







Palaeontology

VOLUME 28 · PART 3 AUGUST 1985



Published by

The Palaeontological Association · London

Price £21·50

THE PALAEONTOLOGICAL ASSOCIATION

The Association was founded in 1957 to promote research in palaeontology and its allied sciences.

COUNCIL 1984-1985

President: Professor C. DOWNIE, Department of Geology, University of Sheffield, Sheffield S1 3JD

Vice-Presidents: Dr. J. C. W. COPE, Department of Geology, University College, Swansea SA2 8PP

Dr. R. RIDING, Department of Geology, University College, Cardiff CF1 1XL

Treasurer: Dr. M. ROMANO, Department of Geology, University of Sheffield, Sheffield S1 3JD

Membership Treasurer: Dr. A. T. THOMAS, Department of Geological Sciences, University of Aston, Birmingham B4 7ET

Institutional Membership Treasurer: Dr. A. R. LORD, Department of Geology, University College, London WC1E 6BT

Secretary: Dr. P. W. SKELTON, Department of Earth Sciences, Open University, Milton Keynes MK7 6AA

Circular Reporter: Dr. D. J. SIVETER, Department of Geology, University of Hull, Hull HU6 7RX

Marketing Manager: Dr. R. J. ALDRIDGE, Department of Geology, University of Nottingham, Nottingham NG7 2RD

Editors

Dr. D. E. G. BRIGGS, Department of Geology, Goldsmiths' College, London SE8 3BU

Dr. P. R. CROWTHER, Leicestershire Museums Service, Leicester LE1 6TD

Dr. L. B. HALSTEAD, Department of Geology, University of Reading, Reading RG6 2AB

Dr. R. HARLAND, British Geological Survey, Keyworth, Nottingham NG12 5GG

Dr. T. J. PALMER, Department of Geology, University College of Wales, Aberystwyth SY23 2AX

Other Members

Dr. E. N. K. CLARKSON, Edinburgh

Dr. C. R. C. PAUL, Liverpool

Dr. D. EDWARDS, Cardiff

Dr. A. B. SMITH, London

Dr. P. D. LANE, Keele

Professor T. N. TAYLOR, Columbus

Dr. A. W. OWEN, Dundee

Overseas Representatives

Australia: Professor B. D. WEBBY, Department of Geology, The University, Sydney, N.S.W., 2006

Canada: Dr. B. S. NORFORD, Institute of Sedimentary and Petroleum Geology, 3303-33rd Street NW., Calgary, Alberta

Japan: Dr. I. HAYAMI, University Museum, University of Tokyo, Hongo 7-3-1, Bunkyo-Ku, Tokyo

New Zealand: Dr. G. R. STEVENS, New Zealand Geological Survey, P.O. Box 30368, Lower Hutt

U.S.A.: Dr. R. CUFFEY, Department of Geology, Pennsylvania State University, Pennsylvania

Professor A. J. ROWELL, Department of Geology, University of Kansas, Lawrence, Kansas 66045

Professor N. M. SAVAGE, Department of Geology, University of Oregon, Eugene, Oregon 97403

South America: Dr. O. A. REIG, Departamento de Ecología, Universidad Simón Bolívar, Caracas 108, Venezuela

MEMBERSHIP

Membership is open to individuals and institutions on payment of the appropriate annual subscription. Rates for 1985 are:

Institutional membership	.	.	.	£45.00 (U.S. \$68)
Ordinary membership	.	.	.	£21.00 (U.S. \$32)
Student membership	.	.	.	£11.50 (U.S. \$18)
Retired membership	.	.	.	£10.50 (U.S. \$16)

There is no admission fee. Correspondence concerned with Institutional Membership should be addressed to **Dr. A. R. Lord, Department of Geology, University College, Gower Street, London WC1E 6BT, England**. Student members are persons receiving full-time instruction at educational institutions recognized by the Council. On first applying for membership, an application form should be obtained from the Membership Treasurer, **Dr. A. T. Thomas, Department of Geological Sciences, University of Aston, Gosta Green, Birmingham B4 7ET**. Subscriptions cover one calendar year and are due each January; they should be sent to the Membership Treasurer. All members who join for 1985 will receive *Palaeontology*, Volume 28, Parts 1-4. All back numbers are still in print and may be ordered from Marston Book Services, P.O. Box 87, Oxford OX4 1LB, England, at £21.50 (U.S. \$33) per part (post free).

THE ORIGINS AND AERODYNAMICS OF FLIGHT IN EXTINCT VERTEBRATES

by KEVIN PADIAN

ABSTRACT. Active (flapping, powered) flight has evolved in only three groups of vertebrates: pterosaurs (late Triassic), birds (late Jurassic), and bats (early Tertiary). Gliding has arisen many times in vertebrates, is a separate adaptation from flying, and does not appear to be a prerequisite for active flight. Skeletal features that distinguish flyers from gliders include modifications of the pectoral and forelimb apparatus, elongation of the distal part of the wing skeleton for thrust, and certain physiological modifications that often leave clues in the skeleton. Soaring evolved in birds and pterosaurs secondarily, after powered flight was well established in both groups: it is a necessary result of phyletic size increase outstripping the ability to meet power requirements for sustained flapping.

The origin of flight can be approached through a combination of phylogenetic, functional, and aerodynamic evidence. A basic question is whether flight evolved in the trees or on the ground. Of the three groups of active flyers, two (pterosaurs and birds) show no trace of gliding antecedents and appear to have evolved flight directly from the ground. Bats show many morphological and phylogenetic indications of an arboreal, gliding ancestry and are very different in all such respects from pterosaurs and birds. The theory of an arboreal origin of flight in birds so far lacks support from phylogenetic and functional-morphologic evidence; arguments in favour of this theory have invoked hypothetical selective advantages of features that either cannot be tested or apply equally to a terrestrial origin. Most of these features were already present in the coelurosaurian dinosaur ancestors of birds. Pterosaurs were structurally and functionally convergent on birds in many locomotory respects, and show prima-facie evidence of a cursorial, non-gliding origin of flight.

Aerodynamic considerations of extinct vertebrates have mainly focused on two animals: *Archaeopteryx* (the first known bird) and *Pteranodon* (a specialized Cretaceous pterosaur). Functional inferences from skeletal evidence imply that *Archaeopteryx* was capable of flapping flight, though most 'modern' avian flight features were not developed; it does not seem well built for gliding. *Pteranodon* (a soarer, not a glider), like many large birds, was capable of active flight but probably only used it to take off, gain altitude, and avert danger. All pterosaurs were strong, active fliers and only large size constrained this ability. Aerodynamics of *Pteranodon* have commanded much productive interest, but nearly all models have been based either on (1) a morphologic analogy to bats, which is structurally incorrect, or (2) an aerodynamic analogy to certain low-speed aircraft or hang-gliders, which is both structurally and aerodynamically incorrect. Reappraisal of the anatomy and aerodynamic parameters indicate that *Pteranodon*'s flight range was higher and that it was more active and manoeuvrable than previous studies have suggested, and so more comparable to modern soaring birds. Studies of flight in extinct organisms cannot rely solely on engineering models or presumed selective advantages or pressures; they must take into consideration all aspects of phylogeny, function, and aerodynamics.

POWERED flight is a difficult and complex adaptation which commands attention as a truly 'major feature' of adaptive evolution. Aerodynamic requirements are severe, and they constrain the kinematics of the flight stroke (the defining feature of powered flight) and the morphology of the wing into adaptive channels that have converged in several vertebrate lineages. For this reason the problem of the origin of flight is especially approachable in macroevolutionary terms (Padian 1982). By comparing the morphology, phylogeny, and ecology of various kinds of flying vertebrates the evolutionary origins of flight may be studied. This approach shows that, although many features of vertebrate flight are common to all flyers, the differences in morphology and

ecology suggest different evolutionary pathways to the same ends (Pennycuick 1972; Rayner 1981; Padian 1983b).

The purpose of this work is to assess the flying abilities of extinct animals. The first step is to review briefly the several modes of air travel, and to show how skeletal indicators of these modes may appear in the fossil record. A basic introduction to the known fossil flyers is followed by a consideration of the origins of flight in birds, pterosaurs, and bats. Finally, treatments of the aerodynamics of extinct vertebrates are reviewed, and new interpretations suggested.

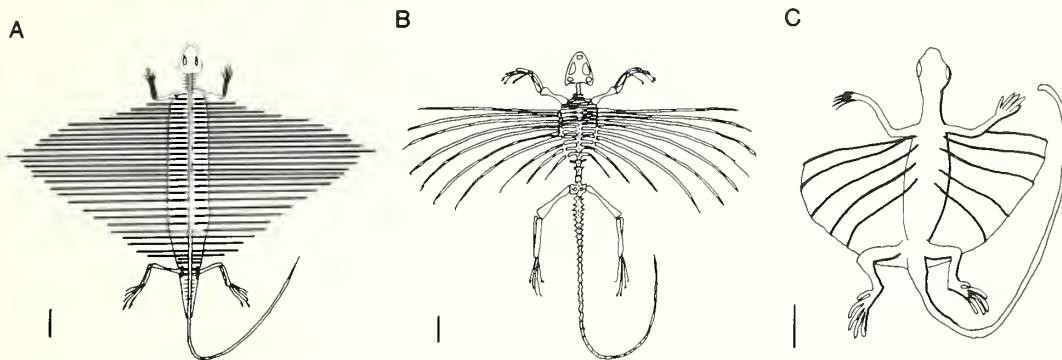
It should be noted that in the present context 'flight' denotes active, powered, flapping flight only. Other modes of air travel that are not self-powered (gliding, parachuting, and soaring) are thereby differentiated; unfortunately space does not permit extensive treatment of the latter. The scope of this review is by no means exhaustive, but is an introduction to current issues. Important problems such as energetics, neurology, and migration must be largely omitted, as there is little direct evidence of them from the fossil record.

TYPES OF VERTEBRATE FLIGHT

Air travel in living vertebrates has often been divided into four modes: parachuting, gliding, flapping, and soaring (Lull 1906; Savile 1962; Hildebrand 1982). These have recently been defined and contrasted by Rayner (1981) in an excellent review of flight adaptations in living vertebrates. Parachuting is usually distinguished from gliding in two ways: the force responsible for the majority of aeronautic support (lift for gliding, drag for parachuting), and the angle of descent (shallower than 45° for gliding, steeper than 45° for parachuting). This can be reduced to a consideration of lift/drag ratio. In evolutionary terms, parachuting may require less morphologic modification, for it is merely a way of slowing a fall; gliding implies a greater horizontal component and a longer time in the air, often with a relatively precise pre-selected landing point. Some authors believe that only radially symmetrical organisms can really qualify as parachuters, though others define parachuting as drag force exceeding lift force. Flapping flight, as its name implies, is defined by the flight stroke, which imparts power in the form of forward thrust. When the resulting increase in air speed from the flight stroke is applied over the surfaces of an aerodynamically efficient airfoil, a pressure differential creates thrust, enabling the animal to gain altitude regardless of assistance from winds or a high starting point. Soaring is a secondary adaptation in large birds and (apparently) large pterosaurs that evolved from flappers and still retain some capacity to flap. Soaring, which has often been likened to falling down an up escalator, allows the animal to make use of thermals (convection rings of rising air) to gain energy that offsets the animal's weight. Such energy may also be gained from winds, as well as from wind speeds that vary with altitude (Pennycuick 1972; Brower 1983). Soaring is both energetically inexpensive and advantageous to predators with acute long-distance vision; the low energetic cost appears to have enabled many soaring birds and pterosaurs to grow phyletically to a size at which flapping for extended periods is energetically impossible. One would think that there is no reason why gliding animals, incapable of powered flight, could not directly evolve a soaring habit. However, gliders have a wing of poor aspect ratio for optimal soaring performance, they cannot easily avoid various kinds of aeronautical hazards, and there are few ecological advantages of soaring to them because they are not visually oriented predators. Rayner (1981) has pointed out that bats do not soar because there are no convective air currents at night. In the absence of selective pressure to become diurnal, seek large prey, and develop acute vision, soaring probably would not be useful for bats. Gliding animals, by virtue of their ecology and diets, also have no reason to soar and it is not surprising that this mode of air travel is largely restricted to a secondary adaptation in groups of predatory and scavenging flappers.

Skeletal correlates of aerial adaptations can provide insight into the aerodynamic abilities of extinct vertebrates. Gliding adaptations are difficult to recognize in the fossil record because they often leave no skeletal clues, and airfoils are seldom preserved. In the absence of an airfoil, adaptations to some form of air travel may be recognized by analogy to modern forms (text-fig. 1). For example, the hyperelongated ribs of the lizard-like *Kuehneosaurus* (upper Triassic, Bristol

Channel; Robinson 1962) and the closely related *Icarosaurus* (upper Triassic, New Jersey; Colbert 1966, 1970) are quite similar to those of the modern agamid lizard *Draco*, which uses its ribs to support a gliding membrane (Colbert 1967). Morphologic features can also indicate functional, aerodynamic, and even physiological abilities and limitations in fossil forms. Several such criteria are available to distinguish active flyers from passive gliders (Padian 1983b).



TEXT-FIG. 1. Three reptiles that modified their ribs as gliding organs. A, *Weigeltosaurus*, upper Permian (after Evans); B, *Icarosaurus*, upper Triassic; C, the living agamid lizard *Draco*. Scale bars represent 2 cm.

1. The defining feature of a flying vertebrate is its flight stroke. Adaptations related to the generation of the power stroke include an expanded bony sternum or breastbone (including a pronounced median keel) for anchoring the flight muscles, a shoulder girdle that is braced to the sternum, an enlarged deltopectoral crest on the humerus for the insertion of flight muscles, and a shoulder articulation that limits forearm movement to activities compatible with the flight stroke (text-fig. 2). Flying vertebrates have developed these features to a relatively greater or lesser degree (bats rather less than birds and pterosaurs in some respects), but such features are never found in the skeletons of gliders.

2. The forelimb proportions in aerial vertebrates are often greater than in non-aerial relatives. Flying squirrels, for instance, have humerus and forearm segments significantly elongated over those of other squirrels (Bryant 1945; Thorington and Heaney 1981). True flyers take this a step further in that the outermost segment of the wing, comprising the wrist (birds), hand (bats), or one finger (pterosaurs), is hypertrophied, which never happens in gliders (text-fig. 2). This is the area that provides thrust (forward motion) in active flight, whereas the inner two wing segments provide lift (on which a glide depends for aerial support; see Rayner 1981).

3. The airfoil in gliders is normally a simple extension of skin and superficial muscle, stretched by bony elements (limbs and bone spars in most gliders, but ribs in others), and without any (or with only rudimentary) internal support structures (Jepsen 1970; Thorington and Heaney 1981; Novacek 1982). In flyers the airfoil is always stiffened by anteroposteriorly oriented structural elements. These are the feather shafts of birds, the fingers of bats, and the intercalated wing fibres of pterosaurs (Zittel 1882; Wellnhofer 1975; Padian 1983b). These may reduce spanwise tension in the wing membrane, a problem noted by Bramwell and Whitfield (1974) for pterosaurs, and equally applicable to bats. Such structural elements certainly act in all flyers to give camber to the wing and to provide competence of the airfoil during the flight stroke.

4. Gliders, which are all arboreal, retain most locomotory abilities of their non-gliding relatives. This is not true for flyers, whose limb structures have been modified to accommodate the kinematics of the flight stroke by reducing unrelated mobility at certain joints, lightening and strengthening

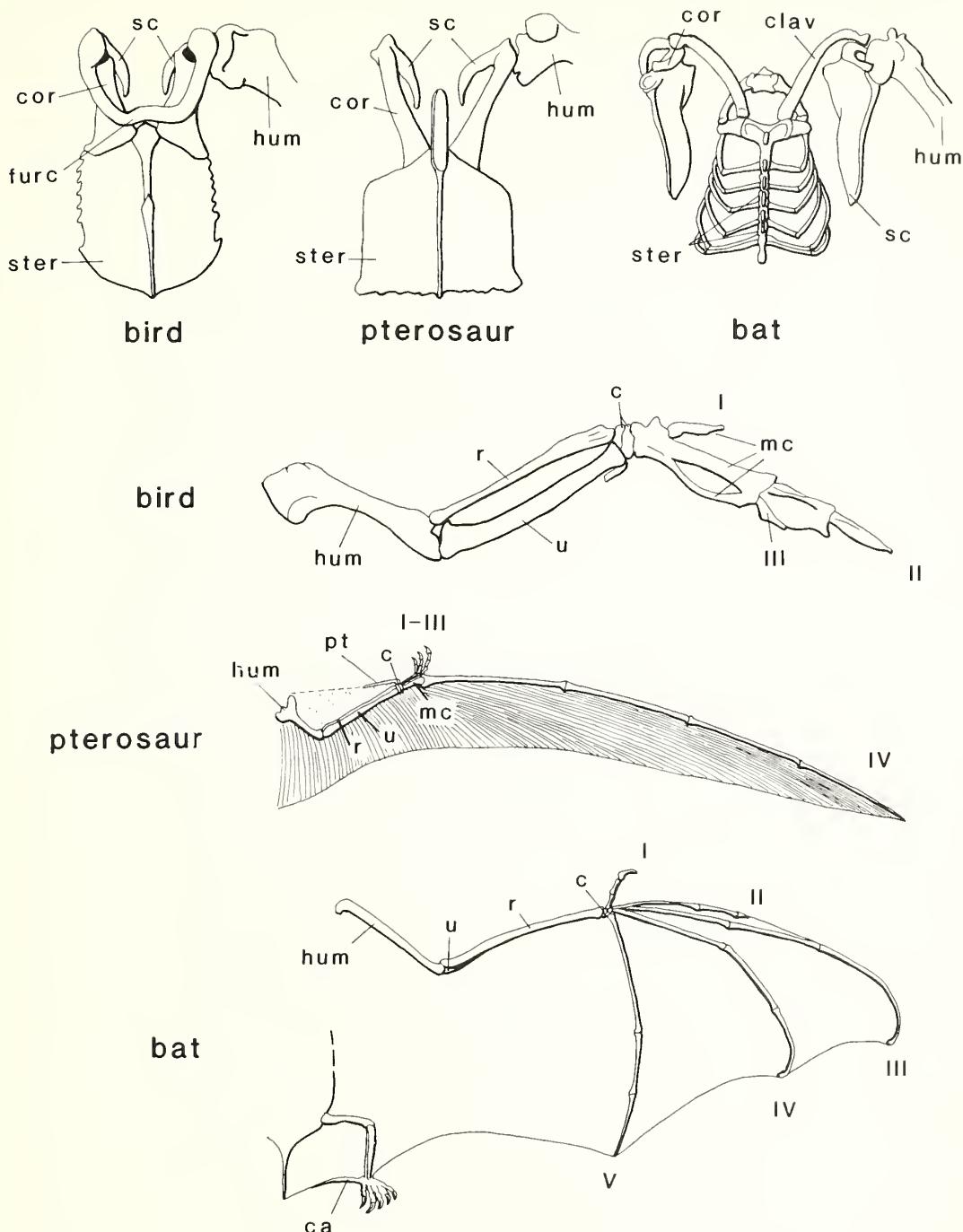
bones, and eliminating unnecessary muscle weight from the wings. Limitations of normal mammalian locomotion are obvious in the bats (except *Desmodus*, the vampire bat, which is secondarily modified for walking and jumping: Altenbach 1979). Ostrom (1976b) demonstrated the restrictions of certain wrist and hand movements in post-*Archaeopteryx* birds, compared to their coelurosaurian dinosaur ancestors. And the limitations on the motion of pterosaur forelimbs, documented by Hankin and Watson (1914), Bramwell and Whitfield (1974), Wellnhofer (1978), and others, have been shown to be modifications related to the down-and-forward flight stroke common to birds and bats (Padian 1983a, b). This stroke and its aerodynamic effects are well understood in living forms (Pennycuick 1972; Rayner 1979).

5. Pneumatic foramina (holes in the skeleton for expansion of respiratory surface into the bone cavities, used to cool the blood), and thermoinsulatory coverings such as feathers and fur, indicate a level of metabolism necessary to sustain active flight. Bats lack pneumatic foramina, though birds and pterosaurs have them. Therefore, whereas such foramina are not necessary for flight, their presence leads to only one inference (Seeley 1870). Pterosaurs and birds, unlike other known diapsids (crocodiles, squamates, and *Sphenodon*), evolved a thermoinsulatory covering. Bats, of course, are furred, but so are other mammals, so this feature by itself does not relate to flight. Indeed, it is not even clear that these features evolved strictly in the context of flight in the other two groups, but knowledge of such fossilized structures is poor.

TRUE VERTEBRATE FLYERS

Pterosaurs have their earliest records in the Norian (upper Triassic) of Italy (Wild 1978), birds in the upper Jurassic of Germany (with apparent occurrences in France and Utah [Jensen 1981]), and bats in the Eocene of North America (Jepsen 1970) and Germany. Pterosaurs died out at the close of the Cretaceous Period, along with all the dinosaurs except birds, which by their coelurosaurian ancestry are properly considered theropod dinosaurs (see below). Pterosaurs coexisted with birds, and have a more extensive and diverse fossil record than birds, throughout the Cretaceous. During this time the record of birds is virtually restricted to open-water forms such as the ternlike *Ichthyornis*, the diving, flightless *Hesperornis*, and its relative *Baptornis* (Marsh 1880). At the close of the Cretaceous some other forms appear, but these are only poorly known (Brodkorb 1963) and only tenuously linked to living orders. Cretaceous pterosaurs are also almost entirely found in marine facies, and have commonly been presumed pelican- or gull-like in their habits. Because the known Cretaceous representatives of these groups evidently had similar ecologies, on face value it may be inferred that pterosaurs did not die out from competition with the birds, but rather from a failure to keep diversifying and replacing taxa, a necessary component of evolutionary persistence. Bats seem to have occupied a nocturnal, originally insectivorous adaptive zone since sometime in the early Tertiary, after the pterosaurs were gone and the birds already well established.

Pterosaurs. Pterosaurs have recently been reviewed and revised by Wellnhofer (1970, 1974–1975, 1978: anatomy and diversity) and Padian (1979, 1980, 1983a, b: locomotion and flight). In light of recent work a summary of salient features of pterosaurs may be given. They were active flyers with a shoulder girdle strongly buttressed to the sternum, which was widely expanded over the ventral thorax and keeled in the midline (Wellnhofer 1978). The sternum anchored the flight muscles, and as in birds the recovery stroke of flight, powered by the *M. supracoracoideus* equivalent, was effected by a pulley mechanism involving the acrocoracoid process of the coracoid, which changed the primitive action of the muscle from an adductor to an elevator (Padian 1983b). The wing could be folded, but the joint separating the second and third of the three major functional units of the wing was between the fourth metacarpal and its phalanx, not at the wrist as in birds (text-fig. 2). The wing was a membrane of skin with a network of closely intercalated 'fibres' that provided strength and camber; these 'fibres' are never found folded but are always gathered, so their structural integrity is evident (Zittel 1882; Wellnhofer 1975; Padian 1983b). They may have been modified scales, and were presumably keratinous. The wing was brought forward through a down-and-forward path



TEXT-FIG. 2. Diagrammatic comparisons of the thoracic regions and forelimbs of the three groups of vertebrate flyers. Thoracic regions (*above*) are seen from the front; right forelimbs (*below*) in dorsal view. Structurally, the coracoids of pterosaurs and birds and the clavicles of bats appear to be analogous, as do the bird's furcula, the cristospine of pterosaurs, and the manubrium of bats; the last two structures are situated at the anterior extreme of the sternum. Abbreviations: *c*, carpus; *ca*, calcar; *clav*, clavicle; *cor*, coracoid; *furc*, furcula; *hum*, humerus; *mc*, metacarpus; *pt*, pteroid; *r*, radius; *sc*, scapula; *ster*, sternum; *u*, ulna; I-V, numbered digits. Not to scale.

during the flight stroke, and retracted by an up-and-backward motion, as in birds and bats (Padian 1983b). The hindlimbs were sufficient for bipedality to be the only means of terrestrial locomotion; pterosaurs could not walk on all fours because the forelimbs could not rotate past the limit of the forward flight stroke (Padian and Olsen 1984; Padian 1983b). The femur was held in a diagonal to horizontal position nearly parallel to the body midline, as in birds and most dinosaurs, and the gait was parasagittal and digitigrade (Padian 1983a, b). The Pterosauria comprise some forty genera, traditionally divided between the paraphyletic Rhamphorhynchoidea and their monophyletic descendants, the Pterodactyloidea; diagnostic differences are reviewed in Wellnhofer (1978) and Padian (1980). Pterosaurs, though not dinosaurs, were very closely related to them and share with them many synapomorphies (Gauthier 1984); their closest known sister taxon appears to be the small ornithosuchian archosaur *Scleromochlus* (von Huene 1914; Padian 1980, 1984; Gauthier 1984).

Birds. The fossil record of birds begins with *Archaeopteryx*, from the upper Jurassic Solnhofen limestones of Bavaria. The history of the five known specimens (plus the original feather) has often been reviewed (see e.g. Ostrom 1979 and references therein). Even more frequently repeated is the concept of the mosaic 'half-reptile, half-bird' morphology of *Archaeopteryx*, although until recent years there was no convincing picture of which 'reptiles' included the direct ancestors of birds. Ostrom, in a series of papers (1973–1979), established that birds were descended from small coelurosaurian theropod dinosaurs, on the basis of a series of unusual and generally overlooked characters that were unique to these dinosaurs and birds (represented by *Archaeopteryx*). Padian (1982) formalized Ostrom's evidence and arguments, along with additional evidence, into a testable cladistic framework in which some fifty synapomorphies of *Archaeopteryx* and coelurosaurs were recognized; Gauthier (1984) has expanded this list to over 120 (Gauthier and Padian, in press). Critics of Ostrom's theory (e.g. Walker 1977; Tarsitano and Hecht 1980; Martin *et al.* 1980; Martin 1983) have quarrelled with interpretations of individual characters or have argued that some proposed synapomorphic features are 'not similar', and have pointed out resemblances of either *Archaeopteryx* or modern birds to other selected fossil archosaurs. However, these critics have not recognized or addressed the structure of cladistic methodology, which is a valuable tool for reconstructing phylogeny precisely because it transforms mere lists of characters (e.g. Martin 1983) into hierarchical distributions of nested sets of characters, thereby forming a more robust logical structure than a list. In this context, non-hierarchical claims of 'similarity' or 'dissimilarity' have no objective meaning. Statements about sister-group relationships between two taxa must be gauged against a third in order to establish phylogenetic homology; the latter is deductive, not declarative, and so, logically, are statements about 'dissimilarity' (non-homology at a given phylogenetic level).

As Martin (1983) and others have pointed out the coelurosaurian hypothesis is based almost exclusively on an extensive series of post-cranial characters (though the skull of *Archaeopteryx* is in all recognizable respects coelurosaurian), which ostensibly evolved independent of the others. Ostrom compared these across a wide range of coelurosaurs and other archosaurs. Walker (1973) and Martin *et al.* (1980), who advocate a common origin of crocodiles and birds (among as yet unspecified 'thecodonts'), have mainly relied upon certain features of the ear region which are unfortunately not preserved in the crucial coelurosaurs. Because two-thirds of a comparison cannot establish anything with respect to the other third, at present the evidence of the ear region is only tantalizing, though potentially quite valuable. Critics of Ostrom's post-cranial theory though have yet to demonstrate or even propose that any other specified taxon is closer in these respects to *Archaeopteryx*; consequently, it must be provisionally accepted that birds are descended from theropod dinosaurs—in fact, they are the closest sister-group of deinonychosaurian coelurosaurs (*sensu* Colbert and Russell 1969; see Padian 1982, and Gauthier and Padian, in press).

This phylogenetic premise is necessary to understand which skeletal features conventionally regarded as 'avian' are really avian and not simply dinosaurian, theropodan, or coelurosaurian. The typical textbook litanies of 'avian' characters include hollow bones, a lightly built skeleton, long forelimbs, fused clavicles, and a keeled sternum; yet all these features are already synapomorphies of coelurosaurian dinosaurs, and the last is not preserved in *Archaeopteryx* (Gauthier and Padian, in

press). At present the only known character distinguishing *Archaeopteryx* as a bird is the flight feathers, which demonstrates that *Archaeopteryx* was an active flier (Feduccia and Tordoff 1979). Later birds are distinguished from *Archaeopteryx* by the fused and reduced wrist and fingers, and the ossified contact of the coracoid with the expanded sternum, both modifications for flight; and by the fusion of pelvic elements, reduction of teeth, and various cranial features. These, however, must be regarded as ancillary to the origin of birds; in an adaptive sense they can be viewed as fine-tuning the flight mechanism and the avian life-style.

Bats. Evidence for the origin of bats is indirect. The earliest fossil bat is *Icaronycteris*, from the Green River (Bridgerian: middle Eocene) of Wyoming (Jepsen 1970). Its complete skeleton, magnificently preserved, has been subjected to some phylogenetic debate, but most workers prefer to assign it, with some reservations, to the Microchiroptera. It has a long tail and many other primitive features, but it is in all respects a flying bat, with fully developed wings. Possible dental records of bats from the early Eocene are provocative but shed no light on the question of bat origins; spectacular skeletal fossils from the Middle Eocene (Lutetian) Messel pits of the Darmstadt region of Germany represent several species of primitive bats. Recent re-evaluation of several ancient, generalized, closely related placental groups (including the Scandentia or tree shrews, bats, primates, and lipotyphlan insectivores) suggest that dermopterans and bats are sister groups (Novacek 1982). If this view prevails the understanding of plesiomorphic characters and ecological factors in the origin of bat flight may fit a cohesive evolutionary pattern (see below).

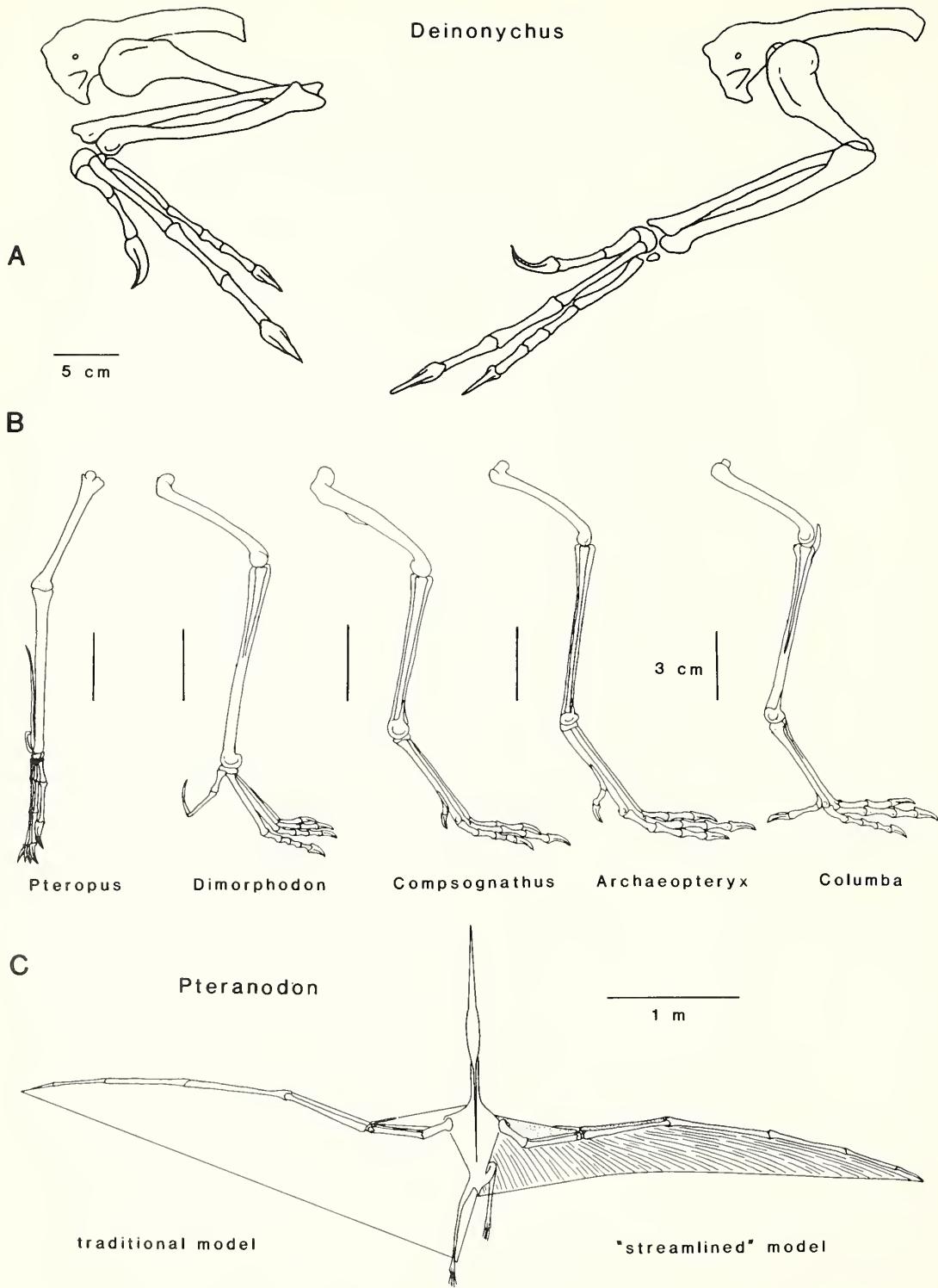
ORIGINS OF FLIGHT

'Origins' has been left plural because mounting evidence suggests that pathways to vertebrate flight have differed, depending as much on phylogenetic constraints as on aerodynamic ones. Powered flight is defined here by the common use in all flyers of the down-and-forward flight stroke of the wings. The wing produces both lift (inner segment) and thrust (outer segment). How such wings evolve is not so clear-cut. In order to be convincing, explanations of the evolution of flight must be consistent with empirical knowledge. Evolutionary theory can support many kinds of adaptive explanations, but only a fusion of many independent lines of evidence can suggest which historical explanations are more appropriate in a given case (Padian 1982).

Bird flight. Far more attention has been paid to birds than to bats and pterosaurs with regard to the origin of flight. Ostrom (1974, 1979) reviewed the old dichotomy between the terrestrial, cursorial origin ('from the ground up': Williston 1879; Nopcsa 1907, 1923)—obscure and unsupported by evidence for nearly a century—and the arboreal, gliding origin (Marsh 1880; Bock 1965), which has predominated in evolutionary thought. The latter is intuitively more convincing, perhaps because the images of climbing, leaping, parachuting, gliding, and finally flapping sail past our eyes like cartoons in a flipbook. The question is not whether this theory is possible; I will argue later that it is, at least for bats. The question is really whether it is supported by evidence; and so far the answer is surprisingly negative, at least for birds. This is odd considering the reliance most modern birds place on arboreal life; however, to study the origin of flight is not to deal with why modern birds live in trees, but how ancient birds got into the air. *Post hoc* arguments are not applicable.

Bock (1965) championed the arboreal theory by showing that it was consistent with the neo-Darwinian Modern Synthesis of evolution—invoking no teleology and no inadaptive stages, with each adaptive level self-sufficient and derivable from the previous one by small steps. Selective advantages of each intergrading stage were self-evident, on the basis of their survival and success in modern forms. But as valid as these assumptions may be, they hold true regardless of any empirical evidence that may be brought to bear on the origin of birds and their flight. Bock's theory, in the absence of evidence, reduces to a statement of belief that flight evolved in accordance with the Modern Synthesis; but many possible explanations can be accommodated by the Synthesis. The point at issue is to discover which factors could discriminate between alternate theories.

There are at least three kinds of factors at work: phylogenetic, functional, and aerodynamic



(Padian 1982). Phylogenetically the most robust hypothesis is that birds began from small, active, carnivorous, bipedal theropod dinosaurs. As Ostrom (1974) realized, any satisfactory theory of bird origins has to begin with *Archaeopteryx*; and any satisfactory theory of *Archaeopteryx* must consider the habits of its closest sister-group. This, the predatory Deinonychosauria, included agile, terrestrial, cursorial bipeds with long arms, large brains, and stereoscopic vision (Hopson 1980; Russell 1980; Ostrom 1980). Trends toward these features in the evolution of coelurosaurs is clear (Padian 1982; Gauthier 1984; Gauthier and Padian, in press). Though perhaps nothing about the skeletons of these animals, including *Archaeopteryx*, precludes at least the smaller forms from climbing trees, no evidence favours it (Ostrom 1979)—despite a wealth of skeletal correlates in modern birds for scansorial and arboreal adaptations (Feduccia 1973; Bock and Miller 1959). Therefore, unless compelling arguments can be adduced for an arboreal stage in the evolution of flight, it seems to me that the phylogenetic and palaeoecological evidence of terrestrial ancestry must be taken at face value.

Coelurosaurs had many structural features that later figured in the evolution of flight. These attributes may be adduced from the extensive skeletal comparisons of coelurosaurs and other archosaurs by Ostrom (1974–1976). Some of these have a direct relationship to the later development of the flight stroke in birds. In addition to the anatomical features mentioned above, Ostrom (1969) noted the semilunate wrist joint in deinonychososaurs (text-fig. 3A), which allowed them to flex their long hands laterally against the forearm—in fact, to fold them exactly as a bird folds its wing (Ostrom 1976b). *Archaeopteryx* shows no specialization of the forelimb bones beyond those of other deinonychososaurs, and the bones themselves are only slightly longer proportionally than in its larger, non-volant relatives. Direct palaeontologic evidence indicates that deinonychososaurs used the forelimbs to grasp prey while attacking it with the teeth and clawed feet (Kielan-Jaworowska 1975)—just as Ostrom (1969) had predicted. To seize prey from a retracted position the humerus must be protracted and adducted, the forearm extended, and the hand extended by swinging forward and mediad, pushed in part by differential movement of the radius relative to the ulna (text-fig. 3A). (When the elbow is flexed the radius slides forward over the ulna and flexes the long hand against the forearm, as in birds.) The shoulder joint is a ball and socket with only partial restriction of movement, the elbow is a hinge, and the wrist another hinge; the mobility of these joints is equivalent to or greater than those of birds, and restricted in similar ways. Therefore only the smallest conceivable modification is necessary to change the functional repertoire of the deinonychosaurian forelimb to accommodate the down-and-forward motion of flight. Because these structures and functions were useful in a very different context for terrestrial predators, it cannot be argued that they evolved specifically for flight. They were co-opted from a predatory function, and this would only have been possible in a terrestrial setting, as Ostrom (1974) explained:

Climbing and flying involve different sets of muscles and require very different movements of the various forelimb components. In all probability, selective forces that tended to perfect one activity would not have been optimal for the other. And while we can rationalize the advantages of climbing into trees as a necessary precursor to the earliest stages of the evolution of flight, from a functional anatomical aspect the two activities are unrelated.

TEXT-FIG. 3. A, left pectoral girdle and forelimb of the coelurosaurian dinosaur *Deinonychus*, in lateral view: *left*, with arm folded, *right*, with arm extended. The semilunate carpal synapomorphic of deinonychososaurs and birds is at the base of the three digits. B, right hindlimbs in lateral view: the fruit bat *Pteropus*, the pterosaur *Dimorphodon*, the small theropod dinosaur *Compsognathus*, the first known bird *Archaeopteryx*, and the pigeon *Columba*. Note the differences in orientation, femoral head, fibular location, and metatarsal-phalangeal structure between the bat and the four archosaurs; the former hangs upside-down in trees, whereas the latter are and were presumably active terrestrial bipeds. C, dorsal view of the Cretaceous pterosaur *Pteranodon* in flight: left side, the traditional ‘wide-winged’ model, after Bramwell and Whittfield 1974; right side, the revised ‘streamlined’ model based on new analysis of the forelimb and hindlimb articulations (Padian 1983b), and on wing impressions preserved in the genus *Rhamphorhynchus*.

What of the role of feathers? Most workers have accepted Regal's (1975) contention that feathers evolved initially as modified scales to enhance thermoregulation, though whether to shed heat, retain it, or both, depends on answers to palaeoenvironmental and palaeophysiological questions that may never be resolved. In any case, Regal's thoughtful analysis applies only to body feathers (down and contour); flight feathers are clearly specially modified contour feathers, and their insulatory function when folded is almost certainly secondary in an evolutionary sense to their development as a flight organ. Ostrom (1975a, b) proposed, following the predatory ecology of the coelurosaurs, that hypertrophied feathers on the forelimbs were selected as an aid to batting down flying insects. Although this use is consistent with generally distributed predatory traits in theropods, it is difficult to see how the improvement of a predatory function such as this would have paved the way for the development of flight, a locomotory function (Padian 1982). (Ostrom produced a parallel argument, quoted above, to dispel the arboreal theory's putative connection between climbing and flying.) Martin (1983) commented that a solid mesh of feathers was a poorly designed 'net' that probably would have only blown the insect prey farther away. Caple *et al.* (1983) showed that the 'insect nets' would have generated severe instability and loss of balance. They proposed instead that if the earliest birds and their immediate forerunners caught prey with their teeth instead of their hands, the arms would have been very effective bilateral stabilizers during a jump into the air. Even a forelimb surface expansion capable of lifting 1% of the animal's body weight would have had a significant effect on stability. A greater surface area would result in even greater stability, which, combined with faster takeoff speed, would result in increased lift, a longer time in the air, and presumably a more successful insect forage. Ostrom and most workers have since conceded the advantages of this model (Lewin 1983).

Caple *et al.* (1983) made the terrestrial flight model a strong contender by overcoming the objection that when the winged proto-bird leapt into the air it would immediately lose speed from its only source of power (the legs). The authors set up the basic requirements for the evolution of the flight stroke itself, but did not pursue it to the specific case of birds; I have shown that this stroke is almost fully evolved already in deinonychosaurians, though nearly inconceivable in any other contemporary animals. Any protraction and extension of an airworthy, feathered forelimb would have increased lift and time in the air—whether useful for pursuit of prey (Ostrom 1975a, b), escape from predators (Harrison 1976), or simply more agile running over broken ground (Padian 1982), is not important. Any repetition of such a stroke sustains the animal in flight even longer. From these modest beginnings the flight of birds evolved by steps no less adaptive, incremental, or self-sufficient than those of the arboreal scenario. The difference is that ecological stages for which no evidence exists are not invoked. (See Harrison 1976 for several perceptive comments on this issue.)

The fossil record indicates that the immediate ancestors of birds were terrestrial, agile, bipedal, cursorial, and predatory. It does not indicate that they were arboreal, climbers, parachuters, or gliders. Bock (1983) suggested that feathers would have evolved to advantage in treetops, where heat loss is allegedly greater than on the ground; that stereoscopic vision would have been useful for proto-birds clambering through branches; and that long feathers would have helped break an accidental fall from the trees. These hypothetical advantages have yet to be supported by evidence for arboreality. Martin (1983) asserted that *Archaeopteryx* 'was more adapted for moving about in the trees than for a life in the open plain', based on an analogy to primates. His contention that *Archaeopteryx* could not run or even stand fully erect hinges on an interpretation that the proximal femur is obliquely oriented in the acetabulum; however, this orientation applies to dinosaurs, modern birds, pterosaurs, and most mammals, all of which walk parasagittally (text-fig. 3B). This advanced condition is sharply contrasted with the 'semi-erect' condition in 'thecodonts' and crocodiles, all of which have a primitive sigmoid femur with a head that is continuous with the shaft, not set off by a distinct neck. The mobility and anatomy of every joint in the hindlimb of *Archaeopteryx* must be considered; Martin (1983) dealt only with the long proportions of the hindlimb, which he suggested was an adaptation to jumping. He did not detail his scenario in which 'a small arboreal reptile with a tendency toward bipedality . . . [which] was improved by vertical climbing

and leaping', developed flight, nor how fully terrestrial abilities might have re-evolved. It seems, on balance, that many unnecessary steps must be invoked only to get the trees in there somehow. Though both hypotheses demand further work, most workers in the recent literature seem to have accepted Ostrom's ideas on the anatomy, phylogenetic relationships, and functional morphology of *Archaeopteryx* (e.g. Bakker and Galton 1974; Wellnhofer 1974; Desmond 1975; Padian 1983a, b; Thulborn and Hanley 1982; Gauthier 1984; Cracraft 1977; Colbert 1980; Russell 1980; Hotton 1980; Bakker 1980; Halstead and Halstead 1981; McGowan 1980; Caple *et al.* 1983; etc.). The aerodynamic model of Caple *et al.* (1983) promises to be highly productive in further investigations of the evolution of bird flight (Lewin 1983).

Bat flight. The question of the origin of bat flight is in some ways at about the same stage as the question of bird flight was a decade ago, perhaps because so little is known about the ancestry of bats. Once Ostrom proposed a specific origin of birds the question of the origin of their flight assumed a whole new dimension, because models could be constructed on actual taxa. This was particularly important with birds because they have no living relatives that are the least bit like them ecologically.

Though the fossil record does not reveal much about the origin of bats, they share a close common ancestry with other orders of small mammals of nocturnal, arboreal, insectivorous, or omnivorous habits (lipotyphlan insectivores, Dermoptera, and Scandentia). Dermopterans are at least as ancient as bats, if the fossil record gives any indication. However, no one would propose that the modern dermopteran is a plausible *Urtyp* for the earliest bat: for reasons laid out by Jepsen (1970) the colugo is highly specialized for its inverted, fruit-eating lifestyle. But the forests in which the colugo now lives were certainly not always of their present compositions, and therefore it is reasonable to assume that dermopterans have changed with their environment, as bats have. It is highly probable that in the early Eocene or Palaeocene the members of the two groups looked more like each other than their modern representatives do.

Perhaps from these considerations a general idea of proto-bat ecology may be extrapolated. Let us assume, as nearly all workers on the problem have, that the ancestors of bats had the ecological characteristics noted above. As in many primitive mammals, there may also have been a rudimentary sense of echolocation, though perhaps the mechanism was not homologous to the organs used in chiropteran echolocation. Because these features are generally distributed among the sister-groups of bats, no special explanation of the adaptive value of these characters to bats is necessary. At this point, to go further in the investigation of the origin of bat flight requires a more specific statement about the closest sister-taxon of bats. If, for example, the Dermoptera were so established (Novacek 1982) the investigation is reduced to three alternatives: (1) bats did not go through a gliding stage, and evolved powered flight completely independently of the dermopterans' evolution of gliding; (2) the common ancestors of bats and dermopterans went through a gliding stage, and the two lineages subsequently diverged; (3) bats and dermopterans independently evolved a gliding stage, and the bats went on from there to evolve powered flight. The phylogenetic milieu is a powerful source of information about the context of functional evolution. Without a better fossil record of the earliest bats and proto-bats the most promising line of evidence for the origin of bat flight would seem to be analysis of the interrelationships of known orders and the trends that mark their histories. However, some interesting ideas and approaches of previous workers suggest that even in the absence of phylogenetic information, the functional problem can be explored.

Jepsen (1970) proposed three stages in the evolution of bat flight. Stage 1, the pre-bat, was much like the animals described above, except that Jepsen postulated 'large (and, possibly, webbed) front feet' useful in leaping after prey, with hind legs and feet that 'could be extended outward (laterally) from the body when it moved around in crevices'. It also could hang by its hind feet, as flying squirrels can, and could leap from this posture to a nearby target. Stage 2, the sub-bat, had 'webbed large hands (or small wings) which were used principally in catching flying prey', and the proto-wings of skin 'enabled the sub-bat to be very briefly sustained in the air by rapid flapping' after prey. The legs were now fixed laterally. Stage 3 is the essentially modern bat, with fully grown wings and

refined skeleto-muscular adaptations. It is important to note that Jepsen did not believe that bats ever passed through a gliding stage: he regarded gliding as a separate evolutionary plateau (or dead end). Instead, like Ostrom, he placed great reliance on the hypertrophy of the hands as prey-catchers.

Two problems with this are: (1) how did a (normally) quadrupedal mammal get around in trees with these large webbed hands, and (2) once again, why should the improvement of a predatory function pave the way for a locomotory function? The evolution of inverted posture is indeed very important, and (as Sam McLeod once suggested to me) may have evolved well before the other features: otherwise, how would the forelimbs be freed for flight? Once suspended upside down, it is easier to drop to a lower target than to climb up, so presumably the advantage of a gliding ability is not eliminated (see below).

Smith (1977), working from the model of a typical gliding proto-bat, regarded the expansion of the wrist and hand membranes almost as a developmental by-product of elongating the digits along with the other forelimb bones. (Fair enough, but why then do not other mammalian gliders have hypertrophied hands?) He suggested that 'the continued development of the wing, in this manner, eventually would have produced an ungainly and clumsy structure that necessitated movement as a wing rather than a fixed gliding device'. The theory stresses the random nature of raw materials upon which selection may act, but the development of the flight stroke and the form-function complexes of bat limbs and girdles is left unexplained. Smith, however, concluded that bats passed through a gliding stage. His view contrasts with that of Pirlot (1977), who suggested that bat flight began as brief periods of hovering while jumping at insects from the ground, again without a gliding stage. Clark (1977) argued against this because the curve of power requirements for increasing flight speed is U-shaped; therefore it would have been far less costly for bats to begin with medium-speed flight, because hovering is as expensive as high-speed flight. Clark concluded that 'it is more reasonable to suggest that bat ancestors were gliders which gradually evolved the capacity for sustained (and controlled) flight at speeds where power requirements were minimal'.

One argument in favour of a gliding origin for bats is that, if their ancestors were indeed arboreal, they would almost have had to have been gliders first: an animal that experiments with powered flight in the treetops risks mortal danger at each outing without some kind of airfoil to break the fall. Evidence for such a glider-type design is found in the configuration of the wing in bats, the only flyers to incorporate the hindlimbs into the airfoil, as all mammalian gliders do (Padian 1982). Without a gliding stage, it must be postulated that the legs became incorporated into the wing only after flapping flight evolved, which did not happen in birds or pterosaurs. An alternative is that enlargement of the hand, and evolution of the flight stroke, occurred in bats after the gliding habit was established. The gliding membrane could have been the 'safety net' for the evolution of flight in an arboreal setting.

Pterosaur flight. The section is quite brief because there is almost no discussion of the origin of pterosaur flight in the literature. This is hardly surprising, as most writers have considered pterosaurs mere gliders, and their exact phyletic origins have not been well understood. Von Huene (1914) suggested that pterosaurs evolved from small arboreal 'thecodonts' like *Scleromochlus*, which jumped from branch to branch, then developed parachuting, gliding, and flapping flight. Romer repeated von Huene's origin of flight theory nearly verbatim in all editions of his *Vertebrate Paleontology*, but leaving out mention of *Scleromochlus*, which he considered a dinosaur. Elsewhere I argue the opposite (Padian 1984): that von Huene got the phylogeny right, but the scenario wrong. *Scleromochlus* is the closest known sister-group to pterosaurs, as von Huene thought (Padian 1980; Gauthier 1984). But in locomotory adaptations it was a small, light, bipedal runner, and so were pterosaurs for nearly the first hundred million years of their existence (upper Triassic–upper Cretaceous).

Pterosaurs parallel birds in so many adaptive respects that every argument applicable to the terrestrial theory given above for birds also applies to pterosaurs (Padian 1983b). They stood, held their limbs, and moved their joints in almost exactly the same ways (text-fig. 3B), and such adaptations as the acrocoracoid process of the shoulder girdle, the restricted glenoid fossa, the

coracoids buttressed to the sternum, the narrow wings unconnected to the feet, the pelvic configuration, the reduced fibula, and the mesotarsal ankle suggest, even with the regrettable paucity of supporting fossils, that pterosaurs evolved flight in a cursorial, terrestrial context, without a gliding stage. They never developed an avian-style perching foot, their hind claws were never sharply curved (unlike their fore claws), and they always kept a low femur/tibia ratio and a high metatarsal/tibia ratio characteristic of lightly built, active animals (Coombs 1978), and uncharacteristic of non-avian arboreal forms. Perhaps they could climb trees; but as in the earliest birds, no evidence currently supports this point, whereas ample evidence indicates high proficiency as terrestrial bipeds. The origin of the first group of vertebrate flyers, unfortunately, is far more poorly known than the origins of flight in the other two groups, and their comparative biology far more difficult to approach.

AERODYNAMIC PERFORMANCE OF FOSSIL VERTEBRATES

Apart from calculations made by Colbert (1966, 1967, 1970), Evans (1982), Thorington and Heaney (1981), and others of the weight, wing area, and wing loadings of various gliders, studies of aerodynamic performance in fossil vertebrates have centred on two animals: *Archaeopteryx* and *Pteranodon*. In both, estimates have been made of gliding performance, with some consideration of minimal power requirements for flapping flight.

Archaeopteryx. It is important to remember that most work on the aerodynamics of *Archaeopteryx* preceded Ostrom's hypotheses of theropod ancestry and terrestrial origin of flight. In this aerodynamic work it was assumed that *Archaeopteryx* was arboreal and mainly a glider, which flew weakly if at all. If Ostrom's ideas (later modified and developed mathematically by Caple *et al.* 1983) are correct, a gliding stage would have been aerodynamically obviated, because gliding from the ground up is so ineffective. There is no way to tell how much, if any, gliding *Archaeopteryx* did, but there is certainly value in estimating its gliding performance, as well as its power requirements.

Flying animals can glide at a range of speeds, merely by varying the incidence of the glide. They also flex the wings at high speeds in order to obtain a range of glide performance (J. M. V. Rayner, pers. comm.). Gliding performance is maximized when the gliding angle (proportional to the sinking speed) is low, because the lift is high relative to drag. But if the lift is too high, the animal slows until it stalls. The minimum flying speed (V_{\min}) is achieved when lift is maximized ($C_{L\max}$: just before stalling) and is inversely correlated with it. This is expressed by the formula

$$V^2 = 2W/\rho SC_L$$

in which W , the weight (mass \times gravity), approximates the lift (L) in a steady glide, ρ is the density of air, and S the area of the airfoil. $C_{L\max}$ is best calculated empirically, and ranges from 1.3 to 1.6 in modern birds and bats (Pennycuick 1972). Because ρ is usually assumed, the critical biologic variables are the weight and wing area, the quotient of which is called the wing loading, and is roughly proportional to gliding speed.

The aerodynamic analysis, then, begins with calculations of weight and wing area. Heptonstall (1970) confirmed Jerison's (1968) estimate of the former at 500 g, and calculated the wing area at 373 cm², exclusive of body and tail surfaces. Bramwell (1971) and Yalden (1971a) argued for lower weights (200–250 g) and larger lift areas (479 cm², including 91 cm² on the body between the wings). Yalden (1971b) compared *Archaeopteryx* to birds of similar wing span (58 cm) and found a weight range of 170–300 g; the same range was found for mammals of similar head–body length (21.8 cm). Yalden used estimates of 150, 200, and 250 g in his calculations, favouring the intermediate value.

Heptonstall (1970) used the formula given above to calculate what he believed to be the maximum flying speed of *Archaeopteryx* at 20.9 m/s. Heptonstall calculated L by estimating maximum bending moments possible on a humerus with a tensile strength commensurate with experimental results, thus deriving the maximum lift possible. In his formula the expression L was equated with W , a common practice when calculating performance in a steady glide, in which maximum lift is generated

(Pennycuick 1972). However, Bramwell (1971) argued that the formula only works for minimum speed (V_{\min}): maximum lift is not generated with maximum speed, and vice versa. Yalden (1971b), using a similar formula from Pennycuick (1969), calculated the minimum power speed at 6·9, 7·6, and 8·2 m/s, depending on the weights listed above. Because in modern birds some 15% of body weight is pectoral muscle, Yalden took 30 g as the available weight for the power stroke, and derived a power requirement of 105–140 watts/kg. All these figures are well within avian range, but Yalden noted that this is not surprising, as he based all estimated values on those observed in modern birds. He concluded that if *Archaeopteryx* approached modern birds in muscle physiology, it probably could have flown.

The important point to be made about all the work discussed above is that the calculated values are within the ranges of modern birds. Despite differences in estimates and derivations the results agree to within a factor of two, and usually much closer, and are therefore reliable if not precise. In this context it is interesting to consider Yalden's estimates of minimum power speed, the speed at which the least work has to be done. Once again, the U-shaped curve relating power requirements to flight speed shows that very low and very high speeds are most expensive. Starting flight from a standing position, then, requires a lot of energy to be expended initially, before getting up to an economical speed. A running takeoff can minimize the effort required by the wings to build up this speed, and if the wings are merely spread significant lift can be generated. Caple *et al.* (1983) based calculations on a cursorial model of 100 g, shaped as a cylinder 15 cm long and 3 cm diameter, and applied a ground speed of 3–4 m/s derived from empirical observations by Taylor (1973). Because maximum running speed is observed to vary proportionally with mass, it is clear that an animal the size of *Archaeopteryx*, endowed with the cursorial skeletal adaptations of coelurosaurs, would have had no trouble bringing its ground speed up to minimum flying speed.

Once in the air, the flapping performance can be estimated only if the physiology is known or assumed. The gliding performance depends on wing loading and aspect ratio (the shape of the wing: wingspan squared divided by wing area). Of great importance is the ability of a flying animal to land. To land slowly and easily, most animals reorient the body and beat the wings vigorously to achieve minimum speed flight. (This discussion applies only to landing on the ground, as Caple *et al.* (1983) have shown the difficulty of landing on a branch to an animal that is not already extremely sophisticated in its flight.) Heptonstall (1970) reckoned that the high wing loading and sinking speed of *Archaeopteryx* would have made landing very rough, though Bramwell (1971) figured that the tail would have reduced the stalling speed; Yalden (1971b) and Bramwell (1971) both calculated lower wing loadings. In view of the cursorial adaptations of *Archaeopteryx*, it may be surmised that a running landing was possible, so that the airspeed need only have been reduced to the minimum flying speed in order for the legs to take over. Heptonstall (1970) calculated optimal gliding speeds at 10–15 m/s, but the lower wing loading suggested by other authors would have reduced this figure considerably. By my calculations, stalling speed for *Archaeopteryx* would have been on the order of 5–6 m/s, and a short burst of flapping (generating enough lift to slow airspeed) would have enabled a running landing at a speed of 3–4 m/s. (Use of the alula in landing was probably not available to *Archaeopteryx*.)

Pterosaurs. Fascination with the aerodynamics of these extinct archosaurs began well before man invented powered flight. Early work particularly reflected the hope that pterosaurs would reveal possibilities for human flight, though as soon as workable aircraft were invented interest in pterosaurs quickly cooled. In the past decade it has been rekindled by the opposite hope, that modern advances in aviation might reveal how pterosaurs flew.

Most attention by far has centred on the crested pterodactyloid, *Pteranodon*. *Rhamphorhynchus*, an earlier, smaller, long-tailed form, was studied by von Kripp (1943) and a flapping model built and flown by von Holst (1957); however, the model would work properly only when the leaf-shaped vane at the end of the tail, preserved in several fossil specimens, was oriented horizontally, whereas its true orientation is vertical. Apart from these studies, modern work has been almost entirely devoted to *Pteranodon*, and a general overview of this work will now be given.

The problem initially faced was to determine the upper size limit of *Pteranodon*, because until 1975 it was believed to be the largest flying creature of all time. Most studies drew material from the worn and broken bone ends of the *Pteranodon*-like *Ornithocheirus* in the Cambridge University collection, or from the more complete but thoroughly crushed material of *Pteranodon* itself in the Yale University collections (described by Eaton 1910). A typical wing span used in the modern aerodynamic work is about 7 m (Heptonstall 1971; Bramwell 1971; Bramwell and Whitfield 1974; Brower 1983; etc.), though Eaton described a partial radius and ulna that, if projected isometrically, would have yielded a wing span of 8·16 m (Heptonstall 1971). My study of the Yale collections and Eaton's work reveal that the largest size for which complete wings exist is about 5 m. Even at this size, measurements from many incomplete specimens must be pooled in order to arrive at a mean figure. The exact size of the largest *Pteranodon*, however, matters little because in 1975 Lawson described remains of a pterodactyloid he later named *Quetzalcoatlus northropi*, which had a wing-span initially projected at 15·5 m. This estimate proved to be too high, and a figure of about 12 m (35–40 ft), based on additional material and further proportional comparisons, is now generally accepted (Langston 1981). Numerous remains of apparent juveniles of this species, almost exactly half the length of the larger form in all dimensions, have a wing span of approximately 5·8 m (19 ft).

An up-to-date review of aerodynamic assessments of *Pteranodon* and its relative *Nyctosaurus* was given by Brower (1983), which obviates long discussion here; I will summarize only the major outlines and conclusions of other authors (Table 1), and point out possible directions for future research. The most influential work, of course, is the classic monograph by Bramwell and Whitfield (1974) on the biomechanics of *Pteranodon*, which wedded the early functional-morphologic work of Hankin and Watson (1914) to modern concepts of aerodynamics in a beautifully written and lucid paper. According to their findings, echoed by Heptonstall (1971), Stein (1975), Sneyd *et al.* (1982), Brower (1983), and others, *Pteranodon* was a superb low-speed soaring animal that had difficulty flying in high winds and landing, but had a low sinking speed, an excellent lift/drag profile, a light wing loading, low turning radius, high manœuvrability, and optimal performance at 7–10 m/s. It was presumed to spend most of its time gliding at sea, trapping fish at the surface in its great beak. However, its existence must have been marginal, because it was so large that

TABLE 1. Calculated aerodynamic performance of the cretaceous pterosaur *pteranodon*

Author	W Weight (kg)	S Wing area (m ²)	Wing Loading (kg/m ²)	B Wingspan (m)	X Mean Chord (m)	AR Aspect ratio	V Speed (m/s)
von Kripp 1943*	30	3·5	8·5	7	1	14	15
	15	2·25	6·6	6	0·75	16	13·27
Heptonstall 1971	22·7	3·44	6·6	6·8	[0·51]	13	7
Bramwell 1971	18	5·8	3·1	8·2	[0·70]	11·7	6·7
Bramwell and Whitfield 1974†	16·6	4·62	3·6	6·95	[0·66]	10·5	7·7–8·0
Brower 1983‡	14·94	2·53	5·9	6·95	[0·36]	19·1	9·5

Values I calculated from data in other works are in brackets.

* Two configurations were given, based on different aerodynamic performance models.

† Bramwell and Whitfield (1970) considered three weight estimates (11·36, 18, and 25 kg) and used 18; in 1974 they considered 12·8, 16·6, and 23·8, accepting the intermediate value. This is very close to Brower's (1983) estimate, and reflects a range comparable to those of large modern birds.

‡ Brower calculated that *Pteranodon* could fly as fast as 17 m/s under certain conditions.

it was only barely capable of level flight; how it managed to catch fish, recover from the weight of the prey, and overcome the sudden strain on the neck to rise above the water's surface was not clear.

These studies have been very constructive in their efforts to determine parameters of flight mode, and they continue to be productive. It is worth noting, however, that most recent work on the palaeobiology of pterosaurs post-dated the aerodynamic work, and the former has important implications for the latter. Far from suggesting that aerodynamic approaches should be abandoned, I would like to provoke further discussion and investigation into the basis of understanding the aerodynamics of extinct vertebrates by raising the following questions and alternate interpretations to previous work. For some of these interpretations there is good evidence; others require only a change of attitude or modification of assumptions which are, I believe, as plausible as those of other authors.

Many palaeobiological problems, usually overlooked, relate to the structure, function, and ecology of *Pteranodon*, which was phylogenetically only a bizarre sideline of 140 million years of pterosaur evolution. Its smaller forerunners were active fliers; and *Pteranodon*, though neither the last nor the largest of pterosaurs, and not a sustained flapper, retained both limited flapping ability and full bipedal terrestrial locomotion. Any trade off of flapping ability for increased size in this lineage must have been conditional on great advantages to that way of life, and it is unlikely that millions of years of biological and aerodynamic fine-tuning would have been sacrificed in the process. Analyses of *Pteranodon*'s flight have so far ignored this legacy and have overlooked or misinterpreted many important morphological factors. For example, Bramwell and Whitfield (1974) described a 'locking mechanism' in the shoulder joint of *Pteranodon* that, they argued, would have enabled the wing to be fixed in gliding position without expending much energy. This idea has been picked up by many later authors. The form of the glenoid facet, however, is not especially modified as they claim; it merely reflects the suture of the scapula and coracoid, which are fused in most adult diapsids. The corresponding 'ridge' they identify on the head of the humerus is not present on the articular surface but at its margin; this ridge is formed where the superficial laminar bone of the shaft gives way to the porous epiphyseal surface which was covered by cartilage, as was the glenoid. Therefore the 'locking joint' is very questionable. Also, the glenoid fossa faces postero-laterally, not anterolaterally as their Figure 22 shows. These factors greatly influence interpretation of the articulation and movement of the wing, which in reconstructions is almost always swept too far forward.

The structure of the wing membrane is also very important. Most aerodynamic treatments have overlooked palaeobiological considerations of the fine, stiff, intercalated 'fibres' that permeate the wing membrane (Zittel 1882; Wellnhofer 1975; Padian 1979, 1980, 1983b). Brower (1983) notes that they are 'approximately parallel to the wingspan [and to] the major direction of tensioning of the membrane', which is incorrect. These strong, rodlike 'fibres' of keratin or perhaps collagen are never found bent or folded, and their orientation parallels that of the feather shafts of birds and the fingers of bats (text-figs. 2, 3C). Hence they are precisely perpendicular to the direction of spanwise tension at any point along the wing, not parallel to it. Brower, like most other analysts, concluded that pterosaur wings, lacking internal structure, could not have been as manœuvrable as those of bats and could not have flapped at low speeds. But it is precisely the overlooked internal structure of the wing that suggests the opposite: because the spanwise tension would have been resisted by the network of 'fibres', the wing could have been collapsed much more than in bats without loss of aerodynamic competence. Ability to draw in the wing (that is, to reduce its surface area, thereby increasing wing loading) without losing the aerodynamic competence has been denied by most authors, and so most aspects of flight performance observed in modern soaring birds have not been applied to pterosaurs. The flight of *Pteranodon* at all speeds and under all conditions has therefore been modelled as if the animal needed to keep its wings fully outstretched, which is unrealistic in view of the animal's biology.

The configuration of the pterosaur wing, as discussed earlier, was narrow and the aspect ratio high, as in a gull or albatross (Zittel 1882). Most aerodynamic analyses of the flight of *Pteranodon*

(Bramwell and Whitfield 1974; Stein 1975; McMasters 1975; Sneyd *et al.* 1982) have used a model in which the comparatively broad wings were attached to the feet, as in bats, and most of these authors have agreed that a strong tendon along the trailing edge of the wing, anchored to the feet, would have been necessary to control the membrane (text-fig. 3C, *left*). In fact, preserved wings of pterosaurs show incontrovertibly both that the hindlimbs were free of the wing and that no trailing wing tendon existed: further evidence for the structural integrity of the 'fibres'. Without these fibres, a strong trailing tendon would have been necessary, and in that case it would indeed, as aerodynamicists have argued, been very difficult for *Pteranodon* to draw in the wing at all without collapsing it. Furthermore, the extreme forward sweep of the wings commonly pictured (e.g. Bramwell and Whitfield 1974; Brower 1983; Sneyd *et al.* 1982) was impossible, being based on incorrect anatomical interpretations and the assumption of a wide wing. With a narrow wing and correct articulations, the centre of lift is further back, and the wing profile slimmer and more laterally directed (text-fig. 3C, *right*).

What are the aerodynamic consequences of these considerations? Only Brower (1983) has used a narrow wing configuration in aerodynamic calculations, and his calculated wing area is 55% of that used by Bramwell and Whitfield and others. (My own estimate is closer to 45%.) The wing loading is then effectively doubled, which has a significant effect on calculated flying and sinking speeds, polar curves, turning radius, mass distribution, and flapping performance. These will be considered in detail elsewhere, but it may be noted for instance that the wing chord and induced drag are halved, and wing profile drag is probably no longer comparable to that of the Gottingen 417a airplane, which lacks the large leading spar of the pterosaur's wing and is very dissimilar to it in aspect and cross-section.

Accepting that the wing did not lose its shape (i.e. its aerodynamic competence) when partially drawn in, *Pteranodon* need no longer be considered only in fully extended position. The larger wing loadings, higher flying speeds, and lower sinking speeds that result are characteristic of the performances of modern soaring birds. For instance, Bramwell (1971) calculated that in a typical thermal *Pteranodon* would gain half a mile in altitude in five minutes. But what if *Pteranodon* wished to use the thermal to search for food without gaining altitude? One can now see that it had only to flex the wings to achieve lower wing area, higher wing loading, greater airspeed, and even lower sinking speed. Using Bramwell's configurations and calculations, a thermal rising at 4·1 m/s would have carried *Pteranodon* up at a rate of about 3·45 m/s. This value is also her calculated sinking speed at a flying speed of 16·5 m/s. Therefore *Pteranodon* could have flown level in a thermal at 16·5 m/s. This is more than twice the calculated 'optimal' flying speed in still air, and the wings are fully outstretched. How would *Pteranodon*'s performance improve if the ability to flex the wings to control flight were considered?

In general, a palaeobiological view of *Pteranodon*'s flight appears to give greater ranges for most calculated flight variables: higher speeds, more manœuvrability, and better take off and landing performance. The typical calculated polar curve of *Pteranodon* (e.g. Bramwell and Whitfield 1974; Brower 1983) is much more attenuated compared to those of birds and aircraft; but of course, the latter curves were discerned by empirical observation, not by calculation. What would happen if values for albatrosses and falcons were calculated based on the kinds of data estimates used for *Pteranodon*, and then compared with empirical results? Until this is done there is no way to judge the accuracy of approaches that have so far been taken to pterosaur flight. Pterosaurs were not aircraft, and their wings were in no way comparable to those of hang-gliders (*contra* Brower 1983 and McMasters 1975) or sailplanes (*contra* Bramwell and Whitfield 1974); nor were their wing skeletons inflexible spars with the membranes under considerable spanwise tension (*contra* these authors and Sneyd *et al.* 1982). Their wings were comparable in biological and aerodynamic respects to the wings of birds and bats, with a design inherited from their ancestors, shaped by natural selection, and fine-tuned by evolutionary constraints and opportunities. Until these factors are considered in engineering approaches, we shall probably lack a realistic view of the flight performance of pterosaurs, and continue to view them as inferior precursors to birds and bats.

CONCLUSION

Over the past two decades knowledge of animal flight has deepened considerably. Much more is known of the mechanics of flight, and the ability to calculate flight energetics accurately (see Pennycuick 1972) augurs well for the understanding of the evolution of flight and for the significance of the differences among modern flyers in the physiology of flight. Preliminary results of the attempts to fuse engineering with palaeontology to arrive at realistic appraisals of the flight performances of extinct taxa have been pioneering in their approaches. Yet most of this work has yet to take advantage of recent palaeobiological advances in the phylogenetic and functional understanding of these animals. If, as current research indicates, birds evolved from small theropod dinosaurs and developed flight from the ground up, the utility of studying gliding performance in *Archaeopteryx* is uncertain; the earliest birds may seldom, if ever, have glided. The main problem is still getting up in the air and staying up, which requires a realistic analysis of the evolution of flapping. In pterosaurs the efficiency of the wings as flying organs seems to have been underestimated, because considerations of the aerodynamics and functional morphology of the large soaring form *Pteranodon* have neglected the functional and phylogenetic evolution of pterosaurs. Bats, unfortunately, remain largely shrouded in mystery with respect to the means by which they evolved flight; it can be hoped that as their phylogenetic relationship with other mammals is clarified, the characteristics clearly distinguishing bats from these groups may shed light on the evolution of flight in these most unusual of flying vertebrates.

Acknowledgements. I am most grateful to G. R. Caple, W. A. Clemens, D. Yalden, J. A. Gauthier, E. J. Laitone, S. McLeod, M. J. Novacek, J. H. Ostrom, C. Pennycuick, J. M. V. Rayner, M. K. Smith, P. Wellnhofer, and R. Wild for helpful discussions of their work and comments on my own. Their concordance with my views is, of course, not implied, and any errors or misinterpretations are purely mine.

REFERENCES

- ALTENBACH, J. S. 1979. Locomotor morphology of the vampire bat, *Desmodus rotundus*. *Amer. Soc. Mamm. Special Publ.* **6**, 1–137.
- BAKKER, R. T. 1980. Dinosaur heresy—dinosaur renaissance: why we need endothermic archosaurs for a comprehensive theory of bioenergetic evolution. In THOMAS, R. D. K. and OLSON, E. C. (eds.). *A cold look at the warm-blooded dinosaurs*, 351–462. AAAS Selected Symposium Series 28, Westview Press, Boulder, Colorado, 514 pp.
- and GALTON, P. M. 1974. Dinosaur monophyly and a new class of vertebrates. *Nature, Lond.* **248**, 168–172.
- BOCK, W. J. 1965. The role of adaptive mechanisms in the origin of higher levels of organization. *Syst. Zool.* **14**, 272–287.
- 1983. On extended wings. *The Sciences*, **23** (2), 16–20.
- and MILLER, A. H. 1959. The scansorial foot of the woodpeckers, with comments on the evolution of perching and climbing feet in birds. *Amer. Mus. Novit.* **1931**, 1–45.
- BRAMWELL, C. D. 1970. Flying speed of the largest aerial vertebrate. *Nature, Lond.* **225**, 660.
- 1971. Aerodynamics of *Pteranodon*. *Biol. J. Linn. Soc.* **3** (4), 313–328.
- and WHITFIELD, G. R. 1974. Biomechanics of *Pteranodon*. *Phil. Trans. R. Soc. Lond. B* **267**, 503–581.
- BRODKORB, P. 1963. Birds from the Upper Cretaceous of Wyoming. *Proc. 13th Int. Orn. Congr.* 1962, **1**, 55–70.
- BROWER, J. C. 1983. The aerodynamics of *Pteranodon* and *Nyctosaurus*, two large pterosaurs from the Upper Cretaceous of Kansas. *Jour. Vert. Paleo.* **3** (2), 84–124.
- BRYANT, M. D. 1945. Phylogeny of Nearctic Sciuridae. *Amer. Midl. Nat.* **33** (2), 257–390.
- CAPLE, G. R., BALDA, R. T. and WILLIS, W. R. 1983. The physics of leaping animals and the evolution of pre-flight. *Am. Nat.* **121**, 455–467.
- CLARK, B. D. 1977. Energetics of hovering flight and the origin of bats. In HECHT, M. K., et al. (eds.). *Major Patterns of Vertebrate Evolution*, 423–425. Plenum Press, New York.

- COLBERT, E. H. 1966. A gliding reptile from the Triassic of New Jersey. *Amer. Mus. Novit.* **2246**, 1–23.
— 1967. Adaptations for gliding in the lizard *Draco*. *Ibid.* **2283**, 1–20.
— 1970. The Triassic gliding reptile *Icarosaurus*. *Bull. Amer. Mus. Nat. Hist.* **143** (2), 87–142.
— 1980. *The evolution of vertebrates* (3rd edn.). John Wiley and Sons, New York.
— and RUSSELL, D. A. 1969. The small Cretaceous dinosaur *Dromaeosaurus*. *Amer. Mus. Novit.* **2380**, 1–49.
- COOMBS, W. P. 1978. Theoretical aspects of cursorial adaptations in dinosaurs. *Quart. Rev. Biol.* **53**, 393–418.
- CRACRAFT, J. 1977. John Ostrom's studies on *Archaeopteryx*, the origin of birds, and the evolution of flight. *Wilson Bull.* **39**, 488–492.
- DESMOND, A. J. 1975. *The hot-blooded dinosaurs*, 238 pp. Blond and Briggs, London.
- EATON, G. F. 1910. Osteology of *Pteranodon*. *Mem. Conn. Acad. Arts Sci.* **2**, 1–38.
- EVANS, S. E. 1982. The gliding reptiles of the Upper Permian. *Zool. Jour. Linn. Soc.* **76**, 97–123.
- FEDUCCIA, A. 1973. Evolutionary trends in the Neotropical ovenbirds and woodpeckers. *Orn. Monogr.* **13**, 1–69.
— and TORDOFF, H. B. 1979. Feathers of *Archaeopteryx*: asymmetric vanes indicate aerodynamic function. *Science*, **203**, 1021–1022.
- GAUTHIER, J. A. 1984. *A cladistic analysis of the higher systematic categories of the Diapsida*. Ph.D. thesis, Department of Paleontology, University of California.
- and PADIAN, K. (in press). Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In HECHT, M. K., OSTROM, J. H., VIOHL, G. and WELLNHOFER, P. (eds.). *The Beginnings of Birds*. Jura Museum, Eichstatt.
- HANKIN, E. H. and WATSON, D. M. S. 1914. On the flight of pterodactyls. *Aeronaut. Jour.* **18**, 324–335.
- HARRISON, C. J. O. 1976. Feathering and flight evolution in *Archaeopteryx*. *Nature Lond.* **263**, 762–763.
- HEPTONSTALL, W. B. 1970. Quantitative assessment of the flight of *Archaeopteryx*. *Ibid.* **228**, 185–186.
— 1971. An analysis of the flight of the Cretaceous pterodactyl *Pteranodon*. *Scott. J. Geol.* **7** (1), 61–78.
- HILDEBRAND, M. 1982. *Analysis of Vertebrate Structure* (2nd edn.). John Wiley and Sons, New York.
- HOLST, E. VON. 1957. Der Saurierflug. *Palaeont. Z.* **31**, 15–22.
- HOPSON, J. A. 1980. Relative brain size in dinosaurs: implications for dinosaurian endothermy. In THOMAS, R. D. K. and OLSON, E. C. (eds.). *A cold look at the warm-blooded dinosaurs*, 287–310. AAAS Selected Symposium Series 28, Westview Press, Boulder, Colorado.
- HUENE, F. VON. 1914. Beiträge zur Geschichte der Archosaurier. *Geol. Pal. Abh. N.F.* **13**, 1–53.
- JENSEN, J. A. 1981. Another look at *Archaeopteryx* as the world's oldest bird. *Encyclop.* **58**, 109–128.
- JEPSEN, G. L. 1970. Bat origins and evolution. In WIMSATT, W. A. (ed.). *Biology of Bats*, Vol. I, 1–64. Academic Press, New York.
- JERISON, H. J. 1968. Brain evolution in *Archaeopteryx*. *Nature, Lond.* **219**, 1381.
- KIELAN-JAWOROWSKA, Z. 1975. Late Cretaceous mammals and dinosaurs from the Gobi Desert. *Amer. Sci.* **63** (2), 150–159.
- KRIPP, F. VON. 1943. Ein Lebensbild von *Pteranodon ingens* auf flugtechnischer Grundlage. *Nova Acta Leop. N.F.* **12** (83), 217–246.
- LANGSTON, W., JR. 1981. Pterosaurs. *Sci. Am.* **244**, 122–136.
- LAWSON, D. A. 1975. Pterosaur from the Latest Cretaceous of West Texas: discovery of the largest flying creature. *Science*, **187**, 947–948.
- LEWIN, R. 1983. How did vertebrates take to the air? *Science*, **281**, 38–39.
- ULL, R. S. 1906. Volant adaptation in vertebrates. *Am. Nat.* **40** (476), 537–566.
- MCMASTERS, J. H. 1975. An analytic survey of low-speed flying devices—natural and manmade. *Technical Soaring*, **3** (4), 17–39.
- MARSH, O. C. 1880. Odontornithes: a monograph of the extinct toothed birds of North America. *Rept. U.S. Geol. Explor. 40th Parallel*, **7**, 1–201.
- MARTIN, L. D. 1983. The origin of birds and of avian flight. *Current Ornith.* **1**, 105–129.
- STEWART, J. D. and WHETSTONE, K. N. 1980. The origin of birds: structure of the tarsus and teeth. *The Ank.* **97**, 86–93.
- NOPCSA, F. VON. 1907. Ideas on the origin of flight. *Proc. Zool. Soc. Lond.* **1907**, 223–236.
— 1923. On the origin of flight in birds. *Ibid.* **1923**, 463–477.
- NOVACEK, M. J. 1982. Information for molecular studies from anatomical and fossil evidence on higher Eutherian phylogeny. In GOODMAN, M. (ed.). *Macromolecular Sequences in Systematic and Evolutionary Biology*, 3–42. Plenum Press, New York.

- OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist. Yale*, **30**, 1–165.
- 1973. The ancestry of birds. *Nature, Lond.* **242**, 136.
- 1974. *Archaeopteryx* and the origin of flight. *Quart. Rev. Biol.* **49**, 27–47.
- 1975a. The origin of birds. *Ann. Rev. Earth Planet. Sci.* **3**, 55–77.
- 1975b. On the origin of *Archaeopteryx* and the ancestry of birds. *Coll. Int. CNRS*, **218**, 519–532.
- 1976a. Some hypothetical anatomical stages in the evolution of avian flight. In OLSON, S. L. (ed.). *Collected Papers in Avian Paleontology*. *Smiths. Misc. Coll.* **27**, 1–21.
- 1976b. *Archaeopteryx* and the origin of birds. *Biol. Jour. Linn. Soc.* **8**, 91–182.
- 1979. Bird flight: how did it begin? *Amer. Sci.* **67** (1), 46–56.
- 1980. The evidence for endothermy in dinosaurs. In THOMAS, R. D. K. and OLSON, E. C. (eds.). *A cold look at the warm-blooded dinosaurs*, 15–60. AAAS Symposium Series 28, Westview Press, Boulder, Colorado.
- PAIDAN, K. 1979. The wings of pterosaurs: a new look. *Discovery (New Haven)*, **14**, 20–29.
- 1980. *Studies on the structure, evolution, and flight of pterosaurs*. Ph.D. thesis, Yale University. 309 pp.
- 1982. Macroevolution and the origin of major adaptations: vertebrate flight as a paradigm for the analysis of patterns. *Proc. 3rd N. Amer. Paleont. Conv.* **2**, 387–392.
- 1983a. Description and reconstruction of new material of *Dimorphodon macronyx* (Buckland) (Pterosauria: Rhamphorhynchoidea) in the Yale Peabody Museum. *Postilla*, **189**, 1–44.
- 1983b. A functional analysis of flying and walking in pterosaurs. *Paleobiology*, **9** (3), 218–239.
- 1984. The origin of pterosaurs. In REIF, W.-E. and WESTPHAL, F. (eds.). *Proceedings, Third Symposium on Terrestrial Mesozoic Ecosystems*, 163–168. ATTEMPTO, Tübingen.
- and OLSEN, P. E. 1984. The fossil trackway *Pteralichnus*: not pterosaurian, but crocodilian. *J. Paleont.* **58**, 178–184.
- PENNYCUICK, C. J. 1969. The mechanics of bird migration. *Ibis*, **111**, 525–556.
- 1972. *Animal Flight*, 68 pp. Edward Arnold, London.
- PIRLOT, P. 1977. Wing design and the origin of bats. In HECHT, M. K., et al. (eds.). *Major Patterns of Vertebrate Evolution*, 375–410. Plenum Press, New York.
- RAYNER, J. M. V. 1979. A new approach to animal flight mechanics. *Jour. Exp. Biol.* **80**, 17–54.
- 1981. Flight adaptations in vertebrates. In DAY, M. H. (ed.). *Vertebrate Locomotion*, 137–172. Academic Press, New York.
- REGAL, P. J. 1975. The evolutionary origin of feathers. *Quart. Rev. Biol.* **50**, 35–66.
- ROBINSON, P. L. 1962. Gliding lizards from the Upper Permian of Great Britain. *Proc. Geol. Soc. Lond.* **1601**, 137–146.
- RUSSELL, D. A. 1980. Reflections of the dinosaurian world. In JACOBS, L. L. (ed.). *Aspects of Vertebrate History*, 257–268. Museum of Northern Arizona Press, Flagstaff.
- SAVILE, D. B. O. 1962. Gliding and flight in the vertebrates. *Amer. Zool.* **2**, 161–166.
- SEELEY, H. G. 1870. Remarks on Professor Owen's monograph on *Dimorphodon*. *Ann. Mag. Nat. Hist.* (4) **6**, 129–152.
- SMITH, J. D. 1977. Comments on flight and the evolution of bats. In HECHT, M. K., et al. (eds.). *Major Patterns in Vertebrate Evolution*, 427–437. Plenum Press, New York.
- SNEYD, A. D., BUNDOCK, M. S. and REID, D. 1982. Possible effects of wing flexibility on the aerodynamics of *Pteranodon*. *Am. Nat.* **120**, 455–477.
- STEIN, R. S. 1975. Dynamic analysis of *Pteranodon ingens*: a reptilian adaptation to flight. *J. Paleont.* **49**, 534–548.
- TARSITANO, S. and HECHT, M. K. 1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. *Zool. Jour. Linn. Soc.* **69**, 149–182.
- TAYLOR, C. R. 1973. Energy costs of animal locomotion. In BOTIS, L., et al. (eds.). *Comparative Physiology*, 24–42. North Holland, Amsterdam.
- THOMAS, R. D. K. and OLSON, E. C. (eds.). 1980. *A cold look at the warm-blooded dinosaurs*, 514 pp. AAAS Selected Symposium Series 28, Westview Press, Boulder, Colorado.
- THORINGTON, R. W., JR. and HEANEY, L. R. 1981. Body proportions and gliding adaptations of flying squirrels (Petauristinae). *J. Mamm.* **62**, 101–114.
- THULBORN, R. A. and HANLEY, T. L. 1982. The reptilian relationships of *Archaeopteryx*. *Aust. J. Zool.* **30**, 611–634.
- WALKER, A. D. 1973. New light on the origin of birds and crocodiles. *Nature Lond.* **237**, 257–263.
- 1977. Evolution of the pelvis in birds and dinosaurs. In ANDREWS, S. M., et al. (eds.). *Problems in Vertebrate Evolution*, 319–358. Academic Press, London.

- WELLNHOFER, P. 1970. Die Pterodactyloidea (Pterosauria) der Oberjura Plattenkalke Suddeutschlands. *Abh. Bayer. Akad. Wiss. N.F.* **141**, 1–133.
— 1974. *Campylognathoides liasicus* (Quenstedt), an Upper Liassic pterosaur from Hozmaden. *Ann. Carnegie Mus.* **45** (2), 5–34.
— 1975. Die Rhamphorhynchoidea der Oberjura Plattenkalke Suddeutschlands. *Palaeontographica A* **148**, 1–33, 132–186; *A* **149**, 1–30.
— 1978. Pterosauria. *Handbuch der Palaeoherpetologie, Teil 19*. Stuttgart: Gustav Fischer Verlag.
WILD, R. 1978. Die Flugsaurier (Reptilia, Pterosauria) aus der Oberen Trias von Cene bei Bergamo, Italien. *Boll. Soc. Pal. Ital.* **17** (2), 176–256.
WILLISTON, S. W. 1879. 'Are birds derived from dinosaurs?' *Kansas City Rev. Sci.* **3**, 457–460.
YALDEN, D. W. 1971a. Flying ability of *Archaeopteryx*. *Nature, Lond.* **231**, 127.
— 1971b. The flying ability of *Archaeopteryx*. *Ibis*, **113**, 349–356.
ZITTEL, K. A. VON. 1882. Ueber Flugsaurier aus dem lithographischen Schiefer Bayerns. *Palaeontogr.* **29**, 47–80.

KEVIN PADIAN
Department of Paleontology
University of California
Berkeley
California 94720
U.S.A.

Typescript received 28 June 1984

Revised typescript received 13 November 1984

THE MICROSTRUCTURE OF TOOTH ENAMEL IN MULTITUBERCULATE MAMMALS

by G. FOSSE, Z. KIELAN-JAWOROWSKA and S. G. SKAALE

ABSTRACT. The enamel microstructure of single teeth and teeth *in situ* in whole jaws of late Jurassic, late Cretaceous, and Palaeocene multituberculates belonging to the Plagiaulacoidea, Taeniolabidoidea, Ptilodontoidea, and *Meniscoessus* (Cimolomyidae, suborder indet.) is examined by incident light microscopy, scanning electron microscopy (SEM), and polarized light microscopy. For comparison one docodont tooth and some single late Cretaceous and Recent eutherian teeth are included. The enamel of the Plagiaulacoidea like that of the docodont tooth is not prismatic, but consists of radially arranged, closely packed 5 µm thick columns of crystals, which diverge from the central axis of each column towards the outer enamel surface. The Asian as well as the North American Taeniolabidoidea have gigantoprismatic enamel, the numerical density of prisms per unit area being four to five times lower than in the Ptilodontoidea and Eutheria. In most taeniolabidoid jaws the prism density is somewhat higher in the molars than in the incisors. The oldest gigantoprismatic enamel was found in some undescribed multituberculate teeth from the early Cretaceous of Asia. As *Meniscoessus* (suborder indet.) has gigantoprismatic enamel, it is suggested that this feature may be useful in establishing the taxonomic position of some multituberculate groups.

THIS paper examines the tooth enamel of multituberculate mammals from the upper Jurassic, Kimmeridgian to the late Palaeocene, in order to discover differences in enamel microstructure among the suborders Plagiaulacoidea, Ptilodontoidea, and Taeniolabidoidea, to elucidate their relationships.

Moss (1969) found that multituberculate enamel was a non-prismatic, continuous structure, and that it contained tubules which followed a zigzag course. Fosse *et al.* (1973) confirmed the presence of these zigzag tubules but challenged Moss' view on the non-prismatic enamel structure on the basis of six unidentified multituberculate teeth from the late Cretaceous in which the enamel was discontinuous and prismatic, the prisms being extremely large in comparison with those of other mammals. Subsequently Fosse *et al.* (1978) investigated the teeth of four identified multituberculate species, *Catopsalis joyneri* and *Stygimys kuszmauli* (Taeniolabidoidea) and *Mesodma thompsoni* and *M. formosa* (Ptilodontoidea). The number of prisms per mm² ranged from 3650 to 5860 in the members of the Taeniolabidoidea and from 26 600 to 27 200 in the Ptilodontoidea. The taeniolabidoid prism density was the lowest observed in any group of mammals.

Sahni (1979) studied the enamel microstructure in several late Cretaceous North American Ptilodontoidea and Taeniolabidoidea, as well as Eutheria (from the Hell Creek Formation of Montana, Sloan and Van Valen (1965)) and found large prisms in all the multituberculate genera. According to Sahni the prism density per mm² in *Mesodma* and *Meniscoessus* (suborder indet.—see Hahn and Hahn 1983) was 9000 and 7400 respectively, while in *Catopsalis* and *Stygimys* it was 8700 and 4500. The data for *Mesodma* differ considerably from those obtained by Fosse *et al.* (1978). Using the scales given on the *Mesodma* micrographs in Sahni's paper we calculated a mean prism density of 21 400 per mm².

In view of the differences between the results obtained by Fosse *et al.* (1978), by Sahni (1979, Table 1), and by us on Sahni's micrographs, concerning *Mesodma*, we decided to examine once more isolated teeth of *Mesodma* sp. and to compare them with a molar of *Meniscoessus* sp. (Cimolomyidae, suborder indet.), all from the late Cretaceous of North America, and with various taeniolabidoid teeth from the late Cretaceous of Asia (Kielan-Jaworowska 1970, 1974a), the Late Palaeocene of Asia (Matthew and Granger 1925), and the late Cretaceous of North America (Sloan

and Van Valen 1965). All the North American late Cretaceous material comes from the Hell Creek Formation of Montana (Clemens *et al.* 1979). The late Cretaceous Asian material which forms the bulk of the material comes from the Djadokhta and Barun Goyot formations, or the stratigraphic equivalent of the latter: the red beds of Khermeen Tsav. We tentatively accept, after Gradzinski *et al.* (1977) that the Djadokhta Formation belongs to the upper Santonian and/or lower Campanian Stage, while the Barun Goyot Formation (and the red beds of Khermeen Tsav) belong to the middle Campanian Stage.

We also examined the enamel microstructure of isolated teeth from the early Cretaceous of Asia, which are at present being studied by Kielan-Jaworowska, Dashzeveg, and Trofimov. Some of these teeth (genus *Arginbaatar*) were assigned to the Taeniolabididae by Trofimov (1980), while Hahn and Hahn (1983) erected the family Arginbaataridae within the Plagiaulacoidea. Consequently at present we assign all the early Cretaceous Mongolian multituberculates to a suborder indet.

The earliest multituberculate teeth examined by us belong to the suborder Plagiaulacoidea and come from the late Jurassic, Kimmeridgian, of Portugal (Hahn 1969, 1971, 1978). From the same location we also included an unidentified docodont tooth for comparison, as well as teeth of late Cretaceous and Recent eutherian mammals.

ABBREVIATIONS

GI	Institute of Geology, Academy of Sciences of the Mongolian People's Republic, Ulan Bator.
IAUB	Institute of Anatomy, University of Bergen, Bergen.
PIFU	Palaeontologishes Institut, Freie Universität, Berlin.
UM	University of Minnesota, Minneapolis, U.S.A.
ZPAL	Institute of Palaeobiology, Polish Academy of Sciences, Warsaw.

I incisor dp deciduous premolar P permanent premolar M molar.

MATERIAL

Docodonta

Docodontidae

gen. et sp. indet., Kimmeridgian, Portugal, Leiria, Guimarota: PIFU no number (a molar)

Multituberculata

Plagiaulacoidea

Family, gen. et sp. indet., Kimmeridgian, Portugal Leiria, Guimarota: PIFU no number (a molar)

Paulchoffatidae (all from the Kimmeridgian of Portugal, Leiria, Guimarota):

Paulchoffatia sp.: PIFU VJ 270-155 (dp¹); PIFU VJ 272-155 (P¹); PIFU VJ 273-155 (P¹)

Kuehneodon sp.: PIFU VJ 303-155 (P⁵); PIFU VJ 308-155 (P⁵)

Suborder indet. (all from the ?Aptian or Albian Guchin beds of Mongolia, Guchin Us):

Arginbaataridae

Arginbaatar dimitrievae Trofimov: GI PST 10/11 (P₄); GI PST 10/13 (P₄)

Family, gen. et sp. indet.: GI PST 10/29 (I¹); GI PST 10/23 (P₄)

Taeniolabidoidea

Eucosmodontidae

(*Chulsanbaatar*, *Nemegtbaatar*, and *Kryptobaatar* are from the upper Cretaceous of Asia, Gobi Desert, *Stygimys* from the upper Cretaceous, Hell Creek Formation, North America, Montana, Bug Creek):

Chulsanbaatar vulgaris Kielan-Jaworowska, Barun Goyot Formation, Khulsan: ZPAL MgM-I/62 (I₁, M₁); ZPAL MgM-I/157 (I₁, P₄, M₁); Barun Goyot Formation, Nemegt: ZPAL MgM-I/111 (I₁); red beds of Khermeen Tsav, Khermeen Tsav II: ZPAL MgM-I/108 (I₁); ZPAL MgM-I/109 (I₁, P₄)

Nemegtbaatar gobiensis Kielan-Jaworowska, red beds of Khermen Tsav, Khermen Tsav II: ZPAL MgM-I/81 (I₁, M₁); ZPAL MgM-I/82 (I₁, P₄, M₁)

Kryptobaatar dashzevegi Kielan-Jaworowska, Djadokhta Formation, Bayn Dzak: ZPAL MgM-I/7 (P₄); ZPAL MgM-I/9 (P₄, M₁); ZPAL MgM-I/37 (I₁, M₁); ZPAL MgM-I/53 (I₁, P₄, M₁)

Stygimys kuszmaudi Sloan and Van Valen, Hell Creek Formation, Bug Creek: UM no. 5 (I₁, M₂)

Taeniolabididae (all from Asia, Gobi Desert):

Kamptobaaatar and *Catopsalis* are from the upper Cretaceous, *Prionessus* from the Upper Palaeocene
Kamptobaaatar kuczynskii Kielan-Jaworowska, Djadokhta Formation, Bayn Dzak: ZPAL MgM-I/38
(P₄)

Catopsalis catopsaloides (Kielan-Jaworowska), red beds of Khermeen Tsav, Khermeen Tsav II: ZPAL
MgM-I/78 (I₁, M₁); ZPAL MgM-I/80 (M₁)

Prionessus lucifer Matthew and Granger, Naran Bulak: ZPAL MgM-II/67 (I₁, M₁, M₂)

Ptilodontoidea

Neoplagiaulacidae (all from the upper Cretaceous Hell Creek Formation, North America, Montana, Bug Creek):

Mesodma thompsoni Clemens: UM no. 3 (P₄)

Mesodma sp.: ZPAL MK-I/7 (P₄); ZPAL MK-I/8 (P₄); ZPAL MK-I/3 (M¹); ZPAL MK-I/6 (M¹)

Suborder indet.

Cimolomyidae, Bug Creek, Montana, Hell Creek formation:

Meniscoessus sp.: ZPAL MK-I/9 (M₂)

Eutheria

Proteutheria

Kennalestidae, Djadokhta Formation, Gobi Desert, Bayn Dzak:

Kennalestes gobiensis Kielan-Jaworowska: ZPAL MgM-I/3 (P³)

Rodentia

Muridae, Recent, Europe:

Rattus norvegicus (Berkenhout): IAUB no number (I₁, M₁)

Primates

Hominidae, Recent, Europe:

Homo sapiens L.: IAUB no number (P²).

METHODS

The Asian multituberculate material investigated in Warsaw consisted of whole mandibles with teeth *in situ*. The right or left mandible was positioned in plasticine on a microscope slide under a dissection microscope in such a way that a selected region of enamel on the tooth to be studied was the highest point of the whole dentition. This region was then carefully planed horizontally by hand using 0/2 and then 0/4 grit emery paper (Buchler Ltd., Evanston, Ill., U.S.A.), each grade having been glued and trimmed to either of the two long, narrow sides of a 10 × 2 × 0.3 cm rectangular, planed wood stick. The horizontal, tiny but relatively flat enamel surface, less than 1 mm in diameter formed in this way was then etched with a very small amount of 0.37 N HNO₃ applied by a fine-pointed brush. The etching was interrupted after 5 sec with plain water, using a similar brush. Next, to micrograph the etched surface, the microscope slide with the specimen still in the original position on it was transferred to a Leitz Laborlux microscope equipped with camera, an Ultropak incident light condenser and a U-O-11 objective. A Leitz microscale with 10 µm divisions was micrographed with the same magnification.

At IAUB the films of the etched surfaces with cross-cut enamel prisms were copied on 23 × 30 cm film sheets with a standard magnification.

The smallest unit that describes the number of cross-sectioned prisms per mm² (numerical prism density) is a triangle consisting of central distances between three adjacent prisms. Determining the prism density in the enamels consisted of measuring the distances between centres of adjacent prisms in several such triangular units within each micrographed enamel area (Fosse, 1968a).

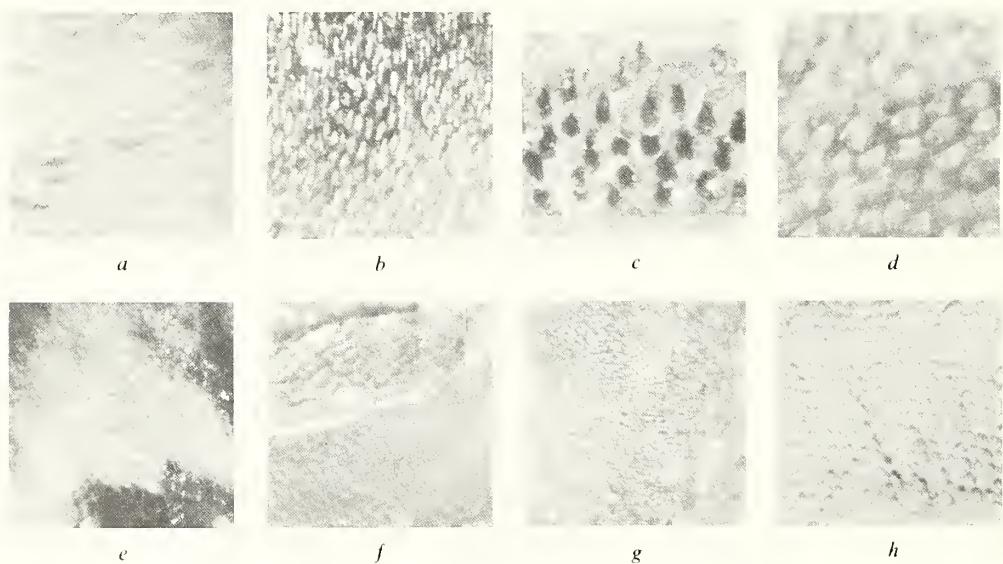
Table 1 presents prism densities (a), mean central distances between adjacent prisms (D), and the new parameter A which signifies the theoretical mean cross-sectional area in µm² of the enamel producing end of the ameloblasts (Fosse 1968d; Fosse *et al.* 1973, *et al.* 1978). The prism density values presented were calculated from incident light micrographs of superficially planed and etched natural outer enamel surfaces which are nearly planoparallel with an original layer of ameloblasts (Fosse *et al.* 1973). As it is still generally believed that each prism rod is produced by one ameloblast (Fosse *et al.* 1978), the number of prisms per mm² in such planes should reflect the number of original enamel producing ameloblasts per mm² in that plane, irrespective of its angle with the prism rods underneath (Fosse 1968c).

Two multituberculate lower jaws, *Chulsanbaatar vulgaris* Kielan-Jaworowska, ZPAL MgM-I/62, and *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/53, as well as docodont and plagiulaocoid single teeth

(gen. et sp. indet.), and five plagiulaacoid single teeth determined at generic level, all from the Kimmeridgian, Leiria, Guimarota, Portugal, were sectioned by a wire string saw (Fosse *et al.* 1974) to obtain cut surfaces or thin sections for transmitted light microscopy. For the SEM micrographs a Jeol T-200 instrument was used. The specimens were covered by gold-palladium before SEM micrography. A Leitz Ortholux Pol microscope was used for transmitted light micrographs of thin tooth sections.

RESULTS

In the material in Warsaw, clusters of prisms were usually quickly recognized in the planed and etched enamel surfaces. Text-fig. 1*a* represents P_4 of *K. dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/7. With the same magnification text-fig. 1*b*, *c*, and *d* respectively show the prism densities in *Mesodma* sp. (P_4), *Stygimys kuszmauli* (I_1), and *Meniscoessus* sp. (M_2) enamels, all three from the late Cretaceous, Lancian (Maastrichtian), North America, Montana, Bug Creek. In incident light planed and etched enamel surfaces of Kimmeridgian plagiulaacoid and docodont teeth showed regularly packed structures in a pattern resembling cross-cut prism rods, (text-fig. 1*e*, *f*). Their numerical density and mean interproximate central distance were of a magnitude between those of the eutherians: late Cretaceous *Kennalestes gobiensis* and Recent *Rattus norvegicus*, (text-fig. 1*g*; Table 1). Human enamel had considerably larger prisms than *R. norvegicus*. The prism density near the cusp on the outer surface of a human premolar was about the same as that of *Mesodma* sp.,



TEXT-FIG. 1. Incident light micrographs of planed and etched surfaces of various enamels reproduced with the same magnification, $\times 250$. *a* represents the enamel surface of a tooth micrographed *in situ*, *c* and *f* represent the cut and etched enamels of sectioned teeth, all the others represent superficially planed and etched outer enamel surfaces of teeth embedded in plastic blocks. *a*, *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/7, P_4 , occlusal edge above. *b*, *Mesodma* sp., ZPAL MK-I/8, P_4 , occlusal edge above. *c*, *Stygimys kuszmauli* Sloan and Van Valen, UM no. 5, I_1 , showing longitudinal section through medial enamel facet seen in the lingual direction, dentine below. *d*, *Meniscoessus* sp., ZPAL MK-I/9, M_2 , occlusal surface above. *e*, *Paulchoffatia* sp., PIFU VJ 273-155, P^1 , showing prism-like pattern of structures without distinct borders, occlusal surface to right. *f*, docodont molar (gen. et sp. indet.), PIFU no number, obliquely cut through one of the cusps, showing prism-like pattern, montage. *g*, *Rattus norvegicus* (Berkenhout), IAUB no number, M_1 , occlusal surface above. *h*, *Homo sapiens* L., IAUB no number, P^2 , occlusal surface above.

TABLE 1. The number of prisms per mm² (a), the mean central distance in microns between adjacent prisms (D), and the theoretical mean cross-sectional area in µm² of the enamel producing cells (A) (see Methods) in the enamel of some specimens of European, Asian, and North American multituberculates from different ages, of one undetermined docodont molar, one Cretaceous, and two recent eutherian species. The ZPAL specimens were represented by whole jaws from which the enamel parameters of more than one tooth were usually available, see Material.

Species/specimen	a	D	A	
Docodont, gen. & sp. indet.				
PIFU no number	34 514	5·78	28·9	M
<i>Paulchoffatia</i> sp.				
PIFU VJ 273-155	43 080	5·17	23·2	P ¹
PIFU VJ 272-155	59 987	4·38	16·6	P ¹
<i>Kuehneodon</i> sp.				
PIFU VJ 303-155	50 983	4·75	19·6	P ⁵
<i>Arginbaatar dimitrievae</i> Trofimov				
GI PST 10/11	7123	12·73	140·3	P ₄
GI PST 10/13	5426	14·58	184·2	P ₄
Multituberculata subord. fam. gen. and sp. indet.				
GI PST 10/29	4891	15·36	204·4	I ¹
GI PST 10/23	11 365	10·07	87·9	P ₄
<i>Chulsanbaatar vulgaris</i> Kielan-Jaworowska				
ZPAL MgM-I/62	5812	14·09	172·0	I ¹
	10 001	10·74	99·9	M ₁
ZPAL MgM-I/157	4960	15·25	201·5	I ₁
	5734	14·18	174·3	P ₄
	11 623	9·96	86·0	M ₁
ZPAL MgM-I/111	6519	13·30	153·4	I ₁
ZPAL MgM-I/108	7219	12·64	138·5	I ₁
ZPAL MgM-I/109	6258	13·58	159·7	I ₁
	9520	11·01	105·0	P ₄
<i>Nemegthaatar gobiensis</i> Kielan-Jaworowska				
ZPAL MgM-I/81	5399	14·62	185·1	I ₁
	12 133	9·75	82·4	M ₁
ZPAL MgM-I/82	5435	14·57	183·9	I ₁
	4241	16·49	235·7	P ₄
	8271	11·81	120·9	M ₁
<i>Kryptobaatar daszevegi</i> Kielan-Jaworowska				
ZPAL MgM-I/7	6314	13·52	158·3	P ₄
ZPAL MgM-I/9	3379	18·48	295·9	I ₁
	6349	13·48	157·4	P ₄
ZPAL MgM-I/10	4464	16·08	223·9	I ₁
	5271	14·79	189·6	P ₄
ZPAL MgM-I/21	3705	17·65	269·8	I ₁
	4908	15·33	203·7	P ₄
	3980	17·03	251·2	M ₁
ZPAL MgM-I/37	4292	16·40	232·9	I ₁
	3753	17·53	266·4	M ₁
ZPAL MgM-I/53	3415	18·38	292·7	I ₁
	5812	14·09	172·0	P ₄
	6039	13·82	165·5	M ₁
<i>Stygimys kuszmauli</i> Sloan and Van Valen				
UM no. 5	3860	17·29	259·0	I ₁
<i>Kryptobaatar kuczynskii</i> Kielan-Jaworowska				
ZPAL MgM-I/38	6776	13·05	147·5	P ₄

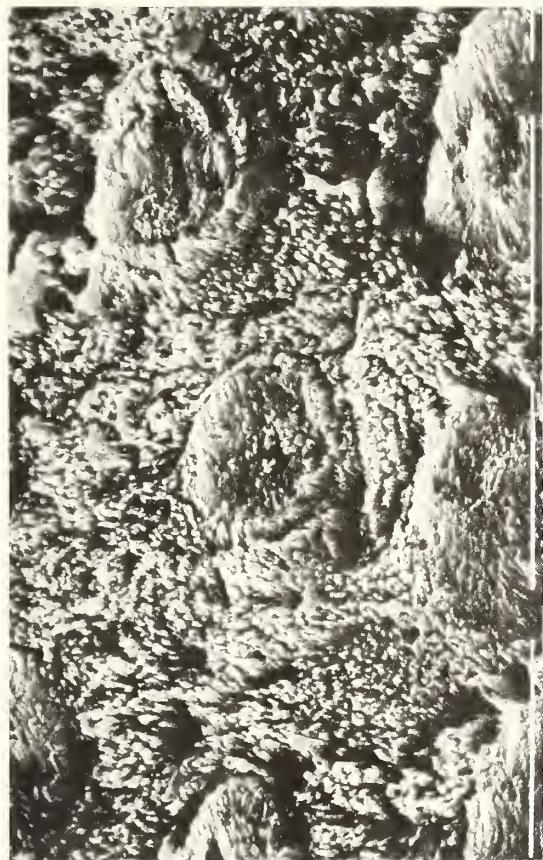
TABLE 1 (cont.)

Species/specimen	a	D	A	
<i>Catopsalis catopsalooides</i> (Kielan-Jaworowska)				
ZPAL MgM-I/78	4740	15.60	210.9	I ₁
	6650	13.17	150.3	M ₁
ZPAL MgM-I/80	6063	13.79	164.9	M ₁
<i>Prionessus lucifer</i> Matthew and Granger				
ZPAL MgM-II/67	6440	13.38	155.2	I ₁
	5776	14.13	173.1	M ₁
	6138	13.71	162.9	M ₂
<i>Mesodma</i> sp.				
ZPAL MK-I/7	28 627	6.35	34.9	P ₄
ZPAL MK-I/8	26 321	6.62	37.9	P ₄
ZPAL MK-I/3	26 694	6.58	37.5	M ¹
ZPAL MK-I/6	21 557	7.32	46.4	M ¹
<i>Meniscoessus</i> sp.				
ZPAL MK-I/9	4088	16.80	244.5	M ₂
<i>Kenalestes gobiensis</i> Kielan-Jaworowska				
ZPAL MgM-I/3	31 599	6.04	31.6	P ³
<i>Rattus norvegicus</i> (Berkenhout)				
IAUB no number	65 703	4.19	15.2	I ₁
	67 095	4.14	14.9	M ₁
<i>Homo sapiens</i> L.				
IAUB no number	25 335	6.75	39.5	P ²

(text-fig. 1b, h; Table 1). In most ZPAL taeniolabidoid jaws with more than one tooth micrographed, the prism density of the incisor was lower than that of P₄ or M₁, see Table 1. The higher density in the molars apparently is caused not so much by smaller prisms as by less interprismatic enamel (Pl. 48, figs. 1 and 2). The great difference between the microstructure of taeniolabidoid and *Mesodma* enamels is demonstrated in Plate 48, figs. 1–4, where it is also seen that the crystal structure of the *Kryptobaatar* enamels was coarser than that of the *Mesodma* enamels. Near the outer surface of human enamel there is very little interprismatic substance (Pl. 48, fig. 5). The human prism diameters

EXPLANATION OF PLATE 48

Figs. 1–5. SEM micrographs of superficially planed and etched outer enamel surfaces reproduced with the same magnification, $\times 2900$, documented by the automatically recorded scale divisions of $10 \mu\text{m}$ having been retained in the micrographs. 1, *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/53, I₁, showing that the prisms are widely separated by interprismatic enamel consisting of crystals being normal to the surface and that the crystals of the prism cores are obliquely orientated relative to the surface and inclined in an incisal direction above. 2, M₁ from the same dentition as I₁ in fig. 1, showing that the spatial arrangement of the crystals in the prisms and interprismatic enamel is less distinct and that the prisms are nearly of the same size but more closely packed than in I₁. 3, *Mesodma* sp., ZPAL MK-I/8, P₄, showing that the prisms are smaller and their numerical density per unit area considerably lower than in *Kryptobaatar* enamel, also that the crystals are more delicate and densely packed. In the interprismatic enamel the crystals are normal to the surface, while those of the prism cores are inclined in a cuspal direction to the left. 4, *Mesodma* sp., ZPAL MK-I/3, M¹, not belonging to the same individual as P₄ in fig. 3, but showing similar prism size, numerical density of prisms, and crystal orientation. Cuspal direction is to the left. In the upper half are some openings of enamel tubules. 5, *Homo sapiens* L., IAUB no number, P², showing that prisms are nearly as large as in *Kryptobaatar* enamel (fig. 1), but that their numerical density approximates that of the *Mesodma* enamels (figs. 3 and 4). Cuspal direction is to the right.



1



2



3



4



5

FOSSE, KIELAN-JAWROWSKA and SKAALE, multituberculate enamel

are about as large as those of the *Kryptobaatar* (Pl. 48, figs. 1 and 2) and *Chulsanbaatar* enamels (Pl. 49, fig. 3), whereas the distances between centres of adjacent prisms equal those of the *Mesodma* enamels (Pl. 48, figs. 3 and 4; Table 1). Thus there is no interdependence between prism diameters and number of prisms per unit area.

Longitudinal and transverse sections of taeniolabidoid incisors showed cross-cut prisms; in longitudinal sections when they passed through the medial enamel facets where the prism rods were inclined in a dorsomedial (mesiolingual) direction in a transversal plane relative to the incisors, in transversal sections in the ventrolateral facets where the prism rods were inclined in an anterior (incisal) direction in a sagittal plane relative to the tooth. Regardless of the orientation of the enamel surfaces represented by Plate 48, figs. 1–4 and Plate 49, figs. 1 and 3, they all demonstrate that the crystals in the interprismatic enamel are orientated with their long axis nearly normal to the natural outer enamel surface. The crystals of the prism cores are parallel with the prism rods, and the apices of the arcades are pointing in the direction of the acute angle between prism rods and the dentine enamel junctional surface.

In the SEM discrete enamel prisms in the Kimmeridgian enamels could not be discerned. Plate 49, figs. 2 and 5 show plagiocalcoid and docodont enamels at the same magnification. A certain regular pattern in the crystal orientation may be observed. This pattern seemed to consist of 5 µm thick, closely packed columns of crystals, the latter diverging from the central axis of each column towards the external enamel surface. In Table 1 are given the values for three plagiocalcoid teeth and one docodont molar from the Kimmeridgian, Portugal, based on measurements in incident light micrographs.

Longitudinal sections, about 80 µm thick, were prepared from three plagiocalcoid teeth of which two were determined on the generic level, and one docodont molar (gen. et sp. indet.) from the Kimmeridgian. In the microscope one of the plagiocalcoid enamels (gen. et sp. indet.) showed large black spots along lines that might correspond to the course of growth lines (striae of Retzius, Pl. 50, fig. 1). In polarized transmitted light with crossed polars and the dentine enamel junction at

EXPLANATION OF PLATE 49

Figs. 1–5. SEM micrographs of various multituberculate enamels reproduced with the same magnification, ×2900, documented by the automatically recorded scale divisions of 10 µm having been retained along the right margins of the micrographs. Figs. 1, 2, and 3 represent sectioned and etched enamel surfaces, figs. 4 and 5 superficially planed and etched outer enamel surfaces. 1, *Stygimys kuszmauli* Sloan and Van Valen, UM no. 5, I₁, enlargement of the same enamel surface as figured in text-fig. 1c, but rotated 90°, dentine enamel border at right. The prisms are large and widely separated by interprismatic enamel where the crystals are orientated with their long axes in the figured plane, from left to right, e.g. perpendicularly to the outer enamel surface, while the crystals of the prisms are normal to the figured surface. Towards the dentine at right the borders of two prisms consist of an amorphous material. 2, *Paulchoffatia* sp., PIFU VJ 270-155, dp¹, showing oblique section through cusp where the enamel consists of crystals without preferential orientations in prisms and interprismatic material. In some places it may be seen that the crystals are arranged in fan-shaped clusters. Dentine in lower left corner. 3, *Chulsanbaatar vulgaris* Kielan-Jaworowska, ZPAL MgM-I/62, I₁, showing transversal section through ventrolateral enamel facet. The prisms are somewhat smaller and their numerical density higher than in *Kryptobaatar* (Pl. 48, fig. 1) and *Stygimys* (fig. 1) enamels. The interprismatic enamel consists of crystals orientated with their long axes in the figured plane from top to bottom, e.g. normal to the outer enamel surface while the crystals of the prism cores are nearly normal to the figured plane. Arcade shaped grooves surround the prisms, the apices of which point towards the dentine at top. 4, *Meniscoessus* sp., ZPAL MK-I/9, M₂, showing arcade shaped grooves surrounding the large prisms, the apices of which point in the cuspal direction at left. Crystals of interprismatic enamel are generally normal to the figured surface, while the crystals of the prisms are inclined to the left. 5, docodont molar (gen. et sp. indet.), PIFU no number. There is no organization of crystals in prisms and interprismatic enamel, but the uneven appearance of the etched surface indicates the presence of crystal clusters about 5 µm wide.



1



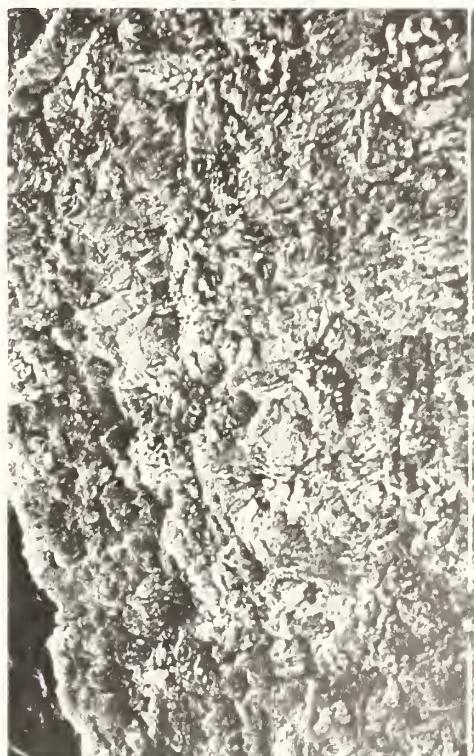
3



4



2



5

a small angle with the polarizer axis, poorly defined band-like 5–6 µm thick structures could be seen in plagiulaucoid as well as docodont enamels, running radially from the inner to the outer surface (Pl. 50, figs. 2–5). Enamel tubules were very scarce. In polarized light the longitudinally cut *Chulsanbaatar*, *Kryptobaatar*, and *Stygimys* enamels showed discrete broad and straight bands of a regular width, running at an angle of approximately 45° to the outer enamel surface. Enamel tubules were abundant, coursing from the dentine enamel junction along the bands for short distances, but mostly crossing them, running mainly in a radial direction (Pl. 50, figs. 6–8). Longitudinally sectioned *Mesodma* premolar enamel like that of the taeniolabidoid enamels showed discrete bands of a regular but much narrower width. A few enamel tubules were seen (Pl. 50 fig. 9). Black spots like those seen in the plagiulaucoid enamel, but irregularly arranged, were observed in some sections of taeniolabidoid enamels. The bands of the docodont and plagiulaucoid enamels were most distinctly seen when their long axes were parallel with one of the polarizer planes. They were negatively birefringent when positioned with their long axes diagonally in the field of vision; in this position these enamels seemed structureless. The bands of the taeniolabidoid and *Mesodma* enamels shown in Plate 50, figs. 6–9, were also negatively birefringent with respect to their length, and most distinctly seen by maximum prism extinction which occurred when they were inclined a little, relative to one of the polarizer planes; from 0° to 20° for the different sections and different enamel areas within each section. This maximum extinction was obtained by rotating the stage with the section in the direction of the prism inclination towards the cusp from the position where the prisms were parallel with one of the polarizer planes.

DISCUSSION

Poole (1956) found that tooth enamel in synapsid reptiles was non-prismatic as the crystals were arranged in closely packed cylindrical groups that were normal to the enamel surface. They were called pseudo-prisms. Poole (1957) stated that prismatic enamel generally originated in primitive mammals. Moss (1969) studied fossil therapsid, non-therian and therian enamels, including the enamel of fossil marsupials and placentals, and concluded that therapsid and all non-therian enamels are continuous, but with a banded appearance in longitudinal thin sections when viewed in the polarizing microscope. According to the same author true prismatic enamel which is characteristic

EXPLANATION OF PLATE 50

Figs. 1–9. Thin sections of enamel of longitudinally sectioned teeth micrographed in transmitted light with the same magnification, ×875. Excepting fig. 1 where normal light was used, the sections were micrographed in polarized light with crossed filters. The incisal/cuspal direction is to the left, dentine below. 1, late Jurassic, Kimmeridgian plagiulaucoid molar (gen. et sp. indet.). Black spots within the enamel lie in rows probably along growth lines (striae of Retzius). A few enamel tubules are seen, section thickness 60 µm. 2, the same section showing indistinct band-like structures of irregular width normal to the dentine where hair-pin bends of dentinal tubules are seen. 3, late Jurassic, Kimmeridgian docodont molar (gen. et sp. indet.), showing band-like structures normal to the dentine enamel junction, section thickness 55 µm. 4, *Paulchoffatia* sp., PIFU VJ 273–155, P¹, showing band-like structures nearly normal to the dentine, section thickness 90 µm. 5, *Kuehneodon* sp., PIFU VJ 308–155, P⁵, showing band-like structures normal to the dentine, section thickness 90 µm. 6, *Chulsanbaatar vulgaris* Kielan-Jaworowska, ZPAL MgM-I/62, I₁, showing distinct, broad bands of regular width inclined about 45° to the dentine enamel junction, enamel tubules cross the bands, section thickness 80 µm. 7, *Kryptobaatar dashzevegi* Kielan-Jaworowska, ZPAL MgM-I/53, P₄, showing distinct bands of similar width and orientation as in fig. 6, section thickness 90 µm. 8, *Stygimys kuszmauli* Sloan and Van Valen, UM no. 5, M₂, showing slightly broader bands but of similar orientation as in figs. 6 and 7, enamel tubules crossing bands, section thickness 60 µm. 9, *Mesodma thompsoni* Clemens, UM no. 3, P₄, showing distinct curved bands, but of a narrower width than in figs. 6, 7, and 8, a few enamel tubules are seen, section thickness 50 µm.



1



2



3



4



5



6



7



8



9

only for Theria first appeared in the early Cretaceous (Albian) forms. Poole (1971) studying Jurassic dryolestids, suggested that prismatic enamel originated in Theria. Poole and Cooper (1971) found prismatic enamel in the extant agamid *Uromastix* however, and concluded that enamel prisms are not confined to mammals. Osborn and Hillman (1979) studied by polarizing microscopy the enamel of the pelycosaur *Dimetrodon*, the therapsids *Thrinaxodon*, *Probainognathus*, *Proboleodon*, *Diademodon*, and *Massetognathus*, the early Jurassic primitive triconodont *Eozostrodon* (? = *Morganucodon*), a late Cretaceous dryolestid, and therian mammals. They found that prismatic enamel only appeared in the Cretaceous non-therian and therian mammals. In the Permian *Dimetrodon* the enamel was micromorphologically homogeneous with regard to crystal orientation, whereas all Triassic–early Jurassic enamels are characterized by ‘an arrangement of close-packed hexagonal columns of crystals (Osborn and Hillman 1979, p. 58). In a longitudinal section of *Diademodon* enamel a column of crystals was about 5 µm wide. There was no interprismatic enamel. These observations concerning crystal orientation in Triassic–early Jurassic enamels are consistent with the results of our light and SEM microscopic study of the late Jurassic plagioulacoid and docodont enamels as radially orientated bands about 5 µm wide were seen in longitudinal sections (Pl. 50, figs. 2–5) and prism-like structures with interproximate central distances of about 5 µm in tangential planes (text-fig. 1e, f). In SEM the late Jurassic enamels studied by us showed crystals spraying out towards the outer enamel surface from the centre of 5 µm thick closely packed ‘columns’ (Pl. 49, figs. 2 and 5).

Grine *et al.* (1979) by SEM studies found discrete prisms with interprismatic enamel between them in *Eozostrodon* teeth. Grine and Vrba (1980) also demonstrated prismatic enamel in the cynodont *Pachygenelus*. Interprismatic central distances according to magnifications were about 5 µm. Frank *et al.* (1984) described ‘preprismatic’ enamel in late Triassic haramiyids and so did Sigogneau-Russell *et al.* (1984) in the early Jurassic therian *Kuehneotherium*. Preprismatic enamel according to these latter authors consists of radially arranged columns of crystals similar to those described by Osborn and Hillman (1979) and by us in this paper. Excepting the results of Grine *et al.* (1979) and Grine and Vrba (1980), it may be concluded at present from the reports cited above that prismatic enamel originated in non-therian mammals and not before the Cretaceous as stated by Osborn and Hillman (1979), whereas preprismatic enamel where crystals are arranged in 5 µm thick closely packed columns originated in cynodonts, therapsids, and persisted in some non-therians and therians from the Triassic through the late Jurassic. In light of this the findings of Grine *et al.* (1979) and Grine and Vrba (1980) are perplexing and should encourage further studies on enamel microstructure of non-therian forms of pre-Cretaceous age.

Our findings support the hypothesis of Fosse *et al.* (1978) that the multituberculate suborder Taeniolabidoidea was characterized by remarkably large and widely separated enamel prisms. Osborn and Hillman (1979) have confirmed the existence of such large prisms in *Catopsalis* sp. and *Stygimys* sp. Carlson and Krause (1982) with a few exceptions found large prisms in Taeniolabidoidea. The oldest ZPAL multituberculates derive from the late Cretaceous, Gobi Desert, Djadokhta Formation, which is of ?late Santonian and/or ?early Campanian age (see Material). However, due to the courtesy of Dr. Demberlyin Dashzeveg we were able to examine by incident light microscopy the enamel microstructure of two identified and two unidentified multituberculate teeth from the early Cretaceous (?Aptian or ?Albian) of Guchin Us, Gobi Desert, Mongolian People’s Republic (see Clemens *et al.* 1979). They are the specimens GI PST 10/11, GI PST 10/13, GI PST 10/29, and GI PST 10/23 housed in the Institute of Geological Sciences of the Mongolian Academy of Sciences in Ulan Bator. These teeth show the same size and numerical density of prisms as do the Taeniolabidoidea from late Cretaceous of Asia (Table 1). The Guchin Us multituberculates are currently being investigated by Kielan-Jaworowska, Dashzeveg, and Trofimov and if it can be demonstrated that the Early Cretaceous Asian multituberculates are close to the ancestors of late Cretaceous Taeniolabidoidea, which the enamel structure indicates, it may be concluded that this peculiar prismatic enamel structure was established and persisted in Taeniolabidoidea through a time span ranging from Aptian or Albian to late Palaeocene.

Our finding that *Mesodma* (suborder Ptilodontoidea) enamel had a mean prism density of 25800

per mm² agrees with the results of Fosse *et al.* (1978), but disagrees with the conclusion of Sahni (1979) with regard to *Mesodma* enamel. By our method we calculated the densities 24120, 22300, and 19840 respectively in his figured *Mesodma* enamels (Sahni 1979, pl. 1, figs. 2, 3, and 6), which represent cross-cut prisms in *Mesodma* enamel in his paper. Therefore, we submit that in *Mesodma* enamel, there is a significantly higher prism density and smaller prisms than in the representatives of Taeniolabidoidea. Carlson and Krause (1982) in other ptilodontoid taxa also found prism diameters similar to those we observed in *Mesodma* enamels. It seems that Ptilodontoidea do not differ significantly with respect to numerical prism density from many recent representatives of Eutheria (Fosse 1968b, d) and Metatheria (Fosse *et al.* 1973), nor from the late Cretaceous eutherians *Protungulatum donnae* (Fosse *et al.* 1978) and *Kennalestes gobiensis* (Table 1 in this paper). Thus the enamel in Taeniolabidoidea is gigantoprismatic, meaning that the prism density per unit area is four to five times lower than in the ptilodontoid *Mesodma* sp. and in all other known mammals. Poole (1956) suggested that during amelogenesis each column in pseudoprismatic enamel may be the product of one ameloblast. Assuming that columns in preprismatic enamel and prisms in 'normal' as well as gigantoprismatic enamel are the products of single ameloblasts, the present documentation concerning the range of column and prism dimensions, see text-fig. 1, demonstrates the enormous diversity in ameloblast diameters in mammals. It may be speculated that each prism and half the thickness of interprismatic enamel surrounding it were formed by more than one ameloblast in taeniolabidoid enamel. Considering the similarity of crystal orientation in prisms and interprismatic material between gigantoprismatic and 'normal' enamel (Pl. 48, figs. 1, 3, and 4), this seems improbable and would represent a very unique and special organization of the active ameloblasts in Taeniolabidoidea compared with Ptilodontoidea and other extinct and all Recent mammals.

Fosse *et al.* (1973, Figs. 1, 12, and 13) in the medial facet (not explicitly named so) of a multituberculate incisor from the Hell Creek Formation, Montana, later identified as belonging to the Taeniolabidoidea (Fosse *et al.* 1978), observed that the prism rods deviated in a transversal plane relative to the tooth. In the ventrolateral facet (named buccodistal, Fosse *et al.* 1973) of the same tooth the prism rods in the inner two thirds of the enamel deviated towards the tip of the crown. In the present study the same general arrangement of prism rods was observed in sections of the incisors of *Chulsanbaatar vulgaris*, ZPAL MgM-I/62 (Pl. 49, fig. 3), and *S. kuszmauli*, UM no. 5 (Pl. 49, fig. 1), and we tentatively suggest that this prism rod orientation in incisor enamel may be common to all late Cretaceous Taeniolabidoidea.

Fosse *et al.* (1973, Fig. 6) described the crystal orientation in multituberculate enamel, stating also that the prisms are arcade shaped in cross-section, and that the apices of the arcades point in the direction of the inclination of the prism rods relative to the dentine enamel junction. The same orientation of the crystals and the same morphology of the cross-cut prism rods were found in the present study of taeniolabidoid and ptilodontoid late Cretaceous enamels by SEM (Pls. 48 and 49). Polarized light microscopy indicated that the c-axes of the crystals in the prisms are inclined slightly in a cervical direction relative to the long axes of the prism rods, as the acute angle between prism rods and polarizer plane in the extinction position was cervically positioned relative to the prism rods.

In twelve mandibles from the ZPAL collection we were able to compare the prism density of incisors, premolars, and molars and in ten of them the numerical density was lower in incisors than in premolars or molars; in two of these it increased as much as twofold from incisor to molar (Table 1). It should, however, be stressed that the lowest prism densities of *Mesodma* or other mammalian teeth studied were about twice as high as the highest in taeniolabidoid molars.

Like Sahni (1979, Table 1 and pl. 3, fig. 6) we found gigantoprismatic enamel in the late Cretaceous North American *Meniscoessus*. If other genera of Cimolomyidae are distinguished by gigantoprismatic enamel this may indicate a relation of that family to Taeniolabidoidea, although the lower incisors in Cimolomyidae (Archibald 1982) are completely covered by enamel, a feature characteristic of Ptilodontoidea.

In view of the documented large difference between the microstructure of taeniolabidoid and ptilodontoid enamel, we believe that future studies of enamel microstructure may assist in

establishing the systematic position and phylogenetic relationships of some poorly known multituberculate groups regarded at present as *incertae sedis*.

Acknowledgements. We wish to express our gratitude to Dr. B. Krebs and the late Dr. S. Henkel (Palaeontologisches Institut, Freie Universität, Berlin) for the loan of the Kimmeridgian multituberculate and docodont specimens from Portugal and the permission to study them, and to Dr. D. Dashzeveg (Institute of Geological Sciences of the Mongolian People's Republic, Ulan Bator) for the permission to study the enamel of early Cretaceous multituberculates from Guchin Us in Mongolia. We are grateful to Dr. D. Sigogneau-Russell (Institut de Paleontologie, Muséum National d'Histoire Naturelle, Paris) and Professor G. Hahn (Department of Geology, University of Marburg) for reading the manuscript and offering useful comments. The second author thanks Professor M. C. McKenna (The American Museum of Natural History, New York) for donating to the Institute of Paleobiology in Warsaw a sample of Hell Creek Formation teeth, some of which are studied in this paper.

We also wish to thank the photographer at ZPAL Mr. M. Dziewinski and the photographer at IAUB Mr. R. Jensen for their assistance in the preparation of the micrographs.

REFERENCES

- ARCHIBALD, J. D. 1982. A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. *Univ. Calif. Publ. Geol. Sci.* **122**, 1-286.
- CARLSON, S. J. and KRAUSE, D. W. 1982. Multituberculate phylogeny: evidence from tooth enamel ultrastructure. *Ann. Meeting 1982 Geol. Soc. Amer., Abstr.*, 460.
- CLEMENS, W. A., LILLEGRAVEN, J. A., LINDSAY, E. H. and SIMPSON, G. G. 1979. Where, when, and what—a survey of known mammal distribution. In LILLEGRAVEN, J. A., KIELAN-JAWOROWSKA, Z. and CLEMENS, W. A. (eds.) *Mesozoic mammals: the first two-thirds of mammalian history*, 7-58. University California Press, Berkeley, Los Angeles, London.
- FOSSE, G. 1968a. The calculation of prism diameters and number of prisms per unit area in dental enamel. *Acta odont. scand.* **26**, 315-336.
- 1968b. Prism density and pattern on the outer and inner surface of the enamel mantle of canines. *Ibid.* 501-543.
- 1968c. The vertical compression of the prism pattern on the outer enamel surface of human permanent teeth. *Ibid.* 545-572.
- 1968d. The numbers of cross-sectioned ameloblasts and prisms per unit area in tooth germs. *Ibid.* 573-603.
- RISNES, S. and HOLMBAKKEN, N. 1973. Prisms and tubules in multituberculate enamel. *Calc. Tiss. Res.* **11**, 133-150.
- ROLI, J. and KNUDSEN, H. 1974. A sectioning machine for teeth and other brittle materials. *Acta odont. scand.* **32**, 299-304.
- ESKILDSEN, O., RISNES, S. and SLOAN, R. E. 1978. Prism size in tooth enamel of some Late Cretaceous mammals and its value in multituberculate taxonomy. *Zool. Scripta*, **7** (1), 57-61.
- FRANK, R. M., SIGOGNEAU-RUSSELL, D. and VOEGEL, J. C. 1984. Tooth ultrastructure of Late Triassic Haramiyidae. *Jl dent. Res.* **63** (5), 661-664.
- GRADZINSKI, R., KIELAN-JAWOROWSKA, Z. and MARYANSKA, T. 1977. Stratigraphy of the Upper Cretaceous Djadokhta, Barun Goyot and Nemegt formations of Mongolia. *Acta Geol. Polonica*, **27** (3), 281-318.
- GRINE, F. E. and VRBA, E. S. 1980. Prismatic enamel: a pre-adaptation for mammalian diphycodonty? *South Afr. Jl Sci.* **76**, 139-141.
- and CRUICKSHANK, A. R. I. 1979. Enamel prisms and diphycodonty: linked apomorphies of mammalia. *Ibid.* **75**, 114-120.
- HAHN, G. 1969. Beiträge zur Fauna der Grube Guimaraota Nr. 3. Die Multituberculata. *Palaeontographica*, A, **133** (1-3), 1-100.
- 1971. The dentition of the Paulchoffatidae (Multituberculata, Upper Jurassic). *Memoria Serv. Geol. Portugal*, (n.s.), **17**, 7-39.
- 1978. Die Multituberculata, eine fossile Säugetiere-Ordnung. *Sonderbd. Naturwiss. Ver. Hamburg*, **3**, 61-95.
- and HAHN, R. 1983. Multituberculata. In WESTPHAL, F. (ed.). *Fossilium Catalogus, I: Animalia, pars 127*, 1-409. Kugler Publications, Amsterdam.

- KIELAN-JAWOROWSKA, Z. 1970. New Upper Cretaceous multituberculate genera from Bayn Dzak, Gobi Desert. In KIELAN-JAWOROWSKA, Z. (ed.). Results Polish-Mongolian Paleont. Expeditions, II. *Palaeontologia Polonica*, **21**, 5-41.
- 1974a. Multituberculate succession in the late Cretaceous in the Gobi Desert (Mongolia). In ibid. V. *Palaeontologia Polonica*, **30**, 23-44.
- MATTHEW, W. D. and GRANGER, W. 1925. Fauna and correlation of the Gashato Formation of Mongolia. *Amer. Mus. Novitates*, **189**, 1-12.
- MOSS, M. L. 1969. Evolution of mammalian dental enamel. *Ibid.* **2360**, 1-39.
- OSBORN, J. W. and HILLMAN, J. 1979. Enamel structure in some therapsids and Mesozoic mammals. *Calcif. tissue Int.* **29**, 47-61.
- POOLE, D. F. G. 1956. The structure of the teeth in some mammal-like reptiles. *Quart. Jl. Micr. Sci.* **97**, 303-312.
- 1957. The formation and properties of the organic matrix of reptilian tooth enamel. *Ibid.* **98**, 349-367.
- 1971. An introduction to the phylogeny of calcified tissues. In DAHLBERG, A. A. (ed.). *Dental morphology and evolution*, 65-79. Chicago University Press, Chicago and London.
- and COOPER, J. S. 1971. Prism structure in the enamel of a reptile. *Jl dent. Res.* **50**, 681.
- SAHNI, A. 1979. Enamel ultrastructure of certain North American Cretaceous mammals. *Palaeontographica*, A, **166** (1-3), 37-49.
- SIGOGNEAU-RUSSELL, D., FRANK, R. M. and HEMMERLE, J. 1984. Enamel and dentine ultrastructure in Early Jurassic therian, *Kuehneotherium*. In PATTERSON, C. (ed.). Commemorative volume of Professor K. A. Kermack. *Zool. Jl Linn. Soc. Lond.* **82**, 207-215.
- SLOAN, R. and VAN VALEN, L. 1965. Late Cretaceous mammals from Montana. *Science*, **148** (3667), 220-227.
- TROFIMOV, B. A. 1980. Multituberculata i Symmetrodonta iz nizhnego miela Mongolii. *Dokl. Akad. Nauk SSSR*, **251** (1), 209-212. [In Russian.]

G. FOSSE

S. G. SKAALE

Institute of Anatomy
University of Bergen
5000 Bergen, Norway

Z. KIELAN-JAWOROWSKA

Zaklad Paleobiologii
Polska Academia Nauk
al. Zwirki i Wigury 93
02-089 Warszawa
Poland

Typescript received 5 March 1984

Revised typescript received 31 July 1984

MICROPALAEONTOLOGY OF THE LATE PROTEROZOIC VETERANEN GROUP, SPITSBERGEN

by ANDREW H. KNOLL and KEENE SWETT

ABSTRACT. Shales and siltstones of the Upper Proterozoic Veteranen Group, Spitsbergen, contain abundant and well-preserved microfossil populations. Plankton assemblages from open coastal deposits include a number of taxa previously known from Upper Riphean sequences in Scandinavia, the Soviet Union, and North America. Microfossils from more restricted coastal environments are dominated by small coccoidal unicells and filamentous sheaths of probable cyanobacteria, with locally abundant rod-shaped fossils of blue-greens or other bacteria. Biostratigraphic considerations indicate that the Veteranen Group, which comprises the earliest unmetamorphosed sedimentary sequence in Spitsbergen, was deposited between 800 and 900 Ma ago; this nearly 4000 m sequence was deposited within a relatively brief interval during the early stages of subsidence in a basin that eventually opened to become Iapetus. The preservation of delicate prokaryotic microfossils in lagoonal black shales contributes to the resolution of systematic problems arising from the development of two distinct research traditions in Precambrian palaeontology.

DURING the past decade, it has become clear that the Late Proterozoic earth supported a taxonomically diverse and ecologically heterogeneous biota of micro-organisms, as well as, in its later stages at least, early representatives of the multicellular (tissue grade) kingdoms. This diversity is well documented in the sedimentary successions of the Svalbard archipelago, where beautifully preserved microfossil assemblages are found at numerous stratigraphic horizons throughout a 7000 m sequence that spans some 400 million years of Late Proterozoic to Early Cambrian time. Both planktic and microbenthic fossils are found in rocks representing a variety of sedimentary environments (Knoll 1982a, b, 1984; Knoll and Calder 1983), and this record is augmented by stromatolites and microphytolites which are widely distributed in carbonate portions of the succession (Golovanov 1967; Golovanov and Raaben 1967; Raaben and Zabrodin 1972; Swett and Knoll 1985). During the 1981 and 1982 field seasons we conducted detailed stratigraphic and sedimentological studies of several localities in north-eastern Spitsbergen (text-figs. 1, 2). In this paper we describe the distribution of microfossil assemblages preserved in the lowermost unmetamorphosed units of the Spitsbergen Proterozoic succession, the Veteranen Group.

GEOLOGICAL SETTING

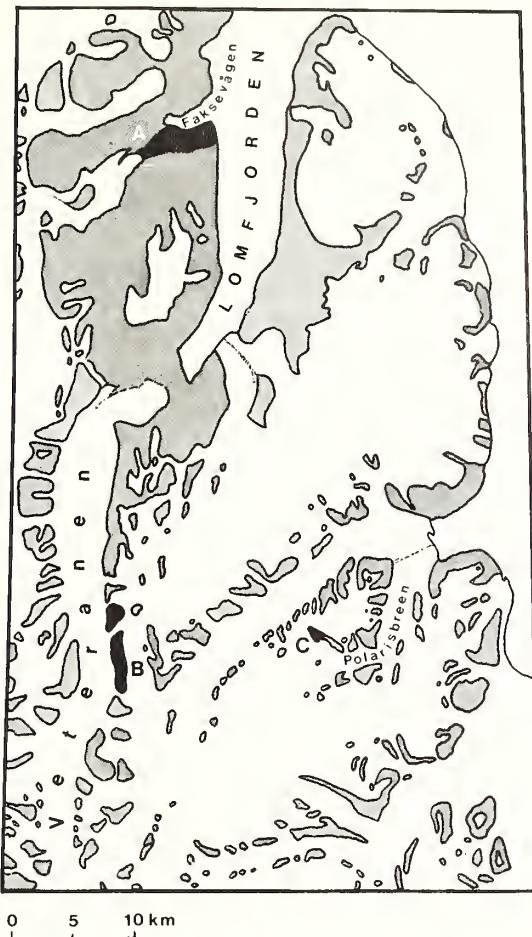
The late Precambrian and Palaeozoic geological history of the North Atlantic region centres on the inception, development, and ultimate destruction of the Iapetus Ocean. The closing of this ocean basin is documented by the igneous intrusions, metamorphism, sedimentary patterns, and structural features associated with the Caledonian orogeny. Its early development is reflected in the late Proterozoic sedimentary sequences of the region. In north-eastern Spitsbergen, some 6600 m of unmetamorphosed sedimentary rocks lie beneath the lowermost Cambrian strata of the island; this succession is in turn underlain by a comparably thick sequence of metasedimentary and metavolcanic rocks (Harland 1959; Harland and Wright 1979). The thickness and almost uniformly shallow marine nature of the unmetamorphosed sequence indicates that it was deposited near the margin of a slowly subsiding trough, genetically linked to, but perhaps antedating, the opening of a substantial ocean basin. Fairchild and Hambrey (1985) interpret palaeocurrent data from glaciogenic rocks near



TEXT-FIG. 1. Map of Svalbard showing the location of the study area in northern Spitsbergen. The shaded study area is enlarged in text-fig. 2.

the top of the Proterozoic section as indicating glacial flow from the south-west, a finding that supports the concept of a late Vendian opening for the ocean basin (Harland, pers. comm. 1984). Except for a few hundred metres of well-laminated graded siltstone and shale couplets that may reflect fault control of local deposition, and two thin lava flows at the same general stratigraphic level (Wilson 1958), there is little to suggest an early rifting stage of basin evolution. Evidence for such an event may lie in the metamorphic rocks at the base of the sequence.

In north-eastern Spitsbergen the unmetamorphosed Proterozoic section comprises three easily contrasted groups: the immediately sub-Cambrian Polarisbreen Group, approximately 800–900 m of



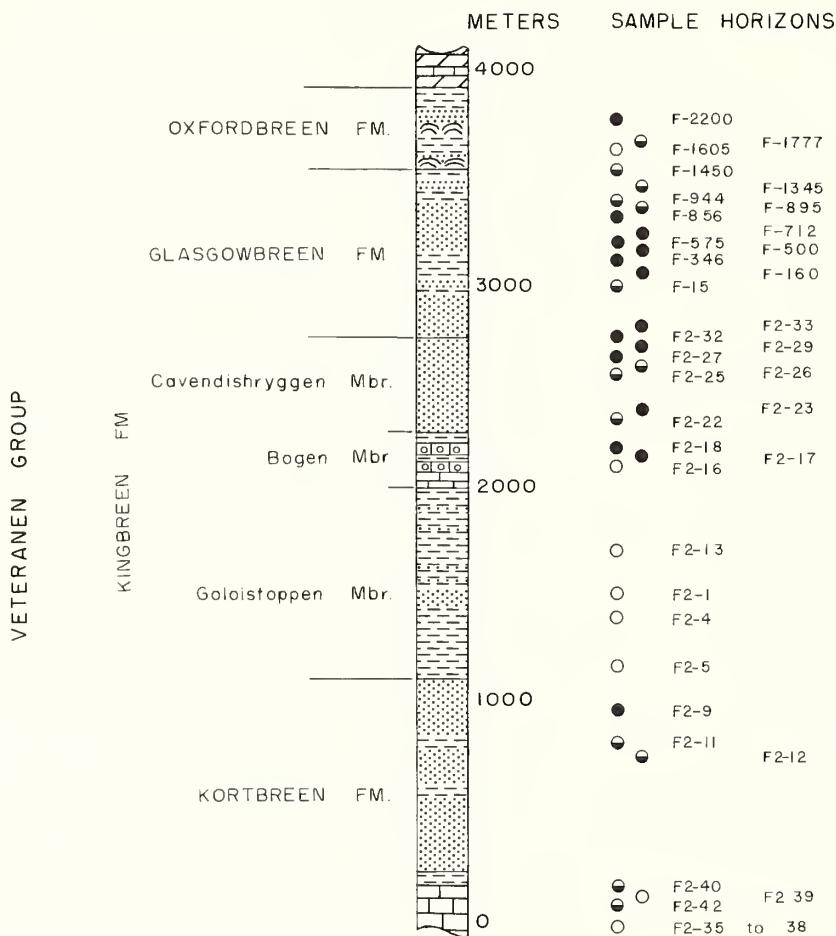
TEXT-FIG. 2. Enlargement of shaded area in text-fig. 1. Stippled areas represent outcrop; white areas indicate glacial ice, except for Lomfjorden and the Hinslopenstretet (upper right edge of figure) which are water covered. Detailed examinations of the Veteranen Group were undertaken at Faksevågen (A) and Cavendishryggen (B). The upper part of the group was also studied in the Polarisbreen area (C).

predominantly fine-grained siliciclastic rocks with extensive tillites (Wilson and Harland 1964; Hambrey 1982); the underlying Akademikerbreen Group, up to 2000 m thick and consisting largely of carbonates (Wilson 1961); and, at the base of the succession, the sequence of greatest interest here—the Veteranen Group (Wilson 1958).

The Veteranen Group has been divided into four formations (in ascending stratigraphic order): Kortbreen, Kingbreen, Glasgobreen, and Oxfordbreen (Harland *et al.* 1966). Basing our field studies on the thorough stratigraphic description of this group by Wilson (1958), we measured sections along the eastern wall of Veteranen Glacier at Cavendishryggen and in the Faksevågen area west of Lomfjorden (text-figs. 2, 3). The oldest Veteranen strata located are thinly laminated and occasionally cross-laminated calcisiltites of the lower Kortbreen Formation, exposed in the core of an anticline at Faksevågen. These limestones are tectonically deformed, but Wilson's (1958) thickness estimate of 300 m agrees well with our observations. Tan-weathering dolomitic units are common in this section, as are thin intercalations of quartzarenite and dark shales. The limestones become increasingly shaly in their uppermost 20 m and are overlain abruptly, but with apparent conformity, by the thick quartzarenites of the upper Kortbreen Formation. These sandstones are well-rounded, fine to medium grained quartzarenites, variously white or tinted pink, buff, maroon, or light green. Ripple marks with wavelengths of a few to 6 cm abound, as do cross-beds with set thicknesses of up to about 15 cm. Mudcracks occur intermittently throughout the unit, and

fossiliferous black shales also occur as thin interbeds. Wilson (1958) characterized these sandstones as 'typically shallow water deposits'. We concur and further suggest that they accumulated in shallow, tidally influenced environments marginal to the exposed continent.

Conformably overlying the Kortbreen quartzarenites is the Kingbreen Formation. This formation is 1200 m thick at Faksevågen and slightly thicker in the wall of Cavendishryggen; it has been divided into three members (Harland *et al.* 1966). At Cavendishryggen the basal Galoistoppen Member contains a thick sequence of millimetre-laminated dark siltstones and shales. As noted above the laminae in this unit comprise distinct graded couplets that are quite similar to beds from the somewhat younger Ocoee Supergroup of Tennessee. Keller (1979) has interpreted the Ocoee couplets as indications of the waning stages of fault influenced sedimentation, prior to the transition from a rift



TEXT-FIG. 3. Stratigraphic column of the Veteranen Group at Faksevågen, based on Wilson (1958) and our own measurements. Palynological sample horizons (with sample numbers) are indicated by circles. Filled circles indicate well-preserved microfossil assemblages; half-filled circles indicate poorly preserved assemblages; samples marked by open circles are barren. In the column, dashed lines indicate shales and siltstones; dotted lines signify sandstones; and rectangles and rhombic patterns indicate limestones and dolostones, respectively. Circles indicate ooids and concave downward arcs signify stromatolitic carbonates.

basin setting to a passive margin continental shelf. Bedding surfaces of the lower Galoistoppen sequence contain textural lineations that indicate unidirectional flow.

In the upper portion of the Galoistoppen Member, quartzose sandstone interbeds become increasingly common, and the dominant character of the sequence shifts to quartzarenites and interbedded black shales, with conspicuous calcareous units that contain low angle cross-beds, shallow channels, and intraformational conglomerates. The section at Cavendishryggen is more conspicuously calcareous than the correlative beds at Faksevågen, where variegated and often mudcracked shales and dolomitic shales are the dominant lithologies.

The overlying Bogen Limestone Member contains frequent oolite and microphytolite-bearing limestones, as well as cross-bedded (including herringbone cross-beds) calcarenites and intercalated siliciclastic units. The uppermost Cavendishryggen Quartzite Member contains massive, cross-bedded quartzarenites with thinner interbedded units of sandy and silty flagstones and shale.

The Kingbreen Formation is conformably overlain by the Glasgowbreen Formation, a 900 m unit that bears many similarities to the underlying Cavendishryggen sequence. This formation contains massive thicknesses of pink, green, and buff quartzarenites. Like those near the base of the Veteranen Group, the Glasgowbreen sandstones are generally compositionally mature, well rounded quartzarenites, marked by conspicuous ripple marks, interference ripples, megaripples, and cross-bedding (including herringbone cross-beds). Interbedded carbonaceous shales are common in some horizons within the formation. Wilson (1958) referred to these carbonaceous units as greywackes, but it is clear that they are discrete shales and sandy shales environmentally related to the tidal sandstones with which they are intercalated. The succeeding Oxfordbreen Formation contains proportionally fewer sandstones and more shales, and is distinguishable by the presence of carbonate interbeds (including oolitic and stromatolitic units). The stromatolites are low profile, laterally linked hemispheres up to 1 m high and 1·7 m across. Maximum synoptic relief developed during deposition was about half this height. Red shales are common in the upper part of the formation; these are generally flat-laminated, but can contain ripples, cross-laminations (in intercalated sandstones), mudcracks, and ripped-up mud flake clasts. These sedimentary features are particularly conspicuous at a locality along the north face of Polarisbreen Glacier (text-fig. 2). The top of the formation is fixed at the base of the massive dolomites and limestones that characterize the Akademikerbreen Group.

It can be seen from the foregoing summary that the rocks of the Veteranen Group document a variety of sedimentary environments, but that variation occurs within fairly strict limits. Almost the entire sequence records shallow marine depositional environments, ranging from below wave base to tidally influenced conditions and quiet lagoons marked by occasional subaerial exposure and storms.

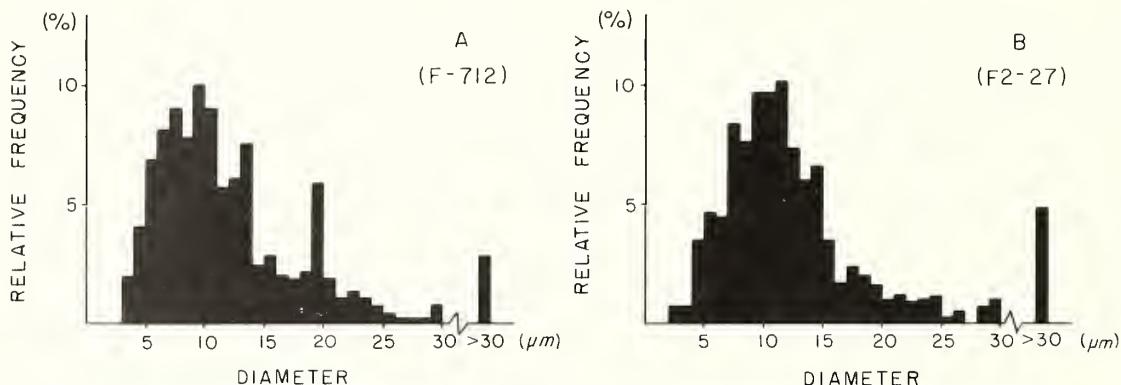
Available radiometric dates from Precambrian rocks of north-eastern Spitsbergen reflect Caledonian overprints of isotopic systems. On the basis of stromatolite and microphytolite distributions, Milstein and Golovanov (1979) have suggested that the Veteranen Group is late Riphean (950–670 Ma) in age. Acritarchs in this group, coupled with those in the correlative Franklinsundet and Celsiusberget groups of Nordaustlandet (Knoll 1982a) and those found in overlying units, indicate that the group as a whole probably exceeds 800 Ma in age, but is unlikely to be much older than 900 Ma (see discussion below).

MICROFOSSIL ASSEMBLAGES

Extensive collections of Veteranen Group samples were made from both the Cavendishryggen and Faksevågen sections. The Cavendishryggen area is characterized by more severe diagenetic alteration, approaching chlorite grade metamorphism. Strata are more highly indurated; they commonly develop a platy aspect, and a weak slaty cleavage is developed in the lower units. As a consequence the organic matter in Cavendishryggen rocks is black and fossil preservation is poor. In contrast, twenty-eight of the thirty-six samples taken from an approximately 3500 m section at Faksevågen contained identifiable fossils. Preservation at this locality is poorest in the youngest formation examined, the Oxfordbreen Formation, despite the abundance of reddish-brown organic matter in dark green to black shales. Preservation is much better in the Glasgowbreen and Kingbreen

formations, where microfossils are often abundant and relatively diverse. The colour of microfossil walls changes systematically as one descends the local stratigraphic column, but identifiable microfossils can still be seen in the dark grey to black organic residues isolated from grey shales within the carbonates at the base of the Kortbrean Formation.

Small ($< 25 \mu\text{m}$) coccoidal unicells are the most abundant fossils in every sample examined (Pl. 51, figs. 8, 11–18). Variation in wall thickness, wall ornamentation, and clustering patterns suggests that these unicell populations are taxonomically heterogeneous, an inference that can also be drawn from the size frequency distributions of sample populations (text-fig. 4A, B). Many taxonomic names have been applied to previously described fossils of similar aspect (e.g. Timofeev 1969) but, because diagnoses have often been based on characters likely to be diagenetic in origin and because published illustrations are often difficult to interpret, it would be hazardous to apply names without first making a careful study of the type materials. In so far as many of the observable differences between these small unicells may be related to intraspecific and/or diagenetically introduced variation, the formal recognition of each discernible morphotype would lead to an overestimate of species diversity. On the other hand the simple morphology of these fossils and the inevitable loss of taxonomically important characters (such as pigment complements) during post-mortem degradation must lead to an underestimate of original species diversity (Knoll and Golubic 1979). We have for these reasons not attempted to quantify the preserved diversity within this size class, preferring instead to treat these fossils as a unit, while acknowledging their probable biological heterogeneity.



TEXT-FIG. 4. Size frequency distribution of small coccoidal unicells from samples F-712, Glasgowbreen Formation (A), and F2-27, Kingbreen Formation (B). For both A and B, $N = 500$.

Among larger spheroidal microfossils, *Leiosphaeridia asperata* (Naumova) Lindgren, 1982 (= *Kildinella hyperboreica* Lindgren, 1982) is easily the most abundant acritarch (Pl. 52, figs. 4–8, 10, 11). It is found in all samples analysed and is common in most. *L. asperata* is morphologically simple, consisting of flexible, smooth-walled vesicles approximately 15–80 μm in diameter (usually 25–45 μm) that apparently dehisced by means of a median split mechanism. It is likely that these fossils are the remains of algal cysts (e.g. Lindgren 1981; Vidal and Knoll 1983) but, as Lindgren (1981, 1982) has pointed out, a variety of taxonomically and functionally different algal remains could be lumped within this form species.

Other common microfossils include *Kildinospaera chagrinata* Vidal in Vidal and Siedlecka, 1983 (= in part *Kildinella sinica*, according to Vidal and Siedlecka 1983), *Synsphaeridium* sp., and cf. *Stictosphaeridium* spp. (sensu Vidal 1976). More complex acritarchs are rare; these include *Kildinospaera granulata* Vidal in Vidal and Siedlecka, 1983, *Tasmanites riphejicus* Jankauskas, 1978, *Satka colonialica* Jankauskas, 1979a, *Bavlinella faveolata* (Schepeleva) Vidal, 1976, *Favoso-*

sphaeridium sp., and fragmentary remains of very large acritarchs, probably *Chuaria circularis* Walcott, 1899 (Pl. 51, figs. 1, 2). Tubular microfossils, the probable extracellular sheaths of filamentous cyanobacteria, occur in many samples (Pl. 51, fig. 19; Pl. 52, figs. 1–3, 12), and small rod-shaped remains are common in sample F-712 (Pl. 51, figs. 5, 6, 9, 10). Within any one sample, morphological diversity is low (text-fig. 5), a characteristic of late Riphean acritarch assemblages previously noted by Vidal and Siedlecka (1983).

TAXON	SAMPLE HORIZON			KO F2-9	KI F2-40	GL F-346	OX F-2200
	F2-17	F2-23	F2-27				
<i>Bavlinella faveolata</i> (Schepeteva) Vidal		R				R	
<i>Eosynechococcus</i> sp.		R R			R	C	
<i>Tasmanites rifejicus</i> Jankauskas			R		R R	R	
? <i>Chuaria circularis</i> Walcott	R	R			R R R R	R	
<i>Favosphaeridium</i> sp.					R		
<i>Kildinospaera chagrinata</i> Vidal	R	R	R C	R R	C	R	
<i>Kildinospaera granulata</i> Vidal					R R	C	R
<i>Leiosphaeridia asperata</i> (Naumova) Lindgren	C C	R C	R R C	C C C	R C C C		
<i>Satka colonialica</i> Jankauskas					R R R R	R	
cf. <i>Stictosphaeridium</i> sp. (<i>sensu</i> Vidal)		C	C C R	C			
<i>Synsphaeridium</i> sp.		R	R C R	R R R R R	R		
Small Unicells	C C A A A C	A A C A A A A A C C					
Filaments	C R A A A C R	R R R C C R R					
Number of taxa	4	4	6	7	5	7	11
					11	11	7
					14	8	

TEXT-FIG. 5. Chart showing the distribution of microfossil taxa within selected samples of the Veteranen Group. Samples are arranged stratigraphically, with the oldest sample on the left. KO, Kortbreen Formation; KI, Kingbreen Formation; GL, Glasgowbreen Formation; OX, Oxfordbreen Formation. R, rare; C, common; A, abundant.

Despite the thickness of the Veteranen Group, there is no evidence for stratigraphically significant changes in assemblage composition within the sequence. This is not to say that all recovered assemblages are identical; certainly, they are not. Gray and Boucot (1975) have noted, however, that variation in assemblage composition can reflect taphonomic and/or palaeoecological, as well as stratigraphic differences. Relatively poor preservation through much of the Oxfordbreen Formation may mask evolutionary changes in the plankton biota: fossils in the overlying Akademikerbreen Group do differ in ways that are most likely a consequence of evolutionary turnover. On the other hand, one well-preserved assemblage from the Oxfordbreen Formation (sample F-2200) is indistinguishable from assemblages found in the lower formations of the group.

Much of the variation evident in the relative abundance of microfossil groups represented is thought to reflect palaeoenvironmental variation within the coastal marine sedimentary deposits. Filamentous sheaths provide a case in point. In several samples (e.g. F2-27), filaments are conspicuously abundant, comprising some 40% or more of all preserved specimens. The filaments are long (often more than 100 µm in length) and not infrequently intertwined with one another. Large acritarchs (> 30 µm diameter) comprise only 3–5% of the assemblage, and biostratigraphically significant taxa are generally rare or absent. Filament rich assemblages are found in thin, black to greenish shale interbeds within predominantly cross-bedded and rippled quartz sandstones or oolitic and cross-bedded calcarenites. We interpret these assemblages as the remnants of very near-shore

coastal to lagoonal communities. The filaments are thought to represent autochthonous or nearly autochthonous, probably benthic, cyanobacterial populations.

At the other end of the spectrum are assemblages in which filaments occur only as rare, fragmented and probably allochthonous individuals. In these assemblages, large acritarchs are relatively common (10–15% of all individuals in sample populations from sample F-575) and diverse. Such assemblages tend to occur within thicker, green to black siltstone and shale units, with only minor sandstone intercalations. We interpret these biological and sedimentary assemblages as representing the most off-shore or ‘normal marine’ setting within the Veteranen Group. Most if not all of the spheroidal microfossils found in these assemblages are thought to have been planktic.

DISCUSSION

Biostratigraphy

The Veteranen biota contains several taxa that have long stratigraphic ranges and hence limited biostratigraphic utility. Among these fossils are: *Leiosphaeridia asperata*, cf. *Stictosphaeridium* sp., *Synsphaeridium* sp., and the small unicells, filaments, and rods. More useful are *Kildinosphaera granulata*, *Tasmanites riphejicus*, and *Satka colonialica* which to date are known only from Upper Riphean rocks. Along with co-occurring *L. asperata*, *K. chagrinata*, and probable *Chuaria*, these fossils form an assemblage similar to previously described assemblages from Upper but not uppermost (Kudashian, possibly equivalent to Vidal’s (1976) Lower Vendian) Riphean rocks elsewhere in the Northern Hemisphere.

Two forms, *Favosphaeridium* sp. and *Bavlinella faveolata*, are morphologically similar to taxa best known from uppermost Riphean to Cambrian rocks. The occurrence of *Bavlinella* is particularly interesting because this distinctive fossil has sometimes been considered an index fossil for Vendian rocks. Its actual range is now known to extend from the latest Riphean to the Cambrian, and this new population confirms earlier reports of its questionable occurrence in Upper Riphean rocks (see discussion in Vidal 1976). *Bavlinella* is often an abundant constituent of Vendian assemblages associated with glaciogenic rocks and has been interpreted as an opportunistic taxon by Knoll *et al.* (1981). Such an interpretation carries with it the prediction that *B. faveolata* should occur as a minor component of earlier and later microfloras, and this seems to be the case.

The apparent stratigraphic homogeneity of the Veteranen assemblages may reflect a slower rate of morphological evolution among early algae, a rapid rate of deposition for the Veteranen Group, or both. Comparable thicknesses of miogeosynclinal sediments are known to have accumulated during the approximately 70 million year long Cambrian Period along the eastern and western margins of North America (Bond *et al.* 1983; Cook and Bally 1975). The relatively rapid subsidence required for such accumulation is thought to be related to the cooling of the lithosphere following rifting (McKenzie 1978; Bond *et al.* 1983; Armin and Mayer 1983). It is also true, however, that our present understanding of late Riphean palaeontology is such that it is only possible to divide the period into a handful of assemblage zones, each the same order of length as the Cambrian (Vidal and Knoll 1983). This may reflect slow rates of morphological (but not necessarily physiological) evolution. Thus, the stratigraphic indivisibility of the Veteranen Group may well be a consequence of both rapid deposition and slow morphological change.

Absolute age estimates for the Veteranen assemblages must be inferred from radiometric dates assigned to comparable microbiotas from other areas. Biotas containing the distinctive elements that characterize the Veteranen Group are found in the Klubbnes and Andersby formations of the Vads^m Group, East Finnmark (Vidal 1981); the lower Båtsfjord Formation of the upper Barents Sea Group, also in East Finnmark (Vidal and Siedlecka 1983); the Chuar Group, Arizona (Vidal and Ford 1985); the Red Pine Shale of the Uinta Mountain Group, Utah (Vidal and Ford 1985); the ‘type’ Upper Riphean beds of the southern Urals (Jankauskas 1982); and the lower part of the Upper Visingsö Beds, Sweden (Vidal 1976; Vidal and Ford 1985).

With the exception of a K-Ar determination recalculated as approximately 640 Ma for dolerite dykes that cut the Barents Sea Group in northern Norway (Beckinsale *et al.* 1975), available radio-

metric dates on Upper Proterozoic sequences in Scandinavia are largely Rb-Sr whole rock analyses of shales (reviewed in Vidal and Knoll 1983). Klubbnes Formation shales have yielded dates of 807 ± 19 Ma (recalculated by Vidal from Sturt *et al.* 1975), while Visingsö occurrences are overlain by shales dated at 707 ± 37 Ma (Vidal 1981). Western North American assemblages antedate a structural disturbance bracketed at 820–770 Ma (reset K-Ar dates on basalts) and postdate an episode of basaltic extrusion dated at 1070 ± 70 Ma by Rb-Sr whole rock analyses (Elston and McKee 1982). Rb-Sr whole rock determinations of Red Pine Shale specimens yield an age of 950–925 Ma for that formation (Crittenden and Peterman 1975; Chaudhuri and Hanson 1980). K-Ar dates for Upper Riphean sedimentary rocks in the Urals suggest a depositional age of 850–940 Ma (Keller 1982).

Whole rock chronometric analyses of detrital sedimentary rocks have been the subject of much debate, as have many K-Ar determinations of presumably early diagenetic glauconites from Precambrian sediments. None the less, available radiometric data, coupled with corroborative tectonic and palaeomagnetic considerations (Elston, pers. comm. 1984) suggest that assemblages of the type found in the Veteranen Group very likely fall in the 800–900 Ma range. While it is clear that planktic microfossils are of demonstrated value in Proterozoic biostratigraphy (e.g. Vidal and Knoll 1983), it is also apparent that the full stratigraphic potential of early plankton will be realized only when better radiometric, palaeoecological, and biogeographic control is available.

Palaeoecology

The palaeoenvironmental variability of late Proterozoic microfossil assemblages has frequently been discussed in the literature (Vidal 1976, 1981; Knoll 1981, 1982b, 1984; Knoll and Calder 1983; Vidal and Knoll 1983). Recognition of palaeoecological patterns of distribution is important for both biological and geological reasons: biological because 'lateral' variation must be taken into account in any evolutionary interpretation of the fossil record (e.g. Strother *et al.* 1983); and geological in that Proterozoic fossils, like their Phanerozoic counterparts, are potentially valuable as indicators of sedimentary environment. In the Veteranen Group, both the diversity and the relative abundance of large ($> 30 \mu\text{m}$) acritarchs increase along a gradient from inshore, often lagoonal deposits to more open coastal siltstones and shales. As noted above, the abundance and preservational quality of filament populations decreases along the same gradient. (Environments are established on the basis of sedimentary structures, textures, and bedding sequences.) Similar distributions have been recognized in other Upper Proterozoic sequences, both carbonate and siliciclastic (reviewed by Vidal and Knoll 1983); the Veteranen observation serves to increase one's faith in the generality of the pattern.

Palaeoecological and biogeographic distributions are also relevant to biostratigraphic determinations. For example, *Trachysphaeridium laminaritum* Timofeev, 1966 is an important constituent of many late Riphean microfloras but has not been found in the Veteranen Group. Vidal and Ford (1985) have observed that in rocks of the Grand Canyon and elsewhere this species and *Kildinospaera chagrinata* have mutually exclusive distributions. *K. chagrinata* is relatively common in the Veteranen Group, so perhaps some poorly defined environmental parameter excluded *T. laminaritum* from the Veteranen sea. A more problematic example concerns the distinctive microfossil *K. lophostriata* (Jankauskas) Vidal in Vidal and Siedlecka, 1983 which occurs in late Riphean assemblages from the Soviet Union, Scandinavia, and North America, but which has not been recognized in Veteranen assemblages. Does this absence indicate that *K. lophostriata* had not evolved at the time of Veteranen deposition, that it was extinct by the time the Svalbard shelf originated, or that *K. lophostriata* is missing for reasons of ecology, biogeography, or chance? We simply do not know, it being impossible to eliminate any one of these possible explanations on the basis of present evidence. Once again this underscores the need for further investigations of late Proterozoic microbiotas conducted within a framework of strict stratigraphic and sedimentological control.

Systematics and palaeobiology

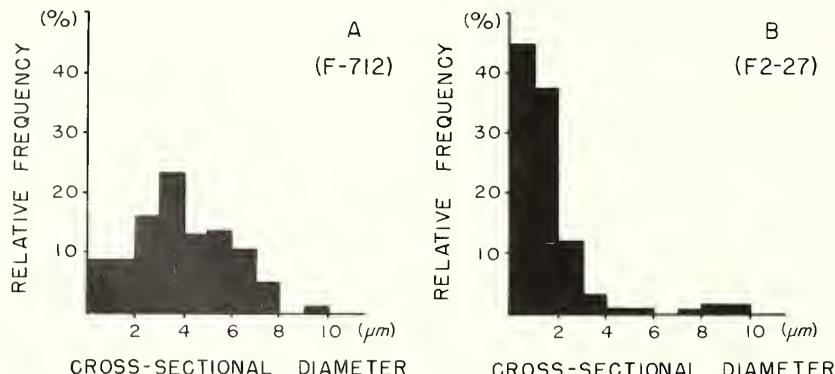
Proterozoic microfossils are generally studied by the petrographic examination of silicified carbonates or by the palynological maceration of siliciclastic rocks. In a critique of the systematic

problems created by this dichotomy of approach, Diver and Peat (1979) have suggested that many of the apparent differences between 'chert' and 'shale' biotas are illusory, the result of separate research schools with independently evolved taxonomic practices. Systematic traditions certainly pose a serious problem for comparative studies of Precambrian microbiotas, as do differences in preservation potential that may separate shales and silicified carbonates. On the other hand, some of the observed differences among assemblages are real and reflect the ecological partitioning of Proterozoic environments. Recognition of this aspect of the problem suggests a path toward the solution of the 'chert-shale' dilemma.

Most of the known biostratigraphically useful, open shelf acritarch assemblages come from carbonaceous siltstones and shales (e.g. Timofeev 1969; Vidal 1976); however, not all open coastal rocks are siliciclastic. Compacted and compressed acritarchs have been isolated from carbonaceous limestones and dolomites of the Upper Visingsö Beds of Sweden (Vidal 1976) and the Båtsfjord Formation of East Finnmark, Norway (Vidal and Siedlecka 1983); and open coastal carbonates from the uppermost Riphean Hunnberg and Ryssö formations of Nordaustlandet, Svalbard, contain microfossils preserved by early diagenetic silicification (Knoll 1984; Knoll and Calder 1983). The assemblages in these cherts are comparable to contemporaneous 'shale' biotas and demonstrate that, if present in silicified carbonates, large acritarchs such as *Trachysphaeridium*, *Kildinosphaera*, *Chuaria*, or *Trachyhystrichosphaera* species can be recognized and identified. Silicified carbonates from lagoonal and intertidal facies of the same formations do not contain abundant large acritarchs.

Several assemblages from lagoonal shales of the Kingbreen (samples F2-27, F2-29) and Glasgowbreen (F-712) formations of the Veteranen Group exemplify the converse distribution. Here, colonies of small spheroidal unicells, filaments, and rods—the stuff of most 'cherty' microbiotas—constitute the fossil populations. This demonstrates that early diagenetic silicification is not a prerequisite for the preservation of delicate prokaryotic remains, and it provides a second opportunity to compare assemblages from similar physical environments preserved in different ways. In the relative abundance and size frequency distribution of unicell and filament populations (text-figs. 4, 6), the Veteranen lagoonal assemblages closely resemble those from lagoonal silicified carbonates of the slightly younger Draken and Ryssö formations of Svalbard, as well as the subtidal associations of the approximately contemporaneous Bitter Springs Formation, Australia (Schopf 1968; Knoll 1981). They do not closely resemble microbiotas from open coastal shales or intertidal to supratidal silicified carbonates.

Similar preservation of delicate 'cherty' microfossils in shales has been reported from the approximately 1300 Ma old Roper Group of northern Australia (Peat *et al.* 1978) and the Upper Riphean of the southern Urals (Jankauskas 1982). Thin-section examination of microbiotas



TEXT-FIG. 6. Size frequency distribution of filamentous sheaths from samples F-712, Glasgowbreen Formation (A) and F2-27, Kingbreen Formation (B). For both A and B, $N = 200$.

preserved in shales has been successful in a few instances (Moorman 1974; Peat *et al.* 1978; Horodyski 1980, *et al.* 1980; Knoll *et al.* 1981; Chauvel and Mansuy 1981) but most siliciclastic microfloras are best observed in maceration residues. A principal disadvantage of this procedure is that it loses the important information of spatial distributions of populations within rock. Such data are valuable in both systematic and palaeoecological studies (Knoll and Golubic 1979; Knoll 1981, 1982b). Of particular significance to the present discussion is the fact that when populations can be defined spatially their size frequency distribution, degradational variability, and (sometimes) cell division sequences can be determined. Comparisons of small unicell populations from the Draken, Hunnberg, Ryssö, and Bitter Springs formations with those from the Veteranen Group and other siliciclastic units suggests that, although different names have been applied to permineralized and compressed populations, they are very similar in their morphological modes and ranges of variation. The same is true of filament and rod populations. In these cases, parallel taxonomic schemes hinder biological comparisons, and some systematic revision is necessary. However, drawing a lesson from analogous comparative studies of Carboniferous coal ball and compression floras, any revisions must be undertaken on a case by case basis using all available fossil materials. Simplistic taxonomic solutions will obscure biological differences as surely as the present systems hide similarities.

In summary, most Proterozoic open coastal and shelf microbiotas are preserved as compressions or compactations in siltstones and shales, while most late Precambrian petrifications come from restricted coastal environments where early diagenetic silicification was most likely. Many algae that were thus precluded from restricted lagoonal and intertidal habitats are found as acritarchs in shales, while some mat building micro-organisms (e.g. *Eoentophysalis* Hofmann, 1976) characteristic of intertidal zones are preserved only or predominantly in silicified carbonates. Because the correspondence of environments and preservational modes is not absolute, silicified shelf biotas and compressed or compacted lagoonal assemblages allow hypotheses of differential preservational effects to be tested. The limited observations available to date suggest that the most serious problems of taxonomic obfuscation concern populations of small unicells and, to a lesser extent, filaments.

A geophysical aside

Although taxa differ in the rates at which their remains change colour with increasing temperature, colour characterization of fossil pollen, spores, and algal cysts is useful in studies of organic thermal maturation (Gutjahr 1966; Staplin 1969; Hunt 1979). Acritarchs in the Hecla Hoek succession of north-eastern Spitsbergen vary systematically from amber in Cambrian shales to an opaque black in the oldest parts of the Veteranen Group. Within the Veteranen succession exposed at Faksevågen, colours range from a slightly reddish Moderate Brown (Kelly and Judd 1976) in sample F-2200 from the upper Oxfordbreen Formation to a dark Brownish Black to Black in the lowermost Kingbreen and Kortbreen formations. In so far as the Faksevågen section comprises the limb of an open folded anticline without apparent intrusions in the immediate vicinity, one can hypothesize that observed colour changes are primarily due to maximum burial depth achieved in the Ordovician Period, just prior to Caledonian deformation. Oxfordbreen sample F-2200 sits beneath some 4300 m of preserved late Precambrian and Cambro-Ordovician strata. Assuming that any additional (now eroded) thickness of Upper Ordovician and Silurian strata was minimal, and assigning a maximum temperature to this rock of 125–150 °C based on the organic maturation index (Hunt 1979, p. 324), one can estimate an early Palaeozoic geothermal gradient of about 1 °C per 29–35 m. Estimates based on the occurrence of Dark Greyish Brown acritarchs and filaments in the upper Kingbreen Formation (samples F2-17 to 33) and nearly black materials in the Kortbreen Formation (F2-12, and slightly lighter in F2-40) fall in the same range. This falls within the normal range for continental geothermal gradients and suggests that at Faksevågen the temperature history of the Veteranen Group was controlled primarily by burial. At Cavendishryggen and in correlative rocks on Nordaustlandet other factors, probably related to Caledonian tectonism, intensified the thermal regime.

SYSTEMATIC PALAEONTOLOGY

No new or emended taxa are here proposed and we have limited our systematic discussions to brief remarks designed to complement existing data and interpretations of the taxa found in the Veteranen Group. All samples and prepared slides are housed in the Paleobotanical Collections of the Botanical Museum, Harvard University.

Kingdom MONERA Haeckel, 1866
 Division CYANOPHYTA (Sachs) Pascher, 1931
 Class COCCOGONAE Thuret, 1875
 Order PLEUROCAPSALES Geitler, 1925
 Family UNKNOWN
 Genus BAVLINELLA (Scheppeleva) Vidal, 1976

Type species. *Bavlinella faveolata* (Scheppeleva) Vidal, 1976.

Bavlinella faveolata (Scheppeleva) Vidal, 1976

Plate 51, figs. 3, 4

Discussion. This distinctive fossil occurs in small numbers in samples F2-27 and F-856. Multisphere size is 5–12 µm, and individual microsphere units are less than 1 µm in diameter. Chauvel and Mansuy (1981) noted that in the Brioherian of Normandy and Brittany, *B. faveolata* specimens with small unit cells characterize older (> 670 Ma) portions of the sequence, while Vendian (640–580 Ma) deposits additionally contain many specimens having a significantly larger unit cell size. (Chauvel and Mansuy used the name *Sphaerocongregus variabilis* Moorman, regarded by Vidal (1976) as a junior synonym of *B. faveolata*.) Veteranen specimens are consistent with these unit cell size observations.

B. faveolata reached its acme in the Vendian, when it apparently expanded opportunistically with the climatic restriction and extinction of other previously dominant taxa. Its complete stratigraphic range runs at least from the late Riphean (this paper) to the early Cambrian (Vidal 1981). Moorman (1974) and Knoll *et al.* (1981) compared *B. faveolata* with pleurocapsalean cyanobacteria, noting the close correspondence in size frequency distribution, unit cell or baecocyte size frequency, and multiple fission pattern of reproduction (see Waterbury and Stanier 1978). Mansuy and Vidal (1983) suggested a chroococcacean origin for *B. faveolata*, comparing the fossil populations with species of the colonial chroococcacean genera *Gomphosphaeria*, *Coelosphaerium*, and *Microcystis*. Although most species of these genera differ from *Bavlinella* in colony size and shape, colony architecture, unit cell size frequency distribution, or unit cell shape (see Geitler 1932; Desikachary 1959), some species of *Microcystis* do form tightly packed spheroidal colonies. Ecologically, *Bavlinella* does resemble some modern colonial chroococcaceans in its inferred planktic mode of life and tendency to bloom under eutrophic conditions (Knoll *et al.* 1981; Mansuy and Vidal 1983).

The critical data bearing on the affinities of *B. faveolata* concern patterns of cell division. Pleurocapsalean multispheres and tightly packed chroococcacean colonies may have similar morphologies, but the development of these morphologies occurs quite differently in the two orders.

EXPLANATION OF PLATE 51

For each figure, slide number (which includes a sample number from text-fig. 3), stage co-ordinates (where 'x' on slide F500-14 = 23·7 × 102·2) and Harvard University Paleobotanical Collection number are given. Bar in fig. 2 = 40 µm for figs. 1, 2, and = 10 µm for all other figures.

Figs. 1, 2. ?*Cluaria circularis* Walcott. Fragmentary remains; note small unicell (comparable in size to fig. 18) in fig. 1. 1, F575-5, 52·2 × 107·8, 60754. 2, F575-5, 45·5 × 95·6, 60755.

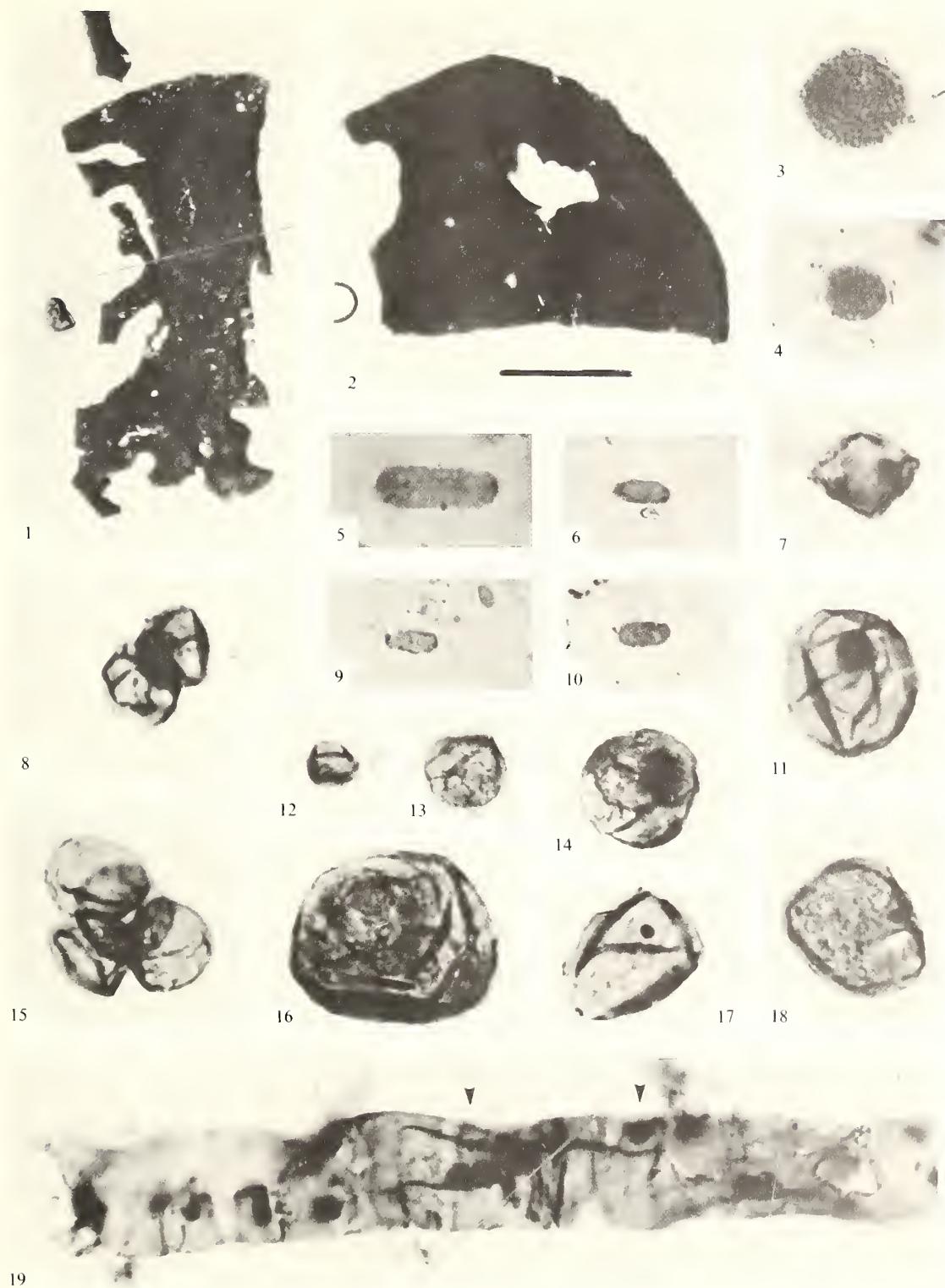
Figs. 3, 4. *Bavlinella faveolata* (Scheppeleva) Vidal. 3, F2-29-2, 55 × 96·5, 60756. 4, F2-29-2, 33·3 × 102·3, 60757.

