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Cover: This specimen of *Calymene blumenbachii* from the Wenlock of Dudley is mounted in gold, forming the centrepiece of a nineteenth century brooch presented to the Natural History Museum by Miss E. Begg.

THE ORIGIN OF ALGAL-BIVALVE PHOTO-SYMBIOSIS



by TERUFUMI OHNO, TETZUYA KATOH *and* TERUFUMI YAMASU

ABSTRACT. The photo-symbiotic bivalves *Fragum fragum* and *Fragum lochooanum* burrow in sediments and supply light through a posterior shell gape to zooxanthellae within their internal soft parts. This newly discovered mode of photo-symbiosis in bivalves can be termed *sciaphilous* (shade loving), and the hitherto known one, in which bivalves expose mantles or transparent shells out of the sediment to harvest light, as *heliophilous* (sun loving). *Fragum unedo*, also examined here, is heliophilous. Sciaphilous photo-symbiosis in *F. fragum* is enabled by the zooxanthellae's low compensation point of photosynthesis ($50 \mu\text{Einstein m}^{-2} \text{s}^{-1}$), a point far lower than the ambient light intensity of their habitat. The zooxanthellae's pre-adaptation to low light intensity might have played an important role in originating the zooxanthella-bivalve symbiosis. Sciaphilous photo-symbiosis allows bivalves to profit from photo-symbiosis without risking predation or epibiont attachment, and thus may have been common among fossil photo-symbiotic bivalves. The disproportionately rapid increase in the length of the posterior shell gape and the very rapid decrease of the angle between the posterior and ventral valve margins during the growth of two sciaphilous *Fragum* species, which ensure effective light harvesting by the zooxanthellae, can be used as criteria in searching for fossil sciaphilous microbial-bivalve photo-symbiosis.

SYMBIOSIS between bivalves and contained photosynthetic zooxanthellae has been known since the detailed study by Yonge (1936). This occurs in the genera *Tridacna* (Yonge 1936), *Hippopus* (Yonge 1936) and *Corculum* (Kawaguti 1941), all of which are Indo-Pacific tropical shallow-water dwellers. Symbiosis between non-photosynthetic organisms and photosynthetic microbes will be termed photo-symbiosis hereafter. The symbiotic unicellular, brown-coloured algae, traditionally called zooxanthellae, are currently placed in the dinoflagellate genus *Symbiodinium* (Blank and Trench 1986). This same genus is harboured within all the modern hermatypic corals. Although Yonge (1936) observed zooxanthellae contained within cells (phagocytic blood-cells) of the animals, the zooxanthellae are more commonly located intercellularly in the host bivalve's soft tissues (Trench *et al.* 1981).

With the exception of *Tridacna crocea* Lamarck, which bores in reef coral, all the taxa above are epifaunal. The hitherto known living photo-symbiotic bivalves, both epifaunal and infaunal, place their hypertrophied mantle edges (*Hippopus* and *Tridacna*, including *T. crocea*) or transparent windows on extremely flat posterior valve surfaces (*Corculum cardissa* (Linnaeus); Vogel 1975; Watson and Signor 1986) above the sediment surface in order to expose part of the animal to sunlight. This life habit can be termed *heliophilous* (sun loving).

All the known photo-symbiotic bivalves belong to the superfamilies Cardiacea and Tridacnacea, which are closely related to each other. The majority of the bivalves of the superfamily Cardiacea adopt an infaunal mode of life. Thus the ancestors of the photo-symbiotic bivalves mentioned above were most probably infaunal bivalves. This raises the question of how the symbiotic relationship originated between the infaunal ancestors of these bivalves and the light-demanding photosynthetic zooxanthellae.

Photo-symbiosis has been inferred in fossil bivalves (Philip 1972; Vogel 1975; Loriga and Benini 1977; Skelton 1979; Thiele and Tichy 1980; Yancey and Boyd 1983; Skelton and Wright 1987; Seilacher 1990) as well as among fossil brachiopods (Cowen 1970, 1982). This inference is based on

features of their shell morphology, shell microstructures and their palaeoecology, which are similar to those of living photo-symbiotic bivalves or hermatypic corals.

Recently, Kawaguti (1983) and Yamasu (1988*a, b*) have reported new examples of zooxanthella–bivalve symbiosis in *Fragum fragum* (Linnaeus) and *Fragum unedo* (Linnaeus). Umeshita and Yamasu (1985) found another example in a third species, *Fragum mundum* (Reeve). In contrast with the highly specialized shell forms of other known photo-symbiotic bivalves, the shell shape of the *Fragum* species is similar to other non-symbiotic cardiid bivalves, except for their long and straight posterior margin as well as the angular corner where the posterior and ventral valve margins meet. This suggested that a detailed investigation of bivalves belonging to the genus *Fragum* could provide us with information about the initial stage of zooxanthella–bivalve symbiosis. Further, information on the zooxanthella–symbiosis of the genus would also contribute to a safer basis for inferring the existence of photo-symbiosis among fossil bivalves. For these reasons, three living specimens of strawberry cockles, *F. fragum*, *F. unedo* and *F. loochooanum* Kira, were examined on the basis of their ecology, anatomy, distribution of zooxanthellae within their soft tissues, shell form and shell microstructure. For *F. fragum*, shell transparency and photosynthetic activity of symbiotic zooxanthellae were also examined.

The present investigation reports the finding of the new life mode for photo-symbiotic bivalves, in *F. fragum* and *F. loochooanum*, which may be termed *sciaphilous* (shade loving). The adaptive significance and origin of photo-symbiosis in bivalves, as well as the criteria for inferring sciaphilous photo-symbiosis in fossil bivalves, are discussed.

MATERIALS AND METHODS

Habitats of the examined bivalves

The majority of the observations of the life habits of the three species of *Fragum*, as well as the collection of materials for the further studies, were carried out by numerous scuba dives on the shallow sand flat of Amitori Bay in front of the Okinawa Regional Research Centre, Tokai University, Iriomote Island, Okinawa Prefecture, Japan, between November 1988 and November 1991. The substratum consists of light grey silty coarse sand. The sand grains are mainly calcareous bioclasts. The flat is exposed during the low tides of Spring and late Autumn, when the tidal range is largest. At average high tides, it is covered with about 2 m sea water. The mean monthly temperature fluctuates between 22 °C in February and 29 °C in July (from data for the period May 1977 to December 1989; Okinawa Regional Research Centre 1990).

On test-dives to the deeper part of the bay, a few living individuals with zooxanthellae were also found at a depth of 20 m in muddy sand substrata. They were not incorporated into the material of the present study.

Additional samples of living *F. unedo* were collected from the adjacent sandy flats within the bay and from the sandy flat at the mouth of Sakiyama Bay, which is located about 1.5 km south of the centre and separated from Amitori Bay by a small peninsula. For the study of shell allometry, *F. unedo* specimens collected from the Kabira Bay on Ishigaki Island, which is located about 50 km from Amitori Bay, were incorporated.

The specimen for Plate 1, figures 5 and 8 was collected at Bise, Okinawa Island, Okinawa Prefecture.

All the examined specimens, except for those photographically documented in the field study, are stored in the Museum of the Department of Geology and Mineralogy, Faculty of Science, Kyoto University (JCTO0014–JCTO0019).

Burrowing rate index

The collected samples were kept in a laboratory aquarium filled with a sufficient thickness of silty coarse sand from their natural habitats before measurement of burrowing rate indexes. The samples were provided with running sea water and received ambient light from windows. The burrowing of

the cockles was recorded by a video-camera. Burrowing periods (time between erection of shells and complete burrowing of the posterior shell margin), and number of rocking motions during burrowing were determined from video-images. Mass (wet weight) and shell length of the samples were also measured. For each individual, burrowing rate index (BRI), defined by Stanley (1970), was calculated according to the following equation:

$$\text{BRI} = \frac{[\text{mass (g)}]^{1/3}}{\text{burrowing period (s)}} \times 100.$$

Shell transparency of Fragam fragum

Measurements were carried out using a spectro-photometer (Hitachi Type 3400). The shell surface is exposed to a light source. Behind it is a hole 3 mm in diameter in an opaque board. The light transmitted through the shell and the hole is then gathered and measured using a photo-multiplier equipped with an integrating sphere.

Measurements of the photosynthesis-irradiance profile of the zooxanthellae of Fragam fragum

The cockles were collected on the sandy flat in Amitori Bay in October, 1990 and kept in an aquarium for several days under the same conditions as the samples for the measurement of the burrowing index, and then examined for the photosynthetic activity of the zooxanthellae.

Zooxanthellae in the cockles were isolated from the mantle tissues by squeezing them in sterilized and filtered sea water. The sea water with liberated zooxanthellae was then passed through a nylon mesh (50 μm) to remove tissue fragments, and then centrifuged at 1200 g for 10 min to separate bacteria and various small particles which were left in the supernatant. The red precipitate of zooxanthellae was then suspended in filtered sea water and placed in a 3.0 ml vessel with a rotating platinum electrode, fitted with a circulating water-jacket to keep a constant temperature of 20 $^{\circ}\text{C}$. The light beam from a 350 W incandescent lamp was passed through two infrared-absorbing filters (Hoya, HA-30) and a diaphragm, to attenuate the light intensity in a step-wise fashion, and then focused on the vessel. Light intensity at the surface of the vessel was monitored with a Licor Quantum Sensor. Both O_2 concentration in the vessel, as monitored by the platinum electrode, and the light intensity were automatically recorded.

SCIAPHILOUS LIFE MODE AND POSTERIOR MANTLE EDGES

More than two hundred living *F. fragum* were observed on the tidal flat in front of the Okinawa Regional Research Centre. Their population density here seldom exceeds one or two individuals per square metre, although an exact determination was not carried out.

On burrowing, the valves become completely immersed in the sediment, with the flattened posterior valve slopes just beneath the thin sediment cover (Pl. 1, fig. 3; Text-fig. 1B). The posterior shell gape is covered by partly fused mantle edges (Pl. 1, figs 1 and 2; Text-figs 1A and 2). From both posterior valve margins, mantle edges extend laterally. They are furnished with numerous tentacles, and are moderately hypertrophied, especially ventral to the inhalant siphon. The tentacles secrete mucus and sand grains adhere around them. Consequently, the extended mantle edges and tentacles are covered by sand grains (Pl. 1, fig. 9). Therefore in the natural life position of *F. fragum*, it is only the exhalant and inhalant siphons and a part of the posterior mantle edges covering the shell gape that are continuously exposed through the sediment (Pl. 1, fig. 3; Text-fig. 1B). These exposed soft parts covering the posterior shell gape are spotted with transparent and non-transparent patches and are as a whole semitransparent (Pl. 1, fig. 2). Large transparent patches commonly occur around the exhalant and inhalant siphons.

More than eighty living *F. loochooanum* were observed. They have a life habit rather similar to *F. fragum*, and burrow completely into the sediment. Their very weakly hypertrophied lateral

expansions of posterior mantle edges, together with numerous tentacles (Text-fig. 1A), are covered by the sediment (Pl. 1, fig. 6; Text-fig. 1B). Therefore, only the posterior mantle edges covering the posterior shell gape, including the inhalant and exhalant siphons, are continuously exposed through the sediment. Transparent and non-transparent patches spot these exposed soft parts and make them semitransparent. Large transparent patches occur on the mantle edges covering the notches of the marginal crenulations along the posterior valve margins in addition to those around the exhalant and inhalant siphons. This species does not fix sand grains around its tentacles.

Five living *F. unedo* were available for observation. They bury their valves completely in the sediment. Their posterior mantle edges are furnished with tentacles and are strongly hypertrophied, especially ventral to the inhalant siphon. Here, they form fan-shaped lobes (Pl. 1, fig. 7; Text-figs 1A–B). The lobes continue as broad fleshy stripes along the rest of the posterior margin. These hypertrophied mantle edges are spread over the surface of the substratum (Pl. 1, fig. 7; Text-fig. 1B). The mantle edges covering the posterior gape, including inhalant and exhalant siphons, are thick and less transparent. Most of the individuals show a negative reaction to shade and draw back their posterior mantle edges when a shadow crosses over them.

All the examined samples of these three species contain zooxanthellae within their soft tissues. Therefore, their coexistence with zooxanthellae is not purely fortuitous but very probably symbiotic.

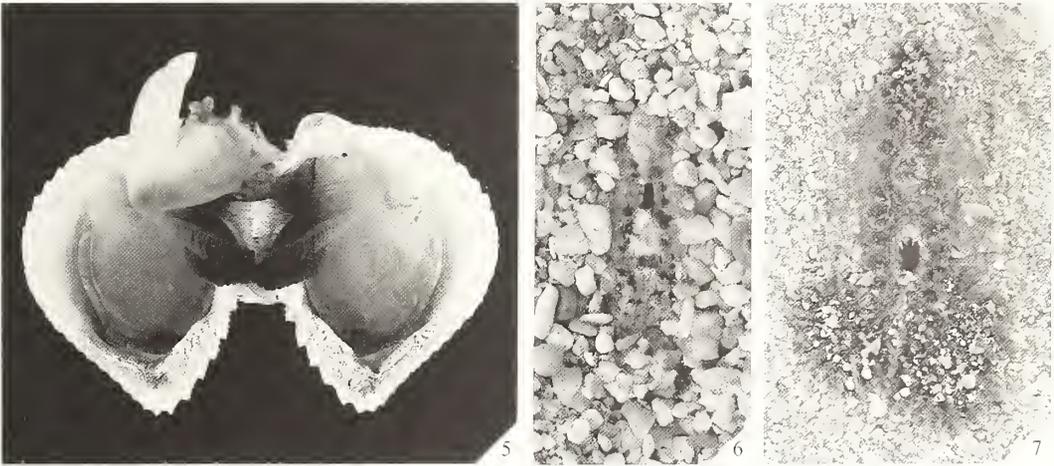
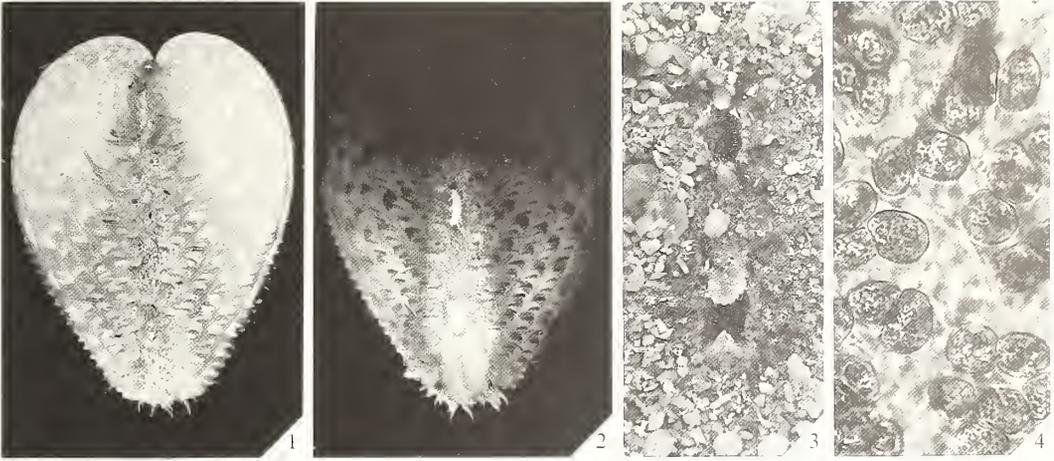
F. fragum and *F. loochooanum* adopt infaunal life habits and do not extend their mantle margins and valves out of the sediment, except for the regions around the inhalant and exhalant siphons. Furthermore, *F. fragum* apparently deliberately minimizes the exposure on sediment by mucus secretion from the tentacles and adhesion of sediment grains around them. This previously unrecognized photo-symbiotic life mode, in which the host bivalves do not expose their mantle edges to the light, except for small areas stretched between the posterior shell gape, can be called *sciaphilous* (shade loving; Text-fig. 7). In contrast, all the hitherto known living photo-symbiotic bivalves, both epifaunal and infaunal, can be termed *heliophilous* (sun loving), because they put their hypertrophied mantle margins or transparent shells out of the sediment to expose them directly to the light. *F. unedo*, which is infaunal and extends its hypertrophied mantle margins and tentacles out of the sediment, belongs to this latter category.

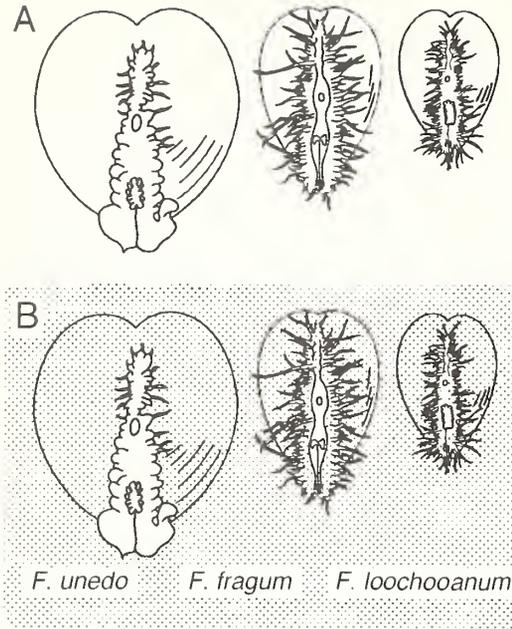
EXPLANATION OF PLATE I

Figs. 1–5, 8–9. *Fragum fragum*. 1–2, with moderately expanded mantle edges and tentacles. 1, illuminated from above. 2, illuminated from below in dark room. Mantle edges covering the shell posterior gape are more transparent than the semi-transparent valves. Non-fused part of the mantle edges meet together along the dark line running along the middle of the shell gape from the inhalant siphon to the ventral margin. Both $\times 1.7$. 3, in natural life position, posterior part of the shell covered with foraminiferal sand, $\times 3.3$. 4, zooxanthellae in the mantle tissue, $\times c. 600$. 5, soft parts: gills and mantle covering the inner shell surface, especially near the posterior gape, containing abundant zooxanthellae, are dark coloured. Condensation of zooxanthellae, partly caused by the contraction of muscles, has darkened the pallial lines. The bottom wall of the supra-branchial chamber (triangular white area in the middle of the photograph) contains fewer zooxanthellae than the area of the foot surface (upper left of the bottom wall of the supra-branchial chamber), which faces the bottom wall in life, $\times 1.4$. 8, soft parts: abundant zooxanthellae darken both the outer and the inner gill demibranchs. In contrast, the posterior mantle edges are spotted with transparent flecks (dark in the photo) and white flecks, and contain very few zooxanthellae. The distal half of the L-shaped foot, and the mantle covering the anterior part of the shell interior, both located rather distant from the posterior shell gape from which light penetrates into the shell interior, are white and contain very few zooxanthellae, $\times 1.9$. 9, the posterior slopes of shells are covered with sand grains, adhering to them because of the presence of mucus secreted by the tentacles.

Fig. 6. *Fragum loochooanum* in natural life position. Only the posterior gape is visible through the sediment, $\times 4.3$.

Fig. 7. *Fragum unedo* in natural life position with strongly expanded mantle edges lying on the sediment, $\times 1.7$.





TEXT-FIG. 1. Sketch of three *Fragum* species. A, Mantle edges fully expanded. B, Exposure of mantle edges through sediment cover (sediment is stippled).

ACTIVE BURROWING ABILITY

As a measure of locomotion ability, the burrowing time and burrowing rate index (BRI) were determined for ten individuals of *F. fragum*, six individuals of *F. loochooanum* and one individual of *F. unedo* (Table 1).

For the Cardiacea, to which *Fragum* also belongs, Stanley (1970) reported BRI values for seven species. Following Stanley's statement that temperature has a minor effect on BRI value within the range 20–30 °C, a comparison of BRI values between the present species and Stanley's six species was made, all measured within this temperature range. Stanley's seventh species, *Dinocardium robustum* shows an exceptionally large BRI value of 5 (measured at 18 °C) in comparison with his other six species.

Three of Stanley's (1970) species have a BRI value of 1, and of the other three, one species has a value of 0.9, another 0.5, and the last 0.4. Thus *F. fragum* (mean BRI = 0.7) burrows as effectively as Stanley's six cardiacean species without symbiotic zooxanthellae. For *F. unedo* only one measurement is available (BRI = 0.4) which does not allow us to draw any conclusion, although it is comparable to the BRI values of Stanley's six cardiaceans.

F. loochooanum has a very low BRI value (mean BRI = 0.075) in comparison with the above discussed species. Perhaps the BRI value underestimates locomotive activity of small sized animals, which cannot use weight, for example, to help in cutting themselves into the sediment. If locomotive activity is measured in terms of burrowing period, *F. loochooanum* (114 s) burrows far faster than *F. fragum*.

BIVALVE ANATOMY

Mantle edges

When the three examined strawberry cockle species open their valves, the mantle edges cover the shell gape along its whole length (Text-fig. 2). They are fused between the beak and the inhalant siphon. Along the rest of the gape, they are not fused, yet meet tightly together. The ventral mantle edges as well as the anterior mantle edges are thin, except for the rather thick ventral mantle edges near the angular postero-ventral shell corner.

TABLE 1. Burrowing index of three *Fragum* species. Abbreviations: M, mass; L, length; BP, burrowing period; R, number of rocking motions; BR1, burrowing rate index; std., standard deviation. The centre referred to is the Okinawa Regional Research Centre.

	M (g)	L (mm)	BP (s)	R (times)	BR1
<i>Fragum fragum</i> *					
(n = 10)					
	1.86	14.4	891	3	0.14
	3.24	17.0	129	4	1.15
	3.44	17.4	231	3	0.65
	3.89	17.9	115	3	1.37
	4.48	19.2	316	4	0.52
	4.54	18.9	305	4	0.54
	4.89	19.0	1347	4	0.13
	6.36	20.3	543	6	0.34
	6.49	22.7	824	6	0.23
	10.99	24.5	103	4	2.16
Mean	5.02	19.13	480.4	4.1	0.72
SD	2.39	2.73	395.1	1.0	0.62
<i>Fragum loochooanum</i> †					
(n = 6)					
	0.16	7.1	50	4	0.076
	0.24	8.6	129	4	0.073
	0.25	8.5	122	5	0.074
	0.27	8.5	124	5	0.076
	0.29	8.6	160	4	0.077
	0.39	9.7	100	4	0.075
Mean	0.27	8.5	114.2	4.3	0.075
SD	0.07	0.75	33.7	0.5	0.001
<i>Fragum unedo</i> ‡					
(n = 1)					
	6.86	25.1	484	11	0.40

* Samples from the sandy bottom in front of the centre; collected between 26 and 29 Oct. 1990; measured on 30 Oct. 1990 at water temperature of 26.8 °C.