Figs. 5, 6, 9, 10. *Eosynechococcus* sp. 5, F500-13, 54·9 × 106·2, 60758. 6, F712-4, 42·4 × 110·4, 60759. 9, F712-4, 13 × 109·6, 60760; note second, small specimen at the upper right corner of the figure. 10, F712-6, 33·4 × 107, 60761.

Fig. 7. A coccoidal unicell distorted by diagenetic crystal growth. Similar morphologies have been described as *Octodryxium* spp., but genuine *O. truncatum* specimens (e.g. Vidal 1976) do not resemble this specimen.

Figs. 8, 11–18. Small coccoidal unicells. Note small blebs of internal organic matter in 11, 17, and 18. 8, F2-27-2, 29·4 × 113·7, 60762. 11, F2-23-1, 30·6 × 101·7, 60763. 12, F856-1, 38·9 × 108·5, 60764. 13, F500-13, 49·8 × 108·8, 60765. 14, F575-5, 38·2 × 114·9, 60796. 15, F712-6, 52·8 × 105·5, 60766. 16, F575-6, 39 × 107·6, 60767. 17, F575-5, 50·5 × 114·3, 60768. 18, F575-7, 44 × 106·1, 60769.

Fig. 19. Filamentous sheath containing degraded remnants of cells (arrows). F500-14, 45·2 × 96, 60770.



In modern pleurocapsalean cyanobacteria, baecocyte clusters are formed by repeated binary fissions of a large initial cell, without intervening cell growth (Waterbury and Stanier 1978). In *Microcystis* and related genera, colonies arise by cell divisions interspersed with growth, so that at no point in the life cycle are any individual cells significantly larger than the cells that are found in the multicellular colony. Thus, if *B. faveolata* has pleurocapsalean affinities, its multispheres should co-occur with unicells, dyads, and tetrads having the same approximate total volume. If *Bavlinella* is a chroococcalean blue-green, no large cells should occur in the population and colony size might be expected to be somewhat variable. In samples processed by maceration, it is risky to infer that unicells are part of the life cycle of multispheres in the same assemblage, especially when the multispheres themselves are as rare as they are in the Veteranen Group. *Bavlinella*-rich assemblages from the Hector Formation, Alberta (Moorman 1974), the Mineral Fork Formation, Utah (Knoll *et al.* 1981), and the Brioverian of France (Chauvel and Schopf 1978; Chauvel and Mansuy 1981; Mansuy 1983) have been studied in thin-section; in at least two of these assemblages (Hector and Mineral Fork), *Bavlinella* multispheres occur in intimate spatial association with unicells and rare spheroidal dyads and tetrads whose maximum diameters are about the same size as the *B. faveolata* multispheres. It can be argued correctly that close spatial association of planktonic populations need not imply taxonomic identity. On the other hand the cell morphologies predicted by the 'pleurocapsalean hypothesis' do occur, while micron-sized unicells and variable colony sizes that might represent a chroococcalean growth series have not been observed. Therefore, pending further morphological data, we prefer to keep this fossil among the Pleurocapsales.

Order CHROOCOCCALES Wettstein, 1924
 Family CHROOCOCCACEAE Nägeli, 1849
 Genus EOSYNECHOCOCCUS Hofmann, 1976

Type species. Eosynechococcus moorei Hofmann, 1976.

Eosynechococcus sp.

Plate 51, figs. 5, 6, 9, 10

Description. Isolated rod-shaped vesicles; 2–9 µm long and 1–3 µm wide (mean dimensions = 3·6 × 1·8 µm, $s_x = 1 \mu\text{m}$, $s_y = 0\cdot5 \mu\text{m}$, $N = 50$).

Discussion. *Eosynechococcus* is a form genus for small rod-shaped microfossils, most of which are probably, but not demonstrably, cyanobacteria (see Knoll 1982a). Although many previously described *Eosynechococcus* populations occur as dense aggregations in stromatolitic laminae, occurrences of non-clustered solitary rods and dyads have been described (Hofmann 1976; Knoll 1982a; Jankauskas 1982; Strother *et al.* 1983), and some of these are known to occur in non-stromatolitic muds. The generic diagnosis of *Eosynechococcus* Hofmann, 1976 specifically states that individuals may be solitary or clustered, so there is no question that this generic name is appropriate for the Veteranen fossils. In its size frequency distribution, the Veteranen population resembles *E. moorei* Hofmann, 1976 and *E. brevis* Knoll, 1982b, but maceration has destroyed the evidence of spatial distribution and division patterns that would allow these two species to be distinguished. Thus, we have elected to use the designation *Eosynechococcus* sp. That these are fossils and not modern contaminants can be demonstrated by the colour of their walls, which indicates thermal alteration under conditions of deep burial.

Class HORMOGONAE Thuret, 1875
 Order OSCILLATORIALES Copeland, 1936 or NOSTOCALES Geitler, 1925
 Filamentous microfossils
 Plate 51, fig. 19; Plate 52, figs. 1–3, 12

Discussion. Filamentous microfossils are abundant constituents of several Veteranen samples,

particularly those from the Bogen Member of Kingbreen Formation. Specimens are uniformly non-septate and are interpreted as extracellular sheaths; however, internal patterns of thickening and attenuation often faithfully record the dimensions of trichome cells that originally occupied sheath interiors (Pl. 52, fig. 2). These 'ghosts' suggest that the micro-organisms had a single trichome composed of undifferentiated cells, much like modern *Lyngbya*. In rare instances, partially degraded trichome fragments are preserved inside the sheaths (Pl. 51, fig. 19). Size frequency distributions (text-fig. 6) indicate that several taxa are represented. Like silicified microbiotas from the Bitter Springs (Schopf 1968; Knoll 1981), Draken (Knoll 1982b), and Sukhaya Tunguska (Mendelson and Schopf 1982) formations, the Veteranen populations fall into several size classes having modes in the 1, 2-4, 4-8, and 10-12 μm diameter ranges. The widest sheath observed is 16 μm in diameter.

In terms of permineralization taxonomic practice, these populations can be described as species of *Tenuofilum*, *Eomycetopsis*, and *Siphonophycus*, with the generic distinctions based largely on size. Macerated filaments have been assigned to these genera (e.g. Jankauskas 1982) or to the form genus *Taeniatum*. Biologically, most filamentous sheath populations were probably produced by oscillatoriacean or nostocalean cyanobacteria. The absence of well-preserved trichomes precludes further comparison, although 'ghosts' of cells impressed on sheath interiors do indicate an oscillatoriacean affinity for many specimens.

Kingdom PROTOCTISTA Copeland, 1956 emend. Margulis, 1971
 Division PRASINOPHYTA Round, 1971
 Order PTEROSPERMATALES Schiller, 1925
 Family TASMANITACEAE Sommer, 1956 ex. Tappan, 1980
 Genus TASMANITES Newton, 1875

Type species. Tasmanites punctatus Newton, 1875.

Tasmanites rifejicus Jankauskas, 1978

Plate 53, fig. 11

Discussion. Specimens of *T. rifejicus* are rare in the Veteranen Group, but they are easily distinguished by the numerous pores that perforate the vesicle. One Veteranen specimen (112 μm) falls in the size range for the species observed by Jankauskas (1978, 1982) and Vidal and Ford (1985), but others range from 43 to 52 μm . Despite their smaller size, these specimens have been placed in *T. rifejicus* by virtue of their wall structure.

Group ACRITARCHA Evitt, 1963
 Genus ?CHUARIA Walcott, 1899

Type species. Chuaria circularis Walcott, 1899.

?*Chuaria circularis* Walcott, 1899

Plate 51, figs. 1, 2

Discussion. No complete specimens of *C. circularis* have been observed in Veteranen material, but large fragments of robust, and often differentially coalified, spheroidal vesicles are common in some samples. Individual fragments range up to 140 μm in maximum dimension, and the curvature of these broken specimens indicates that the original vesicles were often in excess of 300 μm diameter. Several species of *Trachysphaeridium* and *Kildinosphaera* exceed 200 μm in diameter but, given the robust nature of the walls and the commonness of the fragments, we suggest that the large shards belong to *C. circularis*. *Chuaria* is known to occur in correlative beds in Nordaustlandet, Svalbard (Knoll 1982a), and East Greenland (Vidal 1979), and indeed is common in Upper Riphean rocks from many localities throughout the world (Ford and Breed 1973; Hofmann 1977).

Genus FAVOSOPHAERIDIUM Timofeev, 1959, ex Timofeev, 1966

Type species. Favosphaeridium scandicum Timofeev, 1966.*Favosphaeridium* sp.

Plate 53, figs. 7, 10

Discussion. A single specimen 95 μm in diameter was observed in sample F-575. The size and irregularly reticulate surface ornamentation of this specimen (Pl. 53, fig. 10) are comparable to those characterizing the specimens of Timofeev described by Vidal (1976) from the Visingsö Beds, Sweden. Poor preservation makes specific comparison impossible.

Genus KILDINOSPHEAERA Vidal, 1983

Type species. Kildinosphaera chagrinata Vidal, 1983.*Kildinosphaera chagrinata* Vidal, 1983

Plate 53, figs. 1-3

Discussion. Vidal (*in* Vidal and Siedlecka 1983) cut a Gordian knot in Proterozoic acritarch taxonomy by creating the new genus *Kildinosphaera* and describing as its type species *K. chagrinata*. The new genus was necessitated by Lindgren's (1982) transfer of *Kildinella hyperboreica* (the type species of *Kildinella*) to *Leiosphaeridia* Eisenack, and the species was described to impart rigor to a troubled system of morphologically overlapping form species, most prominently *K. sinica* Timofeev, 1966. The Veteranen specimens have flexible, easily foldable walls with a subdued chagrinate surface. Size range is 26-78 μm ($\bar{x} = 40 \mu\text{m}$, $s_x = 10.6 \mu\text{m}$, $N = 50$).

Kildinosphaera granulata Vidal, 1983

Plate 53, figs. 9, 12-14

Discussion. Veteranen specimens of *K. granulata* have flexible walls with a conspicuous, finely granulate surface texture. Size range is 30-85 μm ($\bar{x} = 52.2 \mu\text{m}$, $s_x = 15.2 \mu\text{m}$, $N = 20$). This species is common only in the most diverse, open coastal assemblage, sample F-856 and, less so, F-575.

Genus LEIOSPHAERIDIA Eisenack, 1958

Type species. Leiosphaeridia baltica Eisenack, 1958.*Leiosphaeridia asperata* (Naumova) Lindgren, 1982

Plate 52, figs. 4-8, 10, 11

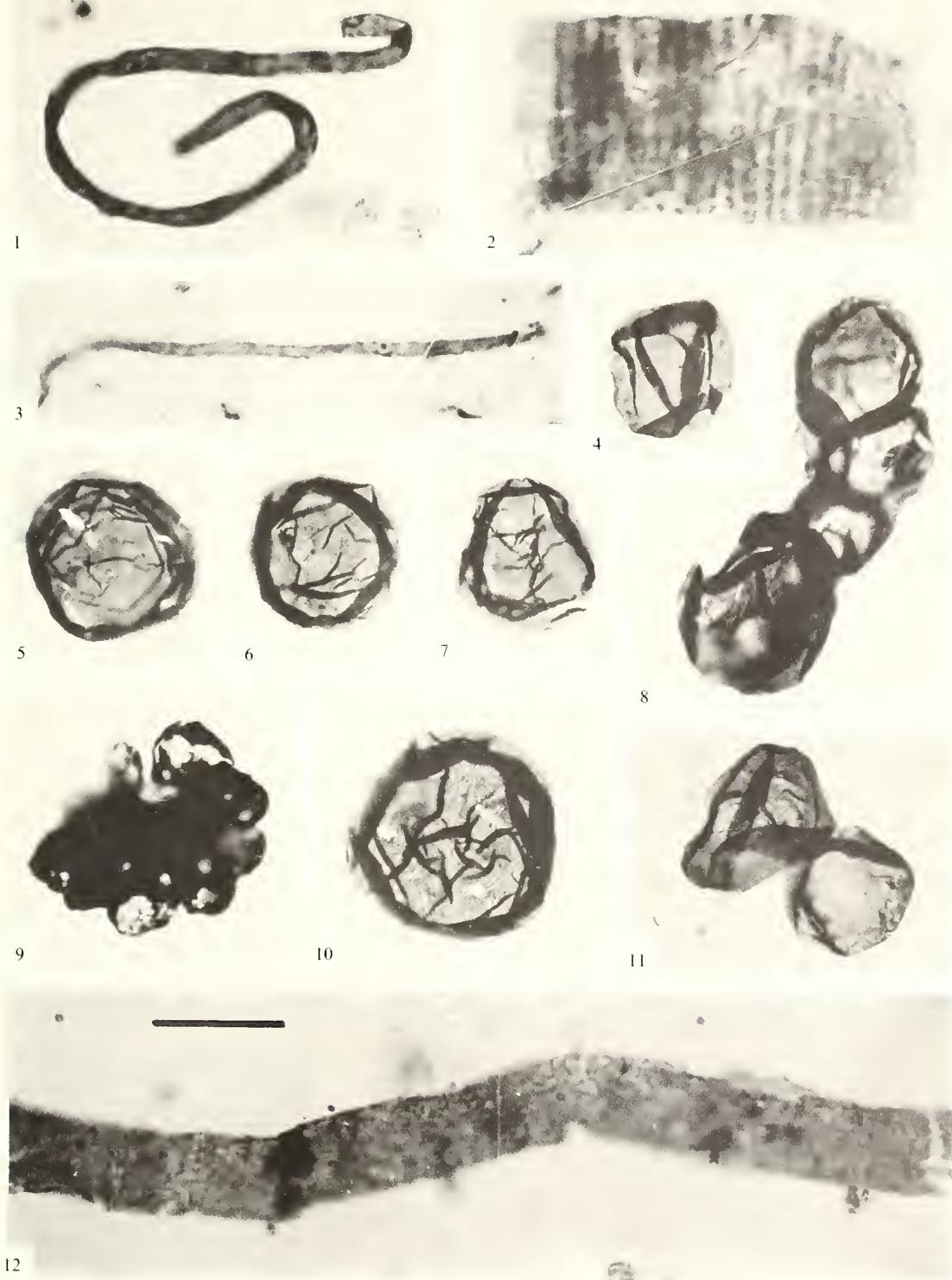
EXPLANATION OF PLATE 52

For each figure, slide number (which includes a sample number from text-fig. 3), stage co-ordinates (where 'x' on slide F500-14 = 23.7 \times 102.2) and Harvard University Paleobotanical Collection number are given. Bar in fig. 12 = 10 μm for figs. 1-3, 12, and = 20 μm for all other figures.

Figs. 1-3, 12. Filamentous microfossils. 1, F500-12, 43.1 \times 103.4, 60771. 2, F2-17-2, 48.5 \times 116.5, 60772. 3, F2-29-2, 40.2 \times 104.3, 60773. 12, F712-2, 42 \times 112.4, 60774.

Figs. 4-8, 10, 11. *Leiosphaeridia asperata* (Naumova) Lindgren. 4, F712-6, 21 \times 107.2, 60775. 5, F500-12, 49 \times 95.5, 60776. 6, F500-6, 50.5 \times 95.7, 60777. 7, F500-12, 48 \times 90.1, 60779. 8, a cluster of vesicles, F2200-1, 47.7 \times 105.3, 60780. 10, F500-10, 31.4 \times 109.1, 60781. 11, F712-6, 34 \times 100.3, 60795.

Fig. 9. *Synsphaeridium* sp. F575-5, 58.4 \times 110.6, 60782.



KNOLL and SWETT, Late Proterozoic microfossils

Discussion. Lindgren (1982) synonymized the well-known Proterozoic acritarch species *Kildinella hyperboreica* Timofeev, 1966 with *L. asperata*. Veteranen *L. asperata* specimens have smooth, flexible walls 20–52 µm in diameter ($\bar{x} = 32.9 \mu\text{m}$, $s_x = 7.7 \mu\text{m}$, $N = 52$).

Genus SATKA Jankauskas, 1979a

Type species. *Satka favosa* Jankauskas, 1979a.

Satka colonialica Jankauskas, 1979b

Plate 53, figs. 4–6, 8

Discussion. Vidal and Ford (1985) have interpreted *S. colonialica* as a thin, chagrinate to finely granular envelope whose outline reflects the dimensions of the numerous, smaller ellipsoidal cells about which it was compressed. Veteranen specimens support this interpretation; both in the Spitsbergen population and in previously described colonies, the ellipsoidal internal bodies are generally absent. Individual *S. colonialica* specimens reach 100 µm in length, but most fall in the 40–50 µm range. Ellipsoidal internal bodies are 7–14 µm long.

Genus STICTOSPHAERIDIUM Timofeev, 1962

Type species. *Stictosphaeridium podolense* Timofeev, 1962.

cf. *Stictosphaeridium* sp. *sensu* Vidal, 1976

Discussion. Very thin-walled, spheroidal vesicles with diameters of 25–63 µm are common in several Veteranen samples.

Genus SYNSPHAERIDIUM Eisenack, 1965

Type species. *Synsphaeridium gotlandicum* Eisenack, 1965.

Synsphaeridium sp.

Plate 52, fig. 9

Discussion. Microfossils assigned to *Synsphaeridium* differ from other small unicells of the Veteranen Group in their possession of a thick (but not brittle) psilate wall that compresses to yield rounded folds rather than the sharp, pleated folds seen in many other taxa. Specimens have diameters of 13–17 µm and commonly occur in clusters.

EXPLANATION OF PLATE 53

For each figure, slide number (which includes a sample number from text-fig. 3), stage co-ordinates (where 'x' on slide F500-14 = 23.7 × 102.2) and Harvard University Paleobotanical Collection number are given. Bar in fig. 14 = 20 µm for figs. 1–6, 8–14, and = 60 µm in fig. 7.

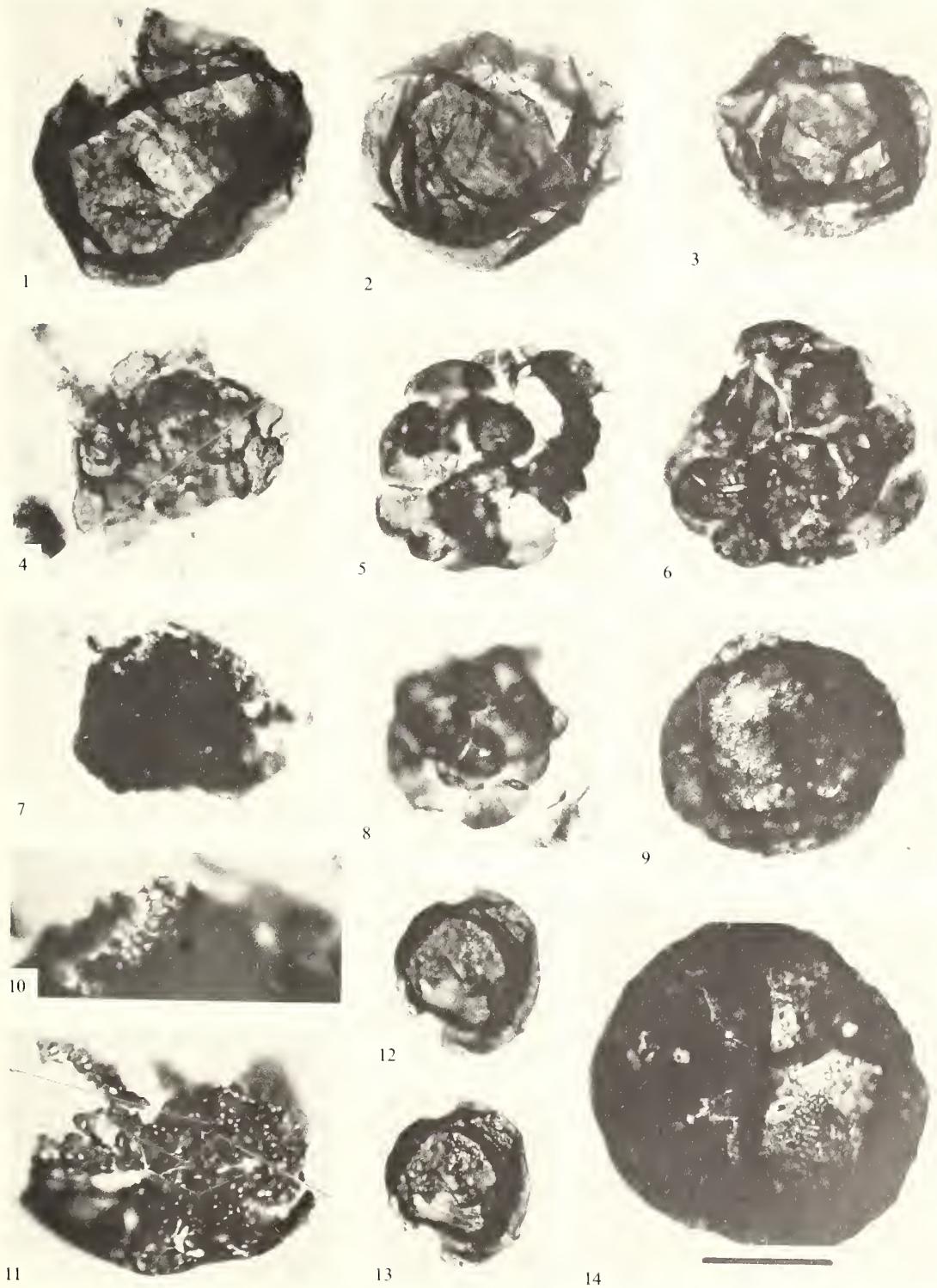
Figs. 1–3. *Kildinospaera chagrinate* Vidal. 1, F575-7, 34 × 95.8, 60783. 2, F500-10, 57 × 95.2, 60784. 3, F575-5, 44.2 × 114.9, 60785.

Figs. 4–6, 8. *Satka colonialica* Jankauskas. 4, F500-12, 42.3 × 104, 60786. 5, F500-10, 57 × 95.2, 60787. 6, F575-5, 44.2 × 114.9, 60788. 8, F500-12, 45.5 × 102, 60789.

Figs. 7, 10. *Favosphaeridium* sp. 7, F575-1, 42.4 × 109.7, 60790. Fig. 10 is an enlargement of a portion of fig. 7 showing the structure of the vesicle wall.

Figs. 9, 12–14. *Kildinospaera granulata* Vidal. 9, F500-10, 51 × 110.4, 60791. 12, F2200-1, 39.5 × 113.1, 60792. 13, same specimen as fig. 12, photographed using interference contrast. 14, F500-10, 58.2 × 97.4, 60793.

Fig. 11. *Tasmanites rifejicus* Jankauskas. F575-7, 34.3 × 110.1, 60794.



MICRO-ORGANISMS INCERTAE SEDIS

Small coccoidal unicells

Plate 51, figs. 8, 11–18

Discussion. Numerous taxonomic names have been proposed for the classification of the small (3–25 µm), psilate to granular, spheroidal vesicles that occur as common constituents of late Proterozoic microbiotas (Timofeev 1966, 1969). If found as permineralizations, most of these populations would be assigned to the genus *Myxococcoides* Schopf, especially *M. minor* Schopf, 1968 or *M. cantabrigiensis* Knoll, 1982a. Because maceration destroys original spatial relationships and often scatters individuals from loose clusters, some of the characters that are important in the recognition of *Myxococcoides* species are lost in the acid-resistant residues herein under consideration. Jankauskas (1982) treated comparable materials from the Upper Riphean of the southern Urals as species of the genera *Synsphaeridium*, *Leiosphaeridia*, *Margominiscula*, *Arctacellularia*, *Leiominuscula*, and unnamed spheroids. Pending the opportunity to examine type specimens in the Soviet Union, we prefer to treat these populations informally. Size frequency distributions of two sample populations are shown in text-fig. 4.

Acknowledgements. We thank the Norsk Polarinstitutt and the Cambridge Spitsbergen Expedition for logistical and intellectual co-operation, E. Burkhardt and S. Goldberg for assistance in preparing the plates and text-figures, and G. Vidal and W. B. Harland for helpful criticisms of our manuscript. This research was supported in part by NSF Grants DPP 80-19998 and DPP 83-01226.

REFERENCES

- ARMIN, R. A. and MAYER, L. 1983. Subsidence analysis of the Cordilleran miogeoclinal: implications for the timing of late Proterozoic rifting and amount of extension. *Geology, Boulder, Colo.* **11**, 702–705.
- BECKINSALE, R. D., READING, H. G. and REX, D. C. 1975. Potassium-argon ages for basic dykes from East Finnmark: stratigraphical and structural implications. *Scott. J. Geol.* **12**, 51–65.
- BOND, G. C., KOMINZ, M. A. and DEVLIN, W. J. 1983. Thermal subsidence and eustasy in the Lower Paleozoic miogeoclinal of western North America. *Nature, Lond.* **306**, 775–779.
- CHAUDHURI, S. G. and HANSON, W. R. 1980. Rb-Sr ages of the Uinta Mountain Group of Utah and Colorado. *Abstr. Prog. geol. Soc. Am.* **12** (6), 269.
- CHAUVEL, J. J. and MANSUY, C. 1981. Micropaléontologie du Protérozoïque du Massif Armoricain (France). *Precamb. Res.* **15**, 25–42.
- and SCHOPF, J. W. 1978. Late Precambrian microfossils from Brionian cherts and limestones of Brittany and Normandy, France. *Nature, Lond.* **275**, 640–642.
- COOK, T. D. and BALLY, A. W. (eds.). 1975. *Stratigraphic Atlas of North and Central America*, 271 pp. Princeton University Press, Princeton.
- COPELAND, J. L. 1936. Yellowstone thermal Myxophyceae. *Ann. N.Y. Acad. Sci.* **36**, 1–232.
- CRITTENDEN, M. D. and PETERMAN, Z. E. 1975. Provisional Rb/Sr age of the Precambrian Uinta Mountain Group, northeastern Utah. *Utah Geol.* **2**, 75–77.
- DESIKACHARY, T. V. 1959. *Cyanophyta*, 686 pp. New Delhi.
- DIVER, W. L. and PEAT, C. J. 1979. On the interpretation and classification of Precambrian organic-walled microfossils. *Geology, Boulder, Colo.* **7**, 401–404.
- EISENACK, A. 1958. *Tasmanites* Newton 1875 und *Leiosphaeridia* n.g. als der Hystrichosphaeridea. *Palaeographica, A*, **110**, 1–19.
- 1965. Microfossilien aus dem Silur Gotlands. Hystrichosphären, Problematika. *Neues Jb. Geol. Paläont. Abh.* **122**, 257–274.
- ELSTON, D. P. and MCKEE, E. H. 1982. Age and correlation of the Late Proterozoic Grand Canyon Orogeny, Northern Arizona. *Bull. geol. Soc. Am.* **93**, 681–699.
- EVITT, W. R. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs, II. *Proc. natn. Acad. Sci. U.S.A.* **49**, 298–302.
- FAIRCHILD, I. J. and HAMBREY, M. J. 1985. The Vendian succession of northeastern Spitsbergen: petrogenesis of a dolomite-tillite association. *Precamb. Res.* **26**, 111–167.
- FORD, T. D. and BREED, W. J. 1973. The problematical Precambrian fossil *Chuaria*. *Palaeontology*, **16**, 535–550.

- GEITLER, L. 1925. Synoptische Darstellung der Cyanophyceen in morphologischer und systematischer Hinsicht. *Beih. bot. Zbl.* **41**, 163.
- 1932. Cyanophyceae. In KOLKWITZ, R. (ed.). *Kryptogamenflora von Deutschland, Österreich und der Schweiz*, **14**, 1196 pp. Akademische Verlagsgesellschaft, Jena.
- GOLOVANOV, N. P. 1967. Stromatolites from the Riphean deposits of Murchisonfjorden, Nordaustlandet. In KRASIL'SHCHIKOV, A. A. (ed.). *Documents on the stratigraphy of Spitsbergen*, 6–20. Trudy NIIGA, Leningrad.
- and RAABEN, M. E. 1967. Upper Riphean analogues in the Spitsbergen Archipelago. *Dokl. Akad. Nauk SSSR*, **173**, 1141–1144. [In Russian.]
- GRAY, G. and BOUCOT, A. J. 1975. Color changes in pollen and spores: a review. *Bull. geol. Soc. Am.* **86**, 1019–1033.
- GUTJAHR, C. C. M. 1966. Carbonization measurements of pollen-grains and spores and their application. *Leids. geol. Meded.* **38**, 1–29.
- HAECKEL, E. H. 1866. *Generelle Morphologie*, 2 vols., 1036 pp. Georg Reimer Verlag, Berlin.
- HAMBREY, M. J. 1982. Late Precambrian diamictites of northeastern Svalbard. *Geol. Mag.* **119**, 527–551.
- HARLAND, W. B. 1959. The Caledonian sequence in Ny Friesland, Spitsbergen. *Q. Jl. geol. Soc. Lond.* **114**, 307–342.
- WALLIS, R. H. and GAYER, R. A. 1966. A revision of the Lower Hecla Hoek succession in Ny Friesland, Spitsbergen. *Geol. Mag.* **93**, 265–286.
- and WRIGHT, N. J. R. 1979. Alternative hypothesis for the pre-Carboniferous evolution of Svalbard. *Skr. norsk Polarinst.* **167**, 89–117.
- HOFMANN, H. J. 1976. Precambrian microflora, Belcher Islands, Canada: significance and systematics. *J. Paleont.* **50**, 1043–1073.
- 1977. The problematic fossil *Chnaria* from the late Precambrian Uinta Mountain Group, Utah. *Precamb. Res.* **4**, 1–11.
- HORODYSKI, R. J. 1980. Middle Proterozoic shale-facies microbiota from the lower Belt Supergroup, Little Belt Mountains, Montana. *J. Paleont.* **54**, 649–663.
- DONALDSON, J. A. and KERANS, C. 1980. A new shale-facies microbiota from the Middle Proterozoic Dismal Lakes Group, District of Mackenzie, Northwest Territories, Canada. *Can. J. Earth Sci.* **17**, 1166–1173.
- HUNT, J. M. 1979. *Petroleum geochemistry and geology*, 617 pp. W. H. Freeman, San Francisco.
- JANKAUSKAS, T. V. 1978. Plant microfossils from the Riphean of the southern Urals. *Dokl. Acad. Sci. USSR, Earth Sci. Section*, **242**, 913–915. [In Russian.]
- 1979a. Lower Riphean microfossils of the southern Urals. *Ibid.* **247**, 1465–1467. [In Russian.]
- 1979b. Middle Riphean microbiota from the southern Urals and the Bashkirian Urals. *Ibid.* **248**, 190–193. [In Russian.]
- 1982. Microfossils from the Riphean of the Southern Urals. In KELLER, B. M. (ed.). *Stratotype of Riphean: palaeontology and palaeomagnetics*, 84–120. Acad. Sci. USSR, Geol. Inst., Nauka, Moscow. [In Russian.]
- KELLER, B. M. (ed.). 1982. *Stratotype of Riphean: palaeontology and palaeomagnetism*, 175 pp. Acad. Sci. USSR, Geol. Inst., Nauka, Moscow. [In Russian.]
- KELLER, F. 1979. Stratigraphy and structure of the Ocoee Supergroup in Eastern Tennessee, 320 pp. Ph.D. thesis (unpublished), Yale University.
- KELLY, K. L. and JUDD, D. B. 1976. Color: universal language and dictionary of names. *U.S. Nat. Bur. Standards, Spec. Publ.* **440**, 184 pp.
- KNOLL, A. H. 1981. Paleoecology of late Precambrian microbial assemblages. In NIKLAS, K. (ed.). *Paleobotany, paleoecology, and evolution*, 1, 17–54. Praeger, New York.
- 1982a. Microorganisms from the late Precambrian Draken Conglomerate, Ny Friesland, Spitsbergen. *J. Paleont.* **56**, 755–790.
- 1982b. Microfossil based biostratigraphy of the Precambrian Hecla Hoek sequence of Nordaustlandet, Svalbard. *Geol. Mag.* **119**, 269–279.
- 1984. Microbiotas of the Late Precambrian Hunnberg Formation, Nordaustlandet, Svalbard. *J. Paleont.* **58**, 131–162.
- BLICK, N. and AWRAMIK, S. M. 1981. Stratigraphic and ecologic implications of late Precambrian microfossils from Utah. *Am. J. Sci.* **281**, 247–263.
- and CALDER, S. 1983. Microbiotas of the late Precambrian Ryssö Formation, Nordaustlandet, Svalbard. *Palaeontology*, **26**, 467–493.
- and GOLUBIC, S. 1979. Anatomy and taphonomy of a Precambrian algal stromatolite. *Precamb. Res.* **10**, 115–151.
- LINDGREN, S. 1981. Remarks on the taxonomy, botanical affinities, and distribution of leiospheres. *Stockh. Contr. Geol.* **38**, 1–20.

- LINDGREN, S. 1982. Algal coenobia and leiospheres from the Upper Riphean of the Turukhansk region, eastern Siberia. *Ibid.* 37–45.
- MCKENZIE, D. 1978. Some remarks on the development of sedimentary basins. *Earth planet. Sci. Lett.* **40**, 25–32.
- MANSUY, C. 1983. Les Microsphères de Proterozoïque Supérieur Armoricain (Brioverien): nature, répartition stratigraphique, affinités biologiques, 76 pp. Thèse (unpublished), Rennes.
- and VIDAL, G. 1983. Late Proterozoic Brioverian microfossils from France: taxonomic affinity and implications of plankton productivity. *Nature, Lond.* **302**, 606–607.
- MARGULIS, L. 1971. Whittaker's five kingdoms: minor modifications based on considerations of the origins of mitosis. *Evolution*, **25**, 242–245.
- MENDELSON, C. V. and SCHOPF, J. W. 1982. Proterozoic microfossils from the Sukhaya Tunguska, Shorikha, and Yudoma formations of the Siberian Platform, USSR. *J. Paleont.* **56**, 42–83.
- MILSTEIN, V. E. and GOLOVANOV, N. P. 1979. Upper Precambrian microphytolites and stromatolites from Svalbard. *Skr. norsk Polarinst.* **167**, 219–224.
- MOORMAN, M. 1974. Microbiota of the Late Proterozoic Hector Formation, southwestern Alberta, Canada. *J. Paleont.* **48**, 524–539.
- NÄGELI, C. 1849. *Gattungen einzelliger Algen*, 139 pp. Friedrich Schutthess, Zürich.
- NEWTON, E. T. 1875. On 'Tasmanite' and Australian 'White Coal'. *Geol. Mag. (n.s.)*, **12**, 337–342.
- PASCHER, A. 1931. Systematische Übersicht über die mit Flagellaten in Zusammenhang stehenden Algenreihen und Versuch einer Einreihung dieser Algenstämme in die Stämme des Pflanzenreiches. *Beih. bot. Zbl.* **175**, 417–428.
- PEAT, C. J., MUIR, M. D., PLUMB, K. A., MCKIRDY, D. M. and NORVICK, M. S. 1978. Proterozoic microfossils from the Roper Group, Northern Territory, Australia. *BMR J. Aust. Geol. Geophys.* **3**, 1–17.
- RAABEN, M. E. and ZABRODIN, V. E. 1972. Algal problematics of the Upper Riphean (stromatolites, oncolites). *Trudy Inst. Geol. Acad. Sci. USSR*, **217**, 130 pp.
- ROUND, F. E. 1971. The taxonomy of the Chlorophyta II. *Br. phycol. J.* **6**, 235–264.
- SCHILLER, J. 1925. Die planktonischen vegetation des adriatischen meers: B. Chrysomonadina, Heterokontae, Cryptomonadina. *Arch. Protistenk.* **53**, 59–123.
- SCHOPF, J. W. 1968. Microflora of the Bitter Springs Formation, late Precambrian, central Australia. *J. Paleont.* **42**, 651–688.
- STAPLIN, F. L. 1969. Sedimentary organic matter, organic metamorphism, and oil and gas occurrence. *Bull. Can. Petrol. Geol.* **17**, 47–66.
- STROTHER, P. K., KNOLL, A. H. and BARGHOORN, E. S. 1983. Micro-organisms from the Late Precambrian Narssârssuk Formation, North-West Greenland. *Palaeontology*, **26**, 1–32.
- STURT, B. A., PRINGLE, I. R. and ROBERTS, D. 1975. Caledonian nappe sequence of Finnmark, northern Norway, and the timing of the orogenic deformation and metamorphism. *Bull. geol. Soc. Am.* **86**, 710–718.
- SWETT, K. and KNOLL, A. H. 1985. Stromatolitic bioherms and microphytolites from the late Proterozoic Draken Conglomerate Formation, Spitsbergen. *Precamb. Res.* (in press).
- TAPPAN, H. 1980. *The paleobiology of plant protists*, 1028 pp. W. H. Freeman, San Francisco.
- THURET, G. 1875. Essai de classification des Nostochinées. *Ann. Sci. Nat.*, **1** (6), 372.
- TIMOFEEV, B. V. 1959. The ancient flora of the Baltic and its stratigraphic significance. *Trud vses. nest. nauchno-issled. geol.-razv. Inst.* **129**, 320 pp. [In Russian.]
- 1962. The Theodolite Stage in palaeontology. *Ibid.* **196**, 601–647. [In Russian.]
- 1966. *Microphytological investigations of ancient formations*, 145 pp. Acad. Sci. USSR, Lab. Precamb. Geol., Nauka, Leningrad. [In Russian.]
- 1969. *Proterozoic sphaeromorphs*, 146 pp. Acad. Sci. USSR, Inst. Precamb. Geol. Geochronol., Nauka, Leningrad. [In Russian.]
- VIDAL, G. 1976. Late Precambrian microfossils from the Visingsö Beds in southern Sweden. *Fossils Strata*, **9**, 1–56.
- 1979. Acritarchs from the Upper Proterozoic and Lower Cambrian of East Greenland. *Bull. Gronlands geol. Unders.* **134**, 1–55.
- 1981. Micropaleontology and biostratigraphy of the Upper Proterozoic and Lower Cambrian sequence in East Finnmark, northern Norway. *Norg. geol. Unders.* **362**, 1–53.
- and FORD, T. D. 1985. Planktonic microfossils (acritarchs) from the Upper Proterozoic of North America and their chronostratigraphic implications. *Precamb. Res.* (in press).
- and KNOLL, A. H. 1983. Proterozoic plankton. *Mem. geol. Soc. Am.* **161**, 265–277.
- and SIEDLECKA, A. 1983. Planktonic, acid-resistant microfossils from the Upper Proterozoic strata of the Barents Sea region of the Varanger Peninsula, East Finnmark, northern Norway. *Norg. geol. Unders.* **382**, 45–79.

- WALCOTT, C. D. 1899. Pre-Cambrian fossiliferous formations. *Bull. geol. Soc. Am.* **10**, 199–244.
- WATERBURY, J. B. and STANIER, R. Y. 1978. Patterns of growth and development in Pleurocapsalean cyanobacteria. *Microbiol. Rev.* **42**, 2–44.
- WETTSTEIN, R. VON. 1924. *Handbuch der systematischen Botanik* (Third edition), 1017 pp. Wien, Leipzig.
- WILSON, C. B. 1958. The Lower Middle Hecla Hoek rocks of Ny Friesland, Spitsbergen. *Geol. Mag.* **94**, 305–327.
- 1961. The Upper Middle Hecla Hoek rocks of Ny Friesland, Spitsbergen. *Ibid.* **98**, 89–116.
- and HARLAND, W. B. 1964. The Polarisbreen Series and other evidence of Late Pre-Cambrian Ice Ages in Spitsbergen. *Ibid.* **101**, 198–219.

ANDREW H. KNOLL

Department of Organismic and Evolutionary Biology
Harvard University
Cambridge, Massachusetts 02138
U.S.A.

KEENE SWETT

Department of Geology
University of Iowa
Iowa City, Iowa 52242
U.S.A.

Typescript received 15 May 1984

Revised typescript received 14 January 1985

LOWER CRETACEOUS INOCERAMID BIVALVES FROM THE ANTARCTIC PENINSULA REGION

by J. A. CRAME

ABSTRACT. The occurrence of rich faunas of Lower Cretaceous inoceramid bivalves in the Antarctic Peninsula region further emphasizes their widespread distribution, and enhances their potential for regional biostratigraphic correlations. The Antarctic material is contained in approximately seven of twelve species groups that are recognized on a worldwide scale. Six of these are assigned to the genus *Inoceramus* and one to *Birostrina*. The comparatively rare genus, *Anopaea*, is left undivided.

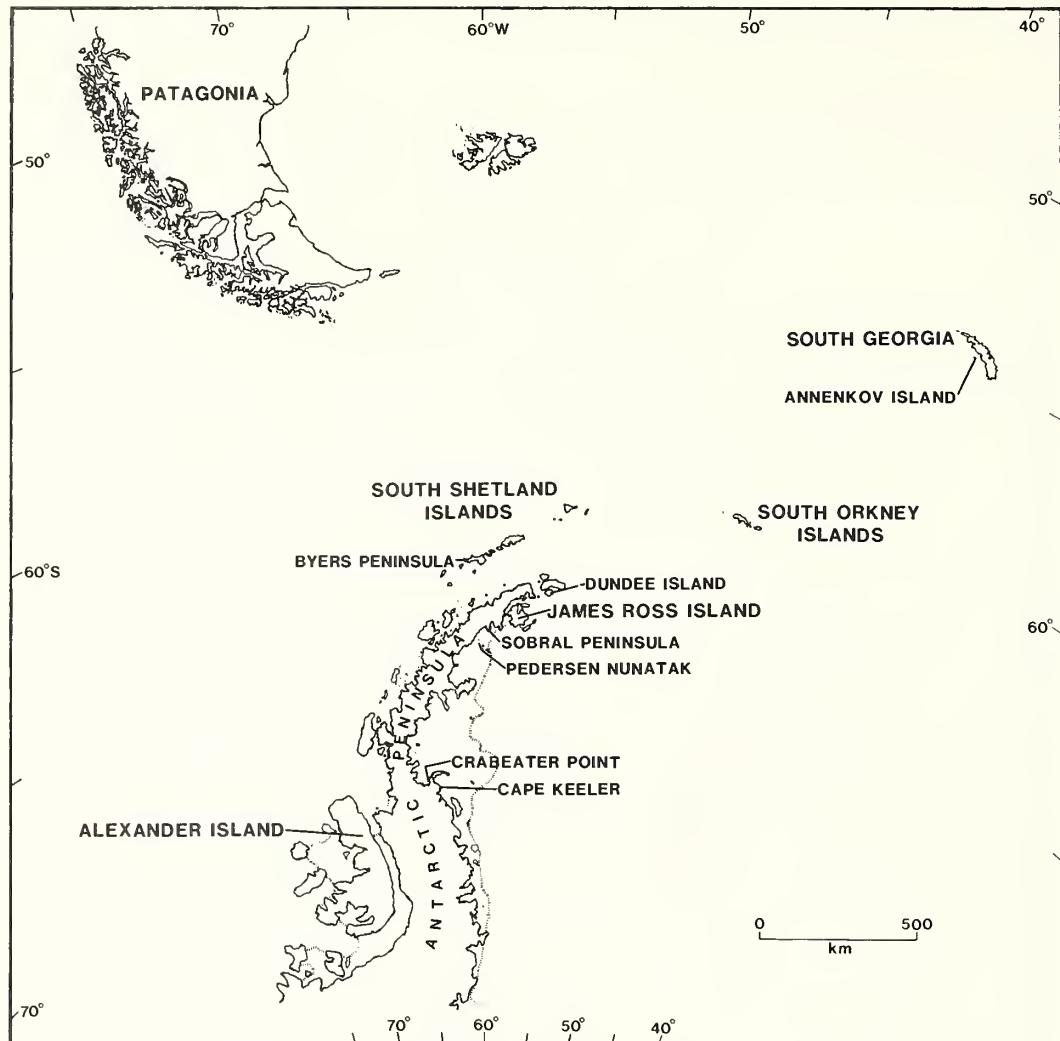
In the Fossil Bluff Formation of Alexander Island, Berriasian representatives of the *I. ovatus* group (*I. cf. ovatus* Stanton and *I. sp. aff. ellioti* Gabb) are succeeded by *A. trapezoidalis* (Thomson and Willey) which has undifferentiated Berriasian–Aptian affinities. This is in turn followed by an Aptian member of the *I. neocomiensis* group (*I. deltoides* sp. nov.) and in the Albian there are occurrences of *Anopaea* sp. nov. aff. *mandibula* (Mordvilko), *B. cf. concentrica* (Parkinson) (*B. concentrica* gp.), *I. cf. anglicus elongatus* Pergament, *I. sp. aff. belluensis* Reeside, *I. sp. aff. comancheanus* Cragin (all *I. anglicus* gp.), and *I. flemingi* sp. nov. (*I. lherowskyae* gp.). Aptian–Albian strata on James Ross Island have yielded both *I. stoneleyi* sp. nov. (*I. lherowskyae* gp.) and *Anopaea* sp. nov. β . These are followed by the Albian species *I. cf. sutherlandi* M'Coy and *I. carsoni* M'Coy (both *I. carsoni* gp.) and the highest Lower Cretaceous specimens within this sequence have been referred to *B. concentrica* (Parkinson).

Although specimens of *I. cf. heteropterus* Pokhialainen (*I. heteropterus* gp.) and *I. annenkovensis* sp. nov. (unclassified) from Annenkov Island are of probable Hauterivian–Barremian age, it is noticeable that there is a marked lack of Valanginian–Barremian inoceramids in the Antarctic Peninsula region. This gap probably reflects a period of regional uplift and non-deposition.

Representatives of the *I. ovatus* and *I. heteropterus* groups provide a means of correlation between the Berriasian–Barremian of the Antarctic Peninsula and the North Pacific region. *I. deltoides* sp. nov. can be closely matched with Northern Hemisphere Aptian members of the *I. neocomiensis* group and *I. stoneleyi* sp. nov. and *I. flemingi* sp. nov. have possible counterparts within the Aptian–Albian of Spitzbergen, south-east USSR and far eastern USSR. Of the various Albian species groups, that based on *I. carsoni* provides a direct link between Antarctica and Australia and those based on *I. anglicus* and *B. concentrica* facilitate a range of long-distance correlations. The latter category, in particular, may be one of the first truly cosmopolitan inoceramid groups.

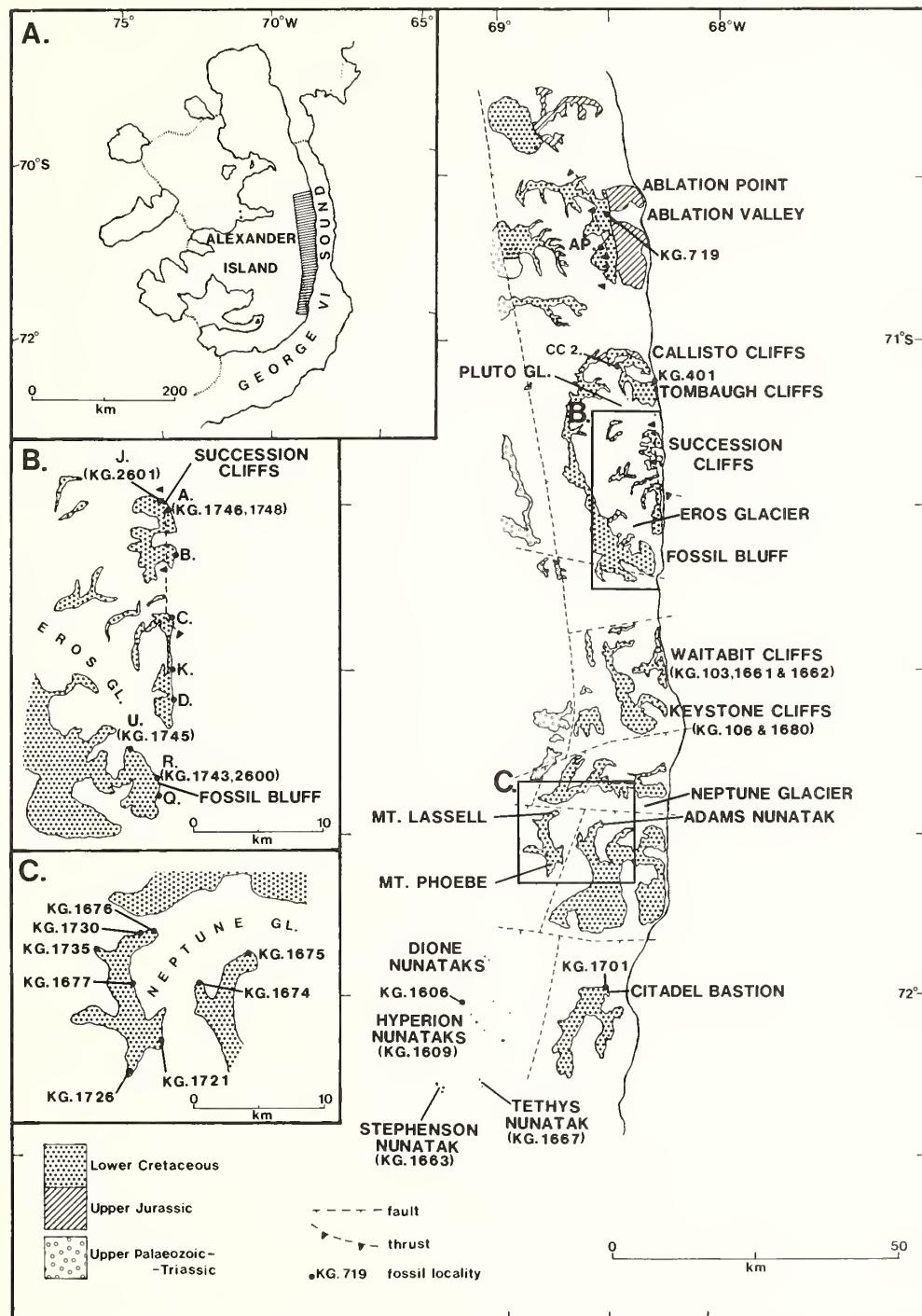
IN comparison with their Upper Cretaceous counterparts, Lower Cretaceous inoceramid bivalves have received little attention from palaeontologists. It is usually assumed that a few meagre lineages persisted from the Jurassic–Cretaceous boundary through to the beginning of the Upper Cretaceous, when a remarkable diversification occurred. In an early paper on the evolution of *Inoceramus* through the period, Woods (1912) depicted the entire range of English Upper Cretaceous species as originating from just two Aptian species. Possible Neocomian (i.e. Berriasian–Valanginian) and Barremian ancestors were not considered.

We now know that there was in fact a considerable diversity of Lower Cretaceous inoceramids. In the Neocomian they can be traced around the North Pacific margins from California to Kamchatka (Pokhialainen 1974) as well as in Northern Siberia (Zakharov 1966; Zakharov and Turbina 1979) and parts of Europe (Gillet 1924). In the Barremian–Aptian there is a notable development of the *I. neocomiensis* group, and in the Albian a variety of species is known from regions such as the North Pacific (e.g. McLearn 1943; Imlay 1961; Pergament 1965), the Russian Platform (Saveliev 1962), Western Europe (e.g. Woods 1911), and Australasia (e.g. Day 1969; Stevens and Speden 1978). The distribution of Lower Cretaceous *Inoceramus* species would seem to be such as to offer considerable potential for regional biostratigraphic correlations.

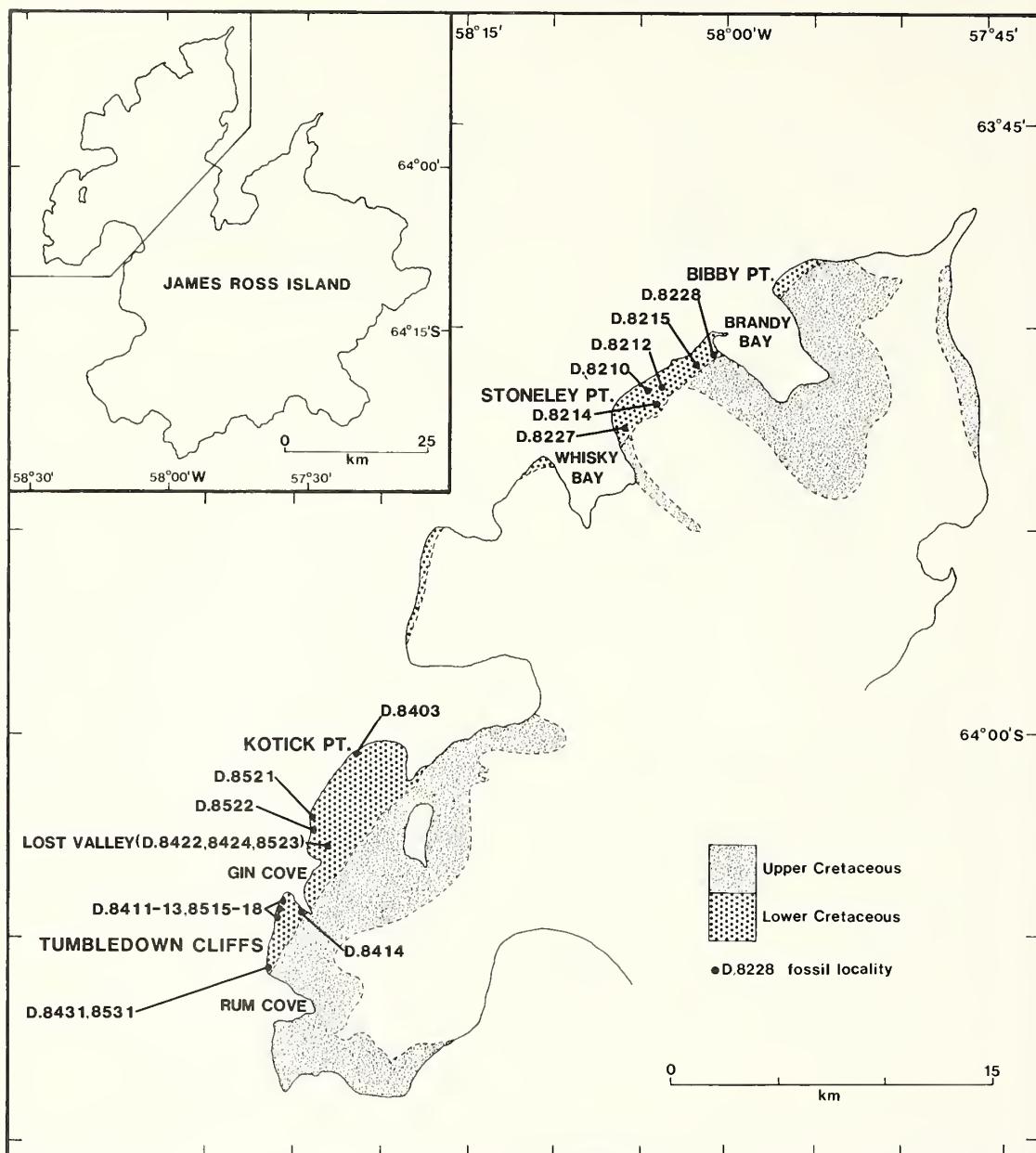


TEXT-FIG. 1. Locality map for the Antarctic Peninsula region.

One further region in which Lower Cretaceous inoceramids are well represented is the Antarctic Peninsula (text-fig. 1). On the south-western flanks of the peninsula, along the inner or eastern margin of Alexander Island (text-fig. 2), they occur through the greater part of the Fossil Bluff Formation (?Kimmeridgian–Albian). This unit, which is at least 4 km thick and composed of a variety of fine- to coarse-grained volcaniclastic sediments, accumulated in a fore-arc environment (Taylor *et al.* 1979). On the north-eastern side of the peninsula, within the James Ross Island group (text-fig. 3), further Cretaceous sediments are encountered that were deposited in a rear-arc setting. Recent fieldwork has shown the lower stratigraphic units mapped by Bibby (1966) in this area to be lower Cretaceous. They are approximately 1400 m thick, and are composed of lithologies ranging from bioturbated siltstones to breccio-conglomerates, and contain both ammonites and inoceramids. They pass up into a predominantly finer grained Upper Cretaceous sequence (the Hidden Lake Beds and Snow Hill Island Series of Bibby, 1966), that may be in excess of 3 km thick. Further fossiliferous Cretaceous sediments



TEXT-FIG. 2. Locality and geological map of the central east coast of Alexander Island. The Fossil Bluff Formation comprises the Upper Jurassic and Lower Cretaceous strata. Inset A shows the position of the enlarged area on the east coast of Alexander Island, inset B is an enlargement of localities in the Succession Cliffs-Fossil Bluff area, and inset C of localities in the Adams Nunatak-Mt. Lassell-Mt. Phoebe area.



TEXT-FIG. 3. Locality and geological map of NW James Ross Island. The inset shows the position of the enlarged area on the NW coast of James Ross Island.

can be traced through the Scotia arc in both the South Shetland Islands and the South Georgia Island group. In the former of these areas, early Cretaceous fossils have been collected from a sequence of fine- to coarse-grained clastic sediments on Byers Peninsula, Livingston Island (text-fig. 1) (Smellie *et al.* 1980). These sediments are intimately associated with a series of contemporaneous island-arc volcanic rocks in a setting similar to that described on Annenkov Island, close to South Georgia (text-

fig. 1) (Pettigrew 1981). Indeed, similar fossiliferous Lower Cretaceous sediments associated with volcanic rocks can be traced into the regions of southern Patagonia that were once contiguous with the island-arc marginal basin systems of the Scotia arc (e.g. Tanner *et al.* 1981; Tanner 1982).

It is the aim of this paper to describe the Lower Cretaceous inoceramids from the Antarctic Peninsula region and assess their potential for both local and regional biostratigraphic correlations. Until a formal re-classification has been completed (Crame, in prep.), it will be necessary to divide the two principal genera (*Inoceramus* J. Sowerby, 1814 and *Birostrina* J. Sowerby, 1821) into a series of informal species groups (Table 1). These groups are partly based on those of previous authors (Woods 1911, 1912; Gillet 1924; Maury 1936; McLearn 1943; Hayami 1960; Saveliev 1962; Pergament 1965; Sornay 1966; Pokhialainen 1969, 1974) and are partly new herein. *Inoceramus* is subdivided into nine species groups and *Birostrina* (which is here taken to be a valid genus, *sensu* Kauffman 1977, 1978a-c) into three. In Table 1 these twelve categories are arranged in approximate stratigraphic order. The comparatively rare genus, *Anopaea* Eichwald, 1861, is left undivided.

Wherever possible, the following measurements were taken:

shell length (L)—the length of the valve as measured along the direction of maximum growth (or growth axis).

shell width (W)—the maximum dimension perpendicular to the length.

apical angle (α)—the angle between the hingeline and the anterior margin.

All the specimens are currently held in the collections of the British Antarctic Survey, Cambridge, UK. In the systematic descriptions the following abbreviations are used: WS—whole specimen (i.e. bi-valved specimen); LV—left valve; RV—right valve.

SYSTEMATIC PALAEONTOLOGY

Family INOCERAMIDAE Giebel, 1852

Genus INOCERAMUS J. Sowerby, 1814

Type species. *Inoceramus cuvierii* J. Sowerby, 1814 from the 'Upper Chalk' of Sussex, England; by subsequent designation (Cox 1969, p. N315).

Inoceramus ovatus group

Inoceramus cf. *ovatus* Stanton, 1895

Text-fig. 4a

- cf. 1895 *Inoceramus ovatus* Stanton, p. 47, pl. 4, fig. 15.
- cf. 1938 *Inoceramus ovatus* Stanton; Anderson, p. 99, pl. 4, fig. 9.
- cf. 1966 *Inoceramus ovatus* Stanton; Zakharov, p. 98, pl. 35, fig. 3.
- 1972 *Inoceramus* sp. a, Thomson and Willey, p. 9, fig. 7c.

Holotype. *Inoceramus ovatus* Stanton (1895, p. 47, pl. 4, fig. 15); Paskenta group (Berriasian–Valanginian), Shasta series, California (see Anderson 1938); by monotypy.

Material. One slightly distorted internal mould (WS) KG.719.15 from approximately the 1675 m level in the Ablation Valley section, Alexander Island (70° 49' S., 68° 28' W.; text-figs. 2 and 10).

Occurrence. As for material; specimen KG.719.15 occurs in association with a Berriasian *Haplophylloceras-Bochianites* ammonite assemblage (Thomson 1979, p. 31); Tithonian–Valanginian (and Hauterivian?) range established in the Northern Hemisphere.

Description. The left valve (text-fig. 4a), which is the better preserved of the two, clearly has a sub-symmetrical pyriform outline; the narrow, pointed umbonal region is curved gently forwards and there are well-rounded anteroventral, ventral, and posteroventral regions. The length of the valve is 62 mm and width is 45 mm (W/L = 0.73). It is moderately convex, with the maximum inflation occurring in the umbonal region and centre of the valve. There are steep descents to the antero- and posterodorsal regions, but much shallower gradients in a ventral direction. Ornament consists of

TABLE 1. Classification of Lower Cretaceous inoceramids. The table summarizes the morphological features, and stratigraphical and geographical distributions of the principal Lower Cretaceous species. The genera *Inoceramus* and *Birostrina* are subdivided into informal species groups and it is envisaged that these will eventually form the basis of a series of subgenera. References used in establishing the various categories are as follows:

<i>Inoceramus ovatus</i> sp.: Whiteaves 1883; Stanton 1895; Anderson 1938, 1945; Zakharov 1966, 1968; Pokhialainen 1974; Zakharov and Turbina 1979. <i>I. proconcentricus</i> sp.: Zakharov 1966; Pokhialainen 1969, 1974; Glazunova 1973. <i>I. colonicus</i> sp.: Anderson 1938; Inlay 1960; Pergament 1965; Zakharov 1968; Pokhialainen 1969, 1974; Anderson 1938; Inlay 1960; Jones and Gryc 1960; Pergament 1966; Pokhialainen 1969; Kauffman <i>et al.</i> 1978. <i>I. neocomiensis</i> sp.: d'Orbigny 1846; Whiteaves 1883; Wollemann 1906; Woods 1911; Sornay 1965; Pokhialainen 1969; Glazunova 1973; Zakharov and Turbina 1979. <i>I. litorinowskyae</i> sp.: Newton 1909; Stolley 1912; Wellman 1959; Saveliev 1962; Pergament 1965; Glazunova 1973. <i>I. anglicus</i> sp.: Woods 1911, 1912; McLean 1919, 1933, 1943; Reeside 1923; Inlay 1961; Saveliev 1962; Pergament 1965; Glazunova 1973; Jeletzky 1977; Kauffman 1978a-c; Kauffman <i>et al.</i> 1978; Matsumoto <i>et al.</i> 1978. <i>I. carsoni</i> sp.: McCoy 1865, 1866, 1867; Etheridge 1872; Etheridge Jr. 1892, 1901, 1905; Ludbrook 1966. <i>Birostrina salomonii</i> sp.: Woods 1911, 1912; Casey 1961; Saveliev 1978a. <i>B. concentrica</i> sp.: J. Sowerby 1821; Etheridge 1907; Woods 1911, 1912, 1917; Heinz 1930; Maury 1936; Nagao and Matsumoto 1939; Warren and Stelck 1940; Saveliev 1962; Parkinson 1966; Glazunova 1973; Kauffman 1977, 1978a-c; Speden 1977; Wiedmann and Kauffman 1978; Crane 1980. <i>B. sulcata</i> sp.: Parkinson 1849; J. Sowerby 1821; d'Orbigny 1846; Wollmann 1906; Woods 1911, 1912; Jones 1960; Kauffman 1978a-c. <i>Anopaea</i> (undivided): Etheridge Jr. 1901; Saveliev 1962; Pokhialainen 1969; Thomson and Willey 1972; Crame 1981; Kelly 1984.			
--	--	--	--

Genus and group name	Component species	Diagnostic features	Stratigraphic range	Distribution
<i>Inoceramus ovatus</i> sp.	<i>I. ovatus</i> Stanton, <i>I. ellioti</i> Gabb, <i>I. quadrinotatus</i> Whiteaves, <i>I. impurus</i> Zakharov, <i>I. carinatus</i> Zakharov, <i>I. bojarkensis</i> Zakharov, <i>I. golberrii</i> Zakharov and Turbina (pars)	Small to medium; oval to pyriform outline; generally erect but may include some obliquely elongated forms; only slightly inequivalve; weakly to moderately inflated; subdued or irregular concentric ornament	Tithonian–Valanginian; ?Hauterivian	Pacific Coast of USA; northern Siberia
<i>I. proconcentricus</i> sp.	<i>I. proconcentricus</i> Pokhialainen, <i>I. murgadensis</i> Pokhialainen, <i>I. pronatus</i> Pokhialainen, <i>I. tainniricus</i> Zakharov, <i>I. vassiljevskovi</i> Pokhialainen, <i>I. apicatus</i> Pokhialainen	Small to medium; oval to well rounded; moderately to strongly inequivalve; most gryphacoid forms bear superficial resemblance to <i>Birostrina concentrica</i> ; weakly to moderately inflated (LV always more convex); subdued to prominent, irregular concentric ornament	Berriasian–Valanginian; Lower Hauterivian	Far East of USSR; Far East of USSR;
<i>I. ancella</i> sp.	<i>I. ancella</i> Trautschold, <i>I. pseudopropinguinus</i> Pergament, <i>I. inaequata</i> Hayami, <i>I. gagensis</i> Pokhialainen	Medium; pyriform to rounded-elongate; LVs sometimes have angular (almost trapezoidal) outline; moderately to strongly inequivalve; moderately inflated (LV more than RV); LV umbo only moderately enrolled; broad, low, regular concentric folds	possibly some extension into both the Lower Hauterivian and Lower Barremian	Pacific Coast of North America; Spitzbergen; Russian Platform; Crimea; northern Siberia
<i>I. colonicus</i> sp.	<i>I. colonicus</i> Anderson, <i>I. ovatoides</i> Anderson, <i>I. sub-colonicus</i> Pokhialainen	Medium to large; pyriform to rounded-elongate; strongly gryphacoid; LV always much more inflated than RV; narrower than <i>I. ancella</i> or <i>B. concentrica</i> ; long, narrow RVs have 'pinnid' appearance; long, curving ligamentum; almost smooth	Upper Hauterivian–Lower Barremian	Far East of USSR; Pacific Coast of North America

<i>I. heteropterus</i> sp.	<i>I. heteropterus</i> Pokhialainen, <i>I. semicostatus</i> Pokhialainen, <i>I. peltiformis</i> Pokhialainen, <i>I. solus</i> Pokhialainen, <i>I. terechonae</i> Pokhialainen, ? <i>I. vallejensis</i> Anderson, ? <i>I. dunveganensis</i> McLean, ? <i>I. scutulatus</i> Whitehouse, ? <i>I. procerus</i> Whitehouse	Medium to large; rounded, rounded-triangular, or oval outline; tapering dorsally; prominent narrow, pointed beaks rise slightly above hinge-line and curve forwards; moderately inflated; slightly inequivale?; RV often with steep, shelf-like anterior margin; prominent ligamentarium bearing large rounded-rectangular resilifers; almost smooth or faint, broad, concentric ribs	Essentially Upper Hauterivian; if <i>I. vallejensis</i> is a true member, then range may extend down into the Valangian; if <i>I. danveganensis</i> , <i>I. scutulatus</i> , and <i>I. procerus</i> are true members, then the range may be extended up to the Upper Albian, and possibly even Middle Cenomanian	Far East of USSR; ?Antarctic Peninsula; possible extension to Japan; Pacific Coast of North America; north-east Australia
<i>I. neocomiensis</i> sp.	<i>I. neocomiensis</i> d'Orbigny, <i>I. subneocomiensis</i> Glazunova, <i>I. volgensis</i> Glazunova, ? <i>I. quatsinoensis</i> Whiteaves, ? <i>I. ewaldi</i> Schlueter, ? <i>I. curacaoensis</i> Weaver, ? <i>I. borealis</i> Glazunova, ? <i>I. obtusus</i> Glazunova, ? <i>I. gusselaensis</i> Glazunova, ? <i>I. pochialaynen</i> Zakharov and Turbinia	Small to medium; broad, rounded-triangular outline; weakly to moderately inflated; LV slightly larger and more convex than RV; straight anterior margin; apical angle approx. 95°–115°; narrow, closely and evenly spaced ribs which occasionally split or become irregular; ribs have acute to rounded summits and are sometimes superimposed on primary low folds	Upper Aptian to Middle or Upper Albian	Europe; south-western USSR; ?Far East of USSR; Pacific Coast of North America; southern Argentina
<i>I. lherowowskya</i> sp.	<i>I. lherowowskya</i> Saveliev, <i>I. kedrovensis</i> Pergament, <i>I. choffatii</i> Newton, <i>I. spitzbergensis</i> Stolley, <i>I. saratoviensis</i> Glazunova, ? <i>I. urirus</i> Wellman	Small, erect, rounded-triangular to rounded-square outline; equivale; moderately to strongly inflated in centre of valve and umbonal region, often flattening towards valve margins; prominent, prosogyrous beaks; faint, narrow concentric ornament which may become irregular ventrally; occasional coarse ribs with acute summits	Upper Aptian to Middle or Upper Albian	South-western USSR; Far East of USSR; Spitzbergen; South Africa; ?New Zealand
<i>I. anglicus</i> sp.	<i>I. anglicus</i> Woods, <i>I. subanglicus</i> Pergament, <i>I. anglicus elongatus</i> Pergament, <i>I. anglicus conjugalis</i> Pergament, ? <i>I. dowlingi</i> McLearn, ? <i>I. cadiotensis</i> McLearn, ? <i>I. comancheanus</i> Cragin, ? <i>I. bellinensis</i> Reeside	Small to very large; broad rounded to rounded-triangular outline; length approximately equal to width; anterior region more prominent and apical angle larger than in <i>I. neocomiensis</i> group; weakly inflated; slightly inequivale?; narrow, regular concentric ribs usually have well-rounded summits and are separated by broad, flat interspaces; ribs typically symmetrical about growth axis and occasionally weaken or bifurcate	Essentially Middle–Upper Albian, but may also range into both Lower Albian and Lower Cenomanian	Europe; south-western USSR; Far East of USSR; Japan; Pacific Coast of North America; East Greenland; eastern Mexico
<i>I. carsoni</i> sp.	<i>I. carsoni</i> McCoy, <i>I. sutherlandi</i> McCoy	Medium to very large; sub-erect to strongly obliquely elongated; both narrow and broad forms exist; equivale to slightly inequivale?; moderately to strongly inflated over the umbonal region but flattened ventrally; pointed umbonal region strongly projecting; anterior margin often in the form of a shallow sigmoidal curve; narrow, regular concentric ornament which may be in two distinct phases	Upper Albian	North-east Australia

TABLE 1. Classification of Lower Cretaceous inoceramids. The table summarizes the morphological features, and stratigraphical and geographical distributions of the principal Lower Cretaceous species. The genera *Inoceramus* and *Birostrina* are subdivided into informal species groups and it is envisaged that these will eventually form the basis of a series of subgenera. References used in establishing the various categories are as follows:

Inoceramus ovatus gp.: Whiteaves 1883; Stanton 1895; Anderson 1938, 1945; Zakharov 1966, 1968; Pokhvalainen 1974; Zakharov and Turbina 1979. *I. proconcentricus* gp.: Zakharov 1966, 1969; Zakharov and Turbina 1979. *I. aucterior* gp.: Traushold 1865; Hayami 1960; Pergament 1965; Pokhvalainen 1969, 1974; Glazunova 1973. *I. colomae* gp.: Anderson 1938; Imay 1960; Pergament 1966; Pokhvalainen 1969, 1974; Jetletsky 1970. *I. heteropterus* gp.: Whitehouse 1924; Anderson 1938; Imay 1960; Jones and Gryc 1960; Pergament 1966; Pokhvalainen 1969; Kauffman *et al.* 1978. *I. neocomensis* gp.: d'Orbigny 1846; Whiteaves 1883; Wollmann 1906; Woods 1911; Gillett 1924; Weaver 1931; Hayami 1960; Imay 1960; Casy 1961; Sorray 1965; Pokhvalainen 1969; Glazunova 1973; Zakharov and Turbina 1979. *I. kievrawskyan* gp.: Newton 1909; Stolley 1912; Wellman 1959; Saveliev 1962; Pergament 1965; Glazunova 1973. *I. anglicus* gp.: Woods 1911, 1912; McLarn 1919, 1933; Reeside 1923; Imay 1961; Saveliev 1962; Pergament 1965; Glazunova 1973; Jetletsky 1977; Kauffman 1978a-c; Kauffman *et al.* 1978; Matsutomo *et al.* 1978. *I. carsoni* gp.: McCoy 1865, 1866, 1867; Etheridge 1872; Etheridge Jr 1892, 1901, 1905; Ludbrook 1966. *Birostrina salomonis* gp.: Woods 1911, 1912; Casey 1961; Saveliev 1962; Kauffman 1978a; *B. concentrica* gp.: J. Sowerby 1821; Etheridge 1907; Woods 1911, 1912, 1917; Heinrich 1930; Maury 1936; Nagao and Matsutomo 1939; Warren and Stelek 1940; Saveliev 1962; Pergament 1966; Glazunova 1973; Kauffman 1977, 1978a-c; Spele 1977; Wiedmann and Kauffman 1978; Crane 1980. *B. sulcata* gp.: Parkinson 1819, J. Sowerby 1821; d'Orbigny 1846; Wollmann 1906; Woods 1911, 1912; Jones 1960; Kauffman 1978a; *v. anapara* (undivided); Etheridge Jr 1901; Saveliev 1962; Pokhvalainen 1969; Thomson and Willey 1972; Crane 1981; Kelly 1984.

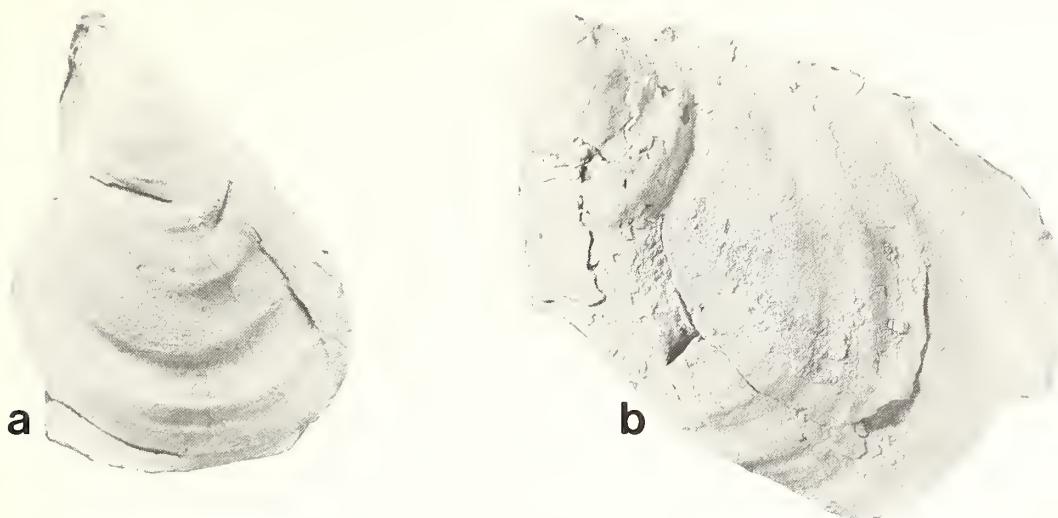
Genus and group name	Component species	Diagnostic features	Stratigraphic range	Distribution
<i>Inoceramus ovatus</i> gp.	<i>I. ovatus</i> Stanton, <i>I. ellioti</i> Gabb, <i>I. quasinoensis</i> Whiteaves, <i>I. imparius</i> Zakharov, <i>I. curvum</i> Zakharov, <i>I. bojaricum</i> Zakharov, <i>I. galberthi</i> Zakharov and Turbina (pars)	Small to medium; oval to pyriform outline; generally erect but may include some obliquely elongated forms; only slightly inequivalve; weakly to moderately inflated, subdued or irregular concentric ornament	Tithonian–Valanginian; ?Hauterivian	Pacific Coast of USA, northern Siberia
<i>I. proconcentricus</i> gp.	<i>I. proconcentricus</i> Pokhvalainen, <i>I. murgalensis</i> Pokhvalainen, <i>I. primatus</i> Pokhvalainen, <i>I. tenuiricus</i> Zakharov, <i>I. vassilenkovi</i> Pokhvalainen, <i>I. spinatus</i> Pokhvalainen	Small to medium; oval to well rounded, moderately to strongly inequivalve, most gryphaeoid forms bear superficial resemblance to <i>Birostrina concentrica</i> ; weakly to moderately inflated (LV always more convex), subdued to prominent, irregular concentric ornament	Bernesian–Valanginian; Lower Hauterivian	Far East of USSR, northern Siberia
<i>I. aucterior</i> gp.	<i>I. aurilla</i> Trautschold, <i>I. pseudopropinqua</i> Pergament, <i>I. inaequata</i> Hayami, <i>I. gagatensis</i> Pokhvalainen	Medium; pyriform to rounded-elongate; LV sometimes has angular (almost trapezoidal) outline; moderately to strongly inequivalve; moderately inflated (LV more than RV); LV umbro only moderately enrolled; broad, low, regular concentric folds	Essentially Upper Hauterivian; possibly some extension into both the Lower Hauterivian and Lower Barremian	Far East of USSR, Japan; Pacific Coast of North America, Spitsbergen, Russian Platform; Crimea, northern Siberia
<i>I. colanicus</i> gp.	<i>I. colanicus</i> Anderson, <i>I. ovatoides</i> Anderson, <i>I. subvolvulus</i> Pokhvalainen	Medium to large, pyriform to rounded-elongate, strongly gryphaeoid; LV always much more inflated than RV; narrower than <i>I. aurilla</i> or <i>B. concentrica</i> , long, narrow RVs have 'pinnid' appearance; long, curving ligamental; almost smooth	Upper Hauterivian–Lower Barremian	Far East of USSR, Pacific Coast of North America
<i>I. heteropterus</i> gp.	<i>I. heteropterus</i> Pokhvalainen, <i>I. semicostatus</i> Pokhvalainen, <i>I. peltiformis</i> Pokhvalainen, <i>I. sulci</i> Pokhvalainen, <i>I. teretifrons</i> Pokhvalainen, <i>I. valvergensis</i> Anderson, <i>I. shunvengensis</i> McLarn, <i>I. scutulatus</i> Whitehouse, <i>I. procerus</i> Whitehouse	Medium to large; rounded, rounded-triangular, or oval outline; tapering dorsally, prominent narrow, pointed beaks rise slightly above hinge-line and curve forwards; moderately inflated; slightly inequivalve?; RV often with steep, shelf-like anterior margin, prominent ligamental bearing large rounded-rectangular resilifers; almost smooth or faint, broad, concentric ribs	Essentially Upper Hauterivian; if <i>I. valvergensis</i> is a true member, then range may extend down into the Valanginian; if <i>I. shunvengensis</i> , <i>I. scutulatus</i> , and <i>I. procerus</i> are true members, then the range may be extended up to the Upper Albian, and possibly even Middle Cenomanian	Far East of USSR, "Antarctic Peninsula"; possible extension to Japan; Pacific Coast of North America, north-east Australia
<i>I. neocomensis</i> gp.	<i>I. neocomensis</i> d'Orbigny, <i>I. subneocomensis</i> Glazunova, <i>I. volgensis</i> Glazunova, <i>I. quasineocomensis</i> Whiteaves, <i>I. ovalis</i> Schlüter, <i>I. uracanthus</i> Weaver, <i>I. borealis</i> Glazunova, <i>I. obtusus</i> Glazunova, <i>I. gusevkensis</i> Glazunova, <i>I. pischiahaeanus</i> Zakharov and Turbina	Small to medium; broad, rounded-triangular outline; weakly to moderately inflated, LV slightly larger and more convex than RV; straight anterior margin; apical angle approx. 95°–115°; narrow, closely and evenly spaced ribs which occasionally split or become irregular; ribs have acute to rounded summits and are sometimes superimposed on primary low folds	Barremian–Aptian, with a possible downward extension into Hauterivian and Valanginian	Europe; south-western USSR, "Far East of USSR, Pacific Coast of North America, southern Argentina
<i>I. kievrawskyan</i> gp.	<i>I. kievrawskyan</i> Saveliev, <i>I. kedrovnikovi</i> Pergament, <i>I. choffati</i> Newton, <i>I. spitzbergensis</i> Stolley, <i>I. saratovensis</i> Glazunova, <i>I. urinus</i> Wellman	Small, erect, rounded-triangular to rounded-quadrilateral; equivalve; moderately to strongly inflated in centre of valve and umbonal region, often flattening towards valve margins; prominent, prosogyrous beaks; faint, narrow concentric ornament which may become irregular ventrally; occasional coarse ribs with acute summits may also develop ventrally	Upper Aptian to Middle or Upper Albian	South-western USSR, Far East of USSR, Spitsbergen, South Africa; ?New Zealand
<i>I. anglicus</i> gp.	<i>I. anglicus</i> Woods, <i>I. subanglicus</i> Pergament, <i>I. anglicus elongatus</i> Pergament, <i>I. anglicus conglobatus</i> Pergament, <i>I. dawlingi</i> McLarn, <i>I. calotectus</i> McLarn, <i>I. conancharinus</i> Cragin, <i>I. belluriensis</i> Reeside	Small to very large; broad rounded to rounded-triangular outline; length approximately equal to width; anterior region more prominent and apical angle larger than in <i>I. neocomensis</i> group; weakly inflated; slightly inequivalve?; narrow, regular concentric ribs usually have well-rounded summits and are separated by broad, flat interspaces; ribs typically symmetrical about growth axis and occasionally weaken or bifurcate	Essentially Middle–Upper Albian, but may also range into both Lower Albian and Lower Cenomanian	Europe; south-western USSR; Far East of USSR; Japan; Pacific Coast of North America; East Greenland; eastern Mexico
<i>I. carsoni</i> gp.	<i>I. carsoni</i> McCoy, <i>I. sutherlandi</i> McCoy	Medium to very large; sub-erect to strongly obliquely elongated; both narrow and broad forms exist; equivalve to slightly inequivalve?; moderately to strongly inflated over the umbonal region but flattened ventrally; pointed umbonal region strongly projecting; anterior margin often in the form of a shallow sigmoidal curve; narrow, regular concentric ornament which may be in two distinct phases	Upper Albian	North-east Australia

TABLE I (cont.)

Genus and group name	Component species	Diagnostic features	Stratigraphic range	Distribution
<i>B. salmoni</i> gp.	<i>I. salmoni</i> d'Orbigny, <i>I. imitans</i> Casey	Small to medium; rounded-rectangular to obliquely elongated, moderately to strongly inequivale; LV moderately inflated, RV only weakly so, LV umbo strongly incurved, broad, shallow sulcus on LV variably developed, simple, regular concentric ornament	Essentially Lower Albian, but <i>I. salmoni</i> may range into the Middle Albian	Although originally restricted to southern England, <i>I. copinus</i> may also occur in South Africa and Angola; <i>I. salmoni</i> —Western Europe, southwestern USSR, Far East of USSR, Pacific Coast of USA, ?Peru
<i>B. concentrica</i> gp.	<i>I. concentrica</i> Parkinson, <i>I. rostratrica</i> nippensis Nagao and Matsumoto (pars?), <i>I. concentrica</i> costatus Nagao and Matsumoto (pars?), <i>I. zuvolpeensis</i> Glazunova, <i>I. vulnibonita</i> Etheridge, <i>I. warakius</i> Wellman, <i>I. trinitatis</i> Mintell, <i>I. cornutus</i> McLearn (pars), <i>I. involvibrans</i> Pergament, <i>I. radicans</i> Pergament	Small to medium, occasionally large; obliquely oval to pyriform; noticeably longer than wide; short lunigeline; posterior wing missing; moderately to very strongly inequivale; LV always more strongly inflated than RV; narrow, prominent, and strongly enrolled umbo LV gives gryphaeoid appearance; thin prismatic shell layer; simple regular concentric ornament which may be traversed by weakly developed radial folds and sulci	Essentially Middle and Upper Albian, but with the possibility of a few Lower Albian records; may also extend well into the Cenomanian	Europe, southwestern USSR, Far East of USSR, Pacific Coast of North America, eastern Mexico, Brazil; ?Peru, ?southern Argentina; South Africa; New Zealand, Antarctic Peninsula
<i>B. sulcata</i> gp.	<i>I. sulcatus</i> Parkinson, <i>I. sub-sulcatus</i> Wiltshire, <i>I. sulcatus</i> Saveliev, <i>I. sub-sulcatus</i> Böse	Similar to small <i>B. concentrica</i> but with strong radial plicae covering all or part of shell	May well be restricted to Upper Albian, but there are a few possible Middle Albian records	Europe; southwestern USSR, Far East of USSR, Japan, Pacific Coast of North America; eastern Mexico; South Africa
<i>Ahiopara</i>	<i>A. brachowi</i> (Rouillier), <i>A. trapezoidalis</i> (Thomson and Willey), <i>A. constrictus</i> (Etheridge), <i>I. mordvilkoi</i> Pokhvalainen, <i>I. mordvilkoi</i> Mordvilko	Small to medium; elongate-pyriform outline, with high rounded posterior and narrow, pointed anterior, deep anterodorsal lunule; variably developed anterior sulcus; long, gently sloping lunigeline; equivale to slightly inequivale, slightly to moderately inflated, thin prismatic shell layer; ornament of low commarginal folds with superimposed secondary growth lamellae	Bernesian-Albian	Eastern England; ?Far East of USSR, ?southwestern USSR; Queensland; Antarctic Peninsula

TABLE 1 (cont.)

Genus and group name	Component species	Diagnostic features	Stratigraphic range	Distribution
<i>B. salomonii</i> sp.	<i>I. salomonii</i> d'Orbigny, <i>I. copensis</i> Casey	Small to medium; rounded-rectangular to obliquely elongated; moderately to strongly inequivalve; LV moderately inflated; RV only weakly so; LV umbo strongly incurved; broad, shallow sulcus on LV variably developed; simple, regular concentric ornament	Essentially Lower Albian, but <i>I. salomonii</i> may range into the Middle Albian	Although originally restricted to southern England, <i>I. copensis</i> may also occur in South Africa and Angola; <i>I. salomonii</i> —Western Europe, southwestern USSR, Far East of USSR, Pacific Coast of USA, ?Peru
<i>B. concentrica</i> gp.	<i>I. concentrica</i> Parkinson, <i>I. concentrica nipponica</i> Nagao and Matsumoto (pars?), <i>I. concentrica costatus</i> Nagao and Matsumoto (pars?), <i>I. zavoljensis</i> Glazanova, <i>I. voluumbonatus</i> Etheridge, <i>I. warakius</i> Wellman, <i>I. tenuis</i> Mantell, <i>I. cornificatus</i> McLearn (pars), <i>I. incelebratus</i> Pergament	Small to medium, occasionally large; obliquely oval to pyriform; noticeably longer than wide; short hinge-line; posterior wing missing; moderately to very strongly inequivalve; LV always more strongly inflated than RV; narrow, prominent, and strongly enrolled umbo LV gives gryphaeoid appearance; thin prismatic shell layer; simple regular concentric ornament which may be traversed by weakly developed radial folds and sulci	Essentially Middle and Upper Albian, but with the possibility of a few Lower Albian records; may also extend well into the Cenomanian	Europe; south-western USSR; Far East of USSR; Pacific Coast of North America; eastern Mexico; Brazil; ?Peru, ?southern Argentina; South Africa; New Zealand; Antarctic Peninsula
<i>B. sulcata</i> gp.	<i>I. sulcatus</i> Parkinson, <i>I. subsulcatus</i> Wilshire, <i>I. sulcoides</i> Savileev, <i>I. subsulciformis</i> Böse	Similar to small <i>B. concentrica</i> but with strong radial plicae covering all or part of shell	May well be restricted to Upper Albian, but there are a few possible Middle Albian records	Europe; south-western USSR; Far East of USSR; Japan; Pacific Coast of North America; eastern Mexico; South Africa
<i>Anopaea</i>	<i>A. brachovi</i> (Rouillier), <i>A. trapezoidalis</i> (Thomson and Willey), <i>A. constrictus</i> (Etheridge), <i>I. mandibula-formis</i> Pohjalainen, <i>I. mandibula</i> Mordvilko	Small to medium; elongate-pyriform outline, with high rounded posterior and narrow, pointed anterior; deep antero-dorsal lunule; variably developed anterior sulcus; long, gently sloping hinge-line; equivale to slightly inequivale; slightly to moderately inflated; thin prismatic shell layer; ornament of low commarginal folds with superimposed secondary growth lamellae	Berriasian-Albian	Eastern England; ?Far East of USSR; ?south-western USSR; Queensland; Antarctic Peninsula



TEXT-FIG. 4. *Inoceramus* cf. *ovatus* Stanton and *I.* sp. aff. *ellioti* Gabb from the Fossil Bluff Formation of Alexander Island. *a*, internal mould of a whole specimen of *I.* cf. *ovatus* (KG.719.15) viewed from the left side; specimen from Ablation Valley. *b*, internal mould of an incomplete left valve of *I.* sp. aff. *ellioti* (KG.401.51) from Tombaugh Cliffs. Both specimens $\times 1$.

poorly developed primary concentric folds with a spacing of 5–7 mm. Superimposed on this initial pattern, especially in the dorsal half of the valve, are finer, closely spaced secondary ribs (text-fig. 4*a*).

The right valve has been partially crushed and its true form is uncertain. However, it probably agrees closely in size and shape with the left and it can be concluded that the specimen was, at most, only slightly inequivale. The hinge appears to have been short and oblique and the apical angle is approximately 73° .

Remarks. The pyriform outline, narrow pointed umbones, subdued ornament, and near equality of the valves all suggest affinity with the *I. ovatus* group, and more especially with *I. ovatus* itself. However, poor preservation prevents positive identification with this species.

Inoceramus sp. aff. *ellioti* Gabb, 1869

Text-fig. 4*b*

- cf. 1938 *Inoceramus ellioti* Gabb; Anderson, p. 99, pl. 7, fig. 1.
1972 *Inoceramus* sp. *a*; Thomson and Willey, p. 9, fig. 7*b*.

Holotype. *Inoceramus ellioti* Gabb; ?Paskenta group (Berriasian–Valanginian), Shasta series, California; refigured in Anderson (1938, pl. 7, fig. 1).

Material. One incomplete internal mould (with traces of a thin prismatic shell layer) (WS) (KG.401.51); 30 m level at Tombaugh Cliffs, Alexander Island ($71^\circ 04' S.$ $68^\circ 18' W.$; text-figs. 2 and 10).

Occurrence. As for material. Associated fossils include Berriasian ammonites, belemnites, and bivalves (Taylor *et al.* 1979, p. 36; Crame 1982, text-fig. 9). *I. ellioti* has a probable Tithonian–Valanginian age-range in California (Anderson 1938; Zakharov 1968).

Description. Although the anterior and ventral regions of this specimen are incomplete, it can be judged to have had a slightly oblique, oval outline. The better preserved left valve (text-fig. 4*b*) has an estimated length of 82 mm and a width of 59 mm ($W/L = 0.72$). The umboinal region is not so clearly isolated as in the specimen of *I. cf. ovatus* and not noticeably inclined forwards either. It merges

ventrally with the moderately inflated central region of the valve and there are gentle descents to the posterior and posterodorsal margins. The latter is noticeably flatter and more pronounced than in the previous species.

Both valves bear the impressions of two phases of concentric ornament. The larger ribs have widths of 3–5 mm and low, rounded profiles. Regularly spaced and symmetrically curving over the central part of the valve, they sweep strongly forwards in the posterodorsal region. Finer secondary ribs (up to 2 mm in width) are superimposed on the primary ornament (text-fig. 4b).

Remarks. Even though there are similarities between this and the previous species (*I. cf. ovatus*) in style of ornament (see Thomson and Willey 1972, p. 9), it is apparent that there are significant differences in their respective shell forms. This specimen, with its more prominent posterodorsal region, is closer to broad forms in the *I. ovatus* group such as *I. quatsinoensis* and *I. ellioti* (Table 1). It is judged to be marginally closer to the latter, although poor preservation means that it can be only tentatively assigned to it.

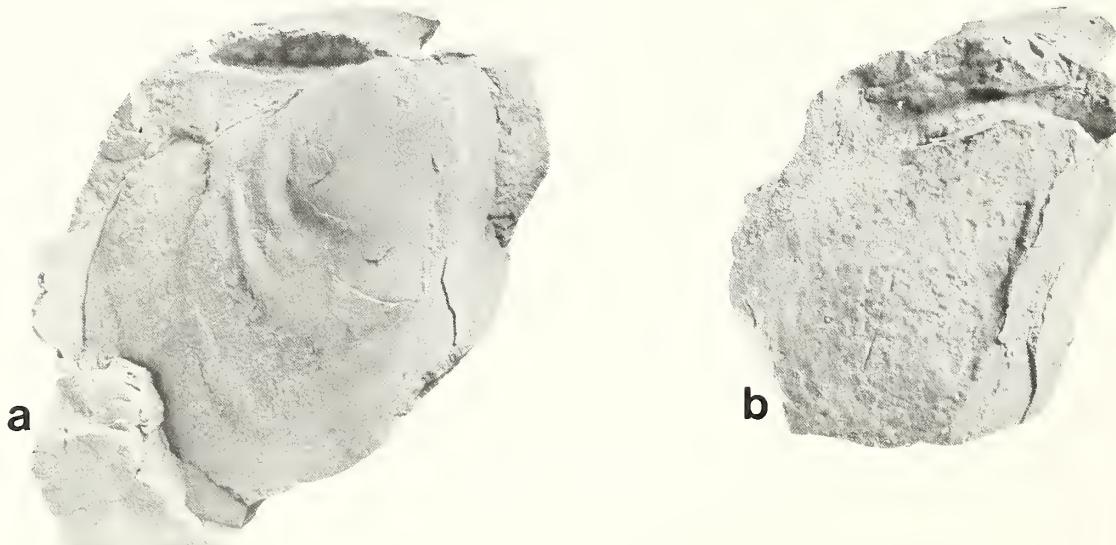
Inoceramus heteropterus group
Inoceramus cf. *heteropterus* Pokhialainen, 1969

Text-fig. 5a, b

cf. 1969 *Inoceramus heteropterus* Pokhialainen, p. 141, pl. 14, figs. 2–4; pl. 17, fig. 4; pl. 20, fig. 3; pl. 21, fig. 4.

Holotype. *Inoceramus heteropterus* Pokhialainen (1969, p. 141, pl. 14, fig. 4; pl. 17, fig. 4); specimen No. 46a/3, Museum of the NE Complex Scientific Research Institute, Magadan; Upper Hauerivian, basin of the River Veseloy, NW Kamchatka; by original designation.

Material. Five incomplete internal moulds of whole specimens bearing traces of shell material (M.1196.3a–e); approximately the 715 m level in the Lower Tuff Member, Annenkov Island (54° 29' S., 37° 03' W.; text-fig. 1) (Pettigrew 1981, fig. 5; Crame 1983a, figs. 6 and 7).



TEXT-FIG. 5. *Inoceramus* cf. *heteropterus* Pokhialainen from Annenkov Island. a, internal mould (with traces of a thick prismatic shell layer) of an incomplete whole specimen (M.1196.3c) viewed from the right side. b, internal mould (with traces of a thick prismatic shell layer) of an incomplete whole specimen (M.1196.3d) viewed from the right. Both specimens $\times 1$.

Occurrence. As for material. The *I. heteropterus* group is Upper Hauterivian in the Far East of USSR (Table 1), but this age may have to be extended down to at least the Valanginian if *I. vallejoensis* Anderson is a true member of the group. Similarly, if certain younger species are subsequently referred to it, it may have to be extended to the Albian or even Cenomanian (Table 1). The Annenkov Island Formation (which includes the lower Tuff Member) is imprecisely dated in the interval Neocomian–Aptian (Thomson *et al.* 1982).

Description. The specimens are conspicuous for their oval outlines, very reduced ornament, and narrow, pointed umbones. The latter project strongly above the hinge and forwards, but are not significantly curved inwards (text-fig. 5a, b). The mean shell length of the five specimens is 84.8 mm (S.D. = 17.95; range = 71–113) and mean width is 62.4 mm (S.D. = 15.27; range = 49–86). There is some evidence that the left valves may be slightly longer than the right valves but the specimens are not well enough preserved for this to be accurately determined.

The best preserved right valve is that of specimen M.1196.3c (text-fig. 5a). It is moderately convex, with the maximum inflation occurring in the umbonal region and along the growth axis. There is a gentle gradient from the centre of the valve to the ventral region and also to the posterodorsal region where there is an indistinctly recessed wing. There is a significantly steeper descent from the anterior margin of the valve to the plane of commissure. This occurs across a flat to gently concave shelf up to 13 mm wide (text-fig. 5a). At its dorsal end, directly beneath the umbo, the shelf assumes a more strongly concave profile and could be described as a gutter. Its presence is related to the curve of the umbo up and away from the hinge margin. The beak is missing, but by comparison with specimens M.1196.3b and d, it can be judged to have been narrow, pointed, and prosogyrous. A similar, but slightly shallower, concave gutter separates it from the hinge margin.

The left valves are not so well preserved as the right valves. In outline and general form they appear to be close to the latter and there are some indications that they may be marginally narrower and more evenly inflated. Specimen M.1196.3d has a very pronounced anterior shelf which again runs steeply from the anterior margin to the plane of commissure and has an approximate width of 15 mm. The net effect of the very pronounced anterior shelf on both valves must have been to produce a projection with a distinctly ‘V’ shaped cross-section.

The anterior shelf of the left valve also narrows and deepens directly beneath the umbo (text-fig. 5a, b). The separation of the left umbo from the hingeline is best seen from the right side where a smooth, narrow, triangular area can be clearly distinguished between the beak and the dorsal surface of the ligamentat (text-fig. 5a, b). The latter feature, which is the surface on which the ligament pits are arranged (Pokhialainen 1969), is partially displayed on specimens M.1196.3b–d; on M.1196.3c it has an approximate length of 30 mm and a depth of 5 mm in the centre. There is some evidence that it may have had a convex upper (dorsal) surface but this could not be definitely confirmed. The largest ligament pits certainly seem to be in the centre of the ligamentat where they are preserved as a rather irregular row of barrel-like protuberances with convex sides (text-fig. 5a). Much of the surface detail of the pits has been lost and it is uncertain whether they are simple or composed of composite elements.

On both valves there are faint traces of broad, low concentric folds.

Remarks. These almost smooth, oval shells with prominent, pointed umbones can be readily linked to the *I. heteropterus* group from the Soviet Far East. Unfortunately, this group is almost exclusively known from a single taxonomic study (Pokhialainen 1969) and the relationships between the component species are not always clear. The Annenkov Island specimens are judged to be closest to *I. heteropterus* itself, which exhibits a very similar range of shell sizes and morphologies (cf. Pokhialainen 1969, pl. 14, figs. 2 and 3; pl. 17, fig. 4; pl. 20, fig. 3; pl. 21, fig. 4). In particular, this species has a steeply descending anterior margin on the right valve which assumes a deep concave profile at its dorsal end, as well as a conspicuous ligamentat bearing large rounded-rectangular ligament pits (Pokhialainen 1969, pl. 15, fig. 6; pl. 20, fig. 3). As the specimens may be slightly less inequivalve than the Russian material, and have more prominent left anterior margins, they are only tentatively referred to *I. heteropterus*.

I. sohs Pokhialainen (1969, pl. 13, fig. 6; pl. 20, fig. 7) is very close to *I. heteropterus* but can be

distinguished by a slightly larger apical angle, distinctive ligamentat, and less prominent hollow (gutter) on the anterior margin. *I. peltiformis* Pokhialainen (1969, pl. 12, fig. 2; pl. 13, figs. 1–5) is a rounder and more convex form with traces of a distinct posterodorsal wing. The same feature is also present on *I. semicostatus* Pokhialainen (1969, pl. 14, fig. 1; pl. 17, figs. 1–3) which is an elongate-rounded form with prominent concentric ornament present on the smaller (?juvenile) specimens. It too, has a distinctive ligamentat and lacks a deep concave hollow along the anterodorsal margin.

Inoceramus neocomiensis group
Inoceramus deltoides sp. nov.

Plate 54, figs. 1–7; Plate 55, figs. 1, 2

Type material. Holotype: KG.1678.7 (RV?). Paratypes: KG.1677.2–4; KG.1678.5–7, 9; KG.1701.33, 34; KG.1730.13–16, 18, 20–22, 24; KG.1735.4–9, 13–24, 26–30, 32–37; KG.1743.1–7, 9; KG.1745.15; KG.2800.9, 31, 33, 84–86, 88, 264, 281, 282, 343, 344, 347, 348, 1113–1121, 1127–1130, 1133, 1136–1139 (both int.m. + ext. m.; RV's, LV's + indet. V's). From the following localities (see text-fig. 2): KG.1677—ridge between Mt. Lassell and Mt. Phoebe ($71^{\circ} 45' 30''$ S., $68^{\circ} 49'$ W.); KG.1678/1730—N face of Mt. Lassell, Neptune Glacier ($71^{\circ} 43'$ S., $68^{\circ} 45'$ W.); KG.1701—Citadel Bastion ($71^{\circ} 59'$ S., $68^{\circ} 32'$ W.) (probably loose); KG.1735—nunatak 0·6 km W of Mt. Lassell ($71^{\circ} 43' 30''$ S., $68^{\circ} 52'$ W.); KG.1743/2800—Fossil Bluff ($71^{\circ} 19'$ S., $68^{\circ} 17'$ W.); KG.1745—locality U—2 km NW of Fossil Bluff ($71^{\circ} 18'$ S., $68^{\circ} 20'$ W.). At locality KG.1743/2800 the specimens occur between 96 and 133 m in a 426 m section (text-fig. 10); their occurrence at localities to the south of Fossil Bluff (text-fig. 2) is due to tectonic repetition of the Fossil Bluff Formation.

Occurrence. As for the type material. Associated aconecceratid and heteromorph ammonites strongly suggest an Aptian age, although there is a possibility that some of them may have Barremian affinities too (Thomson 1974, 1983). Co-occurring specimens belonging to the *Aucellina andina-radiostriata* group suggest an Aptian-Albian age (Crame 1983a).

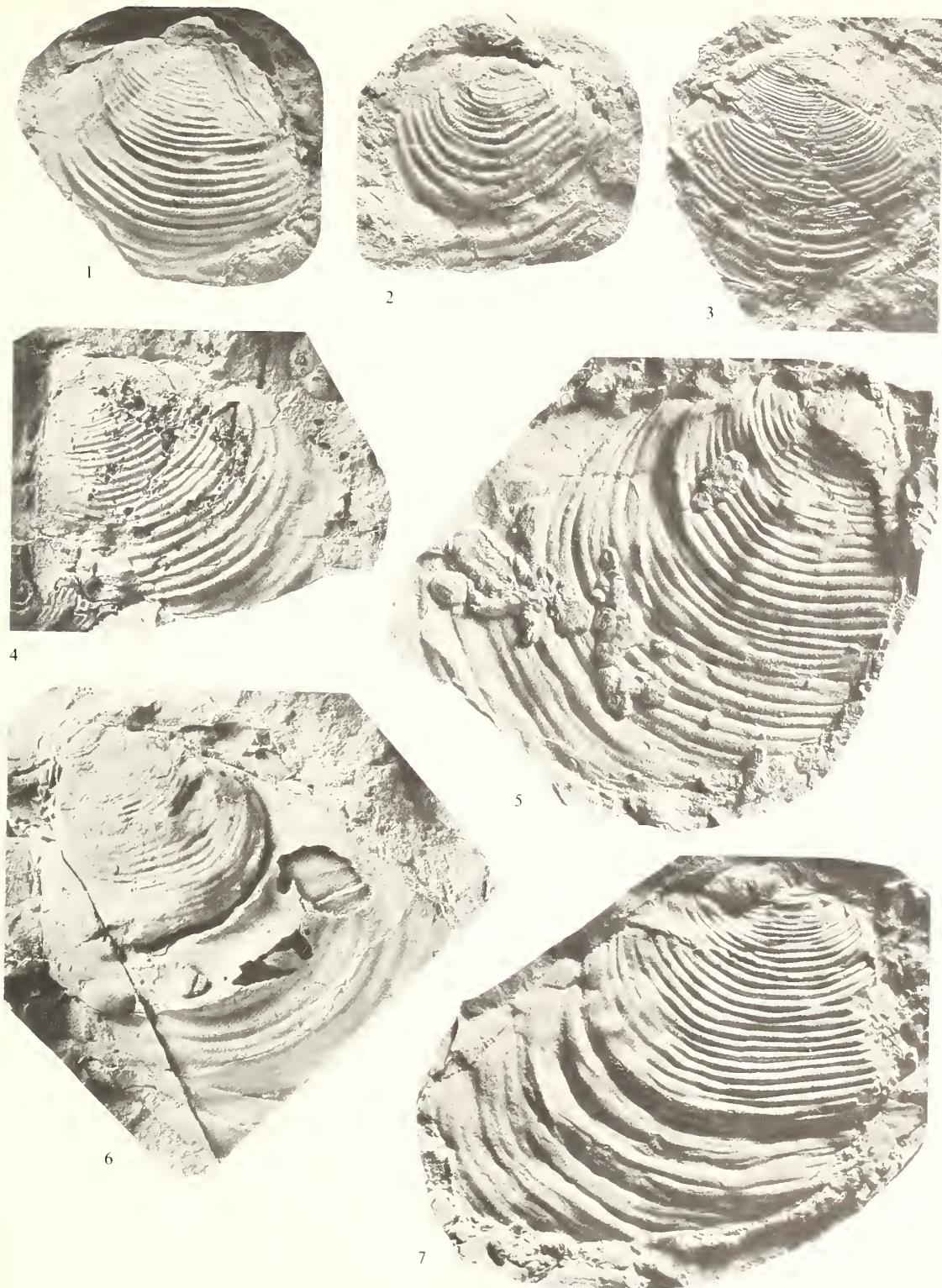
Derivation of name. From the distinctive delta-like, or triangular, outline.

Diagnosis. Medium to large, weakly inflated *Inoceramus* with a triangular outline; ornament of narrow, regularly spaced concentric ribs that are slightly asymmetric about the growth axis; ornament lacking in the ventral regions of the largest specimens; slightly inequivalve.

Description. First impressions of this species are those of a medium-sized, flat triangular shell that varies from roughly equilateral in outline (e.g. KG.1678.6 and 7; Pl. 54, fig. 1 and Pl. 55, fig. 2) to slightly oblique and inequilateral (e.g. KG.1677.4 and 1735.9; Pl. 54, figs. 4 and 6). Although it is often difficult to distinguish between right and left valves, it is apparent that, in all the asymmetric specimens, it is the anterior region which becomes reduced; the extent of this reduction varies from barely detectable to the pronounced state seen in two of the three articulated specimens (e.g. KG.1745.15; Pl. 54, fig. 2). The latter specimens are also of interest in that their left valves are slightly larger and have more inflated umbonal regions than the right valves. There is also a general impression from study of the single valves that at least some of the left valves have more inflated umbones than the right valves (e.g. KG.1677.4; Pl. 54, fig. 6).

EXPLANATION OF PLATE 54

Figs. 1–7. *Inoceramus deltoides* sp. nov. from the Fossil Bluff Formation of Alexander Island. 1, internal mould of probable right valve (KG.1678.6); Mt. Lassell. 2, internal mould of small whole specimen (KG.1745.15) viewed from the right side; locality U near Fossil Bluff. 3, rubber peel from the external mould of indeterminate valve (KG.2800.1128); Fossil Bluff. 4, internal mould of probable left valve (KG.1735.9); nunatak 0·6 km due W of Mt. Lassell. 5, rubber peel from external mould of probable right valve (KG.1678.9); Mt. Lassell. 6, internal mould of left valve (KG.1677.4); Mt. Lassell–Mt. Phoebe ridge. 7, rubber peel from external mould of probable right valve (KG.1678.5); Mt. Lassell. All specimens $\times 1\cdot5$, except for fig. 2 which is $\times 1\cdot5$.

CRAME, *Inoceramus* from Antarctica

Owing to the uncertainty of the orientation (i.e. left or right) of many valves the following measurements are based on an undifferentiated sample. It should be borne in mind that the left valves may be very slightly longer than the right valves, and also that, owing to the poor state of preservation, most specimens are probably incomplete. The mean estimated shell length is 69·11 mm (S.D. = 22·65; range = 41–175; N = 44), mean width is 62·30 mm (S.D. = 31·48; range = 32–210; N = 44), and mean ratio of width to length is 0·89 (S.D. = 0·23; range = 0·62–1·55; N = 44). Thus, the average shell shape is roughly that of an isosceles triangle that is marginally taller than it is broad (e.g. KG.1678.7; Pl. 55, fig. 2); common variants are narrower, oblique types (e.g. KG.1677.4; Pl. 54, fig. 6) and squatter, broader forms with expanded ventral regions (e.g. KG.1735.14a; Pl. 55, fig. 1). Where preserved the anterior and posterior margins appear to be essentially straight features that enclose an apical angle that approximates to a right angle ($\bar{x} = 91\cdot16^\circ$; S.D. = 14·69; range = 73°–132°; N = 45) (e.g. KG.1678.6, 7, 1735.9, and 2800.1128; Pl. 54, figs. 1, 3, 4 and Pl. 55, fig. 2). In those valves with attenuated anterior regions, a short, straight anterodorsal margin passes into a gently to strongly convex anteroventral margin (e.g. KG.1677.4; Pl. 54, fig. 6). The ventral margin always appears to be well rounded.

The valves are weakly to moderately inflated with the maximum inflation occurring in the umbonal region. As well as the single left valves with more inflated umbones (e.g. KG.1677.4), there are some large right valves in which the umbones rise steeply from a weakly inflated valve surface (e.g. KG.1677.2 and 3). A distinctive feature of this species is its narrow, regularly spaced concentric ornament. This is best seen in the early stages of the shell where the ribs are typically 1–1·5 mm in width, have acute to rounded profiles, and are separated by narrow interspaces (e.g. KG.1678.7, 1735.9, 2800.1128; Pl. 54, figs. 3, 4; Pl. 55, fig. 2). Usually arranged slightly asymmetrically about the growth axis, they occasionally anastomose or die out (e.g. KG.1678.6, 1735.14a, 2800.1128; Pl. 54, figs. 1, 3; Pl. 55, fig. 1); for the most part, however, they are remarkably uniform in their size and distribution. On some of the larger specimens there is a tendency for the ribs to become coarser and irregular in the posteroventral and ventral regions. Here they are bunched into thicker features 4–5 mm in width, which, when traced into the posterodorsal region, sweep strongly forwards and diminish in intensity (e.g. KG.1678.5 and 9; Pl. 54, figs. 5 and 7). On the largest specimens the concentric ribs can be up to 2 mm in width and are separated by shallow, flat-floored interspaces of similar, or even slightly greater, size. They are essentially restricted to the umbonal and central regions of the valve and, when traced towards the anterior, posterior, and ventral margins, are seen to die out rapidly (e.g. KG.1677.2, 3 and 1735.8). They are replaced by areas of smooth, undulatory shell and it can be concluded that this dimorphic ornament pattern is a consistent feature of all the largest valves. A final characteristic to be noted about the ornament is the tendency for the fine concentric ribs of some specimens to be grouped (and slightly raised) on low primary folds. This is best seen in the umbonal region of the largest specimen (KG.1677.3) but can also be detected on a number of smaller valves. This style of ornament is close to Heinz's (1928a) *Anwachsringreifen*.

Those specimens with the most strongly reduced anterior regions show obvious similarities in outline to *Anopaea* (e.g. KG.1745.15; Pl. 54, fig. 2); these are enhanced by the presence on some valves of a very shallow anteroventral sulcus (e.g. KG.1735.4). Such material can be taken as further evidence of possible morphological transitions between *Inoceramus* and *Anopaea*.

Remarks. The flat, triangular form and regular, closely spaced concentric ornament readily link *I. deltoides* sp. nov. with either the *I. neocomiensis* or *I. anglicus* groups. Features which suggest a greater affinity to the former of these include: a mean apical angle in the region of 90°, the absence of a protruding anterior region, the slightly inequivale nature of the shell (with the left valve being the more convex), comparatively narrow ornament with acute to rounded summits, and the occasional presence of *Anwachsringreifen* (Table 1). There are in fact considerable similarities, especially in style of ornament, with *I. neocomiensis* itself, although this species is usually interpreted as a comparatively small and more strongly inequivale form (e.g. d'Orbigny 1846, pl. 403, figs. 1 and 2; Woods 1911, pl. 45, figs. 1 and 2; Glazunova 1973, pl. 19, fig. 1a, b). *I. subneocomiensis* reaches larger sizes (> 100 mm in length) and shows a distinct tendency to develop *Anwachsringreifen* (e.g. Glazunova 1973, pl. 16,

fig. 4 and pl. 17, fig. 1); however, on the early stages of the valve the ribbing is less distinct than on *I. deltoides* sp. nov. and on some of the smaller specimens it is noticeably less regular (e.g. Glazunova 1973, pl. 17, fig. 2). Much clearer regular ornament is seen on both *I. borealis* and *I. obtusus* from the Russian Platform (Glazunova 1973, pl. 13, figs. 1–3; pl. 14, figs. 1 and 2; pl. 15, figs. 1–3; pl. 16, figs. 1 and 2), but in both these species the interspace width exceeds that of the ribs and the overall ornament style is closer to that of *I. anglicus* than *I. neocomiensis*. Large specimens of *I. cadottensis* McLearn from the Albian of the Canadian west coast and Alaska also show a pronounced change from narrow, regularly spaced ribs over the central regions of the valve to almost smooth ventral and posterior margins (e.g. Imlay 1961, pl. 9, fig. 1; Jeletzky 1964, pl. 27, fig. 7). However, it is apparent that this species typically has a longer hinge and more rounded-rectangular form than *I. deltoides* sp. nov. The early ribbing is also more typical of the *I. anglicus* group.

Inoceramus licherowskya group

Inoceramus stoneleyi sp. nov.

Plate 55, figs. 3–12

Type material. Holotype: D.8212.135 (int.m. WS with traces of outer shell layer). Paratypes: D.8210.25 (ext.m., WS); D.8210.50, 8212.103 (both int.m., LV); D.8212.180, 181 (both ext.m., LV); D.8212.101, 104, 136, 138, 139, 141–144, 182, 212, 213, 228 (all int.m., RV); D.8212.73, 140, 177 (all int.m., indet. V). Locality D.8210—N flank of pale ridge 1 km NE of Stoneley Point ($63^{\circ} 51' 40''$ S., $58^{\circ} 06' 20''$ W.); D.8212—floor of valley to S of pale ridge ($63^{\circ} 51' 40''$ S., $58^{\circ} 05' 20''$ W.) (text-fig. 3). These localities occur between 600 and 925 m in the combined stratigraphic section measured on NW James Ross Island (text-fig. 11).

Occurrence. As for the type material. Aptian–Albian, with a possible downward extension into the Barremian (Crame 1983a, b).

Some of the poorly preserved inoceramids recorded from the Crabeater Point region on the east coast of the Antarctic Peninsula (text-fig. 1) (Thomson 1967) may also belong within this species. In particular, a series of internal moulds bearing traces of thin, blade-like concentric ribs (BMNH specimens LL16068 and 16069) closely resemble the smaller and smoother forms of *I. stoneleyi* sp. nov. (cf. Pl. 55, fig. 9; Pl. 55, figs. 6, 7, 10, 12).

Derivation of name. In recognition of the pioneer geological work in the area by Professor R. Stoneley.

Diagnosis. A small, erect *Inoceramus*; moderately inflated in the central regions but with noticeably flattened and extended valve margins; ornament weak and irregular in the centre of each valve and almost absent on the margins; equivalve.

Description. This species is judged to have been equivalve, or very nearly so. The mean estimated shell length is 25·43 mm (S.D. = 6·02; range = 15–37; N = 14) and mean shell width is 16·86 mm (S.D. = 4·47; range = 10–25; N = 14); (N.B. these measurements exclude two very small right valves (D.8212.101 and 228) with lengths of 10 and 12 mm and widths of 6 and 7 mm, respectively; these are almost certainly juveniles). The right valve of the holotype has an erect, oval outline which is slightly accentuated by the missing tip of the umbo (Pl. 55, fig. 5). However, this feature is present on other right valves and is clearly narrow and turned weakly forwards (e.g. D.8212.104; Pl. 55, fig. 7). It is apparent that the apical region is always considerably narrower than the ventral and that the valves are more asymmetric about an imaginary midline than the first impression gained by cursory examination of the holotype. The maximum degree of inflation occurs in the centre of the valve and usually follows the growth axis from the beak to a point close to the ventral margin. On the anterior, ventral, and posterior margins there is an abrupt flattening to form a distinct rim (or shelf) between 4 and 6 mm in width; the junction between the main part of the valve and this rim is marked by a shallow depression (Pl. 55, figs. 3 and 5). Apparently restricted to just the largest specimens, there are some indications that this rim may diminish in the anterodorsal region where there is usually the steepest descent from the centre of the valve to the margin. On some specimens, such as D.8212.212 (which is a small, flattened right valve), there appears to have been a steep descent along the greater part of the anterior margin (Pl. 55, fig. 8), and thus the rim may have been essentially restricted to the ventral and posterior regions.

The ornament on the right valve of the holotype, which is preserved in prismatic shell material, consists of narrow (< 1 mm wide) concentric ribs that are slightly asymmetric about the growth axis (Pl. 55, fig. 5). Their spacing is close but by no means regular, and, when traced towards the valve margins, they show some tendency to anastomose or disappear. In any event, all the ornament disappears at the annular depression and the marginal rim is smooth (Pl. 55, figs. 3 and 5). The style of ornament over the central region of the valve is characteristic of all the right valves in the collection, although there is some variation in intensity of ribbing (Pl. 55, figs. 5, 7, 8, 10–12). On specimen D.8212.212, ribs of up to 2 mm in width are preserved in thick shell material in the posterodorsal region; here they are closely intercalated with narrower, discontinuous ribs (Pl. 55, fig. 8). Along the dorsal margin of this specimen the same thick shell layer has preserved a ligamentat measuring approximately 19 mm in length and 4·5 mm in height. This feature, which is set at an angle to the plane of commissure, bears the remnants of three large and four small, intercalated, ligament pits. The larger types have rectangular flask-shaped profiles, tapering gradually from the ventral to dorsal margins of the ligamentat, whilst the smaller, narrower ones taper correspondingly in the opposite direction. A large, oval, posterior adductor muscle scar is visible in the posterodorsal quadrant of the holotype's right valve (Pl. 55, fig. 5).

Although less well preserved, the left valve of the holotype appears to be essentially similar in form and style of ornament to the right. Left valves as a whole are less well represented in the collection but those that are present suggest that they exhibit a range of variation very similar to that seen in the rights (D.8210.50, 8212.103, 135; Pl. 55, figs. 3, 4, 6).

Remarks. Originally thought to be a small member of the *I. neocomiensis* group (Crame 1983a, b) it is now apparent that this species is better classified within the *I. licherowskyae* group (Table 1). Perhaps its closest resemblance is with *I. spitzbergensis* Stolley (1912, p. 20 and pl. 1, figs. 5 and 6) from the Aptian/Albian of Spitzbergen. This species too, is small and erect, and shows a similar transition from a well-inflated central region to much flatter margins. It has narrow, closely spaced concentric ribs which occasionally become larger, irregular in their course and wedge-shaped in cross-section. Nevertheless, despite these similarities, it would appear that *I. spitzbergensis* has a more quadrate outline, due principally to the presence of a right-angled posterodorsal wing, and there is also the possibility that it has a more angular ventral margin (Stolley 1912, pl. 1, fig. 5). The narrower form of *I. licherowskyae* Saveliev (1962, p. 228 and pl. 5, figs. 2–8) from the Upper Albian of Mangishlak is close to specimens such as D.8212.104 and 141 which lack an outer rim (Pl. 55, figs. 7 and 12), although it would seem that this species has consistently finer and closer spaced ornament. It also has slightly more pointed umbones and there is some tendency towards the formation of a small posterodorsal wing (e.g. Saveliev 1962, pl. 5, fig. 2). Both *I. kedrovensis* Pergament (1965, p. 28 and pl. 9, figs. 3 and 4) from the Albian of north-west Kamchatka and *I. saratoviensis* Glazunova (1973, p. 46, pl. 21, figs. 3 and 4) from the late Aptian of the Russian Platform could be matched with some of the

EXPLANATION OF PLATE 55

Figs. 1 and 2. *Inoceramus deltoides* sp. nov. from the Fossil Bluff Formation of Alexander Island. 1, rubber peel from an external mould of an indeterminate valve (KG.1735.14a); small nunatak 0·6 km due W of Mt. Lassell. 2, holotype (KG.1678.7), an internal mould of a probable right valve; Mt. Lassell. Both specimens $\times 1$.

Figs. 3–8, 10–12. *Inoceramus stoneleyi* sp. nov. from the Stoneley Point region, NW James Ross Island. 3, posterodorsal view of holotype (D.8212.135); the specimen, which is an internal mould bearing traces of a prismatic shell layer, is joined at the hinge but gapes widely ventrally. 4, internal mould of left valve (D.8212.103). 5, right valve of holotype. 6, internal mould of left valve (D.8210.50). 7, internal mould of right valve (D.8212.104). 8, internal mould of right valve (D.8212.212) partly covered by a thick prismatic shell layer. 10, internal mould of incomplete right valve (D.8212.138). 11, internal mould of right valve (D.8212.144). 12, internal mould of right valve (D.8212.141). All specimens $\times 1\cdot5$.

Fig. 9. Possible specimens of *I. stoneleyi* sp. nov. (BMNH LL.16068) from Crabeater Point, Kenyon Peninsula. Both specimens are internal moulds of right valves. $\times 1\cdot5$.

CRAME, *Inoceramus* from Antarctica

smoother forms of *I. stoneleyi* sp. nov. (e.g. Pl. 55, figs. 7, 10, 12). However, there is some evidence to suggest that the former of these Russian species is narrower and closer in outline to *I. licherowskyae*, whilst the latter has a much more rounded-triangular outline.

Inoceramus flemingi sp. nov.

Plate 56, figs. 1, 2

Type material. Holotype: KG.1726.10 (int.m., LV). Paratypes: KG.1726.2, 3, 14 (all int.m., LV); KG.1726.7 (ext.m., LV); KG.1726.5, 8 (both int.m., RV); ?KG.1682.36 (int.m., RV). Locality KG.1726 is on the ridge running SSW from Mt. Phoebe ($71^{\circ} 48' 30''$ S., $68^{\circ} 48' 00''$ W.) and KG.1682 is at a high level in Waitabit Cliffs, Alexander Island ($71^{\circ} 30'$ S., $68^{\circ} 48'$ W.; text-fig. 2). At both these localities the specimens occur in close association with *Birostrina?* cf. *concentrica*.

Occurrence. Albian (probably Middle–Upper Albian), from its close association with *B.? cf. concentrica* at both localities KG.1682 and 1726.

Derivation of name. In honour of the Rt. Revd. W. L. S. Fleming, geologist on the British Graham Land Expedition (1934–1937) and the first person to collect fossils from Alexander Island.

Diagnosis. A small, erect *Inoceramus* with prominent concentric ornament, slightly prosogyrous umbones, and a flange-like posterodorsal wing; prominent ligamentat bearing flask-shaped ligament pits; equivalve, or very nearly so.

Description. This is a small species with a mean shell length of 27·38 mm (S.D. = 7·96; range = 18–38; N = 8) and a mean width of 17·13 mm (S.D. = 5·64; range = 11–27; N = 8). Both valves have erect, rounded-quadrata outlines and prosogyrous umbones that terminate in narrow, pointed beaks (Pl. 56, figs. 1 and 3). The latter reach up to the level of the long, straight hingeline which subtends a mean apical angle of $75\text{--}88^{\circ}$ (S.D. = 6·56; range = $68^{\circ}\text{--}84^{\circ}$; N = 8) with the straight to gently convex anterior margin. The ventral margin is well rounded but the posterior is much less steeply convex and in some specimens comes to lie subparallel to the anterior. On the holotype a prominent ligamentat is displayed (Pl. 56, fig. 1), which, when complete, would have had dimensions of approximately 14×2 mm. The prominent ligament pits are distinctly flask-shaped, with well-rounded, bulbous bases tapering up into narrow necks.

Both valves are moderately inflated, with the maximum degree of inflation occurring along the growth axis. There are even descents from the apex of convexity to all the margins and in the posterodorsal region there is a narrow, indistinctly recessed wing. This is best seen on the holotype where it forms a smooth flange-like feature up to 6 mm in width (Pl. 56, fig. 1). The ornament consists of a simple pattern of clearly defined and regularly spaced concentric ribs that are symmetrically arranged about the growth axis (e.g. KG.1726.8, 10; Pl. 56, figs. 1 and 3); in cross-section these ribs

EXPLANATION OF PLATE 56

Figs. 1 and 3. *Inoceramus flemingi* sp. nov. from the Fossil Bluff Formation of Alexander Island. 1, holotype, an internal mould of a left valve (KG.1726.10) from the ridge running SSW from Mt. Phoebe. 3, internal mould of right valve (KG.1726.8) from the same locality. Both specimens $\times 1\cdot5$.

Fig. 2. *Inoceramus urius* Wellman. Plaster cast of the holotype (a left valve, NZGS TM2116) from the Upper Albian Motuan stage of New Zealand. $\times 1$.

Figs. 4, 5, and 7. *Inoceramus* cf. *anglicus elongatus* Pergament from the Fossil Bluff Formation of Alexander Island. 4, internal mould of left valve (KG.1680.72); Keystone Cliffs. 5, internal mould of left valve (KG.1680.2); same locality. 7, internal mould of left valve (KG.106.3); same locality. All specimens $\times 1$.

Figs. 6 and 8. *Inoceramus* sp. aff. *comancheanus* Cragin from the Fossil Bluff Formation of Alexander Island. 6, internal mould of right valve (KG.1606.18); Hyperion Nunataks. 8, internal mould of left valve (KG.1680.73); Keystone Cliffs. Both specimens $\times 1$.

Fig. 9. *Inoceramus* sp. aff. *anglicus* Woods. Rubber peel from an external mould of a large, incomplete right valve (BR.151.12); Welchness, western Dundee Island. $\times 1$.

CRAME, *Inoceramus* from Antarctica

typically have an acute profile, tapering from a broad base to a summit no more than 0·5 mm in width. On most specimens the interspace width increases from approximately 0·5 mm over the umbo to 2·0–2·5 mm close to the ventral margin. Although there may be some difference in the size of the posterodorsal wing between the left and right valves, they are in all other aspects very similar.

Remarks. This small, erect, equivalve (or nearly so) species probably has its closest links with the *I. liverowskyae* group (Table 1). However, it should be noted that the ornament seems to be consistently stronger and more regular than almost all members of this group, with the possible exception of *I. liverowskyae* itself from the Upper Albian of Mangishlak. The holotype of this species does bear moderately strong, regular concentric ribs (cf. Saveliev 1962, pl. 5, fig. 6; Pl. 56, fig. 1) but all Saveliev's (1962, pl. 5, figs. 2–5, 7, 8) other illustrated material is characterized by much finer ribbing. The prominent ligamentum suggests a possible link with *I. urius* Wellman from the Upper Albian of New Zealand (see Pl. 56, fig. 2), but this species has a slightly different outline and much less uniform ornament. Although *I. flemingi* sp. nov. is similar in size to *I. stoneleyi* sp. nov. and some specimens possess a flattened posterodorsal area, it can be readily distinguished by its prominent ligamentum and strong, regular ornament.

Inoceramus anglicus group
Inoceramus sp. aff. *anglicus* Woods, 1911

Plate 56, fig. 9

- cf. 1911 *Inoceramus anglicus* Woods, p. 264, text-fig. 29.
- cf. 1961 *Inoceramus anglicus* Woods; Imlay, p. 52, pl. 9, figs. 4 and 6; pl. 10, fig. 9.
- cf. 1965 *Inoceramus* cf. *anglicus* Woods; Pergament, pl. 3, fig. 2.
- cf. 1965 *Inoceramus* sp. aff. *anglicus* Woods; Pergament, pl. 6, fig. 4.
- cf. 1973 *Inoceramus anglicus* Woods; Glazunova, p. 49, pl. 19, fig. 4; pl. 21, figs. 1 and 2.

Lectotype. *Inoceramus anglicus* Woods (1911, pl. 45, fig. 8a, b), Red Limestone (Albian), Hunstanton; designated by Saveliev (1962, p. 223).

Material. Two large fragments (with traces of shell material): BR.151.12 (ext.m., RV); BR.151.11 (int.m., LV). From the large lateral moraine at Welchness, western Dundee Island (63° 29' S., 56° 15' W.) (text-fig. 1).

Occurrence. *I. anglicus* is Middle–Upper Albian, with possible extensions into both the Lower Albian and Lower Cenomanian (Table 1). The predominantly Middle–Upper Albian species, *B. concentrica*, has also been recorded from Dundee Island (Crame 1980).

Description and remarks. Whereas specimen BR.151.12 had an original shell length of approximately 160 mm and a width of 100 mm, specimen BR.151.11 appears to have been significantly smaller, with corresponding dimensions of approximately 105 and 75 mm. All the valve margins are incomplete, but it can be judged, from the course of the ornament, that the form was sub-erect to erect. Both specimens are only weakly inflated. The most characteristic feature of this material is its strong, regular, and widely spaced concentric ornament; the component ribs, which are 1–2 mm in width and have well-rounded cross-profiles, are separated by broad, flat interspaces that vary from 2–3 mm in width on the early part of the shell to up to 7 mm towards the ventral margin (e.g. BR.151.12; Pl. 56, fig. 9). This style of ornament is reminiscent of that found on both large specimens of *I. anglicus typica* (e.g. Woods 1911, text-fig. 29; Imlay 1961, pl. 9, figs. 4 and 6, pl. 10, fig. 9; Glazunova 1973, pl. 19, fig. 4, pl. 21, figs 1 and 2) and large fragments tentatively assigned to the *I. anglicus* group (e.g. Pergament 1965, pl. 3, fig. 2, pl. 6, fig. 4).

Inoceramus cf. *anglicus elongatus* Pergament, 1965

Plate 56, figs. 4, 5, 7

- cf. 1965 *Inoceramus anglicus elongatus* Pergament, p. 19, pl. 2, figs. 3 and 4; pl. 6, fig. 3.
- 1972 *Inoceramus* sp. β; Thomson and Willey, p. 11 and fig. 7d.

Holotype. *Inoceramus anglicus elongatus* Pergament; specimen 3/70a from the Albian of the River Kedrovoy region, Kamchatka (Pergament 1965, p. 19, pl. 2, fig. 3); by original designation.

Material. KG.106.3, 1680.2, 3, 30, 72, 75 (all int.m., LV); KG.1680.59 (ext.m., RV); RV.1680.5 (ext.m., ?RV); KG.1663.33, 1680.4 (both int.m., ?RV); KG.1681.5. (ext.m., indet.V). Localities KG.106 and 1680 are in the lowest 32 m of the section at Keystone Cliffs ($71^{\circ} 33' 00''$ S., $68^{\circ} 15' 30''$ W.) and KG.1681 is from an equivalent stratigraphic level at the top of Waitabit Cliffs ($71^{\circ} 30' 00''$ S., $68^{\circ} 14' 30''$ W.). Locality KG.1663 is on the W side of Stephenson Nunatak ($72^{\circ} 08' 30''$ S., $69^{\circ} 09' 00''$ W.; text-figs. 2 and 10).

Occurrence. On balance the upper levels of Waitabit Cliffs and lower levels of Keystone Cliffs have an Albian age (Taylor *et al.* 1979); however, a few ammonites from these localities have older affinities (Thomson 1974, 1983) and their presence has yet to be fully explained. *I. anglicus elongatus* is Middle–Upper Albian in Kamchatka (Pergament 1965, fig. 6) and in England specimens provisionally identified as *I. cf. anglicus elongatus* occur in the lower Cenomanian (Kauffman 1978b, p. IV.5).

Description. This is a small to medium-sized species with an erect to slightly obliquely elongated outline; the mean shell length is 46·36 mm (S.D. = 9·00; range = 36–63; N = 11) and mean width is 30·73 mm (S.D. = 5·95; range = 22–40; N = 11). At first sight, it would appear to be significantly narrower than the similarly ribbed *I. deltoides* sp. nov. (cf. Pl. 54, figs. 1–7; Pl. 56, figs. 5–7), but, when the respective mean apical angles (*I. anglicus elongatus* = $82\cdot3^{\circ}$; *deltoides* sp. nov. = $91\cdot16^{\circ}$) are compared, they are not found to be significantly different (Student's *t*-test, $p > 0\cdot05$). This is largely due to the presence of a prominent hinge region on some specimens of *I. cf. anglicus elongatus* which rises well above the posterodorsal margin of the valve (e.g. KG.106.3 and 1680.2; Pl. 56, figs. 5 and 7). There is no evidence of a corresponding feature of similar magnitude on *I. deltoides* sp. nov., although it should be stressed that the hinge region of this species is never well preserved. The W/L ratio for *I. cf. anglicus elongatus* is 0·66 and this is significantly less (Student's *t*-test, $p < 0\cdot001$) than that for *I. deltoides* sp. nov. (0·89).

The long, gently convex anterior margin forms an acute angle at the beak with an almost straight posterodorsal margin (e.g. KG.1680.72; Pl. 56, fig. 4). The latter is sharply differentiated from a prominent ligamentum which appears to have had a length up to two-thirds that of the total valve length and a height of 1·5–2·0 mm. It bears the remnants of rounded-quadrata to rectangular ligament pits with a mean width in the region of 1 mm; these may be either closely spaced (e.g. KG.1680.30) or separated by interspaces of up to 1 mm. All the specimens are weakly inflated and there are very gentle descents from the centre of the valve to all the margins. On some specimens (e.g. KG.106.3; Pl. 56, fig. 7) the umbo is slightly differentiated from the main body of the valve, but in others (e.g. KG.1680.72, 1681.5; Pl. 56, fig. 4) it is barely discernible as a separate entity. In all cases it terminates in a narrow, pointed beak which does not rise above the level of the hingeline.

The style of ornament is very similar to that seen in the early stages of *I. deltoides* sp. nov. Typically less than 0·5 mm in width at their summits, the ribs are closely and regularly spaced, sub-symmetrical about the growth axis and rounded in cross-section (Pl. 56, figs. 4, 5, 7). There is a slight increase in both rib and interspace width towards the ventral margin of the largest specimens and occasional ribs anastomose or become irregular in their course. The irregularities in the early stage of specimen KG.1680.72 (Pl. 56, fig. 4) may be due to shell damage during growth. Although the right valves are less well preserved than the left valves, it would appear that the species was equivalve.

Remarks. These comparatively small, finely ribbed individuals closely resemble a number of juvenile and incomplete specimens that have been assigned to the *I. anglicus* group (e.g. Imlay 1961, pl. 9, fig. 3; Saveliev 1962, pl. 1, figs. 1–5; Pergament 1965, pl. 1, fig. 3, pl. 4, fig. 3, pl. 5, fig. 2, pl. 9, fig. 6; Glazunova 1973, pl. 19, fig. 5a–c) (see Table 1). In particular, the broader, more erect forms (e.g. KG.1680.2; Pl. 56, fig. 5) compare well with certain specimens of *I. anglicus forma typica* from Mangishlak (e.g. Saveliev 1962, pl. 1, fig. 5b) and the narrower, more oblique ones (e.g. KG.1680.72; Pl. 56, fig. 4) with the subspecies *I. anglicus elongatus* from NW Kamchatka (Pergament 1965, p. 19, pl. 2, figs. 3 and 4; pl. 6, fig. 3). Although lack of a hinge means that the true orientation of some of the Alexander Island material is unknown, it is likely that the majority of specimens are at least slightly obliquely elongated; as such, they are closer to *anglicus elongatus* than *forma typica*. For two

of his specimens. Pergament (1965, p. 19) gives lengths of 47 and 44 mm, widths of 32 and 37 mm, and apical angles of 62° and 72°. One of these (Pergament 1965, pl. 2, fig. 3) clearly has a few bifurcating ribs, and, were it not for the fact that no hinge regions are preserved, it would appear that the Russian specimens closely resemble those from Alexander Island. *I. volgensis* from the Aptian of the Russian Platform (Glazunova 1973, p. 43, pl. 12, figs. 1–5) is a finer ribbed species whilst *I. borealis* (Glazunova 1973, p. 43, pl. 13, figs. 4 and 5; pl. 14, figs. 1 and 2; pl. 15, figs. 1–3; pl. 16, figs. 1 and 2), even though it has a similar style of ornament, has a much wider apical angle.

Inoceramus sp. aff. *bellyuensis* Reeside, 1923

Text-fig. 6

cf. 1923 *Inoceramus bellyuensis* Reeside 1923, p. 203, pl. 46, fig. 1.

Holotype. *Inoceramus bellyuensis* Reeside; USNM 32514 (LV); N of Bellvue, Colorado; Dakota Formation (late Albian–early Cenomanian?) (Reeside 1923, p. 203, pl. 46, fig. 1); by original designation.

Material. KG.1675.3 (ext.m., LV), from Adams Nunatak, Neptune Glacier, Alexander Island (71° 44' 00" S., 68° 33' 30" W.); KG.1606.16 (ext.m., ?LV) from near the top of a 600 m section on the north-westernmost



TEXT-FIG. 6. *Inoceramus* sp. aff. *bellyuensis* Reeside from the Fossil Bluff Formation of Alexander Island; rubber peel from an external mould of a left valve (KG.1675.3) from Adams Nunatak. $\times 0.75$.

nunatak in the Hyperion Nunataks group (approximately 5 km south of Dione Nunataks) ($71^{\circ} 58' 30''$ S., $68^{\circ} 59' 00''$ W.; text-fig. 2).

Occurrence. *I. bellvuensis* is probably late Albian–early Cenomanian in the Western Interior USA (Scott 1970; Kauffman *et al.* 1978). In the Far East of the Soviet Union, specimens referred to *I. cf. bellvuensis* by Pergament (1965, p. 22, pl. 4, figs. 1 and 2) occur in association with members of the *I. anglicus* group in Middle–Upper Albian strata.

Description. Specimen KG.1675.3 (text-fig. 6) had an original shell length in excess of 190 mm and a width of at least 140 mm. The outline is judged to have been roughly oval and the orientation slightly oblique; although the hinge is only partially preserved and there has been a certain amount of post-mortem distortion, it would appear that the blunt umbonal region was slightly opisthogynous. The apical angle of approximately 110° is formed between a comparatively short straight hinge and a long, gently convex anterior margin. The ventral margin is incomplete but the posterior is a long convex feature slightly more strongly curved than the anterior. One of the most striking features of this specimen is the extensive crescent-shape posterior wing which can be traced from the hinge to the ventral margin and has a maximum width in its central region of 50 mm (text-fig. 6). Whereas the umbonal and central regions of the valve are slightly inflated and bear strong, regular concentric ornament, the posterior wing is flat and bears very reduced ornament. The ribs of the former regions are up to 2 mm in width, well rounded in cross-section and separated by flat-floored interspaces of similar dimensions. As they pass on to the wing these ribs sweep strongly forwards and become very much finer (text-fig. 6).

Specimen KG.1606.16 is a less complete left valve with an original shell length in the 90–100 mm range. The ribbing over its umbonal region is similar to that of KG.1675.3 but ventrally some of the ribs fuse in the centre of the valve and have widths of up to 3 mm. There are again indications of a flattened, crescentic posterior wing (up to 18 mm in width) bearing very fine, strongly recurved ribs.

Remarks. The North American species *I. comancheanus* Cragin and *I. bellvuensis* Reeside have generally been regarded as less regularly ribbed members of the *I. anglicus* group (e.g. Reeside 1923; Imlay 1961; Pergament 1965). The latter species, which is the larger and more erect, is characterized by an extensive, flattened, almost smooth posterior region; specimen KG.1675.3 (text-fig. 6) is close to the holotype (Reeside 1923, pl. 46, fig. 1) but has, if anything, a slightly more oval outline. It is also apparent that at least some specimens of *I. bellvuensis* possess a terminal, pointed beak that rises slightly above the hinge and is gently prosogyrous (e.g. Reeside 1923, pl. 46, figs. 1 and 2; Kauffman *et al.* 1978, pl. 7, fig. 9).

Inoceramus sp. aff. *comancheanus* Cragin, 1895

Pl. 56, figs. 6, 8

cf. 1923 *Inoceramus comancheanus* Cragin; Reeside, p. 202, pl. 45, fig. 2.

cf. 1965 *Inoceramus* cf. *comancheanus* Cragin; Pergament, p. 27, pl. 9, figs. 1 and 2.

cf. 1978 '*Inoceramus*' *comancheanus* Cragin; Kauffman, Cobban and Eicher, p. XXIII.29 and pl. 7, fig. 4.

Lectotype. *Inoceramus comancheanus* Cragin; USNM 32686 (RV); 2–3 miles NE of Denison, Texas; Duck Creek Formation; designated by Kauffman *et al.* (1978, p. XXIII.29 and pl. 7, fig. 4).

Material. KG.1606.18 (int.m., RV); KG.1677.9, 1680.73 (both int.m., LV); KG.1735.11 (int.m. ?RV). Locality KG.1606—near the top of a 600 m section on the north-northwesternmost nunatak of the Hyperion Nunataks group ($71^{\circ} 58' 30''$ S., $68^{\circ} 59' 00''$ W.); KG.1677—ridge between Mt. Lassell and Mt. Phoebe ($71^{\circ} 45' 30''$ S., $68^{\circ} 49' 00''$ W.); KG.1680—lower levels, Keystone Cliffs ($71^{\circ} 33' 00''$ S., $68^{\circ} 15' 30''$ W.); KG.1735—small nunatak 0·6 km W of Mt. Lassell ($71^{\circ} 43' 30''$ S., $68^{\circ} 52' 00''$ W.) (text-fig. 2).

Occurrence. Associated fossils indicate an undifferentiated Albian age. *I. comancheanus* is Upper Albian–Lower Cenomanian.

Description. These four poorly preserved specimens have lengths in the region of 60 mm and widths of approximately 42 mm. They all have erect profiles, apical angles between 90° and 110° , and weak,

somewhat irregular concentric ornament. The anterior margin, which is long and comparatively straight, leads into moderately well-rounded ventral and posterior margins (e.g. Pl. 56, figs. 6 and 8). There are traces of a short, straight hinge and on specimen KG.1680.73 (Pl. 56, fig. 8) four rounded-rectangular ligament pits (measuring approximately 2.5×1.5 mm) are preserved. The valves are weakly inflated in the umbonal and anterior regions and compressed posteriorly. Narrow (< 1 mm), fairly regularly spaced concentric ribs cover the former of these regions but they become noticeably less distinct on the posterior (e.g. KG.1606.18; Pl. 56, fig. 6). In places the course of the ribs is irregular and on specimen KG.1680.73 (Pl. 56, fig. 8) they are slightly asymmetric about the growth axis.

Remarks. The slightly irregular style of ornament and flattened, faintly ribbed posterior region links these specimens with *I. comancheanus* Cragin. Although this species is usually regarded as an obliquely elongated one (e.g. Reeside 1923, pl. 45, figs. 1, 3, 4, 6, 7; Eigenheer and Sornay 1974, pl. 1, fig. a), it does include some more erect individuals (e.g. Reeside 1923, pl. 45, figs. 2 and 5; Kauffman *et al.* 1978, pl. 7, fig. 4). The density of ribbing on the Antarctic specimens is perhaps not so high as is usually encountered on *I. comancheanus* and there is also less of a tendency for individual ribs to split (Pl. 56, figs. 6 and 8). Nevertheless, Pergament (1965, p. 27, pl. 9, figs. 1 and 2) has illustrated two specimens of *I. cf. comancheanus* from the Middle–Upper Albian of the Soviet Far East with regular, more widely spaced ornament and these are comparable to the Alexander Island material.

Inoceramus carsoni group
Inoceramus carsoni M'Coy, 1865

Plate 57, figs. 1–3; Plate 58, fig. 2a, b; text-fig. 7

- 1865 *Inoceramus carsoni* M'Coy, p. 334.
- 1866 *Inoceramus carsoni* M'Coy; M'Coy, p. 50.
- 1867 *Inoceramus carsoni* M'Coy; M'Coy, p. 196.
- 1872 *Inoceramus pernooides* Etheridge (*non* Goldfuss), p. 343, pl. 22, fig. 3.
- 1892 *Inoceramus carsoni* M'Coy; Etheridge Jr., p. 463 (*non* pl. 25, figs. 9 and 10 = *I. sutherlandi*).
- 1892 *Inoceramus pernooides* Etheridge; Etheridge Jr., p. 464, pl. 25, figs. 7, 8, 12.
- 1892 *Inoceramus* sp. indet.; Etheridge Jr., pl. 21, fig. 19.
- 1901 *Inoceramus etheridgei* Etheridge Jr. (*non* Woods), p. 22.
- 1905 *Inoceramus etheridgei* Etheridge Jr., p. 13, pl. 2, figs. 7–9.
- 1928b *Inoceramus pictus* Sowerby; Heinz, p. 129 (*pars*).
- 1966 *Inoceramus carsoni* M'Coy; Ludbrook, p. 157, pl. 17, figs. 2 and 3.

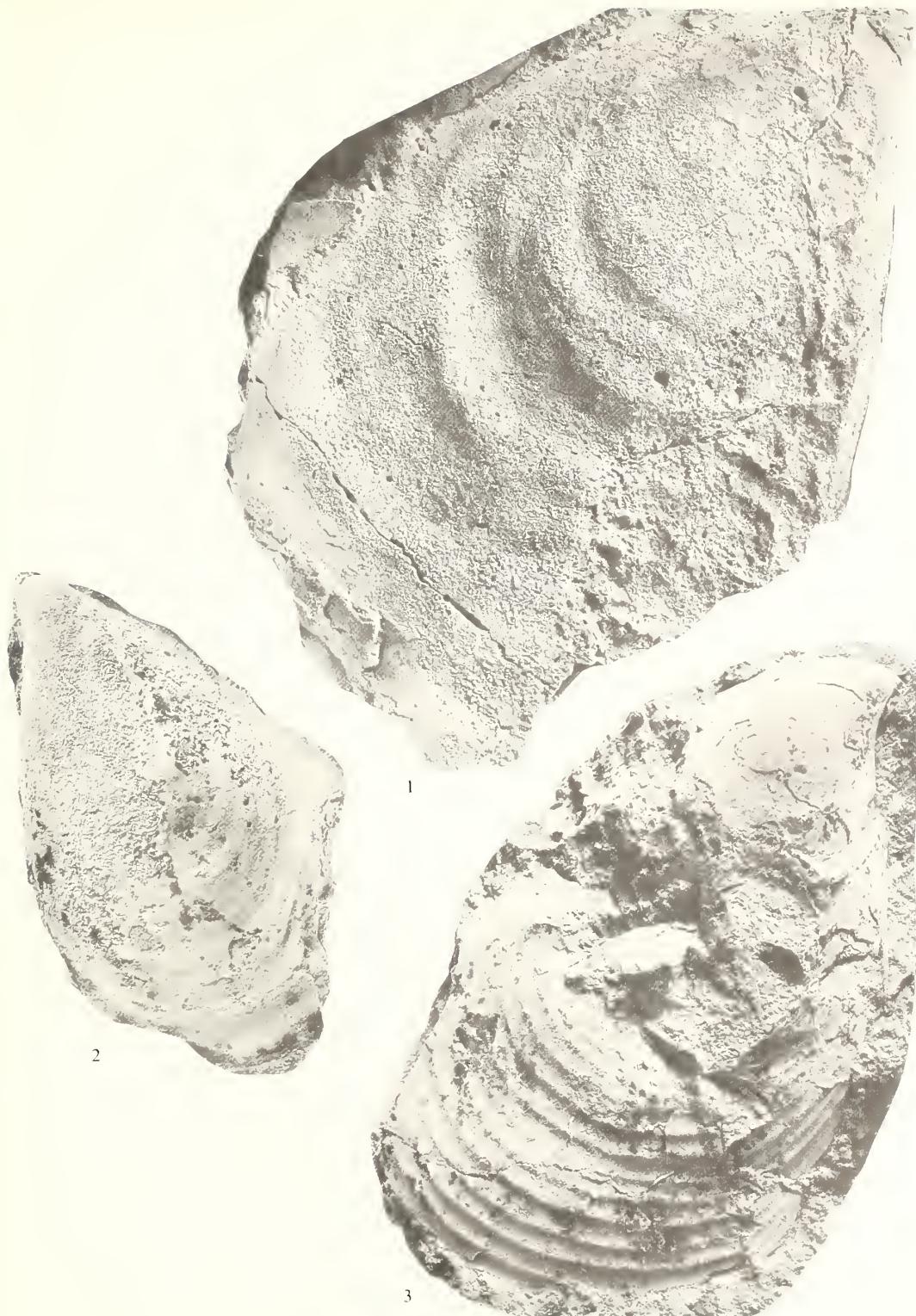
Lectotype. P.2712 (RV) (National Museum of Victoria): base of Walker's Table Mountain, W bank of Flinders River, Queensland; Albian; designated by Ludbrook (1966, p. 157 and pl. 17, fig. 3).

Material. D.8411.11, 12b, 13, 16, 8412.73, 8413.1, 8422.96c, 108, 114, 134–136, 8424.3 (all int.m., RV); D.8412.57 (int.m., ?RV); D.8411.12a, 14, 17, 37, 38, 58, 8412.59–61, 8422.66, 69, 74b, 75, 76, 80, 89, 95, 96a, b, 122–127, 131, 132, 137, 141, 8424.4a–c (all int.m., LV); D.8422.70 (ext.m., LV); D.8411.10, 15, 61, 66, 8412.62, 66, 68, 74, 75, 8413.3, 8422.64, 65, 71–74, 77, 78, 89, 97–99, 106, 115–117, 127–129 (probable juveniles). Localities D.8411 and 8413—reworked nodules in a breccio-conglomerate unit at 151 m in the composite 346 m section (D.8515–8518) at N end of Tumbledown Cliffs, NW James Ross Island ($64^{\circ} 03' 50''$ S., $58^{\circ} 26' 00''$ W.); D.8412–67–121 m interval in the same section; D.8422 and 8424—uppermost 121.5 m of a 483.5 m section (D.8521–8523) in Lost Valley, NW James Ross Island ($64^{\circ} 02' 20''$ S., $58^{\circ} 24' 10''$ W.) (text-figs. 3 and 11).

Occurrence. As for material; associated throughout both the Lost Valley and Tumbledown Cliffs sections with *Maccoyella* and *Ancellina* (? *A. hughendenensis*) (Etheridge). An upper Albian age inferred for the James Ross

EXPLANATION OF PLATE 57

Figs. 1–3. *Inoceramus carsoni* M'Coy from NW James Ross Island. 1, internal mould of right valve (D.8422.136); Lost Valley, $\times 0.75$. 2, internal mould of left valve (D.8422.123); same locality, $\times 1$. 3, internal mould of right valve (D.8413.1); northern Tumbledown Cliffs, $\times 1$.



CRAME, *Inoceramus* from Antarctica

Island material by analogy with Great Artesian Basin faunas (Ludbrook 1966; Day 1969), is compatible with the occurrence of the ammonite *Ptychoceras* at approximately the 466 m level in the Lost Valley section and presence of *B. concentrica* and a turrilitid ammonite in the upper levels of the Tumbledown Cliffs section (text-fig. 11).



TEXT-FIG. 7. *Inoceramus carsoni* M'Coy; internal mould of a large left valve (D.8422.132) from Lost Valley, NW James Ross Island. $\times 0.75$.

Description. Adult specimens have a mean shell length of 105.33 mm (S.D. = 39.36; range = 56–225; N = 46) and a mean width of 58.26 mm (S.D. = 21.56; range = 28–127; N = 46). With their narrow, pointed umbones and broader, rounded ventral regions, they have a distinctive mytiloid (or pernoid) outline, although it is noticeable that the orientation (with respect to a horizontal hinge) varies from sub-erect to strongly oblique (e.g. Pl. 57, figs. 1–3; text-fig. 7). In the more erect forms the long anterior margin varies from almost straight to a sigmoidal curve composed of an initial concave portion beneath the umbonal region and a subsequent long, gently convex portion (e.g. D.8413.1; Pl. 57, fig. 3). The posterodorsal margin in these types is usually slightly convex and the posteroventral and ventral margins well rounded. In the obliquely elongated forms the anterior region is usually divisible into an early short sigmoidal section and a later, and much longer, gently convex one (e.g. D.8411.12, 8422.132; Pl. 58, fig. 2a and text-fig. 7). The latter lies subparallel to the long, feebly convex posterodorsal border and there is a narrow, very convex ventral region. As might be expected the obliquely elongated specimens are consistently narrower than the more erect ones, and have W/L values well below 0.5. Some of the erect types are narrow too, but others show a pronounced trend towards ventral expansion (e.g. D.8422.136; Pl. 57, fig. 1); overall, a mean W/L value of 0.56 was obtained (S.D. = 9.35; range = 0.36–0.76; N = 46). The hinge, which is never well preserved, is short and straight and sometimes forms a low, oblique-angled wing at its junction with the posterodorsal margin (e.g. D.8411.12; Pl. 58, fig. 2a). The umbo rises sharply above the hinge, curves moderately strongly forwards and inwards, and terminates in a narrow, acuminate beak. The slim form of the whole umbonal region is reflected in the narrow apical angle ($\bar{x} = 62.85^\circ$; S.D. = 10.61; range = 46–92°; N = 47).

From the umbonal region, which is moderately inflated, there is typically a steep descent to the anterior margin and a slightly less sharp one to the posterodorsal border. There is also a smooth, even gradient to the ventral region, which, in the largest specimens, is almost flat (e.g. D.8422.132, 136; Pl. 57, fig. 1 and text-fig. 7). The basic ornament pattern is one of simple, narrow (< 1 mm) concentric rings (*Anwachsringen* of Heinz 1928a) that are remarkably regular in their course and distribution; very few tapering or anastomosing ribs are seen. The only significant variation in ornament style is in the rib density, with some specimens having interspaces of only slightly greater dimensions than the ribs (e.g. D.8411.12; Pl. 58, fig. 2b) and others exhibiting a spacing of 3–4 mm, especially in their ventral regions (e.g. D.8413.1; Pl. 57, fig. 3). Very occasionally, interspaces up to 10 mm in width developed, and on the largest specimen (D.8412.57), which has an estimated length of 215 mm, there is evidence of extensive disruption of coarsely spaced ribs in the ventral region. Some of the closely spaced ornament shows signs of being grouped on low primary folds into *Anwachsringreifen* (e.g. D.8411.12, 8422.132; Pl. 58, fig. 2b and text-fig. 7). Although no adult whole specimens were found, it is judged that this species was equivalve, or very nearly so.

Juvenile specimens tend to have more erect profiles than adults and less obviously protruding umbonal regions. Nevertheless, the umbones are still consistently narrow and at least some terminate in slender, pointed beaks. Many juveniles display closely spaced *Anwachsringen* ornament.

Remarks. The narrow, pointed and strongly projecting umbones of these specimens, together with their sub-erect to obliquely elongate form and simple, regular concentric ribs, readily link them to the Australian *I. carsoni* group (Table 1). In particular the comparatively low width to length ratio, shallow sigmoidal curve of many of the anterior margins, and predominance of fine, closely spaced ornament, suggest that they are closest to *I. carsoni* itself (cf. Etheridge 1872, pl. 22, fig. 3; Etheridge Jr. 1892, pl. 25, figs. 7, 8, 12; Etheridge Jr. 1905, pl. 2, figs. 7–9; Ludbrook 1966, pl. 17, figs. 2 and 3; Hill *et al.* (ed.) 1968, pl. K.V., fig. 11). However, it should be stressed here that the principal distinction between *I. carsoni* and *I. sutherlandi* is one of size, with the latter being broader, and usually longer, than the former (M'Coy 1865, 1866, 1867; Ludbrook 1966, p. 159). It is not always easy to separate large *carsoni* from small *sutherlandi* and the possibility that some of the Antarctic specimens may be at least transitional to *sutherlandi* should be born in mind. Specimen D.8411.12 (Pl. 58, fig. 2a), for example, has a higher than average ventral expansion for its length and approaches some small forms of *sutherlandi* (cf. Ludbrook 1966, pl. 17, figs. 4 and 6), whilst one of the largest specimens, D.8422.136 (Pl. 57, fig. 1), has a distinctive rounded-triangular form that may be better accommodated in *sutherlandi* than *carsoni* (cf. Ludbrook 1966, pl. 18, fig. 1). Re-examination of the extensive Australian material may yet show that these two species can be combined.

Inoceramus cf. sutherlandi M'Coy, 1865

Plate 58, fig. 1

- cf. 1865 *Inoceramus sutherlandi* M'Coy, p. 334.
- cf. 1866 *Inoceramus sutherlandi* M'Coy, p. 50.
- cf. 1867 *Inoceramus sutherlandi* M'Coy, p. 196.
- cf. 1872 *Inoceramus* allied to *I. problematicus* d'Orbigny; Etheridge, p. 344, pl. 22, fig. 4.
- cf. 1889 *Inoceramus maximus* Lumholtz, p. 367, fig.
- cf. 1892 *Inoceramus carsoni* M'Coy (pars); Etheridge Jr., p. 463, pl. 25, figs. 9 and 10.
- cf. 1892 *Inoceramus sutherlandi* M'Coy; Etheridge Jr., p. 463.
- cf. 1901 *Inoceramus maximus* Lumholtz; Etheridge Jr., p. 24.
- cf. 1924 *Inoceramus maximus* Lumholtz; Whitehouse, p. 128, pl. 7, figs. 1 and 2a, b.
- cf. 1928b *Inoceramus sutherlandi* M'Coy; Heinz, p. 144.
- cf. 1966 *Inoceramus sutherlandi* M'Coy; Ludbrook, p. 157, pl. 18, fig. 1.

Holotype. *Inoceramus sutherlandi* M'Coy; P.2170 (RV) (National Museum of Victoria); base of Walker's Table Mountain, Flinders River, Queensland; Albian; illustrated by Ludbrook (1966, pl. 18, fig. 1).

Material. D.8403.53–57: numerous large, incomplete valves contained within a series of mudstone concretions; approximately the 200 m level in the section measured at Kotick Point (D.8403, 64° 00' S., 58° 21' W.), NW James Ross Island (text-figs. 3 and 11).

Occurrence. As for material. Lithological correlations between the Kotick Point and Lost Valley sections indicate that *I. cf. sutherlandi* occurs approximately 100–150 m beneath the first appearance of *I. carsoni* (text-fig. 11). The specimens are associated with *Aucellina* and probable representatives of the ammonite *Silesites*. Both these types are present at approximately the 900–1000 m level in the Brandy Bay–Whisky Bay area (text-fig. 11) in Aptian–Albian beds that have also yielded *I. stoneleyi* sp. nov. and *Anopaea* sp. nov. β. *I. sutherlandi* is an Upper Albian species in Australia (Ludbrook 1966; Day 1969).

Description. There are indications that some of these specimens had lengths and widths in excess of 150 mm, and occasionally substantially more. The prismatic shell layer is in places up to 4 mm thick and it is readily apparent that the original species was a broad, thick-shelled form. Some idea of the original form can be obtained from three imperfect internal moulds of right valves (D.8403.53a, b and 57); these have estimated lengths of 144, 142, and 110 mm, corresponding widths of 105, 107, and 88 mm, and W/L values of 0.73, 0.75, and 0.80. Specimens D.8403.53a and b seem to have erect, rounded-triangular outlines, with narrow, pointed umbones and much broader, rounded ventral regions. They are moderately and evenly inflated and exhibit smooth, gentle descents from the centre of the valve to the ventral margins and slightly steeper ones from the umbonal region to the antero- and posterodorsal margins. The umbones, which are not sharply differentiated from the valve surface, curve gently forwards and inwards and appear to taper to a point.

Specimen D.8403.57 (Pl. 58, fig. 1) also has an erect profile but seems to have been considerably broader than the previous two. In addition, it is more strongly inflated in the umbonal region and there is an almost vertical descent from the latter to the anterodorsal margin. There is a shallower gradient in the opposite direction to the posterodorsal region, which is considerably extended by the presence of an extensive, flat, obtuse-angled wing. This feature is separated from the inflated umbo by a well-marked radial groove and bordered dorsally by the remnants of a long, straight hinge. On all three specimens there are only very faint traces of shallow, widely spaced, concentric folds.

Remarks. These broad, erect, almost smooth valves immediately invite comparison with medium-sized and large forms of *I. sutherlandi* (e.g. *I. maximus* Lumholtz 1889, fig. on p. 367; *I. carsoni* M'Coy in Etheridge Jr. 1892, pl. 25, fig. 9; *I. maximus* Lumholtz in Whitehouse 1924, p. 128, pl. 7, figs. 1 and 2; all of which = *I. sutherlandi* in Ludbrook 1966, p. 157). The holotype itself (Ludbrook 1966, pl. 18, fig. 1) is very similar in style to these specimens, although of somewhat larger dimensions (L = 187 mm, W = 130 mm). It should be noted, however, that the posterodorsal wing on specimen D.8403.57 (Pl. 58, fig. 1) is rather more clearly defined than that normally seen on *I. sutherlandi* and that the Antarctic specimens lack sigmoidally curved anterior margins. It is only possible, at present, to suggest a tentative assignment to *I. sutherlandi*.

Inoceramus of uncertain group affinity
Inoceramus annenkovensis sp. nov.

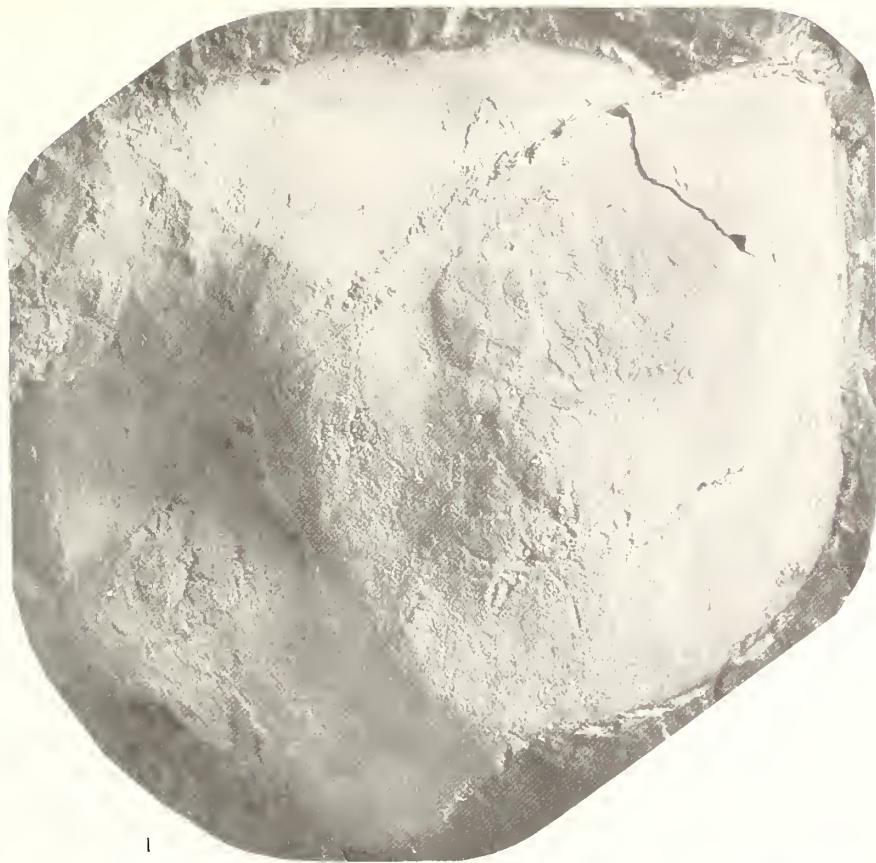
Text-fig. 8a–c

- 1947 *Inoceramus* sp.; Wilckens, p. 37, pl. 5, figs. 2–4.
?1982 *Inoceramus* sp.; Thomson, Tanner and Rex, p. 179, fig. 19.2g.

EXPLANATION OF PLATE 58

Fig. 1. *Inoceramus* cf. *sutherlandi* M'Coy. Internal mould of right valve (D.8403.57); Kotick Point, NW James Ross Island, × 1.

Fig. 2. *Inoceramus carsoni* M'Coy. a (left), internal mould of left valve (D.8411.12a); b (right), internal mould of right valve (with traces of shell material) (D.8411.12b); specimens from northern Tumbledown Cliffs, James Ross Island, × 1.



CRAME, *Inoceramus* from Antarctica

Type material. Holotype: M.1165.30c.1 (int.m., RV). Paratypes: M.1165.30c.2, 1165.32a (both int.m., RV); M.1165.32b (ext.m., ?RV); M.1165.32c (int.m., indet. V). Locality M.1165 occurs at approximately the 518·5 m level in the Lower Tuff Member, Annenkov Island ($54^{\circ} 29' S.$, $37^{\circ} 03' W.$; text-fig. 1) (Pettigrew 1981, fig. 5; Crame 1983a, figs. 6 and 7).

Occurrence. As for material. The Annenkov Island Formation is imprecisely dated in the interval Neocomian–Aptian (Thomson *et al.* 1982). The overlying species, *I. cf. heteropterus*, suggests a late Hauterivian age and the closely related species, *I. anomiaeformis*, a Hauterivian–Barremian one.

Derivation of name. From the occurrence on Annenkov Island.

Diagnosis. A small, weakly inflated *Inoceramus* with a rounded, sub-symmetrical outline; irregular and ill-defined ornament is mainly confined to the umbonal region; prominent ligamentat comprises a sequence of complex ligament pits; equivalence of valves undetermined.

Description. The holotype has a length and width of 44 mm and specimens M.1165.32b and c are of similar dimensions; M.1165.32a and M.1165.30c.2, however, are significantly smaller, with lengths and widths in the 20–25 mm range. The outline appears to be well rounded and the holotype is sub-symmetrical about an axis joining the midpoints of the dorsal and ventral margins (text-fig. 8a). All the valves are weakly inflated, with the only significant convexity occurring in the umbonal region. A steep descent from the latter towards the anterodorsal margin leads into a narrow, concave gutter which, on the holotype, has a length of approximately 10 mm and a maximum width of 3 mm. At its deepest directly beneath the umbo, this feature progressively diminishes in strength when traced in a ventral direction (text-fig. 8a).

The umbo is slightly prosogyrous and terminates in a narrow, pointed beak (text-fig. 8a). Although the tip of the latter must have been approximately level with the dorsal surface of the hinge, it was separated from it by another narrow, deep gutter (text-fig. 8a). This feature merges anteriorly with the anterodorsal gutter and also diminishes in intensity when traced in a direction away from the umbo (i.e. posteriorly). The ligamentat is well preserved on M.1165.30c.2 (text-fig. 8b) and partially preserved on M.1165.30c.1 and M.1165.32a. On the former two of these specimens it can clearly be seen to slope steeply inwards towards the plane of commissure between the valves; this indicates that the ligament area had a ‘V’ shaped cross-section. The ligamentat varies from 15–20 mm in length and 2–3 mm in depth and comprises somewhere between seven and ten ligament pits. These pits are complex features with essentially rounded-quadratae to rounded-rectangular outlines and at least two structural elements. On specimen M.1165.30c.2 these can be resolved into a simple, striated, square, or rectangle which alternates with a more deeply impressed figure ‘J’ (text-fig. 8b).



TEXT-FIG. 8. *Inoceramus annenkovensis* sp. nov. from Annenkov Island. a, holotype, internal mould of a right valve (M.1165.30c.1). b, internal mould of a right valve (M.1165.30c.2). c, latex peel from external mould of a probable right valve (M.1165.32b). All specimens $\times 1$.

The ornament on four of the specimens (M.1165.30c.1, 2; M.1165.32a, c) is extremely weak and irregular. Narrow, concentric ribs can be made out over the umbonal regions but these vary from acute to well rounded in profile and are noticeably irregular in their distribution (text-fig. 8a, b). On the holotype (M.1165.30c.1) and specimen M.1165.32c, this style of ornament rapidly diminishes away from the umbo and much of the ventral surface of the valve has an uneven, undulatory appearance (text-fig. 8a). Stronger ornament is preserved on the external mould (M.1165.32b), which, at first sight, seems to be readily distinguishable from the other material by its slightly posteriorly directed umbo (text-fig. 8c). Nevertheless, it is apparent that this specimen has been crushed and it very probably is a right valve with a slightly displaced umbo. Narrow, irregular ribs with acute summits on the earliest shell stages give way ventrally to closely spaced ones with rounded summits and widths in the 1–2 mm range. These ribs, which are slightly erratic in their course and variable in thickness, sweep strongly forwards to fuse along the anterior margin (text-fig. 8c). On the posterior and ventral margins there are indications of a marked reduction in rib intensity.

Specimen M.1165.32b is of particular importance as it provides a possible link with a hitherto unique specimen of *Inoceramus* previously described from the Lower Tuff Member of Annenkov Island (*Inoceramus* sp. of Thomson *et al.* 1982, p. 179, fig. 19.2g). This external mould of a whole specimen was collected loose from locality L on Lawther Knoll (Thomson *et al.* 1982, fig. 19.1) and thus probably came from a stratigraphic level equivalent to either station M.1165 or M.1196 (Pettigrew 1981, fig. 2). It has clearly defined, narrow, and closely spaced concentric ornament that shows some considerable similarities in style to that of specimen M.1165.32b (cf. text-fig. 8c and Thomson *et al.* 1982, fig. 19.2g). Although both valves appear to be mytiliform, it is apparent that this specimen has been crushed and that the anterior margins may have been foreshortened.

Remarks. The three small, rather poorly preserved specimens of *Inoceramus* sp. described by Wilckens (1947, p. 37, pl. 5, figs. 2–4) from the north-east coast of Annenkov Island most likely belong within this new species. Their outlines are slightly more elongate than those of the valves just described, but in degree of inflation and ornament pattern they agree closely. They were collected from a series of localities that are very close to Pettigrew's (1981, fig. 2) M.1153 and locality J of Thomson *et al.* (1982, table 19.1); thus, they probably originate from somewhere within the lowest 80 m of the Lower Tuff Member (Pettigrew 1981, fig. 5; Crame 1983a, figs. 6, 7). The only existing species with which *I. annenkovensis* sp. nov. could be compared is *I. anomiaeformis* Feruglio (1936, p. 29, pl. 2, figs. 1 and 2) from Tithonian-Lower Cretaceous strata of the Lago Argentino region of Patagonia. This species was based on the internal moulds of two rounded, almost symmetrical, right valves, the larger of which (Feruglio 1936, pl. 2, fig. 1) was subsequently designated the lectotype (Leanza 1967, p. 150). This specimen has a moderately inflated, centrally positioned umbo whose tip is turned very slightly forwards. Either side of the umbo are two small, subequal ears that are moderately well differentiated from the main disc of the valve. On both Feruglio's illustrated specimens there is an ornament of fine narrow concentric ribs that occasionally anastomose or intergrade. This style of ornament is close to that of *I. annenkovensis* sp. nov., but the sub-symmetrical form, distinct ears, and apparent lack of a prominent ligamentum probably serve to distinguish it as a separate species. Riccardi (1977, p. 222, fig. 2a) has described a single incomplete specimen of *I. aff. anomiaeformis* from the Springhill Formation of southern Patagonia which is notable for the more pointed, prosogyrous form of its umbones as well as its indistinct ornament. It may well provide a link with the Annenkov Island specimens but at present there is insufficient material available for this to be firmly established. In Patagonia, *I. anomiaeformis* occurs in association with the ammonite *Favrella* in beds that are generally assigned to the Hauterivian-Barremian (Riccardi 1970, 1977; Riccardi *et al.* 1971).

Genus *Birostrina* J. Sowerby, 1821

1864 *Actinoceramus* Meek.

Type species. *Inoceramus sulcatus* Parkinson, 1819, from the Gault (middle-upper Albian) of Folkestone, England; by subsequent designation (Cox 1969, p. N315).

Birostrina concentrica group
Birostrina concentrica Parkinson, 1819

Plate 59, figs. 1–11, 13

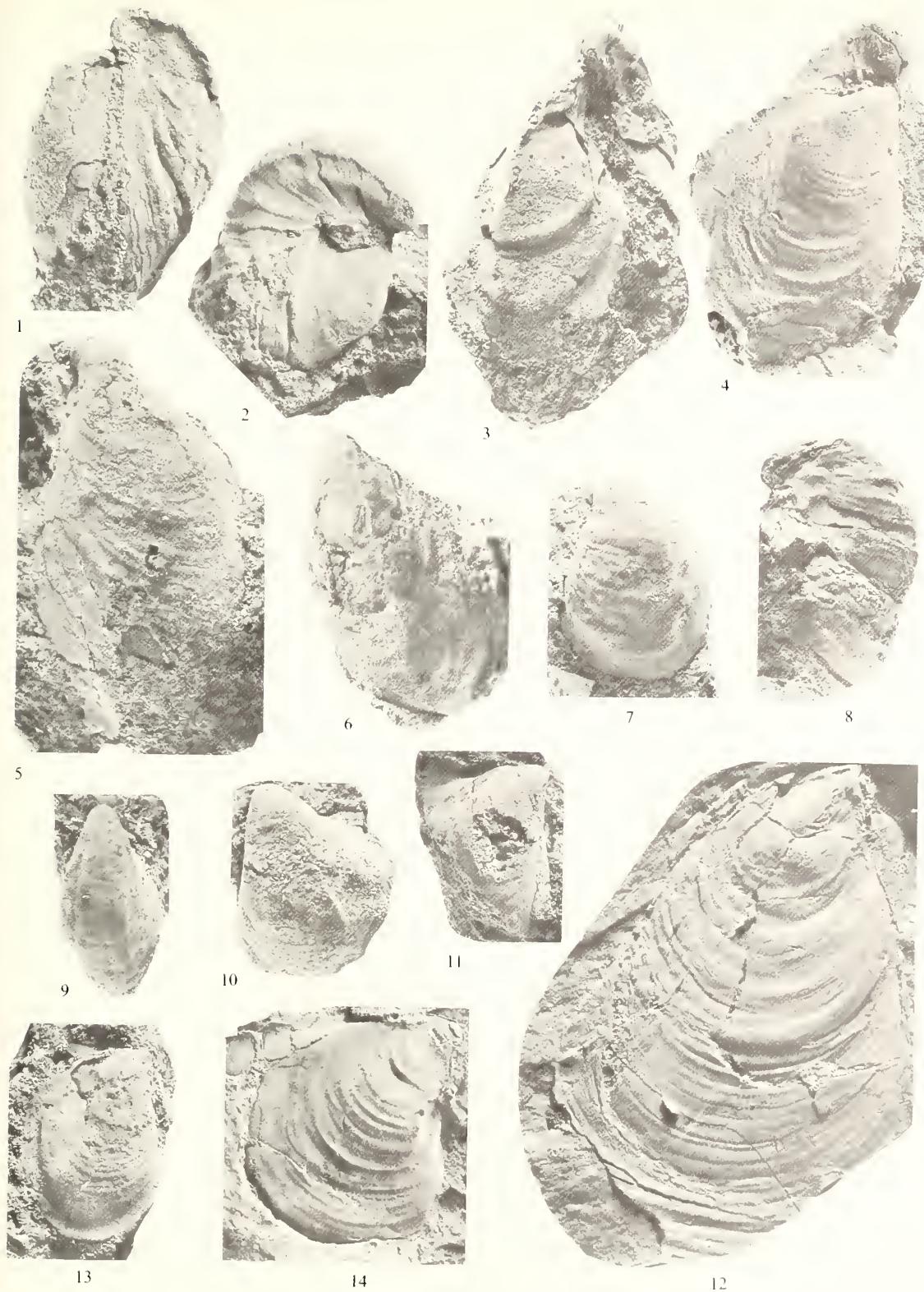
- 1819 *Inoceramus concentricus* Parkinson, p. 58, pl. 1, fig. 4.
 1821 *Inoceramus concentricus* Parkinson; J. Sowerby, p. 183, pl. 305, figs. 1–6.
 1846 *Inoceramus concentricus* J. Sowerby; d'Orbigny, p. 506, pl. 404, figs. 1–5.
 1876 *Inoceramus concentricus* Parkinson; Whiteaves, p. 79.
 1904 *Inoceramus concentricus* Parkinson; Airaghi, p. 183, fig. 2.
 ?1907 *Inoceramus volviunbonatus* Etheridge, p. 73, pl. 2, figs. 1–6.
 1911 *Inoceramus concentricus* Parkinson; Woods, p. 265, pl. 45, fig. 11; pl. 46, figs. 1–10; pl. 47, figs. 1 and 2.
 ?1911 *Inoceramus concentricus* Parkinson; Schlagintweit, p. 94.
 1917 *Inoceramus concentricus* Parkinson; Woods, p. 9, pl. 3, figs. 9 and 10.
 ?1921 *Inoceramus concentricus* Parkinson; Bonarelli and Nágera, p. 22, pl. 2, fig. 9.
 1930 *Inoceramus concentricus* Parkinson; Heinz, p. 683, fig. 1.
 1933 *Actinoceramus (Taenioceramus) concentricus* Parkinson; Heinz, p. 245.
 1936 *Inoceramus concentricus brasiliensis* (White); Maury, p. 107, pl. 8, figs. 9, 10, 13.
 ?1939 *Inoceramus concentricus* Parkinson var. *nipponicus* Nagao and Matsumoto, p. 267, pl. 24, fig. 2; pl. 25, figs. 1–6.
 ?1939 *Inoceramus concentricus* Parkinson var. *costatus* Nagao and Matsumoto, p. 270, pl. 24, figs. 1, 4, 5; pl. 27, fig. 2.
 ?1960 *Inoceramus (Actinoceramus) concentricus* Parkinson; Jones, p. 157, pl. 29, figs. 1 and 2.
 1962 *Inoceramus concentricus* Parkinson; Saveliev, p. 235, pl. 7, figs. 3–7 and pl. 8, figs. 1 and 2.
 ?1966 *Inoceramus* cf. *concentricus* Parkinson; Pergament, p. 30, pl. 1, figs. 1–4.
 ?1976 *Inoceramus (Inoceramus) concentricus* Parkinson; Chiplonkar and Badve, p. 199, pl. 1, fig. 5.
 1978a *Birostrina concentrica* (Parkinson) (*sensu lato*); Kauffman, p. IV.2.
 1978b *Birostrina concentrica* (Parkinson) (*sensu lato*); Kauffman, p. XVII.1 and pl. 1, figs. 1–3, 5–16, 18.
 1978 *Birostrina concentrica* (Parkinson) (*sensu lato*); Wiedmann and Kauffman, p. III.4, pl. 1, figs. 1–10 and 12–14.
 1980 *Inoceramus concentricus* Parkinson; Crame, p. 283, fig. 2a–c.

N.B. this synonymy comprises only those references that were useful in identifying the Antarctic material. No attempt has been made here to fully revise all the European and Japanese specimens of *I. concentricus*. Woods

EXPLANATION OF PLATE 59

Figs. 1–11, 13. *Birostrina concentrica* (Parkinson) from James Ross and Dundee Islands. 1, anterior view of internal mould of a whole specimen (D.8228.12); Brandy Bay. 2, posterodorsal view of internal mould of a whole specimen (D.8228.5); umbonal region of the left valve slightly displaced across that of the right; same locality. 3, internal mould of a whole specimen (D.8413.58) that bears traces of a thin prismatic shell layer; viewed from the right side; northern Tumbledown Cliffs. 4, internal mould of a whole specimen (D.3862.6), viewed from the right side; Welchness (Dundee Island). 5, internal mould of left valve (D.8227.5); Whisky Bay. 6, internal mould of left valve (D.8214.13); small gully approximately 2 km E of Stoneley Point. 7, internal mould of left valve (D.8214.31); same locality. 8, left valve of specimen D.8228.5 viewed from the anterior. 9, internal mould of left valve (D.8413.42); northern end of Tumbledown Cliffs. 10, internal mould of left valve (D.8413.38); same locality. 11, internal mould of right valve (D.8214.29); small gully approximately 2 km E of Stoneley Point. 13, internal mould (with traces of prismatic shell) of right valve (D.8215.11); gully approximately 3 km ENE of Stoneley Point. All the specimens are from NW James Ross Island, except for fig. 4 which is from western Dundee Island. All $\times 1$, except for fig. 1 which is $\times 1.5$.

Figs. 12 and 14. *Birostrina?* cf. *concentrica* (Parkinson) from the Fossil Bluff Formation of Alexander Island. 12, rubber peel from external mould of right valve (KG.1680.74); Keystone Cliffs. 14, internal mould (with traces of shell material) of small right valve (KG.2801.250); northern end of Succession Cliffs. Both specimens $\times 1$.

CRAME, *Birostrina* from Antarctica

(1911) and Saveliev (1962) contain references to a number of early European works not cited here and Kauffmann (1977) gives a preliminary revision of the Japanese forms.

Type specimen. *Inoceramus concentricus* Parkinson (1819, p. 58, pl. 1, fig. 4); by monotypy.

Material. D.3862.6, 8215.3, 28, 8227.6, 8, 8228.5, 10, 12, 14, 20, 8413.58, 60, 8414.4, 5, 8431.97, 98, 8531.1 (all int.m., WS); D.8214.3, 5, 6, 8, 13, 30, 31, 37, 39, 40, 44, 45, 48, 50, 8215.1, 4, 9, 12–14, 16, 25, 8227.5, 10, 12, 8228.2, 3, 7, 13, 16, 19, 8413.35–42, 59, 8414.6, 8531.5–11, BR.151.2 (all int.m., LV); D.8414.8, 8431.95 (int.m., ?LV); D.8214.4, 7, 9, 12, 14–17, 20, 22, 26–29, 32, 33, 42, 46, 51, 52, 8215.2, 7, 11, 19, 20, 23, 8227.11, 13, 8228.6, 11, 17, 18, 8344.1, 3, 8413.43, 44, 8431.96, 8531.2–4, BR.151.1, 4, 5a, b, 6, 10 (all int.m., RV); D.8414.7 (int.m., ?RV); D.8413.69 (ext.m., RV). Many of the internal moulds bear traces of a thin outer shell layer. All the following localities (except for D.3862 and BR.151) are on NW James Ross Island (text-fig. 3): D.8214—small gully approx. 2 km E of Stoneley Pt. ($63^{\circ} 52' S.$, $58^{\circ} 04' 30'' W.$); D.8215—small gully approx. 4 km ENE of Stoneley Pt. ($63^{\circ} 51' 15'' S.$, $58^{\circ} 03' 20'' W.$); D.8227—NE shore of Whisky Bay ($63^{\circ} 52' 40'' S.$, $58^{\circ} 06' 55'' W.$); D.8228—SW shore of Brandy Bay ($63^{\circ} 51' S.$, $58^{\circ} 01' W.$); D.8344—2 km E of Bibby Pt. ($63^{\circ} 48' 20'' S.$, $57^{\circ} 54' 30'' W.$); D.8413—N of Tumbledown Cliffs ($64^{\circ} 03' 00'' S.$, $58^{\circ} 24' 30'' W.$); D.8431/8531—S end of Tumbledown Cliffs ($64^{\circ} 05' 00'' S.$, $58^{\circ} 26' 40'' W.$); D.3862/BR.151—moraine ridge, Welchness, Dundee Island ($63^{\circ} 29' S.$, $56^{\circ} 15' W.$) (text-fig. 1).

Occurrence. As for material. On James Ross Island, *B. concentrica* is associated with an Albian-Cenomanian turritiid ammonite in the northern Tumbledown Cliffs assemblage (D.8413) and at locality D.8414 (text-fig. 3). In the combined section for western James Ross Island (text-fig. 11) it occurs 125 m above the highest occurrence of *I. carsoni* and approximately 400 m above the *I. stoneleyi* sp. nov.—*Silesites* assemblage of the Whisky Bay-Brandy Bay area.

The Middle–Upper Albian age range established by Woods (1911, 1912) for *B. concentrica* has been widely accepted by other authors (e.g. Pergament 1981; Tröger 1981). However, the possibility that this species both extends into the top of the Lower Albian and the base of the Lower Cenomanian should not be discounted (Kauffman 1978a, fig. 1; Sornay 1981). If forms such as *I. concentricus nipponicus* and *I. cf. concentricus* (Pergament 1966) prove to be true members of the *B. concentrica* group (see Table 1), then extension of the range into well within the Cenomanian will be established. There is also a possibility of Cenomanian representatives of '*I. concentricus*' in New Zealand (see below). Other definite Southern Hemisphere occurrences of *B. concentrica* are in South Africa (Middle–Upper Albian of Zululand; Heinz 1930; Kauffman 1978b) and Brazil (?Middle–Upper Albian; Maury 1936), whilst there are further possible records from the Albian of Argentinian Patagonia (Bonarelli and Nágera 1921) and the Albian of Madagascar (Heinz 1933).

Description. The James Ross Island specimens agree closely with those previously described from Dundee Island (Crame 1980, p. 283). They are comparatively small, with the left valves having a mean shell length of 34·48 mm (S.D. = 8·58; range = 16–56; N = 42) and the right valves 26·88 mm (S.D. = 7·49; range = 11–50; N = 49). These respective mean shell lengths are significantly different (Student's *t*-test, $p < 0\cdot001$) and attest to the strongly gryphaeoid form of the species. This is clearly exhibited by the whole specimens, each of which has a left valve with an inflated umbonal region that towers over that of the right (e.g. D.3862.6, 8228.5, 12, 8413.58; Pl. 59, figs. 1–4). The larger volume of material from James Ross Island enables the range of variation of this biostratigraphically important species to be more fully assessed.

The outline of the left valve is variable and at least three main types can be made out: obliquely elongated, elongate-pyriform, and rounded-quadrata. The first of these is the most strongly asymmetric, possessing a comparatively narrow, pointed umbonal region that slopes gently forwards (e.g. D.8214.13 and 8227.5; Pl. 59, figs. 5 and 6); the second is more upright and pear- (or tear-)shaped (e.g. D.8214.31, 8228.5, 12; Pl. 59, figs. 1, 7, 8); and the third is similar to the second but considerably squatter (e.g. D.8413.38; Pl. 59, fig. 10). No rigid morphologic or stratigraphic divisions can be placed between these types and it is almost certain that they intergrade. In profile, all the left valves are strongly convex (i.e. incurved) and in lateral view the maximum degree of inflation can be seen to lie in the central regions of the valve and along the growth axis. The form of the central region varies from a broad, shallow dome, with only moderate descents on either side (e.g. D.8227.5; Pl. 59, fig. 5) to a narrow, strongly convex ridge that is bounded laterally by extremely steep drop-offs (e.g. D.8228.5 and 8413.42; Pl. 59, figs. 2, 8, 9). A particularly noticeable feature of all the left valves is the almost

vertical descent along the anterior margin; this forms a prominent flat, smooth shelf of anything up to 15 mm in height. There is a shallower descent to the ventral and posterior margins and at the posterodorsal extremity a small flange-like wing is delimited by a sharp break in slope on one side and the short, straight hinge on the other. The strongly incurved, slightly to strongly prosogyrous umbo rises above the hingeline by anything up to 11 mm and frequently tapers to a beak of less than 2 mm width. The apical angle generally lies in the 85°–95° range.

The smaller right valve of *B. concentrica* has an erect outline and is typically somewhat longer than wide (\bar{x} W/L = 0.71; S.D. = 0.12; range = 0.48–1.08; N = 61) (e.g. D.8215.11; Pl. 59, fig. 13); there are, however, both occasional narrow, elongate forms and squatter, rounded ones. The hinge typically forms an apical angle with the anterior margin of between 90° and 110°. The latter feature is straight to very slightly concave and usually measures at least half the total shell length. It leads into well-rounded anteroventral, ventral, and posteroventral margins, but the posterior margin proper is less steeply curved (Pl. 59, fig. 13). The small, prosogyrous umbo, which is not nearly so prominent as that on the left valve, does not rise above the hingeline and a narrow posterodorsal wing is indistinctly recessed. The principal mode of variation in the right valve is in its degree of inflation. Normally, they are moderately and evenly inflated, with smooth, regular descents occurring to the valve margins (e.g. D.8215.11; Pl. 59, fig. 13). Nevertheless, some specimens are more strongly convex, with the maximum degree of inflation being concentrated along the growth axis (e.g. D.3862.6 and 8228.5; Pl. 59, figs. 2 and 4). There are even some indications of this variation being carried to the extreme form that has a convex ridge extending from the beak to the ventral margin with very steep drop-offs on either side (e.g. D.8214.29; Pl. 59, fig. 11). Such a form is similar to that described by Woods (1911, p. 267, pl. 46, figs. 8–10) in some specimens from the Blackdown Greensand and Hunstanton Red Limestone of England.

Owing to the poor state of preservation of many of the moulds the precise nature of the original ornament is difficult to define. Whenever traces of concentric ribs are present, on either valve, they always appear to be simple, narrow, regular, and closely spaced. Typically less than 1 mm wide and separated by interspaces of slightly greater dimensions, they may have either sharp or rounded summits (e.g. D.3862.6, 8214.31, 8227.5; Pl. 59, figs. 4, 5, 7). On some valves slightly coarser secondary ribs, with a 3–10 mm spacing, appear to be superimposed on the primary ones (e.g. D.8228.5 and 8413.58; Pl. 59, figs. 2, 3, 8) and there are some indications too, of both occasional growth pauses and irregularities.

A small number of internal moulds bear traces of up to five radial riblets (e.g. D.8214.27, 8215.25, 8228.13, 8413.38, 42; Pl. 59, figs. 9, 10). These have a maximum width of 1 mm and seem to radiate from the umbo to the ventral margin; however, it should be emphasized that they are nearly all weak and discontinuous. Some of the interspaces between them are slightly concave and as such can be described as sulci.

Remarks. Kauffman (1978a) suggested that this highly variable species may eventually be split into as many as six subspecies, but these have yet to be formally described. The stratigraphic control on the present collections does not permit such an approach here, and all the material is referred to a single taxonomic category.

Small to medium-sized elongate-pyriform whole specimens (e.g. D.3862.6, 8228.10, 20, 8413.58, 60; Pl. 59, figs. 3 and 4) as well as more obliquely elongated forms (e.g. D.8214.13 and 8227.5; Pl. 59, figs. 5 and 6) compare well with the majority of European specimens illustrated by Parkinson (1819, pl. 1, fig. 4), J. Sowerby (1821, pl. 305, figs. 1–6), Woods (1911, pl. 46, figs. 1–10; pl. 47, figs. 1 and 2) and Saveliev (1962, pl. 7, figs. 3–7; pl. 8, figs. 1 and 2). It is worth noting too that the latter two works illustrate collections with a range of variation comparable in scale, if not in precise detail, with the Antarctic material. The tendency towards a more pyriform outline of specimens such as D.8214.31 and 8228.5 (Pl. 59, figs. 2, 7, 8) can be matched to that of Woods's (1911, pl. 45, fig. 11) largest illustrated specimen and, probably, to Maury's (1936, pl. 8, figs. 9 and 10) subspecies *I. concentricus brasiliensis* (White) too.

The squatter, more rounded-quadrata Antarctic left valves (e.g. D.8413.38, Pl. 59, fig. 10) fit in less

well with the traditional European concepts of *B. concentrica*. Nevertheless, they appear to grade into obliquely elongated forms and Kauffman (1978a, b; Wiedmann and Kauffman 1978) has shown how they can also be distinguished in both European and South African collections. Types such as specimen D.8413.38 closely resemble '*B. concentrica* n. subsp. 2' and associated forms from Spain (cf. Pl. 59, fig. 10 and Wiedmann and Kauffman 1978, pl. 1, figs. 3–6, 8–10, 13), and *B. concentrica brasiliensis* and '*B. concentrica* n. subsp. C' from South Africa (Kauffman 1978b, pl. 1, figs. 11, 16, 18). Kauffman's (1978a) '*B. concentrica* n. subsp. A', which is characterized by an anterior sulcus and a few coarse, widely spaced ribs, has no direct counterparts in the Antarctic collections. The European and South Africa '*B. concentrica* n. subsp. B', with its slanting and strongly projecting umbo (e.g. Kauffman 1978b, pl. 1, figs. 5 and 10), also seems to be missing, and it would appear that the bulk of the Antarctic specimens fall within Kauffman's (1978a, b) concepts of *B. concentrica concentrica* and the more quadrate forms, *B. concentrica brasiliensis* and '*B. n.* subsp. C'.

Birostrina? cf. *concentrica* Parkinson, 1819

Plate 59, figs. 12, 14; Plate 60, figs. 1–4; Plate 61, figs. 1–4

- cf. 1846 *Inoceramus concentricus* J. Sowerby; d'Orbigny, p. 506, pl. 404, figs. 1 and 2.
- cf. 1911 *Inoceramus concentricus* Parkinson; Woods, p. 265, pl. 45, fig. 11.
- cf. 1914 *Inoceramus aff. concentricus* Parkinson; Spangler, p. 235, pl. 15, fig. 18.
- cf. 1917 *Inoceramus concentricus* Parkinson; Woods, p. 9, pl. 3, figs. 9 and 10.
- cf. 1936 *Inoceramus concentricus brasiliensis* (White); Maury, p. 107, pl. 8, figs. 9 and 10.
- 1972 *Inoceramus aff. concentricus* Parkinson; Thomson and Willey, p. 13, figs. 9a and 10.

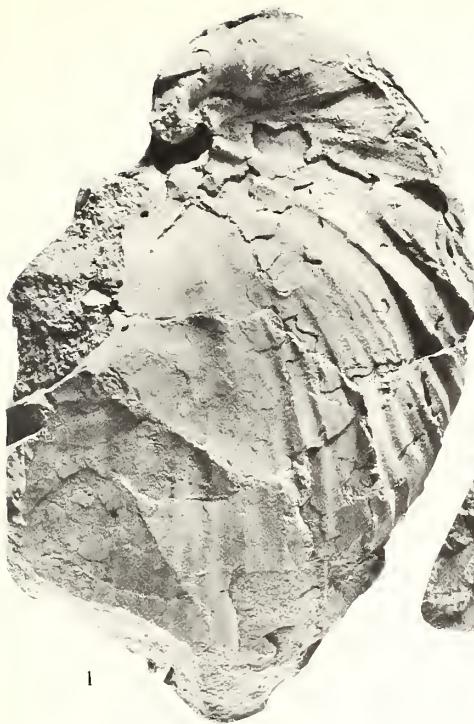
Material. KG.1674.7 (int.m., WS); KG.103.181, 1609.16, 1675.2, 1681.6, 1721.23, 1746.7, 9, 1748.24, 2801.158, 182, 183, 206, 215, 218, 239, 262 (all int.m., LV); KG.1674.8 (?int.m., LV); KG.1663.35, 2801.180, 223 (all ext.m., LV); KG.103.158, 1674.6, 9, 1677.1, 1746.8, 2801.185, 207, 250, 256 (all int.m., RV); KG.1677.8, 1726.9b (both ?int.m., RV); KG.1677.3, 1674.5, 1680.74, 2801.150, 184, 214, 216 (all ext.m., RV). All the following localities are within the Fossil Bluff Formation of Alexander Island (text-fig. 2): KG.103/1681—upper levels, Waitabit Cliffs ($71^{\circ} 30' 00''$ S., $68^{\circ} 14' 30''$ W.); KG.1609—westernmost nunatak, Hyperion Nunataks group ($72^{\circ} 02' 30''$ S., $68^{\circ} 55' 00''$ W.); KG.1663—W side, Stephenson Nunatak ($72^{\circ} 08' 30''$ S., $69^{\circ} 09' 00''$ W.); KG.1667—small nunatak immediately to NW Tethys Nunatak ($72^{\circ} 08' 00''$ S., $68^{\circ} 59' 30''$ W.); KG.1674—small nunatak approximately 2 km SW Adams Nunatak ($71^{\circ} 08' 00''$ S., $68^{\circ} 38' 45''$ W.); KG.1675—Adams Nunatak, Neptune Glacier ($71^{\circ} 44' 00''$ S., $68^{\circ} 33' 00''$ W.); KG.1677—ridge between Mt. Lassell and Mt. Phoebe ($71^{\circ} 45' 30''$ S., $68^{\circ} 49' 00''$ W.); KG.1680—lower levels, Keystone Cliffs ($71^{\circ} 33' 00''$ S., $68^{\circ} 15' 30''$ W.); KG.1721—ridge running E of Mt. Phoebe ($71^{\circ} 47' 00''$ S., $68^{\circ} 43' 45''$ W.); KG.1726—ridge running SSW from Mt. Phoebe ($71^{\circ} 48' 30''$ S., $68^{\circ} 48' 00''$ W.); KG.1746/1748/2801—upper levels, North Succession Cliffs ($71^{\circ} 08' 30''$ S., $68^{\circ} 17' 30''$ W.).

Occurrence. As for material. The age in the upper Waitabit Cliffs and lower Keystone Cliffs is almost certainly Albian (?Middle–Upper Albian) (text-fig. 10) (Willey 1972; Thomson 1974; Taylor *et al.* 1979); however, as previously mentioned, the presence of some ammonites with older (?Barremian) affinities at Waitabit Cliffs (Thomson 1983) has yet to be fully explained.

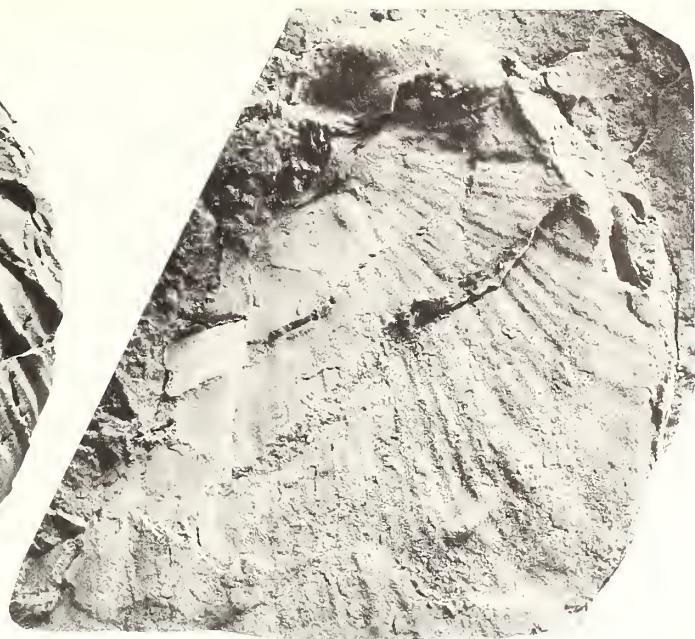
Description. These specimens show all the typical features of *B. concentrica*, except that they are somewhat larger. The respective mean shell lengths of the left and right valves, for example, are 89.77 mm (S.D. = 12.64; range = 68–114; N = 13) and 84.80 mm (S.D. = 19.31; range = 54–118; N = 10), and these values are significantly greater (Student's *t*-test, *p* < 0.001) than the corresponding

EXPLANATION OF PLATE 60

Figs. 1–4. *Birostrina?* cf. *concentrica* (Parkinson) from the Fossil Bluff Formation of Alexander Island. 1, anterior view of internal mould of left valve (KG.1674.8); some prismatic shell material visible; small nunatak approximately 2 km SW of Adams Nunatak. 2, anterior view of internal mould of incomplete left valve (KG.2801.262); northern end of Succession Cliffs. 3, exterior view of the left valve of a whole specimen (KG.1674.7); small nunatak approximately 2 km SW of Adams Nunatak. 4, the same specimen, which is an internal mould, viewed from the right. All specimens $\times 1$.



1



2



3



4

CRAME, *Birostrina?* from Antarctica

ones (34.48 and 26.88) from the James Ross Island specimens. The foregoing measurements suggest that the degree of inequality between the valves may not be so great in the Alexander Island material but it should be emphasized that they are nearly all incomplete single valves. The one articulated specimen (KG.1674.7; Pl. 60, figs. 3 and 4) has a left valve of 100 mm length and a right of 76 mm and it is likely that this scale of difference may be close to the true value for the species.

The left valves consistently have obliquely oval to pyriform outlines and prominent, strongly enrolled umbones (e.g. KG.103.181, 1674.7, and 8, 2801.262; Pl. 60, figs. 1-3 and Pl. 61, fig. 2). They were moderately to strongly inflated, with the maximum convexity occurring in the central region along the growth axis. From the latter there was a very steep descent to the anterior margin and a somewhat gentler one towards the posterior. One specimen, however, is noticeable for its very steep descents to both the anterior and posterior margins; this gives it a markedly 'humpback' cross-profile (KG.1681.6; Pl. 61, figs. 3 and 4). The basic ornament pattern preserved on internal moulds of left valves is one of narrow (generally < 1 mm in width) closely and regularly arranged concentric ribs (e.g. KG.1674.7 and 2801.262; Pl. 60, figs. 2 and 3). On some specimens there is evidence of extremely fine ribbing on the early stages (e.g. KG.1674.7; Pl. 60, fig. 3), whilst on others somewhat coarser ones develop towards the ventral margin (e.g. KG.103.181; Pl. 61, fig. 2). There are also indications that secondary stronger ribs developed in certain specimens (e.g. KG.1674.8; Pl. 60, fig. 1), in a manner similar to that described for specimens D.8228.5 and 8413.58 (Pl. 59, figs. 2, 3, 8) from James Ross Island. These ribs have approximately 3-7 mm spacings and their sharper profiles rise significantly higher than those of the primary ribs. A small number of the internal moulds are almost smooth, their surfaces being broken only by occasional shallow concentric depressions which may indicate growth pauses (e.g. KG.1681.6; Pl. 61, figs. 3 and 4).

The right valve has an erect outline and a moderately to strongly prosogyrous umbo that scarcely rises above the level of the hingeline (e.g. KG.1674.7, 1680.74, 2801.250; Pl. 59, figs. 12, 14 and Pl. 60, fig. 4). Where preserved the anterior margin is seen to be a nearly straight feature that is equal in length to at least half the total valve length. It normally subtends an angle close to a right angle with the hinge, although some compressed specimens have values considerably greater than this (e.g. KG.103.158; Pl. 61, fig. 1). The anterior margin leads into well-rounded ventral and posteroventral margins but the posterodorsal border is somewhat straighter. The degree of inflation is considerably less than that of the left valve, with most of it being concentrated in the umbonal and central regions; the descents to the valve margins are correspondingly gentler, with only the anterior edge being sharply defined. Specimen KG.1674.7 (Pl. 60, fig. 4) has a narrow, smooth flange running along the anterior margin which tapers from approximately 9 mm in width at the ventral end to less than 3 mm beneath the umbo. This feature could be interpreted as an anterior wing but it is also possible that it represents a near vertical anterior edge that has collapsed on compression. The same specimen bears traces of a narrow, tapering posterodorsal wing but this is not a prominent characteristic of the right valve.

One right valve, KG.1674.6, is considerably more inflated than all the others. This inflation is concentrated in the dorsal half of the valve, especially along the growth axis. There are steep descents to both the antero- and posterodorsal margins and the overall form of the valve is similar to that of specimen D.8214.29 (Pl. 59, fig. 11) from James Ross Island. The fine regular ornament of the left valve is generally repeated on the right (e.g. KG.1680.74 and 2801.250; Pl. 59, figs. 12 and 14). There are occasional interruptions to the basic pattern caused by growth pauses or superimposition of the fine ribs on low primary folds (e.g. KG.1680.74; Pl. 59, fig. 12). Both rib width (which is generally

EXPLANATION OF PLATE 61

Figs. 1-4. *Birostrina?* cf. *concentrica* (Parkinson) from the Fossil Bluff Formation of Alexander Island. 1, internal mould of possible right valve (KG.103.158); Waitabit Cliffs. 2, anterodorsal view of internal mould of incomplete left valve (KG.103.181); same locality. 3, exterior view of internal mould of large left valve (KG.1681.6); same locality. 4, anterior view of same specimen. All specimens $\times 1$.



CRAME, *Birostrina?* from Antarctica

<1·5 mm) and interspace width increase slightly towards the ventral margin. Notable variants include types such as specimen KG.103.158 (Pl. 61, fig. 1), which has acute, more widely spaced ribs that show some tendency to anastomose, and KG.1674.6, which is an almost smooth form bearing traces of fine radial striae. No obvious radial folds or sulci were observed on either valve.

Remarks. The strongly gryphaeoid form and regular concentric ornament link these specimens with *B. concentrica*. However, as their mean dimensions are considerably greater than those normally associated with this species, and their preservation rather poor, they are only tentatively assigned to it. There is a fairly close correspondence with the few known large forms of *B. concentrica* from Europe and Brazil (e.g. d'Orbigny 1846, pl. 404, figs. 1 and 2; Woods 1911, pl. 45, fig. 11; Maury 1936, pl. 8, figs. 9 and 10). The correspondence is less precise with the large specimens of '*I. concentricus*' from New Zealand (Woods 1917, pl. 3, figs. 9 and 10) as the latter have somewhat broader and more symmetrical left valves. Some specimens currently assigned to the New Zealand species, *I. warakius* Wellman (see Speden 1977, figs. 10–16), may well be a better match for the Antarctic material, but this taxon is currently in need of extensive revision. It certainly seems to possess a strongly graphaeoid form and probably forms part of a lineage of '*I. concentricus*'-like forms which span the Albian–Cenomanian Motuan and Ngaterian stages. A left valve described by Spengler (1914, pl. 15, fig. 18) as *I. aff. concentricus* from the Lower Utatur Group of southern India shows some similarities to the Antarctic specimens but is less strongly inflated. In view of their size and apparent lack of radial ornament, all the foregoing large specimens can only be tentatively linked with *Birostrina*.

The affinity of specimen KG.103.158 (Pl. 61, fig. 1) to *B.?* cf. *concentrica* must be held in some doubt as it is both considerably broader (apical angle 128°) than any other right valve and bears sharper, more irregular ornament. It could just be closer to certain members of the *I. anglicus* group. There are some doubts too about the allegiance of specimen KG.1681.6 (Pl. 61, figs. 3 and 4), whose strongly inflated profile and almost smooth surface could be matched to Cenomanian species such as *I. corpulentus* from Canada (e.g. Warren and Stelck 1940, pl. 4, figs. 4–6) and *I. redundus* from the Soviet Far East (e.g. Pergament 1966, p. 40, pl. 16, fig. 1a; pl. 18, figs. 1a, b and 2a) (see Table 1). However, no other Cenomanian fossils have yet been recognized in the Fossil Bluff Formation.

Genus *Anopaea* Eichwald, 1861

Type species. *Inoceramus lobatus* Auerbach and Frears (1846, p. 492, pl. 7, figs. 1–3) = *I. brachovi* Rouillier (1849, p. 439), from the Upper Jurassic of the Ural Mts., USSR; by monotypy (Cox 1969, p. N317).

Anopaea trapezoidalis (Thomson and Willey, 1972)

Text-fig. 9a

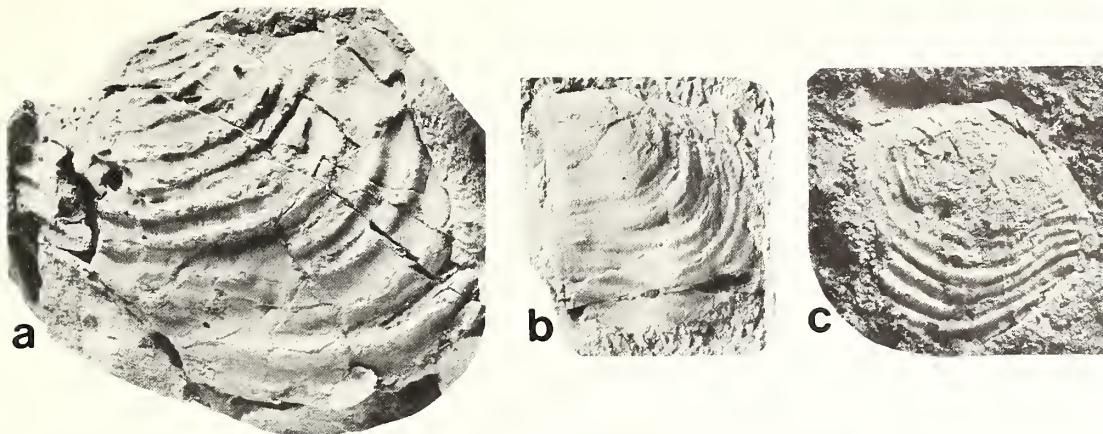
- 1972 'Inoceramus' *trapezoidalis* Thomson and Willey, p. 11, fig. 8a–b.
 1981 *Anopaea trapezoidalis* (Thomson and Willey); Crame, p. 215, pl. 2, figs. a–d.

Holotype. KG.18.31a (int.m., LV) from the Fossil Bluff Formation of Alexander Island; illustrated in Thomson and Willey (1972, fig. 8a) and Crame (1981, pl. 2, fig. a); by original designation.

Additional material. KG.2880.225, 293, 296 (all int.m., LV); KG.1745.10 (ext.m., LV); KG.1745.11 (ext.m., RV). Both localities are in the Fossil Bluff Formation of Alexander Island (text-fig. 2): KG.1745—locality U, 2 km NW of Fossil Bluff (71° 18' S., 68° 20' W.); KG.2800—locality Q, Fossil Bluff (71° 19' S., 68° 17' W.). The specimens at the latter locality occur between 88·5 and 111·0 m in a 426 m section (text-fig. 10).

Occurrence. As for material. Previously regarded as Berriasian in age (Crame 1981, fig. 5), it is now apparent that *A. trapezoidalis* may be, in part at least, as young as Aptian (Crame 1983a).

Description and remarks. Specimens KG.1745.10 and 11, with shell lengths (as measured from anterior to posterior extremities) in the region of 15 mm, and specimen KG.2800.295, with a length of approximately 32 mm, closely resemble the smallest members of this species previously described from locality K (Thomson and Willey 1972, fig. 8b; Crame 1981, pl. 2, figs. b–d). The two smallest specimens bear traces of a distinct anterior sulcus and specimen KG.2800.293, although lacking this



TEXT-FIG. 9. *Anopaea* from the Antarctic Peninsula region. *a*, incomplete internal mould of a large left valve of *A. trapezoidalis* (Thomson and Willey) (KG.2800.255); specimen from Fossil Bluff, Alexander Island. *b*, incomplete internal mould of a left valve of *A. sp. nov. aff. mandibula* (Mordvilko) (KG.1682.37); specimen from Waitabit Cliffs, Alexander Island. *c*, internal mould of a right valve of *A. sp. nov. β* (D.8212.261) from a locality approximately 1.5 km ENE of Stoneley Point, NW James Ross Island. All specimens $\times 1$.

feature, has the remnants of a very deep anterior lunule. Specimen KG.2800.225 (text-fig. 9*a*) is similar in general form to the holotype (KG.18.31*a*; Thomson and Willey 1972, fig. 8*a*; Crame 1981, pl. 2, fig. *a*), but slightly larger. It has a very high, rounded posterior region and much narrower anterior, and, like the holotype, lacks a clearly defined anterior sulcus. This seems to be a characteristic of the largest individuals of this species, as is the presence of coarse concentric ornament. On specimen KG.2800.225 (text-fig. 9*a*) the ribs are in the region of 3 mm apart over the centre of the valve and 5 mm apart towards the ventral margin. Specimen KG.2800.296 is a very incomplete large left valve with a height in the posterior region of about 65 mm and an estimated length of 80 mm. It is covered with closely set, coarse concentric ribs separated by deep interspaces.

Anopaea sp. nov. aff. *mandibula* (Mordvilko, 1949)

Text-fig. 9*b*

cf. 1962 *Inoceramus mandibula* Mordvilko; Saveliev, p. 230, pl. 6, figs. 1–11.

Material. KG.1682.37 (int.m., LV), from a high level in Waitabit Cliffs, Alexander Island ($71^{\circ} 30' 00''$ S., $68^{\circ} 14' 30''$ W.; text-figs. 2 and 10).

Occurrence. As for material. Albian (?Middle–Upper Albian), from its position at a high level in Waitabit Cliffs.

Description. The estimated length of this specimen is 35 mm and the maximum height (dorsal to ventral margins) is 32 mm. Although most of the anterior region is missing it can be judged to have been much narrower than the posterior with a height of approximately 17 mm. The well-rounded posterior region can be traced forward into a short, straight hinge which is partially obscured by the strongly prosogyrous umbo. The latter terminates in a narrow, pointed beak which overhangs a deeply excavated anterodorsal lunule (text-fig. 9*b*). The ventral margin is slightly sinuous due to the presence of a broad, shallow sulcus of some 12 mm width in its mid-region. This sulcus can be traced right up into the beak where it sweeps forwards and narrows to just under 2 mm in width (text-fig. 9*b*). The weakly to moderately inflated valve surface is covered with narrow (predominantly < 1 mm in width) concentric ribs that are regularly spaced but somewhat variable in their intensity; some tend to fade across the sulcus and others in the posterodorsal region (text-fig. 9*b*). Slightly coarser ribs

approaching 1 mm in width and separated by interspaces of up to 2 mm occur close to the ventral margin.

Remarks. The form of this specimen is too rounded and the ornament too fine for it to be related to *A. trapezoidalis*. It would seem instead to be closer to *A. mandibula* (Mordvilko) from the Lower Albian of Mangishlak (Saveliev 1962, p. 230, pl. 6, figs. 1–11). This is an erect, moderately inflated and finely ribbed species whose left valve can be closely matched with the Alexander Island specimen. However, there may be some differences between the two (especially in the form of the anterior sulcus) and specific separation seems to be necessary. *B. salomoni* (d'Orbigny) also has a strongly sulcate left valve, but this is typically more rounded-rectangular in outline and bears a broad, orthogyrous umbo (e.g. Woods 1911, pl. 45, figs. 3–7; Saveliev 1962, pl. 9, figs. 6–9).

Anopaea sp. nov. β

Text-fig. 9c

Material. D.8212.261 (int.m., RV); D.8212.262 (int.m., LV). Locality D.8212—valley floor approx. 1·5 km ENE of Stoneley Point, James Ross Island ($63^{\circ} 51' 40''$ S., $58^{\circ} 05' 20''$ W.; text-fig. 3); the specimens originate from approximately the 980 m level in the combined section measured on NW James Ross Island (text-fig. 11).

Occurrence. As for material. Aptian–Albian, from its association with *I. stoneleyi* sp. nov. and probable silesitid ammonites.

Description. The right valve (D.8212.261; text-fig. 9c) has an extremely accentuated rounded-wedge shaped profile; over a length of 23 mm it tapers from a height of 23 mm in the posterior region to approximately 8 mm at the anterior. The straight hinge has a length of 10 mm and subtends an angle of 140° with the anterior margin. It leads posteriorly into what appear to have been well-rounded posterior and posteroventral margins and these in turn pass into an anteroventral region whose outline is interrupted by a broad, shallow sinus (text-fig. 9c). Although incomplete, it would appear that the latter region was extremely narrow and pointed. A slender, tapering posterodorsal wing with a height at its posterior end of 2 mm and a concave cross-section is sharply demarcated from the main surface of the valve. Ornament consists of narrow (< 1 mm), regular concentric ribs separated by flat interspaces of 1·0–1·5 mm width (text-fig. 9c).

Remarks. Although there are some similarities in style of ornament between these specimens and the Tithonian species, *A. stoliczkai* (Holdhaus) (Crame 1981, pl. 1, figs. a–f), they differ significantly in shell form. In particular, specimen D.8212.261 (text-fig. 9c) has a less deeply excavated lunule but more prominent anterior sulcus. There are differences too in shell form from *A. trapezoidalis*, and in style of ornament from *A.* sp. nov. aff. *mandibula*.

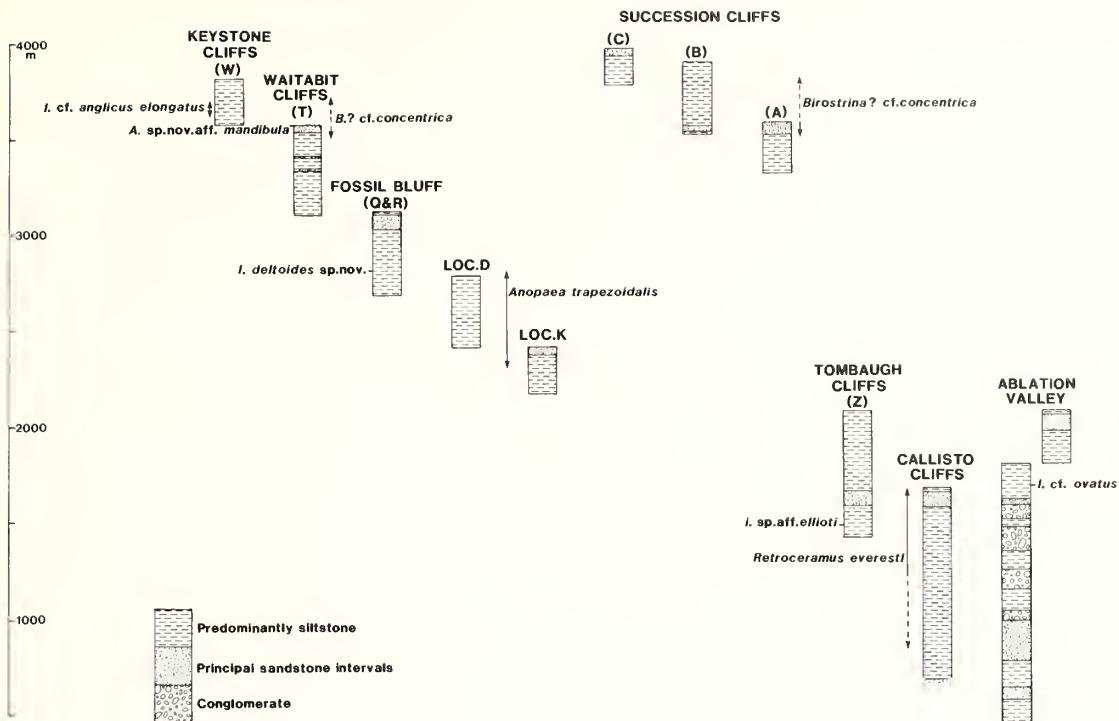
This material most likely represents a new species. The suffix β is used as a new but unnamed species of *Anopaea* has already been described from probable Upper Jurassic strata within the Fossil Bluff Formation (Crame 1981, p. 213).

STRATIGRAPHIC DISCUSSION

Alexander Island

Preliminary accounts of the distribution of Lower Cretaceous inoceramid bivalves through the Fossil Bluff Formation have already been given (Crame 1983a, b). In these works a simplified stratigraphic correlation scheme was presented for a series of major localities between Ablation Point and Keystone Cliffs (text-fig. 2; Crame 1983a, fig. 3; 1983b, fig. 2); these were thought to comprise the greater part of the Fossil Bluff Formation and total approximately 3820 m in thickness. With the more detailed taxonomic and stratigraphic information given in this study, it is necessary to briefly re-examine these distributions and further assess their stratigraphic implications.

In the lower levels of Tombaugh Cliffs and highest parts of Callisto Cliffs (text-fig. 10), *Retroceramus everesti* is of Berriasian age (Crame 1982). It is probably also present towards the top of



TEXT-FIG. 10. Occurrence of Lower Cretaceous inoceramids in the Fossil Bluff Formation of Alexander Island. Localities given in text-fig. 2. Correlations based in part on Taylor *et al.* 1979, fig. 6 and Crame 1982, text-fig. 9. Vertical scale in metres (lowest 500 m omitted).

the main Ablation Valley section and it is thought that the uppermost limit of its range can be set at 1675 m. Thus, it overlaps with the occurrences of *I. sp. aff. ellioti* (1480 m) and *I. cf. ovatus* (1675 m) (text-fig. 10), both of which have also been well established as Berriasian (Taylor *et al.* 1979; Crame 1983a, b). Moving southwards, structural, lithological, and faunal considerations all suggest that the top of the Tombaugh Cliffs section correlates with a level slightly beneath the base of the section at locality K (text-fig. 10). The next inoceramid to appear in the sequence, *A. trapezoidalis*, commences in the mid-levels of the section at locality K (2300 m) and continues upwards through locality D to the 2810 m level at localities Q and R (text-fig. 10). The extension of the range of this species into the base of the Fossil Bluff sections means that it may be, in part at least, as young as Aptian in age; indeed, it is even possible that it is also Aptian at locality K, as was originally suggested by Thomson and Willey (1972). At present there is no palaeontological evidence for the age of the beds occurring between *I. cf. ovatus* and *A. trapezoidalis* (text-fig. 10).

I. deltoides sp. nov. at the 2800–2820 m level (text-fig. 10) is most likely Aptian in age, although previous comments about possible late Neocomian or Barremian affinities of certain heteromorph ammonites occurring above it should be borne in mind. If various ammonite species of the genera *Aconeoceras*, *Theganeceras*, and *Sanmartinoceras*, and belemnites of the genera *Peratobelus* and *Neohibolites*, are taken as Aptian (Taylor *et al.* 1979), then it would appear that this stage is well represented in the sections at localities Q and R and in the lower levels of Waitabit Cliffs (text-fig. 10). The transition up into the Albian seems to occur at the latter locality with specimens of *B.? cf. concentrica* (3500–3700 m) and *Eotetragonites* being taken as indicators of the younger stage. Notwithstanding the possible Barremian affinities of ammonites such as *Antarcticoceras* and *Silesites*

(Thomson 1983), both *Anopaea* sp. nov. aff. *mandibula* (3560 m) and *I. cf. anglicus elongatus* (3620–3680 m) are also taken to be Albian (?Middle–Upper Albian) in age (text-fig. 10).

The gradual southerly younging of the Fossil Bluff Formation between Ablation Valley and Fossil Bluff is interrupted by the abrupt occurrence of Albian strata at localities A, B, and C, Succession Cliffs (text-figs. 2 and 10). These beds, which have yielded *B.? cf. concentrica* together with ammonites such as *Antarcticoceras antarcticum* Thomson and *Ptychoceras* sp., are thought to have been emplaced by a combination of thrusting and normal faulting (Taylor *et al.* 1979). Further evidence of stratigraphic repetition of the Fossil Bluff Formation by faulting is provided by the recurrence of both *I. deltoides* sp. nov. and *B.? cf. concentrica* at several localities between the Neptune Glacier and Stephenson Nunatak (text-fig. 2). The exact stratigraphic positions of *I. flemingi* sp. nov., *I. sp. aff. bellvuensis*, and *I. sp. aff. comancheanus* are uncertain but it is assumed that they occupy a level at least as high as that of *B.? cf. concentrica* (text-fig. 10).

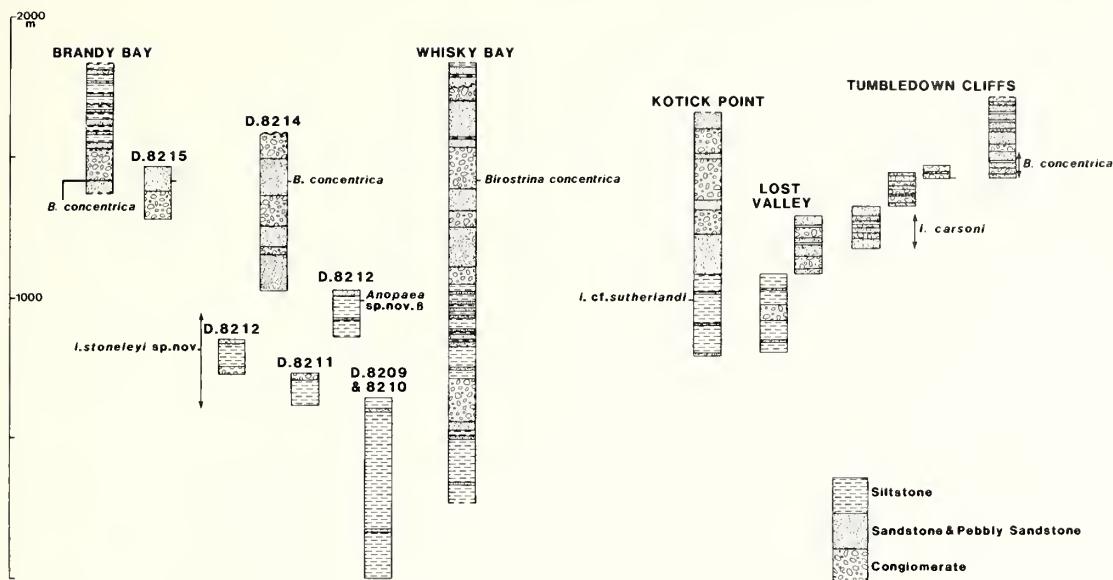
James Ross Island

The Lower Cretaceous biostratigraphy established for the Brandy Bay–Whisky Bay region (Crame 1983a, b) can now be extended to the Gin Cove–Rum Cove area (text-fig. 3). This correlation is based primarily on the occurrence of *B. concentrica*, which, although unrecorded in poorly exposed strata at Kotick Point, is present in both the North and South Tumbledown Cliffs sections (text-figs. 3 and 11). It is enhanced by certain broad lithological comparisons between the two regions and by similar levels of occurrence of the ammonite provisionally identified as *Silesites*.

I. stoneleyi sp. nov. (previously identified as a member of the *I. neocomiensis* group—Crame 1983a, b) occurs in the combined section between approximately 600 and 925 m (text-fig. 11). Associated fossils, such as '*Ancyloceras*' *patagonicum*, small aconeceratids and *Aucellina*, suggest an Aptian–Albian age, as do close relatives within the *I. licherowskyae* group; nevertheless, the possibility that at least some ancyloceratids and aconeceratids may be Barremian (or even older) in Alexander Island should be considered in any final age-determination of these beds. To date the only fossils collected from the lowest 600 m of strata on James Ross Island are a series of juvenile buchiid/oxytomid bivalves and a small gaudryceratid ammonite. If the beds containing *I. stoneleyi* sp. nov. are confirmed as Aptian–Albian, then this lowest biostratigraphic unit (text-fig. 11) may well prove to be Barremian or even earlier in age.

Anopaea sp. nov. β from the 980 m level at locality D.8212 (text-fig. 11) is also judged to be Aptian–Albian. The silesitid ammonites with which it is associated can be traced again at the 900–1000 m level in the Kotick Point section (text-fig. 11). Other fossils occurring in the lower half of the Kotick Point section include occasional phylloceratid and lytoceratid ammonites, *Aucellina* and *I. cf. sutherlandi*; the latter species in particular has been used to assign an undifferentiated Aptian–Albian age to this interval. *Inoceramus carsoni*, an Upper Albian species in Australia, occurs in the Lost Valley and North Tumbledown Cliffs sections between 1140 and 1250 m (text-fig. 11). Throughout this range it is associated with a species of *Aucellina* close to *A. hughendenensis* and a so far unidentified species of *Maccoyella*. The heteromorph *Ptychoceras* (Upper Aptian–Upper Albian) has been recorded from the top of the Lost Valley section and a probable specimen of *Beudanticeras* (Lower–Upper Albian) from an equivalent stratigraphic level nearby (M. R. A. Thomson, pers. comm.). Neither *I. cf. sutherlandi* nor *I. carsoni* has yet been found in the Brandy Bay–Whisky Bay region, where the 1000–1300 m interval is predominantly composed of unfossiliferous conglomeratic beds.

B. concentrica occurs in the combined section at approximately the 1375 m level (text-fig. 11). The Middle–Upper Albian age for this species established in other regions would seem to be confirmed by its position above *I. carsoni* and its association at North Tumbledown Cliffs and locality D.8414 (text-figs. 3 and 11) with turrilitid ammonites (M. R. A. Thomson, pers. comm.). At South Tumbledown Cliffs there appears to be a regular transition upwards from the *B. concentrica* beds into Cenomanian strata characterized by acanthoceratid ammonites and probable members of the *I. pictus* Sowerby group (M. R. A. Thomson, pers. comm.). However, at all other localities so far investigated the Lower–Upper Cretaceous boundary is obscured by poorly exposed conglomeratic strata and local unconformities (Crame 1983b).



TEXT-FIG. 11. Occurrence of Lower Cretaceous inoceramids on the NW coast of James Ross Island. Localities given in text-fig. 3. Correlations based in part on unpublished information kindly supplied by J. R. Ineson. Vertical scale in metres.

Annenkov Island and South Georgia

Comparisons with similar forms suggest that the most likely age affinities of both *I. annenkovensis* sp. nov. (= *I. cf. anomiaeformis* of Crame 1983a) and *I. cf. heteropterus* from the Lower Tuff Member of the Annenkov Island Formation are Hauterivian–Barremian. Nevertheless, it should be emphasized that these comparisons are somewhat tenuous and the precise age of the sediments on this island remains in some doubt. A slightly younger age (Barremian or Aptian) age is suggested by the poorly preserved specimens of aconceratid ammonites and *Aucellina* that occur in the upper levels of the range of *I. annenkovensis* sp. nov. (Crame 1983a, figs. 6 and 7), but there are also a number of other faunal elements in both the Lower Tuff and Upper Breccia Members whose significance is as yet uncertain (Thomson *et al.* 1982). There is still considerable scope for clarification of the biostratigraphy of Annenkov Island.

Only a single indeterminate specimen of *Inoceramus* has been recorded from the Cumberland Bay Formation of South Georgia (Thomson *et al.* 1982, p. 178).

SYNTHESIS

Berriasian representatives of the *I. ovatus* group (*I. cf. ovatus* and *I. sp. aff. ellioti*) from Alexander Island provide a possible means of correlation between the earliest Cretaceous strata of Antarctica and those of the Pacific coast of North America and Siberia. Moving up through the succession of Antarctic Lower Cretaceous inoceramids, it is apparent that there is then a pronounced stratigraphic gap before the probable Aptian–Albian faunas of the upper Fossil Bluff Formation and the lower part of the James Ross Island succession. There is very little evidence of Valanginian, Hauterivian, or Barremian inoceramids. Of course this time interval may be at least partially filled in the Fossil Bluff Formation when taxonomic revisions of certain ammonites (notably the heteromorphs) have been undertaken and stratigraphic studies at localities AP and CC2 (text-fig. 2) completed. Nevertheless, at present, there is very little firm palaeontological evidence for the Valanginian–Barremian stages in

Alexander Island. *Anopaea trapezoidalis* (text-fig. 10) may be late Neocomian or Barremian in the early part of its range but this has yet to be confirmed.

Although the Cretaceous sedimentary succession in the James Ross Island area is thought to commence at approximately the Aptian stage, there is evidence of lower stratigraphic horizons at least two localities on the east coast of the Antarctic Peninsula. Late Hauterivian–Barremian dinoflagellates and coccoliths have been recovered from a 750–1000 m conglomeratic sequence on the Sobral Peninsula (text-fig. 1), and at Pedersen Nunatak (text-fig. 1) a 142 m sequence of conglomerates and sandstones has yielded ammonite fragments referable to the South American Hauterivian species, *Favrella wilckensi* (Favre) (Farquharson 1982; Thomson and Farquharson 1984). Further north, *I. annenkovensis* sp. nov. and *I. cf. heteropterus* from the Lower Tuff Member of Annenkov Island have Hauterivian–Barremian affinities. The latter species in particular, through its link with a distinctive North Pacific inoceramid group, suggests an Upper Hauterivian age, but balanced against this is the presence of both aconeceratid ammonites and *Aucellina* in the same stratigraphic unit. Perhaps the best compromise is to regard the age of this unit as Barremian. Early Cretaceous marine sediments on Byers Peninsula (South Shetlands) are probably confined to the Berriasian and Valanginian (Smellie *et al.* 1980) but isolated marine intervals within the Mesozoic alluvial fan conglomerates of the South Orkney Islands (text-fig. 1) may range as high as the Hauterivian (Thomson 1981).

The paucity of Valanginian–Barremian inoceramids from the Antarctic Peninsula region as a whole enhances the impression of a general hiatus at this time gained from the study of other faunal groups (notably the ammonites, e.g. Thomson 1974, 1982). This may well be linked with a significant marine regression as the Antarctic Peninsula underwent a major phase of uplift and magmatic activity (Farquharson 1982). It has been suggested that the simplest explanation of this orogenic pulse was an increased rate of subduction of the Pacific Aluk plate beneath the Antarctic Peninsula margin of Gondwana. Such an event is thought to have been a likely precursor to the Valanginian opening of the South Atlantic and Weddell Sea basins (Farquharson 1983).

I. stoneleyi sp. nov., the lowest species to occur in the James Ross Island succession, can be matched with Aptian–Albian members of the *I. licherowskyae* group from Spitsbergen, south-western USSR, and the far-eastern USSR. Similarly, *I. deltoides* sp. nov. from the Fossil Bluff Formation is close to specimens of *I. subneocomiensis* and *I. neocomiensis* known from a number of Northern Hemisphere localities. The *I. neocomiensis* group is a particularly interesting one in that it may be one of the earliest Cretaceous inoceramid groups with a cosmopolitan distribution. It is succeeded by the *B. concentrica* group which is truly worldwide in its occurrence. The Middle–Upper Albian age of *B. concentrica* on James Ross Island is supported by ammonites and this species is generally regarded as one of the most useful for both local and regional correlations in the Antarctic Lower Cretaceous. On Alexander Island the presence of *B.?* cf. *concentrica* in the Waitabit Cliffs and Keystone Cliffs sections suggests that a general correlation can be made between the uppermost levels of the Fossil Bluff Formation and the 1375 m level on James Ross Island (text-figs. 10 and 11).

Other high level inoceramids in the Fossil Bluff Formation include *I. flemingi* sp. nov., a probable member of the *I. licherowskyae* group, and three species (*I. cf. anglicus elongatus*, *I. sp. aff. bellvuensis*, and *I. sp. aff. comancheanus*) that have their strongest affinities with the cosmopolitan *I. anglicus* group. Both the latter three and *I. sp. aff. anglicus* from Dundee Island can be compared with specimens from a wide range of Northern Hemisphere localities. Representatives of the *I. carsoni* group in the James Ross Island succession provide a direct link between the Antarctic Peninsula and Great Artesian Basin of Australia; in particular, *I. carsoni* indicates a correlation of the 1140–1250 m interval with stratigraphic units such as the Allaru Mudstone of Queensland (Day 1969). *Anopaea* sp. nov. aff. *mandibula* may furnish another connection between the Aptian–Albian Fossil Bluff Formation faunas and those of the south-western USSR.

The Fossil Bluff Formation apparently terminates in the Albian (Taylor *et al.* 1979), but the James Ross Island succession passes up into Cenomanian and younger beds (Crame 1983b).

Acknowledgements. I would like to thank Mr. C. P. Nuttall, Dr. N. J. Morris, and Mr. R. Cleevley for allowing me ready access to the Mesozoic Mollusca collections of the Department of Palaeontology, British Museum (Natural History). On a visit to Australia, Dr. N. H. Ludbrook kindly arranged for me to examine the collections held in the South Australian Department of Mines and Energy and Dr. B. P. Webb (Director-General) subsequently allowed me to borrow a number of specimens from them. Mr. P. J. G. Fleming facilitated my examination of the Geological Survey of Queensland's collections and I would also like to acknowledge use of a set of inoceramid plaster casts supplied by the New Zealand Geological Survey.

My colleagues Dr. M. R. A. Thomson, Mr. J. R. Ineson, and Dr. G. W. Farquharson offered constructive criticisms of a number of points raised in the text. Dr. B. Haigh (Cambridge) translated some of the cited Russian material and Mr. C. Gilbert of the British Antarctic Survey took the photographs.

REFERENCES

- AIRAGHI, C. 1904. Inocerami del Vento. *Boll. Soc. geol. ital.* **20**, 178–198.
- ANDERSON, F. M. 1938. Lower Cretaceous deposits in California and Oregon. *Spec. Pap. geol. Soc. Am.* **16**, 1–339.
- 1945. Knoxville Series in the California Mesozoic. *Bull. geol. Soc. Am.* **56**, 909–1014.
- AUERBACH, J. and FREARS, H. 1846. Notices sur quelques passages de l'ouvrage de MM. Murchison, E. de Verneuil et la Comte A. de Keyserling: Géologie de la Russie d'Europe et des montagnes de l'Oural. *Byull. mosk. Obshch. Ispyt. Prir.* **35**, 486–500.
- BIBBY, J. S. 1966. The stratigraphy of part of north-east Graham Land and the James Ross Island group. *Scient. Rep. Br. Antarct. Surv.* **53**, 1–37.
- BONARELLI, G. and NÁGERA, J. J. 1921. Observaciones geológicas en las inmediaciones del Lago San Martín (Territorio de Santa Cruz). *Boln Dir. gen. Minas Geol. Hidrol., B. Aires, Ser. B,* **27**, 1–39.
- CASEY, R. 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology*, **3**, 487–621.
- CHIPRONKAR, G. W. and BADVE, R. M. 1976. On some inoceramid species occurring in the Bagh Beds of Narmada Valley. *J. Univ. Poona*, **48**, 195–209.
- COX, L. R. 1969. Family Inoceramidae Giebel, 1852. In MOORE, R. C. (with TEICHERT, C., MCCORMICK, L. and WILLIAMS, R. B.) (eds.). *Treatise on invertebrate paleontology. Pt. N, Vol. 1, Mollusca 6. Bivalvia*, N314–N321. Geological Society of America and University of Kansas Press.
- CRAME, J. A. 1980. The occurrence of the bivalve *Inoceramus concentricus* on Dundee Island, Joinville Island group. *Bull. Br. Antarct. Surv.* **49**, 283–286.
- 1981. Upper Cretaceous inoceramids (Bivalvia) from the James Ross Island group and their stratigraphical significance. *Ibid.* **53**, 29–56.
- 1982. Late Jurassic inoceramid bivalves from the Antarctic Peninsula and their stratigraphic use. *Palaeontology*, **25**, 555–603.
- 1983a. Lower Cretaceous bivalve biostratigraphy of Antarctica. *Zitteliana*, **10**, 399–406.
- 1983b. Cretaceous inoceramid bivalves from Antarctica. In OLIVER, R. L., JAMES, P. R. and JAGO, J. B. (eds.). *Antarctic Earth Science*, 298–302. Australian Academy of Science, Canberra.
- DAY, R. W. 1969. The Lower Cretaceous of the Great Artesian Basin. In CAMPBELL, K. S. W. (ed.). *Stratigraphy and palaeontology. Essays in honour of Dorothy Hill*, 140–173. Australian National University Press, Canberra.
- EIGHENHEER, R. and SORNAY, J. 1974. Sur une forme apparentée à *Inoceramus comancheanus* Cragin dans le Cénomanien basal de Montlaux (Alpes-de-Provence). *Bull. Mus. natn. Hist. nat., Paris*, **229**, 141–144.
- ETHERIDGE, R. 1872. Description of the Palaeozoic and Mesozoic fossils of Queensland. In DANTREE, R. Notes on the geology of the colony of Queensland. *Q. Jl geol. Soc. Lond.* **28**, 317–350.
- 1907. Cretaceous fossils of Natal collected by Mr William Anderson, Government Geologist. Part II. The Umsinene River deposit. In ANDERSON, W. *Third and final report of the Geological Survey of Natal and Zululand*, 67–90.
- ETHERIDGE, R. JR. 1892. In JACK, R. L. and ETHERIDGE, R. JR. *The geology and palaeontology of Queensland and New Guinea, with sixty-eight plates and a geological map of Queensland*. 2 vols. Dulau and Co., London.
- 1901. Additional notes on the palaeontology of Queensland (part 2). *Bull. geol. Surv. Qld*, **13**, 1–37.
- 1905. Contributions to the palaeontology of South Australia. No. 14. Cretaceous fossils from Dalhousie Springs. In *Report on geological explorations in the west and north-west of South Australia*, 13–17. C. E. Bristow, Government Printer, Adelaide.
- FARQUHARSON, G. W. 1982. Late Mesozoic sedimentation in the northern Antarctic Peninsula and its relationship to the southern Andes. *J. geol. Soc. Lond.* **139**, 721–728.

- FARQUHARSON, G. W. 1983. Sedimentation associated with the Late Mesozoic volcanic arc of the northern Antarctic Peninsula. Unpubl. Ph.D. thesis, C.N.A.A.
- FERUGLIO, E. 1936. Palaeontographica patagonica. Pt. 1. *Memoire 1st. geol. miner. Univ. Padova*, **11**, 1–192.
- GILLET, S. 1924. Études sur les lamellibranches néocomiens. *Mém. Soc. geol. Fr. (N.S.)*, **1**, fasc. 3–4, 1–224.
- GLAZUNOVA, A. E. 1973. *Paleontological evidence of the stratigraphic separation of Cretaceous deposits in the Volga region*, 200 pp. Lower Cretaceous. 'Nedra', Moscow. [In Russian.]
- HAYAMI, I. 1960. Jurassic inoceramids in Japan. *J. Fac. Sci. Tokyo Univ., ser. II*, **12**, 277–328.
- HEINZ, R. 1928a. Über die bisher wenig beachtete Skulptur der Inoceramen-Schale und ihre stratigraphische Bedeutung. Beiträge zur Kenntnis der oberkretazischen Inoceramen IV. *Mitt. miner.-geol. Stinst. Hamb.*, **10**, 3–39.
- 1928b. Über die Kreide-Inoceramen Australiens und ihre Beziehungen zu denen Europas und anderer Gebiete. Beiträge zur Kenntnis der oberkretazischen Inoceramen VIII. *Ibid.* 131–147.
- 1930. Ueber Kreide-Inoceramen der südafrikanischen Union. *C.r. 15th Int. geol. Congr., Pretoria*, 1929, **2**, 681–687.
- 1933. Inoceramen von Madagaskar und ihre Bedeutung für die Kreide-Stratigraphie. *Z. dt. geol. Ges.* **85**, 241–259.
- HILL, D., PLAYFORD, G. and WOODS, J. T. (eds.). 1968. *Cretaceous fossils of Queensland*, 35 pp. Queensland Palaeontographical Society, Brisbane.
- IMLAY, R. W. 1960. Ammonites of early Cretaceous age (Valanginian and Hauterivian) from the Pacific Coast states. *Prof. Pap. U.S. geol. Surv.* **334-F**, 167–228.
- 1961. Characteristic Lower Cretaceous megafossils from northern Alaska. *Ibid.* **335**, 74 pp.
- JELETZKY, J. A. 1964. Illustrations of Canadian fossils. Lower Cretaceous marine index fossils of the sedimentary basins of western and Arctic Canada. *Geol. Surv. Pap. Can.* **64-11**, 1–101.
- 1970. Cretaceous macrofaunas. In DOUGLAS, R. J. W. (ed.). *Geology and economic minerals of Canada*, 649–662. Department of Energy, Mines and Resources, Ottawa.
- 1977. Mid-Cretaceous (Aptian to Coniacian) history of Pacific slope of Canada. In KANMERA, K. (ed.). *Mid-Cretaceous Events. Hokkaido Symposium, 1976. Spec. Pap. palaeontol. Soc. Japan*, **21**, 97–126.
- JONES, D. L. 1960. Lower Cretaceous (Albian) fossils from southwestern Oregon and their paleogeographic significance. *J. Paleont.* **34**, 152–160.
- and GRYC, G. 1960. Upper Cretaceous pelecypods of the genus *Inoceramus* from northern Alaska. *Prof. Pap. U.S. geol. Surv.* **334E**, 149–165.
- KAUFFMAN, E. G. 1977. Systematic, biostratigraphic and biogeographic relationships between Middle Cretaceous Euro-American and North Pacific Inoceramidae. In KANMERA, K. (ed.). *Mid-Cretaceous Events. Hokkaido Symposium, 1976. Spec. Pap. palaeontol. Soc. Japan*, **21**, 169–212.
- 1978a. British Middle Cretaceous inoceramid biostratigraphy. In *Événements de la partie moyenne du Crétacé. Uppsala 1975–Nice 1976. Annls. Mus. Hist. nat. Nice*, **4** (1976), IV.1–IV.12.
- 1978b. South African middle Cretaceous Inoceramidae. *Ibid.* XVII.1–XVII.6.
- 1978c. Middle Cretaceous bivalve zones and stage implications in the Antillean subprovince, Caribbean province. *Ibid.* XXX.1–XXX.11.
- COBBAN, W. A. and EICHER, D. L. 1978. Albian through lower Coniacian strata. Biostratigraphy and principal events in western interior states. *Ibid.* XXIII.1–XXIII.52.
- KELLY, S. R. A. 1984. Bivalvia of the Spilsby Sandstone and Sandringham Sands (Late Jurassic–Early Cretaceous) of eastern England. Part 1. *Palaeontogr. Soc. [Monogr.]*, 94 pp., 20 pls.
- LEANZA, A. F. 1967. Anotaciones sobre los fósiles jurásico-cretácicos de Patagonia austral (colección Feruglio conservados en la Universidad de Bologna). *Acta geol. illoana*, **9**, 121–188.
- LUDBROOK, N. H. 1966. Cretaceous biostratigraphy of the Great Artesian Basin in South Australia. *Bull. geol. Surv. S. Aust.* **40**, 1–223.
- LUMHOLTZ, C. 1889. *Among Cannibals*, 395 pp. John Murray, London.
- M'COY, F. 1865. Note on the Cretaceous deposits of Australia. *Ann. Mag. nat. Hist.* **16**, 333–334.
- 1866. On the discovery of Cretaceous fossils in Australia. *Trans. Proc. R. Soc. Vict.* **7**, 49–51.
- 1867. On the Recent Zoology and palaeontology of Victoria. *Ann. Mag. nat. Hist.* **20**, 175–202.
- MCLEARN, F. H. 1919. New species of pelecypods from the Cretaceous of northern Alberta. *Bull. geol. Surv. Can. Mus.* **29**, 9–12.
- 1933. Pelecypods of the Lower Cretaceous Clearwater Formation, northern Alberta. *Trans. R. Soc. Can.* **27**, 139–156.
- 1943. Trends in some Canadian species of *Inoceramus*. *Can. Fld. Nat.* **57**, 36–46.

- MATSUMOTO, T., OKADA, H., HIRANO, H. and TANABE, K. 1978. Mid-Cretaceous zonation in Japan. In *Événements de la partie moyenne du Crétacé. Uppsala 1975–Nice 1976. Annls Mus. Hist. nat. Nice*, **4** (1976), XXXIII.1–XXXIII.6.
- MAURY, C. 1936. O Cretaceo de Sergipe. *Monografias Serv. Geol. Min. Brasil*, **11**, 1–25.
- MEEK, F. B. 1864. Check list of the invertebrate fossils of North America. Cretaceous and Jurassic. *Smithson. misc. Collns*, **7**, 1–40.
- NAGAO, T. and MATSUMOTO, T. 1939. A monograph of the Cretaceous *Inoceramus* of Japan. *J. Fac. Sci. Hokkaido Univ.*, **4**, 241–299.
- NEWTON, R. B. 1909. Cretaceous Gastropoda and Pelecypoda from Zululand. *Trans. R. Soc. S. Afr.*, **1**, 1–106.
- ORBIGNY, A. D'. 1846. *Paléontologie française. Description des mollusques et rayonnés fossiles. Terrains Crétacés. 3. Lamellibranches*, V, 449–520. Masson, Paris.
- PARKINSON, J. 1819. Remarks on the fossils collected by Mr Phillips near Dover and Folkestone. *Trans. geol. Soc. Lond.*, **5**, 52–59.
- PERGAMENT, M. A. 1965. Inocerams and Cretaceous stratigraphy of the Pacific region. *Trudy Inst. geol. Nauk, Mosk.*, **118**, 1–102. [In Russian.]
- 1966. Zonal stratigraphy and inocerams of the lowermost Upper Cretaceous on the Pacific coast of the USSR. *Ibid.*, **146**, 1–83. [In Russian.]
- 1981. Pacific regions of the USSR. In REYMENT, R. A. and BENGTSON, P. (eds.). *Aspects of Mid-Cretaceous regional geology*, 69–102. Academic Press, London.
- PETTIGREW, T. H. 1981. The geology of Annenkov Island. *Bull. Br. Antarct. Surv.*, **53**, 213–254.
- POKHIALAINEN, V. P. 1969. Neocomian inocerams of the Anadyrskiy-Koryakskiy folded region. *Trudy sev.-vost. kompl. nauchno-issled. Inst.*, **32**, 118–123. [In Russian.]
- 1974. Osobennosti rasprostraneniya inotseramid neokoma Tikhookeanskoi oblasti (Spreading of the Neocomian Pacific inoceramids). *Trudy Inst. Geol. Geofiz. sib. Otd.*, **80**, 174–187. [In Russian.]
- REESIDE, J. B. 1923. The fauna of the so-called Dakota Formation of northern central Colorado and its equivalent in southeastern Wyoming. *Prof. Pap. U.S. geol. Surv.*, **131H**, 199–212.
- RICCARDI, A. C. 1970. *Favrella* R. Douvillé, 1909 (Ammonitina, Cretácico inferior): edad y distribucion. *Ameighiniana*, **7**, 119–138.
- 1977. Berriasian invertebrate fauna from the Springhill Formation of Southern Patagonia. *Neues Jb. Miner. Geol. Paläont. Abh.*, **155**, 216–252.
- WESTERMANN, G. E. G. and LEVY, R. 1971. The Lower Cretaceous Ammonitina *Olcostephanus*, *Leopoldia* and *Favrella* from west-central Argentina. *Palaeontographica*, **136**, Abt. A, Lief. 1–6, 83–121.
- ROUILLIER, C. 1849. *In ROUILLIER, C. and VOSSINSKY, A. Études progressives sur la géologie de Moscou; quatrième étude. Byull. Mosk. Abshch. Ispyt. Prir.*, **22**, 237–355.
- SAVELEV, A. A. 1962. Albian inoceramids of Mangishlak. *Trudy vses. nauchno-issled. geol.-razv. nefte Inst.*, **196**, 219–254. [In Russian.]
- SCHLAGINTWEIT, O. 1911. Die fauna des Vracon und Cenoman in Peru. In STEINMAN, G. Beiträge zur Geologie und Paläontologie von Südamerika. XVII. *Neues Jb. Miner. Geol. Paläont. BeilBd.*, **33**, 43–135.
- SCOTT, G. R. 1970. Paleoecology and paleontology of the Lower Cretaceous Kiowa Formation, Kansas. *Paleont. Contr. Univ. Kans.*, **52**, 1–94.
- SMELLIE, J. L., DAVIES, R. E. S. and THOMSON, M. R. A. 1980. Geology of a Mesozoic intra-arc sequence on Byers Peninsula, Livingston Island, South Shetland Islands. *Bull. Br. Antarct. Surv.*, **50**, 55–76.
- SORNAY, J. 1965. Les Inoceramés du Crétacé Inférieur en France. *Mém. Bur. Rech. géol. nucléaire*, **34**, 393–397.
- 1966. Idées actuelles sur les Inocéramés d'après divers travaux récents. *Annls. Paléont.*, *Invertébrés*, **52**, 59–92.
- 1981. Inocérames. In *Travail de synthèse du groupe de travail sur les "Événements Biologiques" (Mid-Cretaceous Events)*. *Cretaceous Res.*, **2**, 417–425.
- SOWERBY, J. 1821. *The Mineral Conchology of Great Britain*, 3, 127–186, pls. 272–306. London.
- SPEDEN, I. G. 1977. Taitai Series (Early Cretaceous) and the elimination of the Mokoian stage. *N.Z. Jl Geol. Geophys.*, **20**, 537–562.
- SPENGLER, E. 1914. Nachträge zur Oberkreidefauna des Trichinopoly-Distriktes in Südinidien. *Beitr. Paläont. Geol. Ost.-Ung.*, **26**, 213–239.
- STANTON, T. W. 1895. Contributions to the Cretaceous palaeontology of the Pacific coast. The fauna of the Knoxville Beds. *Bull. U.S. Geol. Surv.*, **133**, 1–132.
- STEVENS, G. R. and SPEDEN, I. G. 1978. New Zealand. In MOULLADE, M. and NAIRN, A. E. M. (eds.). *The phanerozoic geology of the world, II. The Mesozoic*, A. 251–328. Elsevier, Amsterdam, Oxford, and London.

- STOLLEY, E. 1912. Über die Kreideformation und ihre fossilien auf Spitzbergen. *K. svenska Vetensk Akad. Handl.* **47**, 1-29.
- TANNER, P. W. G. 1982. Geologic evolution of South Georgia. In CRADDOCK, C. (ed.). *Antarctic geoscience*, 167-176. University of Wisconsin Press, Madison.
- STOREY, B. C. and MACDONALD, D. I. M. 1981. Geology of an Upper Jurassic-Lower Cretaceous island-arc assemblage in Hauge Reef, The Pickersgill Islands and adjoining areas of South Georgia. *Bull. Br. Antarct. Surv.* **53**, 77-117.
- TAYLOR, B. J., THOMSON, M. R. A. and WILLEY, L. E. 1979. The geology of the Ablation Point-Keystone Cliffs area, Alexander Island. *Scient. Rep. Br. Antarct. Surv.* **82**, 1-65.
- THOMSON, M. R. A. 1967. A probable Cretaceous invertebrate fauna from Crabeater Point, Bowman Coast, Graham Land. *Bull. Br. Antarct. Surv.* **14**, 1-14.
- 1974. Ammonite faunas of the Lower Cretaceous of south-eastern Alexander Island. *Scient. Rep. Br. Antarct. Surv.* **80**, 1-44.
- 1979. Upper Jurassic and Lower Cretaceous ammonite faunas of the Ablation Point area, Alexander Island. *Ibid.* **97**, 1-37.
- 1981. Late Mesozoic stratigraphy and invertebrate paleontology of the South Orkney islands. *Bull. Br. Antarct. Surv.* **54**, 65-83.
- 1982. A comparison of the ammonite faunas of the Antarctic Peninsula and Magallanes Basin. *J. geol. Soc. Lond.* **139**, 763-770.
- 1983. 'European' ammonites in the Lower Cretaceous of Antarctica. *Zitteliana*, **10**, 407-412.
- and FARQUHARSON, G. W. 1984. Discovery and significance of the ammonite genus *Favrella* in the Antarctic Peninsula area. *Bull. Br. Antarct. Surv.* **62**, 7-14.
- and WILLEY, L. E. 1972. Upper Jurassic and Lower Cretaceous *Inoceramus* (Bivalvia) from south-east Alexander Island. *Ibid.* **29**, 1-19.
- TANNER, P. W. G. and REX, D. C. 1982. Fossil and radiometric evidence for ages of deposition and metamorphism of sedimentary sequences on South Georgia. In CRADDOCK, C. (ed.). *Antarctic geoscience*, 177-184. University of Wisconsin Press, Madison.
- TRAUTSCHOLD, H. 1865. Der Inoceramen-Thon von Simbirsk. *Bull. Soc. Nat. Moscou*, **38**, 1-24.
- TRÖGER, K.-A. 1981. German Democratic Republic. In REYMENT, R. A. and BENGTSON, P. (eds.). *Aspects of Mid-Cretaceous regional geology*, 1-28. Academic Press, London.
- WARREN, P. S. and STELCK, C. R. 1940. Cenomanian and Turonian faunas in the Pouce Coupe district, Alberta and British Columbia. *Trans. R. Soc. Can.* **34**, 143-152.
- WEAVER, C. 1931. Palaeontology of the Jurassic and Cretaceous of west central Argentina. *Mem. Univ. Wash.* **1**, 1-169.
- WELLMAN, H. W. 1959. Divisions of the New Zealand Cretaceous. *Trans. R. Soc. N.Z.* **87**, 99-163.
- WHITEAVES, J. F. 1876. On some invertebrates from the coal-bearing rocks of the Queen Charlotte Islands, collected by Mr James Richardson in 1872. In *Mesozoic fossils*, 1, Pt. I, 1-92, Geological Survey of Canada, Montreal.
- 1883. On the Lower Cretaceous rocks of British Columbia. *Trans. R. Soc. Can.* **1**, 81-86.
- WHITEHOUSE, F. W. 1924. The Queensland Inocerami collected by M. Lumholz in 1881. *Proc. R. Soc. Qd.* **35**, 127-132.
- WIEDMANN, J. and KAUFFMAN, E. G. 1978. Mid-Cretaceous biostratigraphy of northern Spain. In *Événements de la partie moyenne du Crétacé. Uppsala 1975-Nice 1976. Annls Mus. Hist. nat. Nice*, **4** (1976), III.1-III.34.
- WILCKENS, O. 1947. Paläontologische und geologische Ergebnisse der Reise von Kohl-Larsen (1928-29) nach Süd-Georgien. *Abh. senckenb. naturforsch. Ges.* **474**, 1-66.
- WILLEY, L. E. 1972. Belemnites from south-eastern Alexander Island: 1. The occurrence of the family Dimitobelidae in the Lower Cretaceous. *Bull. Br. Antarct. Surv.* **28**, 29-42.
- WOLLEMAN, A. 1906. Die Bivalven und Gastropoden des nordeutschen Gaults (Aptiens und Albiens). *Jb. preuss. geol. Landesanst.* **27**, 259-300.
- WOODS, H. 1911. A monograph of the Cretaceous Lamellibranchia of England. *Palaeontogr. Soc. [Monogr.]*, **2**, Pt. 7, 261-284.
- 1912. The evolution of *Inoceramus* in the Cretaceous period. *Q. Jl geol. Soc. Lond.* **68**, 1-20.
- 1917. The Cretaceous faunas of the north-eastern part of the South Island of New Zealand. *Palaeont. Bull., Wellington*, **4**, 1-41.
- ZAKHAROV, V. A. 1966. *Late Jurassic and early Cretaceous bivalve molluscs of the north of Siberia and their ecology. Part 1. Order Anisomyaria*, 191 pp. 'Nauka', Moscow. [In Russian.]
- 1968. Changes of complexes of bivalve species at the boundary between the Jurassic and Cretaceous

- periods in the Boreal Arctic zoogeographic regions. *Trudy Inst. Geol. Geofiz. sib. Otd.* **48**, 90–100. [In Russian.]
- and TURBINA, A. S. 1979. Early Neocomian inoceramids from northern Siberia and their role in benthic assemblages. In SAKS, V. N. and ZAKHAROV, V. A. (eds.). *Conditions of the existence of the Mesozoic marine Boreal fauna*. *Ibid.* **411**, 23–36. [In Russian.]

J. A. CRAME

British Antarctic Survey
Natural Environment Research Council
High Cross
Madingley Road
Cambridge CB3 0ET

Manuscript received 23 May 1984

Revised manuscript received 28 September 1984

CORONATE ECHINODERMS FROM THE LOWER PALAEZOIC OF BRITAIN

by STEPHEN K. DONOVAN and CHRISTOPHER R. C. PAUL

ABSTRACT. Coronates are pelmatozoan echinoderms with a functional stem, a bud-shaped theca, and erect, biserial, pinnate arms. They evolved early in the Middle Ordovician, probably from the 'eocrinoid' *Bockia*, and gave rise to the blastoids *sensu stricto*. The subclass Coronata contains six genera. *Mespilocystites* (early Caradoc–Ashgill) had geniculate radial furrows, while all later genera had planar or gently convex radii. Of these *Stephanoblastus* (Caradoc–Wenlock) had a very narrow stem and triradiate keels at the base of the theca. All other genera had triangular thecal bases. *Tornoblastus* (Ashgill) had a conical theca with a protruding base bearing three flanges, *Paracystis* (Caradoc) had a bowl-shaped theca with a sunken base, *Stephanocrinus* (Ashgill–Ludlow) a tall, steeply conical theca, and *Cupulocorona* gen. nov. (Ashgill–Wenlock) a conical to cup-shaped theca with a protruding base. The British coronate fauna includes five new species: *S. ramsbottomi* (Hirnantian) characterized by a large, angular conical theca with low coronal processes, *C. salopiae* (early Wenlock) characterized by a pyriform theca with low coronal processes and low ridges at the plate sutures, *C. rugosa* (Cautleyan–Rawtheyan) with a conical theca bearing very coarse ornament, *C. digitalis* (Cautleyan–Rawtheyan) with a conical theca and very long coronal processes, and *Stephanocrinus sensu lato* sp. (Cautleyan) which is poorly known but had very fine ribbing.

CORONATES are a small but distinctive group of Lower Palaeozoic pelmatozoans with a functional stem, a small theca with five interradial coronal processes ventrally and a fixed arrangement of thecal plates very similar to that of blastoids, and erect, biserial, pinnate arms. Opinions as to their affinities have varied in the past, but we believe they were most closely related to the blastoids. Although thecae of coronate echinoderms are not uncommon in the Ordovician and Silurian of Britain (no columns or arms have yet been discovered), the only previous references to their occurrence are in Bather (1900, pp. 96, 145), who mentioned that *Stephanocrinus* was found in the Silurian of Britain, and King and Wilcockson (1934, p. 17), in which Bather recognized a calyx from the Upper Ordovician at Hunterstyke as *Stephanocrinus*. The latter is described below as *S. ramsbottomi* sp. nov. In 1952 W. H. C. Ramsbottom prepared an unpublished manuscript on some coronates including a proposed new species, *S. salopiae*, which is probably the species referred to by Bather (1900) and is redescribed here as *Cupulocorona salopiae*. Otherwise British coronates have been ignored or referred to as 'new cystidean' (Reed 1907, p. 537). Following the recent reassessment of *Stephanocrinus* (Brett *et al.* 1983), which elevated the Coronata to class status, it is timely to describe British representatives of the group.

GENERAL MORPHOLOGY OF THE CORONATES

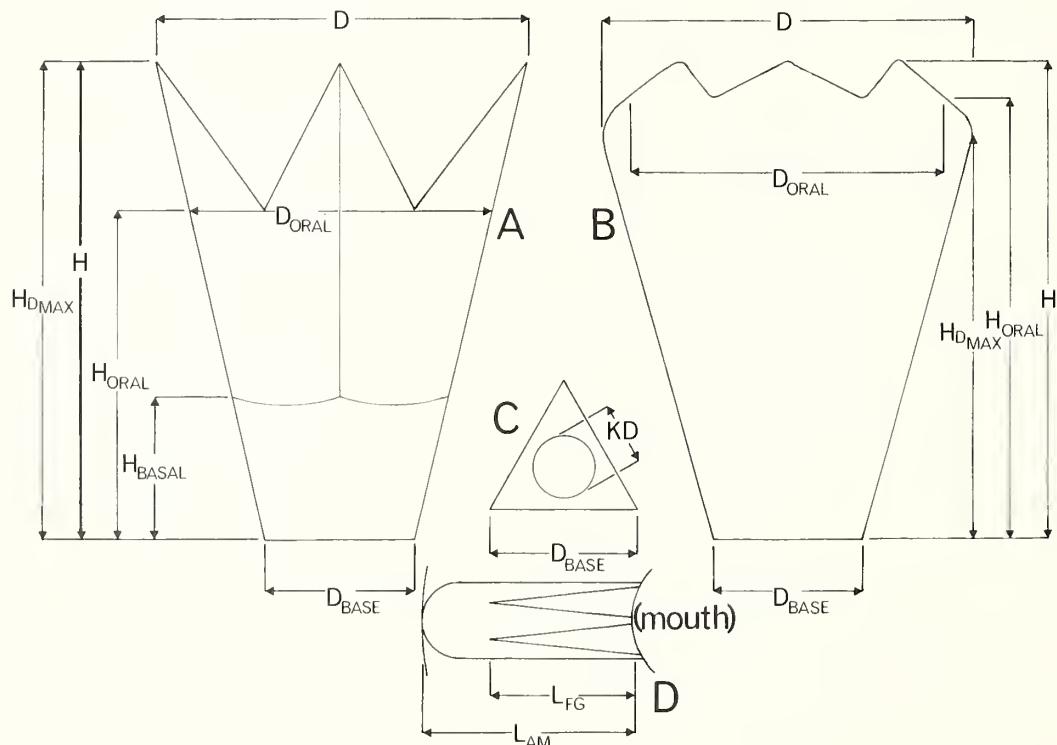
Stem. Apparently homeomorphic, composed of small circular columnals with convex latera, narrow ($\frac{1}{8}$ – $\frac{1}{10}$ thecal diameter) or extremely narrow ($\frac{1}{25}$ thecal diameter), circular in section and with a circular lumen as far as is known. Brett *et al.* (1983, fig. 1k) illustrated a discoidal holdfast which they associated with *S. angulatus*.

Theca. Elongate-conical through conical to cup- or bowl-shaped, base triangular or triradiate, top with five distinct coronal processes. Constant plate arrangement (text-fig. 5A) consisting of three basals of which the azygous basal occupies the AB interray; five radials all with cleft upper margins, the two 'wings' each forming half of the aboral side of a coronal process; six deltoids, a sub- and super-deltoid in the CD (posterior) interray adoral to the anus and one deltoid in each of the other

four interrays, deltoids triangular and raised to form the adoral portions of the coronal processes; five primary ambulacrals at the tip of each ambulacrum and in the radial furrows between the coronal processes; five oral cover plates over the central mouth, the posterior of which is very slightly the largest; ten elongate ambulacral cover plates, one pair per ambulacrum. The basals and radials are usually ornamented with fine ridges or rows of granules which form rhombic patterns. In some genera there are also major ridges on the theca diverging upwards from the basals and forming a V W pattern, the base of the V being centred on the azygous basal.

Three orifices all in the oral surface (text-fig. 5B). A central, nearly circular mouth. An anus, almost as large as the mouth, situated at the base of the CD coronal process on the adoral side, and covered with an anal pyramid of three or four cover plates. Just adoral to the anus on the common suture of the sub- and super-deltoid a small tubercle with a transverse slit is sometimes found. This has been interpreted as a possible hydropore (Brett *et al.* 1983, p. 632). Both suture and orifice are frequently cryptic.

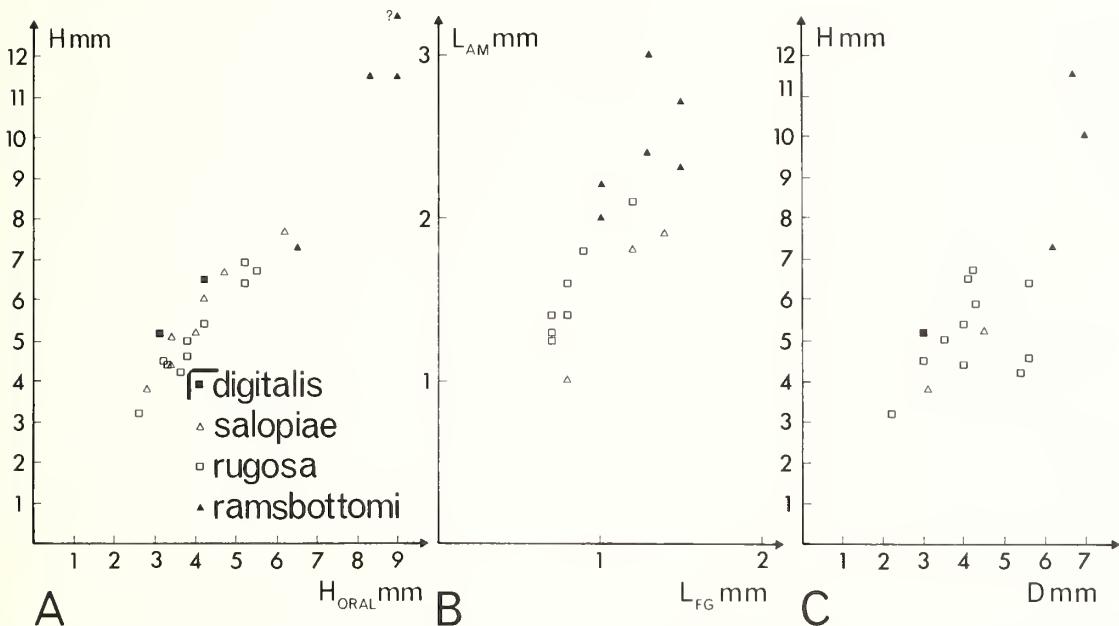
Subvective system. The ambulacra commence as five broad main grooves in the radial furrows between the coronal processes. In the floor of each main groove are two narrow food grooves which may unite near the mouth, but in some species remain separate along the entire length of the main groove. The main grooves terminate in a primary ambulacral plate, which bears two rounded facets of which the left (as viewed from the mouth down the ambulacrum) is always the smaller. The free arms are biserial and give rise to biserial lateral branches (brachioles) alternately. The arms are strongly



TEXT-FIG. 1. Standard measurements of coronate thecae. A, B, lateral views of thecae. C, base of theca. D, ambulacrum. H, height of theca, $H_{D\text{MAX}}$, height of theca at maximum diameter, H_{ORAL} , height of oral surface, H_{BASAL} , height of basal circlet, D, maximum diameter of theca, D_{ORAL} , diameter of oral surface, D_{BASE} , diameter of base of theca, KD, diameter of columnal facet, L_{AM} , length of ambulacrum, L_{FG} , length of food groove.

coiled when at rest (like the proboscis of a butterfly) and must have been considerably longer than the coronal processes when extended for feeding.

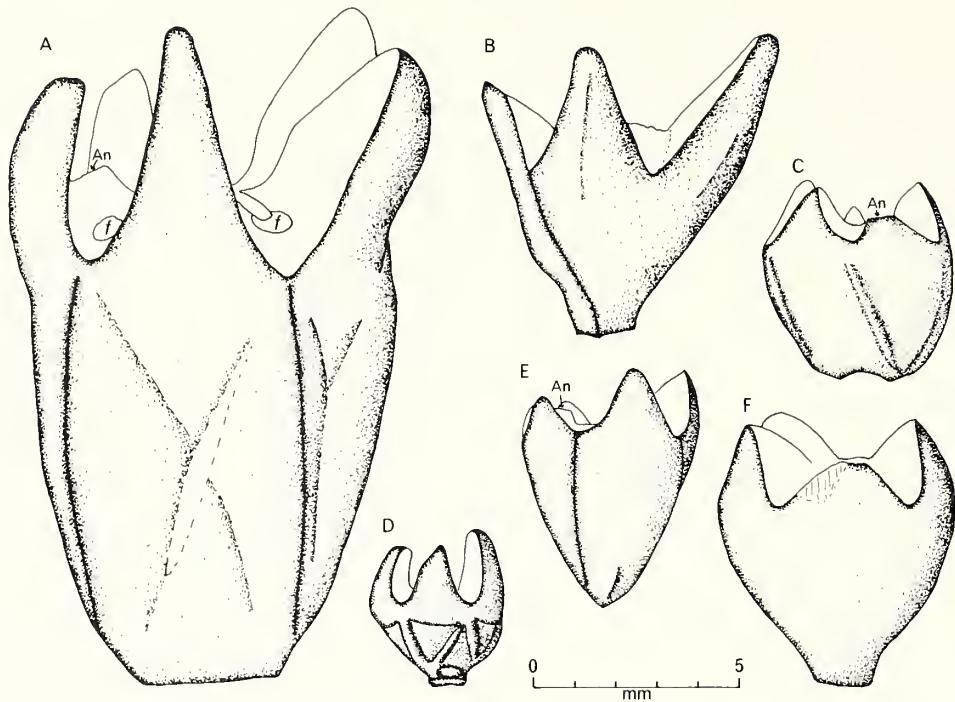
Measurements taken from specimens are explained in text-fig. 1 and summarized in Table 1. Although many parameters can be defined, it is not easy to differentiate between species graphically (text-fig. 2) due to the extreme similarity of thecae. Three bivariate plots are given; thecal height against height of the oral surface (2A), ambulacrual length against length of radial furrows (2B), and thecal height against thecal diameter (2C). The best separation is given by text-fig. 2B, although the graphs suffer from a lack of data as most of the available specimens are not sufficiently well preserved to allow many measurements to be taken.



TEXT-FIG. 2. Bivariate plots of some of the measurements shown in text-fig. 1. A, height against height of oral surface. B, length of ambulacrum against length of food groove. C, height against diameter.

CHARACTERS OF THE INCLUDED GENERA

Brett *et al.* (1983) provided a very detailed and accurate description of *S. angulatus* Conrad, 1842, the first coronate to be described. They thus settled the basic characters of the type species of the type genus of the only family recognized within the Coronata. However, the status and detailed morphology of the other genera remain uncertain, as do the phylogenetic relationships of the group as a whole. North American coronates, including *S. angulatus*, are exclusively Silurian, whereas in Europe Ordovician representatives are definitely known in Britain (King and Wilcockson 1934, and herein), Bohemia (Barrande 1887), France (Chauvel and Le Menn 1973), Spain (Chauvel and Le Menn 1979), and Sweden (Regnell 1945) and probably occur in Portugal as well (Delgado 1908). Coronates form a small but very distinctive group of pelmatozoan echinoderms. As far as is known all species and genera share an identical arrangement of thecal plates. Features which vary are general thecal shape, relative proportions of the coronal processes, surface ornament, and relative size of the stem (text-fig. 3), none of which is usually considered the type of character on which genera should be defined. Indeed it is not difficult to argue the case for assigning all known species to one genus, for which *Stephanocrinus* Conrad, 1842, is the oldest available name.



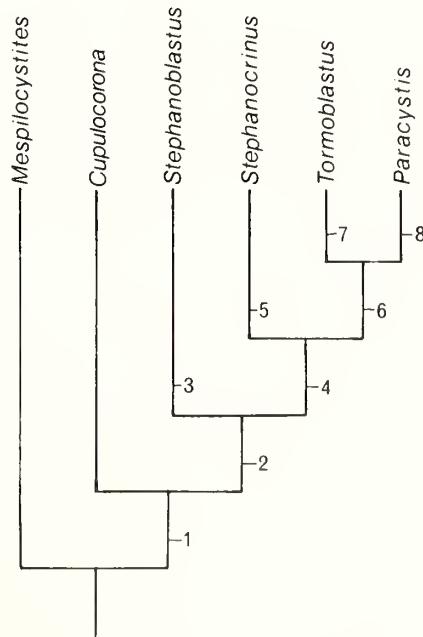
TEXT-FIG. 3. Thecal profiles in coronate genera. A, *Stephanocrinus*. B, *Mespilocystites*. C, *Paracystis*. D, *Tormoblastus*. E, *Stephanoblastus*. F, *Cupulocorona* gen. nov. All based on the type species of the genera. An, anus, f, primary ambulacral plate.

Nevertheless, some of the variations within the Coronata seem to be of phylogenetic significance. *Mespilocystites bohemicus* Barrande, 1887 (text-fig. 3B) from the Lower Caradoc of Trubsko, Czechoslovakia, is the oldest known species and a suitable starting point for comparisons (see Paul 1985, for a full description). It is characterized by a relatively low, broadly conical cup with very prominent coronal processes reaching half the total height which flare outwards so that their tips mark the widest part of the theca. All later forms have coronal processes that curve inwards towards their tips and in most the widest part of the theca is level with the oral surface. *M. bohemicus* also has strongly geniculate radial furrows between the coronal processes. The ambulacral grooves radiate horizontally from the mouth and terminate in facets for the arms which lie about half-way from the mouth to the periphery of the oral surface. Beyond the arm facets the radial furrows slope steeply downwards at an angle of about 40°. All other species, except *M. tregarvanicus* Le Menn from the Ashgill of Brittany, have planar or gently convex radial furrows, although the position of the arm facet varies from species to species. The base of the theca in *M. bohemicus* protrudes slightly and is triangular in cross-section. Within the triangle is a narrow, circular stem facet about one-tenth the diameter of the oral surface. The ornament of the main cup plates consists of obvious fine ridges which form rhombic patterns across plate sutures.

Several changes to this basic morphology had already occurred in the Caradoc, from which two Swedish species are known. *Paracystis ostrogothicus* Sjöberg, 1915 (text-fig. 3C), differs in having planar radial furrows, much lower coronal processes, and a stem facet which is impressed into the base of the theca. The corners of the basal triangle hang down slightly over the stem and the profile of the cup is a regular bowl shape. The surface ornament is composed of much coarser ridges than those of *M. bohemicus* and there are even more prominent ridges which form a V W pattern

around the theca, with the base of the V centred on the azygous basal, i.e. in the AB interray. The other Swedish Caradoc species, although discovered by F. A. Bather in 1907, has yet to be described. It has a slightly angular, bud-shaped theca with a minute stem facet about one-twenty-fifth of the diameter of the oral surface. From this facet three sharp ridges radiate to the points of the V and W angles on the lateral surface of the theca, so that the base of the theca is triradiate, not triangular. Otherwise cup plates are almost completely smooth and show only faint traces of concentric growth lines. *Stephanoblastus mirus* (Barrande 1887), from the Wenlock of Czechoslovakia is the only other described species with a triradiate base (text-fig. 3E) and is similar to the Swedish species, but it is more elongate and has very fine rhombic ridges on cup plates. *S. mirus* was made type species of *Stephanoblastus* by Jaekel (1918, p. 110) and it seems that this line became established in the Caradoc.

Tormoblastus bodaee Jaekel, 1927 (text-fig. 3D), is known from a unique type specimen which has a conical theca with prominent VW ridges and a protruding triangular base which bears three horizontal flanges. Each flange is formed by two adjacent basals. Most of the remaining species fall into two distinct genera, *Stephanocrinus* and a new genus. *S. angulatus* Conrad, 1842 (text-fig. 3A), type species of *Stephanocrinus*, has a tall, steeply conical theca with tall coronal processes and a thecal profile that is slightly concave at the level of the basal : radial sutures. It also has prominent ridges in a VW pattern as well as finer ridges in rhombs. The second genus has a low, conical to cup-shaped theca with a triangular basal prominence, no VW ridges but finer ridges in rhombic sets, and generally low coronal processes (text-fig. 3F). It resembles *M. bohemicus* except that the coronal processes do not flare, the radial furrows are usually planar, and the theca is generally cup-shaped rather than conical. This genus lacks a suitable name and we propose *Cupulocorona* for it (see below). Both *Stephanocrinus* and *Cupulocorona* were already present in the Ashgill. *S. ramsbottomi* occurs in the Hirnantian of northern England, south-west Wales, and in the Boda Limestone (Ashgill) at Osmundsberget and Skålberget, Dalarna, Sweden, while a species of *Cupulocorona* also occurs in the Boda Limestone at Boda and Osmundsberget, and three new species from the Ashgill of Britain are described below. Our view of the evolutionary relationships of these genera is shown in text-fig. 4.

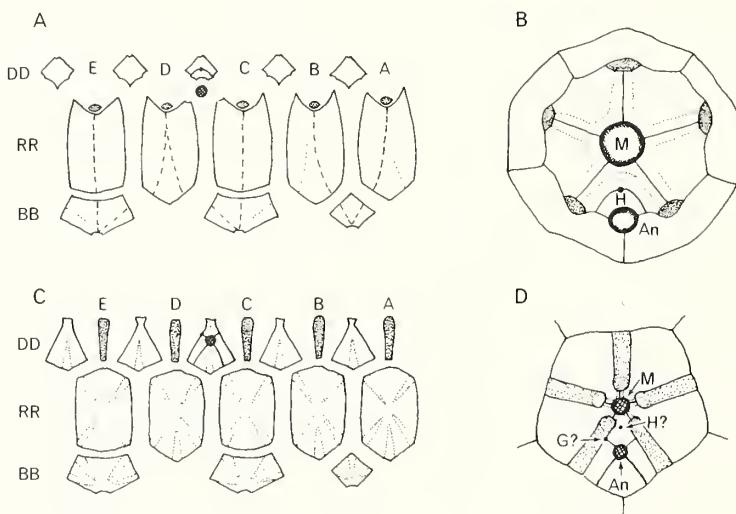


TEXT-FIG. 4. Cladogram showing inferred relationships between coronate genera. Synapomorphies (1-8) as follows: 1, loss of geniculate radial furrows; 2, development of VW pattern of ridges or angles; 3, very narrow stem and triradiate base to theca; 4, development of two additional ridges between V and W ridges; 5, tall conical theca with concave lateral surfaces; 6, ornament of coarse ridges only; 7, basal flanges; 8, bowl-shaped theca.

PHYLOGENETIC RELATIONSHIPS

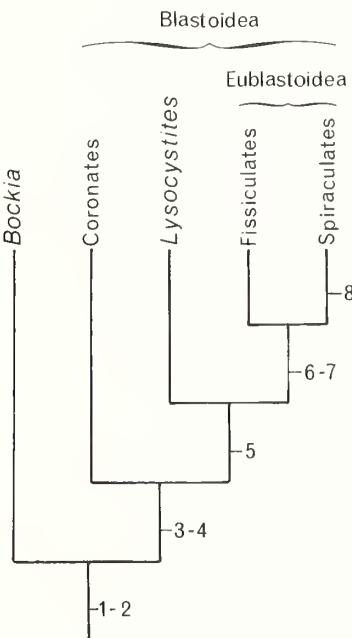
The systematic position of coronates has given rise to considerable debate. Coronates have been variously assigned to the crinoids (e.g. Wachsmuth and Springer 1886, p. 283; Bather 1900, p. 145; Fay 1962, p. 209; 1978, p. T575) or the blastoids (e.g. Etheridge and Carpenter 1886; Jaekel 1918, p. 109). Sprinkle (1980) considered them to be ancestral to the blastoids, while Brett *et al.* (1983) erected a new class, the Coronoidea, for them. Coronates share common features with blastoids and the enigmatic Silurian genus *Lysocystites*, most recently described by Sprinkle (1973, p. 139). Blastoids, coronates, and *Lysocystites* all have very similar arrangements of cup plates, including the following: three basals with the azygous basal in the AB interray, five radials, four single deltoids and two or more anal deltoids in the CD interray, and five radially positioned plates at the bases of the ambulacra. This combination of characters is not found in any other group of pelmatozoans.

The radially positioned plates at the bases of the ambulacra demonstrate most clearly the close affinities of blastoids, coronates, and *Lysocystites*. Blastoids differ from all other pelmatozoans in having hydrospires and lancet plates beneath the ambulacra. Hydrospires are an autapomorphy of the Blastoidea, being without homologue in other echinoderms; the lancet plate is not. Coronates have a single plate at the base of each arm which lies between the radial and two adjacent deltoids (text-fig. 5B). An erect arm with alternate biserial branches (brachioles) arises from this plate. As Sprinkle (1980) pointed out, to derive a blastoid ambulacrum from a coronate arm requires extension of the primary ambulacral plate to become the lancet and the development of a recumbent ambulacrum on top of it. *Lysocystites* (text-fig. 5C, D) has five elongate, radially positioned plates between the deltoids at the adoral ends of which are facets for erect ambulacra of unknown structure.



TEXT-FIG. 5. Plate diagrams in coronates and *Lysocystites*. A, B, Coronates. A, lateral view (broken lines indicate V and W ridges, dotted lines additional ridges found in *Stephanocrinus*, *Tormoblastus*, and *Paracystis*); B, oral surface. C, D, *Lysocystites*. C, lateral view (dotted lines indicate outlines of triradiate thecal pore structures); D, oral surface. A-E, Carpenter radia; An, anus; BB, basal plates; DD, deltoid plates; G, gonopore; H, hydropore; M, mouth; RR, radial plates; supposed homologues of blastoid lancet plates stippled. Note that these plates bear the facets for erect arms and always lie in a radial position between a radial plate and two deltoids. Note also that the mouth frame is composed of five deltoids even in *Lysocystites* where they are elongate.

These plates lie between two deltoids and are in contact with a radial. In our view they, too, are homologues of the lance plate in blastoids. Coronates, blastoids, and *Lysocystites* differ in their pore structures. *Lysocystites* has unique pore structures running to the corners of the basals, radials, and deltoids. Coronates have n-shaped canals within the coronal processes (see Brett *et al.* 1983, for a thorough description), while blastoids have hydrospires. Brett *et al.* (1983) have argued that the differences between the ambulacra and pore structures in the Blastoidea and Coronata warrant the recognition of a separate class for the latter. Whether one accepts this new class or not, *Lysocystites* has the same taxonomic status as coronates and blastoids. Since it is clearly possible to infer relationships between blastoids, coronates, and *Lysocystites* (text-fig. 6), an alternative course of action is to unite the three within an enlarged class Blastoidea. With the exception of the inclusion of *Lysocystites* and the omission of the parblastoids, this is essentially the classification advanced by Jaekel (1918, p. 107 *et seq.*).



TEXT-FIG. 6. Cladogram showing inferred relationships between the 'eocrinoid' *Bockia*, the coronates, and blastoids. Synapomorphies (1–8) as follows: 1, three basal plates; 2, erect, biserial, pinnate arms; 3, cup formed by BB, RR, and DD only; 4, ambulacra on distinct base-plate (= lance in eublastoids); 5, elongate ambulacral base-plate; 6, recumbent ambulacra; 7, hydrospires; 8, spiracles.

There remains the question of the ancestry of the Blastoidea, as modified and enlarged here. The most likely candidate is the 'eocrinoid' *Bockia*, even though at first sight it differs dramatically from blastoids. *Bockia* shares the following characters with blastoids *sensu lato*: a narrow circular stem, a cup with three basal plates (unfortunately the position of the smallest basal with respect to the Carpenter ambulacra remains unknown), and erect, biserial arms with alternating biserial lateral branches (brachioles) which arise from an oral prominence that had four normal deltoids and three posterior deltoids in the CD interray. The ambulacral structure is similar to that found in coronates, although not absolutely identical (see Bockelie 1981, for a more complete description of *Bockia*). To transform *Bockia* into a corinate requires cessation of plate addition early in growth, but after the basals, radials, and deltoids had formed, development of coronal processes, and the incorporation of the primary ambulacral plates into the theca. These last plates may have been derived from the small plates in the oral prominence of *Bockia* or alternatively they may be enlarged ambulacral plates. Regrettably the details of this part of the cup in *Bockia* are insufficiently known to

settle this point. The blastoid lineage was relatively successful, but ultimately became extinct in the Permian.

SYSTEMATIC PALAEONTOLOGY

Subphylum BLASTOZOA Sprinkle, 1973

Class BLASTOIDEA Say, 1825

Subclass CORONATA Jackel, 1918

Family STEPHANOCRINIDAE Wachsmuth and Springer, 1886

Definition. Pelmatozoans with a slender homeomorphic stem; theca formed of three basals (the azygous in the AB interray), five radials, six deltoids (a sub- and super-deltoid in the CD interray and one each in the other four interrays), five primary ambulacral plates each bearing two ambulacral facets, five interradial oral cover plates of which the one in the CD interray is slightly the largest, ten long, thin ambulacral cover plates (a pair in each ambulacrum); deltoids and radials produced into erect coronal processes containing n-shaped canals; oral surface with three orifices, a large central mouth, a moderately large anus in the CD coronal process and covered by a pyramid of three or four anal cover plates, and a small slit-like hydropore on the sub-superdeltoid suture between the anus and the mouth; primary ambulacral plates bearing erect, biserial, pinnate arms with biserial lateral branches (brachioles), the two facets of the primary ambulacral plate bearing the main arm trunk and the first lateral branch.

Genus STEPHANOCRINUS Conrad, 1842

Type species. By monotypy, *Stephanocrinus angulatus* Conrad, 1842, from the Middle Silurian, Rochester Shale, of New York State.

Diagnosis. Narrow stem, large, elongate, conical theca with a triangular base, often with concave sides and with low or high coronal processes, planar radial furrows, and ornament of very strong VW ridges as well as finer ridges in rhombic sets.

Stephanocrinus ramsbottomi sp. nov.

Plate 62, figs. 1, 5, 6, 8; Plate 63, fig. 6; text-figs. 7A, 8B

v1907 New cystidean; Reed, p. 537.

v1934 *Stephanocrinus* sp.; Bather in King and Wilcockson, p. 17.

Derivation of species name. In honour of Dr. W. H. C. Ramsbottom.

EXPLANATION OF PLATE 62

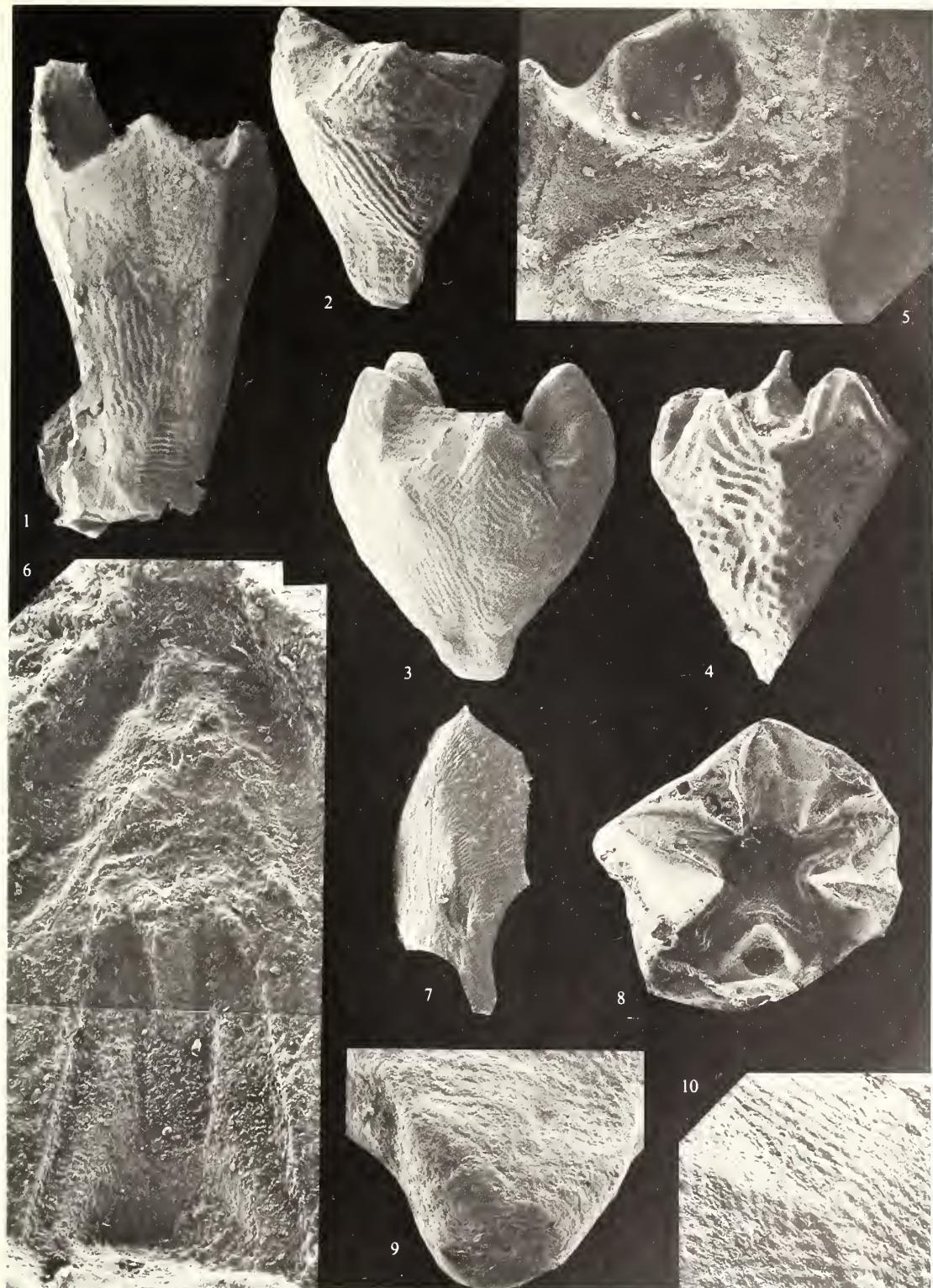
Figs. 1, 5, 6, 8. *Stephanocrinus ramsbottomi* sp. nov. 1, 8, holotype, BMNH E25427. 1, lateral view of theca, $\times 8$. 8, oral surface, $\times 8\cdot3$. 5, BMNH E25428. Anus, two ambulacra, and part of the mouth, $\times 22$. 6, BMNH E25426. Ambulacrum showing paired food grooves (mouth below), $\times 50$.

Figs. 2, 3, 9, 10. *Cupulocorona salopiae* gen. et sp. nov. 2, BMNH E45531. Lateral view of the theca, $\times 15$. 3, BMNH E45532. Lateral view of theca, $\times 11$. 9, BMNH E6393. Oblique view of the triangular base of theca. The stem articulated on the depressed, circular facet, $\times 28$. 10, BMNH E45530. Sutures between two radials (left) and a basal, preserved in positive relief, $\times 24$.

Fig. 4. *Cupulocorona rugosa* gen. et sp. nov. SM A31002a. Lateral view of theca, $\times 12$.

Fig. 7. ?*Stephanocrinus* s. l. sp. BMNH E69218. Lateral view of theca (orientation unknown), $\times 13$.

All scanning electron micrographs of latex casts from natural moulds, except figs. 2, 3, 9, 10.



DONOVAN and PAUL, coronate echinoderms

Diagnosis. Low, triangular coronal processes, with ambulacratal facets about half-way from the mouth to the periphery of the oral surface, and with a prominent convex ridge aboral to the facets.

Types. Holotype, British Museum, Natural History, (BMNH) E25427 from the Hirnantian at Hunterstye, north-west Yorkshire. Eighteen paratypes in BMNH and Sedgwick Museum, Cambridge (SM).

Other material. Twenty-one thecae, all of which are external moulds unless otherwise stated. BMNH E25426, E25427a, b, E25428a-d (a = internal mould); SM A31830, 1, 2a, b, 3a, b, 4-7 (internal moulds), A32077, A39061, 2a, b, A41084a-d (a = internal mould), A109797/8 (part and counterpart), X.772-X.774.

Horizons and localities. This species is known from three British localities, two of which indicate a definite Hirnantian age.

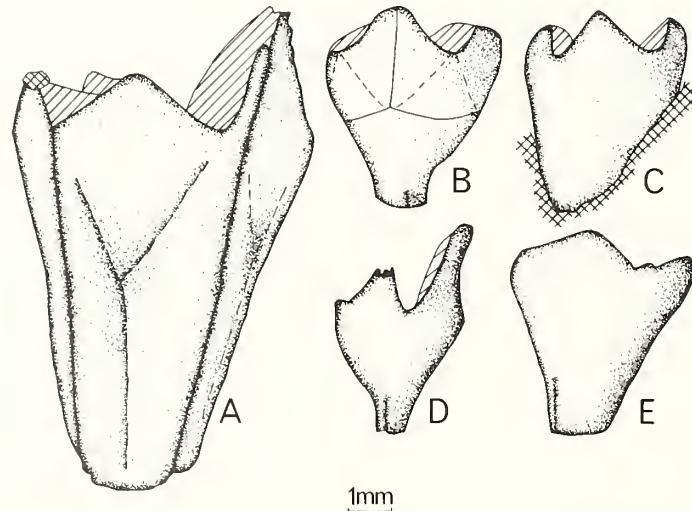
1. Ashgill Shales, old quarry on Hunterstye, Upper Crummackdale, Austwick district, north-west Yorkshire, NGR SD 780716. King and Wilcockson (1934, p. 17) also identified *Phacops* cf. *mucronata*, *Meristina crassa*, and *Rafinesquina* cf. *Strophomena hirnantensis* from this locality. Williams *et al.* (1972) regard the Ashgill Shales in this area to be of Hirnantian age, based on assessment of the brachiopod fauna by Wright (1968, table 3).

2. St. Martin's Cemetery Beds, roadside 110 m west of St. Martin's Cemetery, Haverfordwest, Dyfed, South Wales (Reed 1907, Cantrill 1907). Hirnantian (Williams *et al.* 1972, fig. 5).

3. North side of the bend in the lane from Keisley Hamlet to the west quarry, Keisley, Westmorland, NGR NY 712238. The precise horizon is unknown, but may be Lower Llandovery in age (Wright 1982).

In addition, specimens from the Boda Limestone (Ashgill) at Osmundsberget and Skålberget, Dalarna, Sweden, appear to belong to this species.

Description. Theca angular, elongate conical, with a pentagonal oral surface (Pl. 62, fig. 8; text-fig. 8B) and triangular base. The five angles of the oral surface joined to the three at the base by prominent ridges which form a V (Pl. 63, fig. 6) with its base in the AB interray, and a W with the tops in the C, D, and E rays. Faces of the theca slightly concave (Pl. 62, fig. 1; Pl. 63, fig. 6; text-fig. 7A). Stem facet round, usually more than half the diameter of the triangular base. Coronal processes triangular, varying from low with straight sides (Pl. 63, fig. 6) to high with incurved sides (Pl. 62, fig. 1). Ornament of low ridges arranged in rhombic patterns (Pl. 62, fig. 1; Pl. 63, fig. 6). Ambulacratal grooves extend about half-way along the radial furrows (Pl. 62, fig. 5). Ambulacratal, oral, and anal



TEXT-FIG. 7. Thecal profiles in British coronates. A, *Stephanocrinus ramsbottomi*, holotype, BMNH E25427. B, *Cupulocorona salopiae*, holotype, BMNH E6390. C, E, *C. rugosa*, C, paratype, SM A31002a. E, paratype, SM A31261b. D, *C. digitalis*, holotype, SM A40229.

cover plates unknown. Mouth central, circular. Anus circular, about half the diameter of the mouth (Pl. 62, figs. 6, 8; text-fig. 8B). Oral surface slopes slightly away from the mouth.

Discussion. *S. ramsbottomi* is the largest British coronate and is also the earliest member of the genus *Stephanocrinus* as we understand it. The earliest American species are from the Upper Llandovery (C_5), Hopkington Formation (Brett *et al.* 1983, p. 632). The present species differs from *S. angulatus* in having a plate ornament of ridges rather than rows of tubercles, lower coronal processes, the ambulacral facets nearer the mouth, and a more angular theca. It differs from other British coronates in not having a cup-like outline (text-fig. 7).

?*Stephanocrinus sensu lato* sp.

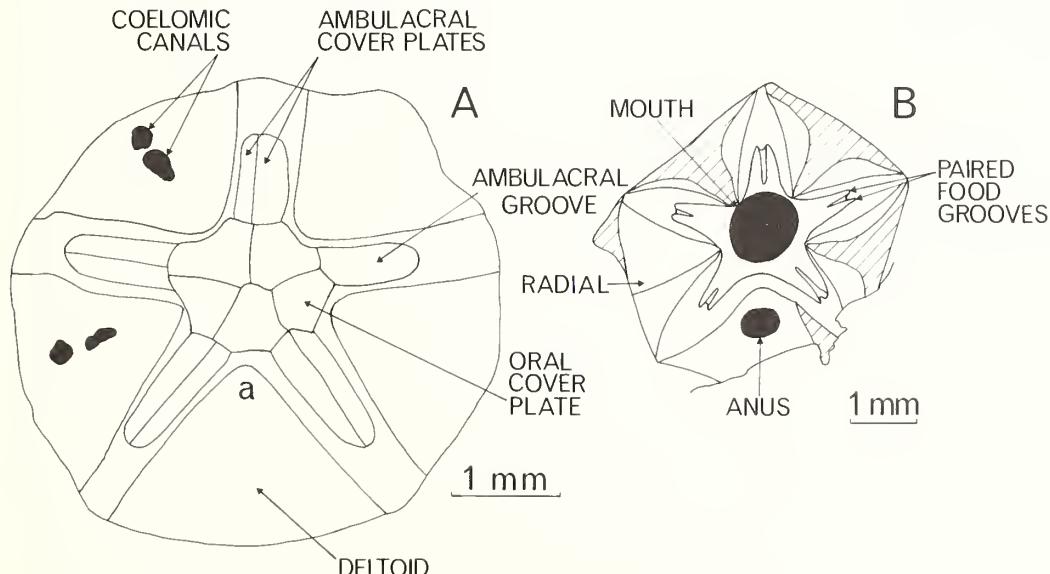
Plate 62, fig. 7; Plate 63, fig. 1

Material. A single, incomplete external mould, BMNH E69218, collected by C.R.C.P.

Horizon and locality. Sholeshook Limestone (Cautleyan; Price 1973, 1980), Sholeshook railway cutting, near Haverfordwest, Dyfed, South Wales, NGR SM 968171.

Description. The specimen is an external mould, without counterpart, of part of a theca (Pl. 62, fig. 7). Neither oral surface nor base of the cup visible. Part of two sides of theca apparent, the junction between them angular, suggesting a species of *Stephanocrinus*. Theca probably pentagonal in cross-section. On one side an ornament of fine striae is preserved (Pl. 63, fig. 1) which fan out and lie between 40° and 80° to the angle between the sides of the theca. On the second side the striae are subparallel to this ridge. The specimen is 3.2 mm wide by 7.6 mm long, individual striae about 0.07 mm wide.

Discussion. This specimen has a much finer ornament than other specimens from the Sholeshook Limestone (i.e. *Cupulocorona rugosa* gen. et sp. nov.). The theca is more angular and, apparently, proportionately more conical. The incomplete preservation precludes a more detailed description. The specimen seems to represent a stephanocrinid with an angular theca, but without better material a definite generic assignment cannot be made.



TEXT-FIG. 8. Oral surfaces of British coronates. A, *Cupulocorona salopiae*, holotype, BMNH E6390, a, approximate position of anus. B, *Stephanocrinus ramsbottomi*, holotype, BMNH E25427.

Genus CUPULOCORONA gen. nov.

Type species. Cupulocorona salopiae sp. nov.

Derivation of generic name. From the Latin *cupula* = a small cask, *corona* = a crown.

Diagnosis. Narrow stem, conical to cup-shaped theca with protruding triangular base and generally low coronal processes, planar or gently convex radial furrows, ornament of fine to coarse ridges in rhombic sets, but no prominent V W ridges.

Cupulocorona salopiae sp. nov.

Plate 62, figs. 2, 3, 9, 10; Plate 63, figs. 2, 3; text-figs. 7B, 8A

v1952 *Stephanocrinus salopiae*; Ramsbottom ms.

Derivation of species name. From the adjective Salopian = of Shropshire.

Diagnosis. Blunt coronal processes, pyriform theca with plate suture emphasized by low ridges.

Types. Holotype, BMNH E6390, paratypes, BMNH E6392–6394, E45530–45532.

Other material. Seven complete thecae, five of which are distorted.

Horizon and locality. The specimen labels state: 'Silurian. Lower Wenlock Shales, Buildwas Beds. E. bank of River Severn, a short distance above Buildwas Bridge, Shropshire.' Vine (1882, table, p. 48) records calyces of echinoderms from Maw's samples 36 and 37 in the Buildwas Beds, and the records probably refer to this species. The Buildwas Beds are of early Wenlock age, from mid-*centrifugus* zone to mid-*riccartonensis* zone (Cocks *et al.* 1971). It is not known if Maw's samples came from a single horizon or were gathered from throughout the outcrop. The specimen labels seem to refer to locality 132 of Dean (1968).

Description. Theca pear-shaped (Pl. 62, figs. 2 and 3). Base triangular with rounded corners (Pl. 62, fig. 9), stem cicatrix circular and depressed. Thecal cross-section changes from triangular to rounded pentagonal just above the base. Coronal processes large and triangular, with blunt angles (text-fig. 7B). Sutures between adjacent plates bear broad ridges (Pl. 62, fig. 10). Aboral surface of theca ornamented with fine ridges in rhombic patterns. Ambulacra bear paired food grooves, which slope gently away from the mouth and extend about 65% of the way to the periphery of the oral surface (Pl. 63, figs. 2 and 3; text-fig. 8A). Food grooves concealed by paired ambulacral cover plates. Five oral cover plates lie interradially over the mouth. The anus has not been identified with certainty, although the approximate position can be predicted (text-fig. 8A). The hydropore has not been seen. Two broken coronal processes, in the DE and EA interrays of the holotype, expose paired coelomic canals within. Measurements are given in table 1.

Cupulocorona rugosa sp. nov.

Plate 62, fig. 4; Plate 63, figs. 4, 7–9; text-fig. 7C, E

Derivation of species name. From the Latin *rugosa* = rough, corrugated.

EXPLANATION OF PLATE 63

Fig. 1. ?*Stephanocrinus* s. l. sp. BMNH E69218. Detail of ornament, $\times 55$.

Figs. 2, 3. *Cupulocorona salopiae* gen. et sp. nov. Holotype, BMNH E6390. 2, oral cover plates (centre) and five pairs of ambulacral cover plates (A ray above), $\times 30$. 3, oral surface (anus below), $\times 12.3$.

Figs. 4, 7–9. *Cupulocorona rugosa* gen. et sp. nov. 4, SM A31813. Oral surface (anus below), $\times 12.3$. 7, SM A40187. Lateral view showing base of theca, $\times 21$. 8, holotype, SM A31004b. Lateral view, $\times 15.5$. 9, SM A53930a. Lateral view, $\times 13$.

Fig. 5. *Cupulocorona digitalis* gen. et. sp. nov. Holotype, SM A40229, $\times 15$.

Fig. 6. *Stephanocrinus ramsbottomi* sp. nov. SM A109798. Lateral view of crushed theca, $\times 8$.

All scanning electron micrographs of latex casts from natural moulds, except figs. 2, 3.



DONOVAN and PAUL, coronate echinoderms

TABLE 1. Measurements in mm of British coronate echinoderms

Spec. No.	D	D _{BASE}	D _{ORAL}	H	H _{DMAX}	H _{ORAL}	H _{BASAL}	KD	L _{FG}	L _{AM}
<i>Stephanocrinus ramsbottomi</i>										
BM E25426	6.8	?	6.7	?	?	?	?	?	1.0	2.2
BM E25427	6.7	2.0	6.3	11.5	= H	9.0	?	0.7	1.3	2.4
BM E25428	7.0	?	7.0	10.0	= H?	7.7?	?	?	1.5	2.3
BM E30485	Internal mould									
SM A31830	Poorly preserved base of a theca									
SM A31831	6.0	1.1	6.0	?	= H?	6.0	?	1.1	?	?
SM A31832	8.0	1.8	= D	12.0	9.2	9.2	?	1.3	0.7	2.4
SM A31833	8.1+	2.0?		13.0?	= H	9.0?	?	?	1.3	3.0
SM A31834-7	All internal moulds									
SM A32077	Deformed oral surface only									
SM A39061	7.3+	?	7.3	?	?	?	?	?	1.5	2.7
SM A39062	6.2	1.0	5.7?	7.3	= H	6.5	?	0.8	1.0	2.0
SM A40184	Poorly preserved									
SM A109797/8	?	?	?	11.5	= H?	8.3	?	?	?	?
<i>Cupulocorona salopiae</i>										
BM E6390	4.5	1.2	4.4	5.2	= H	4.0	2.0	0.6	1.2	1.8
BM E6392	?	1.6	?	6.7	= H	4.7	?	0.6	?	?
BM E6393	?	1.4	?	6.0	= H	4.2	3.2?	0.8	?	?
BM E6394	?	1.1	= D	4.4	= H	3.4	?	0.5	?	?
BM E45530	?	1.6	?	7.7	6.2	6.2	4.0	0.8	1.4	1.9
BM E45531	3.1	1.2	3.1	3.8	3.4	2.8	1.6?	0.65	0.8	1.0
BM E45532	?	1.2	?	5.1	3.8	3.4	2.4	0.6	?	?
<i>Cupulocorona digitalis</i>										
BM E30484	?	1.0	4.1	6.5	?	4.2	?	?	?	?
SM A40229	3.0	0.6	= D	5.2	= H	3.1	?	?	?	?
<i>Cupulocorona rugosus</i>										
SM A31001	5.6	?	5.4	4.6	= H	3.8	?	?	1.2	2.1
SM A31002	4.0	?	4.0	4.4	3.3	3.3	?	?	0.8	1.6
SM A31003	4.0?	?	3.8	5.4	4.2	4.2	?	?	?	1.7
SM A31004	4.2+	?	4.2	?	?	?	?	?	0.8	1.4
SM A31259	5.6	?	5.6	6.4+	5.2+	5.2+	?	?	0.9	1.8
SM A31260	4.2+	0.7?	4.0+	6.7+	= H	5.5+	?	0.7	?	?
SM A31261	4.3?	0.9	4.1	5.9	= H	5.2	?	0.6	0.7?	1.7
SM A31813	4.3	?	4.0	?	= H	?	?	?	0.7	1.4
SM A40185	Preserves part of the cup ornament only									
SM A40186	3.0+	0.8	= D	4.5	= H	3.2	?	0.6	?	?
SM A40187	2.2	0.6	= D	3.2	= H	2.6	?	0.5	?	?
SM A40188	3.5	0.9	= D	5.0	= H	3.8	?	0.6	0.7	1.4
SM A40189	3.2?	?	3.2	?	?	?	?	?	0.7	1.25
SM A53929	5.4	1.6	5.0	4.2	= H	3.6	?	?	?	?
SM A53930	Poorly preserved									

Diagnosis. Coarse-ribbed ornament and coronal processes which are lower than wide.

Types. Holotype, SM A31004, from the Upper Ordovician, Redhill Beds, at Prendergast Place near Haverfordwest, Dyfed, South Wales, plus fourteen paratypes (SM).

Other material. Fifteen specimens in the Sedgwick Museum collections (all external moulds unless otherwise indicated). A31001a, b (part and counterpart), A31002a, b (part and counterpart), A31003, 4a, b (a = internal

mould), A31259a, b (part and counterpart), A31260, 1a, b (part and counterpart), A31813, A40185–40187, 8a, b (part and counterpart), 9a, b (a = internal mould), A53929a, b (b = artificial cast), A53930a, b (b = artificial cast).

Horizons and localities. This species is known from five localities and horizons, all of which are Ashgill in age.

1, 2. The Sholeshook Limestone, both in the railway cutting (NGR SM 968171) and at Prendergast Place (NGR SM 957166), near Haverfordwest, Dyfed, South Wales. Most of the Sholeshook Limestone is Cautleyan in age, but the youngest rocks at Prendergast Place are Rawtheyan, Zone 5, according to Price (1980).

3. The Redhill Beds at Prendergast Place which Price (1980, p. 486, table 1) considered to be confined to the Rawtheyan, Zone 5.

4. The Lower Phillipsinella Beds at locality 1 of King (1923, p. 494, fig. 2), Aber Marchnant, SW Berwyn Hills, Powys (NGR SJ 039194). These beds contain *Kloucekia robertsi* (Reed 1904) which Ingham (1977, p. 118) regarded as an important index fossil for Rawtheyan, Zone 5.

5. The Dolhir Beds (mid-Cautleyan to Rawtheyan; Hiller 1981) at two localities in the Glyn Ceiriog district, Clwyd. (a) 'Tram cutting ENE of Coed-y-Glyn-isaf' (specimen label) and (b) on the road close to, and north of, Gelli (NGR SJ 184367; Groom and Lake 1908).

Description. Thecal cross-section round (Pl. 63, fig. 8) to pentagonal (Pl. 62, fig. 4), with circular to pentagonal oral surface (Pl. 63, fig. 4) and triangular base (Pl. 63, fig. 7). Stem facet round. Coronal processes triangular, lower than wide. Ornament of coarse ridges in rhombic patterns (Pl. 62, fig. 4; Pl. 63, figs. 7–9). Ambulacral, oral, and anal cover plates unknown. Ambulacral grooves about 50% of the length of the radial furrows, with paired food grooves at their distal ends. Mouth circular to weakly pentagonal; anus circular.

Cupulocorona digitalis sp. nov.

Plate 63, fig. 5; text-fig. 7D

Derivation of species name. From the Latin *digitus* = finger.

Diagnosis. Long finger-like coronal processes, ornament of coarse ridges, conical thecal profile, and constricted base.

Types. Holotype, SM A40229, from the Ashgill, Phillipsinella Beds at Aber Marchnant, SW Berwyn Hills. Paratype, BMNH E30484.

Other material. Two thecae, the holotype being an external mould with a counterpart.

Horizons and localities. 1, type locality (see *C. rugosa*) and 2, 5 m above the Pusgillian Pen-y-Garnedd black shales at Powys Arms Quarry, Pen-y-Garnedd, south-east of Llanfyllin, Powys, possibly Cautleyan (P. J. Brenchley, pers. comm.).

Description. Theca low, conical, with a nipple-like triangular base. Stem facet not seen. Coronal processes finger-like or triangular with curved sides (neither specimen shows both sides of the theca so the precise nature of the coronal processes is not established). Ornament of coarse rhombic ridges. Oral surface not seen.

Acknowledgements. We thank Dr. D. Price, Sedgwick Museum, Cambridge, and Dr. A. B. Smith and Mr. D. N. Lewis, British Museum, Natural History, for the loan of specimens. Dr. W. H. C. Ramsbottom kindly gave us a copy of his unpublished manuscript on British and Swedish coronates. Scanning electron micrographs were produced by Mr. C. J. Veltkamp of the Botany Department, Liverpool University, and Table 1 was typed by Ms. Grainne Moloney. Some of the photomicrographs were printed by Mr. D. J. McCabe. Finally, part of this work was undertaken during the tenure of NERC research grant GR3/4732, which is gratefully acknowledged.

REFERENCES

- BARRANDE, J. 1887. *Système Silurien du centre de la Bohême. Ie partie: Recherches paléontologiques. v. 7. Classe des Échinodermes. Ordre des Cystidés*, xix + 233 pp., 39 pls. Leipzig and Prague.
 BATHER, F. A. 1900. The Echinoderma. In LANKESTER, E. R. (ed.), *A Treatise on Zoology*, vol. 3, 344 pp. London.

- BOCKELIE, J. F. 1981. The Middle Ordovician of the Oslo Region, Norway. 30. The eocrinoid genera *Cryptocrinites*, *Rhipidocystis* and *Bockia*. *Norsk geol. Tidskr.* **61**, 123–147.
- BRETT, C. E., FREST, T. J., SPRINKLE, J. and CLEMENT, C. R. 1983. Coronoidea: a new class of blastozoan echinoderms based on taxonomic reevaluation of *Stephanocrinus*. *J. Paleont.* **57**, 627–651.
- CANTRILL, T. C. 1907. Stratigraphical note. *Geol. Mag.* **44**, 537–538.
- CHAUVEL, J. and LE MENN, J. 1973. Échinodermes de l'Ordovicien Supérieur de Coat-Carrec, Argol (Finistère). *Bull. Soc. géol. miner. Bretagne Ser. c*, **4**, 39–61, pls. 1–3.
- 1979. Sur quelques échinodermes (Cystoïdes et Crinoïdes) de l'Ashgill d'Aragon (Espagne). *Géobios*, **12**, 549–587, 3 pls.
- COCKS, L. R. M., HOLLAND, C. H., RICKARDS, R. B. and STRACHAN, I. 1971. A correlation of Silurian rocks in the British Isles. *Quart. Jl geol. Soc. Lond.* **127**, 103–136.
- CONRAD, T. A. 1842. Observations on the Silurian and Devonian systems in the United States, with descriptions of new organic remains. *J. Acad. nat. Sci. Philad.* **8**, 228–280, pls. 12–17.
- DEAN, W. T. 1968. Geological itineraries in south Shropshire. *Geol. Ass. Guide*, **27**, 48 pp.
- DELGADO, J. F. N. 1908. *Système Silurian du Portugal Étude de Stratigraphie Paléontologique*, 247 pp., 4 pls. Lisbon.
- ETHERIDGE, R. JN. and CARPENTER, P. H. 1886. *Catalogue of the Blastoida in the Geological Department of the British Museum (Natural History)*, xv + 322 pp., 20 pls. London.
- FAY, R. O. 1962. Ventral structures of *Stephanocrinus angulatus* Conrad. *J. Paleont.* **36**, 206–210, pl. 35.
- 1978. Order Coronata Jaekel, 1918. In MOORE, R. C. and TEichert, C. (eds.). *Treatise on Invertebrate Paleontology. Part T. Echinodermata 2*, pp. T574–T578. Geol. Soc. Am. and Univ. Kansas Press.
- GROOM, T. and LAKE, P. 1908. The Bala and Llandovery rocks of Glyn Ceiriog (North Wales). *Quart. Jl geol. Soc. Lond.* **64**, 546–595.
- HILLER, N. 1981. The Ashgill rocks of the Glyn Ceiriog district, North Wales. *Geol. J.* **16**, 181–200.
- INGHAM, J. K. 1977. The Upper Ordovician trilobites from the Cautley and Dent districts of Westmorland and Yorkshire. *Palaeontogr. Soc. [Monogr.]*, **3**, 89–121, pls. 19–27.
- JAEKEL, O. 1918. Phylogenie und System der Pelmatozoen. *Paläont. Z.* **3**, 1–128.
- 1927. Über *Tormoblastus* n.g., eine coronate Blastoides, aus dem Ordovicium Schwedens. *Ark. Zool.* **19A** (4), 6 pp., 1 pl.
- KING, W. B. R. 1923. The Upper Ordovician rocks of the southwestern Berwyn Hills. *Quart. Jl geol. Soc. Lond.* **79**, 487–507, pl. 26.
- and WILCOCKSON, H. W. 1934. The Lower Palaeozoic rocks of Austwick and Horton-in-Ribblesdale, Yorkshire. *Ibid.* **90**, 7–31.
- PAUL, C. R. C. 1985. Ordovician and Silurian coronates from Czechoslovakia. *Geol. J.* **20**, 21–29.
- PRICE, D. 1973. The age and stratigraphy of the Sholeshook Limestone of southwest Wales. *Ibid.* **8**, 225–246.
- 1980. A revised age for the topmost Sholeshook Limestone Formation (Ashgill) of South Wales. *Geol. Mag.* **117**, 485–489.
- REED, F. R. C. 1904. New fossils from the Haverfordwest district. *Ibid.* **41**, 106–109, pl. 5.
- 1907. The base of the Silurian near Haverfordwest. *Ibid.* **44**, 535–537.
- REGNELL, G. 1945. Non-crinoid Pelmatozoa from the Palaeozoic of Sweden: a taxonomic study. *Medd. Lunds geol-miner. Instn.* **108**, 255 pp., 15 pls.
- SAY, T. 1825. On two genera and several species of Crinoidea. *J. Acad. nat. Sci. Philad.* **4**, 289–296.
- SJÖBERG, S. 1915. *Paracystis ostrogothicus* g. et sp. n., en egendomlig Pelmatozo från Östergötlands Chasmopskalk. *Geol. For. Stockholm Forhandl.* **37**, 171–178, pls. 2–3.
- SPRINKLE, J. 1973. Morphology and evolution of blastozoan echinoderms. *Spec. Publ. Mus. comp. Zool. Harv.* 284 pp., 43 pls. Cambridge, Mass.
- 1980. Origin of blastoids: new look at an old problem. *Geol. Soc. Am. Abstr. Progr.* **12**, 528.
- VINE, G. R. 1882. Notes on the Polyzoa of the Wenlock Shales, Wenlock Limestone, and Shales over Wenlock Limestone. From material supplied by G. Maw, Esq., F.L.S., F.G.S. *Quart. Jl geol. Soc. Lond.* **38**, 44–68.
- WACHSMUTH, C. and SPRINGER, F. 1886. Revision of the palaeocrinidae, pt. 3, sect. 2. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions. *Proc. Acad. nat. Sci. Philad.* (1885), 225–364, pls. 4–9.
- WILLIAMS, A., STRACHAN, I., BASSETT, D. A., DEAN, W. T., INGHAM, J. K., WRIGHT, A. D. and WHITTINGTON, H. B. 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.* **3**, 74 pp.
- WRIGHT, A. D. 1968. A westward extension of the Upper Ashgillian *Hirnantia* fauna. *Leithaia*, **1**, 352–367.

— 1982. The Ordovician-Silurian boundary at Keisley, northern England. In BRUTON, D. L. and WILLIAMS, S. H. (eds.). Abstracts for meetings 20, 21 and 23 August 1982, IVth International Symposium on the Ordovician System. *Palaeont. Contr. Oslo Univ.* **280**, 60.

S. K. DONOVAN

Department of Geology
Trinity College
Dublin 2, Eire

Present address:

Natural Environment Research Council
Polaris House
North Star Avenue
Swindon SN2 1EU
England

C. R. C. PAUL

Department of Geology
Liverpool University
Liverpool L69 3BX
England

Typescript received 1 June 1984

Revised typescript received 29 November 1984

CORTICAL DEVELOPMENT IN *CHALONERIA CORMOSA* (ISOETALES), AND THE BIOLOGICAL DERIVATION OF COMPRESSED LYCOPHYTE DECORTICATION TAXA

by KATHLEEN B. PIGG and GAR W. ROTHWELL

ABSTRACT. Several anatomically preserved stem fragments showing a wide range of surface features have been discovered among specimens of the Upper Pennsylvanian isoetalean *Chaloneria cormosa*. A comparison of the specimens demonstrates that stems produced a narrow zone of periderm, and that tissues external to the periderm accounted for a moderate increase in stem circumference by two distinctive modes of cell divisions. Depending on the presence or absence of secondary cortical tissues, on differential taphonomy, and on the level at which the cortex is exposed, the surface of a specimen may be comparable to one of several distinctive decortication morphotypes. The outer surface is similar to *Bothrodendron* and *Cyclostigma*, while specimens with leaf bases removed are reminiscent of *Stigmaria*. When fractured through the periderm a *Knoria* surface is produced, while secondary cortical features immediately external to the periderm conform to *Asolamus*. Specimens reveal the anatomical bases for decortication morphotypes and demonstrate that such genera are produced by members of Isoetales as well as Lepidodendrales.

OUR current understanding of Carboniferous vegetation relies upon plant remains that are preserved by several different modes, including compression/impresion, cellular permineralization, and mold/cast (Schopf 1975). Upper Carboniferous and Pennsylvanian fossils of varying preservational types typically exhibit differential suites of characters, and traditionally have been studied independently of one another. As a result, a great deal is known about fossils within each group, but remains preserved by different modes seldom have been correlated with the precision necessary to demonstrate whether they represent the same or different taxonomic species.

One group in which correlations of this type are of particular value is Carboniferous Lycopida. Large Palaeozoic lycophytes produced massive amounts of cortical tissue. Fractured at different surface and subsurface levels, stems typically display characteristic, widely differing features (Renault and Zeiller 1888; Weiss and Sterzel 1893; Thomas and Watson 1976). When preserved as compressions, such morphotypes (DiMichele 1983) are given generic rank but their mode of production, anatomical origin, and biological significance remain poorly understood. Among the most prominent genera are *Asolamus* Wood (1860) and *Knoria* Sternberg (1825). Although *Asolamus* has been described from numerous localities throughout North America, Europe, and Northern Africa (White 1899; Janssen 1940; Crookall 1964; Daber and Kahlert 1970; Lejal-Nicol 1972; Boersma 1978), and is a common component of many compression floras from the Appalachian Basin (Darrah 1969), it is understood only as a characteristic configuration on the rock surface. Through the years it has been described as, or confused with, such diverse structural forms as *Lepidodendron*, *Sigillaria*, *Sigillarioides*, *Pseudosigillaria*, and *Stigmaria* (Crookall 1964). It also has been interpreted as a decortication layer of numerous Carboniferous compression genera (e.g. Daber and Kahlert 1970), or as the outer surface of an otherwise unknown lycophyte stem (White 1899; Janssen 1940). In contrast, *Knoria* is known to represent a decortication surface of lepidodendreal stem genera (Solms-Laubach 1891; Thomas and Watson 1976).

Several additional taxa of Carboniferous lycophyte stem compressions exhibit features unlike those of typical lepidodendrid taxa. The genus *Bothrodendron* Lindley and Hutton (1833) originally was

described as a Carboniferous stem compression with tiny leaf scars and conspicuous halonal branch scars, but it now includes several diverse forms which undoubtedly represent more than one genus of plants. Morphotypes such as *Bothrodendron*, *Pinakodendron* (Weiss and Sterzel 1893), and some species of *Cyclostigma* Haughton (1859) are delimited by overlapping taxonomic criteria. All are characterized by rounded or lenticular leaf scars (or leaf bases) borne in a low helix and widely separated on the stem surface (Crookall 1964). Despite detailed studies of some features (e.g. cuticle and compression surfaces; Thomas 1967), anatomical features of these taxa are poorly known. Consequently, the whole plants represented by Upper Carboniferous specimens of such taxa remain poorly understood (Crookall 1964; Stubblefield and Rothwell 1981).

During the recent study of a new family of Pennsylvanian lycophytes, the Chaloneriaceae Pigg and Rothwell (1983b), several permineralized stems of *Chaloneria cormosa* were revealed on split coal-ball surfaces. Some were exposed at the outer surface of the stem (figs. 21, 22, of Pigg and Rothwell 1983a) with intact leaf bases, epidermis, and cuticle, while others were split at a variety of subsurface levels. The specimens display a wide array of configurations that are very distinct from one another. When compared to compression-impression taxa, they are similar to a variety of genera including *Cyclostigma*, *Pinakodendron*, *Bothrodendron*, *Stigmaria*, *Asolanus*, and *Knoria*. Because the histology and ontogeny of *Chaloneria* are well known, it is now possible to determine anatomical, taphonomic, and ontogenetic bases for the surface configurations that delimit several morphotypes of decortication compression taxa, and to relate more precisely these to the types of plants by which they were produced.

METHODS AND MATERIALS

Specimens of *C. cormosa* are preserved by calcareous cellular permineralization in coal balls from the Duquesne coal (Upper Pennsylvanian) where it outcrops in a roadcut on Ohio State Route 22, approximately 8 km west of Steubenville, Ohio, USA (Rothwell 1976). Surfaces were etched in 5% HCl for 30 sec. to increase contrast for photography. Some coal balls were cut perpendicular to the stem surface and peeled to determine the exact level at which the cortical tissue had split. Other specimens were peeled parallel to the stem surface to identify the anatomical basis for the surface features. Peels were mounted on microscope slides for photography.

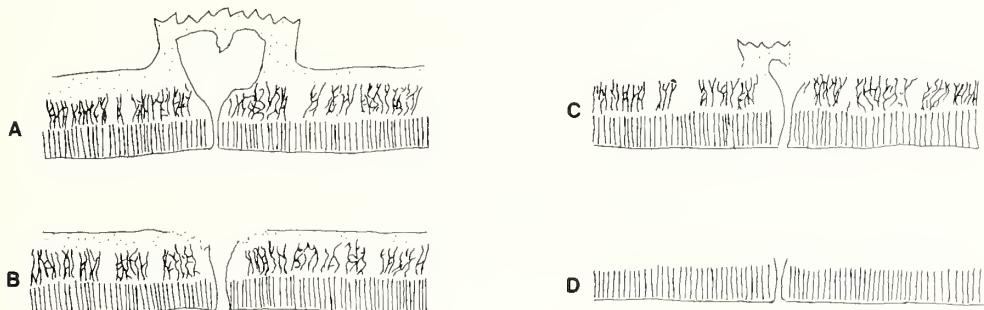
Compression specimens of *A. camptotaenia* and *cf. Bothrodendron* photographed for comparative purposes were collected from two Middle Pennsylvanian localities in eastern Ohio. The first is Dorr Run located approximately 1.7 km northwest of Nelsonville (NE $\frac{1}{4}$, NE $\frac{1}{4}$, sec. 30, Wayne Twp., Nelsonville 7.5 min. Quadrangle), Athens Co., Ohio. Stratigraphically these specimens occur in the Snow Fork shale below the Middle Kittanning coal, Middle Kittanning cyclothem, Allegheny Group. The second locality is a strip mine operated by the James Bros. Coal Co., at Mineral City (South centre, Sec. 26, Rose Twp., 7.5 min. Quadrangle), Carroll Co., Ohio. At this locality, fossils are preserved in the shale over the Lower Kittanning (Ohio no. 5 coal), Lawrence-Lower Kittanning cyclothem, Allegheny Group. Pertinent specimens and slides are housed in the Paleobotanical Herbarium, Department of Botany, Ohio University, where they bear acquisition numbers 584, 3375, 3825, 7640-7662.

DESCRIPTION

Surface Morphologies. *C. cormosa* is an Upper Pennsylvanian member of Isoetales characterized by a cormose base and an unbranched stem bearing helically arranged leaves (Pigg and Rothwell 1983a, b). Unlike typical members of Lepidodendrales that often have abutting leaf cushions prior to periderm development, the leaf bases of *Chaloneria* are separated by wide areas of stem surface (Pl. 64, fig. 1). Also unlike the leaf cushions of Lepidodendrales, *Chaloneria* leaf bases have irregularly shaped scars where the leaves become detached.

Coal-ball specimens fractured at the outer surface of the stem are characterized by helically arranged leaf bases, about 8–10 mm wide and 5 mm high separated from one another by wide areas of stem surface (Pl. 64, fig. 1; text-fig. 1A). In this regard, *Chaloneria* is similar to several other taxa (e.g. *Bothrodendron*, *Cyclostigma*; Crookall, 1964) that typically lack abutting leaf cushions (Pl. 64, figs. 6, 7; Jennings 1979). Leaf bases of *Chaloneria* have blunt lateral wings, a rounded keel, and either an

apical notch or a ligule pit (Pl. 64, figs. 1, 2). They are also somewhat bulbous, bulging out from the stem surface (Pl. 64, fig. 2), and in this regard are similar to the leaf scars popularly attributed to *Asolanus* (Crookall 1964; Darrah 1969). Distally the leaves of *Chaloneria* abruptly become much narrower (Pigg and Rothwell 1983a). No distal portions of leaves were present on fractured surfaces. When a leaf is detached at a single level the base displays either one or two vascular strands. More frequently, leaves are broken off unevenly, resulting in irregular appearing bases (Pl. 64, fig. 1) in which vascular strands are obscured. There is no evidence of an abscission zone that would provide for the production of regular scars like those on the leaf cushions of Lepidodendrales. Dark, longitudinal strips of tissue are often present on the interfoliar stem surface (Pl. 64, fig. 1), and these represent strips of epidermis and cuticle.



TEXT-FIG. 1A-D. Diagrams of cortical tissues in stems of *Chaloneria cormosa* that have significant periderm; stippled area includes outer cortex in which randomly oriented internal cell divisions occur; distorted lines indicate level at which *Asolanus*-pattern is produced; straight lines indicate periderm. Outer surface of A will appear as *Chaloneria* unless pattern of distorted cortex is impressed on surface, in which case specimen will be recognized as *Asolanus*. Outer surface of B will resemble *Stigmaria* unless pattern of distorted cortex is impressed on surface, in which case specimen will be recognized as *Asolanus*. Outer surface of C has been split at level where regardless of whether leaf bases are detached above (at left) or at interfoliar surface, specimen will exhibit *Asolanus* configuration. Cortex in D has been split at level of periderm such that both inner and outer surfaces will produce *Knoria* pattern.

In other specimens the epidermis is intact in interfoliar areas, but leaves have broken off near or below the stem surface (Pl. 64, fig. 5; text-fig. 1B). In some specimens of this type the interfoliar surface is smooth. On others there are vertically oriented, undulating striations (Pl. 64, fig. 5 at arrows) that conform to the subsurface primary cortical tissue as seen in tangential section (Pl. 64, fig. 3). The most conspicuous features of many specimens are the prominent circular or elliptical parichnos strands that accompany the leaf traces (Pl. 64, fig. 3). They are similar to appendage scars on stigmarian axes, with the rounded parichnos strands of *Chaloneria* (Pl. 64, fig. 5) corresponding to the aerenchymatos middle cortex of stigmarian appendages. There is a further resemblance with *Cyclostigma*, which in the past also has been confused with *Stigmaria* (Crookall 1964).

Two additional cortical patterns of *Chaloneria* are commonly represented on split coal-ball surfaces. Several specimens are characterized by an anastomosing pattern of diagonal striations (text-figs. 1C, 2a, b). Of these, some exhibit bulbous leaf base scars (text-fig. 2b), while in others the leaf base is broken off at a more proximal level, revealing axially elongate rather than rounded parichnos strands (text-fig. 2a). This pattern conforms to the compression taxon *Asolanus* (Wood 1860) based on the characteristic interfoliar pattern (Pl. 64, fig. 8; text-fig. 2a, b).

An additional, commonly preserved surface of *Chaloneria* cortex is characterized by densely compact cells (text-fig. 2e, g) and lacks striations or other prominent interfoliar features (text-figs. 1d,

2e). Specimens of that type each possess a vascular strand that is surrounded by an oval or vertically elongate, lenticular parichnos strand (text-fig. 2e). This type of decortication pattern is comparable to *Knorria* (Sternberg 1825).

Anatomical origin of surface features. In transverse section an immature specimen of *Chaloneria* exhibits a medullated protostele surrounded by primary cortical tissues; this pattern is also present in distal stem regions (Pigg and Rothwell 1983a). Most stems are flattened (Pl. 64, fig. 4), lacking preserved pith and inner cortex. In the inner zone of commonly preserved primary cortex the cells possess differentially thickened walls and frequently broken tangential walls (Pl. 64, fig. 4 at top). This results in a resemblance to distorted radial rows of periderm (Pigg and Rothwell 1979). Tangential sections through the zone (Pl. 64, fig. 3) reveal the undulating, vertically oriented pattern that is sometimes present on the epidermis (Pl. 64, fig. 5 at arrows). This pattern is also characteristic of the interfoliar region on the stems of many compressions, where it is interpreted as the result of distortion during diagenesis (Pl. 64, fig. 7; Rex and Chaloner 1983).

Older and more proximal stem segments exhibit secondary cortical tissues that are derived both from a continuous cambium (viz. periderm) and from the internal subdivision of individual cortical cells (Pl. 64, fig. 2). Periderm is represented by a zone of radially aligned cells with differentially thickened radial walls, and is present along the inside of the commonly preserved cortex (Pl. 64, fig. 2). In stems with little periderm (Pl. 64, figs. 4, 5) the primary cortex and epidermis remain relatively intact and unaltered. In stems with larger amounts of periderm the epidermis and cuticle are separated into longitudinally oriented strips of tissue at the periphery of the stem (Pl. 64, fig. 1). In these specimens, cortex outside the periderm appears distorted (Pl. 64, fig. 2 at sides; text-fig. 1A-C). Tangential sections of the tissue reveal narrow, vertically elongated lenticular regions where the cells are laterally expanded, and in which some internal cell divisions have occurred (text-fig. 2f). These regions alternate with areas of narrow primary cortical cells (text-fig. 2d,f). The alternation of these zones produces a pattern of discontinuous light and dark strips (text-fig. 2c) in specimens with little periderm (e.g. Pl. 64, fig. 4). Stems with a thicker zone of periderm (e.g. Pl. 64, fig. 2) have a distinctive pattern of diagonal lines in the interfoliar region. When seen on split surfaces this pattern produces the *Asolanus* configuration (text-fig. 2a,b). Cortical growth of this type undoubtedly could accommodate only a moderate increase in circumference of the stem, and this is consistent with the periderm of *Chaloneria* being up to only about 2 mm thick (Pl. 64, fig. 2). Expansion of the subepidermal cortex is accomplished by the randomly oriented subdivision of many cells (Pl. 64, fig. 2 at arrow), another

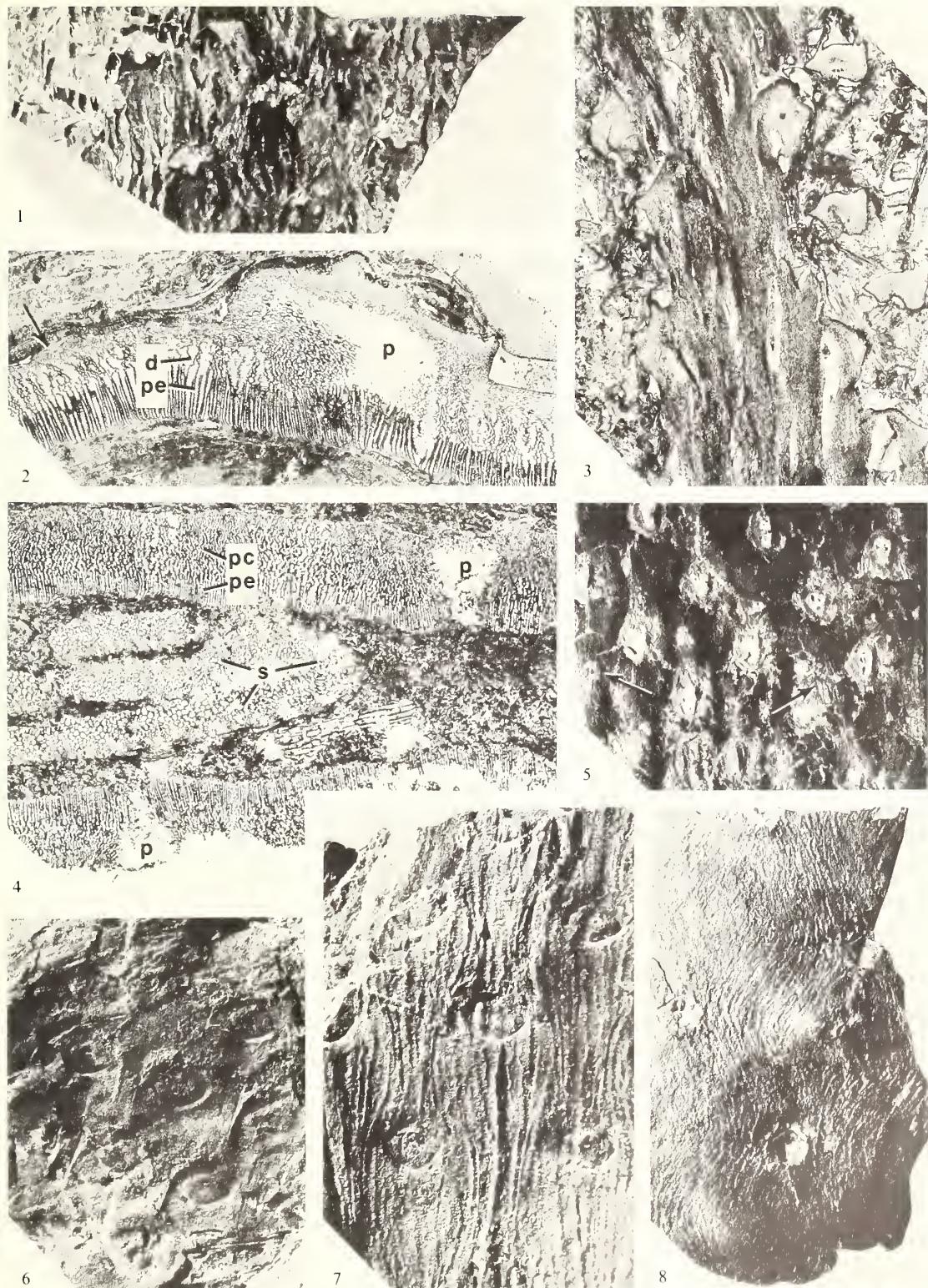
EXPLANATION OF PLATE 64

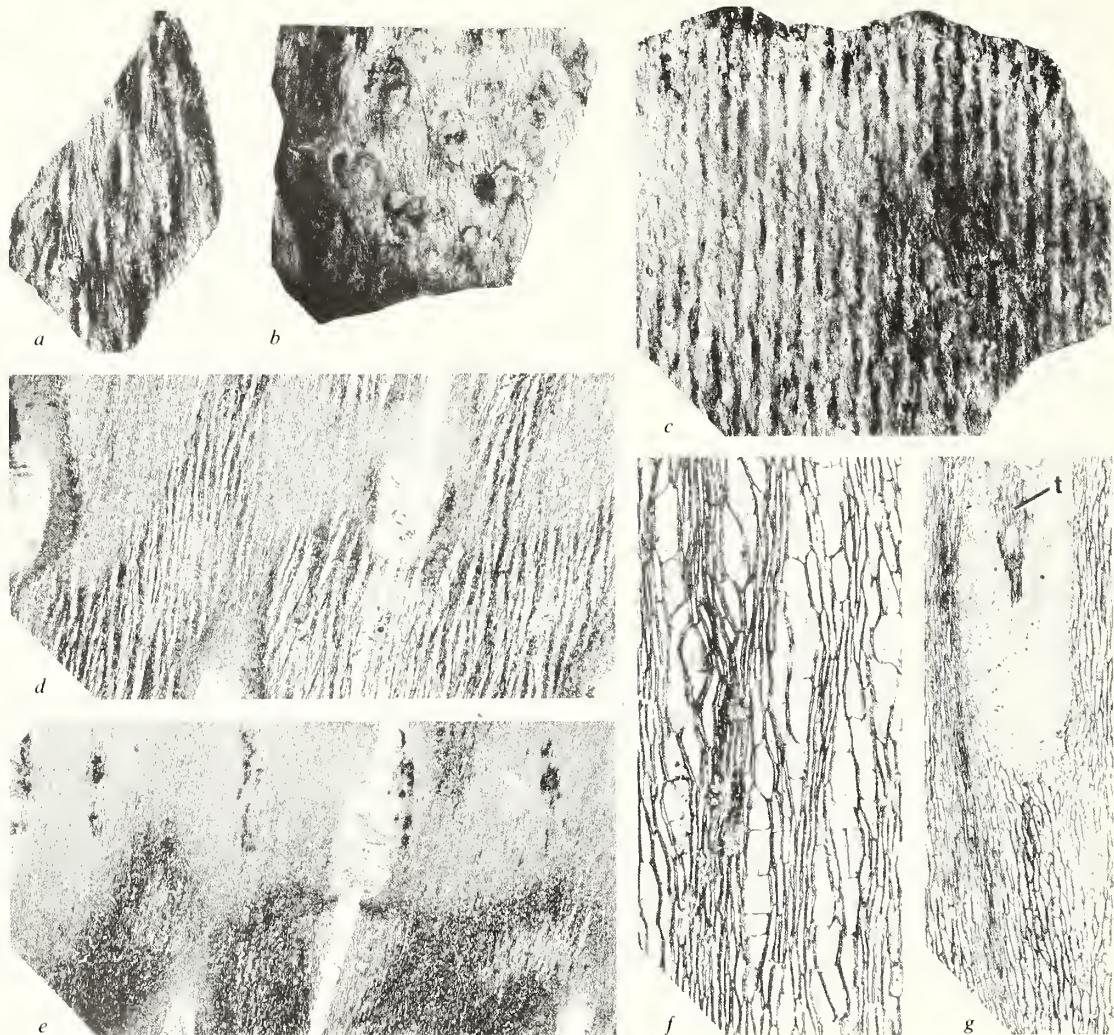
Figs. 1-5. *Chaloneria cormosa*. d, distorted cortex; p, parichnos; pc, primary cortex; pe, periderm; s, stele. 1, surface view of stem in which secondary growth has split epidermis into longitudinally oriented strips, O.U.P.H. no. 3825, $\times 1$. 2, transverse section of cortex showing leaf base and interfoliar region after significant secondary growth. Arrow indicates position of outer cortex in which randomly oriented internal cell divisions have occurred, C.B. 1399A top no. 9, $\times 7$. 3, tangential section near surface of stem with only primary growth. Primary cortex exposed at centre and leaf bases sectioned at sides, C.B. 1398D(1) side no. 310, $\times 25$. 4, transverse section of flattened stem with little periderm. Outer surface of cortex at top comparable to that in fig. 5, outer surface of cortex at bottom comparable to that in text-fig. 2c. C.B. 2126A bottom $\times 7$. 5, surface view of stem with leaf bases broken off at level of interfoliar stem surface and intact epidermis. Note vertically undulating, longitudinal pattern (at arrows) that conforms to cellular pattern of primary cortex in fig. 3, C.B. 2127A(2), $\times 1$.

Fig. 6. *Bothrodendron*-type impression of stem surface with relatively smooth interfoliar surface. O.U.P.H. no. 7642, $\times 2.5$.

Fig. 7. *Bothrodendron*-type impression of stem surface with longitudinally oriented, vertical pattern similar to that of primary cortex in *Chaloneria*, O.U.P.H. no. 7643, $\times 2.5$.

Fig. 8. *Asolanus* impression of stem with leaf bases similar to those in figs. 6 and 7, and interfoliar pattern similar to that of *Chaloneria* specimens in text-fig. 2a, b. O.U.P.H. no. 7644, $\times 1$.

PIGG and ROTHWELL, Carboniferous *Chaloneria* (*Isoetales*)



TEXT-FIG. 2a-g. *Chaloneria cormosa* cortex in surface views and in tangential sections; t, leaf trace. a, cortex of specimen with well-developed periderm, split at level of 'd' in Plate 64, fig. 2, C.B. 2126, $\times 1$. b, cortex of same specimen as a, but with leaf bases split slightly further toward periphery, at level comparable to specimen in Plate 64, fig. 5, C.B. 2126, $\times 1$. c, surface of cortex at level similar to that in Plate 64, fig. 1, but from specimen with only limited periderm, comparable to outer surface of cortex at bottom of Plate 64, fig. 4, C.B. 2126, $\times 1$. d, tangential section through cortex of specimen with significant periderm, comparable to surface in b, C.B. 2127A(1) Side no. 6, $\times 2.5$. e, tangential section through periderm of specimen in d showing anatomical derivation of *Knoria* configuration, C.B. 2127A(1) side no. 9, $\times 2.5$. f, enlargement of anatomical detail in d, C.B. 2127 no. 7, $\times 17$. g, enlargement showing anatomical detail of tissue that compresses to produce *Knoria* configuration, C.B. 1398D(1) side no. 310, $\times 17$.

indication of only limited increase in girth due to secondary growth. The interfoliar pattern similar to *Asolanus* commonly found among specimens of *Bothrodendron*, *Cyclostigma*, and *Pinakodendron* is consistent with the interpretation that they also had limited periderm production, and a cortical zone that became distorted by secondary growth similar to that in *Chaloneria*. If some species of these

genera represent small trees, as supposed by some authors, then the majority of the ultimate stem diameter must have been produced by primary growth.

Tangential sections or fractures through the periderm of *Chaloneria* reveal homogeneous tissue traversed by leaf traces and accompanying parichnos (text-figs. 1D, 2e, g), and produce a *Knorria* configuration (text-fig. 2e). The occurrence of *Knorria* in association with many lepidodendrid specimens probably also represents tangential sections through the periderm. Considering the massive amounts of periderm they produced, it is not surprising that *Knorria* is of such common occurrence among lepidodendrids. However, because smaller forms such as *Chaloneria* also produced periderm, *Knorria* should be expected to occur among specimens of them as well.

DISCUSSION

Plant Size Estimation. Because the broad inner cortical region and pith are rarely present in anatomically preserved stems of *Chaloneria*, specimens are almost always represented by a highly flattened cylinder (DiMichele *et al.* 1979; Pigg and Rothwell 1983a) that must have collapsed quite early during diagenesis. Under these circumstances, instead of the width of the flattened *Chaloneria* stems being a rough approximation of their diameter in life (as proposed in the compression model of Walton 1936; Rex and Chaloner 1983), it was probably exaggerated significantly. A more realistic approximation of the original diameter of the flattened stems is obtained by considering their width to represent one-half the circumference. In such a case the original diameter can be calculated by doubling the width of the stem, and considering that figure to represent the original circumference. The stem diameter is then easily calculated by considering circumference (C) to be equal to πD , where D = stem diameter. If this interpretation of the taphonomic alteration of stems is correct, then the size of compressed plants with a similar mode of cortical growth (e.g. as in *Asolanus*) may have been overestimated by many previous authors.

Developmental Interpretation. Some stems of *C. cormosa* exhibit only primary growth, and in these axes the preserved cortical tissues are relatively homogeneous (Pl. 64, fig. 3 at centre). Variations from specimen to specimen are due primarily to taphonomic processes including uneven leaf detachment, differential preservation, dissimilar amounts of crushing, and the impression of subsurface cortical patterns (Pl. 64, fig. 3) on to the epidermis (Pl. 64, fig. 5; Rex and Chaloner 1983). The cortex in specimens of this type lacks regions of anastomosing cells and radially aligned cells.

By contrast the onset of secondary growth produced several distinctive layers of cortical tissues. The most regular of these is the zone of radially aligned peridermal cells that are located at the inner margin of the commonly preserved cortex. This is also the zone that initiated an increase in the girth of the stem. In stems with prominent periderm, lenticular areas that are characterized by internally septate cells developed to the periphery of the periderm (Pl. 64, fig. 2; text-fig. 2d). Such areas represent a mechanism for maintaining tissue continuity immediately outside the periderm during the increase in girth. It is clear that many cells in the outermost cortex also remained meristematic at the onset of periderm production, such that the longitudinal fissures on the stem surface are restricted primarily to the epidermis. However, the outermost zone of cortical cells grew by more random patterns of internal cell divisions (Pigg and Rothwell 1983a).

Systematic Implications. Documentation among specimens of *C. cormosa* of the anatomical and taphonomic features that produce several morphotypes of lycophyte stem surface patterns provides a basis for relating such morphotypes to a diverse assemblage of Palaeozoic plants. It also provides evidence for the modes of cortical development in compression/impression forms that previously have been known primarily as surface patterns. In taxa of compressed stems with distantly spaced leaf bases such as *Bothrodendron*, *Cyclostigma*, and *Pinakodendron*, a relatively smooth interfoliar region (Pl. 64, fig. 6) probably displays a less distorted outer surface than specimens with characteristic interfoliar patterns (Pl. 64, figs. 7, 8; Rex and Chaloner 1983). Among the latter specimens, those with gently undulating patterns (Pl. 64, fig. 7) show features similar to those of the primary cortex in *Chaloneria*, and were undoubtedly preserved prior to, or distal to, secondary cortical development. In contrast,

stems with the *Asolanus*-type diagonal interfoliar pattern (Pl. 64, fig. 8) reveal that significant secondary cortical activity like that of *Chaloneria* had occurred prior to fossilization. Some specimens of this type represent decortication external to the periderm (text-fig. 2a, b), while others have had the subepidermal configuration impressed on the outer surface of the stem (text-fig. 2e). As emphasized by Rex and Chaloner (1983) specimens of the latter type may show both surface and subsurface features at the same level. This accounts for the occurrence of external leaf-base scars that are separated by a subsurface *Asolanus*-type cortical pattern on some specimens (Pl. 64, fig. 8). While isoetaleans like *Chaloneria* were probably the most common source of such decortication surfaces, some lepidodendraleans with relatively moderate secondary development (e.g. *Lepidodendron dicentricum*, Eggert 1961) produced 'phellem meshes' that may appear similar to *Asolanus* when seen on a split surface. The specimens of *Asolanus* interpreted as a *Lepidodendron* by Daber and Kahlert (1970) could reflect this mode of growth.

It is now clear that the *Knoria* pattern is produced when the cortex is split through or at the surface of the periderm in both Lepidodendrales and Isoetales, and that its more common occurrence with lepidodendraleans is probably the result of the much more massive periderm produced by the group. Likewise, the *Asolanus* configuration results from either decortication peripheral to the periderm or from the imprinting of subsurface features on the epidermis in plants with the capacity for only limited periderm production after much of the secondary cortical production had been completed.

Through continuing efforts to determine the biological and taphonomic origins of compression features (e.g. Rex and Chaloner 1983) and the anatomical basis for morphological features, the significance of many lycophyte morphotypes is becoming increasingly clear. In terms of both taxonomic significance and ontogenetic potential the increased knowledge allows for a better understanding of lycophyte evolution, and provides the basis for more accurate interpretations of remains preserved as coalified compressions or impressions.

Acknowledgements. The specimens figured in Plate 64, figs. 7 and 8 were collected by Mr. L. J. Millhorn, and provided by Dr. M. T. Sturgeon, Department of Geology, Ohio University. We wish to thank Dr. T. N. Taylor for reading the manuscript. This study was supported in part by National Science Foundation grant BSR831-0576 (to G. W. R.).

REFERENCES

- BOERSMA, M. 1978. A survey of the fossil flora of the 'Illinger Flozone' ('Heusweiller Schichten', Lower Stephanian, Saar, German Federal Republic). *Rev. Palaeobot. Palynol.* **26**, 41-92.
- CROOKALL, R. 1964. Fossil plants of the Carboniferous rocks of Great Britain (2nd sect.), *Mem. Geol. Surv. G.B., Palaeontol.* **4**, 217-354.
- DABER, R., and KAHLERT, E. 1970. *Lepidodendron (Asolanus) camptotaenia* (Wood, 1860) comb. n. *Paläontol. Abh., B. Palaeobot.* **3**, 349-355.
- DARRAH, W. C. 1969. A critical review of the Upper Pennsylvanian floras of eastern United States with notes on the Mazon Creek flora of Illinois. Privately publ., 219 pp.
- DIMICHELE, W. A. 1983. *Lepidodendron hickii* and generic delimitation in Carboniferous lepidodendrid lycopods. *Syst. Bot.* **8**, 317-333.
- MAHAFFY, J. F. and PHILLIPS, T. L. 1979. Lycopods of Pennsylvanian coals: *Polysporia*. *Can. J. Bot.* **57**, 1740-1753.
- EGGERT, D. A. 1961. The ontogeny of Carboniferous arborescent Lycopsida. *Palaeontographica, Abt. B*, **108**, 43-92.
- HAUGHTON, S. 1859. On *Cyclostigma*, a new genus of fossil plants from the Old Red Sandstone of Kiltorcan, Co. Kilkenny; and on the general law of phyllotaxis in natural orders—Lycopodiaceae, Equisetaceae, Filices, etc. *J. Roy. Dublin Soc.* **2**, 407-420.
- JANSEN, R. E. 1940. Some fossil plant types of Illinois. *Sci. Papers Illinois State Museum*, Springfield, **I**, 1-123.
- JENNINGS, J. R. 1979. Lower Pennsylvanian plants of Illinois. III. *Bothrodendron* from the Drury Shale. *J. Paleontol.* **53**, 519-523.
- LEJAL-NICOL, A. 1972. Contribution à l'étude des lycophytes paléozoïques de Bassin de Fort-Polignac (Illizi). *Nord. Alger Bull. Soc. Hist. nat. Afr.* **63**, 49-79.

- LINDLEY, J. and HUTTON, W. 1833. *The fossil flora of Great Britain*. Vol. 1, 218 pp. James Ridgway, London.
- PIGG, K. B. and ROTHWELL, G. W. 1979. Stem-root transition of an Upper Pennsylvanian woody lycopsid. *Am. J. Bot.* **66**, 914–924.
- 1983a. *Chaloneria* gen. nov., heterosporous lycophtyes from the Pennsylvanian of North America. *Bot. Gaz.* **144**, 132–147.
- 1983b. Megagametophyte development in the Chaloneriaceae fam. nov., Paleozoic Isoetales (Lycopsida). *Ibid.* 295–302.
- RENAULT, B. and ZEILLER, R. 1888. Études sur le terrain houiller de Commentary—Flore fossile, Pt. 1. *Soc. industrie mineral St. Etienne Bull.* **2**, 1–366.
- REX, G. M. and CHALONER, W. G. 1983. The experimental formation of plant compression fossils. *Palaeontology*, **25**, 231–252.
- ROTHWELL, G. W. 1976. Petrified Pennsylvanian age plants of eastern Ohio. *Ohio J. Sci.* **76**, 128–132.
- SCHOPF, J. M. 1975. Modes of fossil preservation. *Rev. Palaeobot. Palynol.* **20**, 27–53.
- SOLMS-LAUBACH, H. 1891. *Fossil Botany* (English Translation), 401 pp. Clarendon Press, Oxford.
- STERNBURG, K. 1825. *Versuch einer geognostisch botanischen Darstellung der Flora der Vorwelt*, 1 (pt. 4), 1–48. Leipzig.
- STUBBLEFIELD, S. P., and ROTHWELL, G. W. 1981. Embryogeny and reproductive biology of *Bothrodendrostrobus mundus* (Lycopsida). *Am. J. Bot.* **68**, 625–634.
- THOMAS, B. A. 1967. The cuticle of two species of *Bothrodendron* (Lycopsida: Lepidodendrales). *J. Nat. Hist.* **1**, 53–60.
- and WATSON, J. 1976. A rediscovered 114-foot *Lepidodendron* from Bolton, Lancashire. *Geol. J.* **11**, 15–20.
- WALTON, J. 1936. On the factors which influence the external form of fossil plants; with descriptions of the foliage of some species of the Palaeozoic Equisetalean genus *Annularia* Sternberg. *Phil. Trans. R. Soc. Lond. B.* **226**, 219–237.
- WEISS, C. E. and STERZEL, T. 1893. Die Sigillarien der preussischen Steinkohlen- und Rothliegenden-Gebiete. II. Gruppe der Subsigillarien. *Abhandl. könig. preuss. geol. Landesanst. n.F.* **2**, 1–255.
- WHITE, D. 1899. Fossil flora of the Lower Coal Measures of Missouri. *U.S. Geol. Survey Mon.* **37**, 467 pp.
- WOOD, H. C. 1860–1861. Contributions to the Carboniferous flora of the United States. *Proc. Acad. Nat. Sci. Philadelphia for 1860*, **12**, 236–240, 436–443, 519–522.

KATHLEEN B. PIGG

Department of Botany
The Ohio State University
Columbus, Ohio 43210
USA

GAR W. ROTHWELL

Department of Botany
Ohio University
Athens, Ohio 45701
USA

Typescript received 4 June 1984

Revised typescript received 27 November 1984

WEALDEN OCCURRENCE OF AN ISOLATED BARREMIAN DINOCYST FACIES

by N. F. HUGHES and I. C. HARDING

ABSTRACT. Records of occurrence are presented in the form of two new taxa of peridinioid dinoflagellate cysts and twenty-three comparison records from Upper Wealden strata of Barremian age in the British Geological Survey's Warlingham Borehole, Surrey. Because these well-preserved dinocysts are not accompanied by any other dinocyst palynomorphs, their presence is interpreted as a short-lived and local record of very low palaeosalinity. Other occurrences at different levels in the Wealden usually contain three or four dinocysts of known marine taxa, and appear to represent more widespread and perhaps stronger marine incursions. Palynofacies, ostracods, and clay minerals are briefly discussed in connection with the possibility that these new dinocysts may represent the earliest known occurrences of non-marine dinoflagellates to produce fossilisable cysts.

THE purpose of this paper is to illustrate and to describe the circumstances of occurrence of a new dinoflagellate cyst which has been found in abundance in some palynomorph-bearing Wealden samples. No other dinocysts have been found in these samples which are from the upper part of the Weald Clay in the British Geological Survey (B.G.S.) Warlingham Borehole in Surrey (Worssam and Ivimey-Cook 1971) and appear to be of late Barremian age. The new dinocysts, first illustrated by Hughes (1980), have no close parallels in the literature and appear to be relatively simple peridinioids; their occurrence without other dinocysts may indicate a palaeosalinity less than the marine salinity of the time, and if so the beginning of a trend towards the fresh-water dinocysts of today. It may therefore be necessary to qualify the generally accepted view (e.g. Hughes and Moody-Stuart 1967) that through the Mesozoic any dinocyst occurrence indicates a marine environment.

PREPARATION METHOD

Samples have been treated by a standard palynologic extraction method for light microscope study: dilute HCl, HF, conc. HNO_3 oxidation (time stated with record sample description), dilute NH_4OH (to avoid using KOH which causes swelling), and zinc bromide (S.G.2.0) as heavy liquid. Although residues are now stored in glycerine/water, some early preparations twenty-five years ago were stored in glycerine jelly and have been successfully brought into use with hot water and/or HCl/HF.

Slides for light microscopy were made by a standard Hydramount/Depex method; some of the older preparations mentioned below for comparison records were mounted in Clearcol or even in glycerine jelly. Micrographs were taken on Kodak Technical Pan Film 2415 (rated 100 ASA) using a Nikon FX35A camera on Nikon Labophot microscope 01819.

SEM stubs were prepared with strew residue over a Cambridge Mark 2 nickel grid (see Hughes *et al.* 1979). Micrographs were taken on Ilford 70 mm film FP4, using a Phillips 501B Scanning Electron Microscope. All specimens and preparations are lodged in the Sedgwick Museum.

RECORD OF SPECIMENS

All specimens observed are here listed as belonging either to a biorecord (unchangeable reference taxon) or to a graded comparison record (see Hughes 1976, p. 26). To distinguish this separate treatment in which neither emendation of a taxon definition nor unqualified attribution of specimens to a taxon are admissible, the taxa are not arranged in any formal hierarchy nor are the names latinized.

Qualified attribution in the form of graded comparison records is set out as follows:

cfA = variation in the comparison record agrees with that described for the reference taxon in all qualitative aspects, but minor quantitative differences may be included. This grade (cfA) is taken to indicate such close resemblance as would indicate stratigraphic correspondence.

cfB = variation in the comparison record may differ from that of the reference taxon in one specified qualitative aspect. This comparison is taken to indicate less close stratigraphic correspondence. The grade cfB occurrences would normally stratigraphically enclose those of cfA.

cfC = adequate resemblance to the reference taxon to be useful in discussion, but normally used for occurrences which would be made into new biorecords if such were justified by geological necessity. Any one occurrence may be compared cfC with more than one reference taxon.

Any of these records may be placed by others in attribution to a Linnean taxon if that procedure appears to be rewarding, but the records themselves are designed to remain unchanged and separately retrievable for any purpose.

Group DINOCYST PERIDINIOID CRETACEOUS
Genusbox CINCTURO-

Diagnosis. Peridiniod dinocyst with ambitus subcircular to ovoidal, without pericoels or horns. Apex usually exhibits slight asymmetry. Periphramg thickness < 0.5 µm; sculpture rugulae and/or verrucae. Paratabulation obscure except where indicated by archaeopyle, believed to be (3I) or (A₃,3I). Pericingulum distinctly sculptured; perisulcus devoid of sculpture.

Comparison. *Cyclopsiella* Drugg and Loeblich is unsulptured.

Archaeopyle references. Evitt (1967) and Norris (1978, p. 303).

Biorecord CINCTURO-JUDITH

Plate 65, figs. 1–9; Plate 66, figs. 1–5; text-fig. 1

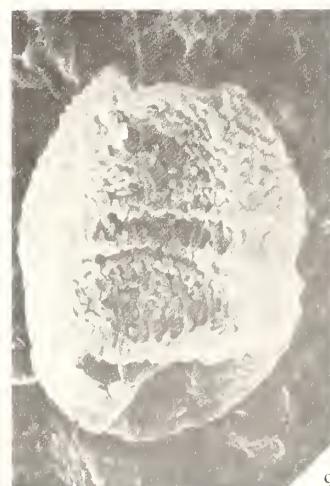
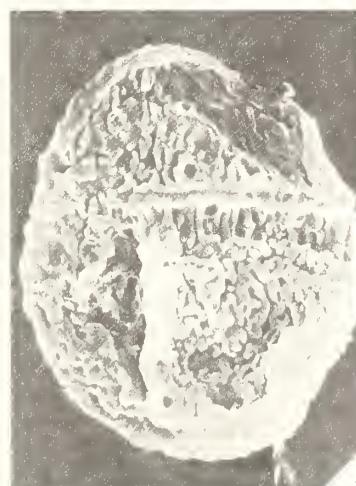
Record sample. B.G.S. Warlingham Borehole, depth (ft) 1258/2–4 (in.); greenish-grey compacted mudstone (blocky with weak lamination) with pyrite as streaks, burrow infillings and coatings on small fossils; small red-brown oxidation patches. Fauna: ostracods, small black fish spines, fish vertebrae, bone fragments, and brown spines. Preparation CH053/1(W120): oxidation 10 min cold conc. HNO₃, centrifuged, heavy liquid mineral separation. Palynologic facies (200 counted): palynomorphs compressed, little damage, little corrosion; 48.5% Cincturo-Judith, 1% tectate-columellates, 34% saccates; 1.5% *Classopollis*, 1% *Eucommiidites*, 2.5% *Cicatricosisporites*, 11.5% other triletes.

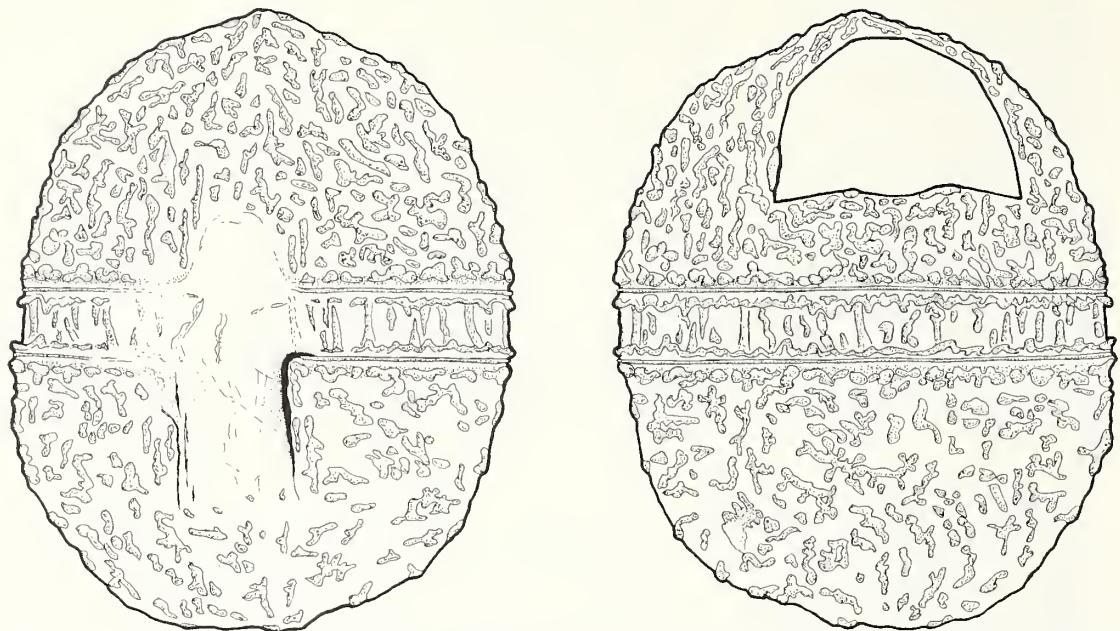
Dimensions (100 specimens). Length (31.4) 37.0 (45.7) µm; breadth (25.7) 33.1 (42.8) µm.

Description. Shape and structure. Pericyst: ambitus ovoidal or sub-circular, elongated anterior to posterior, widest immediately post-cingulum; slight dorsoventral flattening. Epicyst and hypocyst of approximately equal size. Apical region rounded; apex asymmetrically located in 40% of observed specimens; 24% displayed a short broad apical papilla. Antapex rounded. Periphramg thickness 0.4 µm (2 specimens; SEM photos); sculpture of rugulae (max. width 0.75 µm) and verrucae (max. diameter 0.6 µm). The specimens with apical papilla have 8 to 10

EXPLANATION OF PLATE 65

Figs. 1–9. Cretaceous dinoflagellate. Biorecord Cincturo-Judith: Barremian age; Upper Wealden, Warlingham Borehole, depth 1258' 2–4"; stub IC 105, preparation CH053, sample WM 1258' 2–4". Films HSF62 and 67. 1, 2, 4, 5, 7–9, ×1500; 3, ×3000; 6, ×6500. Scanning electron micrographs. 1, ref. 213789, dorsal view (HSF67/07); 2, ref. 360823, dorsal view (HSF62/08); 3, detail of same, sculpture in percingular region (HSF62/09); 4, ref. 238786, ventral view showing broad perisulcus (HSF62/06); 5, ref. 246892, oblique dorsal view, with prominent pericingulum (HSF62/07); 6, ref. 358875, endocyst exposed where pericyst is torn (HSF62/10); 7, ref. 315915, dorsal view (HSF62/11); 8, ref. 345910, slightly oblique ventral view showing perisulcal fold (HSF67/01); 9, ref. 337796; oblique view (HSF67/03).