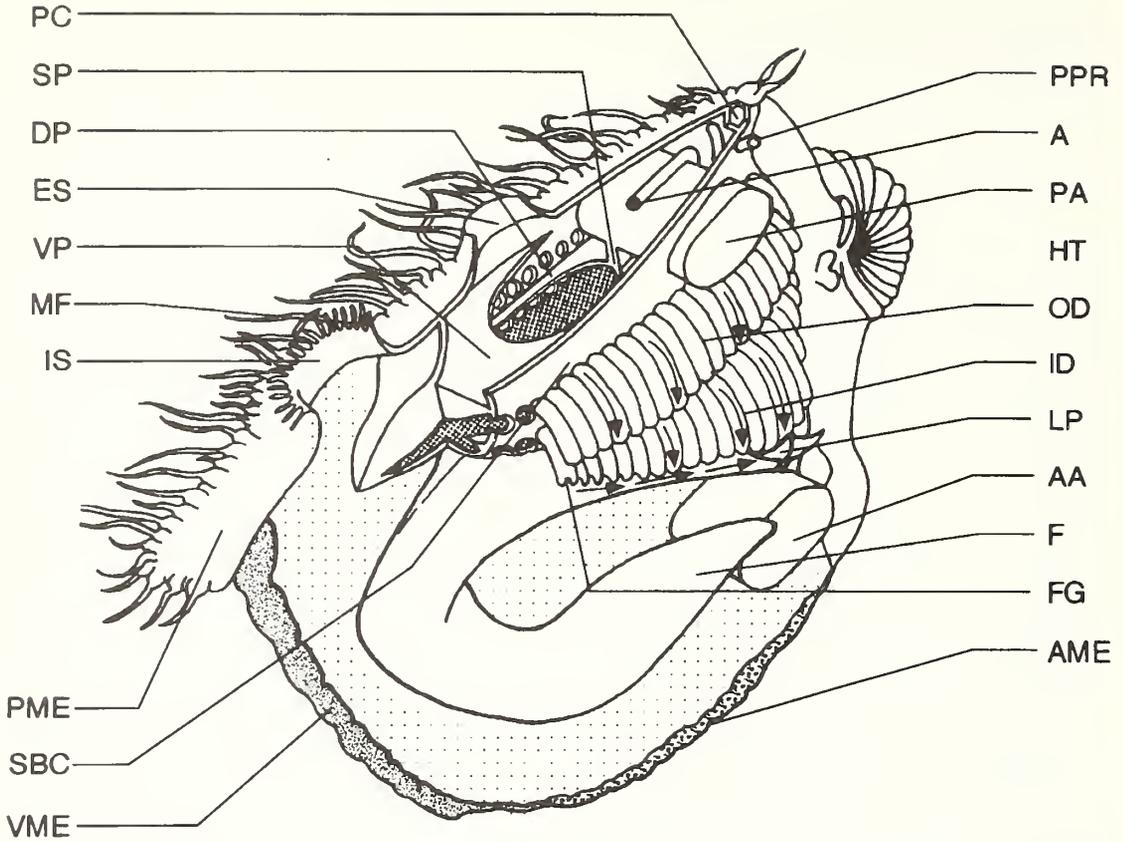
† Samples from the sandy bottom in front of the centre; collected between 26 and 31 Oct. 1990; measured on 5 Nov. 1990 at water temperature of 26.2 °C.

‡ Sample from sandy flat at the mouth of Sakiyama Bay; collected on 31 May 1989; measured on 2 June, 1989 at water temperature of 25.9 °C.

As already described, the mantle edges along the posterior valve margins show considerable variation between the sciaphilous and the heliophilous species. In brief, the sciaphilous *F. fragum* and *F. loochooanum* have less hypertrophied, less extensively laterally expanded, and more transparent posterior mantle edges than the heliophilous *F. unedo*. It is difficult to estimate quantitatively the proportion of the incident light that is transmitted through the mantle edges covering the posterior gape of the sciaphilous *F. fragum* and *F. loochooanum*. In *F. fragum*, however, they are more transparent than the semitransparent posterior slope of their valves (Pl. 1, fig. 2).

Soft parts within the shell interior

The anatomy of the soft parts within the shell interior is quite similar in all three *Fragum* species. The description below is mainly based on *F. fragum* (Pl. 1, figs 5 and 8; Text-fig. 2).



TEXT-FIG. 2. Anatomy of *Fragum fragum*. Inner surface of the bottom (anterior side) of the supra-branchial chamber is densely stippled. Mantle covering the inner surface of the shell is weakly, but regularly, stippled. Ventral and anterior mantle edges are irregularly stippled. Arrows on inner and outer demibranchs indicate the direction of ciliary grain transportation. Abbreviations: A, anus; AA, anterior adductor muscle; AME, anterior mantle edge; DP, dorsal partition of supra-branchial chamber; ES, exhalant siphon; F, foot; FG, food groove (inner marginal food groove of ctenidium); ID, inner demibranch; IS, inhalant siphon; LP, labial palp; MF, ventral end of mantle fusion; OD, outer demibranch; PA, posterior adductor muscle; PC, pericardium; PME, posterior mantle edge; PPR, posterior pedal retractor muscle; SBC, supra-branchial chamber; SP, sagittal partition connecting posterior adductor muscle and dorsal partition of supra-branchial chamber; VME, ventral mantle edge; VP, ventral partition of supra-branchial chamber.

Just under the posterior shell gape there is an elongated tube separated off by a thin membrane (supra-branchial chamber; Purchon 1955) running parallel to the posterior valve margins. Its dorsal end reaches to the foot, yet the membrane is not fused with the latter but is separated by a very narrow slit. The tube is bipartite ventral to the exhalant siphon, where a thin membrane divides a lower (anterior) chamber, with attachment of demibranchs, from the upper chamber. Dorsal to the exhalant siphon it is tripartite. Here, there is a hollow between the mantle edge and the posterior adductor muscle. The anus opens in this hollow. Below it, a thin membrane separates two chambers, each with attachment areas for outer and inner demibranchs, respectively. The upper of the two chambers has a sagittal partition. The three examined species have inner and outer gill demibranchs which hang from the lateral wall of the supra-branchial chamber. The inner demibranchs are considerably larger than the outer demibranchs and have food grooves along their free edges (inner marginal food grooves of ctenidium). The inner demibranchs are connected by a

pair of labial palps to the mouth on the ventral side of the foot. The palps, considerably smaller than those illustrated in *Clinocardium nuttali* (Stasek 1961), are located at about one-third of the length of the inner demibranchs from their dorsal ends. Each of the labial palps is composed of two small triangular lobes. The adductor muscles are located near the beak. The foot is large and L-shaped.

DISTRIBUTION OF ZOOXANTHELLAE

Zooxanthellae (Pl. 1, fig. 4) are contained intercellularly among the tissues of the strawberry cockles. Their brown colour makes it easy to determine their occurrence and relative abundance within the cockle tissues.

In the two sciaphilous species, *F. fragum* and *F. loochooaman*, the zooxanthellae are contained in the innermost part of the hypertrophied lateral expansions of the posterior mantle edges, but in only small quantities. Their tentacles, as well as the mantle covering the posterior margins, both of which are more or less transparent, do not contain abundant zooxanthellae. The ventral mantle edges contain abundant zooxanthellae just near the corner where the posterior and ventral margins meet. The zooxanthellae content of the mantle edges gradually decreases towards the anterior mantle edges.

In the shell interior of these sciaphilous species, the thin membranes of the supra-branchial chamber contain zooxanthellae, but not very abundantly. The surfaces of the gill demibranchs are strongly dark brown coloured (Pl. 1, figs 5 and 8). On the outer surfaces of the demibranchs, the brown colour fades gradually towards the beak. The inner sides of the demibranchs are brown coloured, especially strongly along the line of their attachment to the supra-branchial chamber wall. Weak brown coloration is also observed on the foot facing the floor of the supra-branchial chamber. The membrane covering the posterior adductor muscle is strongly brown coloured. Abundant zooxanthellae also exist within the mantle lining the shell interior: in the smallest species, *F. loochooaman*, the whole surface is coloured dark brown; in *F. fragum* the coloration is more vivid along the posterior valve margins and posterior part of the ventral margin.

The hypertrophied and laterally expanded mantle edges of the heliophilous *F. unedo*, which are exposed to light on the sediment surface, harbour a large number of zooxanthellae under their thick, almost non-transparent tissue. Zooxanthellae are also abundant in the ventral mantle edge just near the corner where it meets with the posterior mantle edge. Their abundance gradually decreases towards the anterior mantle edges. In the shell interior, the thin membrane of the walls and floor of the supra-branchial chamber contains a large number of zooxanthellae. The coloration of the gills and the mantle lining the shell interior is much weaker than the two sciaphilous species. In particular, the anterior part of the mantle lining the shell interior is almost white and contains very few zooxanthellae.

In summary, the sciaphilous *F. fragum* and *F. loochooaman* farm the zooxanthellae mainly within their internal soft tissues, whereas the heliophilous *F. unedo* farms them chiefly in its exposed and hypertrophied posterior mantle edges. In the two sciaphilous species, the mantle edges covering the posterior shell gape and supra-branchial chamber, which aligns the gills just beneath and parallel with the posterior shell gape, are semi-transparent. They ensure the penetration of light to the gills and other internal soft tissues with abundant zooxanthellae. The heliophilous *F. unedo* also has a long supra-branchial chamber. This species, however, uses it as an area for farming the zooxanthellae rather than as a device for ensuring light supply to the gills. The light for the zooxanthellae within the tissues of the supra-branchial chamber is supplied from the inhalant and exhalant siphons.

ACTIVE GRAIN TRANSPORTATION ON THE GILL SURFACE

Transportation of grains by ciliary action (Text-fig. 2) was monitored by sprinkling fine grinding powder over the gill surfaces of *F. fragum*. On each outer demibranch grains are transported from the ascending branch to its free edge, and then on, over the descending branch on to and along the

ctenidial axis. On the inner demibranch, grains are transported on both the descending and ascending branches to the food groove along its free edge. The action of cilia in the food groove then transports fine particles, via the labial palps, to the mouth. In one specimen it takes about a minute for the grains to cross the brightest part of the descending lamella of the inner demibranch from the ctenidial axis to the food groove, even after three hours have elapsed since the beginning of dissection. Excess grains are sorted by the labial palps, mixed with mucus to form small round balls and then expelled from its pointed end. The above construction of the gill as well as the manner of fine grain transportation on it closely resembles that of *Clinocardium nuttali* described by Stasek (1961).

The similar construction of the gills and the labial palps of the three examined *Fragum* species suggests that these species actively transport and sort grains on the gills and labial palps, as observed in *F. fragum*, which in turn indicates that the three examined *Fragum* species retain active filter feeding.

SHELL FORM AND ALLOMETRIC GROWTH

Shell form

In accordance with the diagnosis of the genus *Fragum* (Keen 1980), the three examined *Fragum* species have fairly inflated valves, flattened posterior valve slopes, well defined umbonal ridges along the intersection of the posterior and ventral valve slopes, as well as an angular postero-ventral corner of the valve margins. The posterior valve margin is very long and almost straight except near the beak. It meets with a more or less straight ventral margin and forms an angular corner. In the present study the angle of this corner is referred to as the PV-angle. In some specimens the umbonal ridge protrudes weakly at the shell margin postero-ventrally. In this case the margin ventral to it is weakly concave near the angular corner.

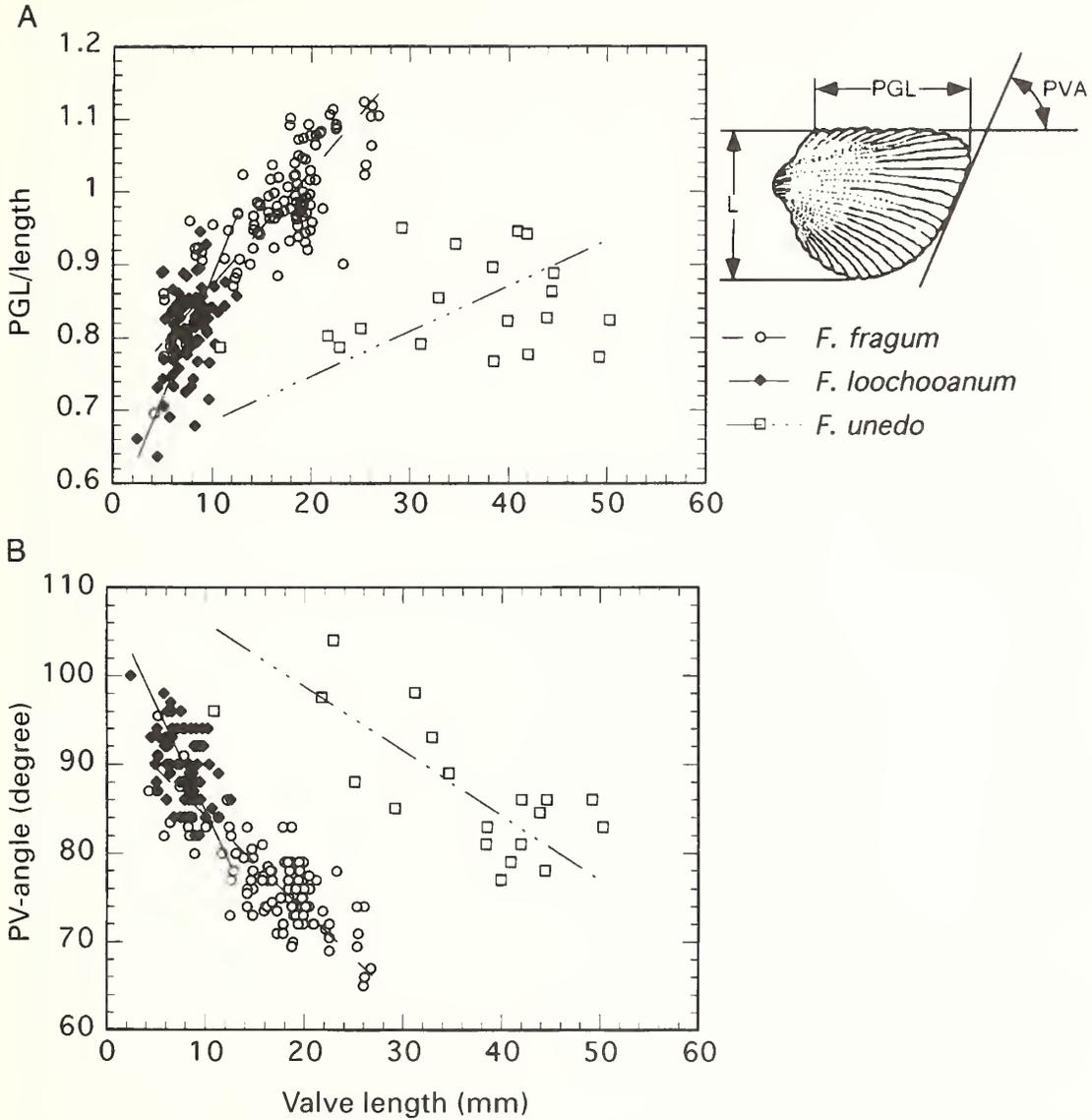
Allometric growth

The sciaphilous *F. fragum* and *F. loochooanum* show a very conspicuous disproportionate increase in the length of the posterior gape (PGL) in comparison with the increase in shell length (L) as expressed by the rapid increase in PGL/L ratio (Text-fig. 3A; Table 2). In the heliophilous *F. unedo*, on the other hand, this tendency is not present.

The angles between posterior and ventral margins (PV-angle) of the two sciaphilous species are far smaller than that of the heliophilous one, when compared for the same L value (Text-fig. 3B). The average PV-angle of the largest specimens (L = about 25 mm) of *F. fragum* is 20 degrees smaller than that of *F. unedo* of comparative L value. The average for *F. loochooanum* is smaller by about 10 degrees than that of *F. unedo*, for comparable shell sizes (L = 10 mm).

Furthermore, the PV-angle decreases very rapidly with increased shell length (L) in the sciaphilous *F. fragum* and *F. loochooanum* (Text-fig. 3B; Table 2). The heliophilous *F. unedo* also shows this tendency, but weakly.

The strongly disproportionate increase in the length of the posterior shell gape (PGL) during the growth of *F. fragum* and *F. loochooanum* leads to a rapid enlargement of the area of the posterior shell gape through which light penetrates into the shell interior. The rapid decrease in the PV-angle during shell growth keeps an increasingly larger area of the ventral mantle edges near the angular postero-ventral corner in a short distance from the posterior shell gape. Thus the allometric growth of these two shell characters ensures a light supply to the areas rich in zooxanthellae in the soft tissues of the shell interior and along the shell margins of the two sciaphilous species. The heliophilous *F. unedo* farms its zooxanthellae mainly in its hypertrophied mantle edges exposed above the sediment. Therefore, for this species the above mentioned two shell characters are not so important and allometry is weakly developed.



TEXT-FIG. 3. Allometric shell growth of *Fragum* species. A. Posterior gape length (PGL)/length (L) ratio plotted against length (L). B. Angle between posterior and ventral valve margins (PV-angle) plotted against length (L). (Registration numbers of samples: *Fragum fragum* = CTO0014; *F. loochooanum* = CTO0015; *F. unedo* = CTO0016). Parameters of reduced major axes are listed in Table 2.

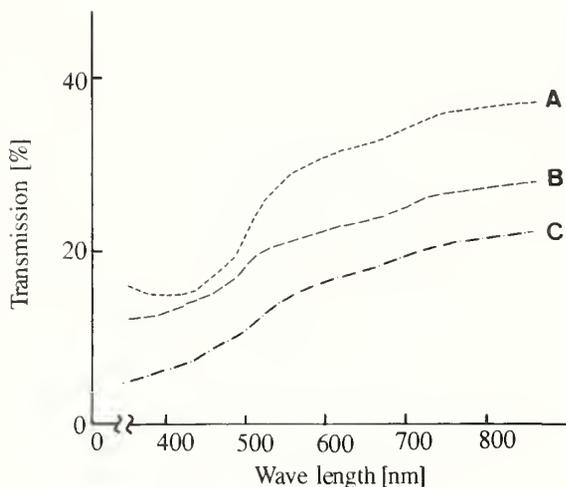
TRANSMISSION OF LIGHT THROUGH THE SHELL

The shell of *F. unedo* is thick and non-transparent. In contrast, *F. fragum* and *F. loochooanum* have rather thin and semi-transparent shells. The shell of *F. fragum* transmits more light than that of *F. loochooanum*. The shell structure and the transmission of light through the shell was examined for *F. fragum*.

The shell of *F. fragum* is composed of a mosaic of transparent and non-transparent domains of mm order. The shell consists of an outer layer of needle-shaped crystallites radiating in a fan-shape

TABLE 2. Reduced major axis ($Y = aX + b$) related to allometric shell growth of *Fragum* species. Abbreviations: L, shell length (mm); n , number of samples; PGL, posterior gape length (mm); PVA, angle between posterior and ventral valve margins (PV-angle) (degrees); r , correlation coefficient; n.s., not significant. For the definition of the reduced major axis, see Agterberg (1974, p. 122).

	Y	X	a	b	r	Level of significance
<i>F. fragum</i> ($n = 109$; CTO0014)	PGL/L	L	0.0157	0.7169	0.78813	$P < 0.001$
	PVA	L	-1.0707	95.0033	0.80577	$P < 0.001$
<i>F. loochooanum</i> ($n = 80$; CTO0015)	PGL/L	L	0.0331	0.5551	0.38645	$P < 0.001$
	PVA	L	-2.4040	108.4430	0.41084	$P < 0.001$
<i>F. imedo</i> ($n = 19$; CTO0016)	PGL/L	L	0.0061	0.6233	0.18729	n.s.
	PVA	L	-0.7236	113.1170	0.70156	$P < 0.01$



TEXT-FIG. 4. Transmission of light through the posterior slopes of *Fragum fragum* shells. A, the smallest specimen (shell length = 22.1 mm; CTO0017); B, the largest specimen (shell length = 31.5 mm; CTO0018); C, a medium-sized specimen (shell length = 15.8 mm; CTO0019).

towards the growth margin and an inner layer of crossed-lamellar structure. These two shell layers show no microstructural modifications producing different transparency, thus the transparency must be achieved by factors other than microstructure.

The posterior slope is the most transparent part of the shell of *F. fragum*. In Text-figure 4, the transmission/wavelength curves of this part are shown for three specimens of different sizes. The most transparent sample is the smallest one, but the least transparent sample is a medium sized specimen. Therefore the shell transparency of *F. fragum* may have considerable individual variability. The transparency of the posterior slope is between 13 and 18 per cent. for the least transparent specimen and between 14 and 22 per cent. in the most transparent one for light with wavelengths in the range 400–500 nm. As the wavelength increases to 800 nm this value increases to 27 per cent. in the least transparent specimen and 36 per cent. in the most transparent one.

The needle-shaped crystallites of the outer shell layer radiate and those of the crossed lamellae in the inner shell layer are differently orientated from one lamella subunit to another. Therefore the light penetrating into the shell of this species will be scattered by these variously orientated crystallites and illuminates the shell interior uniformly. This is in contrast with the transparent windows of the photo-symbiotic bivalve *Corculum cardissa*. In the latter, bundles of fine needle-like

crystallites radiate inwards from the shell external surface to form windows (Watson and Signor 1986), which transmit light effectively, with minimum dispersion, into the shell interior where there are abundant zooxanthellae.

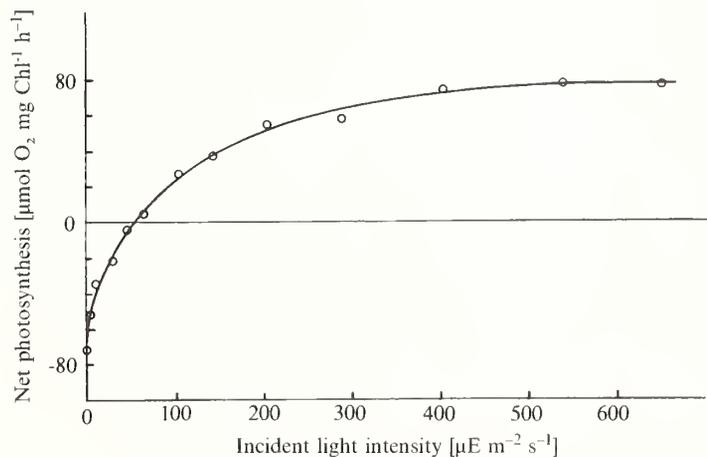
A direct comparison of the shell transparency of *Corculum cardissa* and *F. fragum* is not possible because Watson and Signor (1986) do not give the size of their measured shells. However, the lower transmission values of the present three specimens compared with the samples studied by Watson and Signor (maximum light transmission value of 40 per cent. at 620 nm) does not contradict our impression that the transparency of the shell in *Corculum cardissa* is higher.