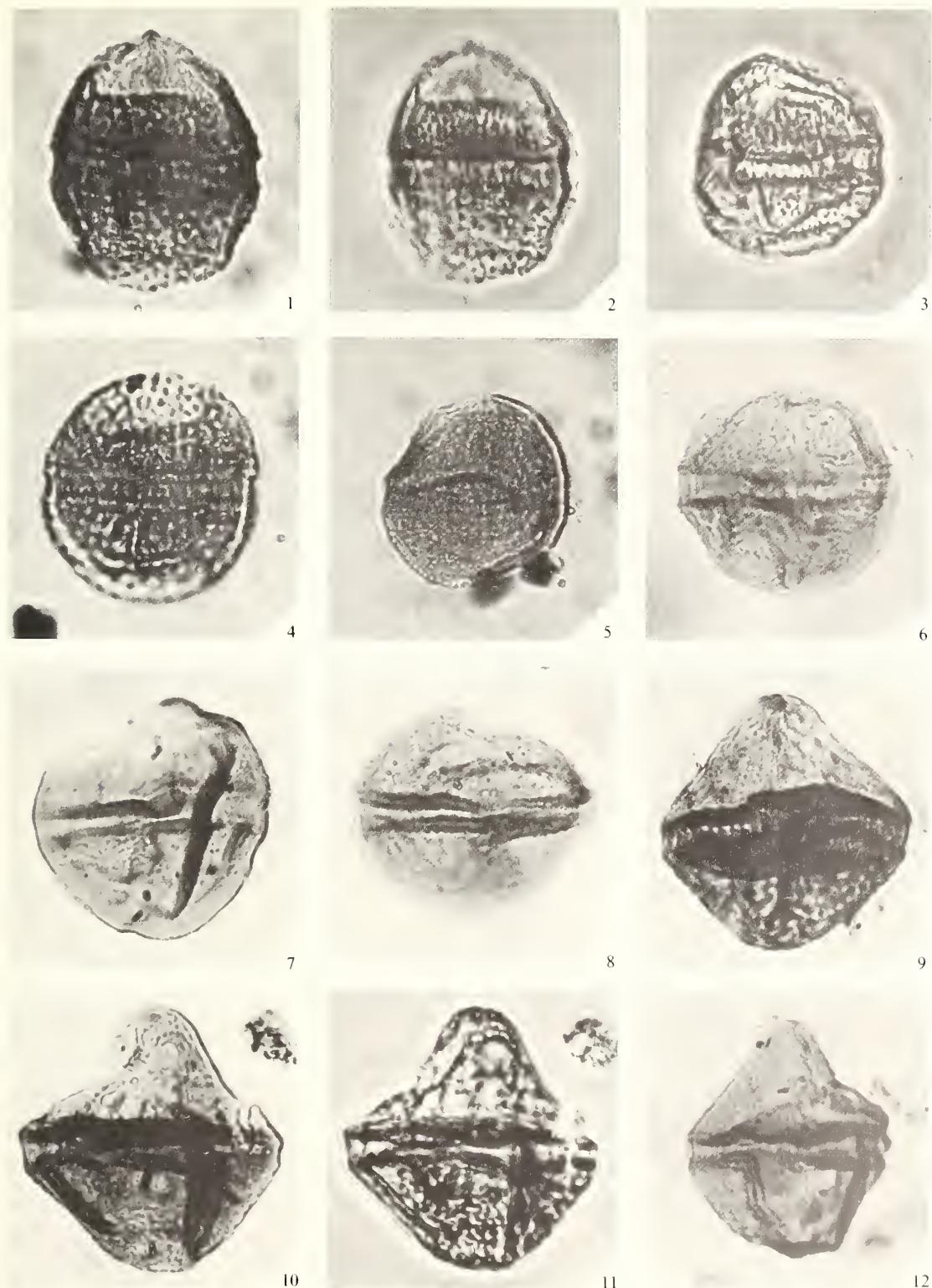


TEXT-FIG. 1. Generalized reconstruction of *Cincturo-Judith*, designed to show important morphological characters. *Left*, ventral view; *right*, dorsal view. $\times 1750$.

rugulae radiating irregularly from the papilla. Endocyst: distinguishable in specimens with antapical 'pericoel' (4%); closely adpressed to pericyst in most other specimens but separation of two walls seen when cyst is ruptured. Endophragm laevigate, 0.5 μm thick but considerably thinner in apical third of epicyst. Paratabulation. Pericingulum: planar, always prominent; anterior and posterior parasutures shown as continuous ridges 0.3 μm wide set in smooth pandasutural zone 0.8 μm wide; a row of papillate verrucae borders the pericingulum above and below, while the main sculpture of parallel cross striae (rugulae) fills the whole 3 μm width effectively obscuring any paratabulation. Perisulcus: strongly developed, mainly on hypocyst; depressed area of much reduced sculpture, bounded (in 59 % of specimens) by prominent parallel sulcal folds 4–6 μm apart. Archaeopyle: (3I) or (A₃3I) type, recognizable (4 % of specimens) by broadly triangular opening extending almost to apex; 59 % of cysts showed no excystment feature, but 35 % were torn or ruptured in the apical region perhaps as a result of archaeopyle formation.

EXPLANATION OF PLATE 66

Figs. 1–12. Cretaceous dinoflagellates. Barremian age; Upper Wealden, Warlingham Borehole. Films HOF 13 and 14. 1–5, depth 1258' 2–4", slide CH053/1, biorecord *Cincturo-Judith*; 6–8, depth 1209' 9", slide W124/1, cfB *Cincturo-Judith*; 9–12, depth 1198' 2', slide BP556/3, biorecord *Cincturo-Domed*. All figures $\times 1000$, light micrographs. 2, 3, 10, phase contrast. Microscope reference SM306(OR3)Leitz646388. 1, 2, ref. 52.9/122.3, specimen focussed to show archaeopyle (HOF13/32, 13/35); 3, ref. 35.3/120.4, specimen showing asymmetry of apex (HOF13/12); 4, ref. 44.0/116.6, subcircular specimen with ?archaeopyle (HOF13/24); 5, ref. 38.3/124.6, focussed on pericingulum (HOF13/17); 6, ref. 29.5/124.1, slightly oblate specimen (HOF14/16); 7, ref. 28.1/126.2, specimen with reduced sculpture and thin apical region (HOF14/18); 8, ref. 50.4/123.1, showing prominent perincingular folds (HOF14/14); 9, ref. 43.5/119.9, specimen showing 'domed' epicyst and perisulcal fold (HOF14/19); 10, 11, ref. 49.7/113.2, showing general morphology (HOF14/33, 14/34); 12, ref. 59.2/118.3, displaying broad perisulcus (HOF14/32).



Distinction. The single unnamed peridinacean cyst (Batten 1982, fig. 8.11f) with a prominent sculptured pericinctum appears to have a (4A3I) archaeopyle and dissimilar sculpture.

Comparison. Taxa in the genusbox Cincturo- are readily distinguishable from those in such genera as *Palaeoperidinium* (Deflandre) Sarjeant and *Subtilisphaera* (Jain and Millepied) Lentin and Williams, by their lack of apical and antapical horns. They can also be distinguished from the Tertiary genus *Saeptodinium* Harris by the strongly developed pericinctum, and from *Geiselodinium* Krutzsch by the lack of pericoels. The overall morphology bears some resemblance to *Cyclopsiella mura* Duxbury, although this is an unsculptured species of a genus which Stover and Evitt (1978) regarded as acritarchs.

Name. The first observations were made by Mrs. Judith C. Moody-Stuart in 1966.

COMPARISON RECORDS

cfA Cincturo-Judith: Warlingham Borehole; lithology as for WM1258/2-4, except for differences noted. Specimen counts represent whole content of one slide in each case.

WM 1254/1-3	(18 specimens): plus bivalves, <i>Euestheria</i> . Prep. W067/1.
WM 1254/8	(56 specimens): darker and more brownish colour. Prep. K127/1.
WM 1255/3-6	(309 specimens): Prep. W100/1.
WM 1255/7-8	(34 specimens): plus bivalves, gastropods. Prep. W121/1.
WM 1256/3-4	(95 specimens): darker and more brownish colour. Prep. M68/1.
WM 1258/2-4	(428 specimens): Biorecord (see above).
WM 1258/9	(401 specimens): Prep. Z212/3.
WM 1259/0	(63 specimens): plus <i>Euestheria</i> . Prep. Z182/3.
WM 1259	(2 specimens): Prep. CH009/2.
WM 1259/6-9	(78 specimens): Prep. Z207/1.
WM 1260/-	(210 specimens): Prep. W119/2.
WM 1261/10-11	(588 specimens): plus <i>Euestheria</i> . Prep. W068/1.
WM 1262/0-1	(294 specimens): plus <i>Euestheria</i> . Prep. W069/1.
WM 1262/2-3	(490 specimens): Prep. K098/2.
WM 1262/6	(126 specimens): plus <i>Euestheria</i> . Prep. W108/1.
WM 1277/9	(21 specimens): brownish; flaser bedding, pale brown; rare ostracods. Prep. Z216/3.
WM 1278/8	(7 specimens): brownish; no ostracods. Prep. BP558/1.
WM 1279/2	(2 specimens): brownish; no ostracods. Prep. W118/1.
WM 1279/3	(5 specimens): brownish; no ostracods. Prep. Z217/3.
WM 1297/10	(11 specimens): brownish; flaser bedding, pale brown; no ostracods. Prep. Y563/4.

cfB. CINCTURO-JUDITH

Plate 66, figs. 6-8; Plate 67, figs. 1-3

Record sample. B.G.S. Warlingham Borehole, depth (ft) 1209/9 (in); olive green compacted mudstone with brownish tint (blocky with very weak lamination); few pyrite patches. Fauna: numerous fish fragments, black

EXPLANATION OF PLATE 67

Figs. 1-8. Cretaceous dinoflagellates. Barremian age; Upper Wealden, Warlingham Borehole. 1-3, stub IC112, preparation W124, sample WM1209' 9", cfB Cincturo-Judith; 4-8, stub IC161, preparation BP556, sample WM1187' 2", biorecord Cincturo-Domed. Films HSF62, 63, and 66. 1, 4, 5, 7, 8, $\times 1500$; 3, 6, $\times 3000$. 1, 3, ref. 232754, 1, oblique ventral view showing perisulcal fold (HSF62/15); 3, detail of sculpture (HSF62/16); 2, ref. 236784, showing reduced size of epicyst (HSF62/14); 4, ref. 363771, dorsal view showing domed epicyst (HSF63/09); 5, ref. 361775, oblique ventral view showing epicystal archaeopyle (HSF63/08); 6, ref. 365760, detail of sculpture (HSF66/02); 7, ref. 350761, dorsal view (HSF63/13); 8, ref. 351762, oblique apico-ventral view (HSF63/12).



bones, vertebrae, spines. Preparation W124/1: oxidation 10 min cold conc. HNO_3 , centrifuged, heavy liquid mineral separation. Palynologic facies: 31% cfB. Cincturo-Judith, 1% tectate-columellates and monosulcates, 28.5% saccates, 10% *Classopollis*, 3% *Eucommiidites*, 3.5% *Cicatricosisporites*, 22% other triletes, 1% fungal debris.

Dimensions (50 specimens). Length (45.6) 38.5 (34.2) μm ; breadth (45.6) 38.3 (31.4) μm .

Distinction from biorecord. Pericyst shape: high proportion (42%) broader than long; hypocyst larger, about six-tenths of whole. Periphram: thickness 0.5 μm (one SEM photo); sculpture less prominent as verrucae (max. diameter 0.6 μm) or short rugulae (max. length 3 μm). Paratabulation: pericingulum wider, up to 4 μm , but often reduced by secondary folding; cingular sculpture of less distinct uneven vertical corrugations; pandasutural zone bordered by discrete verrucae; parasulcus emphasized by folds (70% of specimens); archaeopyle not seen, but apical rupture frequent.

Other cfB records

WM 1180/6 (36 specimens): Prep. K345/1.

WM 1181/2-10 (85 specimens): same lithology as biorecord, more fish remains. Prep. M679/1.

WM 1184/0-2 (40 specimens): more fish remains. Prep. K125/1.

WM 1209/9 (672 specimens): (see above).

Palynofacies. All of the cfA and cfB records occur in palynofacies rich in amorphous finely comminuted organic matter ('mush'). This material may be a partial case of the greenish colouration of the samples. *Botryococcus* has rarely been observed in these preparations and without it there is no reason to regard the 'mush' as indicative of an anoxic lacustrine environment in the sense of Sladen and Batten (1984).

Biorecord CINCTURO-DOMED

Plate 66, figs. 9-12; Plate 67, figs. 4-8

Record sample. B.G.S. Warlingham Borehole, depth (ft) 1187/2 (in.); khaki greenish compacted blocky mudstone, almost conchoidal fracture, 'greasy' to touch, weak lamination, small pyrite patches. Fauna: fish vertebrae and spines (brown), *Euestheria*. Preparation BP556/3; oxidation 60 min cold conc. HNO_3 , centrifuged; mounted in glycerine jelly. Palynologic facies (200 counted): 51.5% Cincturo-Domed, 45% tectate-columellates, 15.5% saccates, 10% *Classopollis*, 1% *Eucommiidites*, 3% *Cicatricosisporites*, 3% other triletes, 6.5% *Celyphus rillus*.

Dimensions. (50 specimens). Length (48.5) 42.3 (31.4) μm , breadth (48.5) 39.6 (28.5) μm .

Description. Shape and structure. Pericyst: ambitus pear-shaped, elongated anterior to posterior; epicyst blunt-ended concave-sided; hypocyst rounded, of comparable overall dimensions with epicyst; greatest width immediately post-cingular; slight dorsoventral flattening. Periphram: thickness 0.3-0.4 μm (observed on two SEM photos); sculpture more pronounced on hypocyst, short rugulae (up to 5 μm long) and/or verrucae; epicyst rugulae of low relief, continuous, radiating from blunt apex. Endocyst: laevigate, 0.4-0.5 μm thick (SEM photos), thinning rapidly in apical third of epicyst. Paratabulation. Pericingulum: planar, narrow, distinct; width (3-4 μm), sculpture uneven vertical corrugations and striae obscuring tabulation; width reduced by secondary compression; pandasutural zones without sculpture. Perisulcus: mainly on hypocyst, 4 μm wide; bounded by parallel ridges, secondarily developed into folds. Archaeopyle: not clearly observed, but frequent dorsal rupturing of cyst wall in 'intercalary' position, affecting up to one-third of epicyst.

Distinction. Only known from this sample (1258 specimens); differs in shape and excystment feature from *Cyclopsiella mura* Duxbury 1983. Accompanied by very rare *Veryhachium*-type acritarchs.

STRATIGRAPHIC POSITION OF SAMPLES

Succession. The main occurrences of Cincturo-Judith are in the strata immediately below Topley's Bed 6 'Large Paludina' at 1252 ft (Worssam and Ivimey-Cook 1971, p. 22). The occurrence of Cincturo-Domed and most of the cfB records of Cincturo-Judith are from just above Topley's

Bed 7 'Sandstone' at 1210–1238 ft. The base of the Lower Greensand (Aptian) is taken at 1047 ft, making all these samples Barremian or earlier.

Ostracods. F. W. Anderson (in Worssam and Ivimey-Cook 1971) placed all these beds in his *Cypridea bogdenensis* beds of his *C. clavata* Zone, and further placed his Gillmans Cycle of 'C' and 'S' phases between 1248 and 1263 ft. Our samples (1254–1263 ft), which were taken from the cores after those used by Anderson, included identifications of *C. clavata* (spinose), *C. valdensis* (large, punctate), *C. rotundata* (medium size, punctate), *C. spinigera* (unispinose), *Theriosynoecum fittoni* (especially from WM1258/9 in great numbers), *Darwinula leguminella*, and *D. oblonga*. Less certain identifications were of rare *Mantelliana mantelli* and ?*Fabanella boloniensis* (both from WM1258/9) and ?*Miocytheridea henfieldensis* (from WM1255/7–8). Of these all the *Cypridea*, *Darwinula*, and *Miocytheridea* species form part of Anderson's 'C' phase of fresh/brackish water; *Theriosynoecum* is found in association with *Cypridea* and is probably from fresh-water (Kilenyi and Allen 1968, and our data); the others relate to Anderson's 'S' phase, which he regarded as 'marine'. The age indication by Anderson (1973) and Kilenyi and Neale (1978) for these samples would be Late Hauterivian to Early Barremian.

Angiospermid pollen. Various tectate-columellate pollen from lower levels in the Warlingham Borehole down to 1415 feet (Hughes *et al.* 1979) are believed from correlation with similar occurrences from north of the London–Brabant uplift to be of early Barremian age.

PALYNOMORPHS AND WEALDEN PALAEOSALINITIES

Hitherto the presence of dinocysts in Mesozoic palynomorph assemblages in which reworking was considered unlikely, has normally been taken as straightforward indication of marine conditions.

Recently it has been pointed out (Hughes 1980; Batten 1982; Batten and Eaton 1980) that several horizons through the otherwise fresh-water Wealden provide restricted dinocyst assemblages; individual horizons may contain up to four dinocyst species normally found in marine rocks of comparable age. These horizons have been interpreted as resulting from marine incursions; but presumably these incursions were both incomplete and short-lived because stenohaline marine megafossils have not been found except in one case at the very top of the Weald Clay in Kent, just below the main Aptian incursion (Casey 1961).

The occurrences described in this paper differ in each featuring only one dinocyst taxon that is in abundance up to 75% and that is not known to exist elsewhere in any fully marine circumstances.

Finally the great majority of Wealden palynomorph assemblages include no dinocysts or acritarchs at all and are consequently interpreted as of fresh-water origin.

It is tempting to regard these occurrences as a gradation from fully marine, through major fluctuations say down to one half salinity (with three or four dinocyst taxa) to minor fluctuations with say some such low level as one quarter salinity (with one unique taxon) to fresh water. No salinity percentage figures could be suggested because the Cretaceous general marine salinity was probably not 34·4‰. In addition it is perhaps more likely that incursive water-masses bearing living dinocysts were both local and transient, and that no sector of the Wealden 'lake' settled down to a distinct geographical salinity gradient as in the present Baltic Sea with steady conditions and organism representation for any length of time.

OTHER INDICATIONS OF WEALDEN PALAEOSALINITY

It is important that in the Wealden of Southern England from beginning Berriasian to end Barremian no cephalopod, echinoderm, coral, foraminiferan, or brachiopod has been recorded and there were thus no fully marine situations.

Anderson (1973) claimed that his 'S' phase ostracods represented marine conditions, alternating with his more usual 'C' phase ostracods representing fresh/brackish water. All of our samples from

Warlingham 1254 to 1263 contained ostracods in quantity and of these only rare specimens of ?*Mantelliana* and ?*Fabanella* at WM1258/9 could be taken to represent 'S' phase; all others were 'C' phase ostracods. Anderson (1971) regarded the triple 'S' phase, styled by him, Gillman's cycle, as a distinct incursion; our ostracod fossils from fifteen samples in these 10 ft of strata do not indicate anything dramatic. Possibly there was a minor fluctuation as indicated by the dinocysts, which is also in keeping with the findings of Kilenyi and N. W. Allen (1968) but scarcely with those of P. Allen and Keith (1965).

Dr. C. V. Jeans has kindly examined by X-ray diffraction the clay mineral assemblages ($< 2 \mu\text{m}$ e.s.d.) from a series of eight samples spanning the horizons of occurrence of these dinocysts (Jeans 1978, p. 625 for method). Identification was carried out at the level of clay mineral groups and he concluded that no systematic variations within these assemblages could be related to these particular horizons. Such a view does not conflict with our interpretation that these consistently greenish samples bearing ostracods, fish fragments, and pyrite, in addition to abundance of a unique dinocyst, represent a minor salinity fluctuation. We further do not accept the suggestion of Sladen and Batten (1984, p. 161) that these salinity changes could reflect evaporation cycles in the basin.

Clearly, chemical investigations should have been and have been attempted (Allen *et al.* 1973) but the results are cautious and appear inconclusive in the context of our present observations. The bivalve *Filosina* referred to by Allen *et al.* (1973) as marine, has not been observed in the borehole sector we are studying.

CONCLUSIONS

Our evidence and that of previous papers suggests that in general early Cretaceous dinocysts were confined to marine conditions which their presence may be taken to indicate.

On the other hand the dinocysts Cincturo-Judith and Cincturo-Domed as described above appear to be genuine dinocysts which occur in a facies which is distinct from the rocks above and below and represented perhaps some slight degree of salinity. The occurrence of these dinocysts in abundance, without any others present, suggests the beginning of a trend that may have led in late Tertiary and Recent time to the freshwater armoured dinoflagellate thecae.

Acknowledgements. We are grateful to assistance from Mrs. Audrey McDougall with sample preparation, to Mr. David Newling with Scanning Electron Microscopy, and to Mr. R. Lee and Mr. R. Hill with light microscopy. I. C. H. acknowledges a NERC studentship GT4/82/GS/122 and N. F. H. a NERC Research Grant 3/4048.

REFERENCES

- ALLEN, P. and KEITH, M. L. 1965. Carbon isotope ratios and palaeosalinities of Purbeck-Wealden carbonates. *Nature, Lond.* **208**, 1278-1280.
- , TAN, F. C. and DEINES, P. 1973. Isotopic ratios and Wealden environments. *Palaeontology*, **16**, 607-621.
- ANDERSON, F. W. 1971. The sequence of ostracod faunas in the Wealden and Purbeck of the Warlingham bore-hole. *Bull. Geol. Surv. Gt. Br.* **36**, 122-138.
- 1973. The Jurassic-Cretaceous transition: the non-marine ostracod faunas. In CASEY, R. and RAWSON, P. F. (eds.), *The Boreal Lower Cretaceous*, 101-110. Geol. Jl, Spec. Issue No. 5. Liverpool.
- BATTEN, D. J. 1982. Palynofacies and salinity in the Purbeck and Wealden of southern England. In BANNER, F. T. and LORD, A. R. (eds.), 278-295. Allen & Unwin.
- and EATON, G. L. 1980. Dinoflagellates and salinity variations in the Wealden (Lower Cretaceous) of southern England, 32. In *Abstracts 5th Int. Palynological Conf. Cambridge 1980*.
- CASEY, R. 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology*, **3**, 487-621.
- DUXBURY, S. 1983. A study of dinoflagellate cysts and acritarchs from the Lower Greensand (Aptian to Lower Albian) of the Isle of Wight, Southern England. *Palaeontogr. Abt. B.* **186**, 18-80.
- EVITT, W. R. 1967. Dinoflagellate studies II, the archaeopyle. *Stanford Univ. Publ. Geol. Sci.* **10** (3), 1-83.
- HUGHES, N. F. 1976. *Palaeobiology of angiosperm origins*, pp. 24-31. Cambridge University Press, Cambridge.
- 1980. Palynological correlation of Early Cretaceous freshwater to marine strata. *Proc. IV Int. Palynol. conf. Lucknow (1976-1977)*, **2**, 497-499.

- DREWRY, G. E. and LAING, J. F. 1979. Barremian earliest angiosperm pollen. *Palaeontology*, **22**, 513–525.
- and MOODY-STUART, J. C. 1967. Palynological facies and correlation in the English Wealden. *Rev. Palaeobot. Palynol.*, **1**, 259–268.
- JEANS, C. V. 1978. The origin of the Triassic clay assemblage of Europe with special reference to the Keuper Marl and Rhaetic of parts of England. *Phil. Trans. Roy. Soc. A* **289**, 549–639.
- KILENYI, T. J. and ALLEN, N. W. 1968. Marine-brackish bands and their microfauna from the lower part of the Weald Clay of Sussex and Surrey. *Palaeontology*, **11**, 141–162.
- and NEALE, J. W. 1978. The Purbeck/Wealden. In BATE, R. H. and ROBINSON, E. (eds.). *A stratigraphical index of British Ostracoda*, 299–324. Geol. Jl Spec. Issue No. 8. Liverpool.
- NORRIS, G. 1978. Phylogeny and a revised supra-generic classification for Triassic–Quaternary organic-walled dinoflagellate cysts (Pyrrophyta). Part I, Cyst terminology and assessment of previous classifications. *Neues Jahrb. für Geol. und Paläont. Abhandl.* **155**, 300–317.
- SLADEN, C. P. and BATTEN, D. J. 1984. Source-area environments of Late Jurassic and Early Cretaceous sediments in Southeast England. *Proc. Geol. Assoc.* **95** (2), 149–164.
- STOVER, L. E. and EVITT, W. R. 1978. Analyses of pre-Pleistocene organic-walled dinoflagellates. *Stanford Univ. Publ. Geol. Sci.* **15**, 1–300.
- WORSSAM, B. C. and IVIMEY-COOK, H. C. 1971. The stratigraphy of the Geological Survey Borehole at Warlingham, Surrey, *Bull. Geol. Surv. Gt. Br.* **36**, 1–146.

N. F. HUGHES

I. C. HARDING

Department of Earth Sciences
University of Cambridge
Downing Street
Cambridge CB2 3EQ

Typescript received 10 July 1984

Revised typescript received 13 November 1984

A NEW GENUS OF CARBONIFEROUS SPIRIFERID BRACHIOPOD FROM SCOTLAND

by MARIE LEGRAND-BLAIN

ABSTRACT. The microsculpture and vascular markings of the classical species '*Spirifer*' *trigonalis* are described, mainly from Scottish Brigantian (late Viséan) specimens. The genus *Angiospirifer* and subfamily Angiospiriferinae are created. *Angiospirifer* is related to the genus *Brachythyrina*, which became widespread during the upper Carboniferous.

CARBONIFEROUS spiriferids present unusual systematic difficulties, especially when specimens have a simple external shape and ornamentation, and when the microsculpture and internal features become taxonomically important. Among upper Palaeozoic spiriferids, in addition to the dental plates, the mantle canals are important taxonomic and evolutionary features (Ivanova 1960, 1971; Lazarev and Poletaev 1982). However, good internal surfaces or moulds are needed for such observations: in consequence, mantle canals are unknown on many of the long-established Dinantian species that were collected from limestone facies.

'S.' *trigonalis* (Martin, 1809) *sensu* Muir-Wood 1956, a species often cited from the Eurasian and North African Carboniferous, has been studied in detail by Dunlop (1961), so its biometry and shell structure are well established. This paper adds to Dunlop's study by researching the microsculpture and mantle canals of 'S.' *trigonalis*: a species previously attributed to a variety of genera, but here assigned to a new genus, *Angiospirifer*.

SYSTEMATIC PALAEONTOLOGY

Genus ANGOSPIRIFER nov.

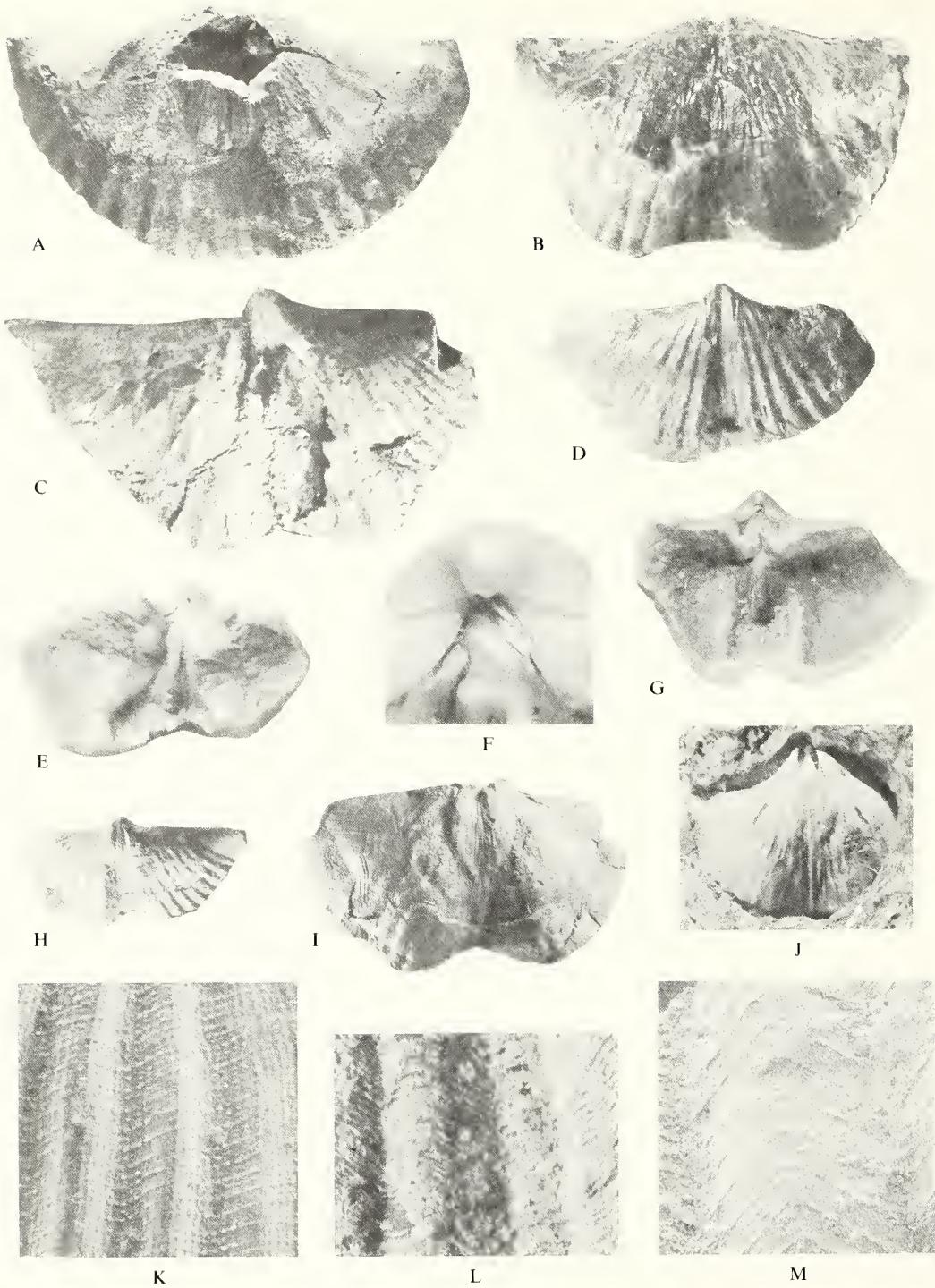
Type species. *Spirifer trigonalis* (Martin, 1809) *sensu* Muir-Wood 1956; Brigantian, Scotland.

Derivatio nominis. From the Greek word *aggeion* (= vessel): a reference to the development of the vascular markings.

Diagnosis. Shell of trigonal shape, megathyrid to slightly brachythryid; lateral ribs conspicuous, rarely divided, median sinus and fold costate; sub-imbricated micro-lamellae bearing faint radial tubercles; adminicula short, intra-sinal; elongated apical callosity located between apex and muscle scar; genital markings surrounding the apical-muscular area; vascular markings roughly reticulated, developed on adult interior lateral ventral region.

Description of the type species: *S. trigonalis*

The type specimen of the species *trigonalis* is a neotype, proposed by Muir-Wood to the International Commission on Zoological Nomenclature (1956, p. 112). It bears British Museum (Natural History) number BB 7340; and is figured by Davidson (1858, pl. 5, fig. 33; 1863, pl. 50, fig. 4) and Dunlop (1961, pl. 64, figs. 1–3). The locality 'Cousland, near Dalkeith, Midlothian', is a well-known old quarry in the North Greens Limestone and underlying shales (Wilson 1974, locality 32; P. Brand, pers. comm.), of upper Brigantian age (George *et al.* 1976, fig. 14j). The lost original specimens described by Martin came from a different locality: 'Derbyshire', with an imprecise age of Asbian to Brigantian. So, the neotype choice may have altered the original sense of the species *trigonalis*.



Newly collected topotypes would have provided the firmest basis for this study, but they proved impossible to obtain. P. Brand (British Geological Survey, Edinburgh) recently visited Cousland quarry and found it partly filled. Some specimens collected from Cousland have been examined in the British Geological Survey, Edinburgh (EV 517–519, 524, B 1735^D, B 1787^D, T 3277), but they are poorly preserved.

On the other hand, D'Arcy quarry, 4 km S-SW of Cousland in the North Greens Limestone (Wilson 1974, locality 31), has yielded good specimens (British Geological Survey, Edinburgh, T 3278; text-fig. 1C, M). In addition the *S. trigonalis* material described by Dunlop (1961) is from another Scottish locality: Brockley, near Coalburn, Lanarkshire. This locality is 65 km SW from Cousland, in the Douglas Main Limestone, at the base of the lower Limestone group, and a little below the *stratum typicum* (George *et al.* 1976, fig. 14B). Dunlop (1961) has established statistically that the Brockley spiriferid population belongs to the species *trigonalis*. I have collected extra specimens from this locality (text-fig. 1B, D). Therefore, in the absence of good *trigonalis* topotypes, D'Arcy and Brockley specimens may be used. In both localities the shells are preserved in shaly limestones, those from D'Arcy being rather fragile and distorted. Internal moulds have been prepared by partly removing the shell material with needles (text-fig. 2A, D, F).

Other specimens are natural internal moulds from outside Scotland: British Geological Survey no. RV 733, figured in Burgess and Holliday (1979, pl. 6, fig. 14) and herein (text-fig. 1A), from the Pendleian of Cumbria; British Museum (Natural History), Gilbertson Collection no. B 244, figured by Waterhouse (1970, pl. 2, figs. G–J), from an unknown locality, probably Bolland, Yorkshire; B.M.(N.H.) nos. BD 2062–2063 (text-fig. 1E, F, G), from the late Dinantian of Alnwick, Northumberland. These latter specimens show apical interiors.

Morphological terms. Most morphological terms are in current use, as in Williams and Rowell (1965). Some less common terms not cited by Dunlop (1961) are listed in Table 1.

Biometry. The Brockley population has been studied statistically by Dunlop (1961, p. 480, text-fig. 1, tables 1, 2). Some specimens from D'Arcy attain 42 mm in width, whereas the Brockley shells never exceed 39.3 mm wide. The external variability of *A. trigonalis* is important, and more so than previously recognized. The neotype is decidedly narrower than the largest members of these populations (maximum width 27.8 mm; hinge width 24.9 mm; length 24 mm; thickness 18.2 mm).

TEXT-FIG. 1A–G, M., *Angiospirifer trigonalis* (Martin, *sensu* Muir-Wood). A, British Geological Survey, Keyworth, RV 733; natural internal mould of adult specimen, formerly figured by Pattison in Burgess and Holliday (1979, pl. 6 fig. 14). Knutton Shell Beds, Pendleian, Coldberry Gutter (Cumbria), $\times 2$. B, British Museum (Nat. Hist.) BD 1700, prepared internal mould of adult pedicle valve collected by the author. Douglas Main Limestone of Lower Limestone Group, Brigantian, Brockley (Lanarkshire), $\times 2$. C, British Geological Survey, Edinburgh, T 3278-1, prepared internal mould of adult pedicle valve. North Greens Limestone of Lower Limestone Group, Brigantian, D'Arcy quarry (Midlothian), $\times 2$. D, B.M.(N.H.) BD 1701, prepared internal mould of young pedicle valve collected by the author. Same locality as B, $\times 2$. E, F, B.M.(N.H.) BD 2062, adult pedicle valve; Carboniferous Limestone (Brigantian), Alnwick (Northumberland). E, interior, showing delthyrium, elongated apical callosity, muscle scar, $\times 2$. F, fragments of stegidial plates, $\times 5$. G, B.M.(N.H.) BD 2063, pedicle valve interior. Same locality as E and F, $\times 2$. M, B.G.S., Edinburgh, T 3278-2, external microsculpture. Same locality as in C, $\times 20$. H and K, *Anthracospirifer pellaensis* (Weller); H, B.M.(N.H.) BD 1703, prepared internal mould of adult specimen given to the author by Dr. G. A. Cooper; Pella beds, Meramecian, 2 miles S of Pella (Iowa, USA), $\times 1$. K, B.M.(N.H.) BD 1704, external microsculpture of specimen given to the author by Dr. A. S. Horowitz; Pella Formation, Meramecian, Mahaska quarry (Iowa, USA), $\times 10$. I, J, L, 'Parachoristes' (*sensu* Lazarev and Poletaev 1982). I, J, Cayton Gill beds, Kinderscoutian, Ripley, Harrogate (N. Yorkshire). I, B.G.S. Keyworth, 50261, natural internal mould of adult pedicle valve, formerly figured as 'Spirifer ♂' by George (1932, text-fig. 8), $\times 1$. I, B.M.(N.H.) BD 1702, natural mould of rather young pedicle valve collected by the author, $\times 1$. L, B.M.(N.H.) BD 1705, external microsculpture of specimen collected by the author. Oued el Hamar Formation, upper Bashkirian, Oued Tagnana section, loc. ML 290, 15 km W-NW. of Béchar (Algeria), $\times 10$.

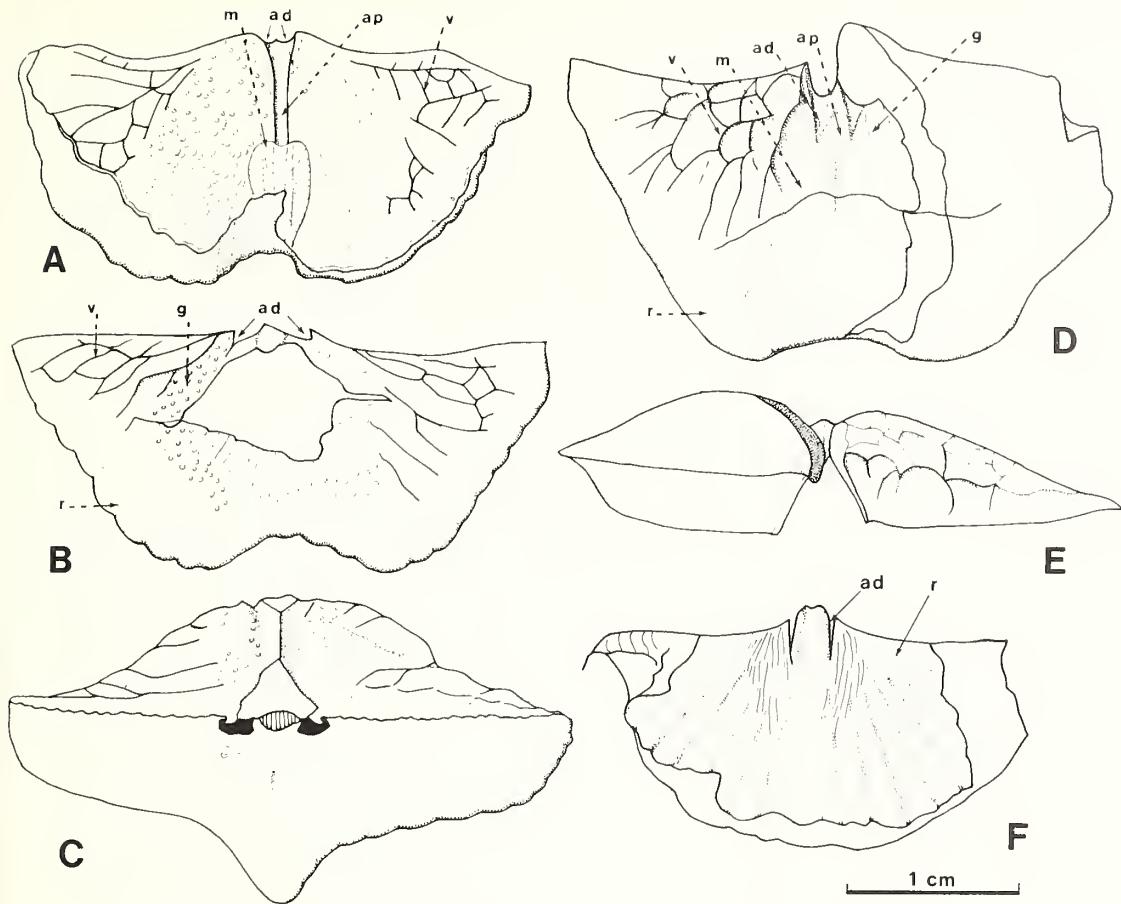
TABLE 1. Morphological terms not cited in Dunlop (1961) or differently interpreted, and their equivalents in the literature

Terms and their authors (when post <i>Treatise</i> , 1965)	Definitions	Equivalents in: (1) Dunlop 1961; (2) Vandercammen 1959, 1962; (3) Lazarev and Poletaev 1982
Adminicula	Ventral parts of dental plates, joining to the bottom of the pedicle valve	(1) dental plates
Apical callosity	Secondary thickening inside the umbo of the pedicle valve	(1) 'ventral septum'
Delthyrial plate	Transverse plate connecting the two dental plates in their apical part, below the inter-area level	
Genital markings	Radial ridges or pits on inside of shell within genital areas	(2) gonoglyphe (3) alveolate vascular system
Stegidial plates: Cowen 1968; Grant 1976	Pairs of laminate plates making up the delthyrial cover, forming a convex arch above the interarea level; they are fragile and rarely entirely preserved	(1) a part of the 'delthyrial plate' (2) plaques deltidales
Tabellae: Waterhouse 1968	Dorsal supporting plates, called crural plates by some authors	(1) crural plates
Vascular markings	Impressions of mantle canals on shell interior	(2) angioglyphe (3) pinnate, ramified, reticulate vascular system

Microsculpture. The neotype exhibits fine but worn concentric lamellae. Davidson (1863, pl. 50, fig. 9a) figured the microsculpture of a specimen from Barrhead, Renfrewshire, Scotland. This specimen is not preserved in the British Museum collections. However, Davidson's observation is confirmed on specimens from D'Arcy (text-fig. 1M). The concentric lamellae are variously spaced (4–10 per mm) and are slightly raised and imbricated, like a tiled roof; their anterior borders display a festoon aspect, due to fine tubercles being arranged regularly in radial rows. Sometimes, traces of these tubercles form very fine radial lirae.

Delthyrium and stegidial plates. Dunlop (1961) described the area and delthyrial structures. None of the Scottish specimens displays externally preserved stegidial plates, but fragments of these structures are seen on specimens from Alnwick (text-fig. 1F) and on B.M.(N.H.) B 244 (Waterhouse 1970, fig. 2J). Stegidial structures are found on apical sections of Brockley specimens, as described below.

Internal moulds and surfaces (text-figs. 1A–G, 2). On adult internal moulds the adminicula appear as extremely short apical incisions, close to each other and within the sulcus. A narrow median apical callosity forms a depression that runs from the inter-adminicular region to the posterior end of the muscle scar; its length and shape are very variable, from short rhombic form (text-fig. 2D) to an elongate septum-like shape (text-figs. 1G, 2A). The muscle scar is moderately to slightly depressed into the shell substance, pyriform, and more or less separated from the apex, occurring either just in front of the adminicular distal extremities (text-fig. 2D) or at some distance from them (text-fig. 2A). The genital markings surround the region of the muscle scar and apical callosity, extending up on to the inside of the interarea on both sides of the delthyrium (text-fig. 2C). This area bears small pits which may be arranged in an indistinct radial pattern. The vascular markings, around the genital area, extend over the whole posterolateral interior surface, including the lateral regions of the interarea. Two distinct canals run from the tops of lateral apical cavities towards the lateral extremities. They widen, divide into transverse canals, and form a rough reticulation upon the insides of the interarea.



TEXT-FIG. 2. *Angiospirifer trigonalis* (Martin, *sensu* Muir-Wood), internal moulds. A, British Museum (Nat. Hist.) BD 1700, adult pedicle valve. Douglas Main Limestone, Brigantian, Brockley (Lanarkshire). B, C, British Geological Survey, Keyworth, RV 733, adult specimen, broken in the ventral muscular area. Knutton Shell Beds, Pendleien, Coldberry Gutter (Cumbria). B, ventral view. C, dorsal view. D, E, British Geological Survey, Edinburgh, T 3278-1, adult pedicle valve. North Greens Limestone, Brigantian, D'Arcy Quarry (Midlothian). D, ventral view. E, dorsal view. F, B.M.(N.H.) BD 1701, young pedicle valve. Same locality as in A. ad = adminicula or their internal moulds; ap = apical callosity; g = genital markings; m = muscle scar; r = external ribs on their internal moulds; v = vascular markings.

and ears. Other radial canals extend from the lateral parts of the genital area, to branch and anastomose together (text-fig. 2A, B, D). The shape of the external ribs is seen internally only anteriorly. Brachial valve internal moulds (text-fig. 2C) display short thick tabellae; the cardinal process and muscle scar are poorly preserved; reduced genital markings appear on both sides of the muscle area.

A young pedicle valve, 25 mm wide, with a shell thickness of 0.4 mm, shows internally the external ribs pattern within 7 mm of the apex (text-figs. 1D, 2F). The adminicula are represented by two slender incisions, 2 mm apart and 2.4 mm long; their apical parts are extra-sinal, whereas their distal extremities coincide with the sinal borders. There is no apical callosity. The muscle scar is hardly distinguishable, but posteriorly it projects to between the adminicula, whereas its anterior border

seems to extend beyond them. The genital and vascular markings are not differentiated. Lateral to the adminicula, thin radiating canals run in different directions from the external ribs.

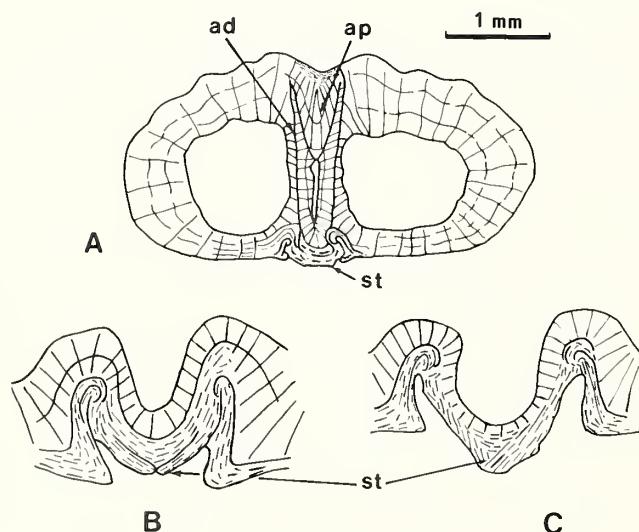
On another young pedicle valve, 41 mm wide and 1 mm thick (T 3278-3, not figured), the external ribs are seen internally after one third of the length of the valve. Already the muscle scar is located anterior of the apex, from which it is separated by a median callosity 4 mm long. The genital and vascular markings are again poorly differentiated.

The characteristic adult pattern of genital and vascular markings appears on the pedicle valves when the shell, in the posterior region, is at least 2 mm thick. Thus the ontogeny of *A. trigonalis* is characterized by a rapid forward migration of the muscle scar; the development of the vascular markings is linked with a thickening of the shell in the whole posterolateral ventral region.

Apical sections of pedicle valves. Apical sections have been described by Dunlop (1961, text-figs. 4e-f, 7e, 12a-e; pl. 65, fig. 7), and again here (text-fig. 3A-C). The dental plates are well developed, made of two distinctive parts: 1, short converging dental 'flanges' bordering the delthyrium; 2, long parallel or slightly diverging adminicula. Both parts are made of tertiary columnar shell, on both sides of a slender median fibrous layer (Vandercammen and Plodowski 1967). The 'median septum' of Dunlop (1961, text-figs. 4d, 12a, d, e) corresponds mainly to the median apical callosity, posterior to the muscle scar. The growth surfaces (as seen in sections, e.g. Dunlop 1961, text-fig. 12e) show that there is no fibrous layer such as occurs in true septa. On the other hand, in the umbo infilling, the 'V' structure called a septum by Dunlop (1961, text-fig. 12a), resembles a recrystallization figure ('faux coussinet septal' of Vandercammen and Plodowski 1967). The 'delthyrial plate' described by Dunlop poses a problem: its anterior part is convex, protruding above the level of the interarea. In fact, it is *pro parte* a stegidial cover, as is strongly suggested by sections exhibiting paired but unequally developed plates (text-fig. 3B, C). A true single internal delthyrial plate is restricted to the top of the delthyrial cavity, but on most adult specimens it is obliterated by the umbonal infilling and recrystallization.

Remarks. The species *trigonalis* has been attributed in the literature to several spiriferid genera: to *Spirifer* by most authors in the past, and by Dunlop (1961); to *Fusella* by Buckman (1906), Beznosova (1959), and (with some uncertainty) Brunton and Rissoné (1976); to *?Anthracospirifer* by Thomas (1971); and to *?Unispirifer* by Afanas'eva (1975).

Spirifer Sowerby 1816 attains a greater size than *Angiospirifer*, and has frequently divided radial ribs and a microsculpture of radial lirae; vascular markings are absent or reduced to fine and short canal traces. *Fusella* M'Coy 1844 has dental plates comparable to those of *Angiospirifer*, being



TEXT-FIG. 3. *Angiospirifer trigonalis* (Martin, *sensu* Muir-Wood), transverse sections of pedicle valves showing structures reinterpreted from Dunlop (1961). A, Dunlop's text-fig. 12e. B, Dunlop's text-fig. 11e. C, Dunlop's text-fig. 11g. Douglas Main Limestone, Brigantian, Brockley (Lanarkshire). ad = adminicula or their internal moulds; ap = apical callosity; st = stegidial plates.

positioned within the sinus (Brunton and Rissoné 1976, fig. 2A). The muscle scars are indistinguishable, the median callosity is restricted to the tip of the umbo, and the vascular markings are reduced. A further important difference is the virtual absence of ribbing in the ventral sulcus of *Fusella*. *Unispirifer* Campbell 1957 has an ornamentation of finer and more numerous ribs than on *Angiospirifer* and a microsculpture of radial lirae. Its adminicula diverge and surround the posterior part of the muscle scar and the vascular markings are not differentiated. *Anthracospirifer* Lane 1963 has the same external shape and ornamentation as *Angiospirifer*, but it differs in: *a*, its microsculpture, with radial lirae as prominent as the concentric lamellae, forming a characteristic reticulation (text-fig. 1K; Sutherland and Harlow 1973, pl. 16, fig. 10); *b*, the position of the ventral muscle scar, which on adult internal moulds creates a strong apical relief (text-fig. 1H; Sutherland and Harlow 1973, pl. 16, fig. 4); *c*, the adminicula, which diverge around the posterior part of the muscle scar, in an extra-sinal position; *d*, the vascular markings, which seem to be absent. In the pedicle valve of *Anthracospirifer* the posteriorly thickened shell thins rapidly towards the margins, so that the internal surface shows the external ribbing. *Prochoristitella* Legrand-Blain 1968 resembles *Angiospirifer* by the position of the adminicula, apical callosity, and muscle scar; however, the microsculpture differs from that of the latter genus by better development of the radial lirae; mantle cavities are reduced. *Brachythyrina* Fredericks 1929 has the same shape and ornamentation as *Angiospirifer*. Its apical callosity, muscle scar, and mantle canals are comparable, but *Angiospirifer* is distinguished by possessing adminicula. Choristitids, like *Angiospirifer*, are provided with slightly diverging or parallel adminicula, and reticulate vascular markings (Lazarev and Poletaev 1982, pl. 1, figs. 4, 5): this pattern is well exhibited on British specimens from the Kinderscoutian Cayton Gill beds (text-fig. 1I, J). The choristtid microsculpture, seldom figured in Russian literature, is not preserved on the Cayton Gill material. On Algerian Bashkirian specimens (text-fig. 1L) the microsculpture is rather similar to that of *Angiospirifer*, although the concentric lamellae are more closely spaced. The differences between choristitids and *Angiospirifer* are: *a*, the radial ribs are generally more slender and bifurcating in choristitids; *b*, the adminicula are longer and the apical callosity reduced or absent; *c*, the vascular markings are more extensive, especially in the anterior part of the pedicle valve, and their reticulation is more delicate than in *Angiospirifer*. Finally, the genus *Subspirifer* Shan and Zhao 1981, which resembles *Angiospirifer* by shape and costation, differs by its smooth dorsal fold. Its microsculpture is unknown and its internal structure inadequately figured.

Generic composition

It is difficult to assign with certainty species of the broad *trigonalis* group to *Angiospirifer*. Some of the '*trigonalis*' specimens widely cited in the Eurasian and North African Carboniferous may not belong to *Angiospirifer*. For example, '*Spirifer trigonalis*' from Silesia (Zakowa 1958, pl. 3, fig. 9; 1966, pl. 15, figs. 3, 6) of probable Asbian age, displays a prominent apical muscle scar and pinnate mantle canals; it is probably not congeneric. The species *bisulcatus* Sowerby, sometimes considered synonymous with *trigonalis*, does not belong to *Angiospirifer*, since the syntypes in the Sowerby Collection, examined in the British Museum (Natural History), have a lirate microsculpture.

Some Serpukhovian Russian species, described by Semikhhatova (1941) as '*trigonalis* group', may be true *Angiospirifer*: their adminicula show a tendency towards reduction and the muscle scar is located far from the apex (*S. gamma* Semikhhatova, 1941, pl. 5, figs. 14b, 16b). The microsculpture of the species *parabisulcatus* Semikhhatova is identical to that of *A. trigonalis* (Ivanova 1971, text fig. 4; pl. 1, fig. 4). The assignment of these species to *Angiospirifer* should be checked by observations of the vascular markings.

In addition the present author is currently investigating several undescribed *Angiospirifer* species in the upper Viséan and Serpukhovian of the northern Algerian Sahara.

Phyletic and systematic position of the genus Angiospirifer

The evidence of reticulate vascular markings as early as the upper Viséan is a significant feature for the phyletic trends of Spiriferidae. Ivanova (1972) pointed that the complex choristtid canal system evolved from a spiriferid stock. In the diagram of Lazarev and Poletaev (1982), such a development

was recorded only from Bashkirian choristitids, and regarded as an important criterion for distinguishing lower and upper Carboniferous Spiriferids. There is now evidence for the existence of reticulate vascular markings as early as the end of lower Carboniferous, both in *Angiospirifer* and in *Brachythyrina* (*Anthracothyrina*) Legrand-Blain, 1984. These taxa are related to each other, displaying a reduction in their dental plates (studied in some Russian species of the *trigonialis* group by Yanichewsky (1935), Semikhatova (1941), and observed also in Algerian species). On the other hand, *Angiospirifer* is a possible ancestor of choristitids. The origin of *Angiospirifer* should be sought in pre-Brigantian specimens, probably among the genera *Unispirifer* or *Prochoristitella*.

Placing *Angiospirifer* within its correct position and amongst the spiriferids is currently impossible. Ivanova (1972) attaches importance to the canal system which characterizes the families Brachythrididae and Choristitidae. The existence in *Angiospirifer* of a denticulate interarea separates it from the Brachythrididae. The Choristitidae of Ivanova (1972) have well-developed adminicula, so it is impossible to include both *Angiospirifer* and *Brachythyrina* in that family.

Carter (1974) distinguished many subfamilies in the Spiriferidae, but without considering the mantle canals. He doubtfully placed *Brachythyrina* in the Prospirinae (the microsculpture of which is lirate). His sub-family Choristitinae includes several genera characterized by numerous divided ribs.

Brunton and Rissoné (1974), followed by Waterhouse (1981), placed *Fusella* and *Brachythyrina* in the subfamily Strophopleuridae, which they considered as belonging to the family Mucospiriferidae, and not Spiriferidae. In my opinion the sinal costation of *Angiospirifer* is strongly different from the ornamentation of Mucospiriferids.

Thus, since *Angiospirifer* does not fit into existing families, I propose a new sub-family, belonging to the family Spiriferidae King 1846 *sensu* Carter 1974.

Subfamily ANGIOSPIRIFERINAE nov.

Diagnosis. Transverse shape; ribs not numerous, sometimes dividing; microsculpture sub-imbricated; adminicula short or lacking; apical callosity and vascular markings more or less developed.

Genera included. *Angiospirifer* gen. nov.; *Brachythyrina* Fredericks, 1929; *Prochoristitella* Legrand-Blain, 1968; *Kinghuria* Litvinovitch, 1969; ?*Quizhouspirifer* Xian, 1979; ?*Subspirifer* Shan and Zhao, 1981.

Stratigraphic range. Lower Carboniferous (Viséan) to lower Permian.

Acknowledgements. The author thanks Dr. C. H. C. Brunton for his advice, supervision of the manuscript, and loan of British Museum (Natural History) specimens; Dr. P. Brand for information about Scottish localities and loan of Edinburgh Geological Survey specimens; Drs. W. H. C. Ramsbottom and J. Pattison for demonstrating the Cayton Gill locality and for the loan of British Geological Survey specimens; Drs. G. A. Cooper and A. S. Horowitz for the gift of American *Anthracospirifer*.

REFERENCES

- AFANAS'YEVA, G. A. 1975. The genus *Unispirifer* (Brachiopoda) in the Soviet Union. *Paleont. J.* **1975**, 412–413.
- BEZNOSOVA, G. A. 1959. Lower Carboniferous Brachiopods of the Kuznetsk basin (families Cyrtospiriferidae and Spiriferidae). *Tr. Pal. Inst. A.N. SSSR.* **75**, 1–136. [In Russian.]
- BRUNTON, C. H. C. and RISSONÉ, A. 1976. *Fusella* McCoy 1844, a problematic brachiopod genus from the lower Carboniferous. *Bull. Br. Mus. Nat. Hist. (Geol.)* **27**, 275–284.
- BUCKMAN, S. S. 1906. Brachiopod nomenclature. *Ann. Mag. Nat. Hist.* **58**, 321–327.
- BURGESS, I. C. and HOLLIDAY, D. W. 1979. Geology of the country around Brough-under-Stainmore. *Mem. Geol. Surv. G.B.* sheet 31.
- CARTER, J. L. 1974. New genera of Spiriferid and Brachythridid brachiopods. *J. Paleont.* **48**, 674–696.
- COWEN, R. 1968. A new type of delthyrial cover in the Devonian brachiopod *Mucospirifer*. *Palaeontology*, **11**, 317–327.
- DAVIDSON, T. 1858–1863. A monograph of British Carboniferous brachiopods. *Palaeont. Soc. [Monogr.]* **2**, 5, 1–280.
- DUNLOP, G. M. 1961. Shell development in *Spirifer trigonalis* from the Carboniferous of Scotland. *Palaeontology*, **4**, 477–506.

- GEORGE, T. N. 1932. Brachiopoda from the Cayton Gill beds. *Trans. Leeds Ass.* **5**, 37–48.
- JOHNSON, G. A. L., MITCHELL, M., PRENTICE, J. E., RAMSBOTTOM, W. H. C., SEVASTOPULO, G. D. and WILSON, R. B. 1976. A correlation of Dinantian rocks in the British Isles. *Geol. Soc. London Spec. Rep.* **7**, 1–87.
- GRANT, R. E. 1976. Permian brachiopods from Southern Thailand. *Mem. Paleontol. Soc.* **9**, 1–269.
- IVANOVA, E. A. 1960. Order Spiriferida. In ORLOV, Y. A. (ed.). *Principles of Palaeontology*, (7) *Bryozoa and Brachiopoda*, 264–280. Mosk. A.N. SSSR.
- 1971. Introduction to the study of Spiriferids. *Tr. Pal. Inst. A.N. SSSR*, **126**, 1–104. [In Russian.]
- 1972. Main features of Spiriferid evolution (Brachiopoda). *Paleont. J.* **1972**, 309–320.
- LAZAREV, S. S. and POLETAEV, V. I. 1982. The development of the brachiopod mantle canal system at the early–middle Carboniferous boundary. In: RAMSBOTTOM, W. H. C. et al. (eds.). *Biostratigraphic data for a mid-Carboniferous boundary*, 89–94. Subcommittee on Carboniferous Stratigraphy, Institute of Geological Sciences, Leeds.
- LEGREND-BLAIN, M. 1968. Spiriferacea carbonières et permiens d'Afghanistan central. *Notes et Mém. Moyen-Orient, Museum d'Hist. nat. Paris*, **9**, 187–253.
- DELVOLVÉ, J. J. and PERRET, M. F. 1984. Les brachiopodes carbonières des Pyrénées Centrales françaises. 2—Etude des Orthida et des Spiriferida. Biostratigraphie, Paléoécologie, Paléobiogéographie. *Geobios*, **17**, 297–325.
- MUIR-WOOD, H. M. 1956. Request for the substitution of neotype as the standard of reference for six nominal species belonging to the Class Articulata (Phylum Brachiopoda), the names published for which by Martin (W.) in 1809 have been validated by the International Commission on Zoological Nomenclature, in place of the figures previously proposed for adoption as such standards. In: Opinion 419. *Opin. and Decl. Intern. Comm. Zool. Nomencl.* **14**, 107–119.
- SEMIKHATOVA, S. V. 1941. 'The group of *Spirifer trigonalis* Martin' from the lower Carboniferous supracoalbearing beds of Moscow basin. *Tr. Pal. Inst. A.N. SSSR*, **12**, 1–175. [In Russian.]
- SUTHERLAND, P. K. and HARLOW, F. H. 1973. Pennsylvanian brachiopods and biostratigraphy in Southern Sangre de Cristo Mountains, New Mexico. *Mem. New Mexico Bur. Mines Miner. Res.* **27**, 1–173.
- THOMAS, G. A. 1971. Carboniferous and early Permian Brachiopods from Western and Northern Australia. *Bull. Austr. Bur. Min. Res. Geol. Geophys.* **56**, 1–276.
- VANDERCAMMEN, A. 1959. Essai d'étude statistique des *Cyrtospirifer* du Frasnien de la Belgique. *Mém. Inst. roy. Sci. nat. Belg.* **145**, 1–175.
- and LAMBIOTTE, M. 1962. Observations sur les sarcoglyphe dans *Atrypa reticularis* (C. Linné, 1767). *Bull. Inst. roy. Sci. nat. Belg.* **38**, 1–15.
- and PLODOWSKI, G. 1967. La question du genre *Spirifer* s. str. et des genres voisins. *Ibid.* **43**, 1–11.
- WATERHOUSE, J. B. 1968. The classification and description of Permian Spiriferida (Brachiopoda) from New Zealand. *Palaeontographica*, A, **129**, 1–94.
- 1970. The lower Carboniferous brachiopod genus *Fusella* McCoy 1844. *Occ. Pap. Roy. Ontario Mus. Life Sci.* **15**, 1–12.
- 1981. The Permian Stratigraphy and Palaeontology of Southern Thailand. *Mem. Thailand Geol. Surv.* **4**, 1–213.
- WILLIAMS, A. and ROWELL, A. J. 1965. Morphological terms applied to Brachiopods. In: MOORE, R. C. (ed.) *Treatise on Invertebrate Paleontology, Part H, Brachiopoda 1*, H139–H155. Geological Society of America and University of Kansas Press, New York and Lawrence.
- WILSON, R. B. 1974. A study of the Dinantian marine faunas of South-East Scotland. *Bull. Geol. Surv. G.B.* **46**, 35–65.
- YANICHEWSKY, M. E. 1935. On some peculiarities of the shells of Spiriferida. *Annuaire Soc. Paleont. Russie*, **10**, 11–27.
- ZAKOWA, H. 1958. Biostratigraphy of the lower Carboniferous marine deposits of the area of Walbrzych Miasto (Lower Silesia). *Inst. Geol. Prace*, **19**, 1–211.
- 1966. Zone *Goniatites crenistria* Phill. in the vicinity of Sokolec and Jugow, at the foot of the Sowie Gory Mountains (Central Sudetes). *Ibid.* **43**, 1–197.

MARIE LEGREND-BLAIN

Laboratoire de Géodynamique des Bassins Sédimentaires
Université de Pau et des Pays de l'AdourAvenue de l'Université
64000 Pau
France

Typescript received 19 July 1984

Revised typescript received 2 January 1985

OSTRACODES ACROSS THE IAPETUS OCEAN

by ROGER E. L. SCHALLREUTER and DAVID J. SIVETER

ABSTRACT. A pilot study comparing ostracode faunas from the North American and European plates dispels the notion that Ordovician ostracodes show strict endemicity. Problems addressed include: how some ostracodes managed to cross the Ordovician Iapetus Ocean estimated at 3,000 + km wide; and why some of their ostracode counterparts in the Silurian show provinciality? It is concluded that, from the point of view of ostracode dispersal, opposing Ordovician plates may have been in closer effective geographical proximity than hitherto supposed. Ostracodes recovered only slowly and with general provincial aspect from global sea level changes at the Ordovician-Silurian boundary.

Ostracode distributions support other biogeographic evidence that Tornquist's Sea, the ocean between the Gondwanan plate (containing southern Britain) and Baltica, had contracted by mid to late Ordovician and that the Rheic Ocean, separating northern and southern Europe, was developing during the Silurian. Much more work on Lower Palaeozoic ostracodes is needed to test these findings further.

MOST of present day Europe and North America were separated by an ocean during the early Palaeozoic. Wilson's (1966) idea that the 'proto-Atlantic' had opened and closed again during the Cambrian to Silurian has been amplified in many accounts which document sedimentological, structural, and tectonic evidence for what has been termed the Iapetus Ocean (e.g. Dewey 1969; Phillips *et al.* 1976; Mitchell 1984). Palaeontologists have independently tested for the existence and distance apart of the plates by comparing Lower Palaeozoic faunas and floras from both sides of the presumed ocean, and assessing their relative provincial or cosmopolitan nature (e.g. Spjeldnaes 1978). Faunal evidence relating to continental separation has been elaborated mainly using trilobites (e.g. Whittington and Hughes 1972; Fortey 1975), brachiopods (Williams 1973, 1976), and graptolites (Skevington 1978). Some microfossil groups (e.g. conodonts; Fortey and Barnes 1977) have been similarly employed but ostracodes have been neglected in this respect.

There is no recognized Lower Palaeozoic equivalent of the ostracode fauna of the later (Tertiary-Recent) deep-sea psychrosphere. Thus, no Lower Palaeozoic (benthic) ostracodes can be regarded as diagnostically 'oceanic'. However, ostracode endemicity can be used as a good independent test for the presence of an ocean recognized from other geological and faunal evidence. Ordovician ostracodes have previously been assumed to be endemic across the Iapetus Ocean: in a paper which provided the standard reference model for progressive faunal migration across the Iapetus Ocean, McKerrow and Cocks (1976, fig. 1) charted ostracodes as the last major animal group, apart from freshwater fish, to migrate (in the middle Silurian) across the former oceanic barrier.

The present paper represents a pilot study to assess the possible occurrence of generic or species level links between pertinent ostracode faunas of the North American and European plates, particularly during Ordovician times, and also to assess what implications such possible links may have for palaeogeography and for the palaeozoology of Lower Palaeozoic Ostracoda. Supporting the model of development of the Iapetus Ocean based on structural and allied evidence (Phillips *et al.* 1976), distributional patterns of trilobites and brachiopods indicate that the discrete lower Ordovician faunal provinces, which help define each plate, had by Caradoc-Ashgill times broken down as the ocean narrowed. Ostracode faunal links between the two plates are herein shown to occur and increase throughout the Ordovician. It is concluded that, bearing in mind the possible dispersal capabilities of Ordovician ostracodes, opposing Ordovician plates may have been in closer effective geographical proximity than hitherto supposed.

According to recent palaeogeographic reconstructions based on facies and faunal analysis (Cocks and Fortey 1982, figs. 2, 3; see text-fig. 1 herein), during the Arenig–early Llanvirn a North American continent straddled the equator, while Baltic and Gondwanan continents were positioned at southerly, relatively temperate and high latitudes respectively. North America included Britain north of the Lake District, Spitzbergen, Greenland, and western Newfoundland, but excluded parts of the present day American Atlantic seaboard. The Baltic continent extended from Scandinavia eastwards to parts of the Russian platform. Gondwana included southern Britain, Africa, South America, Iberia, Bohemia, and eastern Newfoundland. Tornquist's Sea, the proposed ocean (Cocks and Fortey 1982) separating the Baltic and Gondwanan continents, is thought to have closed during mid to late Ordovician times, thus creating a latitudinally more continuous southern continental margin to the Iapetus Ocean. Cocks and Fortey (1982) also document mid to late Silurian faunal evidence supporting the presence of a widening Rheic Ocean between the latter southern continental area and Gondwana–southern Europe (including France, Iberia, and Bohemia) further south.

SILURIAN OSTRACODE FAUNAS OF THE NORTH ATLANTIC REGION

Unusually for Silurian invertebrates, a barrier to geographical dispersal of many characteristic ostracodes apparently still existed along the site of the remnant Iapetus Ocean. Late Silurian (Ludlow–Přídolí) ostracode faunas of the European plate indicate widespread faunal links, particularly in the distribution of kloedeniine beyrichiaceans (Martinsson 1963, 1965, 1967, 1970, 1977; Siveter 1978b). Combinations of the genera *Kloedenia*, *Londonia*, and *Frostiella*, and concomitant beyrichiine and amphitoxotidine taxa define a late Silurian faunal region incorporating parts of Maritime Canada and New England (eastern Maine, southern New Brunswick, eastern Nova Scotia), southern Britain including the Lake District, Scania, subsurface rocks in the Baltic and Poland and extending into Podolia, Ukrainian SSR. Corresponding faunas on the North American plate (Lundin 1971; Berdan 1983) are mostly different, being rare in ostracodes with strong 'Baltic' affinities. Thus, a parallel 'Appalachian belt' is traceable from westernmost Virginia to Gaspé and the Silurian faunas of Anticosti Island, Canada (Berdan 1970; Copeland 1977a; Copeland and Berdan 1977). This belt has an essentially endemic beyrichiacean fauna (Copeland 1980) characterized, for example, by early Silurian zygodoblines and a later Silurian–early Devonian 'false *Kloedenia*' fauna. Silurian faunas from central Europe (Czechoslovakia), dominated by non-palaeocopes (see Bouček 1936), are largely different again from those of northern Europe and eastern North America, and thus could support the notion of a second more southerly barrier (the Rheic Ocean) hindering the dispersal of invertebrates.

These three ostracode regions are broadly defined, largely on the occurrence and type of beyrichiaceans present (a distinctive group of shallow-water benthic ostracodes), and are conspicuous during the late Silurian. Concurring with the faunal migrational patterns proposed by McKerrow and Cocks (1976), Cocks and Fortey (1982, p. 474) concluded that in the Silurian, 'The assumption, from faunal grounds alone, that there was still a Iapetus Ocean is based on continued provinciality of the thelodont fish and ostracods'. This seemed to confirm the migrational pattern one might expect of ostracodes from a knowledge of the life history of extant forms, which lack pelagic larvae.

The regions inevitably have some ostracode genera in common. For example, *Beyrichia*, *Craspedobolbina*, and *Aechmina* are also known from the early Silurian sequence of Anticosti (Copeland 1974a, 1982a). In Britain, where remnants of the North American and European plates are sutured, the rare ostracode species known from the Silurian of Scotland are endemic, although some of the genera (e.g. *Beyrichia*, *Craspedobolbina*) are also known from the prolific faunas of southern Britain (Siveter 1978b). Further afield, other 'European'–'North American' Silurian ostracode contacts are more difficult to explain palaeogeographically, such as those few (pelagic?) podocopid genera from Bohemia and Soviet Asia which are also recorded from the mid to late Silurian of north-western Canada (Copeland 1977b). This part of Canada belongs to the late Silurian–Devonian Cordilleran ostracode province extending from Nevada to Alaska (Berdan 1983).

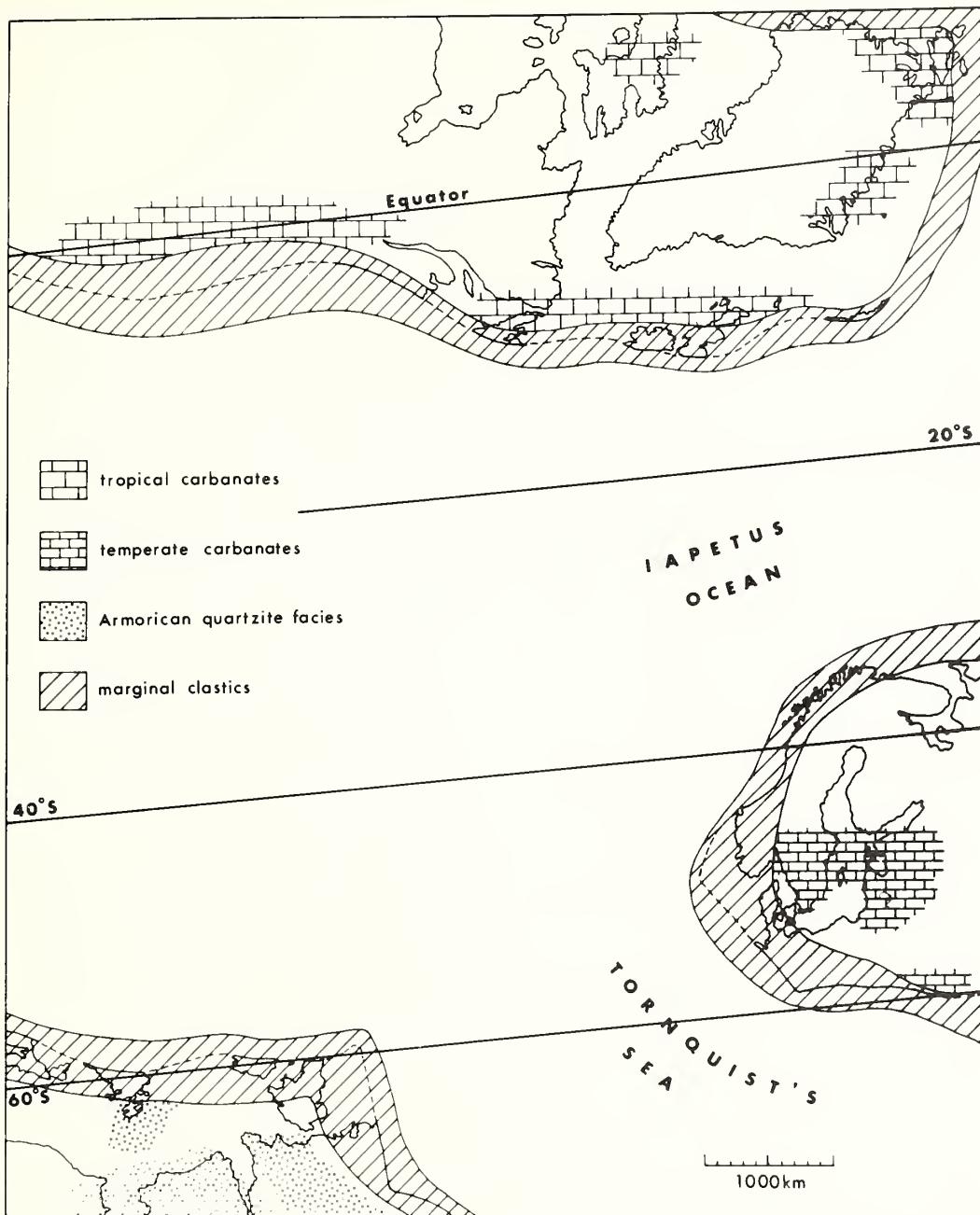


FIG. 1. Palaeogeography and chief sedimentary facies of the area surrounding Britain in Arenig times (from Cocks and Fortey 1982).

which, although on the opposite side of the North American plate to the western margin of the Iapetus Ocean, was nevertheless capable of recruiting a few north 'European' type beyrichiacean genera in addition to central European podocopids.

OSTRACODES AS INDICATORS OF ENVIRONMENT

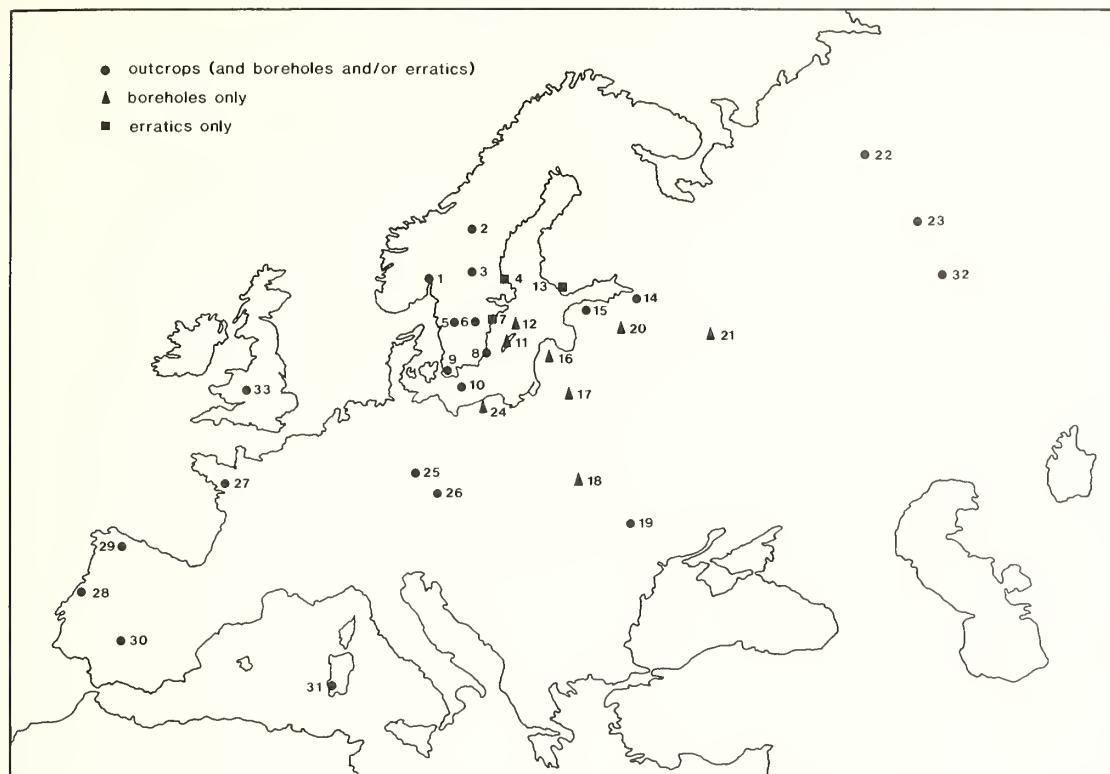
Studies of the life cycle and ecology of modern species (for example Elofson's (1941) classic paper on marine forms from Sweden) indicate that benthic ostracodes have no known pelagic larval stage and that ontogeny normally proceeds within a single biotope. Unaided dispersal across deep oceanic barriers would logically be a formidable task for benthic ostracodes, which generally live on, or sometimes burrow into, the substrate. Although some ostracode groups such as the Myodocopida are pelagic, the overwhelming number of both living and fossil marine forms have, or are thought to have had, a benthic mode of life. The vast majority of extant marine ostracodes live in the typically high diversity littoral and shallow marine zones. By contrast, the present day deep-ocean (psychrospheric) benthic ostracode faunas (those living at depths of about 500–5000 m) are global and cosmopolitan in distribution but relatively poorly diverse (Benson and Sylvester-Bradley 1971; Benson 1979). The junction between the psychrosphere and the shallower, warmer 'thermosphere' represents a fundamental biological frontier (Hessler and Saunders 1967)—an environmental barrier which, if breached, induces amongst ostracodes skeletal and diversity changes in response to the new stresses imposed (Benson 1975c, 1981).

Ostracodes can be good palaeoenvironmental indicators, particularly in post-Palaeozoic rocks where closer taxonomic correlation with modern groups facilitates easier ecological interpretation than for Palaeozoic forms. Ostracodes are opportunistic colonizers, occurring in marine, brackish, freshwater, and even terrestrial environments. Unlike the plankton, extant benthic ostracodes are affected by such environmental factors as the nature of the substrate (Elofson 1941). However, salinity and depth-related factors, such as bottom-water temperatures, exert the most significant control on their overall distribution. As Benson elegantly demonstrated in his studies of Tethys and its Messinian salinity crisis (1972, 1973, 1975a, 1976), and of the early Tertiary origin of the psychrosphere (1975b), the development of a sedimentary basin or the evolution of oceanic systems can be independently charted using ostracode faunal evidence. Ostracodes—often facies controlled—have the capacity to crawl into or out of basins as changing geological and environmental controls dictate. The history of Lower Palaeozoic ostracodes is presumably controlled in like fashion and would similarly betray major events such as the relative movements of plates.

OCCURRENCE OF EUROPEAN AND NORTH AMERICAN ORDOVICIAN OSTRACODES

The occurrence of described Ordovician ostracode faunas is shown in text-figs. 2 and 3. Ostracodes are known from much of Scandinavia, with important faunas from the lower Ordovician of the Siljan district (Hessland 1949) and the Oslo region (Henningsmoen 1954a); from the middle Ordovician of Jämtland and Tvären (Thorslund 1940), central Sweden (Jaanusson 1957), and the Oslo region (Henningsmoen 1953); and from the upper Ordovician of Västergötland (Henningsmoen 1948), the Oslo region (Henningsmoen 1954b), and Scania (Troedsson 1918; Schallreuter 1980). Sarv (e.g. 1959, 1963) has described Estonian Ordovician ostracodes and Schallreuter (1983; full bibliography) has extensively documented faunas from Baltoscandian erratic boulders. Faunas described from eastern Europe embrace the middle and upper Ordovician of Latvia and Lithuania (Gailīte *in* Ulst *et al.* 1982; Sidaravičienė 1971, 1975) together with records from the Leningrad region (Männil 1963), Volhyn (Krandievsky 1975), and Podolia (Krandievsky 1969). In central Europe ostracodes are recorded from nearly all Ordovician stages in Bohemia, the late Ordovician of Thuringia, and a borehole in Pomerania (Schmidt 1941; Blumenstengel 1965; Knüpfer 1968; Přibyl 1979).

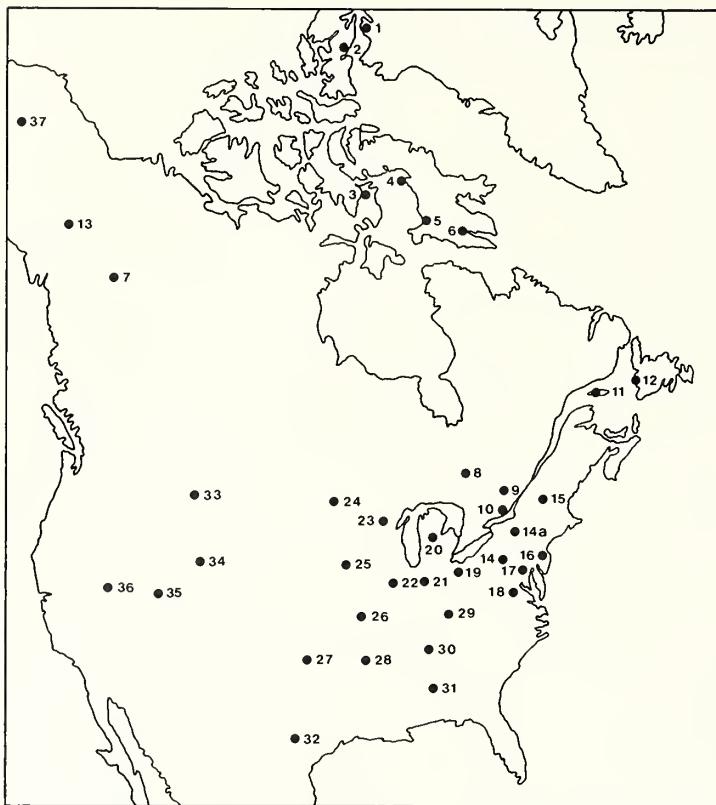
Ostracodes occur in many Ordovician areas in Britain; Siveter (1978a) has reviewed all known



TEXT-FIG. 2. Occurrence and key papers of the main Ordovician ostracode faunas from Europe: 1, Oslo Region (Henningsmoen 1953, 1954a, b; Qvale 1980); 2, Jämtland (Thorslund 1940); 3, Siljan district (Hessland 1949; Jaanusson 1957); 4, South Bothnian area (Jaanusson 1957); 5, Västergötland (Henningsmoen 1948; Jaanusson 1957); 6, Östergötland (Jaanusson 1957); 7, Tvären area (Thorslund 1940; Jaanusson 1957); 8, Öland (Jaanusson 1957; Schallreuter 1977c); 9, Scania (Troedsson 1918; Schallreuter 1980); 10, Bornholm (Poulson 1978); 11, Gotland and Baltic erratics in general (e.g. see Schallreuter 1983, and references therein); 12, Gotska Sandön (Jaanusson 1966); 13, Nyland (Martinsson 1956); 14, Leningrad district (Männil 1963); 15, Estonia (Sarv 1959, 1963); 16, Latvia (Gailīte *in Ulst et al.* 1982); 17, Lithuania (Siduravičienė 1971, 1975); 18, Volyn (Krandievsky 1975); 19, Podolia (Krandievsky 1969); 20, Pskov district (Neckaja 1973); 21, Moscow syneclyse (Prokofiev and Kuznetsov 1982); 22, Pečorskian Urals (Zenkova 1977); 23, Central Urals (Persina *et al.* 1971); 24, Pomerania (Bednarczyk 1974); 25, Thuringia (Knüpfer 1968); 26, Bohemia (Přibyl 1979); 27, Armorican Massif (Vannier 1984); 28, Portugal (Vannier 1984); 29, Cantabrian Mountains (Bassler and Kellett 1934); 30, Almaden (Bassler and Kellett 1934); 31, Sardinia (Bassler and Kellett 1934); 32, Central Urals (Varganov *et al.* 1970); 33, Great Britain (Siveter 1978a, 1982b, c, 1983; Schallreuter and Siveter 1983a).

faunal associations and revised key taxa. Vannier (1984) has recently provided comprehensive faunal records from the Armorican Massif, France, and a comparison with Ordovician ostracodes from Iberia.

The better known faunas from the North American plate include those from Oklahoma (Harris 1957), Kentucky (Warshauer and Berdan 1982), Virginia (Kraft 1962), Michigan (Kesling 1960; Kesling *et al.* 1962), Missouri (Keenan 1951), Iowa and Ontario (Kay 1934, 1940), Minnesota and Iowa (Swain *et al.* 1961; Burr and Swain 1965), and various eastern states (e.g. Swain 1957, 1962). Many faunas, particularly of middle and upper Ordovician age, have been described from Canada by Copeland (e.g. 1962, 1965, 1966, 1970, 1973, 1974b, 1977a, b, c, 1978, 1982b, 1983). Unrevised faunas



TEXT-FIG. 3. Occurrence and key papers of the main Ordovician ostracode faunas from United States, Canada, and Greenland. 1, Greenland (Teichert 1937a, b); 2, Ellesmere Island (Teichert 1937a, b); 3-6, Melville Peninsula and Baffin Island (Copeland 1977c); 7, District of McKenzie (Copeland 1974b, 1977b, 1982b); 8, Lake Timiskaming and vicinity (Copeland 1965); 9, Ottawa Valley (Copeland in Steele and Sinclair 1971); 10, Napanee, Ontario (Copeland 1962); 11, Anticosti Island (Copeland 1970, 1973); 12, Newfoundland (Copeland and Bolton 1977; Whittington and Kindle 1963); 13, Yukon (Copeland 1966, 1977b, 1978); 14, 14a, Pennsylvania and New York (Swain 1957, 1962); 15, Vermont (Creath and Shaw 1966); 16, 17, New Jersey and Maryland (Bassler and Kellett 1934); 18, Virginia (Kraft 1962); 19, Ohio (Warshauer 1975; Guber 1971); 20, Michigan (Kesling 1960; Kesling *et al.* 1962); 21, Indiana (Guber 1971); 22, Illinois (Bassler and Kellett 1934); 23, Wisconsin (Kay 1940); 24, Minnesota (Burr and Swain 1965; Swain *et al.* 1961); 25, Iowa (Burr and Swain 1965); 26, Missouri (Keenan 1951); 27, Oklahoma (Harris 1957); 28, Arkansas (Harris 1957); 29, Kentucky (Warshauer and Berdan 1982); 30, 31, Tennessee and Alabama (Bassler and Kellett 1934); 32, 33, Texas and Montana (Harris 1957); 34, Wyoming (Guber and Jaanusson 1964; Berdan 1976); 35, 36, Utah and Nevada (Berdan 1976); 37, Alaska (Copeland 1983).

occur in Greenland (Teichert 1937b) and Scotland (see Siveter 1978a), and ostracodes are also known to occur in the Arenig of Spitsbergen (Fortey 1975).

AFFINITIES BETWEEN EUROPEAN AND NORTH AMERICAN ORDOVICIAN OSTRACODES

Ordovician ostracodes have previously been assumed to be endemic across the North Atlantic region (McKerrow and Cocks 1976; Cocks and Fortey 1982), but the evidence indicates that this is not the case.

Rader (1965), Copeland (1977a, p. 5; 1978, p. 97; 1981, p. 185; 1983), Copeland and Berdan (1977, p. 22), Swain (1977, p. 39), Siveter (1978a), and Schallreuter and Siveter (1982, 1983b) indicate some Ordovician genera common to Europe and North America but no comprehensive comparison of Ordovician faunas from opposite sides of the Iapetus Ocean has been made, partly because of inherent difficulties. Most Ordovician faunas are incompletely known and taxonomic revision is required for several major faunas, especially those described from North America. In general, early Ordovician ostracode faunas are poorly represented or are less well documented than those of the middle and late Ordovician. In addition, within the Palaeocopa, homeomorphy, misidentification, and classificatory difficulties are widespread. Nevertheless, as Ordovician ostracodes are documented from virtually all North American states and relevant western European countries, a faunal comparison is possible.

Plates 68–70 illustrate just a few of the Ordovician ostracode genera common to two or more relevant continents. They embrace a wide variety of both palaeocopes (Pls. 68, 70) and non-palaeocopes such as Eridostraca (Pl. 69, figs. 1, 2), Metacopa (Pl. 69, figs. 3, 4), Leiocopa (Pl. 69, figs. 5, 6), Binodicopa (Pl. 69, figs. 7, 8), and Leperditiocopa (Pl. 69, figs. 9, 10). Taxonomic revision and improved documentation (of, for example, British faunas) will undoubtedly produce an extended list of cosmopolitan genera (and possibly some conspecific taxa) from opposite sides of the Iapetus Ocean.

Earliest contacts

Ostracode faunas of the North American and European plates reveal elements in common from at least the later part of early Ordovician times. *Eobromidella* provides an early link, occurring in the lower Ordovician of Sweden (Hessland 1949) and the Tulip Creek Formation (early Champlanian), Simpson Group of Oklahoma (Harris 1957); differences between the two forms appear minimal (Pl. 68, figs. 5, 6). This early ostracode contact across the Iapetus Ocean confirms the migrational pattern defined from palaeogeography: an equatorial North America opposed a southerly, approaching Baltica, with the Gondwanan continent further to the south beyond a contracting Tornquist Sea.

Other initial links would possibly be recognized if early Ordovician faunas were better known, particularly from North America. Moreover, compared with the Scandinavian limestone-and-shale successions in which Ordovician palaeocopes flourished from Arenig to Ashgill, known British faunas are notably deficient in the Arenig and early Llanvirn. For instance, the oldest known ostracode faunas of significance from Wales and the Welsh Borderland are from the Llandeilo of South Wales (Siveter 1978a). In the strongly contrasted facies of the British Ordovician, representative ostracode assemblages belong mostly to the shelly associations and not to the alternative basin facies; it seems a valid generalization to group Ordovician ostracodes with trilobites and brachiopods as shelf-sea benthos. It may be significant, therefore, that British ostracode faunas largely come from post-Llanvirn sequences when the contrast between shelly and graptolitic facies was strongest, and lithologies similar to 'Llandeilo Flags' prevailed.

Middle Ordovician

Most of the genera with supposed European affinities mentioned by Swain (1962, 1977) we consider misidentified. Nevertheless, in the middle Ordovician clearly increased affinities exist between opposing Iapetus Ocean ostracode faunas, presumably reflecting a closer proximity of plates than in earlier times. Many middle Ordovician ostracode genera are common to both North American and European plates; there is ample evidence also of contemporaneous ostracode contact between Baltica and part of the old Gondwanan continent, as represented by southern Britain. The notion that Gondwana moved north, so that Tornquist's Sea had virtually ceased to exist by mid to late Ordovician (Cocks and Fortey 1982), is corroborated in as much as any remnant of this ocean evidently failed to provide an effective barrier to ostracode dispersal. Whittington and Hughes (1972) and Williams (1973, 1976) showed that, by the late Caradoc, certain trilobite and brachiopod faunas of southern Britain and Scandinavia respectively were very similar; generic links between the ostracode faunas of the two areas, and between Britain and North America, can be traced somewhat

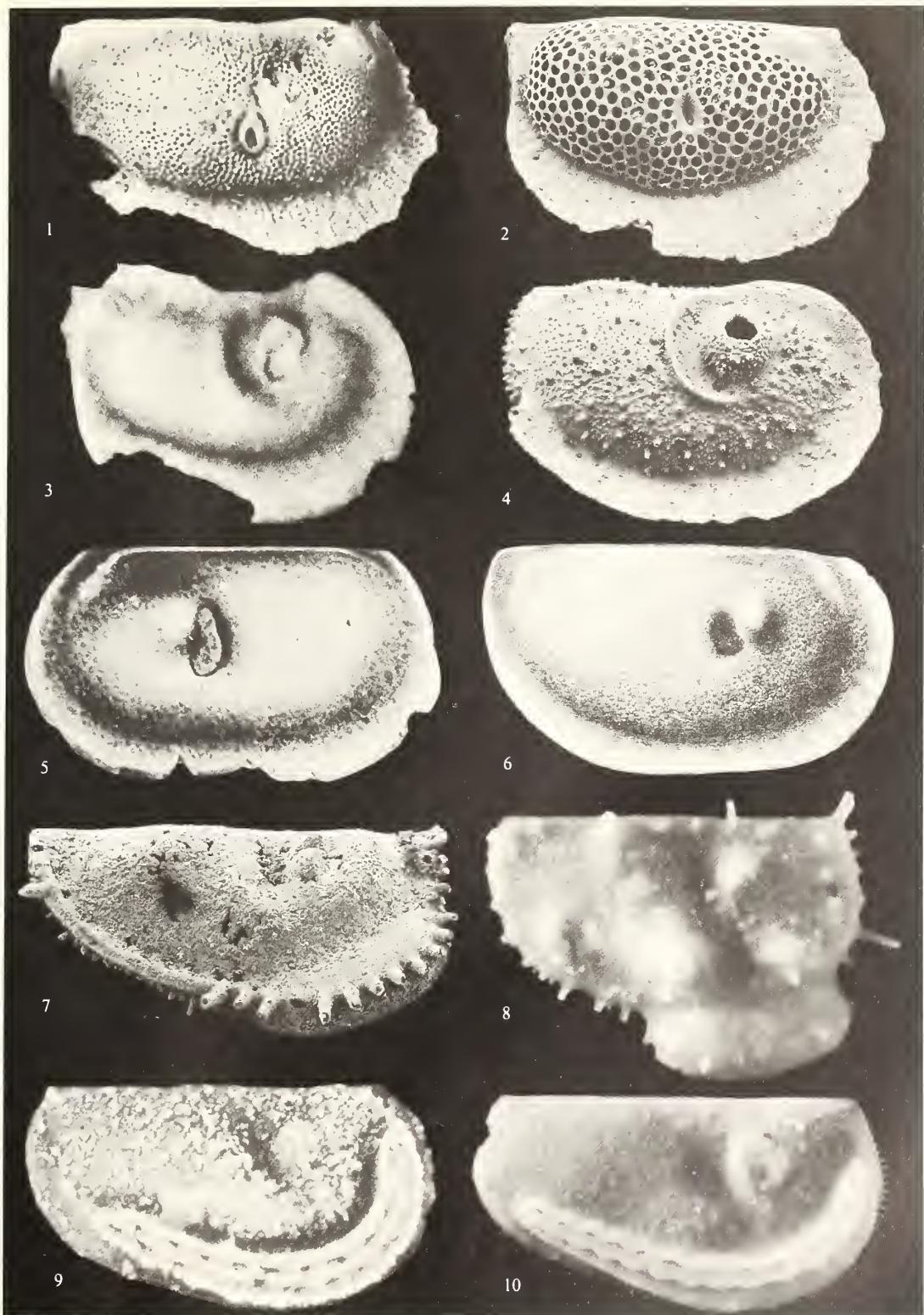
earlier to the Llandeilo Series of Wales. Additionally, the presence in the Caradoc and possibly the Ashgill of southern Britain (Siveter 1978a, pl. 3, fig. 5 and p. 46 respectively) of the Bohemian genus *Crescentilla* suggests that, unless the ostracode was pelagic, the postulated developing Rheic Ocean was not yet a formidable obstacle to migration. Obviously many middle Ordovician ostracode genera are endemic to one particular plate, but the fact that ostracode faunal links between the plates were firmly established by mid Ordovician is also clear and requires explanation.

Homeokiesowia, *Vittella*, *Klimphores*, *Pseudulrichia*, and *Tallinnellina* are amongst many ostracode genera occurring in the Llandeilo Series of South Wales and the middle Ordovician of Baltoscandia (Siveter 1978a, 1982b, 1983; Schallreuter and Siveter 1983a). For example, the Llandeilo material includes a form close to *Pseudulrichia bucura*, a species recorded from middle Ordovician Backsteinkalk boulders of North Germany and Gotland and from the higher part of the Idavere Stage (C_3) (= early Caradoc) in the Pskov district, Russia (Siveter 1978a). *Cryptophyllus* (Pl. 69, figs. 1, 2) is one of the rare ostracodes to show moult retention and occurs as far afield as the Llandeilo Series of South Wales (Siveter 1978a), the Öjlemyrflint erratics of the Baltic (Schallreuter 1977a), the early to mid Ordovician of Oklahoma (Harris 1957), and the Whiterockian Sunblood Formation of north-western Canada (Copeland 1978). *Ceratopsis* is equally as distinctive morphologically and characteristic of mid to late Ordovician sequences in the United States (e.g. Kentucky: Warshauer and Berdan 1982; Ohio: Warshauer 1975) and north-western and eastern Canada (Copeland 1974b, 1977a); it is represented by *C. britannica*, *C. duftonensis*, and undescribed species variously from the

EXPLANATION OF PLATE 68

Palaeocopes from the lower and middle Ordovician of both sides of the Iapetus Ocean (*left* North America, *right* Europe).

- Fig. 1. *Platybolbina (Rimabolbina) omphalota* Kesling, 1960, middle Ordovician (Bony Falls Limestone, Blackriverian), Bony Falls on the Escanaba River, Delta County, Michigan, U.S.A.; right valve (holotype, UMMP 37355), $\times 34$ (from Kesling 1960, pl. 8, fig. 4 *left*).
- Fig. 2. *P. (Rimabolbina) rima* Schallreuter, 1964, middle Ordovician (Skagen Formation, Upper Viruan), Backsteinkalk erratic boulder (no. Sta1, 1B1 type), Staberhuk, Isle of Fehmarn (Baltic Sea), Germany; right valve (GPIMH 2717), $\times 47$.
- Fig. 3. *Hesperidella michiganensis* Kesling, Hall and Melik, 1962, same bed and locality as fig. 1; immature female right valve (paratype, UMMP 37225), $\times 87$ (from Kesling *et al.* 1962, pl. 2, fig. 2 *left*).
- Fig. 4. *H. estonica* (Bonnema, 1909), same boulder as fig. 2; tecnomorphic right valve (GPIMH 2718), $\times 48$.
- Fig. 5. *Laccochilina [Eobromidella] eurychilinoides* (Harris, 1957), middle Ordovician (Tulip Creek horizon, Blackriverian), Sycamore Creek Simpson section, Oklahoma, U.S.A.; left valve (holotype, Museum of Comparative Zoology, Harvard University, Boston, no. 4631), $\times 29$ (from Harris 1957, pl. 8, fig. 1a).
- Fig. 6. *L. dorsoplicata* Hessland, 1949, lower Ordovician (Upper Oelandian, Kundan), Silverberg II, Eastern Siljan District, Dalecarlia, Sweden; right valve (holotype, Museum of the Palaeontological Institute, University of Uppsala, no. ar.os.398), $\times 42$ (from Hessland 1949, pl. 6, fig. 6).
- Fig. 7. *Hithis colonus* Schallreuter and Siveter, 1982, middle Ordovician (lower part of Edinburg Formation), section in field on south side of road, 0.2 km south-east of Strasburg Junction, just west of Strasburg, Shenandoah County, Virginia, U.S.A.; female right valve (paratype, GPIMH 2675; valve tilted 10°), $\times 45$.
- Fig. 8. *H. hithis* Schallreuter, 1964, middle Ordovician (Skagen Formation, Upper Viruan), Backsteinkalk erratic boulder (no. 1B16, 1B1 type), beach at Dornbusch, Isle of Hiddensee (Baltic Sea), Germany; female right valve (holotype, SGWG 3/3; Schallreuter 1964b, pl. 12, fig. 2), $\times 80$.
- Fig. 9. *Hippula (Hippula) varicata* (Harris, 1957), middle Ordovician (Lower Esbataottine Formation, Chazyan), Sunblood Mountain, southwestern District of Mackenzie, Canada; female right valve (GSC 49378), $\times 67$ (from Copeland 1982b, pl. 1, fig. 2).
- Fig. 10. *H. (H.) latonoda* (Schallreuter, 1964), middle Ordovician (Skagen Formation, Upper Viruan), Backsteinkalk erratic boulder (no. 1B4, 1B1 type), beach at Dornbusch, Isle of Hiddensee (Baltic Sea), Germany; female right valve (holotype, SGWG 2/3; Schallreuter 1964a, pl. 10, fig. 1), $\times 60$.



SCHALLREUTER and SIVETER, palaeocopes from the lower and middle Ordovician of North America (*left*) and Europe (*right*)

Llandeilo, Caradoc, and Ashgill of South Wales, the Welsh Borders, and Cross Fell in southern Britain (Siveter 1978a). *Hithis* (Pl. 68, figs. 7, 8) is present in the mid and late Ordovician of Baltoscandia and the Edinburg Formation of Virginia (Schallreuter and Siveter 1982), while *Hippula* (Pl. 68, figs. 9, 10) occurs in the mid Ordovician of Baltoscandia, Thuringia, Bohemia, Siberia, and Oklahoma (Schallreuter and Krúta 1980), and in the District of Mackenzie, Canada (= *Oecematobolbina* of Copeland 1982b).

Later Ordovician

Many ostracode genera from the late Ordovician of the North American continent are typical of the fairly homogeneous coeval faunas of the Baltic regions (see Pl. 70) and also occur to a varying extent in Scandinavian and southern British faunas. On Anticosti Island alone, the late Ashgill Ellis Bay and underlying Vaureal formations (Copeland 1970, 1973) have the following genera in common with the Baltic: *Moeckowia*, *Anticostiella*, *Caprabolbina*, *Platybolbina*, *Tetradella*, *Eoaquapulex*, *Pseudulrichia*, *Antiaeclimina*, *Cryptophyllus*, *Eographiodactylus*, *Hemeaschmidtella*, *Trianguloschmidtella*, *Warthinia*, *Byrsolopsina*, *Monotiopleura*, *Brevibolbina*, *Pseudolippula* (Pl. 70, figs. 3, 4), *Rectella*, and *Brevidorsa*. *Distabolbina warthini* Copeland, 1977, from the late Mohawkian of Baffin Island, Canada, and *D. grekoffi* Schallreuter, 1977, from upper Ordovician Baltic erratics, may be conspecific (Pl. 70, figs. 1, 2). Furthermore, Copeland (1983) has recently reported the typical circum-Baltic species *Steusloffina cuneata* from the latest Ordovician/earliest Silurian of Anticosti Island. The ostracode fauna of the Ashgill Brachiopodskiffer of Scania (Troedsson 1918) includes the characteristic American genus *Quadrijugator*, whilst that of the late Ordovician Maquoketa Shale of Missouri (Keenan 1951) contains many genera also found in the Baltic, exemplified *inter alia* by the species *Eoaquapulex barbatus*, *Byrsolopsina irregularis*, *Deefgella? septinoda*, *Spinaechmina taura*, and *Antiaeclimina maquoketensis*.

EXPLANATION OF PLATE 69

Non-palaeocopes from the middle Ordovician of both sides of the Iapetus Ocean (*left* North America, *right* Europe).

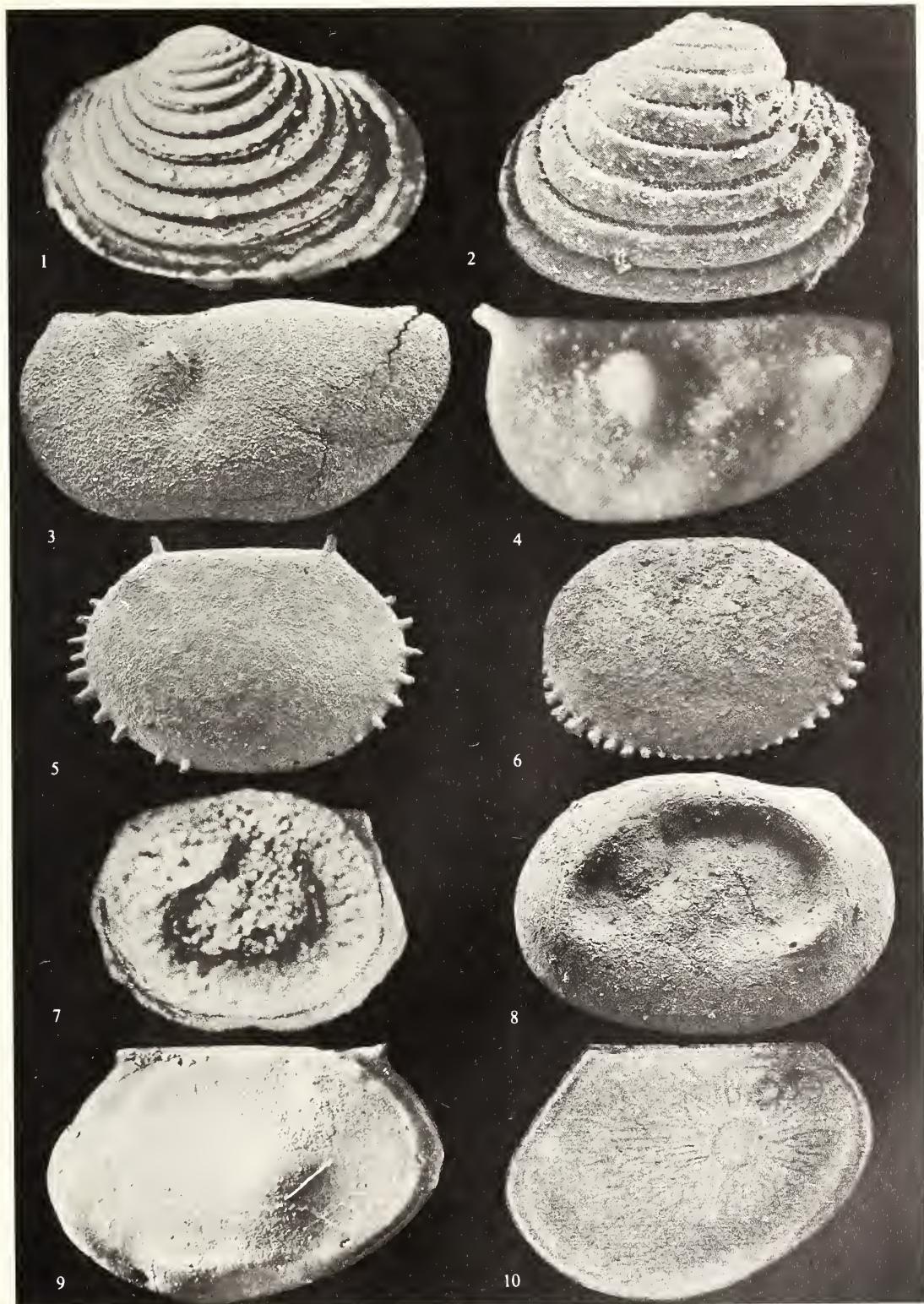
Figs. 1, 2. Eridostraca. 1, *Cryptophyllus magnus* (Harris, 1931), middle Ordovician (Sunblood Formation, Whiterockian, Chazyan), Esbataottine Mountain, southwestern District of Mackenzie, Canada; left valve (GSC 38417), $\times 36$ (from Copeland 1978, pl. 1, fig. 7). 2, *Cryptophyllus?* sp. of Siveter 1978, middle Ordovician ('Llandeilo Flags'), old quarry 300 m north of Big House, Lampeter Velfrey, east of Narberth Dyfed, Wales; right valve (BM(NH) no. OS 6676), $\times 76$ (from Siveter 1978a, pl. 1, fig. 1).

Figs. 3, 4. Metacopa. 3, *Balticella deckeri* (Harris, 1931), middle Ordovician (lower part of Edinburg Formation, Blackriverian), Strasburg Junction, Virginia, U.S.A.; left valve (GPIMH 2719), $\times 45$. 4, *B. binodis* (Krause, 1897) (= *B. oblonga* Thorslund, 1940), middle Ordovician [Idavere- (C_3) or Johvi-Stage (D_1), Upper Viruan], Backsteinkalk erratic boulder (type and no. 14B2), Teschenhagen near Stralsund, Pomerania, Germany; juvenile left valve (SGWG 28/9; Schallreuter 1968, fig. 10.4), $\times 64$.

Figs. 5, 6. Leiocopa. 5, *Brevidorsa fimbriata* (Ulrich, 1892), from same bed and locality as fig. 3; left valve (GPIMH 2720), $\times 32$. 6. *B. crassispinosa* (Schallreuter, 1973), from same bed and locality as Plate 68, fig. 2; left valve (GPIMH 2721), $\times 67$.

Figs. 7, 8. Binodicopa. 7, *Pedomphalella intermedia* Swain and Cornell in Swain *et al.* 1961, middle Ordovician (Decorah Shale), 3 miles east of Rochester, Minnesota, U.S.A.; imperfect left valve (paratype, Univ. Minnesota), $\times 115$ (from Swain *et al.* 1961, pl. 48, fig. 7a). 8, *P. jonesii* (Krause, 1897) (= *Schmidtella egregia* Sarv, 1963), same boulder as fig. 4; left valve (GPIMH 2722), $\times 99$.

Figs. 9, 10. Leperditiocopa. 9, *Bivia duncanae* Berdan, 1976, middle Ordovician (Llanvirn-Llandeilo; upper part of Kanosh Shale, Pogonip Group, Chazyan), Crystal Peak section, Ibex Area, Millard County, Western Utah, U.S.A.; right valve (paratype, USNM 235540), $\times 8$ (from Berdan 1976, pl. 5, fig. 4). 10. *B.? ordoviciana* (Kummerow, 1924), middle Ordovician light grey limestone erratic boulder corresponding in age to the Echinosphärenkalk (Lower Viruan), Voigtsdorf, Mecklenburg, Germany; right valve (lectotype, Museum für Naturkunde der Humboldt-Universität Berlin, MB.O.65), $\times 4$ (from Kummerow 1924, pl. 20 [numbered 21], fig. 1).



SCHALLREUTER and SIVETER, non-palaeocopes from the middle Ordovician of North America (left) and Europe (right)

By contrast the faunas of the Maquoketa Shale in Iowa (Burr and Swain 1965) bear more resemblance to those from Scania. Ostracoda in common with the upper Viru (Caradoc) Sularp Shale fauna (Schallreuter 1980) include *Pariconchoprimitia*, *Vogdesella*, *Orechina*, *Conchoprimitiella*, and *Klimphores*; the last two genera also occur in the mid to late Ordovician of southern Britain.

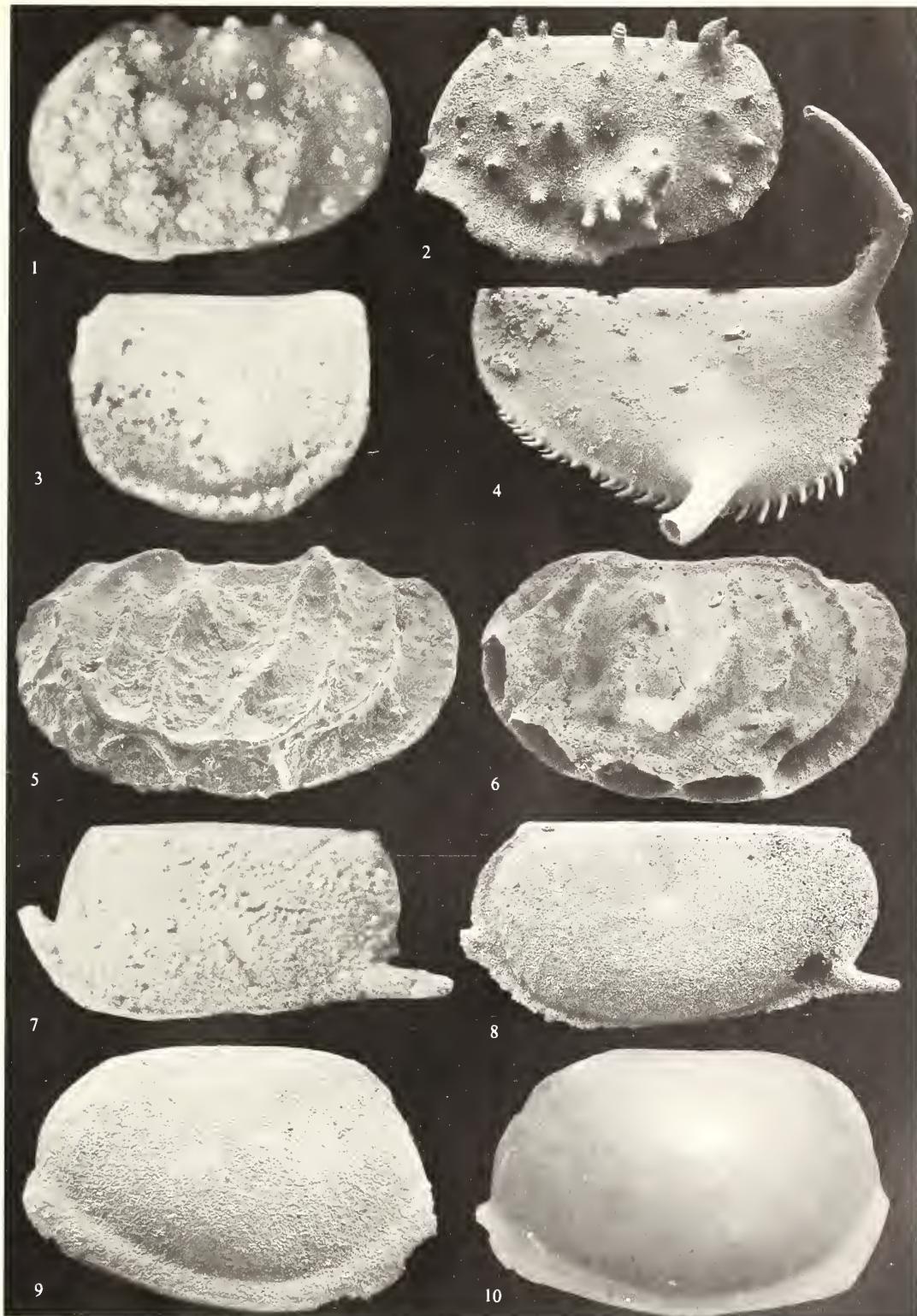
While the appearance of ostracode genera in common is often broadly contemporaneous between continents, the origins of many ostracode groups apparently lie on the North American plate with subsequent migration to 'Europe'. The Leperditiocopa (e.g. Pl. 69, figs. 9, 10), for example, occurs in North America throughout the Ordovician whereas in Europe only four species are known, including one from the middle Ordovician of Norway. Other groups, such as the Lomatopisthiidae, the Nodambichilinae, and genera such as *Eoaquapulex* (Pl. 70, figs. 9, 10), *Tetradella* (Pl. 70, figs. 5, 6), and *Eographiodactylus* (Pl. 70, figs. 7, 8) occur in North America by the middle Ordovician but not in Baltoscandia until the end of the Ordovician.

In summary, ostracodes display progressively increasing faunal connections between the North American and Baltica/Gondwanan continents throughout the Ordovician. The earliest known connections occur in the late early Ordovician; there are many genera in common in the middle Ordovician; and by the late Ordovician the ostracode faunas of the two areas show even greater similarity, including possibly conspecific material. There are correspondingly increasing ostracode links between the Gondwanan and Baltic continents as the intervening ocean waned. The pattern of ostracode distribution across the Iapetus Ocean seems to mirror that shown by Ordovician brachiopods and trilobites, with progressively increasing contacts associated with the approaching continents.

EXPLANATION OF PLATE 70

Palaeocopes from the middle and upper Ordovician of both sides of the Iapetus Ocean (*left* North America, *right* Europe).

- Fig. 1. *Distobolbina warthini* Copeland, 1977, middle Ordovician (late Mohawkian), Silliman's Fossil Mount, southern Baffin Island, Canada; female left valve (paratype, USNM 216133), $\times 82$ (from Copeland 1977c, pl. 6, fig. 9).
- Fig. 2. *D. grekoffi* Schallreuter, 1977, upper Ordovician (Upper Harjuan), Öjlemyrflint erratic boulder (no. G8), beach at Gnisvärd, Isle of Gotland (Baltic Sea), Sweden; female left valve (holotype, GPIMH 1926; Schallreuter 1977b, pl. 4.26, fig. 1a), $\times 63$.
- Fig. 3. *Pseudolippula castorense* (Copeland, 1970), upper Ordovician (Vauréal Formation), Anticosti Island, Quebec, Canada; posteriorly incomplete right valve (paratype, GSC 24004) with spines broken away, $\times 68$ (from Copeland 1970, pl. 4, fig. 21).
- Fig. 4. *P. pseudopokornina* Schallreuter, 1975, upper Ordovician (Upper Harjuan), Öjlemyrflint erratic boulder (no. Wie2), Wielen, west of Uelsen, Emsland, Niedersachsen, Germany; right valve (GPIMH 2723), $\times 97$.
- Fig. 5. *Tetradella scotti* Guber, 1971, upper Ordovician (Elkhorn Formation), Fairhaven, Preble County, Ohio, U.S.A.; female left valve (GPIMH 2724, valve tilted 20°), $\times 70$.
- Fig. 6. *T. separata* Sidaravičienė, 1971, upper Ordovician (Upper Harjuan), Öjlemyrflint erratic boulder (no. G16), beach north of Lickershamn, Isle of Gotland (Baltic Sea), Sweden; female left valve (GPIMH 1992, valve tilted 20°), $\times 59$.
- Fig. 7. *Eographiodactylus eos* Kraft, 1962, middle Ordovician (Edinburg Formation, Blackriverian), Tumbling Run section, Virginia, U.S.A.; left valve (paratype, USNM 136637), $\times 71$ (from Kraft 1962, pl. 16, fig. 9).
- Fig. 8. *E. sulcatus* Schallreuter, 1975, same boulder as fig. 4; left valve (GPIMH 2725), $\times 100$.
- Fig. 9. *Eoaquapulex* sp. (= *Oepikella frequens* of Kraft, 1962), same bed and locality as Plate 69, fig. 3; female right valve (GPIMH 2726), $\times 30$.
- Fig. 10. *E. frequens* (Steusloff, 1895), upper Ordovician (Upper Harjuan), Leptaenakalk erratic boulder, Neu-Brandenburg, Mecklenburg, Germany; female right valve (lectotype, SGWG 114/37), $\times 27$.



SCHALLREUTER and SIVETER, palaeocopes from the middle and upper Ordovician of North America (*left*) and Europe (*right*)

SIGNIFICANCE OF THE PATTERNS OF OSTRACODE DISTRIBUTIONS

How did many ostracode genera manage to cross the Iapetus Ocean in the Ordovician and why were some corresponding ostracodes still provincial during the Silurian?

Width of the Iapetus Ocean

Estimated widths of the Iapetus Ocean pose problems in explaining the pattern of ostracode migration. Based on structural and stratigraphic palinspastic restoration of Iapetus, Williams (1980) estimated a minimum width of 2000 km at its maximum development. He concluded (1980, p. 435) that it was unlikely that such a geographically continuous orogen (10,000 km) 'which included equally continuous tectonic-stratigraphic facies belts related to ancient continental margins and an ocean basin, could have been produced by the opening of a narrow rift, a marginal ocean, or even a narrow major ocean'. Analysis of structural telescoping and palinspastic restoration of coeval sedimentary facies across the western margin of Iapetus implies a continental slope/rise of at least 200 km width; modern continental margins of comparable width and length border major oceans (Williams 1980, p. 421).

Cocks and Fortey (1982, p. 474) noted that ostracodes would have been unable to cross an ocean barrier, even one quite narrow. Cocks *et al.* (1980) estimated an ocean 900 km wide by the early Silurian. By analogy with modern subduction rates and with the survival periods and dispersal rates of modern pelagic larvae, McKerrow and Cocks (1976) suggested a minimal 2000–3000 km width, even during late Ashgill, with the first closure occurring in the north-east by the Silurian collision of Greenland and the Baltic. They believed that a mid Silurian trans-Iapetus migration of benthic ostracodes demonstrated closure of the ocean along part of its length.

Pelagic larvae?

One can speculate that ostracodes crossed the Ordovician Iapetus Ocean because, unlike modern forms, they had pelagic larvae. This is improbable, a conclusion supported by the fact that many Ordovician ostracodes apparently brooded their young (dimorphism believed to be associated with egg/brood care dominates palaeocope morphology) and thus would be unlikely to also have had widely dispersed larvae.

Benthic migration?

Fortey (1975) and Fortey and Owens (1978) have demonstrated shelf to slope related Iapetus trilobite communities showing increasing cosmopolitanism with depth. Could the trans-Iapetus ostracodes possibly represent deeper water assemblages, or did they perhaps migrate stepwise down shelf and across the ocean? Alternatively, is the trans-Iapetus ostracode mixing due in part to transgressive events in the manner recently modelled and persuasively tested by Fortey (1984) when assessing biological effects of Ordovician eustatic events? The biological implications of a transgressive pulse include not only generation of endemic taxa on flooded cratonic areas but also migration shelf-wards of previously extra-cratonic, deep-water faunas, thereby giving a false impression of provincial breakdown in response to tectonic events (Fortey 1984, p. 39). Thus, the pronounced Llandeilo-Caradoc transgression augments tectonic explanations for the late Ordovician trilobite mixing across Iapetus (Fortey 1984, pp. 46–47, fig. 4).

That some ostracode faunal mixing may be explained either by trans-oceanic migration or by cratonic migration during transgressions undoubtedly justifies detailed investigation, but this lies beyond the scope of the present study. As noted above, however, depth barriers are generally formidable for ostracodes and, even though community and detailed facies related analyses of Ordovician ostracode faunas have not yet been attempted, in broad terms they belong to the relatively shallow-water shelf/platform environment and not to the outer slope (e.g. Copeland 1982b). The existence of a Lower Palaeozoic psychrospheric (deep-sea) ostracode fauna is not documented, but a controlling inflow of the cold polar waters necessary to create a more universal psychrosphere (Benson 1979) within a two-layer ocean model (Bruun 1957), similar to that determining global

distribution of extant oceanic ostracodes, was apparently a possibility during the Ordovician. Late Ordovician glaciation is amply attested and Fortey (1984, p. 48, fig. 10) has suggested that a possible early Ordovician South Polar ice sheet was twice as large as Antarctica today. We need to search the right kind of deposits for possible Ordovician psychrospheric ostracodes; the oceanic deposits of the Ordovician of the Southern Uplands of Scotland (Leggett 1979) are an example, but from which ostracodes are so far unknown.

Chance dispersal?

Dispersal of larvae (or even eggs or adults) by the passive transport of ocean currents is another possibility, as with many other marine invertebrates (Scheltema 1977). The ostracode dispersal patterns noted above suggest that, if current action was a factor, the significant current direction may have been from the North American to the European plate. Rafting on 'floats' (of, for example, marine algae) is yet another viable method of dispersal of modern marine animals, but is less effective (Scheltema 1977) because most benthic invertebrates are not well-adapted to survive long periods as epiplankton in the open sea.

The eggs of freshwater ostracodes are quite hardy; they are able to tolerate cold (Sohn and Kornicker 1979) and, in the case of some (though not all: McKenzie and Hussainy 1968), to withstand decades of desiccation (Van Morkhoven 1962, p. 139). Freshwater ostracode eggs can also possibly survive transport by high altitude winds (Sohn and Kornicker 1979) and have been found viable after ingestion and defecation by aquatic animals such as fish (Kornicker and Sohn 1971). The same has not been demonstrated for marine ostracodes, but they themselves form part of the diet of marine fish (Kornicker and Sohn 1971) and their eggs, when laid (outside the carapace), are usually deposited as clusters on bottom sediment or vegetation—an obvious potential food for many marine invertebrates.

Even though their dispersal mechanism is not in many cases understood, some modern ostracode faunas (from such island sites as Hawaii, for example) combine genera from distant regions separated by deep and in some cases almost 'barren' ocean floors (R. H. Benson, pers. comm.). It is thus possible that Ordovician ostracode dispersal was the result of nothing more than chance rafting or passive transport by other animals. Against this argument, however, is the fact that the ostracode migrational pattern copies that of trilobites and brachiopods, indicating that it reflects something more tangible than chance. Moreover, as noted above, there is reason to believe that in palaeocope ostracodes the well-being of possibly eggs and young depends to some degree on parental care. Potential Ordovician conveyors would also have been limited to cephalopods and possibly early fish, whereas modern ostracodes have many other passive dispersal mechanisms, including carriage by birds (e.g. De Deckker 1977) and man (Van Morkhoven 1962, p. 139).

Pelagic ostracodes?

Another solution is to reinterpret the palaeoecology of palaeocopes, but their shape, centre of gravity, and ventral and adventral structures favour the notion that most were benthic crawlers (or maybe bottom swimmers) and not pelagic; swimmers possibly included, for example, those forms with ventrally open (unprotected) antra, like *Foramenella* (Henningsmoen 1965). Pelagic ostracodes are characteristically planktonic forms and free-swimmers belonging to the Order Myodocopida; they are typically poorly calcified with a limited potential for preservation and have a scant fossil record. The origins of a free-swimming mode of life in Ostracoda is an untackled question but we know of no convincing pelagic myodocopid earlier than the Silurian. The bolbozooids and associates, known from basinal facies of the Ludlow Series of the Welsh Borderland and from coeval horizons of France, Sardinia, and Czechoslovakia, are possibly amongst the pioneer ostracodes adapted to a life off the bottom (Siveter 1984).

Closer geographical proximity?

Unless Ordovician ostracodes had some elusive mechanism of dispersal, their crossing of the Iapetus Ocean may have been aided by geographical proximity of opposing plates, which were possibly much

closer together and the ocean shallower at some point along the 10 000 km length of the Appalachian-Caledonides tract than estimates and palaeogeographical reconstructions have indicated. Bearing in mind the contacts demonstrated above (for example, by the ostracode fauna of South Wales as early as the early Llandeilo), the separation distance of 60° latitude between Britain and North America proposed by Cocks and Fortey (1982) (text-fig. 1 herein) appears to be an overestimate. This argument supports the tectonic model of Phillips *et al.* (1976) of oblique collision as early as the late Ordovician. Likewise the occurrence of only major-sized plates is possibly too simplistic; geographically intermediate 'islands' (microplates?) (e.g. see Neuman 1972) would obviously have provided easier pathways for the long distance oceanic migration of ostracodes. A number of extra-cratonic island faunas occur, for example, in the Llandeilo of the mobile belt of Newfoundland, in sites which concur with both regressive conditions and models, and which might engender speciation events imprinted on later transgressions (Fortey 1984, pp. 40, 45, 47–48). The Llandeilo marks approximately the initial, extensive mixing of trans-Iapetus ostracodes, though no ostracode faunas are as yet documented from supposed island sites.

Effects of late Ordovician eustatic changes

Animals on both the American and European plates, as typified by benthic brachiopods and planktic graptolites, suffered a marked decline during the latest Ordovician—a time of eustatic regression associated with the Gondwanan glaciation centred on North Africa (McKerrow 1979; Leggett *et al.* 1981). Ostracodes are no exception: the late Ordovician in eastern North America marks a period of extinction of, for example, many hollinomorphs, followed by the re-establishment of new ostracode faunas (Copeland 1977a); similar changes can be recognized in Europe (e.g. Siveter 1982a). In one of the best known and conformable Ordovician–Silurian ostracode successions, that from Anticosti Island, Quebec, about 15 m of strata across the boundary are barren of diagnostic ostracode faunas (Copeland 1970, 1973, 1981). In the Welsh basin of Britain, latest Ordovician and particularly earliest Silurian (early Llandovery) ostracodes are notably few. New Silurian stock in many of these regions is characterized by the occurrence of pioneer representatives of beyrichiacean palaeocopes. The faunal differences between Silurian beyrichiacean ostracodes across the Iapetus Ocean (see above) resulted possibly from the Llandovery, post-glacial transgression which isolated the shelf-living ostracodes into two stocks (Copeland 1977a; Copeland and Berdan 1977). Fortey (1984) has indeed predicted that one of the biological implications of a transgressive episode is the generation of high diversity and endemism on separated cratonic areas. The recovery of the shelf benthos was apparently slow (Leggett *et al.* 1981) but, ecological conditions being generally similar on both sides of the remnant Iapetus Ocean, this does not explain why some ostracodes display an endemicity which is particularly marked during the Ludlovian, and at the level of the Ludlow–Přídolí transition (and which is atypical of Silurian animals in general; Holland 1971).

CONCLUSIONS

1. Evidence from ostracode distributions can be used to test independently other faunal and geological data which indicate the site of oceans. As no psychrospheric-type ostracodes are yet documented from the Lower Palaeozoic, ostracodes *alone* cannot be used to diagnose the presence of oceans.

2. A pilot study comparing ostracode faunas from the North American and European plates dispels the notion of McKerrow and Cocks (1976) that Ordovician ostracodes show strict endemicity. Many middle and late Ordovician ostracode genera are common to both sides of an ocean which is recognized from the weight of geological and other faunal evidence.

3. In order for ostracodes to migrate across a mid Ordovician Iapetus Ocean which is estimated, from independent geological evidence, to have been at least several thousands of kilometres wide, it is concluded that opposing plates were at some point possibly in much closer proximity, or the ocean shallower, than hitherto supposed. Alternatively, the existence of intermediately placed islands or microplates may have aided animal dispersal.

4. The provincial aspect of some Silurian ostracodes may be related back to global changes in sea level at the Ordovician-Silurian boundary.

5. Ostracode distributions support other biogeographic evidence for the contraction of Tornquist's Sea by mid to late Ordovician, and for the development of the Rheic Ocean during the Silurian.

6. The use of ostracodes to help solve Lower Palaeozoic biogeographic problems is at a rather crude stage compared with equivalent trilobite or brachiopod studies. The data base is nowhere as comprehensive and there has been no sophisticated analyses of, for example, facies and any associated ostracode 'communities'. A few specialists are fully engaged documenting the ostracode faunas. Much remains to be done, for example, on the taxonomy of North American Ordovician ostracodes. Detailed studies on the autecology of palaeocope species also need to be undertaken to elucidate modes of life. Nevertheless, previous assumptions concerning the timing of ostracode contacts across the Iapetus Ocean must now change and their implications be reappraised. The more we examine the record, the more contacts emerge, even during the Silurian. Endemism is often a reflection of the current state of knowledge.

Plates 68–70. The plates are designed to demonstrate congeneric ostracode occurrence across the Iapetus Ocean in the middle and upper Ordovician, using examples from a variety of major taxa. The figures include scanning electron micrographs of our own material and pertinent illustrations after previous authors. Restrictions on the availability of several relevant specimens have prevented their illustration by scanning electron microscopy. Abbreviations used in plate explanations: GPIMH, Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, Federal Republic of Germany; SGWG, Sektion Geologische Wissenschaften der Universität Greifswald, German Democratic Republic; USNM, United States National Museum, Washington, D.C., U.S.A.; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan, U.S.A.; GSC, Geological Survey of Canada, Ottawa, Canada.

Acknowledgements. We thank Dr. R. A. Fortey and Professor R. F. Lundin for kindly suggesting improvements to the original manuscript, and Drs. R. H. Benson and J. M. Berdan for their helpful comments. D. J. S. gratefully acknowledges support for this work from N.E.R.C., the Royal Society, the Research Board of the University of Leicester, and the Deutsche Forschungsgemeinschaft in combination with the Geologisch-Paläontologisches Institut, Universität Hamburg. Text-fig. 1 is reproduced by kind permission of the Geological Society of London and Drs. L. R. M. Cocks and R. A. Fortey.

REFERENCES

- BASSLER, R. S. and KELLETT, B. 1934. Bibliographic index of Paleozoic Ostracoda. *Spec. Pap. geol. Soc. Am.* **1**, xiii + 500 pp.
- BEDNARCZYK, W. 1974. The Ordovician in the Koszalin-Chojnice region (Western Pomerania). *Acta geol. pol.* **24**, 581–600, 2 pls.
- BENSON, R. H. 1972. Ostracodes as indicators of threshold depth in the Mediterranean during the Pliocene. In STANLEY, D. J. (ed.). *The Mediterranean Sea*, 63–73. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania.
- 1973. An ostracodal view of the Messinian salinity crisis. In DROOGER, C. W. (ed.). *Messinian events in the Mediterranean*, 235–242. North Holland Publ. Co., Amsterdam.
- 1975a. Ostracodes and Neogene history. *Micropaleont. spec. Publs.* **1**, 41–48.
- 1975b. The origin of the psychrosphere as recorded in changes of deep-sea ostracode assemblages. *Lethaia*, **8**, 69–83.
- 1975c. Morphologic stability in Ostracoda. *Bull. Am. Paleont.* **65**, 13–46.
- 1976. Changes in the ostracodes of the Mediterranean with the Messinian salinity crisis. *Palaeogeogr. Palaeoclimat. Palaeoecol.* **20**, 147–170.
- 1979. In search of lost oceans; a paradox in discovery. In GRAY, J. and BOUCOT, A. J. (eds.). *Historical biogeography, plate tectonics and the changing environment*, 379–389. Oregon State University Press.
- 1981. Form, function and architecture of ostracode shells. *A. Rev. Earth planet. Sci.* **9**, 59–80.
- and SYLVESTER-BRADLEY, P. C. 1971. Deep-sea ostracodes and the transformation of Ocean to Sea in the Tethys. In OERTLI, H. J. (ed.). *Paléoécologie Ostracodes*. *Bull. Cent. Rech. Pau*, **5**, 63–91.

- BERDAN, J. M. 1970. American ostracode zonation. In BERRY, W. B. N. and BOUCOT, A. J. (eds.). Correlation of the North American Silurian rocks. *Spec. Pap. geol. Soc. Am.* **102**, 39–40.
- 1976. Middle Ordovician leperditicopid ostracodes from the Ibex area, Millard County, western Utah. *Geology Stud. Brigham Young Univ.* **23** (3), 37–65, 9 pls.
- 1983. Biostratigraphy of Upper Silurian and Lower Devonian ostracodes in the United States. In MADDOCKS, R. F. (ed.). *Applications of Ostracoda*, 313–337. University of Houston, Texas.
- BLUMENSTENGEL, H. 1965. Zur Ostracodenfauna eines Kalkgerölls aus dem Thüringer Lederschiefer (Ordovizium). *Freiberger ForschHft.* **C182**, 63–78, 2 pls.
- BONNEMA, J. H. 1909. Beitrag zur Kenntnis der Ostrakoden der Kuckerschen Schicht (C_2). *Mitt. miner.-geol. Inst. Reichsuniv. Groningen*, **2**, 1–84, pls. 1–8.
- BOUČEK, B. 1936. Die Ostracoden des böhmischen Ludlows (Stufe e β). *Neues Jb. Miner.* **76**, 31–98, pls. 2–6.
- BRUUN, A. 1957. Deep sea and abyssal depths. In HEDGPETH, J. W. (ed.). *Treatise on marine ecology and paleoecology*, **1**, 641–672. Geological Society of America.
- BURR, J. H. and SWAIN, F. M. 1965. Ostracoda of the Dubuque and Maquoketa formations of Minnesota and northern Iowa. *Spec. Publs Minn. geol. Surv.* **3**, 40 pp., 6 pls.
- COCKS, L. R. M. and FORTEY, R. A. 1982. Faunal evidence for oceanic separations in the Palaeozoic of Britain. *J. geol. Soc.* **139**, 465–478.
- MCKERROW, W. S. and LEGGETT, J. K. 1980. Silurian palaeogeography on the margins of the Iapetus Ocean in the British Isles. *Mem. Dept. geol. Sci. Virginia Polyt. Inst.* **2**, 49–55.
- COPELAND, M. J. 1962. Two new Ordovician Ostracoda from southern Ontario. In Canadian fossil Ostracoda, Conchostraca, Eurypterala and Phyllocarida. *Bull. geol. Surv. Can.* **91**, 55–57, pl. 12.
- 1965. Ordovician Ostracoda from Lake Timiskaming, Ontario. *Ibid.* **127**, 1–52, 11 pls.
- 1966. Some Leperditiid Ostracoda from the Richardson Mountains, northern Yukon Territory. *Proc. geol. Ass. Can.* **17**, 43–51, 1 pl.
- 1970. Ostracoda from the Vauréal Formation (Upper Ordovician) of Anticosti Island, Quebec. *Bull. geol. Surv. Can.* **187**, 15–29, pls. 4, 5.
- 1973. Ostracoda from the Ellis Bay Formation (Ordovician), Anticosti Island, Quebec. *Geol. Surv. Pap. Can.* **72-43**, 1–49, 9 pls.
- 1974a. Silurian Ostracoda from Anticosti Island, Quebec. *Bull. geol. Surv. Can.* **117**, 1–13, 1 pl.
- 1974b. Middle Ordovician Ostracoda from southwestern District of Mackenzie. *Ibid.* **244**, 1–55, pls. 1–9.
- 1977a. Early Paleozoic Ostracoda of eastern Canada. In SWAIN, F. M. (ed.). *Stratigraphic micropaleontology of Atlantic Basin and Borderlands*, 1–17, 3 pls. Elsevier, Amsterdam.
- 1977b. Early Paleozoic Ostracoda from southwestern District of Mackenzie and Yukon Territory. *Bull. geol. Surv. Can.* **275**, 1–88, 16 pls.
- 1977c. Ordovician Ostracoda, southeastern District of Franklin. *Ibid.* **269**, 77–97, 6 pls.
- 1978. Early Paleozoic ostracode assemblages, northwestern Canada. *Spec. Pap. geol. Ass. Can.* **18**, 93–111, 3 pls.
- 1980. *Innuibeyrichia*, a new Silurian ostracode genus from the Canadian arctic. *Geol. Surv. Pap. Can.* **80-1B**, 29–37.
- 1981. Latest Ordovician and Silurian ostracode faunas from Anticosti Island, Québec. In LESPÉRANCE, P. J. (ed.). *IUGS Subcommission on Silurian Stratigraphy, Ordovician–Silurian Boundary working group. Field meeting, Anticosti, Gaspé, Québec, II: Stratigraphy and paleontology*, 185–195.
- 1982a. An occurrence of the Silurian ostracode *Beyrichia* (*Beyrichia*) from Anticosti Island, Quebec. *Geol. Surv. Pap. Can.* **82-1B**, 223–224.
- 1982b. Bathymetry of early middle Ordovician (Chazy) ostracodes, Lower Esbataottine Formation, District of Mackenzie. *Bull. geol. Surv. Can.* **347**, 1–39, 9 pls.
- 1983. *Steusloffina cuneata* (Steusloff), 1895, from Anticosti Island, Quebec. *Geol. Surv. Pap. Can.* **83-1B**, 201–204.
- and BERDAN, J. M. 1977. Silurian and early Devonian beyrichiacean ostracode provincialism in northeastern North America. *Ibid.* **77-1B**, 15–24, 3 pls.
- and BOLTON, T. E. 1977. Additional paleontological observations bearing on the age of the Lourdes Formation (Ordovician), Port au Port Peninsula, Western Newfoundland. *Ibid.* **77-1B**, 1–13, 4 pls.
- CREATH, W. B. and SHAW, A. B. 1966. Paleontology of northwestern Vermont. XIII. *Isochilina* from the Ordovician Highgate Formation. *J. Paleont.* **40**, 1331–1334, pl. 164.
- DE DEKKER, P. 1977. The distribution of the ‘giant’ ostracods (Family Cyprididae Baird, 1845) endemic to Australia. In LÖFFLER, H. and DANIELOPOL, D. (eds.). *Aspects of ecology and zoogeography of recent and fossil Ostracoda*, 285–294. W. Junk, The Hague.

- DEWEY, J. F. 1969. Evolution of the Appalachian/Caledonian Orogen. *Nature, Lond.* **222**, 124–129.
- ELOFSON, O. 1941. Zur Kenntnis der marinen Ostracoden Schwedens, mit besonderer Berücksichtigung des Skagerraks. *Zool. Bidr. Upps.* **19**, 215–534.
- FORTÉY, R. A. 1975. Early Ordovician trilobite communities. *Fossils Strata*, **4**, 339–360.
- 1984. Global earlier Ordovician transgressions and regressions and their biological implications. *Palaeont. Contr. Univ. Oslo*, **295**, 37–50.
- and BARNES, C. R. 1977. Early Ordovician conodont and trilobite communities of Spitsbergen: influence on biogeography. *Alcheringa*, **1**, 297–309.
- and OWENS, R. M. 1978. Early Ordovician (Arenig) stratigraphy and faunas of the Carmarthen district, south-west Wales. *Bull. Br. Mus. nat. Hist. (Geol.)* **30**, 225–294.
- GUBER, A. L. 1971. Problems of sexual dimorphism, population structure and taxonomy of the Ordovician genus *Tetradella* (Ostracoda). *J. Paleont.* **45**, 6–22, pls. 1–4.
- and JAANUSSON, V. 1964. Ordovician ostracodes with posterior domiciliar dimorphism. *Bull. geol. Instn Univ. Uppsala*, **43** (1/3) 2, 43 pp., 6 pls.
- HARRIS, R. W. 1931. Descriptions and illustrations of ostracodes and conodonts. In DECKER, C. E. and MERRITT, C. A. The stratigraphy and physical characteristics of the Simpson Group. *Bull. Okla. geol. Surv.* **55**, 112 pp., 15 pls.
- 1957. Ostracoda of the Simpson Group of Oklahoma. *Ibid.* **75**, vi + 333 pp., 10 pls.
- HENNINGSMOEN, G. 1948. The Tretaspis Series of the Kullatorp core. *Bull. geol. Instn Univ. Uppsala*, **42**, 374–432, pls. 23–25.
- 1953. The Middle Ordovician of the Oslo region, Norway. 4. Ostracoda. *Norsk geol. Tidsskr.* **32**, 35–56, 5 pls.
- 1954a. Lower Ordovician ostracods from the Oslo region, Norway. *Ibid.* **33**, 41–68, 2 pls.
- 1954b. Upper Ordovician ostracods from the Oslo region, Norway. *Ibid.* 69–108, 6 pls.
- 1965. On certain features of palaeocoope ostracodes. *Geol. För. Stockh. Förh.* **86**, 329–334.
- HESSLAND, I. 1949. Investigations of the Lower Ordovician of the Siljan district, Sweden. I. Lower Ordovician ostracods of the Siljan district, Sweden. *Bull. geol. Instn Univ. Uppsala*, **33**, 97–408, 26 pls.
- HESSLER, R. R. and SAUNDERS, H. L. 1967. Faunal diversity in the Deep Sea. *Deep-Sea Res.* **14**, 56–78.
- HOLLAND, C. H. 1971. Silurian faunal provinces? *Geol. J. spec. Issue*, **4**, 61–76.
- JAANUSSON, V. 1957. Middle Ordovician ostracodes of central and southern Sweden. *Bull. geol. Instn Univ. Uppsala*, **37**, 173–442, 15 pls.
- 1966. Ordovician ostracodes with supravelar antra. *Ibid.* **43**, (6/8) 7, 30 pp., 3 pls.
- JONES, C. R. and SIVETER, D. J. 1983. On *Harperopsis scripta* (Harper). *Stereo-Atlas Ostracod Shells*, **10**, 5–12, 4 pls.
- KAY, G. M. 1934. Mohawkian ostracoda: species common to Trenton faunules from the Hull and Decorah formations. *J. Paleont.* **8**, 328–343, pls. 44–46.
- 1940. Ordovician Mohawkian Ostracoda: Lower Trenton Decorah fauna. *Ibid.* **14**, 234–269, pls. 29–34.
- KEENAN, J. E. 1951. Ostracodes from the Maquoketa Shale of Missouri. *Ibid.* **25**, 561–574, pls. 78, 79.
- KESLING, R. V. 1960. Middle Ordovician Black River ostracods from Michigan. Part II. *Levisulculus* and *Eurychilina*. *Contr. Mus. Paleont. Univ. Mich.* **15**, 349–363, 4 pls.
- HALL, D. D. and MELIK, J. C. 1962. Middle Ordovician Black River ostracods from Michigan. Part IV. Species of *Colacchilina* (new genus), *Laccochilina*, and *Hesperidella*. *Ibid.* **17**, 205–213, 2 pls.
- KNÜPFER, J. 1968. Ostracoden aus dem Oberen Ordovizium Thüringens. *Freiberger ForschHft (C)*, **234**, 5–29, 6 pls.
- KORNICKER, L. S. and SOHN, I. G. 1971. Viability of ostracode eggs egested by fish and effect of digestive fluids on ostracode shells—ecologic and paleoecologic implications. *Bull. Cent. Rech. Pau*, **5**, 125–135, 1 pl.
- KRAFT, J. C. 1962. Morphologic and systematic relationships of some Middle Ordovician Ostracoda. *Mem. geol. Soc. Am.* **86**, viii + 104 pp., 19 pls.
- KRANDIEVSKY, V. S. 1969. Stratigraphic distribution of Ostracoda in the Ordovician deposits of the Volyn-Podolye. *Trans. Akad. Sci. Ukrain. SSR (B)* **1969**, 870–874. [In Ukrainian.]
- 1975. First occurrences of the Lower Ordovician ostracods in western Volyn. *Ibid.* **1975**, 691–694. [In Ukrainian.]
- KRAUSE, A. 1897. Ueber die Ostrakodenfauna eines holländischen Silurgeschiebes. *Z. dt. geol. Ges.* **48**, 932–939, pl. 25.
- KUMMEROW, E. 1924. Beiträge zur Kenntnis der Ostracoden und Phyllocariden aus nordischen Diluvialgeschieben. *Jb. preuss. geol. Landesanst. BergAkad.* **44**, 405–448, pls. 20, 21.
- LEGGETT, J. K. 1979. Oceanic sediments from the Ordovician of the Southern Uplands. *Spec. Publs geol. Soc. Lond.* **8**, 495–498.

- LEGGETT, J. K., MCKERROW, W. S., COCKS, L. R. M. and RICKARDS, R. B. 1981. Periodicity in the early Palaeozoic marine realm. *J. geol. Soc.* **138**, 167–176.
- LUNDIN, R. F. 1971. Possible paleoecological significance of Silurian and early Devonian ostracode faunas from midcontinental and northeastern North America. *Bull. Cent. Rech. Pan.* **5**, 853–868.
- MCKENZIE, A. H. G. and HUSSAINY, S. U. 1968. Relevance of a freshwater cytherid (Crustacea, Ostracoda) to the continental drift hypothesis. *Nature, Lond.* **220**, 806–808.
- MCKERROW, W. S. 1979. Ordovician and Silurian changes in sea level. *J. geol. Soc.* **136**, 137–145.
- and COCKS, L. R. M. 1976. Progressive faunal migration across the Iapetus Ocean. *Nature, Lond.* **263**, 304–306.
- MÄNNIL, R. M. 1963. On the correlation of the Ordovician strata of Estonia and Leningrad region. *Eesti NSV Tead. Akad. Geol. Inst. Uurim.* **13**, 3–40. [In Russian.]
- MARTINSSON, A. 1956. Neue Funde kambrischer und ordovizischer Geschiebe im südwestlichen Finnland. *Bull. geol. Instn Univ. Uppsala*, **36**, 79–105, 2 pls.
- 1963. *Kloedenia* and related ostracode genera from the Silurian and Devonian of the Baltic area and Britain. *Ibid.* **42** (1/6) 2, 63 pp.
- 1965. The Siluro-Devonian ostracode genus *Nodibeyrichia* and faunally associated kloedeniines. *Geol. För. Stockh. Förh.* **87**, 109–138.
- 1967. The succession and correlation of ostracode faunas in the Silurian of Gotland. *Ibid.* **89**, 350–386.
- 1970. Ostracodes: correlation with Europe. *Spec. Pap. geol. Soc. Am.* **102**, 41–44.
- 1977. Palaeocene ostracodes. *Int. Un. geol. Sci. (Ser. A)* **5**, 327–332.
- MITCHELL, A. H. G. 1984. The British Caledonides: interpretations from Cenozoic analogues. *Geol. Mag.* **121**, 35–46.
- NECKAJA, A. I. 1973. Ostrakody ordovika i silura SSSR. *Trudy vses. nest. nauchno-issled. geol.-razy. Inst.* **324**, 104 pp. [In Russian.]
- NEUMAN, R. B. 1972. Brachiopods of early Ordovician volcanic islands. *Int. Geol. Congr.*, sec. 7, 297–302.
- PERŠINA, A. I. et al. 1971. *Biostratigrafija silurijskikh i devonskikh otloženij Pečorskogo Urala*, 131 pp. Nauka, Leningrad. [In Russian.]
- PHILIPS, W. E. A., STILLMAN, C. J. and MURPHY, T. 1976. A Caledonian plate tectonic model. *J. geol. Soc.* **132**, 579–610.
- POULSEN, V. 1978. *Dahnianitina* beds (late Ordovician) on Bornholm. *Dann. geol. Unders.* **1976**, 53–87.
- PŘIBYL, A. 1979. Ostracoden der Šárka- bis Králův Dvůr-Schichten-gruppe des böhmischen Ordoviziums. *Sb. nar. mus. Praze* (B), **33**, 53–145, 8 pls.
- PROKOFIEV, V. A. and KUZNETZOV, A. G. 1982. Fauna and certain stratigraphic problems in Ordovician deposits of Moscow synecline. *Bull. Mosc. Soc. Naturalists (Geol. Ser.)* **57**, 67–82.
- QVALE, G. 1980. New Caradocian ostracodes from the Oslo–Asker district, Norway. *Norsk geol. Tidsskr.* **60**, 93–116.
- RADER, E. K. 1965. First discovery of the hollinacean Ostracoda *Pseudorakverella* from the United States (Trenton Member, Martinsburg Formation, Virginia). *J. Paleont.* **39**, 159–161.
- SARV, L. I. 1959. Ordovician ostracods in the Estonian S.S.R. *Eesti NSV Tead. Akad. Geol. Inst. Uurim.* **4**, 211 pp., 32 pls.
- 1963. New ostracods from the Ordovician of East Baltic. *Ibid.* **13**, 161–188, 7 pls.
- SCHALLREUTER, R. E. L. 1964a. Neue Ostrakoden der Gattungen *Platybolbina*, *Brevibolbina* und *Oecematobolbina* aus mittelordovizischen Backsteinlkalkgeschieben. *Ber. geol. Ges. D.D.R.* **9**, 381–383, 422–425.
- 1964b. *Hithinae*—eine neue Unterfamilie ordovizischer Ostrakoden. *Ibid.* 385–387, 426–429.
- 1968. Ordovizische Ostracoden mit geradem Schloßrand und konkavem Ventralrand. *Wiss. Z. Ernst Moritz Arndt-Univ. Greifswald*, **17**, 127–152.
- 1973. Die Ostracodengattung *Hyperchilarina* und das *Aparachites*-Problem. *Geol. För. Stockh. Förh.* **95**, 37–49.
- 1975. Ostrakoden aus Öjlemyrgeschieben (Ordoviz) II. *Neues Jb. Geol. Paläont. Abh.* **150**, 270–293.
- 1977a. On *Cryptophylus gutta* Schallreuter. *Stereo-Atlas Ostracod Shells*, **4**, 1–8.
- 1977b. On *Distobolbina grekoffi* Schallreuter sp. nov. *Ibid.* 25–28.
- 1977c. Eine neue Art der Ostrakodengattung *Pelecybolbina* aus dem Ordoviz von Öland. *Geol. För. Stockh. Förh.* **99**, 409–411.
- 1980. Ostrakoden aus dem Sularpschiefer (Mittelordoviz) von Schonen (Schweden). *Palaeontographica*, A, **169**, 1–27, pls. 1–9.
- 1983. Glossomorphitiniae und Sylthinae (Tetradellidae, Palaeocopa, Ostracoda) aus Backsteinlkalk-Geschieben (Mittelordoviz) Norddeutschlands. *Ibid.* **180**, 126–191, pls. 15–29.

- and KRŮTA, M. 1980. Taxonomy and nomenclature of the Ordovician ostracode genus *Hippula*. *Neues Jb. Geol. Paläont. Mh.* **1980**, 505–512.
- and SIVETER, D. J. 1982. On *Hithis columus* Schallreuter & Siveter sp. nov. *Stereo-Atlas Ostracod Shells*, **9**, 85–88.
- 1983a. On *Tallinnellina dissita* Schallreuter & Siveter sp. nov. *Ibid.* **10**, 1–4.
- 1983b. Ostrakoden beiderseits des Iapetus-Ozeans. *Paläont. Ges.* **53**. *Jahresversammlung Mainz*, 66.
- SCHELTEMA, R. E. 1977. Dispersal of marine invertebrate organisms: paleobiogeographic and biostratigraphic implications. In KAUFFMAN, E. G. and HAZEL, J. E. (eds.). *Concepts and methods in biostratigraphy*, 73–108. Dowden, Hutchinson & Ross, Stroudsberg, Pennsylvania.
- SCHMIDT, E. A. 1941. Studien im böhmischen Caradoc (Záhořan-Stufe). 1. Ostrakoden aus den Bohdalec-Schichten und über die Taxonomie der Beyrichiacea. *Abh. senckenb. naturforsch. Ges.* **454**.
- SIDARAVIČIENĖ, N. 1971. New Ostracoda from Middle and Upper Ordovician of Lithuania. In *Palaeontology and stratigraphy of the Baltic and Byelorussia*, **3**, 23–36.
- 1975. New Ordovician Ostracoda of the South Baltic Area. In GRIGELIS, A. (ed.). *The fauna and stratigraphy of Paleozoic and Mesozoic of Baltic and Byelorussia*, 21–43.
- SIVETER, D. J. 1978a. The Ordovician. *Geol. J. Spec. Issue*, **8**, 41–56.
- 1978b. The Silurian. *Ibid.* 57–100.
- 1982a. Late Ordovician and early Silurian ostracodes from the Oslo region, Norway. In WORSLEY, D. (ed.). *IUGS Subcommission on Silurian Stratigraphy. Field Meeting, Oslo Region, 1982*, 121–127.
- 1982b. On *Homeokiesowia epicopa* Siveter sp. nov. *Stereo-Atlas Ostracod Shells*, **9**, 89–92.
- 1982c. On *Schallreuteria superciliata* (Reed). *Ibid.* 93–100.
- 1983. On *Vittella fecunda* Siveter sp. nov. *Ibid.* **10**, 13–16.
- 1984. Habitats and modes of life of Silurian ostracodes. In BASSETT, M. G. (ed.). *Autecology of Silurian organisms. Spec. Pap. Palaeont.* **32**, 71–85, 2 pls.
- SKEVINGTON, D. 1978. Latitudinal surface water temperature gradients and Ordovician faunal provinces. *Alcheringa*, **2**, 21–26.
- SOHN, I. G. and KORNICKER, L. S. 1979. Viability of freeze-dried eggs of the freshwater *Heterocypris incongruens*. In KRSTIĆ, N. (ed.). *Taxonomy, biostratigraphy and distribution of ostracodes*, 1–4, 1 pl. Geological Society of Serbia, Belgrade.
- SPJELDNAES, N. 1978. Faunal provinces and the Proto-Atlantic. *Geol. J. Spec. Issue*, **10**, 139–150.
- STEELE, H. M. and SINCLAIR, G. W. 1971. A Middle Ordovician fauna from Braeside, Ottawa Valley, Ontario. *Bull. geol. Surv. Can.* **211**, 97 pp.
- STEUSLOFF, A. 1895. Neue Ostrakoden aus Diluvialgeschieben von Neu-Brandenburg. *Z. dt. geol. Ges.* **46**, 775–787, pl. 58.
- SWAIN, F. M. 1957. Early Middle Ordovician Ostracoda of the eastern United States. Part I. Stratigraphic data and description of Leperditidae, Aparchitidae and Leperditellidae. *J. Paleont.* **31**, 528–570, pls. 59–62.
- 1962. Early Middle Ordovician Ostracoda of the eastern United States. Part II. Leperditellacea (part), Hollinacea, Kloedenellacea, Bairdiacea and Superfamily Uncertain. *Ibid.* **36**, 719–744, pls. 109–111.
- 1977. Early Paleozoic Ostracoda of the Atlantic margin, other than eastern Canada. In SWAIN, F. M. (ed.). *Stratigraphic micropaleontology of Atlantic Basin and Borderlands*, 19–48. Elsevier, Amsterdam.
- CORNELL, J. R. and HANSEN, D. L. 1961. Ostracoda of the families Aparchitidae, Aechminidae, Leperditellidae, Drepanellidae, Eurychilinidae and Punctaparchitidae from the Decorah Shale of Minnesota. *J. Paleont.* **35**, 345–372, pls. 46–50.
- TEICHERT, C. 1937a. Ordovician and Silurian faunas from Arctic Canada. *Rep. Fifth Thule Exped. 1921–1924*, **1** (5), 169 pp., 24 pls.
- 1937b. A new Ordovician fauna from Washington Land, North Greenland. *Meddr. Gronland*, **119** (1), 65 pp., 7 pls.
- THORSLUND, P. 1940. On the Chasmops Series of Jemtland and Södermanland (Tvären). *Sver. geol. Unders. Afh. (Ser. C)*, **436**, 191 pp., 15 pls.
- TROEDSSON, G. T. 1918. Om Skånes Brachiopodskiffer. *Acta Univ. Lund. (N.F. 2)*, **15** (3), 110 pp., 2 pls.
- ULRICH, E. O. 1892. New lower Silurian Ostracoda, no. 1. *Am. Geol.* **10**, 263–270, pl. 9.
- ULST, R. Z., GAILĪTE, L. K. and JAKOVLEVA, V. I. 1982. *Ordovik Latvii*, 295 pp., 8 pls. Zinatne Riga. [In Russian.]
- VAN MORKHOVEN, F. P. C. M. 1962. *Post-Paleozoic Ostracoda; their morphology, taxonomy and economic use*, **1**, 204 pp. Elsevier, Amsterdam.
- VANNIER, J. 1984. *Ostracodes ordoviciens du Massif Armoricain*. Unpublished thesis, University of Rennes, 158 pp., 26 pls.

- VARGANOV, V. G. *et al.* 1970. Ordovik central'noj časti Ufimskogo amfiteatra. *Sov. Geol.* **1970** (6), 44–57. [In Russian.]
- WARSHAUER, S. M. 1975. The sexual dimorphism and ontogeny of *Ceratopsis chambersi* (Miller) (Ostracoda, Palaeocopida) from the Upper Ordovician of southwestern Ohio and northern Kentucky. *Bull. Am. Paleont.* **67**, 443–456, 3 pls.
- and BERDAN, J. M. 1982. Palaeocapid and Podocapid Ostracoda from the Lexington Limestone and Clays Ferry Formation (Middle and Upper Ordovician) of Central Kentucky. *Prof. Pap. U.S. geol. Surv.* **1066** (H), 80 pp., 19 pls.
- WHITTINGTON, H. B. and HUGHES, C. P. 1972. Ordovician geography and faunal provinces deduced from trilobite distribution. *Phil. Trans. R. Soc., B*, **263**, 235–278.
- and KINDLE, C. H. 1963. Middle Ordovician Table Head Formation, western Newfoundland. *Bull. geol. Soc. Am.* **74**, 745–758, 2 pls.
- WILLIAMS, A. 1973. Distribution of brachiopod assemblages in relation to Ordovician palaeogeography. *Spec. Pap. Palaeont.* **12**, 241–269.
- 1976. Plate tectonics and biofacies evolution as factors in Ordovician correlation. In BASSETT, M. G. (ed.). *The Ordovician System*, 29–66. University of Wales Press and National Museum of Wales, Cardiff.
- WILLIAMS, H. 1980. Structural telescoping across the Appalachian Orogen and the minimum width of the Iapetus Ocean. *Spec. Pap. geol. Ass. Can.* **20**, 422–440.
- WILSON, J. T. 1966. Did the Atlantic close and then re-open? *Nature, Lond.* **210**, 678–681.
- ZENKOVA, G. G. 1977. Novye vidy ostrakod ordovika zapadnogo sklona Srednego Urala. *Novye vidy drevnih rastenij i bespozvonočnych SSSR*, **4**, 74–75, 87, 180, 203. [In Russian.]

ROGER E. L. SCHALLREUTER

Geologisch-Paläontologisches Institut
Universität Hamburg
Bundesstrasse 55, D 2000 Hamburg 13
Federal Republic of Germany

DAVID J. SIVETER

Department of Geology
University of Leicester
Leicester LE1 7RH, U.K.

Typescript received 20 July 1984

Revised typescript received 31 January 1985

TWO NEW SPECIES OF HERBACEOUS LYCOPODS FROM THE DEVONIAN OF VENEZUELA WITH COMMENTS ON THEIR TAPHONOMY

by D. EDWARDS and J. L. BENEDETTO

ABSTRACT. Two new species of herbaceous lycopods, *Haskinsia sagittata* and *Colpodexylon cachiriense*, are described from Devonian strata in the Cano Grande–Rio Cachiri region (north central Sierra de Perija) of Venezuela. The recently discovered diverse assemblage of megafossils also contains the first record of progymnosperms in South America as well as possible cladoxylaleans. The lycopods exhibit a number of preservation forms, and these are related to their putative preservational history. The assemblage is of Laurentian aspect, showing greatest similarity to those from New York State. Its biogeographical significance is briefly discussed in relation to the distribution of continents in Devonian times.

MOST of our knowledge of terrestrial vegetation in Devonian times derives from assemblages collected in North America, Europe, and Asia (Chaloner and Sheerin 1979; Banks 1980; Gensel and Andrews 1984). With the exception of Australia, records from southern continents are based on fragmentary, usually poorly preserved megafossils which often lack independent faunal or palynological evidence for their age. In the course of a biostratigraphical study of Devonian outcrops in northern Venezuela, one of us (J. L. B.) and Dr. P. Rachebouef (University of Brest) discovered a completely new fossil plant assemblage, more diverse and better preserved than hitherto recorded from the Devonian of South America.

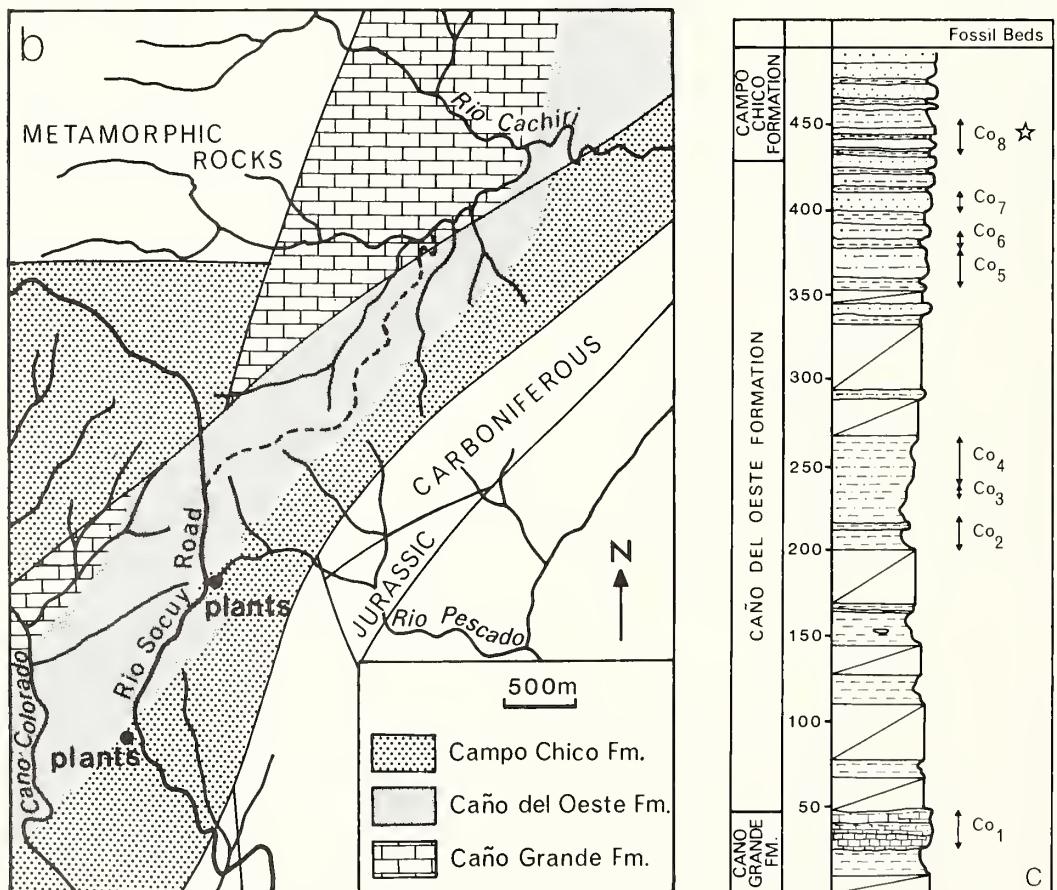
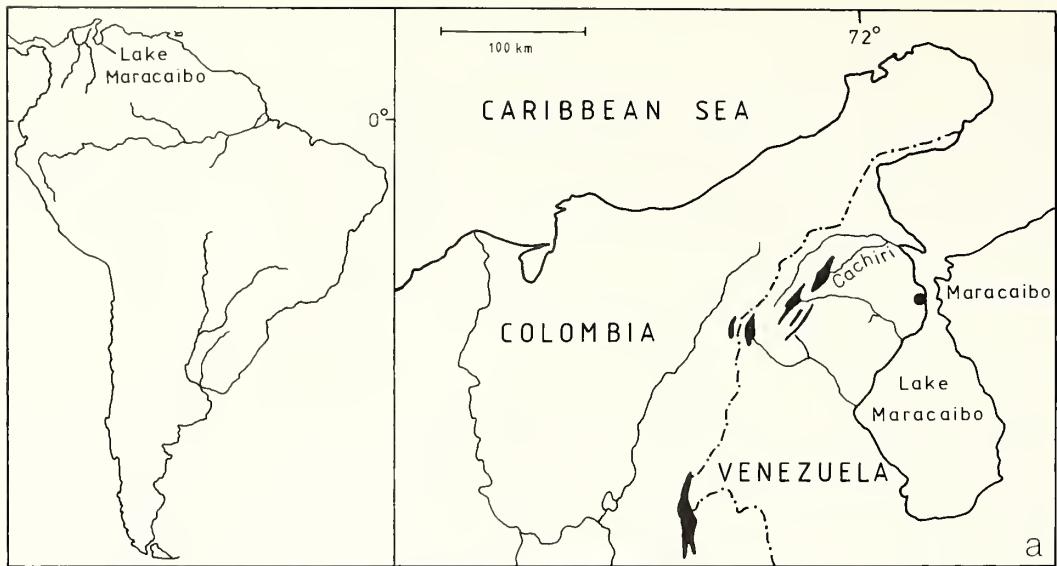
STRATIGRAPHY AND LOCALITIES

The Devonian of the Colombian–Venezuelan basin in the northern Andes comprises a number of outcrops extending from the eastern cordillera in Colombia to the Sierra de Perija in Venezuela (text-fig. 1a). The strata exposed in the Cano Colorado–Rio Cachiri area, c. 70 km west of Maracaibo, are the most northerly (text-fig. 1b). The geology and biostratigraphy of the area have been summarized by Benedetto (1980, 1984). The fossil plants occur at two exposures of the same horizon (Co_8) towards the base of the Campo Chico formation in the Cano Colorado section (text-fig. 1c). There were no animal fossils present, but a rich brachiopod fauna collected about 50 m below the plant beds (Co_6 horizon) is of Givetian age.

MATERIAL AND METHODS

The fossil plants occur in laminated micaceous siltstones ranging in colour from a light olive grey to whitish or pinkish buff depending on the degree of weathering. The lycopod stems are strongly compressed and usually incompletely preserved. Many comprise a thin fragmentary layer of fine-grained sediment sandwiched between two coalified layers. Others are iron-stained impressions often with a dusting of coaly matter. The complete range of preservation forms is discussed more fully below.

All specimens were photographed under uniform and unilateral lighting. The most useful technique for this extremely soft matrix was dégagement (Leclercq 1960), tungsten wire sharpened in molten sodium nitrite being used to loosen the grains of sediment. Areas of cuticle were removed on



TEXT-FIG. 1. *a*, locality map indicating Devonian outcrops in the northern part of the Colombian-Venezuelan basin of South America. *b*, Devonian geology in the Cano Colorado–Rio Cachiri region. *c*, Stratigraphical log of the section along the road to the Rio Socuy from the Cano Colorado. Plant horizon is indicated by a star. Co₁₋₈ refer to horizons with faunal assemblages recorded in detail by Benedetto (1984).

cellulose nitrate film pulls. Latex replicas (Dunlop) taken from impressions with cellular imprints were coated with gold and examined by SEM. Palynological samples were prepared by standard techniques.

The specimens and preparations are housed in the Palaeontology Laboratory, University of Brest, France (prefix LPB).

SYSTEMATIC PALAEONTOLOGY

Class LYCOPSIDA

Order PROTOLEPIDODENDRALES

Family HASKINSIACEAE Grierson and Banks, 1983

Genus HASKINSIA Grierson and Banks, 1983

Type species: *Drepanophycus colophyllus* Grierson and Banks, 1963 (transferred to *H. colophylla* by Grierson and Banks 1983) from the Kiskatom Formation, Tioughniogan Stage, Erian Series, Middle Devonian (= Givetian) in New York State, U.S.A.; also recorded from Lower Frasnian strata of New York State.

Haskinsia sagittata sp. nov.

Plate 71, figs. 1–8; Plate 72, figs. 1–13; Plate 73, figs. 1–8; text-fig. 2

Derivation of name. Latin *sagitta*, arrow, referring to the arrowheaded shape of the leaf.

Holotype. LPB16046 (Pl. 71, fig. 6; Pl. 72, figs. 1, 2, and 12).

Locality. Exposures on the road from the town, Villa del Rosario, to the Socuy River in the Colorado valley, some 950 and 1500 m NNW of the farm 'Alemania', c. 70 km west of Maracaibo, north-western Venezuela.

Horizon. Carbonaceous lutites at base of the Campo Chico Formation; Devonian (?Givetian–Frasnian).

Diagnosis. Herbaceous lycopod with occasional dichotomous branching. Axes at least 10·5 cm long, 4·8–6·8 mm wide ($\bar{x} = 5\cdot7$ mm, $n = 34$) exclusive of leaves. Longitudinal lines separate leaf bases. Leaves spirally arranged, sometimes pseudowhorled; 7–9 leaves per gyre (usually 7). Lateral margins of adjacent leaf blades touch or overlap: apices of leaves of one gyre at same level as bases of leaves in that above. Leaves simple and upright, comprising petiole 0·45–1·2 mm wide ($\bar{x} = 0\cdot7$ mm, $n = 35$) widening into conspicuous lamina, at maximum width 1·13–1·92 mm ($\bar{x} = 1\cdot48$ mm, $n = 30$) with two downwardly directed lateral projections and tapering into an acuminate tip. Leaf length, including petiole, at least 2·47 mm.

Description. Seven small slabs, almost all of slightly differing lithology, contain some forty sterile leafy stems of variable appearance. The variability is due to different forms of preservation and planes of fracture. With one exception (LPB16051, Pl. 71, fig. 2) the possession of distinctive sagittate leaves indicates that the stems belong to a single taxon.

Stem morphology: Except in the two branching specimens the stems show little change in diameter along the short lengths available for study. Branching is dichotomous (Pl. 71, fig. 1). Depending on the preservation/fracture state the stem surface displays elevations or depressions, sometimes both, marking the attachment of leaves, the surface between the leaf bases being smooth (Pl. 71, fig. 2). Leaves borne on the straight margins of the stem are falcate in profile. Further conspicuous features of a few stems are longitudinal dark lines (Pl. 71, fig. 1) which, on any one surface, pass between but not across leaf bases: their number is thus related to the number of orthostichies. They are either parallel or curve slightly outwards around a leaf base. In a few cases much finer, closely spaced, longitudinally orientated striations occur on a thin brown layer, presumed to be cuticular, but when this is removed on a film pull no further detail is visible. A similar patterning is present on a few impressions, but again scanning electron micrographs of latex casts of these stems failed to reveal any precise details of surface cells (Pl. 73, fig. 8).

Leaf morphology and arrangement: Leaves are most commonly seen in profile. A typical example before uncovering (Pl. 72, fig. 5) shows a prominent base tapering upwards into a simple linear blade, which in this case is parallel to the edge of the axis, but may occasionally be directed away from it (Pl. 72, fig. 6). Removal of

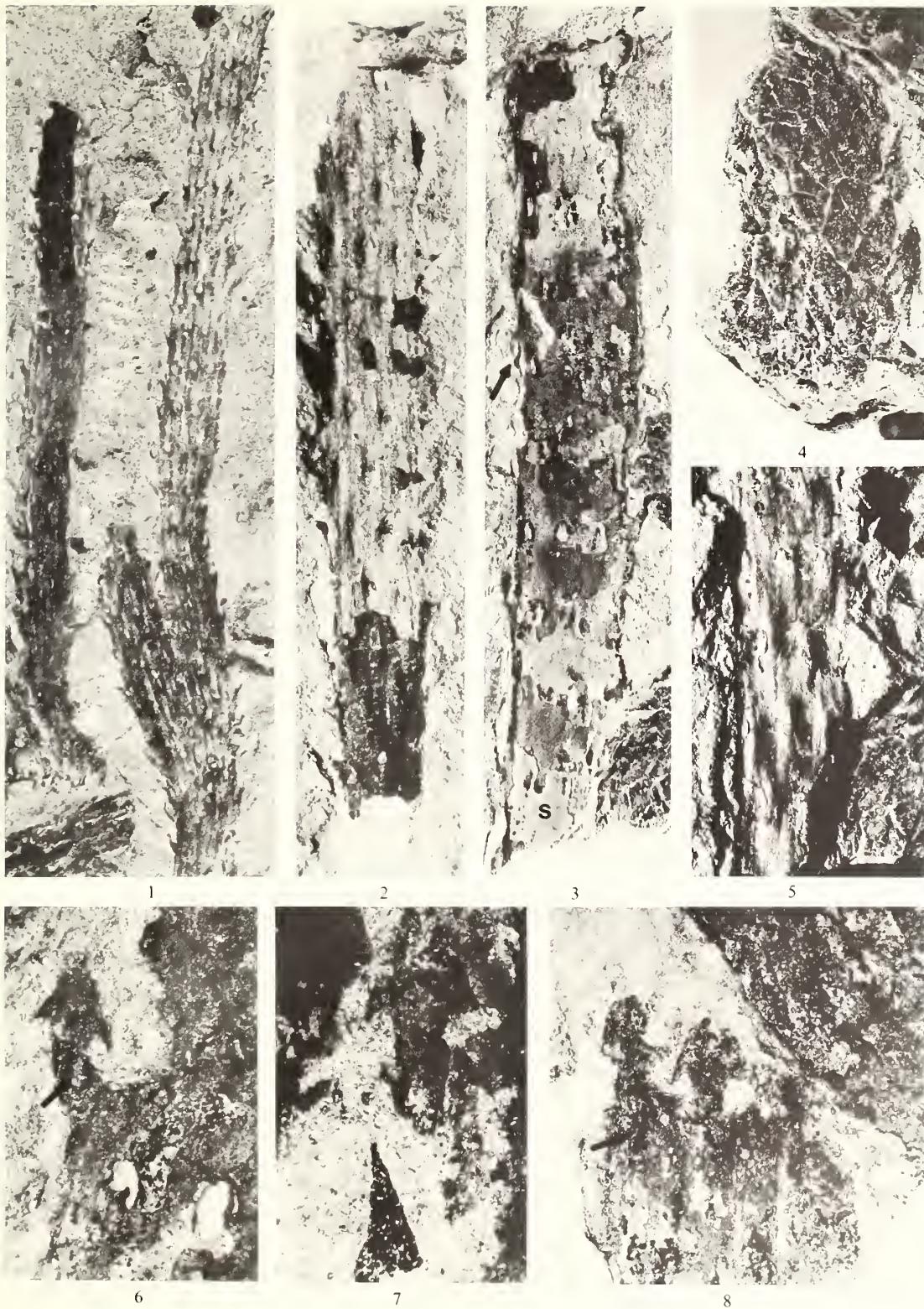
sediment between the leaf and axis, and sometimes removal of the axis itself, reveals an approximately parallel-sided petiole and approximately half of a lamina with a downwardly directed lobe (Pl. 72, fig. 8). The tapering apex of the lamina often extends down into the matrix, so that the length of the leaf is actually greater than that visible in profile. At its base the petiole is vertically extended in cross-section, becoming circular and then flattened distally in the same plane as the lamina. The presence of a thick layer of coalified material suggests that the petiole possessed abundant, probably peripheral, strengthening tissues. Except for one fortuitously fractured specimen (Pl. 71, fig. 4) leaf shape in face view was elucidated by dégagement. Text-fig. 2, where all the leaves are drawn to the same scale, summarizes the range in shape. The leaf blade is roughly triangular with entire margin, and widest point more or less at the level of the junction of the petiole (Pl. 72, figs. 9–11). Two pronounced downwardly directed projections produce the sagittate form (Pl. 72, figs. 9–11) but very occasionally these flare outwards so that the overall shape is hastate (Pl. 72, fig. 12). A midrib is absent. The parallel-sided petiole widens slightly below the blade, but the actual junction is impossible to define. We are not sure of the exact shape of the extremities of the leaf blades since removal of a few grains of sediment can radically alter a tapering outline. At the leaf apex the blade frequently fades away as if it were thinner distally (Pl. 71, figs. 6 and 8). Evidence from isolated tips and iron-stained impressions in addition to uncovered specimens suggests that the apices were originally acuminate (Pl. 71, fig. 7; Pl. 72, fig. 11). The measurements for leaf lengths (blade plus petiole = 2·47–4·7 mm, $\bar{x} = 3\cdot2$, $n = 19$) are therefore too low. The downward projections were probably pointed, but ended somewhat more abruptly than the apices. Any cuticle remaining on blades or petioles is featureless.

The positions of leaf bases on the stems indicate that the leaves were borne in a low spiral, sometimes approaching a pseudowhorled condition, with 7 to 9 leaves in a gyre, the former being the more usual number. The external appearance of leafy shoots in life must have been similar to that of the fossils figured in Plate 71, fig. 4, where the plane of fracture passes through the laminae of the leaves leaving a dusting of coalified material on part and counterpart. The width of this specimen is explained by a change in level which more or less bisects the leafy surface longitudinally and indicates that there were probably two axes lying side by side. The fortuitous and very informative fracture is thus even more remarkable. The subtending stems, originally completely obscured by leaves and sediment, were revealed by dégagement on the larger block. Adjacent leaves in a single gyre meet or just overlap at their lateral extremities and the attenuated leaf apex just extends beyond the base of the petiole in the gyre above. From the attitudes of the leaves it seems that the blades were rigid in life but gently curved inwards and tangentially so that they formed a continuous sheath around the stem.

Comparisons. Grierson and Banks (1983) review Palaeozoic herbaceous lycopods, including the families Drepanophycaceae, Protolepidodendraceae, Archaeosigillariaceae, Eleutherophyllaceae, and Lycopodiaceae. The Venezuelan specimens most closely resemble their new taxon, *H. colophylla*. They originally (1963) placed the leafy remains from New York State in *Drepanophycus*, but new information on the leaves, originally considered falcate, and on stem anatomy, led to the generic reassignment. The leaves of the American specimens are not as markedly sagittate and the vertical files of strengthening cells in the outer cortex are more sinuous. On the basis of such differences, and because the Venezuelan plants lack anatomy, we regard them as a new species.

EXPLANATION OF PLATE 71

Figs. 1–8. *Haskinsia sagittata* sp. nov. 1, LBD16050, branching, leafy stem with traces of coalified material, $\times 1\cdot7$. 2, LBD16051, leafless stem, probably attributable to *H. sagittata*, seen at base as a cleavage compression (*sensu* Chaloner and Collinson 1975) and as a cleavage impression distally. Note persistence of coalified material at points of departure of leaves and on truncated petioles attached to sides of stem, unilateral illumination, $\times 2\cdot8$. 3–5, LBD16052. 3, coalified stem with sedimentary infill (s) and one uncovered leaf (arrowed), $\times 2\cdot8$. 4, leaf lamina cleaved compressions of two aligned stems, $\times 3\cdot7$. 5, base of stem illustrated in fig. 3, unilateral illumination, $\times 10$. 6, LBD16046, uncovered leaf on holotype. It was attached ('scar' is arrowed) to lower surface of the stem and shows the typical lateral displacement of the petiole, $\times 11$. 7, LBD16054(i), acuminate apex of leaf, probably incomplete at tip. Note that it ends at approximately same level as base of leaf above. 8, LBD16046, petioles and lamina bases of three leaves uncovered above fractured end of ridged stem. Arrowed is the elongate raised area in the oval depression marking attachment of petiole on lower surface, $\times 10$. (Photographs under uniform illumination except where otherwise stated.)

EDWARDS and BENEDETTO, *Haskinsia sagittata*

There remain a number of very fragmentary fossils with similarly shaped leaves, which on further investigation may be assigned to *Haskinsia*. Grindley *et al.* (1980) described some stems from the Middle Devonian of Marie Byrd Land, western Antarctica, with similar dimensions and numbers of leaves per gyre. The leaves themselves are slightly smaller but rarely completely preserved, and are sickle-shaped in profile. Face view drawings of the leaves show that their shape is variable: the one just below no. 3 in their fig. 10 has a downwardly projecting tip on the left hand side reminiscent of *H. sagittata*. A major difference is the presence of a central line presumably representing a vein or midrib in the Antarctic specimens. The latter were placed in a new species, *D. schloppfi*, but on the basis of leaf shape they clearly do not belong to that genus (Grierson and Banks 1983).

Far more problematic are the short lengths of lycopod stems, usually lacking leaves but with leaf bases or scars, that are superficially similar to some of the preservation forms seen in the Venezuelan material. These include *Haplostigma furquei* from the Middle Devonian of Argentina (Frenguelli 1954), *H. irregularis*, Middle Devonian of Brazil (Kräusel 1960) and the Falkland Islands (Seward and Walton 1923) as well as from the type area in South Africa, and *Palaeostigma sewardi* first described from the Middle Devonian of Brazil (Kräusel and Dolianiti 1957). The most recent assessment of these two genera is in a preliminary survey of South African Palaeozoic floras by Anderson and Anderson (in press). They note that *Palaeostigma* is atypical among South African lycopods in that it invariably occurs as impressions with the leaves or granulae of the lower surface of the stem showing through to the upper. We have described this preservation state in *Haskinsia sagittata*, but the taxa differ in that the Andersons interpret the projections and depressions on the stem as leaves, describing them as 'rudimentary, rounded to oval granulate projections about as high as wide, well spaced, irregularly aligned into imperfect low angle spiral'. *Haplostigma*, originally based on South African material, has a more regular appearance and the leaves although rarely preserved are described as 'squat conical, acute tipped, length around 1 to 2 times basal width with gentle distal inclination'. Anderson and Anderson placed *H. furquei* in synonymy with *H. irregularis*. We have not had the opportunity to examine specimens of either genus, but from photographs it seems that their relatively featureless stems more closely resemble leafless *Haskinsia sagittata* than those lycopods with a characteristic surface patterning such as *Archaeosigillaria*. The latter, represented by *A. picosensis* (placed in synonymy with *A. caespitosa* by Anderson and Anderson (in press)) occurs with *Protolepidodendron kegeli* at the same Middle Devonian horizon as *Palaeostigma sewardi* in Brazil. It is easily separated from *H. sagittata* (as is *A. conferta* from Argentina (Menendez 1965a)) on the grounds of leaf base characteristics (Kräusel and Dolianiti 1957).

Finally a predominantly lycopod flora from the late Silurian–early Devonian of Libya (Klitzsch *et al.* 1973; Boucot and Gray 1982) contains a number of fragmentary stems with leaf attachment sites, but not leaves, visible. Their preservation states appear to parallel some of those we have described. In particular, the illustrations of *Protolepidodendron helleri* (Klitzsch *et al.* 1973, figs. 1, 12, 13) and *Precyclostigma tadrartense* (*ibid.*, figs. 2, 6, 9, 10) resemble *H. sagittata* in size, leaf arrangement, and

EXPLANATION OF PLATE 72

Figs. 1–13. *Haskinsia sagittata* sp. nov. 1, 2, LBD16046, holotype. 1, stem with some uncovered leaves. Those near the base are attached to the upper surface of the stem, $\times 2.4$. 2, unilateral lighting to show surface features such as leaf bases and ridges, $\times 2.6$. 3, 4, LBD16047, pink stem impressions with dusting of coaly powder. 3, $\times 1.4$. 4, unilateral illumination, $\times 1.7$. 5–7, leaves in profile before uncovering. 5, LBD16052, $\times 9.4$. 6, LBD16047, $\times 10$. 7, LBD16049, $\times 7$. 8, LBD16047, half of leaf revealed on removal of overlying stem and matrix, $\times 9$. 9–11, face views of uncovered leaves. 9, LBD16047; 10, 11, LBD16052 all $\times 10$. 12, LBD16046, hastate leaf exposed when sediment was removed from above holotype; probably attached to upper surface of stem, $\times 12$. 13, LBD16052, stem on left has more or less continuous covering of coalified material (leaf attachment sites are more obvious under unilateral illumination) and shows numerous leaves in profile, successive gyres being close together, $\times 1.6$. (Photographs under uniform illumination except where otherwise stated.)

EDWARDS and BENEDETTO, *Haskinsia sagittata*

the presence of longitudinal grooves between leaf bases, although there are differences in the orientation of the leaf bases. In contrast the much larger leafy lycopod axes recorded from the overlying Lower Devonian Tadrart Formation (Lejal-Nicol 1975) are completely different and more comparable to arborescent forms reported from later in the Devonian elsewhere (Chaloner and Sheerin 1979).

Order PROTOLEPIDODENDRALES
Family PROTOLEPIDODENDRACEAE Kräusel and Weyland, 1949
Genus *COLPODEXYLON* Banks, 1944

Type species. *Colpodexylon deatsii* Banks, 1944 from the Delaware River Flags, equivalent to the marine Upper Ithaca or Enfield formation, Finger Lakes Stage, Senecan Series, lower Upper Devonian (= Frasnian) of New York State, U.S.A.

Colpodexylon cachiriense sp. nov.

Plate 73, fig. 9; Plate 74, figs. 1-9

Derivation of name. From the Rio Cachiri, after which the most northern outcrop of Devonian rocks in Venezuela is named.

Holotype. LPB16045 (Pl. 74, figs. 1 and 2).

Locality. Roadside exposures on the road from the town, Villa del Rosario, to the Socuy River in the Colorado valley, some 950 to 1500 m NNW of the farm 'Alemania', c. 70 km west of Maracaibo, north-western Venezuela.

Horizon. Carbonaceous lutites at the base of the Campo Chico Formation, Devonian (?Givetian-Fresnian).

Diagnosis. Vegetative stems at least 10 cm long, 5.3 to 9.5 mm wide ($\bar{x} = 7.7$ mm, $n = 10$) with persistent leaves borne spirally or in pseudowhorls. Leaf bases not contiguous with 7-9 leaves per gyre (9 being the commonest number); successive gyres also widely spaced. Stem surface between leaf bases probably smooth. Divaricate leaves with broad, flat, or abaxially curved bases, three forked; 0.62-0.96 mm ($\bar{x} = 0.76$ mm, $n = 14$) wide in basal unbranched region, trifurcating 4.0 to 7.5 mm ($\bar{x} = 5.6$ mm, $n = 11$) from attachment. The central fork (0.5-0.72 mm) is approximately twice as wide as the laterals (0.26-0.3 mm) and at least twice as long. All tips acuminate. Leaves at least 14.7 mm long.

EXPLANATION OF PLATE 73

Figs. 1-8. *Haskinsia sagittata* sp. nov. 1, LBD16050, short length of stem with coalified covering, prominent ridges, and leaf bases with sedimentary infill (text-fig. 3d, e), $\times 3$. 2-6, LBD16046. 2, part of lower surface of rock bearing holotype showing predominantly impression fossils, unilateral illumination. Lustre surface produces brighter areas. Note range in form of projection marking bases of leaves attached to upper surface, $\times 2.4$. 3, area of left-hand stem in fig. 2 magnified to show detail of such projections and the infilled bases of leaves (arrowed) attached on lower surface of stem, $\times 6$. 4, two stems on same surface as holotype; latex cast made from one on right, unilateral illumination, $\times 3.1$. 5, part of stem on same surface as holotype, lighter areas comprise fine-grained sedimentary infill; darker areas comprise granular coalified material. Inverted U mark sites of attachment of leaves on lower surface, $\times 9.2$. 6, oval area marking attachment of leaf passing down into matrix; powdery coalified material has been removed to reveal sediment filling base of petiole, $\times 20$. 7, scanning electron micrograph of indeterminate spores recovered on surface of latex cast (stub no. 620), $\times 650$. 8, scanning electron micrograph of latex cast of stem impression illustrated in fig. 4 (stub no. 628), $\times 16$.

Fig. 9, *Colpodexylon cachiriense* sp. nov. LBD16052(i), coalified compression fossil with very fine-grained sedimentary infill (s) sometimes iron-stained on surface (r) and near base an uncovered trifurcating leaf extending from a crescentic depression on lower surface. Arrow indicates possible vascular strand, $\times 29$. (Photographs under uniform illumination except where otherwise stated.)

EDWARDS and BENEDETTO, *Haskinsia, Colpodexylon*

Description. The diagnosis is based on short lengths of unbranched stems showing a variety of preservation forms united in the possession of trifurcating leaves. Apart from two isolated impressions, all the leaves were uncovered. As they are small in number and generally incomplete or distorted, we anticipate that the dimensions recorded in the diagnosis will be emended on the discovery of further specimens.

Stem characteristics: The parallel-sided stems are almost featureless except for the presence of leaf bases or attachment sites marked by inverted crescentic (Pl. 74, fig. 7) or more strongly arched lines (Pl. 74, fig. 1) enclosing depressions and, less frequently, by inverted crescentic ridges. The persistent leaves vary in their arrangement from pseudowhorled to a more steeply pitched spiral condition, but in all cases successive gyres are widely spaced, as are individual leaves in a gyre. The number of leaves per gyre ranges from 7 in the narrower stems to 9 or possibly more in the wider, uncertainty arising from the fact that usually only one surface of a stem is preserved.

Some evidence of a vascular strand comes from a stem 9.5 mm wide, with a longitudinal strip of sedimentary infill and coalified material 1 mm wide, bearing coarse longitudinal striations (arrowed in Pl. 73, fig. 9). The coalified material was macerated in Schulze's solution, but no tracheids were recovered. Latex replicas taken from rock surfaces show faint impressions of cells, but failed to reveal further detail under the SEM.

Leaf characteristics: The most complete leaves are long, slender, and trifurcating, showing no distinction between petiole and blade. (Pl. 74, figs. 2, 4, 5). The proximal unbranched region is parallel-sided and strongly flattened in the plane of the trifurcation, widening slightly before branching. The crescentic attachment sites and bases of leaves uncovered below such sites (Pl. 74, fig. 8) suggest that the basal region was abaxially curved, but this is not apparent on the leaves attached to stems fortuitously fractured transversely (Pl. 74, fig. 7). Nor do they show the broad longitudinal grooves visible on the proximal regions of some of the more complete leaves (Pl. 74, figs. 2 and 3).

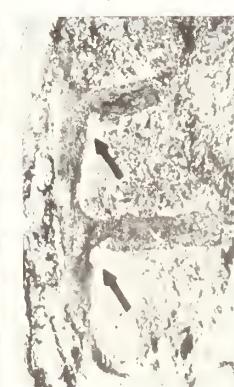
Almost all the branching leaves were uncovered. The lateral segments are usually slightly more than half the width of the central one, the three separated basally by U-shaped embayments of sediment where all are preserved in the same plane. All three taper, the lateral ones being much shorter than the central. We doubt that any of the extreme tips remained intact after uncovering as the sediment grains were wider than the distal parts of the leaves, which were very easily dislodged. Vague outlines of cells are visible as impressions of the adaxial surface near the base, but no further anatomical details of the leaf were obtained. The leaves were persistent, but in the majority of cases only the divaricate basal parts are preserved showing tapering (Pl. 74, fig. 7), truncated (Pl. 74, fig. 9), or more rarely, hooked tips (Pl. 74, fig. 3). Such incompleteness suggests that the branches were more delicate and also explains the change in orientation sometimes observed between the two regions. Whether or not the entire leaf in life was a stiff spreading organ with all parts in the same plane, or was more flexuous, as seen on the holotype, remains conjectural.

All the leaves were sterile. However, we noted two isolated possible sporangia preserved near typical axes. One is elliptical and featureless; the other, 2.5 mm long and 1.8 mm wide, has a notch at one end which is extended into a central longitudinal depression (Pl. 74, fig. 6). Neither structure yielded spores and we have no evidence, apart from association, that they belonged to *C. cachiriense*.

Comparisons. The diagnosis of *Colpodexylon* is based on sterile and fertile leafy stems from the Devonian of New York State (Banks 1944). Most are compression fossils, but some have pyritized

EXPLANATION TO PLATE 74

Figs. 1-9. *Colpodexylon cachiriense* sp. nov. 1, LBD16045, holotype, impression fossil, unilateral light showing attachment sites of leaves borne on the lower surface of the stem, $\times 1.8$. 2, enlargement of part of holotype to show the single attached trifurcating leaf, $\times 3.6$. 3, LBD16048, impression fossil with incomplete attached leaves with hooked tips, unilateral illumination, $\times 3.3$. 4, LBD16049, iron-stained impression of leaf with traces of coalified material, central segment of trifurcation missing, $\times 4$. 5-8, LBD16048. 5, detached leaf with incomplete tips, $\times 3.7$. 6, possible isolated sporangium, $\times 10$. 7, coalified stem with leaf bases in profile. Arrow indicates another stem fractured transversely showing abaxial or adaxial surfaces of leaf bases, $\times 2$. 8, distal part of stem figured in fig. 7, preserved as impression fossil. Leaf scars have been developed to expose adaxial surfaces of two leaves (arrowed) originally projecting down into the matrix below the stem. Isolated leaf shows two of the three distal segments and typical curvature just below the trifurcation, $\times 7.4$. 9, LBD16045, stem impression on same surface as holotype. Incomplete leaves show fracture at point of attachment (arrowed), $\times 5$. (Photographs under uniform illumination except where otherwise stated.)



anatomy. The Venezuelan plants, although far more fragmentary and lacking both reproductive and anatomical details, are assignable to *Colpodexylon* because they possess persistent trifurcating leaves which Grierson and Banks (1963) considered 'the chief diagnostic character' (p. 253) of the genus. Banks originally distinguished two species, the type *C. deatsii* from Frasnian strata and the anatomically less completely known *C. trifurcatum* from the Eifelian. The two are readily separated from the South American plant in that their stems bear a greater number of leaves per gyre with leaf bases both laterally and vertically contiguous. The preservation of the Venezuelan plants is such that usually only the inside of leaf bases are visible, but these are so widely spaced that considerable areas of stem surface must have been exposed between leaf bases. There are however certain similarities in the structure of the leaves. When describing the basal segment of the leaf of *C. deatsii*, Banks (1944) noted that it was necessary to remove matrix from 'alongside the leaf margin in order to expose the true widths' (p. 654) and concluded that this was evidence for a slightly revolute margin. He also recorded two longitudinal furrows on the leaf surface. In describing isolated sporangia he mentioned that a few showed an apical notch sometimes extended into a median line. These were not illustrated but may be similar to the isolated structure we figure in Plate 74, fig. 6.

Lemoigne and Ishchenko (1980) described a putative third species from the Famennian of the Ukraine. In the leaves, only the lateral branches beyond the trifurcation are visible (a similar preservation to that illustrated in Pl. 74, fig. 4), the authors suggesting that the central one is present in a different plane. The stem surface looks quite different from the other species including *C. cachiriense* because each leaf base has an adaxial depression. The leaves are considered ligulate.

Of the herbaceous lycopods reported from South America the only taxon with distinctly divided leaves is *Protolepidodendron kegeli* (Kräusel and Dolianiti 1957) from the Maranhao Basin of Brazil. The leaves as illustrated differ from those in *C. cachiriense* in that they resemble tuning forks, being at least 15 mm long with a bifurcation about 2 mm from the base, although there is always the possibility that further uncovering will show them to be more complexly branched.

TAPHONOMY

Several recent investigations demonstrate that both the type of preservation and subsequent planes of fracture are responsible for the diversity of appearance in the stems of herbaceous and arborescent lycopods (Chaloner and Collinson 1975; Thomas and Purdy 1982; Grierson and Banks 1983; Rex and Chaloner 1983). Such studies greatly facilitate interpretations and descriptions of our fossils and, in particular, the leaf bases of *H. sagittata*. Indeed, the leafy specimen illustrated in Plate 71, fig. 4 allows a leaf lamina cleaved compression plane to be added to the fracture plane terminology summarized by Grierson and Banks (1983). However it has sometimes been difficult to apply their terminology, based mainly on coalified compression fossils, to the heavily weathered Venezuelan examples, where at best the original stem is replaced by a thin layer of sedimentary infill coated by a film of coalified material, and where counterparts are missing. Our fossils exhibit a range of appearances and preservation states (compare, for example, Pl. 71, figs. 1-5) and the entombing sediments vary in colour and hardness, a reflection of the degree of weathering. Some of the more perplexing structures occur in those fossils where little or no organic material remains. The range of types of preservation present permits the poorly preserved forms to be interpreted by reference to the more complete and well-preserved stems. Such an assessment of different preservation types is necessary as the identification and description of lycopods from the Devonian of South America, South Africa, and Antarctica have been based on similar fragmentary impression fossils.

Types of preservation

a. Fossils with layer of sediment sandwiched between two coalified layers that presumably represent the outer tissues of the stem. The amounts of coalified material, sedimentary infill, and compression vary between specimens.

H. sagittata. The least compressed specimen (Pl. 71, fig. 2) lacks the diagnostic leaf blades, but the shape, orientation, and arrangement (7 per gyre) of leaf bases and its size permit assignation to *H. sagittata*. The

coalified stem, a cleavage compression *sensu* Chaloner and Collinson, exposed by a fracture plane running between the upper surface and the matrix is present only at the base of the specimen. A fractured example of the poorly defined elongate projections, the bases of the petioles, show them to be filled with sediment. Leaf arrangement is much clearer where the fossil has dropped out revealing an impression of its lower surface, a cleavage impression. Fine striations are visible under a dissecting microscope.

The stem illustrated in Plate 71, figs. 3 and 5 is similar in composition, but looks quite different as a result of greater compression and irregular fracture removing parts of the upper surface. It comprises a papery layer of very fine-grained whitish sediment(s), stained orange on the outside, and sandwiched between two sporadic powdery coaly layers. Both impression and infill have areas of indistinct cell outlines. Removal of the rock distal to a depression reveals the characteristically shaped leaf of *H. sagittata* (arrowed in Pl. 71, fig. 3). In some cases the depressions are filled with sediment and some additional coalified material producing mounds with irregular topography, but in addition to these, smooth mounds of relatively low relief may be seen on the lower impression surface as well as less regular ones on the sedimentary infill (see Pl. 71, fig. 4 where the stem is illuminated unilaterally). The latter are the incomplete leaf base infills of the leaves attached to the upper surface (i.e. that closer to the observer) and the former show that the stem has been so compressed that its lower surface is pressed into the bases of these leaves producing these 'false leaf bases' (text-fig. 4e, f). Their positions indicate that they do not represent the inward collapse of the stem between leaf bases on the lower surface.

C. cachiriense. The most complete fossils are of this preservation form. The unbranched stem (40 mm long) in Pl. 73, fig. 9, has a variable appearance due to uneven fracture. The extremely fine-grained infill is silvery internally (s) but iron-stained on the surface (r). It lies above a thick coalified layer, but a similar layer representing the organic remains of the stem closer to the observer is rarely preserved above the sedimentary infill. The impression fossil on the rock below is also iron-stained and while some areas bear faint traces of cells, others are distinctly warty. The sediment infill does not extend to the edges of the stem which are marked by a strip of coaly material of variable width (0.3–0.4 mm) although this has sometimes broken. The bases of leaves attached to the sides of the stem, represented by tapering, needle-like projections before developing, are heavily coalified compressions continuous with this marginal band. The attachment sites of the widely spaced superficial leaves are not conspicuous. On the lower impression surface they are shallow depressions limited at one end by a crescentic coalified line. The depression is sometimes filled with sediment and additional coalified material. On the cleaved sedimentary layer their positions are marked by short transverse furrows. Attachment sites on the upper surface of the infill are marked by crescentic ridges, abruptly truncated on the convex edge and tapering gradually on the other. They are most conspicuous where the surface stain has rubbed off.

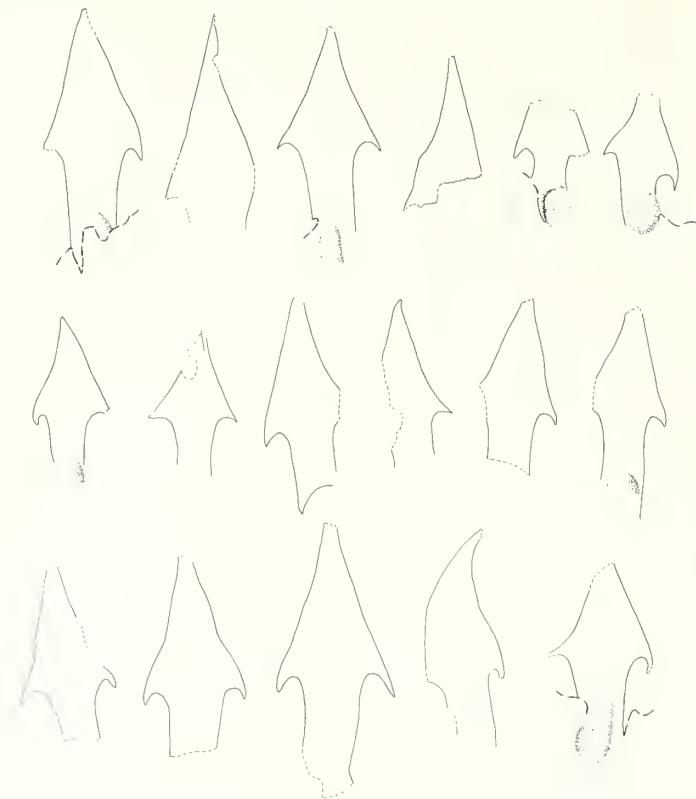
Another example (Pl. 74, fig. 7) has a more untidy appearance because the layers of coalified material and sediment are not continuous over wide areas. They are easily dislodged; the impression below has been developed (Pl. 74, fig. 8) to demonstrate the broad abaxial curved junctions between leaves and stem.

b. Strongly compressed fossils comprising a granular mixture of inorganic and coalified material, only rarely showing distinct layering.

H. sagittata. The holotype and about twenty other axes occurring at different levels in the rock, but most orientated in the same direction, show this preservation type. The matrix was the least weathered of all the slabs examined. The specimen provided an opportunity to study part and counterpart as during preparation one stem was split. Its plane of fracture was irregular but more fossil remained on one surface (the part) than the other (counterpart) thus paralleling the situation on the two major faces of the rock. The surface equivalent to the part bears a number of stems of variable colour (ranging from grey to brown to rust) and appearance. Depending on the plane of fracture and amount of weathering or damage since collection, granular sediment, sporadic coaly or rusty material or stained rock below may be exposed. In some areas the impression beneath has a metallic sheen, the entombing sediment being much finer grained than the general matrix and displaying longitudinally aligned evenly spaced depressions presumably representing the outlines of epidermal cells. SEM examination of latex casts of such stems failed to show the precise shape of individual cells (Pl. 73, fig. 8). The predominantly impressions on the reverse of the block (equivalent to the counterpart) are similar in appearance ranging from those with a striking gold-lustre surface (Pl. 73, fig. 2) to those stained brown and visible only in unilateral lighting.

Before developing only a few leaves were visible in profile, but removal of sediment above and adjacent to stems showed that they were ensheathed in leaves, slightly smaller than the mean, but identical in shape (see base of holotype; Pl. 72, figs. 1, 2 and Pl. 71, fig. 8).

The most conspicuous macroscopic features of these axes, enhanced by unilateral illumination, are the depressions and elevations, the latter sometimes standing over a millimetre above the stem surface marking the positions of leaves. Here again the positions of the bases of leaves of both sides of the stem may be visible on one



TEXT-FIG. 2. Outlines of uncovered leaves showing range in shape and size, drawn from specimens LPB16046, 16047, 16049, 16052, and 16054. All $\times 24$.

exposed surface. The depressions marking the leaves passing down into the matrix are most clearly defined and, on the parts, have three different appearances. In the complete absence of the compression fossil they appear as inverted Us (Pl. 73, fig. 5), often delimited by a line of coalified material (the remains of the peripheral tissues of the leaf base), enclosing a shallow depressed area which sometimes bears a central, longitudinally aligned fold (Pl. 71, fig. 8; text-fig. 2). More usually the attachment site is marked by a circular, elliptical, or ovate area of fine-grained sediment frequently covered by a thin film of coalified matter (Pl. 73, figs. 3, 4, 6). Although this may represent the peripheral tissues of the side of the stem closer to the observer, in a few rare cases, it is further obscured by the infill layer. The plug of sediment may be flat and almost flush with the stem surface or possess a central, barely visible, fold. Finally, less regular mounds of coarser sediment mark the leaf bases.

The elevations are more variable and may be truncated with unevenly contoured tips or more usually are smooth attenuated mounds (Pl. 73, fig. 4). Little sediment or coalified material persists on the flanks of the projections, but occurs sporadically on the surface of the stem particularly in the vicinity of the margins.

The projections are far more distinct on the counterparts accentuated to some extent by the lack of compression fossil. The tips of the pegs are either rounded, irregularly fractured, or have a central crater-like depression surrounded by a rim (Pl. 73, figs. 2 and 3). Depressions or circular to elliptical areas of sediment (sometimes covered by a thin dark layer) mark the attachment of leaves beneath the stem. These may alternate regularly with the pegs or almost coincide with them (Pl. 73, fig. 3).

A few of the stems (e.g. the holotype) bear prominent elongate ridges or depressions of varying lengths (Pl. 72, fig. 2; Pl. 73, figs. 1 and 4). On the specimens equivalent to parts, longitudinally aligned ridges occur between, but never traverse, the leaf base depressions and are sometimes interrupted by the mounds. Between the vertically superimposed depressions they are parallel, 0.6 to 0.9 mm apart, but may widen slightly to enclose the

depressions. Where the body fossil is missing on this surface, ridges also occur on the impression below. A latex replica of such a surface, a cast of the stem (Pl. 73, fig. 8), suggests that the leaves of a single orthostichy were borne on a broad probably slightly raised band isolated from each adjacent one by a groove. On the stems (= counterparts) exposed on the reverse of the slab, longitudinally orientated grooves pass between the projections and across some of the depressions, but there are no ridges.

c. Coalified compressions

One short length of *H. sagittata* stem (Pl. 73, fig. 1) comprises an almost continuous thin layer of coaly material interrupted by approximately circular areas of sediments, thought to be trapped within the bases of leaves attached to the lower surface. Also present are longitudinal ridges separating the leaf bases, and occasional indistinct mounds on the surface of the coalified layer. The latter may mark the portions of the leaves attached to the upper surface of the stem, i.e. that closer to the observer. A very thin film of coaly material has been noted on two of the circular areas of sediment. This may represent the remains of the tissues of the upper surface of the stem. A drawing of a transverse section through this stem is given in text-fig. 3d. Unfortunately its counterpart is missing and no further information was gained on removing the sediment overlying one end.

In most fossils of this type the coalified layer is more powdery and rarely continuous, frequently revealing an iron-stained impression on the rock beneath. Such a stem, figured on the left in Plate 72, fig. 13, is typical in that the attachment sites of the leaves on the lower surface are marked by shallow depressions and on the upper by elongate smooth mounds. Leaf bases in a single orthostichy are widely spaced. The stem surface bears numerous faint longitudinal ridges and grooves that are not continuous over any great distance. The stem on the right looks quite different: it has more pronounced relief and less coaly material. The leaves in profile are more numerous. Although approximately the same width, it has at least nine leaves per gyre and successive gyres are more closely spaced.

The most striking fossils in the assemblage are those where the coalified material is replaced by a granular reddish brown layer.

d. Impressions. Many of the fossils available for study were of this type. Some may have been produced by tropical weathering of originally rather fragmentary coalified compressions or coalified material plus sedimentary infill, but others may be artifacts of collecting in that only the counterpart was originally retained and the body fossil may have been dislodged and lost on subsequent transport.

H. sagittata: The weathered specimens obviously intergrade with some of the coalified compressions just described (Pl. 72, fig. 13). All occur in a very soft, buff to pink matrix, one most useful in deducing leaf morphology by uncovering. The stems illustrated in Plate 72, figs. 3 and 4 are pink iron-stained impressions with traces of black powder associated with leaf bases. Also present on parts of the stem and certain leaves is a brown film which may represent the remains of a cuticle, but this lacks cellular imprints.

The leafy stem figured in Plate 71, fig. 1 superficially resembles the cleavage compression illustrated by Grierson and Banks (1983, fig. 4). The most obvious common features are the circular and oval areas of sediment (0.96 mm long and 0.83 mm wide) marking the attachment sites of leaves. In the Venezuelan fossils, just above and slightly to one side of each leaf base is a slight mound, a false leaf base, marking the position of the leaf on the surface nearer the observer. The stems have a high relief but very little organic material persists. Some of this is in the form of a thin layer of cuticle with traces of cellular markings and more prominent widely spaced longitudinally orientated dark lines delimiting orthostichies. These are sometimes replaced by less regular ridges or furrows. Film pulls showed no further cellular detail.

C. cachiriense: The holotype (Pl. 74, figs. 1 and 2) is predominantly an impression fossil, stained dull red towards one end; leaves are preserved as compressions. Their attachment sites are marked by shallow inverted U-shaped depressions containing oval or elliptical mounds of fine-grained sediment plus some coalified material. The curves of the U extend as shallow ridges, almost to the level of the gyre below, giving the striated appearance best seen in unilateral light. The strongly curved junction between leaf base and stem is represented by a pronounced strip of coalified material much greater in thickness than the coalified film, presumed to be the remains of the outer tissues of the stem, exposed on removing the sedimentary infill. Some very low mounds perhaps marking the sites of leaves on the upper surface are just visible between the depressions on the surface of the impression towards its base, but are sometimes superimposed on the sedimentary infill distally.

A representative of the commonest preservation type of *C. cachiriense* is shown in Plate 74, fig. 3. Its surface has a yellow, silky, almost bone-like, texture. Excavations around the ends of similar small fragments indicate that originally present was a crumbling mixture of small irregular sheets of coalified material and sedimentary infill. Leaf attachment sites on the impression resemble those on the holotype, but when sediment and coalified material are removed, the surface of the stem impression is also convex, suggesting that the stem had collapsed

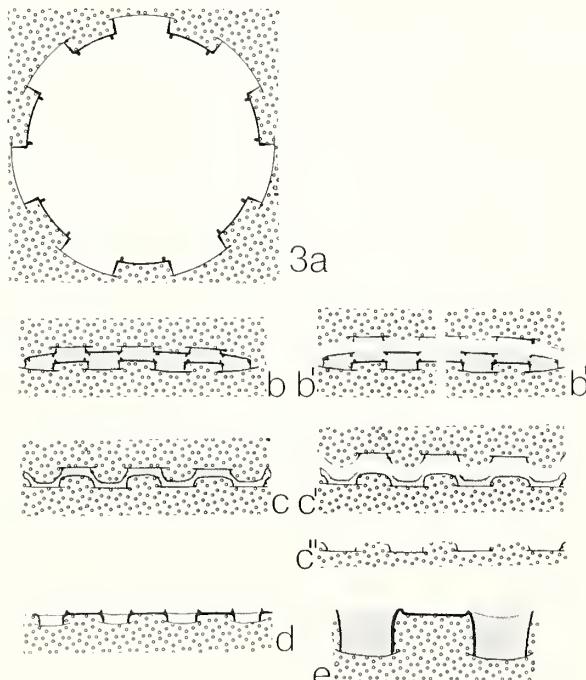
inwards just below a leaf. That this was a topographic feature of the stem in life is considered unlikely; similar but more pronounced examples are seen on stems showing distortion from twisting and stretching.

Preservational history. The sequence of events that produced these preservation forms is broadly similar for the stems of both species. Biodegradation of internal tissues of stems and leaves would have resulted in collapse of these organs, but as emphasized by Rex and Chaloner (1983) exactly when this occurred in relation to burial, possible infiltration by sediment and then further compaction under a mass of sediment, is difficult to determine. The situation is further complicated by the differing rates of decay of soft and hard (strengthening) tissues. Here major problems in interpretation relate to the resilient leaf bases and other strengthening tissues in *Haskinsia* and to the compression of the flat divaricate leaves of *Colpodexylon*.

Impressions of epidermal cells in the extremely fine-grained matrix immediately around some of the fossils suggest that an iron-rich layer quickly encrusted the plant surface after immersion (Spicer 1977). Decay of soft tissues continued during immersion and subsequent burial, but as the stems began to collapse the bases of leaves retained their shape because of the presence of decay-delaying peripheral strengthening tissues. In some instances sediment began to accumulate within the increasingly hollow stems and may well have become trapped in the leaf bases early on, thus further reinforcing them (text-fig. 3). As overlying sediment increasingly compressed the stems perhaps squeezing more grains into the leaf bases, a cast of the inside of the stem surrounded by a very thin layer of disintegrating tissues would have resulted.

Further compression of the infill would have resulted in considerable distortion (Rex and Chaloner 1983) with parts of stem and embombing matrix pressed into leaf bases (text-fig. 3c) thus producing the false leaf bases already noted (Pl. 71, fig. 5). A similarly undulating cross-section would be seen in fossils lacking any sedimentary infill (e.g. Pl. 72, figs. 3, 4, 13). As is often the case features of one surface appear less compressed than the other (text-fig. 3).

Rex and Chaloner (1983) investigating the behaviour of spines in a plant like *Sawdonia* during compression used a hollow cylindrical foam rubber model, which in section looks remarkably like



TEXT-FIG. 3 a-c. Diagrams showing postulated behaviour of stem of *H. sagittata* on compression and subsequent fracture. Coarse stippling represents matrix, fine stippling sedimentary infill. For ease of drawing a whorled arrangement of leaves is shown with those at the margin both directed downwards (a). The fossil above the fracture is equivalent to the counterpart, that below, the part. b, fossil with well-defined coalified layers and sedimentary infill with fracture plane passing between matrix and upper surface of stem and across (b') or around sediment infill of leaf bases (b''). c, highly compressed fossil with fracture plane passing over upper surface and across leaf bases (c'). c'' shows a weathered example with surface of matrix below the compression exposed. In even more compressed forms, sometimes lacking infill, fracture is less regular across stem surface. d, e, postulated section through the stem illustrated in Plate 73, fig. 1 where fracture occurs across upper surface of coalified compression and across bases of leaves attached to lower surface. e is enlarged to show detail of the longitudinal ridges.

our stems. On compression the 'spines' on the upper surface became much shorter, those on the lower surface shortened but less so. Thus the rock surface with stems showing the most pronounced depressions and the most compression material (the parts) was probably the original surface of the sediment.

The longitudinal ridges and grooves on some of the preservation forms are more difficult to interpret. The presence of dark lines in similar positions on certain stems (Pl. 71, fig. 1) suggest that they were indeed regions of thick-walled strengthening tissues equivalent to those described for *H. colophylla* by Grierson and Banks (1983) who considered them hypodermal. In many of the Venezuelan examples (type *b*, Pl. 71, fig. 8, Pl. 72, fig. 2; type *c*, Pl. 73, fig. 1) they seem to be part of the stem surface, where they are associated with the leaf bases on the lower surface of the stem. They thus appear as ridges on the impression fossil below that surface, ridges on the body fossil (part), and grooves on the impression counterpart. The latex cast of the lower surface of such a stem (Pl. 73, fig. 8) shows narrow grooves separating broad ridges on which the vertical files of leaves are borne.

The sequence of events that produced such an arrangement remains problematic. Inwardly projecting rods of more persistent hypodermal tissues could have produced longitudinal grooves on the surface of the sediment filling the hollow (decomposed) centre of the stem in a sequence analogous to the production of grooves on pith casts of *Calamites* (text-fig. 3b). During further diagenesis the organic matter may have almost disappeared so that the entombing matrix was pressed against the surface of the cast. The resulting impression in the surrounding rock would have longitudinal ridges but these have nothing to do with the original surface of the plant (also seen in *Calamites*). However, in these Venezuelan examples, as there is little or no sedimentary infill, it seems likely that the longitudinal strands themselves projected into the matrix and subsequently became coalified. While preferential preservation may account for their presence on one side only of the stem, it is also possible that the positions of the strands on the two surfaces were coincident on compression, thus reinforcing each other to produce the observed feature. Indeed on stems which are twisted or where leaf bases on the two surfaces do not regularly alternate, the longitudinal features, if present, are more closely spaced, cannot be traced over long distances, and occasionally occur as furrows as well as ridges on the same surface.

Also puzzling is the presence of a raised area at the centre of certain depressions marking leaf bases (text-fig. 2). Those illustrated in Plate 71, fig. 8 occur on a stem (type *b* preservation) adjacent to the holotype: removal of the stem distal to the leaf attachment sites has revealed the leaves themselves. The raised area on the left is elongate, that on the right more circular. The anatomical feature responsible for such a topography remains unknown.

Considering *Colpodexylon*, different appearances of the leaves may be related to the behaviour on compression of dorsoventrally flattened structures with extended horizontal connections with the stem. Seen sideways-on, such leaves appear as linear structures with slightly expanded bases (horizontal stem on Pl. 74, fig. 7) produced by the lateral compression of the unbranched proximal regions of the leaf. However, we encountered some such specimens in which removal of matrix immediately adjacent to the straight edge, believed to represent the abaxial limits of the leaf, revealed a further strip of more delicate coalified material below. This change in level and thickness suggests that the originally gently abaxially curved leaf had been twisted slightly on compression so that part of the dorsal (abaxial) surface has become visible at the lower level. A similar explanation fits the zoned appearance of certain quite broad leaf bases in which the adaxial quarter or one third is more heavily coalified or stained than the remainder below. Twisting or fracture of the extended flat or crescentic junction may account for the constrictions sometimes visible at leaf junctions (Pl. 74, fig. 9). As a result of twisting in the basal region of the leaf attached to the holotype (Pl. 74, fig. 2) the abaxial or adaxial surface is preserved in the same plane as the flattened stem.

PALAEOBIOGEOGRAPHY

Lack of information from southern continents has, more than any other factor, frustrated attempts to detect provincialism in Devonian floras (Edwards 1973; Edwards and Fanning 1985). The situation

in South America is typical, the plants (e.g. *Haplostigma* and *Palaeostigma*) are often poorly understood and independent dating of assemblages absent. Even for this relatively well-preserved assemblage from Venezuela the age determination is equivocal in that animal fossils are lacking in the beds containing the plants (Co_8 horizon in the Campo Chico Formation): an assemblage of brachiopods and pelecypods (Co_6 horizon) suggests a Givetian age (probably middle to late Givetian: Benedetto 1980, 1984) for the Co_6 horizon some 50 m below. Brachiopods and pelecypods from 300 m above the plant horizons are late Mississippian–early Pennsylvanian. Bowen (1972) mentions an assemblage of Middle to Upper Devonian palynomorphs (presumably Frasnian) from the upper part of the Campo Chico Formation but we have been unable to correlate this horizon with the plant beds. We have failed to isolate a spore assemblage from the matrix and spores found adpressed to several of the axes are not sufficiently well preserved to permit an age determination (Pl. 73, fig. 7). The plants described here support a Givetian–Frasnian age (Grierson and Banks 1963), although *C. trifurcatum* and *Haskinsia colophylla* are also recorded from Eifelian sediments in New York State. Of the assemblages from Argentina originally described by Frenguelli (1954) and reinvestigated by Menendez (1965a, b) only one, that containing *Haplostigma furquei*, is independently dated and considered Middle Devonian from associated trilobites. The far more diverse assemblage from the Quebrada de la Chavela including *Drepanophycus eximius* (Menendez 1965b) and *Archaeosigillaria conferta* (Menendez 1965a) as well as *Furqueia angulatae*, *Charnelia dichotoma*, *Hyenia argentina*, and *Adiantites devonica* was originally thought to be Devonian but Cuerda *et al.* (1968) consider it younger (Carboniferous) after re-examination and re-identification of some of the plants.

Considering Brazil the assemblage from the Upper Porta Grossa Beds with a number of species of *Spongiophyton* and *Haplostigma* (Kräusel 1960) was originally described as Lower Devonian. Chaloner *et al.* (1974) reviewed recent palynological and micropalaeontological (acritarchs and chitinozoans) studies and concluded that the sediments are probably Givetian. Associated palynomorphs suggest that the lycopod assemblage (*Palaeostigma sewardi*, *Protolepidodendron kegeli*, and *Archaeosigillaria picosensis*) in the Picos Formation of the Maranhao Basin (Kräusel and Dolianiti 1957) is Middle Devonian (Bär and Riegel 1974) although age determinations of other workers range from Emsian to Frasnian (Sampaio and Northfleet 1973; Brito 1967). Finally, strata on the Falkland Islands containing *H. irregularis* are considered Middle Devonian on the basis of the plants themselves (Seward and Walton 1923). These are being reinvestigated by Dr. Sergio Archangelsky.

Thus on current evidence, vascular plant assemblages from South America are of Middle Devonian age, and are dominated by lycopod genera, most of which are known from the northern hemisphere. The recent taxonomic and stratigraphic review of African lycopods (Anderson and Anderson (in press)) includes some revision of American lycopods, which reinforces similarities between the floras of the two southern continents. Further support for a uniform world-wide flora in mid-Devonian times comes from the description of *Leclercqia complexa* from Queensland (Fairon-Demaret 1974), and late Devonian sediments of New South Wales contain species of the northern hemisphere genera *Leptophloium*, *Barinophyton*, and *Archaeopteris* (Gould 1975).

Our studies provide evidence for a uniform vegetation between a part of north Gondwana and the Old Red Continent (Laurentia) in mid- to late-Devonian times, but in isolation do not provide compelling evidence for global uniformity during that period. The similarities may simply reflect the palaeogeographic proximity of the localities or their occurrence in the same climatic zone encompassing more than one palaeocontinent. As far as is known the Venezuelan plants were homosporous with the potential for colonizing very wide areas (Chaloner and Sheerin 1979) and thus provide inconclusive evidence for the past distribution of continents. Many Devonian palaeogeographic reconstructions show an east–west (Rheic) ocean separating north and southern land masses (see e.g. Smith *et al.* (1981) where continent positions are based on palaeomagnetic data; Scotese *et al.* (1979); and Scotese (1984) late Devonian (B) map). Some recent reconstructions have closed or narrowed this ocean. That of Heckel and Witzke (1979), based on the distribution of palaeoclimatically significant rock types, e.g. carbonates, show northern parts of Africa and South America close to Laurentia (Old Red Continent), while Scotese (1984) presents an alternative

reconstruction for the late Devonian (map A) based on new palaeomagnetic data which positions Venezuela closer to north-east America, but Australia is at a much higher latitude and a considerable distance from the Old Red Continent. Such a juxtapositioning of Venezuela and eastern North America appears to complement our conclusions based on floras and receives further support from similarities in marine faunas comprising brachiopods, pelecypods, and corals (Benedetto 1980, 1984).

Finally, considering climatic zones, Barrett (in press) has predicted global climates for four reconstructions of continents in early- to mid-Devonian times including those of Smith *et al.* (1981) and Scotese *et al.* (1979). In all the models, he finds that northern South America (Amazon-Colombian) is likely to have been cool, the land vegetation growing under wet temperate conditions with eastern North America (Appalachian Basin) at lower latitudes in a tropical to subtropical wet climate. This suggests that these early pteridophytes with small or divided leaves and an abundance of strengthening tissues may have been tolerant of a range of climates and thus may provide an explanation for the apparent uniformity of vegetation in Devonian times. Alternatively it may merely indicate that such plants possessed a higher fossilization potential.

Acknowledgements. We thank Dr. Patrick Racheboeuf for his assistance and advice throughout the Venezuelan project, Dr. J. B. Richardson for palynological help, Ms. Jan Cawley for photographic expertise, and Dr. S. Barrett for access to unpublished data.

REFERENCES

- ANDERSON, J. and ANDERSON, H. (in press). *Prodromus of South African Megafloras, Devonian to Lower Cretaceous*, 400 pp. A. A. Balkema, Rotterdam.
- BANKS, H. P. 1944. A new Devonian lycopod genus from southern New York. *Am. Jl Bot.* **31**, 649–659.
- 1980. Floral assemblage zones in the Siluro-Devonian. In DILCHER, D. and TAYLOR, T. N. (eds.). *Biostratigraphy of fossil plants: successional and paleoecological analysis*, 1–24. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.
- BÄR, P. and RIEGEL, W. 1974. Microfloras of the Palaeozoic of Ghana and their palaeofloristic relations. *Sci. Geol. Bull.* **27**, 39–58.
- BARRETT, S. F. (in press). Early Devonian continental positions and climate: a framework for paleophytogeography. In TIFFNEY, B. (ed.). *Geologic factors and the evolution of plants*. Yale University Press.
- BENEDETTO, J.-L. 1980. Sintesis bioestratigráfica del Paleozoico tardío de la Sierra de Perija, Venezuela. *An. Acad. Brasil Cienc.* **52**, 827–839.
- 1984. Les Brachiopodes devonicus de la Sierra de Perija (Venezuela). *Biostratigraphie du Paléozoïque* (Brest), **1**, 1–191.
- BOUCOT, A. J. and GRAY, J. 1982. Geologic correlates of early land plant evolution. *Proc. Third N. Am. Paleontol. Conv.* **1**, 61–66.
- BOWEN, J. M. 1972. Estratigrafia del Precretaceo en la parte norte de la Sierra de Perija. *Mem. V. Congr. Geol. Venezuela*, **2**, 729–761.
- BRITO, I. M. 1967. Silurian and Devonian Acritarcha from Maranhao basin, Brazil. *Micropalaeontology*, **13**, 473–482.
- CHALONER, W. G. and COLLINSON, M. E. 1975. Application of SEM to a sigillarian impression fossil. *Rev. Palaeobot. Palynol.* **20**, 85–101.
- MENSAH, M. K. and CRANE, M. D. 1974. Non-vascular land plants from the Devonian of Ghana. *Palaeontology*, **17**, 925–947.
- and SHEERIN, A. 1979. Devonian macrofloras. In HOUSE, M. R., SCRUTTON, C. T. and BASSETT, M. G. (eds.). *The Devonian System. Spec. Pap. Palaeont.* **23**, 145–161.
- CUERDA, A. J., WAGNER, R. H. and ARRONDO, O. G. 1968. Observaciones sobre algunas floras del Carbonífero Argentino. *Ameghiniana*, **5**, 265–269.
- EDWARDS, D. 1973. Devonian floras. In HALLAM, A. (ed.). *Atlas of Palaeobiogeography*, 105–115. Elsevier, Amsterdam.
- and FANNING, U. 1985. Evolution and environment in the late Silurian–early Devonian: the rise of the pteridophytes. *Phil. Trans. R. Soc. Lond. B*, **309**, 147–165.
- FAIRON-DEMARET, M. 1974. Nouveaux spécimens du genre *Leclercqia* Banks, H. P., Bonamo P. M. et Grierson, J. D. 1972, du Givétien (?) du Queensland (Australie). *Bull Inst. r. Sci. nat. Belg.* **50**, 1–4.

- FAIRON-DEMARET, M. and BANKS, H. P. 1978. Leaves of *Archaeosigillaria vanuxemii*, a Devonian lycopod from New York. *Am. Jl Bot.* **65**, 246–249.
- FRENGUELLI, J. 1954. Plantas Devonicas de la Quebrada de la Charnela en la Precordillera de San Juan. *Not. Mus. La Plata*, **17**, 359–376.
- GENSEL, P. G. and ANDREWS, H. N. 1984. *Plant life in the Devonian*, 381 pp. Praeger, New York.
- GOULD, R. E. 1975. The succession of Australian pre-Tertiary megafossil floras. *Bot. Rev.* **41**, 453–483.
- GRIERSON, J. D. and BANKS, H. P. 1963. Lycopods of the Devonian of New York State. *Palaeontogr. Am.* **4**, 220–295.
- — — 1983. A new genus of lycopods from the Devonian of New York State. *Bot. Jl Linn. Soc.* **86**, 81–101.
- GRINDLEY, G. W., MILDENHALL, D. C. and SCHOPF, J. M. 1980. A mid-late Devonian flora from the Ruppert Coast, Marie Byrd Land, West Antarctica. *Jl Roy. Soc. New Zealand*, **10**, 271–285.
- HECKEL, P. H. and WITZKE, B. J. 1979. Devonian world palaeogeography determined from distribution of carbonates and related lithic palaeoclimatic indicators. In HOUSE, M. R., SCRUTTON, C. T. and BASSETT, M. G. (eds.). *The Devonian System. Spec. Pap. Palaeont.* **23**, 99–123.
- KLITZSCH, E., LEJAL-NICOL, A. and MASSA D. 1973. Le Siluro-Dévonien à psilophytes et lycophytes du bassin de Mourzouk (Libye). *C.r. hebd. Séanc. Acad. Sci., Paris. Série D*, **277**, 2465–2467.
- KRÄUSEL, R. 1960. *Spongiphyton* nov. gen. (Thallophyta) e *Haplostigma* Seward (Pteridophyta) no Devoniano Inferior do Paraná. *Depart. Nac. Prod. Miner., Div. Geol. Miner., Monogr.* **15**, 1–41.
- — — and DOLIANITI, E. 1957. Restos vegetais das Camadas Picos, Devoniano Inferior do Piauí. *Minest. Agr. Dep. Nac. Prod. Miner. Div. Geol. Miner. Bull.* **173**, 7–19.
- — — and WEYLAND, W. 1949. Pflanzenreste aus dem Devon. XIV. *Gilboaphyton* und die Protolepidophytale. *Senckenbergiana*, **30**, 129–152.
- LECLERCQ, S. 1960. Réfendage d'une roche fossilifère et dégagement de ses fossiles sous binoculaire. *Senckenberg leth.* **41**, 483–487.
- LEJAL-NICOL, A. 1975. Sur une nouvelle flore à lycophytes du Dévonien inférieur de la Libye. *Palaeontographica*, **151B**, 52–96.
- LEMOIGNE, Y. and ISHCHENKO, T. 1980. Deux lycophytes avec structures conservées du Dévonien Supérieur d'Ukraine (U.R.S.S.). *Geobios*, **13**, 671–681.
- MENENDEZ, C. A. 1965a. *Archaeosigillaria conferta* (Frenguelli) nov. comb. del Devonico de la Quebrada de la Chavela, San Juan. *Ameghiniana*, **4**, 67–68.
- — — 1965b. *Drepanophycus eximius* (Frenguelli) nov. comb. del Devonico de la Quebrada de la Chavela, San Juan. *Ibid.* 139–140.
- REX, G. M. and CHALONER, W. G. 1983. The experimental formation of plant compression fossils. *Palaeontology*, **26**, 231–252.
- SAMPAIO, A. V. and NORTHFLEET, A. 1973. Estratigrafia e correlação das bacias sedimentares Brasileiras (abs.). *Congr. Bras. Geol.* **27**, 148.
- SCOTSESE, C. R. 1984. Palaeozoic palaeomagnetism and the assembly of Pangaea. In VAN DER VOO, R., SCOTSESE, C. R. and BONHOMMET, N. (eds.). *Plate reconstruction from Palaeozoic palaeomagnetism, Geodynamics series*, **12**, 1–10. American Geophysical Union, Washington, D.C.
- — — BAMBACH, R. K., BARTON, C., VAN DER VOO, R. and ZIEGLER, A. M. 1979. Paleozoic base maps. *Jl geol.* **87**, 217–277.
- SEWARD, A. C. and WALTON, J. 1923. On fossil plants from the Falkland Islands. *Q. Jl geol. Soc. Lond.* **79**, 313–333.
- SMITH, A. G., HURLEY, A. M. and BRIDEN, J. C. 1981. *Phanerozoic palaeocontinental world maps*, 102 pp. Cambridge University Press, Cambridge.
- SPICER, R. A. 1977. The pre-depositional formation of some leaf impressions. *Palaeontology*, **20**, 908–912.
- THOMAS, B. A. and PURDY, H. M. 1982. Additional fossil plants from the Drybrook Sandstone, Forest of Dean, Gloucestershire. *Bull. Br. Mus. Nat. Hist. (Geol.)* **36**, 131–142.

D. EDWARDS

Department of Plant Science
University College
Cardiff

J. L. BENEDETTO

Departamento de Geología
Universidad Nacional de Córdoba y CONICET
Argentina

Typescript received 3 December 1984

Revised typescript received 16 January 1985

NOTES FOR AUTHORS

The journal *Palaeontology* is devoted to the publication of papers on *all aspects* of palaeontology. Review articles are particularly welcome, and short papers can often be published rapidly. A high standard of illustration is a feature of the journal. Four parts are published each year and are sent free to all members of the Association. *Typescripts* should conform in style to those already published in this journal, and should be sent to Dr. D. E. G. BRIGGS, Department of Geology, Goldsmiths' College, University of London, Creek Road, London SE8 3BU, England, who will supply detailed instructions for authors on request (these were published in *Palaeontology* 1977, 20, pp. 921-929).

Special Papers in Palaeontology is a series of substantial separate works conforming to the style of *Palaeontology*.

SPECIAL PAPERS IN PALAEONTOLOGY

In addition to publishing *Palaeontology* the Association also publishes *Special Papers in Palaeontology*. Members may subscribe to this by writing to the Membership Treasurer: the subscription rate for 1985 is £33 (U.S. \$53) for Institutional Members, and £16.50 (U.S. \$27) for Ordinary and Student Members. A single copy of each *Special Paper* is available to Ordinary and Student Members *only*, for their personal use, at a discount of 25% below the listed prices. Non-members may obtain copies, but at the listed prices, from Marston Book Services, P.O. Box 87, Oxford OX4 1LB, England.

RECENT PALAEONTOLOGICAL ASSOCIATION PUBLICATIONS

Special Papers in Palaeontology

Numbers 1-19 are still in print and are available (post free) together with those listed below:

20. (for 1977): Fossil Priapulid Worms, by S. C. MORRIS. 155 pp., 99 text-figs., 30 plates. Price £16 (U.S. \$24).
21. (for 1978): Devonian Ammonoids from the Appalachians and their bearing on International Zonation and Correlation, by M. R. HOUSE. 70 pp., 12 text-figs., 10 plates. Price £12 (U.S. \$18).
22. (for 1978, published 1979): Curation of Palaeontological Collections. A joint Colloquium of the Palaeontological Association and Geological Curators Group. Edited by M. G. BASSETT. 279 pp., 53 text-figs. Price £25 (U.S. \$38).
23. (for 1979): The Devonian System. A Palaeontological Association International Symposium. Edited by M. R. HOUSE, C. T. SCRUTTON and M. G. BASSETT. 353 pp., 102 text-figs., 1 plate. Price £30 (U.S. \$45).
24. (for 1980): Dinoflagellate Cysts and Acritarchs from the Eocene of Southern England, by J. P. BUJAK, C. DOWNIE, G. L. EATON and G. L. WILLIAMS. 100 pp., 24 text-figs., 22 plates. Price £15 (U.S. \$23).
25. (for 1980): Stereom Microstructure of the Echinoid Test, by A. B. SMITH. 81 pp., 20 text-figs., 23 plates. Price £15 (U.S. \$23).
26. (for 1981): The Fine Structure of Graptolite Periderm, by P. R. CROWTHER. 119 pp., 37 text-figs., 20 plates. Price £25 (U.S. \$38).
27. (for 1981): Late Devonian Acritarchs from the Carnarvon Basin, Western Australia, by G. PLAYFORD and R. S. DRING. 78 pp., 10 text-figs., 19 plates. Price £15 (U.S. \$23).
28. (for 1982): The Mammal Fauna of the Early Middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset, by M. J. BISHOP. 108 pp., 47 text-figs., 6 plates. Price £25 (U.S. \$38).
29. (for 1982): Fossil Cichlid Fish of Africa, by J. A. H. VAN COUVERING. 103 pp., 35 text-figs., 10 plates. Price £30 (U.S. \$45).
30. (for 1983): Trilobites and other early Arthropods. Edited by D. E. G. BRIGGS and P. D. LANE. 276 pp., 64 text-figs., 38 plates. Price £40 (U.S. \$60).
31. (for 1984): Systematic palaeontology and stratigraphic distribution of ammonite faunas of the French Coniacian, by W. J. KENNEDY. 160 pp., 42 text-figs., 33 plates. Price £25 (U.S. \$38).
32. (for 1984): Autecology of Silurian organisms. Edited by M. G. BASSETT and J. D. LAWSON. 295 pp., 75 text-figs., 13 plates. Price £40 (U.S. \$60).

Field Guides to Fossils

1. (1983): Fossil Plants of the London Clay, by M. E. COLLINSON. 121 pp., 242 text-figs. Price £7.95 (U.S. \$12).

Other Publications

1982. Atlas of the Burgess Shale. Edited by S. C. MORRIS. 31 pp., 24 plates. Price £20 (U.S. \$44).

Palaeontology

VOLUME 28 · PART 3

CONTENTS

The origins and aerodynamics of flight in extinct vertebrates [<i>Palaeontology Review</i>]	
KEVIN PADIAN	413
The microstructure of tooth enamel in multituberculate mammals	
G. FOSSE, Z. KIELAN-JAWOROWSKA and S. G. SKAALE	435
Micropalaeontology of the Late Proterozoic Veteranen Group, Spitsbergen	
ANDREW H. KNOLL and KEENE SWETT	451
Lower Cretaceous inoceramid bivalves from the Antarctic Peninsula region	
J. A. CRAME	475
Coronate echinoderms from the Lower Palaeozoic of Britain	
STEPHEN K. DONOVAN and CHRISTOPHER R. C. PAUL	527
Cortical development in <i>Chaloneria cormosa</i> (Isoetales), and the biological derivation of compressed lycophyte decortication taxa	
KATHLEEN B. PIGG and GAR W. ROTHWELL	545
Wealden occurrence of an isolated Barremian dinocyst facies	
N. F. HUGHES and I. C. HARDING	555
A new genus of Carboniferous spiriferid brachiopod from Scotland	
MARIE LEGRAND-BLAIN	567
Ostracodes across the Iapetus Ocean	
ROGER E. L. SCHALLREUTER and DAVID J. SIVETER	577
Two new species of herbaceous lycopods from the Devonian of Venezuela with comments on their taphonomy	
D. EDWARDS and J. L. BENEDETTO	599

Palaeontology

VOLUME 28 · PART 4 NOVEMBER 1985



Published by

The Palaeontological Association · London

Price £21·50

THE PALAEONTOLOGICAL ASSOCIATION

The Association was founded in 1957 to promote research in palaeontology and its allied sciences.

COUNCIL 1985-1986

President: Professor C. DOWNIE, Department of Geology, University of Sheffield, Sheffield S1 3JD

Vice-Presidents: Dr. M. G. BASSETT, Department of Geology, National Museum of Wales, Cardiff CF1 3NP
Dr. R. RIDING, Department of Geology, University College, Cardiff CF1 1XL

Treasurer: Dr. M. ROMANO, Department of Geology, University of Sheffield, Sheffield S1 3JD

Membership Treasurer: Dr. A. T. THOMAS, Department of Geological Sciences, University of Aston, Birmingham B4 7ET

Institutional Membership Treasurer: Dr. A. R. LORD, Department of Geology, University College, London WC1E 6BT

Secretary: Dr. P. W. SKELTON, Department of Earth Sciences, Open University, Milton Keynes MK7 6AA

Circular Reporter: Dr. D. J. SIVETER, Department of Geology, University of Hull, Hull HU6 7RX

Marketing Manager: Dr. R. J. ALDRIDGE, Department of Geology, University of Nottingham, Nottingham NG7 2RD

Editors

Dr. D. E. G. BRIGGS, Department of Geology, University of Bristol, Bristol BS8 1RJ

Dr. P. R. CROWTHER, Leicestershire Museums Service, Leicester LE1 6TD

Dr. D. EDWARDS, Department of Plant Science, University College, Cardiff CF1 1XL

Dr. L. B. HALSTEAD, Department of Geology, University of Reading, Reading RG6 2AB

Dr. R. HARLAND, British Geological Survey, Keyworth, Nottingham NG12 5GG

Dr. T. J. PALMER, Department of Geology, University College of Wales, Aberystwyth SY23 2AX

Other Members

Dr. M. J. BENTON, Belfast

Dr. C. R. C. PAUL, Liverpool

Dr. M. E. COLLINSON, London

Dr. A. B. SMITH, London

Dr. P. L. FOREY, London

Professor T. N. TAYLOR, Columbus

Dr. A. W. OWEN, Dundee

Overseas Representatives

Australia: Professor B. D. WEBBY, Department of Geology, The University, Sydney, N.S.W., 2006

Canada: Dr. B. S. NORFORD, Institute of Sedimentary and Petroleum Geology, 3303-33rd Street NW., Calgary, Alberta

Japan: Dr. I. HAYAMI, University Museum, University of Tokyo, Hongo 7-3-1, Bunkyo-Ku, Tokyo

New Zealand: Dr. G. R. STEVENS, New Zealand Geological Survey, P.O. Box 30368, Lower Hutt

U.S.A.: Dr. R. CUFFEY, Department of Geology, Pennsylvania State University, Pennsylvania

Professor A. J. ROWELL, Department of Geology, University of Kansas, Lawrence, Kansas 66045

Professor N. M. SAVAGE, Department of Geology, University of Oregon, Eugene, Oregon 97403

South America: Dr. O. A. REIG, Departamento de Ecología, Universidad Simón Bolívar, Caracas 108. Venezuela

MEMBERSHIP

Membership is open to individuals and institutions on payment of the appropriate annual subscription. Rates for 1985 are:

Institutional membership	£45.00 (U.S. \$68)
Ordinary membership	£21.00 (U.S. \$32)
Student membership	£11.50 (U.S. \$18)
Retired membership	£10.50 (U.S. \$16)

There is no admission fee. Correspondence concerned with Institutional Membership should be addressed to **Dr. A. R. Lord, Department of Geology, University College, Gower Street, London WC1E 6BT, England.** Student members are persons receiving full-time instruction at educational institutions recognized by the Council. On first applying for membership, an application form should be obtained from the Membership Treasurer, **Dr. A. T. Thomas, Department of Geological Sciences, University of Aston, Aston Triangle, Birmingham B4 7ET.** Subscriptions cover one calendar year and are due each January; they should be sent to the Membership Treasurer. All members who join for 1985 will receive *Palaeontology*, Volume 28, Parts 1-4. All back numbers are still in print and may be ordered from Marston Book Services, P.O. Box 87, Oxford OX4 1LB, England, at £21.50 (U.S. \$33) per part (post free).

Cover: The dinoflagellate cyst *Impagidinium patulum* (Wall) Stover and Evitt from bottom sediments in the North Atlantic Ocean. British Geological Survey specimen MPK 4234. $\times 2500$.

XIPHOSURID BURROWS FROM THE LOWER COAL MEASURES (WESTPHALIAN A) OF WEST YORKSHIRE

by J. I. CHISHOLM

ABSTRACT. Bilobate burrows lying parallel to bedding are described from a shallow-water sandstone. The burrows are linked to structures produced by oblique movement through the sediment, the outlines of these suggesting that the animal responsible was a xiphosurid, perhaps *Bellinurus*. The internal structure of the burrows shows transverse markings on either side of a median furrow but the external surfaces are poorly preserved and it is uncertain to which of the existing bilobate ichnogenera the trace fossil belongs. It is provisionally referred to *Aulichnites* Fenton and Fenton, 1937 as *Aulichnites? bradfordensis* ichnosp. nov.

TRACE fossils attributed to limulid movements are known from many parts of the geological column but the majority of those described are walking (or half-swimming) traces (*Kouphichnium* Nopsca; see Häntzschel 1975, p. W75), or are resting traces (*Limulicubichnus* Miller, 1982). Records of these in the Silesian rocks of the central Pennines are summarized by Eagar *et al.* (1985). Limulid burrowing traces have been described less commonly, which is surprising in view of the known burrowing habits of Recent *Limulus*; the structures described here are thought to have been produced by this process.

GEOLOGICAL SETTING

The trace fossils were found at Bolton Wood Quarries (British National Grid Reference SE 162 366) in Bradford, West Yorkshire. Some of the burrows were found in place, distributed sparsely through some 1·2 m of fine-grained sandstone exposed in the north-western part of the quarry but the best-preserved material, including the holotype, was found in slabs lying loose at the foot of this face.

The following section was visible in 1983:

Top of section at SE 1627 3660	thickness (metres)
8. Coal, interlaminated with black mudstone.	0·0·05
7. Alternations of grey striped siltstone and ripple-laminated sandstone; rooty top.	4·80
6. Sandstone, fine and very fine-grained, mainly trough cross-bedded in sets up to about 1·0 m thick, with palaeocurrent flow to east-south-east; some mudstone clasts and tree trunks; some ripple- and parallel-laminated bands. Uneven erosive base.	13·50
5. Siltstone, striped, draped over eroded surface of bed below.	0·0·20
4. Sandstone, fine and very fine-grained, with low-angle wedge-bedding; <i>Arenicolites carbonarius</i> (Binney) sparsely present in top few cm of some beds.	1·70
3. Siltstone, striped, argillaceous.	3·90
2. Sandstone, fine and very fine-grained, with low-angle wedge bedding.	1·80
1. Sandstone, fine and very fine-grained; ripple lamination and parallel lamination alternating in bands 0·06 to 2·26 m thick; parting lineation and rib and furrow structures indicate consistent palaeocurrent flow to west; <i>Aulichnites? bradfordensis</i> ichnosp. nov. sparsely distributed through the top 1·20 m.	7·00

Base of section at SE 1605 3643.

The section is similar to one recorded at the quarries by Stephens *et al.* (1953, pp. 84–85). These authors identified the sandstone (beds 1–6 of the section detailed above) as the Gaisby Rock, which was formerly quarried at Gaisby, some 500 m to the north-west of Bolton Wood Quarries. They regarded the Gaisby Rock (*ibid.*, pp. 75–76) as a locally thickened representative of a thin sandstone known in the Bradford area as the 80-Yard Rock, but a more likely correlation has been put forward by C. G. Godwin (pers. comm.). He points out that the Gaisby Rock is about the same thickness as the ‘main lower leaf’ of the Elland Flags (terms defined by Godwin 1984, fig. 1), and in the absence of indications to the contrary, he prefers to correlate the two, as no local variations in thickness are thereby implied. This correlation is accepted here, with the implication that the Gaisby Rock lies about 30 m higher in the sequence than is indicated by Stephens *et al.* (1953, p. 70). On either correlation, the section lies within the lower half of Westphalian A.

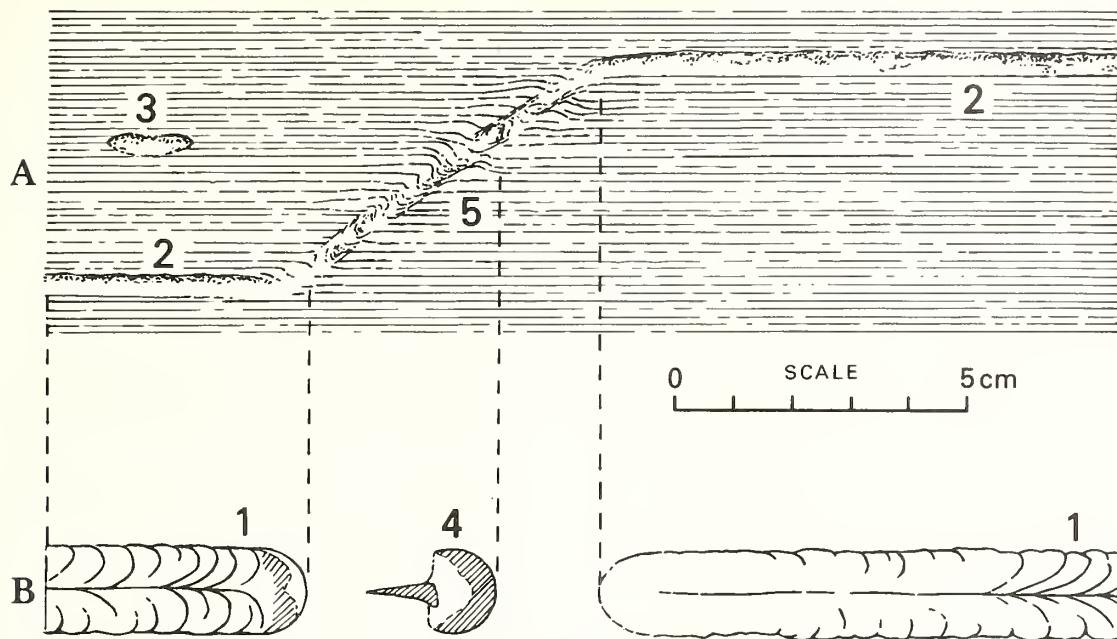
The Coal Measures of the Pennine region are of fluvial or fluvio-deltaic origin (Elliott 1969; Haszeldine and Anderton 1980) and in this context bed 6, the thick, cross-bedded sandstone with tree trunks and mudstone pebbles, is likely to represent a river or distributary channel deposit. The origin of beds 1–5 is less certain, though their position beneath the channel deposit suggests that they may represent a set of crevasse-splay, mouth-bar and barrier-beach sediments. Whether all of these environments are present here, or only some of them, cannot be determined from the limited exposures available. The presence of *Arenicolites carbonarius* suggests that the environment was non-marine (Hardy 1970b, p. 9).

DESCRIPTION OF TRACE FOSSILS

Most of the specimens were collected from the top few centimetres of a loose slab measuring about 6 square metres in surface area. Others were obtained from smaller slabs. The traces were also found in place but only a few of these could be collected, due to the hardness of the rock. The way-up of the loose material was determined by comparison with that obtained *in situ*. All the traces are full reliefs (endichnia), preserved entirely within the sandstone; there are no epireliefes or hyporeliefes. Cut sections suggest that all were produced within the sediment and that no traces formed at the sediment/water interface have been preserved. The structures are of two kinds, about equal in abundance, with a few connected examples that prove their common origin; they are distinguished as ‘oblique penetration structures’ and ‘horizontal burrows’. An idealized reconstruction of the trace fossils is shown in Text-fig. 1.

Oblique penetration structures. These are bedding disturbances, irregularly shaped or roughly quadrangular as seen from above (Pl. 75, figs. 3, 5, 10; Pl. 76, figs. 1, 3) and measuring 10–25 mm in width by 10–35 mm in length. The average width (22 examples) is 15 mm. A section cut across the width of one example (Pl. 75, fig. 6) shows irregular distortion of dark bedding-laminae within an ill-defined biconvex area of disturbance. Side views (Pl. 75, figs. 1, 2, 4, 9) show that most of the disturbances extend obliquely through the sediment at angles of about 35° from the horizontal; a few are steeper. The greatest thickness of sediment penetrated in this way is 30 mm, but the specimen concerned is incomplete both at top and base. When a specimen is split along the bedding, roughly similar quadrangular shapes appear at all levels in the structure. In two of the specimens (Pl. 75, figs. 3, 5) the outline is hoof-shaped or lunate with a pointed projection at the centre of the concave side: strong evidence for a xiphosurid origin. In one of these specimens the lamination bulges upwards at the convex (head) end and downwards at the pointed (tail) end, but in the other is depressed throughout. A few other specimens show signs of the ‘xiphosurid’ shape, the asymmetry of which enables the forward end to be distinguished from the rear. Cut sections of these oriented examples show that more of them were formed by upward movement through the sand than by downward movement.

Horizontal burrows. The burrows are ribbon-like structures, flattened parallel to the bedding. They are straight or variably curved, and incomplete lengths up to 250 mm are present. In width they range



TEXT-FIG. 1. Idealized diagram to show structure of *Aulichnites?* *bradfordensis* in side view (A) and on bedding planes viewed from above (B). Movement of animal from left to right. Horizontal burrows are shown on bedding planes (1), in lengthwise section (2), and in cross-section (3). Oblique upward penetration structure shown on bedding (4) and in lengthwise section (5).

from 10 to 19 mm, the majority being about 15 mm across, and the thickness of most examples lies between 2 and 4 mm; a single specimen is 7 mm thick. The more complete burrows pass at one or both ends into oblique penetration structures and the outline of these can be used (as described above) to determine the direction of movement. The anterior end in such cases tends to have a sharp, convex outline whereas the posterior end is more vague (Pl. 75, figs. 7, 8; Pl. 76, figs. 1, 5).

The outer surfaces of the burrows do not separate cleanly from the matrix and so cannot be observed directly; all the specimens have split through the middle, revealing the internal structure. Cross-sections suggest that both the upper and lower surfaces are generally ill defined, but that the upper are in some cases vaguely bilobate, with a faint median furrow, whereas the lower tend to be flat or unilobate. The sediment inside the burrows shows a disturbed texture in which dark flaky grains of mica and carbon have been reoriented from their original position parallel to bedding, and have also been concentrated at the top of the burrow (Pl. 76, fig. 2). In many specimens the disturbed material, as seen on bedding surfaces, shows a bilobate pattern, with a well-marked median groove and less regular lateral grooves (Pl. 76, figs. 1, 3, 4). Transverse markings, often arranged in a chevron pattern, are present in parts of some specimens (Pl. 76, figs. 1, 3); in the best preserved examples the chevrons open towards the anterior (Pl. 76, fig. 1). In one specimen (GSL 1839) the transverse lines are seen to mark the ends of faint laminae in the burrow fill, but details of this texture are not clear.

INTERPRETATION OF TRACE FOSSILS

The hoof-shaped outlines of some of the penetration structures (Pl. 75, figs. 3, 5) compare well with the shapes produced in soft sediment by juveniles of the Recent horseshoe crab, *Limulus polyphemus* (Caster 1938, pl. 12; Miller 1982, fig. 3), and are good evidence for the xiphosurid origin of the whole burrow assemblage. Burrowing is a normal activity of *L. polyphemus* (Caster 1938,

pp. 17–19; Vosatka 1970) and is thought to have been a characteristic feature of xiphosurid behaviour since Ordovician times (Bergström 1975, p. 301). The initial burrowing movements of juvenile *L. polyphemus* have been described by Vosatka (1970, p. 283) and by Eldredge (1970). The sediment is excavated and displaced by the limbs while the prosoma is pushed forwards and downwards into the sediment by flexing movements of the body. The processes involved in continuous burrowing have not been described in detail, however, but are supposed by Caster (1938, p. 19) to involve a combination of leg and tail movements with the ploughing action of the headshield. The deformation produced in the sediment by burrowing was not described by any of these authors, so that the interpretation of the Bradford burrows is necessarily conjectural.

The median groove of the burrow-fill was probably made by the telson, the straightness of the groove indicating that it did not lash from side to side during burrowing but probably was pressed downwards against the sediment or trailed passively. The internal structure of the burrows is interpreted as a back-fill texture. It roughly reflects the outline of the rear of the animal (Pl. 75, fig. 7; Pl. 76, fig. 1), so was probably produced by repeated backward pressure against the sediment that had been displaced and passed back under the animal by the action of the limbs. The marginal furrows were probably produced by the outer margins of the prosoma and the average width of the burrows, 15 mm, is therefore a measure of the width of this feature.

The penetration structures are not regarded as escape-traces from rapid sedimentation or erosion, because rising and descending structures are present in the same few centimetres of sandstone; it is more likely that oblique movements were part of normal burrowing behaviour. This conclusion is consistent with the lack of any preferred orientation of burrows or penetration structures relative to the current direction shown by parting lineation (Pl. 76, fig. 1) and ripple lamination. The assemblage is thought more likely to have resulted from scavenging for food than from concealment or resting, these types of behaviour being more probably represented by the closely related trace fossil *Limulicubichnus rossendalensis* (Hardy, 1970).

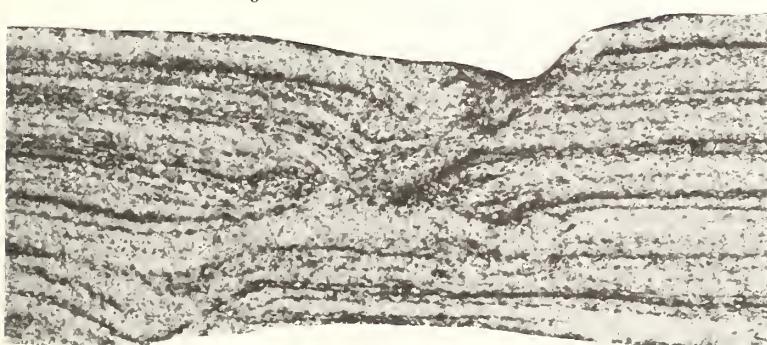
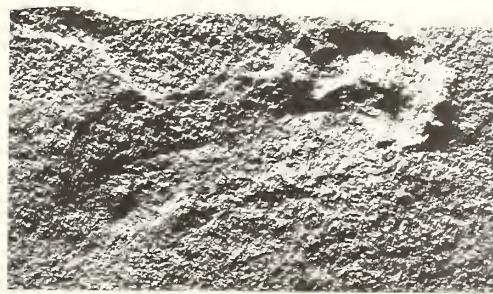
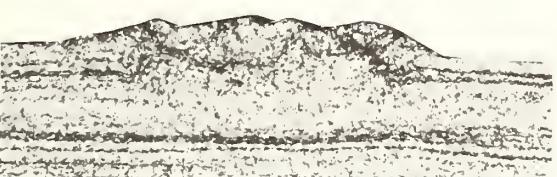
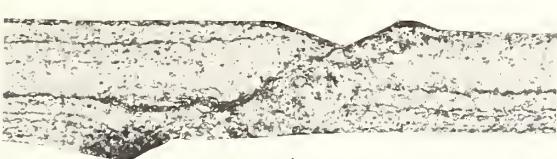
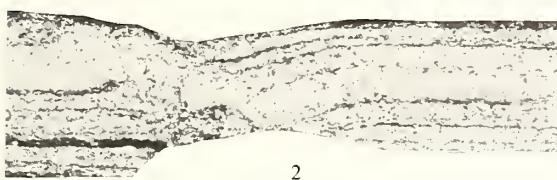
Of the two genera of xiphosurids known to occur in Upper Carboniferous sediments of the region, *Bellinurus* and *Euproops* (Calver 1968, pp. 159–160), the former is thought to have lived in open-water habitats, whereas the latter probably lived in the coal swamps (van der Heide 1951, pp. 63–65); *E. danae* may even have been able to live on subaerial vegetation (Fisher 1979). *Bellinurus* is thus more likely to have produced the burrows described here, which occur in fluvial crevasse-splay or delta-front sandstones.

DISCUSSION

Burrows that can be regarded as incomplete examples of *Aulichnites? bradfordensis* have been found at other localities in the Upper Carboniferous of the Pennine region. One specimen (British Geological Survey, Palaeontology Collection, Keyworth, JIC 1259–60) was found by the author in loose blocks of fine-grained, micaceous, parallel-laminated sandstone at Catlow Quarry, Lancashire (grid reference SD 8873 3676). The quarry is in the Dyneley Knoll Flags (Earp *et al.* 1961, p. 137), which lie at about the same stratigraphical level as the Elland Flags (Wray 1929, p. 272). The burrow

EXPLANATION OF PLATE 75

Figs. 1–10. *Aulichnites? bradfordensis*, ichnosp. nov. 1, 2, 4, 9. Oblique penetration structures, vertical sections cut parallel to direction to travel; note variable nature of lamination disturbance but consistency of angle at which sediment was penetrated. British Geological Survey, Palaeontology Collection, Keyworth: GSL 1844, 1845^A, 1845, 1836, all $\times 2$. 3 and 5. Oblique penetration structures showing 'xiphosurid' outline; view from above, light from top left. 3, paratype, GSL 1832, $\times 2$; 5, GSL 1846, $\times 1$. 6. Oblique penetration structure, section across width. GSL 1843^A, $\times 2$. 7 and 8. Horizontal burrows, view from above, light from top centre. Bilobate pattern; 'head' at right. 7, GSL 1834, $\times 1$; 8, GSL 1830, $\times 1$ (*in situ* specimen). 10. Oblique penetration structure, view from above, light from top left. GSL 1842, $\times 1$.



CHISHOLM, *Aulichnites?* *bradfordensis*

is preserved on a bedding plane as an internal section 12 mm broad by 60 mm long, with a well-marked median furrow but only faint transverse markings. The anterior end has a sharp semi-circular outline, whereas the posterior end fades off more gradually. *L. rossendalensis* is common as hypichnial mounds on blocks in the same quarry. Another example (University of Manchester, Department of Geology Collection, MGSF 95), collected by Dr J. E. Pollard from the Milnrow Sandstone (equivalent of the 80-Yard Rock) at Sycamore Quarry, Kerridge, Cheshire (SJ 940 766), is about 22 mm wide, with curved transverse chevron markings and a median furrow, and follows a gently curved course, with one sharper bend, for a distance of about 30 cm. The traces described from sandy siltstones above the Butterly Marine Band at Standedge, West Yorkshire, by Eagar *et al.* (1983, p. 298) under the provisional name '*Scolicia*', are also similar in many ways to *A.? bradfordensis*, being endichnial burrows flattened parallel to bedding, with bilobate structure and a pattern of transverse markings in places. The maximum width of the burrows is about the same as that of the Bradford traces, but no 'xiphosurid' outlines are associated. The Standedge traces are somewhat older (Kinderscoutian) than those from Bradford but they likewise occur in sediments laid down in a river mouth or interdistributary bay environment (Eagar *et al.* 1983, pp. 287–288). They are thought to have been produced by small arthropods which, in view of the similarities with *A.? bradfordensis*, may well have been xiphosurids. Some bilobed traces from the Grassington Grit (Pendleian) of West Yorkshire were referred by Eagar *et al.* (1985, pl. 1E, F) to cf. *Aulichnites*. They are more sinuous than any so far mentioned and more closely resemble *A. parkerensis*; they appear to be burrows but their greater sinuosity suggests that they were made by a different arthropod.

Three different aspects of xiphosurid behaviour have now been identified as trace fossils in Upper Carboniferous sediments of the Pennine region. Resting, alternating with short forward movements, is represented by *L. rossendalensis* (Hardy 1970a, b), walking and half-swimming movements by *Kouphichnium* aff. *variabilis* (Chisholm 1983), and burrowing movements by *A.? bradfordensis*. The outlines of *L. rossendalensis* and *A.? bradfordensis* are very similar in shape and size, suggesting that they were made by the same animal. All the traces were probably produced by members of the genus *Bellinurus* (Hardy 1970a; Chisholm 1983; and above). Bilobate burrows showing a more sinuous pattern may have been produced by other arthropods.

SYSTEMATIC PALAEONTOLOGY

Ichnogenus AULICHNITES Fenton and Fenton, 1937

Remarks. The type species, *A. parkerensis* Fenton and Fenton, 1937, is a bilobate burrow consisting of an epichnial ridge 5 to 11·4 mm wide with a strong median furrow. The burrow filling is of sand in oval layers which are concave anteriorly and convex upwards (Fenton and Fenton 1937, pp. 1079–1080). An examination of the holotype by Hakes (1977, p. 218) has shown that the undersurface is unilobate and convex downwards, the depth below the median furrow being about 3 mm.

EXPLANATION OF PLATE 76

Figs. 1–5. *Aulichnites?* *bradfordensis*, ichnosp. nov. 1. Horizontal burrow; 'head' at right, chevron ornament at left. Penetration structures and a second burrow also visible. View from above, light from top centre. Holotype, GSL 1831, $\times \frac{1}{2}$. 2. Horizontal burrow, side view of lengthwise section showing disturbed texture and local concentration of dark material towards top. Undisturbed lamination in lower half of specimen. GSL 1837, $\times 2$. 3. Horizontal burrow showing bilobate structure and ornament; penetration structures also present. View from above, light from top centre. Paratype, GSL 1833, $\times \frac{1}{2}$. 4. Horizontal burrow showing irregular bilobate pattern. View from below, light from left. GSL 1835, $\times \frac{1}{2}$. 5. Horizontal burrow with sinuous shape; 'head' end at right. View from below, light from top centre. Paratype, GSL 1832, $\times 1$.



1



2



3



5



4

CHISHOLM, *Aulichnites?* *bradfordensis*

Aulichuites? *bradfordeusis* ichnosp. nov.

Plates 75 and 76; text-fig. 1

- 1976 ?*Gyrochorte*, Hakes, p. 26; pl. 5, fig. 4.
1977 ?*Aulichnites* sp., Hakes, p. 218; pl. 1b.
1983 'Scolicia', Eagar *et al.*, p. 298; pl. 24A-C.

Derivation of name. From the city of Bradford, where the trace fossils were found.

Holotype. British Geological Survey, Palaeontology Collection, Keyworth, Nottingham, GSL 1831.

Paratypes. GSL 1832-1834.

Type locality. Bolton Wood Quarries, Bradford, Yorkshire.

Horizon. Gaisby Rock (but see above); age Westphalian A.

Occurrence. Sparsely in fine-grained sandstone, about 22 m below top of Gaisby Rock.

Diagnosis. Horizontal bilobate burrows linked to obliquely rising or descending traces, some of which have a hoof-shaped outline in plan view. The bilobate burrows are straight or variously curved with a median furrow and variable transverse markings, chevron-shaped in places. The width is generally about 15 mm.

Description. A detailed description of the two main elements, oblique penetration structures and horizontal burrows, is given on pp. 620-621.

Remarks. The 'xiphosurid' outline of the best-preserved penetration structures (Pl. 75, figs. 3, 5) closely resembles, both in size and shape, that of the resting trace *L. rossendalensis* described by Hardy (1970a) from an Upper Carboniferous sandstone in Lancashire, but it would be inappropriate to apply this name to the Bradford structures since these are extensive burrow systems, not short resting traces.

All burrows collected are full-reliefs made up of material disturbed by the passage of the animal. The majority are preserved on parting surfaces parallel to bedding as upwardly convex bilobate ridges and show internal structure rather than the ornament of the top surface. Most bilobate ichnogenera are based on material preserved as epirelief or hyporelief rather than as full-reliefs, so the choice of a suitable name is not straightforward; however, the evidence of cross-sections shows that the structures are closer to epirelief than to hyporelief, in that the upper surfaces are in places convex and vaguely bilobate, whereas the lower surfaces are poorly defined and appear to be unilobate or flat. Of the bilobate epirelief ichnogenera *Halopoa*, *Scolicia*, *Gyrochorte*, and *Aulichnites*, the first is considered unsuitable because it has an irregular surface ornament, not notably transverse, and is only bilobate in places (Martinsson 1965, figs. 29-32). The name 'Scolicia' has been used for trails or burrows of a broadly similar nature from Upper Carboniferous sandstones elsewhere in the Pennine region (Eagar *et al.* 1983, p. 298), but is not used here because most examples of *Scolicia* (and its synonyms) illustrated by Häntzschel (1975, p. W107) show surface patterns or internal structures more complex than those of the Bradford burrows. *Gyrochorte* has a simple, plaited pattern on the bilobate upper surface but the depth of the structure can be greater than its width and Heinberg (1973) has suggested that the trace was made by a worm-like animal burrowing obliquely through the sediment. Because of these differences of structure and interpretation, *Gyrochorte* is considered less appropriate than *Aulichuites*, an ichnogenus with a similar surface pattern but in which the width of the burrow is greater than the depth (Fenton and Fenton 1937, pl. 1, fig. 1; Hakes 1977, p. 218).

The new trace fossil is only tentatively assigned to *Aulichuites* in view of the uncertain nature of the outer surfaces, which in the type ichnospecies, *A. parkerensis*, are bilobate above and unilobate below (Hakes 1977, p. 218). These uncertainties apart, it is clearly different from *A. parkerensis* in several notable respects. First, it is linked to hoof-shaped structures; secondly, the pattern of transverse

markings is much less regular, and less consistently present, than in *A. parkerensis*; thirdly, where the transverse markings are chevron-shaped these open towards the anterior rather than to the posterior; and fourthly, the chevrons meet the centre line at a more acute angle.

Acknowledgements. I would like to thank Mr C. G. Godwin for clarification of his views on the sequence in the Bradford area, and Dr J. E. Pollard for many useful comments on a draft manuscript. The paper is published with the approval of the Director, British Geological Survey (N.E.R.C.).

REFERENCES

- BERGSTRÖM, J. 1975. Functional morphology and evolution of xiphosurids. *Fossils and Strata*, **4**, 291–305.
- CALVER, M. A. 1968. Coal Measures invertebrate faunas. In MURCHISON, D. G. and WESTOLL, T. S. (eds.), *Coal and coal-bearing strata*, 147–177. Oliver and Boyd, Edinburgh and London.
- CASTER, K. E. 1938. A restudy of the tracks of *Paramphibius*. *J. Paleont.* **12**, 3–60.
- CHISHOLM, J. I. 1983. Xiphosurid traces, *Kouphichnium aff. variabilis* (Linck), from the Namurian Upper Haslingden Flags of Whitworth, Lancashire. *Rep. Inst. Geol. Sci.*, No. **83/10**, 37–44.
- EAGAR, R. M. C., OKOLO, S. A. and WALTERS, G. F. 1983. Trace fossils as evidence in the evolution of *Carbonicola*. *Proc. Yorks. geol. Soc.* **44**, 283–303.
- BAINES, J. G., COLLINSON, J. D., HARDY, P. G., OKOLO, S. A. and POLLARD, J. E. 1985. Trace fossil assemblages and their occurrence in Silesian (mid-Carboniferous) deltaic sediments of the Central Pennine Basin, England. In CURRAN, H. A. (ed.), *Biogenic structures; their use in interpreting depositional environments*. Special Publication, SEPM.
- EARP, J. R., MAGRAW, D., POOLE, E. G., LAND, D. H. and WHITEMAN, A. J. 1961. *Geology of the country around Clitheroe and Nelson*, ix + 346 pp. Mem. Geol. Surv. U.K.
- ELDREDGE, N. 1970. Observations on burrowing behaviour in *Limulus polyphemus* (Chelicerata, Merostomata), with implications on the functional anatomy of trilobites. *Am. Mus. Novitates*, **2436**, 1–17.
- ELLIOTT, R. E. 1969. Deltaic processes and episodes: the interpretation of productive coal measures occurring in the East Midlands, Great Britain. *Mercian Geol.* **3**, 111–135.
- FENTON, C. L. and FENTON, M. A. 1937. Burrows and trails from Pennsylvanian rocks of Texas. *Am. Midl. Nat.* **18**, 1079–84.
- FISHER, D. C. 1979. Evidence for subaerial activity of *Euproops donae* (Merostomata, Xiphosurida). In NITECKI, M. H. (ed.), *Mazon Creek Fossils*, 379–447. Academic Press, New York, San Francisco and London, xv + 581 pp.
- GODWIN, C. G. 1984. Mining in the Elland Flags: a forgotten Yorkshire industry. *Rep. Br. Geol. Surv.* **16** (4), 17 pp.
- HAKES, W. G. 1976. Trace fossils and depositional environment of four clastic units, Upper Pennsylvanian megacycloths, northeast Kansas. *Paleont. Contr. Univ. Kans.*, Article 63, 1–46.
- 1977. Trace fossils in late Pennsylvanian cycloths, Kansas. In CRIMES, T. P. and HARPER, J. C. (eds.), *Trace fossils 2*. Geol. J. Special Issue No. 9, 209–226.
- HÄNTZSCHEL, W. 1975. In TEICHERT, C. (ed.), *Treatise on Invertebrate Paleontology*. Part W: *Miscellanea*. Supplement 1, W1–269. Geol. Soc. Amer. and Univ. Kansas Press.
- HARDY, P. G. 1970a. Xiphosurid trails from the Upper Carboniferous of northern England. *Palaeontology*, **13**, 188–190.
- 1970b. Aspects of palaeoecology in the arenaceous sediments of Upper Carboniferous age in the area around Manchester. Ph.D. thesis (unpubl.), University of Manchester.
- HASZELDINE, R. S. and ANDERTON, R. 1980. A braidplain facies model for the Westphalian B Coal Measures of north-east England. *Nature, Lond.* **284**, 51–53.
- HEINBERG, C. 1973. The internal structure of the trace fossils *Gyrochorte* and *Curvolithus*. *Lethaia*, **6**, 227–238.
- MARTINSSON, A. 1965. Aspects of a Middle Cambrian thanatotope on Öland. *Geol. För. Stockh. Förh.* **87**, 181–230.
- MILLER, M. F. 1982. *Limulicubichnus*: a new ichnogenus of limulid resting traces. *J. Paleont.* **56**, 429–433.
- STEPHENS, J. V., MITCHELL, G. H. and EDWARDS, W. 1953. *Geology of the country between Bradford and Skipton*, vii + 180 pp. Mem. Geol. Surv. U.K.

- VAN DER HEIDE, S. 1951. Les arthropodes du terrain houiller du Limbourg méridional. *Meded. geol. Sticht. (C) IV*, No. 5, 1-84.
- VOSATKA, E. D. 1970. Observations on the swimming, righting and burrowing movements of young horseshoe crabs, *Limulus polyphemus*. *Ohio J. Sci.* **70**, 276-283.
- WRAY, D. A. 1929. The Carboniferous succession in the central Pennine area. *Proc. Yorks. geol. Soc.* **21**, 228-287.

J. I. CHISHOLM

British Geological Survey
Murchison House
West Mains Road
Edinburgh EH9 3LA

Typescript received 27 July 1984

Revised typescript received 18 February 1985

EARLY CRETACEOUS *ISOCRINUS* FROM NORTHEAST JAPAN

by TATSUO OJI

ABSTRACT. Two species of *Isocrinus*, one of which is new (*Isocrinus (Chladocrinus) hanaii* sp. nov.), are described from the upper Aptian of the Miyako Group, Northeast Japan. The skeletons of *I. (C.) hanaii* are preserved intact at several localities, so it is presumed that they were rapidly buried either alive or shortly after death, the animals having lived on a sandy bottom in agitated water. In contrast to the relatively deep-water occurrence of modern isocrinids (mostly 200–1000 m), those from Miyako lived in shallow water, indicating that certain stalked crinoids persisted at shallow depths until mid-Cretaceous times. They were among the last isocrinids to have lived in an almost predator-free environment. Soon afterwards, a diversification of predatory teleostean fish was reflected in the contemporaneous appearance of new types of isocrinids.

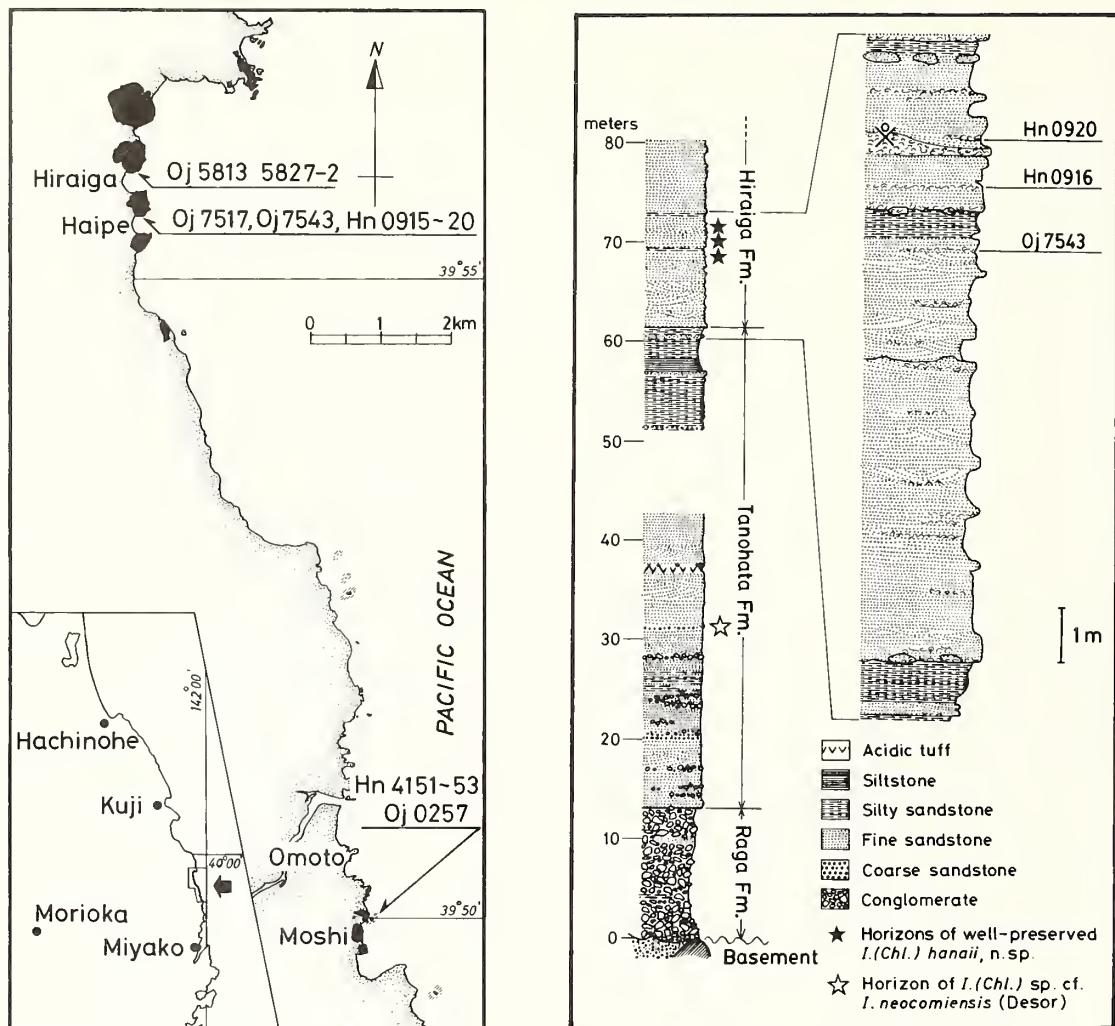
VARIOUS marine invertebrates are known from the Lower Cretaceous Miyako Group in Northeast Japan; crinoids are among the most common, yet they remain undescribed and have even been ignored in some faunal lists. This study presents systematic descriptions of two species of elegantly preserved isocrinids and discusses the implications of their occurrence with respect to changes in the bathymetric distribution of isocrinids through the Mesozoic and the Cainozoic. They are the first crinoids to be described from the Cretaceous of Japan.

The pioneer work on the stratigraphy of the Miyako Group by Yabe and Yehara (1913) recorded the occurrence of excellently preserved crinoids which were identified as *Pentacrinus*. In the late 1940s, T. Hanai carried out detailed field surveys and excavated fine specimens of crinoids, including nearly complete crowns. R. C. Moore examined these specimens during a visit to Japan and suggested their assignment to *Isocrinus*. Since then, crinoids from the Miyako Group have been cited or listed as a species of *Isocrinus* (e.g. Kobayashi *et al.* 1954; Tamura 1982). Excavations by Hanai and his coworkers in the 1960s led to the discovery of additional material. The present study is based mostly on this material, together with material newly collected by the author.

The Miyako Group ranges from the upper Aptian to the lower Albian. Except for the lowest unit (Raga Formation) the Miyako Group is characterized by rich marine faunas which include a variety of bivalves, gastropods, ammonites, and encrusting organisms such as hermatypic corals and calcareous algae. At present, seventy species of bivalves (Hayami 1975), eighty-seven species of gastropods (Kase 1984), and approximately sixty species of cephalopods (Obata and Matsumoto 1977) have been recorded. These fossils indicate a shallow, open marine environment in a warm climate (Hanai *et al.* 1968). Recently discovered fossil beachrock indicates an ancient strand line and further substantiates the dominance of a tropical or subtropical climate (Hanai and Oji 1981).

Isocrinids occur abundantly in almost all the shallow marine strata of the Miyako Group. They normally occur as disarticulated segments of stem and cirri, as is usually the case with fossil crinoids, either associated with other marine fauna or scattered throughout the sediments. At a few localities, however, unusually well-preserved specimens of *Isocrinus* occur commonly with their arms spread on bedding planes. In addition to their palaeontological significance, such exceptional modes of occurrence also give an indication of the nature of the sedimentary environment.

The crinoid fauna of the Miyako Group is of low diversity despite the abundance of specimens, and contains only a few species of isocrinids and one species of comatulid; only two isocrinid species are represented by sufficient material for description.



TEXT-FIG. 1 (left). Location of the collecting localities and distribution of the Miyako Group (black), Northeast Japan.

TEXT-FIG. 2 (right). Columnar section of the Miyako Group along the northern coast of Haipe, showing horizons of collecting sites (left, whole section; right, partly enlarged).

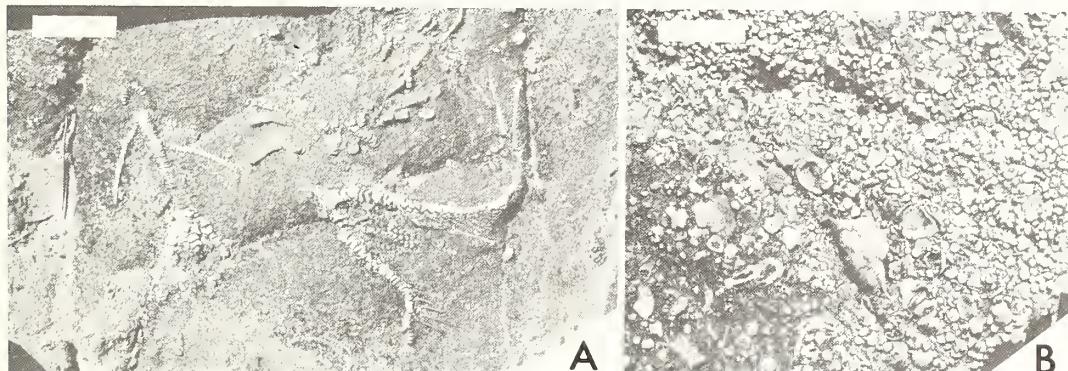
OCCURRENCE AND SEDIMENTARY ENVIRONMENT

Isocrinus (Chladocrinus) hanaii sp. nov.

Specimens are from the lower part of the Hiraiga Formation (uppermost Aptian) in the Tanohata and Moshi areas (text-fig. 1). In the Tanohata area, almost completely preserved specimens occur in several restricted layers approximately 10 m above the base of the Hiraiga Formation (Locs. Oj 7543, Hn 0915, Hn 0916, Hn 0920) along the northern coast of Haipe (text-fig. 2). At these localities a calcareous fine-grained sandstone with large-scale cross-stratification contains abundant bivalves, gastropods, annelid tubes, and fragmented ossicles of *I. (C.) hanaii* sp. nov. The ossicles are mostly concentrated in the lowermost part of a single cross-stratification, or in continuous thin layers. The highly calcareous, well-washed sandstone, the sedimentary structures, and the mode

of occurrence all indicate a high-energy environment in which the disarticulated crinoids were subjected to transport and sorting.

At Loc. Hn 0920 (the type locality for *I. (C.) hanaii* sp. nov.) well-preserved articulated specimens with cup, arms, and column occur sparsely in a single horizon within a light-grey, fine-grained, and well-sorted calcareous sandstone (text-fig. 3A). The specimens have been brought into relief on the bedding plane by selective natural weathering and etching of the matrix. Other marine fossils are rare at this horizon. In contrast a bed several centimetres lower has produced numerous cirrals of *I. (C.) hanaii* sp. nov. associated with many small-sized bivalves (text-fig. 3B), identified as *Glycymeris (Hanaia) densilineata* (Nagao), *Astarte (Tranitscholdia) minor* Nagao, *A. (Nicaniella) semicostata* Nagao. These two distinct modes of occurrence, nearly complete individuals and dissociated cirrals, appear in almost the same lithology and are possibly due to different modes of burial of the skeletons. The former, with well-preserved but fewer specimens, strongly indicates rapid burial of living crinoids, or shortly after their death. Experiments on several species of Recent comatulid crinoids have shown that within two or three days of death they collapse into fragments (Cain 1968; Meyer 1971; Liddel 1975), but there has been no equivalent report on the post-mortem decomposition of Recent isocrinid skeletons. It is unlikely, however, that the well-preserved Cretaceous isocrinids considered here were subjected to much transport. On the other hand the occurrence of *I. (C.) hanaii* sp. nov. almost exclusively as cirrals may possibly result from the sorting of crinoidal fragments along with sand grains during transport, or during reworking by wave action.



TEXT-FIG. 3. Mode of occurrence of *Isocrinus (Chladocrinus) hanaii* sp. nov. at Loc. Hn 0920, northern coast of Haipe. A, well-preserved specimens in fine-grained sandstone. B, slightly below the horizon of A, consisting mostly of cirrals. Both figures are views of bedding plane surfaces. Scale bars 2 cm.

In the Moshi area, *I. (C.) hanaii* sp. nov. is restricted to an interval 24–27 m above the base of the Hiraiga Formation (Locs. Hn 4151, Hn 4153, Oj 0257). The specimens are contained in a calcareous, fine-grained sandstone; while sometimes they retain nearly complete skeletons, they frequently occur as ossicles in calcareous concretions together with wood fragments and small molluscs such as *Mesosacella insignis* (Nagao), *A. (N.) semicostata* Nagao, *A. (Freiastarte) subomaliaoides* Nagao, and the venerid *Nagaoella corrugata* (Nagao).

Isocrinus (Chladocrinus) sp. cf. Isocrinus? neocomiensis (Desor)

Specimens occur in the middle and upper part of the Tanohata Formation (upper Aptian) of the Tanohata area. Those from the middle part of the formation are scattered through calcareous sandstone at the following localities: Loc. Oj 5813, cross-stratified, calcareous, fine-grained sandstone on the northern coast of Hiraiga; Loc. Oj 7517, pebble conglomeratic, calcareous, coarse-grained sandstone, with fragmented ostreids and other bivalves, on the northern coast of Haipe. Specimens from the upper part of the formation are in sandy siltstone at the following localities on the northern coast of Hiraiga: Loc. Oj 5827-2, just below the base of the overlying Hiraiga Formation; Loc. Oj 5825-2, 4 m below the base of the Hiraiga Formation. The siltstones are extensively bioturbated; disarticulated columns and brachials occur scattered throughout the sediment. Specimens from the siltstone are better preserved than those from the sandstone. This species probably lived in relatively calm water.

DISCUSSION

Direct information on the bathymetry of the sediments within which the specimens occur is not available. However, the two species described herein are considered to have been shallow-water isocrinids. Nearly complete specimens of *I. (C.) hanaii* sp. nov. occur associated with transported blocks of hermatypic corals and coralline algae at Haipe. Columnals and a series of brachials of *I.* sp. cf. *I.? neocomiensis* are found in siltstone just above fossil beachrock at Hiraiga. Consequently both species are considered to have been shallow-water dwellers, probably living in depths less than several tens of metres.

Living stalked crinoids are mainly distributed in relatively deep water, mostly 200–1000 m (isocrinids), deeper than 200 m (bourgueticrinids), and 500–5000 m (cyrtocrinids) (Breimer 1978b, p. T329). However, a few examples of Mesozoic stalked crinoids (including the species of *Isocrinus* described here) are found in apparently shallow-water lithofacies. Because of this, it has been proposed that the living stalked crinoids are 'living fossils' which disappeared from shallow water to take refuge in deep water. According to Breimer (1978a, p. T10) they are approaching extinction.

Fossil stalked crinoids for which bathymetric information may be inferred are few. *Seirocrinus subangularis* (Miller), an early Jurassic pentacrinitid from Holzmaden, was once regarded as pseudoplanktonic (Seilacher *et al.* 1968), but has subsequently been reinterpreted as benthonic by Rasmussen (1977) who estimated that the crinoid lived at depths of 100–600 m. If Rasmussen is right this pentacrinitid was present in relatively deep water during the early Jurassic. Nearly complete specimens of *Chariocrinus andreae* (Desor) from the Bajocian of Switzerland occur in apparently shallow-water oolitic sediments (Hess 1972). Other than this occurrence, records of shallow-water isocrinids are scarce, and the two species of *Isocrinus* from the Miyako Group described herein represent the youngest such shallow-water isocrinids so far reported. Apart from the Isocrinidae, a rather different stalked crinoid, the bathycrinid *Dunnicrinus mississippiensis* R. C. Moore, is known from apparently shallow-water facies of Maastrichtian age (Moore 1967). This may suggest that some bathycrinids persisted in shallow seas after the isocrinids had disappeared from such depths.

Despite differing opinions on their taxonomy, it is possible to split the isocrinids into two groups on the basis of the kind of articulation in the primibrachials. One group has synarthrial articulation and the other has cryptoszygial articulation (including the 'synostosis' of several authors). This subdivision of isocrinids was first proposed by Carpenter as early as 1882. Synarthry is characterized by a prominent transverse ridge in the centre of each opposing articular facet, and the ligamentary bundles are distributed in two fossae on either side of the ridge. Synarthrial articulation allows slight movement between two connected ossicles. On the other hand, cryptoszygy is a weak form of articulation; joint facets are almost flat so that each ossicle is tightly connected. Cryptoszygy also occurs in more distal brachitaxes than IBr, and frequently in the proximal part within each brachitaxis.

Observations of living crinoids show that isocrinid arms are easily disarticulated at the cryptoszygy just after specimens have been dredged, and that regeneration of the arms is usually found at the distal facet of a hypozygal. I have frequently observed this in specimens of the isocrinid *Metacrinus rotundus* Carpenter dredged off the southern coast of Japan. Such regeneration indicates that disarticulation at the cryptoszygy occurs while the crinoids are living. Consequently the cryptoszygy of isocrinids may be a specialized articulation for autotomy (as is the case for comatulids) as suggested by Roux (1974). Arms are easily disarticulated at the cryptoszygy in both living and dead specimens of Recent isocrinids. There has been no report of regenerated arms growing from the distal facet of a synarthry.

The group which has synarthrial articulation (named here the 'old group') lived from the Triassic to the Recent, while those which have cryptoszygy in IBr (named here the 'new group') appeared in the early Cretaceous and diversified after the mid-Cretaceous (Table 1). In the present-day Pacific the 'new group' is characterized by many species of *Metacrinus* and *Saracrinus* living mostly between 100–600 m water depth, while a member of the 'old group', *Hypalocrinus naresianus* (Carpenter),

	GENERA	IBr	IIBr~	STRATIGRAPHIC DISTRIBUTION					
				TRIASSIC	JURASSIC	CRETACEOUS	PALEOGENE	NEOGENE	QUAT.
OLD GROUP	<i>Isocrinus</i>	SYN	SYN + CZ	---			
	<i>Hypalocrinus</i>	SYN	SYN + CZ						
	<i>Chariocrinus</i>	SYN	SYN + CZ		—				
	<i>Balanocrinus</i>	SYN	SYN + CZ	—	—				
NEW GROUP	<i>Nielsenicrinus</i>	CZ	SYN + CZ			—	—		
	<i>Austinocrinus</i>	CZ	unknown				—		
	<i>Isselicrinus</i>	CZ	CZ				—	—	
	<i>Doreckicrinus</i>	CZ	CZ				—	—	
	<i>Cainocrinus</i>	CZ	SYN + CZ				—	
	<i>Teliocrinus</i>	CZ	CZ (+SYN)				—		
	<i>Endoxocrinus</i>	CZ	CZ						
	<i>Diplocrinus</i>	CZ	CZ						
	<i>Cenocrinus</i>	CZ	CZ						
	<i>Metacrinus</i>	CZ	CZ						
	<i>Saracrinus</i>	CZ	CZ						

TABLE 1. Stratigraphic distribution of ligamentary articulation type within 'old' and 'new' groups of Isocrinidae (see text); genera and stratigraphic information modified after Rasmussen (1978). IBr, type of ligamentary articulation in primibrachials; IIBr, type of ligamentary articulation in more distal brachitaxes than secundibrachials; SYN, synarthry; CZ, cryptosyzygy (including synostosis and symmorphys).

is restricted to depths greater than 600 m. Data on distribution are still insufficient, especially for the 'old group', but I conclude that the 'new group' lives at shallower depths than the 'old group'.

Teleostean fish are considered to be the main predators of crinoids (Meyer and Macurda 1977) and this may well apply to isocrinids. There is some evidence from a deep-sea photograph of Conan *et al.* (1981, fig. 4) which shows predation by a fish on *Diplocrinus wyvillethomsoni* (Carpenter). An adaptive radiation of teleostean fish took place in shallow water after the mid-Cretaceous (Thomson 1977); if teleosts were the predators of isocrinids, this radiation would have led to some selection pressure on these shallow-water stalked crinoids.

I consider that isocrinids of the 'new group' probably had an advantage over the 'old group' with regard to predation by bony fish because of their greater ability to shed arms in times of emergency. It is not apparent whether they shed their arms deliberately or passively, but it is presumed that they underwent autotomy just as comatulids do. Autotomy or disarticulation of the arms probably guarded the central soft body of isocrinids from predation. Crinoids of the 'new group' have a greater number of cryptosyzygies near the central soft body mass and therefore are presumably better protected from predation and better adapted for regeneration. Consequently, some of the 'new group' have overcome the selection pressure and revived in relatively shallow depth (sometimes less than 100 m) in the present-day Pacific.

Apparent regeneration is absent in *Isocrinus* from Miyako, strongly suggesting that it seldom if ever suffered from predation; the late Aptian shallow sea of Miyako was still then a favourable environment for the 'old group'.

It has not yet been documented whether the isocrinids shed arms by autotomy, and the above discussion is based only on the fact that the arms of living or dead specimens of isocrinids are easily disarticulated at the cryptosyzygy. Further investigation, and particularly experiments on living specimens, are needed to resolve this matter.

SYSTEMATIC PALAEONTOLOGY

Family ISOCRINIDAE Gislén, 1924

Genus ISOCRINUS von Meyer, 1936

Subgenus CHLADOCRINUS Agassiz, 1836 emend. Sieverts-Doreck, 1971

Remarks. *Chladocrinus* was first introduced by Agassiz, and loosely defined for fossil species of '*Pentacrinus*' with relatively numerous internodal plates. Owing to his brief diagnosis and failure to designate a type species, this genus has long been ignored. Recently, Sieverts-Doreck (1971) discussed the validity of the genus, designated as type species *P. basaltiformis* Miller, and emended the diagnosis. She included five early Jurassic species in the genus and treated the two closely related forms *Isocrinus* von Meyer, 1936 (type species *I. pendulus* von Meyer) and *Neocrinus* Thomson, 1864 (type species *P. (Neocrinus) decorus* Thomson) as distinct genera. According to Sieverts-Doreck, *Chladocrinus* is easily distinguished from *Isocrinus* by its lack of symmorphial articulation, and from *Neocrinus* by its more ramified arms. On the other hand, Hess (1972) regarded *Chladocrinus* as a subgenus of *Isocrinus* because the two are differentiated only by the types of ligamentary articulation between IIBr_{3-4} (cryptoszygy versus symmorph). Hess (1972) also treated *Neocrinus* as a distinct genus. Rasmussen (1978) accepted the emended diagnosis of Sieverts-Doreck (1971) and considered *Chladocrinus* a distinct genus. He did not restrict *Chladocrinus* to the early Jurassic species but included within it those early Cretaceous to Recent species of *Neocrinus* whose ligamentary articulation fitted the diagnosis given by Sieverts-Doreck, i.e. IBr_{1-2} (synarthry), IIBr_{1-2} (synarthry), and IIBr_{3-4} (cryptoszygy).

If *Chladocrinus* in the sense of Rasmussen (1978) is adopted, what is the essential difference between *Chladocrinus* and *Isocrinus*? *Isocrinus* possesses symmorphial articulation, generally at IIBr_{3-4} , which is replaced by cryptoszygial articulation in *Chladocrinus*. Consequently, the two genera are separated only by differences in the types of ligamentary articulation.

Both cryptoszygy and symmorph are considered to be modified forms of sphyzyg (Breimer 1978a), differentiated as follows: in cryptoszygy the joint facets are almost flat; in symmorph they are not flat, and instead a prominent transverse culmination of the epizygial brachial fits into a corresponding depression of the hypozygal to form an interlocked structure. *Isocrinus* is characterized by symmorph, but the degree of prominence and depression varies between species. For example, the articular facet of *I. cingulatus* (Münster) drawn by Hess (1972, fig. 3) has a hypozygal which is almost flat, the depression being conspicuous only near the margin. *I. (C.) hanaii* sp. nov. shows an almost flat suture between IIBr_{3-4} (Pl. 77, fig. 2), but the articular facets are somewhat undulating; the distal facet of the hypozygal is more or less concave and the adoral part is slightly elevated (Pl. 78, figs. 7, 8). Similar articulation is also present in an epizygial of *I. (C.)* sp. cf. *I.? neocomiensis* (Desor) (Pl. 78, fig. 6). Considering the various degrees of prominence and depression observed in symmorph and cryptoszygy, it seems difficult to draw a line between the two forms of articulation. I follow Hess (1972) in treating *Chladocrinus* as a subgenus of *Isocrinus*, and regard the Miyako examples as a species of the subgenus *Chladocrinus* because of their slightly depressed, almost flat cryptoszygy.

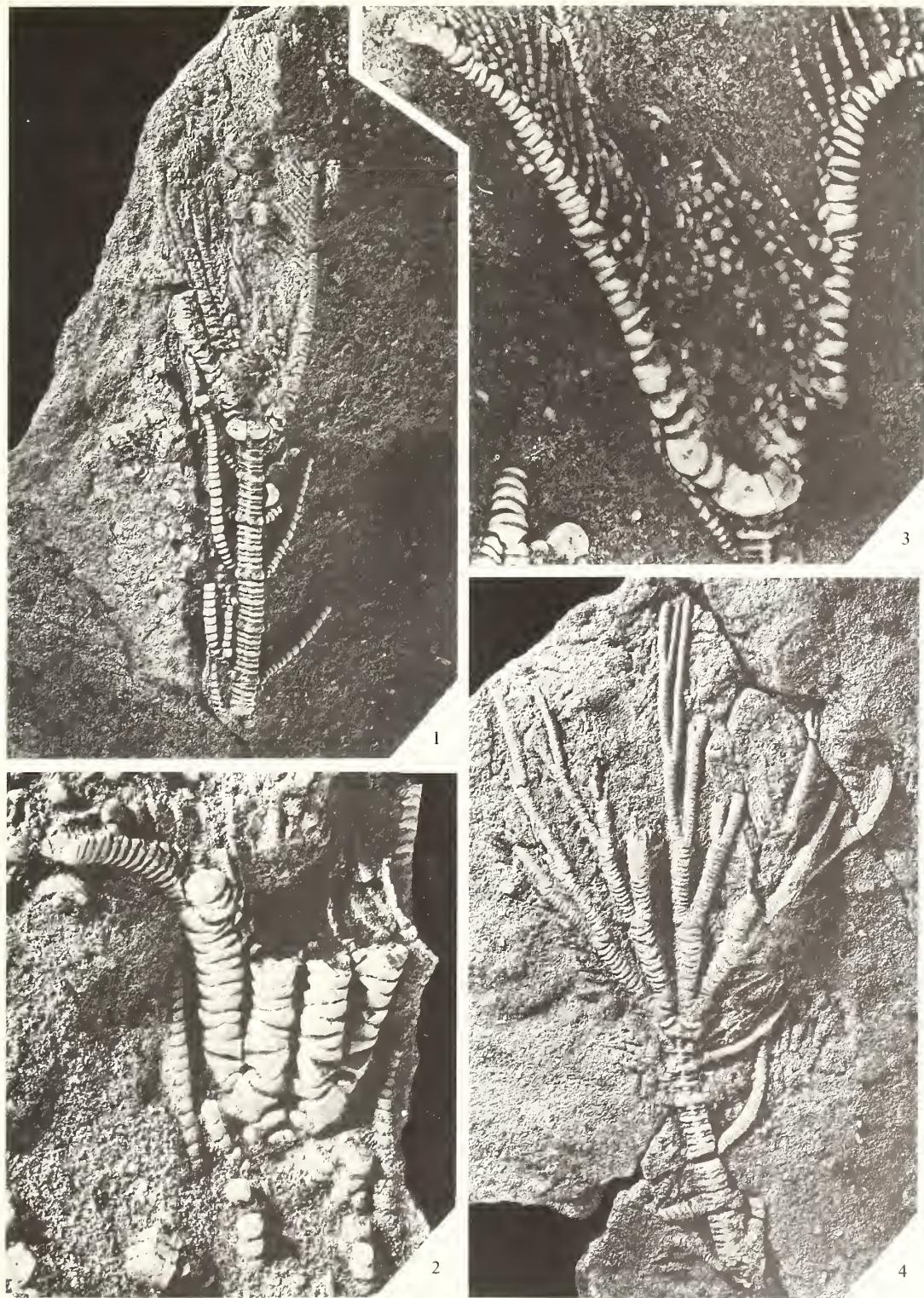
Another classification of the Isocrinidae is that of Roux (1977). Based on columnal morphology, Roux emphasized a strong similarity between the fossil *Balanocrinus* and Recent *N. blakei* and *N. decorus*. Later Roux (1981) placed the two living species in his Balanocrininae; he included fossil *Isocrinus* in his Isocrininae. His subdivisions were based mostly on columnal microstructure, and

EXPLANATION OF PLATE 77

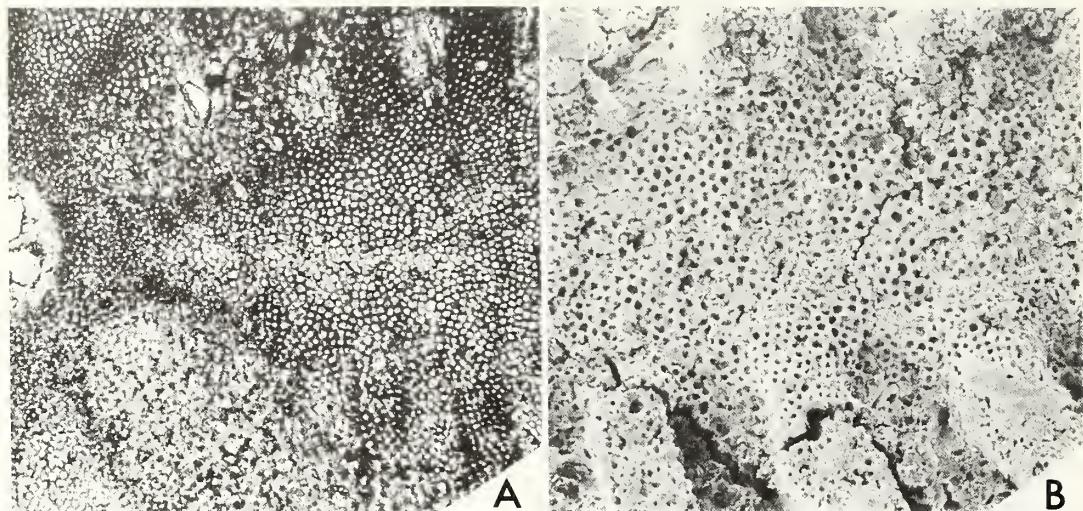
Figs. 1-4. *Isocrinus (Chladocrinus) hanaii* sp. nov., lower part of Hiraiga Formation, northern coast of Haipe.

1, ME6945, Loc. Hn 0916, paratype, $\times 1$. 2, ME6936, Loc. Hn 0920, holotype, $\times 2$. 3, ME6943, Loc. Hn 0920, paratype, $\times 2$. 4, ME6950, Loc. Hn 0916 or Hn 0920 (precise locality unknown), paratype, $\times 1$.

Figs. 1, 2, and 4 whitened; Fig. 3 submerged in water.



OJI, *Isocrinus (Chladocrinus)*



TEXT-FIG. 4. Stereom in columnal; note rounded meshes of α -stereom. A, *Isocrinus (Chladocrinus) hanaii* sp. nov. from Loc. Hn 0920, light micrograph of thin section of columnal, cut transversely near surface, $\times 57$. B, *I. (C.) sp. cf. I.? neocomiensis* (Desor), ME6962 from Loc. Oj 5825-2, SEM micrograph, $\times 95$ (treated in HF following the method of Sevastopulo and Keegan 1980).

especially on the shape of the meshes of the α -stereom. The two species of *Isocrinus (Chladocrinus)* from the Miyako Group are characterized by rounded-polygonal to rounded meshes, and fall into his Isocrininae (text-fig. 4). The controversy surrounding the classification of the Isocrinidae, especially regarding the recognition of reliable taxonomic criteria, remains unsolved.

Isocrinus (Chladocrinus) hanaii sp. nov.

Plate 77; Plate 78, figs. 1-5, 7, 8; Plate 79, figs. 1-7; text-fig. 4A

- 1913 *Pentacrinus*, Yabe and Yehara, pp. 12, 13.
- 1913 *Pentacrinus?*, Yabe and Yehara, p. 17.
- 1954 *Isocrinus*, Kobayashi *et al.*, p. 309.
- 1966 *Isocrinus* sp., Masutomi and Hamada, p. 143, pl. 72, fig. 3.
- 1982 *Isocrinus* sp., Tamura, p. 20, table 1.

Diagnosis. Medium- to small-sized species of *Isocrinus (Chladocrinus)* characterized by very low and tumid columnals, and by regular distribution of slightly embayed cryptosyzygy between the third and fourth brachials in each brachitaxis.

EXPLANATION OF PLATE 78

Figs. 1-5, 7, 8. *Isocrinus (Chladocrinus) hanaii* sp. nov., lower part of Hiraiga Formation, Matsushima islet in Moshi (Locs. Hn 4151, Hn 4153), and on northern coast of Haipe (Oj 7543). 1, ME6962, Loc. Hn 4153, paratype in lateral (*a*, *b*) and dorsal (*c*) views, $\times 2$. 2, ME6964, Loc. Hn 4151, paratype in lateral (*a*) and dorsal (*b*) views, $\times 2$. 3, ME6949, Loc. Oj 7543, in ventral (*a*), dorsal (*b*), and lateral (*c*) views, $\times 2$; arrow indicates one of distal facets of IIBr_3 (also shown in Fig. 7). 4*a*, *b*, ME6955, Loc. Oj 7543, paratype, stereo pair of distal facet of IBr_1 , synarthry, $\times 8.5$. 5, ME6955, Loc. Oj 7543, paratype in ventral view, $\times 4$. 7*a*, *b*, ME6949, Loc. Oj 7543, paratype, stereo pair of distal facet of IIBr_3 , $\times 8.2$. 8*a*, *b*, ME6954, Loc. Oj 7543, paratype, stereo pair of distal facet of IIBr_3 , $\times 10$.

Fig. 6. *Isocrinus (Chladocrinus)* sp. cf. *Isocrinus? neocomiensis* (Desor), ME6974, Loc. Oj 5825-2, proximal facet of brachial, $\times 8.3$.

OJI, *Isocrinus (Chladocrinus)*

Types. ME6936, holotype, well-preserved crown and column from Loc. Hn 0920 (Pl. 77, fig. 2). ME6937–6959, paratypes from Locs. Hn 0915, Hn 0916, Hn 0920, and Oj 7543, northern coast of Haipe. ME6960–6964, paratypes from Locs. Hn 4151, Hn 4153, and Oj 0257, Moshi. All the types are housed in the University Museum, University of Tokyo.

Description. Cup bowl-shaped, low, and wide. Basals small, triangular, and separated on surface. Radials low and broad, with smooth and evenly curved dorsal surface. Articular facet for IBr inclined 50–60°. Dorsal ligament fossa relatively large, approximately one half as large as the articular facet.

Arms more slender towards distal ends, but almost uniform in diameter within each brachitaxis. Nearly isotomous branching until fourth axillary (IVAx). In paratype ME6950, after IVAx, one of two VBrr forks to form VIBrr, and the other remains undivided (Pl. 77, fig. 4). If there is no further division of arms distally and every brachitaxis follows such a pattern of ramification, the finials can number 120. Brachial plates generally thin and smooth on surface. IBr₁ very thin. Articulation IBr_{1–2} embayed synarthrial (Pl. 78, fig. 4). On dorsal surface, distal facet of IBr₁ slightly concave and in contact with strongly convex proximal facet of IBr₂. IBr₂ axillary. Dorsal surface of IBr₂ nearly rhombic in outline, a little wider than high. Secundibrachials twelve or thirteen, rarely eleven or fourteen in number. II
₁ strongly wedge-shaped. Articulation II
{1–2} embayed synarthrial as between IBr{1–2}. II
₂ a little higher than the other secundibrachials. First pinnules on II
₂. II
_{2–3} oblique muscular. II
₃ and II
₄ wedge-shaped, a little thinner than the other secundibrachials. Articulation II
_{3–4} slightly embayed cryptosyzygial, showing nearly straight suture on dorsal surface. Distal facet of II
₃ smooth and marginal crenulation invisible (Pl. 78, figs. 7, 8). Ligamentary articulation of this kind developed between third and fourth brachials of every brachitaxis, with only one exception (one secundibrach of ME6962). Tertiibrachials seventeen, nineteen, or twenty-one in number. Quartibrachials twenty-one or twenty-five, rarely thirty-seven. Proximal pinnules composed of approximately ten pinnulars, which are rectangular in lateral view.

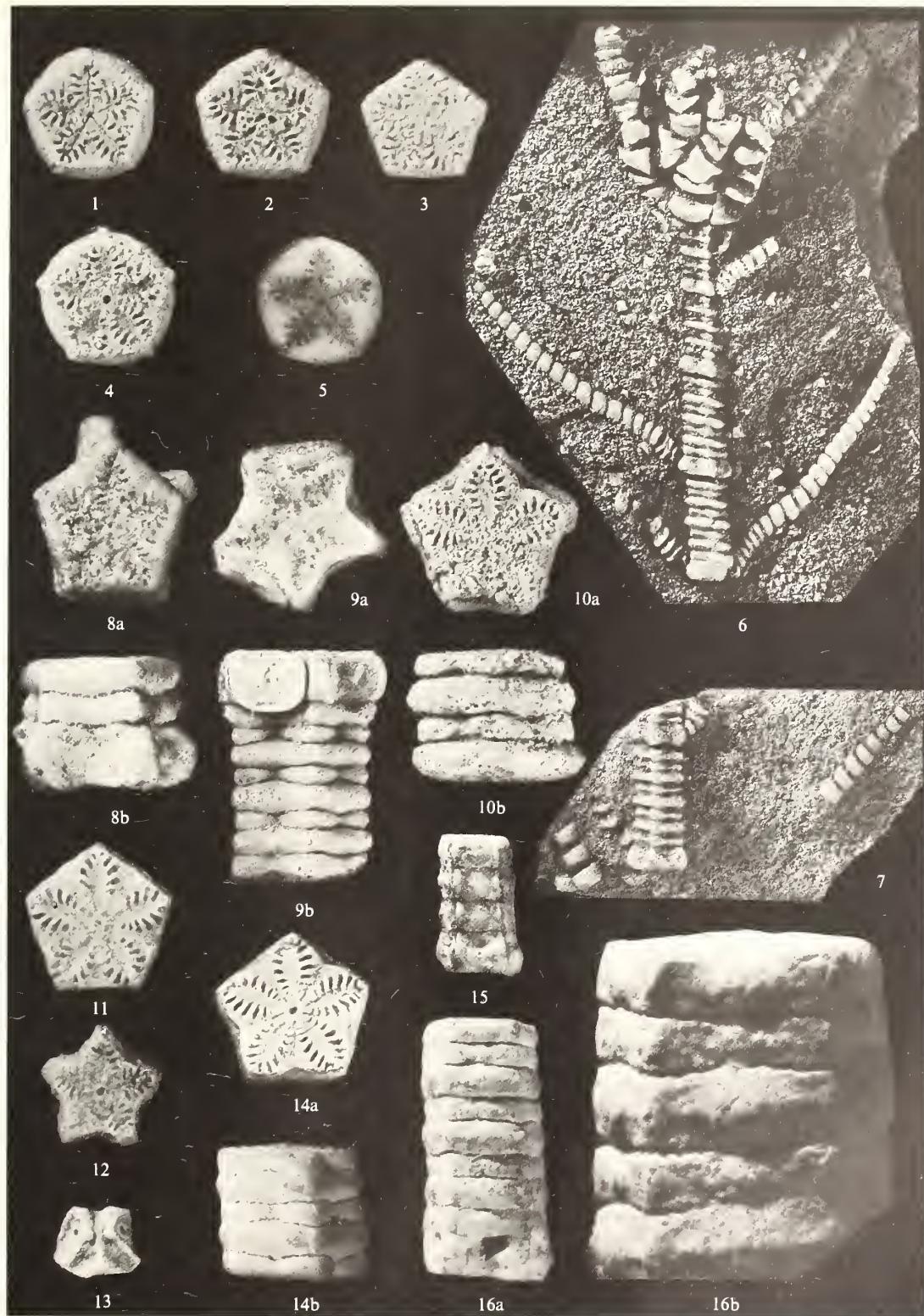
Column short and slender; proximal part highly variable in diameter but gradually modified distally to uniform diameter. Distal part slightly larger than the proximal part. Internodal plates low and tumid, with pentagonal to rounded subpentagonal outline in transverse section. Suture almost straight on surface. Articular facet of columnals petaloid; floors subguttiform, outwardly a little broad, surrounded by culmina and crenellae. Crenulae vary in size from the adradial to the marginal position, with the greatest length between radial and marginal areas. Culmina small in number for the diameter; two or three along margin, three or four along radius in columnals of diameter 4·1 mm. Canal narrow and rounded. Number of internodal plates seven or eight, rarely nine in the distal part. Radial pore developed in the proximal part of paratype ME6947, but otherwise absent. Nodal plates higher (approximately twice as high as internodal), wider, and more stellate in outline than internodal. Interradial edge sharp and arched. Articulation between nodal and infranodal synostosial. Periphery of the distal facet of nodal slightly raised. Cirrus sockets always five in number, large and wide, occupying almost entire height and width of lateral side of nodal, but not interfering with adjacent columnals. Articular ridge of cirrus socket weakly protruding with slightly tuberculated triangular ends. Proximal cirral plates thin and disc-shaped, with circular to slightly ovate outline in transverse section. Height of cirral plates suddenly increases distally in several plates, becoming almost as high as wide. Articular ridge slightly raised, canal passing a little above the centre.

EXPLANATION OF PLATE 79

Figs. 1–7. *Isocrinus (Chladocrinus) hanai* sp. nov., lower part of Hiraiga Formation, northern coast of Haipe. 1–5, Loc. Hn 0920, articular facets of columnals, all $\times 5$; 1 and 5, ME6956, paratype; 2, ME6957, paratype; 3, ME6958, paratype; 4, ME6959, paratype. 6, ME6942, Loc. Hn 0920, paratype, lateral view of column, cirri, and crown, $\times 2$. 7, ME6947, Loc. Hn 0916, paratype, proximal column and cirri, $\times 2$.

Figs. 8–16. *Isocrinus (Chladocrinus)* sp. cf. *Isocrinus? neocomiensis* (Desor), Tanohata Formation. 8, ME6965, Loc. Oj 5813, northern coast of Hiraiga, articular facet (a) and lateral view (b) of columnals, $\times 4$. 9, ME6966, Loc. Oj 5813, northern coast of Hiraiga, articular facet (a) and lateral view (b) of columnals, $\times 4$. 10, ME6967, Loc. Oj 7517, northern coast of Haipe, articular facet (a) and lateral view (b) of columnals, $\times 4$. 11, ME6968, Loc. Oj 5827-2, northern coast of Hiraiga, articular facet of internodal plate, $\times 5$. 12, ME6969, Loc. Oj 5827-2, northern coast of Hiraiga, articular facet of nodal plate, $\times 5$. 13, ME6970, Loc. Oj 5827-2, northern coast of Hiraiga, underside view of radial plate, $\times 4$. 14, ME6971, Loc. Oj 5825-2, northern coast of Hiraiga, articular facet (a) and lateral view (b) of columnals, $\times 4$. 15, ME6972, Loc. Oj 5825-2, lateral view of column, $\times 5\cdot9$. 16, ME6973, Loc. Oj 5825-2, lateral views of column, (a) $\times 4$, (b) $\times 9\cdot9$.

Figs. 1–4, 9b, 10a, 13, and 14a whitened; Fig. 5 submerged in water.

OJI, *Isocrinus (Chladocrinus)*

Discussion. The description above is based on material from Haipe and Moshi. Specimens from the two areas are considered conspecific because of the agreement (or strong similarity) in form of the dorsal cup and brachials, the arrangement of ligamentary articulation, and the pattern of ramification. Relatively complete specimens from Haipe are almost uniform in size, and may represent an adult stage. On the other hand, those from Moshi include relatively small columns which may represent a younger stage; these columns show a more pronounced alternating variation in diameter and columnals are higher with respect to the diameter. Columns of *I. (C.) hanaii* sp. nov. almost lack radial pores and crenulated sutures between columnals, suggesting that their rate of the accretionary growth was high.

I. (C.) hanaii sp. nov. is similar to *N. australis australis* (C. Moore) and *N. a. albascopularis* (Etheridge) from the lower Cretaceous of Australia in the form of the crown (Moore 1870, pl. 3, figs. 1–3; Etheridge 1901, pl. 1, fig. 4, pl. 3, figs. 1–3; Etheridge 1902, pl. 4, figs. 7–10) but the surface of the radials and brachials of *I. (C.) hanaii* sp. nov. is smooth in contrast to the rugose surface of theca and brachials of *N. australis* (which has, in addition, higher IBr₂ and more strongly wedge-shaped IBr₁).

I. (C.) hanaii sp. nov. is distinguished from *Percevalicrinus aldingeri* Klikushin (Rasmussen 1961, pl. 10, figs. 1–11) as *N. tenellus* (Eichwald); Klikushin 1981, pl. 9, figs. 1, 2) by the more tumid columnals of the former which show an alternating variation in diameter in the proximal part of the column. The present species is also distinguished from *P. tenellus* (Eichwald) from the lower Cretaceous of the USSR (Klikushin 1979, pl. 11, fig. 5; text-fig. 1d) by the latter's regular arrangement of meshes in the α-stereom.

There are many species of isocrinids which are tentatively assigned to *Isocrinus* only on the basis of stem elements (e.g. Rasmussen 1961). *I. (C.) hanaii* sp. nov. differs from all of these Cretaceous species in having strongly tumid columnals with a smooth lateral surface.

Although the Miyako examples from calcareous sandstone have been subjected to secondary precipitation of calcite around the ossicles, and the details of the articular facets are more or less obscured, they often retain an almost complete crown and most of the original pattern of ramification. In paratype ME6962 the number of secundibrachials is exceptionally small, eleven in one brachitaxis; this is probably related to the absence of ligamentary articulation at IBr_{3–4} in the brachitaxis. No apparent regeneration has been observed in any of the material.

Isocrinus (Chladocrinus) sp. cf. *Isocrinus? neocomiensis* (Desor)

Plate 78, fig. 6; Plate 79, figs. 8–16

1961 *Isocrinus? neocomiensis* (Desor); Rasmussen, p. 143, pl. 18, figs. 4, 5.

Material. ME6965 and 6966, columns from Loc. Oj 5813, northern coast of Hiraiga. ME6967, column from Loc. Oj 7517, northern coast of Haipe. ME6968–6970, columnals and a radial plate from Loc. Oj 5827–2, northern coast of Hiraiga. ME6971–6974, columns and brachials from Loc. Oj 5825–2, northern coast of Hiraiga.

Description. Brachials smooth on dorsal surface. A brachial (epizygial) with slightly convex and almost smooth proximal facet of cryptosyzygial articulation, as in IBr_{3–4} of *I. (C.) hanaii* sp. nov. (ME6974; Pl. 78, fig. 6). Marginal crenulation inconspicuous.

Column fairly constant in diameter in the small- and medium-sized specimens ME6972 and 6973, slightly variable in diameter in the larger specimens ME6965–6967 and 6971). In the small specimen ME6972, column pentagonal in section, with columnals almost uniform in height and diameter. In the larger column ME6973, a row of a few tubercles is aligned horizontally on the side of a large columnal, and also along the suture. In still larger columns, the kind most commonly represented, internodals are a little tumid and slightly variable in diameter; larger columnals are almost pentagonal and higher compared with smaller ones, which are slightly stellate to pentalobate and less high (ME6965–6967 and 6971). Internodals eight in number. Articular facet of columnals with subguttiform floors surrounded by culmina and crenellae. Crenulae with gradual transition in size from adradial to marginal position, attaining greatest length between radial and marginal areas. Culmina seven or eight in number in a column of diameter 5·7 mm. Canal narrow and rounded. Nodal plate higher, wider, and more stellate in outline than internodal plates, especially in large specimens. Cirrus sockets five in number,

large and wide, occupying almost the entire height and width of lateral side of nodal. Articular ridge weakly protruding with slightly tuberculated triangular ends. Articular ridge of cirral plate weakly raised, with canal passing a little above centre.

Remarks. This species is assigned to the subgenus *Chladocrinus* because of the slightly convex cryptoszygial articular facet of the epizygial. Small- and medium-sized columns with longitudinal ridge and tubercles are strongly reminiscent of *I.? neocomiensis* (Desor) from the Hauterivian of France (Rasmussen 1961, pl. 18, figs. 4, 5), which is represented only by columns. The present species, however, occurs in younger strata (upper Aptian). Because the brachial plates of *I.? neocomiensis* from Europe are unknown, strict specific identification is difficult.

The present species resembles *I. (C.) hanaii* sp. nov. in the form of its brachial plates (especially in the facet of ligamentary articulation) but differs in that its succeeding columnals show little or no variation in diameter and tubercles are present on the lateral side of small- to medium-sized columns.

Acknowledgements. I sincerely thank Emeritus Professor T. Hanai (University of Tokyo) for introducing me to the study of crinoids, for providing excellent specimens, and for encouragement and various suggestions throughout this work. Mr J. C. Grimmer (Scripps Institute of Oceanography) also made helpful suggestions and sent several reference papers. Thanks are due to Dr R. V. Kesling for reading an earlier draft of the paper. Drs. I. Hayami and K. Chinzei (University of Tokyo) offered valuable advice and encouraged the author. Dr T. Kase (National Science Museum) provided specimens from the Moshi area.

REFERENCES

- BREIMER, A. 1978a. General morphology, Recent crinoids, pp. T9–T58. In MOORE, R. C. and TEICHERT, C. (eds.). *Treatise on invertebrate paleontology, Part T. Echinodermata 2, Crinoidea (I)*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.
- 1978b. Ecology of Recent crinoids. *Ibid.*, T316–T330.
- CAIN, J. D. B. 1968. Aspects of the depositional environment and palaeoecology of crinoidal limestones. *Scott. J. Geol.* **4**, 191–208.
- CARPENTER, P. H. 1882. The stalked crinoids of the Caribbean Sea. *Bull. Mus. comp. Zool. Harv.* **10**, 165–181.
- CONAN, G., ROUX, M. and SIBUET, M. 1981. A photographic survey of a population of the stalked crinoid *Diplocrinus (Annacrinus) wyvillethomsoni* (Echinodermata) from the bathyal slope of the Bay of Biscay. *Deep-Sea Res.* **28**, 441–453.
- ETHERIDGE, R. JR. 1901. Additional notes on the palaeontology of Queensland, part 2. *Bull. geol. Surv. Qd.* **13**, 1–37.
- 1902. A monograph on the Cretaceous invertebrate fauna of New South Wales. *Mem. geol. Surv. N.S.W.*, Palaeont. Ser. **11**, 1–50.
- HANAI, T., OBATA, I. and HAYAMI, I. 1968. Notes on the Cretaceous Miyako Group. *Mem. natn. Sci. Mus., Tokyo*, **1**, 20–28. [In Japanese.]
- and OJI, T. 1981. Early Cretaceous beachrock from the Miyako Group, Northeast Japan. *Proc. Japan Acad.*, B, **57**, 362–367.
- HAYAMI, I. 1975. Systematic survey of the Mesozoic Bivalvia from Japan. *Bull. Univ. Mus. Tokyo*, **10**, 1–249.
- HESS, H. 1972. *Chariocrinus* n. gen. für *Isocrinus andreae* (Desor) aus dem unteren Hauptrogenstein (Bajocien) des Basler Jura. *Eclog. geol. Helv.* **65**, 197–210.
- KASE, T. 1984. *Early Cretaceous marine and brackish-water Gastropoda from Japan*, 262 pp. National Science Museum, Tokyo.
- KLIKUSHIN, V. G. 1979. Microstructural features of isocrinid stem. *Paleont. J.* **13**, 83–90.
- 1981. Sea lilies of the genus *Percevalicrinus*. *Ibid.* **15**, 84–95.
- KOBAYASHI, T., HANZAWA, S., ASANO, K., KIMURA, T., HAYASAKA, I., EGUCHI, M., HATAI, K., MAKIYAMA, J., MATSUMOTO, T. and NISIYAMA, S. 1954. ‘*Koseibutsugaku*’ **1**, 372 pp. Asakura-shoten, Tokyo. [In Japanese.]
- LIDDEL, W. D. 1975. Recent crinoid biostratinomy. *Abstr. Progm. geol. Soc. Am.* **7**, 1169.
- MASUTOMI, K. and HAMADA, T. 1966. *Fossils in color*, 258 pp. Hoikusha, Osaka. [In Japanese.]
- MEYER, D. L. 1971. Post mortem disarticulation of Recent crinoids and ophiuroids under natural conditions. *Abstr. Progm. geol. Soc. Am.* **3**, 645–646.
- and MACURDA, D. B. JR. 1977. Adaptive radiation of the comatulid crinoids. *Paleobiol.* **3**, 74–82.

- MOORE, C. 1870. Australian Mesozoic geology and palaeontology. *Q. Jl geol. Soc. Lond.* **26**, 226–261.
- MOORE, R. C. 1967. Unique stalked crinoids from Upper Cretaceous of Mississippi. *Paleont. Contr. Pap. Univ. Kans.* **17**, 1–35.
- OBATA, I. and MATSUMOTO, T. 1977. Correlation of the Lower Cretaceous formations in Japan. *Scient. Rep. Dept. Geol. Kyushu Univ.* **12**, 165–179. [In Japanese.]
- RASMUSSEN, H. W. 1961. A monograph on the Cretaceous Crinoidea. *Biol. Skr.* **12** (1), 428 pp.
- 1977. Function and attachment of the stem in Isocrinidae and Pentacrinitidae: review and interpretation. *Lethaia*, **10**, 51–57.
- 1978. Systematic description, Articulata, pp. T813–T928. In MOORE, R. C. and TEICHERT, C. (eds.). *Treatise on invertebrate paleontology. Part T. Echinodermata 2, Crinoidea (3)*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.
- ROUX, M. 1974. Les principaux modes d'articulation des ossicles du squelette des Crinoïdes pédonculés actuels. Observation microstructurales et conséquences pour l'interprétation des fossiles. *C. r. hebd. Séanc. Acad. Sci., Paris, D*, **278**, 2015–2018.
- 1977. The stalk joints of Recent Isocrinidae (Crinoidea). *Bull. Br. Mus. nat. Hist. (Zool.)*, **32**, 45–64.
- 1981. Echinoderms: Crinoïdes Isocrinidae. Résultats des Campagnes M.U.S.O.R.S.T.O.M. 1. Philippines. *Mému. O.R.S.T.O.M.* **91**, 477–543.
- SEILACHER, A., DROZDZEWSKI, G. and HAUDE, R. 1968. Form and function of the stem in a pseudoplanktonic crinoid (*Seirocrinus*). *Palaeontology*, **11**, 275–282.
- SEVASTOPULO, G. D. and KEEGAN, J. B. 1980. A technique for revealing the stereom structure of fossil crinoids. *Ibid.* **23**, 749–756.
- SIEVERTS-DORECK, H. 1971. Über *Chladocrinus* Agassiz (Isocrinidae) und die nomenklatorische Verankerung dieser Gattung. *Neues Jb. Geol. Paläont. Mh.* **5**, 314–320.
- TAMURA, M. 1982. *Isocrinus* columnal bearing limestones in Sambosan Belt and Japanese Triassic *Isocrinus* columnals. *Mému. Fac. Educ. Kumamoto Univ. Nat. Sci.* **31**, 19–24. [In Japanese.]
- THOMSON, K. S. 1977. The pattern of diversification among fishes, 374–404. In HALLAM, A. (ed.). *Patterns of evolution, as illustrated by the fossil record*, 591 pp. Elsevier, Amsterdam, Oxford, and New York.
- YABE, H. and YEHARA, S. 1913. The Cretaceous deposits of Miyako. *Scient. Rep. Tohoku Imp. Univ.* **2**, 1 (2), 9–15.

TATSUO OJI

Geological Institute
University of Tokyo
Tokyo 113, Japan

Typescript received 31 July 1984

Revised typescript received 29 January 1985

STRUCTURE AND FUNCTION OF THE PECTORAL GIRDLE AND FORELIMB OF *STRUTHIOMIMUS ALTUS* (THEROPODA: ORNITHOMIMIDAE)

by ELIZABETH L. NICHOLLS and ANTHONY P. RUSSELL

ABSTRACT. The forelimb and pectoral girdle of *Struthiomimus altus* are described for the first time. The ornithomimid pectoral girdle differs from that of other theropods in having a higher scapular prominence (acromion process), an anterior flange on the supraglenoid buttress, and a narrow, attenuated coracoid.

Osteological and myological comparisons with recent reptiles and birds, combined with muscle scar evidence, suggests that the primary girdle of *Struthiomimus* was oriented somewhat laterally, as in recent crocodiles and lizards, and that it was mobile with respect to the body wall. The potential for extensive protraction and retraction of the humerus is evident, endowing *Struthiomimus* with extensive forereach abilities, combined with limited rotational potential.

In the manus the offset first digit differs from the usual theropod condition in being rotated outwards, away from the midline of the hand. Digits II and III are incipiently coalesced and functioned as a unit. The osteological evidence suggests that the manus of *Struthiomimus* operated as a hooking and clamping structure, rather than as a grasping or raking one.

WHILE the forelimb of ornithomimids is ‘coelurosaurian’ in length, it lacks the raptorial characteristics of that group, and there has been considerable speculation regarding its function. Osborn (1916) suggested that the first digit was opposable and described the manus as a grasping hand. Later workers, however, have questioned both the opposability of digit I and the grasping ability of the manus (Ostrom 1969; Galton 1971; Osmólska *et al.* 1972).

The forelimb of *Struthiomimus* was figured by Osborn (1916), but only a brief description was given and the scapulocoracoid was not described. The complete forelimb and shoulder girdle are preserved in only a few specimens of North American ornithomimids and in most cases these are either mounted (AMNH 5339, ROM 851) or unprepared (NMC 8632). Consequently most subsequent comparative work has been based on Osborn’s incomplete description.

A specimen of *S. altus* with a well-preserved, articulated pectoral limb and shoulder girdle is now available (Nicholls and Russell 1981). We here redescribe the forelimb and describe and figure the scapulocoracoid for the first time. The presence of clear muscle scars on both the humerus and the scapulocoracoid have prompted us to reconsider forelimb function in this species. Inferences drawn with respect to function are based upon Recent comparative material described herein.

Abbreviations used in this work are as follows: AMNH, American Museum of Natural History; BM(NH), British Museum (Natural History); NMC, National Museum of Canada; ROM, Royal Ontario Museum; TMP, Tyrrell Museum of Palaeontology; UA, University of Alberta; UCMZ, University of Calgary, Museum of Zoology; USNM, United States National Museum.

SYSTEMATIC PALAEOONTOLOGY

Family ORNITHOMIMIDAE Marsh 1890

Genus *Struthiomimus* Osborn 1916 (Emended Russell 1972)

Struthiomimus altus (Lambe 1902)

UCMZ(VP)1980.1. Incomplete skeleton consisting of limbs, girdles, gastralia, and fragments of vertebral column and ribs. The specimen was collected from the Judith River Formation (Judithian,

Upper Cretaceous), of southern Alberta, Canada. The left forelimb and pectoral girdle are complete (text-fig. 1) and were found articulated. A description of the specimen and its taxonomic relationships appear elsewhere (Nicholls and Russell 1981).

Little comparative material is available. Scattered podial fragments of ornithomimids are abundant in the bone scrap of the Judith River Formation, but articulated specimens, or even complete elements, are rare. The two best specimens are ROM 851 (*Ornithomimus edmontonicus*) and AMNH 5339 (*S. altus*). ROM 851 is so crushed that few surface details are discernible. Both of these specimens are mounted, making detailed anatomical comparison difficult. They have been described and figured by Parks (1933) and Osborn (1916) respectively. Comparisons of UCMZ(VP)1980.1 with other North American ornithomimids is based primarily on examination of the following specimens: NMC 12441, 8632, 12228, 8902; UA 16182; ROM 851, 840; and also on literature reports.

Russell (1972) defined three genera of North American ornithomimids: *Ornithomimus*, *Struthiomimus*, and *Dromiceiomimus*. We here recognize only the first two, which may be distinguished on the basis of the manus (Nicholls and Russell 1981)—the manus of *Dromiceiomimus* is incompletely known.

OSTEOLOGY OF THE PECTORAL GIRDLE AND FORELIMB OF *STRUTHIOMIMUS ALTUS*

(a) Orientation

Throughout the subsequent descriptions we have attempted to standardize directional terminology. Due to the difficulty of orienting adult structures in a standard fashion we have chosen to employ developmental terminology and orientation as they relate to the main body and limb axes. In this context all structures have developmental dorsal-ventral, anterior-posterior, and either lateral-medial (limb girdles) or proximal-distal (limbs) axes. All descriptive terminology relates to these axes (refer to orientation arrows on figures for clarification).

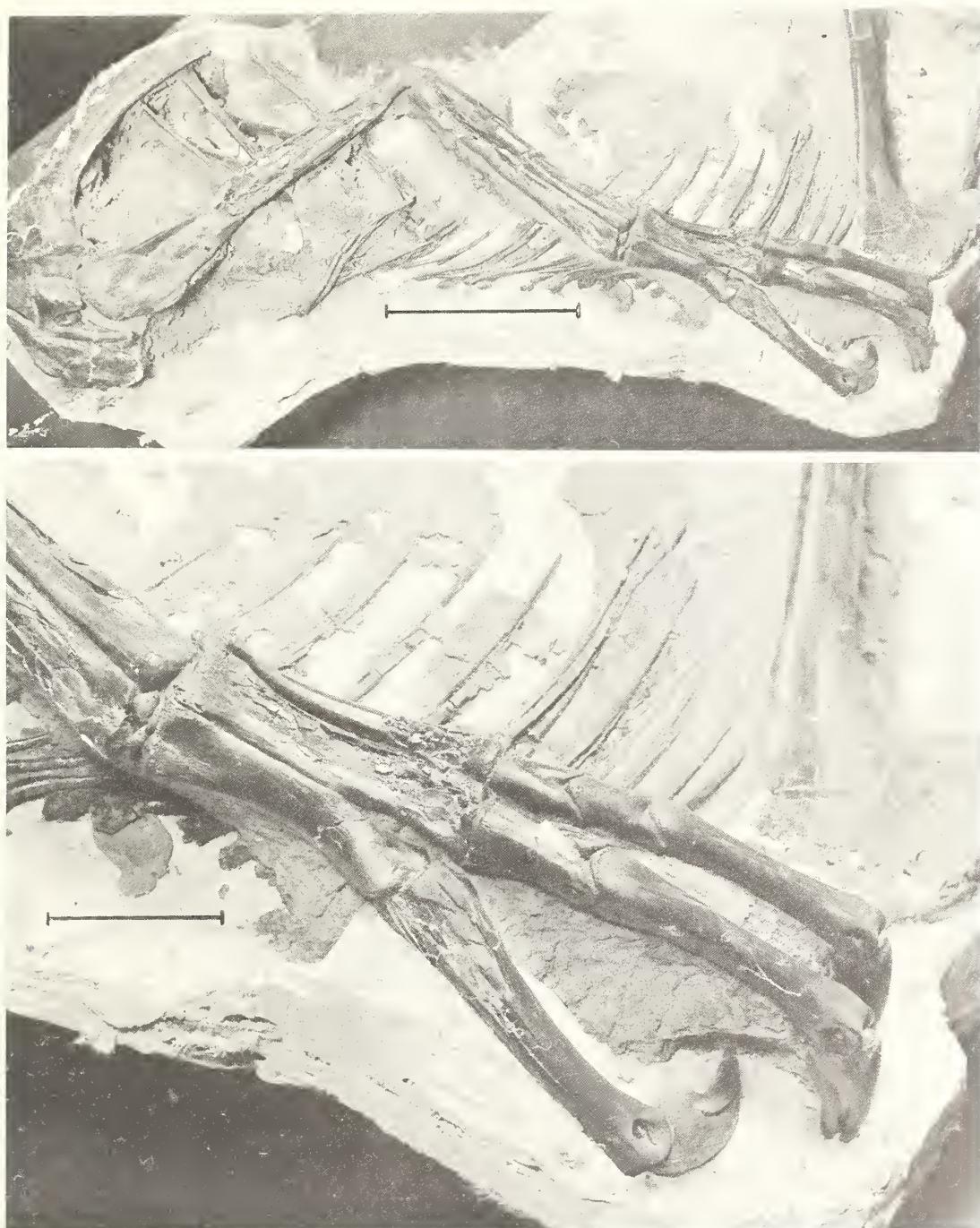
(b) Scapulocoracoid

In UCMZ(VP)1980.1 the left scapulocoracoid is complete, except for the dorsal tip of the scapular blade (text-fig. 1). Both coracoids are complete and overlap along the ventral midline. As the left coracoid is partially covered by the right element, the description of the coracoid is a composite, based on the coracoids of both sides. Measurements of the girdle and forelimb are given in Table 1.

The exact length of the scapula is not known, but assuming the scapulo-femoral ratio of UCMZ(VP)1980.1 to be the same as that of AMNH 5339 (Osborn 1916), we estimate the length of the scapula to be 380 mm. It is long and slender and ventrally the shaft is oval in cross-section, but dorsally becomes compressed and blade-like (text-fig. 2) and the shaft has a slight posterior curvature. Although the dorsal tip of the blade is missing, there is no evidence that it was significantly expanded, in accordance with the situation in other ornithomimids.

Situated anteriorly on the scapula, just dorsal to the scapulocoracoid suture, is a compressed, keel-like prominence (text-fig. 2) that has been referred to as the 'acromion process' by several authors (Ostrom 1969, 1978; Osmólska and Roniewicz 1970; Cooper 1981). Its homology with that tuberosity has not been demonstrated, however, and in the absence of clavicles the existence of an acromion can only be surmised. For this reason we have chosen to refer to this structure as the scapular prominence. It is very well developed in *Struthiomimus* (text-fig. 2) as it is also in *Ornithomimus* and *Gallimimus*. It differs, however, from the situation found in most theropods, where the scapular prominence is more pronounced anteriorly but does not extend as far dorsally (text-fig. 3). The anterior edge of the scapular prominence is quite rugose and porous in texture, suggesting the attachment of either muscle or ligament.

The glenoid fossa is deep and sellar. It is equally developed on both scapula and coracoid and has prominent supra- and infraglenoid buttresses. The scapular portion of the glenoid bears an anteriorly directed flange (text-fig. 2), representing an extension of the supraglenoid buttress that resists dorsal deflection of the humerus during extreme humeral protraction.



TEXT-FIG. 1. *a*, the left pectoral girdle and forelimb of *Struthiomimus altus*, UCMZ(VP)1980.1. The scale bar represents 150 mm. *b*, detail of the left manus and wrist. The scale bar represents 50 mm.

TABLE 1. Measurements of the pectoral girdle and forelimb of
Struthiomimus altus (UCMZ(VP)1980.1).

Scapula—dorsoventral length	380*
—anteroposterior width at midshaft	46
—dorsoventral length of scapular prominence	62
—anteroposterior width of scapulocoracoid suture	88
Coracoid—dorsoventral length, posterior to glenoid	66
—anteroposterior width	179
—length of biceps tubercle	21
—height of biceps tubercle	9
Humerus—proximodistal length	362
—anteroposterior width at midshaft	40
Ulna—proximodistal length	256
—anteroposterior width at midshaft	17
Radius—proximodistal length	239
—anteroposterior width at midshaft	15
Metacarpals, proximodistal length	
—I	102
—II	109
—III	109
Phalanges, proximodistal length	
—I-1	127
—I-2 (ungual)	95
—II-1	40
—II-2	113
—II-3 (ungual)	127*
—III-1	24
—III-2	29
—III-3	89
—III-4 (ungual)	98*

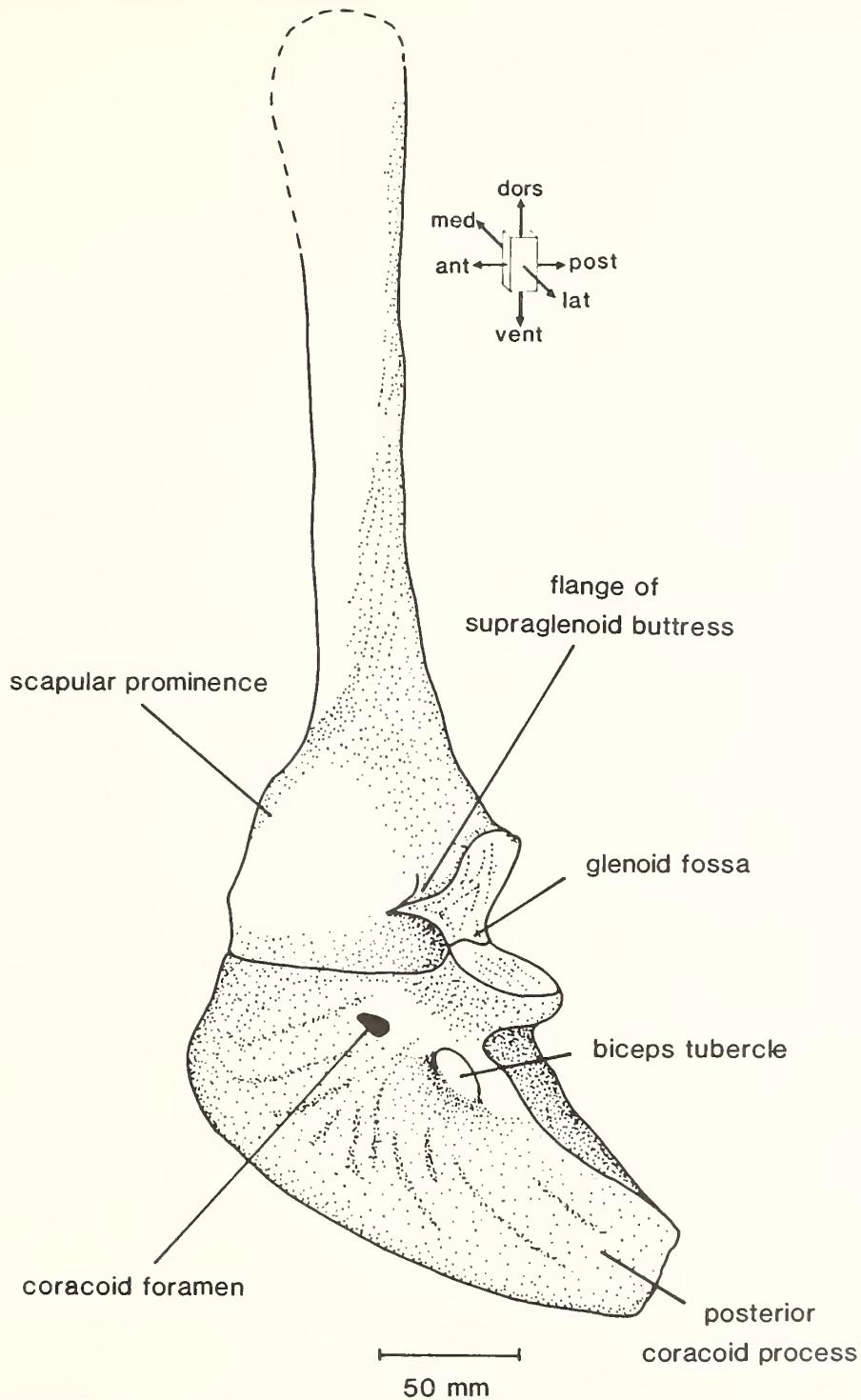
Ungual articular surface dimensions:	Dorsoventral articular height
	Anteroposterior articular width
I-2	21/16
II-3	18/16
III-4	17/15

All measurements are in mm, and refer to the left limb and girdle, except for the coracoid which is represented by the right element. Measurements marked with an asterisk (*) are estimates.

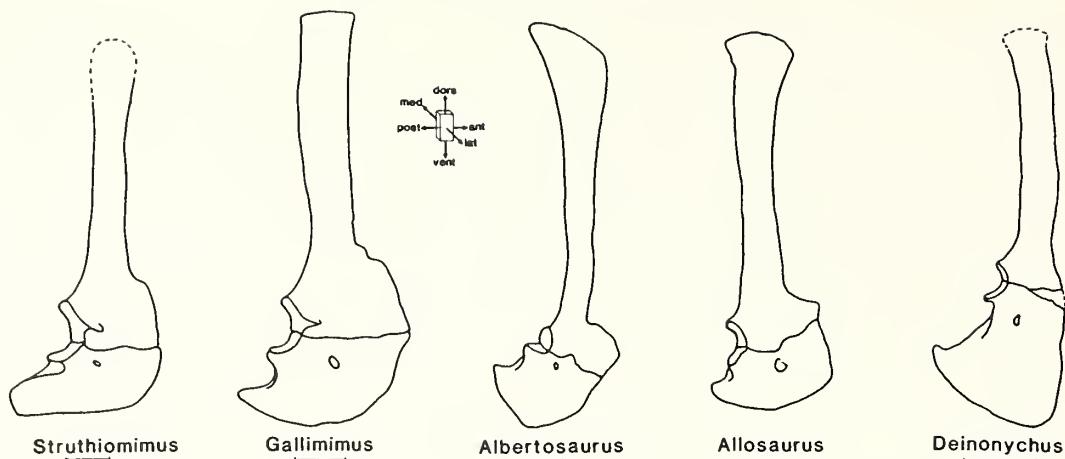
On the dorsal surface of the scapular lip of the glenoid is a narrow, oval depression. A similar depression has been noted in other theropods, notably *Deinocheirus* (Osmólska and Roniewicz 1970) and *Gallimimus* (Osmólska *et al.* 1972) and probably represents the site of origin of the scapular head of the triceps.

The coracoid is about three times as long as deep, the majority of the length being due to the extension of the posterior coracoid process beyond the glenoid fossa (text-fig. 2). This process does not terminate in a curved apex as it does in most theropods, but is truncated posteriorly. The coracoid is thickest along the dorsal edge of the posterior coracoid process, where it forms a conspicuous infraglenoid buttress.

On the lateral surface of the coracoid plate, ventral to the glenoid, is a pronounced elongate tuberosity, the biceps tubercle (text-fig. 2; Table 1). This corresponds to the 'coracoid tuber' described by Osmólska *et al.* (1972) for *Gallimimus* and to the 'biceps tubercle' of *Deinonychus* (Ostrom 1974)



TEXT-FIG. 2. Left scapulocoracoid of *Struthiomimus altus*, UCMZ(VP)1980.1. Ventro-medial curvature removed.



TEXT-FIG. 3. Representative theropod scapulocoracoids compared with that of *Struthiomimus*. All are drawn to approximately the same length for ease of comparison. The scale bar represents 50 mm. In *Struthiomimus* note the narrow, attenuated posterior coracoid process, the anterior flange on the supraglenoid buttress, and the height of the scapular prominence. The latter two characteristics are shared by *Gallimimus*. Diagrams are based on ROM 762 (*Albertosaurus libratus*), ROM 5091 (*Allosaurus fragilis*), and a cast of *Gallimimus bullatus* at the ROM. Data on *Deinonychus* from Ostrom (1974).

and the prosauropod *Massospondylus* (Cooper 1981). It is also well developed in *Dromeosaurus* (TMP 79.20.1) and is present in most long-armed theropods. Ostrom (1974) suggested that the relative size of the biceps tubercle may be related to forelimb length, but this seems unlikely in view of Madsen's (1976) comment that, at least in *Allosaurus*, the development of the biceps tubercle is extremely variable.

There are three clearly defined areas of muscle attachment on the coracoid plate. The most prominent of these is a triangular depression on the dorsal edge of the posterior coracoid process, ventral to the infraglenoid buttress (text-figs. 2 and 11). The depression is very broad and deep, narrows posteriorly, and its surface is quite smooth. This region is interpreted as being the site of origin of the *M. coracobrachialis brevis* (see below).

The other two areas indicative of muscle attachment both lie on the lateral surface of the coracoid plate. The first of these is a broad depression anterior to the glenoid (text-figs. 2 and 11). It overlies the region of the scapulocoracoid suture and the coracoid foramen, extending from the ventral edge of the scapular prominence to the biceps tubercle. This is interpreted as being the site of origin of the *M. supracoracoideus* (see below).

Posterior to the biceps tubercle, the lateral surface of the long posterior coracoid process bears a heavily striated scar (text-figs. 2 and 11), here interpreted as the site of origin of the *M. coracobrachialis longus* (see below). Identical muscle scars were reported by Osmólska *et al.* (1972) for *Gallimimus*.

In overall form the scapulocoracoid of *S. altus* (UCMZ(VP)1980.1) is very like that of the other North American ornithomimids. It does, however, differ considerably from that of other theropods, as noted by Sternberg (1933) in his description of *O. edmontonicus*. In most theropods the depth of the coracoid plate greatly exceeds its length, and the posterior coracoid process is short, terminating in a curved apex ventral to the glenoid (text-fig. 3). A long, shallow coracoid plate with an attenuated coracoid process, an anterior flange extending from the supraglenoid buttress, and a high scapular prominence are all characteristic of the ornithomimid scapulocoracoid. These features are also present in the Mongolian ornithomimids *G. bullatus* (Osmólska *et al.* 1972) and *Archaeornithomimus asiaticus* (USNM 6567, as figured by Gilmore 1933).

Deinocheirus, however, sometimes considered to be an ornithomimid (Ostrom 1976a, 1978), has a more typical theropod scapulocoracoid. The scapular prominence is broken in *Deinocheirus*, but appears to extend considerably far dorsally, as in ornithomimids. There is, however, no accessory flange on the supraglenoid buttress and the coracoid is very deep dorsoventrally, and exhibits little extension of the posterior coracoid process.

(c) Humerus

The left humerus (text-fig. 4) of UCMZ(VP)1980.1 is complete, although the middle of the shaft has been crushed dorsoventrally. It closely resembles the humerus of *Gallimimus* and *Deinocheirus*, although the deltopectoral crest is not as strongly developed as that of the latter genus.

The distal end of the humerus is set at an angle of approximately 40° to the proximal end, a higher degree of torsion than is usual in ornithomimids. In *Gallimimus* this angle is 25–30° (Osmólska *et al.* 1972) and in NMC 8632, 12441, and ROM 840 it is closer to 20°. Osborn (1916) does not mention the degree of torsion in AMNH 5339 (*S. altus*), although his figures 7 and 8 indicate that some torsion is present. The high degree of torsion in UCMZ(VP)1980.1 may be due to post-mortem deformation, as humeral torsion is also high in ROM 851 (35–40°), which has been crushed in a similar manner.

The anterior tuberosity is fully as high as the head and proximally bears an elongate articular surface that juxtaposes the articular surface of the head (text-fig. 4). This accessory articular surface also encroaches on to the dorsal surface of the humerus and is as well developed as the head. It fits beneath the anterior flange of the glenoid during extreme humeral protraction. Distally, the anterior tuberosity merges gradually with the deltopectoral crest. The latter is poorly developed compared with that of other theropods, its apex being located less than one-fifth of the way along the humeral shaft. It is set at an angle of about 40° to the proximal end of the humerus. On the dorsal surface of the edge of the crest is a thickened lip which possibly marks the separation of the insertion of the M. pectoralis and the M. supracoracoideus.

Posterior to the deltopectoral crest, on the dorsal surface, a shallow depression extends along the humeral shaft, possibly marking the insertions of the deltoideus musculature.

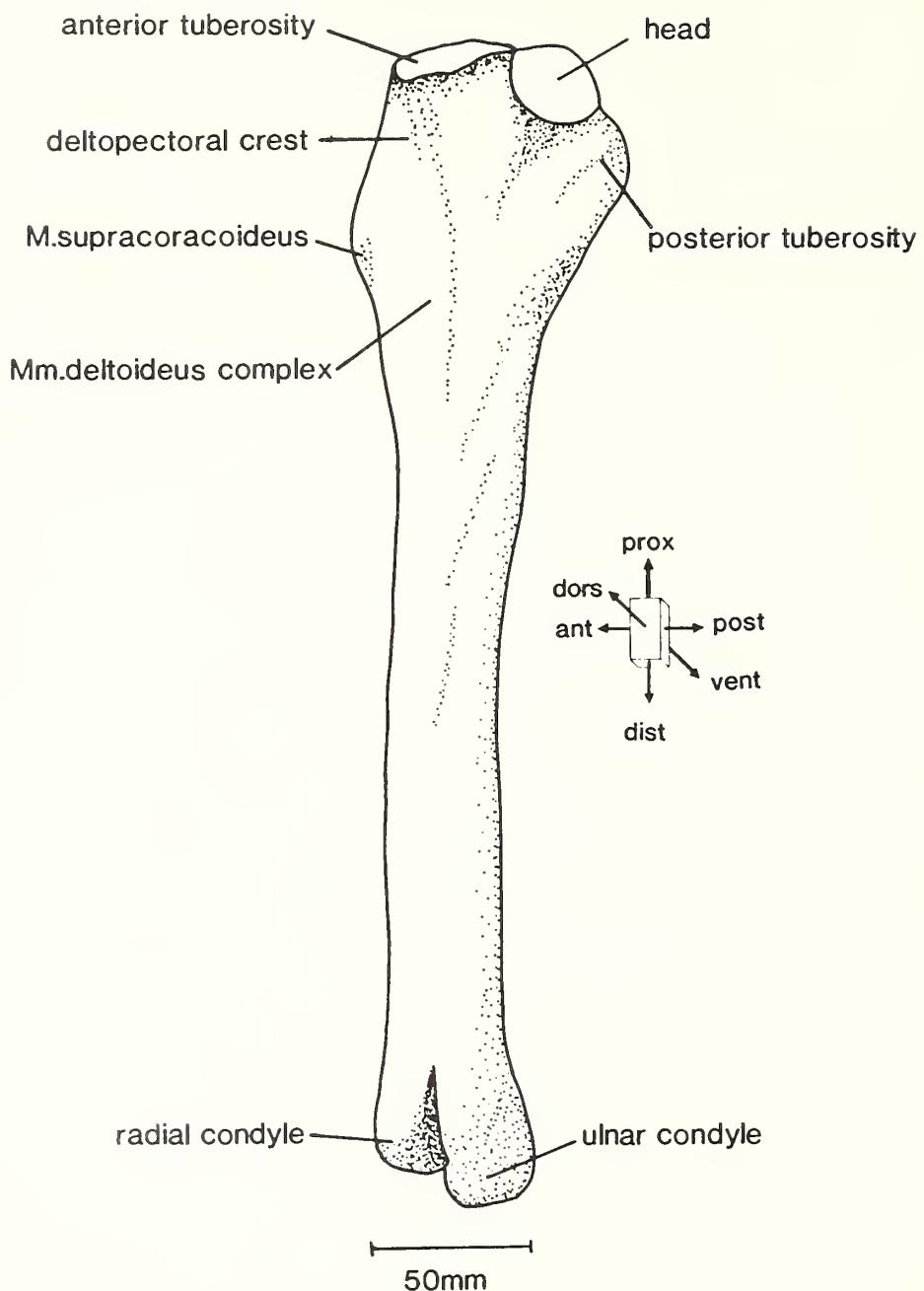
The posterior tuberosity is only moderately developed. It does not project far out from the shaft, as it does in *Deinonychus* or *Allosaurus*, but extends further along the shaft.

The distal end of the humerus is expanded into a pair of condyles. The ulnar, or posterior, condyle is the larger of the two, extends the furthest distally and is bulbous and symmetrical in plan. The anterior, (radial) condyle is narrow, elongated, and continuous with the ectepicondylar ridge. The two condyles are separated ventrally by a broad fossa. Dorsally the olecranon fossa is present only as a faint depression. The entire distal end of the bone has a rugose, porous surface texture, suggesting the presence of extensive articular cartilage.

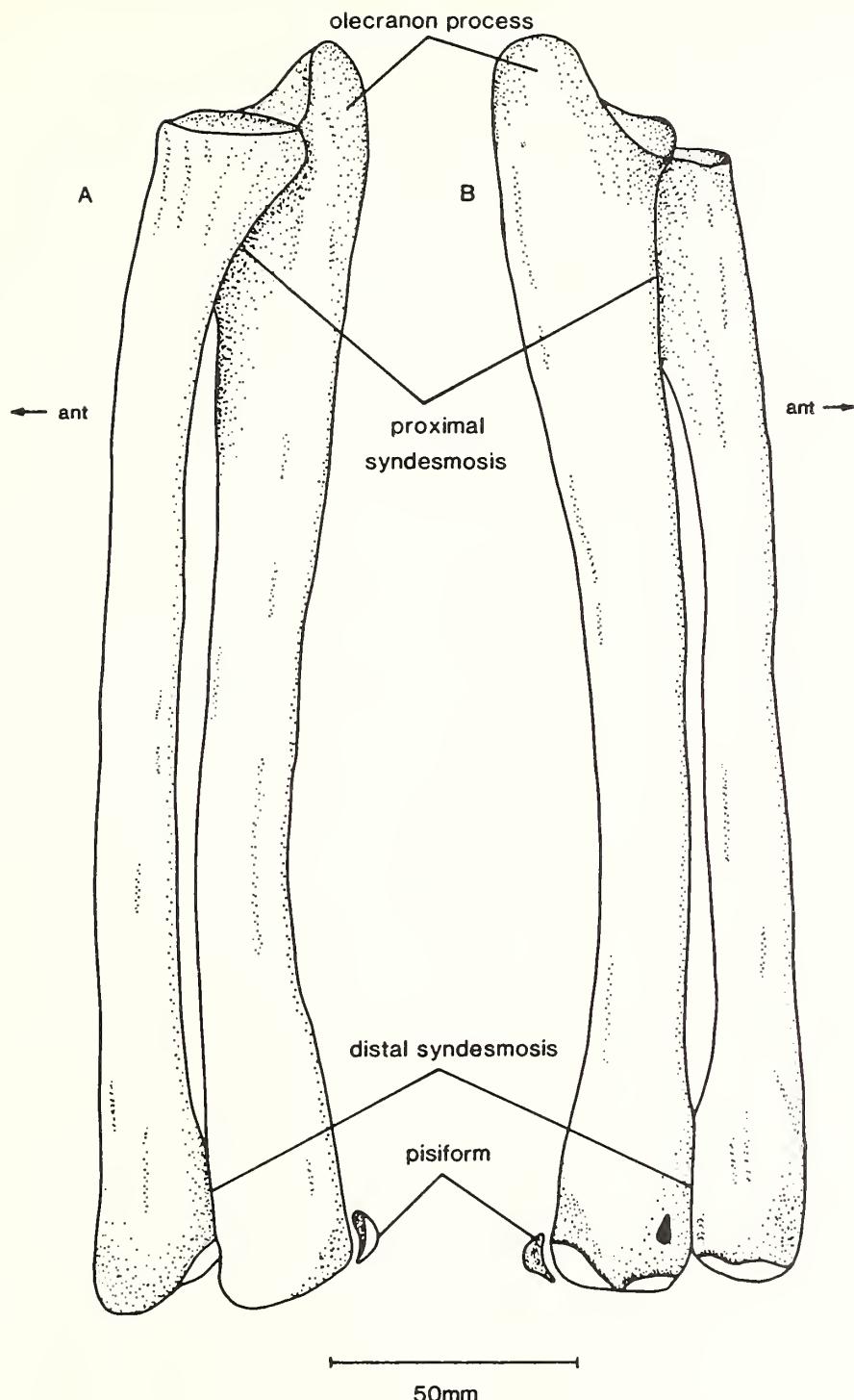
(d) Ulna

The ulna of UCMZ(VP)1980.1 resembles that of *S. altus*, as figured by Osborn (1916, fig. 8). It is triangular in cross-section and gently curved, being convex toward the radius (text-fig. 5). The olecranon process is long, extending 20 mm proximal to the articular surface of the radius. It is significantly deflected from the ulnar shaft, and manipulation of the osteological preparation at the elbow joint indicates that full extension of the forearm was possible. The concave articular facet for receipt of the radius is deep and well developed. The form of both the proximal and distal radioulnar articulations is suggestive of the presence of syndesmotic unions in life. Such joints, binding the elements by way of collagenous fibres, would permit slight play between the elements but limit rotatory ability.

The distal end of the ulna is crescentic and its anterior edge is flattened along its syndesmotic contact with the radius. On the ventral surface are two condyles separated by a broad, shallow groove (text-fig. 5). The anterior of these is only weakly developed, while the posterior one is larger. A small convexo-concave pisiform is situated adjacent to the posterior condyle. The concave surface of the



TEXT-FIG. 4. Left humerus of *Struthiomimus altus*, UCMZ(VP)1980.1. Dorsal view. M. supracoracoideus and Mm. deltoideus complex refer to the implied insertional areas for these muscles (see text for details).



TEXT-FIG. 5. Radius and ulna of *Struthiomimus altus*, UCMZ(VP)1980.1. A, dorsal view; B, ventral view.

pisiform fits snugly against the posterior ulnar condyle, forming a rotational surface between the ulna and the third metacarpal (text-fig. 6). The entire distal end of the ulna bears numerous striations, suggesting the presence of articular cartilage.

(e) Radius

The radius is almost straight, except at the proximal end where it curves toward the ulna. The proximal articular surface is oval and flat and thus fits perfectly the syndesmotic articular facet of the ulna, allowing little rotation (text-fig. 5).

Distally the radius is oval in cross-section, except at its contact with the ulna where it is extensively flattened. The distal end of the radius terminates almost 10 mm short of that of the ulna when the two elements are articulated, a point not evident in Osborn's (1916) illustration. This discrepancy in length reflects the form and disposition of the carpals, most of which are concentrated distal to the radius (text-fig. 6).

The distal articular surface of the radius is convex for articulation with the radiale, and the entire distal end of the radius is heavily striated.

(f) Carpus

All of the carpals are excellently preserved, three of them adhering to the distal end of the radius and one to the proximal surface of the metacarpals (text-fig. 6).

The radiale is ovoid in outline, convex distally and concave proximally where it fits the convex surface of the radius. The distal surface of the intermedium is convex and its dorsal outline triangular. The apex of the triangle forms a low ridge which extends along its proximal surface between the radius and ulna. Distally, between the radiale and intermedium, is a small, disc-like bone, probably a centrale. It thins rapidly toward its ventral surface and fits in a slight depression on the proximal end of metacarpal I. The fourth carpal is extremely flattened and closely adherent to the proximal surface of metacarpals I and II. It is so broad and irregularly shaped that it may represent two or more distal carpals in fusion and is here interpreted as distal carpals 2 and 3. The fifth carpal bone is the pisiform, already described under the consideration of the ulna.

Compared with the carpus of other theropods, that of *Struthiomimus* is most like that of *Albertosaurus*, as described by Lambe (1917), although the distal carpals appear to be more specialized. The carpus lacks the well-defined articular facets present in the carpals of *Deinonychus* (Ostrom 1969), and to a lesser extent *Allosaurus* (Madsen 1976). Apparently the carpus of *Struthiomimus* operated as a hinge-joint, permitting little or no rotation, but was not as 'stiff' as indicated by Gregory (in Osborn 1916).

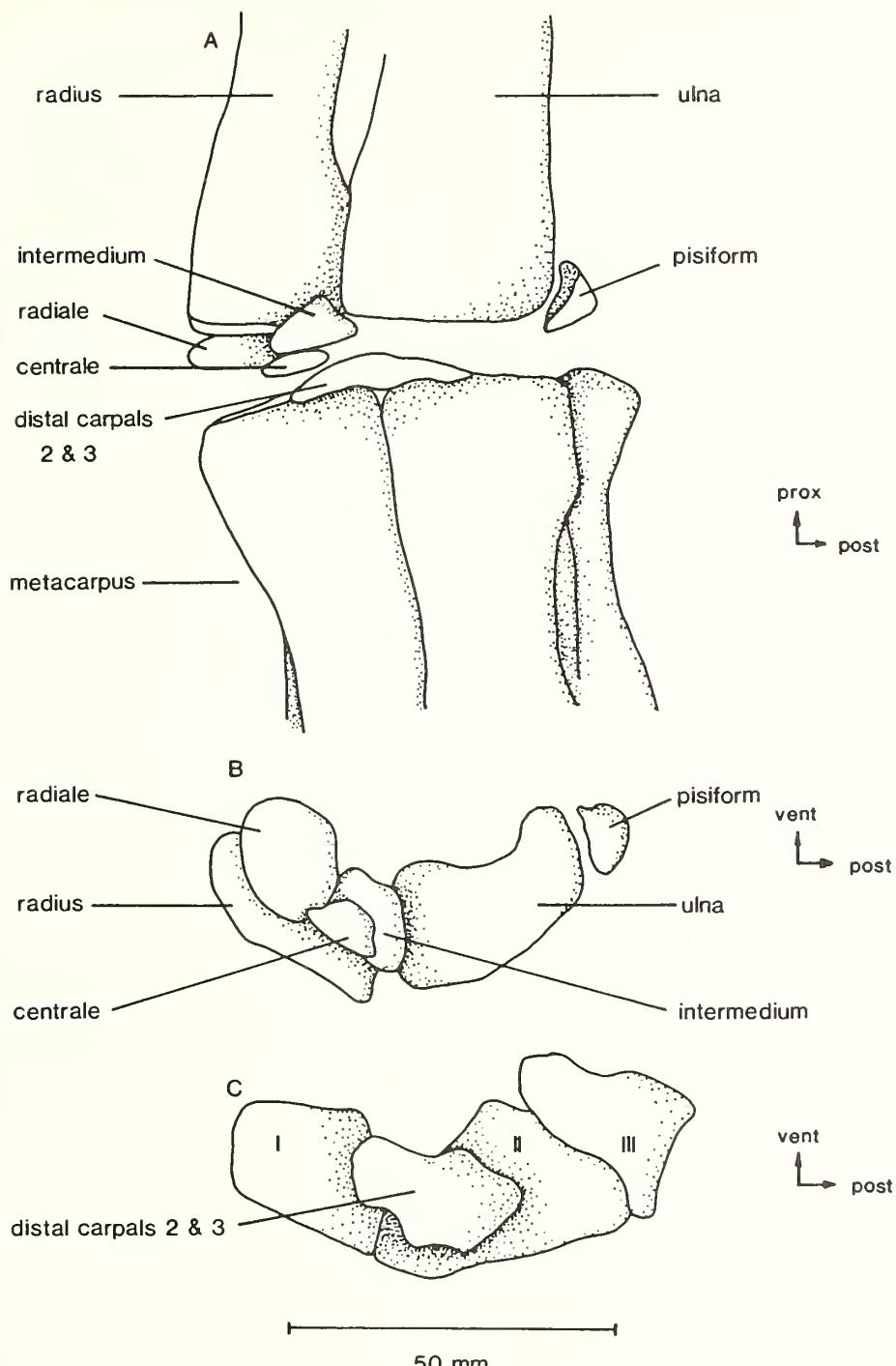
Galton (1971) illustrated six carpals in *Syntarsus* and briefly pared them with the carpals of *Struthiomimus*, although no attempt was made to describe them or to identify the individual elements. The broad, flat anterior distal carpal of *Syntarsus* (Galton 1971, figs. 1 and 3) resembles the fused distal carpals of *Struthiomimus*. The proximal carpals of *Syntarsus*, however, are much flatter than the corresponding elements of *Struthiomimus*, and there is no concentration of the carpals distal to the radius in *Syntarsus*.