The shell transparency of *F. fragum*, as well as of *Corculum cardissa*, is relatively low up to a wavelength of 500 nm, where the photosynthetic pigments (peridinin) of zooxanthellae have a strong absorption peak (Jeffrey and Haxo 1968). *Corculum cardissa* additionally exhibits a relatively low transparency around 675 nm (Watson and Signor 1986), close to where a second peak of the zooxanthellae's action spectrum exists (at 672 nm; Scott and Jitts 1977; Dustan 1982). Therefore the shells of these two bivalves are not perfectly adapted to transmit light in the optimal wavelengths for the zooxanthellae's photosynthesis.

PHOTOSYNTHESIS-IRRADIANCE PROFILE OF ZOOXANTHELLAE

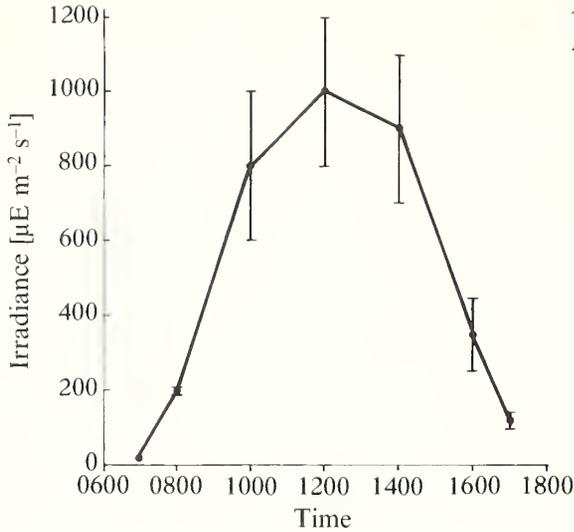
The photosynthesis versus irradiance curve was measured for the zooxanthellae extracted from *F. fragum* (Text-fig. 5). This curve indicates that the compensation light level of photosynthesis of

TEXT-FIG. 5. Photosynthesis-irradiance profile of zooxanthellae extracted from *Fragum fragum*.



the zooxanthellae is $50 \mu\text{Einstein m}^{-2} \text{s}^{-1}$ (an Einstein equals Avogadro's number $- 6.02 \times 10^{23}$ of quanta). Above this light level, zooxanthellae can produce organic matter in excess of their respiration. With increasing irradiance intensity, the rate of photosynthesis gradually increases until it attains a maximum value of about $80 \mu\text{mol O}_2 \text{ mg Chl}^{-1} \text{ h}^{-1}$ at an intensity of $400-500 \mu\text{Einstein m}^{-2} \text{s}^{-1}$.

The daily variation in light intensity at a depth of 2 m on a sunny day is shown in Text-fig. 6. The measurement was carried out in front of the Okinawa Research Centre at Amitori, the habitat of the three examined *Fragum* species, on 6 Nov. 1991. Even during late Autumn, the light intensity greatly exceeds the compensation point of the zooxanthellae of *F. fragum* ($50 \mu\text{Einstein m}^{-2} \text{s}^{-1}$) for at least 9 hours each day (08.00 to 17.00 hours). Because of the tide, the sandy flats where the three *Fragum* species live are submerged to a water depth of about two m only during spring high tides. At other times the water depth is less. The light intensity at the sea bottom will therefore, in general, be greater than that shown by the curve of Text-figure 6.



TEXT-FIG. 6. Light intensity at 2 m water depth in Amitori Bay measured on an Autumn sunny day (6 Nov. 1991).

DISCUSSION

*Sciaphilous photo-symbiosis in *Fragum* and its advantages*

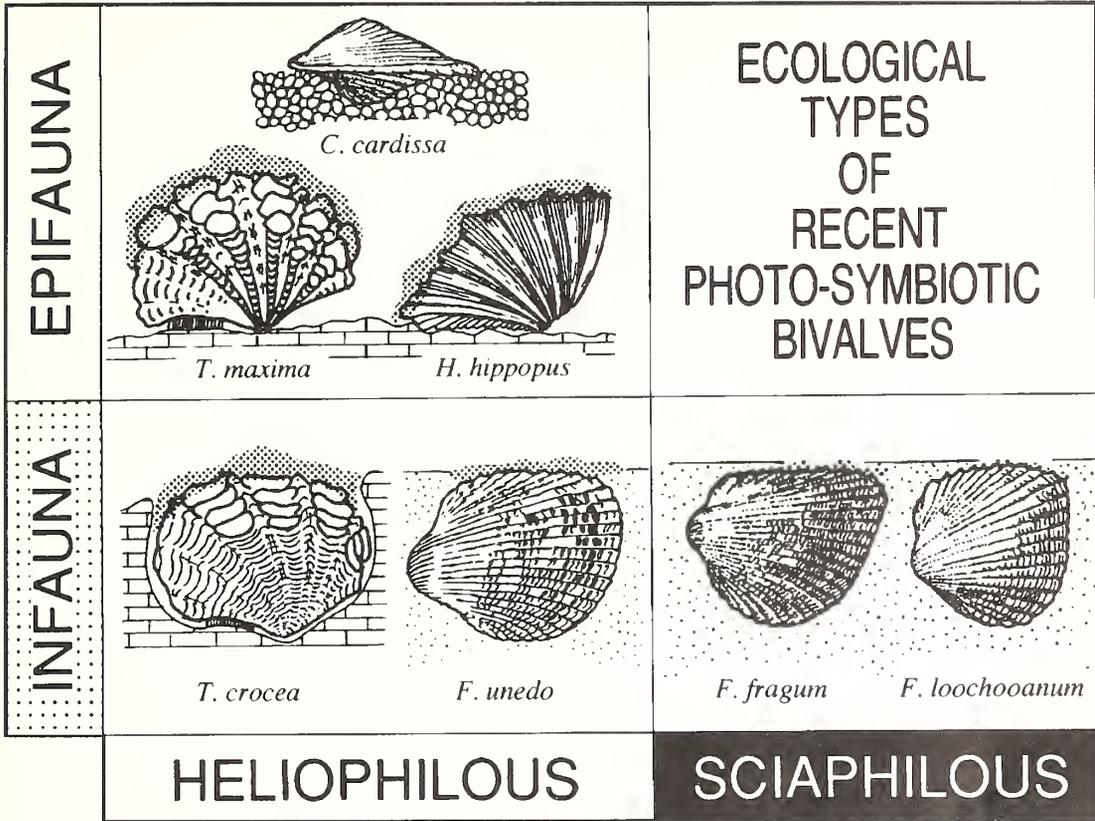
Fragum loochooanum adds a new fourth example of symbiosis with zooxanthellae (*Symbiodinium*) in the genus *Fragum*. The present study also reveals that *F. fragum* and *F. loochooanum* have adopted a new and previously unrecognized life mode among photo-symbiotic bivalves, i.e., sciaphilous (shade loving) photo-symbiosis, in which they do not expose their soft tissues and shells out of the sediment (Text-fig. 7). *F. fragum* even seems to hide itself actively by adhering sand grains to its posterior shell slope by extensively secreting mucus (Pl. 1, fig. 9). The mucus is probably derived from the zooxanthellae's photosynthetic product, as in the two slugs studied by Trench *et al.* (1972).

In the warm shallow seas of the present day, epifaunal bivalves are susceptible to bivalve-eating predators (Vermeij 1977, 1987, p. 167), or suffer from uncomfortable epibiont growth (Stanley 1970, pl. 116, figs 10 and 11; Dörjes 1978, p. 130). *F. fragum* and *F. loochooanum* are well protected from predation and epibiont attachment. Their active locomotion ability (Table 1) also allows them to escape from these disadvantages. Therefore these two sciaphilous bivalves enjoy the benefit of photo-symbiosis without trading their security.

Symbiodinium

To enable photosynthesis in a wide range of daily and seasonal as well as depth-dependent fluctuations of light intensity, marine algae can evolve molecular level adaptations. Shade adaptation is one such, and has been observed in a wide range of marine algae (Falkowski and Owens 1980). It is achieved by increase in number and/or size of photosynthetic units per algal cell (Falkowski and Owens 1980; Falkowski and Dubinsky 1981). Some dinoflagellates also increase the amount of their light-harvesting pigment-protein complex (peridinin-chlorophyll-*a* proteins) when cultured under low light (Prézelin 1976).

It is this shade adaptation which enables the zooxanthellae within *F. fragum* to photosynthesize with the limited amount of light coming through the host's narrow shell gape. In fact, the compensation point of photosynthesis of the zooxanthellae of *F. fragum* (Table 3) is about one-quarter of that of the zooxanthellae of epifaunal and heliophilous *Tridacna maxima* (Roeding) (Scott and Jitts 1977), and about one-twentieth of the maximum intensity of the ambient light of the cockle's habitat measured on a sunny Autumn day (Text-fig. 6). The photosynthesis irradiance



TEXT-FIG. 7. Life habits of photo-symbiotic bivalves.

TABLE 3. List of reported I_c (= compensation point) values (in $\mu\text{Einstein m}^{-2} \text{s}^{-1}$).

Host species	Remarks	I_c	Authors
Measured on hosts			
Hermatypic coral			
<i>Stylophora pistillata</i>	Light adapted	c 250	Falkowski and Dubinsky (1981)
	Shade adapted	c 30	(estimated from their fig. 2)
<i>Stylophora pistillata</i>	Light adapted	127	Porter <i>et al.</i> (1984)
	Shade adapted	26	<i>ibid.</i>
<i>Anthopleura elegantissima</i>	Starved	c 30	Fitt and Pardy (1981) (estimated from their fig. 1)
Bivalve			
<i>Tridacna maxima</i>		c 160–240	Trench <i>et al.</i> (1981) (estimated from their fig. 17)
Measured on zooxanthellae extracted from host bivalve			
<i>Tridacna maxima</i>		c 230	Scott and Jitts (1977) (estimated from their fig. 6)
<i>Fragum fragum</i>		50	Present study

curve for the zooxanthellae of *F. loochooanum* is not available. However, we suggest that the same behaviour of zooxanthellae is essential for the sciaphilous photo-symbiosis of this species.

Symbiodinium belongs to the 'naked' dinoflagellate order Gymnodiniales, which has a very sparse fossil record (Sarjeant and Downie 1974; Norris 1978; Williams 1978). Circumstantial evidence, however, suggests that it has a long symbiotic history. The changes in the relative importance of sponges and corals during the Middle Triassic–Late Jurassic interval probably coincided with the development of a symbiotic relationship between zooxanthellae (= *Symbiodinium*) and corals (Fagerstrom 1987, p. 292). Since then, some of the *Symbiodinium* may have become successfully shade adapted, either as they accompanied hosts exploiting deeper and darker habitats, or because their built-in flexibility enabled them to photosynthesize in very low light intensity allowing corals to exploit darker habitats. In fact the present day shade-adapted *Symbiodinium* of the hermatypic coral *Stylophora pistillata* shows a compensation point of about $30 \mu\text{Einstein m}^{-2} \text{s}^{-1}$ (Falkowski and Dubinsky 1981) which is even lower than that of the zooxanthellae living in *F. fragum* (Table 3).

Besides bivalves, *Symbiodinium* is present in a wide range of hosts such as the jellyfish *Cassiopea*, and numerous species of hermatypic corals (Trench and Blank 1987). The genus's ability to overcome the self-defence system of a wide variety of invertebrate host taxa may also be related to its long symbiotic history.

Scarcity of photo-symbiosis

The zooxanthellae's shade adaptation makes all shallow sea bivalves potential hosts. Yet, among living bivalves, symbiosis with zooxanthellae is confined to the genera *Tridacna*, *Hippopus*, *Corculum* and *Fragum*. *Microfragum festivum* (Deshayes), belonging to the subfamily Fraginae and closely related to *Fragum* and *Corculum*, or *Pinna* sp., which exposes a considerable part of its transparent shell out of the sediment, do not harbour zooxanthellae in their soft tissues (personal observation), although they are living in the same sand flats as the three examined *Fragum* species. These observations suggest that the scarcity of zooxanthella–bivalve photo-symbiosis may not be the result of insufficient observation but is reality.

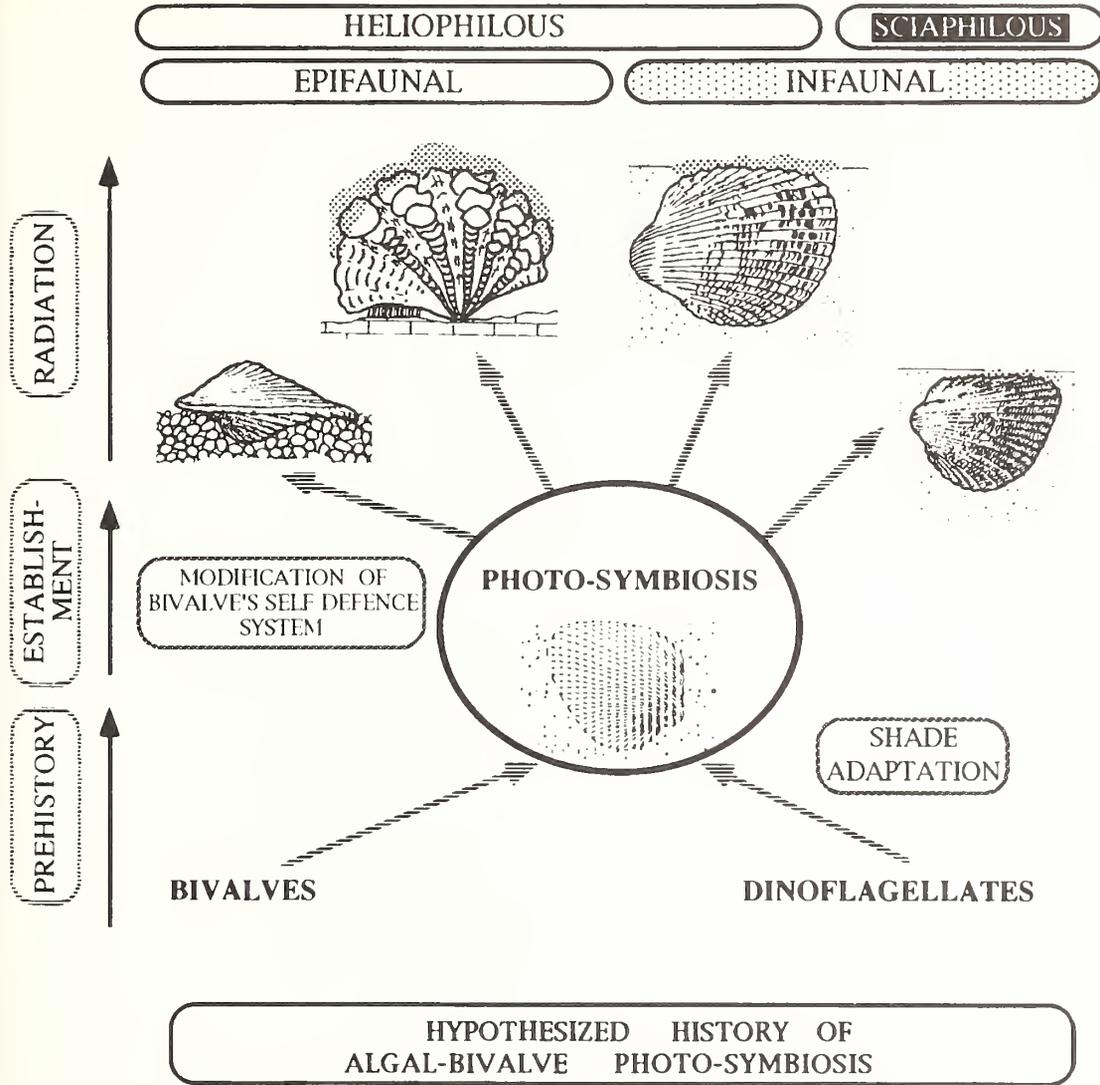
Smith (1991) also pointed out that very few animals are involved in symbiosis with photosynthetic microbes. He considered that costs imposed upon the animal hosts, including those of mechanisms for control of symbiont cell division and regulation of symbiont population size and location, might make photo-symbiosis less economic than the greatly prevalent herbivory for gaining access to photosynthetically-fixed carbon.

Palaeontological implications

The recognition of sciaphilous photo-symbiosis in *F. fragum* and *F. loochooanum* with shade adapted zooxanthellae has several palaeontological implications. Firstly, the photo-symbiosis in this genus and other extant photo-symbiotic bivalves seems to have initiated as a sciaphilous one. Secondly, a sciaphilous origin of photo-symbiosis seems applicable also to some fossil photo-symbiotic bivalves. Finally, several fossil bivalve taxa are now becoming candidates for being (sciaphilous) photo-symbiotic bivalves. In the following we discuss these points in some detail.

Sciaphilous origin of extant photo-symbiotic bivalves. The sciaphilous *F. fragum* and *F. loochooanum* do not show any indication that they once had mantle edges similarly expanded like those of *F. unedo*. Thus they seem to retain a more ancestral form than the latter. Yet they harbour zooxanthellae in their inner soft tissues. Therefore it seems that the photo-symbiosis in the genus *Fragum* was initiated by the association of shade (pre-)adapted *Symbiodinium* and an ancestral infaunal bivalve which was not pre-adapted for light harvesting for symbionts.

As mentioned earlier, the symbiotic relationship between *Symbiodinium* and hermatypic corals was initiated between the Middle Triassic and Late Jurassic, which predates the known range of the genus *Fragum* (Miocene–Recent) by at least about 80 My. It is probable that some *Symbiodinium*



TEXT-FIG. 8. Highly simplified hypothesized history of zooxanthella–bivalve photo-symbiosis (figure of bivalve in ellipse after Stasek 1961).

TABLE 4. Features related to the sciaphilous life mode of *Fragum fragum* and *Fragum loochooanum*.

1. More or less transparent mantle edges covering the posterior shell gape allows light penetration into the shell interior.
2. Long and rather transparent supra-branchial chamber aligns the gills with abundant zooxanthellae just beneath and along the posterior shell gape, through which light penetrates.
3. The rapid increase in the length of the straight shell posterior gape during shell growth increases the area of light penetration.
4. The rapid decrease in the angle between the posterior and ventral valve margins (PV-angle) during shell growth keeps soft parts with abundant zooxanthellae near the shell gape.

species might have successfully shade adapted prior to the initiation of the photo-symbiosis with *Fragum*.

Like *Fragum*, other extant photo-symbiotic bivalves (*Tridacna*, *Hippopus* and *Corculum*) either belong to, or are closely related to, the superfamily Cardiacea, the majority of the members of which are infaunal. Thus the ancestors of these photo-symbiotic bivalves were also most probably infaunal. If so, the above stated scenario may also be applied to the origination of photo-symbiosis of these bivalves. The varied geological ranges of these photo-symbiotic bivalves (*Tridacna* since Miocene; Stasek 1961; *Hippopus* since ?Miocene, but with certainty in Recent; Stasek 1961; and *Corculum* in Recent; Keen 1980) suggests that the establishment of zooxanthella–bivalve photo-symbiosis took place several times.

Once photo-symbiosis is established in a sciaphilous form, the selection pressure would favour the tendency to optimize the benefits of the symbiosis. There is not a unique solution in optimizing (Text-fig. 8). *F. fragum* and *F. loochooanum* sustained their sciaphilous life mode, which would minimize the danger of predation. Infaunal *F. uedo* evolved hypertrophied mantle edges and exposes them widely on the sediment surface to collect more light. *Tridacna*, *Hippopus* and *Corculum* shifted to epifaunal life. The former two expose their mantle tissues out of the shell to collect light, whereas *Corculum* makes its shell transparent to illuminate algae nesting in their soft parts which are protected within the host's valves. Indeed the acquisition of photo-symbiosis with zooxanthellae led to a strong radiation in bivalve morphology and ecology.

Sciaphilous origin of fossil photo-symbiotic bivalves. When considering the origin of photo-symbiosis in bivalves, earlier studies have emphasized the bivalve's adaptations for supplying light to the photosynthetic microbial symbionts. Yonge (1936) suggested infection of zooxanthellae in the siphonal area of tridacnids as the starting point for the photo-symbiosis. Cowen (1982) postulated that symbiosis can only develop in a host that is pre-adapted by tissue exposure to light. Skelton (1979) also suggested pre-adaptation of bivalves for the establishment of the inferred photo-symbiosis in an extinct radiolitid rudist bivalve, *Radiolites* cf. *angeoides* (De Lapeirouse). The latter's extremely narrow valve gape and its small body/mantle cavity ratio were interpreted as indicating atrophy of the gills and the loss of effective filter feeding. Skelton further suggested that the species developed expanded and tentacled mantle margins to make up for its ineffective filter feeding. These tentacled mantle margins, which were expanded out of the shell for collecting food particles, were later infected by the zooxanthellae.

An alternative interpretation of the evolution of photo-symbiosis in this species may be a sciaphilous origin, i.e. the infection of shade adapted microbes within the internal soft tissues of the ancestor of this species. Then the expanded mantle margins of this rudist can be interpreted simply as the result of optimizing light harvesting, followed by the loss of efficient filter feeding. Because this scenario ensures nutrition of the bivalve by photosynthetic products, we can further curtail an evolutionary stage of food collection with expanded and tentacled mantle margins (Skelton 1979). For such a feeding method, it is necessary to conceive a probably very complicated mechanism for smooth transportation of the collected food particles through a very narrow gape and for passing over then to the labial palps or mouth. In future, the initiation of photo-symbiosis in this rudist bivalve and other inferred fossil photo-symbiotic bivalves should not be viewed only as the result of the bivalve's pre-adaptation, but the possibility of their origination in a sciaphilous form should also be considered.

New candidates of fossil photo-symbiotic bivalves. Because sciaphilous photo-symbiosis allows host bivalves to enjoy the benefit of symbiosis without the dangers of predation or epibiont attachment, many fossil photo-symbiotic bivalves, if they ever existed, are likely to have adopted, or even clung to, this option of symbiosis.

F. fragum and *F. loochooanum* show certain morphological features related to their sciaphilous photo-symbiosis with zooxanthellae (Table 4). Among them, rapid increase in the PGL/L ratio as well as a rapid decrease in PV-angle during shell growth (Text-fig. 3; Table 2) can be preserved in

fossil shells. These two features together with the occurrence of fossils from shallow sea sediments would be helpful criteria in the search for sciaphilous photo-symbiosis among fossil bivalves.