Only one carpal is preserved in *Gallimimus*. This was considered by Osmólska *et al.* (1972) to be the radiale, but it bears no resemblance to any of the carpals of UCMZ(VP)1980.1. In ROM 840 the pisiform and radiale are preserved *in situ* and are like the corresponding bones of *Struthiomimus altus*.

(g) Manus

The manus of UCMZ(VP)1980.1 is very like that of AMNH 5339, as illustrated by Osborn (1916, fig. 3). The three metacarpals are subequal in length, metacarpal I being only slightly shorter than the others. All the metacarpals are tightly adpressed proximally and slightly arched. Distally metacarpal I is strongly divergent and its articular surface is rotated anteriorly.

Two types of joint structure are present in the manus (text-fig. 7). The articulations between the metacarpals and the proximal phalanges are of the ball and socket type, allowing considerable flexion, extension, and rotational movement. The interphalangeal joints, in contrast, are ginglymoid



TEXT-FIG. 6. Carpus of *Struthiomimus altus*, UCMZ(VP)1980.1. A, dorsal view; B, distal view of radius and ulna with attached carpals; C, proximal view of metacarpals with attached carpals. Note, C is represented as a mirror image to keep the alignment for the three parts of the figure constant.

and permit extension and flexion, but little or no rotation, as is usual in the manus of theropods. In the more typically raptorial theropods (e.g. *Ornitholestes*, *Allosaurus*, *Chirostenotes*), groove and keel articulations are present on the metacarpals of both digits I and II. The smoothly rounded distal metacarpal articulation is found on all three digits only in ornithomimids. This type of joint surface permits rotational movement and considerable hyperextension of the digits, but little or no flexion below the horizontal. Most of the flexion in the manus occurred at the interphalangeal joints.

Digit I

Metacarpal I is closely applied to metacarpal II for a little more than two-thirds of its length, and its posterior edge is flattened along this contact (text-fig. 7). Distally it diverges from the rest of the metacarpus and the distal articular surface is rotated anteriorly and dorsally. Most of the articular surface is smoothly convex. On the dorsal surface, however, there is a deep groove which guides the phalanx anterodorsally (away from the other digits) on extension (text-fig. 7). On flexion, digit I converges on the other two digits. Pits for the collateral ligaments are not as well developed as in Osborn's figure (1916, fig. 3). The pit is moderately developed on the posterior side (which is rotated to face dorsally), but very poorly developed on the anterior side.

The distal articular surface of metacarpal I in *Struthiomimus* differs from that of *Ornithomimus* (ROM 851, NMC 8632), in which metacarpal I is longer and not offset. In *Ornithomimus* the three metacarpals are parallel throughout and their distal articular surfaces are rotated posteriorly. The first metacarpal of *Struthiomimus* more closely resembles that of *Gallimimus*, which is also shortened and rotated anteriorly.

The first phalanx of digit I is the longest phalanx in the manus. Its proximal articular surface is concave and rotated anteriorly. Dorsally there is an enlarged tubercle which fits into the dorsal groove on the distal end of its metacarpal. Distally the grooved articular surface encroaches considerably on to the ventral surface of the phalanx, allowing the ungual to be flexed up to 65–70° below the horizontal. Pits for the collateral ligaments are very deep.

Digit II

The second metacarpal is flattened anteriorly along its contact with the first. On the proximal articular surface there is a low, broad ventral tubercle. During flexion of the wrist this tubercle fits into the shallow groove between the condyles on the distal end of the ulna (text-fig. 6). Distally the tubercle extends as a stout ridge on the ventral side of the metacarpal.

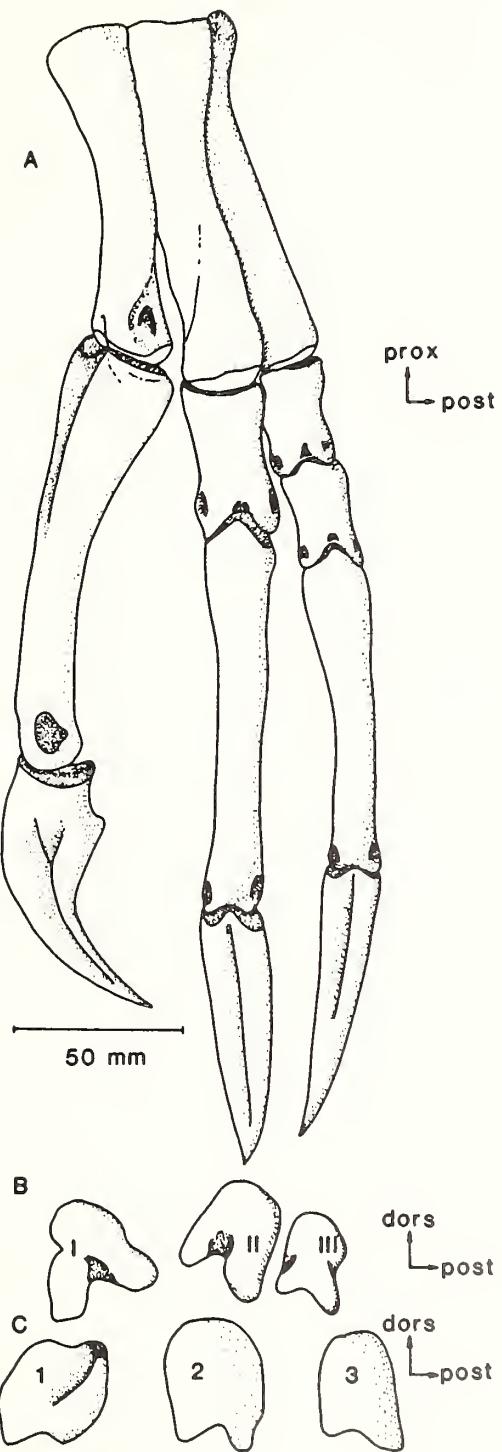
The distal articular surface of metacarpal II lacks any suggestion of the dorsal groove present on metacarpal I. The articular surface is slightly asymmetrical, extending further on the posterior than the anterior side. Pits for the collateral ligaments are only moderately developed.

In the first phalanx the proximal articular surface is smoothly concave, with ventral tubercles for the attachment of the collateral ligaments. The anterior tubercle is much more strongly developed than the posterior one. When articulated with the metacarpal, extension moves the phalanx dorsally and posteriorly away from digit I, and flexion moves it anteriorly and ventrally toward it. The grooved distal articular surface is well developed ventrally, allowing considerable flexion. Pits for collateral ligaments are only moderately developed.

The penultimate phalanx in digit II is very long, being longer than the metacarpal. Pits for the collateral ligaments are well developed and the distal articular surface is of the normal groove and keel type, extending far on to the ventral surface, permitting considerable flexion of the ungual.

Digit III

The third metacarpal is very slender and is closely adherent to metacarpal II. The distal articular facet is broadly rounded and symmetrically developed. Pits for the collateral ligaments are well developed and open distally, forming a broad groove. On the first phalanx the anterior tubercle for the collateral ligament is more strongly developed than the posterior one, making the proximal articular surface asymmetric in the same manner as the corresponding phalanx in digit II. Extension moves the phalanx posterodorsally.



TEXT-FIG. 7. Manus of *Struthiomimus altus*, UCMZ (VP)1980.1. A, dorsal view of entire manus; B, distal articular surfaces of the three metacarpals in natural position; C, proximal articular surfaces of phalanx 1 for the three digits. Note, for ease of comparison C is represented as a mirror image so that the alignment of the digits in the three parts of the figure may be kept constant.

The remaining phalanges in digit III all have the normal symmetrical phalangeal ridge and groove articulations. The grooves are very deep and form tightly interlocking joints which permit no lateral displacement. The pits for the collateral ligaments are correspondingly reduced. They are practically non-existent in phalanges 1 and 2, although they are strongly developed in the penultimate phalanx.

Unguals

In UCMZ(VP)1980.1 the ungual of digit I is complete but the extreme distal tips of unguals II and III have been broken. The unguals are very long and, when covered with a horny sheath during life, must have constituted more than one-third of the length of the manus. The unguals differ from the narrow, highly curved talons of typically raptorial theropods. They are longer, straighter, and broader, being slightly expanded proximoventrally. The articular surface covers the entire proximal end of the ungual and is strongly keeled. The flexor tubercle is not situated directly ventral to the articular surface as in most theropods, but is instead displaced distally about one-quarter of the distance along the phalanx. This greatly enhanced the mechanical advantage of the ungual flexor muscles.

All of the unguals were capable of being highly flexed, forming an angle of almost 70° with the long axis of the penultimate phalanx. The ungual of digit I is the most trenchant of the three, being narrower and more sharply curved than the other two.

The unguals of *Struthiomimus* differ slightly from those of other ornithomimids. Compared to *Ornithomimus*, as defined by Russell (1972), the unguals of *Struthiomimus* are much more robust and more strongly curved. (This, however, may be an allometric feature, as all the specimens identifiable as *Ornithomimus* are smaller animals.) In *Gallimimus* the unguals are shorter and curved, resembling the first ungual of *Struthiomimus*. Osmólska *et al.* (1972) indicated that only a minimal amount of flexion of the unguals was possible in *Gallimimus*, in contrast to the situation in *Struthiomimus* (see above).

Isolated ornithomimid unguals were illustrated and discussed by Ostrom (1969, 1978) in his consideration of the manus of *Deinonychus* and *Compsognathus*. The parameters he used to compare the unguals of theropods were the somewhat equivocal ratio of the length (extension) of the ungual relative to its height, and the angle formed between the cutting edge of the ungual and its arc of rotation. The ornithomimid ungual he used for comparison was that of *O. sedens*, and his figure clearly shows the long, straight, non-raptorial nature of the unguals of *Ornithomimus*. In text-fig. 8 the unguals of UCMZ(VP)1980.1 are compared with those of other theropods. Employing Ostrom's (1969) criteria for claw form and function, the ungual of digit I appears 'subraptorial' and is comparable to those of *Ornitholestes* and *Compsognathus*. The unguals of digits II and III are decidedly non-raptorial.

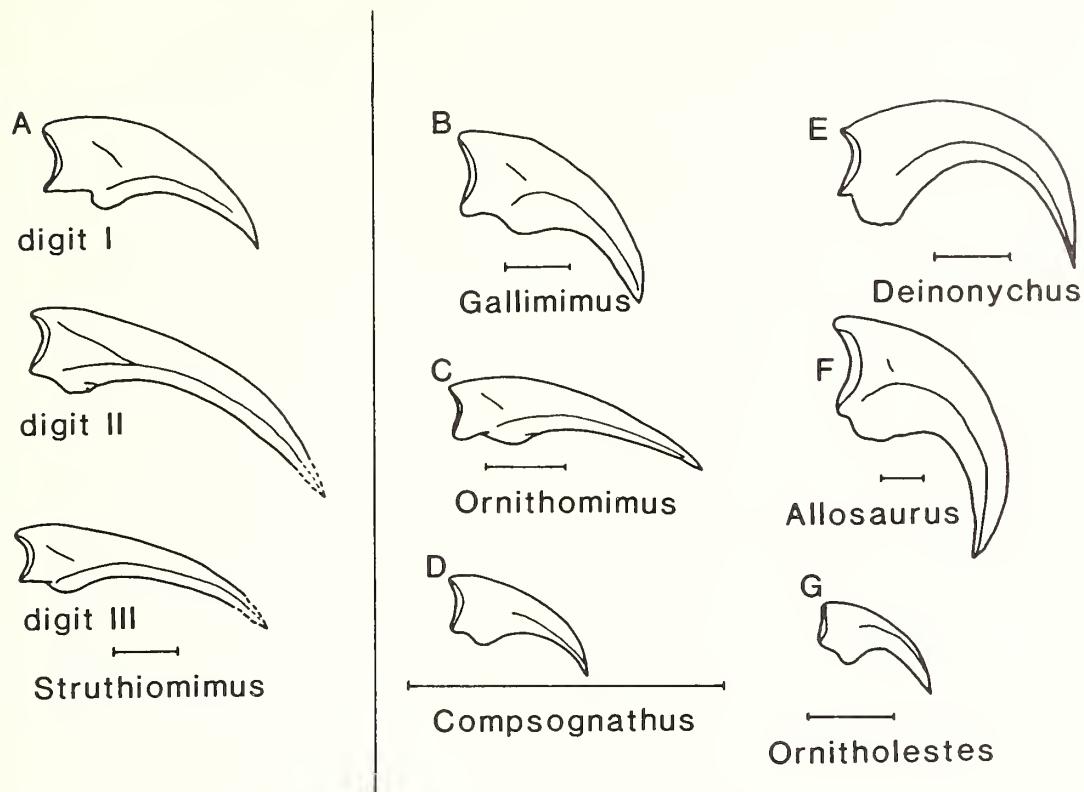
Another parameter useful in comparing unguals is the width of the articular surface, relative to the height, and this is a more reliable criterion for evaluating claw function than the degree of curvature. The true curvature of a claw is formed by its horny sheath, which is seldom preserved in the fossil record. In highly raptorial theropods the unguals are very narrow, with their articular height being almost twice their articular width. As can be seen from Table 1 the unguals of *Struthiomimus* are very broad, their width being almost equal to their height. Again this indicates that they are non-raptorial.

COMPARATIVE RESULTS—THE BASIS FOR A FUNCTIONAL ASSESSMENT

(a) Levels of comparison

In order to attempt to gain a mechanically feasible assessment of the form and possible functional attributes of the breast-shoulder apparatus and forelimb of *Struthiomimus*, comparisons of various types were made. Two 'obvious' comparative models come to mind. The first is a comparison with the equivalent structures of crocodilians in an attempt to investigate, as far as possible, similarities due to the existence of homologies (see, for example, Coombs 1978a; Gardiner 1982; Lauder 1981).

In overall body form, however, crocodilians and ornithomimid dinosaurs are relatively dissimilar and, by inference, it seems reasonable to suspect that their way of life was relatively dissimilar also.



TEXT-FIG. 8. The manual unguals of *Struthiomimus altus* compared with those of other theropods. The ungual of digit I is sub-raptorial and comparable with that of *Compsognathus*. The unguals of digits II and III are decidedly non-raptorial. The horizontal scale represents 20 mm. A, *S. altus*, UCMZ(VP)1980.1, digits I, II, and III; B, *Gallimimus bullatus*, cast at ROM; C, *Ornithomimus edmontonicus*, ROM 851; D, *C. longipes*, adapted from Ostrom (1978); E, *Deinonychus autirrhopus*, adapted from Ostrom (1969); F, *Allosaurus fragilis*, ROM 5091; G, *Ornitholestes hermanni*, adapted from Ostrom (1969).

This leads to the second comparison—that with ratite birds. Similarity of form here is not founded upon congruence of homologies but on homoplastic resemblance (similarity due to convergence). This comparison between ornithomimids and ratites can be considered to be somewhat ‘classical’ in approach, but one in which the basic assumptions have never been tested. The similarity of the ratite pectoral girdle to that of theropod dinosaurs has been most recently discussed by McGowan (1982).

To arrest the comparison at this point, however, and include only *Struthiomimus*, *Alligator*, and *Struthio* cannot fail to produce the expected result—that the breast–shoulder apparatus of the former is structurally and functionally similar to that of *Struthio* due to the great resemblance of form. Such an outcome may or may not be reasonable, but the addition of a third comparison allows a more objective assessment of the resemblances. This third comparison is with chameleons. Chameleons are unusual among normal-limbed lizards in the morphology of their breast–shoulder apparatus and in their mode of progression (Gasc 1963; Peterson 1984). Ostrom (1976a) stated that the narrow form of the scapula found in *Archaeopteryx* occurs only in obligate bipeds (birds, *Archaeopteryx*, and theropod dinosaurs). This is not accurate and, indeed, the primary shoulder girdle of chameleons bears a striking resemblance to that of coelurosaurians, a resemblance that has not gone unnoticed in the

past (Peterson 1973; Bakker 1975). Such similarity, without the influence of potential ancestral-descendant relationships affecting interpretation, forms the basis of the third level of comparison.

(b) Comparative material

The following specimens were dissected (numbers in parentheses refer to number of individuals): *Alligator mississippiensis** (1), *Caiman sclerops** (1), *Crocodylus niloticus* (BMNH 62.1.24.52) (2), *Struthio camelus** (1), *Dromiceius novaehollandiae** (2), *Chamaeleo* sp. (3), *Chamaeleo jacksoni** (1). Those specimens marked with an asterisk (*) form part of the University of Calgary Museum of Zoology anatomical collection. Representative skeletal material for all taxa represented was also examined.

(c) The breast-shoulder apparatus: general considerations

In order to be able to more fully appreciate and assess the structural and functional attributes of the breast-shoulder apparatus of *Struthiomimus*, it is necessary to first outline some general points of shoulder structure.

The primary subject of this paper, *Struthiomimus altus*, was apparently an obligate biped. Here the forelimbs and breast-shoulder apparatus have been released from their traditional role in quadrupedal locomotion and exhibit certain features associated with the relative freedom of the limbs. Such differences reflect not only different functions but also different mechanical potentials of the system.

In its most complete (primitive) form the breast-shoulder apparatus consists of paired primary girdles (the scapulocoracoid complexes) of endoskeletal origin, the secondary girdle complex, consisting of paired clavicles and a median unpaired interclavicle, of dermal origin, and an axial endoskeletal component, the sternum (together with its associated ribs). The costosternal complex forms an integral part of the breast-shoulder apparatus. As the primary girdle does not contact the vertebral column, the secondary girdle and costosternal complexes act as a system of braces preventing excessive displacement of the primary girdles but, at the same time, permitting a limited amount of movement with respect to the body wall. The relative structure of the various components, and the nature of the joints between them are, to a large extent, indicative of the functional potentials of the breast-shoulder apparatus (Dvir and Berme 1978).

The release of the forelimb from weight-bearing and its retention as a well-developed structure in an obligately bipedal, non-brachiating form such as *Struthiomimus* has influenced the structure of the breast-shoulder apparatus considerably. The multiple comparisons discussed below attempt to place the form of the apparatus seen in *Struthiomimus* into a biomechanically consistent framework.

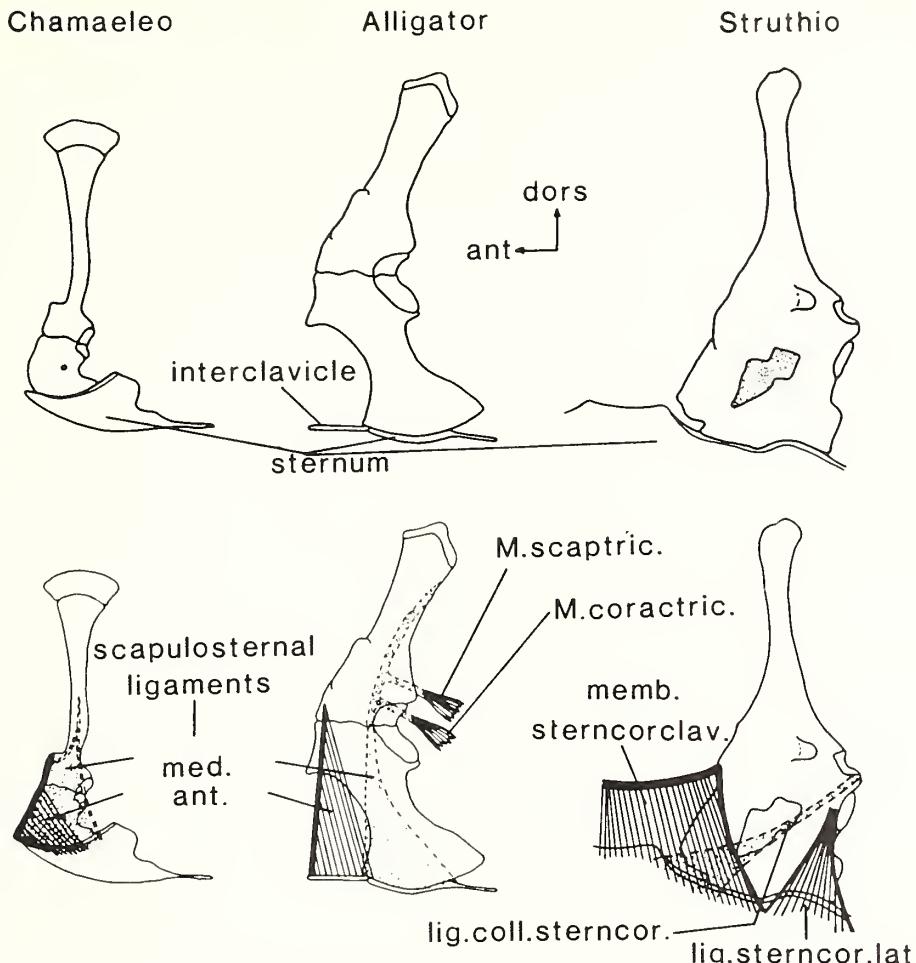
(d) Osteological comparative material

(i) Pectoral girdle of *Alligator* (text-fig. 9)

The breast-shoulder apparatus of crocodilians consists of the scapula, coracoid, interclavicle, and a costosternal system (Kalin 1929). The clavicle is absent and the scapula and coracoid are not fused into a scapulocoracoid plate. The scapula is flattened and blade-like, considerably broader than the scapula of the other forms being discussed, but is only slightly expanded distally. The blade faces laterally and is gently curved to fit the contours of the body wall. The anterior scapular prominence extends well above the level of the glenoid, as in *Struthiomimus*. Posteroventrally the scapula broadens into a stout supraglenoid buttress, on the dorsal lip of which is an oval, roughened area representing the point of origin of the scapular head of the triceps.

The glenoid fossa, to which both the scapula and coracoid contribute equally, is located at the posterior edge of the girdle and faces posterolaterally. The infraglenoid buttress of the coracoid is situated ventral, anterior, and slightly medial to the supraglenoid buttress.

The coracoid is short and deep, its greatest dimension being in the dorsoventral plane. There is no biceps tubercle. The infraglenoid buttress is strongly developed and is situated ventral, anterior, and slightly medial to the supraglenoid buttress. This part of the coracoid plate faces laterally.



TEXT-FIG. 9. Basic form of the primary girdle of the three comparative models discussed in the text. All are viewed from the developmentally lateral aspect regardless of their actual orientation in life. The torsion of the primary girdle of *Struthio* has been artificially removed for ease of presentation. Upper row, primary girdles only; lower row, girdles with major ligament systems superimposed. Ligaments outlined in dashed lines and with their expanse stippled are located on the medial face of the girdle. Each girdle has been drawn to the same dorsoventral linear dimension for ease of comparison. Abbreviations: ant., anterior; lig. coll. sterncor., ligamentum collateralia sternocoracoidea; lig. sterncor. lat., ligamentum sternocoracoideum laterale; M. coractric., M. coracotriceps; M. scaptric., M. scapulotriceps; med., medial.

Ventral to the glenoid the coracoid curves ventrally and medially to meet the sternum. Posteriorly it forms a small but distinct posterior coracoid process. The ventral edge of the coracoid abuts the lateral edge of the sternum in a frontal plane. The coracosternal angle (the angle the coracosternal articulation makes with the sagittal axis of the sternum) is low.

(ii) Pectoral girdle of *Struthio* (text-fig. 9)

In most birds the forelimb is modified for flight and the morphology of the sternum, coracoid, and limb elements are considerably altered from the 'typical' tetrapod form. In ratites flight has been

secondarily lost (Cracraft 1974), the scapula and coracoid are fused into a single plate and the humerus is less severely rotated.

In *Struthio* the secondary girdle is absent. The pectoral girdle consists only of the scapula and coracoid, fused into a single plate. In this respect the shoulder girdle of *Struthio* resembles that of *Struthiomimus* and other theropods, although no suture is present between the two bones. The distal parts of the forelimb of *Struthio* are much reduced and the shoulder structure is reflective of this. The glenoid fossa is very small relative to the size of the girdle and faces laterally. There is a marked flexure between the scapula and the coracoid, with about 60° of torsion between the plane of the two bones.

Deserving of particular mention is the orientation of the scapulocoracoid plate in life. Whereas in *Alligator* the coracoid is elongated and oriented ventromedially to abut the coracoid sulcus of the sternum, the coracoid of *Struthio*, as is the case in birds in general, has been rotated anteromedially, in association with the reorientation of the coracoid sulcus of the sternum. Here the coracoid abuts the functionally anterodorsal aspect of the sternum and the coracosternal angle is very high. The broad coracoid plate is thus oriented anterolaterally and, as a consequence, the glenoid has come to lie in a much more lateral position. Apart from its torsion the scapulocoracoid plate is essentially planar, the coracoid showing little angulation. The ventral border of the coracoid is straight, not curved, and the posterior coracoid process is reduced.

The coracoid plate is very broad and triangular. There is a large centrally located foramen, but it is not homologous with the coracoid foramen of reptiles and is a derived feature of ratites (Cracraft 1974). Broom (1906) indicated that, developmentally, it is formed by an anterior extension of the scapula ('prescapular process') which extends ventrally to join the coracoid at the sternum.

Two distinct tuberosities are present on the scapulocoracoid plate of *Struthio*. The larger of the two was referred to as the 'coracoid tuber' by Cracraft (1974) and was stated to be unique to some ratites. Broom (1906) referred to this tuberosity as the 'acromion process' and McGowan (1982), in his work on the shoulder girdle of kiwis, referred to it as 'the acromial tuberosity'. It is the site of origin of much of the deltoid musculature and it is here referred to as the 'scapular prominence', although its homology with the scapular prominence in other aequipalavate forms has not been demonstrated.

The second tuberosity is situated on the coracoid, ventral and slightly anterior to the glenoid. It is oval in shape with its long axis oriented dorsoventrally. McGowan (1982) calls a similar tuberosity in the kiwi the 'acrococoracoid process'. This structure, by correlation with muscle origins, is the biceps tubercle. It is situated much closer to the glenoid than is the biceps tubercle in *Struthiomimus*.

(iii) Pectoral girdle of *Chamaeleo* (text-fig. 9)

In outline the pectoral girdle of *Chamaeleo* resembles that of both *Struthio* and theropod dinosaurs. The secondary girdle is absent and the pectoral girdle consists only of a scapula and coracoid, which are fused into a single scapulocoracoid plate. Skinner (1959) reported the transient appearance of clavicles and an interclavicle during chameleontid development, but stated that they disappeared rapidly.

The scapula is a long, thin rod which lacks fenestrae. Ventrally it expands into a scapular prominence anteriorly and the glenoid fossa posteriorly. The scapular prominence is well developed (Siebenrock 1893; Skinner 1959), but does not extend far dorsally, reaching only a little above the level of the supraglenoid buttress. The scapula contributes to a little over one-third of the glenoid fossa and there is a well-developed supraglenoid buttress.

The remaining two-thirds of the glenoid is formed by the unfenestrated coracoid. There is a well-developed infraglenoid buttress which is situated ventral and slightly medial to the supraglenoid buttress. The coracoid is relatively flat, lies in the same plane as the scapula, and faces laterally. The ventral edge is extended posteriorly to form a posterior coracoid process. While this posterior coracoid process is not as well developed as in *Struthiomimus*, it is more prominent than in either *Struthio* or *Alligator* and is comparable to that of many theropods (e.g. *Dromeosaurus* TMP P79.29.1, *Albertosaurus* NMC 2120).

Anterior to, and considerably ventral to, the glenoid is the biceps tubercle. It is in a similar position to the biceps tubercle in *Struthiomimus*, although it is not as prominent as in that genus. It is not at all

like the biceps tubercle of *Struthio*, which is an elongate prominence situated much closer to the glenoid.

The coracoid abuts the anterolateral edge of the sternum *via* a dorsally facing coracoid sulcus. The coracosternal angle is low, being about 30°.

Lecuru (1968a, b) distinguished particular features of the lacertilian breast-shoulder apparatus associated with arboreal locomotion, including reduction in the number of scapulocoracoid fenestrae, a tall, narrow scapular blade, modifications of the anteroventral border of the coracoid, and a relatively ventral acromion process (or scapular prominence). Such features reflect adaptation for mobility of the primary girdle on the body wall (Peterson 1973).

(e) Ligament systems of the breast-shoulder apparatus

The ligaments of the breast-shoulder apparatus are seldom considered in studies of the shoulder region, but form an extremely important part of this apparatus when considered as a functional complex. Indeed, consideration of the breast-shoulder apparatus without consideration of the ligament systems means that the functional potential of this apparatus cannot be fully appreciated. Obviously, such systems cannot be reconstructed for fossil forms in any detail, but an appreciation of their architecture in living forms permits some predictive statements to be made.

(i) *Alligator*

In crocodilians a stout anterior scapulosternal ligament is present (text-fig. 9). It arises from the ventral aspect of the scapular prominence and from here fans out as it passes ventrally. Anteriorly it is thickened and forms a stout band which attaches to the anteriormost extremity of the interclavicle. From here it passes posteriorly as a thin sheet which attaches to the interclavicle and the ventral border of the coracoid sulcus of the sternum. It restricts the degree of excursion that can occur at the coracosternal articulation, especially when the humerus is depressed and the limbs become semi-erect. The stout anterior band has the orientation of a clavicle but represents a tensile rather than a compressive structure. Muscular origin from the anterior scapulosternal ligament is meagre.

The medial scapulosternal ligament is continuous with the anterior one on the medial face of the primary girdle. The medial ligament spans the dorsal aspect of the coracosternal articulation and tapers as it passes dorsally across the medial face of the coracoid. At the point where the coracoid curvature is most pronounced it separates from the anterior ligament and attaches to the medial face of the coracoid. From here a slender strand continues dorsally across the coracoscapular joint, passing anterior to the glenoid, and attaches to the medial face of the scapula on its posterior aspect, relatively high up on the shaft. Just dorsal to the glenoid a band of tissue associated with the origin of the M. scapulotriceps diverges at right angles from the main course of the ligament, and slightly ventral to this are bands associated with the M. coracotriceps.

(ii) *Struthio*

The ligaments of the breast-shoulder apparatus of birds are complex and their nomenclature profuse (see Baumel 1979, pp. 148–151). Essentially, however, the arrangement of ligaments about the coracoid is quite similar to that found in *Alligator*. The furcula, when present, is involved, but the absence of this structure in *Struthio* relieves some of the complication.

Two primary sheets can be recognized. The membrana sternocoracoclavicularis extends from the rostral border of the sternum and crosses the coracosternal articulation to attach to the anterior part of the coracoid and the region of the relatively reduced scapular prominence (text-fig. 9). The membrana sternocoracoclavicularis can be topographically equated with the anterior scapulosternal ligament described for *Alligator* (above). In the case of *Struthio* the interclavicle is absent and the orientation of the coracoid on the sternum is different, but essentially the same topographical points are interconnected. The ligamentum sternocoracoideum laterale of *Struthio* governs the ventrolateral aspect of the coracosternal articulation (text-fig. 9).

The developmentally dorsal lip of the coracoid sulcus of the sternum is spanned by the ligamentum collateralia sternocoracoidea in *Struthio* (text-fig. 9). It passes on to the medial face of the coracoid

for much of its length. There is no association with the M. scapulotriceps and no extension up on to the scapular shaft. The M. coracotriceps, generally a vestigial muscle in birds (Berger 1966), is absent in *Struthio* and thus also has no association with the ligamentum collateralia sternocoracoidea.

Topographically the ligamentum collateralia sternocoracoidea of *Struthio* occupies the same basic position as the medial scapulosternal ligament of *Alligator* (above), but morphologically it is more equivalent to the same ligament of *Chamaeleo* (see below). The three ligaments together (membrana sternocoracoclavicularis, ligamentum sternocoracoideum laterale, and ligamentum collateralia sternocoracoidea) govern the mobility at the coracosternal articulation. Mobility of this joint in birds, however, differs from that typically seen in reptiles and the implications of this with respect to coracoid shape and orientation will be more fully considered below.

(iii) *Chamaeleo*

In *Chamaeleo* the coracoidal arm of the medial scapulosternal ligament of other lizards is absent, permitting greater mobility at the coracosternal articulation (Peterson 1973) (text-fig. 9). There is no connection between the forearm extensor musculature and the medial scapulosternal ligament and the absence of a secondary girdle has, as a correlate, the absence of the mesocleidosternal ligament of other lizards (Peterson 1973).

Among lizards, only in chameleons has an anterior scapulosternal ligament been reported. It is very similar in form to that described for *Alligator* (see above), but no interclavicle is present. The anterior scapulosternal ligament arises from the scapular prominence and passes ventrally along the anterior margin of the scapulocoracoid plate, becomes free of the anterior margin of the girdle, and passes slightly anteroventrally to meet its fellow of the opposite side in the ventral midline. The bilateral ligaments fuse to give rise to a short sagittal ligament which passes posteriorly to attach to the ventral lips of the sternal grooves where they approach each other. Broad bands of fascia connect the transverse and longitudinal arms of the ligament (Peterson 1973).

(f) Comparative myological material

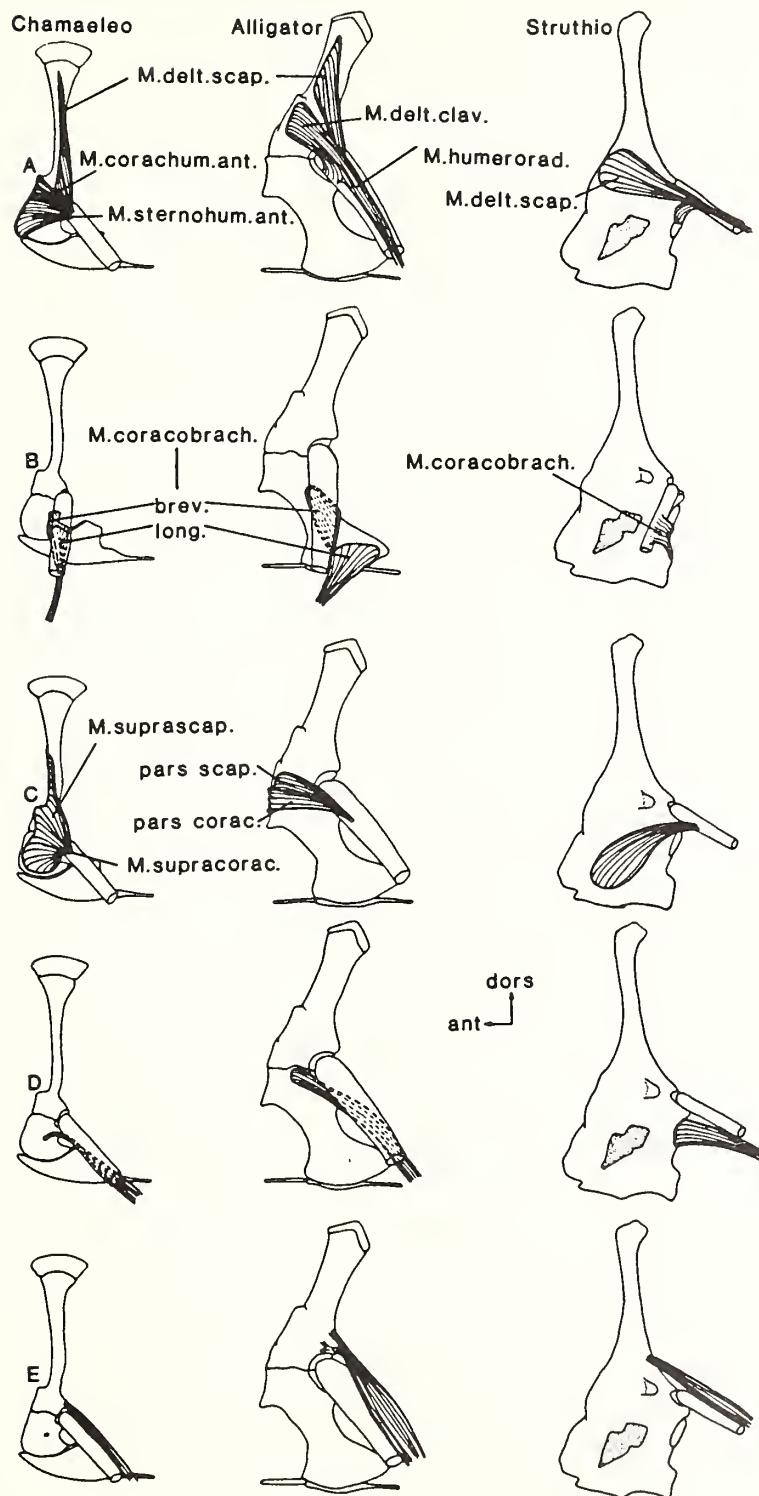
No attempt has been made to reconstruct all the muscles of the pectoral region of *Struthiomimus*; rather we have restricted our work to those muscles for which there is good evidence in the form of muscle scars. The muscles considered are the following: (i) M. deltoides scapularis; (ii) M. deltoides clavicularis; (iii) M. supracoracoideus; (iv) M. coracobrachialis; (v) M. biceps brachii; (vi) M. scapulotriceps. Terminology used is that of Romer (1944), unless otherwise noted.

(i) M. deltoides scapularis (text-fig. 10A) (M. teres major, Haughton 1867a; M. dorsalis scapulae, Fürbringer 1876)

In *Alligator* this muscle arises from the anterolateral surface of the scapular blade. It has a tendinous insertion on the anterodorsal surface of the humerus, just distal of the head.

In *Struthio* the scapulodeltoid (M. deltoides major, Berger 1960) arises from the scapular prominence and the anteromedial edge of the scapulocoracoid plate. There is a small secondary head arising from the biceps tubercle. It inserts along the dorsal surface of the humerus, extending more than half way along its shaft. Similar origin and insertion patterns, except for the small accessory

TEXT-FIG. 10. The form of the muscles discussed for the three comparative models. All are viewed from the (primitively) lateral aspect of the primary girdle. The humerus has been represented in simplified form as a cylindrical rod. A, the Mm. deltoideus complex; B, M. coracobrachialis with the humerus represented in a protracted and depressed attitude. Dashed portions represent parts of the muscle lying ventral to the humerus; C, M. supracoracoideus; D, M. biceps brachii. Dashed portions represent parts of the muscle lying ventral to the humerus; E, M. scapulotriceps. Abbreviations: brev., brevis; long., longus; M. corachum. ant., M. coracohumeralis anterior; M. coracobrach., M. coracobrachialis; M. delt. clav., M. deltoides clavicularis; M. delt. scap., M. deltoides scapularis; M. humerorad., M. humeroradialis; M. sternohum. ant., M. sternohumeralis anterior; M. supracorac., M. supracoracoideus; M. suprascap., M. suprascapularis; pars corac., pars coracoideus; pars scap., pars scapularis.



head, which appears not to have been reported previously, are described for the emu and rhea by Haughton (1867b, c). The accessory head may be the homologue of the *M. deltoideus minor, caput ventrale* of carinate birds (Van den Berge 1979, p. 200).

The absence of an origin of the scapulodeltoid from the scapular blade and the increased insertional length of this muscle are typical avian characteristics (Berger 1960). The origin of this muscle has been brought to lie in a plane which essentially runs along the scapulocoracoid suture and the glenohumeral joint. In so doing its leverage has been altered. Its involvement in humeral elevation is decreased but its part in protraction is enhanced. Its transformation in birds may be associated with the reorientation of the scapulocoracoid and the relative immobility of this element.

In *Chamaeleo* the scapulodeltoid arises from the anterolateral surface of the scapular blade and inserts at the proximal end of the deltopectoral crest of the humerus.

- (ii) *M. deltoides clavicularis* (text-fig. 10A) (*M. deltoides scapularis inferior*, Fürbringer 1876; *M. scapulohumeralis anterior*, Romer 1922; Coombs 1978a).

None of the forms under consideration have a clavicle. In *Alligator* this muscle arises from the external surface of the scapular prominence, crosses the glenohumeral joint, and inserts on to the dorsal surface of the humerus, medial to the deltopectoral crest. Its insertion interdigitates with the origin of the *M. humeroradialis* (Alix 1874), a developmental derivative of this muscle (Romer 1944).

In birds this muscle is known as the *M. tensor propatagialis brevis* (Van den Berge 1979), or the *Mm tensores patagii longus et brevis* (Berger 1966). It is absent in *Struthio*, possibly in association with the loss of flight and the reduction of the forelimb and patagium.

In *Chamaeleo* the clavicular deltoid is considerably altered from the usual lacertilian situation and has been subdivided into the *M. coracohumeralis anterior* and the *M. sternohumeralis anterior* (Skinner 1959). Their continuous origin is from the anterior scapulosternal ligament, and their insertion is on to the dorsal surface of the deltopectoral crest.

- (iii) *M. coracobrachialis* (text-fig. 10B)

In crocodilians the *M. coracobrachialis longus* is usually considered to be absent (Fürbringer 1876; Romer 1944; Holmes 1977). The most prominent component of the *M. coracobrachialis* (*M. coracobrachialis brevis*, Romer 1944) takes origin from much of the lateral surface of the coracoid plate. It inserts on the proximal ventral surface of the humerus, between the deltopectoral crest and the posterior tuberosity. Dissection of both *Crocodylus* and *Alligator*, however, indicates that this muscle arises by way of two heads—the *M. coracobrachialis brevis* (described above) arising from the broad, external surface of the coracoid plate, and the *M. coracobrachialis longus* having its origin from the posterior coracoid process. The muscle can also be separated into two heads at its insertion on the humerus.

In *Struthio* the single *coracobrachialis* (*M. coracobrachialis externus*, Romer 1944; *M. coracobrachialis posterior*, Berger 1960; *M. coracobrachialis cranialis*, McGowan 1982) is considered to be homologous, at least in part, to the *M. coracobrachialis brevis* of reptiles (Romer 1944). It arises on the posterolateral edge of the coracoid plate, ventral to the glenoid, and inserts on the ventral surface of the proximal end of the humerus, between the deltopectoral crest and the posterior tuberosity. In *Struthio* it is strongly developed.

The reorientation of the coracoid on the sternum, the reduction of the posterior coracoid process, and the lateral orientation of the glenoid have had a profound influence on the functioning of the *M. coracobrachialis* in *Struthio*. Leverage in humeral retraction is markedly reduced while its role in depression has been enhanced. As in *Chamaeleo* (see below) it has essentially become a part of the glenoid cuff musculature, playing a role in control at the glenohumeral articulation.

In *Chamaeleo* the *M. coracobrachialis longus* arises from the postero-lateral surface of the coracoid plate and inserts on the entepicondyle of the humerus. The regression of the posterior coracoid process has reduced its leverage in humeral retraction. The *M. coracobrachialis brevis* arises on the posterior edge of the coracoid, ventral of the glenoid. It inserts on the ventral surface of the humerus, about half-way along the shaft.

(iv) M. supracoracoideus (text-fig. 10c)

In *Alligator* the supracoracoideus is divided into two heads. The pars scapularis (Fürbringer 1876) arises on the lateral surface of the scapula, ventral to the scapular prominence. The pars coracoideus (Fürbringer 1876) arises from the medial surface of the coracoid, ventral to the scapular prominence. It curves around the anterior edge of the coracoid to join with the pars scapularis. Together they insert on the deltopectoral crest of the humerus, medial to the insertion of the M. pectoralis.

In *Struthio* the M. supracoracoideus arises from the broad, anterior surface of the coracoid plate, covering the large coracoid foramen. It soon becomes tendinous, its tendon passing between the scapular prominence and the biceps tubercle. The tendon inserts on the dorsal surface of the humerus, just distal to the head. The importance of the biceps tubercle in supporting the tendon of the M. supracoracoideus in birds was noted by Walker (1972) and Ostrom (1976b). The particular morphology of the M. supracoracoideus in *Struthio* may again be related to the secondary absence of flight capabilities. Its role is in humeral elevation and protraction, but its effectiveness in the former is limited by the relatively ventral position of the biceps tubercle. Similar descriptions of this muscle have been furnished by Haughton (1867b, c) for the emu and rhea.

In *Chamaeleo* the supracoracoideus is subdivided into a dorsal M. suprascapularis and a ventral M. supracoracoideus (Skinner 1959; Peterson 1973). The suprascapularis originates on the anterolateral surface of the scapular ramus, adjacent to the anterior border of the M. scapulodeltoideus. The ventral M. supracoracoideus takes origin from the anterolateral surface of the coracoid. The two branches have a common insertion at the humeral head, in the plane of the glenohumeral joint.

(v) M. biceps brachii (text-fig. 10D)

There is little variation in the biceps in all the forms considered. It arises on the external surface of the coracoid, anteroventral to the glenoid, and inserts on the proximal end of the radius and ulna. In *Struthio* it is considerably reduced in size, probably in association with the reduction in size of the antebrachium. Macalister (1867) reported a separate slip of this muscle arising from the M. coracobrachialis in *Struthio*, but we did not locate this, and neither did Haughton (1867c) in his examination of the rhea. In *Struthio* and *Chamaeleo* a distinct biceps tubercle is present.

(vi) M. scapulotriceps (text-fig. 10E)

In *Alligator* this muscle (M. anconeus scapulae lateralis externus, Fürbringer 1876; M. triceps caput scapularis, Romer 1922) has a complex origin. It arises by way of three tendons: from the medial surface of the scapula, dorsal to the glenoid; from a branch of the medial scapuloternal ligament; and from the lateral surface of the scapula, at the supraglenoid buttress. It inserts on the olecranon of the ulna.

In both *Struthio* and *Chamaeleo* the M. scapulotriceps arises by a single head from the lateral surface of the scapula, dorsal to the glenoid fossa. It inserts on the olecranon process. In *Struthio* it is greatly reduced in size and takes origin considerably further dorsal on the scapula with respect to the glenoid. In *Chamaeleo* origin is close to the glenohumeral joint, but has no connection with the medial scapuloternal ligament. This lack of connection with the ligaments of the breast–shoulder apparatus is a major contributory factor to the enhancement of forereach.

DISCUSSION

(a) The form and orientation of the primary girdle of *Struthiomimus* in the context of the comparative models

On reviewing the three comparative models, it is immediately apparent that, as expected, there are few overt similarities between the shoulder girdle of *Struthiomimus* and that of *Alligator*. The shoulder girdle of *Alligator* must fulfil the role of both locomotion and support of the animal, and neither of these demands apply to the bipedal *Struthiomimus*.

In comparing the shoulder girdle of *Struthiomimus* with that of *Struthio* and *Chamaeleo*, a number of similarities are apparent. In all three forms the secondary girdle is absent, there is a single scapulocoracoid plate, a long thin scapular blade, and a biceps tubercle.

On closer comparison, however, these similarities in *Struthio* appear to be rather superficial. The scapulocoracoid of *Struthio* consists of a very large coracoid plate but a greatly reduced scapula. This is reflective of the reduced forelimb in the ostrich. The coracoid faces anteriorly and there is about 60° of torsion between the planes of the scapula and the coracoid. The coracosternal articulation is basically a hinge-type structure (Baumel 1979) with a markedly transverse orientation in association with a similar orientation of the coracoid sulci. Manipulation of articulated elements and reports of rhea (Porteijle 1925; Raikow 1969, fig. 3) and ostrich (Sauer and Sauer 1966, figs. 16, 18, and 20) behaviour indicate that the mobility of the forelimbs, important in courtship and aggression, is restricted to the glenohumeral joint and joints distal to this. The ability of the coracoid to slide in the coracoid sulcus is severely limited, and is tightly bound by the ligaments of the breast-shoulder apparatus.

In contrast the scapulocoracoids of both *Struthiomimus* and *Chamaeleo* have well-developed scapulae. There is no torsion and the entire scapulocoracoid faces laterally. Indeed the pectoral girdle of *Chamaeleo* so closely approaches the typical theropod condition that the only obvious difference is that of size. The pectoral girdle of *Chamaeleo*, however, differs markedly from that of terrestrial, sprawling lizards. In terrestrial forms, such as *Iguana*, the secondary girdle is present and the scapulocoracoid is shorter, broader, fenestrated and the coracosternal angle is high. These differences were discussed by Peterson (1971, 1973), who pointed out that the features typical of *Chamaeleo* are associated with the mobility of the scapulocoracoid during arboreal locomotion.

Mobility of the scapulocoracoid plate relative to the sternum plays an important role in the locomotion of many lizards (see Jenkins and Goslow 1983 for an account of locomotion in *Varanus*) but it is particularly well developed in chameleons. The forelimbs of chameleons have been brought closer under the body, in what Bakker (1971) called the 'semi-erect' stance. The absence of a clavicle, the low coracosternal angle, and the modifications of the ligaments of the breast-shoulder apparatus permit the coracoid to slide anteriorly and posteriorly in the coracoid sulcus, concomitantly rotating the girdle in the parasagittal plane. The long scapular blade of chameleons increases the leverage of the muscles that attach dorsally and rotate the girdle. The outcome of girdle rotation in *Chamaeleo* is to increase forereach of the pectoral limb as the animal moves through a discontinuous network of branches (Peterson 1973, 1984).

The relevance to dinosaurs of Peterson's work on chameleonid lizards was recognized by Bakker (1975), but he applied it to quadrupedal dinosaurs. These would incur problems of weight support irrelevant to chameleons because of their small size, and unencountered in bipedal dinosaurs. The biomechanical implications of scapular rotation in quadrupedal dinosaurs were evaluated by Coombs (1978b) and found to be incompatible with the basic morphology of these forms. In *Struthiomimus*, however, the forelimbs are freed from the role of locomotion and weight support.

Considerable mobility also exists in the primary girdle of crocodilians. As in both *Chamaeleo* and *Struthiomimus*, the primary girdle faces laterally and the coracosternal angle is low. At moderate speeds crocodilians exhibit the high walk, essentially a trotting gait (Sukhanov 1968; Whetstone and Whybrow 1983). With increasing speed the high walk gives way to the gallop (Zug 1974; Webb and Gans 1982). Lateral bending in the trunk is not pronounced, this being reflected in the nature of the intervertebral articulations (Hofstetter and Gasc 1969). The intergirdle distance is relatively short (only 15 vertebrae between girdles) and the animals are short-coupled (Peabody 1959). In the relative absence of whole body movements which shift the primary girdle (Daan and Belterman 1968), the rotation of the girdle in the parasagittal plane, with respect to the sternum, performs a similar function.

Thus, the scapulocoracoid plate in crocodilians is mobile in association with speed, while in chameleons it is associated with movement through a discontinuous substrate (Peterson 1984). In both cases, however, the end result is increased forereach.

Another example taken from within the lizards serves to corroborate the utility of the comparisons

based upon *Chamaeleo*. Most geckos are dorsoventrally depressed lizards that exhibit sprawling locomotion with the proximal segments of the limbs held out to the sides of the body (Russell 1975). In one genus, however, there has been a remarkable departure from this typical facies—*Uroplatus* is quite chameleon-like in its habits and overall appearance (Angel 1942). In association with this many of the attributes of the breast–shoulder apparatus of *Chamaeleo* are duplicated or closely approached (Wellborn 1933, pp. 159–160, 193–196, fig. 38). Our interpretation of the breast–shoulder apparatus of *Struthiomimus* indicates similar structural attributes for promoting forereach and forelimb mobility, particularly in the anterior quadrants of the glenohumeral joint.

The problem of orientation of the scapulocoracoid plate on the body wall in theropods has been a persistent one. Ostrom (1974) discussed the scapulocoracoid of *Deinonychus* and proposed an orientation for it similar to that in modern birds, with the scapulocoracoid oriented anteriorly, as in *Struthio*. No consideration, however, was given to the problem of why the coracosternal articulation should be immobile in a form with highly raptorial forelimbs, and it is clear that this would impose severe limitations on forereach. Subsequently, he has represented the scapulocoracoid orientation of *Deinonychus* in both a *Chamaeleo*-like manner (Ostrom 1976c, fig. 2) and an anterior orientation, as in birds (Ostrom 1976a, b). The latter orientation has been disputed by Tarsitano and Hecht (1980).

The long forelimb and well-developed manus of *Struthiomimus* are inconsistent with an immobile, anteriorly oriented scapulocoracoid. Taken over all, and in comparison with recent models, the osteological evidence suggests that the primary girdle of *Struthiomimus* was oriented somewhat laterally, as in *Chamaeleo*, and that considerable excursion was possible with respect to the body wall.

In UCMZ(VP)1980.1 parts of the vertebral column and ribs are preserved. As articulated, the scapular blade curves dorsally and posteriorly, making an angle of approximately 35° with the axis of the preserved vertebrae. The ventral edge of the coracoid plate lies in the same plane as the gastralia and ossified xiphisternal processes (Nicholls and Russell 1981) and this was probably its orientation during life. It is consistent with orientation of the scapulocoracoid in other articulated ornithomimids (ROM 851, NMC 8632, AMNH 5339). In this orientation the medial surface of the scapular blade lies flat against the dorsal ribs and the blade faces laterally. The ventral edge of the scapular prominence curves medially, resulting in an anterior inclination of the scapulocoracoid plate anterior to the glenoid. The glenoid fossa itself faces posterolaterally.

In the region of the scapulocoracoid suture the lateral face of the coracoid plate faces anterolaterally (see above). In the region of the biceps tubercle, however, the coracoid plate curves medially and the external face of the posterior coracoid process faces ventrally while its dorsal edge faces laterally. Consequently the coracoid plate of *Struthiomimus* lies in two distinct planes: anterolaterally, ventral to the scapular prominence and ventrally, in the region of the posterior coracoid process.

The same condition is present in NMC 8632, 8902 and ROM 851, 840. Tarsitano and Hecht (1980), in their discussion of *Archaeopteryx*, state that the coracoid of this genus is more complex than that of other reptiles, in that it lies in two different planes. In fact, the flexure of the coracoid plate that they describe for *Archaeopteryx* is very similar to that present in *Struthiomimus*. Tarsitano and Hecht's statement (1980, p. 163) that the coracoid of theropods 'is a fairly simple plate lying essentially in the same plane as the scapula' is incorrect. Indeed the coracoid of many theropods is curved medially, although not to the extent of that of *Struthiomimus*.

The structure of the sternum in *Chamaeleo* is suggestive of a possible solution for the orientation of the primary girdle in *Struthiomimus*, being compressed, with dorsally turned coracoid sulci. A sternum of this basic type was figured for a specimen of *Albertosaurus* (NMC 2120) by Lambe (1917, figs. 29 and 30). Along the anterior edges of this are notches that appear to represent the coracoid sulci. The curved nature of this sternum (Lambe 1917, fig. 29a) places the sulci in an anterolateral orientation, directed dorsally, quite similar to the situation in *Chamaeleo*. Unfortunately, the restoration of the sternum (Lambe 1917, fig. 30) represents it as a flat plate, artificially placing the coracoid sulci in an anterior orientation, reminiscent of that of birds. That the sternum was a curved or angulated structure is much more likely, however, as only in the former case could the scapular blade take up its orientation against the ribs, as indicated by Lambe (1917, figs. 5, 7, and 49). A similar form for the

sternum of *Massospondylus* is hinted at by Cooper (1981). The coracoid of *Albertosaurus* is discussed by Lambe (1917, p. 47) as being a curved structure. The medial inflection of the coracoid plate would have permitted articulation with the coracoid sulcus, provided a sliding articulation, and placed the scapulocoracoid plate in an appropriate orientation to follow the contour of the body wall. In such an orientation the glenoid would have faced posterolaterally but would have been relatively laterally situated, as in *Chamaeleo*. Orientation of the glenoid into a relatively more lateral situation provides the potential for greater anterior excursion of the forelimb, allowing the humeral head to move more freely into the anterior quadrants of the glenoid.

It is likely, given the structure of the primary girdle and the nature of its ventral coracoid surface, that the sternum of *Struthiomimus* was similar in form to that described for *Albertosaurus* (above). Suggestions that the coracoids of theropods may have overlapped along the midline in life (referred to as arcifery and reminiscent of the pectoral structure in arciferous frogs) (Osmólska and Roniewicz 1970), seem anatomically untenable.

Given this mode of orientation of the scapulocoracoid plate, comparative analysis suggests that the ligament systems of the breast–shoulder apparatus of *Struthiomimus* probably bore most resemblance to those of *Chamaeleo* and *Alligator*. The medial scapulosternal ligament would probably have exhibited the basic form and relationships seen in *Chamaeleo*, permitting freer coracosternal movement and also allowing more degrees of freedom to the mobility of the humeral head. It is also probable that an anterior scapulosternal ligament was present, taking on the form of that seen in *Chamaeleo* and helping to maintain the integrity of the coracosternal articulation during extreme forereach and retraction (Peterson 1973).

(b) Myological reconstruction of the primary girdle of *Struthiomimus*, with reference to humeral mobility

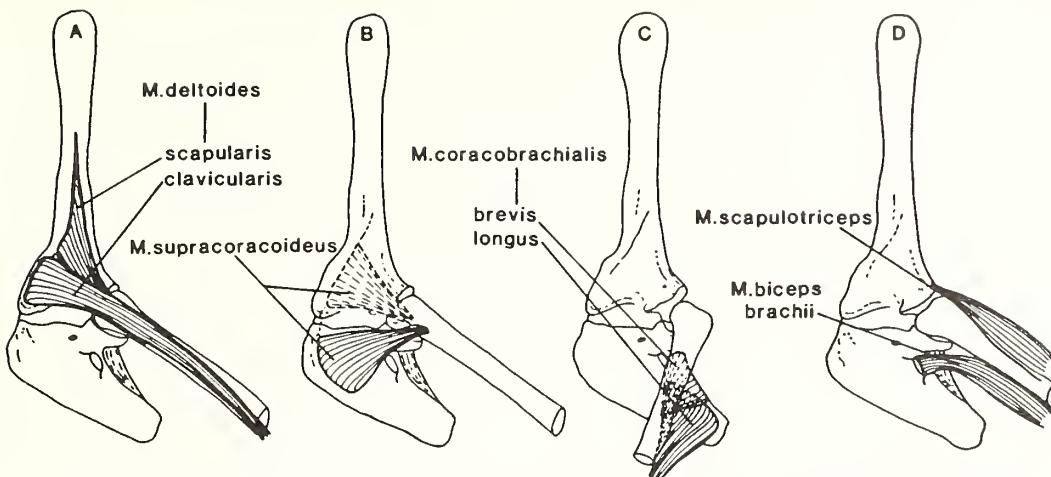
A rather pessimistic view of the utility of muscle scars in muscle reconstruction has been presented by McGowan (1979, 1982). He carried out a detailed study of the musculoskeletal system of the fore and hind limbs of the brown kiwi and stated that it would be impossible to reconstruct musculature from the available osteological data. This view is in general accordance with our own dissections. Only a few muscles were found to leave a discernible scar in *A. mississippiensis* and *Struthio camelus*. Brown (1981), in his work on the Upper Jurassic Plesiosauroida, expressed the opinion that there was no osteological evidence for the detailed muscular reconstruction of the plesiosaur humerus as presented by Watson (1924) and Robinson (1975). The question of the propriety of reconstructing the muscles of extinct vertebrates on osteological features is thus raised.

We feel that a compromise probably exists between the views of McGowan and Brown on the one hand and those of other workers who have apparently employed muscle scar evidence to great advantage. Reconstruction of anatomical minutiae seems beyond the scope of muscle scar evidence, but in strongly sculptured regions such as the shoulder, bone architecture is probably a reasonable indicator of at least the major muscles once present in the area. We have restricted ourselves to the attempted reconstruction of major muscles for which good evidence, in the form of scars or major topographical features, seem to exist.

In considering the breast–shoulder apparatus, the location of each muscle in relation to the glenoid and the nature of the muscle belly are important in functional interpretations. The location of muscles with respect to the glenoid will determine the leverage and control over the glenohumeral joint and will influence adduction, abduction, protraction, and retraction. The muscles considered are discussed in the context of the comparative models and their potential actions assessed.

In *Struthiomimus* no distinct muscle scar is present to indicate the point of origin or the M. deltoides scapularis. The unreduced nature of the laterally facing scapular blade, however, is reminiscent of the situation in *Chamaeleo* and *Alligator*. It is thus probable that the scapulodeltoid of *Struthiomimus* arose from the anterolateral surface of the scapular blade, as it does in the former two genera (text-figs. 10A, 11A), and promoted extensive humeral protraction and elevation.

Given the carriage of the forelimbs of *Struthiomimus*, their probable involvement in prehension (see below) and their unreduced state, it is unlikely that the M. deltoides clavicularis was reduced, as it



TEXT-FIG. 11. Proposed reconstruction of the discussed musculature for *Struthiomimus*. The humerus is represented as a simple cylinder, retracted in A, B, and D, protracted in C. A, the M. deltoideus complex; B, the M. supracoracoideus, the dashed portion is an anatomical equivalent to the dorsal portion of this muscle in *Chamaeleo* (see text-fig. 10c), but its presence is conjectural; C, the M. coracobrachialis, dashed portions represent parts of the muscle lying ventral to the humerus; D, the M. biceps brachii and M. scapulotriceps. For further details see text.

is in *Struthio*. The form of the scapular prominence in *Struthiomimus* most closely resembles that of *Alligator* and it is probable that the clavodeltoid arose from the lateral surface of the scapular prominence (text-figs. 10A, 11A). With this configuration the M. deltoides clavicularis would operate primarily as a protractor and elevator of the humerus, and the height of the scapular prominence suggests that these actions were well developed. In comparison with *Chamaeleo* (text-fig. 10A) the M. deltoides clavicularis of *Struthiomimus* appears to be functionally equivalent to the M. coracohumeralis anterior, but not to the M. sternohumeralis which is concerned with humeral protraction in the parasagittal plane.

One of the most prominent features of the coracoid of *Struthiomimus* is the elongate posterior coracoid process. Its lateral surface is heavily striated and there is a deep trough along its dorsal edge. This suggests that the M. coracobrachialis was bipartite. The M. coracobrachialis brevis probably arose from the trough-like depression ventral to the glenoid (text-fig. 11C). This branch would have been most effective in humeral adduction. The M. coracobrachialis longus probably took origin from the lateral face of the extensive posterior coracoid process. Such a posterior origin, relative to the glenoid, suggests powerful humeral retraction and humeral adduction.

Previous considerations of the pectoral myology of dinosaurs (e.g. Ostrom 1974, Borsuk-Bialynicka 1977, Coombs 1978a, Cooper 1981) have generally considered the M. coracobrachialis longus to be absent. This follows Romer's (1944) contention that it is absent in crocodilians. The two heads of the coracobrachialis complex in *Alligator* (text-fig. 10B), and the morphology of the coracoid plate in *Struthiomimus* suggests that the latter bore both branches. As it is closer in its overall orientation to the M. coracobrachialis complex of *Alligator* than *Chamaeleo* or *Struthio* (text-fig. 10B) it is indicative that the humerus could not be elevated greatly above the horizontal plane.

In *Struthiomimus* it is unlikely that the M. supracoracoideus would have been largely tendinous in the region of the glenoid, as it is in *Struthio*. The latter is an avian characteristic and has been much discussed by Ostrom (1976b) and Olson and Feduccia (1979). Ostrom (1976b) associated a prominent biceps tubercle with translating the direction of pull of a ventrally situated M. supracoracoideus, but this need not always be the case, as is evident from *Chamaeleo* (text-figs. 9, 10C).

It is more likely that the supracoracoideus in *Struthiomimus* was a bipartite muscle, as in both *Alligator* and *Chamaeleo* (text-figs. 10c, 11b). The broad depression anterior to the glenoid (text-fig. 2) appears to indicate the origin of the M. supracoracoideus, but this would correspond only to the ventral part of the muscle in *Chamaeleo*. The structure of the glenoid in *Struthiomimus* suggests that the humeral protractors were well developed. Under these circumstances it seems likely that the supracoracoideus would resemble the condition in *Chamaeleo*, extending dorsally along the scapular blade (text-fig. 10c). This would have provided greater versatility of humeral protraction as well as significant elevation. It would have promoted movement of the humeral head into the anterior quadrants of the glenoid, thus enhancing forereach.

The M. biceps brachii of *Struthiomimus* probably arose from the biceps tubercle (text-fig. 11d), inserting on the radius and ulna. The presence of a well-developed antebrachium and manus implies that it would have been a strongly developed muscle, and not a reduced one as in *Struthio*. There is no evidence for a humeral origin of the biceps, as suggested for *Massospondylus* by Cooper (1981).

The anatomical evidence available for *Struthiomimus* suggests that the condition of the M. biceps brachii was intermediate between that of *Chamaeleo* and *Struthio* (text-fig. 10d). Action over the glenohumeral joint would be small and leverage at the elbow strong. It would have been most effective in elbow flexion with the brachium in the forereach position and the humeral head occupying the anterior quadrants of the glenohumeral joint. The closeness of origin to the glenoid would mean that the role of this muscle in protraction would be reduced. The position of the biceps tubercle in *Struthiomimus* may indicate a slightly more medial orientation of the scapulocoracoid plate than is found in *Chamaeleo*.

In *Struthiomimus* a distinct scar is present on the dorsal lip of the supraglenoid buttress close to the glenohumeral joint, that probably represents the point of origin of the M. scapulotriceps (text-fig. 11d). The morphology of the primary girdle suggests that the M. scapulotriceps of *Struthiomimus* would have resembled most closely that of *Chamaeleo* (text-fig. 10e). The M. coracotriceps was probably absent and the humeral head was, therefore, probably endowed with greater degrees of freedom of movement. In summary, the muscles that have been reconstructed by way of comparison with the alligator, ostrich, and chameleon, indicate some particular features of the mobility of the humerus. In *Struthiomimus* the head of the humerus had considerable mobility within the glenoid cavity. The prominent supra- and infraglenoid buttresses of the glenoid and the well-developed anterior and posterior tuberosities of the humeral head suggest that significant degrees of anteroposterior displacement of the humerus, via rotation and translation, were possible, but elevation and depression were much more restricted. Elevation of the humerus could not extend much above the horizontal, but the deltoid complex and the supracoracoideus were developed to bring about powerful elevation to this level, coupled with strong protraction, pulling the humeral head into the anterior quadrants of the glenoid. The biceps was well placed to produce strong flexion of the elbow when the humerus was elevated and protracted. Combined with the mobility of the primary girdle on the sternum (see above), these activities would bring about extensive forereach, resulting in the antebrachium and manus being pushed forward at, or just above, shoulder height, with the potential for the biceps to draw the antebrachium and manus towards the head when the neck was extended.

Acting in an antagonistic fashion the coracobrachialis complex was positioned to bring about powerful humeral retraction and depression, enhanced by the origin arising from the elongate posterior coracoid process. It is unlikely that the M. pectoralis was well developed as the deltopectoral crest is relatively small, compared with that of other theropods, and the angle the crest makes with the proximal articular surface is low. These factors were taken by Ostrom (1969, p. 109) to be indicative of only poorly developed adduction and retraction of the humerus in ornithomimids. It is likely, however, that the coracobrachialis complex assumed a good deal of the responsibility for humeral retraction, but with the humerus in a more horizontal orientation.

In conjunction with this, the scapulotriceps was positioned to extend the elbow, while the absence of the coracotriceps would greatly increase the mobility of the primary girdle on the sternum by eliminating one of the chief stabilizing ligaments.

(c) Significance of antebrachial and carpal mobility

The elbow joint of *Struthiomimus* was essentially a hinge joint and the radius and ulna were not freely mobile on each other, but functioned as a unit (see above). Thus, with the humerus elevated and protracted the antebrachium could be flexed and extended to move the manus away from or toward the head.

The concentration of the carpal elements distal to the radius is worthy of comment. That this is their natural position is indicated by the close fit of the proximal ridge of the intermedium between the radius and ulna, and a distinct depression on the proximal end of metacarpal I for reception of the centrale. The same orientation of carpals is seen in AMNH 5339. This concentration of bones proximal to metacarpal I would act like a wedge to displace the metacarpus posteriorly, when the wrist was extended, thus effectively increasing the reach of the first digit.

(d) Functional significance of the manus

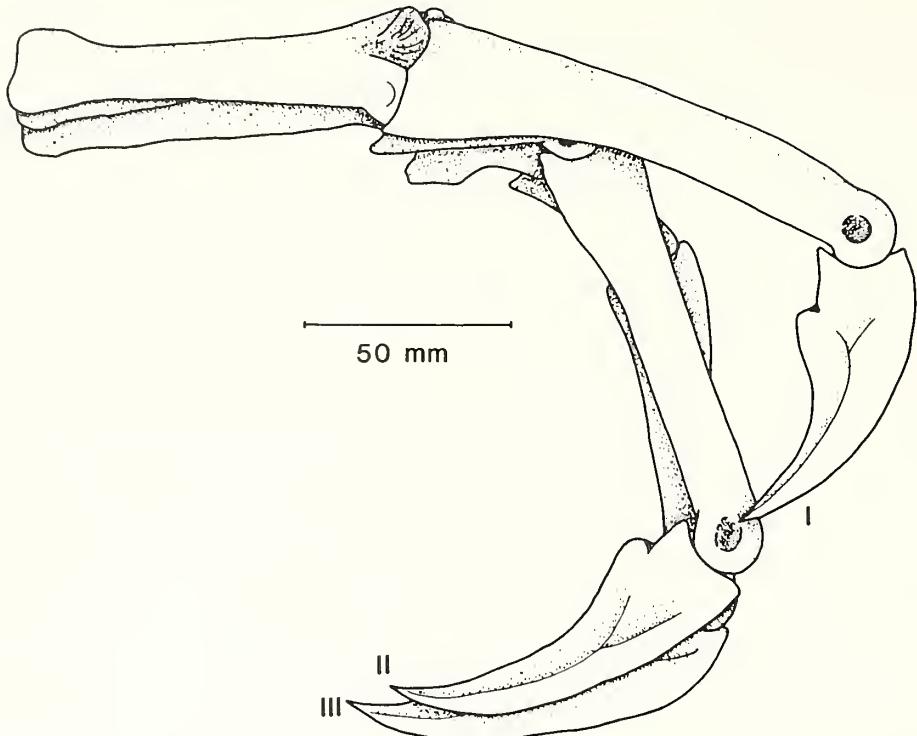
Ostrom (1969) presented a functional analysis of the forelimb of *Deinonychus*, and compared it with that of ornithomimids. He concluded that the forelimb of *Struthiomimus* could not be considered a raptorial grasping structure, as digit I was not truly opposable, the carpus was relatively inflexible and both the internal (our posterior) tuberosity and the deltopectoral crest were poorly developed. Subsequent workers have described the manus of ornithomimids as being relatively weak, and have suggested that the long straight claws were used for lightly raking the surface of the ground to gain access to food (Osmólska *et al.* 1972; Russell 1972). Osmólska *et al.* (1972) have indicated that only very limited flexion was possible in the manus of *Gallimimus*.

We agree with Ostrom that the manus of *Struthiomimus* cannot be considered a grasping or raptorial structure, in the manner of that of *Deinonychus*, but neither can it be considered to be the ineffective, weak structure typical of *Gallimimus* (Osmólska *et al.* 1972). Considerable flexion of all the digits in the manus was possible (text-fig. 12). In a typically raptorial manus, such as that of *Deinonychus* or *Allosaurus*, digits II and III are of unequal length and there is considerable divergence between them. Significant pronation and supination of the manus was also possible, as is evidenced by the articular surfaces of the carpus (at least in *Deinonychus*) and freedom of movement between the radius and ulna. In contrast the forelimb of *Struthiomimus* is characterized by an absence of any significant rotation. The carpus operated as a simple hinge joint and the radius and ulna were firmly syndesmotically united and incapable of independent rotation.

Unique features of the manus of *Struthiomimus* are the nearly equal length of all the digits, the incipient coalescence of digits II and III, and the extreme divergence between digit I and the two lateral digits. The incipient coalescence of digits II and III and their nearly equal length results in these two digits acting in unison. In this regard the manus of *Struthiomimus* resembles that of chameleonid lizards and tree sloths. In chameleons the digits are arranged in opposing sets, while in tree sloths they are in a single set. In both cases, however, the digits are of equal length, are closely applied, and are enclosed in a common sheath of skin that extends to the base of the ungual, holding the digits parallel and causing them to operate as a single unit. Such a sheath may have been present around digits II and III in the manus of *Struthiomimus*.

The divergence of the first digit in *Struthiomimus* has been considered to be a typical theropod characteristic (Ostrom 1969), and Gilmore (1920, p. 61) compared it to that of *Ornitholestes* and *Allosaurus*. While the distal end of the first metacarpal is offset anteriorly in these two genera, as it is in *Struthiomimus*, the nature of the metacarpophalangeal articulation is quite different. In both *Allosaurus* and *Ornitholestes* this articular surface is rotated posteriorly (text-fig. 13). Consequently hyperextension carries digit I dorsally and posteriorly, towards the other digits. When flexed the first digit moves away from the midline of the hand, spreading the digits and broadening the grasp of the raptorial manus.

In *Struthiomimus* the opposite situation exists. The distal articulation of metacarpal I has been rotated anteriorly (text-fig. 13). Hyperextension carries digit I dorsally and anteriorly, resulting in a very wide divergence between digit I and digits II and III. When flexed, digit I moves posteriorly,

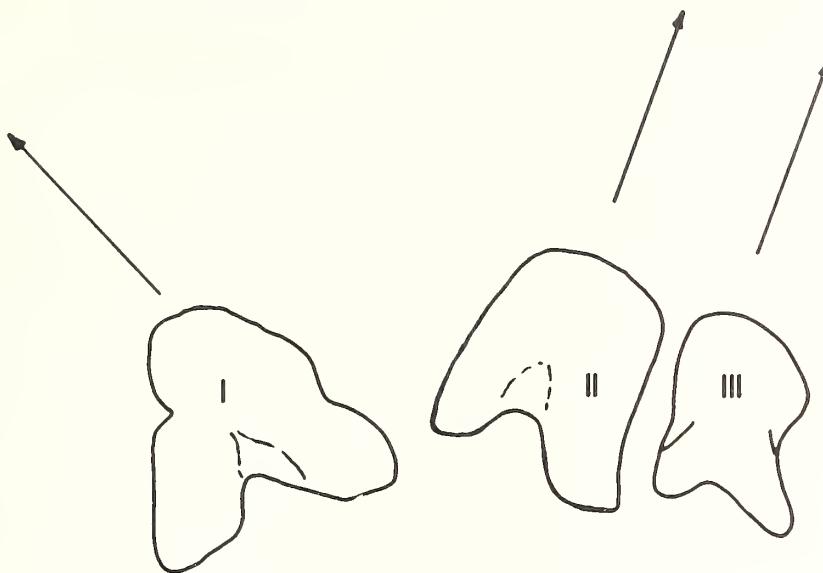
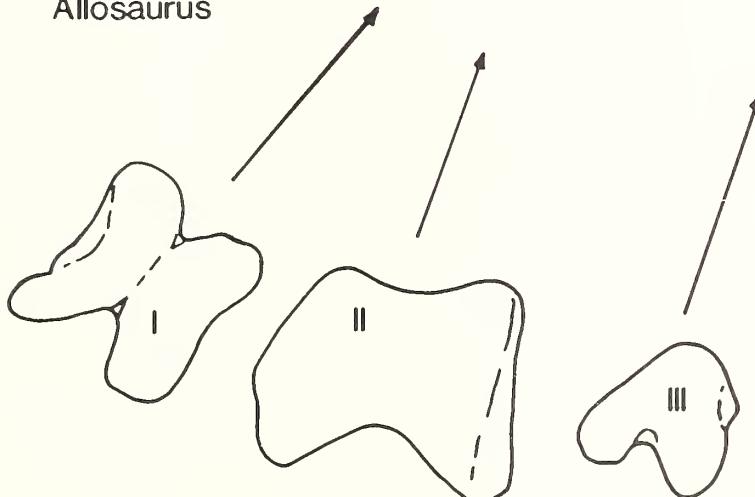


TEXT-FIG. 12. Manus of *Struthiomimus altus* in flexed position, viewed from the anterior aspect.

towards the midline of the hand, effectively narrowing the manus. Flexion also brings digits II and III anteriorly, towards the midline of the hand. With the manus fully flexed the three digits lie close together with digits II and III parallel to one another and digit I converging on these.

The anterior rotation of the distal articular surface of metacarpal I was responsible for Galton's (1971) misinterpretation of Osborn's (1916, fig. 3) figure of the manus of *Struthiomimus*. Galton (1971, pp. 5, 6) suggested that Osborn had incorrectly represented the articular orientation of the first phalanx of digit I, and proposed that instead this phalanx should be rotated clockwise (for the left manus, viewed distally) through 45°. Such a reorientation would result in a more typical theropod configuration of the first digit. Such a reorientation, however, does not accord with the available anatomical evidence. Indeed, Osborn's (1916) interpretation of the orientation of digit I was correct, and the same configuration is evident in UCMZ(VP)1980.1 (text-fig. 1). Rotation of the first phalanx to the position suggested by Galton (1971) results in an anatomically untenable disposition, with the articular surfaces of the first metacarpal and first phalanx not being aligned and, upon extension, the dorsal edge of the first phalanx cutting across the collateral ligament pit on the metacarpal.

Convergence of the digits in flexion is not what would be expected if the manus operated as a raking structure, as has been suggested by Osmólska *et al.* (1972) and Russell (1972). In a rake the prongs are spread to cover a wide area, and a certain amount of digital splay would be expected. Similarly, the manus should be capable of enough pronation to bring the palmar surface parallel to the ground. As has been shown, however, the manus of *Struthiomimus* was capable of little pronation and when fully flexed, the digits of *Struthiomimus* form a very effective hook. The hook-like effect of the manus is enhanced by the elongation of the penultimate phalanx. While this is a characteristic of many theropods, it is particularly well developed in *Struthiomimus*. (The penultimate phalanx makes up

A Struthiomimus**B Allosaurus**

TEXT-FIG. 13. Distal articular surfaces of left metacarpals of *Struthiomimus* compared with those of *Allosaurus*. The arrows indicate the directional path of the first phalanx on hyperextension. In *Struthiomimus* the distal articular surface of metacarpal I has been rotated in a counter-clockwise direction, away from the midline of the hand. Hyperextension results in a very wide divergence between digit I and the remaining digits. In *Allosaurus*, as in most theropods, the distal articular surface of digit I has been rotated in a clockwise direction. When fully extended, the three digits converge. A, *S. altus*, UCMZ(VP)1980.1; B, *A. fragilis*, ROM 5091. (Not drawn to scale.)

29% of the length of digit II on UCMZ(VP)1980.1, compared with 25·6% in *Deinonychus* and 24·6% in *Deinocheirus*. Data from Ostrom 1969, and Osmólska and Roniewicz 1970, respectively.) In an effective grasping structure the phalanges would be of more uniform length, allowing the digits to curl around their object.

In the elongation of the penultimate phalanx, and in the long, straight unguals, the ornithomimid manus resembles the hook-like manus of tree sloths and anteaters (pers. obs.). The joint structure of the two is different, however. In the edentates there is very little flexion between the short, proximal phalanges, most of the proximal flexion being restricted to the metacarpophalangeal joints (Humphry 1869). In *Struthiomimus* the reverse is true. In both, however, there is considerable potential for flexion of the unguals. The end result is similar—a hook is formed by the elongate unguals. In addition, however, the convergence of the first digit on the second and third in *Struthiomimus*, would also add a clamping function to the manus.

Exactly what *Struthiomimus* was hooking and clamping with its manus can only be surmised. It lacks both the fossorial and the suspensory specialization of living edentates. With their flat, edentulous beaks it is most likely that ornithomimids were herbivorous. Jarzen (1982) has discussed the palynology of the Judith River Formation and indicated that ferns (Polypodiaceae) and tree ferns (Cyatheaceae and Dicksoniaceae) were a significant part of the flora. Cycads were also still abundant. If these were utilized as a food source the hooking action of the ornithomimid manus could be employed to pull fronds, sporangia, or even small branches within reach of its mouth.

CONCLUSIONS

The comparative evidence presented has enabled the breast-shoulder apparatus and forelimb of *Struthiomimus* to be reconsidered structurally and functionally. Previous considerations of coelurosaurians and related forms, based chiefly upon avian models, appear to be inadequate. The avian breast-shoulder apparatus exhibits a number of unique specializations associated with the flight mechanism, and these impose several limitations upon the mobility of certain parts of the breast-shoulder apparatus. Extending the comparison to include *Alligator* and *Chamaeleo* has led to the postulation that the primary girdle of *Struthiomimus* was mobile with respect to the body wall and that the forelimb had considerable degrees of freedom of movement.

It is unlikely that the humerus of *Struthiomimus* could have been elevated much above the horizontal, due to the presence of a strong dorsal glenoid buttress, but it could be depressed considerably. The comparative and reconstructed myology, in association with skeletal and ligamentous data, suggest that the forelimb was capable of undergoing considerable protraction with the humerus in the horizontal or semi-vertical position, and that humeral retraction and adduction were relatively powerfully developed. The absence of stabilization of the primary girdle by a secondary girdle and the structural attributes of the forelimb skeleton are consistent with the concept of a highly mobile forelimb. Restriction of primary girdle mobility, as seen in recent birds, is not supported by available morphological evidence.

S. altus had elongate forelimbs. In UCMZ(VP)1980.1 the forelimbs are 58% as long as the hindlimbs. Unlike other long-armed coelurosaurians, however, the long forelimbs are decidedly non-raptorial. Rotational movements in the forelimb are limited, there is little digital splay in the manus, and the claws are long and comparatively broad. The major movements of the forelimb appears to have been protraction and retraction at the glenohumeral joint and extension and flexion of the antebrachium and manus.

The manus of *Struthiomimus* was adapted for neither grasping nor raking the ground, as has been previously suggested, but instead appears to have been a specialized clamping and hooking structure. The extreme divergence between digit I and the two lateral digits, when the manus was fully extended, is unequalled in other theropods. The incipient coalescence of digits II and III, and their ability to be strongly flexed suggests that they were enclosed in a common sheath of skin. This hook-like structure of the manus, combined with the extensive forereach of the limb as a whole, suggests that

Struthiomimus may have used its long arms for hooking small branches, or the fronds of ferns and cycads, and pulling them within reach of its long neck and edentulous head.

Acknowledgements. We would like to thank Dr D. A. Russell, Dr R. C. Fox, and Dr P. Currie for allowing E. L. N. to examine specimens in their charge. We are grateful to the staff at the Royal Ontario Museum for their time and assistance in making their collections of ornithomimids available for study and to Dr Christopher McGowan of that institution for helpful discussions on ratite shoulder musculature. Dr H. Osmólska kindly supplied us with excellent photographs of the Mongolian ornithomimid material. Drs E. N. Arnold, B. G. Gardiner, P. L. Forey, and J. Thomason provided helpful comments on earlier drafts of the manuscript. Typing of the various drafts was capably handled by Mrs Ronica Pacholok and Miss Marg Hunik. Financial support for this work was provided by University of Calgary Special Projects grants 69-7994 and 69-7940 to A. P. R. and by NSERC grant A-9745 to A. P. R.

REFERENCES

- ALIX, E. 1874. *Essai sur l'appareil locomoteur des oiseaux*. Paris: G. Masson.
- ANGEL, F. 1942. Les Lizards de Madagascar. *Mém. Acad. Malagache*, **36**, 1-193.
- BAKKER, R. T. 1971. Dinosaur physiology and the origin of mammals. *Evolution, Lancaster, Pa.* **25**, 636-658.
- 1975. Dinosaur renaissance. *Scient. Am.* **232**, 58-78.
- BAUMEL, J. J. 1979. Arthrologia, pp. 123-173. In BAUMEL, J. J., KING, A. S., LUCAS, A. M., BREAZILE, J. J., and EVANS, H. E. (eds.). *Nomina Anatomica Avium*. Academic Press, New York.
- BERGER, A. J. 1960. The musculature, pp. 301-344. In MARSHALL, A. J. (ed.). *Biology and Comparative Physiology of Birds*. Vol. 1. Academic Press, New York.
- 1966. The musculature, pp. 224-500. In GEORGE, J. C. and BERGER, A. J. (eds.). *Avian Myology*. Academic Press, New York.
- BORSUK-BIAŁYNICKA, M. 1977. A new camarasauroid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. Results of the Polish-Mongolian palaeontological expeditions, pt. VII. *Palaeont. Pol.* **37**, 5-64.
- BROOM, R. 1906. On the early development of the appendicular skeleton of the ostrich with remarks on the origin of birds. *Trans. S. Afr. Phil. Soc.* **16**, 355-368.
- BROWN, D. S. 1981. The English Upper Jurassic Plesiosauroida (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. *Bull. Br. Mus. Nat. Hist. A, Geol.* **35**, 253-347.
- COOMBS, W. P. JR. 1978a. Forelimb muscles of the Ankylosauria (Reptilia: Ornithischia). *J. Paleont.* **52**, 642-657.
- 1978b. Theoretical aspects of cursorial adaptation in dinosaurs. *Q. Rev. Biol.* **53**, 393-418.
- COOPER, M. R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occ. Pap. Natn. Mus. Monuments, Rhodesia*. Series B, Natural Sciences, **6**, 689-840.
- CRACRAFT, J. 1974. Phylogeny and evolution of the ratite birds. *Ibis*, **116**, 494-521.
- DAAN, S. and BELTERMAN, T. 1968. Lateral bending in locomotion of some lower tetrapods I and II. *Proc. K. ned. Akad. Wet. Series C* **71**, 245-266.
- DVIR, Z. and BERME, N. 1978. The shoulder complex in elevation of the arm: a mechanism approach. *J. Biomech.* **11**, 219-225.
- FÜRBRINGER, M. 1876. Zur vergleichenden Anatomie der Schultermuskeln. *Morph. Jb.* **1**, 636-816.
- GALTON, P. M. 1971. Manus movements of the coelurosaurian dinosaur *Syntarsus* and opposability of the theropod hallux (*sic*). *Arioldia (Rhodesia)*, **15**, 1-8.
- GARDINER, B. G. 1982. Tetrapod classification. *Zool. J. Linnean Soc.* **74**, 207-232.
- GASC, J.-P. 1963. Adaptation à la marche arboricole chez le caméléon. *Archis. Anat. Hist. Embryol.* **46**, 81-115.
- GILMORE, C. W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum. *Bull. U.S. Natn. Mus.* **110**, 1-159.
- 1933. On the dinosaurian fauna of the Iren Dabsu formation. *Bull. Amer. Mus. Nat. Hist.* **67**, 23-78.
- HAUGHTON, S. 1867a. Notes on animal mechanics No. VI—On the muscular anatomy of the crocodile. *Proc. R. Ir. Acad.* **9**, 268-277.
- 1867b. Notes on animal mechanics No. X—Muscular anatomy of the emu (*Dromaeus Novae Hollandiae*). *Ibid.* 487-497.
- 1867c. Notes on animal mechanics No. XI—Muscular anatomy of the rhea (*Struthio rheo*). *Ibid.* 497-504.
- HOFTSTETTER, R. and GASC, J.-P. 1969. Vertebrae and ribs of modern reptiles, pp. 210-310. In GANS, C., BELLAIRS, A. D'A., and PARSONS, T. S. (eds.). *Biology of the Reptilia*, Volume 1. Academic Press, London.

- HOLMES, R. 1977. The osteology and musculature of the pectoral limb of small captorhinids. *J. Morph.* **152**, 101–140.
- HUMPHRY, G. M. 1869. The myology of the limbs of the Unau, the Ai, the 2-toed anteater and the pangolin. *J. Anat. Physiol., Lond.* **4**, 17–78.
- JARZEN, D. M. 1982. Palynology of Dinosaur Provincial Park (Campanian) Alberta. *Syllogeus*, **38**, 1–69.
- JENKINS, F. A. JR. and GOSLOW, G. E. JR. 1983. The functional anatomy of the shoulder of the savannah monitor lizard (*Varanus exauthematicus*). *J. Morph.* **175**, 195–216.
- KALIN, J. A. 1929. Über den Brustschulterapparat der Krokodile. *Acta Zool., Stockh.* **10**, 343–399.
- LAMBE, J. M. 1902. On the Vertebrata of the mid-Cretaceous of the Northwestern Territory. Part 2. New genera and species from the Belly River series (mid-Cretaceous). Geological Survey of Canada Separate Report 774. *Contr. Can. Palaeont.* **2**, 25–81.
- 1917. The Cretaceous theropodus dinosaur *Gorgosaurus*. *Canada Department of Mines, Memoir*, **100**, 1–84. Government Printing Bureau, Ottawa.
- LAUDER, G. V. 1981. Form and function: structural analysis in evolutionary morphology. *Paleobiol.* **7**, 430–442.
- LECURU, S. 1968a. Remarques sur le scapulo-coracoïde des lacertiliens. *Annales. Sci. Nat., Zoologie et Biologie Animale*, Paris 12^e série **10**, 475–510.
- 1968b. Étude des variations morphologiques du sternum, des clavicules et de l'interclavicule des lacertiliens. *Ibid.* **511**–544.
- MACALISTER, A. 1867. On the anatomy of the ostrich (*Struthio canuehus*). *Proc. R. Ir. Acad.* **9**, 1–25.
- MCGOWAN, C. 1979. The hind limb musculature of the brown kiwi, *Apteryx australis mantelli*. *J. Morph.* **160**, 33–74.
- 1982. The wing musculature of the brown kiwi *Apteryx australis mantelli* and its bearing on ratite affinities. *J. Zool., Lond.* **197**, 173–219.
- MADSEN, J. H. JR. 1976. *Allosaurus fragilis*: A revised osteology. *Bull. Utah Geol. Miner. Surv.* **109**, 1–163.
- MARSH, O. C. 1890. Description of new dinosaurian reptiles. *Amer. J. Sci.* **39**, 81–86.
- NICHOLLS, E. L. and RUSSELL, A. P. 1981. A new specimen of *Struthiomimus altus* from Alberta, with comments on the classificatory characters of ornithomimids. *Can. J. Earth Sci.* **18**, 518–526.
- OLSON, S. L. and FEDUCCIA, A. 1979. Flight capability and the pectoral girdle of *Archaeopteryx*. *Nature, Lond.* **278**, 247–248.
- OSBORN, H. F. 1916. Skeletal adaptations of *Ornitholestes*, *Struthiomimus* and *Tyrannosaurus*. *Bull. Amer. Mus. Nat. Hist.* **35**, 733–771.
- OSMÓLSKA, H. and RONIEWICZ, E. 1970. Deinocheiridae, a new family of theropod dinosaurs. Results of the Polish–Mongolian palaeontological expeditions, pt. II. *Palaeont. Pol.* **21**, 5–19.
- and BARSOLD, R. 1972. A new dinosaur *Gallimimus bullatus*, N.gen., N.sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. Results of the Polish–Mongolian palaeontological expeditions, pt. IV. *Palaeont. Pol.* **27**, 103–143.
- OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Bull. Peabody Mus. Nat. Hist.* **30**, 1–165.
- 1974. The pectoral girdle and forelimb function of *Deinonychus* (Reptilia: Saurischia): A correction. *Postilla*, **165**, 1–11.
- 1976a. *Archaeopteryx* and the origin of birds. *Biol. J. Linn. Soc.* **8**, 91–182.
- 1976b. Some hypothetical anatomical stages in the evolution of avian flight. *Suihksou. Contr. Paleobiol.* **27**, 1–21.
- 1976c. On a new specimen of the Lower Cretaceous Theropod dinosaur *Deinonychus antirrhopus*. *Breviora*, **439**, 1–21.
- 1978. From dinosaur to bird: The missing link. *Natu. Geogr. Mag.* **154**, 152–185.
- PARKS, W. A. 1933. New species of dinosaurs and turtles from the Upper Cretaceous formations of Alberta. *Univ. Toronto Stud. Geol. Ser.* **34**, 1–33.
- PEABODY, F. E. 1959. Trackways of living and fossil salamanders. *Univ. Calif. Publs. Zool.* **63**, 1–72.
- PETERSON, J. A. 1971. Functional morphology of the shoulder in *Chamaeleo* and *Anolis*. *Amer. Zool.* **11**, 704–705.
- 1973. Adaptation for arboreal locomotion in the shoulder region of lizards. Ph.D. Thesis, University of Chicago.
- 1984. The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. *J. Zool., Lond.* **202**, 1–42.
- PORTEILJE, A. F. J. 1925. Zur Ethologie bzw. Psychologie der *Rhea americana* L. *Ardea*, **14**, 1–14.
- RAIKOW, R. J. 1969. Sexual and agonistic behaviour of the common rhea. *Wilsou Bull.* **81**, 196–206.

- ROBINSON, J. A. 1975. The locomotion of plesiosaurs. *Neues Jb. Geol. Paläont. Abh.* **149**, 286–332.
- ROMER, A. S. 1922. The locomotor apparatus of certain primitive and mammal-like reptiles. *Bull. Amer. Mus. Nat. Hist.* **46**, 517–603.
- 1944. The development of tetrapod limb musculature—the shoulder girdle of *Lacerta*. *J. Morph.* **74**, 1–41.
- RUSSELL, A. P. 1975. A contribution to the functional analysis of the foot of the tokay, *Gekko gecko* (Reptilia: Gekkonidae). *J. Zool., Lond.* **176**, 437–476.
- RUSSELL, D. A. 1972. Ostrich dinosaurs from the late Cretaceous of Western Canada. *Can. J. Earth Sci.* **9**, 375–402.
- SAUER, E. G. F. and SAUER, E. M. 1966. The behavior and ecology of the South African ostrich. *Living Bird*, **5**, 45–75.
- SIEBENROCK, F. 1893. Das skelet von *Brookesia superciliaris* Kuhl. *Sber. Akad. Wiss. Wien.* **102**, 71–118.
- SKINNER, J. H. 1959. Ontogeny of the breast–shoulder apparatus of the South African lacertilian, *Microsaura pumila pumila* (Daudin). *Annale Univ. Stellenbosch.* **35**, 5–66.
- STERNBERG, C. M. 1933. A new *Ornithomimus* with complete abdominal cuirass. *Can. Fld. Nat.* **47**, 79–83.
- SUKHANOV, V. B. 1968. *General system of symmetrical locomotion of terrestrial vertebrates and some features of movement of lower tetrapods*. Amerind Publishing Co., New Delhi.
- TARSITANO, S. and HECHT, M. K. 1980. A reconsideration of the reptilian relationships of *Archaeopteryx*. *Zool. J. Linnaeana Soc.* **69**, 149–182.
- VAN DEN BERGE, J. C. 1979. Myologia, pp. 175–219. In BAUMEL, J. J., KING, A. S., LUCAS, A. M., BREAZILE, J. E. and EVANS, H. E. (eds.), *Nomina Anatomica Avium*. Academic Press, New York.
- WALKER, A. D. 1972. New light on the origin of birds and crocodiles. *Nature, Lond.* **237**, 257–263.
- WATSON, D. M. S. 1924. The elasmosaurid shoulder-girdle and forelimb. *Proc. Zool. Soc. Lond.* **1924**, 885–917.
- WEBB, G. J. W. and GANS, C. 1982. Galloping in *Crocodylus johnstoni*—a reflection of terrestrial activity? *Rec. Aust. Mus.* **34**, 607–618.
- WELLBORN, V. 1933. Vergleichende osteologische Untersuchungen an Geckoniden, Eublephariden und Uroplatiden. *Sber. Ges. Naturf. Freunde Berl.* **1933**, 126–199.
- WHETSTONE, K. N. and WHYBROW, P. J. 1983. Cursorial crocodilian from the Triassic of Lesotho (Basutoland), Southern Africa. *Occ. Pap. Mus. Nat. Hist. Univ. Kansas*, **106**, 1–37.
- ZUG, G. R. 1974. Crocodilian galloping: A unique gait for reptiles. *Copeia*, **1974**, 550–552.

ELIZABETH L. NICHOLLS

Department of Biology
The University of Calgary
2500 University Drive N.W.
Calgary, Alberta, Canada T2N 1N4

ANTHONY P. RUSSELL

Department of Ichthyology and Herpetology
Royal Ontario Museum
Toronto, Ontario, Canada M5S 2C6
and

Department of Biology
The University of Calgary
2500 University Drive N.W.
Calgary, Alberta, Canada T2N 1N4

Typescript received 13 August 1984

Revised typescript received 20 February 1985

CARADOC-ASHGILL CONODONT FAUNAS FROM WALES AND THE WELSH BORDERLAND

by N. M. SAVAGE and M. G. BASSETT

ABSTRACT. Twenty-two multi-element conodont species are described from Caradoc-Ashgill (Ordovician) strata sampled throughout Wales and the Welsh Borderland. *Plectodina bullhillensis*, *P. bergstroemi*, and *Prioniodus deanii* are described as new species. Strata from the Costonian to Soudleyan stages appear to lie within the *tvaeensis* conodont Biozone, with Longvillian to ?Ottoman strata in the *superbus* Biozone, and Pusgillian to Hirnantian strata in the *ordovicicus* Biozone, although in no sections are the zonal boundaries sharply defined. Contrasts in Colour Alteration Index suggest that the Caradoc-Ashgill rocks of the Welsh trough have been subjected to much higher geothermal temperatures than those on the Welsh Borderland platform.

THE starting point for modern work on conodonts of all ages in the British Isles was the description by Rhodes (1953) of four Lower Palaeozoic faunas from Wales and the Welsh Borderland, three from Ordovician rocks and one from Silurian. Given this initial impetus in Ordovician studies, and the fact that numerous faunas of this age have been described subsequently from virtually all parts of the world, it is somewhat surprising at first sight that very few further investigations have been made in the historical type areas of the Ordovician System within the Welsh region. In fact only three additional publications (Lindström 1959; Bergström 1964; Orchard 1980) contain systematic accounts of Ordovician conodont faunas from this area, covering seven discrete stratigraphical units over and above those described by Rhodes. To these should also be added Bergström's (1971a) wider biostratigraphical review, which does contain comments on undescribed faunas from other horizons and localities, plus brief mention of the correlative significance of a late Llandeilo (*Nemagraptus gracilis* Biozone) fauna from limestone blocks in the Garn Formation of Anglesey (Bergström 1981b) and other Llandeilo elements from the type area (Bergström *et al.* 1984). Some elements from South Wales and Shropshire were also noted and illustrated by Bergström (1983, pp. 50, 51, fig. 6A-H) in a discussion of Llandeilo-Caradoc correlations.

This somewhat limited systematic coverage has inevitably restricted the interpretation in the Welsh area of various aspects of Ordovician history based on conodonts, such as biostratigraphy, palaeobiogeography, and palaeotemperatures (e.g. see Bergström 1973, 1977, 1981a for summaries). However, the relative paucity of data is certainly not a reflection of lack of interest in the area but is a result of one dominant factor—the absence of stratigraphically and geographically widespread carbonate units suitable for the techniques of acid digestion that are now standard practice in conodont studies. Throughout both the platform and trough areas of the Wales-Welsh Borderland depositional basin, Ordovician sediments are developed mainly in clastic facies ranging from boulder down to clay grade, with a predominance of fine sands and silts; the relatively few, locally developed carbonate units in the sequence were naturally those first subjected to study for conodonts in the investigations referred to above. This has resulted in a somewhat piecemeal and restricted analysis of the faunas.

Notwithstanding the problems of extraction and stratigraphical/geographical coverage, our studies suggest that the potential for collecting further data on Ordovician conodont faunas in Wales and the Welsh Borderland is far from exhausted. Apart from the carbonate units already investigated, there are a number of other thin, lensoid limestone levels that have not been analysed, and there are also units of calcareous-cemented clastic strata in thin macro-shelly partings that can be broken down by standard techniques. This paper represents an attempt to expand our knowledge of

Ordovician conodont faunas from the region, first by concentrating on a limited part of the sequence (Caradoc and Ashgill) throughout the whole area, and secondly by systematic collecting through vertical sequences rather than from spot samples.

STRATIGRAPHY, LOCALITIES, COLLECTIONS

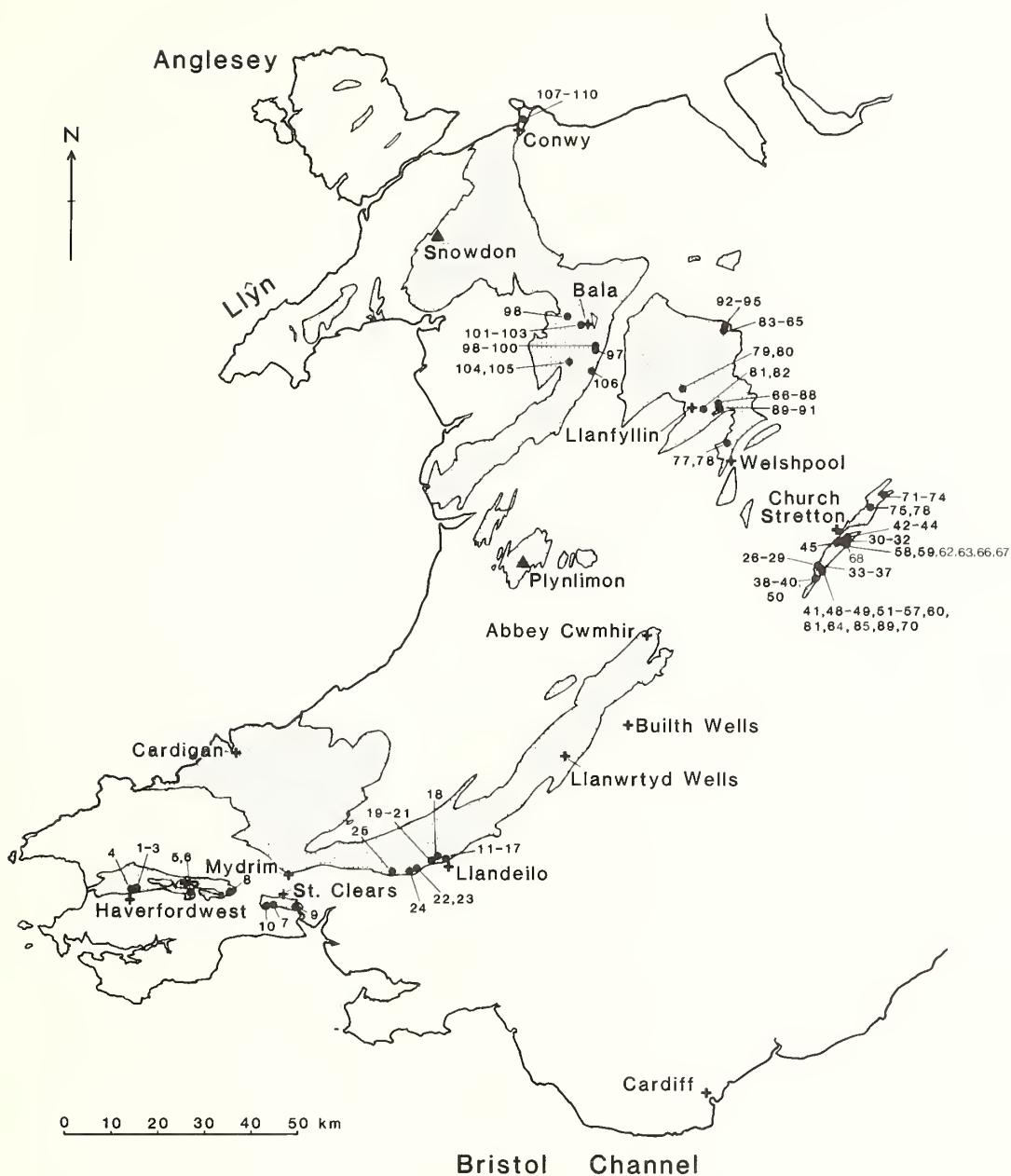
The geographical and stratigraphical coverage of our collections from Caradoc and Ashgill strata throughout Wales and the Welsh Borderland is shown in text-figs. 1–3. Within this coverage we collected 110 samples, ranging in weight from 1·5 kg up to about 4·0 kg, and of these there were forty-eight that yielded no conodont faunas. Text-fig. 4 shows the stratigraphical ranges of species from the forty more productive horizons represented in the collections, and Table 1 gives the yields of all elements in the same samples. Yields from all sixty-two productive samples are plotted in Table 2. As a means of reviewing and interpreting data from previous publications, these samples include new collections of those Caradoc–Ashgill faunas already known from the area. It must be admitted that the results of intensive collecting are still disappointing, and that there is still far from adequate knowledge of conodonts in the region, but our new faunas do represent a substantial increase in data and provide a further base for additional investigations. We believe it likely that many of the seemingly intractable sediments will produce biostratigraphically significant faunas if very large samples are collected in the future.

Williams *et al.* (1972) summarized the distribution of Caradoc–Ashgill sequences in Wales and the Welsh Borderland, and our sampling programme was based initially on this review. In the light of our conodont studies, any departures from this correlation scheme are shown in text-fig. 2 and discussed below. Full details of the stratigraphy and locality of all our 110 samples have been deposited with the British Library, Boston Spa, Yorks UK, as Supplementary Publication No. SUP 14024 (21 pages). They may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, Yorks L23 7BQ. In addition, they are available from the Department of Geology, National Museum of Wales (NMW Geology Open File No. 2). For immediate reference, a summary of the data is given in the Appendix (p. 710). All collections referred to in this paper are housed in the National Museum of Wales (NMW) under Accession Numbers 81.4G, 81.5G, and 81.6G. In the text below, numbers in brackets refer to the sample numbers indicated in text-figs. 1–4 and Tables 1 and 2.

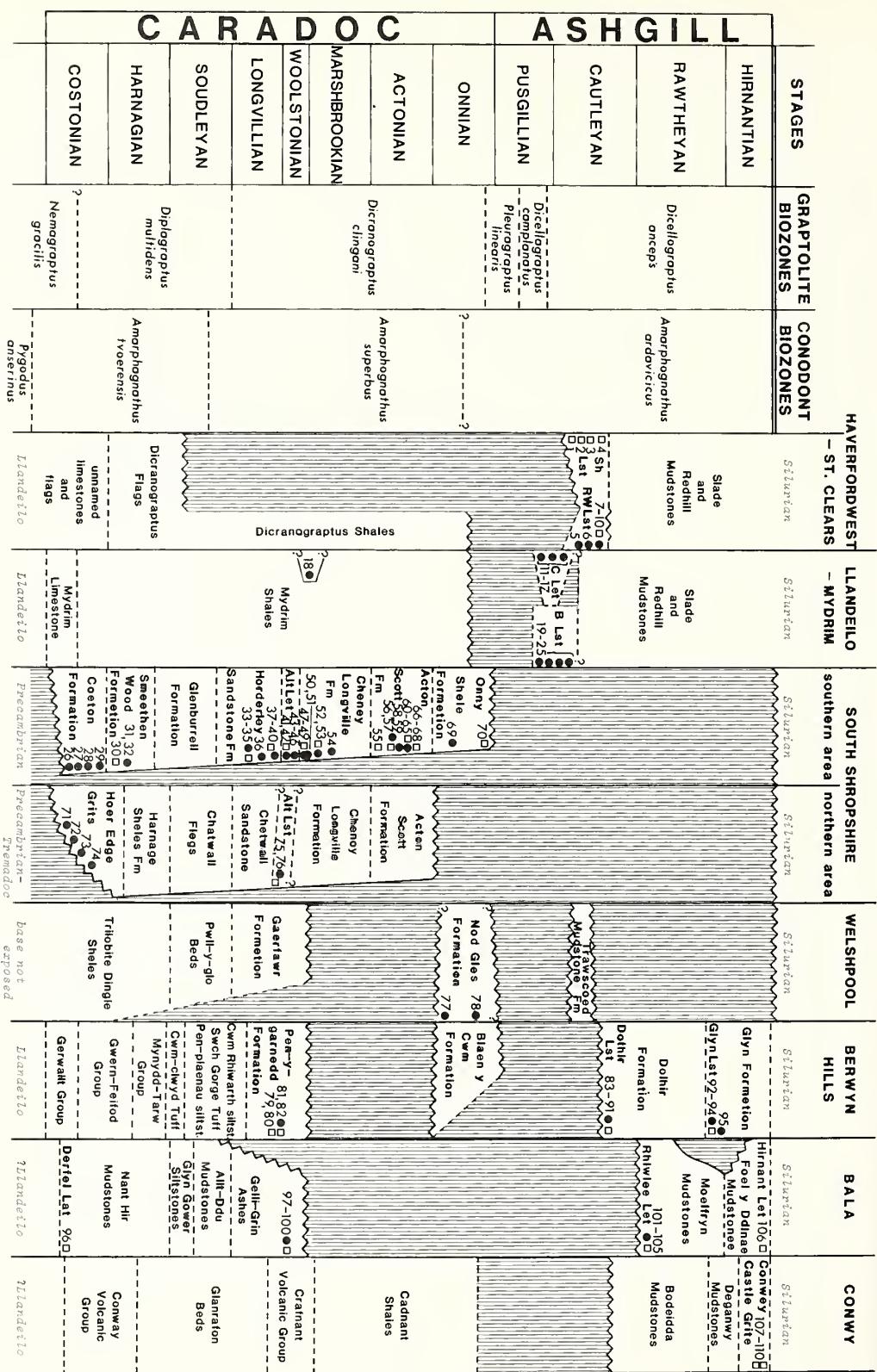
Stratigraphy and correlation (text-fig. 2)

South Wales. Our oldest productive samples (5, 6) from the south-western areas of the Caradoc–Ashgill outcrop (text-fig. 1) were from the Robeston Wathen Limestone in its type development to the west of St Clears (see Price 1973, pp. 231–234, figs. 2 and 3). On the basis of its apparent stratigraphical conformity below calcareous siltstones equivalent to the Sholeshook Limestone that bear a rich shelly fauna, the Robeston Wathen Limestone is dated firmly as early mid Ashgill in age, within Cautleyan zones 1–3 (Price 1973, fig. 6). From these beds we have recovered *Amorphognathus ordovicicus*, which accords well with the general acceptance of this species as an indicator of the Ashgill (e.g. Bergström 1983, fig. 1). Samples (1–4) in the type development of the Sholeshook Limestone further to the west near Haverfordwest were unproductive. Older beds in this region are mostly in graptolitic shales, but a report by Addison (*in* Williams *et al.* 1972, p. 36) suggests that some limestones previously thought to be of Llandeilo age include basal Caradoc (Costonian) shelly faunas; the same report mentions a conodont fauna from this horizon indicative of a *gracilis* graptolite Biozone age, but details are as yet unpublished and we have not collected further samples.

In the Llandeilo region, Price (1973, p. 244; 1984, p. 103) has summarized the shelly faunal evidence for assigning a late Pusgillian to early Cautleyan age to the Birdshill and Crûg limestones (see also Owens 1973, p. 48). Correlation of these levels based on conodonts has been the subject of considerable discussion (cf. Bergström 1971*a*; Orchard 1980) but they have been placed consistently by all authors within the *superbus* Biozone, although Orchard (1980, p. 13) suggested that the Crûg may be the slightly younger of the two and close to the *superbus/ordovicicus* boundary. Our samples from both these horizons (11–17, Crûg Limestone; 19–25, Birdshill Limestone) contain similar faunas



TEXT-FIG. 1. Outcrop of Caradoc-Ashgill strata in Wales and the Welsh Borderland showing the geographical distribution of conodont samples 1-110.



TEXT-FIG. 2. Stratigraphy and correlation of Caradoc-Ashgill successions in Wales and the Welsh Borderland showing the stratigraphical levels of conodont samples 1-110. Sh Lst = Sholeshook Limestone; RW Lst = Robeston Wathen Limestone; C Lst = Crug Limestone; B Lst = Birdhill Limestone; Alt Lst = Alternata Limestone. Solid circles indicate productive samples, open squares unproductive samples.

(Table 1) suggesting a closely similar age, and include what we identify as abundant specimens of *A. ordovicicus* (see discussion below); there are no specimens identified as *A. superbus*. On this basis we see no evidence for a *superbus* age in either the Crûg or Birdshill limestones; their assignment to the *ordovicicus* Biozone is consistent with the early Ashgill age suggested by the shelly faunas and removes this otherwise anomalous extension of the *superbus* Biozone well above the top of the Caradoc. Fragmentary specimens illustrated by Orchard (1980, pl. 4, figs. 23, 26) as *A. cf. A. superbus* from the type Ashgill area of northern England (Cautleyan) are inadequate to show the characteristic features of the species.

An isolated limestone lenticle at Pen-y-banc (sample 18) to the north-west of Llandeilo, generally included previously in the Birdshill outcrop (e.g. see Pringle and George 1948, fig. 11), contains an anomalous fauna; here we identify *A. superbus* but no *A. ordovicicus*. We consider that these beds are probably of mid Caradoc age (text-fig. 2) and are unrelated to the Birdshill-Crûg limestones.

Welsh Borderland and eastern Wales. Most of the stages and lithostratigraphical divisions of the Caradoc Series in the south Shropshire type area (samples 26–76) have yielded conodonts (text-figs. 2 and 3), but they are rarely abundant in the dominantly clastic sediments. No diagnostic zonal forms have been recovered, and correlation with the conodont zonal scheme continues to be based on broader shelly faunal and graptolitic evidence in various areas of Europe (e.g. Bergström 1971a, b, 1977, 1978, 1983). Our collections in the upper part of the succession are based on the revised stratigraphy of Hurst (1979).

In the Gwern-y-Brain section near Welshpool (Cave 1965), two samples (77, 78) from the Nod Glas Formation have yielded fairly common faunas whose age interpretations are problematical. The uppermost Nod Glas beds here contain the trilobite *Onnia gracilis* indicative of the Onnian, while the unconformably underlying Gaerfawr Formation contains a Woolstonian shelly fauna (Cave 1965), so that the limits of the Nod Glas Formation are fairly well circumscribed by comparison with the Shropshire succession (text-fig. 2). However, conodonts from the basal 50 cm (sample 77) of the phosphoritic limestones making up the Nod Glas here contain fairly common *Plectodina bullhillensis* sp. nov., which in Shropshire occurs only in samples from the Costonian to the Woolstonian. In addition the same sample contains *Amorphognathus* aff. *A. tvaerensis* (see p. 694), which again might support an earlier Caradoc age (?pre-mid Soudleyan—text-fig. 2). The full stratigraphical range of *P. bullhillensis* is not yet known from continuous, productive sections, but it cannot be ruled out that the base of the Nod Glas at Gwern-y-Brain is older than has been supposed previously, although the limit may be dictated by the Gaerfawr shelly fauna; it is also possible that the lowest Nod Glas conodonts are reworked although the specimens themselves show no sign of this, and further studies will be necessary to resolve the problem. The top 30 cm of the Nod Glas phosphoritic limestones (sample 78) below the nodular beds (Cave 1965, fig. 1) yielded abundant specimens of *A. ordovicicus*. If the trilobite evidence from here is definitive of the Onnian, then it could be that the *superbus-ordovicicus* Biozone boundary is as low as this below the Ashgill (see discussion above) as we propose tentatively in text-fig. 2, although further investigations are again required to test these relationships.

North Wales. In the Berwyn Hills (79–82) and Bala district (97–100), well-dated Longvillian-Woolstonian formations contain *superbus* Biozone faunas, including *P. bullhillensis* that gives further weight to correlations with the Shropshire succession. Various discontinuous limestone units of Cautleyan–Rawtheyan ages (83–95, 97–105) (text-fig. 2) generally yielded sparse faunas, but all are indicative of the *ordovicicus* Biozone.

None of our samples of Hirnantian age has yielded conodonts. Large samples from the type Hirnant Limestone of Bala (106) and from calcareous-cemented arenites of the Conway Castle Grits at Deganwy (107–110) were processed in the hope of isolating post-*ordovicicus* Biozone faunas to compare with the *Gamachignathus* faunas described from North America and northern England (e.g. McCracken and Barnes 1981a, b; McCracken *et al.* 1980; Orchard 1980; Uyeno and Barnes 1983); the potential of the latter for wider correlation is still unknown as the diagnostic forms have not yet been identified in other regions. *Gamachignathus* is a subjective synonym, apparently junior, of

TABLE I. Number and distribution of individual conodont elements recovered in the forty more productive samples.

TABLE I. Number and distribution of individual conodont elements recovered in the forty more productive samples.

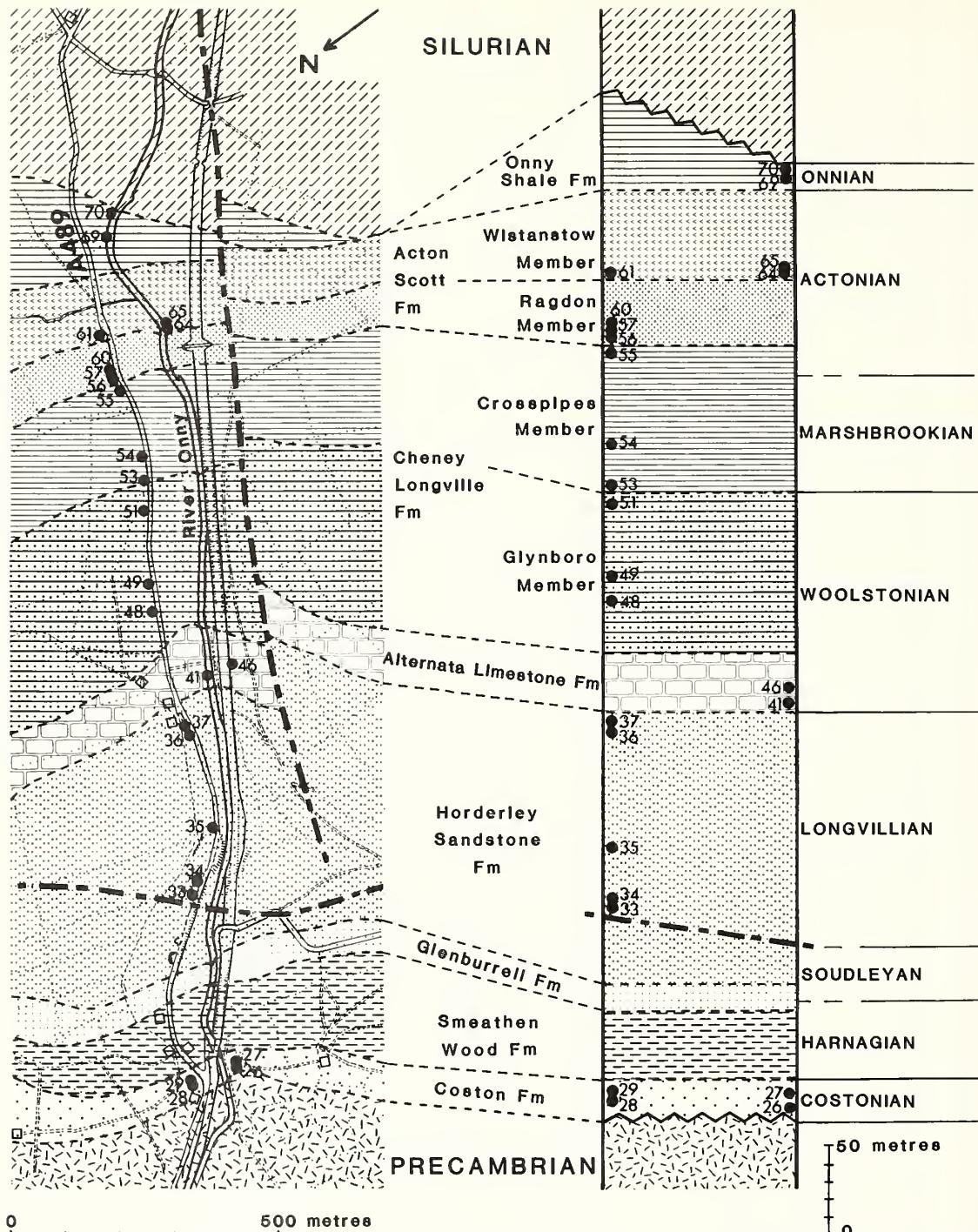
TABLE 2. Number and distribution of conodont species in all 110 samples from Wales and the Welsh Borderland, with details of Colour Alteration Index for each sample.

Conodont Colour Index	Sample no.	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	Total
<i>Anorphognathus ordovicicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>A. sunterius</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>A. aff. A. traerensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Aphelognathus rhodesii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Drepanostodus subrectus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Icriodella superba</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
? <i>Ozarkodina pseudofissilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Panderodus cf. P. gracilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Phragmodus cf. P. undatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Plectiodella bergstroemi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>P. bullitensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>P. tenuis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
? <i>Plectiodina</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Prioniodus deani</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Prioniodus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Protopanderodus litipius</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Pseudoneoneurus</i> sp. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
<i>Pseudoneoneurus</i> sp. B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
? <i>Rhodeognathus elegans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
? <i>Staufferella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
Gen. et sp. indet. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
Indet. fragment	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				

57

TABLE 2. Number and distribution of conodont species in all 110 samples from Wales and the Welsh Borderland, with details of Colour Alteration Index for each sample.

Sample no	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Conodont Colour Index																																								
<i>Amorphognathus ordovicianus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-						
<i>A. aff. A. tuerensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Aploleptognathus rhodesii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Drepanostyliodus subcreucus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Terebellia superba</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
? <i>Ozarkodina pseudofissilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Panderodus cf. P. gracilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Phragmodus cf. P. undatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Pteriodon bergerstroemi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>P. bulbifrons</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>P. tenius</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
? <i>Pteriodon</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Prioniodus deani</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>P. gracilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>P. undatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
<i>Rhodeognathus elegans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
? <i>Staufferella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Gen. et sp. indet. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Gen. et sp. indet. B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Indet. fragment	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-					
Sample no	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78		
Conodont Colour Index																																								
<i>Amorphognathus ordovicianus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	147				
<i>A. aff. A. tuerensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19				
<i>Aploleptognathus rhodesii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	234				
<i>Drepanostyliodus subcreucus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	49				
<i>Terebellia superba</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	214				
? <i>Ozarkodina pseudofissilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	96				
<i>Panderodus cf. P. gracilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	141				
<i>Phragmodus cf. P. undatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10				
<i>Pteriodon bergerstroemi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	34				
<i>P. bulbifrons</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	696				
<i>P. tenius</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	105				
? <i>Pteriodon</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1				
<i>Prioniodus deani</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	17				
<i>P. gracilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	52				
<i>P. undatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19				
<i>Rhodeognathus elegans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1				
? <i>Staufferella</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	97				
Gen. et sp. indet. A	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1				
Gen. et sp. indet. B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	57				



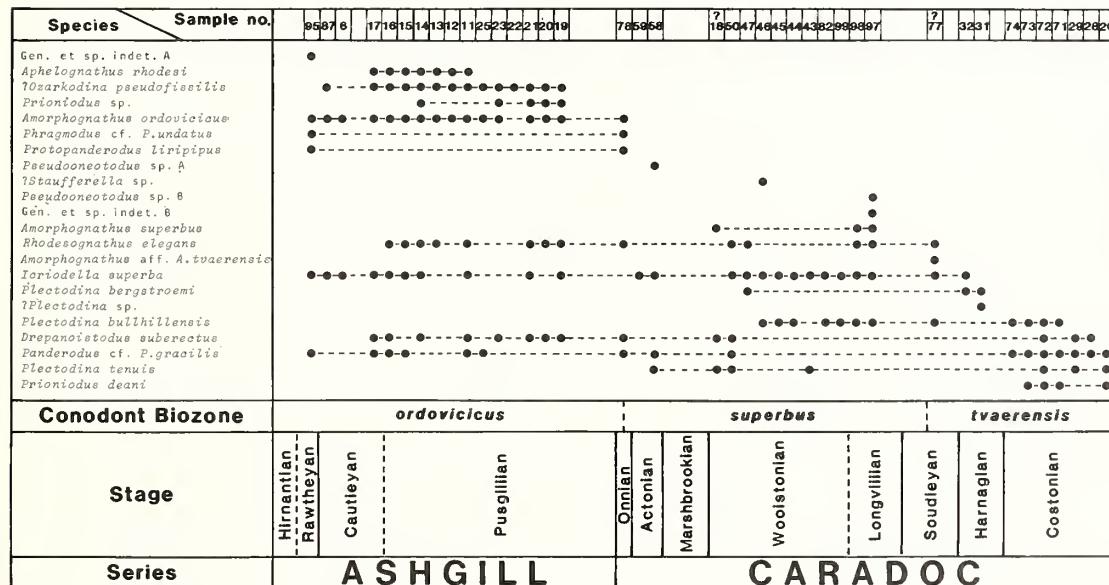
TEXT-FIG. 3. Geological map and stratigraphical section of the Caradoc Series in the Onny valley, Shropshire, showing detail of the distribution of conodont samples; stratigraphical thicknesses are based mainly on measurements made along the section on the north side of the A489 road. Samples plotted on the left of the vertical column are from the A489 road section, those on the right are from the Onny river and old railway section. Details of strike/dip are omitted from the map for clarity, but the dip is fairly constant throughout the section from 8° to 15° (maximum observed 22°) along a bearing of 150° .

Birksfeldia Orchard, 1980, which Orchard recovered from the probably Rawtheyan Cystoid Limestone and Upper Keisley Limestone in northern England, and the middle to late Ashgill Abercwmeiddaw Mudstone, Rhiwlas Limestone, and Robeston Wathen Limestone in North and South Wales. The date of publication of Orchard's paper is August 1980, whereas that of McCracken *et al.* is November 1980. The only other described British Hirnantian conodonts are zonally undiagnostic forms reported by Orchard (1980, pp. 12, 14) from the Swindale Limestone of Cross Fell, northern England.

Conodont biostratigraphy

Text-fig. 4 shows the approximate boundaries between the *ordovicicus*, *superbus*, and *tvaerensis* biozones in relation to our more productive samples. In detail these boundaries are unreliable because of the pronounced facies difference between the Shropshire and Welsh localities. The contrast between the composition of the collections is striking. The Shropshire material has a predominance of *Plectodina* and virtually no specimens of *Amorphognathus*. The Welsh material has an abundance of *Amorphognathus*. Because elements of the *Amorphognathus* lineage are used as zonal indices through this interval elsewhere (e.g. Bergström 1983, fig. 1), their absence in the predominantly shelly facies characteristic of the Caradoc type section is a significant drawback when trying to correlate from Shropshire even to Wales as well as to most other regions. Significant conodont occurrences in our samples are discussed below.

Prioniodus deanii sp. nov. is known from only seventeen elements from the Coston Formation (26) and the Hoar Edge Grit (71–73). It is characterized by a strongly arched, short, Pa element and may be a useful indicator of pre-Harnagian age. It appears to be restricted to the Costonian. *Plectodina tenuis* (Branson and Mehl) is fairly easily recognized in our collections by its strongly arched Pb element and a Sb element possessing a denticle beside the main cusp which is larger than that cusp. It occurs as low as the Coston Formation (26) and other Costonian localities and as high as the limestone at



TEXT-FIG. 4. Stratigraphical range and biostratigraphical zonation of conodonts from the forty more productive samples in Wales and the Welsh Borderland. Within any one Stage there may be some stratigraphical overlap between samples from different regions and sections, but the samples are plotted individually as a means of depicting general ranges; there is no overlap in samples from different Stages; relative durations of Stages are not necessarily true but simply reflect an artificial spacing necessary to accommodate the number of samples plotted.

Pen-y-banc (18) in the probable Marshbrookian. Both ends of its range in Britain are much lower than presently recorded in North America where Sweet (1981b) shows it from the late Kirkfieldian to late Richmondian.

P. bullhillensis sp. nov. is the most abundant species in our collections with almost 700 elements, mostly from the Hoar Edge Grit (71–74) in the Costonian to early Harnagian but with a range extending up to the Cymerig Limestone (97–99) in the probable Longvillian–Woolstonian. It is characterized by a very small Pb element which has a high anterior blade and by a Pa element which is usually large but rather delicate just behind the main cusp and therefore usually broken at that point. In some samples the Pa element is smaller but is still recognizable by its three anterior denticles, backwardly inclined main cusp, and the frequent breakage just behind that cusp. The species is not known from elsewhere but may be a useful indicator of early–mid Caradoc age deposits in Britain.

P. bergstroemi sp. nov. is known mainly from the Smeathen Wood Formation (31, 32) in the Harnagian but also from a few specimens from the lower Cheney Longville Formation (47) in the probable Woolstonian. The complete apparatus is still not known, partly because of the relatively few elements available and partly because most of the known specimens are broken. Nevertheless, it is quite distinctive. *Icriodella superba* Rhodes is a variable species and therefore difficult to subdivide in a meaningful way. It appears to range throughout the upper Caradoc and most of the Ashgill. *A. aff. A. tvaerensis* Bergström is known only from nineteen elements from the lower part of the Nod Glas Formation (77). It has some of the characteristics of *A. inaequalis* (the Pa element) and some of *A. tvaerensis* (the M and Pb elements). As discussed above, the occurrence of this form along with *P. bullhillensis* in this fauna suggests that the lower part of the Nod Glas Formation might be much older than the upper beds which include *A. ordovicicus*.

The type locality of *Rhodesognathus elegans* (Rhodes) is at Rhodes's Locality 3, Pen-y-garnedd, Wales (Rhodes 1953) (our samples 79, 80). According to Lindström (1977) and Sweet *et al.* (1971) the species ranges from the low Caradoc to the end of the Ashgill. In our collections it ranges from the Woolstonian Cheney Longville Formation (47) to the Pusgillian as represented in the Crûg and Birdshill samples (11–17, 19, 20). Thus we seem to be in approximate agreement with Lindström and others.

The type locality of *A. superbus* is Rhodes's Locality 2 (Rhodes 1953, p. 264) in the Cymerig Limestone (our samples 93–100). The holotype is an M element and these are rare and may vary more than earlier suspected. Difficulties in distinguishing *A. superbus* from *A. ordovicicus* may be reduced by noting the differences between the respective Pb elements, as described in the systematic section below. It appears that *A. ordovicicus* is present in the Glyn Formation (92–95), the Crûg Limestone (11–17), the Birdshill Limestone (8–10), the limestones at Dryslwyn (23) and Llanegwad (25), the Robeston Wathen Limestone (5, 6), and the upper part of the Nod Glas Formation (78), whilst *A. superbus* is present in the limestone at Pen-y-banc (18) and the Cymerig Limestone (97, 98).

?*Ozarkodina pseudofissilis* (Lindström) probably does not belong to *Ozarkodina* but is referred to that genus until its affinities can be clarified. The apparatus is currently known only from Pa and Pb elements. The species is characteristic of the Crûg Limestone at Crûg (11–17), which is the type locality, and also of the Birdshill Limestone (19, 20), and the limestones at Dryslwyn (22, 23) and Llanegwad (25). It appears to be an indicator of early Ashgill age. *Aphelognathus rhodesi* (Lindström) occurs in our samples only from the Crûg Limestone (11–17) and may be a useful Pusgillian indicator.

GEOTHERMAL HISTORY OF THE CONODONTS

The colour of conodonts indicates the thermal history of the deposits and largely reflects the thickness and duration of the overburden, although igneous and hydrothermal activity also may be factors. Dynamic (regional) metamorphism should not influence the colour of conodonts. In general the colour, measured as the Colour Alteration Index (CAI) of Epstein *et al.* (1977), will be the same for conodonts of the same age in the same area. Where distances of several tens of kilometres are involved the overburden thickness may have varied sufficiently for conodont colour differences to result (Savage 1983).

The Caradoc age conodonts from Shropshire all exhibit a Colour Alteration Index of 1 to 2 (Table 2), suggesting low geothermal temperatures. The Caradoc conodonts of Central and North Wales, and the Ashgill conodonts from South Wales, all have a CAI of 4·5 or more (Table 2), suggesting much higher geothermal temperatures. Bergström (1981a, p. 385) noted the CAI contrast in the region and suggested that volcanism or heat flow associated with tectonism is a more likely explanation for the high Welsh indices than overburden. If one accepts the calculations of Epstein *et al.* (1977), the overburden on the deposits of the Welsh trough necessary to produce the thermal changes would need to have been several kilometres greater than that on the Borderland platform deposits.

SYSTEMATIC DESCRIPTIONS

In this study we use the element notation of Sweet (1981a) adopted in the recent conodont volume of the *Treatise on Invertebrate Paleontology*. We have attempted to identify dextral and sinistral elements in the descriptions and plate explanations, assuming laterally organized pairs with the elements pointed away from the observer. Illustrations on the plates are arranged in stratigraphical and geographical order, with the older faunas from the Caradoc area on Plates 80–82, and the younger late Caradoc and Ashgill faunas on Plates 83–86. This arrangement is made to emphasize associations in the different areas and to assist in facies comparisons.

Order CONODONTOPHORIDA Eichenberg, 1930

Family BALOGNATHIDAE Hass, 1959

Genus AMORPHOGNATHUS Branson and Mehl, 1933c

Type species. *Amorphognathus ordovicica* Branson and Mehl, 1933c, p. 127.

Remarks. The orientation of the dextral and sinistral Pa elements used here is that used by Bergström (1978, pl. 80, figs. 1–3) but the reverse of that used by Lindström (1977) and by Orchard (1980). Many workers state that dextral elements are distinguished by high anterior blades (Schopf 1966; Lindström 1977; Orchard 1980). In our material both sinistral (Pl. 85, figs. 25 and 26; Pl. 86, figs 25 and 26) and dextral (Pl. 83, figs. 1 and 2; Pl. 84, figs. 1 and 3) elements may have high or low blades.

Amorphognathus ordovicicus Branson and Mehl, 1933c

Plate 84, figs. 1–21; Plate 85, figs. 1–26; Plate 86, figs. 1–13

- 1933c *Amorphognathus ordovicica* n. sp. Branson and Mehl, p. 127, pl. 10, fig. 38 [holotype] [Pa element].
- 1933c *Ambalodus triangularis* n. sp. Branson and Mehl, p. 128, pl. 10, figs. 35–37 [Pb element].
- 1959 *Goniodontus superbis* n. sp. Ethington, p. 278, pl. 40, figs. 1 and 2 [M element].
- 1959 *Trichonodella inclinata* Rhodes; Ethington, p. 290, pl. 41, fig. 6 [Sa element].
- 1959 *Tetraprioniodus parvus* n. sp. Ethington, p. 288, pl. 40, fig. 8 [Sb element].
- 1959 *Eoligonodina elongata* (Rhodes); Ethington, p. 277, pl. 40, fig. 5 [Sc element].
- 1959 *Keislognathus simplex* n. sp. Ethington, p. 280, pl. 40, figs. 9 and 10 [Sd element].
- 1978 *Amorphognathus ordovicicus* Branson and Mehl; Bergström, pl. 80, figs. 1–11 [multielement apparatus].

Remarks. *Amorphognathus ordovicicus* is most easily distinguished from earlier species of the genus by its smaller and more robust Pb elements (Pl. 84, figs. 4–10) as well illustrated in Bergström and Sweet 1966, pl. 28, figs. 7 and 8. The M element is also characteristic (Pl. 84, figs. 15 and 16), and is well illustrated in Bergström 1971a, p. 93, fig. 4(5), but this element is infrequently recovered and is not generally convenient for diagnosis.

Amorphognathus superbus (Rhodes, 1953)

Plate 83, figs. 1-19

- 1953 *Holodontus superbus* n. sp. Rhodes, p. 304, pl. 21, figs. 125-127 [holotype] [M element].
 1953 *Amorphognathus ordovicicus* Branson and Mehl; Rhodes, p. 283, pl. 20, figs. 47-49 [Pa element].
 1953 *Ambolodus triangularis* var. *indentatus* n. var. Rhodes, p. 280, pl. 20, figs. 35-37 [Pb element].
 1953 *Ligonodina elongata* n. sp. Rhodes, p. 305, pl. 21, figs. 130 and 131 [Sc element].
 1953 *Ligonodina extensa* n. sp. Rhodes, p. 306, pl. 21, figs. 128 and 129 [Sc element].
 1953 *Trichonodella gracilis* n. sp. Rhodes, p. 314, pl. 21, figs. 144, 147-150 [Sa element].

Remarks. In this species of *Amorphognathus* the sinistral Pb element is large, deeply excavated, thin-walled, and has a deeply indented and strongly sinuous aboral inner margin (Pl. 83, fig. 8). The dextral Pb element has an aboral inner margin which is deeply indented but non-sinuous (Pl. 83, fig. 6). The M element has an arched aboral margin and bears a low cusp and from one to three subequal denticles (Pl. 83, figs. 11-14).

Confusion about the distinctions between this species and *A. ordovicicus* may have added to the difficulty in correlating the Caradoc and Ashgill in Britain and elsewhere. The type species of *A. superbus* is from the Cymerig Limestone at Locality 2 of Rhodes (1953) in 'the shallow quarry 1750 ft due north of Plas Rhiwalgod and 600 ft east of Y-Garnedd, Merioneth' (our samples 98-100), and the holotype is a M element. M elements of *Amorphognathus* are usually very rare and seem to vary enough within a single fauna to make several specimens desirable for species

EXPLANATION OF PLATE 80

All figs. $\times 40$.

- Figs. 1-5. *Plectodina tenuis* (Branson and Mehl, 1933). 1, inner lateral view of sinistral Pa element, NMW 81.6G.1; 2 and 3, inner lateral and outer lateral views of sinistral M element, NMW 81.6G.2; 4 and 5, outer lateral and inner lateral views of dextral Sc element, NMW 81.6G.3; all from sample 58.
 Figs. 6 and 7. *Pseudooneotodus* sp. A. Lateral and upper views, NMW 81.6G.4, from sample 58.
 Figs. 8-14. *Icriodella superba* Rhodes, 1953. 8-10, outer lateral, upper, and lower views of dextral Pa element, NMW 81.6G.5; 11 and 12, outer lateral and inner lateral views of dextral Pb element, NMW 81.6G.6; 13 and 14, anterolateral and posterolateral views of inner side of dextral M element, NMW 81.6G.7; all from sample 58.
 Figs. 15-22. *Plectodina bullihillensis* sp. nov. 15, inner lateral view of sinistral Pa element, NMW 81.6G.8; 16, outer lateral view of dextral Pb element, NMW 81.6G.9; 17, inner lateral view of dextral Sb element, NMW 81.6G.10; 18, outer lateral view of sinistral Sc element, NMW 81.6G.11; 19, inner lateral view of dextral M element, NMW 81.6G.12; 20, posterior view of Sa element, NMW 81.6G.13; 21, outer lateral view of dextral Pa element, NMW 81.6G.14; 22, outer lateral view of sinistral Sc element, NMW 81.6G.1. Figs. 15-17 from sample 74; figs. 18-21 from sample 73; fig. 22 from sample 74.
 Figs. 23-39. *Prioniodus deani* sp. nov. 23 and 24, outer lateral and inner lateral views of sinistral Pa element, NMW 81.5G.2 (holotype); 25 and 26, inner lateral and outer lateral views of dextral Pa element, NMW 81.5G.3; 27-29, outer lateral, lower, and inner lateral views of dextral Pb element, NMW 81.5G.4; 30-32, lower, outer lateral, and inner lateral views of sinistral Pb element, NMW 81.6G.15; 33 and 34, inner lateral and outer lateral views of sinistral Pb element, NMW 81.6G.16; 35-37, inner lateral, outer lateral, and upper views of sinistral Pb element, NMW 81.6G.17; 38 and 39, lower and upper views of S element, NMW 81.5G.48. Figs. 23-29, 38 and 39 from sample 26; figs. 30-32 from sample 73; figs. 33-37 from sample 71.
 Figs. 40, 41. ?*Plectodina* sp. Inner lateral and outer lateral views of dextral M(?) element, NMW 81.6G.18, from sample 31.
 Figs. 42-47. *Panderodus* cf. *P. gracilis* (Branson and Mehl, 1933). 42, outer view of sinistral compressiform element, NMW 81.6G.19; 43, inner view of dextral compressiform element, NMW 81.5G.5; 44 and 45, outer and inner views of dextral graciliform element, NMW 81.6G.20; 46 and 47, outer and inner views of dextral graciliform element, NMW 81.6G.21. Fig. 42 from sample 74; fig. 43 from sample 26; figs. 44-47 from sample 71.



SAVAGE and BASSETT, Caradoc conodonts

identification. The Pb elements recovered from the type locality were named by Rhodes *Ambolodus triangularis* var. *indentatus* n. var. In our collections from Y Garnedd the M and Pb elements look the same as the Rhodes specimens (Rhodes 1953, figs. 35–37, 125–127). The Pb element is thin-walled, deeply excavated, and deeply indented, with a strongly sinuous inner margin. In contrast, the Pb element of *Amorphognathus ordovicicus* is small and stout. The illustration by Rhodes of Pb elements of *A. superbus* (Rhodes 1953, pl. 20, figs. 30–37), from his Locality 2, with Pb elements from his Locality 3 (Rhodes 1953, pl. 20, figs. 28–31), which is 'a disused quarry about 900 ft east of the Powis Arms at Pen-y-garnedd, Montgomeryshire' (our samples 79, 80) appears to have led to some confusion. These Pb elements from Pen-y-garnedd are the small, stout kind, very similar to those of *A. ordovicicus* but in this case most likely belonging to *A. complicatus* Rhodes, the holotype of which also comes from Rhodes's Locality 3. *A. complicatus* is thought by Bergström (1971a, 1983) to have a range corresponding with the upper half of that of *A. superbus*. This distinction between the Pb elements of *A. superbus* and *A. complicatus* does not seem to have been recognized sufficiently hitherto and it has become common to show the forms, named by Rhodes as *Ambolodus triangularis* var. *indentatus* n. var. and *A. triangularis* Branson and Mehl, as synonyms (Bergström 1964, p. 56; Lindström 1977, p. 44; Orchard 1980, p. 16). Any confusion is probably compounded by the inclusion by Lindström of a small, stout Pb element as part of the illustration of the *Amorphognathus superbus* apparatus in the Catalogue of Conodonts (Lindström 1977, pp. 40, 41). The material used in this illustration is not from the type area in Wales but is from Banklick Creek in Kentucky (Bergström and Sweet 1966, pp. 273, 296, 426, pl. 28, figs. 7 and 8) and probably does not belong to *A. superbus*. Orchard assigned material from the Crûg and Birdshill limestones to *A. superbus* and *A. aff. A. superbus* but illustrated only single views of four broken elements (Orchard 1980, pl. 4, figs. 19–21, and 24). These specimens inadequately support his determination and probably belong variously to *A. ordovicicus* and *Prioniodus* sp.

Amorphognathus aff. *A. tvaerensis* Bergström, 1962

Plate 86, figs. 25–33

- aff. 1962 *Amorphognathus tvaerensis* n. sp. Bergström, p. 36, pl. 4, figs. 7 and 8 [holotype], 9 and 10 [Pa element].
 aff. 1962 *Tvaerenognathus ordovicica* n. gen. et sp. Bergström, p. 57, pl. 1, figs. 1–5 [M element].
 aff. 1962 *Ambalodus triangularis erraticus* n. ssp. Bergström, p. 26, pl. 3, figs. 15–17 [Pb element].

EXPLANATION OF PLATE 81

All figs. × 40.

Figs. 1–17. *Plectodina bullhillensis* sp. nov. 1–3, inner lateral, outer lateral, and lower views of sinistral Pa element, NMW 81.6G.22 (holotype); 4–6, inner lateral, lower, and outer lateral views of sinistral Pb element, NMW 81.6G.23; 7 and 8, outer lateral and inner lateral views of dextral Sb element, NMW 81.6G.24; 9 and 10, lower and inner lateral views of sinistral M element, NMW 81.6G.25; 11 and 12, inner lateral and outer lateral views of sinistral Sc element, NMW 81.6G.26; 13–15, lower, inner lateral, and outer lateral views of asymmetric sinistral Sa element, NMW 81.6G.27; 16 and 17, posterior and postero-lower views of Sa element, NMW 81.6G.28; all from sample 72.

Fig. 18. *Drepanoistodus suberectus* (Branson and Mehl, 1933). Inner lateral view of NMW 81.6G.29, from sample 72.

Figs. 19–35. *Plectodina tenuis* (Branson and Mehl, 1933). 19–21, inner lateral, outer lateral, and lower views of Pa element, NMW 81.5G.6; 22 and 23, lateral and lower views of sinistral Pb element, NMW 81.5G.7; 24 and 25, inner lateral and lower views of sinistral Sb element, NMW 81.5G.8; 26–28, outer lateral, lower, and inner lateral views of dextral M element, NMW 81.5G.9; 29 and 30, outer lateral and inner lateral views of dextral Sc element, NMW 81.5G.10; 31, inner lateral view of dextral Sb element, NMW 81.5G.11; 32 and 33, inner lateral and lower views of asymmetric sinistral Sa element, NMW 81.5G.12; 34 and 35, posterior and lower views of Sa element, NMW 81.5G.13; all from sample 26.

SAVAGE and BASSETT, *Plectodina, Drepanoistodus*

- aff. 1962 *Ambalodus triangularis suecicus* n. ssp. Bergström, p. 28, pl. 3, figs. 11–14 [Pb element].
 aff. 1983 *Amorphognathus tvaerensis* Bergström; Bergström, p. 47, fig. 4H–P [multielement apparatus].

Remarks. A few specimens of *Amorphognathus* from sample 77 comprise what is probably a new species of the genus. The Pa, M, and Pb elements resemble those of the early to middle Caradoc species *A. tvaerensis*. As discussed above (p. 715), the age of sample 77 in the lower Nod Glas Formation was earlier thought to lie within the range of *A. superbus* but the absence of that species from our fauna and the presence of *A. aff. A. tvaerensis* suggests that it may be older.

Genus RHODESOGNATHUS Bergström and Sweet, 1966

Type species. *Ambolodus elegans* Rhodes, 1953, p. 278.

Rhodesognathus elegans (Rhodes, 1953)

Plate 82, figs. 34–37; Plate 83, figs. 26 and 27; Plate 84, figs. 28 and 29; Plate 85, figs. 36–39; Plate 86, figs. 23 and 24

- 1953 *Ambolodus elegans* n. sp. Rhodes, p. 278, pl. 20, figs. 22 and 24 [holotype], 21, 23, and 25 [Pa element].
 1953 *Ambolodus pulcher* n. sp. Rhodes, p. 279, pl. 20, figs. 38–41 [Pb element].
 1953 *Ambolodus robustus* n. sp. Rhodes, p. 279, pl. 20, figs. 26, 27, 32, and 33 [Pa element].
 1977 *Rhodesognathus elegans* (Rhodes); Lindström, p. 535 [multielement apparatus].

Remarks. Sweet (1979a, p. G21) and Orchard (1980, p. 25) have commented on the apparatus of *Rhodesognathus*, and particularly on the possibility that *R. elegans* may have possessed ramiform elements like those of *Amorphognathus*. Orchard (1980) found no evidence of these ramiform elements but considers (pers. comm. 1985) such an apparatus quite likely. We have no ramiform elements with our Pa and Pb elements and we are particularly conscious that the twelve Pa and nine Pb elements recovered from our Cheney Longville Formation sample 50 have no ramiform elements associated with them. In this fauna the absence of *Amorphognathus* and its ramiform elements is helpful in reducing the number of possible associations.

EXPLANATION OF PLATE 82

All figs. × 30.

Figs. 1–16. *Plectodina bergstroemi* sp. nov. 1 and 2, outer lateral and inner lateral views of dextral Sb element, NMW 81.6G.30; 3 and 4, outer lateral and inner lateral views of dextral Pb element, NMW 81.6G.31; 5–7, inner, lower, and outer views of sinistral Sb element, NMW 81.6G.55; 8 and 9, inner lateral and outer lateral views of dextral Sc element, NMW 81.6G.56; 10–12, inner lateral, outer lateral, and lower views of dextral Pb element, NMW 81.6G.32 (holotype); 13–15, inner lateral, outer lateral, and lower views of dextral Pa element, NMW 81.6G.33; 16, inner lateral view of broken M element, NMW 81.6G.34; all from sample 32.

Figs. 17–27. *Plectodina bullhillensis* sp. nov. 17–19, inner lateral, outer lateral, and lower views of dextral Pa element, NMW 81.5G.14; 20–22, outer lateral, lower, and inner lateral views of dextral Pb element, NMW 81.5G.15; 23 and 24, inner lateral and outer lateral views of dextral Sc element, NMW 81.5G.16; 25, inner lateral view of dextral M element, NMW 81.5G.17; 26 and 27, posterior and anterior views of Sa element, NMW 81.5G.18; all from sample 45.

Figs. 28–33. *Icriodella superba* Rhodes, 1953. 28 and 29, inner lateral and outer lateral views of dextral M element, NMW 81.5G.19; 30–32, upper, outer lateral, and lower views of sinistral Pa element, NMW 81.5G.20; 33, outer view of sinistral Pb element, NMW 81.5G.21. Figs. 28–32 from sample 46; fig. 33 from sample 50.

Figs. 34–37. *Rhodesognathus elegans* (Rhodes, 1953). 34, outer lateral view of dextral Pa element, NMW 81.5G.22; 35 and 36, outer lateral and inner lateral views of dextral Pb element, NMW 81.5G.23; 37, outer lateral view of sinistral Pb element, NMW 81.5G.24; all from sample 50.

Fig. 38. *Drepanoistodus subrectus* (Branson and Mehl, 1933). Inner lateral view of NMW 81.5G.25, from sample 50.

Figs. 39–41. ?*Staufferella* sp. Lower, inner lateral, and outer lateral views of NMW 81.5G.26, from sample 45.



SAVAGE and BASSETT, Caradoc conodonts

Family CYRTONIODONTIDAE Hass, 1959
Genus APHELOGNATHUS Branson, Mehl and Branson, 1951

Type species. *Aphelognathus grandis* Branson, Mehl and Branson, 1951, p. 9.

Aphelognathus rhodesi (Lindström, 1959)

Plate 84, figs. 34–46

- 1959 *Ozarkodina rhodesi* n. sp. Lindström, p. 441, pl. 1, figs. 1 and 2 [holotype], 3–9 [Pb element].
- 1959 *Prioniodus pulcherrima* n. sp. Lindström, p. 442, pl. 3, figs. 28–30 [Pa element].
- 1959 *Cordylodus* cf. *spurius* Branson and Mehl; Lindström, pl. 4; figs. 19 and 20 [Sc element], 21 [M element].
- 1959 *Zygognathus crugensis* n. sp. Lindström, p. 451, figs. 11–27 [Sb element].
- 1959 *Trichonodella parabolica* n. sp. Lindström, p. 450, figs. 18–22 [Sa element].
- 1980 *Aphelognathus nudus* sp. nov. Orchard, p. 18, pl. 2, figs. 1 and 2 [Sc element], 3 [Sb element], 4 [Pb element], 8 and 11 [M element].
- 1981b *Aphelognathus rhodesi* (Lindström); Sweet, p. 49, figs. 1–6, p. 51, 52 [multielement apparatus].

Remarks. Lindström (1959) described and figured as form species all the elements of this species from the Crûg Limestone of South Wales (our samples 11–17). The first of these form species is *Ozarkodina rhodesi* on p. 441 and this should thus determine the multielement name. Orchard (1980) believed that the Pa and Pb elements are indistinguishable from those described by Hinde (1879) from Ontario, Canada, and tentatively named the apparatus *Aphelognathus furcatus* (Hinde) based on the Pa element. Sweet (1979b, p. 66) has presented evidence to show that *Prioniodus furcatus* Hinde is part of an *Oulodus* apparatus, and it now seems best to assign the Crûg material to *A. rhodesi*. *A. rhodesi* is easily distinguished from other species of *Aphelognathus* by its short Sb element, lack of denticles anterior of the cusp on the M and Sc elements, and more reclined denticles on the Pa element.

Genus PLECTODINA Stauffer, 1935

Type species. *Plectodina dilata* Stauffer, 1935, p. 152.

EXPLANATION OF PLATE 83

All figs. × 40; all from sample 97.

Figs. 1–19. *Amorphognathus superbus* (Rhodes, 1953). 1–3, upper, outer lateral, and lower views of dextral Pa element, NMW 81.5G.27; 4–7, outer lateral, upper, inner lateral, and lower views of dextral Pb element, NMW 81.5G.28; 8–10, inner lateral, lower outer lateral, and upper views of sinistral Pb element, NMW 81.5G.29; 11 and 12, inner lateral and outer lateral views of sinistral M element, NMW 81.5G.30; 13 and 14, outer lateral and inner lateral views of dextral M element, NMW 81.5G.31; 15, inner lateral views of dextral Sc element, NMW 81.5G.32; 16, inner lateral view of Sa element, NMW 81.5G.33; 17 and 18, inner lateral and outer lateral views of dextral Sc element, NMW 81.5G.34; 19, lateral view of Sd element, NMW 81.5G.35.

Figs. 20–25. *Iciodella superba* Rhodes, 1953. 20 and 21, outer lateral and inner lateral views of sinistral M element, NMW 81.5G.36; 22–24, upper, lower, and inner lateral views of sinistral Pa element, NMW 81.5G.37; 25, outer lateral view of sinistral Pb element, NMW 81.5G.38.

Figs. 26 and 27. *Rhodesognathus elegans* (Rhodes, 1953). 26, outer lateral view of dextral Pb element, NMW 81.5G.39; 27, outer lateral view of dextral Pa element, NMW 81.5G.40.

Figs. 28–35. *Plectodina bullhillensis* sp. nov. 28, outer lateral view of sinistral Pa element, NMW 81.5G.41; 29 and 30, inner lateral and outer lateral views of sinistral Sc element, NMW 81.5G.42; 31 and 32, inner lateral and outer lateral views of dextral M element, NMW 81.5G.43; 33 and 34, inner lateral and outer lateral views of dextral Sb element, NMW 81.5G.44; 35, anterior view of Sa element, NMW 81.5G.45.

Figs. 36 and 37. *Pseudooneotodus* sp. B. Lateral and upper views of NMW 81.5G.46.

Fig. 38. Gen. et sp. indet. B. Lateral view of element, NMW 81.5G.47.



SAVAGE and BASSETT, Caradoc and Ashgill conodonts

Plectodina bergstroemi sp. nov.

Plate 82, figs. 1–16

Diagnosis. A species of *Plectodina* in which all the elements have broad bases containing conspicuous white matter. The denticles are typically discrete and widely spaced.

Holotype. Pb element NMW 81.6G.32, sample 31 (Smeathen Wood Formation, Raggleth, Shropshire); Plate 82, figs. 10–12.

Description. The Pa element bears stout, nodular denticles and a main cusp which is inwardly curved with a distinct ridge up its inner face (Pl. 82, figs. 13–15). The Pb element has large, strongly inclined denticles and an inwardly curved main cusp below which the basal cavity is deeply cupped (Pl. 82, figs. 3, 4, 10–12). A narrow ridge runs up the inner face of the main cusp from the basal margin (Pl. 82, figs. 4, 10). The M element is strongly curved and has sharp anterior and posterior edges; its basal cavity is widely expanded inward (Pl. 82, fig. 16). The Sc element has a gently recurved main cusp and long, discrete denticles along its posterior bar (Pl. 82, figs. 8, 9). The Sb element consists of a large median cusp curving posteriorly and extending below its junction with the anterior and posterior bars. These bars slope sharply downward to enclose an angle of about 90° and bear widely spaced denticles (Pl. 82, figs. 1, 2, 5–7). The Sa element has not been recovered. All the elements have thick, conspicuous white matter in their broadly excavated aboral surfaces. This material does not grade into the darker material comprising the remainder of the element (Pl. 82, figs. 3, 6, 11).

Remarks. This species is named after Stig Bergström in recognition of his contributions to knowledge of Ordovician conodonts.

EXPLANATION OF PLATE 84

All figs. × 40.

Figs. 1–21. *Amorphognathus ordovicicus* Branson and Mehl, 1933. 1–3, upper, lower, and upper outer lateral views of dextral Pa element, NMW 81.4G.1; 4–6, lower, outer lateral, and upper views of sinistral Pb element, NMW 81.4G.2; 7 and 8, outer lateral and inner lateral views of sinistral Pb element, NMW 81.4G.3; 9 and 10, inner lateral and upper views of dextral Pb element, NMW 81.4G.4; 11, lateral view of Sd element, NMW 81.4G.5; 12, lateral view of Sd element, NMW 81.4G.6; 13 and 14 outer lateral and upper views of sinistral Pb element, NMW 81.4G.7; 15 and 16, outer lateral and inner lateral views of dextral M element, NMW 81.4G.8; 17, lateral view of Sd element, NMW 81.4G.9; 18, lateral view of sinistral Sb element, NMW 81.4G.10; 19 and 20, lateral view of Sd element, NMW 81.4G.11; 21, outer lateral view of dextral Sc element, NMW 81.4G.12. Figs. 1–12, 17, and 18 from sample 14; figs. 13, 14, and 19–21 from sample 11; figs. 15 and 16 from sample 17.

Figs. 22–25. *Icriodella superba* Rhodes, 1953. 22, upper view of anterior fragment of sinistral Pa element, NMW 81.4G.13; 23, outer lateral view of sinistral Pa element, NMW 81.4G.14; 24 and 25, inner lateral and outer lateral views of sinistral M element, NMW 81.4G.15; all from sample 14.

Figs. 26 and 27. *Prioniodus* sp. Inner lateral and outer lateral views of dextral Sc element, NMW 81.4G.16, from sample 14.

Figs. 28 and 29. *Rhodesognathus elegans* (Rhodes, 1953). 28, outer lateral view of sinistral Pb element, NMW 81.4G.17, from sample 11; 29, outer lateral view of dextral Pa element, NMW 81.4G.57, from sample 14.

Figs. 30–33. ?*Ozarkodina pseudofissilis* (Lindström, 1959). 30, inner lateral view of dextral Pa element, NMW 81.4G.18; 31 and 32, inner lateral and lower views of sinistral Pa element, NMW 81.4G.19; 33, outer lateral view of dextral Pb element, NMW 81.4G.20. Figs. 30 and 33, from sample 11; figs. 31 and 32, from sample 14.

Figs. 34–46. *Aphelognathus rhodesi* (Lindström, 1959). 34 and 35, lower and inner lateral views of sinistral M element, NMW 81.4G.21; 36 and 37, inner lateral and lower views of sinistral Pb element, NMW 81.4G.22; 38 and 39, inner lateral and lower views of sinistral Pb element, NMW 81.4G.23; 40 and 41, lower and posterior views of Sa element, NMW 81.4G.24; 42, inner lateral view of dextral Pa element, NMW 81.4G.25; 43 and 44, inner lateral and lower views of dextral Sc element, NMW 81.4G.26; 45 and 46, inner lateral and outer lateral views of sinistral Sb element, NMW 81.4G.27. Figs. 34, 35, 38–46 from sample 14; figs. 36 and 37 from sample 11.



SAVAGE and BASSETT, Caradoc and Ashgill conodonts

Plectodina bullhillensis sp. nov.

Plate 80, figs. 15–22; Plate 81, figs. 1–17; Plate 82, figs. 17–27; Plate 83, figs. 28–35

Diagnosis. A species of *Plectodina* in which the Pa element bears discrete, stout denticles, a main cusp more posteriorly inclined than the anterior denticles, and a basal cavity which is widely expanded along the posterior two-thirds of the element. The Pb element is relatively small with an anterior blade twice the height of the posterior blade.

Holotype. Pa element NMW 81.6G.22, sample 72 (Hoar Edge Grit, Bullhill Gutter, Shropshire); Pl. 81, figs. 1–3.

Description. The Pa element shows some ontogenetic range. It may be large and broad, in which case it bears about three short, stout anterior denticles and four to six fairly stout posterior denticles. In these large specimens the entire basal cavity is widely expanded, and particularly so along the posterior two-thirds of the element (Pl. 81, figs. 1–3). In smaller specimens the cusp and denticles are less thickened and the posterior part of the element usually is broken off (Pl. 80, fig. 15; Pl. 82, figs. 17–19). The Pb element is consistently small and delicate. It has an anterior blade twice the height of the posterior blade and a basal cavity expanded beneath the fairly upright main cusp (Pl. 81, figs. 4–6). The M element has a long blade-like main cusp which is sharply twisted inward and backward near its base. There are no anterior denticles. The basal margin of the cusp is quite sharply inclined at an angle of about 110° relative to the basal margin of the posterior bar (Pl. 81, fig. 10). The posterior bar is thin, particularly where it attaches to the cusp, so that in many specimens it is broken from the cusp. It is straight or slightly recurved, tapers posteriorly, and bears seven or more posteriorly inclined denticles which are in contact at their bases but are otherwise discrete. A posteriorly expanded basal cavity is present below the cusp. It is sharply constricted where it extends to the posterior bar but then continues along the bar as a pronounced groove (Pl. 81, figs. 9 and 10). The Sc element has a gently reclined main cusp and a long, straight posterior bar which bears eight or more well-spaced denticles (Pl. 81, figs. 11 and 12). The cusp is laterally compressed apart

EXPLANATION OF PLATE 85

All figs. × 40.

Figs. 1–26. *Amorphognathus ordovicicus* Branson and Mehl, 1933. 1, upper view of sinistral Pa element, NMW 81.4G.28; 2, upper view of sinistral Pa element, NMW 81.4G.29; 3–5, outer lateral and inner lateral views of Sd element, NMW 81.4G.30; 6 and 7, posterior and anterolateral views of Sa element, NMW 81.4G.31; 8 and 9, inner lateral and outer lateral views of dextral Sb element, NMW 81.4G.32; 10 and 11, outer lateral and inner lateral views of sinistral Sb element, NMW 81.4G.33; 12 and 13, outer lateral and inner lateral views of dextral Pb element, NMW 81.4G.58; 14, inner lateral view of dextral Sc element, NMW 81.4G.34; 15, inner lateral view of dextral Sc element, NMW 81.4G.35; 16, outer lateral view of dextral Sb element, NMW 81.4G.36; 17, inner lateral view of dextral Sc element, NMW 81.4G.37; 18–20, anterior and lateral views of Sa element, NMW 81.4G.38; 21, upper view of sinistral Pb element, NMW 81.4G.39; 22, inner lateral view of sinistral Pb element, NMW 81.4G.40; 23, upper view of sinistral Pa element, NMW 81.4G.41; 24, upper view of dextral Pa element, NMW 81.4G.42; 25 and 26, upper and upper lateral views of sinistral Pa element, NMW 81.4G.43. Figs. 1–11 and 22 from sample 19; figs. 12–20 from sample 21; figs. 21 and 23–26 from sample 20.

Fig. 27. ?*Ozarkodina pseudofissilis* (Lindström, 1959). Inner lateral view of sinistral Pa element, NMW 81.4G.44, from sample 21.

Figs. 28–35, 44, and 45. *Prioniodus* sp. 28–30, upper, outer lateral, and inner lateral views of sinistral Pa element, NMW 81.4G.45; 31 and 32, outer lateral and inner lateral views of sinistral Pb element, NMW 81.4G.46; 33, outer lateral view of dextral Pb element, NMW 81.4G.47; 34 and 35 outer lateral and inner lateral views of sinistral Sc element, NMW 81.4G.48; 44 and 45, lateral views of M element, NMW 81.4G.49. Figs. 28–32, 34, and 35 from sample 21; figs. 33, 34, and 45 from sample 19.

Figs. 36–39. *Rhodesognathus elegans* (Rhodes, 1953). 36, inner lateral view of dextral Pb element, NMW 81.4G.50; 37, outer lateral view of sinistral Pb element, NMW 81.4G.51; 38, outer lateral view of sinistral Pa element, NMW 81.4G.52; 39, outer lateral view of dextral Pa element, NMW 81.4G.53. Figs. 36 and 37 from sample 21; fig. 38 from sample 20; fig. 39 from sample 19.

Figs. 40–43. *Icriodella superba* Rhodes, 1953. 40, upper view of fragmentary Pa element, NMW 81.4G.54; 41 and 42, lateral and upper views of fragmentary Pa element, NMW 81.4G.55; 43, lateral view of Pb element, NMW 81.4G.56. Figs. 40 and 43 from sample 20; figs. 41 and 42 from sample 19.



SAVAGE and BASSETT, Caradoc and Ashgill conodonts

from a gentle expansion extending down its inner side (Pl. 81, fig. 11). There are no anterior denticles. The basal cavity beneath the cusp is narrow and continues back along the posterior bar with only minor decrease in width. The Sb element has a weakly sinuous and posteriorly recurved main cusp with basal lips projecting downward on both the anterior and posterior sides (Pl. 81, figs. 7 and 8). The lateral bars are of unequal length and diverge at an angle of 75° to 80°. The shorter lateral bar, which is flexed slightly posteriorly and arched, bears three or four compressed denticles. The longer lateral bar is straighter and bears three or four more widely spaced denticles. The Sa element is usually symmetrical with lateral processes enclosing an angle of about 65°. The posterior face of the cusp bears a median ridge which is cleft where it runs into the basal cavity (Pl. 81, fig. 16). Occasionally the Sa element is slightly asymmetrical and then has the lateral processes more open, to enclose an angle of about 85°, and the cusp ridge twisted sideways (Pl. 81, figs. 13–15).

Remarks. This species is characterized by its broad Pa element, bearing only three or four anterior denticles, and its contrastingly small, delicate Pb element. At present it is known from the lower part of the Costonian to the upper part of the Woolstonian.

Plectodina tenuis (Branson and Mehl, 1933c)

Plate 80, figs. 1–5; Plate 81, figs. 19–35

- 1933c *Ozarkodina tenuis* n. sp. Branson and Mehl, p. 128, pl. 10, figs. 19 [syntype], 20, 21, and 23 [Pa element].
 1933c *Prioniodus*(?) *flexuosus* n. sp. Branson and Mehl, p. 130, pl. 10, fig. 16 [M element].
 1933c *Cordylodus?* *delicatus* n. sp. Branson and Mehl, p. 129, pl. 10, figs. 14 and 15 [Sc element].
 1933c *Phragmodus mirus* n. sp. Branson and Mehl, p. 123, pl. 10, fig. 12 [Sb element].
 1933c *Trichognathus tenuis* n. sp. Branson and Mehl, p. 131, pl. 10, fig. 18 [Sa element].
 1966 *Plectodina furcata* (Hinde); Bergström and Sweet, p. 377, pl. 32, figs. 17–19; pl. 33, figs 1–4; pl. 34, figs. 9–12 [part of multielement apparatus].
 ?1981b *Plectodina tenuis* (Branson and Mehl); Sweet, p. 274, figs. 10–18, pp. 287–290 [multielement apparatus: but note reversal of Pa and Pb notation compared with that used herein and in Sweet 1979b, 1981a].

Remarks. This species has been referred frequently to *Plectodina furcata* (Hinde) but it now appears that the holotype of *furcata* is part of an *Oulodus* apparatus as discussed above in the remarks on

EXPLANATION OF PLATE 86

All figs. × 40.

Figs. 1–13. *Amorphognathus ordovicicus* Branson and Mehl, 1933. 1, upper view of sinistral Pa element, NMW 81.6G.35; 2, upper view of sinistral Pa element, NMW 81.6G.36; 3, upper view of sinistral Pa element, NMW 81.6G.37; 4 and 5, upper and lower views of sinistral Pa element, NMW 81.6G.38; 6, upper view of sinistral Pb element, NMW 81.6G.39; 7, upper view of sinistral Pb element, NMW 81.6G.40; 8 and 9, upper and outer lateral views of sinistral Pb element, NMW 81.6G.41; 10, upper view of dextral Pb element, NMW 81.6G.42; 11–13, anterior and posterior views of Sa element, NMW 81.6G.43; all from sample 95.

Fig. 14. Gen. et sp. indet. A. Lateral view of element, NMW 81.6G.44, from sample 95.

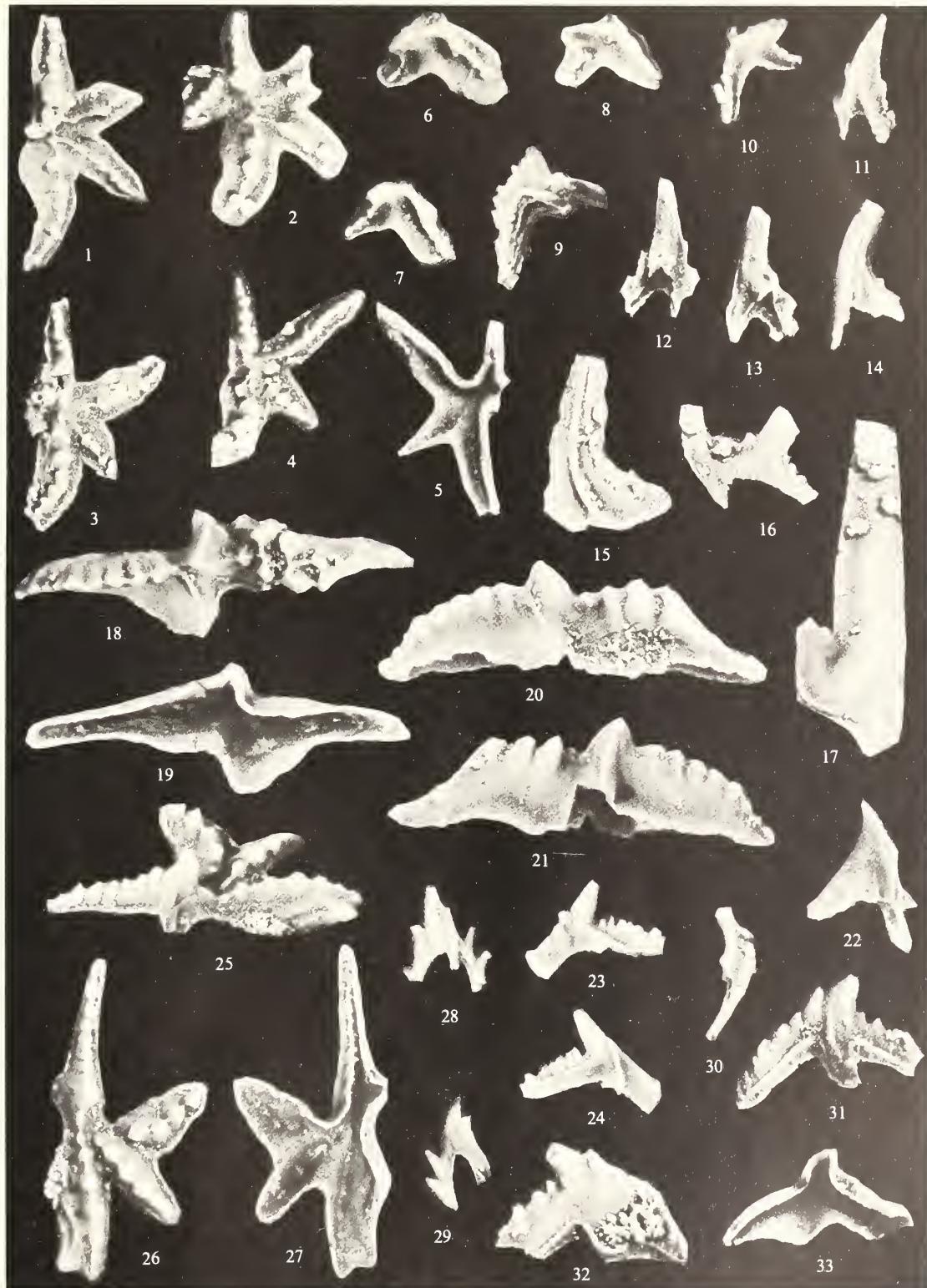
Fig. 15. *Protopanderodus liripipes* Kennedy, Barnes and Uyeno, 1979. Lateral view of NMW 81.6G.45, from sample 95.

Figs. 16 and 17. *Phragmodus* cf. *P. undatus* Branson and Mehl, 1933. 16, inner lateral view of dextral S element, NMW 81.6G.46; 17, inner lateral view of sinistral M element, MNW 81.6G.47; both from sample 95.

Figs. 18–22. *Icriodella superba* Rhodes, 1953. 18–21, upper, lower, inner lateral, and outer lateral views of dextral Pa element, NMW 81.6G.48; 22, inner lateral view of sinistral M element, NMW 81.6G.49; all from sample 77.

Figs. 23 and 24. *Rhodesognathus elegans* (Rhodes, 1953). Inner lateral and outer lateral views of dextral Pa element, NMW 81.6G.50, from sample 77.

Figs. 25–33. *Amorphognathus* aff. *A. tvaerensis* Bergström, 1962. 25–27, inner lateral, upper, and lower views of sinistral Pa element, NMW 81.6G.51; 28 and 29, posterior and anterior views of sinistral M element, NMW 81.6G.52; 30, lateral view of Sa element, NMW 81.6G.53; 31–33, outer lateral, inner lateral, and lower views of sinistral Pb element, NMW 81.6G.54; all from sample 77.



SAVAGE and BASSETT, Caradoc and Ashgill conodonts

Aphelognathus rhodesi. The elements of *Plectodina* in the Branson and Mehl fauna now take the name *P. tenuis* (Branson and Mehl, 1933c). These Shropshire occurrences of this species are from the Costonian to Woolstonian or possibly lowest Marshbrookian. The Costonian occurrences appear to extend the lower range of the species, previously thought to commence in the late Kirkfieldian (Sweet 1981b).

The type material of this species is from the Maquoketa Formation, Clarksville, Missouri. Our material is very similar to the specimens illustrated from that formation by Branson and Mehl (1933c). The multielement apparatus assigned to *P. tenuis* and figured by Sweet (1981b, p. 274) in the Catalogue of Conodonts is from several localities in Kentucky and one in Ohio. The M element is different from the Branson and Mehl specimen (1933c, pl. 10, fig. 16) in having smaller and more upright denticles. The Sa element illustrated by Sweet (1981b, p. 275, figs. 11 and 12) also appears to be more slender and sinuous than the Branson and Mehl specimen (1933c, pl. 10, fig. 12), although the latter is incomplete and difficult to compare.

?*Plectodina* sp.

Plate 80, figs. 40 and 41

Remarks. This M(?) element is relatively short, with closely set inclined denticles along the bar. It cannot be assigned to any known species but is probably part of a *Plectodina* apparatus.

Family ICRIODONTIDAE Müller and Müller, 1957
Genus *Icriodella* Rhodes, 1953

Type species. *Icriodella superba* Rhodes, 1953, p. 288.

Icriodella superba Rhodes, 1953

Plate 80, figs. 8–14; Plate 82, figs. 28–33; Plate 83, figs. 20–25; Plate 84, figs. 22–25; Plate 85, figs. 40–43

- 1953 *Icriodella superba* n. sp. Rhodes, p. 288, pl. 20, figs. 62, 63, 78 [holotype], 54, 58, and 65 [Pa element].
- 1953 *Sagittodontus robustus* n. sp. Rhodes, p. 311, pl. 21, figs. 141 and 142 [M element].
- 1953 *Sagittodontus robustus* var. *erectus* n. var. Rhodes, p. 311, pl. 21, figs. 143, 151, and 152 [M element].
- 1953 *Sagittodontus robustus* var. *distaflexus* n. var. Rhodes, p. 312, pl. 21, figs. 137 and 138 [M element].
- 1953 *Trichonodella divaricata* n. sp. Rhodes, p. 313, pl. 21, figs. 140, 145, and 146 [Pb element].
- 1953 *Icriodella superba* var. *acuta* n. var. Rhodes, p. 288, pl. 20, figs. 59, 60, 64, 65, 71–73, and 77 [Pa element].
- 1953 *Icriodella plana* n. sp. Rhodes, p. 287, pl. 20, figs. 67, 74, and 76 [Pa element].
- 1953 *Icriodella* n. sp. Rhodes, p. 288, pl. 20, fig. 61 [Pa element].
- 1953 *Icriodella deformata* n. sp. Rhodes, p. 286, pl. 20, figs. 67–70 [Pa element].
- 1953 *Icriodella elongata* n. sp. Rhodes, p. 287, pl. 20, figs. 79–81 [Pa element].
- 1981 *Icriodella superba* Rhodes; Klapper and Bergström, pp. W125, W126, fig. 74(1a–j) [multielement apparatus: but note that this figured material is not from the type locality and is quadrimembrate compared with our trimembrate apparatus].

Remarks. Although specimens of *Icriodella* occur at several horizons in Shropshire and Wales, no consistent differences are evident by which the genus can be subdivided. All the specimens are referred to *I. superba* Rhodes, originally described from the Cymerig Limestone of North Wales. Orchard (1980) recognized *I. superba superba* Rhodes and *I. superba deformata* Rhodes from the Cymerig Limestone, the latter being diagnosed by uneven development of the anterior denticles of the Pa elements. Although some specimens in the collections described herein have an uneven development, we are not able to recognize consistent differences. The Pa elements from any particular locality show sufficient range of variation of anterior denticle development, asymmetry of anterior

platform, inclination of denticles and main cusp, and total length of the unit, that the taxonomic subdivisions of Rhodes (1953) commonly have been synonymized by later workers (Bergström 1964; Schopf 1966; Orchard 1980).

Family PHRAGMODONTIDAE Bergström, 1981c
Genus *PHRAGMODUS* Branson and Mehl, 1933b

Type species. *Phragmodus primus* Branson and Mehl, 1933b, p. 98

Phragmodus cf. *P. undatus* Branson and Mehl, 1933b

Plate 86, figs. 16 and 17

- cf. 1933b *Phragmodus undatus* n. sp. Branson and Mehl, p. 115, pl. 8, figs. 22–24 [S element].
cf. 1966 *Phragmodus undatus* Branson and Mehl; Bergström and Sweet, p. 369, pl. 28, figs. 13–20 [Pa, Pb, M, and S elements = multielement apparatus].

Remarks. Only a few specimens of each of the S and M elements have been recovered and these are broken. Nevertheless, the S element is sufficiently diagnostic to make tentative assignation to *Phragmodus undatus* possible.

Family PRIONIODONTIDAE Bassler, 1925
Genus *PRIONIODUS* Pander, 1856

Type species. *Prioniodus elegans* Pander, 1856, p. 29.

Prioniodus deani sp. nov.

Plate 80, figs. 23–39

Diagnosis. A species of *Prioniodus* in which the Pa elements are strongly arched and relatively short. The dextral Pb element has straight lower margins and a prominent lateral process. The sinistral Pb element has arched lower margins and a weak lateral process.

Holotype. Pa element NMW 81.5G.2, sample 26 (Coston Formation, Shropshire); Plate 80, figs. 23 and 24.

Description. The dextral Pa element is short and strongly arched with a small, posteriorly inclined main cusp (Pl. 80, figs. 25 and 26). At least seven small denticles are present on the anterior process and four on the posterior process. The outer lateral process arises from the base of the main cusp. The sinistral Pa element is more strongly arched but otherwise very like the dextral element (Pl. 80, figs. 23 and 24). The dextral Pb element has straight lower margins, a large, slightly inclined main cusp, and a prominent lateral process (Pl. 80, figs. 27–29). The sinistral Pb element has arched lower margins, a relatively small main cusp which is inclined posteriorly and inwards, and a very weak lateral process which arises just anterior of the cusp (Pl. 80, figs. 29–37). The S element has a very weak cusp, one edentate process, and two denticulate process (Pl. 80, figs. 38 and 39). The M element has not been recovered.

Remarks. This species is known at present only from the Costonian and may be a useful indicator of a pre-Harnagian age. The specific name recognizes W. T. Dean's contributions to the Ordovician geology of Shropshire.

Prioniodus sp.

Plate 84, figs. 26 and 27; Plate 85, figs. 28–35, 44, and 45

1980 *Prioniodus* sp. nov. A, Orchard, p. 24, pl. 6, figs. 5, 9, 11, and 12

Remarks. This species is represented by specimens from the Birdshill Limestone and Crûg Limestone. Unfortunately, all the Pa and Pb elements in the collection are broken. Orchard (1980, p. 24) discussed specimens from the Birdshill Limestone which are probably conspecific with this material.

Family PANDERODONTIDAE Lindström, 1970
 Genus PANDERODUS Ethington, 1959

Type species. *Paltodus unicostatus* Branson and Mehl, 1933b, p. 42.

Panderodus cf. *P. gracilis* (Branson and Mehl, 1933b)

Plate 80, figs. 42–47

- cf. 1933b *Paltodus gracilis* n. sp. Branson and Mehl, p. 108, pl. 8, figs. 20 and 21 [graciliform element].
- cf. 1933b *Paltodus compressus* n. sp. Branson and Mehl, p. 109, pl. 8, fig. 19 [compressiform element].
- cf. 1976 *Panderodus gracilis* (Branson and Mehl); Dzik, p. 428, fig. 15a, b, e, f [multielement apparatus].

Remarks. Workers who have attempted to distinguish multielement apparatuses of *Panderodus* include Barrick (1977), Cooper (1975), Dzik (1976), and Barnes *et al.* (1979). We have chosen to adopt a simple distinction in dealing with our specimens and to separate only the more flattened 'compressiform' elements from the narrower 'graciliform' elements.

Family SCOLOPODONTIDAE Bergström, 1981c
 Genus STAUFFERELLA Sweet, Thompson and Satterfield, 1975

Type species. *Distacodus falcatus* Stauffer, 1935, p. 142.

?*Staufferella* sp.

Plate 82, figs. 39–41

Remarks. This species is represented in our collections by a single specimen. It is rounded in cross-section and has a weak carina on one side. It may be a unicarinate element of *Staufferella*.

Family DREPANOISTODONTIDAE Bergström, 1981c
 Genus DREPANOISTODUS Lindström, 1971

Type species. *Oistodus forceps* Lindström, 1955, p. 574.

Drepanoistodus suberectus (Branson and Mehl, 1933b)

Plate 81, fig. 18; Plate 82, fig. 38

- 1933b *Oistodus suberectus* n. sp. Branson and Mehl, p. 111, pl. 35, figs. 22–27.
- 1979b *Drepanoistodus suberectus* (Branson and Mehl); Sweet, p. 79, figs. 7–21, 23, and 30 [multielement apparatus].

Remarks. Only non-geniculate elements of this species have been recovered. They range throughout the full stratigraphical coverage of our samples.

Family PROTOPANDERODONTIDAE Lindström, 1970
 Genus PROTOPANDERODUS Lindström, 1971

Type species. *Acontiodus rectus* Lindström, 1955, p. 549.

Protopanderodus liripipus Kennedy, Barnes and Uyeno, 1979

Plate 86, fig. 15

- 1979 *Protopanderodus liripipus* n. sp. Kennedy, Barnes and Uyeno, p. 546, pl. 1, figs. 9–19 [multi-element apparatus].

Remarks. The sixteen specimens in the sample 78 collection include symmetrical and asymmetrical protopanderodiform elements and a single scandodiform element. The elements are very similar to the type material from the early Caradoc age Tetaugouche Group, New Brunswick.

Family POLYGNATHIDAE Bassler, 1925
Genus OZARKODINA Branson and Mehl, 1933a

Type species. *Ozarkodina typica* Branson and Mehl, 1933a, p. 51.

?Ozarkodina pseudofissilis (Lindström, 1959)

Plate 84, figs. 30–33; Plate 85, fig. 27

- 1959 *Ctenognathus pseudofissilis* n. sp. Lindström, p. 439, pl. 4, figs. 1–9 [Pa element].
1959 *Ozarkodina pseudotypica* n. sp. Lindström, p. 441, pl. 4, figs. 17 and 18 [Pb element].

Remarks. Numerous well-preserved Pa elements of this species have been recovered by us from the Crûg quarry (11–17), which is the type locality, and also farther west along the Towy Anticline. The Pb elements are rare. No other elements of a possible apparatus have been recovered and the species is referred only tentatively to *Ozarkodina*. In these South Wales localities this species is commonly associated with *Amorphognathus ordovicicus* and appears to indicate an Ashgill age.

Orchard (1980) reconstructed this species to include the Pa and Pb elements and, as a possible Sc element, the single *Hindeodella?* sp. specimen recovered from the Crûg Limestone by Lindström (1959, pl. 1, fig. 10). It is surprising that other parts of the apparatus have failed to show up in any of our thirteen samples that yield the Pa or Pb elements, and that Lindström and Orchard had much the same result. There remains the possibility that the species is bimembrate.

Family UNKNOWN
Genus PSEUDOONEOTODUS Drygant, 1974

Type species. *Oneotodus?* *beckmanni* Bischoff and Sannemann, 1958, p. 98.

Pseudooneotodus sp. A

Plate 80, figs. 6 and 7

- 1967 Genus et species ind. B Serpagli, p. 107, pl. 29, figs. 1a, b.

Remarks. This material appears to be identical to that figured by Serpagli (1967) from the Ashgill of the Carnic Alps. The form described as *Pseudooneotodus* aff. *P. beckmanni* by Orchard (1980), from the Ashgill of the English Lake District, appears to have a more acutely angled cone.

Pseudooneotodus sp. B

Plate 83, figs. 36 and 37

Remarks. This single element differs from *Pseudooneotodus* sp. A in having a subrectangular outline, a difference which additional specimens might show to be of no taxonomic significance if a range of variation can be demonstrated. The specimen illustrated by Branson and Mehl (1933b, pl. 9, fig. 3) from the Ordovician Platin Formation of Missouri is even more angular.

Gen. et sp. indet. A

Plate 86, fig. 14

Remarks. This element has a sharply angled triangular cross-section near the base and in this respect is similar to some of the specimens assigned to *Walliserodus debolti* (Rexroad) by Serpagli

(1967, pl. 31). However, the element figured herein is more flared posteriorly and bears some small denticles on this posterior edge.

Gen. et sp. indet. B

Plate 83, fig. 38

Remarks. This element is flattened on its inner side and is convex, with a weak carina on its outer side. The outer base is flared.

Acknowledgements. We thank Professor C. R. Barnes, Dr R. J. Aldridge, and Dr M. J. Orchard for critically reading drafts of the manuscript. Dr D. Price and Dr L. R. M. Cocks gave advice on some collecting localities and stratigraphy. Dr L. Cherns helped with field collecting. Mrs B. J. Savage and Mrs K. Bryant helped with sample preparation; facilities for processing were provided by the University of Oregon and the University of Kent at Canterbury (N.M.S.) and the Department of Geology, University College, Cardiff (M.G.B.). Fieldwork expenses for N.M.S. were defrayed by National Science Foundation grant EAR 77-12908. Contributions from the NSF and the National Museum of Wales towards the costs of publication are gratefully acknowledged.

APPENDIX

Summary of stratigraphical horizon (Formation/Member) and locality of samples 1-110 for immediate reference to data plotted in text-figs. 1-4 and Tables 1 and 2. Locality details are given here as a generalized field name plus an eight figure National Grid Reference. Full topographical descriptions and stratigraphical plots of individual samples within sections are given in the Supplementary Publication deposited in the British Library (see p. 680).

SOUTH WALES

Sample No.(s)

- 1-3 Sholeshook Limestone, Sholeshook railway cutting, SM 9681 1705.
- 4 Sholeshook Limestone, Prendergast quarry, SM 9564 1662.
- 5, 6 Robeston Wathen Limestone, Robeston Wathen quarry, SN 0841 1615.
- 7 Sholeshook Limestone, Llanddowror quarry, SN 2538 1429.
- 8 Sholeshook Limestone, Fron quarry, SN 1711 1711.
- 9 Sholeshook Limestone, Trefenty quarry (Foxhole), SN 2962 1355.
- 10 Sholeshook Limestone, Parke trackside, SN 2392 1335.
- 11-17 Crûg Limestone, Crûg quarry and farm, SN 6270 2306.
- 18 Un-named limestone, Pen-y-banc quarry, SN 6081 2385.
- 19-21 Birdshill Limestone, Birdshill quarry, SN 6014 2312.
- 22, 23 Birdshill Limestone, Dryslwyn Castle, SN 5545 2034.
- 24 Birdshill Limestone, Tŷ-picca quarry, SN 5395 2064.
- 25 Birdshill Limestone, Llanegwad quarry, SN 5151 2130.

WELSH BORDERLAND AND EASTERN WALES

Sample No.(s)

- 26, 27 Coston Formation, Onny section quarry, SO 4118 8624.
- 28, 29 Coston Formation, A489 quarry, SO 4119 8623.
- 30-32 Smeathen Wood Formation, Ragleth quarry, SO 4456 9135.
- 33, 34 Horderley Sandstone Formation, A489 road section, SO 4151 8599.
- 35 Horderley Sandstone Formation, A489 road section, SO 4153 8595.
- 36, 37 Horderley Sandstone Formation, A489 road section, SO 4175 8583.
- 38 Horderley Sandstone Formation, Longlane quarry, SO 4129 8422.
- 39, 40 Horderley Sandstone Formation, High Wood quarry, SO 4119 8522.
- 41 Alternata Limestone, Onny river, SO 4179 8575.
- 42-44 Alternata Limestone, Soudley quarry, SO 4772 9182.
- 45 Alternata Limestone, Marshbrook railway cutting, SO 4403 9049.
- 46 Alternata Limestone, Onny railway, SO 4175 8570.
- 47 Cheney Longville Formation, Glynboro Member, Soudley quarry, SO 4772 9182.
- 48, 49 Cheney Longville Formation, Glynboro Member, A489 road section, SO 4193 8575.
- 50 Cheney Longville Formation, Glynboro Member, Cheney Longville roadside, SO 4185 8501.

- 51 Cheney Longville Formation, Glynboro Member, A489 road section, SO 4201 8571.
 52 Cheney Longville Formation, Crosspipes Member, Cheney Longville roadside, SO 4191 8495.
 53, 54 Cheney Longville Formation, Crosspipes Member, A489 road section SO 4209 8566.
 55 Cheney Longville Formation, Crosspipes Member, A489 road section, SO 4219 8559.
 56, 57 Acton Scott Formation, Ragdon Member, A489 road section, SO 4232 8552.
 58 Acton Scott Formation, Ragdon Member, Hatton stream SO 4645 9013
 59 Acton Scott Formation, Ragdon Member, Hatton stream SO 4642 9018.
 60 Acton Scott Formation, Ragdon Member, A489 road section, SO 4239 8551.
 61 Acton Scott Formation, Wistanstow Member, A489 road section, SO 4241 8550.
 62, 63 Acton Scott Formation, Wistanstow Member, Ragdon stream, SO 4507 9061.
 64, 65 Acton Scott Formation, Wistanstow Member, Onny river, SO 4236 8539.
 66, 67 Acton Scott Formation, Wistanstow Member, Ragdon stream, SO 4505 9054.
 68 Acton Scott Formation, Henley Member, Acton Scott church quarry, SO 4496 8955.
 69, 70 Onny Shale Formation, Onny river, SO 4259 8535.
 71, 72 Hoar Edge Grits, Bullhill Gutter stream, SO 5122 9825.
 73, 74 Hoar Edge Grits, Black Dicks Coppice quarry, SO 5092 9787.
 75, 76 Alternata Limestone, Chatwall farmyard, SO 5135 9741.
 77, 78 Nod Glas Formation, Gwern-y-Brain stream, SJ 2181 1268.

NORTH WALES

Sample No.(s)

- 79, 80 Pen-y-garnedd Formation, Pen-y-garnedd quarry, SJ 1090 2375.
 81, 82 Pen-y-garnedd Formation, Greenhall Park quarry, SJ 1572 1888.
 83-85 Dolhir Formation, Dolhir Limestone Member, Ddôl-hir quarry, SJ 2029 3675.
 86, 87 Dolhir Formation, Dolhir Limestone Member, Gelli Farm quarry, SJ 2360 1939.
 88 Dolhir Formation, Dolhir Limestone Member, Gelli Farm yard, SJ 2368 1924.
 89-91 Dolhir Formation, Dolhir Limestone Member, Cefn goed quarry, SJ 2127 3643.
 92-95 Glyn Formation, Glyn Limestone Member, Ty-draw hill quarry, SJ 2062 3704.
 96 Nant Hir Mudstones, Derfel Limestones Member, Aberderfel stream, SH 8508 3920.
 97 Gelli Grin Ashes, Cymerig Limestone Member, Gelli Grin quarry, SH 9449 3401.
 98-100 Gelli Grin Ashes, Cymerig Limestone Member, Y Garnedd quarries, SH 9451 3537.
 101 Moelfrynn Mudstones, Rhiwlas Limestone Member, Rhiwlas river section, SH 9231 3690.
 102-105 Moelfrynn Mudstones, Rhiwlas Limestone Member, Creigiau Bychan crags, SH 9200 3150.
 106 Foel y Dinas Mudstones, Hirnant Limestone Member, Cwm Hirnant quarry, SH 9510 2963.
 107-110 Conway Castle Grits, Deganwy quarry, SH 7853 7908.

REFERENCES

- BARNES, C. R., KENNEDY, D. J., MCCRACKEN, A. D., NOWLAN, G. S. and TARRANT, G. A. 1979. The structure and evolution of Ordovician conodont apparatuses, *Lethaia*, **12**, 125-151.
- BARRICK, J. E. 1977. Multielement simple-cone conodonts from the Clarita Formation (Silurian), Arbuckle Mountains, Oklahoma. *Geologica Palaeont.* **11**, 47-68.
- BASSLER, R. S. 1925. Classification and stratigraphic use of conodonts (abstr.). *Bull. geol. Soc. Am.* **36**, 218-220.
- BERGSTRÖM, S. M. 1962. Conodonts from the Ludibundus Limestone (Middle Ordovician) of the Tvären area (S.E. Sweden). *Ark. Miner. Geol.* **3**, 1-61.
- 1964. Remarks on some Ordovician conodont faunas from Wales. *Acta Univ. Lund.* **2** (3), 1-66.
- 1971a. Conodont biostratigraphy of the Middle and Upper Ordovician of Europe and eastern North America. *Mem. geol. Soc. Am.* **127**, 83-157.
- 1971b. Correlation of the North Atlantic Middle and Upper Ordovician conodont zonation with the graptolite succession. *Mém. Bur. Rech. géol. minière*. **73**, 177-187.
- 1973. Ordovician conodonts, 47-58. In HALLAM, A. (ed.). *Atlas of palaeobiogeography*. Elsevier Scientific Publishing Company, Amsterdam, London, New York.
- 1977. Early Paleozoic conodont biostratigraphy in the Atlantic borderlands, 85-110. In SWAIN, F. M. (ed.). *Stratigraphic micropaleontology of Atlantic Basin and Borderlands*. Elsevier Publishing Company, Amsterdam.
- 1978. Middle and Upper Ordovician conodont and graptolite biostratigraphy of the Marathon, Texas, graptolite zone reference standard. *Palaeontology*, **21**, 723-758.
- 1981a. Conodonts as paleotemperature tools in Ordovician rocks of the Caledonides and adjacent areas in Scandinavia and the British Isles. *Geol. För. Stockh. Förh.* **102** [for 1980], 377-392.
- 1981b. Biostratigraphical and biogeographical significance of conodonts in two British Middle Ordovician olistostromes. *Abstr. Progr. geol. Soc. Am., North-Central Section*, **13**, 271.

- BERGSTRÖM, S. M. 1981c. Families Phragmodontidae and Scolopodontidae, W129, W141. In CLARK, D. L. et al. *Treatise on Invertebrate Paleontology, W, Supplement 2, Conodonta*. Geological Society of America and University of Kansas Press, Lawrence.
- 1983. Biogeography, evolutionary relationships, and biostratigraphic significance of Ordovician platform conodonts. *Fossils Strata*, **15**, 35–58.
- RHODES, F. H. T. and LINDSTRÖM, M. 1984. Conodont biostratigraphy of the type Llandeilo and associated strata in the Ordovician of Wales. *Abstr. Prog. geol. Soc. Am., Southeastern and North-Central Sections*, **16** (3), 125.
- and SWEET, W. C. 1966. Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky, and its lateral equivalents in Ohio and Indiana. *Bull. Am. Paleont.* **50** (229), 271–441.
- BISCHOFF, G. and SANNEMANN, D. 1958. Unterdevonische Conodonten aus dem Frankenwald. *Notizbl. Hess. Landesamt. Bodenforsch. Wiesbaden*, **86**, 87–110.
- BRANSON, E. B. and MEHL, M. G. 1933a. Conodonts from the Bainbridge (Silurian) of Missouri. *Univ. Mo. Stud. 8*, 39–52.
- 1933b. Conodonts from the Platin (Middle Ordovician) of Missouri. *Ibid.* 101–119.
- 1933c. Conodonts from the Maquoketa–Thebes (Upper Ordovician) of Missouri. *Ibid.* 121–132.
- and BRANSON, C. C. 1951. Richmond conodonts of Kentucky and Indiana. *J. Paleont.* **25**, 1–17.
- CAVE, R. 1965. The Nod Glas sediments of Caradoc age in North Wales. *Geol. J.* **4**, 279–298.
- COOPER, B. J. 1975. Multielement conodonts from the Brassfield Limestone (Silurian) of southern Ohio. *J. Paleont.* **49**, 984–1008.
- DRYGANT, D. M. 1974. Simple conodonts from the Silurian and lowermost Devonian of the Volyno–Podolia area. *Paleont. Sb.* **10**, 64–70. [In Russian.]
- DZIK, J. 1976. Remarks on the evolution of Ordovician conodonts. *Acta palaeont. pol.* **21** (4), 395–455.
- EICHENBERG, W. 1930. Conodonten aus dem Culm des Harzes. *Paläont. Zeitschr.* **12**, 177–182.
- ETHINGTON, R. L. 1959. Conodonts of the Ordovician Galena Formation. *J. Paleont.* **33**, 257–292.
- EPSTEIN, A. G., EPSTEIN, J. B. and HARRIS, L. D. 1977. Conodont color alteration—an index to organic metamorphism. *Prof. Pap. U.S. geol. Surv.* **995**, 1–20.
- HASS, W. H. 1959. Conodonts from the Chappel Limestone of Texas. *Ibid.* **294-J**, 365–400.
- HINDE, G. J. 1879. On the conodonts from the Chazy and Cincinnati Group of the Cambro-Silurian, and from the Hamilton and Genesee-Shale divisions of the Devonian, in Canada and the United States. *Q. Jl geol. Soc. Lond.* **35**, 351–369.
- HURST, J. M. 1979. The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop. *Bull. Br. Mus. nat. Hist.* **32**, 183–304.
- KENNEDY, D. J., BARNES, C. R. and UYENO, T. T. 1979. A Middle Ordovician conodont faunule from the Tetagouche Group, Camel Back Mountains, New Brunswick. *Can. J. Earth Sci.* **16**, 540–551.
- KLAPPER, G. and BERGSTRÖM, S. M. 1981. Family Icriodontidae, W125. In CLARK, D. L. et al. *Treatise on Invertebrate Paleontology, W, Supplement 2, Conodonta*. Geological Society of America and University of Kansas Press, Lawrence.
- LINDSTRÖM, M. 1955. Conodonts from the lowermost Ordovician strata of south-central Sweden. *Geol. För. Stockhl. Förh.* **76**, 517–603.
- 1959. Conodonts from the Crûg Limestone (Ordovician, Wales). *Micropaleontology*, **5**, 427–452.
- 1970. A suprageneric taxonomy of the conodonts. *Lethaia*, **3**, 427–445.
- 1971. Lower Ordovician conodonts of Europe. In SWEET, W. C. and BERGSTRÖM, S. M. (eds.). Symposium on conodont biostratigraphy. *Mem. geol. Soc. Am.* **127**, 21–61.
- 1977. *Amorphognathus; Rhodesognathus*, 21–52; 531–537. In ZIEGLER, W. (ed.). *Catalogue of Conodonts*, Vol. 3. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- MCCRACKEN, A. D. and BARNES, C. R. 1981a. Conodont biostratigraphy and palaeoecology of the Ellis Bay Formation, Anticosti Island, Quebec, with special reference to late Ordovician–early Silurian chronostratigraphy and the systemic boundary. *Bull. geol. Surv. Can.* **329**, 51–134.
- 1981b. Conodont biostratigraphy across the Ordovician–Silurian boundary, Ellis Bay Formation, Anticosti Island, Quebec, 61–69. In LESPÉRANCE, P. J. (ed.). *Field Meeting, Anticosti-Gaspé, Quebec, 1981. Vol. II: Stratigraphy and Paleontology*. IUGS, Subcommission on Silurian Stratigraphy, Ordovician–Silurian Boundary Working Group.
- NOWLAN, G. S. and BARNES, C. R. 1980. *Gamachignathus*, a new multielement conodont genus from the latest Ordovician, Anticosti Island, Quebec. In Current Research, Part C. *Pap. geol. Surv. Can.* **80-1C**, 103–112.
- MÜLLER, K. J. and MÜLLER, E. M. 1957. Early Upper Devonian (Independence) conodonts from Iowa, Part 1. *J. Paleont.* **31**, 1069–1108.

- ORCHARD, M. J. 1980. Upper Ordovician conodonts from England and Wales. *Geologica Palaeont.* **14**, 9–44.
- OWENS, R. M. 1973. British Ordovician and Silurian Proetidae (Trilobita). *Palaeontogr. Soc. [Monogr.]* 1–98.
- PANDER, C. H. 1856. *Monographie der fossilen Fische des silurischen Systems des russisch-baltischen Gouvernements*. Akademie der Wissenschaften, St. Petersburg, 91 pp.
- PRICE, D. 1973. The age and stratigraphy of the Sholeshook Limestone of southwest Wales. *Geol. J.* **8**, 225–246.
- 1984. The Pusgillian Stage in Wales. *Geol. Mag.* **121**, 99–105.
- PRINGLE, J. and GEORGE, T. N. 1948. *British Regional Geology. South Wales*. (2nd edn.), vi + 100 pp. Geological Survey and Museum, HMSO, London.
- RHODES, F. H. T. 1953. Some British Lower Palaeozoic conodont faunas. *Phil. Trans. R. Soc. B* **237**, 261–334.
- SAVAGE, N. M. 1983. The use of conodont occurrence and thermal alteration data as an aid in distinguishing tectonostratigraphic terranes. *Prog. Abstr. a. Mtg. Geol. Ass. Can.* **8**, A60.
- SCHOPF, T. J. M. 1966. Conodonts of the Trenton Group (Ordovician) in New York, southern Ontario, and Quebec. *Bull. N. Y. St. Mus.* **405**, 1–105.
- SERPAGLI, E. 1967. I conodonti dell'Ordoviciano Superiore (Ashgilliano) delle Alpi Carniche. *Boll. Soc. Paleont. Ital.* **6**, 30–111.
- STAUFFER, C. R. 1935. Conodonts from the Glenwood beds. *Bull. geol. Soc. Am.* **46**, 125–168.
- SWEET, W. C. 1979a. Conodonts and conodont biostratigraphy of Post-Tyrone Ordovician rocks of the Cincinnati Region. *Prof. Pap. U.S. geol. Surv.* **1066-G**, 1–26.
- 1979b. Late Ordovician conodonts and biostratigraphy of the western Midcontinent Province. In SANDBERG, C. A. and CLARK, D. L. (eds.). *Conodont biostratigraphy of the Great Basin and Rocky Mountains. Geology Stud. Brigham Young Univ.* **26**, 45–86.
- 1981a. Macromorphology of elements and apparatuses. In CLARK, D. L. et al. W5–W20. *Treatise on Invertebrate Paleontology, W, Supplement 2, Conodonta*. Geological Society of America and University of Kansas Press, Lawrence.
- 1981b. *Aphelognathus; Plectodina*. In ZIEGLER, W. (ed.). *Catalogue of conodonts. Vol. 4*, 27–56; 271–290. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- ETHINGTON, R. L. and BARNES, C. R. 1971. North American Middle and Upper Ordovician conodont faunas. In SWEET, W. C. and BERGSTROM, S. M. (eds.). *Symposium on conodont biostratigraphy. Mem. geol. Soc. Am.* **127**, 163–193.
- THOMPSON, T. L. and SATTERFIELD, I. R. 1975. The Cape Limestone of Missouri. *Rep. Invest. Mo. geol. Surv.* **57**, 1–60.
- UYENO, T. T. and BARNES, C. R. 1983. Conodonts of the Jupiter and Chicotte Formations (lower Silurian), Anticosti Island, Québec. *Bull. geol. Surv. Can.* **355**, i–viii, 1–49.
- WILLIAMS, A., STRACHAN, I., BASSETT, D. A., DEAN, W. T., INGHAM, J. K., WRIGHT, A. D. and WHITTINGTON, H. B. 1972. A correlation of Ordovician rocks in the British Isles. *Spec. Rep. geol. Soc. Lond.* **3**, 1–74.

N. M. SAVAGE

Department of Geology
University of Oregon
Eugene, Oregon 97403
USA

M. G. BASSETT

Department of Geology
National Museum of Wales
Cardiff CF1 3NP
Wales, UK

Typescript received 29 September 1984

Revised typescript received 8 March 1985

CAMBRIAN ELEUTHEROZOAN ECHINODERMS AND THE EARLY DIVERSIFICATION OF EDRIOASTEROIDS

by ANDREW B. SMITH

ABSTRACT. The five genera and thirteen named species of edrioasteroid from the Cambrian are reviewed and, where necessary, redescribed. All are interpreted as sessile suspension feeders, with an external system of radial water vessels and tube feet that functioned in opening the cover plate sheets. The relationships of these five genera to one another and to other edrioasteroid groups is analysed and a revised classification of the Edrioasteroidea is proposed. *Stromatocystites* has fewest autapomorphic characters and is placed as primitive sister group to the other four genera. These fall into two distinct groups: *Totiglobus* and *Walcottidiscus* are rather globular with a reduced dorsal surface, while *Cambraster* and *Edriodiscus* are discoidal with a prominent marginal frame. Three orders are recognized within the Edrioasteroidea: the Edrioasterida, which includes *Totiglobus*, *Walcottidiscus*, and the family Edrioasteridae; the Cyathocystida, for the families Cyathocystidae and Pyrgocystidae; and the Isorophida, which is expanded to include *Cambraster*, *Edriodiscus*, and the families Cyclocystoididae and Agelacrinitidae.

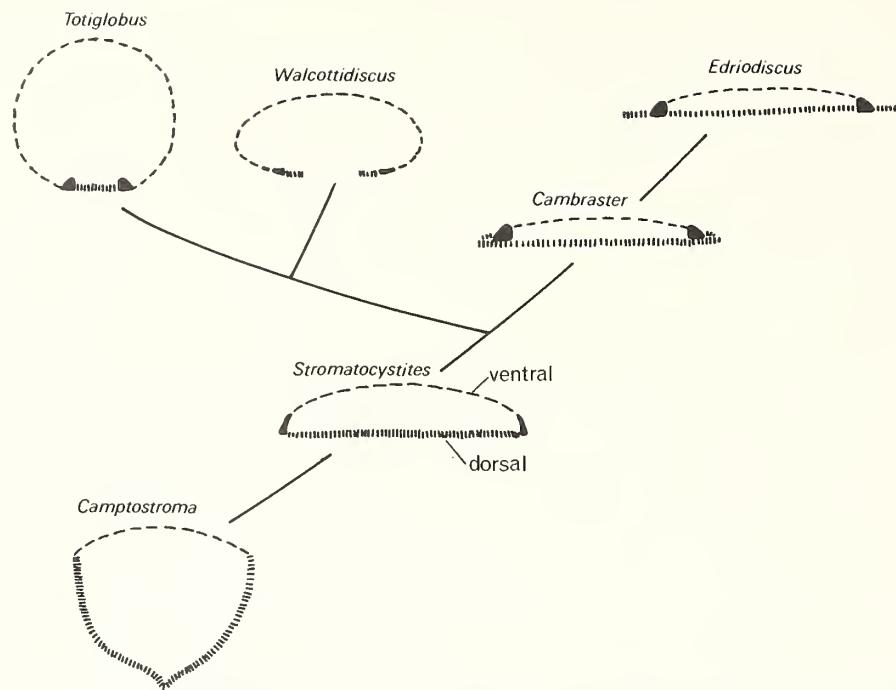
IN the Cambrian there are a small number of echinoderms that have conventionally been classified as edrioasteroids, of which the best known is *Stromatocystites*. Although Pompeckj first described *S. pentangularis* from the Middle Cambrian of Czechoslovakia in 1896, these animals have remained relatively poorly understood. Yet *Stromatocystites* has held an important place in theories of echinoderm phylogeny. Bather (1900, 1915) considered *Stromatocystites* to be ancestral to all eleutherozoan groups and an intermediate between asteroids, echinoids, and holothuroids on the one hand, and cystoids on the other. This view fell largely out of favour when Fell (1962, 1963) proposed that eleutherozoan groups were polyphyletic in origin, and in the *Treatise on Invertebrate Paleontology* (Regnell 1966) *Stromatocystites* is treated as no more than a primitive edrioasteroid. More recently, however, the phylogenetic status of *Stromatocystites* has been reassessed by both Termier and Termier (1969, 1980), who provided a highly novel interpretation, and myself (Smith 1984a, b; Paul and Smith 1984) where a return to the more traditional view is argued for.

Four other genera of edrioasteroid in addition to *Stromatocystites* have been described from the Cambrian: *Cambraster*, *Walcottidiscus*, *Totiglobus*, and *Edriodiscus*. Because of the importance of these genera to theories of the early history of eleutherozoan echinoderms, a detailed appraisal of their morphology and relationships seemed long overdue. Some species have been described recently in considerable detail, such as *C. elegans* by Ubags (1971), *C. tastudorum* by Jell *et al.* (1985), *T. nimius* by Bell and Sprinkle (1978), and *S. walcotti* by Paul and Smith (1984). Others are, however, still poorly known. This paper therefore sets out to review what is known about the morphology of these animals and to examine their relationships, not only with one another but also with other echinoderm groups. However, a detailed comparison between Cambrian edrioasteroids and primitive starfish such as *Archegonaster* will be dealt with in a subsequent paper and is not considered here.

MORPHOLOGY AND ANATOMY

General organization

Although Cambrian edrioasteroids are variable in their overall shape they all share basically the same body plan. All have a skeletal system that is clearly differentiated into dorsal and ventral surfaces. On



TEXT-FIG. 1. Diagrammatic cross-sections through the five Cambrian genera considered here and *Camptostroma* to show the relative development of dorsal (vertical hatching) and ventral (dashed line) plate surfaces.

the ventral surface there is a central mouth and a marginal anus. Five ambulacral zones radiate from the mouth and are separated by wedge-shaped interambulacral zones. The dorsal surface is composed of a marginal ring of somewhat larger plates surrounding a pavement of flat polygonal plates. In *Stromatocystites* and *Cambraster*, dorsal and ventral surfaces are more or less equally developed so that the boundary between them coincides more or less with the ambitus (text-fig. 1). The two genera differ in that *C. taistudorum* appears to have a double layer of plates outside the marginal ring (Jell *et al.* 1985) which *Stromatocystites* lacks. *Edriodiscus* has a single layer. In *Walcottidiscus* the ventral surface has become enlarged relative to the dorsal surface and the boundary between them now lies sub-ambitally. *Totiglobus* has become even more extreme and its dorsal plating is reduced to a relatively minute disc (text-fig. 1); the ventral surface is expanded and extends well below the ambitus. Thus the relative development of dorsal and ventral surfaces is largely responsible for the differences that exist in overall shape. All are sub-circular to sub-pentagonal in outline but whereas *Stromatocystites*, *Edriodiscus*, and *Cambraster* have a fairly flat profile, *Walcottidiscus* has a depressed ovoid profile and *Totiglobus* is almost globular.

Digestive system

The mouth lies centrally on the ventral surface at the point of convergence of the five ambulacra. It does not open directly to the exterior, but is roofed over by a series of cover plates which may or may not have been able to open in life. The peristomial opening is relatively small and in *S. waltoni*, *Cambraster*, and *Totiglobus* is surrounded by a fixed mouth frame of ambulacral plates. In *S. pentangularis*, however, the mouth may have been more flexible as there is some evidence that the two columns of plates in each ambulacrum were able to separate along the perradial suture

proximally, as in many primitive starfish. Unfortunately, the detailed arrangement of plates in the oral area of this species is still unknown.

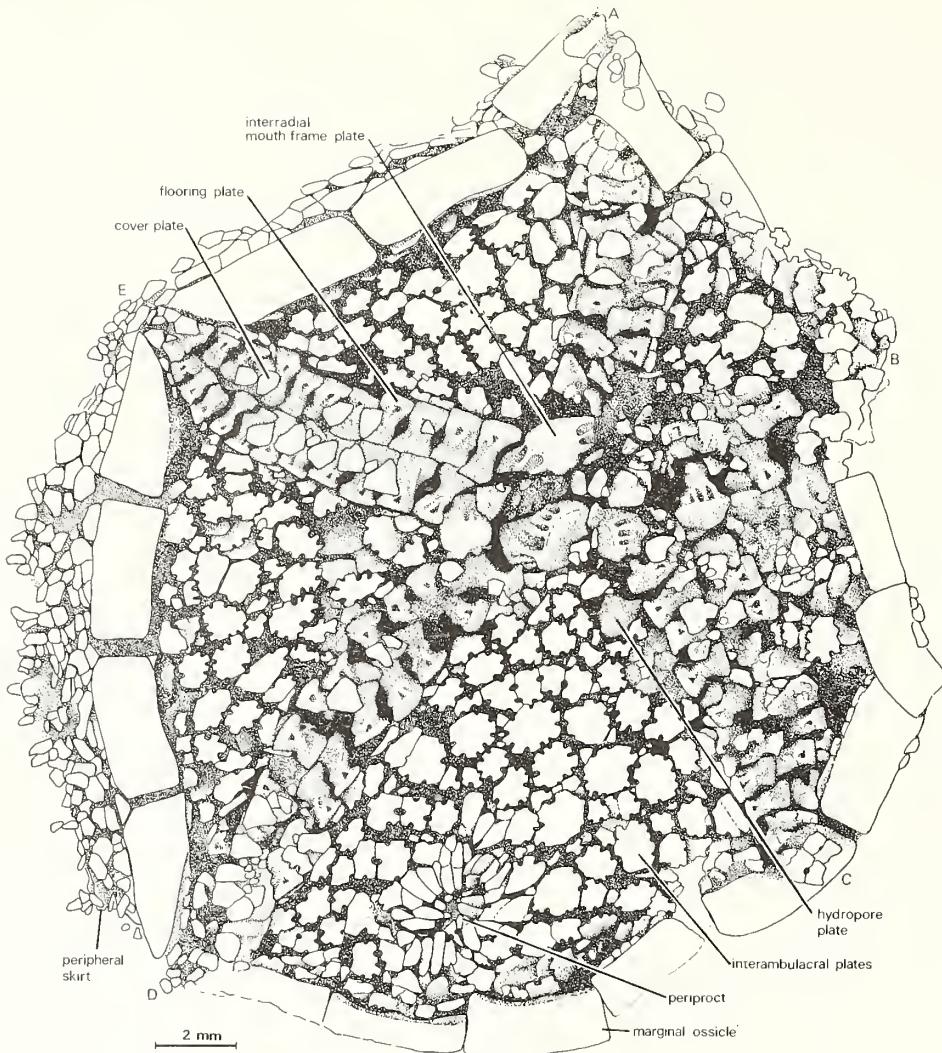
The anus also opens through the ventral surface and is situated marginally in the C/D interambulacrum. In *Stromatocystites* and *Cambraster* the periproct is a moderately large circular zone of lath-like plates arranged radially (text-figs. 2 and 7). A similar periproctal system, but with fewer and more organized plates, is present in *Totiglobus*. The periproctal plates lie either flush with the surrounding interambulacral plates or are slightly raised to form a low conical mound.

Since both mouth and anus lie on the same surface, the digestive system must, at the very least, have been looped. The ubiquity of torsion in the digestive tract of all echinoderms, both larval and adult, suggests that the digestive tract in edrioasteroids was also coiled. Bather (1915) argued that the gut probably coiled anticlockwise in edrioasteroids because of a certain asymmetry in the arrangement of periproctal plates. No such asymmetry can be detected in the Cambrian species and the direction of coiling must remain uncertain. However, an anticlockwise coiling seems the most likely since the hydropore/gonopore opens close to the peristome on the right-hand side of the C/D interambulacrum, and such a direction of coiling of the digestive tract would leave more room for the internal gonad in this position. By inference from living groups the digestive system presumably consisted of a short oesophagus descending from the mouth, leading to a coiled intestine and then to a short rectum.

Dorsal surface

Plates of the dorsal surface can be divided into two groups: those that form the marginal ring and those that form the remainder of the dorsal surface. In *Stromatocystites* plates of the marginal ring are poorly differentiated from the other dorsal plates and lie supra-ambitally. They are moderately large, weakly geniculate plates with a rounded adoral edge and flatter, broader adapical edge which faces the substratum. There are no sutural epispines along any of the plate margins; although adjacent plates abut, their zone of contact is narrow and they would not have been able to form a rigid marginal frame. Internally these marginal plates are gently concave and lack internal processes or other evidence of muscle attachment areas. Marginal plates in *Cambraster* are greatly enlarged and form a prominent frame to the ventral surface (text-fig. 2). There are eighteen to twenty marginal ossicles in the ring. These ossicles are triangular in cross-section and adjacent ossicles firmly abut. Their lateral faces are smooth, without crenulation, so presumably the ossicles were bound together by collagenous ligament to form a fairly inflexible marginal frame. Ossicles at each radius have a V-shaped notch where the ambulacratal flooring plates extend on to the marginal frame (text-fig. 2). *Totiglobus* also possesses a stout marginal ring of abutting ossicles; this ring would have been rather poorly flexible. Marginal ossicles are hardly distinguishable from the exterior but have large internal processes (see Bell and Sprinkle 1978, text-fig. 4) which presumably were associated with muscle attachment. As the processes face towards the centre of the dorsal surface, these could well have been attachment sites for radially arranged dorsal muscle fibres necessary if the dorsal surface acted as a suction pad. Details of the marginal plates in *Walcottidiscus* are poorly known. Externally the marginal plates are not clearly differentiated and, as in *Totiglobus*, there is no recognizable tessellate ring of plates. Whether the marginal ring plates were more clearly differentiated internally is unknown.

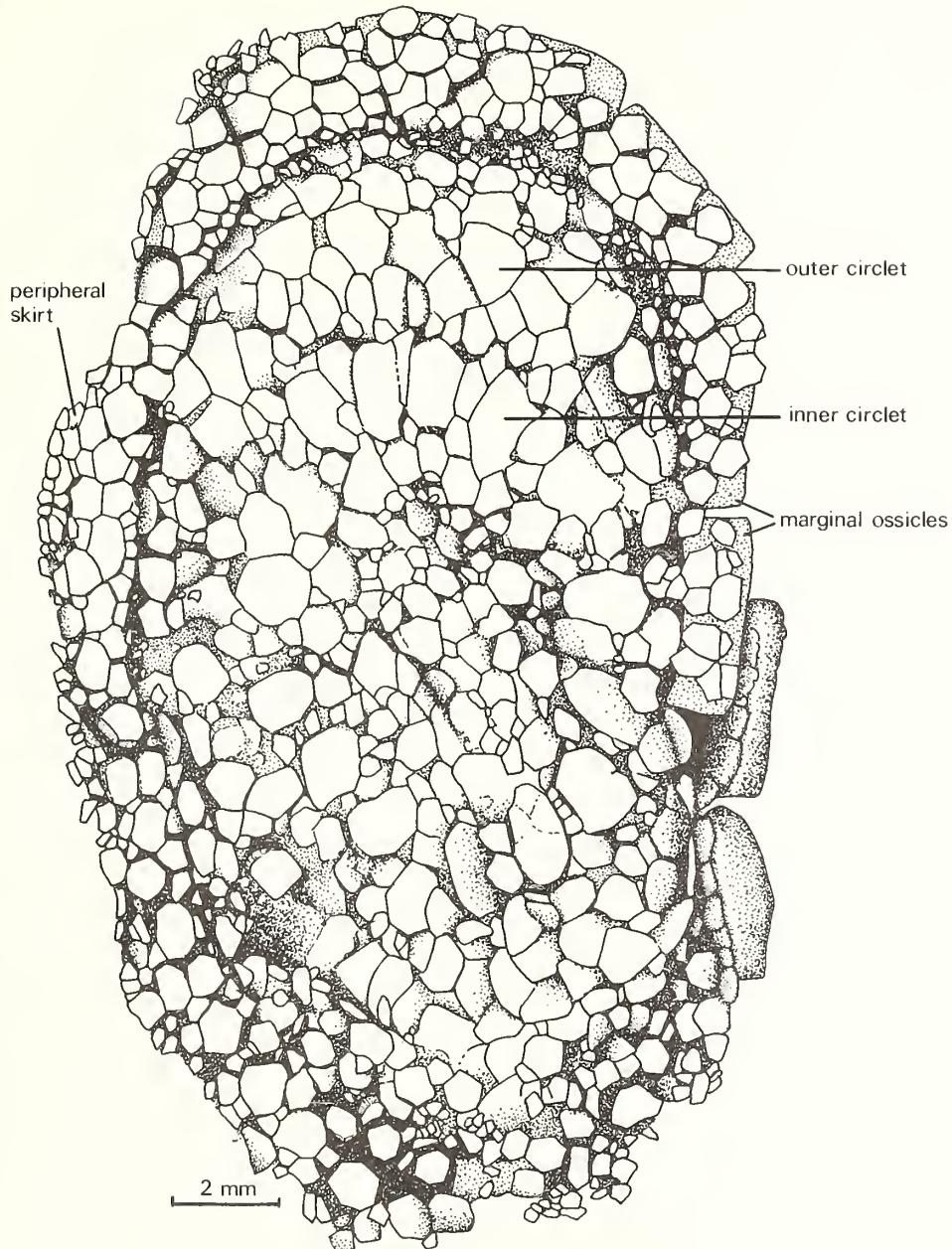
There is an irregular pavement of tessellate, polygonal plates within the marginal ring. The entire dorsal surface is plated in all but *Walcottidiscus* where there is a central uncalcified zone. All of the dorsal plates in *Stromatocystites* are similar in thickness. There is a large equant plate at the centre of the dorsal surface which is surrounded by a variable number of large, radially elongate plates (text-fig. 4). Dorsal plates decrease in size away from the centre of the disc and, immediately adjacent to the marginal ring, there is a zone of tiny lath-like platelets that may not fully abut. This is the region of plate addition where new dorsal plates were added immediately inside the marginal ring. It is also a region of high flexibility. Dorsal plating in *Totiglobus* is very like that in *Stromatocystites* except that there is no clearly distinguishable central plate. Only a small number of polygonal plates lie within the marginal ring and these are smooth externally but weakly ridged and grooved internally (see Bell and



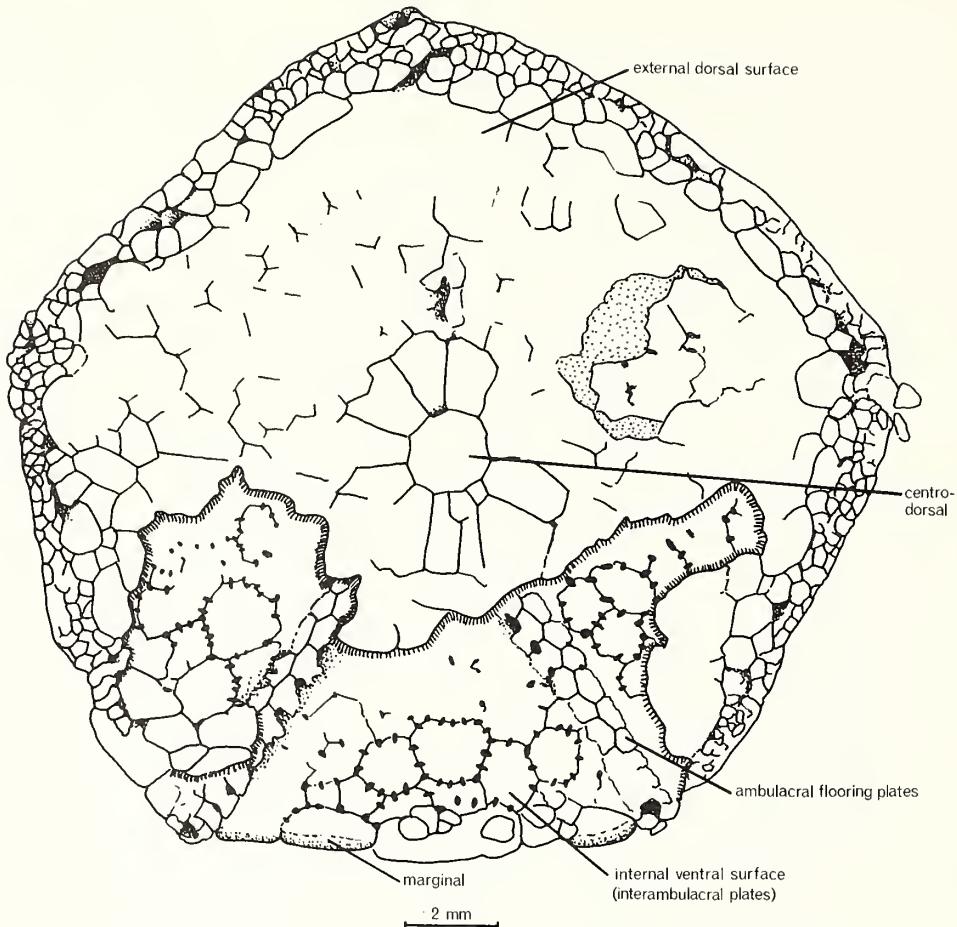
TEXT-FIG. 2. *Cambraster canni* (Miquel, 1894), camera lucida drawing, ventral surface of holotype of *C. elegans* Termier and Termier, 1969, from a latex, BM(NH) E63135 (see text-fig. 19A). Original is in the collections of the Museum of le Havre, France.

Sprinkle 1978, text-fig. 4b). All plates are tessellate and plate size decreases quite noticeably towards the outer edge.

Cambraster has a central zone of small polygonal plates surrounded by one or two circles of large polygonal plates. Over much of the central region of the aboral surface the plates are relatively thin and sub-tessellate, fitting together to form a continuous pavement. All known specimens of *C. canni* show rather distorted and jumbled plating but there are two clear circles of large, radially elongate, polygonal plates which either abut or have small plates intercalated in between (text-fig. 2). There is only one circle of plates in *C. tastudorum*, all of which are contiguous (Jell *et al.* 1985). Plates become thicker and more obviously polygonal towards the margin, but at the very distal edge there are small lath-like plates which probably extended slightly beyond the marginal ossicles (text-fig. 2; see also



TEXT-FIG. 3. *Cambraster cannati* (Miquel, 1894), camera lucida drawing of dorsal surface of holotype of *Eikosacystis miqueli* Termier and Termier, 1969, from a latex, BM(NH) E63136 (see text-fig. 19c, d). Original is in the collections of the Museum of le Havre, France.



TEXT-FIG. 4. *Stromatocystites walcotti* Schuchert, 1919, USNM 66443, camera lucida drawing of the holotype, showing the dorsal surface and part of the interior of the ventral surface where the dorsal surface has been damaged.

Ubaghs 1971). The dorsal surface is slightly larger than the ventral surface, so that the marginal ossicles lie just above the ambitus and are hidden from sight when viewed from beneath.

Edriodiscus, like *Stromatocystites* and *Cambraster*, is fully plated, but here all the plates within the marginal ring are of very much the same size. These are flat, polygonal, and tesselate. There is a ring of flat-based, cylindrical marginal ossicles which form a frame, as in *Cambraster*. Here, however, the marginal ossicles are inserted into the dorsal surface plating so as to separate a peripheral skirt of smaller plates from the main central pavement (text-fig. 20). All plates are covered with radially arranged ridges and grooves, very reminiscent of the ornamentation on the lower surface of peripheral skirt plates in isorophid edrioasteroids.

The structure of the outer zone of calcite plates in *Walcottidiscus* is not clearly seen. There appears to be a large number of small lath-like plates which, in general appearance, resemble the dorsal plating found in *Edrioaster*.

It is quite clear that neither *Stromatocystites* nor *Cambraster* had any means of attaching to the substratum by their dorsal surfaces, at least as adults, and must simply have lain unattached on the

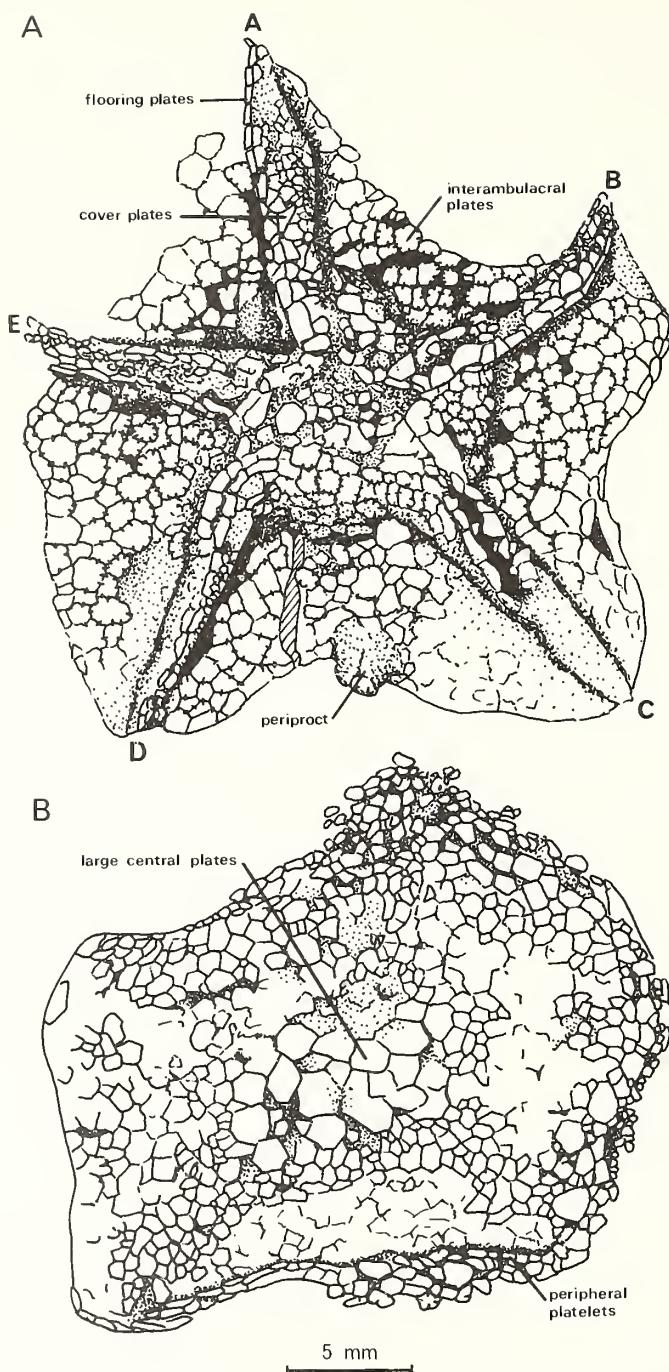
sea floor. *Walcottidiscus*, on the other hand, had a large uncalcified dorsal pad which presumably acted as some form of adhesion disc. *Edriodiscus* has prominent radially arranged ridges and grooves, like those found on the lower surface of peripheral plates in agelacrinitids. This structure is undoubtedly associated with attachment but the precise function of the ridges remains uncertain. The question remains whether *Totiglobus* had any means of attachment. Bell and Sprinkle (1978) thought that the entire dorsal surface within the marginal ring may have acted as a suction pad. Certainly it is hard to imagine how a globular animal such as *Totiglobus* could have been stable with such a small base unless it was able to attach itself. This might have been achieved through various means, but the large internal processes on the marginal ring ossicles suggest that adhesion was achieved through suction. If the dorsal surface was moderately flexible immediately within the marginal ring, then radially arranged muscles running from the centre of the dorsal surface to these internal processes might have been able to pull the dorsal pad inwards to create suction.

Ventral surface

Interambulacral areas. The interambulacral zones in *Stromatocystites* and *Cambraster* are composed of a large number of polygonal, tessellate plates (text-fig. 13). Epispires are present along the plate sutures except immediately adjacent to ambulacral plates, marginal ossicles, and plates of the periproct. Epispires presumably provided egress for external finger-like extensions of the body coelom that functioned in gaseous exchange and presumably resembled papillae of Recent sea-stars. *Totiglobus*, *Walcottidiscus*, and *Edriodiscus* all lack interambulacral epispires and their plating is tessellate to sub-tessellate. New interambulacral plates were added adjacent to the marginal ring.

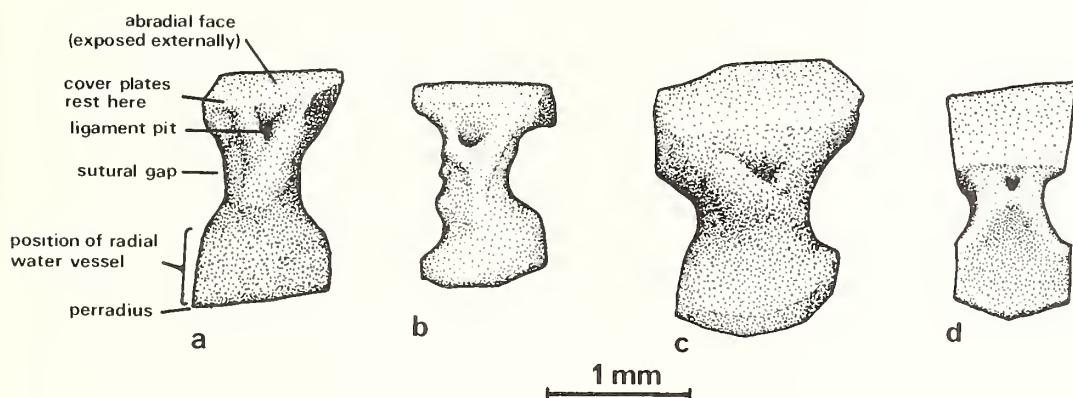
Ambulacral zones. The five ambulacra are arranged in a 2:1:2 pattern. Close to the mouth the A and B and the D and E rays combine to make a T-shaped junction with ambulacrum C above the mouth (text-fig. 15). The ambulacra in *Cambraster* and *Stromatocystites* are straight and continue right to the edge of the ventral surface. The tips of the ambulacra are actually inserted between the ossicles of the marginal ring in both genera and could therefore grow only at the same rate as the body as a whole. *Edriodiscus* has weakly curved ambulacra which still reach the marginal ring. *Totiglobus* has straight ambulacra but, although these extend below the ambitus, they do not reach the marginal ring. The ambulacra in *Walcottidiscus* extend to the ambitus and then curve sinistrally. Ambulacra are initially straight in juveniles but curve to grow around the body in adults. Ambulacra form the animals' food-gathering surfaces, so their length relative to body size is obviously crucial. *Totiglobus* and *Walcottidiscus* arrived at different solutions to the problem of how to increase their food-gathering surface relative to general body size. *Totiglobus* increased its ambulacra by expanding the entire ventral surface relative to the dorsal surface, whereas *Walcottidiscus* evolved curved ambulacra so that their growth was not constrained by the marginal ring but could continue around the periphery.

The detailed structure of the ambulacra is very similar in all genera. Each ambulacrum consists of a biserial column of flooring plates which are roofed over by two multiplated series of cover plates. The morphology of the flooring plates is known in detail only for *Stromatocystites*, *Cambraster*, and *Totiglobus*. Similar flooring plates are probably present in *Walcottidiscus* but here only the narrow external face of the flooring plates can be seen. Individual flooring plates are rather squat, particularly in *Stromatocystites*. There is a small rectangular abradial face which is exposed externally between the interambulacral plates and the cover plates (text-figs. 6 and 8C). This is generally smooth and flat, and adjacent faces abut. The rest of the flooring plate lies hidden beneath the cover plate series. Flooring plates are arranged alternately and the two columns meet perradially along a weakly zigzagged suture. This suture becomes almost straight distally in *Cambraster*, but in *Stromatocystites* and *Totiglobus* the ambulacral plates firmly interlock along the mid-line. There is a moderately large sutural pore between successive plates in each column, passing from the interior of the test to the ambulacral channel. The pore is circular to ovoid in outline and is more or less equally shared between the two plates. It occupies the outer half of the abradial face (text-fig. 6) and therefore opens immediately beneath the cover plates. On the upper face, this pore is sometimes surrounded by a slight rim. In the central region between sutural pores the flooring plate is expanded into a broad



TEXT-FIG. 5. *Stromatocystites pentangularis* Pompeckj, 1896, camera lucida drawings. A, BM(NH) E16004, ventral surface. B, BM(NH) E63138 (latex kindly supplied by Professor G. Ubaghs), dorsal surface of a specimen in the collection of Dr Krantz of Bonn.

V-shaped ridge (text-fig. 6). This ridge has a small but distinct pit situated immediately beneath the cover plates and opening upwards; it is presumably a ligament pit for the collagenous fibres necessary to bind the cover plates to their flooring plates. The perradial portion of the flooring plate is smooth, weakly concave, and forms a shallow channel. The inner face of the flooring plates is unnoteworthy, except in *S. walcotti* where there are paired lateral prongs (text-fig. 7). What the three dimensional shape of these flooring plates is and what purpose the paired prongs served is not at all clear. Where the perradial suture is obviously zigzag, the ambulacral flooring plates must have been more or less rigidly fixed, but in *Cambraster*, where this suture becomes almost linear towards the tips of the arms, it is quite possible that the ambulacra had a certain amount of flexibility and could widen or narrow the ambulacral groove as necessary.

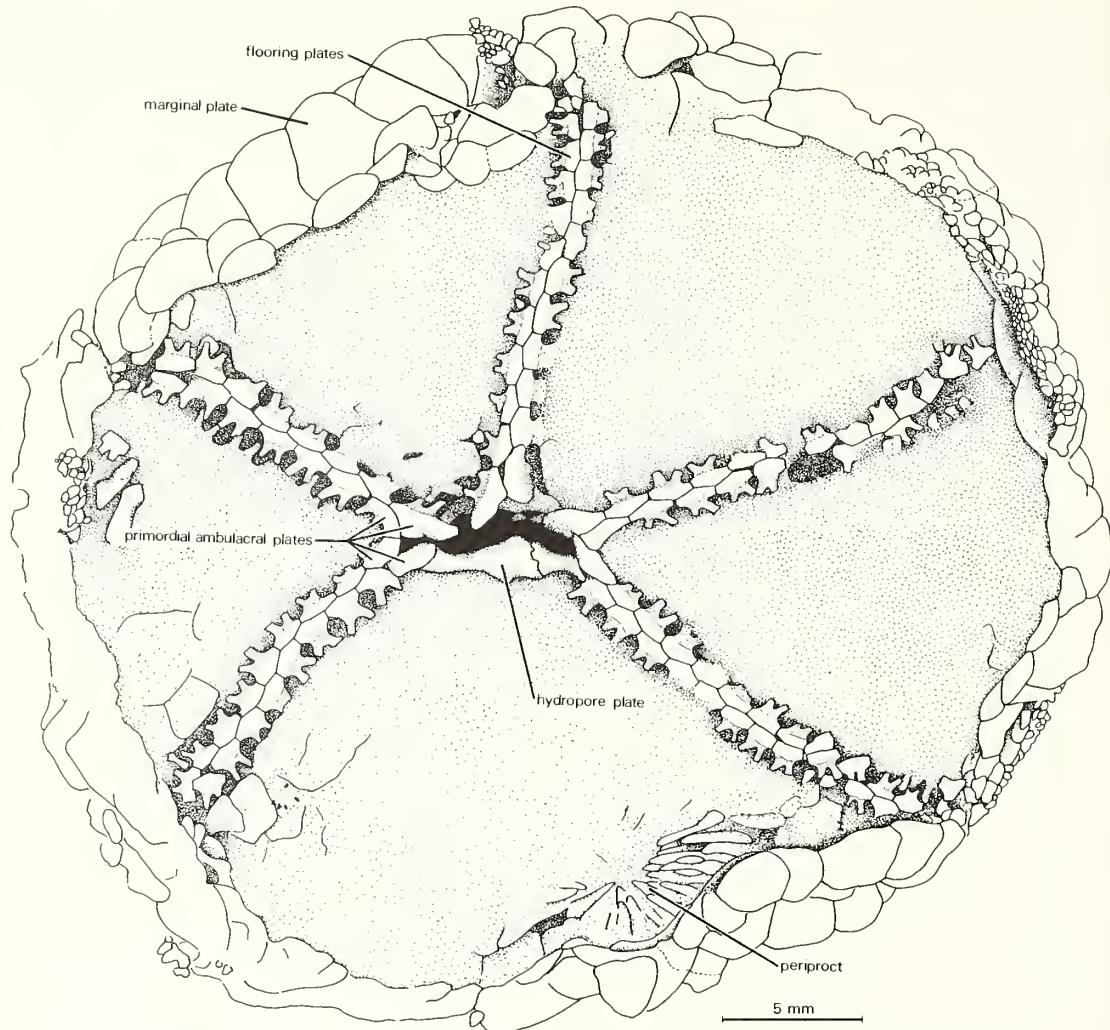


TEXT-FIG. 6. Ambulacral flooring plates, ventral view. *a*, *Cambraster cannati* (Miquel, 1894), detail of one plate from the specimen illustrated in text-fig. 2. *b*, *c*, *Stromatocystites pentangularis* Pompeckj, 1896; *b*, BM(NH) E63099; *c*, BM(NH) E63103. *d*, *Totiglobus nimius* Bell and Sprinkle, 1978, drawn from Bell and Sprinkle (1978, pl. 2, fig. 2).

Cover plates are arranged as a multiple series and attach along the inner border of the flooring plates (text-fig. 14). Distinctly larger primary cover plates are always developed, and towards the distal tip of the ambulacra may be the only cover plates present. Primary cover plates are pentagonal in outline with a broad flat base that rests on the flooring plate, and a distal point. One primary cover plate sits on each flooring plate, except in *Walcottidiscus* where there appear to be two per flooring plate (Pl. 89, fig. 4). Primary cover plates lie either directly above their corresponding flooring plate or slightly offset, as in some specimens of *Totiglobus* (Bell and Sprinkle 1978). There may be smaller plates occasionally inserted between the primary cover plates in *Stromatocystites*, but in other genera the primary cover plates abut each other.

The inner face of each primary cover plate has a distinct ridge that runs slightly obliquely from the proximal edge to the distal point. This becomes less prominent away from the flooring plate and fades. A second, less pronounced ridge can also be made out in some, convergent with the first. This defines a central triangular area on the inner face of the cover plate that possibly marks the position of ligament attachment.

Distal to the primary cover plates comes an irregular array of smaller, secondary cover plates. These are most numerous in *Walcottidiscus*, where there may be four or five irregular rows, whereas in *Stromatocystites* and *Cambraster* they form only a narrow band. In *Totiglobus* there is only a single secondary cover plate inserted between the distal edges of adjacent cover plates. In well-preserved specimens the paired cover plate series meet along the perradius to enclose the ambulacral groove; the perradius often appears slightly sinuous.



TEXT-FIG. 7. *Stromatocystites walcotti* Schuchert, 1919, USNM 376690, camera lucida drawing, showing the interior of the ventral surface and oral frame structure; no locality data, but the matrix is similar to other specimens of *S. walcotti* from Bonne Bay, Newfoundland.

Oral area. The precise arrangement of plates in the oral area is largely unknown in the majority of species. In all except possibly *S. pentangularis* the most proximal ambulacral flooring plates are firmly bound together to form a fixed oral frame. In *S. walcotti* only the most proximal flooring plate in each column, together with the large elongate hydropore plate, are involved in the oral frame (text-fig. 7). The first flooring plates from adjacent ambulacra meet interradially so as to exclude any interambulacral plates from the peristome margin. The hydropore plate is large and asymmetrical, with a broad inward sloping face on the right hand side. This plate lies in interambulacrum C/D. As yet no external hydropore opening has been observed and the stone canal may have opened directly into the peristomial cavity. Both *Cambraster* and *Totiglobus* have an oral frame that consists of five large interradial elements. These appear to have formed through fusion of the first two ambulacral plates in adjacent ambulacral columns (i.e. they are composed of four plates in total). These plates are very

distinctive, having a broad triangular external face and an adradial face with two ridges and pits on each side (text-fig. 2). The pits may represent passageways that have been lost in fusion. The hydropore in *Totiglobus* opens as a slit-like pore between two plates, one of which is the oral frame element in the C/D interray, the other being the next proximal flooring plate in ambulacrum C or an adjacent interambulacral plate (Bell and Sprinkle 1978, text-fig. 2). In *C. caunati* the oral frame is disrupted in the best preserved specimen and the exact location of the hydropore is uncertain. However, there is a large interambulacral plate lying close to the peristome in the C/D interray which is almost certainly the hydropore plate (text-fig. 2); this was probably in contact with the mouth frame plate of that interray in life. The hydropore is clearly seen in *C. tastudorum* where the opening lies between the C/D ambulacral mouth frame and the hydropore plate (Jell *et al.* 1985). As in many edrioasteroids the arrangement of cover plates in the oral area is undifferentiated from that of the ambulacra and no large plates stand out.

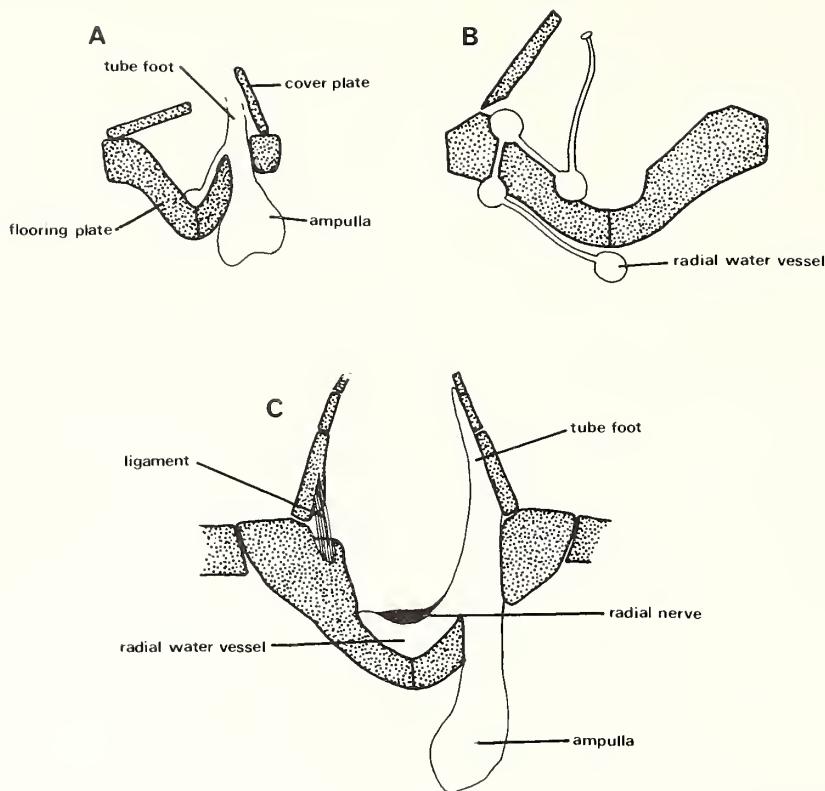
The water vascular system

The presence of radially arranged ambulacra and a hydropore shows that these Cambrian genera possessed a water vascular system, like all other echinoderms. From the single, off-centred hydropore a short stone canal would have descended to the circum-oesophageal ring. There is little direct evidence as to where this ring lay, but the shallow ledge on the adoral face of the mouth frame plates in *Totiglobus* and *Cambraster* may mark its position.

The ambulacra were unquestionably associated with radial water canals that ran from the circum-oesophageal ring to the tip of each ambulacrum. The position of this water vessel has been interpreted in two contrasting ways. Bather (1915), when faced with an almost identical arrangement in *Edrioaster*, thought that the radial water vessel lay above the flooring plates and that the sutural passageways between adjacent flooring plates connected external tube feet to their internal ampullae (text-fig. 8A). This arrangement was also favoured by Paul and Smith (1984) for *Stromatocystites*. Bell (1977), however, argued that edrioasteroids possessed an internal radial water vessel that gave rise to a rather complex arrangement of tubes and bulbs (text-fig. 8B); Bell and Sprinkle (1978) applied this model to *Totiglobus*. Bell produced three arguments in support of his interpretation. First, he noted that in some isorophid edrioasteroids there are pores between adjacent cover plates that lead not into the ambulacral grooves but directly into the thecal interior. These he interpreted as being passageways for tube feet. However, isorophids are a highly derived group with flooring plates that are completely different from those of *Edrioaster* and *Stromatocystites*. Even if Bell is correct in interpreting these cover plate pores as passageways for tube feet, nothing equivalent is found in the Cambrian genera and the arrangement of the water vascular system in the highly derived isorophids is not necessarily the same as in more primitive groups.

Bell's second observation was that in edrioasteroids the hydropore lies on the outer side of the mouth frame, making it rather implausible that the stone canal looped under the mouth frame to reach the externally situated circum-oesophageal ring. He thought it much more likely that the stone canal would simply have descended to an internal ring vessel which then gave rise to internal radial water vessels. Yet this arrangement with external radial water vessels and hydropore situated distal to the mouth elements is precisely what occurs in pelmatozoans, asteroids, and primitive 'ophiuroids'.

Thirdly, Bell suggested that the ambulacral pore lay too close to the cover plates to have allowed the tube feet room to function efficiently, and therefore that the ambulacral pore was for egress of the radial water vessel. This argument collapses if the function of the tube feet in these animals was to open the cover plate skirt, as Paul and Smith (1984) suggested. The tube foot would then need to have been positioned close to the cover plate attachment zone, and possibly even connected to the cover plate sheet. The flooring plate passageways would then have led from the tube feet to their internal ampullae which served as fluid reservoirs and allowed the tube feet to inflate and deflate independently (text-fig. 8C). As embryological studies have shown that an internal radial water vessel is a derived character, and as all pelmatozoans and the more primitive eleutherozoans have external radial water vessels, it seems much more probable that in these Cambrian genera the radial water vessel lay above the flooring plates in the ambulacral tunnel. One of the prime reasons for having



TEXT-FIG. 8. Diagrammatic cross-sections through ambulacra showing flooring plates, cover plates, and the inferred arrangement of the water vascular system according to: A, Bather (1915); B, Bell (1977); C, this paper.

a series of cover plates above the ambulacral tunnel must surely have been to provide protection for the radial water vessel and associated nerves. The smooth perradial channel on the floor of the flooring plates presumably marks the position of this vessel.

MODE OF LIFE

From the preceding description it would appear that Cambrian edrioasteroids were sessile, low-level suspension feeders. They lived either unattached on the sea floor or fixed to the substratum by their dorsal surface, which in some was modified into a suction pad. All lived with their oral surface facing upwards away from the sea floor. This is suggested by their shape, since they have a flat dorsal surface and a weakly to strongly convex ventral surface, and by the presence of ventral epispines in some genera. Epispines are directly connected with gaseous exchange and no echinoderm has respiratory structures on the lower rather than the upper surface. Food must have been captured by the ambulacra and transported to the mouth along the ambulacral grooves, since these converge upon the mouth. When the animal was feeding the cover plate sheets must have been open to expose the ambulacral grooves. The simplest mechanism for raising the cover plate sheets would have been through inflation of the closely adpressed tube feet. If the prominent pit on the outer face of each cover plate is correctly interpreted as a ligament pit, then connective tissue running from this pit to a corresponding depression on the inner face of primary cover plates could have acted like a tension

spring, pulling the cover plate skirt back down over the ambulacral groove when the tube foot deflated. As both mouth and food gathering surfaces were situated on the upper surface, these animals could not have been detritus feeders but must have eaten fine particulate matter in suspension, like pelmatozoan echinoderms. Presumably they were ciliary mucus feeders, using ciliary currents to draw particulate matter into the ambulacral grooves and mucus to trap this material and pass it to the mouth. Both functions could have been performed by the epithelial lining of the flooring plates and the inner surface of the cover plates, although it is possible that there may have been additional crinoid-like tube feet arising directly from the radial water vessel to assist in food capture.

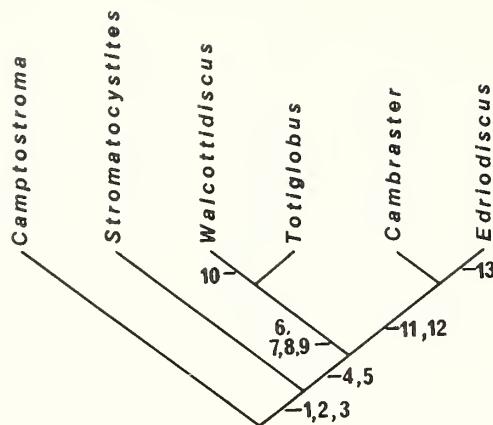
Termier and Termier (1969) suggested that *Stromatocystites* and *Cambraster* were infaunal, living beneath a thin covering of sediment and drawing water with suspended nutrients into permanently sealed ambulacral grooves through orifices at the tip of each ambulacrum. However, the distal orifices that they described are post-mortem artifacts caused by the collapse of the distalmost cover plates in two ambulacra in the holotype of *S. walcotti*. These animals are also unlikely to have lived infaunally since, unlike the asteroids with which the Termiers drew comparison, they had no paxillae to maintain a water-filled space around their buried body, which would have enabled the papillae to continue functioning.

PHYLOGENETIC ANALYSIS

The evolutionary relationships of Cambrian edrioasteroids are important for the analysis of the early history of eleutherozoan echinoderms. The major eleutherozoan groups, such as the asteroids, echinoids, and holothuroids, do not appear in the fossil record until after the Cambrian; the same is true for a number of important edrioasteroid groups. So, can any of these lineages be traced back into the Cambrian? The relationship of *Stromatocystites* to other Lower Cambrian echinoderms has already been analysed by Paul and Smith (1984) who also briefly sketched the later diversification of eleutherozoans. Here I attempt a more detailed analysis of how the Cambrian edrioasteroids relate to later groups.

For this phylogenetic analysis outgroup comparison has been made with the Lower Cambrian genus *Campostroma*. The reasons for placing this genus as one of two primitive sister groups of *Stromatocystites* were fully dealt with by Paul and Smith (1984). They considered *Campostroma* to be intermediate between *Stromatocystites* and the Cambrian pelmatozoans. The characters that seem to be important in determining relationships between the five Cambrian genera are listed in Table 1. Despite our lack of knowledge about certain morphological attributes in some of these genera, a reasonable cladogram can be drawn up (text-fig. 9). All five genera differ from *Campostroma* in having a flattened dorsal surface, rather than a squatly conical dorsal surface capable of some degree of spiral elongation and contraction. Their body-wall skeleton is also only one layer thick and composed of tessellate plates dorsally, whereas in *Campostroma* the skeleton is multilayered and dorsal plating is clearly imbricate.

Of the five Cambrian genera, *Stromatocystites* has the fewest novel characters in comparison with *Campostroma* and other Lower Cambrian echinoderms, and is placed as the primitive sister group to the rest. The remaining four genera fall into two groups of two. *Walcottidiscus* and *Totiglobus* share the synapomorphies of having a rather globular body form (as a result of relative expansion of the ventral surface and reduction of the dorsal surface), the loss of interambulacral epispines, the presence of a basal suction pad, and ambulacra whose distal tips are not inserted into the marginal ring of ossicles. *Cambraster* and *Edriodiscus* are quite different in shape, with an extensive flat dorsal surface and a slightly smaller ventral surface. Their marginal ossicles, which are relatively poorly developed in the other genera, are large and stout with a roughly triangular cross-section; this is taken as a synapomorphy for the group. In both *Cambraster* and *Edriodiscus* the dorsal pavement of plates extends slightly beyond the marginal ring to form a peripheral sheet, although *Edriodiscus* is more advanced in having the marginal ossicles actually inserted into the dorsal pavement. *Totiglobus* and *Cambraster* share two important characters which are not present in *Stromatocystites* but which, by implication, should also be present in *Edriodiscus* and *Walcottidiscus* (although these are too poorly



TEXT-FIG. 9. Cladogram of character distribution for the five genera of Cambrian eleutherozoans; characters 1–13 are given in Table 1.

known at present): 1, an identical mouth frame composed of five interradial elements, each of which is formed by fusion of four proximal flooring plates, two from each adjacent ambulacrum; 2, a discrete hydropore plate that lies adjacent to the mouth frame but is not incorporated into it.

Relationships with other groups

Edrioasterids. The Ordovician family Edrioasteridae currently contains just two genera: *Edrioaster* and *Edriophus*. They have the same overall shape and plating arrangement as *Totiglobus* and *Walcottidiscus*, with ambulacra that extend sub-ambitally, a ring of enlarged ossicles around the dorsal surface, and an uncalcified zone at the centre of the dorsal surface. Their mouth frame consists

TABLE 1. Distribution of characters in Cambrian genera of edrioasteroids. *Camptostroma* is taken as being primitive for outgroup comparison.

Derived character state	<i>Stromatocystites</i>	<i>Cambaster</i>	<i>Edriodiscus</i>	<i>Totiglobus</i>	<i>Walcottidiscus</i>
1. Flat, tessellate dorsal surface	×	×	×	×	×
2. Dorsal plating one layer thick	×	×	×	×	×
3. Marginal ring of plates present	×	×	×	×	×
4. Mouth frame composed of five fused ambulacrual flooring plates, interradially positioned	—	×	?	×	?
5. Hydropore plate excluded from oral frame	—	×	?	×	?
6. Interambulacrual plates tessellate; no epispines	—	—	?	×	×
7. Dorsal surface acting as suction pad	—	—	—	×	×
8. Dorsal growth reduced relative to ventral growth	—	—	—	×	×
9. Ambulacrual tips free of marginal ring	—	—	?	×	×
10. Central region of dorsal surface uncalcified	—	—	—	—	—
11. Marginal ossicles stout, forming a prominent ring	—	×	×	—	—
12. Peripheral skirt extending beyond marginal ossicles	—	×	×	—	—
13. Marginal ossicles inserted into dorsal pavement	—	—	×	—	—

of five interradial elements, each formed through the fusion of proximal flooring plates, but they are unique in also having five radially positioned elements which underlie the flooring plates (see Bell 1976), a feature which can be taken as a synapomorphy for the two genera. The interambulacral zones are identical to those of *Totiglobus* and *Walcottidiscus*; ambulacral zones are similar but possess enlarged primary cover plates and greatly reduced secondary cover plates. Bell and Sprinkle (1978) suggested that *Totiglobus* might be ancestral to edrioasterids. However, *Walcottidiscus* is taken as the primitive sister group here rather than *Totiglobus* since *Walcottidiscus* and edrioasterids share two advanced characters: 1, ambulacra that curve around the ambitus; 2, a central uncalcified zone to the dorsal surface.

Isorophids. The majority of isorophid edrioasteroids have been reviewed recently by Bell (1976) in admirable detail and the group is therefore relatively well understood. Isorophids share the following four advanced characters that distinguish them from other edrioasteroids: 1, uniserial flooring plates lacking sutural passageways; 2, an oral frame composed of the first flooring plate in each ambulacrum; 3, ambulacral cover plates that extend intrathecally and completely conceal the flooring plates; 4, an uncalcified dorsal surface. These are all autapomorphies of the group. Bell (1976) divided isorophids into two suborders and four families, carefully listing the diagnostic features of each. However, he did not distinguish between symplesiomorphic and synapomorphic character states and, in the light of what is now known about the Cambrian edrioasteroids, it is worth examining these groupings cladistically. Table 2 gives an analysis of the characters used by Bell (1976) and identifies those that are apomorphic and can be used in constructing a cladogram (text-fig. 10). Using *Stromatocystites* for outgroup comparison, as primitive, it is apparent that Bell's group Isorophina is based largely on symplesiomorphic characters and that the only possible synapomorphy that they share is the presence of four enlarged primordial cover plates, at least primitively. Of the two families included within the Isorophina, the Agelacrinitidae form a monophyletic group with the following autapomorphies: 1, hydropore structure formed of a large number of small plates, without a clearly differentiated hydropore plate; 2, ambulacral cover plates arranged in distinct cycles. The genus *Lispidecodus*, which Kesling (1967) considered to be sufficiently distinct to merit its own family, also belongs here in my opinion. The other family, Bell's Isorophidae, is paraphyletic as it lacks any unique synapomorphy.

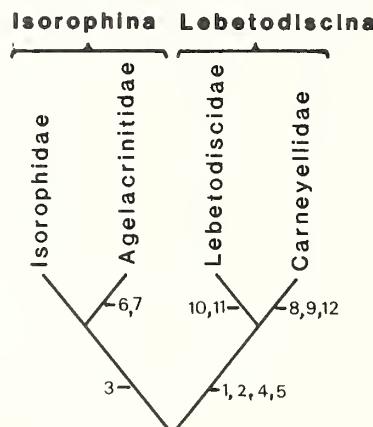
Members of the second suborder, Lebetodiscina, share two good synapomorphies: 1, the loss of all secondary cover plates in all but the oral area; 2, having sutural passageways between adjacent cover plates. The great majority also possess enlarged primordial cover plates, especially in the C/D interray. In the family Carneyellidae the oral area is dominated by three large primordial cover plates; both the secondary cover plates and the shared oral cover plates have been lost from the oral area. The dominance of the primordial cover plates in the oral region and the extremely simple arrangement of ambulacral cover plates are features typical of juvenile lebetodiscinids and suggest that this family may have evolved through heterochrony. The Lebetodiscinae have a less well-differentiated peripheral rim than any other isorophid family, and this may be a shared derived character for the group.

Isorophids are usually considered to have evolved from edrioasterids (Bather 1915; Bockelie and Paul 1983), although Bell and Sprinkle (1978) thought that they were independently derived from some unknown Cambrian group. Some primitive isorophids such as *Savagella* retain a stout ring of marginal ossicles that are triangular in cross-section and very reminiscent of those in *Cambraster* and *Edriodiscus*. Isorophids also have a peripheral skirt of plates lying outside the marginal ring of ossicles, as found in *Edriodiscus*. These apomorphic features suggest that *Cambraster*, *Edriodiscus*, and isorophid edrioasteroids belong to the same clade. Jell *et al.* (1985) have recently reported an isorophid edrioasteroid from the Upper Cambrian of Australia, but this is too poorly preserved to add much to our understanding of their early evolution.

Cyclocystoids. This group has been revised and reinterpreted recently by Smith and Paul (1982). They chose to maintain cyclocystoids as a separate class but suggested that they were closely related to both *Cambraster* and isorophid edrioasteroids. Cyclocystoids are a rather peculiar and

TABLE 2. Analysis of character distribution within Bell's (1976) Order Isorophida. Synapomorphic characters 1–12 (see text-fig. 10) are in bold. Outgroup comparison has been made with Cambrian edrioasteroids.

Suborder LEBETODISCINA Bell, 1976	Suborder ISOROPHINA Bell, 1976
1. Anal structure a periproct	Anal structure a valvular cone
2. Three oral primary cover plates enlarged or none	3. Four oral primary cover plates enlarged or none
4. Primary cover plates only	Primary and secondary cover plates
5. Cover plate sutural passageways	No cover plate sutural passageways
Suborder ISOROPHINA Bell, 1976	Family AGELACRINITIDAE Chapman, 1860
Family ISOROPHIDAE Bell, 1976	Theca domal
Theca domal	Four primary oral cover plates
Four primary oral cover plates	Hydropore incorporated into central oral rise
Hydropore incorporated into central oral rise	Cover plates alternately large and small
Cover plates alternately large and small	Interambulacra squamose and imbricate
Interambulacra squamose and imbricate	Family CARNEYELLIDAE Bell, 1976
Suborder LEBETODISCINA Bell, 1976	Theca domal
Family LEBETODISCIDAE Bell, 1976	8. Lateral shared cover plates absent
Theca domal, discoidal or clavate	9. Secondary shared cover plates absent
Lateral shared cover plates present	Hydropore plate forming part of oral area
Secondary oral cover plates present	Ambulacra low and rounded
10. Hydropore plate adjacent to ambulacrum	Cover plate passageways oblique
Ambulacra high pronounced ridges	Peripheral plates geniculate with differentiated
Cover plate passageways near vertical	marginals
11. Peripheral plates squamose, marginals poorly differentiated	12. Three very large primary cover plates in oral area
Cover plates hardly differentiated in oral area	



TEXT-FIG. 10. Cladogram of character distribution for the major groups within Bell's (1976) group Isorophida. Characters 1–12 are given in Table 2.

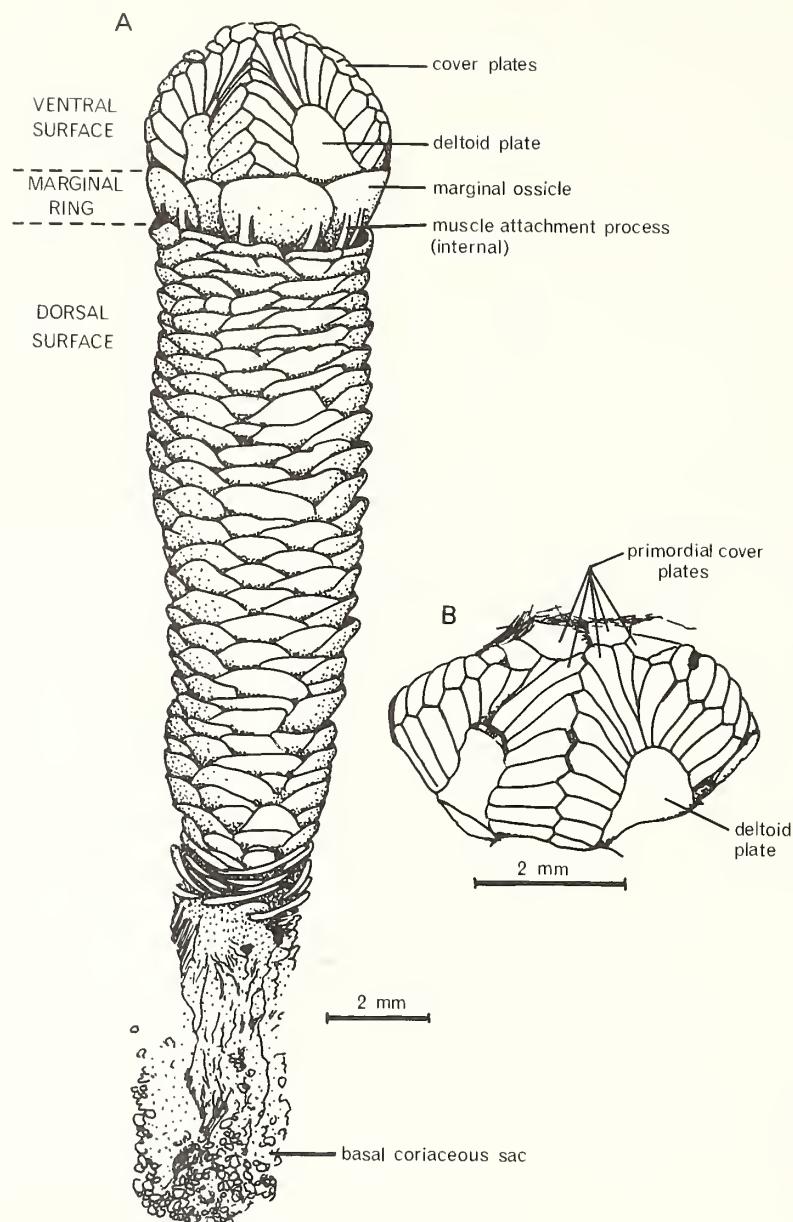
poorly understood group of echinoderms that have all been placed within the single family Cyclocystoididae. They share a number of unique characters which distinguish them from other echinoderms, including the possession of perforate marginal ossicles that have distal cupules roofed over by a movable peripheral skirt of plates, a dorsal plated surface composed of annular plates with a polygonal outline, and the absence of a ventral periproct. However, they share with *Cambraster*, *Edriodiscus*, and isorophids such as *Savagella* the ring of stout marginal ossicles and the peripheral skirt of plates; they share uniserial ambulacral flooring plates with isorophids alone. This suggests that cyclocystoids and isorophids are sister groups.

Cyathocystids. *Cyathocystis* and *Cyathotheca* are two very distinctive genera that were placed in their own family Cyathocystidae by Bather (1899). Although Bell (1980) suggested that *Timeischytes* and *Hadrochthis* should also be included in this family, Bockelie and Paul (1983) convincingly demonstrated that they did not belong here and were in fact isorophids. Bockelie and Paul (1983) identified a number of autapomorphies for this group: 1, the dorsal surface is a single calcite element which is cup-shaped and moulded to the substratum; 2, the five primordial cover plates remain in contact throughout growth; 3, a single large deltoid plate occupies each interambulacral zone; 4, there are no ambulacral flooring plates. They therefore suggested that cyathocystids represented a line of descent from *Stromatocystites* independent of the main edrioasterid-isorophid lineage.

Not all of their supposed synapomorphies are unique to this group, however, since the five primordial cover plates also remain in contact throughout growth in pyrgocystids (text-fig. 11) and pyrgocystids also possess only a single interradial plate in each interambulacrum. Furthermore, the fact that these deltoid plates surround the peristome, abut along the distal edge at the perradial suture, and carry articulating cover plates strongly indicates that these are homologous not with interambulacral plates but with the fused ambulacral mouth frame plates present in *Cambraster*, *Totiglobus*, and edrioasterids. Bockelie and Paul (1983) were therefore mistaken in suggesting that cyathocystids lacked flooring plates; rather they have lost all but the most proximal fused ambulacral flooring plates that form the mouth frame elements. Cyathocystids are so highly modified that their precise phylogenetic position is difficult to ascertain. However, the presence of oral frame elements composed of fused ambulacral flooring plates is a synapomorphy shared with both edrioasterids and the *Cambraster*-isorophid clade. In the cladogram they are therefore placed in a trichotomy with these two groups (text-fig. 12).

Pyrgocystids. Pyrgocystids are fully plated and turret-shaped edrioasteroids with an elongate stalk composed of imbricate dorsal plates and a small ventral surface surmounting the stalk (text-fig. 11). The marginal ossicles lie at the top of the turret and surround the ventral surface. On each marginal plate there is a pair of internal processes similar to those in *Totiglobus* (text-fig. 11). These were presumably attachment sites for the dorsal muscles responsible for contraction of the turret. In some there is a basal sac of minute platelets embedded in a coriaceous membrane. Unfortunately very little is known about the plating of the ventral surface. A single large interradial plate lies in each interambulacrum except posteriorly, where a small number of smaller plates are found (see Holloway and Jell 1984). Pyrgocystids have tall, narrow cover plates very much like those of cyathocystids; the primordial cover plates meet above the oral area (text-fig. 11b), also like cyathocystids. If, as in cyathocystids, the large interradial 'deltoid plates' turn out to be mouth frame plates formed through fusion of proximal flooring plates, as is strongly suspected, then cyathocystids and pyrgocystids are best considered to be sister taxa. The perradial margin of the deltoid plates is scalloped exactly as in cyathocystids and no flooring plates have yet been seen in partially disarticulated specimens. Both groups have the same turret-shaped theca and almost identical cover plate arrangements. The principal difference is that in cyathocystids dorsal plating is formed of a single calcite element, whereas in pyrgocystids it is composed of many plates. Possibly dorsal plating in cyathocystids has become fused.

Text-fig. 12 provides a character matrix for the various groups of edrioasteroid discussed above and a summary of their relationships derived from cladistic analysis of this matrix.



TEXT-FIG. 11. *Rhenopyrgus grayae* (Bather), BM(NH) E23470, Ashgill, Upper Ordovician, Girvan, Scotland; camera lucida drawings of the holotype to show the basic morphological features of pyrrocystids: A, lateral; B, oral surface.

CLASSIFICATION

Edrioasteroids have always been considered a natural grouping and, since 1899, have been assigned the status of class (Bather 1899). However, current classification schemes of this group, such as those of Bell (1980), do not reflect the hierarchical groupings identified in the preceding section and summarized in text-fig. 12. It is therefore necessary to rationalize the classification as a whole in order to place the Cambrian genera into their appropriate monophyletic groups. If the characters used to define edrioasteroids are examined critically, it is difficult to identify any advanced characters that are not also present in other primitive eleutherozoan groups. Instead, edrioasteroids are characterized by having retained primitive features of crown-group echinoderms, such as the ventral periproct, unmodified ambulacral cover plates, an oral mouth frame that is fixed, and an attached mode of life as adults; but they lack the pelmatozoan synapomorphies of a dorsal stem and an exothecal ambulacral subvinctive system. Having interradial mouth frame elements formed by fusion of proximal ambulacral flooring plates is an important shared derived character that unites *Totiglobus*, *Cambraster*, edrioasterids, cyathocystids, and probably pyrgocystids but which is not found in *Stromatocystites* or primitive asteroids and ophiuroids. This implies that all edrioasteroids, with the exception of *Stromatocystites*, form a natural clade which can be considered as a plesion within the stem group of the Eleutherozoa (see Smith 1984b). As this plesion corresponds more or less to the class Edrioastroidea Bather as currently accepted (though with the removal of *Stromatocystites* and the inclusion of cyclocystoids), this seems the obvious name and taxonomic rank to maintain, respecting historical tradition. *Stromatocystites* is then the primitive sister group to all other known eleutherozoan echinoderms and is best classified as a separate and distinct plesion.

Within the plesion Edrioastroidea there are three subgroups forming a trichotomy in the cladogram (text-fig. 12). At present, there are insufficient morphological data to solve this trichotomy convincingly and the three groups identified are best assigned equal rank, even though two of them contain just four genera each whereas the third contains some thirty-five genera and is considerably more diverse. This last group includes *Cambraster*, Bell's Isorophida, and cyclocystoids. Cyclocystoids have in recent years been separated off at class level, even though the few genera known all belong to a single family, the Cyclocystoididae. Similarly, isorophids, as defined by Bell (1976), display an extremely limited range of morphological variation and are a very conservative group. Bell (1976) elevated this group to the rank of order, recognizing two suborders each with two families. However, in comparison with taxonomic assignment in other echinoderm groups, Bell's order Isorophida is more comparable to a family, and the various subdivisions to subfamilies and tribes. It might be more sensible therefore to reduce Bell's Isorophida to a lower rank such as family, where the name Agelacrinitidae Chapman 1860 would have priority. The two suborders erected by Bell could then be transformed to the rank of subfamily; Lebetodiscinae (for the Lebetodiscina) and Isorophinae (for the Isorophina). This would make cyclocystoids and the Agelacrinitidae sister groups. Although *Cambraster*, cyclocystoids, and agelacrinitids differ in a number of striking features, they appear to form a monophyletic group and should therefore be classified together. Taxonomic debasement can be avoided by uniting them within one order and the most obvious available name for this group is the order Isorophida. This then requires the expansion of Bell's original diagnosis for the Isorophida to include the cyclocystoids and *Cambraster*.

If this clade is assigned the rank of order, then the two other monophyletic sister groups should also be ranked as orders. There is already an order Edrioasterida for the genera *Edrioaster*, *Edriophus*, and *Totiglobus*; it is only necessary to include *Walcottidiscus* here and expand the diagnosis for the family Edrioasteridae in consequence. An order Cyathocystida is also currently available, although at present it contains only the single family Cyathocystidae. If the pyrgocystids are correctly interpreted as the sister group to the cyathocystids then the Cyathocystida needs to be redefined to contain two families, the Pyrgocystidae and the Cyathocystidae.

A phylogenetic classification of the plesion Edrioastroidea, using the conventions recommended by Wiley (1979), is presented in Table 3, together with a more traditional scheme for comparison. The precise taxonomic levels that have been chosen are, and always will be, open to dispute, but they are

TABLE 3. Classification of the Edrioasteroidea.

<i>Traditional classification (based on Bell 1980, but with later additions)</i>	<i>Revised classification (this paper)</i>
Order STROMATOCYSTOIDA Termier and Termier, 1969	Genus STROMATOCYSTITES Pompeckj, 1896
Family STROMATOCYSTITIDAE Bassler, 1936	Plesion (Class) EDRCIOASTEROIDEA Billings, 1858
Family CAMBRASTERIDAE Termier and Termier, 1969	Order EDRCIOASTERIDA Bell, 1976 (<i>sedis mutabilis</i>)
Order EDRCIOASTEROIDA Bell, 1976	Family TOTIGLOBIDAE Bell and Sprinkle, 1978
Family EDRCIOASTERIDAE Bather, 1898	Family EDRCIOASTERIDAE Bather, 1898
Family TOTIGLOBIDAE Bell and Sprinkle, 1978	
Order ISOROPHIDA Bell, 1976	Order ISOROPHIDA Bell, 1976 (emend.) (<i>sedis mutabilis</i>)
Suborder LEBETODISCINA Bell, 1976	Genus CAMBRASTER Cabibel, Termier and Termier, 1958
Family LEBETODISCIDAE Bell, 1976	Genus EDRCIODISCUS Smith, 1985
Family CARNEYELLIDAE Bell, 1976	Family CYCLOCYSTOIDIDAE Miller, 1882
Suborder ISOROPHINA Bell, 1976	Family AGELACRINITIDAE Chapman, 1860
Family HEMICYSTITIDAE Bassler, 1936 (= ISOROPHIDAE Bell, 1976)	Subfamily ISOROPHINAE Bell, 1976
Family AGELACRINITIDAE Chapman, 1860	Subfamily LEBETODISCINAE Bell, 1976
Suborder UNCERTAIN	
Family PYRGOCYSTIDAE Kesling, 1967	Order CYATHOCYSTIDA Bockelie and Paul, 1983 (emend.)
Family LISPIDECODIDAE Kesling, 1967	(<i>sedis mutabilis</i>)
Family RHENOCYSTIDAE Holloway and Jell, 1984	Family PYRGOCYSTIDAE Kesling, 1967
Order CYATHOCYSTIDA Bockelie and Paul, 1983	Family CYATHOCYSTIDAE Bather, 1898
Family CYATHOCYSTIDAE Bather, 1899	

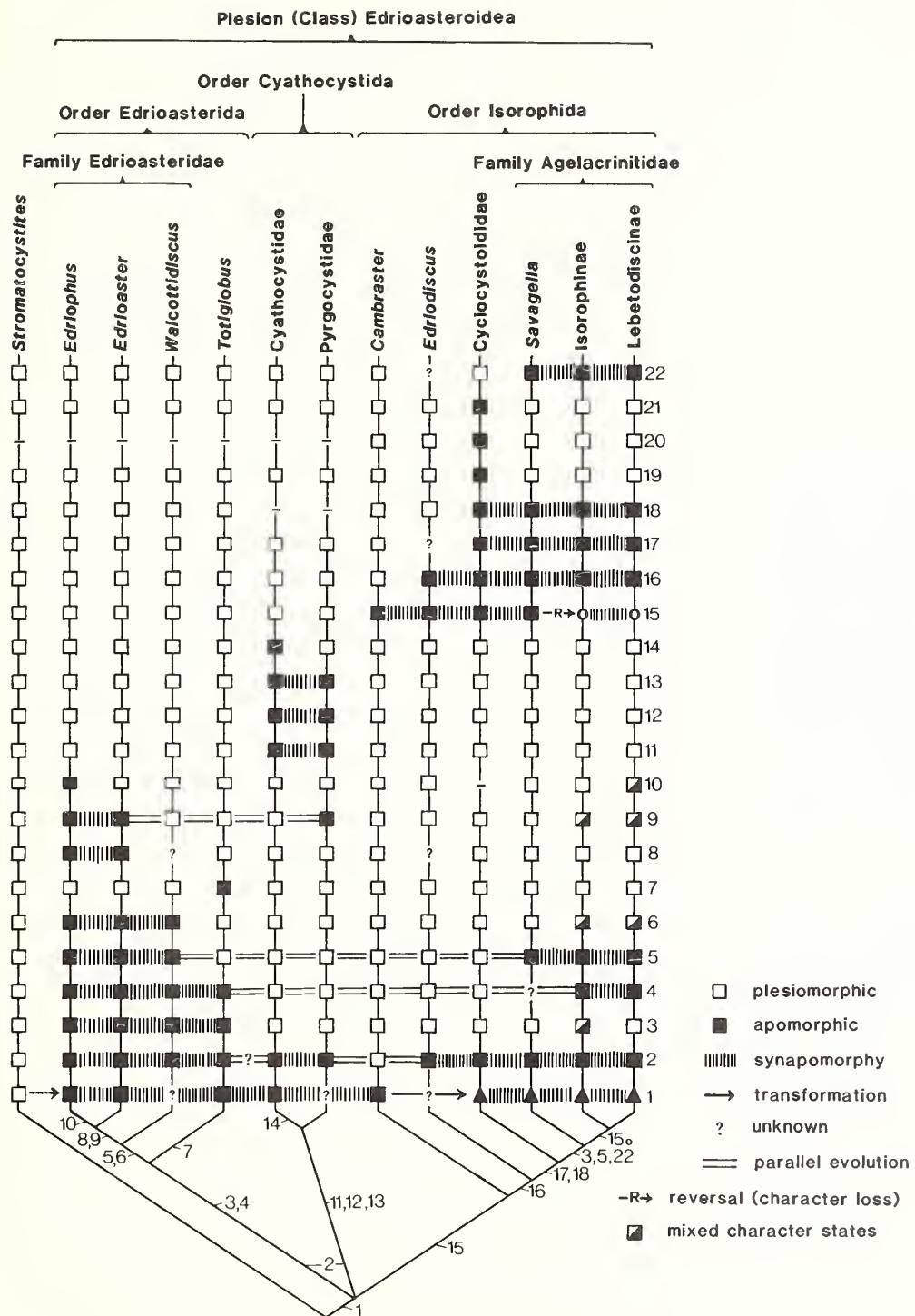
the least important part of the classification scheme. It is the hierarchical and listing orders that convey information and on which the classification should be judged.

Emended taxonomic definitions

Plesion (Class) EDRCIOASTEROIDEA Billings, 1858. Stem group eleutherozoans with a fixed mouth frame of ambulacral flooring plates (primitively five interradial elements). Retained plesiomorphic characters include the sessile mode of life as adults, the periproct opening ventrally in the posterior interambulacrum, and a largely unmodified arrangement of cover plates protecting the ambulacral groove.

Order EDRCIOASTERIDA Bell, 1976. Sub-globular edrioasteroids with biserial flooring plates, a dorsal surface that is reduced relative to the ventral surface, and ambulacra that extend sub-ambitally.

TEXT-FIG. 12. Character distribution and the derived cladogram for principal edrioasteroid groups. Characters 1–22 are as follows: 1, oral frame composed of fused ambulacral flooring plates positioned interradially, transformed to oral frame of radially positioned flooring plates; 2, loss of epispines from interambulacral zones; 3, dorsal growth retarded relative to ventral growth; 4, ambulacral tips free of the marginal ring; 5, central part of dorsal surface uncalcified; 6, ambulacra curve around ambitus; 7, dorsal surface a tiny, plated suction pad; 8, five radial elements in oral frame in addition to the fused flooring plates; 9, secondary cover plates greatly reduced or lost; 10, anal structure a periproct; 11, all five primordial cover plates meet centrally; 12, single large deltoid (= fused ambulacral flooring plates?) occupies interambulacral zones; 13, dorsal surface expanded into a stalk; 14, dorsal surface a single (?fused) calcite element; 15, marginal ossicles stout, forming a distinct frame to the ventral surface; marginal ossicles as imbricate ring (reversed character state); 16, marginal ossicles inserted into the dorsal pavement to form a clearly demarcated peripheral skirt; 17, flooring plates uniserial; 18, loss of sutural pores for internal ampullae; 19, perforate marginal ossicles; 20, dorsal plates annular with central perforation; 21, peripheral skirt modified into a protective canopy for the cupule zone; 22, cover plates extend intrathecally at the interradial suture to conceal the flooring plates externally.



Order CYATHOCYSTIDA Bockelie and Paul, 1983. Turret-shaped edrioasteroids with a greatly expanded dorsal surface, a single large deltoid plate in each interambulacrum (fused ambulacral flooring plate?), and primordial ambulacral cover plates that meet above the peristome. The dorsal stalk may be either multiplated or composed of a single (?fused) calcite element.

Order ISOROPHIDA Bell, 1976. Discoidal to clavate edrioasteroids with a distinct peripheral rim of plates extending beyond the ring of marginal plates.

Family AGELACRINITIDAE Chapman, 1860. Isorophids with uniserial flooring plates and generally unbranched arms, cover plates with adradial intrathecal extensions that conceal the flooring plates externally, and an uncalcified dorsal surface within the peripheral skirt.

Subfamily LEBETODISCINAE (= Suborder LEBETODISCINA Bell, 1976). Agelacrinitids with sutural passages between adjacent cover plates.

Subfamily ISOROPHINAE (= Suborder ISOROPHINA Bell, 1976). Agelacrinitids with primary ambulacral cover plates in two or more sizes, arranged cyclically, and primitively with four enlarged primordial cover plates.

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens referred to below are abbreviated as follows: BM(NH), British Museum (Natural History), London; CPC, Commonwealth Palaeontological Collections, Bureau of Mineral Resources, Canberra, Australia; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NYSM, New York State Museum, Albany; USNM, United States National Museum, Smithsonian Institution, Washington D.C.

Genus STROMATOCYSTITES Pompeckj, 1896

- 1896 *Stromatocystites* Pompeckj, p. 506.
- 1899 *Stromatocystites* Pompeckj; Jaekel, p. 42.
- 1900 *Stromatocystites* Pompeckj; Bather, p. 206.
- 1911 *Chilocystis* Perner MSS; Zelizko, p. 6.
- 1918 *Stromatocystites* Pompeckj; Jaekel, p. 112.
- 1919 *Stromatocystites* Pompeckj; Schuchert, p. 1.
- 1936 *Stromatocystites* Pompeckj; Bassler, p. 3.
- 1966 *Stromatocystites* Pompeckj; Regnell [pars], p. U133.
- 1969 *Stromatocystites* Pompeckj; Termier and Termier, p. 133.
- non 1905 *Stromatocystites* Miquel, p. 476 [= *Cambraster*].

Diagnosis. Theca flattened, discoidal, or weakly pentagonal in outline and fully plated; ambulacra straight, reaching edge of ventral surface; cover plates arranged as multiserial sheets; interambulacral plates with sutural epispires; dorsal plating polygonal, tessellate, with large centro-dorsal.

Type species. *Stromatocystites pentangularis* Pompeckj, 1896, by original monotypy.

Other species. *S. walcotti* Schuchert, 1919.

EXPLANATION OF PLATE 87

Figs. 1–6. *Stromatocystites pentangularis* Pompeckj, 1896. 1, 2, and 5, BM(NH) E16004, Middle Cambrian, Jince, Czechoslovakia: 1, general view showing three individuals, two of which are dorsal surface uppermost, $\times 1$; 2, one individual, ventral surface uppermost, $\times 2$; 5, same individual, dorsal surface, $\times 2$. 3 and 4, BM(NH) E29830, Lower Cambrian, Bonne Bay, Newfoundland: 3, oral, $\times 2$; 4, aboral, $\times 2$. 6, specimen in the collection of Dr Krantz of Bonn, latex BM(NH) E63138, Middle Cambrian, Pod Trnim, Czechoslovakia, dorsal surface, $\times 2$.

All photographs are of latex casts whitened with ammonium chloride sublimate.



SMITH, *Stromatocystites*

Stratigraphical age and distribution. Uppermost Lower Cambrian (*Olenellus* Beds) to Middle Cambrian (*Paradoxides gracilis* Zone) from Jince, Czechoslovakia, Bonne Bay, Newfoundland, and Rostock, northern Germany (in glacial drift, presumably derived from Scandinavia).

Remarks. *Stromatocystites* was first described by Pompeckj in 1896 and his figures have been copied by all later workers. *S. pentangularis* and *S. walcotti* are each known from a large number of specimens and are redescribed below. A third species, *S. balticus* Jaekel, 1899, is represented by only two specimens whose whereabouts are no longer known and it is treated as a *nomen dubium*.

Stromatocystites is distinguished from other Cambrian edrioasteroids by having dorsal and ventral surfaces similar in size, sutural epispires in interambulacral zones, straight narrow ambulacra with multiserial cover plate sheets, poorly developed marginal ring plates, and simple unfused oral frame plates. *Cambraster* likewise has interambulacral epispires but differs in having compound oral frame plates and a stout marginal ring of ossicles. *Walcottidiscus* and *Totiglobus* both lack epispires and have a reduced dorsal surface.

Stromatocystites is stratigraphically the oldest known genus of eleutherozoan echinoderm.

Stromatocystites pentangularis Pompeckj, 1896

Plate 87; Plate 89, fig. 1; text-figs. 5, 6B, C, 13–15

- 1896 *Stromatocystites pentangularis* Pompeckj, p. 506, pl. 13, figs. 1–6.
- 1899 *Stromatocystites pentangularis* Pompeckj; Jaekel, p. 42, figs. 5–8.
- 1900 *Stromatocystites pentangularis* Pompeckj; Bather, p. 206, fig. 1.
- 1911 *Chilocystis bohemica* Perner MSS, in Zelizko, p. 6.
- 1919 *Stromatocystites pentangularis* Pompeckj; Schuchert, p. 2, fig. 1E.
- 1936 *Stromatocystites pentangularis* Pompeckj; Bassler, p. 3, pl. 1, figs. 6 and 7.
- 1958 *Stromatocystites pentangularis* Pompeckj; Cabibel, Termier and Termier, p. 283, fig. 2.
- 1966 *Stromatocystites pentangularis* Pompeckj; Regnelli, p. U160, text-fig. 126.
- 1969 *Stromatocystites pentangularis* Pompeckj; Termier and Termier, p. 133, figs. 1–3.

Diagnosis. A species of *Stromatocystites* with a domed ventral surface and pentagonal outline; marginal ossicles undifferentiated; ambulacra narrow, without V-shaped intrathecal extensions; centro-dorsal plate surrounded by six or seven plates; oral frame large, pentagonal.

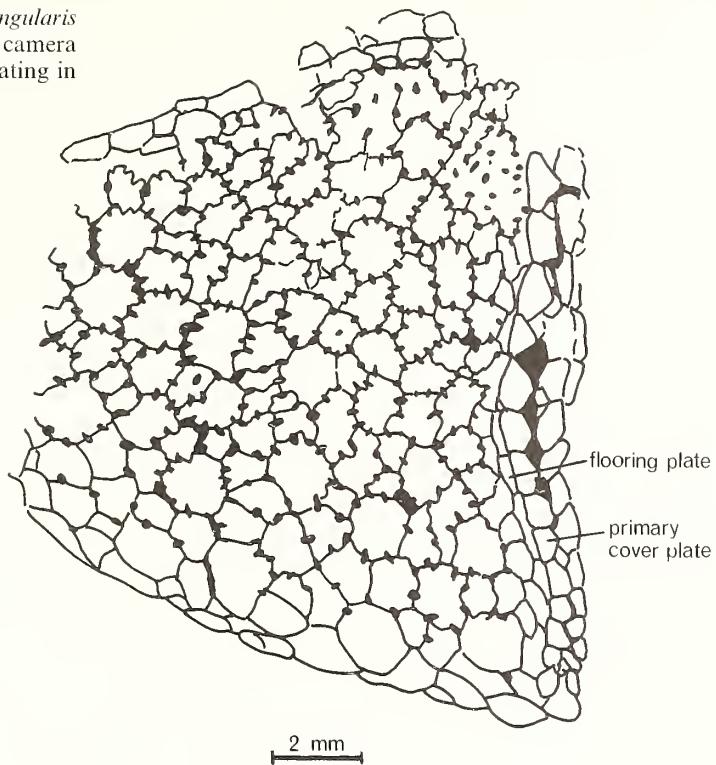
Types. Pompeckj (1896) based his description on forty examples from 'Pod Trnim bei Tejrovice' of which six were illustrated. These were stated to belong to the Geologischen Reichsanstalt, Vienna, but are now housed in the Czechoslovakian Geological Survey, Prague. No holotype was designated by Pompeckj, thus all are syntypes. The holotype of *Chilocystis bohemica* is P/77916, Národní Muzeum, Prague; a cast, BM(NH) E16008, of this specimen was studied (Pl. 89, fig. 1).

Material studied. The following description is based largely on eighteen well-preserved individuals, BM(NH) E15897, E15898, E16004, and E29380, and on the two individuals, USNM 56665. The collections in the Národní Muzeum, Prague, have also been studied, as have three latex casts of specimens in the private collection of Dr Krantz of Bonn, kindly given to me by Professor Ubachs (BM(NH) E63137–63139).

Stratigraphical age and distribution. BM(NH) E29380 (four individuals) comes from the *Olenellus* Beds, Taconian, high Lower Cambrian of Bonne Bay, Newfoundland. Other material comes from the *Paradoxides gracilis* Zone, Upper Jince Beds, Middle Cambrian of Tyrovice and Jince, Czechoslovakia.

Description. All specimens examined are preserved as natural moulds of external surfaces. The theca is pentagonal in outline with the ambulacra running to the five rounded corners. In a number of specimens the interambulacral portions are gently concave suggesting that there may have been internal radially arranged postural muscles present. The entire theca is plated. On the ventral surface the ambulacra form narrow ridges which extend to the margin. These meet centrally in a 2:1:2 pattern with ambulacra B+C and D+E paired and united on either side of the mid-line. Ambulacrum A is unpaired and set almost at right angles to the paired lateral ambulacra (text-fig. 15). The ambulacra form prominent ridges on the theca while interambulacral zones are generally depressed. The ambulacra are straight and composed of biserial flooring plates with left and right cover plate series. Flooring plates are relatively short (in the perradial/interradial direction) and broad (in the

TEXT-FIG. 13. *Stromatocystites pentangularis* Pompeckj, 1896, BM(NH) E16008, camera lucida drawing, showing the ventral plating in one interambulacrum.

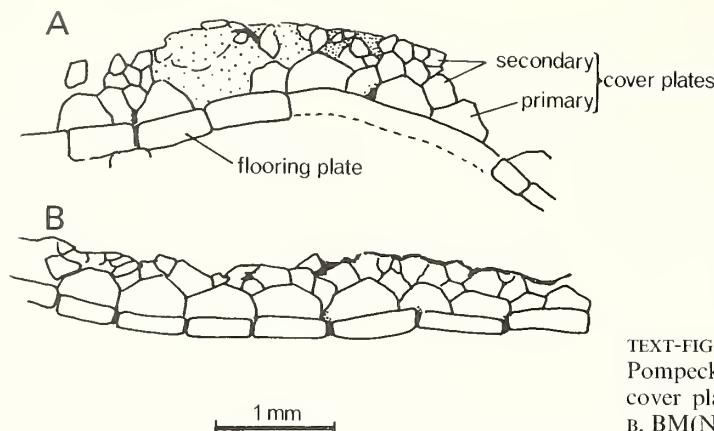


adoral/adambital direction) (text-fig. 6b, c). The perradial edge of each plate is weakly angled and the flooring plates alternate to produce a zigzag perradial suture. Interradially a small part of the flooring plate is exposed between the interambulacral plates and the cover plate sheets. On the adoral/adambital suture, immediately perradial to the site where the cover plates attach, is a small ovoid pore, shared equally between the two flooring plates. The flooring plates appear to be steeply inclined so as to form a deep and narrow ambulacral tunnel.

Cover plates are arranged as two multiserial sheets that attach towards the adradial edge of the flooring plates, one on either side of the ambulacrum. A large pentagonal primary cover plate rests directly on each flooring plate. Between these, more or less directly above the flooring plate sutures, are smaller diamond-shaped cover plates. A further two or so irregular rows of small cover plates lie above the primary and diamond-shaped cover plates (text-fig. 14). The two cover plate sheets meet along the mid-line and, in well-preserved material, form a crenulated crest to the ambulacral ridge. In the oral area the arrangement of cover plates appears identical with that of the more distal ambulacral areas and there are no distinguishably larger plates. The flooring plates and cover plate series are more or less identical to those in helicoplacoids (see Paul and Smith 1984).

In almost all specimens compaction has pressed dorsal and ventral surfaces together so that narrow ridges mark the position of the underlying flooring plates on the dorsal surface. The five ridges do not meet in a 2:1:2 pattern, as might be expected, but bifurcate near the centre and unite interradially to form a pentastellate ring (Pl. 87, figs. 4-6). This suggests that adorally the individual columns of flooring plates could have separated along the perradial suture and that the most proximal flooring plates were united interradially to form a large and flexible peristomial opening, as in primitive asteroids. Unfortunately, no specimens examined showed the internal face of the ventral surface and the precise arrangement of flooring plates in the oral region must remain speculative.

Interambulacral zones on the ventral surface are composed of small polygonal and tessellate plates of variable size and shape (text-fig. 13). There are up to fifteen plates abreast in an interambulacral zone. At the sutures between plates there are small oval or slit-like epispires with neither internal nor external rims. Epispire are absent from a narrow zone bordering the ambulacra and immediately adjacent to the marginal plates. The periproct lies more or less centrally in the C/D interray. It is composed of about twelve to fifteen lath-shaped



TEXT-FIG. 14. *Stromatocystites pentangularis* Pompeckj, 1896, camera lucida drawings of cover plate arrangements: A, USNM 56665b; B, BM(NH) E16004.

plates arranged radially. These plates and those immediately adjacent lack epispires. They generally lie more or less flush with the surrounding interambulacral plates.

No third aperture has been identified amongst the plates of the oral area, probably because no specimen is sufficiently well preserved in this region to reveal such a structure. The dorsal surface is usually concave and pressed against the ventral surface, although in life it was presumably more or less flat. All specimens show a sharp marginal rim suggesting that the large marginal plates formed a more rigid frame, as in *S. walcotti*. Immediately inside this rim there is a very narrow zone of tiny plates. The remainder of the dorsal surface is covered in polygonal, tessellate plates with a pitted surface texture. These plates are more or less irregularly arranged (text-fig. 5B), but a large equant plate at the centre of the disc is surrounded by six or seven other large plates. There is no evidence for any attachment structure by which adult *Stromatocystites* might have attached itself to a hard substratum.

Remarks. *S. pentangularis* is not uncommon at certain horizons and clusters of individuals are preserved together on bedding surfaces. As individuals showing both dorsal and ventral surfaces are found together on the same slab, they probably represent individuals that have been current transported and buried alive. The original description by Pompeckj (1896) was fairly good and, for the most part, later workers have simply repeated his findings without adding any new information.

Stromatocystites walcotti Schuchert, 1919

Plate 88; text-figs. 4, 7, 16

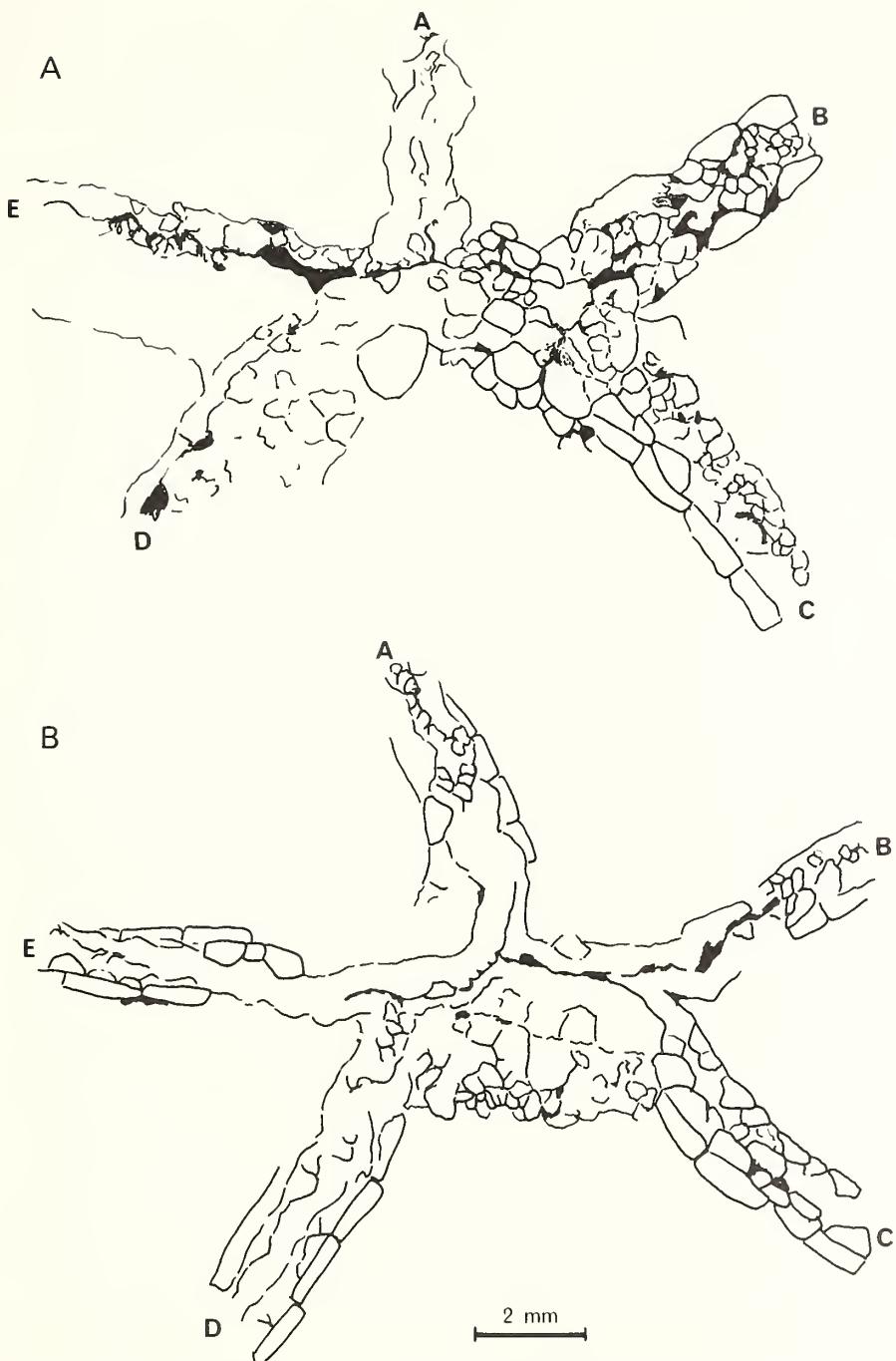
- 1919 *Stromatocystites walcotti* Schuchert, p. 3, pl. 7, figs. 1–3; text-fig. 1.
- 1966 *Stromatocystites walcotti* Schuchert; Regnell, p. U160, text-fig. 126.
- 1969 *Stromatocystites walcotti* Schuchert; Termier and Termier, p. 137, pl. 8, figs. 1–4.
- 1984 *Stromatocystites walcotti* Schuchert; Paul and Smith, p. 452, text-figs. 6 and 7.

Diagnosis. A species of *Stromatocystites* discoidal in shape and with a pentagonal outline; marginal ring plates present and visible externally; ambulacral flooring plates with V-shaped intrathecal extensions; oral frame not large and pentastellate; centro-dorsal plate surrounded by a circle of ten or eleven plates.

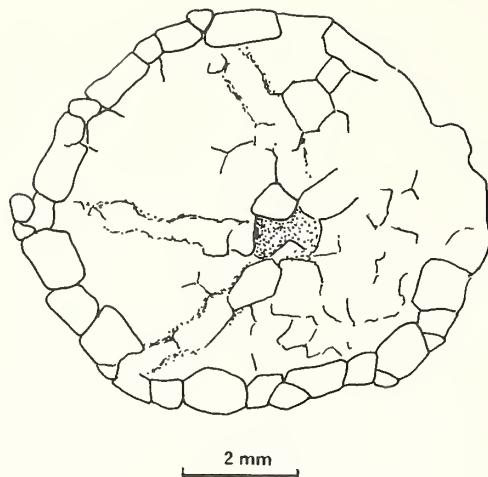
Types. Holotype, USNM 66443 (Pl. 88, fig. 1); paratypes, USNM 66444.

Material examined. In addition to the holotype and paratypes, twenty slabs, USNM 376690 and 384978–384984, with a total of thirty-seven individuals have been examined.

Stratigraphical age and distribution. *Olenellus* Beds, Taconian, upper Lower Cambrian; all specimens come from the eastern arm of Bonne Bay, western coast of Newfoundland.



TEXT-FIG. 15. *Stromatocystites pentangularis* Pompeckj, 1896, camera lucida drawings of plating in the oral area: A, USNM 56665b; B, BM(NH) E16004.



TEXT-FIG. 16. *Stromatocystites walcotti* Schuchert, 1919, USNM 384978, camera lucida drawing of the dorsal plated surface of a juvenile showing the prominent marginal ring plates.

Description. Specimens are 9–22 mm in diameter, weakly pentagonal in outline, and have a flattened profile without the ventral convexity characteristic of *S. pentangularis*. Ambulacra are long and straight and form ridges on the ventral surface. They extend to the ambitus and the tip of each ambulacrum is inserted between the large plates forming the marginal ring. Flooring plates are short and broad and are arranged alternately in two columns with a weakly zigzag perradial suture. Each plate appears to have a pair of short processes that extend intrathecally, but is otherwise very like those of *S. pentangularis*. The arrangement of cover plates is not clearly seen in any of the specimens, but it is quite obviously a multiplated sheet. The ambulacra meet in a 2:1:2 pattern over the oral area and there is no apparent differentiation of the cover plates in this region. The internal aspect of the ventral surface is seen in USNM 376690 and shows the oral frame. The oral frame is transversely elongate and made up of the ten most adoral unfused flooring plates, together with one large asymmetrical interambulacral plate in the C/D interray (the hydropore plate) (text-fig. 7). Unlike *S. pentangularis*, *S. walcotti* shows no evidence of having perradial slits and a flexible mouth frame. There is no obvious hydropore groove in the mouth frame, such as is found in agelacrinitids, but the large hydropore plate is embayed on the D ray side, possibly to allow passage for some soft tissue structure.

The interambulacral zones of the ventral surface are composed of irregularly arranged polygonal plates with epispines. Individual plates are comparatively larger and fewer in number than in *S. pentangularis*, with up to eight plates abreast in any one interambulacrum. The periproct opens in the C/D interray close to the ventral margin and slightly offset towards the C ray. It consists of a large number of elongate plates arranged more or less radially. The periproct is always flush with the surrounding interambulacral plating.

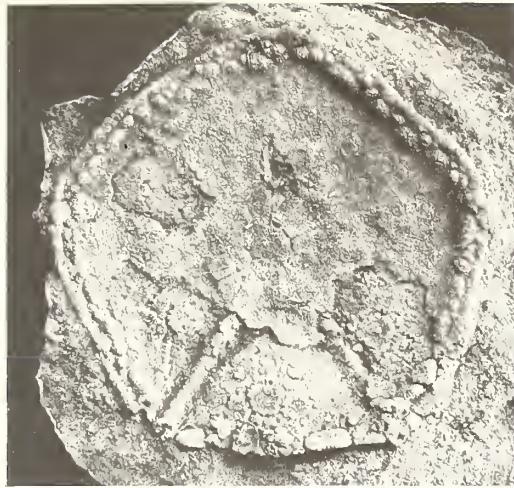
Marginal plating is more strongly developed than in *S. pentangularis* and is sometimes the only part to be preserved. There is a ring of abutting plates which are thickened along the dorsal facing edge. They are held nearly perpendicular to the sea floor around the margin of the theca.

The dorsal surface is covered by a pavement of polygonal, tessellate plates, except immediately adjacent to the marginal ossicles where there are two or three irregular rows of small, loosely fitting plates. At the centre of the disc there is a large, almost circular centro-dorsal plate surrounded by a ring of ten or eleven large, radially elongate plates. Elsewhere the dorsal plating is somewhat smaller and totally irregular in its arrangement.

EXPLANATION OF PLATE 88

Figs. 1–5. *Stromatocystites walcotti* Schuchert, 1919. 1, USNM 66443, holotype, Lower Cambrian, Bonne Bay, Newfoundland; dorsal surface (see text-fig. 4), $\times 2.5$. 2, USNM 384978, Lower Cambrian, Bonne Bay, Newfoundland; dorsal surface of a juvenile showing the prominent marginal ring at this stage, $\times 5$. 3–5, USNM 376690, no locality data: 3, general view of the interior of the ventral surface, $\times 1.8$; 4, detail of the periproct and ambulacral flooring plates (internal), $\times 4$; 5, detail of the oral frame, $\times 5$.

All photographs are of latex casts whitened with ammonium chloride sublimate.



1



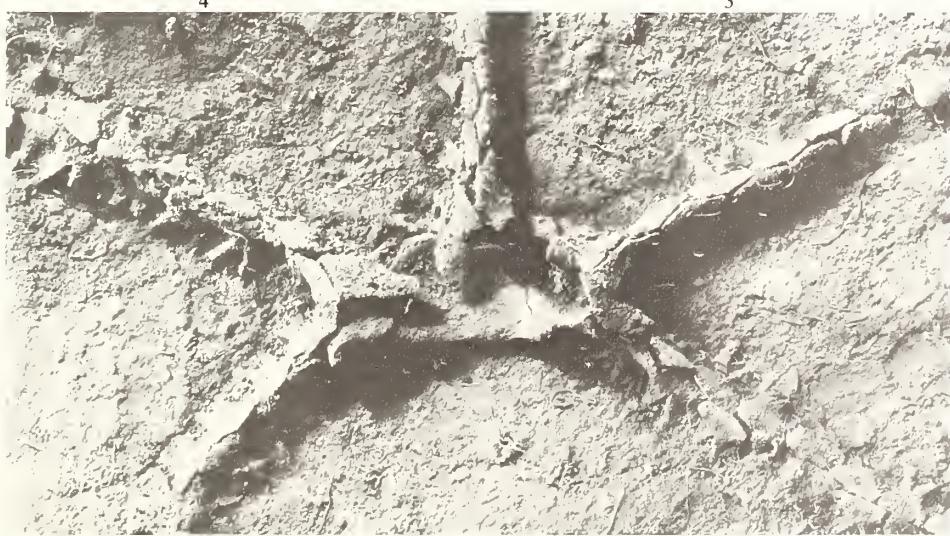
2



3



4



5

SMITH, *Stromatocystites*

Remarks. The original description by Schuchert (1919) is accurate in most respects. Schuchert used the name *S. walcotti* for six larger specimens (including the holotype) but placed all the smaller specimens in a different group which he designated as variety *minor*. As the two forms are indistinguishable and simply represent individuals at different growth stages, Schuchert's variety is not a biologically useful concept.

S. walcotti is similar to *S. pentangularis* in many respects, but is less inflated ventrally, has a smaller, more transversely elongate mouth frame, and has a larger number of dorsal plates in contact with the centrodorsal. Termier and Termier (1969) believed that they could recognize inhalent orifices at the ambulacral tips, suggesting that the ambulacral passageways were enclosed and only opened to the exterior via these terminal orifices. In my opinion such openings did not exist in life and the Termiers were misled by one specimen in which the very terminal cover plates had been displaced during burial and compaction in a couple of the ambulacra.

S. walcotti was tentatively assigned to the genus *Cambraster* by Jell *et al.* (1985) because *C. tastudorum* and *S. walcotti* have rather similar dorsal plating, and *S. walcotti* is supposed to have a ring of marginal ossicles like *Cambraster*. Although marginal ossicles are present in *S. walcotti* and are more prominent than in *S. pentangularis*, particularly in juveniles, they appear to be much less well developed than they are in *Cambraster*. Furthermore, the development of a central zone of large polygonal plates on the dorsal surface is not restricted to *Cambraster* and *S. walcotti* but is also a feature of *S. pentangularis* (see Pl. 87). Therefore, although *S. walcotti* may well be directly ancestral to *C. tastudorum*, it lacks crucial features (such as a marginal skirt and stout marginal ring) that characterize *Cambraster* and cannot be placed within this genus.

Stromatocystites balticus Jaekel, 1899

Remarks. This species was erected on the basis of two specimens, both of which have since been lost. Jaekel's original description is rather vague and the distinction between this species and *Stromatocystites pentangularis* is not at all clear. Regnell (1945) has reviewed all that is known about this species and I can add nothing else. Since no specimens now exist and the original description is too generalized to distinguish *S. balticus* from *S. pentangularis*, I recommend that *S. balticus* be treated as a *nomen dubium*. The original specimens came from the Middle Cambrian *Paradoxides paradoxissimus* Zone of the Baltic and were collected from a glacial erratic block in northern Germany.

Genus WALCOTTIDISCUS Bassler, 1935

- 1935 *Walcottidiscus* Bassler, p. 3.
- 1936 *Walcottidiscus* Bassler; Bassler, p. 2.
- 1943 *Walcottidiscus* Bassler; Bassler and Moody, p. 209.
- 1966 *Walcottidiscus* Bassler; Regnell, p. U161.

Diagnosis. Theca sub-ovoid, circular to roundedly pentagonal in outline; dorsal surface relatively small compared to ventral surface, consisting of an outer zone of tiny platelets and a central uncalcified zone; ambulacra curving sinistrally at the ambitus, extending sub-ambitally, composed of

EXPLANATION OF PLATE 89

Fig. 1. *Stromatocystites pentangularis* Pompeckj, 1896. BM(NH) E16008, latex cast of P/77916, Národní Muzeum, Prague, holotype of *Chilocystis bohemica*, detail of interambulacral zone, $\times 6$.

Figs. 2–6. *Walcottidiscus typicalis* Bassler, 1935. Burgess Shale, Middle Cambrian. 2 and 3, USNM 90754, holotype, part and counterpart (see text-fig. 17), $\times 4$. 4–6, USNM 90755, holotype of *W. magister* Bassler, 1936; 4 and 6, details of cover plate arrangement in ambulacra (f = flooring plates, external portion; c = cover plates), $\times 6$; 5, general view, $\times 1$.

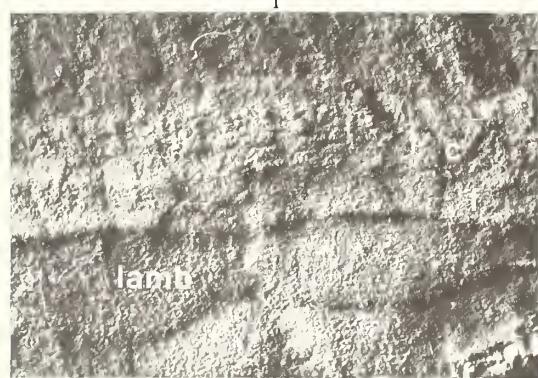
All specimens whitened with ammonium chloride sublimate.



1



2



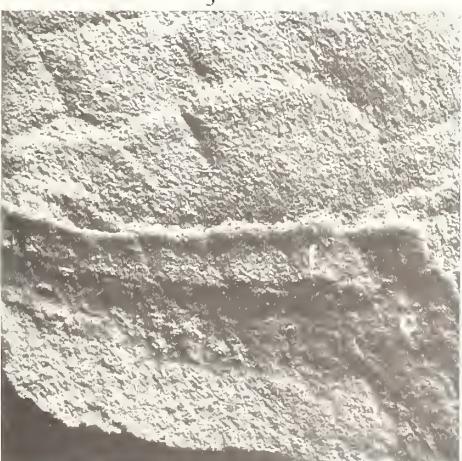
4



3



5



6

SMITH, *Stromatocystites*, *Walcottidiscus*

biserial flooring plates and multiserial cover plate sheets; interambulacral areas subtesselate, lacking epispines; periproct subambital.

Type species. *Walcottidiscus typicalis* Bassler, 1935, by original monotypy.

Stratigraphical age and distribution. Middle Cambrian Burgess Shale, *Bathyuriscus-Elrathina* Zone, British Columbia, Canada.

Remarks. Bassler (1935) described and figured a small edrioasteroid from the Burgess Shale under the name *W. typicalis*. His description was rather sketchy and, in places, somewhat misleading; the specimen has not since been redescribed. A year later, Bassler (1936) described a second specimen from the same locality under the name *W. magister*. This is a much larger specimen and superficially seems to be quite distinct. However, the differences between the two specimens are almost certainly a result of size; I interpret *W. typicalis* as a juvenile and *W. magister* as an adult of the same species.

Neither specimen is particularly well preserved and details of ambulacral plating around the oral area cannot be made out. *Walcottidiscus* has certain characteristics that distinguish it from all other Cambrian edrioasteroids but which it shares with the Ordovician edrioasterids *Edrioaster* and *Edriophus*. These include the sub-oval shape, the strongly curved ambulacra that run around the ambitus, and the reduced dorsal surface with its central uncalcified zone. *Walcottidiscus* differs from both *Edrioaster* and *Edriophus* in the arrangement of ambulacral cover plates. In *Edrioaster* and *Edriophus* there is a series of large primary cover plates, usually with a series of very much smaller secondary cover plates inserted distally, whereas in *Walcottidiscus* cover plates are arranged in a complex multiserial sheet, as in *Stromatocystites*.

Walcottidiscus typicalis Bassler, 1935

Plate 89, figs. 2-6; text-fig. 17

- 1935 *Walcottidiscus typicalis* Bassler, p. 3, pl. 1, fig. 1.
- 1936 *Walcottidiscus magister* Bassler; Bassler, p. 2, pl. 2, fig. 2.
- 1943 *Walcottidiscus typicalis* Bassler; Bassler and Moody, p. 210.
- 1943 *Walcottidiscus magister* Bassler; Bassler and Moody, p. 210.
- 1966 *Walcottidiscus typicalis* Bassler; Regnell, p. U161.

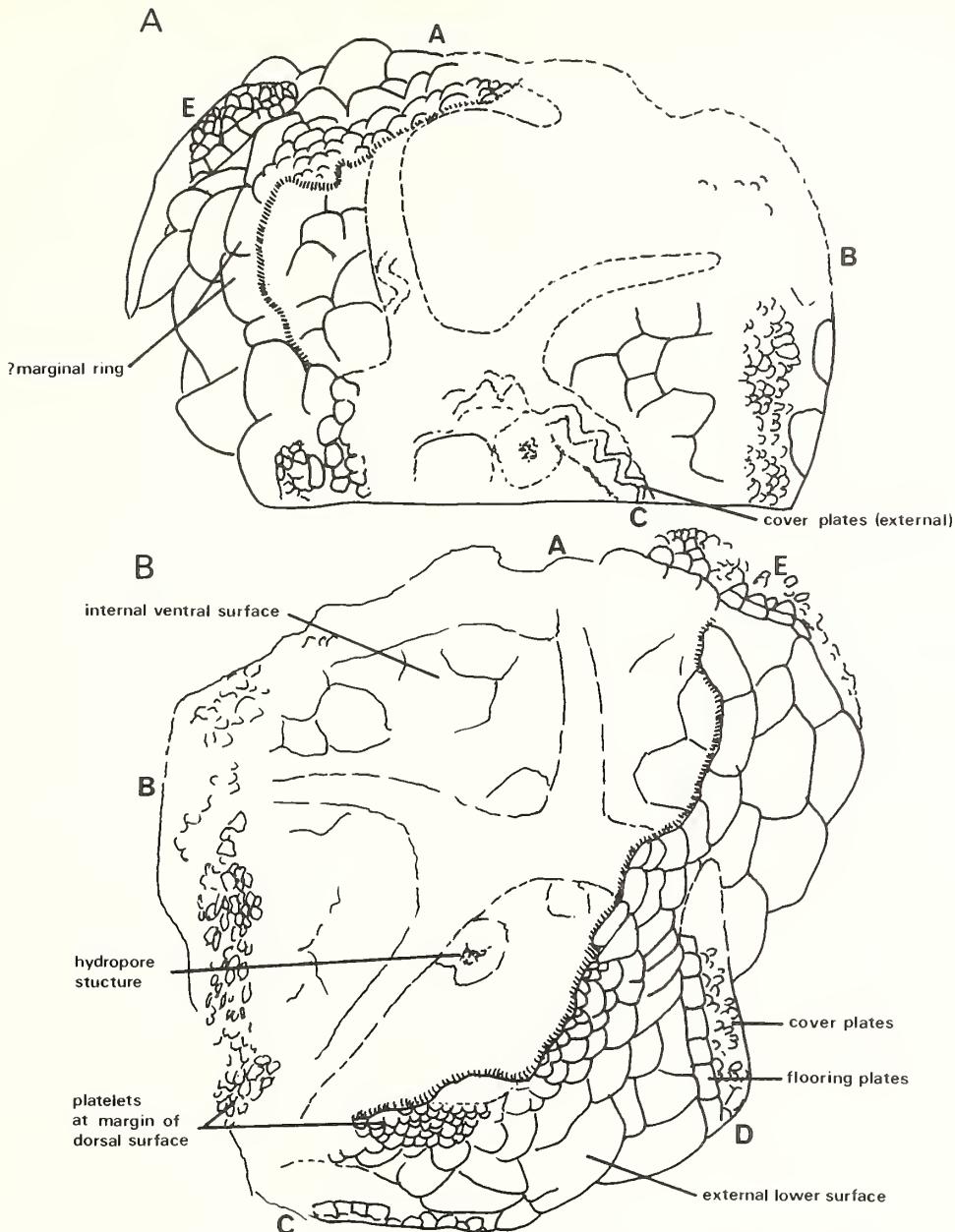
Diagnosis. As for genus.

Types. Holotype, USNM 90754, part and counterpart (Pl. 89, figs. 2 and 3). Holotype of *Walcottidiscus magister*, USNM 90755 (Pl. 89, figs. 4-6).

Stratigraphical age and distribution. Middle Cambrian Burgess Shale, *Bathyuriscus-Elrathina* Zone, Burgess Pass, British Columbia, Canada.

Description. The preservation of the holotype, USNM 90754, is rather difficult to interpret as both part and counterpart show a mixture of mould and original plating. The more complete part shows the exterior of the underside and part of the interior of the upper surface. The less complete counterpart shows the external mould of the underside and the external surface of the upper side (text-fig. 17). The theca is somewhat distorted but appears to have had a rounded pentagonal outline. The maximum diameter of the theca is 15.5 mm and the minimum 12.0 mm, so the diameter in life must have been approximately 14.0 mm. The other specimen, USNM 90755, shows only the exterior of the upper surface and is damaged in places. It has an anterior-posterior diameter of 64.0 mm. Some of the calcite plating is preserved in this specimen. In both specimens the ambulacra extend subambitally and, in the holotype, the dorsal surface can be shown to be smaller than the thecal diameter. *W. typicalis* presumably had a sub-oval to flattened sub-globular shape in life.

Ambulacra are arranged in a 2:1:2 pattern around the mouth. Over much of the upper surface the ambulacra are more or less straight, but on approaching the ambitus all five ambulacra curve sinistrally. In the smaller specimen, ambulacra B, C, and D appear on the lower surface, following a slightly oblique course to the margin. Adjacent ambulacra do not approach one another closely and their tips almost reach the edge of the dorsal plating. The ambulacra in the larger specimen are strongly flexed at the ambitus and run around the outer edge of the theca. The tip of one ambulacrum almost reaches the next ambulacrum to the left (Pl. 89, fig. 5).



TEXT-FIG. 17. *Walcottidiscus typicalis* Bassler, 1935, USNM 90754, camera lucida drawing of the holotype: A, part; B, counterpart.

The detailed structure of the ambulacral flooring plates cannot be made out with any certainty on either specimen. Flooring plates are biserially arranged and alternate in each ambulacrum. On the outer surface the adradial portion of each flooring plate is exposed between the cover plate sheets and the interambulacral plate, as in *Stromatocystites*. This portion of the flooring plate is flat and rectangular in outline, and adjacent faces abut to form a regular border to the arch of cover plates (Pl. 89, figs. 4 and 6). The arrangement of cover plates is best

seen in the larger specimen, but can also be made out towards the tips of ambulacra B and C in the holotype. Cover plates are arranged as a multiserial sheet of abutting plates; they are largest immediately adjacent to the flooring plates and progressively decrease in size towards the free edge. Towards the distal tip in the smaller specimen, the cover plate sheet consists of just two or possibly three irregular rows, but in the larger specimen there are four or possibly five irregular rows of cover plates in each sheet. The first row of cover plates is well defined and these are the largest. They are broader than tall and more or less rectangular but with an angled upper edge making them pentagonal. There are approximately two of these primary cover plates to each flooring plate. The succeeding cover plates are much more randomly arranged and become progressively more equant in shape towards the free edge (Pl. 89, fig. 4).

The oral area is more or less totally obscured in both specimens and nothing can be seen of the oral frame. The location of the hydropore is possibly indicated by a small raised circular rim with a central depression seen on both part and counterpart of the holotype. This lies in the C/D interray, slightly removed from the oral area.

Interambulacral areas are relatively broad and are composed of large sub-polygonal and semi-tesselate plates on the upper surface, with smaller, more imbricate plates sub-ambitally. The plates imbricate adorally so that the more distal plates overlap slightly on to their more proximal neighbours. At the ambitus there are three or four plates abreast in each interambulacrum. There are no epispines.

The holotype exhibits an indistinct area of radially arranged plates in the C/D interray that may be the periproct; this lies sub-ambitally close to the edge of the ventral surface. The dorsal surface is seen only in the holotype. Much of the dorsal surface appears to have been uncalcified, since both part and counterpart reveal the inner face of the upper surface centrally. However, around the edge there is a border, 1–2 mm in breadth, composed of minute plates (3–4 per mm). The diameter of the dorsal surface is approximately 9–10 mm and so is only about 70% of the diameter of the theca. There is a suggestion in the A/B and C/D interambulacra that the dorsal surface may be ringed by a border of broader, rather rectangular plates.

Remarks. Bassler (1935, 1936) placed these two specimens in different species. The principal differences between them are in size and degree of ambulacral curvature. Unfortunately, neither is particularly well preserved and many of the structural details are still unknown. In *W. typicalis*, although the ambulacra curve sinistrally at the ambitus, they are not particularly long and are well separated from each other. In *W. magister*, which is the larger of the two specimens, the ambulacra also curve at the ambitus to run sinistrally around the thecal margin, but in this specimen they are much longer and the tip of one ambulacrum almost touches the neighbouring ambulacrum. *W. typicalis* is only a quarter of the size of *W. magister*, so this difference could simply be a factor of growth. In all edrioasteroids with curved ambulacra, ontogenetic series show that ambulacra are initially straight in juveniles and become progressively more curved as growth proceeds. The two specimens are therefore probably no more than juvenile and adult of the same species and *W. magister* is treated as a junior synonym of *W. typicalis*.

Genus TOTIGLOBUS Bell and Sprinkle, 1978

1978 *Totiglobus* Bell and Sprinkle, p. 247.

Diagnosis. Theca sub-globular and fully plated; dorsal surface greatly reduced, less than half thecal diameter, circular in outline with marginal ring of stout plates surrounding a pavement of small polygonal plates; ambulacra more or less straight, extending sub-ambitally; flooring plates biserial, alternate, with sutural pores; cover plates in two series; oral frame composed of five compound ambulacral flooring plates; interambulacral plates imbricate to sub-tessellate, without epispines; periproct sub-ambital, close to dorsal surface.

Type species. *Totiglobus nimius* Bell and Sprinkle, 1978, by original designation.

Stratigraphical age and distribution. Early Middle Cambrian of Nevada, USA.

Remarks. This is probably the best understood of the Cambrian edrioasteroids because of the careful and detailed work carried out by Bell and Sprinkle (1978). *Totiglobus* can be distinguished easily from *Stromatocystites* and *Cambraster* by its interambulacral zones, which are devoid of epispines, and by its relatively small dorsal surface and swollen ventral surface; it lacks a peripheral skirt of plates, unlike *Edriodiscus*. *Totiglobus* most closely resembles *Walcottidiscus*, but is distinguished by having

more or less straight ambulacra at all sizes and a fully plated dorsal surface. Ambulacra in *Walcottidiscus* curve distally around the ambitus in larger individuals, and the central part of the dorsal surface is uncalcified.

Totiglobus nimius Bell and Sprinkle, 1978

1978 *Totiglobus nimius* Bell and Sprinkle, p. 247, pls. 1–6; text-figs. 1–4.

Diagnosis. As for genus.

Types. Holotype, MCZ 983; paratypes, MCZ 984–996 and NYSM 13293–13326.

Stratigraphical age and distribution. Chisholm Shale, *Glossopleura* Zone, Middle Cambrian of Nevada, USA.

Description. A full and detailed description of this species, together with full locality data, was given by Bell and Sprinkle (1978).

Genus CAMBRASTER Cabibel, Termier and Termier, 1958

- 1894 *Trochocystites* Miquel [*non* Barrande], p. 9.
- 1905 *Stromatocystites* Miquel [*non* Pompeckj], p. 476.
- 1923 *Cambraster* Jaekel, p. 344 [*nomen nudum*].
- 1935 *Cambraster* Jaekel; Stubblefield and Spencer *in Thoral*, p. 35 [*nomen nudum*].
- 1958 *Cambraster* Jaekel; Cabibel, Termier and Termier, p. 284.
- 1958 *Eikosacystis* Cabibel, Termier and Termier, p. 286.
- 1966 *Stromatocystites* Pompeckj; Regnell [*pars*], p. U160.
- 1969 *Cambraster* (Jaekel) *emend.* Cabibel, Termier and Termier; Termier and Termier, p. 137.
- 1969 *Eikosacystis* Cabibel, Termier and Termier; Termier and Termier, p. 141.
- 1971 *Cambraster* Cabibel, Termier and Termier; Ubaghs, p. 182.

Diagnosis. Fully plated, disc shaped edrioasteroid with a pentagonal frame of stout marginal ossicles; ambulacra straight, inserted distally between the marginal ossicles; dorsal surface plated, slightly larger than ventral surface, and composed of a sub-tessellate pavement of plates arranged in cycles; interambulacral zones with epispines.

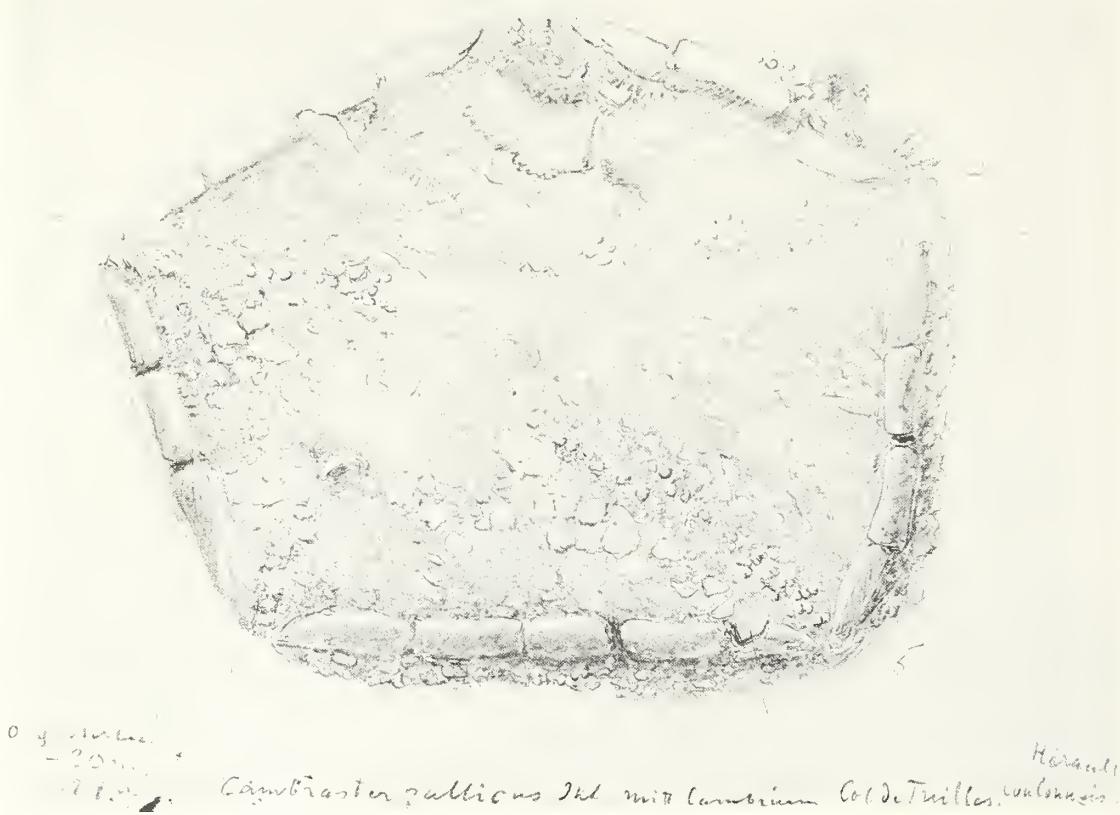
Type species. *Cambraster cannati* (Miquel, 1894), by original designation.

Other species. *C. tastudorum* Jell, Burritt and Banks, 1985.

Stratigraphical age and distribution. *Paradoxides mediterraneus* Zone, Middle Cambrian of the Montagne Noire, southern France; medial Middle Cambrian of Tasmania.

Remarks. This important genus remained poorly understood until Ubaghs (1971) published a detailed morphological description of well-preserved material. The name *Cambraster* was first used by Jaekel (1923) for a species that he believed to be a primitive asteroid from the Middle Cambrian sandy schists of the département of Hérault, France. He interpreted *Cambraster* as intermediate between edrioasteroids and the Ordovician asteroid *Archegonaster*, but failed to describe or figure this animal, or even to designate a specific name. Prior to this, specimens of *Cambraster* had been wrongly identified as the carpoid *Trochocystites* or as *Stromatocystites* by Miquel (1894, 1905). Although later authors have been uncertain as to the identity of Jaekel's *Cambraster*, Stubblefield and Spencer (*in Thoral* 1935) suggested that it was the same as Miquel's (1905) species *S. cannati*, also from the Middle Cambrian of Hérault. Amongst the papers in the possession of W. K. Spencer at his death, and now in the archives of the British Museum (Natural History), is an original line-drawing signed by Jaekel and labelled *Cambraster* (text-fig. 18), proving that Jaekel was indeed referring to the same animal as Miquel.

The name *Cambraster* was finally validated by Cabibel, Termier and Termier (1958) who provided a generic diagnosis and gave a rather sketchy description of the type species, *C. cannati* (Miquel); they also described a new genus *Eikosacystis*, with two species. These were all redescribed in slightly greater detail by Termier and Termier (1969) who placed *Cambraster* and *Eikosacystis* in their own



TEXT-FIG. 18. Original line drawing by Otto Jaekel of a specimen said to be in the Berlin Museum and signed as *Cambraster gallicus* Jkl, Middle Cambrian, Coulounnais, Hérault.

families, the Cambrasteridae and the Eikosacystidae respectively. However, as Ubags (1971) pointed out, *Cambraster* and *Eikosacystis* are synonymous and differ only in their state of preservation. Specimens with the plating of the oral surface preserved more or less intact, and therefore showing ambulacra, were placed by the Termiers into *Cambraster* while more distorted specimens that had either a jumbled muddle of dissociated plates within the marginal ring or had lost the ventral plating altogether (and so revealed the interior of the dorsal surface) were classified as *Eikosacystis*, which was thus believed to lack ambulacra. Ubags's (1971) careful and detailed observations on *Cambraster* have greatly clarified the status of this genus while further morphological information has been added by the discovery of additional material from the Cambrian of Tasmania by Jell *et al.* (1985).

Cambraster is easily distinguished from other Cambrian edrioasteroids by its prominent marginal ring of ossicles which, unlike those of *Edriodiscus*, are not inserted into the dorsal pavement.

Cambraster cannati (Miquel, 1894)

Text-figs. 2, 3, 6A, 18, 19

1894 *Trochocystites cannati* Miquel, p. 9.

1905 *Trochocystites* sp. Miquel, p. 475.

1905 *Stromatocystites cannati* (Miquel); Miquel, pp. 476, 482, pl. 15, fig. 5.

- 1935 *Stromatocystites(?) Cannati* Miquel; Thoral, p. 35.
- 1935 *Trochocystites(?) nov. sp.* Miquel; Thoral, p. 138, pl. 5, fig. 3.
- 1958 *Cambraster cannati* (Miquel); Cabibel, Termier and Termier, p. 284, pl. 1, figs. 2-4; text-figs. 3 and 4.
- 1958 *Eikosacystis couloumanensis* Cabibel, Termier and Termier, p. 286, pl. 1, fig. 5; text-fig. 5.
- 1958 *Eikosacystis? ferralsensis* Cabibel, Termier and Termier, p. 287, pl. 1, figs. 6 and 7.
- 1969 *Canbraster cannati* (Miquel); Termier and Termier, p. 138, pl. 9, figs. 1-3; text-fig. 5.
- 1969 *Canbraster elegans* Termier and Termier, p. 139, pl. 10, figs. 1-4; text-fig. 6.
- 1969 *Eikosacystis couloumanensis* Cabibel, Termier and Termier; Termier and Termier, p. 141, pl. 12, fig. 1; text-fig. 7.
- 1969 *Eikosacystis miqueli* Termier and Termier, p. 142, pl. 11, figs. 1-4; text-fig. 8.
- 1969 *Eikosacystis courte solei* Termier and Termier, p. 143, pl. 12, fig. 2; text-fig. 9.
- 1969 *Eikosacystis ferralsensis* Cabibel, Termier and Termier; Termier and Termier, p. 144, pl. 12, figs. 3 and 4; text-fig. 10.
- 1971 *Canbraster elegans* Termier and Termier; Ubaghs, p. 182, text-figs. 8-11.

Diagnosis. As for genus.

Types. The holotype of *Canbraster cannati*, *C. elegans*, and *Eikosacystis miqueli* are currently held at the Museum of Le Havre, France. Latex casts (BM(NH) E63135, 63136, and 63153) of these specimens were studied (text-fig. 19). The whereabouts of *E. ferralsensis*, *E. couloumanensis*, and *E. courte solei* are currently unknown. They were in the possession of Mme G. Termier at the Département de Géotectonique, Université Pierre et Marie Curie, Paris, but, on enquiry there, could not be located.

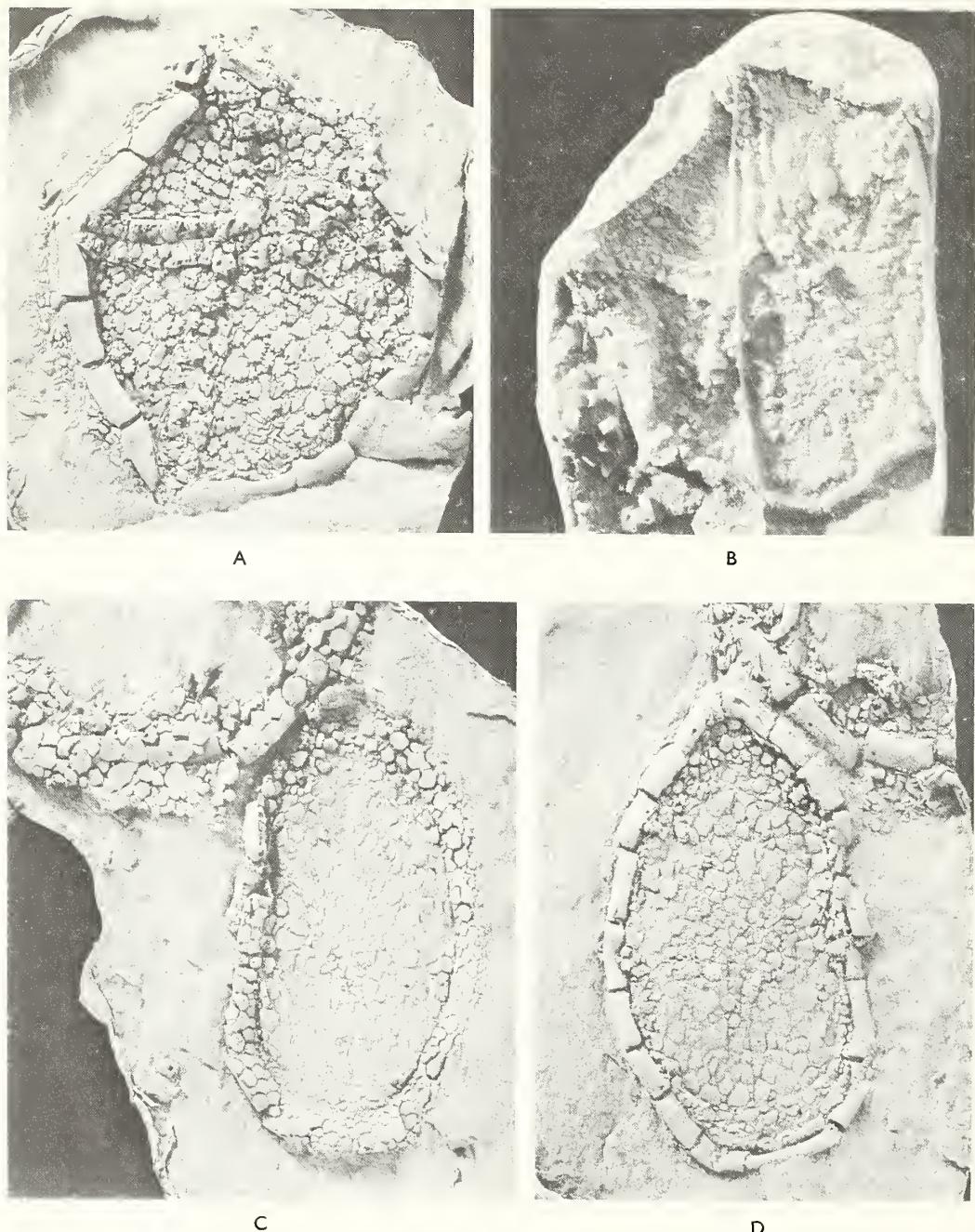
Stratigraphical age and distribution. All the material comes from Beds E and F of Courte sole (1973) in the Middle Cambrian of the Montagne Noire, in the vicinity of Coulouma and Ferrals-les-Montagnes, France.

Description. A complete and detailed description of this species was given by Ubaghs (1971), under the name *C. elegans*, and I have only two additional observations to make. First, although dorsal plating is generally disrupted to a greater or lesser degree in all of the specimens examined, plates do have an angular outline and would have formed a continuous pavement of closely fitting plates in life, as in *Stromatocystites*. These plates are arranged in circles around the centre of the disc with at least two rings of larger plates separated by zones of smaller plates. Secondly, the peripheral zone of dorsal plating does not extend much beyond the ring of marginal ossicles and only a very narrow rim of dorsal plates would have been visible from above.

Remarks. Termier and Termier (1969) recognized two species of *Canbraster* and four of *Eikosacystis*, all of which are treated here as synonymous. Two of their species, *C. cannati* and *C. elegans*, are moderately well preserved and show the plating of the oral surface. These two species were distinguished by the fact that in *C. elegans* rather more of the dorsal surface plating is visible around the margin. This is a post-mortem artifact produced by displacement of some of the marginal ring ossicles and, as the two specimens are otherwise identical, I regard them as synonymous. Two of the Termier's species which show only the marginal ring and dorsal plating, *E. miqueli* and *E. courte solei*, are indistinguishable from one another. Furthermore, as Ubaghs (1971) pointed out, *E. miqueli* and *C. elegans* are specimens of the same species in different states of preservation, one showing the marginal ring and aboral surface, the other showing the marginal ring and oral surface. Specimens referred to as *E. ferralsensis* are large distorted individuals in which most of the plating within the marginal ring lies jumbled together or has been lost. Finally, *E. couloumanensis* is known from only a single small specimen, 12 mm in diameter. This has a stout marginal ring of equant ossicles but the plating within the marginal ring is poorly preserved. I have not been able to examine this specimen but, as it comes from the same beds and the same locality as adult *C. cannati*, I suspect that it is a juvenile specimen of this species.

Canbraster tastudorum Jell, Burrett and Banks, 1985

Remarks. This species has only recently been described by Jell *et al.* (1985) from the Cateena Group, medial Middle Cambrian, of Tasmania. It differs from *Canbraster cannati* in having epispines



TEXT-FIG. 19. *Cambraster cannati* (Miquel, 1894). A, BM(NH) E63135, latex cast of the holotype of *C. elegans* Termier and Termier, 1969, ventral surface, $\times 3$ (see text-fig. 2). B, BM(NH) E63153, latex cast of the holotype of *Trochocystites cannati* Miquel, 1894, $\times 1.4$. C, D, BM(NH) E63136, latex casts of the holotype of *Eikosacystis miqueli* Termier and Termier, 1969 (see text-fig. 3): C, aboral surface, exterior, $\times 3$; D, counterpart showing the ventral surface of the marginal ring and the interior of the dorsal surface (all ventral disc plating having been lost), $\times 3$.

developed only towards the centre of the oral surface and in having a prominent contiguous circle of large polygonal plates near the centre of the aboral surface.

Genus *EDRIODISCUS* Jell, Burrett and Banks, 1985

- 1971 *Cyclocystoides* Henderson and Shergold [non Salter and Billings], p. 706.
 1985 *Edriodiscus* Jell, Burrett and Banks, p. 190.

Diagnosis. Aboral surface fully plated, composed of small polygonal plates with radial ridging; marginal ring circular, composed of forty to fifty plates, surrounded by a peripheral skirt; ventral surface unknown.

Type species. *Cyclocystoides primotica* Henderson and Shergold, 1971, by original designation.

Stratigraphical age and distribution. Early Middle Cambrian of West Queensland, Australia.

Remarks. This genus is very poorly known and contains just one species represented by two specimens, neither of which reveals the ventral surface. It is, however, distinct from any other known echinoderm and clearly deserves generic separation. The species was originally placed in the genus *Cyclocystoides* by Henderson and Shergold (1971), but Smith and Paul (1982) pointed out that it lacked important cyclocystoid features such as perforate marginal ossicles, and removed it from that group.

Edriodiscus, with its stout marginal ring of abutting ossicles, most closely resembles *Cambraster*. However, there are only fifteen to twenty marginal ossicles in *Cambraster*, and these are hidden from view on the lower surface by the pavement of dorsal plates. Marginal ossicles in *Edriodiscus* are more numerous and are inserted into the dorsal pavement. No other Cambrian echinoderm has a peripheral skirt of plates so well developed. The radial ridges that are such a prominent feature of this animal are highly reminiscent of the radial ridging present on the lower surface of peripheral plates of agelacrinitids, and presumably served the same adhesive function. Nothing is known about the oral surface.

Edriodiscus primotica (Henderson and Shergold, 1971)

Text-fig. 20

- 1971 *Cyclocystoides primotica* Henderson and Shergold, p. 706, pl. 138, figs. 1–3.
 1985 *Edriodiscus primotica* (Henderson and Shergold); Jell, Burrett and Banks, p. 190, figs. 7a–c and 8.

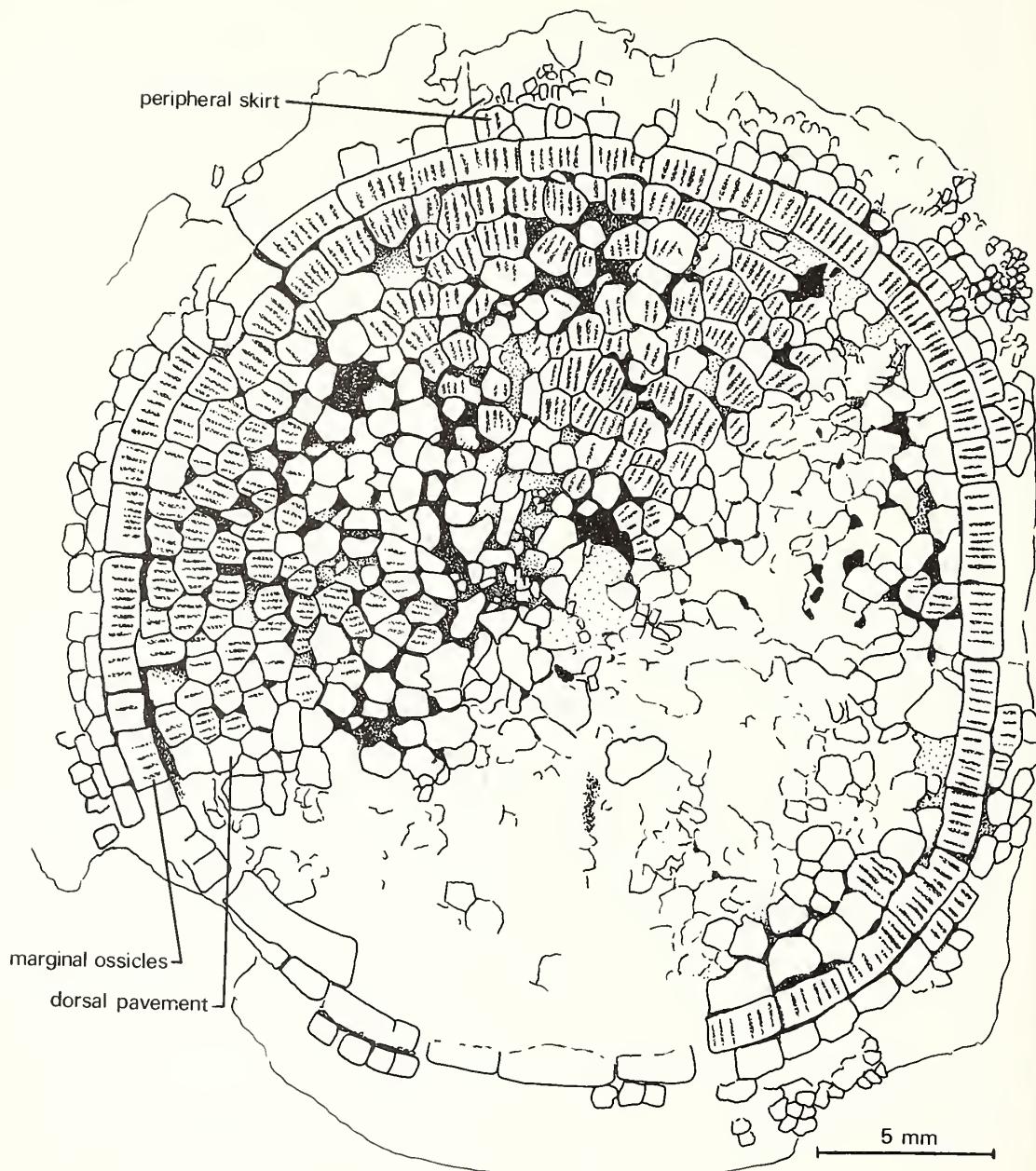
Diagnosis. As for genus.

Types. Holotype, CPC 11395 (text-fig. 20); paratype, CPC 11396.

Stratigraphical age and distribution. Yelvertoft Beds, late Ordian, early Middle Cambrian of West Queensland, Australia.

Description. A full description of the lower surface of this species was given by Henderson and Shergold (1971) and I have nothing new to add. New material, showing details of the ventral surface, has recently been found by Peter Jell and a more complete description has been given by him (Jell *et al.* 1985).

Acknowledgements. Porter Kier (Smithsonian Institution, Washington), Rudolf Prokop (Národní Muzeum, Prague), A. Prieur (Office National de Gestion des Collections Paléontologiques, Lyon), the Abbé Courte sole (Carcassone), G. Breton (Museum of Le Havre), and R. A. Henderson (James Cook University, Australia) have allowed me free access to material in their collections. Peter Jell (Victoria National Museum, Australia), Chris Paul (Liverpool University), and Dick Jefferies (British Museum (Natural History)) have all been kind enough to read an earlier draft of this paper and made many helpful suggestions. Finally, I thank Professor G. Ubags for not only providing me with latexes of specimens in his possession but also for being extremely helpful throughout the duration of this work. Part of this research was carried out with the support of NERC research grant GR3/4732.



TEXT-FIG. 20. *Edriodiscus primoticus* (Henderson and Shergold, 1971), CPC 11395, camera lucida drawing of the holotype, dorsal surface.

REFERENCES

- BASSLER, R. S. 1935. The classification of the Edrioasteroidea. *Smithson. misc. Collns.*, **93**, 1–11.
- 1936. New species of American Edrioasteroidea. *Ibid.*, **95**, 1–33.
- and MOODY, M. W. 1943. Bibliographic and faunal index of Palaeozoic pelmatozoan echinoderms. *Spec. Pap. geol. Soc. Am.*, **45**, 733 pp.
- BATHER, F. A. 1899. A phylogenetic classification of the Pelmatozoa. *Rep. Br. Ass. Advmt Sci.*, D, 916–923.
- 1900. The Echinoderma. In LANKESTER, E. R. (ed.). *A Treatise on Zoology, part 3*, 216 pp. Black, London.
- 1915. *Studies in Edrioasteroidea I–IX*, 403 pp. Published by the author at ‘Fabo’, Marryat Road, Wimbledon, England.
- BELL, B. M. 1976. A study of North American Edrioasteroidea. *Mem. N.Y. St. Mus. Sci. Serv.*, **21**, 447 pp.
- 1977. Respiratory schemes in the Class Edrioasteroidea. *J. Paleont.*, **51**, 619–632.
- 1980. Edrioasteroidea and Edrioblastoidea. In BROADHEAD, T. W. and WATERS, J. A. (eds.). *Echinoderms, notes for a short course. Univ. Tennessee, Dept. geol. Sci. Stud. Geol.* **3**, 158–174.
- and SPRINKLE, J. 1978. *Totiglobus*, an unusual new edrioasteroid from the Middle Cambrian of Nevada. *J. Paleont.*, **52**, 243–266.
- BOCKELIE, F. and PAUL, C. R. C. 1983. *Cyathotheca sneedica* and its bearing on the evolution of the Edrioasteroidea. *Lethaia*, **16**, 257–264.
- CABIBEL, J., TERMIER, H. and TERMIER, G. 1958. Les Échinoderms mésocambriens de la Montagne Noire. *Annls Paléont.*, **44**, 281–294.
- CHAPMAN, E. J. 1860. On a new species of *Agelacrinites* and on the structural relations of that genus. *Can. J. Ind. Sci. & Art*, **5**, 358–365.
- COURTESSOLE, R. 1973. Le Cambrien Moyen de la Montagne Noire: biostratigraphie. Laboratoire de Géologie CEARN, Toulouse.
- FELL, H. B. 1962. A classification of the echinoderms. *Tnatura*, **10**, 138–140.
- 1963. Phylogeny of sea-stars. *Phil. Trans. R. Soc.*, **B246**, 381–435.
- 1965. The early evolution of the Echinozoa. *Breviora*, **219**, 1–17.
- HENDERSON, R. A. and SHERGOLD, J. H. 1971. *Cyclocystoides* from the early Middle Cambrian rocks of north-western Queensland, Australia. *Palaeontology*, **14**, 704–710.
- HOLLOWAY, D. J. and JELL, P. A. 1984. Silurian and Devonian edrioasteroids from Australia. *J. Paleont.*, **57**, 1001–1016.
- JAEKEL, O. 1899. *Stammesgeschichte der Pelmatozoen, I: Thecoidea und Cystoidea*, 442 pp. Berlin.
- 1918. Phylogenie und System der Pelmatozoen. *Paläont. Z.*, **3**, 1–128.
- 1923. Zur Morphologie der Asterozoa. *Ibid.*, **5**, 344–350.
- JELL, P. A., BURRETT, C. F. and BANKS, M. R. 1985. Some Cambrian and Ordovician echinoderms from eastern Australia. *Alcheringa*, **9**, 183–208.
- KESLING, R. V. 1967. Edrioasteroid with unique shape from Mississippian strata of Alberta. *J. Paleont.*, **41**, 197–202.
- MIQUEL, J. 1894. Note sur la géologie des terrains primaires du département de l’Hérault. Le Cambrien et l’Arenig. *Bull. Soc. Étude Sci. nat. Béziers*, **17**, 5–36.
- 1905. Essai sur le Cambrien de la Montagne Noire. Coulouma, l’Acadien. *Bull. Soc. géol. Fr.* (4), **5**, 465–483.
- PAUL, C. R. C. and SMITH, A. B. 1984. The early radiation and phylogeny of echinoderms. *Biol. Rev.*, **59**, 443–481.
- POMPECKJ, J. F. 1896. Die Fauna des Cambrium von Tejrovice und Skrej in Bohmen. *Jb K.-K. geol. Reichsanst.*, **Wien**, **45**, 495–614.
- REGNELL, G. 1945. Non-crinoid Pelmatozoa from the Palaeozoic of Sweden, a taxonomic study. *Medd. Lunds geol.-min. Instn.*, **108**, 255 pp.
- 1966. Edrioasteroids, pp. U136–U172. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part U. Echinodermata 3*. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.
- SCHUCHERT, C. 1919. A Lower Cambrian edrioasteroid *Stromatocystites walcotti*. *Smithson. misc. Collns.*, **70**, 1–7.
- SMITH, A. B. 1984a. *Echinoid palaeobiology*, 190 pp. George Allen & Unwin, London.
- 1984b. Classification of the Echinodermata. *Palaeontology*, **27**, 431–459.
- and PAUL, C. R. C. 1982. A revision of the class Cyclocystoidea (Echinodermata). *Phil. Trans. R. Soc.*, **B296**, 577–684.
- TERMIER, H. and TERMIER, G. 1969. Les Stromatocystitoides et leur descendance: essai sur l’évolution des premiers echinoderms. *Geobios*, **2**, 131–156.

- TERMIER, H. and TERMIER, G. 1980. Modalités de l'évolution des Echinodermes au Cambrien. In JANGOUX, M. (ed.). *Echinoderms: present and past*, 59–65. A. A. Balkema, Rotterdam.
- THORAL, M. 1935. *Contribution à l'étude paleontologique de l'Ordovicien intérieur de la Montagne Noire et révision sommaire de la faune cambrienne de la Montagne Noire*, 362 pp. Imprimerie de la Manufacture de la Charité, Montpellier.
- UBAGHS, G. 1971. Diversité et spécialisation des plus anciens echinoderms que l'on connaisse. *Biol. Rev.* **46**, 157–200.
- WILEY, E. O. 1979. An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Syst. Zool.* **28**, 308–337.
- ZELIZKO, J. C. 1911. Nove prispevky ke studiu jíneckého kambria. *Rozpr. české Akad.* **20** (10), 1–7.

ANDREW B. SMITH

Department of Palaeontology
British Museum (Natural History)
Cromwell Road
London SW7 5BD

Typescript received 7 October 1984

Revised typescript received 25 March 1985

OPTIMUM PREPARATION, PRESERVATION, AND PROCESSING TECHNIQUES FOR GRAPTOLITE ELECTRON MICROSCOPY

by L. W. DUMICAN and R. B. RICKARDS

ABSTRACT. Published guidance on the preparation of ultrathin sections of biological material rarely gives sufficient detail to enable fossil material in general and graptolite material in particular to be prepared to a consistently high standard. The crucial steps relative to pre-microtoming, ultramicrotoming, and post-microtome work, including museum storage, are described together with the 'tricks of the trade' that, taken in total, result in successful micrographs.

TRANSMISSION ELECTRON MICROSCOPY (TEM) has been an important technique in biological and medical science for many years but its application to fossil material poses rather different problems and such material is generally more difficult to prepare. Urbanek (1978) suggested that ultrastructural research may help to resolve some of the problems highlighted by earlier morphological and phylogenetical studies on graptolites. Wide discussion of the mechanism of periderm secretion in graptolites has suggested that TEM studies may aid a better understanding of the relations between inferred soft parts and the skeletal material.

Williams (1965, pp. H254–H255) and Nye *et al.* (1972) described a technique which may be used simultaneously to section both hard and soft tissues for study by reflected light, a technique which may be applied, for example, to recent brachiopods. The initial stages of impregnation with epoxy resins, described by Nye *et al.* (1972), are similar to those which we have used in the preparation of graptolites for TEM.

The use of ultrathin sections in palaeontology has been slowly adopted, largely because of the potential preparation difficulties involved and partly because of costs. Diamond knives commonly exceed £1000 sterling and are not much cheaper to have sharpened. In contrast, stereoscan electron microscopy (SEM) is now used routinely in most groups and especially so in graptolites (Rickards *et al.* 1982). There is no logical reason why TEM studies should not become equally routine, for they are a necessary complement to SEM work, contributing towards our understanding of skeletal morphology, as has been confirmed by recent studies of graptolites (e.g. Crowther 1981). This paper describes how to isolate graptolites from the original matrix, and their subsequent preparation for scanning and transmission electron microscopy. Photographic techniques employed to obtain maximum contrast in the final micrograph are then described briefly and relevant problems of museum documentation discussed.

Graptolite material is quite variable in its preservation of ultrastructural detail, sometimes exquisite but often showing varied forms of degradation. Even the best techniques, coupled with infinite care, occasionally give barely adequate results, whilst some specimens seemingly respond well to very primitive technology (Berry and Takagi 1970). The current procedures evolved during tenureship by the authors of a Research Grant from the Natural Environment Research Council on graptolite ultrastructure, although considerable progress was made in the 1970s and summarized by Crowther and Rickards (1977). A number of the pre-sectioning techniques have not been described before but some were developed many years ago by Professor O. M. B. Bulman and by the junior author.

CHEMICAL ISOLATION

Most SEM and TEM work is enhanced by using specimens chemically freed from the rock matrix. Adhering rock or pyrite can seriously damage diamond knives; but for SEM studies, graptolites in the matrix have been used successfully (Rickards *et al.*, 1971; Crowther and Rickards 1977) in part to test the effect of chemical preparation on the ultrastructural detail, which appears to be negligible.

The procedure for chemical isolation follows two basic routes depending upon whether the matrix is highly calcareous or not. It should always be carried out in a fume cupboard. Many limestones containing graptolites can be immersed as small pieces (a few cm across) in dilute hydrochloric acid (10% HCl; text-fig. 1), in glass beakers, releasing the graptolites often in a matter of hours. There is no way of determining in advance whether the periderm is strong enough to withstand the effervescence, or whether the graptolites may be isolated by any method, other than by trial and error. If the effervescence appears to be breaking up the emerging specimens, then the acid may be diluted to slow down the action, or a non-effervescent or less violently effervescent acid (such as acetic acid, CH_3COOH) can be used.

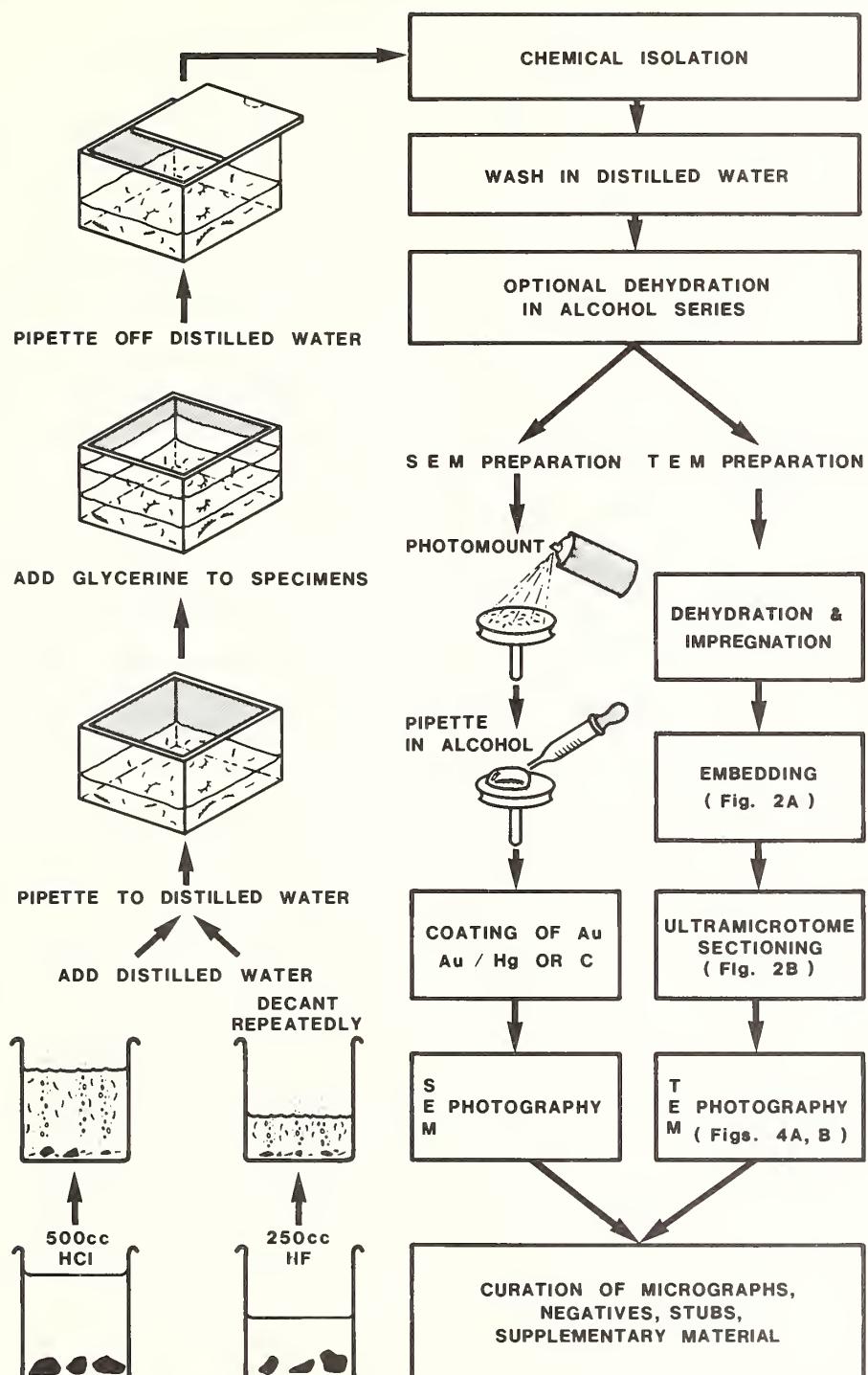
A second procedure may be used when the terriginous content of the limestone is so great that a relatively firm rottenstone remains, failing to release the graptolites. When this happens the blocks must be treated with 10% HCl for up to three weeks, changing the acid daily, until all possible CaCO_3 has been removed. At that stage the rottenstone can be treated with 60% hydrofluoric acid, in polythene beakers, which usually releases the graptolites within a few hours. In all the above treatments, two or three pieces of rock can be placed in up to 500 cc of HCl or up to 250 cc of HF (text-fig. 1), or the whole process can be made into an assembly line using large containers and quantities of fluid.

The next stage is the most laborious and critical if the full suite of isolated specimens is to be retained. Some specimens will have floated in an oily scum, often adhering to the meniscus. These need to be carefully pipetted off, using either glass or polythene hand pipettes (for HCl or HF respectively), into a container of distilled water in which they may still float. The remaining fluid is then carefully decanted and washed away using copious supplies of water from the fume cupboard taps. Specimens 'floating' in mid-fluid can be pipetted out at this stage. As a rule, a majority of specimens lie in the muddy debris at the bottom of the beaker. Distilled water should be added to the beaker, stirring the sunken specimens and mud, and the whole of the above decanting process repeated several times until the acid has been washed out. Pipetting can take place at the same time but eventually the whole remaining mass of mud and graptolites needs to be carefully decanted into a wide, shallow, preferably white-bottomed picking dish. At no stage should the specimens be allowed to dry out or to support their own weight in air, for many collapse, especially if the original rock came from a tectonized region. However, the most delicate rhabdosomes may be supported by fluid and can easily be held in that medium until they are transferred to the long term resting medium, namely viscous glycerine.

Initial picking by hand pipette is from the picking tray into distilled water in glass beakers. The graptolites must not be stored in distilled water for longer than about twenty-four hours, since this encourages the growth of fungus. The main problem at this stage is the number of fragments and early growth stages that may be masked by the mud and missed altogether. Specimens should be washed in several changes of distilled water for a few hours.