Some promising fossil candidates may be expected among the trigoniid bivalves which adopted a life mode similar to the present day cardiids, in warm shallow marine sandy habitats during the Mesozoic (Stanley 1978). Indeed, a specimen of the Bajocian *Trigonia denticulata* Ag. in our possession has an overall shell form quite similar to that of *F. fragum* and *F. loochooanum*. Furthermore, it would be interesting to see if the ancestors of *Opisoma* Stoliczka (Chavan 1969, N572 and fig. E72, 4) have a similar form to *F. fragum* or *F. loochooanum*. The shell morphology of this Lower Jurassic astartid bivalve has an overall resemblance to that of the living photo-symbiotic bivalve *Corculum cardissa*. These fossil bivalves tempt us to examine them and related species in detail, although their geological age suggests that their symbiotic photosynthetic microbes are not necessarily identical or related to the present day *Symbiodinium*.

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REFERENCES

- AGTERBERG, F. P. 1974. *Developments in geomathematics, 1. Geomathematics, mathematical background and geoscience applications*. Elsevier Scientific Publishing, Amsterdam, xvi + 596 pp.
- BLANK, R. J. and TRENCH, R. K. 1986. Nomenclature of endosymbiotic dinoflagellates. *Taxon*, **35**, 286–294.
- CHAVAN, A. 1969. Superfamily Crassatellacea Férussac, 1822. N562–N583. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology. Part N. Volume 2 (of 3), Mollusca, 6. Bivalvia*. The Geological Society of America, Inc. and The University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, ii + N491–N952.
- COWEN, R. 1970. Analogies between the Recent bivalve *Tridacna* and the fossil brachiopods Lyttoniaceae and Richthofeniaceae. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **8**, 329–344.
- 1982. Algal symbiosis and its recognition in the fossil record. 431–478. In TEVESZ, M. J. S. and MCCALL, P. L. (eds). *Biotic interactions in Recent and fossil benthic communities*. (Topics in Geobiology 3). Plenum, New York, 837 pp.
- DUSTAN, P. 1982. Depth-dependent photoadaptation by zooxanthellae of the reef coral *Montastrea annularis*. *Marine Biology*, **68**, 253–264.
- DÖRJES, J. 1978. Das Watt als Lebensraum. 107–143. In REINECK, H. E. (ed.). *Das Watt. Ablagerungs- und Lebensraum* (Zweite, neubearbeitete und erweiterte Auflage). Verlag von Waldemar Kramer, Frankfurt am Main, 185 pp.
- FAGERSTROM, J. A. 1987. *The evolution of reef communities*. John Wiley and Sons, New York, xv + 600 pp.
- FALKOWSKI, P. G. and DUBINSKY, Z. 1981. Light-shade adaptation of *Stylophora pistillata*, a hermatypic coral from the Gulf of Eilat. *Nature*, **289**, 172–174.
- and OWENS, T. G. 1980. Light-shade adaptation, two strategies in marine phytoplankton. *Plant Physiology*, **66**, 592–595.
- FITT, W. K. and PARDY, R. L. 1981. Effects of starvation, and light and dark on the energy metabolism of symbiotic and aposymbiotic sea anemones, *Anthopleura elegantissima*. *Marine Biology*, **61**, 199–205.
- JEFFREY, S. W. and HAXO, F. T. 1968. Photosynthetic pigments of symbiotic dinoflagellates (zooxanthellae) from corals and clams. *The Biological Bulletin*, **135**, 149–165.
- KAWAGUTI, S. 1941. Heart Shell *Corculum cardissa* (L.) and its zooxanthella. *Kagaku Nanyo*, **3**, 45–46. [in Japanese].

- KAWAGUTI, S. 1983. The third record of association between bivalve mollusks and zooxanthellae. *Proceedings of the Japan Academy, Series B*, **59**, 17–20.
- KEEN, A. M. 1980. The pelecypod family Cardiidae: a taxonomic summary. *Tulane Studies in Geology and Paleontology*, **16**, 1–40.
- LORIGA, C. B. and BENINI, C. A. 1977. Analisi morfofunzionale di alcuni lamellibranchi Liassici e loro rapporto con le ostree. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale in Milano*, **118**, 212.
- NORRIS, G. 1978. Phylogeny and a revised supra-generic classification for Triassic-Quaternary organic-walled dinoflagellate cysts (Pyrrhophyta). Part II. Families and sub-orders of fossil dinoflagellates. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **156**, 1–30.
- OKINAWA REGIONAL RESEARCH CENTRE 1990. *Measured data at Amitori, Iriomote Island (I)*, Okinawa Regional Research Centre, Oceanographic Institute of the Tokai University, Shimizu, 110 pp. [in Japanese].
- PHILIP, J. 1972. Paléocologie des formations à rudistes du Crétacé supérieur – l'exemple du Sud-Est de la France. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **12**, 205–222.
- PORTER, J. W., MUSCATINE, L. and DUBINSKY, Z. 1984. Primary production and photoadaptation in light- and shade-adapted colonies of the symbiotic coral, *Stylophora pistillata*. *Proceedings of the Royal Society of London, Series B*, **222**, 161–180.
- PRÉZELIN, B. 1976. The role of peridinin-chlorophyll *a*-proteins in the photosynthetic light adaptation of the marine dinoflagellate, *Glenodinium* sp. *Planta*, **130**, 225–233.
- PURCHON, R. D. 1955. A note on the biology of *Tridacna crocea* Lam. *Proceedings of the Malacological Society of London*, **31**, 95–110.
- SARJEANT, W. A. S. and DOWNIE, C. 1974. The classification of dinoflagellate cysts above generic level: a discussion and revisions. *Birbal Sahni Institute of Palaeobotany Special Publication* no. 3: *Symposium on Stratigraphical Palynology*, 9–32.
- SCOTT, B. D. and JITTS, H. R. 1977. Photosynthesis of phytoplankton and zooxanthellae on a coral reef. *Marine Biology*, **41**, 307–315.
- SEILACHER, A. 1990. Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Historical Biology*, **3**, 289–311.
- SKELTON, P. W. 1979. Preserved ligament in a radiolite rudist bivalve and its implication of mantle marginal feeding in the group. *Palaeobiology*, **5**, 90–106.
- and WRIGHT, V. P. 1987. A Caribbean rudist bivalve in Oman: island-hopping across the Pacific in the Late Cretaceous. *Palaeontology*, **30**, 505–529.
- SMITH, D. C. 1991. Why do so few animals form endosymbiotic associations with photosynthetic microbes? *Philosophical Transactions of the Royal Society of London, Series B*, **333**, 225–230.
- STANLEY, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Memoir of the Geological Society of America*, **125**, 1–296.
- 1978. Aspects of the adaptive morphology and evolution of the Trigoniidae. *Philosophical Transactions of the Royal Society of London, Series B*, **284**, 247–258.
- STASEK, C. R. 1961. The form, growth and evolution of the Tridacnidae (giant clams). *Archives de Zoologie Expérimentale et Générale*, **101**, 1–40.
- THELE, O. and TICHY, G. 1980. Über das Auftreten von *Tanichintongia* (Bivalvia) in Perm des Iran. *Karlinthin*, **82**, 166–173.
- TRENCH, R. K. and BLANK, R. J. 1987. *Symbiodinium microadriaticum* Freudenthal, *S. goreauii* sp. nov., *S. kawagutii*, sp. nov. & *S. pilosum*, sp. nov.: Gymnodinioid dinoflagellate symbionts of marine invertebrates. *Journal of Phycology*, **23**, 469–481.
- TRENCH, M. E. and MUSCATINE, L. 1972. Symbiotic chloroplasts; their photosynthetic products and contribution to mucus synthesis in two marine slugs. *The Biological Bulletin*, **142**, 335–349.
- WETHEY, D. S. and PORTER, J. W. 1981. Observations on the symbiosis with zooxanthellae among the Tridacnidae (Mollusca, Bivalvia). *The Biological Bulletin*, **161**, 180–198.
- UMESHITA, H. and YAMASU, T. 1985. On the morphology of a species of strawberry cockle *Fragum* sp. *The Biological Magazine of Okinawa*, no. 23, 50. [in Japanese].
- VERMEIJ, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**, 245–258.
- 1987. *Evolution and escalation, an ecological history of life*. Princeton University Press, Princeton, New Jersey, xv + 527 pp.
- VOGEL, K. 1975. Endosymbiotic algae in rudists? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **17**, 327–332.

- WATSON, M. E. and SIGNOR, P. W. 1986. How a clam builds windows: shell microstructure in *Corculum* (Bivalvia: Cardiidae). *The Veliger*, **28**, 348–355.
- WILLIAMS, G. L. 1978. Dinoflagellates, acritarchs and tasmanitids. 293–326. In HAQ, B. U. and BOERSMA, A. (eds). *Introduction to marine micropaleontology*. Elsevier, New York, 376 pp.
- YAMASU, T. 1988a. Animals in coral reef 3 – Symbiotic relationships in coral reef. 123–145. In NISHIHIRA, M. (ed.). *The coral reefs in Okinawa*. Okinawaken Kankyokagaku Kensa Centre, Naha, 239 pp. [in Japanese].
- 1988b. Symbiosis between marine animals and algae. *The Heredity*, **42**, 12–20. [in Japanese].
- YANCEY, T. E. and BOYD, D. W. 1983. Revision of the Alatoconchidae: a remarkable family of Permian bivalves. *Palaeontology*, **26**, 497–520.
- YONGE, C. M. 1936. Mode of life, feeding, digestion and symbiosis with zooxanthellae in the Tridacnidae. *Scientific Reports, Great Barrier Reef Expedition, British Museum*, **1**, 283–321.

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THE TETHYAN BIVALVE *ROUDAIRIA* FROM THE UPPER CRETACEOUS OF CALIFORNIA

by M. X. KIRBY and L. R. SAUL

ABSTRACT. The Tethyan genus *Roudairia* is described for the first time from North America. A new species, *Roudairia squiresi*, occurs in the shallow-marine, basal beds of the San Francisquito Formation (uppermost Maastrichtian) at Warm Springs Mountain, Los Angeles County, California. The earliest representatives of the genus *Roudairia* are from the Cenomanian of north and west Africa. The genus later migrated westward to the western Tethyan Realm and into California during the latest Cretaceous. The presence of *R. squiresi* suggests warm water in California at the end of the Cretaceous. The taxonomic status of two closely related genera, *Cicatrea* and *Veniella*, in relation to *Roudairia*, remains unclear. However, among these three related taxa, there are at least two distinct generic groups present. The first is represented by *Veniella* and the second by *Roudairia*. Specimens from Africa and Madagascar, previously ascribed to '*Cicatrea cordialis*', belong in the second group. Whether *Cicatrea cordialis* from India also belongs in this second group cannot be determined until additional specimens provide better morphological data.

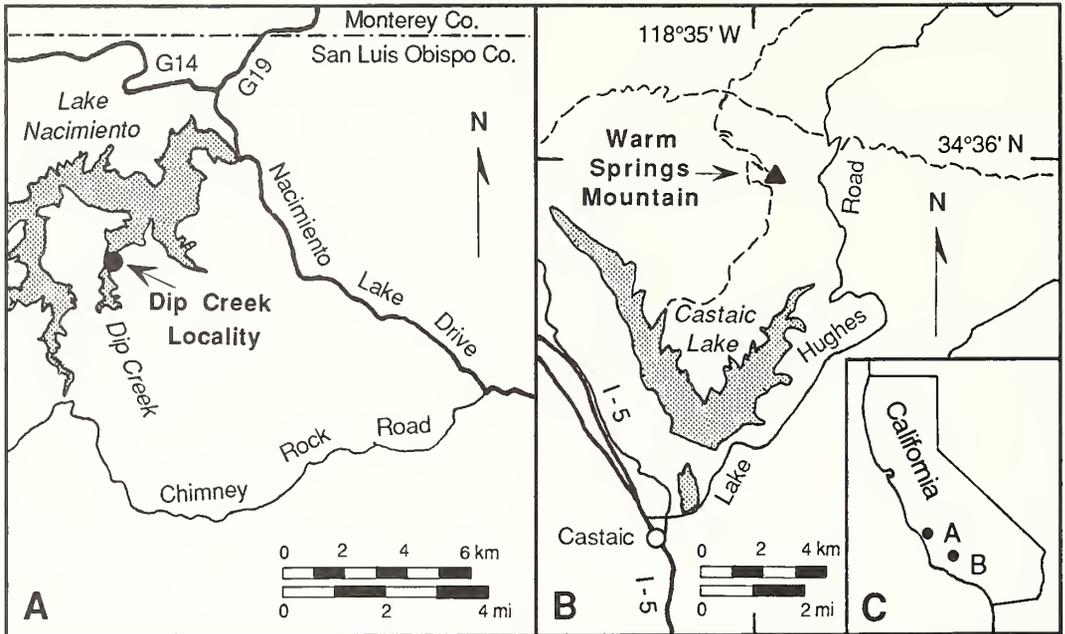
SEVERAL specimens of a new species, *Roudairia squiresi*, were collected from basal beds of the San Francisquito Formation on Warm Springs Mountain, in the San Gabriel Mountains, Los Angeles County, southern California (Text-fig. 1). Turritellid gastropods associated with *R. squiresi* at Warm Springs Mountain indicate a very late Maastrichtian age for the basal San Francisquito Formation (Saul 1983). The basal San Francisquito Formation at Warm Springs Mountain is part of a shallow-marine phase of a transgressive sequence that continued across the Cretaceous/Tertiary boundary into the Palaeocene (Kooser 1980; Kirby *et al.* 1991).

A fragment of a left valve that resembles *R. squiresi* was found in undifferentiated Upper Cretaceous rocks at Dip Creek, south shore of Lake Nacimiento, San Luis Obispo County, central California (Text-fig. 1). Associated Turritellid gastropods and an ammonite indicate a latest Maastrichtian age (Saul 1983).

Roudairia has not previously been reported from North America. One species is known from the Upper Cretaceous of Jamaica (Trechmann 1927), and four species are known from the Upper Cretaceous of Peru (Brüggen 1910; Lisson 1925; Olsson 1934, 1944). A closely related genus, *Veniella* Stoliczka, 1870, is present in Western Interior and Gulf Coast, North American deposits of Turonian to Maastrichtian age. Another closely related taxon, *Cicatrea* Stoliczka, 1870, is from the Upper Cretaceous of India.

The palaeobiogeographical distributions of *Roudairia*, *Veniella*, and *Cicatrea* are clouded by difficulties in determining their generic and specific characters. Many of the pioneering reports of species assignable to these genera failed to note important morphological features and were vague as to stratigraphical position. Darteville and Freneix (1957) considered *Roudairia* and *Cicatrea* to be synonyms of *Veniella*, and therefore placed their species in *Veniella*. They indicated the biogeographical provenance of these species, but did not reassess completely their stratigraphical positions.

A complete review is beyond the scope of this paper, but the work of Darteville and Freneix (1957), which delineates characters of four widely occurring species, '*Cyprina (Cicatrea) cordialis*' Stoliczka, 1870, '*Trigonia auresseensis*' Coquand, 1862, *Roudairia drui* Munier-Chalmas, 1881, and '*Cyprina forebesiana*' Stoliczka, 1870, assists in assigning the first three of these species to *Roudairia* and the fourth to *Veniella*.



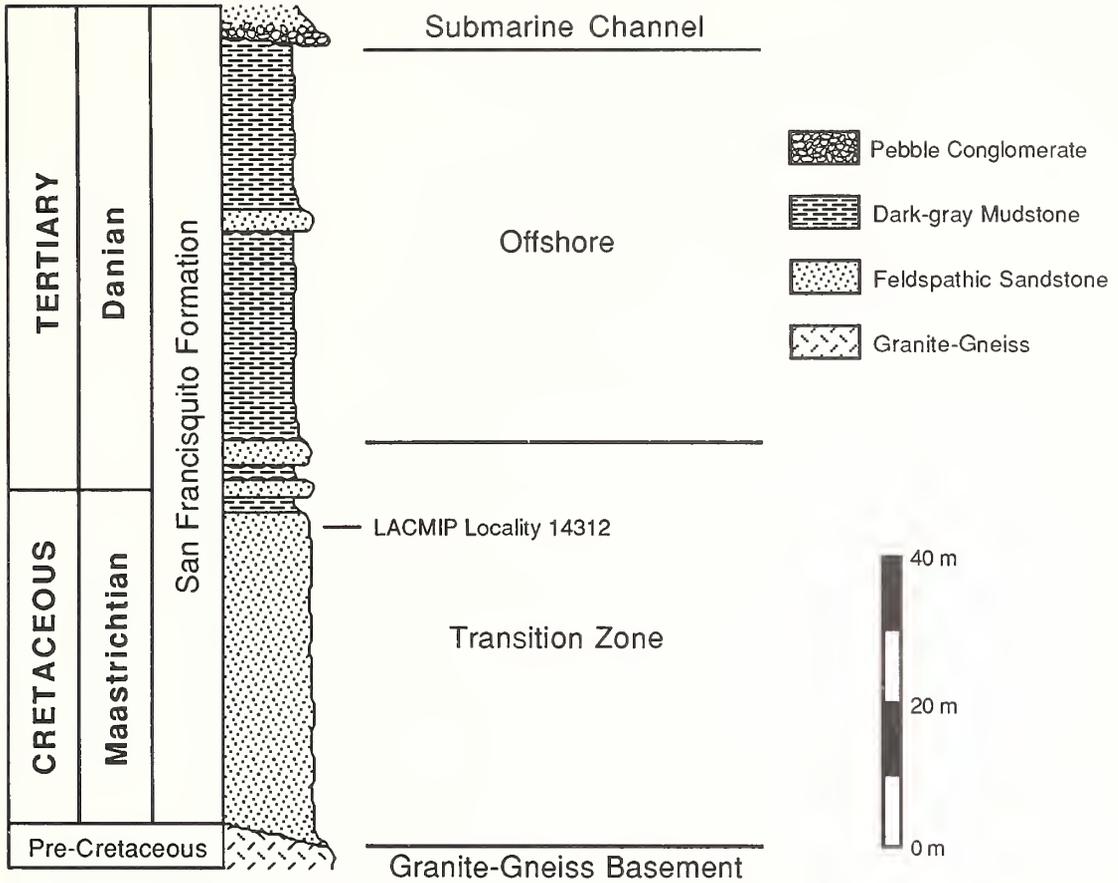
TEXT-FIG. 1. Locality maps showing (A) Dip Creek, (B) Warm Springs Mountain, and (C) California.

This paper describes the stratigraphy and depositional environments associated with *R. squiresi*, discusses the Late Cretaceous palaeobiogeography of the genus *Roudairia*, compares the generic characters of *Veniella* and *Cicatrea* with those of *Roudairia*, and concludes with the description of *R. squiresi*.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

The most complete specimens of *R. squiresi* are from the lowermost San Francisquito Formation at Warm Springs Mountain (Text-fig. 2). The San Francisquito Formation ranges in age from late Maastrichtian to late Palaeocene (Dibblee 1967; Kooser 1980, 1982). At Warm Springs Mountain, the formation was deposited on a granite-gneiss basement that is cut by dykes of early Maastrichtian age (Joseph *et al.* 1982). The San Francisquito Formation represents a marine-transgressive sequence that consists of shallow-marine deposits grading upsection into deeper submarine-fan deposits (Kooser 1980; Kirby 1991). The lower part of the formation contains a conformable section across the Cretaceous/Tertiary boundary (Kirby *et al.* 1991), as defined by the *Turritella* zonation of Saul (1983). *Roudairia squiresi* was found 5 m below this boundary (Text-fig. 2).

Eight unabraded valves, including one right valve, three left valves, two articulated specimens, and one fragment, were found in a feldspathic sandstone at Warm Springs Mountain (Kirby 1991). The single-valved specimens had probably been transported a short distance, whereas the articulated specimens were most likely *in situ*. The specimens were associated with the gastropods *Turritella webbi* Saul, 1983, *Turritella chaneyi orienda* Saul, 1983, *Anchura?* sp., and with the bivalves *Cucullaea* sp. nov., *Brachidontes?* sp. nov., and *Callistalox fragilis* (Gabb, 1869). *Turritella webbi*, *Turritella chaneyi orienda*, and *Brachidontes* are characteristic of a shallow-marine environment (Keen 1971; Saul 1983).

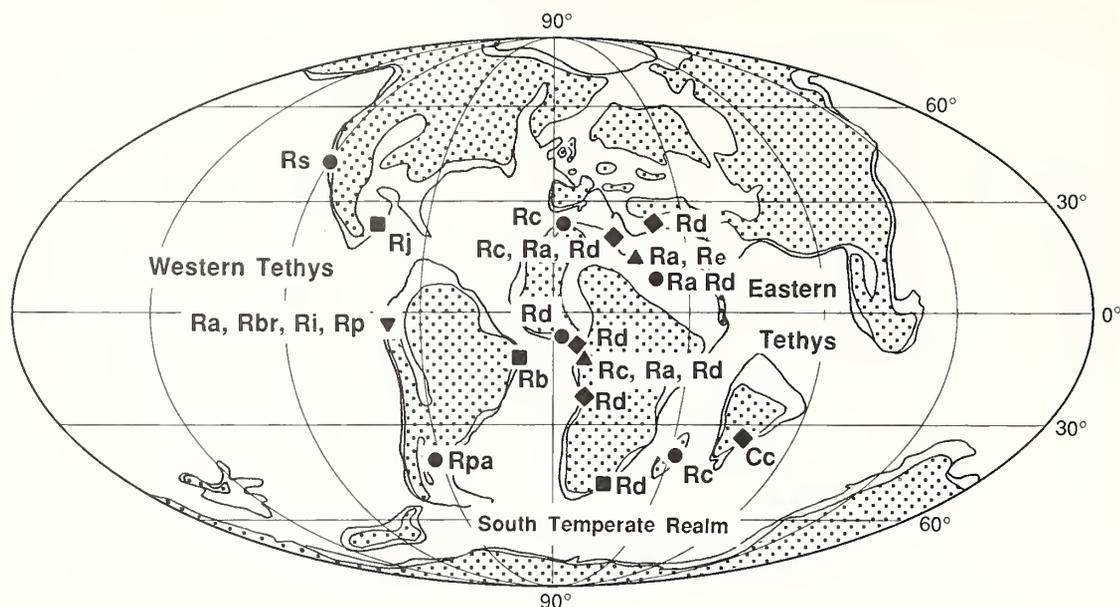


TEXT-FIG. 2. Stratigraphical section of the basal San Francisquito Formation, Warm Springs Mountain, California, showing chronostratigraphy, lithology, depositional environments, and stratigraphical position of *Roudairia squiresi* type locality (LACMIP locality 14312) (after Kirby 1991). Note transgressive nature of stratigraphical section.