The best way to transfer delicate specimens into viscous glycerine is to reduce the amount of distilled water over them by pipetting it off until only a few mm cover the specimens. Then glycerine is added gently around the margins of the container, thus pushing the specimens away from the sides. Eventually, glycerine can be dropped gently on top of them, weighing them down (text-fig. 1). The remaining distilled water floats above the glycerine and, when it is completely separated from the graptolites, can easily be pipetted off to leave the specimens in a firm, supportive, fluid matrix.

Specimens that floated on initial extraction may sink quite quickly; if not, they will have tiny gas bubbles lodged inside the thecae. These can be removed by pipetting the specimen directly into alcohol, a somewhat violent process which may snap the specimens; alternatively they can be cooled



TEXT-FIG. 1. Flow chart summarizing preparatory stages for storage, SEM and TEM work.

in a refrigerator when the small gas bubbles may escape (dishes of alcohol should not be placed in a refrigerator without proper consultation with a laboratory technician, for there is a risk of explosion). Once the specimens have sunk, transfer to glycerine can proceed as above, and the graptolites are now ready for the preparatory stages described below, leading to electron microscopy.

As an important aside, it should be mentioned that in preparing glycerine held specimens for light microscopy (as, for example, in the production of slides or resin mounts; Hutt and Rickards 1967), any chemical clearing using Schultz' Solution (KClO_3 and HNO_3) should be done in the absence of glycerine since there is a slight risk of accidentally producing TNG or TNT.

SEM PREPARATION

Preparation of graptolites for use in the SEM involves mounting the specimen on a stub and subsequently coating it, preferably with gold; other coatings may be tried, such as gold/palladium or carbon, and occasionally it may not be necessary to coat at all if much pyrite adheres to the specimens. The specimen is pipetted from glycerine into absolute alcohol, in which it is washed for approximately thirty minutes. An intermediate distilled water stage has proved unnecessary. The stub is then sprayed with a very thin film of 'Photomount' (see Crowther and Rickards 1977), or double sided adhesive tape may be used, and the specimen is pipetted with a drop of alcohol to the surface of the stub. The graptolite may be oriented at this stage by manoeuvring it with a damp hair, although great care must be taken with very fragile specimens. The alcohol is then allowed to evaporate. Finally, with the Sedgwick Museum material, the stub is placed in an 'EMscope' sputter coater and coated with 200–500 Å of gold, after which it is ready for examination in the SEM.

TEM PREPARATION

The specimen is pipetted from glycerine into a vial containing distilled water and washed in three changes of water for fifteen minutes each. Commonly, a graded series of ethyl alcohol dilutions is then used for dehydration of the specimen but it is possible to use three changes of absolute alcohol (about ten to fifteen minutes each). At this stage the specimens may be stored indefinitely in the alcohol. After dehydration the specimens are soaked in a 50/50 mixture of propylene oxide (1,2—epoxy propane) and absolute alcohol and then in a further two changes of 100% propylene oxide for fifteen minutes each. This facilitates uniform impregnation of the specimen by the epoxy.

During each of the above stages the vial is placed in a rotator so that the liquid circulates freely inside the specimen. Whilst the specimens are soaking in the propylene oxide the epoxy resin mix may be prepared. Propylene oxide should be used in glass rather than plastic containers and only in a fume cupboard because of its toxicity, volatility, and flammability. After use it should be flushed away with continuous water flow for five minutes.

Embedding

The 'Agar 100' embedding kit (equivalent to 'Epon 812') is suitable for embedding graptolite material. The 'Epon' mixture is blended and accelerator added just before use. A graduated cylinder, a small (100 ml) conical flask, and the containers of resin and hardener are warmed in an oven at 60 °C. The four components, resin, DDSA hardener (dodecyl succinic anhydride), MNA hardener (methyl nadic anhydride), and BDMA accelerator (N benzyl N-N dimethylamine) are mixed by pouring them in turn into the graduated cylinder. Before adding BDMA the other three components should be stirred thoroughly since direct mixing of BDMA and MNA may be explosive. The mixture is then poured immediately into the warm conical flask and stirred for about one minute. A few air bubbles may develop but these will dissipate if the mixture is allowed to stand for a short time at 60 °C. Epoxy resins, hardeners, and accelerators should be handled with care in a fume cupboard.

Difficulties may be experienced in obtaining blocks of the correct hardness for ideal sectioning. The following mixture has recently been used successfully to embed specimens of *Monograptus formosus* from the Mielnik borehole in Poland: resin 25 ml; DDSA 11 ml; MNA 14 ml; BDMA 1 ml. The

hardness of the final block may be controlled by varying the proportions of DDSA and MNA in the resin mixture. When proportions of DDSA to MNA were tried in the quantities 12·5/12·5 ml the resultant blocks were too soft, and at 10/15 ml they were too brittle. Hardness may also be increased as the concentration of the accelerator (BDMA) increases, but the block may become brittle and difficult to section as a result.

After the resin components have been stored for about five months, they begin to give inconsistent results. It is suggested that the accelerator should be stored in a dessicator in the dark. Several workers have found that the accelerator for 'Spurr' resin, for example, has a very short shelf life (about two weeks). The liquid epoxy resin is soluble in absolute alcohol and all glassware should be rinsed in alcohol after use.

The specimen is then transferred in propylene oxide to a small tray (a vial top or petri dish is ideal) and an equal volume of epoxy resin mixture is added. These are left for one hour, loosely covered to prevent evaporation. The covers may then be removed and the specimens left in a fume cupboard overnight, during which time the propylene oxide will evaporate. They are then polymerized in a thermostatically controlled oven in three stages (35 °C, 45 °C, and 60 °C), over a period of thirty-six hours: overnight at 35 °C, next day at 45 °C, and overnight at 60 °C. The maximum internal temperature of the epoxy resin obtained during polymerization will affect the properties of the resultant block. If the temperature is too low, the block will be too soft; if the temperature is too high, bubbles may form in the epoxy and the block will be too brittle (Nye *et al.* 1972). Ideally the end product should be an amber colour and of moderate hardness (i.e. will not deform when pressed with a finger nail).

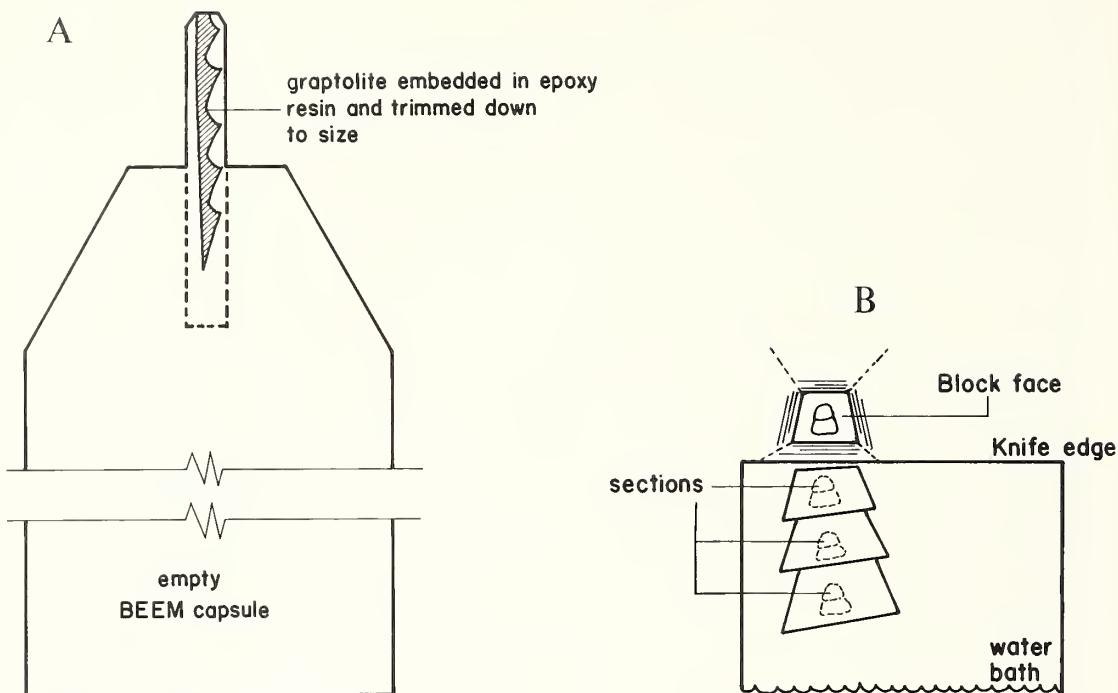
The graptolites are now ready for cutting into blocks and mounting on 'Araldite' stubs made and polymerized in the same way and at the same time. The hardened resin is trimmed from the specimen, which is then stuck to a stub (made in polyethylene capsules known as 'BEEM capsules') in the required orientation, with 2-tube 'Araldite'. The graptolite may be trimmed down to size with a heavy duty, backed razor blade. This step is carried out with the specimen held under water because it is usually too small to be clamped and consequently is easily lost during trimming in air.

Where a series of transverse sections from a specimen of three or more thecae in length is required, it is suggested that a small hole be made in the end of a BEEM capsule and the trimmed specimen then forced through the hole so that the end to be sectioned protrudes from the capsule (text-fig. 2A). The capsule is then filled with liquid epoxy resin and polymerized as before. The specimen will have been polymerized twice but this does not adversely affect the end-product. When specimens of this type were simply stuck on stubs with 2-tube 'Araldite', they often snapped off during sectioning on the ultramicrotome.

Cutting ultrathin sections

After polymerization the block is held in the clamp of the ultramicrotome and the area around the graptolite trimmed into a pyramidal shape (text-fig. 2A). The face to be sectioned should be cut until it reaches the specimen to save time and wear on the knife edge. The block face is shaped so that cut sections will form a ribbon, perpendicular to the knife edge, on the surface of the water bath (text-fig. 2B). It is therefore necessary for two edges of the block to be parallel to each other and orientated in the ultramicrotome so that they are parallel to the knife edge (text-fig. 2B). It is best if one side is longer than the other, forming a trapezium orientated such that each new section pushes along the whole width of the previous one, so detaching it from the knife edge. Neatly rectangular slices do not form such a reliable and straight 'ribbon'.

A diamond knife is held in the knife holder, tilted at approximately 4°, and the water bath is filled with distilled water until it appears white in polarized light (i.e. maximum reflection is obtained with a 'flat' meniscus). The knife is advanced manually towards the block until almost touching it, as seen through the binocular microscope, then locked in position. It is often difficult to see just how close the block is to the knife edge. A mirror placed under the specimen will reflect bright, white light between the knife edge and block face, making it easier to judge the gap between them. The knife should never



TEXT-FIG. 2. A, showing how embedded graptolite (three or more thecae in length) may be orientated for transverse sectioning; the encased specimen is forced through a hole at the shaped end of the BEEM capsule which is then filled with epoxy resin and polymerized (full explanation in text). B, sketch of trapezium-shaped block face which causes the cut sections to form a saw-edged ribbon on the surface of the ultramicrotome's water bath.

touch the block face at the start since this will undoubtedly damage the edge. When the knife and block face are as close as possible the block is advanced $0.5\text{ }\mu\text{m}$ at a time until a complete section is cut from the face, after which the block is advanced automatically by a set thickness.

Interference colours are used to estimate the thickness of cut sections. Peachey (1958) provided a correlation between section thickness and interference colours as follows:

Colour	Thickness Å (1 nm = 10 Å)
grey	600
silver	600–900
gold	900–1500
purple	1500–1900
blue	1900–2400
green	2400–2800
yellow	2800–3200

Ideally sections should have grey interference colours, especially if they are to be used for high resolution work. However, silver and occasionally pale gold sections have been used successfully for work at low magnifications. The position and the meniscus level of the water bath may have to be finely adjusted for optimum viewing of the interference colours. The ultramicrotome is very sensitive to touch and atmospheric conditions. It is therefore necessary to avoid contact with it as far as possible and also to eliminate any draughts in the room, especially those caused by doors opening; a steady temperature of $20\text{ }^{\circ}\text{C}$ should be maintained. A cutting speed of 1.1 mm/s used with a knife angle of approximately 4° provides good sections of graptolite material. In general, hard specimens

are best cut at slower speeds than soft specimens. The optimum settings for all controls can only be realized by experimentation. Sections should float off evenly in a straight line and be of uniform colour, flat, and with no corrugations.

Most of the difficulties in cutting good sections arise from faults with embedding and the knife edge. For a further detailed discussion of faults observed in ultrathin sections, and their possible causes, see Reid (1974). Generally glass knives do not provide such good sections of graptolites as diamond knives, but they may be used to trim specimens prior to sectioning with the diamond knife. When viewed through the binocular microscope the edge of a glass knife can often be seen to crumble after only one cut of the material. When the embedding medium is softer, several cuts are possible but problems with corrugations within the section and the mounting medium may be encountered (text-fig. 3). After a few sections have been cut with a glass knife the edge becomes blunt and it is necessary to move to an unused part of the knife. Diamond knives are more durable and may be used for repeated sectioning over long periods of time (often several weeks or months).



TEXT-FIG. 3. TEM micrograph showing corrugations throughout the section, caused when the embedding medium is too soft, $\times 8000$ (*Dictyonema rarum* Wiman, SM X1193).

A picking brush dipped in chloroform and held over the surface of the water bath causes the sections to flatten, due to the heavy vapour. This eliminates, to a certain extent, deformation that might have occurred during sectioning. An uncoated copper grid is held with fine forceps and placed matt side down on top of the floating sections, which will then adhere to the grid. After drying matt side up on filter paper the grids are ready for use in the electron microscope. We have found that in general it is not necessary to coat prepared grids with carbon (but see also Crowther and Rickards 1977).

It is more informative to study several sections cut in serial order than single sections, since any contaminants introduced during sectioning can be recognized more easily when seen in successive sections. If the 'ribbon' of cut sections is transferred to the grid intact, it may be possible during TEM examination to obtain a three-dimensional understanding of that part of the graptolite ultra-structure.

PHOTOGRAPHY

Initially problems were encountered with lack of contrast in the electron micrographs, a not uncommon feature of electron microscopy; the thinner the section the less contrast there will be between specimen and background. Since thinner sections provide better resolution, it is necessary to

try to increase the contrast in some other way. One such method is to take photographs slightly underfocused. True focus on the electron microscope is found at the point of least contrast. This may be seen by observing fresnel fringes on the edges of the specimen or around the edges of adventitiously placed holes (text-fig. 4). (Fresnel fringes arise from the interference between scattered and unscattered electron beams; see Agar and Chescoe (1974) for a full discussion on their formation.) When the specimen is overfocused, the edge is outlined by a pale diffraction band with a concentric dark one (text-fig. 4B); when underfocused, a pale band (or fresnel fringe) follows the edge (text-fig. 4A). True focus occurs where the fresnel fringe disappears but contrast appears to be minimal. Thus it is often preferable to take photographs slightly out of focus in order to heighten contrast whilst increasing, of course, the risk of lower resolution. Contrast may also be increased at the film development stage. Micrographs are taken using 'Kodalith MP11 Ortho film 2577' on an 'AEI Corinth 500' electron microscope and are developed for three minutes at 13 °C in 'Ilford Phenisol' developer, diluted in the proportion 1:6.



TEXT-FIG. 4. TEM micrographs showing the pattern produced by fresnel fringes. A, overfocused; B, underfocused. Both SM X1193, $\times 5000$ approx.

The micrographs are then printed on 'Ilford Ilfoprint grade 4' paper using a 'Beseler MCX' enlarger. TEM micrographs should be taken as quickly as possible, since contamination builds up quite quickly on the specimen and may adversely affect both contrast and resolution, blurring the section. SEM photographic techniques have been discussed comprehensively by Crowther and Rickards (1977, pp. 11–12) and are not enlarged upon here, except to say that most of our SEM work is now carried out using a 'Philips 501B' electron microscope and 'Ilford FP4 (70 mm)' film processed according to manufacturer's instructions.

MUSEUM STORAGE

Storage of isolated reference material used under the light microscope is a relatively straightforward matter. The authors have been working on graptolites prepared and stored in glycerine, corked, and sealed with candlewax in 1895 and they are as satisfactory today as presumably they ever were. They respond well to both TEM and SEM studies, and the only deterioration evident is of the glycerine, not the graptolite. In some tubes the glycerine has gone slightly brown, though it is still transparent. At the Sedgwick Museum, graptolites have been similarly stored in glycerine for twenty years.

However, in order to facilitate normal examination by research workers, they are stored in the type of plastic container illustrated (text-fig. 1) in which very viscous glycerine only 5–10 mm deep is used, which greatly lessens the chance of spillage. Yet the container is not sealed, has a sliding lid, and the specimens can be easily examined under the light microscope, particularly as there is no problem with the sphericity of the container. There is no reason to suppose that material, so stored, will not last fifty years and normal curatorial procedures can be adopted by the museum staff.

SEM stubs pose a more difficult problem. The Sedgwick Museum has fifteen-year-old mountings which have been re-used successfully, but deterioration is apparent, especially in the glues or gums used to mount the specimens on the stubs but also in the coating used. The question of glues has been examined very thoroughly by Dr Jenny Chapman (*in prep. and pers. commun.*), and it seems unlikely that even well-mounted graptolites will last twenty-five years. Therefore, whilst normal curatorial procedures can be applied to stubs, and are at the Sedgwick Museum, the following items take on greater importance in curation: 1, the photographic negative (and prints); 2, unmounted topotypes (preserved in glycerine); and 3, topotype rock samples known to have yielded the originals.

The most difficult preservational problem concerns TEM ultrathin sections mounted on grids. Although Sedgwick Museum specimens have been re-used successfully after a period of five years, it is unlikely that grids will survive a decade; re-use itself usually causes rapid deterioration so that further use is unlikely. Therefore, the film negatives are vital from a curatorial and research standpoint and there seems no good reason why, properly stored, they should not last for a century. Thus the film negative becomes the 'specimen' for all future research reference. A supplementary part of the specimen is that remaining in the unsectioned stub. Although this has not appeared on film, it is a potential source of at least partial confirmatory work on the same specimen and hence should be catalogued as a very important part of the original. The life of a specimen mounted in resin depends upon the life of the resin, which may deteriorate in, at most, a few years, making further sectioning difficult (at least with a valuable diamond knife), but the mounted specimens may last for several decades as far as light microscopy is concerned.

It is clear from the authors' work that curation must be built into the procedural system and planned for at an early stage of the work. Much the best system is to curate all parts and products immediately after they have been produced, any delay merely contributing to the possibility of very small items being separated from each other and being effectively lost.

Acknowledgements. We gratefully thank Roger Northfield (Department of Zoology, University of Cambridge) for all his help with ultramicrotomy, and David Bursill for his constant assistance during experimental photographic work.

REFERENCES

- AGAR, A. W. and CHESCOE, D. 1974. Image formation in the electron microscope. In GLAUERT, A. M. (ed.). *Practical methods in electron microscopy*, 2.
- BERRY, W. B. N. and TAKAGI, R. S. 1970. Electron microscope investigations of *Orthograptus quadrifimocronatus* from the Maquoketa Formation (Late Ordovician) in Iowa. *J. Palaeont.* **44**, 117–124.
- CROWTHER, P. R. 1981. The fine structure of graptolite periderm. *Spec. Pap. Palaeont.* **26**, 119 pp.
- and RICKARDS, R. B. 1977. Cortical bandages and the graptolite zoid. *Geologica Palaeont.* **11**, 9–46.
- HUTT, J. and RICKARDS, R. B. 1967. An improved transfer technique for the preparation and preservation of pyritized graptolites. *Geol. Mag.* **104**, 180–181.
- NYE, O. B., DEAN, D. A. and HINDS, R. W. 1972. Improved thin section techniques for fossil and recent organisms. *J. Palaeont.* **46**, 271–275.
- PEACHEY, L. D. 1958. Thin sections. A study of section thickness and physical distortion produced during microtomy. *J. biophys. biochem. Cytol.* **4**, 233–242.
- REID, N. 1974. Ultramicrotomy. In GLAUERT, A. M. (ed.). *Practical methods in electron microscopy*, 3.
- RICKARDS, R. B., HYDE, P. J. W. and KRINSLEY, D. H. 1971. Periderm ultrastructure of a species of *Monograptus* (Phylum Hemichordata). *Proc. R. Soc. B* **178**, 347–356.
- CROWTHER, P. R. and CHAPMAN, A. J. 1982. Ultrastructural studies of graptolites—a review. *Geol. Mag.* **119**, 355–370.

- URBANEK, A. 1978. Significance of ultrastructural studies for graptolite research. *Acta palaeont. pol.* **23**, 595–629.
WILLIAMS, A. 1965. Techniques for preparation of fossil and living brachiopods, pp. H251–H256. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part H. Brachiopoda* (1). Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.

LORI W. DUMICAN
BARRIE RICKARDS

Sedgwick Museum
Department of Earth Sciences
University of Cambridge
Downing Street
Cambridge CB2 3EQ

Typescript received 20 October 1984

Revised typescript received 29 January 1985

ON THE IDENTITY OF THE AMPHIBIAN *HESPEROHERPETON GARNETTENSE* FROM THE UPPER PENNSYLVANIAN OF KANSAS

by ANDREW R. MILNER

ABSTRACT. *Hesperoherpeton garnettense* Peabody was first described as an embolomerous anthracosaurian amphibian, based on a small scapulocoracoid and associated neural arch from the Upper Pennsylvanian of Garnett, Kansas. Subsequently, on the basis of a referred specimen from the type locality, *Hesperoherpeton* was claimed by Eaton and Stewart to be the most anatomically primitive tetrapod despite its Upper Pennsylvanian age. Re-examination of the type and the referred specimen leads to the conclusion that the former is indeterminate and the latter is a poorly preserved small specimen of a temnospondyl amphibian of the family Trematopidae. It may be a specimen of the trematopid *Actiobates peabodyi* Eaton from the same locality. The binomen *H. garnettense* is a *nomen dubium* restricted to the type specimen, and Eaton and Stewart's Order Plesiopoda is invalid.

THE Upper Pennsylvanian tetrapod assemblage from Garnett in eastern Kansas is unique among Carboniferous faunas in that it is made up largely of diapsid and pelycosaurian reptiles (Reisz 1981; Reisz *et al.* 1982). Only three amphibian specimens from Garnett have been described. One of these, *Actiobates peabodyi* Eaton 1973 is a temnospondyl of the family Trematopidae (Milner: in prep.). The other two specimens form the subject of this study. In 1958, Peabody described a small scapulocoracoid and associated neural arch from Garnett as the new taxon *Hesperoherpeton garnettense* which he assigned to the family Cricotidae within the embolomerous anthracosaurs. In 1960, Eaton and Stewart described a second specimen from Garnett which they attributed to *Hesperoherpeton*. This specimen comprised the crushed and disarticulated anterior skeleton of a small amphibian, which Eaton and Stewart reconstructed, concluding that it was not an embolomere but was quite unlike any other known fossil amphibian. Despite its late Pennsylvanian age, Eaton and Stewart interpreted *Hesperoherpeton* as the most primitive known tetrapod, a relictual form structurally intermediate between rhipidistian fishes and tetrapods and they made it the basis of a new order Plesiopoda. This order was erected as a grade group characterized by a mixture of choanate fish characters (large notochordal canal, divided braincase, postaxial processes on some fore-limb elements, and probable articulation between tabular and pectoral girdle) and tetrapod characters (tetrapod pectoral girdle, digits, otic notch, nostrils separate from jaw margin and rhachitomous vertebrae). Eaton and Stewart also placed *Hesperoherpeton* in the monogeneric family Hesperoherpetonidae defined by its unique specializations, notably the squamosal bordering the orbit and the loss of most of the circumorbital series. As the skull is both disarticulated and incomplete, it is difficult to understand how such unique characters were identified. The presence of postaxial processes on some limb bones neatly fulfilled a prediction about primitive tetrapod limb structure made by Eaton several years previously (Eaton 1951) and elaborated subsequently (Eaton 1960). Most later workers on Palaeozoic tetrapods who have examined this material or discussed tetrapod origins, have either treated Eaton and Stewart's interpretation with extreme caution (Romer 1968, p. 88; Olson 1971, p. 292) or have ignored it altogether (Thomson and Bossy 1970; Carroll and Winer 1977; Rosen *et al.* 1981; Reisz *et al.* 1982). The only alternative systematic position suggested for it was a doubtful placement within the Seymouriamorpha by Romer (1966, p. 363) followed by Kuhn (1972, p. 43). However, in some more general accounts of amphibian evolution it has been cited as a very primitive tetrapod illustrating an intermediate condition between fishes and

tetrapods (Schmalhausen 1968, pp. 54, 62; Porter 1972, p. 93, Vorob'yeva 1974, p. 222; Alexander 1975, p. 235).

During 1979 I was able to examine the two *Hesperoherpeton* specimens and make a number of observations which suggest a more mundane interpretation of this material. Although precise systematic placement of the two specimens is not possible, this reinterpretation does provide a refutation of the status given to them by Eaton and Stewart.

MATERIAL

- KUVP 9976 The holotype of *H. garnettense* Peabody 1958. Collected in 1954 and figured by Peabody (1958, text-fig. 1), Eaton and Stewart (1960, fig. 8), and in this work (text-fig. 1A, B).
 KUVP 10295 Referred specimen of Eaton and Stewart 1960. Collected in 1955 and figured by Eaton and Stewart (1960, fig. 1-7 and 9-11) and in this work (text-figs. 2B-4).

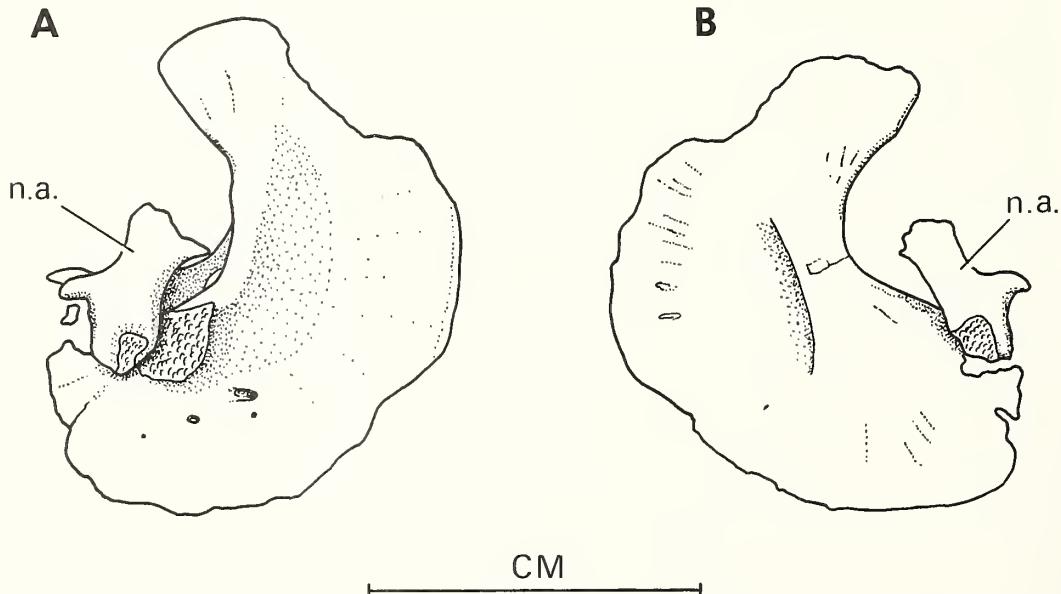
Both specimens are housed in the Vertebrate Paleontology collections (KUVP) of the Museum of Natural History at the University of Kansas, Lawrence, Kansas.

Locality and Horizon. Quarry 10 km north-west of Garnett, Putnam Township, Anderson County, Kansas. Rock Lake Member, Stanton Formation, Lansing Group, Missourian Series, Upper Pennsylvanian. Reisz *et al.* (1982) provide further information on the locality and the detailed local stratigraphy.

DESCRIPTIONS

The holotype specimen

KUVP 9976 consists of a small right scapulocoracoid and a neural arch in close association. The originally exposed surface has been embedded in plastic and the specimen subsequently prepared out



TEXT-FIG. 1. A, B, *Hesperoherpeton garnettense* Peabody (*nomen dubium*). KUVP 9976, the holotype and only specimen from Garnett, Kansas. Right scapulocoracoid in A, external aspect, B, internal aspect, together with associated neural arch. n.a.—neural arch.

so that the two bones are visible from both sides. The specimen was figured by Peabody (1958, text-fig. 1) and, less accurately, by Eaton and Stewart (1960, fig. 8) but is refigured here for ease of reference (text-fig. 1A, B) although the figure, drawn directly from the specimen, contains no new information.

The neural arch is not co-ossified to a centrum and has a low neural spine. The former feature indicates that it cannot be attributed to the orders Nectridea, Aïstopoda, Microsauria, or any amniote group. The absence of swollen neural arches suggests, albeit from negative evidence, that it is not a seymouriamorph. Peabody suggested that it belonged to an embolomerous form as the symmetrical anterior and posterior faces of the pedicels implied the presence of equally large intercentra and pleurocentra. However, although the pedicel faces are asymmetrical in some rhachitomous forms, they are symmetrical or nearly so in others (*Neldasaurus* Chase 1965, fig. 9A; *Eryops* Moulton 1974; *Tersomius* Daly 1973, text-figs. 5A and 6). Thus the neural arch does not characterize the specimen as an embolomerous anthracosaur but simply as either a temnospondyl or an anthracosaur or a more primitive stem-tetrapod.

The scapulocoracoid is well ossified for its size and this suggests that it belonged to a terrestrial form, small aquatic amphibians having unossified or poorly ossified endochondral regions in the pectoral girdle. The shape of the scapulocoracoid resembles that of labyrinthodont-grade amphibians rather than of reptiles. The presence of supracoracoid and glenoid foramina below the glenoid resembles the condition in both temnospondyls (*Greererpeton* Holmes 1980, *Dissorophus* DeMar 1968) and anthracosaurs (*Proterogyrinus* Holmes 1980). The glenoid is large and slightly triangular as originally described by Peabody, not a small ovoid as interpreted by Eaton and Stewart, and it resembles that in terrestrial temnospondyls such as *Trematops* (Olson 1941, fig. 11B).

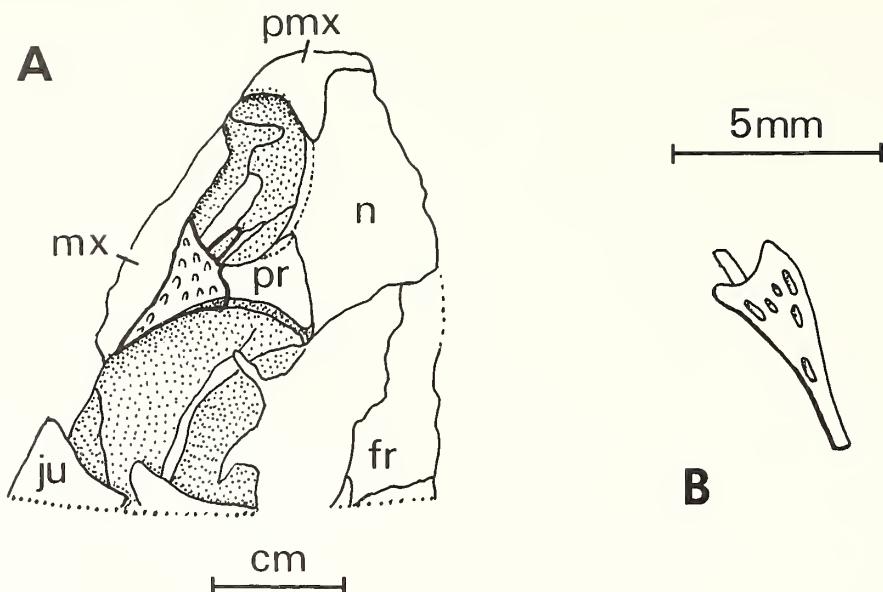
In conclusion, the holotype specimen of *H. garnettense* appears to be an indeterminate labyrinthodont-grade amphibian, possibly a terrestrial temnospondyl. The bones are entirely consistent with attribution to a trematopid temnospondyl such as *Actiobates* which occurs at Garnett, but are equally consistent with attribution to a small member of the Dissorophidae or Eryopidae. Thus the binomen *H. garnettense* is a *nomen dubium* restricted to an indeterminate holotype specimen.

The referred specimen

KUVP 10295 consists of a large number of small bones on a small slab of shale. The originally exposed surface has been embedded in plastic and the specimen has been prepared from the back. As noted by Eaton and Stewart (1960, p. 220) the bones are mostly broken or distorted by crushing and are also scattered. All the identifiable bones are consistent in size, number, and general relative position with the interpretation that they derive from the anterior half of a single, small amphibian skeleton. The anterior appendicular skeleton and the anterior trunk are most readily recognized, being only slightly disarticulated, the posterior skeleton is absent, whilst the skull is severely crushed and scattered. Regrettably, some elements are now difficult to observe through the plastic coat. However, I have been able to identify and draw several bones which I believe are sufficient to permit a reassessment of this specimen. These include some elements of the skull roof, palate, mandible, axial and anterior appendicular skeleton. Unfortunately I was unable to identify the braincase, stapes, or occiput amongst the crushed cranial elements at one end of the slab: those skull bones which are figured and described here being a group which have drifted back towards the pectoral region. Some of the identified bones are figured in text-figs. 2B-4 and are described in the following paragraphs.

Skull. Five cranial elements have been confidently identified, namely a right lachrymal, a left postfrontal, a right squamosal, a right vomer, and a left pterygoid.

The right lachrymal (text-figs. 2B and 3) is the most diagnostic element in the specimen. It is present as a disarticulated bone and was described and figured by Eaton and Stewart (1960, fig. 3C, D) as the right tabular. It consists of an elongate triangular plate of lightly sculptured dermal bone with a long slender process extending ventrolaterally from the unsculptured surface along its long axis (text-fig. 2B). Eaton and Stewart interpreted this as a tabular with a small otic notch supported by a flange of the



TEXT-FIG. 2. A, *Actiobates peabodyi* Eaton. KUVP 17941, the holotype specimen. Left anterior region of the skull based on Eaton 1973, fig. 1a and on first-hand observation of the specimen. The lachrymal is heavily outlined and sculpture pits are depicted on it. Abbreviations are: fr—frontal, ju—jugal, mx—maxillary, n—nasal, pmx—premaxillary, pr—prefrontal. B, indeterminate trematopid. KUVP 10295, isolated ossification interpreted as right tabular by Eaton and Stewart, but here identified as the right lachrymal of a trematopid.

dermal surface and by the slender process. In their discussion they suggested that the slender process may have articulated with the pectoral girdle in a rhipidistian-like manner. There is no precedent for a tabular of this particular shape in the lower tetrapods and as the bone occurs as an isolated structure, its identification as a tabular would appear to have been no more than a guess. However, its precise shape and size relative to the other bones are entirely consistent with it being a lachrymal of a temnospondyl amphibian of the Family Trematopidae. The Trematopidae are a family of dissorophoid amphibians characterized by several features, most conspicuously the elongate external naris (Olson 1941; Bolt 1974a). Within the Order Temnospondyli, this type of external naris, with a posterior extension and a characteristic configuration of surrounding bones is unique to the Trematopidae, although a similar arrangement occurs in the Upper Permian batrachosaur *Chroniosaurus* from Russia (Tverdochlebova 1972). Such a narial structure has been claimed for the dissorophid *Longiscutula houghae* (DeMar 1966; Boy 1981) but Bolt (1974a) notes that this is doubtful and I can confirm, having examined this specimen, that the 'elongate nostril' is an artifact of crushing. In the trematopids the posterior extension of the naris is a manifestation of modifications to the nasal, prefrontal, lachrymal, maxillary, and vomer (Bolt 1974a). The primitive temnospondyl lachrymal condition is a roughly rectangular bone extending from naris to orbit and bearing the lachrymal duct or ducts. In most long-snouted temnospondyls it withdraws from contact with the naris and orbit and is a rhomboidal bone bordered by nasal, maxillary, prefrontal, and jugal. In trematopids however, the enlarged naris, combined with the retention of the lachrymal position on the orbit margin, results in the lachrymal being preserved as a triangular plate of sculptured bone bordering the orbit anterolaterally. This is well shown by the trematopid *Actiobates*, also from Garnett (text-fig. 2A). A ventral process of bone extends anteriorly from the main body of the lachrymal along the floor of

the nasal chamber bordering the maxillary (text-fig. 2A) and this corresponds to the slender process which Eaton and Stewart interpreted as a form of tabular horn. The resultant configuration of a trematopid lachrymal is matched by the bone in KUVP 10295 (text-figs. 2B and 3) and this provides compelling evidence that the bone is a lachrymal and that the specimen is a trematopid temnospondyl.

The left postfrontal is present as an isolated element overlapping the left pterygoid (text-fig. 3). It is anteriorly pointed and posteriorly rectangular with a small posterior lappet which would have extended under the supratemporal. This shape of bone and the position of the lappet identify it as a postfrontal (Boy 1972 Abb. 4K depicts a very similar postfrontal in *Micromelerpeton*). It has temnospondyl-type irregular pitted sculpture and the absence of dermo-sensory pits or canals indicates that it derives from a terrestrial temnospondyl. In these features it is consistent with attribution to the families Eryopidae, Trematopidae, or Dissorophidae. The anterior extension terminating in a point rather than a sutural contact indicates that there was no prefrontal-postfrontal common suture but that both bones terminated as points over the orbit, and that the frontals entered the orbit margin. This derived character occurs in advanced dissorophids (not *Amphibamus*) and in trematopids, but not in eryopids where there is consistently a prefrontal-postfrontal contact. No bone of this precise shape was figured by Eaton and Stewart but it may be the 'postorbital' of their description.

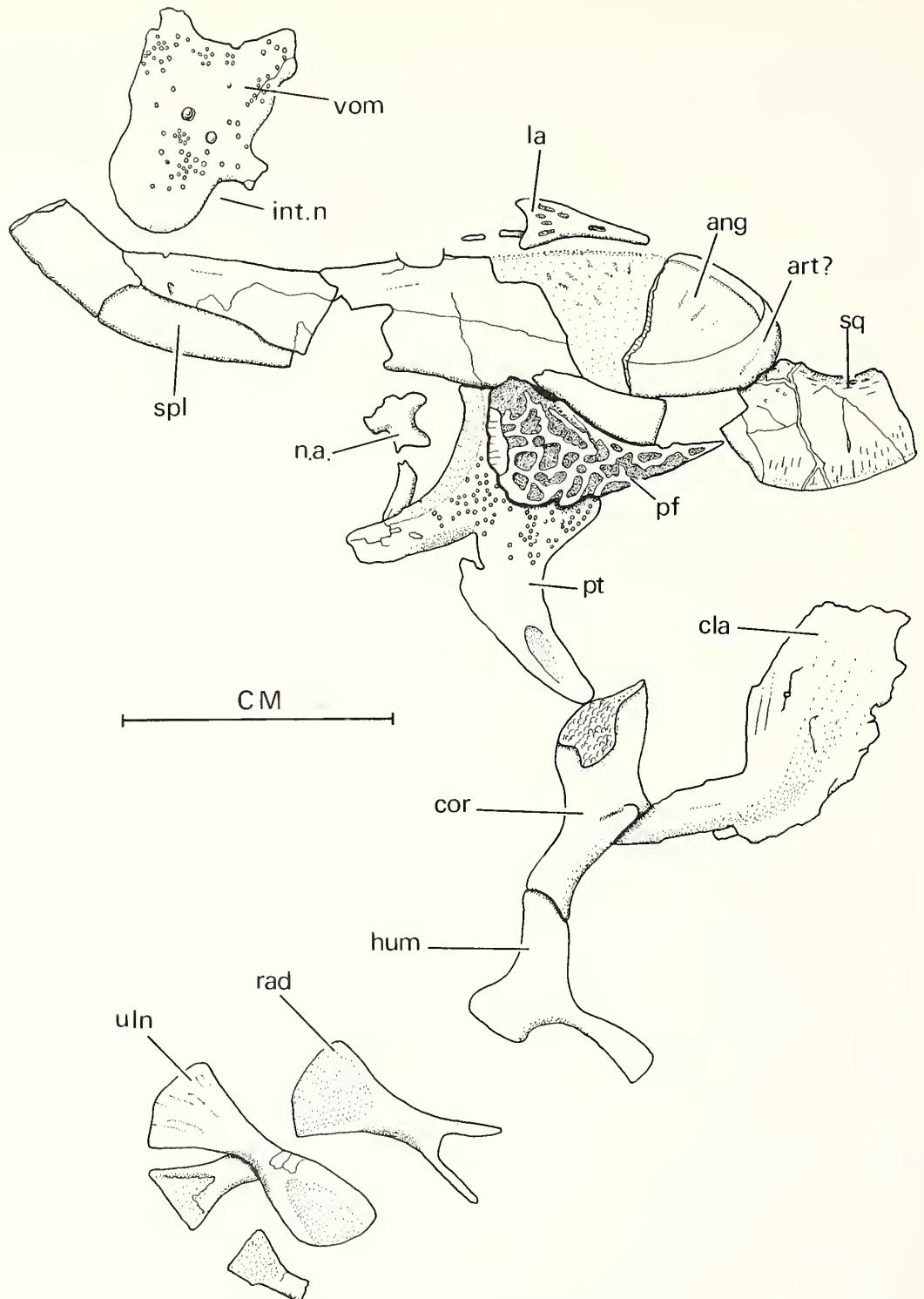
The right squamosal (text-fig. 3) was figured by Eaton and Stewart (1960, fig. 3a, b) as the left squamosal. It is a large rectangular bone, shallowly concave along one edge, which is the border of the tympanic notch, rather than the (unprecedented) orbit margin as suggested by Eaton and Stewart. The unsculptured ventral surface is exposed and on it, next to the otic margin, is a branched crack, the raised edges of which appear to have been figured as flange-like structures by Eaton and Stewart. Such flanges are not certainly present unless cracks have formed along the edges of them so that the structures which appear as raised edges are, in fact, low flanges. Flanges on the ventral surface of the squamosal have been reported in several Palaeozoic temnospondyls including *Edops* (Romer and Witter 1942), *Dendrerpeton* (Watson 1956, fig. 29 as *Platystegos*), *Tersomius* (Carroll 1964, fig. 4), and an unnamed trematopid from Fort Sill (Bolt 1974b, fig. 3). The squamosal only indicates the presence of a large otic notch.

The right vomer (text-fig. 3) is a large irregularly shaped flat plate of bone bearing a covering of tiny denticles and what appear to be the bases of two palatal fangs on the exposed ventral surface. A shallow concavity along one edge may be interpreted as the border of the internal naris. A slightly larger concavity on one of the shorter edges is probably the anterior border of the left interpterygoid vacuity. Such a large, relatively wide, vomer bearing a fang-pair and bordering a large interpterygoid vacuity is only consistent with belonging to a temnospondyl. Other early tetrapods either have narrow vomers, fangless vomers, or no interpterygoid vacuities.

The left pterygoid (text-fig. 3) is also denticle covered on the exposed ventral face and is of the characteristic triradiate form associated with the presence of large interpterygoid vacuities. The quadrate and basipterygoid rami are clearly visible and the palatine ramus is partly obscured by the superimposed postfrontal. There is also a distinct denticle-bearing posterodistal flange. The combination of such a flange with large interpterygoid vacuities identifies the specimen as a dissorophoid, either belonging to the Dissorophidae or the Trematopidae.

The above described elements are the only ones which could be identified as cranial ossifications. I could not recognize the premaxillary, maxillary, parietal, supratemporal, or any of the occipital and braincase ossifications identified by Eaton and Stewart. It would, of course, be futile to attempt a reconstruction of the skull based on the five elements recognized in this work, but they include most of the bones used in Eaton and Stewart's palatal reconstruction and some of the significant components of their skull roof reconstruction.

Mandible. The right mandible (text-fig. 3) is crushed and lightly twisted, being visible in dorsolateral aspect at the back and ventrolateral aspect at the front. It bears temnospondyl-type sculpturing on one large posterior element, partly visible as impression, which appears to me to be the angular rather than the surangular as suggested by Eaton and Stewart. Parts of the mandible may be identified as the



TEXT-FIG. 3. Indeterminate trematopid previously referred to *Hesperoherpeton garnettense* by Eaton and Stewart 1960. KUVP 10295, part of one face of the specimen showing disarticulated cranial and anterior appendicular elements. Abbreviations: ang—angular, art?—articular?, cla—clavicle, cor—coracoid, hum—humerus, int.n.—margin of internal naris, la—lachrymal, n.a.—neural arch, pf—postfrontal, pt—pterygoid, rad—radius, spl—splenial, sq—squamosal, uln—ulna, vom—vomer.

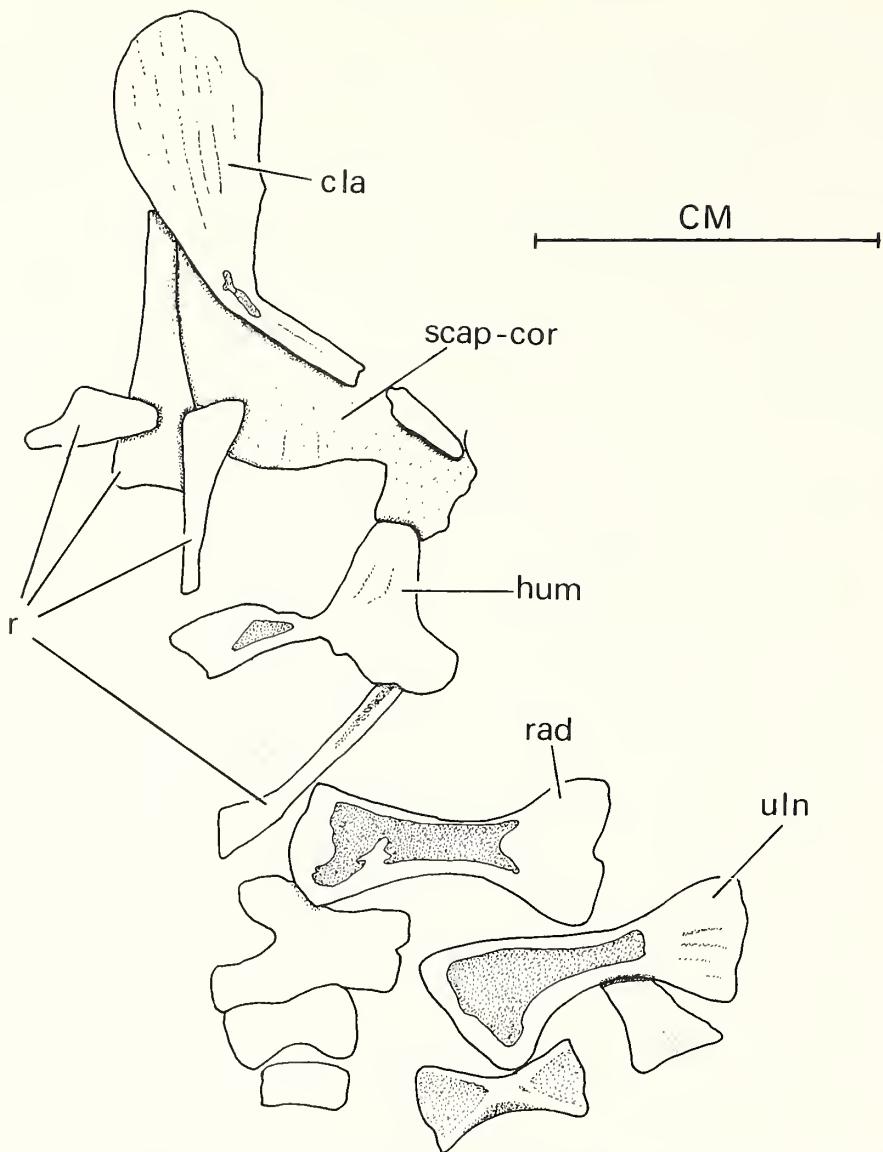
splenial, dentary, and articular with varying degrees of confidence but the only general conclusion that may be drawn from the mandible is that it probably belonged to a temnospondyl.

Postcranial skeleton. There is little to add to Eaton and Stewart's description of the vertebrae. They comprise neural arches, some with slightly elongate neural spines, U-shaped intercentra and large paired pleurocentra. Some neural spines are distinctly lower than depicted by Eaton and Stewart, one is visible in text-fig. 3 between the mandible and the pterygoid. The vertebrae appear to correspond to the typical rhachitomous condition and are consistent with attribution to many Palaeozoic temnospondyl families. Some short straight anterior thoracic ribs are present (text-fig. 4). As Eaton and Stewart note, they are substantially expanded proximally, but this is a common feature of the thoracic ribs of small labyrinthodonts.

Preparation of the slab has permitted both aspects of the preserved anterior appendicular skeleton to be recognized (text-figs. 3 and 4). The clavicle, visible in both aspects, is narrow-bladed with a long stem. The outer face of the blade is lightly striated. The narrow blade resembles those of presumed terrestrial temnospondyls such as eryopids, trematopids, and dissorophids and also of microsaurs and seymouriamorphs. Part of the scapulocoracoid is visible under the clavicle on one side (text-fig. 4). A couple of striations are visible suggesting that part of the exposed bone is the scapular blade and the rest is coracoid. On the other face of the specimen (text-fig. 3) the crushed coracoid is visible in ventral aspect and bears a prominent glenoid fossa. Comparison of text-fig. 3 with figure 11 of Eaton and Stewart shows that their 'humerus' is actually the base of the coracoid with a short humerus closely appressed to it. They interpreted the coracoid as the ridged proximal region of an 'unusually long humerus' and the glenoid surface was depicted as an unfinished cartilage ridge on the proximal end of the humerus (Eaton and Stewart 1960, fig. 11).

The genuine humerus is a short 'propellor-blade' shaped structure with broad ends set at 90° to each other, the proximal end being visible as a flat blade while the distal end is visible only in section (text-figs. 3 and 4). This shape and relative size of humerus characterizes many terrestrial temnospondyls such as *Eryops*, the trematopids, and some dissorophids. In apparently aquatic temnospondyls such as the trimerorhachoids the humerus blades are poorly ossified and less obviously rotated at 90° to one another. Other small temnospondyls such as *Amphibamus* and *Branchiosaurus* have longer, more slender humeri (Carroll 1964; Boy 1972; Milner 1982). The humerus of KUPV 10295 was probably incompletely ossified at the ends and may have been slightly longer. Eaton and Stewart interpreted the entire humerus as the distal portion of a long humerus bearing a slender hook-like ectepicondyle, a supposed relictual fish characteristic. The radius and ulna are close to the humerus and to each other although not in articulation (text-figs. 3 and 4). They are of typical temnospondyl type and I cannot see the pronounced distal expansion of the ulna which Eaton and Stewart figure as homologous to a postaxial process. Several isolated metacarpals and phalanges are present but are not in articulation and do not permit a reconstruction of the carpus or manus. The only unusually shaped manus bone depicted by Eaton and Stewart which does appear to be present is the forked bone which they describe as an ulnare with a posterior hook-like expansion. A bone of approximately this shape is present on one face of the specimen (text-fig. 4). In view of the otherwise orthodox nature of the appendicular skeleton, I suspect that this ossification is made up of two or three metacarpals or phalanges superimposed and crushed across each other. Apart from this I can see nothing in the skeleton of the fore-limb which would justify the unique reconstruction of Eaton and Stewart.

Systematic position. The visible determinate bones of KUPV 10295 are all consistent with attribution to the Temnospondyli. The type of dermal sculpturing on the postfrontal, the shape of the pterygoid and the vomer, and the structure of the vertebrae in particular support this attribution. The postfrontal, squamosal, clavicle, and humerus together specify a temnospondyl with no lateral-linc pits around the interorbital region, an otic notch, a narrow clavicle, and a short, broad-ended humerus showing pronounced torsion. Such characteristics are consistent with the specimen being either an eryopid, a dissorophid, or a trematopid. The pterygoid with the posterodistal flange and the postfrontal coming to an anterior point identify it as either a dissorophid or a trematopid, while the lachrymal is most diagnostic, permitting the specimen to be identified as a trematopid. The only other



TEXT-FIG. 4. Indeterminate trematopid previously referred to *Hesperoherpeton garnettense* by Eaton and Stewart 1960. KUVP 10295, part of reverse face of specimen showing disarticulated axial and anterior appendicular elements. Abbreviations as for text-fig. 3 plus: r—rib, scap-cor—scapulocoracoid.

determinate amphibian described from Garnett is the trematopid *Actiobates peabodyi* (Eaton 1973) and it is probable though not demonstrable that KUVP 10295 is a poor specimen of *Actiobates*. As *Actiobates* has not been fully described or comparatively diagnosed against the Texas red-bed trematopids such as *Acheloma*, there is no basis for assigning KUVP 10295 to any particular genus other than by locality and horizon so it is proposed that the specimen be considered as Trematopidae incertae sedis.

DISCUSSION

Systematic conclusions. Re-examination of the two specimens from Garnett confirms a view, which has been implicit in the tendency of most workers to ignore Eaton and Stewart's paper, that their interpretation was not justified by the material and that there is no foundation for either the Order Plesiopoda or the Family Hesperoherpetonidae. Their limb reconstruction is based on a misinterpretation of the crushed anterior appendicular elements and their skull reconstructions are a frankly imaginative assembly of a series of isolated elements which can be interpreted in a far more justifiable manner by comparison with contemporaneous forms. As noted in the introduction, the nature of this specimen was immediately evident to most workers on Palaeozoic tetrapods and Eaton and Stewart's publication has been widely ignored. However because it was ignored rather than explicitly criticized, *Hesperoherpeton* found its way into several general discussions on the origin and early evolution of tetrapods, by authors who assumed that the absence of refutation meant that the work was accepted. It is, perhaps, a reminder of the value of published critical discussion.

Amphibians in the Garnett tetrapod fauna. The Garnett assemblage is unique among Carboniferous tetrapod assemblages in that it is largely composed of early amniotes, namely pelycosaurs and diapsids. Some of these have been redescribed or newly described in recent years and the known amniote fauna currently comprises the diapsid *Petrolacosaurus* (Reisz 1977, 1981) and four pelycosaurs, namely the sphenacodont *Haptodus* (Currie 1977, 1979), the enigmatic long-spined *Xyrospondylus* and undescribed material of *Edaphosaurus*, and a *Clepsydrops*-like ophiacodont (Reisz *et al.* 1982). The type specimen of the trematopid *Actiobates* (Eaton 1973) and the two specimens redescribed in this paper, are the only described amphibians from Garnett. Reisz *et al.* (1982) reported a further four amphibian specimens recently collected and yet to be described, while Peabody (1958, p. 571) reported an earlier discovery of a series of nectridean vertebrae which were subsequently lost before they could be described. Thus there may be other amphibians in the Garnett assemblage, but at present, all the described material is either trematopid temnospondyl or consistent with attribution to that family.

Reisz *et al.* (1982) discussed the lithology of the productive horizons at Garnett and concluded that it represents a terrestrial environment subject to progressive incursions by brackish water, implying an estuarine mud-flat regime. It is interesting then, that the only determinate amphibians described to date are trematopids, the peculiar naris of which has been interpreted as modified to incorporate a chamber for an enlarged gland, possibly a salt gland (Bolt 1974a). Possession of a salt gland permits tetrapods to be more tolerant of both xeric and saline environments and it is possible that trematopids had such glands and were unusual among temnospondyls in their tolerance of brackish conditions.

Acknowledgements. I should like to thank Dr Larry Martin and Dr Hans-Peter Schultze of the University of Kansas for their hospitality and for permission to examine this material. My research travel was funded by the University of London Central Research Fund.

REFERENCES

- ALEXANDER, R. MCN. 1975. *The Chordates*, 480 pp. Cambridge University Press, London.
- BOLT, J. R. 1974a. Osteology, function and evolution of the trematopsid (Amphibia: Labyrinthodontia) nasal region. *Fieldiana: Geol.* **33**, 11–30.
- 1974b. A trematopsid skull from the Lower Permian, and analysis of some characters of the dissorophoid (Amphibia: Labyrinthodontia) otic notch. *Ibid.* **30**, 67–79.
- BOY, J. A. 1972. Die Branchiosaurier (Amphibia) des saarpfälzischen Rotliegenden (Perm, SW-Deutschland). *Abh. hess. Landesamt. Bodenforsch.* **65**, 1–137.
- 1981. Zur Anwendung der Hennigschen Methode in der Wirbeltierpaläontologie. *Paläont. Z.* **55**, 87–107.
- CARROLL, R. L. 1964. Early evolution of the dissorophid amphibians. *Bull. Mus. comp. Zool. Harv.* **131**, 163–250.
- and WINER, L. 1977. Privately circulated appendix to CARROLL, R. L. Patterns of amphibian evolution: an extended example of the incompleteness of the fossil record. Chapter 13 in HALLAM, A. (ed.). *Patterns of Evolution*. Elsevier, Amsterdam.

- CHASE, J. N. 1965. *Neldasaurus wrightae*, a new rhachitomous labyrinthodont from the Texas Lower Permian. *Bull. Mus. comp. Zool. Harv.* **133**, 153–225.
- CURRIE, P. J. 1977. A new haptodontine sphenacodont (Reptilia: Pelycosauria) from the Upper Pennsylvanian of North America. *J. Paleont.* **51**, 927–942.
- 1979. The osteology of haptodontine sphenacodonts (Reptilia: Pelycosauria). *Palaeontographica Abt. A.* **163**, 130–168.
- DALY, E. 1973. A Lower Permian vertebrate fauna from southern Oklahoma. *J. Paleont.* **47**, 562–589.
- DEMAR, R. E. 1966. *Longiscutula houghae*, a new genus of dissorophid amphibian from the Permian of Texas. *Fieldiana: Geol.* **16**, 45–53.
- 1968. The Permian labyrinthodont amphibian *Dissorophus multicinctus* and the adaptations and phylogeny of the family Dissorophidae. *J. Paleont.* **42**, 1210–1242.
- EATON, T. H. JR. 1951. Origin of tetrapod limbs. *Amer. Midl. Nat.* **46**, 245–251.
- 1960. The aquatic origin of tetrapods. *Trans. Kans. Acad. Sci.* **63**, 115–120.
- 1973. A Pennsylvanian dissorophid amphibian from Kansas. *Occas. Pap. Mus. nat. Hist. Univ. Kans.* **14**, 1–8.
- and STEWART, P. L. 1960. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. *Univ. Kans. Publs Mus. nat. Hist.* **12**, 217–240.
- HOLMES, R. 1980. *Proterogyrinus scheelei* and the early evolution of the labyrinthodont pectoral limb, 351–376. In PANICHEN, A. L. (ed.). *The terrestrial environment and the origin of land vertebrates*, 633 pp. Systematics Assn Spec. Vol. No. 15. Academic Press, London.
- KUHN, O. 1972. Seymourida, 20–69. In CARROLL, R. L., KUHN, O. and TATARINOV, L. P. Teil 5B Batrachosauria (Anthracosauria), Gephyrostegida–Chroniosuchida. *Handbuch der Paläoherpetologie*. Fischer, Stuttgart.
- MILNER, A. R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontology*, **25**, 635–664.
- MOULTON, J. M. 1974. A description of the vertebral column of *Eryops* based on the notes and drawings of A. S. Romer. *Breviora*, No. 428, 1–44.
- OLSON, E. C. 1941. The family Trematopsidae. *J. Geol.* **49**, 149–176.
- 1971. *Vertebrate Paleozoology*, 839 pp. Wiley Interscience, New York.
- PEABODY, F. E. 1958. An embolomerous amphibian in the Garnett fauna (Pennsylvanian) of Kansas. *J. Paleont.* **32**, 571–573.
- PORTER, K. R. 1972. *Herpetology*, 524 pp. Saunders, Philadelphia.
- REISZ, R. R. 1977. *Petrolacosaurus kansensis* Lane, the oldest known diapsid reptile. *Science*, **196**, 1091–1093.
- 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Spec. Publ. Mus. nat. Hist. Univ. Kans.* **7**, 1–74.
- HEATON, M. J. and PYNN, B. R. 1982. Vertebrate fauna of late Pennsylvanian Rock Lake Shale near Garnett, Kansas: Pelycosauria. *J. Paleont.* **56**, 741–750.
- ROMER, A. S. 1966. *Vertebrate Paleontology* (3rd edn), 468 pp. Chicago University Press, Chicago.
- 1968. *Notes and Comments on Vertebrate Paleontology*, 304 pp. Chicago University Press, Chicago.
- and WITTER, R. V. 1942. *Edops*, a primitive rhachitomous amphibian from the Texas red beds. *J. Geol.* **50**, 925–960.
- ROSEN, D. E., FOREY, P. L., GARDINER, B. G. and PATTERSON, C. 1981. Lungfishes, tetrapods, paleontology and plesiomorphy. *Bull. Am. Mus. nat. Hist.* **167**, 159–267.
- SCHMALHAUSEN, I. I. 1968. *The Origin of Terrestrial Vertebrates*, 314 pp. Academic Press, New York and London.
- THOMSON, K. S. and BOSSY, K. H. 1970. Adaptive trends and relationships in early Amphibia. *Forma et Functio*, **3**, 7–31.
- TVERDOCHLEBOVA, G. I. 1972. A new batrachosaurian genus from the Upper Permian of southern Cisuralia. *Paleontol. J.* **6**, 84–90.
- VOROB'YEVA, E. I. 1974. On the formation of tetrapod characters in crossopterygians. *Ibid.* **8**, 219–224.
- WATSON, D. M. S. 1956. The brachyopid labyrinthodonts. *Bull. Br. Mus. nat. Hist. (Geol.)*, **2**, 315–392.

ANDREW R. MILNER

Department of Biology
Birkbeck College
London WC1E 7HX

HOMOTAXY AND BIOSTRATIGRAPHICAL THEORY

by G. H. SCOTT

ABSTRACT. The principal problem in biostratigraphical theory is a justification for using fossils to identify isochronous horizons. Biostratigraphers establish the sequential order of fossil events but there is no theoretical justification for equating constancy in stratigraphical position (homotaxy) with constancy in time of deposition. The problem is important as the way in which it is solved greatly influences the direction of biostratigraphical research. A partial solution is to use homotaxy as a weak test for diachroneity. Events that do not maintain invariant stratigraphical order are regarded as diachronous. While surviving events are not shown to be isochronous the amount of potential diachroneity throughout their individual distributions is inversely related to their stratigraphical spacing. The closer are homotaxial events in stratigraphical space the less they have wandered in time. Thus a major objective of biostratigraphical research should be to make tests of homotaxis more rigorous by raising the density of events.

SINCE William Smith the principal role of biostratigraphers has been to provide classifications of strata useful for estimating time of deposition. Historical geology requires a chronological framework to study ancient geographies and the sequential classifications established with fossils have long been used for this purpose. Indeed, the advent of radiometric and palaeomagnetic chronologies, in which time is directly estimated, has not diminished the utility of biostratigraphical data and there are now interesting applications of fossils as surrogate criteria for datum planes determined by quantitative techniques for measuring age. Cenozoic biostratigraphy, for example, has progressed to the stage where appearances and extinctions of taxa, calibrated at only a few sites with radiometric or magnetostratigraphic chronologies, are used as datum planes expressed in years (e.g. Ryan *et al.* 1974; Poore *et al.* 1984) that are recognized at locations far distant from the sites of calibration. Resolutions of less than 10 000 years have been claimed for such datum planes (Thierstein *et al.* 1977; Berggren and van Couvering 1978). To the bystander, these applications suggest that biostratigraphy has come of age and that the isochronous surfaces envisaged by the *International Stratigraphic Guide* (Hedberg 1976) can be accurately estimated by fossils.

While utility itself may be a justification, there is little theory to underwrite biostratigraphical practice. Further, over a long period there have been denials that fossils can accurately estimate time. A trenchant early critic was Huxley (1862) who argued that occurrences of taxa in fixed order from section to section (the common feature of biostratigraphical classifications since William Smith) did not imply that each datum or unit was isochronous. As correspondence in position did not imply contemporaneity, he alleged by way of demonstration that, 'for anything that geology or palaeontology are able to show to the contrary, a Devonian fauna and flora in the British Islands may have been contemporaneous with Silurian life in North America, and with a Carboniferous fauna and flora in Africa' (Huxley 1862, p. xliv). Modern critics (e.g. Miller 1965; Drooger 1974; Watson 1983), while less dismissive than Huxley, have continued to wrestle with the problems of using fossils to define isochronous surfaces. Kitts (1966) made a detailed investigation of the problem, viewing the events of the biostratigrapher as biological signals which were transmitted from specific centres. Because biological signal velocities (rates of dispersal) are variable and cannot be determined intrinsically from the data, he concluded that 'simultaneous with' relationships cannot be derived from fossils.

The impasse in biostratigraphical theory is that the intrinsic palaeobiological and stratigraphical data for an individual event do not enable its isochroneity to be established. There is no rationale for

progressing from event ordering to event dating. The *International Stratigraphic Guide* states (p. 88) that 'biostratigraphic correlation is one of the most useful approaches to time correlation if used with discretion and judgment', repeating an earlier view (p. 63) that correlation is a matter of judgement. It also mentions 'subtle paleontological discrimination' (p. 88) but in none of the discussions are clear guidance or objective rules given for identifying the most reliable datum planes. The idealistic way in which the *Guide* equates fossil datum planes with isochronous surfaces is echoed in some texts. Krumbein and Sloss (1963, p. 370) wrote that 'Chronospecies and "chronogenera" include the most obvious index fossils, since the synchronism of their range zones may be established without serious doubt'. In like vein, Donovan (1966, p. 32) found it 'inconceivable, in view of what we now know of evolution and dispersal, that a long and complex series of faunal changes should occur at different times in different places'. Certainly, there are grounds for making such assertions but where is the theory that allows them to be tested with biostratigraphical evidence? Other authors (e.g. Dunbar and Rodgers 1957; Weller 1960; Raup and Stanley 1978) focus more on the imperfections of palaeobiological events as time indices. Yet these 'realists' also fail to confront the problem: how to identify the best events for time correlation?

In overview, there is no theory to allow a set of ordered events to be tested for isochroneity with biostratigraphical data. The problem has existed since the advent of biostratigraphy and is ignored or glossed over in the vast majority of the biostratigraphical literature. I believe that this is unsatisfactory as the direction of biostratigraphical research is intimately related to the way in which the gap between sequence and time is to be bridged. Here I outline one approach which, rather than trying to find isochronous events directly, seeks to identify the least diachronous.

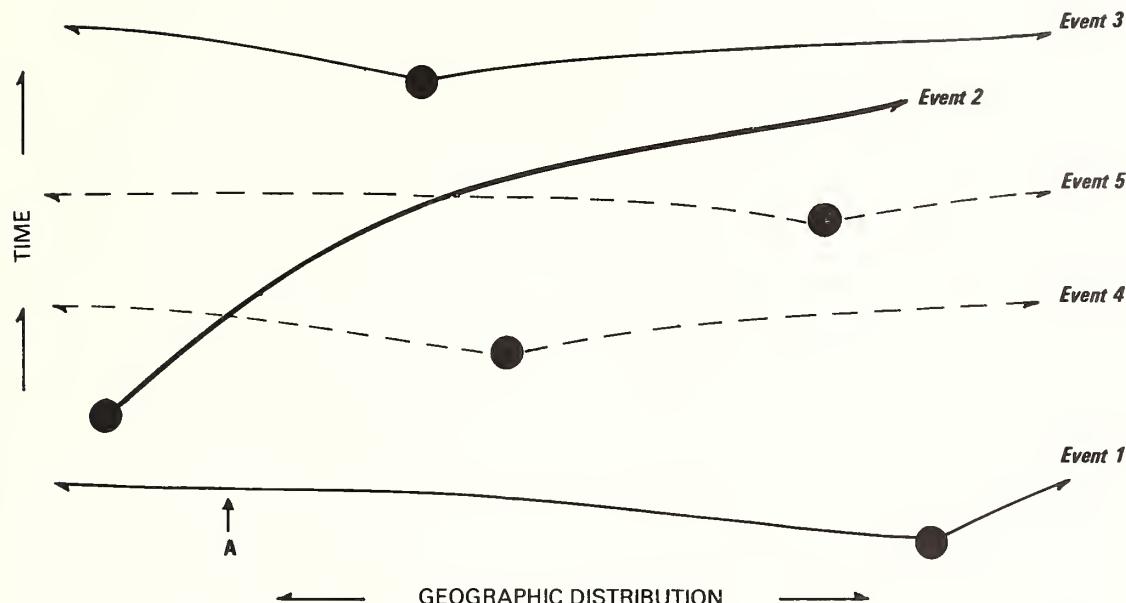
A PARTIAL SOLUTION

Perhaps ironically for Huxley, a basis for biostratigraphical theory lies in his concept of homotaxis. To Huxley (1862) it signified similarity in orders of stratigraphical events without implication of contemporaneity, and he used it with some relish to demolish time stratigraphical correlation with fossils. Huxley was correct in contending that an order of events, maintained from section to section, does not entail that each was isochronous throughout its occurrences. Nevertheless, he did not explore some implications of his concept. Let us simply define as homotaxial those events that occur in fixed stratigraphical order with respect to selected neighbouring events. As graphical representations show, order invariance does not necessarily identify an event as isochronous. Homotaxial events potentially include strictly isochronous events (e.g. those caused by instantaneous global catastrophes) as well as diachronous events that are insufficiently time transgressive to intersect with their immediate neighbours. Conversely, non-homotaxial events include those diachronous events that are time transgressive to the extent that they produce inversions of order. Relative to the time stratigraphical objective, non-homotaxial events can be rejected as certainly unsuitable. Thus the problem focuses on homotaxial events; these may vary considerably in the amount of undetected diachroneity. Huxley denied that this class of event was applicable in time stratigraphy. This is substantially correct given the biogeographical model he implied in which, over a long period (Silurian to Carboniferous), taxa originated in one region and slowly migrated in the same direction to others. But in any model in which events may arise at various geographical loci (text-fig. 1) and disperse at different rates in different directions, homotaxial events will include those that are potentially the most accurate estimators of time. The operational task is to identify the least diachronous.

While tests using various stratigraphical, physical, or chemical techniques are sometimes feasible, it is important from the standpoint of biostratigraphical theory to identify procedures that simply depend on stratigraphical relationships (the intrinsic data of biostratigraphy).

The primary procedure relates to the stratigraphical spacing of homotaxial events and tries to force them into the class of non-homotaxial events. Text-fig. 1 shows a homotaxial triplet (Events 1, 2, 3). Events 1 and 3 are well behaved in the time domain as they dispersed rapidly. Event 2 did not, but it will still be regarded as a homotaxial event as it does not intersect with the adjacent Events 1 and 3.

EVENT SPACING AND HOMOTAXY



TEXT-FIG. 1. Initially, only biostratigraphical Events 1, 2, 3 are known. They maintain homotaxy throughout their joint occurrences. Event 4 is recognized subsequently and it is found that the upward sequence 1-4-2-3 is maintained over most of the region in which they occur jointly. However, in the vicinity of A the order of Events 4 and 2 inverts. Evidence from Event 5 helps establish that Event 2 is strongly diachronous. The slow dispersal of Event 2 was unrecognized when the event set consisted only of Events 1, 2, 3. Decreasing the stratigraphical spacing of events will raise the chance of detecting the most diachronous events provided that the origins of events and their dispersal directions and rates are variable.

Consideration of an additional event (4, perhaps newly recognized) shows that while it maintains homotaxy with Events 1 and 3 it fails with Event 2. At this stage which of Events 2 and 4 is the more diachronous is unknown and further events, such as 5, may be needed to reject Event 2.

Interpolation of additional events in homotaxial sets should tend to eliminate the most diachronous. Thus attempts to falsify the hypothesis that a set of events is homotaxial become increasingly rigorous as event spacing declines. As testing relies only on hypotheses about event orders, there is no indication of the variation in age of events that survive testing. They are not shown to be isochronous, neither is their diachroneity definitely established. Nevertheless, for particular sedimentary regimes, those that are closest in stratigraphical space may be expected to best approximate isochronous horizons.

The signal model (Kitts 1966) provides another perspective on selection of events. Here, events are considered to be transmitted away from a local geographical origin. Speciation by allopatry is an excellent example but some extinctions (such as those caused by an environmental change moving along a geographical gradient, progressively eliminating populations) also conform. The significance of geographical extent is that it provides a test of signal velocity. Any event whose transmission time is slower than those of its neighbours is liable not to maintain its order in the sequence (Event 2 in text-fig. 1). Whether it does so depends on several factors, including its proximity (in time) to the

neighbouring event with faster velocity, and on variation in its own velocity. This may be considerable. For example, zooplankton populations tend to be watermass bounded (McGowan 1971). Within one watermass, biological events are rapidly distributed by physical circulation. But the spread of a taxon to a neighbouring watermass is often a trial and error process. Thus some signals (e.g. first appearances) may terminate near the boundary (possibly indicating that founder populations in the adjacent watermass failed to establish). On the other hand, a successful invasion may lead to rapid expansion over the whole of the new territory.

While estimates of ancient signal velocities are speculative, it is obvious that variation in signal velocity is the more likely to be revealed the greater the area over which homotaxis is checked. It is not simply the global taxa that are the least diachronous, it is those that dispersed most rapidly throughout their entire geographical range. The effectiveness of the geographical test is related to event spacing. If events are widely spaced, velocities are only weakly testable via consideration of geographical distributions. Rather, its effectiveness increases as event spacing decreases. Generally, events that maintain homotaxial order over the widest area at the minimum available stratigraphical spacing are likely to be the least diachronous.

DISCUSSION

Given suitable distributions of event origins and dispersal routes, tests of homotaxy are potentially capable of eliminating all but strictly isochronous events. In this respect the argument simply supports the utility of sequence classifications long used by biostratigraphers in their quest for time. Additionally, however, the formulation raises issues in contemporary theory and practice that would otherwise not be clearly perceived.

1. Testability. Like Donovan (1966), we may appeal to evolutionary theory to 'guarantee' that certain events are isochronous or, like the *International Stratigraphic Guide*, we may cloak our selections under the shrouds of 'discretion' and 'judgment'. The merit of building a theory around homotaxy is that it emphasizes practical testing procedures. Biostratigraphy is not an art, despite the writings of the *International Stratigraphic Guide*.

2. Integration of data. Events used in biostratigraphy come from sources as diverse as protists and vertebrates. However, the potential value of this diversity is rarely realized in biostratigraphical applications. The systematics of groups well represented in the Cenozoic record, for example, have recently been greatly refined, often with large increases in the number of useful biostratigraphical events recognized. Yet this research has been paralleled by the multiplication of biostratigraphical classifications which use only events in one group (e.g. Martini 1971; Riedel and Sanfilippo 1978; Blow 1979). While all represent major advances, no single classification necessarily uses events that are the least diachronous. In general, this will be the integrated set as it will contain the most closely spaced events.

Integration implies more than finding the stratigraphical position of diatom species C relative to coccolith species H in one or two sequences. To fully utilize advances in the systematics of Cenozoic planktonic microfossils the positions of individual events need to be compared with those of their nearest stratigraphical neighbours throughout regions of joint occurrences. While biogeographical compatibility largely controls the severity of testing, any reduction in event spacing while maintaining homotaxy enhances the value of the datum planes for time stratigraphy. There is an increasing effort to correlate events in various planktonic microfossil groups (e.g. Hornbrook and Edwards 1971; Ikebe and Chiji 1981; Abbott 1984) but is testing really rigorous?

3. Stratotypes. The *International Stratigraphic Guide* vigorously promoted the function of stratotypes and type localities as standards for the definition and recognition of stratigraphical units. It views a stratotype (p. 27) as 'the standard of reference on which the concept of the unit is uniquely based'. Thus biostratigraphical units (p. 63) are 'extended away from their type localities by biostratigraphic correlation'. Similarly, the boundaries of stages (chronostratigraphical unit, p. 71) 'as they are extended away from the boundary stratotypes should be in principle isochronous'. Further, the Guide states (p. 86) that 'Only after the type limits (boundary stratotypes) of a chrono-

stratigraphic unit have been established can the limits be extended geographically beyond the type section'.

These views conflict with the theory advocated here. While it is valuable to have a locality that serves as a name bearer for a datum or unit, homotaxial theory does not require any locality to serve as a standard endowed with special status. Homotaxis is recognizable only by occurrences of events in the same order in several sequences. The order of events in one section without reference to the order of the same events in other sequences is completely irrelevant in a homotaxial scheme. Rather than initially identifying a standard and correlating outward from that site, as the *Guide* suggests, a homotaxial datum, or unit, can only be recognized after inspection of events in several sequences. From a different viewpoint Hay (1974) reached a similar conclusion. The equal status of sequences in homotaxial schemes is implied in the test procedure for order invariance. Any sequence in which the order of an event is not maintained becomes crucial in determining the status of the event, irrespective of its relationships in the stratotype.

I suggest that methodological emphasis on stratotypes is misplaced. Biostratigraphy is built on selection of events, not selection of sections.

Biostratigraphers have long advocated the utility of fossils to identify synchronous horizons and independent methods of dating are now establishing that some palaeobiological events in fact dispersed extremely rapidly. Such results, however encouraging, do not resolve the problem of identifying synchronous horizons when only data on the order of events are available. While there may not be a full solution to this problem the value of my formulation is that it points to a coherent approach to event selection and identifies research objectives that should improve biostratigraphical resolution. Rightly, some will say that the procedures are commonplace, used by all biostratigraphers. Nevertheless, the way they may be used to bridge the gap between order of events and age of events is insufficiently recognized either in practice or in the literature.

Acknowledgements. I thank Professor R. M. Carter and colleagues at N.Z. Geological Survey for many constructive comments.

REFERENCES

- ABBOTT, W. H. 1984. Progress in the recognition of Neogene diatom datums along the U.S. Atlantic coast. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **47**, 5–20.
- BERGGREN, W. A. and VAN COUVERING, J. A. 1978. Biochronology, 39–55. In COOKE, G. V., GLAESSNER, M. F. and HEDBERG, H. D. (eds.). *The Geologic Time Scale*. American Association of Petroleum Geologists, Tulsa, Oklahoma.
- BLOW, W. H. 1979. *The Cainozoic Globigerinida*, xv + 1413 pp. E. J. Brill, Leiden.
- DONOVAN, D. T. 1966. *Stratigraphy*, 199 pp. T. Murby, London.
- DROOGER, C. W. 1974. The boundaries and limits of stratigraphy. *Proc. K. ned. Akad. Wet.* **B77**, 159–176.
- DUNBAR, C. O. and RODGERS, J. 1957. *Principles of Stratigraphy*, xii + 356 pp. J. Wiley, New York.
- HAY, W. W. 1974. Implications of probabilistic stratigraphy for chronostratigraphy. *Verh. naturf. Ges. Basel* **84**, 164–171.
- HEDBERG, H. D. (ed.). 1976. *International Stratigraphic Guide*, xvi + 200 pp. J. Wiley, New York.
- HORNIBROOK, N. DE B. and EDWARDS, A. R. 1971. Integrated planktonic foraminiferal and calcareous nannoplankton datum levels in the New Zealand Cenozoic, 649–657. In FARINACCI, A. (ed.). *Proceedings of the Second Planktonic Conference, Roma 1970*. Vol. 1. Edizioni Tecnoscienza, Rome.
- HUXLEY, T. H. 1862. The anniversary address. *Q. Jl geol. Soc. Lond.* **18**, xl–liv.
- IKEBE, N. and CHIJI, M. 1981. Important datum-planes of the western Pacific Neogene (revised) with remarks on the Neogene stages in Japan. In TSUCHI, R. (ed.). *Neogene of Japan*. IGCP-114 National Working Group of Japan, Shizuoka University, 1–14.
- KITTS, D. B. 1966. Geologic time. *J. Geol.* **74**, 127–146.
- KRUMBEIN, W. C. and SLOSS, L. L. 1963. *Stratigraphy and Sedimentation*, vii + 600 pp. W. H. Freeman, San Francisco.
- MARTINI, E. 1971. Standard Tertiary and Quaternary calcareous nannoplankton zonation, 739–785. In FARINACCI, A. (ed.). *Proceedings of the Second Planktonic Conference, Roma 1970*. Vol. 2. Edizioni Tecnoscienza, Rome.

- MCGOWAN, J. A. 1971. Oceanic Biogeography of the Pacific, 3–73. In FUNNELL, B. M. and RIEDEL, W. R. (eds.). *The Micropalaeontology of Oceans*. University Press, Cambridge.
- MILLER, T. G. 1965. Time in stratigraphy. *Palaeontology*, **8**, 113–131.
- POORE, R. Z., TAUXE, L., PERCIVAL, S. F. JR., LABREQUE, J. L., WRIGHT, R., PETERSEN, N. P., SMITH, C. C., TUCKER, P. and HSÜ, K. J. 1984. Late Cretaceous–Cenozoic magnetostratigraphic and biostratigraphic correlations for the South Atlantic Ocean, Deep Sea Drilling Project Leg 73, 645–655. In HSÜ, K. J. et al., *Initial Reports of the Deep Sea Drilling Project*. Vol. 73. National Science Foundation, Washington, D. C.
- RAUP, D. M. and STANLEY, S. M. 1978. *Principles of Paleontology*, x + 481 pp. W. H. Freeman, San Francisco.
- RIEDEL, W. R. and SANFILIPPO, A. 1978. Stratigraphy and evolution of tropical Cenozoic radiolarians. *Micro-paleontology*, **24**, 61–96.
- RYAN, W. B. F., CITA, M. B., RAWSON, M. D., BURCKLE, L. H. and SAITO, T. 1974. A paleomagnetic assignment of Neogene stage boundaries and the development of isochronous datum planes between the Mediterranean, the Pacific and Indian Oceans in order to investigate the response of the world ocean to the Mediterranean salinity crisis. *Riv. Ital. Paleont. Stratigr.* **80**, 631–687.
- THIERSTEIN, H. R., GEITZENAUER, K. R., MOLFINO, B. and SHACKLETON, N. J. 1977. Global synchronicity of late Quaternary coccolith datum levels: validation by oxygen isotopes. *Geology*, **5**, 400–404.
- WATSON, R. A. 1983. A critique chronostratigraphy. *Am. J. Sci.* **283**, 173–177.
- WELLER, J. M. 1960. *Stratigraphic Principles and Practice*, xvi + 725 pp. Harper, New York.

G. H. SCOTT

Typescript received 30 November 1984

N.Z. Geological Survey

Revised typescript received 4 April 1985

P.O. Box 30368

Lower Hutt, New Zealand

THE TYPE SPECIES OF *CALYMENE* (TRILOBITA) FROM THE SILURIAN OF DUDLEY, ENGLAND

by DEREK J. SIVETER

ABSTRACT. The type material of *Calymene blumenbachii* Brongniart in Desmarest 1817 (type species of *Calymene* Brongniart, 1822) and *C. tuberculata* (Brünnich, 1781) has been revised, with that of the latter being figured for the first time. The *nomen dubium* status accorded to *C. tuberculata* by Shirley (1933) can no longer be upheld as the syntype specimens of Silurian age are, on preparation, very well preserved and identifiable, though this species is now recognized as a senior (subjective) synonym of *C. blumenbachii*. In consequence application is being made to the International Commission on Zoological Nomenclature to retain the junior name in the interest of stability.

DURING recent work on the Calymenidae in preparation for the second edition of the *Treatise on Invertebrate Paleontology* (*Trilobita*), nomenclatural problems have resurfaced regarding the conservation of the generic name *Calymene* Brongniart in Brongniart and Desmarest, 1822, type genus for the family, and the right of Milne Edwards (1840) to stand as the author of the family name. These uncertainties prompted Whittington (1983) to petition the International Commission on Zoological Nomenclature (ICZN) in favour of both claims. Subsequent study by the present author has further shown that *C. blumenbachii* Brongniart in Desmarest, 1817, the type species of *Calymene*, is a junior (subjective) synonym of *Trilobus tuberculatus* Brünnich, 1781. The purpose of this paper is to give evidence of this synonymy by providing new data on the type material of both species. Additionally, the paper is a prerequisite to an application to the ICZN (Whittington and Siveter, in press), by way of a rider to Whittington's 1983 proposals, to use its plenary powers to suppress the senior name *tuberculata* in favour of *blumenbachii*, on the grounds that only the latter name has been used for the species by various authors during the last fifty years.

The terminology and photographic and preparation techniques are those previously employed by Siveter (1977, 1979, 1980, 1983). Repositories holding material used in this revision are: Université P. et M. Curie, Laboratoire de Paléontologie des Invertébrés, Paris (UPMC); Geologisk Museum, Københavns Universitet (MGUH).

THE TYPE SPECIES OF *CALYMENE*

The type material of Calymene blumenbachii Brongniart in Desmarest, 1817

No material of *C. blumenbachii* was figured by Desmarest (1817) but Brongniart in Brongniart and Desmarest (1822) illustrated two syntype specimens, one (*ibid.*, pl. 1, fig. 1A, B) a partially enrolled example, the other (*ibid.*, pl. 1, fig. 1C, D) an extended incomplete individual; Dudley was indicated (*ibid.*, pp. 9, 11, and 143) as the type locality (and I can confirm that this name appears on the specimen label accompanying the enrolled form). Shirley (1933) relocated this material in the Sorbonne, Paris, together with a third specimen 'which probably belonged to Brongniart' but which Shirley left out of his account because of its uncertain curatorial history. Shirley also selected the enrolled syntype to stand as 'the type' (that is lectotype) for the species, and figured it (*ibid.*, pl. 1, figs. 1–3), though not the second (now paralectotype) specimen. Since this time the type suite of specimens has remained unstudied.

Dr Francoise Bigey (Université P. et M. Curie, Laboratoire de Paléontologie des Invertébrés, Paris) subsequently rediscovered the lectotype in the collections of her institute, the Sorbonne

Geology Collection having been 'removed to new buildings' (pers. comm. 5 February 1974); I have since fully prepared this specimen and it is refigured herein (Pl. 90, figs. 1–5), but the paralectotype was reported by Dr Bigey as missing. Further, Brongniart's material has 'been shared in the past between the Muséum National d'Histoire Naturelle and Paris University' (pers. comm. Dr Bigey, 23 November 1983), though Dr J.-C. Fischer, sub-director of this museum, informs me (1 September 1984) that the paralectotype is not in their collections, and it does not appear in the recently published catalogue of type and figured trilobites housed there (Carriol 1984). For the present it is missing.

The type material of Trilobus tuberculatus Brünnich, 1781

Four specimens comprised the syntype suite of this species, the type locality of which was indicated by Brünnich (1781, p. 391) as 'Rensnest' (= Wren's Nest), 'Dudley'. Shirley (1933, p. 63) examined this material of *C. tuberculata* and concluded that the specimens which he referred to as the 'third' and 'fourth' were, respectively, the pygidium of an undescribed Ordovician calymenid from Shropshire and an almost complete asaphid from the Ordovician of Scandinavia or the eastern Baltic. He claimed that the 'first' specimen, 'a cranium more than half buried in matrix and six attached thoracic segments . . . is impossible to refer to any of the species . . . occurring at Dudley' and that the 'second' specimen, 'twelve thoracic segments and an attached pygidium . . . cannot be identified with certainty'. Shirley did not name the 'first' or 'second' specimens in his paper but in a letter (23 June 1933) to Dr J. P. J. Ravn, the then Curator of the Geologisk Museum, Københavns Universitet (where the material is housed) he writes: 'I cannot identify specimens one and two further than *Calymene* sp. (at Dudley I have recognised at least four species). They have a matrix which is similar to other specimens from Dudley and there seems to be no doubt that they came from that locality.'

Dr S. Floris, the present Curator, has loaned me (18 January 1984) the first two (MGUH 16.805, 16.806) and fourth (MGUH 16.807) of the syntypes, the third one (Shropshire Ordovician calymenid) being reported as missing. The 'Rensnest' locality information given by Brünnich in his paper is also written on the original labels of all these three syntypes, including that of the Ordovician asaphid. However a Wren's Nest origin is corroborated for at least one of the two syntypes which are of Silurian age, that referred to by Shirley as the 'first' specimen (MGUH 16.805) and which is selected below as the lectotype for the species, by evidence from ostracodes recovered from the surrounding matrix (Pl. 90, figs. 6 and 7). Dr David Siveter has kindly supplied the following comments on these: 'The ostracodes are an almost complete female right valve of the beyrichiacean *Osmotoxotis phalacra* Siveter, 1980, a left valve of the thlipsuracean *Thlipsura v-scripta* Jones and Holl, 1869, and two other indeterminate non-palaeocope specimens. *T. v-scripta* is known from the Homerian Stage and possibly the upper part of the Sheinwoodian Stage, Wenlock Series to the lower Gorstian Stage, Ludlow Series of the West Midlands and the Welsh Borderland, and from at least the Wenlock Series on Gotland (Siveter 1978). *O. phalacra* is unknown outside the Homerian Much Wenlock Limestone Formation of the West Midlands and the Welsh Borderland; it has been recorded (Siveter 1980) from Mayhill, the Malverns, Ledbury, and the type and other localities at the Wren's Nest. The figured *O. phalacra* specimen (Pl. 90, fig. 6) is only the fourth female of the species known from the Wren's Nest and it shows exceptional preservation, having a sculpture of fine reticulo-striation and sparse tubercles not previously observed in females from this locality.' Ostracodes have not been recovered from the matrix around the 'second' specimen of Shirley but there is no reason to doubt that it, too, came from the Wren's Nest.

Photographs of the two Dudley syntype trilobites were taken before (Pl. 91, figs. 7, 10, 12) and after (Pl. 91, figs. 1–6, 8, 9, 11, 13) preparation, so that the nature of the specimens as seen by Shirley and Brünnich is on record; also casts were made of the specimens before they were prepared. Both syntypes were found to have one more thoracic segment, that is seven (Pl. 91, fig. 9) and thirteen (Pl. 91, fig. 1), than the number given by Shirley. In order to fix the concept of *Trilobus tuberculatus* in keeping with the previously held notion of this species as a Silurian *Calymene* from Dudley, the specimen illustrated herein on Plate 91, figs. 3, 6, 8, 9, 11–13 is now selected as lectotype (MGUH 16.805).

The question of synonymy

As Shirley (1933) noted, on priority grounds many Scandinavian and continental authors (e.g. Lindström 1885) used the senior name *C. tuberculata* rather than *C. blumenbachii* for late Wenlock calymenids of this type. Shirley nevertheless effectively declared *C. tuberculata* a *nomen dubium* because of 'inadequate description and types', and said that 'the name *tuberculata* for any species of *Calymene* must be allowed to fall'. After preparing the Silurian material of Brünnich I am convinced that there are no significant morphological differences from that of Brongniart and that they are conspecific (see discussion below and Pls. 90 and 91). All the material is from the Dudley area, though it is unknown in the case of *C. blumenbachii* whether its type locality is specifically the Wren's Nest, as for *C. tuberculata*, there being two other Silurian inliers (Dudley Castle Hill and Hurst Hill; Butler 1939) in the district. The type horizon for all the material is indisputably the Much Wenlock Limestone Formation, of late Homrian age, considering the ostracode evidence presented above and the fact that I have not noted any specimens of this species from Dudley, of which there are very many, in any other formation.

The type species

The type species of *Calymene* Brongniart in Brongniart and Desmarest, 1822 is *C. blumenbachii* Brongniart in Desmarest, 1817, by subsequent designation of Shirley (1933), and not, as stated by Whittington (1983), *Calymena blumenbachii* Brongniart in Desmarest, 1817 by original designation. Bassler's (1915) designation of *C. tuberculata* to stand as the type species pre-dates that of Shirley, but it is invalid (see Whittington and Siveter, in press).

SYSTEMATIC PALAEONTOLOGY

Family CALYMNIDAE Milne Edwards, 1840 Genus CALYMENE Brongniart, 1822

Type species. *Calymene blumenbachii* Brongniart in Desmarest, 1817, from the Much Wenlock Limestone Formation, Homrian Stage, Wenlock Series, Dudley, West Midlands, UK, by subsequent designation of Shirley 1933, p. 53.

Calymene blumenbachii Brongniart, 1817

Plate 90, figs. 1–5; Plate 91

- ?1750 nondescript petrified insect; Lyttelton, p. 105, pl. 1, figs. 9–14; pl. 2 (*par*s). [From the figures it is probably *C. blumenbachii*.]
- ?1750 *scolopendrae aquaticeae scutatae*; Mortimer, p. 106, pl. 1, figs. 15–18. [From the figures it is possibly *C. blumenbachii*.]
- 1781 *Trilobus tuberculatus* Brünnich, p. 389. [Suppression requested, Whittington and Siveter, in press; ICZN pending.]
- 1816 Le Calymène de Blumenbach; Brongniart in Desmarest, p. 50.
- 1817 *Calymena blumenbachii*, Brong.; Brongniart in Desmarest, p. 517. [Suppression of *Calymena* Desmarest, 1817 requested, Whittington 1983; ICZN pending.]
- 1822 *Calymene blumenbachii*; Brongniart in Brongniart and Desmarest, p. 11, pl. 1, fig. 1A–D.
- ?1839 *Calymene blumenbachii* Brongniart; Murchison, p. 653, pl. 7, figs. 6 and 7, *non* fig. 5.
- 1851 *Calymene blumenbachi* (Brong.); M'Coy (*par*s) in Sedgwick and M'Coy, p. 165.
- ?1852 *Calym. blumenbachi*. Brongn.; Barrande, p. 566, pl. 5, fig. 8; *non* pl. 19, fig. 10; *non* pl. 43, figs. 46–48.
- ?1859 *Calymene blumenbachii* Brongniart; Murchison, p. 235, pl. 18, fig. 10.
- 1865 *Calymene blumenbachii*, Brongn.; Salter, p. 93, pl. 8, figs. 8, 10, 12–14, ?figs. 7, 15, 16, *non* figs. 9 and 11, pl. 9, figs. 1 and 2.
- 1868 *Calymene ceratophthalma*; Woodward, p. 489, pl. 21, fig. 1 (*par*s), ?fig. 2.
- 1869 *Calymene blumenbachii*; Woodward, p. 43.
- non 1872 *Calym. blumenbachi*. Brongn.; Barrande, p. 36, pl. 14, fig. 33.
- non 1879 *Calymene blumenbachii*, Brongniart; Nicholson and Etheridge, p. 140, pl. 10, figs. 2–6.

- non 1906 *Calymene blumenbachi*, Brongniart, 1822; Reed, p. 133, pl. 17, figs. 12 and 13.
 1933 *Calymene blumenbachi* Brongniart, 1822; Shirley, pp. 52, 59, pl. 1, figs. 1–5.
 1936 *Calymene lata* sp. nov. Shirley, p. 414, pl. 30, figs. 11–13; pl. 31, fig. 4.
 non 1957 *Calymene (Calymene) blumenbachi blumenbachi* Brongniart, 1822; Tomczykowa, pp. 97, 135, pl. 3, figs. 3 and 4; text-fig. 6a, b.
 1959 *Calymene blumenbachii* Brongniart, 1822; Whittington in Moore, p. O452, fig. 353.1a–c.
 1970 *Calymene blumenbachi blumenbachi*; Schrank, p. 135, pl. 9, figs. 5 and 6.
 non 1977 *Calymene blumenbachi* Brongniart, 1822; Männil, p. 250, pl. 4, figs. 6 and 7; pl. 5, figs. 1–4.
 ?1980 *Calymene blumenbachi* Brongniart; Chatterton and Campbell, p. 95, fig. 4.
 1980 *Calymene blumenbachii blumenbachii* Brongniart, 1822; Siveter, p. 784, pl. 97, fig. 10; pl. 100, figs. 9–11.
 1983 *Calymene blumenbachii* Brongniart in Desmarest, 1817; Whittington, p. 177.
 1984 *Calymene blumenbachii* Brongniart; Thomas, Owens and Rushton, fig. 23 (*pars*).

Lectotype. Subsequently designated Shirley 1933, p. 53. A complete, partially enrolled specimen, Collections de Paléontologie de l'Université P. et M. Curie, No. 3409/77; figured Brongniart in Brongniart and Desmarest 1822, pl. 1, fig. 1a, b; Shirley 1933, pl. 1, figs. 1–3; herein Plate 90, figs. 1–5.

Paralectotype. The more or less complete specimen which formed the basis for Brongniart in Brongniart and Desmarest 1822, pl. 1, fig. 1c, d. This specimen now appears to be lost (see above).

Type stratum and locality. Much Wenlock Limestone Formation, Homrian Stage, Wenlock Series, Dudley, West Midlands. Bassett (1976, pp. 211 and 212) regarded at least the base of this formation at Dudley as being of *lundgreni* Biozone age, with the upper part being most likely of *ludensis* Biozone age.

Additional material. All of the major and most provincial museums in Britain have well-preserved material of this species and there is no attempt here to provide a complete list; the total number of specimens is probably several hundred. It is also well represented in the collections of numerous foreign repositories.

Diagnosis. A species of *Calymene* with a short preglabellar area, about one-tenth as long (sag.) as glabella; anterior border low relative to dorsal surface of frontal glabellar lobe and steeply to more or less vertically inclined, having a fairly sharp dorsal edge; preglabellar furrow very short (sag. and exsag.), moderately deep. Strongly inflated glabella projects well above and well in front of fixed cheek. Pygidium with strongly convex (tr.) axis, six to eight axial rings, five pleural furrows.

Description. Cephalon is subsemicircular in outline, 2·1 (Pl. 90, fig. 1) to 2·2 (Pl. 91, fig. 6) times as wide as long. Glabellar outline is bell-shaped, 1·0 (Pl. 91, fig. 6) to 1·1 (Pl. 90, fig. 1) times as long as wide, projects well in front of fixed cheeks. Occipital ring slightly narrower (tr.) than glabellar width at 1p lobes, gently convex in profile, is longest medially but gradually shortens abaxially and flexes forwards at axial furrow where it is weakly inflated. Occipital furrow moderately long (sag.), not deeply incised behind central glabellar area, becomes slit-like abaxially. Lobe 1p is fairly large, subquadrate, has a quite strongly convex outer margin, is strongly swollen and separated from median lobe by very shallow posterior extension of furrow 1p. The latter is deep and widest (exsag.) at axial furrow, runs inward and backward between lobes 1p and 2p, bifurcates adaxially, longer posterior branch turning first backward then inward, anterior branch directed forward and inward, continuing very weakly anteriorly across inner side of lobe 2p. Distinct intermediate lobe within fork of furrow 1p. Lobe 2p

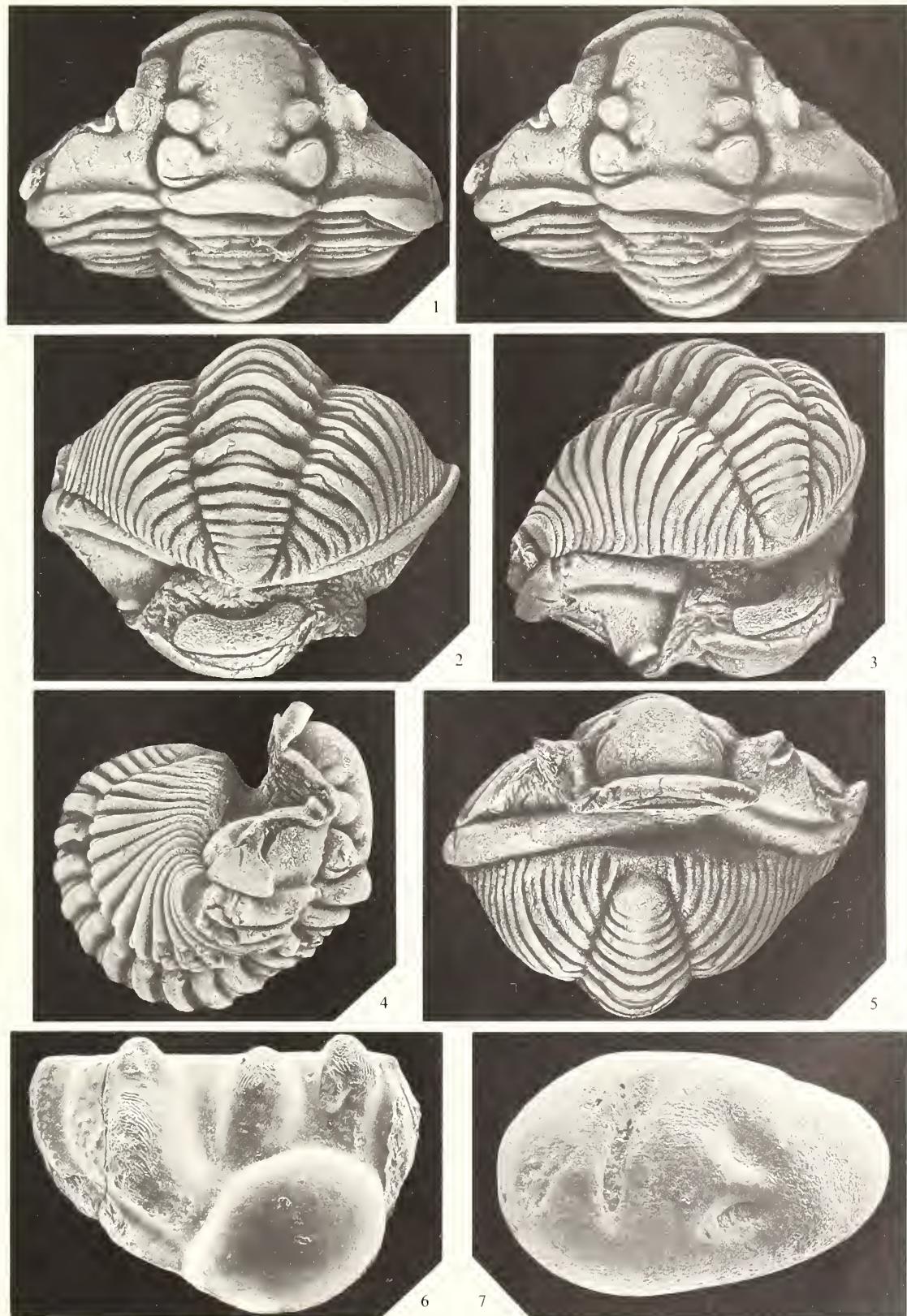
EXPLANATION OF PLATE 90

Figs. 1–5. *Calymene blumenbachii* Brongniart in Desmarest, 1817. UPMC 3409/77, Much Wenlock Limestone Formation, Dudley; lectotype; complete, partially enrolled specimen. 1, dorsal stereo-pair (cephalon); 2, dorsal (pygidium); 3, oblique (pygidium); 4, lateral; 5, frontal (cephalon); all $\times 2$. Figured Brongniart in Brongniart and Desmarest 1822, pl. 1, fig. 1a, b; Shirley 1933, pl. 1, figs. 1–3.

Fig. 6. *Osmotoxotis phalacra* Siveter, 1980. MGUH 16.803, Much Wenlock Limestone Formation, Wren's Nest, Dudley; right valve, female, lateral view, $\times 33$.

Fig. 7. *Thlipsura v-scripta* Jones and Holl, 1869. MGUH 16.804, Much Wenlock Limestone Formation, Wren's Nest, Dudley; left valve, teconomorph, lateral view, $\times 73$.

Ostracodes prepared and photographed by Dr David J. Siveter (Leicester).

SIVETER, *Calymene, Osmotoxotis, Thlipsura*

rather swollen, transversely elongate, papillate. Furrow 2p directed transversely or slightly forward. Lateral lobe 3p longest (exsag.) dorsally, narrows as it runs down side of glabella, confined by shallow though distinct 3p furrow which trends inward and forward. Small 4p lobe present. Frontal lobe with its sides vertically inclined and directed exsagitally or slightly outward posteriorly, in dorsal view anterolateral margins are rounded, anterior outline weakly (Pl. 90, fig. 1) to strongly (Pl. 91, fig. 6) convex forward. Frontal lobe is about 0·7 times as wide as glabella at lobe 1p. In lateral profile (Pl. 90, fig. 4; Pl. 91, fig. 8) dorsal surface of glabella projects well above fixed cheek, is gently convex between occipital furrow and furrow 2p, thereafter moderately to strongly convex to anterior face of frontal lobe, which falls very steeply and is undercut by preglabellar furrow.

Axial furrow very shallow at occipital ring, narrowest at base of lobe 1p, becomes progressively wider (tr.) and much deeper to furrow 1p; around lobe 1p it undercuts and its abaxial face curves very steeply downward and slightly inward; it is just continuous under bridge of lobe 2p and genal buttress, from here to preglabellar furrow it is uniformly narrow, deep, and trench like. Anterior pit is below posterior part of frontal lobe. Preglabellar furrow very short (sag. and exsag.), moderately deep. Anterior border is a very short raised rim, in lateral view (Pl. 90, fig. 4) it curves vertically upward and a little inward, its dorsal surface is quite sharply edged and does not reach far up anterior face of frontal lobe (Pl. 90, fig. 5); opposite axial furrow it is slightly swollen (Pl. 91, fig. 3). Anterior margin moderately convex forward (Pl. 90, fig. 1) and upward (Pl. 90, fig. 5).

Posterior border becomes considerably wider (exsag.) and less convex abaxially from fulcrum before narrowing (exsag.) slightly near genal angle (Pl. 91, fig. 3). Posterior border furrow widest opposite fulcrum, has shallow anterior and steep posterior slope. In lateral profile postocular part of fixed cheek slopes (exsag.) gently to moderately to posterior border furrow, preocular part is rather narrow (tr.), curves steeply downward and forward. Furrow between fixed cheek and anterior border is shallower than preglabellar furrow. Palpebral lobe is moderately (Pl. 91, fig. 11) to quite steeply (Pl. 90, fig. 5) inclined with mid-length opposite anterior part of lobe 2p, it is longer (exsag.) than lobe 2p but not as long as lobe 1p, its outer margin is slightly pointed. At contact of posterior facial suture and ocular suture, palpebral lobes are 1·6 times as wide apart as width of glabella across 2p lobes. Posterior branch of suture runs transversely from palpebral lobe then turns obliquely backward to lateral border where it bends more sharply backward and finally slightly outward to bisect lateral and posterior margins; anterior branch directed forward and slightly inward to anterior border, turns sharply inward on outer face of border to connective suture (Pl. 91, fig. 11). Visual surface of eye is not preserved, reniform in outline, supported by eye socle from which convex main field of free cheek descends very steeply to distinct, broadly U-shaped lateral border furrow (Pl. 91, figs. 3 and 8). Lateral border turns sharply over and under; doublure acutely reflexed.

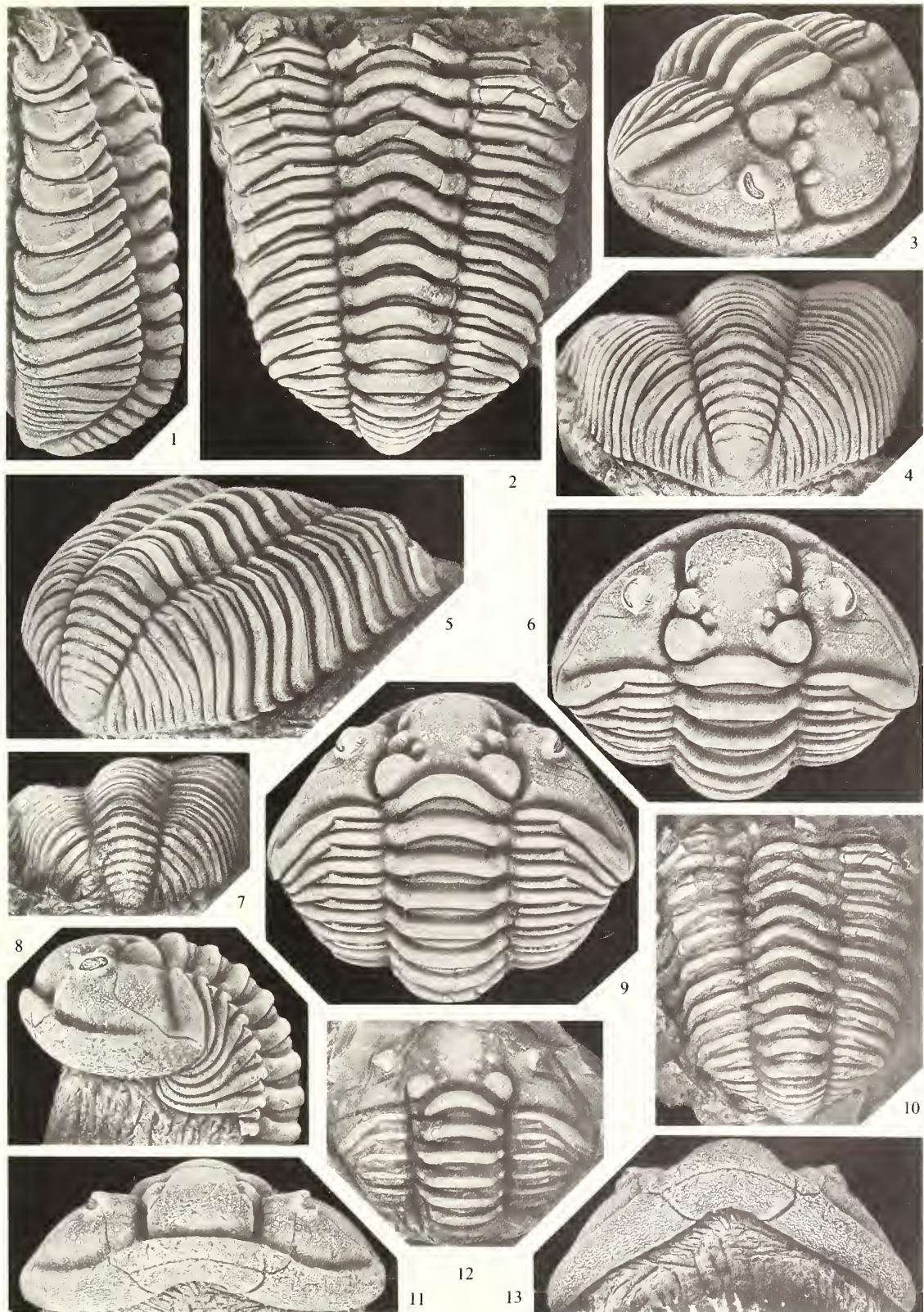
Rostral plate (Pl. 90, fig. 2; Pl. 91, fig. 13) composed of border and doublure sectors. Border sector and rostral suture broadly arched; connective suture abaxially convex. Hypostoma apparently missing on figured material.

Thorax has thirteen segments. Gently convex (sag.) axial ring very gradually widens (exsag.) abaxially from median line and is produced into gently inflated node at axial furrow (Pl. 91, fig. 9). Articulating half-ring about as wide (sag.) as axial ring sagitally; articulating furrow shallow medially, deeper and narrower (exsag.) abaxially. Posterior pleural band strongly convex (exsag.), forms a narrow bounding rim around the flat pleural facet. Dorsally the pleural furrow is relatively wide (exsag.), deep, and U-shaped, reduced to a rill-like slit on pleural facet (Pl. 91, fig. 1). Anterior pleural band tightly convex (exsag.), narrower, and slightly lower than posterior band.

Pygidium is slightly less than twice as wide as long. Axis is slightly less than half the pygidial width (Pl. 90, fig. 2), reaches well above pleural regions, is strongly convex (sag.), has seven (Pl. 90, fig. 2) or eight (Pl. 91, fig. 4) axial rings (other specimens have only six). All axial rings except the last defined posteriorly by complete ring furrows which are weakest medially; last ring furrow discontinuous; terminal axial piece rounded. Axial furrow clearly impressed, weakest posteriorly. Inner part of pleural region falls steeply from axial furrow, outer

EXPLANATION OF PLATE 91

Figs. 1-13. *Calymene blumenbachii* Brongniart in Desmarest, 1817. 1, 2, 4, 5, 7, and 10, MGUH 16.806, Much Wenlock Limestone Formation, Wren's Nest, Dudley; paralectotype of *C. tuberculata* (Brünnich, 1781) and 'second' specimen of Shirley (1933), pygidium and thorax. 1, lateral; 2, dorsal; 4, posterior; 5, posterior-oblique; all views of prepared specimen, $\times 2$. 7, posterior; 10, dorsal; both views of unprepared specimen, $\times 1\cdot5$. 3, 6, 8, 9, and 11-13, MGUH 16.805, Much Wenlock Limestone Formation, Wren's Nest, Dudley; lectotype of *C. tuberculata* (Brünnich, 1781) and 'first' specimen of Shirley (1933), cephalon and partial thorax. 3, oblique; 6, dorsal (cephalon); 8, lateral; 9, dorsal (thorax); 11, frontal; 13, ventral; all views of prepared specimen, $\times 2$. 12, dorsal (thorax) view of unprepared specimen, $\times 1\cdot5$.



part becomes vertically inclined. There are five distinctly impressed pleural furrows which are best marked at their mid-length and almost reach lateral margin (Pl. 90, fig. 3; Pl. 91, fig. 5). Interpleural furrows are slightly longer than pleural furrows, deepest distally, become very faint more proximally though are never completely effaced, are slightly better impressed again immediately adjacent to axial furrow. Fifth interpleural furrow runs on outside of an exsagittally directed ridge which probably represents anterior pleural band of sixth pleura and confines (abaxially) the postaxial sector. Inside this ridge is a very shallow furrow. In lateral profile there is a break in slope between terminal axial piece and postaxial sector. Border rolls under at lateral margin, is widest (tr.) anteriorly.

Sculpture on glabella and fixed and free cheek inside posterior and lateral borders consists of closely spaced large to small granules. Abundance of granules falls off towards furrows and they are absent in deepest part of axial furrow, preglabellar furrow, lateral and posterior border furrows, and occipital furrow. Granules are closely packed and more uniform in size on outer side of anterior border, lateral border, rostral plate, central part of pygidial axis, distal posterior margins of pleurae, outer pleural region, and border roll of pygidium; on posterior part of lateral border roll they are more elongate and scale-like, on cephalic and pygidial borders more flattened. Much more widely scattered fine- to medium-sized granules on thorax, except for pleural, axial, and articulating furrows. Pleural facets have very fine granules. Granules are scarce on inner part of pygidial pleural region and abaxial part of pygidial axis.

Discussion. The description above is of the three trilobites figured herein, but it can be applied to other specimens of the species. In the lectotype of *C. tuberculata* the glabellar and cephalic width to length ratio and convex outline of the frontal glabellar lobe is slightly greater than that of the *C. blumenbachii* lectotype (cf. Pl. 90, fig. 1; Pl. 91, fig. 6), and the paralectotype of *tuberculata* has an extra, very weak eighth pygidial axial ring furrow compared with the *blumenbachii* lectotype (cf. Pl. 90, fig. 5; Pl. 91, fig. 4), but such variation is considered to be intraspecific. A description of the hypostoma and a comparison with other closely related taxa, for example *C. clavicula* Campbell, 1968 from the Silurian of Oklahoma or *C. neotuberculata* Schrank, 1970 from the Wenlock of the Baltic, is in preparation by me for publication elsewhere. *C. ceratophthalma* Woodward, 1868 and *C. lata* Shirley, 1936, both from the Much Wenlock Limestone Formation of Dudley, I consider to be junior synonyms of *C. blumenbachii*.

Occurrence. Much Wenlock Limestone Formation, West Midlands inliers, England; late Wenlock mudstones and siltstones, Penylan, Rumney inlier, Cardiff area, South Wales.

Acknowledgements. I am indebted to the following who helped in the search for the material used in this paper: Dr Francoise Bigey (Laboratoire de Paléontologie des Invertébrés, Université P. et M. Curie, Paris), Dr J.-C. Fischer (Muséum National d'Histoire Naturelle, Paris), Dr Søren Floris (Geologisk Museum, Københavns Universitet), Dr John Peel (Grønlands Geologiske Undersogelse, København). Professor H. B. Whittington (Cambridge) kindly reviewed the manuscript for the author; Mr R. V. Melville (ICZN, London) and Dr J. D. D. Smith (ICZN, London) gave advice on questions of nomenclature. The ostracode work of Dr David J. Siveter (Leicester) is gratefully acknowledged.

REFERENCES

- BARRANDE, J. 1852. *Système Silurien du centre de la Bohême. 1ère partie: Recherches paléontologiques. Vol. 1. Crustacés: Trilobites*, xxx + 935 pp. Prague and Paris.
 —— 1872. *Système Silurien du centre de la Bohême. 1ère partie: Recherches paléontologiques. Supplément au vol. 1. Trilobites, Crustacés divers et Poissons*, xxx + 647 pp. Prague and Paris.
- BASSETT, M. G. 1976. A critique of diachronism, community distribution and correlation at the Wenlock–Ludlow Boundary. *Lethaia*, **9**, 207–218.
- BASSLER, R. S. 1915. Bibliographic index of American Ordovician and Silurian fossils. *Bull. U.S. natn. Mus.* **92**, 2 vols. 1521 pp.
- BRONGNIART, A. 1822. *In BRONGNIART, A. and DESMAREST, A. G. Histoire naturelle des Crustacés fossiles, sous les rapports zoologique et géologique. Savoir: les Trilobites par A. Brongniart. Les Crustacés proprement dits par A. G. Desmarest*, vii + 154 pp. Paris.
- BRÜNNICH, M. T. 1781. Beskrivelse over Trilobiten, en Dyreslaegt og dens Arten, med en nye Arts Aftegning. *Nye Saml. K. dansk. Vid. Selsk. Skr.* **1**, 384–395.

- BUTLER, A. J. 1939. The stratigraphy of the Wenlock Limestone at Dudley. *Q. Jl geol. Soc. Lond.* **95**, 37–74.
- CARRIOL, R.-P. 1984. Types et figurés de trilobites du Muséum national d'Histoire naturelle. *Bull. Mus. natn. Hist. nat. Paris*, 4^e sér. **6**, sect. C, No. 1, 3–32.
- CHATTERTON, B. D. E. and CAMPBELL, K. S. W. 1980. Silurian trilobites from near Canberra and some related forms from the Yass Basin. *Palaeontographica*, **A167**, 77–119.
- DESMAREST, A. G. 1816. In *Nouv. Dict. Hist. nat.* (2nd edn.), **5**, 49–50.
- 1817. In *ibid.* **8**, 517–518.
- LINDSTRÖM, G. 1885. Förteckning på Gotlands Siluriska Crustacéer. *Ofvers K. VetenskAkad. Förh. Stockh.* **6**, 37–100.
- LYTTELTON, C. 1750. A letter from the Rev. Charles Lyttelton, LL.D. and F.R.S., Dean of Exeter, to the President, concerning a nondescript petrified insect. *Phil. Trans. R. Soc.* **46**, 598–599.
- MÄNNIL, R. M. 1977. East Baltic Lower Silurian Calymenidae (Trilobita). In KALJO, D. (ed.). Facies and fauna of the Baltic Silurian. *AKad. Nauk. Eston. SSR. Inst. Geol. Tallinn*, 240–258. [In Russian with English and Estonian summaries.]
- M'Coy, F. 1851. In SEDGWICK, A. and M'Coy, F. *A synopsis of the British Palaeozoic rocks, with systematic descriptions of the Palaeozoic fossils in the geological museum of the University of Cambridge*, 184 pp. Cambridge and London.
- MILNE EDWARDS, H. 1840. *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux*, **3**, 638 pp. Paris.
- MORTIMER, C. 1750. Some further account of the before-mentioned Dudley Fossil, by the Editor of these Transactions. *Phil. Trans. R. Soc.* **46**, 600–602.
- MURCHISON, R. I. 1839. *The Silurian System, founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester and Stafford; with descriptions of the coalfields and overlying formations*, xxxii + 768 pp. London.
- 1859. *Siluria. The history of the oldest fossiliferous rocks and their foundations, with a brief sketch of the distribution of gold over the earth* (3rd edn.), xx + 592 pp. London.
- NICHOLSON, H. A. and ETHERIDGE, R. 1879. A monograph of the Silurian fossils of the Girvan district in Ayrshire with special reference to those contained in the 'Gray Collection', **1** (2), 136–233. Edinburgh and London.
- REED, F. R. C. 1906. The lower Palaeozoic trilobites of the Girvan district, Ayrshire. *Palaeontogr. Soc. [Monogr.]*, **(3)**, 97–136.
- SALTER, J. W. 1865. A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations. *Ibid.* (2), 81–128.
- SCHRANK, E. 1970. Calymeniden (Trilobita) aus Silurischen Geschieben. *Ber. dt. Ges. geol. Wiss.*, A, **15**, 109–146.
- SHIRLEY, J. 1933. A redescription of the known British Silurian species of *Calymene* (s.l.). *Mem. Proc. Manchr. lit. phil. Soc.* **77**, 5–67.
- 1936. Some British trilobites of the family Calymenidae. *Q. Jl geol. Soc. Lond.* **92**, 384–422.
- SIVETER, DAVID J. 1978. The Silurian. In BATE, R. H. and ROBINSON, J. E. (eds.). A stratigraphical index of British Ostracoda. *Geol. J. Special Issue*, **8**, 57–100.
- 1980. British Silurian Beyrichiacea (Ostracoda). *Palaeontogr. Soc. [Monogr.]*, **133**, 1–76.
- SIVETER, DEREK J. 1977. The middle Ordovician of the Oslo Region, Norway, 27. Trilobites of the family Calymenidae. *Norsk geol. Tidsskr.* **56** (for 1976), 355–396.
- 1979. *Metacalymene* Kegel, 1927, a calymenid trilobite from the Kopanina Formation (Silurian) of Bohemia. *J. Paleont.* **53**, 367–379.
- 1980. Evolution of the Silurian trilobite *Tapinocalymene* from the Wenlock of the Welsh Borderlands. *Palaeontology*, **23**, 783–802.
- 1983. *Calymene lawsoni* and allied species from the Silurian of Britain and their stratigraphic significance. In BRIGGS, D. E. G. and LANE, P. D. (eds.). *Trilobites and other arthropods: papers in honour of Professor H. B. Whittington*, F.R.S. *Spec. Pap. Palaeont.* **30**, 69–88.
- THOMAS, A. T., OWENS, R. M. and RUSHTON, A. W. A. 1984. Trilobites in British stratigraphy. *Spec. Rep. geol. soc. Lond.* **16**, 78 pp.
- TOMCZYKOWA, E. 1957. Trilobites from the Wenlock and lower Ludlow graptolitic shales of the Święty Krzyż Mountains. *Biol. Inst. geol.* **122**, 83–143. [In Polish with Russian and English summaries.]
- WHITTINGTON, H. B. 1959. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology*. Part O. *Arthropoda*, 1, xix + 560 pp. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.

- WHITTINGTON, H. B. 1983. *Calymene* Brongniart, 1822 in Brongniart & Desmarest, 1822 (Trilobita): Proposed conservation. Z.N. (S.) 637. *Bull. zool. Nom.* **40**, (3), 176–178.
- and SIVETER, DEREK J. In press. Type species of the genus *Calymene* Brongniart in Brongniart & Desmarest, 1822 and proposed suppression of the name *tuberculatus* Brünnich, 1781: rider to Z.N. (S.) 637. *Bull. zool. Nom.*
- WOODWARD, H. 1868. On a newly-discovered long-eyed *Calymene* from the Wenlock Limestone, Dudley. *Geol. Mag.* **5**, 489–494.
- 1869. On a newly-discovered long-eyed trilobite from Dudley. *Ibid.* **6**, 43–44.

DEREK J. SIVETER

Department of Geology
University of Hull
Cottingham Road
Hull HU6 7RX

Typescript received 13 February 1985

Revised typescript received 22 March 1985

THE PALAEONTOLOGICAL ASSOCIATION

Notes for authors submitting papers for publication in

PALAEONTOLOGY

and

SPECIAL PAPERS IN PALAEONTOLOGY

prepared by the Editors and Council of the Palaeontological Association

PUBLICATION POLICY AND PRACTICE

Scope of publications. Manuscripts on any aspect of palaeontology will be considered for publication. Papers on Recent material may be acceptable if their palaeontological relevance is explicit. Preference is given to manuscripts with more than local significance. Review papers are particularly welcome and a fee may be payable by the Association. Prospective authors of such papers who wish to take advantage of this offer should first contact the Publications Secretary. Papers whose principal purpose is to describe one or two new species of common groups are not usually published. A high standard of illustration is a feature of the journal. The series *Special Papers in Palaeontology* is for papers longer than those normally accepted for *Palaeontology* (see below, p. 800) or for collections of shorter papers with a common theme.

Palaeontology and *Special Papers in Palaeontology* provide opportunity for illustration using both Plates and Text-figures, but authors are required to pay special attention to brevity in the composition of both illustrations and text. Short papers are particularly welcome in *Palaeontology*. The style should be simple. Care should be taken to avoid long complicated sentences and the unnecessary use of unusual words or phrases, so that papers may be read easily by those unaccustomed to the English language.

Submission. Papers should be written in English, with British rather than American spelling. Three complete copies of the typescript (including explanatory text for illustrations and tables) should be submitted. Three sets of good-quality copies of all text-figures and plates should accompany each typescript; these should be reduced to publication size. The original figures (if they are small) may, if necessary, serve as illustrations for one copy. Although failure to provide three copies will usually result in slower handling, no paper will be rejected for this reason. Submissions should be made to the Secretary of the Publications Committee at the address given on the inside cover of the current issue of *Palaeontology*. The Secretary will assign each paper to an editor who will handle all subsequent communication with the author. Papers will be sent to at least two referees, including at least one specialist in the field covered by the paper. The editor will inform authors of referees' comments and will normally require referees' suggestions to be implemented. Changes of an editorial nature will usually be requested at this stage, but these will be kept to a minimum if authors will follow the instructions given below. Adherence to these rules will also improve the chances of publication within the target time, currently less than 12 months from the date the typescript is first received.

Copyright. Authors of papers that are accepted for publication will be asked to sign over the copyright to the Association.

THE FORMAT OF THE MANUSCRIPT

Typing. Papers should be typed on good-quality paper, preferably of International A4 size (297 × 210 mm). All pages of typing, including references and explanations of illustrations, should be numbered consecutively. Plate and text-figure explanations should be put on separate sheets following the rest of the typescript. Double spacing of lines (not one and a half) is required throughout (including references and explanations of text-figures and plates), and there should be a 3-cm left-hand margin.

The *Title* should be short but informative and should normally include fossil group, age, and general location. It should not include the names of new taxa.

A concise *Abstract* of not more than 200 words is required at the beginning of all papers. It should summarize results (rather than contents) of the paper and must mention all new systematic names erected; it should be carefully prepared so that it will serve satisfactorily for international use in abstracting journals.

Style and arrangement. Authors should consult recently published volumes of *Palaeontology* and construct their papers in accordance with the format used there. Attention is drawn to the following practices, adherence to which will keep editorial delays to a minimum.

Three orders of heading are used. In typescript these should be represented as follows: 1st order headings, upper-case letters centred; 2nd order headings, lower-case letters underlined for italics, flush to the left-hand margin, on a line of their own; 3rd order headings, as 2nd order, but followed by a full stop and with the text continuing on the same line. Nothing else should normally be underlined in the text with the exception of words requiring italicization such as generic and specific names, and foreign words and phrases that are not Anglicized.

In the text, references should be cited by the author's name and the date of the publication, without a comma in between. Brackets are used as appropriate, e.g. '... as discussed by Dickens (1963)'; 'as discussed previously (Dickens 1963)'. The page reference to any quotation must be given, e.g. Dickens (1963, p. 20). A work with three or more authors (Squeers, Pickwick and Carton 1964), may be shortened (Squeers *et al.* 1964) unless ambiguity results. Note that the ampersand (&) is *not* used anywhere in the text.

Systematic work is always introduced by the 1st order heading: 'SYSTEMATIC PALAEONTOLOGY'. Second order headings are often not appropriate in this section. The conventions of the journal regarding a marginal or a central position on the page, the order of the different sections, and the format for synonymies, references to illustrations, etc., should be followed with reference to previous issues of *Palaeontology*. Note that information accessory to systematic descriptions such as type data, etymology, stratigraphic position (which should be detailed), curatorial information, description, etc., is set in small type. Such sections should be adjacent to avoid frequent changes between large and small type. Care should be taken to ensure that diagnoses, descriptions, and discussion are kept distinct. Synonymies are also set in small type. Only the most important previous citations should be given. This style is:

- 1841 *Ammonites Requienianus* d'Orbigny, p. 315, pl. 93, figs. 1–4.
- 1903 *Coilopoceras requienianum* (d'Orbigny); Hyatt, p. 99.
- 1975 *Coilopoceras requieni* (d'Orbigny); Dassarma and Sinha, p. 70, pl. 9, fig. 6; text-fig. 8.

Note that figure and plate numbers, etc., that were originally given in Roman numerals are always transliterated into arabic figures. This is also the case in the main text and the references.

Authors are encouraged to use symbols to indicate the degree of confidence with which particular items in the list are referred to the species under discussion. Such symbols are given in MATTHEWS, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, 16, 713–719. For example:

- v1937 = the author has seen the cited material and agrees with the reference.
- v*1937 = the author has seen the type of the species.

Name(s) and correspondence address(es) should be typed on the right-hand side of the page after the reference list.

Footnotes. These will only be allowed in exceptional circumstances. Permission to publish, for instance, should be included with other acknowledgements.

References should be arranged in alphabetical order of authors' names at the end of the paper. The author's name should be typed in capitals, with the initials after the surname. It should be followed by the year of publication, and the title of the paper in full. In the titles of papers, capital letters should be used only for proper nouns, and for all nouns in German. The name of the journal (which should be underlined) should be abbreviated in the style of the fourth edition of the *World List of Scientific Periodicals*, Butterworths, London, 1963–1965. New titles and abbreviations are listed in *British Union Catalogue of Periodicals*, Butterworths, London (quarterly), 1964 onwards. Volume number (part or fascicle number, in brackets, only if really necessary) and pagination should be given in arabic figures with the items separated by commas only. Volume numbers only should be given a wavy underline to indicate bold type. The titles of books should be underlined for printing in italics, and the number of pages (e.g. 560 pp.), publisher, and place of publication should be given in that order. When a reference has been translated or transliterated, the original language should be stated in square brackets at the end. Examples:

- BOUCOT, A. J. 1981. *Principles of benthic marine paleoecology*, xv+463 pp. Academic Press, New York and London.
- and JOHNSON, I. G. 1979. Pentamerinae (Silurian brachiopods). *Palaeontographica*, A163, 87–129.
- COCKS, L. R. M. and MCKERROW, W. S. 1978. Silurian. In MCKERROW, W. S. (ed.). *The ecology of fossils*, 93–124. Duckworth, London.
- 1984. Review of the distribution of the commoner animals in Lower Silurian marine benthic communities. *Palaeontology*, 27, 663–669.
- D'ORBIGNY, A. C. V. D. 1853. Note sur le nouveau genre *Hypotrema*. *J. Conchyliologie*, 4, 432–438, pl. 10.
- HOLLAND, C. H. 1971. Some conspicuous participants in Palaeozoic symbiosis. *Scient. Proc. R. Dubl. Soc.* A4(2), 15–26.
- JAANUSSON, V. 1979. Ecology and faunal dynamics, 253–294. In JAANUSSON, V., LAUFELD, S. and SKOGLUND, R. (eds.). Lower Wenlock faunal and floral dynamics—Vattenfallet section, Gotland. *Sver. geol. Unders. Afh. C762*, 1–294.
- NORTHROP, S. A. 1939. Paleontology and stratigraphy of the Silurian rocks of the Port Daniel—Black Cape Region, Gaspé. *Spec. Pap. geol. Soc. Am.* 21, i–ix, 1–302.
- OBUT, A. M. 1964. Podtip Stomochordata. Stomokhordovye. In ORLOV, Y. A. (ed.). *Osnovy paleontologii: Echinodermata, Hemichordata, Pogonophora, Chaetognatha*, 279–337. Nedra Press, Moscow. [In Russian.]
- RASMUSSEN, H. W. 1978. Articulata. In MOORE, R. C. and TEichert, C. (eds.). *Treatise on invertebrate paleontology*. Part T. *Echinodermata* 2(3), T813–T928. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.
- SHELDON, P. A. 1979. Functional morphology of *Baltoeurypterus*. Ph.D. thesis (unpubl.), University of Cambridge.
- STORMER, L. 1934a. Merostomata from the Downtonian sandstone of Ringerike, Norway. *Skr. norske Vidensk-Akad. Mat.-naturv. kl.* 1933 (10), 1–125.
- 1934b. Downtonian Merostomata from Spitzbergen, with remarks on the suborder Synziphosura. *Ibid. 1934* (3), 1–26.
- WATKINS, R. 1979. Benthic community organization in the Ludlow Series of the Welsh Borderland. *Bull. Br. Mus. nat. Hist. (Geol.)*, 31, 175–280.
- WHITTARD, W. F. 1934. A revision of the trilobite genera *Deiphon* and *Onycopyge*. *Ann. Mag. nat. Hist.* (10), 14, 505–533.
- WHITTINGTON, H. B. 1977. The Middle Cambrian trilobite *Naraoaia*, Burgess Shale, British Columbia. *Phil. Trans. R. Soc.*, B 280, 409–443.

Units and symbols. As far as possible the recommendations contained in *Quantities, Units and Symbols* (second edition, The Royal Society, London, 1975) should be followed; in particular, the International System of Units (SI) should be used whenever it is practicable to do so (e.g. μm , mm, m, kg). Note that no full stop is used after such symbols.

LINE ILLUSTRATIONS AND TABLES

Text-figures. Original drawings, in black on good quality white card or on good quality drawing film, should be submitted. They should preferably be made double the final size but no larger, and when reduced must not exceed the type area of a page 200 × 147 mm. If the caption (explanation) of a full-page figure is long, allowance for its inclusion on the same page should be made by reducing the height of the figure. In composing smaller text-figures, space on the page is best used if the figure is wide rather than high, and the full width of the page should be used if possible. Individual prints and diagrams within one text-figure should be lettered (A, B, C, etc.) and a linear scale bar added where appropriate. All lettering should be inserted by the author, and must be readable when reduced. Good quality photographic copies (unglazed) may be suitable for reproduction and are preferable to excessively large originals; originals may, however, have to be requested by the editor.

Professional preparation of text-figures. The Association has allocated a limited sum of money to help offset the cost of professional preparation of text-figures that require skills above those normally available to authors, where such professional help is not otherwise available. Authors wishing to apply for grants from this fund should approach the Association through the Secretary of the Publications Committee, giving details of the proposed text-figures together with a draft manuscript. Awards will be made at the discretion of the Association and, although funds will only be granted if it appears likely that the manuscript will ultimately satisfy the Association's requirements, the awarding of financial aid will not commit the Association to publication.

Tables. Tables should preferably be carefully drafted to the same standards as text-figures; alternatively, they may be prepared on an electric typewriter, paying special attention to compactness and legibility, and using a carbon ribbon. Two copies at correctly reduced size must be supplied in addition to the originals. Fold-out tables are not acceptable, because of prohibitive cost. If a table of larger than page size is essential, it should be arranged for two facing pages.

EXPLANATION OF PLATE X

This plate has been designed to show the common defects noted in plates submitted for publication. General comment: the plate lacks balance of contrast and is poorly laid out. If your plate shows any of the defects illustrated here, it should not be submitted for publication. Submitted copy should be made up of normal black and white prints, not half-tones. Otherwise, interference dots (as seen here) will result. Top row, in general. The prints do not line up along their top and bottom edges. The gap between 1 and 2 is not parallel sided or perpendicular to the margin. Note the unacceptably variable size and shape of the cut-off corners to allow the insertion of figure numbers.

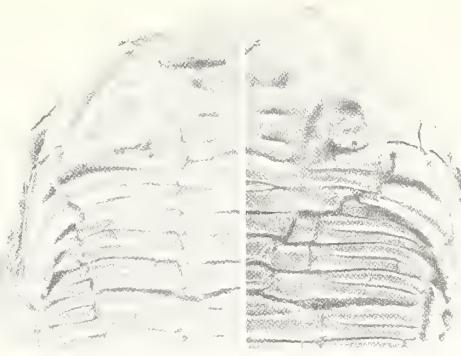
- Fig. 1. Low contrast showing loss of detail. Note that the print is not mounted perpendicular to the margin.
- Fig. 2. Moderate contrast reveals greater detail.
- Fig. 3. Not sharply in focus, and the appearance is therefore fuzzy.
- Fig. 4. Negative scratched, causing lines on the print.
- Fig. 5. SEM. The print is marred by scan lines caused by charging, the gold coating on the background is badly cracked and the lower part of the specimen has been trimmed off.
- Fig. 6. SEM. This print shows excessive contrast. Also, though the illumination should appear to come from the top or top left, the print has been mounted at right angles to the desired orientation. The specimen is dirty and not worth illustrating.
- Fig. 7. A hair on the negative is superimposed on the glabella.
- Fig. 8. The background has been inexpertly painted out with Indian ink. Note the loss of ribs below the aperture and the crude painting-out around the ribs elsewhere. The print was damaged during mounting, causing artefacts near the aperture.
- Fig. 9. The background has been clumsily cut away using scissors. Note the damage to the outline of the ribs and local accidental inclusion of background.
- Fig. 10. The unevenly illuminated specimen merges with the background.



1



2



3



4



5



6



7



8



9



10

How not to make a plate

Explanations of text-figures and tables should be typed (double-spaced) and placed at the end of the typescript. They should be numbered consecutively with the rest of the typescript.

Position in text. The approximate position desired for insertion of text-figures, tables, and plates should be indicated on the typescript.

PLATES AND TEXT-PHOTOGRAPHS

It continues to be editorial policy to maintain a high standard of plate quality. Authors are reminded that the published plate cannot be of better quality than the original. Plate X shows the common defects noted in plates submitted for publication. If your plates show any of these defects, they should be corrected before submitting them to the journal.

Size. The size of plates is 203 × 147 mm. Where authors have photographs which fill less than a full page, they will be referred to as text-figures. These will be reproduced by the same process as plates but to text-figure dimensions (see above). Every effort should be made to ensure that no page space is wasted, particularly with respect to the width of text-figures composed of photographs.

Plates and text-photographs should be submitted at publication size. Large plates cause problems of handling and offer few advantages of improved quality. Magnifications of individual figures should be stated in the caption, not indicated by scale-bars on the photographs.

Lighting. The convention of lighting fossils from the top left should be followed where possible.

Preparation of photographic prints. Photographs should be sharply in focus and printed on glossy paper. They should be of medium contrast, using the range of shades of grey but avoiding extremes of black and white. Artefacts such as dirt on the negative or scratches from the enlarger should be absent from the prints. All prints on a plate should be of even tone and contrast. For this reason, it is often better to avoid mixing conventional photographs with photomicrographs. Where possible, remove labels from macrofossils before photography. Avoid unsightly backgrounds.

Mounting. Mount the prints on clean, white board using dry mounting tissue or a non-aqueous glue. Use the same method for all prints. Avoid glue on the background or on the print surface. Place prints as close together as is reasonable, making full use of plate space. Rectangular prints should not only be cut rectangular but also mounted parallel to each other and to the sides of the plates. Leave space for figure numbers either directly below each print or by cutting off a bottom corner (Pl. X, fig. 3).

Where it is desired to remove the background from around a fossil, the print should be carefully trimmed to the edge of the fossil and mounted on clean white board. Black backgrounds are permitted, but the author is responsible for accurately delimiting the edge of the fossil. Roughly trimmed prints should be precisely outlined using black drafting ink.

Each plate should be protected by a tracing paper overlay attached along the upper edge. The author's name, and title of the paper, should be written on the back of the originals of each text-figure and plate.

Numbering. Figure numbers should run consecutively from left to right from top to bottom of each plate. 1a, 1b, 1c, etc., should only be used to distinguish different views of the same fossil. Numbers should be pencilled on the overlay. Do not stencil numbers on the plates. All numbers are added by the printers, although space for such numbers should be provided when the plate is made up by the author.

Explanations of plates should be typed and placed at the end of the typescript. They should be brief but adequate. The magnification of each figure should be stated. The museum number of the specimen should be given. For example:

Fig. 1. *Ammonia beccarii* (Linné). Repository and catalogue number. Description, locality, horizon, magnification.

Figs. 2–6. *Elphidium crispum* (Linné). 2, repository and catalogue number; description, locality, horizon, magnification. 3a, repository and catalogue number; description, locality, horizon, magnification. 3b, description, magnification. 4, etc.

ADMINISTRATION

Preservation of types and other specimens. In accordance with recommendations of the International Codes of Botanical and Zoological Nomenclature, all illustrated fossils should be registered and deposited in an appropriate permanent institution, preferably a museum with staff and facilities capable of ensuring their availability for future reference in perpetuity. The registered numbers should be quoted. Papers that fail to meet this requirement will not be published.

Proofs. Authors will normally receive one proof; this proof is for the purpose of correcting printer's errors and not for altering the wording or substance of the paper. Authors may be charged for excessive alterations. The editors will only be responsible for author corrections notified by return of post. Whenever possible, plate proofs will be sent to the authors with the text proofs.

Offprints. Fifty offprints of each paper will be sent free of charge; further copies may be purchased at prices shown on the order form which will be sent with the proofs to the author (or corresponding author in the case of multi-author papers).

Deposition of data. The Association makes use of the scheme run by the British Library, Lending Division, whereby publication expenses can be saved by depositing tables of data and other reference material with the British Library rather than printing them. The deposited material is stored on microfiches, and either microfiche or full-size copies may be obtained from the British Library by an applicant (preferably using British Library prepaid coupons) on a standard scale of charges which allows for postage etc.

The British Library will only accept deposited material through the Publications Committee of the Association; all such material will be referred to as part of a published paper. The published paper will bear a reference to deposited copy with full details of its pagination and means of acquisition, e.g. '... have been deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14003 (26 pages)'. Prepaid coupons for such purposes are held by many technical and university libraries throughout the world. They may be purchased from the British Library, Lending Division, Boston Spa, Wetherby, Yorks. LS23 7BQ. Association policy is that neither plates nor formal taxonomic data will be considered for deposition. Authors should indicate and separate as appendices those parts of their papers that they propose for deposition; the Publications Committee may also recommend that part of a paper should be deposited rather than be printed.

Preparation of copy for deposition. Copy must be prepared by the author according to the following specifications. Editors will not undertake the preparation of copy.

- (i) Copy must be camera-ready.
- (ii) Maximum page size for text or tables in typescript or computer print out is 330 mm high × 240 mm. wide, including margins. Optimum page size is A4 size.
- (iii) Tabular matter should be headed descriptively on the first page, with column headings recurring on each page.
- (iv) Prefatory text, which should contain the abstract from the parent paper, should be included.
- (v) All pages must be consecutively numbered.

Authors with large sections for deposition are advised to consult the Secretary of the Publications Committee for further information.

SPECIAL PAPERS IN PALAEONTOLOGY

Preparation of papers for this series should be in the same style as for *Palaeontology*.

Submission. Prospective authors should consult the Editors well in advance of submission, supplying as much information as possible.

Cost of publication. The Association's funds for this series are limited. Authors are asked to obtain grants wherever possible. Manuscripts should not normally exceed the equivalent of 110 published pages.

Offprints. A small number of free offprints will be supplied and further copies may be obtained at a special reduced charge. For multiple author volumes such as conference proceedings, authors will receive one free copy of the volume but no free reprints. Reprints of individual papers may be ordered at the standard charge. Details will be supplied at the time by the editor concerned.

GRANTS IN AID OF PUBLICATION

Palaeontology has no compulsory page or plate charges. However, authors are requested to seek grants in aid of publication from their institutions or from research funds, or to apply for publication costs in research grants. Some financial support is particularly welcome, and may be necessary, for long papers.

Although acceptance of a paper for publication will not be dependent on the receipt of such grants, authors will appreciate that the funds available to the Association are limited. Every grant or donation will therefore directly help the Association's publication programme.

1985

THE PALAEONTOLOGICAL ASSOCIATION

THE PALAEONTOLOGICAL ASSOCIATION

ANNUAL REPORT OF COUNCIL FOR 1984

MEMBERSHIP AND SUBSCRIPTIONS. Membership totalled 1,420 on 31 December 1984, an increase of 7 over the previous year. There were 932 Ordinary Members, an increase of 22; 48 Retired Members, an increase of 5; 123 Student Members, a decrease of 20; and 317 Institutional Members (no change). The number of individuals and institutions subscribing to *Palaeontology* through Marston's agency was 435, a decrease of 7. Subscriptions to *Special Papers in Palaeontology* number 123 individuals, an increase of 1, and 131 Institutions, an increase of 8. Standing orders for *Special Papers* through Marston's agency were about 100 for *Special Paper 31*. Sales of back parts of *Palaeontology* via the Membership Treasurer realized £98·43. Sales of back parts of *Palaeontology* to Institutional Members yielded £21·98 plus US \$34.00. Sales of Special Papers 1-21 under the special offer yielded £2,278, less about £700 in postage; other sales of *Special Papers* to individuals yielded £1,216·19, and to Institutions, £131 plus US \$114. Sales of 26 copies of the *Atlas of the Burgess Shale* through the Marketing Manager yielded £241·50 plus US \$492.94. Sales of *Fossil Plants of the London Clay* through the Marketing Manager yielded £1,162·15 plus US \$311.50 for 281 copies.

FINANCE. During 1984 the Association published Volume 27 of *Palaeontology* at an estimated cost of £53,952 (including postage and distribution). *Special Papers 31* and *32* were published at a cost of £10,305 and £13,450 (provisional) respectively. In addition the *Atlas of Invertebrate Macrofossils* was published jointly with Longman, at a cost to the Association of £2,246. The Association is grateful to all those who made donations.

PUBLICATIONS. Volume 27 of *Palaeontology*, published in 4 parts during 1984, contained 898 pages and 80 plates. *Special Papers 31: Systematic Palaeontology and Stratigraphic Distribution of the Ammonite Faunas of the French Coniacian* by W. J. Kennedy and *32: Autecology of Silurian Organisms* edited by M. G. Bassett and J. D. Lawson were published in November and December respectively.

MEETINGS. Eight meetings were held in 1984. The Association is indebted to the organizers, hosts, and field leaders of these.

- a. *Joint Meeting with the Geological Society* on 'Fossils and Sealevel Changes', held on 8 February at Burlington House, Piccadilly, London. More than 100 attended the meeting, which was convened by Dr R. Riding.
- b. *Review Seminar* on 'Palaeobiogeography', held on 15 February at the University of Bristol. More than 200 attended the meeting. The local secretary was Professor R. J. G. Savage.
- c. *Twenty-seventh Annual General Meeting*, held in the Lecture Theatre of the Geological Society of London on 14 March. Professor Yves Coppens delivered the Annual Address on 'Hominid Evolution'. The Sylvester-Bradley Award was made to Mr P. Doyle.
- d. *Field Meeting*, organized by the Carboniferous Group, to Fife and Lothian, Scotland led by Dr A. R. M. Macgregor. About 50 attended the excursion which was held on 13-16 April.
- e. '*Progressive Palaeontology*' Meeting, aimed at younger researchers, held at Bedford College, London, on 29 May. More than 53 attended the meeting, which was convened by Dr Jane Francis.
- f. *Field Meeting* on the 'Lower Palaeozoic of the Lake District', held on 14-17 September, and organized and led by Dr A. W. A. Rushton and Dr D. E. White. More than 20 attended.
- g. *Review Seminar* on 'Extinctions', held on 14 November at the Open University, Milton Keynes. Over 200 people attended. The local secretary was Dr P. W. Skelton.
- h. *The Annual Conference*, held at Fitzwilliam College, Cambridge, on 19-22 December took the form of a thematic session on taphonomy followed by an open meeting. About 150 attended. The President's Award was made to Dr M. J. Benton. An excursion was led to the Upper Jurassic of Upware by Dr S. R. A. Kelly. The local secretary was Dr C. P. Hughes.

COUNCIL. The following members served on Council following the Annual General Meeting on 14 March 1984: *President*: Professor C. Downie; *Vice-Presidents*: Dr J. C. W. Cope, Dr R. Riding; *Treasurer*: Dr M. Romano;

Membership Treasurer: Dr A. T. Thomas; *Secretary:* Dr P. W. Skelton; *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 C. R. C. Paul, Dr D. J. Siveter (Circular Reporter), Dr A. B. Smith, Professor T. N. Taylor.

CIRCULARS. Four Circulars, numbers 115–118, were distributed to Ordinary, Student, and Retired Members, and on request to over 90 Institutional Members.

COUNCIL ACTIVITIES. Besides the now well-established Review Seminars and Field Meetings, two new kinds of meeting were launched with great success in 1984, to be held annually thereafter: discussions with the Geological Society have led to the institution of a meeting to be held each spring on some aspect of the broader geological applications of palaeontology; and, as a result of requests from younger members of the Association for a regular meeting at which they could informally present their results and discuss their work with each other, the 'Progressive Palaeontology' series was initiated.

The *Atlas of Invertebrate Macrofossils*, edited by Professor J. W. Murray and published by Longman on behalf of the Association came out just in time to go on show at the Annual Conference. A brochure advertising the benefits of Association membership was also published. The special offer for the sale of *Special Papers 1–21* at reduced prices, in order to clear back stock, was extremely successful.

Plans for the future include the organization of a one day session at the 3rd International Conference on Systematic and Evolutionary Biology and also the 6th Meeting of the Geological Societies of the British Isles.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING DECEMBER 1984

BALANCE SHEET AS AT 31 DECEMBER 1984

1983	£	£	1983	£	£
46,586			INVESTMENTS AT COST (see schedule)		50,459
			CURRENT ASSETS		
1,486			Sundry Debtors	2,033	
25,395			Cash at Bank	29,630	
1,912			Sylvester-Bradley Fund	1,816	
<hr/>					
28,793				33,449	
<hr/>					
			CURRENT LIABILITIES		
2,215			Subscriptions Received in Advance	2,337	
13,500			Provision for cost of publication of:		
			<i>Palaeontology 27/4</i>	13,800	
			<i>Special Paper 32</i>	13,450	
—			Sundry Creditors	2,509	
9,631			Loan from Royal Society	2,000	
<hr/>					
27,346				34,096	
<hr/>					
1447					(647)
<hr/>					
£48,033					£49,812
<hr/>					

Represented by:

PUBLICATIONS RESERVE ACCOUNT		
43,165	Balance Brought Forward	44,135
970	Excess of Income over Expenditure for the Year Transferred from Income and Expenditure Account	1,230
<hr/>		
44,135		45,365
SYLVESTER-BRADLEY FUND		
2,021	Balance Brought Forward	1,912
91	Interest	104
(200)	Grant Awarded	(200)
1,912	Balance Carried Forward	1,816
1,986	MEETING RESERVE	2,631
<hr/>		
£48,033		£49,812
<hr/>		

INCOME AND EXPENDITURE ACCOUNT

		INCOME	
1983	£	£	£
SUBSCRIPTIONS			
1984		40,231	
1983		921	
40,593		—	41,152
PALAEONTOLOGY			
Sales		25,997	
Donations		210	
28,939		—	26,207
SPECIAL PAPERS			
Sales		8,123	
Donations		1,373	
7,280		—	9,496
BURGESS SHALE PORTFOLIO			
Sales		1,069	
Postage/Stationery		(58)	
2,257		—	1,011
FOSSIL PLANTS OF THE LONDON CLAY			
Sales		1,729	
Postage/Stationery		(261)	
—		—	1,468
(1,243)			779
—			3,917
8,431			8,947
330			99
SUNDRY INCOME		—	—
£86,587			£93,076
=====			=====

FOR THE YEAR ENDED DECEMBER 1984

EXPENDITURE

1983	£	£
		<i>COST OF PUBLICATION OF PALAEOENTOLOGY</i>
		Volume 27—Part 1
		Part 2
		Part 3
		Part 4 (provisional)
		Over Provision for Volume 26, Part 4
54,821		(50)
		54,002
		<i>COST OF PUBLICATION OF SPECIAL PAPERS</i>
		No. 31
		No. 32 (provisional)
14,729		10,305
		13,450
		23,755
		<i>COST OF PUBLICATION OF:</i>
2,425		<i>Fossil Plants of the London Clay</i>
3,600		Cumulative Index
—		<i>Atlas of Invertebrate Macrofossils</i>
1,212		1,605
650		141
		2,246
		3,992
		<i>WAREHOUSING OF PUBLICATIONS</i>
GRANTS		1,919
—		100
		<i>COST OF CIRCULARS</i>
		Preparation
		Postage
		Credit
4,041		2,709
		1,826
		(480)
		4,055
		<i>ADMINISTRATIVE COSTS</i>
		Postage and Stationery
		Editorial and Expenses
		Meeting Expenses
		Audit Fee
		Membership of Societies
4,139		1,684
		212
		1,842
		225
		60
		4,023
£85,617		£91,846
		EXCESS OF INCOME OVER EXPENDITURE FOR THE YEAR TRANSFERRED TO PUBLICATIONS RESERVE ACCOUNT
£970		£1,230

INCOME AND EXPENDITURE ACCOUNT

FOR THE YEAR ENDED DECEMBER 1984

INCOME		£	£
1983			
£			
SUBSCRIPTIONS			
1984	40,231		
1983	921		
40,593		41,152	
PALAENTOLOGY			
Sales	25,997		
Donations	210		
28,939		26,207	
SPECIAL PAPERS			
Sales	8,123		
Donations	1,373		
7,280		9,496	
BURGESS SHALE PORTFOLIO			
Sales	1,069		
Postage/Stationery	(58)		
2,257		1,011	
FOSSIL PLANTS OF THE LONDON CLAY			
Sales	1,729		
Postage/Stationery	(261)		
		1,468	
(1,243)		779	
OUTPRINTS			
PROFIT ON SALES OF INVESTMENTS	3,917		
8,431		8,947	
INVESTMENT INCOME (see schedule)	99		
330		99	
£86,587		£93,076	

EXPENDITURE		£	£
1983			
£			
COST OF PUBLICATION OF <i>PALAEONTOLOGY</i>			
Volume 27—Part 1			13,222
Part 2			13,431
Part 3			13,599
Part 4 (provisional)			13,800
Over Provision for Volume 26, Part 4		(50)	
54,821			54,002
COST OF PUBLICATION OF <i>SPECIAL PAPERS</i>			
No. 31			10,305
No. 32 (provisional)			13,450
14,729			23,755
COST OF PUBLICATION OF:			
<i>Fossil Plants of the London Clay</i>			1,605
Cumulative Index			141
<i>Atlas of Invertebrate Macrofossils</i>			2,246
2,425			3,992
3,600			
—			
1,212			1,919
650			100
WAREHOUSING OF PUBLICATIONS			
GRANTS			
COST OF CIRCULARS			
Preparation			2,709
Postage			1,826
Credit			(480)
4,041			4,055
ADMINISTRATIVE COSTS			
Postage and Stationery			1,684
Editorial and Expenses			212
Meeting Expenses			1,842
Audit Fee			225
Membership of Societies			60
	4,139		4,023
	£85,617		£91,846
EXCESS OF INCOME OVER EXPENDITURE FOR THE YEAR TRANSFERRED TO			
PUBLICATIONS RESERVE ACCOUNT			£1,230

SCHEDULE OF INVESTMENTS AND INVESTMENTS INCOME AS AT 31 DECEMBER 1984

			Gross Income for Year
		Cost £	£
£12,000	13½% 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	13½% Treasury Stock 1997	5,000	710
£3,280	13½% Exchequer Stock 1996	3,000	435
£2,000	Agricultural Mortgage Corporation Ltd. 9½% Debenture 1980/1985	1,938	185
5,270	M. & G. Charifund Units	4,073	1,070
1,865	Imperial Group p.l.c. 25p Ordinary Shares	1,730	177
10,000	New Throgmorton Trust (1983) p.l.c. 25p Income Shares	1,706	321
700	Clarke, Nicholls & Coombs p.l.c. 25p Shares	668	61
£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	45
570	National Westminster Bank p.l.c. £1 Ordinary Shares	2,788	
£10,150	Agricultural Mortgage Corporation Ltd. 7¾% Debenture Stock 1991/1993	8,251	393
1,600	Commercial Union Assurance Co. p.l.c. 25p Shares (sold August 1984)	—	159
5,000	Thorn EMI p.l.c. 7% Convertible Redeemable Second Cumulative Preference Shares 1992/1999 (sold March 1984)	—	250
			<hr/>
	Bank interest	6,298	2,649
		<hr/>	<hr/>
		50,459	8,947
		<hr/>	<hr/>
	MARKET VALUE at 31 December 1984 (1983—£68,428)	£71,437	
		<hr/>	

REPORT OF THE AUDITOR TO THE MEMBERS OF
THE PALAEONTOLOGICAL ASSOCIATION

In my opinion, the Accounts as set out on pages 803 to 806, give a true and fair view of the state of the affairs of the Association at 31 December 1984 and of its income and expenditure for the year ended on that date.

March 1985
Market Harborough, Leicestershire

G. R. POWELL
Chartered Accountant

INDEX

Pages 1–206 are contained in Part 1; pages 207–412 in Part 2; pages 413–618 in Part 3; pages 619–810 in Part 4. Figures in **Bold** Type indicate plate numbers.

A

- Aldridge, R. J. See Mabillard, J. E. and Aldridge, R. J.
Algae: mound-building coralline alga, Florida, 189
Alocopythere bhandari sp. nov., 371, **44**; *dhansariensis* sp. nov., 372, **44**; *polygona* sp. nov., 374, **45**; *talukdari* sp. nov., 374, **44**
Ammonites: Maastrichtian, Western Australia, 35
Amorphognathus ordovicicus, 691, **84**, **85**, **86**; *superbus*, 692, **83**; aff. *A. tvaerensis*, 694, **86**
Amphibian: Pennsylvanian, Kansas, 767
Anagaudryceras politissimum, 46, **1**; *subtilineatum*, 45, **2**
Antarctica: Lower Cretaceous bivalves, 475
Antropora tintata, **31**
Aphelognathus rhodesi, 698, **84**
Arsenault, M. See Schultze, H.-P. and Arsenault, M.
Aulatornoceras auris, **17**; cf. *A. auris*, **16**; '*A.*' *leoschmanni*, **16**
Aulichnites? *bradfordensis* ichnosp. nov., 626, **75**, **76**
Australia: Maastrichtian ammonites from Miria Formation, 35

B

- Bairdia berguaensis*, 365, **42**
Balticella binodis, **69**; *deckeri*, **69**
Bassett, M. G. See Savage, N. M. and Bassett, M. G.
Bavilinella faveolata, 462, **51**
Beania simplex, **27**
Belemnite: sexual dimorphism in *Youngibelus*, 133
Beltina danai, 344, **39**
Benedetto, J. L. See Edwards, D. and Benedetto, J. L.
Benton, M. J. and Walker, A. D. Palaeoecology, taphonomy, and dating of Permo-Triassic reptiles from Elgin, northeast Scotland, 207
Bergaueria? sp., 350, **38**
Biorecord Cincturo-Judith, 556, **65**, **66**; cf. Biorecord Cincturo-Judith, 560, **66**, **67**; Biorecord Cincturo-domed, 562, **66**, **67**
Birostrina concentrica, 506, **59**; *B.?cf. concentrica*, 510, **59**, **60**, **61**
Biva duncanae, **69**; *B.?ordoviciana*, **69**
Bivalvia: Lower Cretaceous, Antarctica, 475
Boscence, D. W. J. The morphology and ecology of a mound-building coralline alga (*Neogoniolithon strictum*) from the Florida Keys, 189
Boyd, M. J. A protothyridid captorhinomorph (Reptilia) from the Upper Carboniferous of Newsham, Northumberland, 393
Brachiopoda: Taxonomy, shell structure, and palaeoecology of *Gasconia*, 243; Carboniferous, Scotland, 567
Brachycycloceras koniuckianum, 237, **25**; *obtusum*, 247, **24**; *?obtusum*, **23**; *B. sp.*, **24**
Brahmaites (Brahmaites) kossmati sp. nov., 68, **6**, **7**
Brevidorsa crassispinosa, **69**; *fimbriata*, **69**

- Britain: Upper Carboniferous nautiloid *Brachycycloceras*, 235; Lower Palaeozoic echinoderms, 527; see also England, Scotland, Wales, and Ireland
Bryozoa: earliest fenestrate bryozoan and a short review of Ordovician Bryozoa, 147; zooid and colony growth of cheilostome bryozoans, 255
Buntonia royi sp. nov., 374, **45**

C

- Cainozoic: taxonomy and evolution of *Protenaster*, 311
Calymene blumenbachii, 783, **90**, **91**
Cambrian: Echinoderms and edrioasteroids, 715
Canada: mid-Proterozoic macro-biota, 331
Carboniferous: *Brachycycloceras*, Britain, 235; reptilia, Northumberland, 393; brachiopoda, Scotland, 567; trace fossils in Westphalian A, West Yorkshire, 619
Celleporaria magnifica, **30**
Celleporella hyalina, **29**
Chaloneria cornosa, **64**
Chamberlain, J. A. Jr. and Pillsbury, S. W. Fluid transport properties of *Nautilus* siphuncular tube: within camera distribution of flow rate, 121
Chisholm, J. I. Xiphosurid burrows from the Lower Coal Measures (Westphalian A) of West Yorkshire, 619
Chuaria circularis, 342, **35**, **36**, **37**, **38**, **39**; ?*C. circularis*, 465, **51**
Chulsanbaatar vulgaris, **49**, **50**
Colpodexylon cachiense sp. nov., 606, **73**, **74**
Communities: Estimating biomass and energy flow of molluscs, 1
Conodont: Ordovician, Welsh Borderland, 679
Crame, J. A. Lower Cretaceous inceramid bivalves from the Antarctic peninsula region, 475
Crassotornoceras annissi sp. nov., 168, **16**; *belgicum*, 169, **16**; *crassum*, 165, **16**; *guestfalicum*, 170, **16**
Cretaceous: non-heteromorph ammonites, Western Australia, 35; medusoid hydrozoan, Japan, 101; bivalves, Antarctica, 475; Barremian dinoflagellate cysts, 555; *Isocrinus*, Japan, 629
Cryptophyllum magnum, **69**; *C.? sp.*, **69**
Cupuladria biporosa, **27**
Cupulocrona digitalis sp. nov., 541, **63**; *rugosa* sp. nov., 538, **62**, **63**; *salopiae* sp. nov., 538, **62**, **63**
Curry, G. B. See Taylor, P. D. and Curry, G. B.
Cushmanidea distincta sp. nov., 370, **46**
Cyclodendron leslii, 114, **11**, **12**, **13**
Cytherella antheriformis sp. nov., 362, **41**; *assamensis* sp. nov., 359, **40**; *barpatharensis* sp. nov., 360, **40**; *deapanica* sp. nov., 358, **40**; *hastata* sp. nov., 360, **41**; *ventroconcava* sp. nov., 364, **41**; *C. sp.*, 364, **42**
Cytherelloidea sp. juv., 364, **42**
Cytheropteron reticulariadiata sp. nov., 380, **46**
Cytherura eocaenica sp. nov., 376, **46**

D

- Daltaenia mackenziensis* sp. nov., 346, 39
Desmophyllites diphylloides, 54, 4
 Devonian: tornoceratid goniaticite, 159; lycopods, Venezuela, 599
Distobolbina grekoffi, 70; *warthini*, 70
 Donovan, S. K. and Paul, C. R. C. Coronate Echinoderms from the Lower Palaeozoic of Britain, 527
 Doyle, P. Sexual dimorphism in the belemnite *Youngibelus* from the Lower Jurassic of Yorkshire, 133
Drepanoistodus subrectus, 708, 81, 82
 Dumican, L. W. and Rickards, R. B. Optimum preparation, preservation, and processing techniques for graptolite electron microscopy, 757

E

- Echinodermata: Cainozoic spatangoid *Protenaster*, 311; Lower Palaeozoic, Britain, 527; Cambrian, 715
 Edrioasteroids: Cambrian, 715
 Edwards, D. and Benedetto, J. L. Two new species of herbaceous lycopods from the Devonian of Venezuela with comments on their taphonomy, 599
 El-Khayal, A. A. and Romano, M. Lower Ordovician trilobites from the Handir Shale of Saudi Arabia, 401
 Electron microscopy: preparation and processing of graptolite material for electron microscopy, 757
 England: type species of *Calymene*, Silurian, 783
Eoaquaplex sp. (= *Oepikella frequens* of Kraft 1962), 70; *frequens*, 70
 Eocene: ostracoda, India, 355
Eographiodactylus eos, 70; *sulcatus*, 70
Eosynechococcus sp., 464, 51

F

- Falcitornoceras* gen. nov., 18, 19
Falcitornoceras falcatum, 172, 17, 18, 19, 20; *falciculum* sp. nov., 178, 18; *f. falculatum* subsp. nov., 180, 17, 18, 19, 20; *f. constrictum* subsp. nov., 182, 18, 19; *f. wagueri* subsp. nov., 183, 19, 20
Favosphaeridium sp., 466, 53

Fish: the panderichthyid *Elpistostege*, 293

- Fosse, G., Kielan-Jaworowska, Z. and Skaale, S. G. The microstructure of tooth enamel in multituberculate mammals, 435

G

- Gasconsia worsleyi* sp. nov., 246
Gaudryceras kayei, 46, 1, 2
 Gen. et sp. indet. A, 709, 86; Gen. et sp. indet. B, 710, 83
 Goniaticites: Devonian, 159
 Graptolite: preparation and processing for electron microscopy, 757
Grossonrites genumatns, 66, 5
Grypania spiralis, 349, 39
Guimarites kalika, 59, 5; *raggatti* sp. nov., 60, 6

H

- Hanken, N.-M. and Harper, D. A. T. The taxonomy, shell structure, and palaeoecology of the trimerillid brachiopod *Gascousia* Northrop, 243

- Harding, I. C. See Hughes, N. F. and Harding, I. C.
 Harper, D. A. T. See Hanken, N.-M. and Harper, D. A. T.
Haskinsia sagittata sp. nov., 601, 71, 72, 73
 Henderson, R. A. and McNamara, K. J. Maastrichtian non-heteromorph ammonites from the Miria Formation, Western Australia, 35
Hesperiella esthonica, 68; *michigauensis*, 68
Hesperoherpeton garnettense, 76
Hippula (Hippula) latonoda, 68; (*H.*) *varicata*, 68
Hithis colonus, 68; *hithis*, 68
 Hoffmann, A. Biotic diversification in the Phanerozoic: diversity independence, 387
 Hoffmann, H. J. The Mid-Proterozoic Little Dal macrobiota, Mackenzie Mountains, north-west Canada, 331
Homo sapiens, 48
 House, M. R. and Price, J. D. New late Devonian genera and species of tornoceratid goniaticites, 159
 Hughes, N. F. and Harding, I. C. Wealden occurrence of an isolated Barremian dinocyst facies, 555
 Hydrozoan: first Mesozoic chondrophorine, Japan, 101

I

- Icriodella superba*, 706, 80, 82, 83, 84, 85
 India: Eocene Ostracoda, 355
Inoceramus deltoides sp. nov., 486, 54, 55; *carsoni*, 498, 57, 58; *flemingi* sp. nov., 492, 56; *stoneleyi* sp. nov., 489, 55; *urus*, 56; sp. aff. *anglicus*, 494, 56; cf. *anglicus elongatus*, 494, 56; sp. aff. *comancheanus*, 497, 56; cf. *sutherlandi*, 501, 58
 Instructions for Authors, 793
Isocrinus (Chaladocrinus) huanai sp. nov., 636, 77, 78, 79; (C.) sp. cf. *I.? neocomiensis* (Desor), 640, 78, 79

J

- Japan: Cretaceous medusoid hydrozoan, 101; *Isocrinus*, Cretaceous, 629
 Jurassic: sexual dimorphism in *Youngibelus* from Yorkshire, 133

K

- Kanie, Y. See Stanley, G. D. Jr. and Kanie, Y.
Kerfornella sp., 405, 47
Kildinospaera chagrinata, 466, 53; *granulata*, 466, 53
Kitchinites spath sp. nov., 57, 4
Kloneckia sp., 408, 47
 Knoll, A. H. and Swett, K. Micropalaeontology of the late Proterozoic Veteranen Group, Spitzbergen, 451
Kossiaticeras (Natalites) brunnschweileri sp. nov., 63, 6, 7; *K. (N.)* sp. juv., 64, 7
Krithe oryza sp. nov., 370, 43, 46; cf. *K. oryza*, 371, 44

L

- Laccochiliua dorsoplicata*, 68; *L. (Eobromidella) eurychilioides*, 68
 Legrand-Blain, M. A. A new genus of Carboniferous spiriferid brachiopod from Scotland, 567
Leiosphaeridia asperata, 466, 53
 Lidgard, S. Zooid and colony growth in encrusting cheiostome bryozoans, 255
Loufengshania stipitata, 343, 38

- Loxochoncha?* sp., 375, 46
 Lycopod: Permian, South Africa, 111; Devonian, Venezuela, 599
- M**
- Mabillard, J. E. and Aldridge, R. J. Microfossil distribution across the base of the Wenlock series in the type area, 89
 McNamara, K. J. Taxonomy and evolution of the Cainozoic spatangoid echinoid *Protenaster*, 311
 McNamara, K. J. See Henderson, R. A. and McNamara, K. J.
 Macrobiota: Proterozoic, Canada, 331
 Mammals: microstructure of tooth enamel in multi-tuberculate mammals, 435
Maorites densicostatus, 64, 4
Meniscoessus sp., 49
Mesodina thompsoni, 50; *M.* sp., 48
Metrarabdotox unguiculatum cookae, 26
 Microfossils: distribution in Wenlock type area, 89; Proterozoic, Spitzbergen, 451
 Milner, A. R. On the identity of amphibian *Hesperoherpeton garnettense* from the Upper Pennsylvanian of Kansas, 767
 Mollusca: Estimating biomass and energy flow of molluscs in palaeo-communities, 1
Monoporella nodulifera, 28
- N**
- Neale, J. W. and Singh, P. Ostracoda from the Middle Eocene of Assam, 355
Neogoniolithon strictum, 22, 23
Neogrammmites caronensis sp. nov., 71, 6
Neseuretus (*Neseuretus*) cf. *tristani*, 495, 47
 Nicholls, E. L. and Russell, A. P. Structure and function of the pectoral girdle and forelimb of *Stratiomimus altus* (Theropoda: Orthinomimidae), 643
- O**
- Oji, T. Early Cretaceous *Isocrinus* from north-east Japan, 629
 Ordovician: review of Bryozoa, 147; trilobites, Saudi Arabia, 401; conodont faunas, Wales, 679
Orthoceras anceps, 25; *obnusum*, 24
Osmotoxotis phalacra, 90
 Ostracoda: Middle Eocene, India, 355; from Iapetus ocean, 577
? *Ozarkodina pseudofissilis*, 709, 84, 85
- P**
- Pachydiscus* (*Pachydiscus*) *fresvillensis*, 78, 8, 9; *P.* (*P.*) *jacquoti australis* subsp. nov., 76, 8; *P.* (*P.*) *neubergicus dissitus* subsp. nov., 72, 7, 9
 Padian, K. Palaeontology Review: The origins and aerodynamics of flight in extinct vertebrates, 413
Paijenborchella (*Eopaijenborchella*) sp., 366, 43; (*E.*) *assamensis* sp. nov., 365, 42, 43
 Palaeontology Review: The origins and aerodynamics of flight in extinct vertebrates by Kevin Padian, 413
Palaeophacmaea annulata, 104, 10
 Palaeozoic: echinoderms, Britain, 527
Panderodus cf. *P. gracilis*, 708, 80
Paracytheridea? *superdimorphica* sp. nov., 375, 45
Parasmittina nitida, 27
Partschiceras (*Phyllopachyceras*) *forbesianum*, 43, 1
 Paul, C. R. C. See Donovan, S. K. and Paul, C. R. C.
- Pandchoffatia* sp., 49, 50
Pedomphatella intermedia, 69; *jonesii*, 69
 Pennsylvanian: amphibian, Kansas, 767
 Permian: lycopod, South Africa, 111; reptiles, Scotland, 207
 Phanerozoic: Biotic diversification, 387
 Phillips, D. The nautiloid *Brachycycloceras* in the Upper Carboniferous of Britain, 235
Phragmodius cf. *P. undatus*, 707, 86
Phylloceras (*Neophylloceras*) *ramosum*, 40, 1; (*N.*) *surya*, 42, 1, 2
 Pigg, K. B. and Rothwell, G. W. Cortical development in *Chaloneria cornosa* (Isoetales), and the biological derivation of compressed lycophyte decortication taxa, 545
 Pillsbury, S. W. See Chamberlain, J. A. Jr. and Pillsbury, S. W.
Plaesiacomia vacuvertis, 406, 47; sp. aff. *P. rara*, 406, 47
Platybolbina (*Rimabolbina*) *omphalata*, 68; (*R.*) *rima*, 68
Plectodina bergstroemii sp. nov., 700, 82; *bullhillensis* sp., 702, 80, 81, 82, 83; *tennis*, 704, 80, 81; ?*P.* sp., 706, 80
Polonoceras planum, 17
 Powell, E. N. and Stanton, R. J. Jr. Estimating biomass and energy flow of molluscs in palaeocommunities, 1
 Price, J. D. See House, M. R. and Price, J. D.
Prioniodus sp., 709, 84, 85
Propontocypris eocaenica, sp. nov., 365, 42
Protenaster antiaustralis, sp. nov., 318, 33; *australis*, 313, 32, 33; *philipsi* sp. nov., 322, 34; *preatustralis* sp. nov., 321, 33, 34
 Proterozoic: macrobiota, Canada, 331; microfossils from Spitzbergen, 451
Protopanderodus firipipus, 708, 86
Pseudohippula castorensis, 70; *pseudoporkornina*, 70
Pseudooneotodus sp. A, 709, 80, 83; sp. B, 709, 83, 86
Pseudophyllites indra, 50, 2, 3; *latns*, 50, 3
Pyriporopsis? *texana*, 28
- R**
- Rayner, R. J. The Permian lycopod *Clyciodendron lesliei* from South Africa, 111
 Reptilia: Permo-Triassic, Scotland, 207; protorothyridid captorhinomorph, Carboniferous, Northumberland, 393
Reticycloceras sp. juv., 25; ?*R.* sp., 25
Rhodesognathus elegans, 696, 82, 83, 84, 85, 86
 Rickards, R. B. See Dumican, L. W. and Rickards, R. B.
 Romano, M. See El-Khayal, A. A. and Romano, M.
 Rothwell, G. W. See Pigg, K. B. and Rothwell, G. W.
 Russell, A. P. See Nicholls, E. L. and Russell, A. P.
- S**
- Satka colonialica*, 468, 53
 Saudi Arabia: Ordovician trilobites, 401
 Savage, N. M. and Bassett, M. G. Caradoc-Ashgill conodont faunas from Wales and the Welsh Borderland, 679
 Schallreuter, R. E. L. and Siveter, D. J. Ostracodes across the Iapetus Ocean, 577
Schizocythere deopanica sp. nov., 368, 43
Schizoporella floridana, 27; *floridana?*, 29
 Schultze, H.-P. and Arsenault, M. The panderichthyid fish *Elpistostege*: a close relative of tetrapods, 293
 Scotland: Permo-Triassic reptiles from Elgin, 207; Carboniferous brachiopods, 567
 Scott, G. H. Homotaxy and biostratigraphical theory, 777
Semicytherura indica sp. nov., 378, 45, 46; *S. indica* sp. nov. ?subsp. nov., 380, 46

- Silurian: microfossil distribution in Wenlock type area, 89; type species of *Calymene*, England, 783
 Singh, P. See Neale, J. W. and Singh, P.
 Siveter, D. J. See Schallreuter, R. E. L. and Siveter, D. J.
 Siveter, D. J. The type species of *Calymene* (Trilobita) from the Silurian of Dudley, England, 783
 Skaale, S. G. See Fosse, G., Kielan-Jaworowska, Z. and Skaale, S. G.
 Smith, A. B. Cambrian eleutherozoan echinoderms and the early diversification of edrioasteroids, 715
 South Africa: Permian lycopod, 111
 Stanley, G. D. Jr. and Kanie, Y. The first Mesozoic chondrophorine (medusoid hydrozoan) from the Lower Cretaceous of Japan, 101
 Stanton, R. J. Jr. See Powell, E. N. and Stanton, R. J. Jr.
?Staufferella sp., 708, 82
Steginoporella sp. nov., 31
Stephanocrinus ransbottomi sp. nov., 534, 62, 63; *?S. sensu lato* sp., 537, 62, 63
Stromatocystites pentangularis, 738, 87, 89; *walcotti*, 740, 88
Struthioninthus altus, 643
Stygimys kuznaudi, 49, 50
Stylopoma spongites, 30
 Swett, K. See Knoll, A. H. and Swett, K.
Synsphaeridium sp., 468, 52
- T
- Tasmanites rifijicus*, 465, 53
Tawnia dalensis, 334, 35, 36, 37, 38
 Taylor, P. D. and Curry, G. B. The earliest known fenestrate
- bryozoan, with a short review of Lower Ordovician Bryozoa, 147
Tetradelli scotti, 70; *separata*, 70
Thilipsura v-scripta, 90
 Trace Fossils: Westphalian A, West Yorkshire, 619
 Triassic: reptilia, Scotland, 207
 Trilobita: Ordovician, Saudi Arabia, 401
Tyrasotaenia sp., 349, 35; *T.? sp.*, 349, 35, 36, 37
- U
- Uroleberis armeniaca* sp. nov., 381, 46
- V
- Venezuela: Devonian lycopods, 599
 Vertebrates: origins and aerodynamics of extinct vertebrates, 413
- W
- Walcottidiscus typicalis*, 746, 89
 Wales: Ordovician conodont faunas, 679
 Walker, A. D. See Benton, M. J. and Walker, A. D.
Wilbertopora mutabilis, 28
- X
- Yestoleberis?* sp., 381, 46
- Y
- Youngibelus levius*, 138, 15; *tubularis*, 136, 14

NOTES FOR AUTHORS

The journal *Palaeontology* is devoted to the publication of papers on *all aspects* of palaeontology. Review articles are particularly welcome, and short papers can often be published rapidly. A high standard of illustration is a feature of the journal. Four parts are published each year and are sent free to all members of the Association. *Typescripts* should conform in style to those already published in this journal, and should be sent to **Dr. D. E. G. Briggs, Department of Geology, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, England**, who will supply detailed instructions for authors on request (these are published in *Palaeontology* 1985, 28, pp. 793–800).

Special Papers in Palaeontology is a series of substantial separate works conforming to the style of *Palaeontology*.

SPECIAL PAPERS IN PALAEONTOLOGY

In addition to publishing *Palaeontology* the Association also publishes *Special Papers in Palaeontology*. Members may subscribe to this by writing to the Membership Treasurer: the subscription rate for 1985 is £33 (U.S. \$53) for Institutional Members, and £16.50 (U.S. \$27) for Ordinary and Student Members. A single copy of each *Special Paper* is available to Ordinary and Student Members *only*, for their personal use, at a discount of 25% below the listed prices. Non-members may obtain copies, but at the listed prices, from Marston Book Services, P.O. Box 87, Oxford OX4 1LB, England.

RECENT PALAEONTOLOGICAL ASSOCIATION PUBLICATIONS

Special Papers in Palaeontology

Numbers 1–19 are still in print and are available (post free) together with those listed below:

20. (for 1977): Fossil Priapulid Worms, by S. CONWAY MORRIS. 155 pp., 99 text-figs., 30 plates. Price £16 (U.S. \$24).
21. (for 1978): Devonian Ammonoids from the Appalachians and their bearing on International Zonation and Correlation, by M. R. HOUSE. 70 pp., 12 text-figs., 10 plates. Price £12 (U.S. \$18).
22. (for 1978, published 1979): Curation of Palaeontological Collections. A joint Colloquium of the Palaeontological Association and Geological Curators Group. Edited by M. G. BASSETT. 279 pp., 53 text-figs. Price £25 (U.S. \$38).
23. (for 1979): The Devonian System. A Palaeontological Association International Symposium. Edited by M. R. HOUSE, C. T. SCRUTTON and M. G. BASSETT. 353 pp., 102 text-figs., 1 plate. Price £30 (U.S. \$45).
24. (for 1980): Dinoflagellate Cysts and Acritarchs from the Eocene of Southern England, by J. P. BUJAK, C. DOWNIE, G. L. EATON and G. L. WILLIAMS. 100 pp., 24 text-figs., 22 plates. Price £15 (U.S. \$23).
25. (for 1980): Stereom Microstructure of the Echinoid Test, by A. B. SMITH. 81 pp., 20 text-figs., 23 plates. Price £15 (U.S. \$23).
26. (for 1981): The Fine Structure of Graptolite Periderm, by P. R. CROWTHER. 119 pp., 37 text-figs., 20 plates. Price £25 (U.S. \$38).
27. (for 1981): Late Devonian Acritarchs from the Carnarvon Basin, Western Australia, by G. PLAYFORD and R. S. DRING. 78 pp., 10 text-figs., 19 plates. Price £15 (U.S. \$23).
28. (for 1982): The Mammal Fauna of the Early Middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset, by M. J. BISHOP. 108 pp., 47 text-figs., 6 plates. Price £25 (U.S. \$38).
29. (for 1982): Fossil Cichlid Fish of Africa, by J. A. H. VAN COUVERING. 103 pp., 35 text-figs., 10 plates. Price £30 (U.S. \$45).
30. (for 1983): Trilobites and other early Arthropods. Edited by D. E. G. BRIGGS and P. D. LANE. 276 pp., 64 text-figs., 38 plates. Price £40 (U.S. \$60).
31. (for 1984): Systematic palaeontology and stratigraphic distribution of ammonite faunas of the French Coniacian, by W. J. KENNEDY. 160 pp., 42 text-figs., 33 plates. Price £25 (U.S. \$38).
32. (for 1984): Autecology of Silurian organisms. Edited by M. G. BASSETT and J. D. LAWSON. 295 pp., 75 text-figs., 13 plates. Price £40 (U.S. \$60).
33. (for 1985): Evolutionary Case Histories from the Fossil Record. Edited by J. C. W. COPE and P. W. SKELTON. 202 pp., 80 text-figs., 4 plates. Price £30 (U.S. \$45).
34. (for 1985): Review of the upper Silurian and lower Devonian articulate brachiopods of Podolia, by O. I. NIKIFOROVA, T. L. MODZALEVSKAYA and M. G. BASSETT. 66 pp., 6 text-figs., 16 plates. Price £10 (U.S. \$15).

Field Guides to Fossils

1. (1983): Fossil Plants of the London Clay, by M. E. COLLINSON. 121 pp., 242 text-figs. Price £7.95 (U.S. \$12).

Other Publications

1982. Atlas of the Burgess Shale. Edited by S. CONWAY MORRIS. 31 pp., 24 plates. Price £20 (U.S. \$30).
1985. Atlas of Invertebrate Macrofossils. Edited by J. W. MURRAY. Published by Longman in collaboration with the Palaeontological Association. xiii + 241 pp. Price £13.95. Available in the USA from Halsted Press at U.S. \$24.95.

Palaeontology

VOLUME 28 · PART 4

CONTENTS

Xiphosurid burrows from the Lower Coal Measures (Westphalian A) of West Yorkshire J. I. CHISHOLM	619
Early Cretaceous <i>Isocrinus</i> from Northeast Japan TATSUO OJI	629
Structure and function of the pectoral girdle and forelimb of <i>Struthiomimus altus</i> (Theropoda: Ornithomimidae) E. L. NICHOLLS and ANTHONY P. RUSSELL	643
Caradoc–Ashgill conodont faunas from Wales and the Welsh Borderland N. M. SAVAGE and M. G. BASSETT	679
Cambrian eleutherozoan echinoderms and the early diversification of edrioasteroids ANDREW B. SMITH	715
Optimum preparation, preservation, and processing techniques for graptolite electron microscopy L. W. DUMICAN and R. B. RICKARDS	757
On the identity of the amphibian <i>Hesperoherpeton garnettense</i> from the Upper Pennsylvanian of Kansas ANDREW R. MILNER	767
Homotaxy and biostratigraphical theory G. H. SCOTT	777
The type species of <i>Calymene</i> (Trilobita) from the Silurian of Dudley, England DEREK J. SIVETER	783
Instructions for authors	793





SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01375 6960