Feldspathic sandstone crops out from the base of the San Francisquito Formation to 47 m above the base of the formation (Text-fig. 2). The sandstone is silty, very fine- to medium-grained, and poorly sorted. Although mostly structureless, the sandstone contains indistinct planar bedding locally. Bioturbation is very abundant. Fossiliferous lenses, up to 210 mm thick, are present throughout the feldspathic sandstone. These lenses are inferred to be storm-lag deposits (Kirby 1991).

Abundant bioturbation indicates deposition below fair weather wave base, and storm-lag deposits indicate deposition above storm wave base. Both these features indicate deposition of the feldspathic sandstone in the shallow-marine, transition zone (Kirby 1991).

These transition-zone deposits are part of a shallow-marine, transgressive sequence that grades upsection into offshore deposits. The underlying granite-gneiss basement and an overlying submarine-channel conglomerate stratigraphically bound the sequence (Text-fig. 2). This 110 m thick sequence is between 68.5 Ma and 63.8 Ma in age, based on the *Turritella* zonation of Saul (1983). Deposition of this transgressive sequence probably resulted from both basinal subsidence and eustatic transgression.



TEXT-FIG. 3. Palaeobiogeographical distribution of *Cicatrea* and *Roudairia* species on a Maastrichtian palaeogeographic map (Ziegler *et al.* 1982). Cretaceous palaeobiogeographical names after Kaufmann (1973). Plotted occurrences range from the Cenomanian to the Maastrichtian. Key to species: **Cc** = *Cicatrea cordialis* (Stoliczka 1870); **Ra** = *R. auressensis* (Coquand 1862) (Darteville and Freneix 1957); **Rb** = *R. brasiliensis* Maury, 1930; **Rbr** = *R. brüggeni* (Lisson 1925) (Olsson 1944); **Rc** = *R. cordialis* (Stoliczka 1870) (Douvillé 1904; Boule and Thevenin 1906; Darteville and Freneix 1957); **Rd** = *R. druī* Munier-Chalmas, 1881 (Rennie 1930; Darteville and Freneix 1957); **Re** = *R. elongata* Naldini, 1948; **Ri** = *R. intermedia* (Brüggen 1910) (Darteville and Freneix 1957; Willard 1966); **Rj** = *R. jamaicensis* Trechmann, 1927; **Rp** = *R. peruviana* Olsson, 1934; **Rpa** = *R. pampaensis* Leanza and Hünicken, 1970; **Rs** = *R. squiresi* sp. nov. (this paper). Symbols indicate the age of the oldest specimens found at each locality: ▲ = Cenomanian; ▼ = Turonian; ■ = Campanian; ● = Maastrichtian; ◆ = Late Cretaceous.

A fragment of a left valve resembling *R. squiresi* was found at Dip Creek. This fragment was found associated with turritellid gastropods and other shallow-water molluscs in very coarse-grained, conglomeratic sandstone and conglomerate beds. Grove (1986) interpreted these sandstone and conglomerate beds to be turbidites that were deposited in deep water.

Taliaferro (1944) referred the Dip Creek strata to his 'Dip Creek formation'. But Durham (1968) mapped outcrops along the north shore of Lake Nacimiento as unnamed Upper Cretaceous and Lower Tertiary rocks. Grove (1986) used this designation for the outcrops along the south shore of Lake Nacimiento. Confident assignment of the Dip Creek section to a formation can only be done after detailed geological mapping in the Lake Nacimiento area is undertaken (V. M. Seiders, pers. comm. 1992).

PALAEOBIOGEOGRAPHY

The genus *Roudairia* has a South Temperate to Tethyan distribution (Text-fig. 3. Cretaceous palaeobiogeographical names as defined by Kauffman 1973.) The genus *Veniella*, which as plotted by Darteville and Freneix (1957, text-fig. 3) included *Cicatrea* and *Roudairia*, has a South Temperate to North Temperate distribution. Text-figure 4 shows the biogeographical distributions of *Cicatrea*,

Location Age	California	Peru	WI & GC USA	Jamaica	Argentina	Brazil	N. Africa	W. Africa	S. Africa	Madagascar	India
Maastrichtian	R	R	V		R		R V	R V		R V	C
Campanian		R	V	R V		R	R V	R V	R V		C
Santonian/ Coniacian		R	V				V	R V	V	V	C V
Turonian		R	V				V	R V	V	V	
Cenomanian							R V	R V			

TEXT-FIG. 4. Location of *Cicatreia* spp. (C), *Roudairia* spp. (R), and *Veniella* spp. (V) through time (based on Stoliczka 1870; Meek 1876; Douvillé 1904; Boule and Thevenin 1906; Trechmann 1927; Maury 1930; Rennie 1930; Olsson 1934, 1944; Naldini 1948; Darteville and Freneix 1957; Willard 1966; Leanza and Hünicken 1970). Note that ages are not to scale. WI = Western Interior. GC = Gulf Coast.

Roudairia, and *Veniella* through time. The earliest record of *Roudairia* is from the Cenomanian of north and west Africa (Naldini 1948; Darteville and Freneix 1957; Cooper 1978). Specimens from these areas range in age from Cenomanian to Maastrichtian. Willard (1966) reported *Roudairia* from the Turonian of Peru. In the Coniacian, *Roudairia* is found in Peru and west Africa (Olsson 1934, 1944; Darteville and Freneix 1957). In the Campanian, *Roudairia* is reported from Peru, Jamaica, Brazil, north Africa, west Africa, and south Africa (Trechmann 1927; Maury 1930; Rennie 1930; Olsson 1934, 1944; Darteville and Freneix 1957). In the Maastrichtian, *Roudairia* is reported from California (this paper), Peru, Argentina, north Africa, west Africa, and Madagascar (Douvillé 1904; Olsson 1934, 1944; Darteville and Freneix 1957; Leanza and Hünicken 1970).

Abbass (1962) described a new species of *Roudairia* from the Danian of Egypt. If his new species, *Roudairia awadi*, is indeed a *Roudairia*, then *Roudairia* evidently survived the Cretaceous/Tertiary mass extinction and lived on into the Palaeocene. His description and figures of *R. awadi*, however, permit doubt as to whether his specimens actually belong to *Roudairia*.

The palaeobiogeographical distribution of *Roudairia* suggests that the genus evolved either in the northern part of the South Temperate Realm or in the Tethyan Realm before or during the Cenomanian. The genus later migrated westward to the western Tethys during the Late Cretaceous. *Roudairia squiresi*, or one of its antecedents, migrated from Central or South America into California in the Maastrichtian (Text-figs 3–4). The migration of the Tethyan *Roudairia* into the northeastern Pacific at this time suggests the presence of warm water in California at the end of the Cretaceous.

Roudairia squiresi of California is most similar to *Roudairia peruviana* Olsson, 1934, which is present in the Maastrichtian Monte Grande Formation and undifferentiated rocks of Campanian to Maastrichtian age in northern Peru (Olsson 1934, 1944). *Roudairia peruviana* is older than *R. squiresi*. *Roudairia jamaicensis* Trechmann, 1927, from the Campanian of Jamaica (Trechmann 1927), is less similar to, and is also older than *R. squiresi*. The present findings extend the palaeobiogeographical range of *Roudairia* from Jamaica and Peru northward to California (Text-fig. 3). The age range of *Roudairia* in the eastern Pacific is extended to the latest Maastrichtian (Text-fig. 4).

SYSTEMATIC PALAEOLOGY

Abbreviations. The following abbreviations are used with catalogue and locality numbers mentioned in the text: CIT, California Institute of Technology; CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; PRI, Paleontological Research Institution; UCLA, University of California, Los Angeles. CIT and UCLA collections are currently at the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

Phylum MOLLUSCA Linnaeus, 1758
 Class BIVALVIA Linnaeus, 1758
 Order VENEROIDA Adams and Adams, 1856
 Family ARCTICIDAE Newton, 1891
 Genus ROUDAIRIA Munier-Chalmas, 1881

Type species. *Roudairia drui* Munier-Chalmas, 1881 from the Campanian and Maastrichtian of Tunisia.

Diagnosis. Inflated arctid bivalves of trigonal to subquadrate outline with a strongly carinate posterior; sculpture of undulating ribs on the flank. Hinge of right valve with three cardinals and four laterals: 1 at the ventral hinge border, anterior to 3a; 3a dorsal to 1; 3b bifid; AI short, subtrigonal; AIII elongate. Hinge of left valve with two cardinals and two laterals; 2b obscurely bifid; 4b elongate, thin; AII chevron-shaped; PII elongate with transverse striations on both sides. Posterior adductor muscle scar bordered anteriorly by a strong myophoric flange.

Discussion. A number of problems with respect to the appropriate generic name for the specimens from Warm Springs Mountain cannot be solved solely on the basis of the Warm Springs Mountain specimens. Of the three generic taxa, *Veniella* Stoliczka, 1870 (type species *Veniella conradi* Morton, 1833), *Cicatrea* Stoliczka, 1870 (type species '*Cyprina*' (*Cicatrea*) *cordialis* Stoliczka, 1870), and *Roudairia* Munier-Chalmas, 1881, the specimens from Warm Springs Mountain are least like *Veniella*. Darteville and Freneix (1957) reviewed the status of the generic names *Veniella*, *Cicatrea*, and *Roudairia*. They considered *Cicatrea* and *Roudairia* to be synonyms of *Veniella* because: (1) the separation of *Veniella* and *Roudairia* required well-preserved adult hinges; (2) '*Cyprina*' *forbesiana* Stoliczka, 1870, was considered by Vokes (1954) to have a left valve hinge like *Roudairia* and a right valve hinge resembling *Veniella*; and (3) some species, such as the Indian *Cicatrea cordialis*, combine the hinge of *Veniella* and the external shape and sculpture of *Roudairia*. Although the types species of *Roudairia* and *Veniella* are sufficiently dissimilar to be recognized as representatives of distinct supraspecific taxa, Darteville and Freneix (1957) believed that '*Cyprina*' *forbesiana* and *Cicatrea cordialis* bridge this morphological gap. Vokes (1954) suggested that *Veniella* is a North American Late Cretaceous group, but he considered *Cicatrea cordialis*, from India and Madagascar, to be closer to *Veniella* than to *Roudairia*. The following discussion outlines what is known of the generic characters of *Veniella*, *Roudairia*, and *Cicatrea*.

The type species of *Veniella*, *V. conradi*, has been illustrated by Vokes (1954). Characters of the genus are discernable from his illustrations and from well-preserved specimens of the type species from the Ripley Formation of Tennessee (Pl. 2, figs 2-4). Exteriorly, the shell has a strong posterior

angulation. Commarginal sculpture anterior to the angulation consists of irregularly developed ridges, the strongest of which are flanged. In the right valve, *V. conradi* has three cardinals, one anterior lateral AIII, and two posterior lateral teeth (Pl. 2, fig. 2). In the left valve, *V. conradi* has two cardinals, one elongate to somewhat triangular anterior lateral AII, and one posterior lateral tooth (Pl. 2, fig. 3). *Veniella conradi* lacks an internal myophoric flange bordering the anterior side of the posterior adductor muscle scar. The *Treatise on invertebrate paleontology* illustration of the left valve of *V. conradi* is misleading (Casey 1969, p. N651, text-fig. E129, 6a). Cardinal 2b is never so bifid in mature specimens as depicted (see ontogenetic hinge changes in Vokes (1954, text-figs 1-4, 6-9)) and the adductor muscle scars are discrepant in size and shape. The posterior adductor muscle scar is actually larger and rounder than the semicircular anterior adductor muscle scar.

The nominal type species of *Rondairia*, *R. drui*, has been variously synonymized with the prior *Opis nudatus* Conrad, 1852, and *Trigonia auressensis* Coquand, 1862. But Darteville and Freneix (1957, p. 141) rejected the synonymy of *R. drui* with *Rondairia nudata* and *Rondairia auressensis*, and listed several characters, including a second posterior carina present in *R. nudata* and finer, more uneven ribbing in *R. auressensis*, that separate these two species from *R. drui*. *Rondairia drui* has been recognized from several horizons and locations (Text-fig. 3), and not all of these specimens are conspecific (Darteville and Freneix 1957). This confusion and the poor preservation of some of the material has made generic characters of *Rondairia* difficult to determine. Exteriorly, *R. drui* has a carinate posterior angulation accentuated by a strongly raised keel. *Rondairia drui* is higher than long, and squarely truncated posteriorly. Commarginal ribbing on the anterior portion of the shell is strong and even near the beaks, but becomes more uneven ventrally. The commarginal ribs, although over-steepened, do not give rise to flanges. Vokes (1954) discussed the hinge teeth based on illustrations in Quaas (1902) and Pervinqui re (1912). The hinge of *R. drui* differs from that of *V. conradi* in having a chevron-shaped anterior lateral AII in the left valve and a pustular anterior lateral AI in the right valve. In contrast, *V. conradi* has an elongate trigonal AII in the left valve and lacks AI in the right valve. Darteville and Freneix (1957) did not indicate whether *R. drui* has an internal myophoric flange along the anterior side of the posterior adductor muscle scar or not. But Quaas' figure (1902, pl. 24, fig. 22) of a left valve of *R. drui* indicates that such a flange is present.

Abbass (1962) described several *Rondairia* species from Egypt. Regrettably, he did not refer to Darteville and Freneix (1957), nor did he indicate the relationship of his Egyptian taxa to those discussed by Darteville and Freneix (1957). In order to settle discrepancies between Abbass (1962) and Darteville and Freneix (1957), we would need to examine and compare Abbass' specimens with those described by Darteville and Freneix (1957).

The type species of *Cicatrea*, *Cyprina (Cicatrea) cordialis* Stoliczka, 1870, has been recognized in various parts of Africa, as well as in India and Madagascar (Darteville and Freneix 1957) (Text-fig. 3). Discussions of the validity of *Cicatrea* (Douvill  1904; Vokes 1954) refer to Stoliczka's figure (1870, pl. 10, fig. 2) of a left valve hinge to define generic characters. Darteville and Freneix (1957) did not figure a hinge for this species and did not have any available for study. Although they did not mention an internal myophoric flange, illustrations of specimens identified as *C. cordialis* by Darteville and Freneix (1957) clearly show the presence of an internal flange bounding the anterior side of the posterior adductor muscle scar. Exteriorly, *C. cordialis* has a high keel along the strong posterior angulation. This keel is particularly pronounced near the beaks. Commarginal sculpture on the anterior portion of the valve is even and roundly ripple-ribbed near the beaks. The commarginal ribs evanesce ventrally. Stoliczka's figure (1870, pl. 10, fig. 2) of the left valve hinge gives the impression of a double exposure. Two hinges appear to be present, one superposed on the other. One hinge is offset higher and to the left of the other hinge. Compared to *Veniella* and *Rondairia*, Stoliczka's figure is peculiar in having no upright, flanged posterior end to the nymph. Although broad ligament grooves are indicated, the usual nymph flange is not. Stoliczka (1870) did comment on its absence. If two valves are superposed, one set of the ligament grooves and subumbonal pits would be above and to the left of the other. Cardinal 2b is drawn as a moderately broad triangle and is more like 2b of *V. conradi* than of *R. squiresi* and *R. peruviana*. This broadly triangular cardinal 2b is somewhat surprising as *C. cordialis* is more elongate with a strong forward

twist to the shell. In *V. conradi*, mature shells of greater elongation and forward twist have a narrower, more elongate 2b, but shorter shells have a more trigonal 2b. The left anterior lateral AII is also peculiar. It is more equantly triangular than that of *V. conradi* and is drawn with the hint of a basal dimple suggesting the possibility of a socket for AI. If *C. cordialis* should be shown to have AI, then its hinge formula would be the same as that of *Roudairia*. Stoliczka (1870, p. 199) said that the base of cardinal 2b is united to the top of AII by a low rib. In *R. squiresi* and *R. peruviana*, a ridge drops from the tip of AII toward the base of 2b, but it encircles the socket for 1 and does not join 2b. Additionally, Stoliczka wrote (1870, p. 199), 'a distinct rib is seen in front of the anterior muscular impression, it has the appearance of an anterior lateral tooth, but has in reality nothing to do with hinge-teeth'. If this figure (Stoliczka, 1870, pl. 10, fig. 2) were drawn from superposed impressions of two shells, the 'distinct rib' would be the anterior margin of the upper, more leftward specimen. *Roudairia squiresi* has a raised anteroventral margin to the anterior adductor muscle scar, but this margin is not sufficiently raised to have the appearance of a tooth.

Drawings of *C. cordialis* credited to Douvillé are in Boule and Thevenin (1906, text-figs 4-6). The drawings are based on rock moulds from Madagascar. Their text-figure 6 of the left hinge greatly resembles Stoliczka's figure 2 (1870, pl. 10) in shape and position of hinge-teeth 2, 4 and AII, except that in Douvillé's text-figure 6, AII is depicted as having a chevron-shape with a well-developed socket for AI in its base. Douvillé's figures (Boule and Thevenin 1906, text-figs 4-6) do not depict any nymph or ligament groove. Their omission may have been caused by incomplete rock moulds.

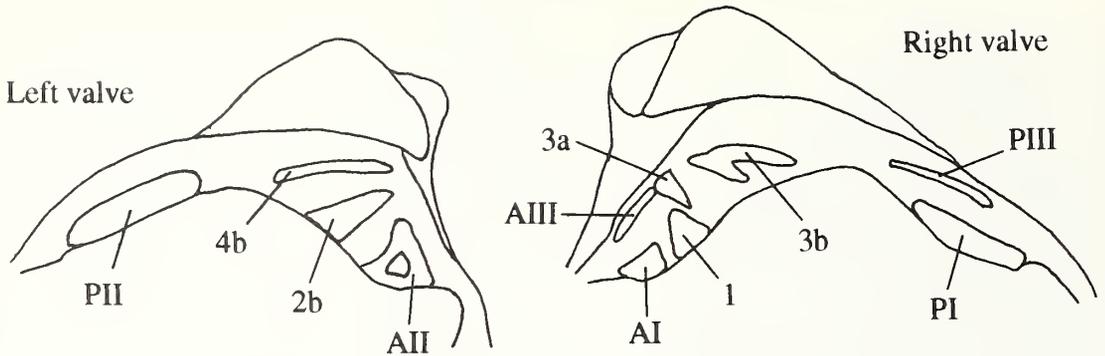
If Stoliczka's left hinge (1870, pl. 10, fig. 2) is drawn accurately, then the hinge of *Cicatrea* differs from that of *Roudairia* in the absence of an alate nymph and in having both 2b and AII broadly triangulate. But Douvillé's tooth AII (Boule and Thevenin 1906, text-fig. 6) is more like that of *Roudairia* and his right valve hinge (Boule and Thevenin 1906, text-fig. 4) shows a well-developed AI similar to that of *Roudairia* but much more elongate than that seen in *R. squiresi* or *R. peruviana*. Differences between illustrations of the Indian *C. cordialis* of Stoliczka and the Madagascan *C. cordialis* of Douvillé permit doubt as to whether they are both the same species, especially as the Indian specimens are probably of early Senonian age rather than the Maastrichtian age of the Madagascan specimens. Despite the comments of several palaeontologists (Douvillé 1904; Boule and Thevenin 1906; Rennie 1929; Cox 1952; Vokes 1954; Darteville and Freneix 1957), the generic characters of *Cicatrea* remain ambiguous. Adequate material from the type locality of *C. cordialis* is necessary to determine how closely Stoliczka's figure (1870, pl. 10, fig. 2) depicts the features these palaeontologists have variously reinterpreted. Based on available illustrations, specimens assigned to *C. cordialis* by Douvillé (Boule and Thevenin 1906) and Darteville and Freneix (1957) are herein referred to *Roudairia*.

In summary, the present taxonomic status of *Veniella*, *Roudairia*, and *Cicatrea* remains unclear due to the lack of well-preserved specimens of *Cicatrea*. Based on previous work (Boule and Thevenin 1906; Vokes 1954; Darteville and Freneix 1957), there are at least two distinct generic groups present. The first group, represented by *Veniella*, is characterized by uneven commarginal

EXPLANATION OF PLATE I

Figs 1-7. *Roudairia squiresi* sp. nov. LACMIP locality 14312, Warm Springs Mountain, California; San Francisquito Formation. 1-5, LACMIP 12204, holotype; left valve; 1, exterior showing strong carina on posterior angulation and rounded ripple ribs developed near beak; 2, anterior showing lunule and development of rounded ripple ribs near beak; 3, posterior, shell removed to show mark of internal myophoric flange on rock cast and posterior adductor muscle scar (rough area to right of myophore impression); 4, interior showing myophoric flange and position of adductor muscle scars; 5, hinge, nymph broken, posterior lateral PII, cardinal 4b elongate slender, cardinal 2b elongate trigonal with faint medial groove, anterior lateral AII chevron-shaped. 6-7, LACMIP 12205, paratype; right valve; 6, hinge, nymph nearly complete, anterior laterals AI and AIII, cardinal 1, 3a, and 3b, 3b bifid, posterior laterals PI and PIII; 7, exterior showing strong carina on posterior angulation. All figures $\times 1$ and coated with ammonium chloride.





TEXT-FIG. 5. Left and right valve hinge areas of *Roudairia squiresi* with the hinge teeth labelled.

ribbing on the anterior margin that tends to develop flanges, by an angulate but not carinate posterior angulation, by the absence of the anterior-lateral tooth AI, and by the absence of an internal myophoric flange on the anterior side of the posterior adductor muscle scar. The second group, represented by *Roudairia*, is characterized by even commarginal ribbing which commonly becomes roundly ripple-ribbed on the anterior portion of the shell near the beaks and which evanesces toward the ventral margin in large specimens, by a strongly carinate posterior angulation that is accentuated by a keel, by the anterior-lateral tooth AI, and by an internal myophoric flange bordering the anterior side of the posterior adductor muscle scar. The specimens from Africa and Madagascar previously described as *Cicatrea* belong in this second group. The Indian specimens described as *Cicatrea* may also belong in this second group. But until better preserved specimens of *Cicatrea* from India are available, the relationship of *Cicatrea* to *Veniella* and *Roudairia* will remain unclear.

The specimens from Warm Springs Mountain are distinct from *V. conradi*. They are externally more similar to *R. drui* and *C. cordialis*. Internally, they are more similar to *R. drui*. Previous workers (e.g. Douvillé 1904; Olsson 1934; Vokes 1954) have used various stratagems to avoid replacing the more commonly used and better-based *Roudairia* Munier-Chalmas, 1881, with the enigmatic and ill-defined *Cicatrea* Stoliczka, 1870. Although the similarity of the Warm Springs

EXPLANATION OF PLATE 2

Fig. 1. *Roudairia squiresi* sp. nov. LACMIP 12209, paratype; articulated specimen, anterior view; LACMIP locality 14316, Warm Springs Mountain, California; San Francisquito Formation.

Figs 2-4. *Veniella conradi* (Morton). 2, LACMIP 12211, hypotype; right valve, interior view showing hinge, muscle scars, and lack of internal myophoric flange bordering posterior adductor muscle scar; LACMIP locality 8063, Coon Creek, Tennessee; Ripley Formation. 3-4, LACMIP 12212, hypotype; left valve; LACMIP locality 8063, Coon Creek, Tennessee; Ripley Formation; 3, interior view showing hinge, muscle scars, and lack of myophoric flange bordering posterior adductor muscle scar. 4, exterior with commarginal flanges developing into distant rib crests.

Figs 5-8. *Roudairia peruviana* Olsson. 5-6, PRI 3716, holotype; right valve; Monte Grande, Peru; Monte Grande Formation; 5, exterior with strong carina on posterior angulation and rounded ripple ribs near beak; 6, hinge, lunular margin and anterior portion of hinge damaged, nymph broken. 7, PRI 4825 (exterior figured by Olsson, 1944, pl. 2, fig. 7), hypotype; left valve, interior view, hinge damaged but shows nymph, cardinal teeth 4b and 2b, and chevron-shaped anterior lateral AII, also myophore along posterior muscle scar; Monte Grande, Peru; Monte Grande Formation, specimen not coated. 8, LACMIP 12210, hypotype; right valve, hinge with well-preserved nymph, anterior laterals AI and AIII, cardinals 1, 3a and 3b, 3b widely bifid, posterior laterals PI and PIII; UCLA locality 5261, north of Tortuga, Paita Peninsula, north-western Peru; 'Baculites beds'.

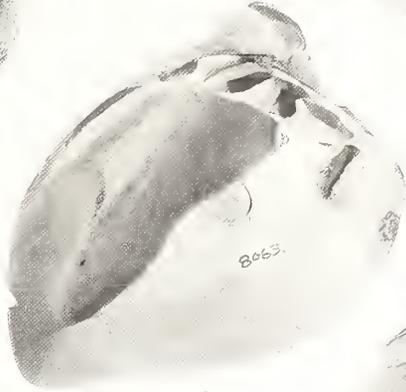
All figures $\times 1$ and coated with ammonium chloride, except where noted otherwise.



1



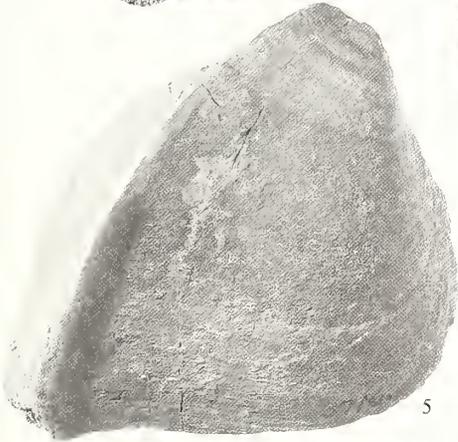
2



3



4



5



6



7



8

Mountain specimens to *Cicatrea* is unclear, they are in shape, sculpture, internal myophoric flange, and hinge most similar to *Roudairia*. *Roudairia squiresi* is the first species of this group to be found in North America.

Roudairia squiresi sp. nov.

Plate 1, figures 1–7; Plate 2, figure 1

1991 *Roudairia peruviana?* Olsson, 1934; Kirby, p. 133, pl. 3, figs 6, 7.

Derivation of name. The species is named for Richard L. Squires whose work on Eocene molluscs of the eastern Pacific has greatly improved our understanding of Tethyan migrations into California.

Holotype. LACMIP 12204; San Francisquito Formation (uppermost Maastrichtian); LACMIP locality 14312, Warm Springs Mountain, Los Angeles County, southern California, USA.

Paratypes. Five specimens: LACMIP 12205–12206 from LACMIP locality 14312; LACMIP 12207–12208 from UCLA locality 1591; LACMIP 12209 from LACMIP locality 14316; all from San Francisquito Formation (uppermost Maastrichtian); Warm Springs Mountain, Los Angeles County, southern California, USA.

Diagnosis. A large *Roudairia* of nearly equant proportions, but with the beaks curled well forward, sculptured near the beaks by ten to fourteen undulatory commarginal ribs that evanesce ventrally, with a strong posterior carina along the posterior angulation. Cardinals 3b and 2b relatively narrow and posteriorly directed (Text-fig. 5).

Description. Shell large, higher than long, subquadrate, inflated, thick; beaks strongly enrolled, strongly prosogyrous; lunular margin nearly straight; anterior end broadly rounded; ventral border nearly straight with a slight sulcus to the anterior of the posterior carination and a little rostrate at the carination; posterior border nearly straight, rounding into dorsal border; lunule large, depressed, bounded by an inscribed line; no escutcheon; posterior carination high, alate near the beaks, abruptly carinate at the ventral border; paralleled anteriorly by a shallow sulcus. External sculpture of about ten to fourteen strong, broad, undulatory, commarginal ribs on beak, diminishing in height ventrally, extending from anterior slope break to sulcus anterior to carina. Entire surface marked by uneven commarginal growth lines.

Ligament groove deep, arched behind strong alate nymphs. Hinge of right valve with short, strong 1 at the hinge border anterior to 3a (Text-fig. 5); short, ventrally directed 3a; strong, bifid, posteriorly directed 3b; anterior laterals AI and AIII low; AI short subtriangular; AIII elongate, paralleling the valve margin; socket for AII chevron-shaped; PI and PIII elongate with PI longer; PIII paralleling the valve margin; socket for PII deep. Hinge of left valve with 2b elongate, narrowly trigonal, obscurely bifid, posteroventrally directed; 4b elongate, thin, posteriorly directed, dorsal to bifid socket for 3b; anterior lateral AII chevron-shaped around shallow socket for AI, anterior to very deep socket for 1; PII elongate, strong, with transverse striations on both sides. Adductor muscle scars strongly marked, anterior impressed and bounded by raised rim, posterior impressed and bounded along anterior side by a strongly raised myophoric flange beginning near the beak and extending to ventral edge of muscle scar.

Measurements. LACMIP 12204 height 70.0 mm, length 70.0 mm, inflation 35.0 mm; LACMIP 12205 height 69.0 mm, length 66.5 mm incomplete, inflation 29.6 mm.

Remarks. *Roudairia squiresi* is similar to *Roudairia peruviana* Olsson, 1934, and to *Roudairia jamaicensis* Trechmann, 1927. These *Roudairia* are large and very trigoniiform, have strong, undulatory, commarginal sculpture on the flanks near the beaks that evanesce well before the ventral margin, have a strong posterior carina along the posterior angulation, and have an inscribed lunule. Internally, they have a strong myophoric flange bordering the anterior side of the posterior adductor muscle scar. The anterior left lateral AII is strongly hooked and forms a chevron, the right anterior lateral AI is present, and the socket for AII is chevron-shaped (Text-fig. 5).

Roudairia squiresi differs from *R. peruviana* (Pl. 2, figs 5–8) from the Maastrichtian of Peru in being less upright, having the beaks curled more forward, having a shallower sulcus anterior to the carina, and having commarginal ribs that are greater in number, narrower, and closer together. *Roudairia squiresi* contrasts with *R. jamaicensis* from the Campanian of Jamaica in being less elongate and having coarser and more pronounced commarginal ribbing. Trechmann figured a mature left valve and an immature right valve of *R. jamaicensis* (1927, pl. 2, figs 1–2). The immature right valve is more elongate than similar sized specimens of *R. squiresi* and has finer and less pronounced ribbing. Although Trechmann's figure (1927, pl. 2, fig. 1) of a mature left valve appears to be relatively higher, his measurements indicate that mature specimens are also more elongate than high, whereas in *R. squiresi*, height and length are more nearly equal.

Veniella conradi (Morton 1833) is less trigoniiform. It has distant, flanged commarginal sculpture and a strong posterior angulation that does not bear a raised carina like that of *R. squiresi*. *Veniella conradi* lacks the internal posterior myophore, its lunule is not inscribed, anterior lateral AII is elongate, trigonal, and the right anterior lateral AI is not present (Pl. 2, figs 2–4).

Vokes (1954, text-figs 6–9) illustrated the changes in the left cardinal 2b of *V. conradi* from juvenile inverted V-shaped to compressed trigonal, obscurely bifid adult. The obscurely bifid character of 2b in *R. squiresi* suggests that it too results from the compression of a widely bifid, inverted V-shaped, juvenile tooth.

The ligament of *R. squiresi* is enlarged below the beak similar to many large venerids (e.g. *Dosinia ponderosa* (Gray 1838)). A similar subumbonal ligamental pit may be the structure that caused Stoliczka (1870) to describe the ligament of *Cyprina* (*Cicatrea*) *cordialis* as lying in a double groove. In *R. squiresi*, this elongate pit encroaches on the anterior end of the nymph, notching it just behind the beak, and creating exteriorly a pattern of shell and notches similar to that seen in Stoliczka's figure 1b (1870, pl. 10).

Only a few specimens of *R. squiresi* have been found, including eight nearly complete large valves from Warm Springs Mountain. A fragment of a left valve from UCLA locality 6525 on Dip Creek, San Luis Obispo County, central California, consists only of the anterior part of the hinge, the lunule, and a suggestion of undulatory commarginal ribbing. The fragment is too incomplete to identify with certainty, but is probably *R. squiresi*.

Stratigraphical range. Uppermost Maastrichtian.

Geographical distribution. Warm Springs Mountain, Los Angeles County, and Dip Creek, south shore of Lake Nacimiento, San Luis Obispo County, central California, USA.

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REFERENCES

- ABBASS, H. L. 1962. A monograph on the Egyptian Cretaceous pelecypods. *Palaeontological Series Monograph, Geological and Mineral Research Department, Geological Museum, Cairo*, **1**, 1–224, pls 1–24.
- ADAMS, H. and ADAMS, A. 1853–1858. *The genera of recent mollusca arranged according to their organization*. John Van Voorst, London, **1**, xi + 484 pp.; **2**, 661 pp.; **3**, 138 pp.
- BOULE, M. and THEVENIN, A. 1906. Paléontologie de Madagascar, I. Fossiles de la côte orientale. *Annales de Paléontologie*, **1**, 43–59, pls 1–2.
- BRÜGGEN, H. 1910. Die Gastropoden und Lamellibranchier des unteren Senons von Nord-Perú. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B*, **30**, 717–787.

- CASEY, R. 1969. *Veniella*. N650–N651. In MOORE, R. C. and TEICHERT, C. (eds). *Treatise on invertebrate paleontology, part N, Mollusca 6, Bivalvia 2*. Geological Society of America, Boulder, Colorado, and Kansas University Press, Lawrence, Kansas, 952 pp.
- CONRAD, T. A. 1852. Description of the fossils of Syria, collected in the Palestine expedition. 211–235, pls 1–22 and appendices 1–8. In LYNCH, W. F., *Official report of the U.S. expedition to explore the Dead Sea and the River Jordan*. Baltimore, 235 pp.
- COOPER, M. R. 1978. Uppermost Cenomanian-basal Turonian ammonites from Salinas, Angola. *Annals of the South African Museum*, **75**, 51–152.
- COQUAND, H. 1862. Géologie et paléontologie de la région Sud de la Province de Constantine. *Mémoires de la Société Emulation de la Provence*. 346 pp., 35 pls.
- COX, L. R. 1952. Cretaceous and Eocene fossils from the Gold Coast. *Bulletin of the Gold Coast Geological Survey*, **17**, 1–68.
- DARTEVELLE, E. and FRENEIX, S. 1957. Mollusques fossiles du Crétacé de la Côte occidentale d'Afrique du Cameroun à l'Angola. II. Lamellibranches. *Annales du Musée Royal du Congo Belge. Série in-8°, Sciences Géologiques*, **20**, 1–271, pls 1–35.
- DIBBLEE, T. W. JR. 1967. Areal geology of the western Mojave Desert, California. *Professional Paper of the United States Geological Survey*, **522**, 1–153.
- DOUVILLÉ, M. H. 1904. Sur quelques fossiles de Madagascar. *Bulletin de la Société Géologique de France*, **4**, 207–217, pl. 8.
- DURHAM, D. L. 1968. Geology of the Tierra Redonda Mountain and Bradley quadrangles, Monterey and San Luis Obispo Counties, California. *Bulletin of the United States Geological Survey*, **1255**, 1–60.
- GABB, W. M. 1869. Cretaceous and Tertiary fossils. *Geological Survey of California, Palaeontology*, **2**, 1–299.
- GRAY, J. E. 1838. Catalogue of the species of the genus *Cytherea*, of Lamarck, with the description of some new genera and species. *Analyst*, **8**, 302–309.
- GROVE, K. 1986. Field trip boat log: Depositional environments of Upper Cretaceous and lower Tertiary strata around Lake Nacimiento, central California Coast Ranges. 43–59. In GROVE, K. and GRAHAM, S. (eds). *Geology of Upper Cretaceous and lower Tertiary rocks near Lake Nacimiento, California*. Society of Economic Paleontologists and Mineralogists, Pacific Section, Los Angeles, Book Number 49, 63 pp.
- JOSEPH, S. E., EHLIG, P. L. and DAVIS, T. E. 1982. Strontium isotopic correlation of the La Panza Range granitic rocks with similar rocks in the central and eastern Transverse Ranges. *Geological Society of America, Abstracts with Programs*, **14**, 176.
- KAUFFMAN, E. G. 1973. Cretaceous bivalvia. 353–383. In HALLAM, A. (ed.). *Atlas of palaeobiogeography*. Elsevier Scientific Publishing Co., Amsterdam, 531 pp.
- KEEN, A. M. 1971. *Sea shells of tropical West America*. Stanford University Press, Stanford, California, 1064 pp.
- KIRBY, M. X. 1991. Macropaleontology and biostratigraphy across the Cretaceous/Tertiary boundary, San Francisquito Formation, Warm Springs Mountain, Los Angeles County, southern California. Unpublished M.Sc. thesis, California State University, Northridge.
- SQUIRES, R. L. and SAUL, L. R. 1991. A conformable Cretaceous/Tertiary boundary at Warm Springs Mountain, Los Angeles County, southern California. *Geological Society of America, Abstracts with Program*, **23**, 60.
- KOOSER, M. A. 1980. Stratigraphy and sedimentology of the San Francisquito Formation, Transverse Ranges, California. Unpublished Ph.D. thesis, University of California, Riverside.
- 1982. Stratigraphy and sedimentology of the type San Francisquito Formation, southern California. 53–61. In CROWELL, J. C. and LINK, M. H. (eds). *Geologic history of Ridge Basin, southern California*. Society of Economic Paleontologists and Mineralogists, Pacific Section, 1982 Annual Convention, Anaheim, 304 pp.
- LEANZA, A. F. and HÜNICKEN, M. A. 1970. Sobre la presencia del género *Roudaireia* en el Cretácico superior del Salitral de La Amarga (Dpto. Chicalco), Provincia de La Pampa, República Argentina. *Revista de la Asociación Geológica Argentina*, **25**, 489–494.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae. 2, Regnum animale*. Editio decima, reformata, Stockholm, 824 pp.
- LISSON, C. I. 1925. Edad de los fósiles peruanos y distribución de sus depósitos. Tercera edición. *Boletín de la Sociedad Geológica del Perú*, **1**, 23–30, pls 1–3.
- MAURY, C. J. 1930. O Cretáceo de Parahyba do norte. *Monographias, Serviço Geológico e Mineralógico do Brasil*, **8**, 1–305.
- MEEK, F. B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the upper Missouri county. *Territorial Report of the United States Geological Survey*, **9**, 1–269.

- MORTON, S. G. 1833. Synopsis of the organic remains of the ferruginous sand formation of the United States, with geological remarks. *American Journal of Science, Series 1*, **23**, 288–294.
- MUNIER-CHALMAS, E. 1881. *Note paléontologique sur les fossiles recueillis par M. le Commandant Roudaire dans son expédition scientifiques en Tunisie. Extraits de la Mission du M. le Commandant Roudaire dans les chotts tunisiens (1878–1879)*. Chamerot, Paris, 59–79.
- NALDINI, E. 1948. Faune Cretacee della Cirenaica. *Paleontographia Italica*, **45**, 85–110, pl. 13.
- NEWTON, R. B. 1891. *Systematic list [of] British Oligocene and Eocene mollusca*. British Museum (Natural History), London, 365 pp.
- OLSSON, A. A. 1934. Contributions to the paleontology of northern Peru: The Cretaceous of the Amotape Region. *Bulletins of American Paleontology*, **20**, 1–104, pls 1–11.
- 1944. Contributions to the paleontology of northern Peru: Part VII: The Cretaceous of the Paita region. *Bulletins of American Paleontology*, **28**, 5–146, pls 1–17.
- PERVINQUIÈRE, L. 1912. Études de paléontologie tunisienne. Parte 2. Gasteropods et Lamellibranches de terrains Crétacés. *Carte Géologique Tunis*, 1–352.
- QUAAS, A. 1902. Die Faunen der Oberen Kreidebildungen in der Libyschen Wüste. II. Die Fauna der Overwegischichten und der Blätterthone in der Libyschen Wüste. *Palaeontographica*, **30**, 153–336, pls 20–33.
- RENNIE, J. V. L. 1929. Cretaceous fossils from Angola. *Annals of the South African Museum*, **28**, 1–54, pls 1–4.
- 1930. New Lamellibranchia and Gastropoda from the Upper Cretaceous of Pondoland. *Annals of the South African Museum*, **28**, 159–260, pls 16–31.
- SAUL, L. R. 1983. *Turritella* zonation across the Cretaceous–Tertiary boundary, California. *University of California Publications in Geological Sciences*, **125**, 1–165.
- STOLICZKA, F. 1870–1871. Cretaceous fauna of southern India. The Pelecypoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series 6*, **3**, 1–537, pls 1–50.
- TALLAFERRO, N. L. 1944. Cretaceous and Paleocene of Santa Lucia Range, California. *Bulletin of the American Association of Petroleum Geologists*, **28**, 449–521.
- TRECHMANN, C. T. 1927. The Cretaceous shales of Jamaica and their mollusca. *Geological Magazine*, **64**, 27–42, 49–65, pls 1–4.
- VOKES, H. E. 1954. The development of the hinge of *Veniella conradi* (Morton) and some conclusions based on its study. *Journal of the Washington Academy of Sciences*, **44**, 36–44.
- WILLARD, B. 1966. *The Harvey Bassler collection of Peruvian fossils*. Lehigh University, Bethlehem, Pennsylvania, 255 pp.
- ZIEGLER, A. M., SCOTSESE, C. R. and BARRETT, S. F. 1982. Mesozoic and Cenozoic paleogeographic maps. 240–252. In BROSCHE, P. and SUNDRMANN, J. (eds). *Tidal friction and the Earth's rotation, II*. Springer-Verlag, Berlin, 345 pp.

APPENDIX

Cited fossil localities

- 1591UCLA: north-flowing tributary to Warm Springs Canyon; approximately 2.4 km west of Warm Springs Camp; approximately 1372 m north and 671 m west of Warm Springs Mountain; Warm Springs Mountain quadrangle, 1958, Los Angeles County, California. Collected by: R. W. Webb, G. Young, and E. H. Quayle, 6/17/1941. San Francisquito Formation, uppermost Maastrichtian.
- 5261UCLA: 'Baculites beds' north of Tortuga, Paita Peninsula, northwestern Peru. Collected by: A. G. Fischer. Maastrichtian.
- 6525UCLA: south-side of Lake Nacimiento; poorly-sorted conglomeratic sandstone cropping out at narrows of Dip Creek; fossils collected from outcrops on east-side of Dip Creek; about elevation 232 m; 427 m south and 61 m west of the northeastern corner, Section 30, Township 25 South, Range 10 East, Lime Mountain quadrangle, 1948, San Luis Obispo County, California. Collected by: R. B. Saul and L. R. Saul, 12/31/1977. Undifferentiated Cretaceous rocks, uppermost Maastrichtian.
- 8063LACMIP: (= CIT 703) Dave Week's place, on Coon Creek; 5.6 km south of Enville; 12.1 km north of Adamsville, McNairy County, Tennessee. Collected by: W. P. Popenoe, 1929. Ripley Formation, Maastrichtian.
- 14312LACMIP: (= CSUN 1447 O) fine-grained feldspathic sandstone 45 m above nonconformity between granite-gneiss basement and overlying San Francisquito Formation; elevation 1015 m; 442 m north and 152 m west of forest lookout tower on summit of Warm Springs Mountain; Warm Springs Mountain quadrangle, 1958, Los Angeles County, California. Collected by: M. X. Kirby, 2/2/1990. San Francisquito Formation, uppermost Maastrichtian.

14316LACMIP: (= CSUN 1145) feldspathic sandstone; elevation 1061 m; 396 m north and 335 m east of forest lookout tower on summit of Warm Springs Mountain; Warm Springs Mountain quadrangle, 1958, Los Angeles County, California. Collected by: S. Connell and R. L. Squires, 1988. San Francisquito Formation, uppermost Maastrichtian.

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A NEW PLOURDOSTEID ARTHRODIRE FROM THE UPPER DEVONIAN GOGO FORMATION OF WESTERN AUSTRALIA

by JOHN A. LONG

ABSTRACT. A new plourdosteid arthrodire, *Mcnamaraspis kaprios* gen. et sp. nov., is described from the Late Devonian (Frasnian) Gogo Formation of Western Australia. *Mcnamaraspis* is characterized by its very short spinal plate, larger pectoral fenestra and inferognathal with several distinct trenchant cusps. The anterior surface of the nasal capsule is covered by a hemispherical bone not previously recorded in placoderms. This is interpreted as an ossified annular cartilage, and, together with the interpretation of the suborbitalis muscle being present in arthrodires, supports the hypothesis that placoderms are more closely related to chondrichthyans than to osteichthyans. *Mcnamaraspis* is placed as the sister taxon to *Torosteus* in the family Plourdosteidae. The Plourdosteidae is redefined. Interrelationships of plourdosteids and relationships to other eubranchyothoracid arthrodires are discussed.

THE superb three-dimensional preservation of the Gogo fishes is now well documented as many of the placoderms and osteichthyans from the fauna have been formally described (Miles 1971, 1977; Miles and Young 1977; Miles and Dennis 1979; Dennis and Miles 1979*a, b*, 1980, 1981, 1982; Dennis-Bryan and Miles 1983; Dennis-Bryan 1987; Long 1988*a, b, c*, 1990, 1994; Gardiner and Miles 1990). New seasons of field work at Gogo from 1986 to 1992 have yielded many new species, including the arthrodire described in this paper. As the bones are uncrushed and the armour of the placoderms can be accurately reconstructed, descriptions of new material can be kept concise by leaving the photographs, tables and illustrations to show main morphological features and proportions. The new arthrodire described herein is essentially similar to *Torosteus* (Gardiner and Miles 1990) in its general anatomy, so only different features or new anatomical data are here described in detail.

The plourdosteid arthrodires were a widespread group during the Late Devonian, being found in Canada (*Plourdosteus*; Vezina 1986, 1990), Russia (*Janiosteus*; Ivanov 1988), China (*Panxiosteus*; Wang 1991) and Australia (*Harrytoombsia*; Miles and Dennis 1979; *Kimberleyichthys*; Dennis-Bryan and Miles 1983; *Torosteus*; Gardiner and Miles 1990). They appear to have displaced the earlier coccosteid arthrodires that are commonly found in Middle Devonian faunas, particularly in the Old Red Continent of Euramerica (Denison 1978, 1984; Dineley and Loeffler 1993).

The hypothetical presence of annular cartilages in placoderms was one of several characters used by Stensiö (1963) to argue for a close relationship between placoderms and chondrichthyans, despite the absence of any fossil evidence. The new form described here shows, for the first time, the presence of ossified annular cartilages in a placoderm. Comparisons are made with the nasal structures of extant fishes and its bearing on placoderm affinities is discussed. In addition, aspects of the soft anatomy of the head are reconstructed from the structures preserved on the visceral surface of the skull roof and cheek.

Throughout the work the words 'length', 'breadth' and 'height' are abbreviated to as 'L', 'B' and 'H' respectively. Indices are expressed as ratios multiplied by 100. Institutional abbreviations are: BMNH, Natural History Museum, London, UK; WAM, Western Australian Museum, Perth, Australia.

SYSTEMATIC PALAEONTOLOGY

Class PLACODERMI McCoy, 1848
 Order ARTHRODIRA Woodward, 1891
 Infraorder BRACHYTHORACI Gross, 1932
 Family PLOURDOSTEIDAE Vezina, 1990

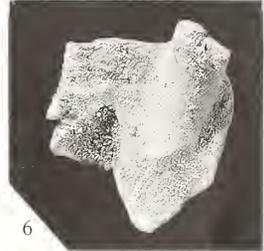
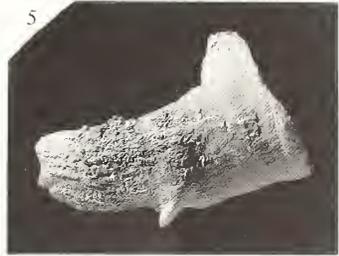
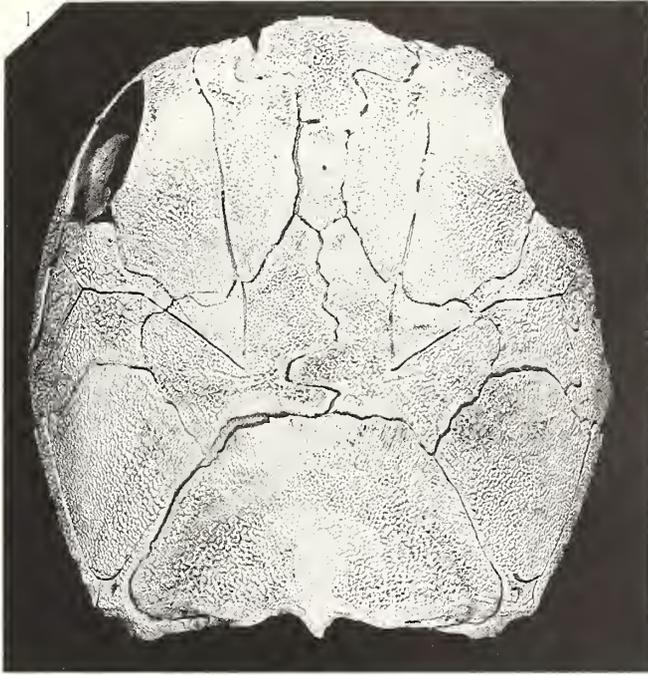
1990 Torosteidae, Gardiner and Miles, p. 162.

Diagnosis. Eubrachythoracid arthrodires with moderately broad heads that lack both internasal and extrascapular plates; the postorbital plates and paranuchal plates are in extensive contact; the visceral surface of the skull-roof has well-developed, prominent postocular processes, and the lateral consolidated area has well-defined, triangular depressions; cheek unit loosely attached to skull-roof and submarginal plate free, well-defined spiracular notch present; parasphenoid with posterior depression immediately behind buccohypophysial foramen and with median hypophysial vein foramen present; trunk shield with a posterior lateral plate that deeply inserts into the ventral margin of the posterior dorsolateral plate; posterior ventrolateral plate has a prepectoral lamina contacting the anterior lateral plate.

Remarks. Vezina (1990) erected the family Plourdosteidae, to include *Plourdosteus*, *Panxiosteus*, *Harrytoombsia*, *Kimberleyichthys*, *Janiosteus* and *Eldenosteus*, based on fifteen characters, although few of these are unique to the referred taxa. Soon after Vezina's paper was published, Gardiner and Miles (1990) proposed the family Torosteidae, to include *Plourdosteus*, *Torosteus*, *Harrytoombsia* and *Kimberleyichthys*, based on fourteen characters, some of which were in agreement with Vezina's definition of the family Plourdosteidae, but again containing few unique characters within the subset of referred taxa. With the description of a new genus, obviously well-preserved, and exhibiting features of both familial diagnoses, it is here appropriate to redefine the family Plourdosteidae, and place Torosteidae in synonymy with this family. The characters used in the definition are all regarded as synapomorphies unique to the referred taxa (as known). In addition, the feature of the well-developed lateral consolidated area with triangular muscle attachment areas has been included, following on from comparisons made on the cheek anatomy of arthrodires in this paper. Other characters used by Vezina (1990) and Gardiner and Miles (1990) which characterize members of the group, but are not unique to the family Plourdosteidae, include: trilobate centrals; loss of internasal plate; skull roofing bones with sinuous suture lines and broad overlap areas; inferognathal plate with well-developed median cusps; postnasal plate large and seen in dorsal view; spinal plate may project laterally from trunk armour; posterior median ventral plate enlarged, being only a little longer than broad. The posterior lateral plate participates in the pectoral fenestra of one coccosteid, *Watsonosteus*, although this genus is regarded as one of the most specialized end members of that lineage and not related to the plourdosteids as it lacks all the defining skull characteristics of the latter group. The most characteristic feature of the posterior lateral plates of plourdosteids is that they possess a dorsal process that inserts deeply into a narrow cavity within the ventral margin of the posterior dorsolateral plate. This arrangement also occurs in

EXPLANATION OF PLATE I

Figs 1–8. *Mcnamaraspis kaprios* gen. et sp. nov. Holotype, WAM 86.9.676. 1, head shield in dorsal view, $\times 1.5$; 2, headshield and cheek bones in left lateral view, $\times 1.5$; 3, left inferognathal in mesial view, $\times 2$; 4–5, right posterior superognathal in 4, mesial and 5, lateral views, $\times 3$; 6–7, right anterior superognathal in 6, posterior and 7, anterior views, $\times 3$; 8, right articular in lateral view, $\times 3$. All specimens whitened with ammonium chloride.



Eastmanosteus calliaspis (Dennis-Bryan 1987), but it appears to be a characteristic feature of all plourdosteids and is thus considered to have been acquired independently by *Eastmanosteus*, a dinichthyid (Long 1987). The genus *Eldenosteus* is currently being restudied by Heidi-Marie Johnstone and David Elliot at Northern Arizona University, based on new finds. It is excluded from comparison with other plourdosteids until descriptions of its anatomy are published.

Genus MCNAMARASPIS gen. nov.

Derivation of name. In honour of Dr Ken McNamara, Western Australian Museum, for his contributions to palaeontology.

Type species. *Mcnamaraspis kaprios* sp. nov., only known species.

Diagnosis. A plourdosteid arthrodire having a head shield slightly broader than long, with a nuchal plate thirty-nine per cent. of the skull length; inferognathals with two prominent anterior cusps; trunk shield with short spinal plate, nineteen per cent. as long as the median dorsal plate, and having greater contact with the interolateral plate than with the anterior ventrolateral plate; pectoral fenestra very large, being longer than the flank length of trunk shield.

Remarks. The unusually short spinal plate separates this genus readily from all other plourdosteids (Text-fig. 1).

Mcnamaraspis kaprios sp. nov.

Plate 1; Text-figures 1–14, 16–17

- 1988a 'a genus of plourdosteid arthrodire new to science', Long p. 442, fig. 6.
 1990 *Torosteus pulchellus*, Gardiner and Miles pp. 175, 180.
 1991 new genus of plourdosteid, Long, pp. 421, 425, pl. 4 C, D.

Derivation of name. Greek 'kaprios', like a boar, alluding to the well-developed lower jaw tusks on the inferognathal.

Holotype. WAM 86.9.676, an almost complete armour, including upper and lower gnathal elements, parasphenoid and partially ossified nasal capsules, wanting only the posterior ventrolateral plates and the left anterior ventrolateral plate (Text-figs 1–4, 6–14; Pl. 1).

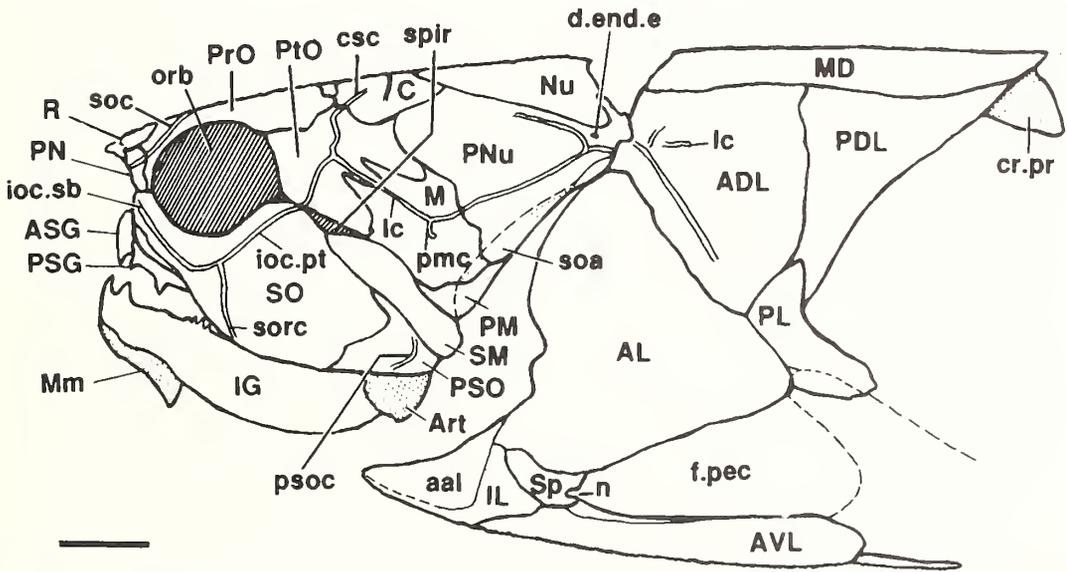
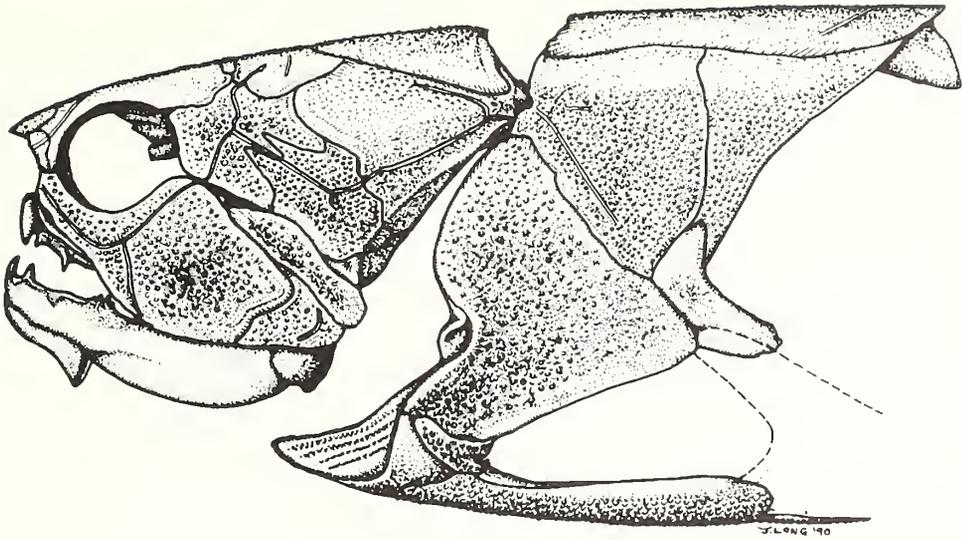
Diagnosis. As for the genus.

Other material. BMNH P52553, a small skull and partial trunk shield, examined and measured by the author (Text-fig. 5).

Type locality. Bugle Gap (near locality 101 of Miles 1971), about 100 km east of Fitzroy Crossing, Western Australia. Gogo Formation (lower Frasnian). Collected by the author in August 1986.

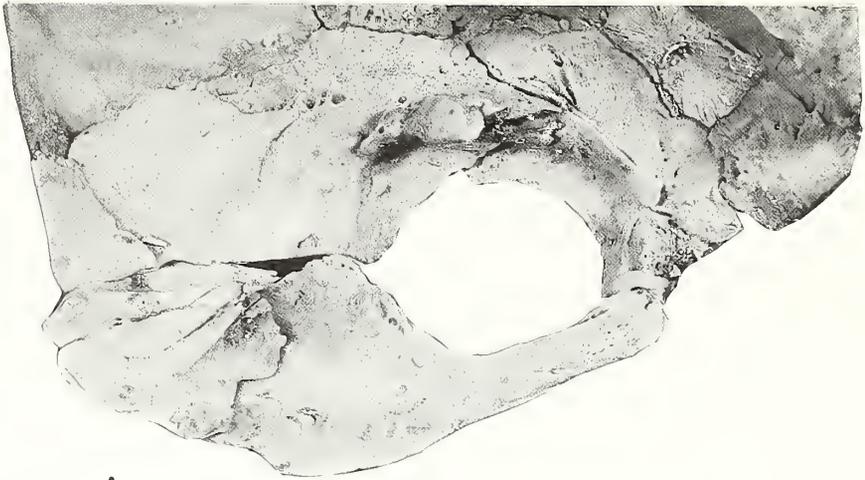
Description

Head shield. The head shield (Pl. 1; Text-figs 2–5) closely resembles that of both *Harrytoombsia* (Miles and Dennis 1979) and *Torosteus* (Gardiner and Miles 1990), but differs principally in the shape of the nuchal plate (Nu) which is shorter in length, has a strongly indented posterior margin, and a weakly convex anterior margin. Skull roof bones generally have sinuous and irregular sutures and relatively broad overlap surfaces. The cheek unit is clearly visible on the skull in dorsal view (Text-fig. 3), and the orbital notches (orb) are also well defined. The nuchal plate on the holotype occupies only thirty-seven per cent. of the skull roof length (Text-fig. 4), and

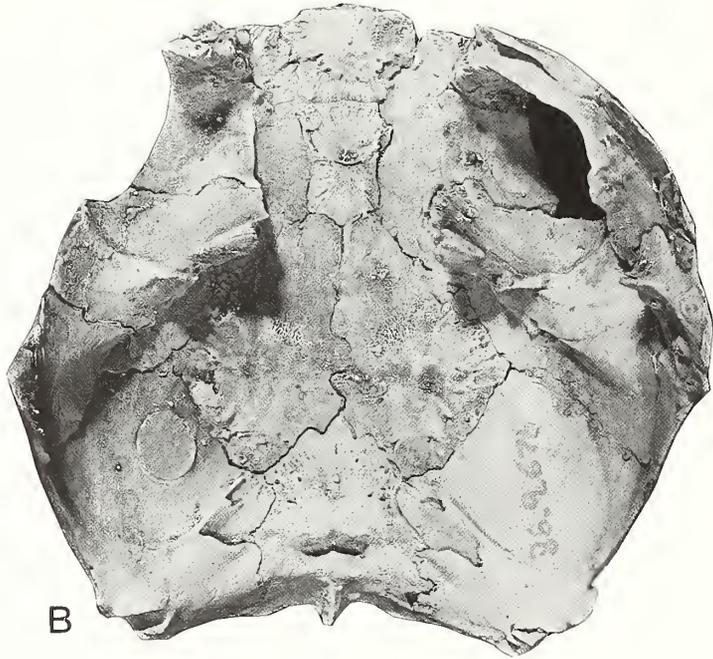


TEXT-FIG. 1. *Menamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Armour in left lateral view. Scale bar represents 10 mm.

has a B/L index of 166 (for P52553 the nuchal is thirty-six per cent. of estimated skull length, B/L index of 162, Text-fig. 5). The nuchal has a weakly convex anterior margin, in contrast to the concave or indented anterior margins of all other plourdosteids. The paranuchal plate (PNu) has extensive contact with the postorbital (PtO), as in other plourdosteids, and the marginal plate (M) is strongly indented into the postorbital plate. The postorbital plate is significantly larger than the marginal. The postmarginal (PM) has a very small externally-ornamented area, most of the plate forming the posteriolaterally-facing subostatic margin (soa). The pineal plate (P) is as long as the T-shaped squat rostral (R), the prepineal length of the skull



A



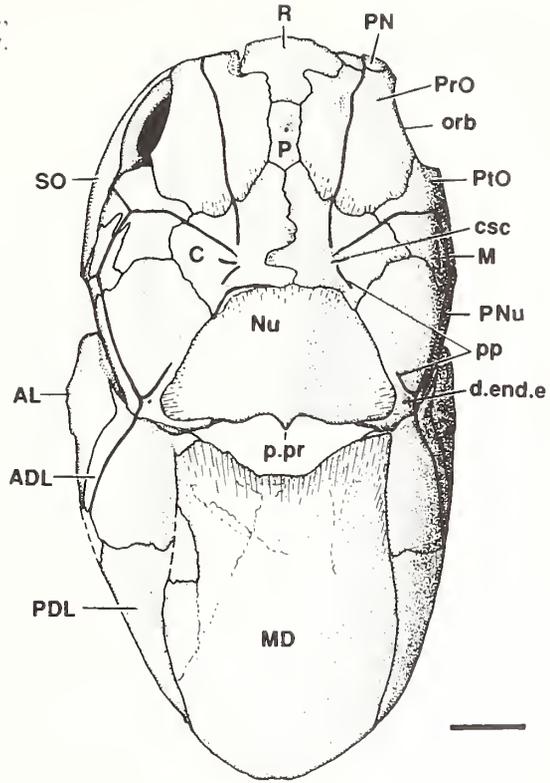
B

TEXT-FIG. 2. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. A, left side of cheek and skull roof in medial view, $\times 2$; B, head shield and cheek bones in ventral view, $\times 1.5$; both whitened with ammonium chloride.

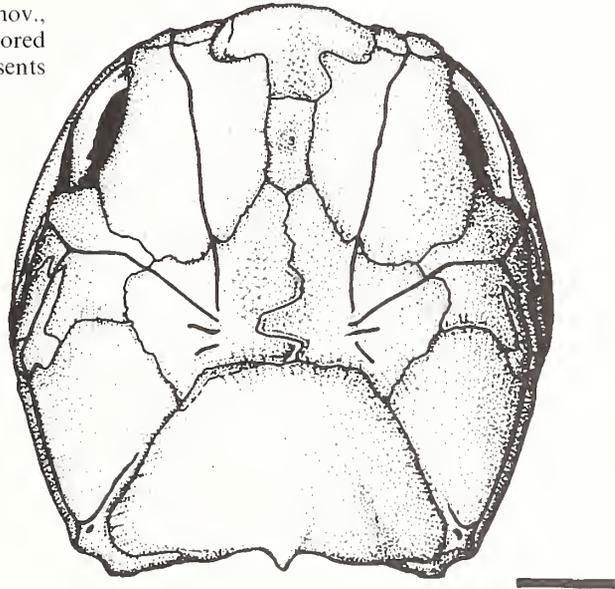
being twenty-five per cent. of the skull length. The postnasal plates (PN) both contact the rostral mesially and there are small accessory postnasal ossifications mesial to the postnasal bones in contact with the rostral (Text-fig. 6, acc. PN).

The visceral surface of the skull-roof shows all the regular morphological landmarks seen in eubrachi thoracic arthrodires (Text-figs 2, 7). Of particular interest are the robust postocular processes (pt.o.pr) which have smaller, secondary processes here termed the 'hyoid processes' (pr.hy), developed

TEXT-FIG. 3. *Mcnamaraspis kaprios* gen. et sp. nov.,
holotype, WAM 86.9.676. Armour in dorsal view.
Scale bar represents 10 mm.

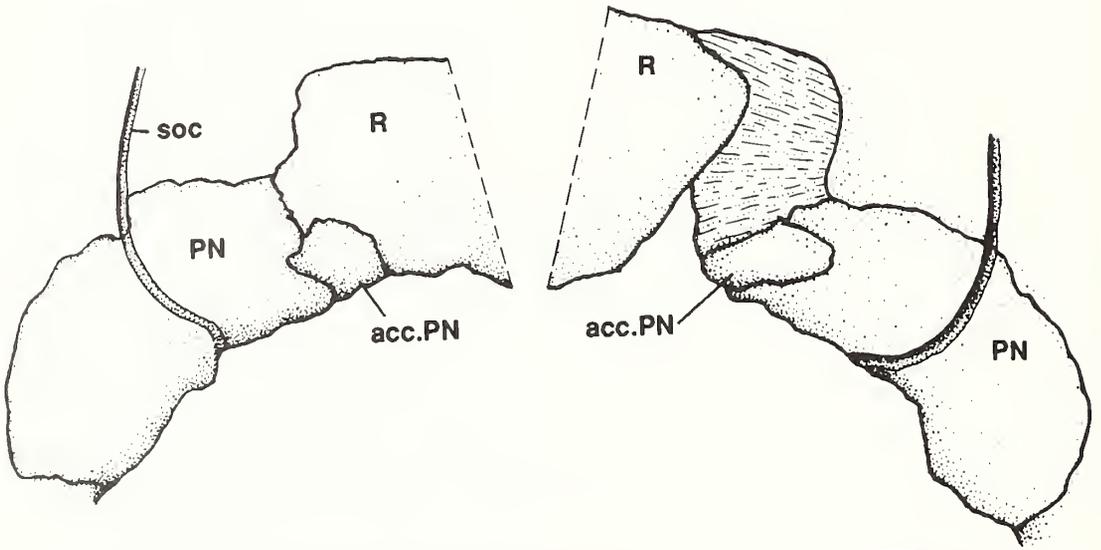
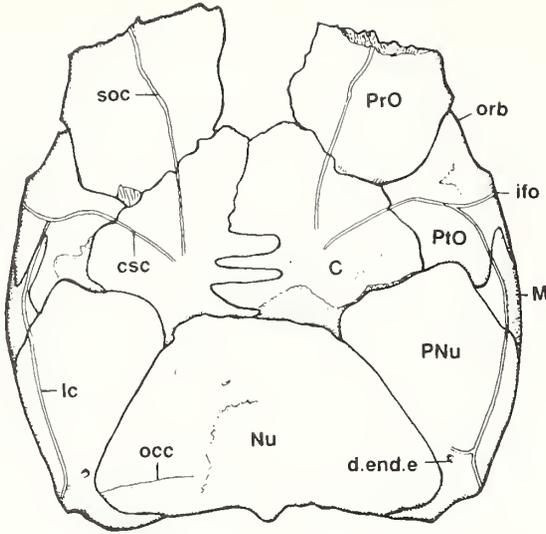


TEXT-FIG. 4. *Mcnamaraspis kaprios* gen. et sp. nov.,
holotype, WAM 86.9.676. Head shield fully restored
with cheek bones, in dorsal view. Scale bar represents
10 mm.



posterior to them. The width between the postorbital processes is 16 mm, narrower than for any other place where dermal bone encloses cartilaginous neurocranium. The triangular area posterolateral to these processes and bounded mesially by the lateral consolidated area (lcp) and anteriorly by a short ridge (ri), the

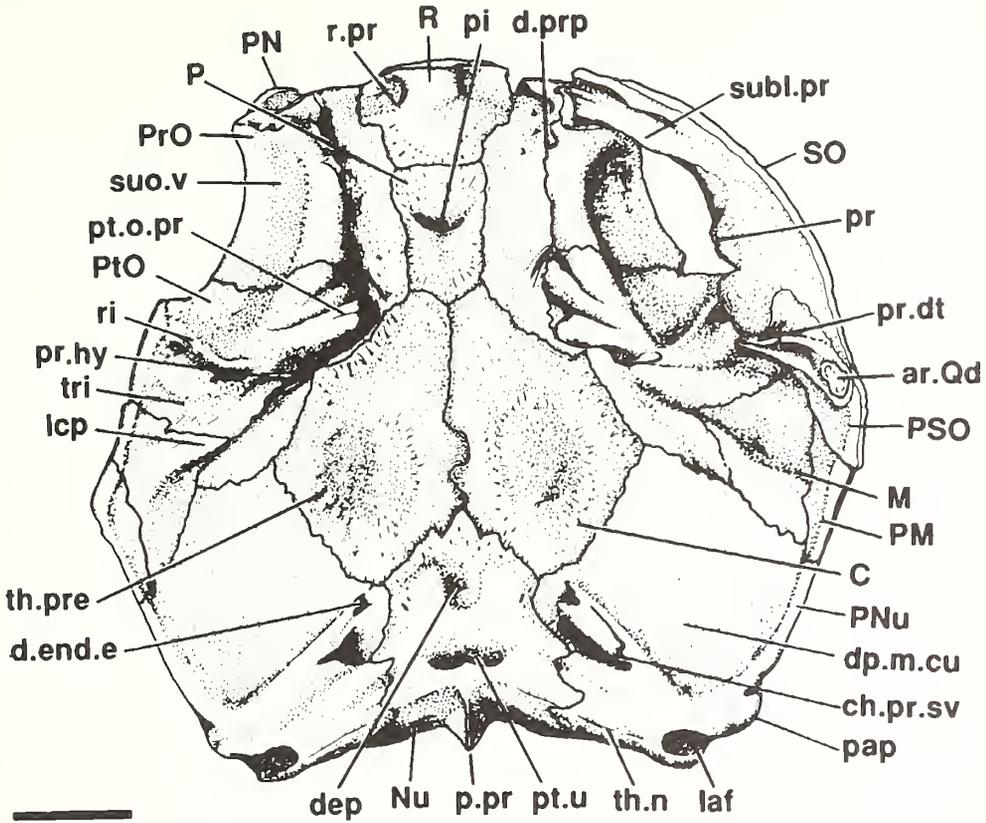
TEXT-FIG. 5. *Mcnamaraspis kaprios* gen. et sp. nov., BMNH P52553. Camera lucida sketch of head shield in dorsal view. Scale bar represents 5 mm.



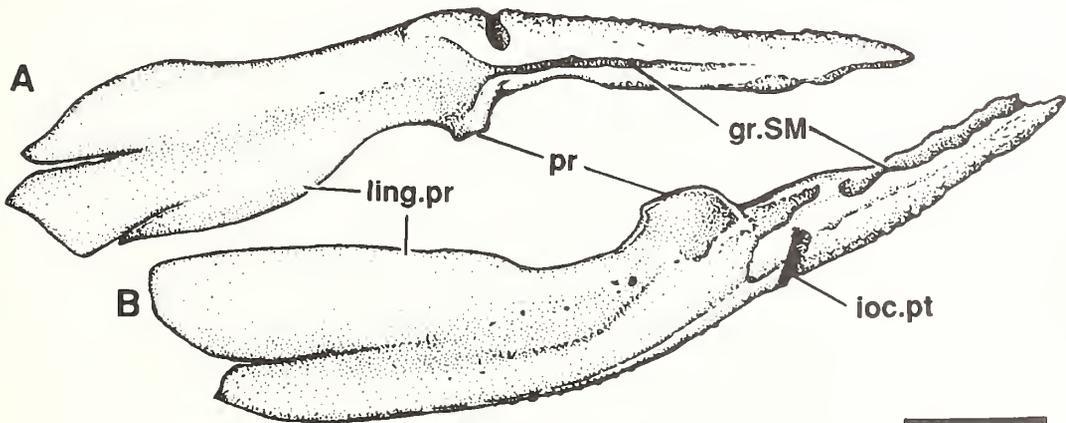
TEXT-FIG. 6. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Camera lucida sketch of left and right anterior margins of the head shield showing position of accessory postnasal bones. Scale bar represents 1 mm.

'postsuborbital crista' of Carr 1991, p. 381). It is a well-defined depression (tri) for muscle attachment coming from the dorsal region of the cheek unit, and is discussed further below.

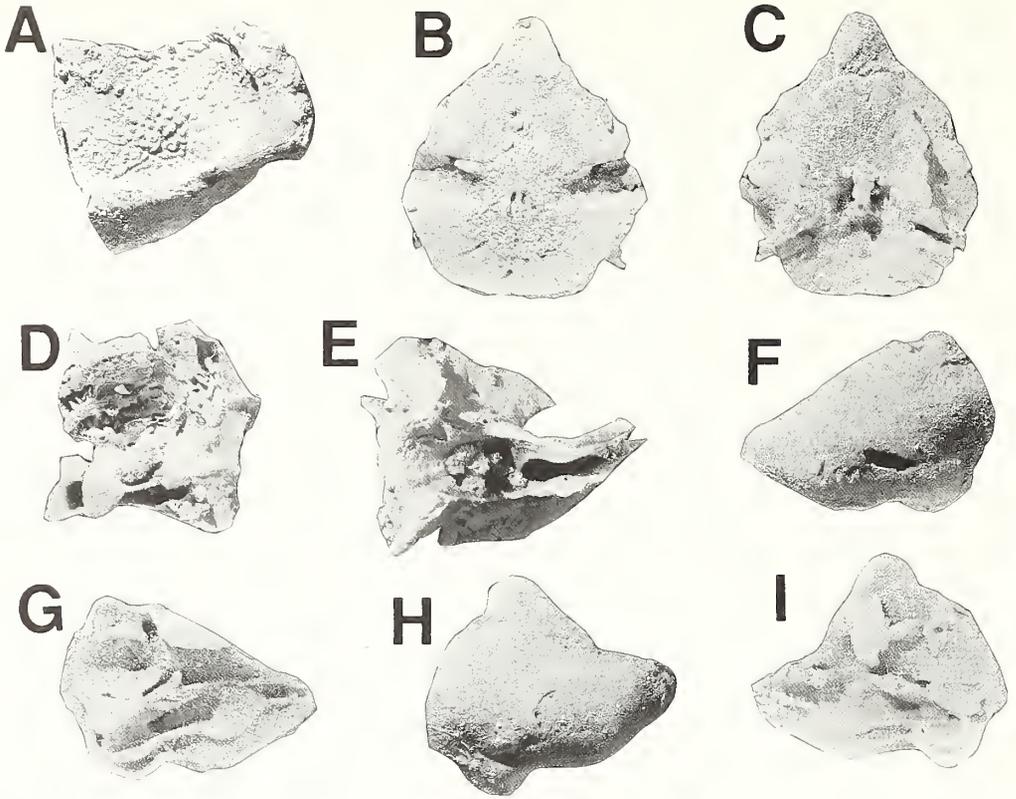
The cheek plates (Pl. 1; Text-figs 1, 8), of both sides are well-preserved and resemble the pattern seen in *Torosteus* except for the narrower suborbital process on the suborbital plate (SO). The submarginal plate (SM) is elongate and contacts the marginal and postmarginal plates, leaving a spiracular notch (spir) between the postorbital plate and the dorsal margin of the suborbital plate. The anterior end of this notch is closed by short contact between the suborbital and postorbital plates, unlike the open spiracular notch in *Torosteus* and *Harrytoombsia*. The postsuborbital plate (PSO) has a well-developed subcutaneous pit and cusped sensory-line groove (psoc), but the suborbital plate lacks the subcutaneous pit seen in other plourdoosteids. The



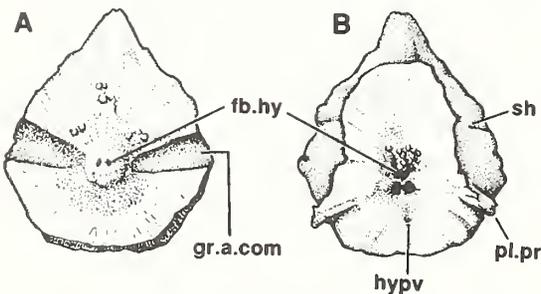
TEXT-FIG. 7. *Menamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Head shield and left cheek bones in ventral view. Scale bar represents 10 mm.



TEXT-FIG. 8. A. *Menamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676; camera lucida sketch of right suborbital plate in dorsal view. B. *Torosteus tuberculatus*, holotype, WAM 40.4.262; left suborbital plate in dorsal view. Scale bar represents 5 mm.



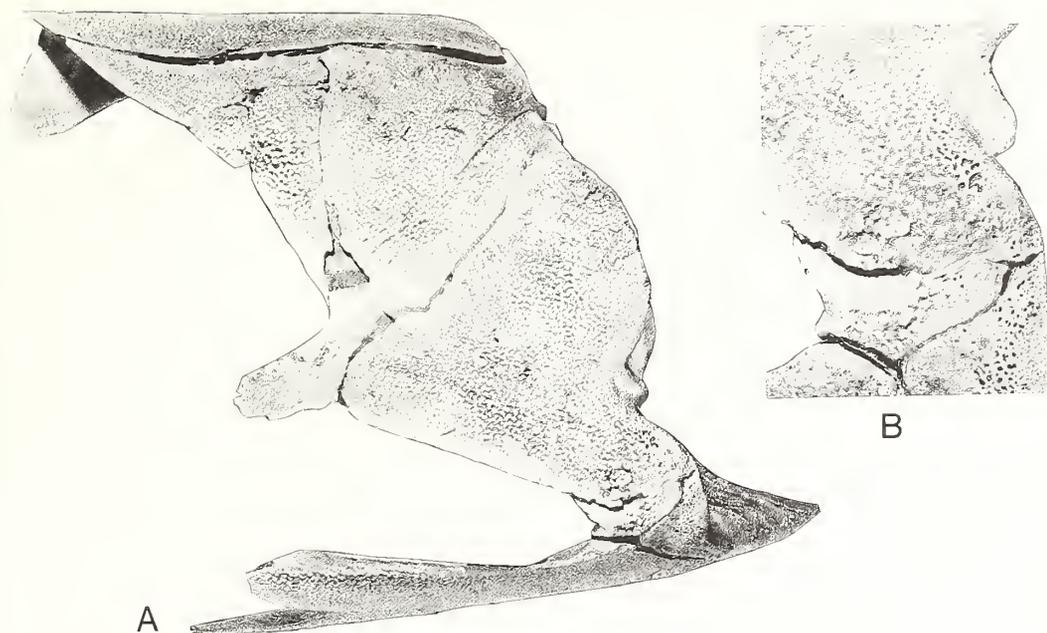
TEXT-FIG. 9. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. A, right articular in mesial view; B–C, parasphenoid in B, ventral view; and C, dorsal view; D–E, left side of ethmoid ossification in D, anterior view; and E, lateral view; F–I, annular cartilages from both sides of nasal capsules in F, H, anterior view; and G, I, posterior view. A–E are $\times 3$; F–I $\times 4$.



TEXT-FIG. 10. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Camera lucida sketch of parasphenoid in A, ventral view; and B, dorsal view. Both $\times 2.73$.

suborbital plate has a well-defined dermal process emanating from near the dorsal end of the orbital margin, along the mesial edge. This process (Text-figs 2, 7–8, pr) occurs in all other Gogo plourdosteids and is discussed more fully below.

The dentition is characteristic for the genus in that the inferognathal (Pl. 1, fig. 3; Text-fig. 1, IG) has three strong mesial 'teeth', two large anterior biting cusps, a trenchant crest with cutting edges on both labial and lingual edges, and well formed posterior teeth at the rear of the biting division of the inferognathal. The anterior superognathal (Pl. 1, figs 6–7; Text-fig. 1, ASG) has three biting cusps, a large trenchant median cusp and two sharp smaller cusps developed on the posteroventral corner of the biting margin. The posterior superognathal (Pl. 1, figs 4–5; Text-fig. 1, PSG) is remarkably thin compared with those of *Harrytoombsia*,



TEXT-FIG. 11. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. A, trunk shield in right lateral view, $\times 1.5$; B, enlargement, showing right spinal plate, $\times 3$.

Torosteus and *Kimberleyichthys*, and has a characteristic sharp cusp directed posteroventrally from its centre. The dorsal process of the posterior superognathal is well-developed, but the greatest width of the bone is still only 0.6 of its length, this being shorter than for the other Gogo plourdosteids.

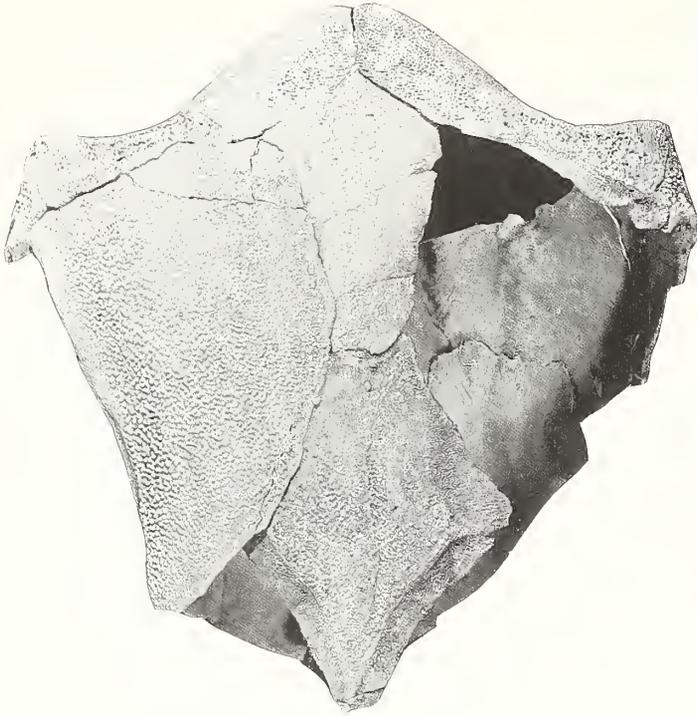
The parasphenoid (Text-figs 9B, C; 10) has a pentagonal shape with a weakly convex posterior margin, although in all other respects it is not unlike that of *Torosteus pulchellus* (Gardiner and Miles 1990, fig. 24). The dorsal surface (Text-fig. 7B) has a well-defined rectangular rim separated from the ventral surface by an extensive prehypophysial shelf (sh). The central area is strongly depressed for the buccohypophysial foramina (fb.hy), with a robust median longitudinal crest separating them. Paired posterolateral processes (pl.pr) are developed. The opening for the median hypophysial vein (hypv) is well-defined.

No extrascapular plate was found in the specimen, and, as all other parts of the anterior of the skeleton were preserved, it is reasonable to assume that an extrascapular plate was lacking from the armour as in other plourdosteids.

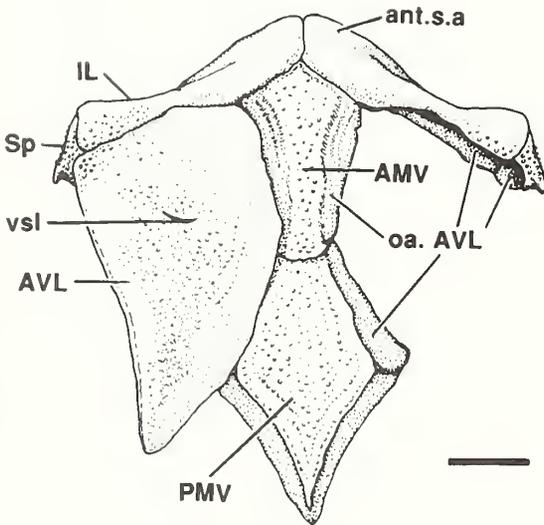
The trunk shield (Text-figs 1, 3, 11–13) is missing only the posterior ventrolaterals and the left anterior ventrolateral plates. The presence of an enclosed pectoral fenestra (f. pec.) is demonstrated by the overlap area on the posterior lateral plate (PL) for the postpectoral lamina of the posterior ventrolateral plate. The pectoral fenestra was very large relative to the size of the lateral wall of the trunk shield, more so than for any other plourdosteid. The anterior lateral plate (AL) is characteristic for the genus within plourdosteids in having a nearly pointed dorsal margin, well-defined semicircular embayment for the overlap of the submarginal plate (the post branchial lamina), short spinal overlap margin, and an extensive, straight margin bordering the pectoral fenestra. The most diagnostic feature of the trunk shield is the very short spinal plate (Text-figs 1, 11B, 13, Sp) which is only twenty-one per cent. of the length of the medial dorsal plate, compared with thirty to thirty-six per cent. in *Torosteus* species. The spinal (Sp) has no posteriorly facing lamina as in *Torosteus*, and is embayed with a small posterior notch (n). The contact margin between the spinal and the interlateral (IL) is more than twice as long as the contact margin between the spinal and anterior ventrolateral plates (AVL).

The median dorsal (MD), anterior dorsolateral (ADL) and posterior dorsolateral (PDL) plates show no special features; their shapes are shown in Text-figures 1–3, 11 and 12. Their proportions are incorporated into the measurements for the trunk shield (Table 1). The posterior lateral (PL) plate is strongly bent, and is much narrower than for *Torosteus* or *Harrytoombsia*.

TEXT-FIG. 12. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676, anterior half of trunk shield in ventral view, $\times 1.5$.



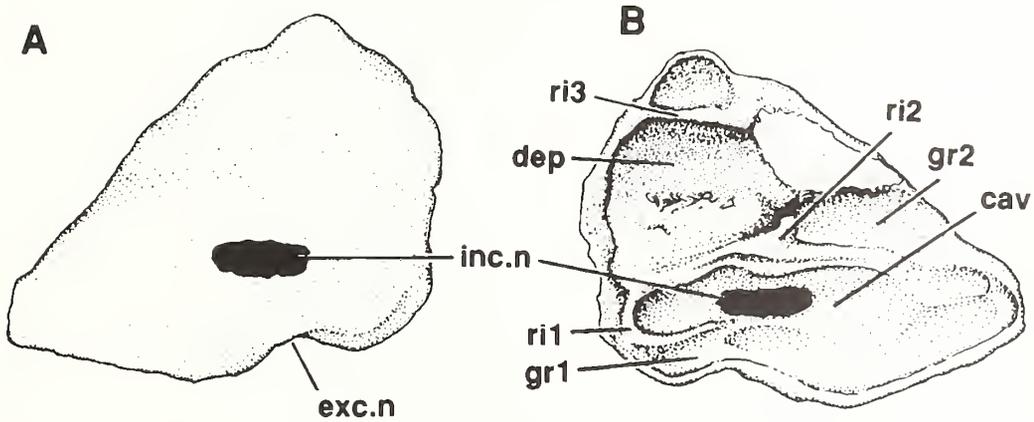
TEXT-FIG. 13. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Anterior half of trunk shield in ventral view. Scale bar represents 10 mm.



The anterior and posterior median ventral plates (Text-figs 11–13, AMV, PMV) are of similar length, the latter being about a third broader than the anterior median ventral plate. The interlateral plate is similar to that in other plourdosteids, such as *Torosteus* and *Harrytoombsia* and shows no special features apart from the well-defined anterior ventral shelf (Text-fig. 13, ant. s.a.).

TABLE 1. Measurements of *Mcnamaraspis kaprios* Holotype, WAM 86.9.676.

1. Skull roof length – 56.3 mm	13. Length of inferognathal – 38.5 mm
2. Breadth skull-roof – 57.7 mm	14. Length of biting division of inferognathal – 17.7 mm
3. Breadth of skull across posteromesial angles – 41.2 mm	15. Breadth of trunkshield – 64 mm
4. Depth of headshield – 35 mm	16. Depth of trunkshield – 63 mm
5. Prepineal length – 13.9 mm	17. Length of rostrocaudal flank of trunkshield – 26.5 mm
6. Length of orbit – 14 mm	18. Length of pectoral fenestra – c. 30 mm
7. Nuchal length – 20.9 mm	19. Median dorsal plate length – 43.8 mm
8. Length of lateral articular fossa – 5.3 mm	20. Median dorsal plate breadth – 35.2 mm
9. Depth of lateral articular fossa – 2.7 mm	21. Length of spinal – 9.4 mm
10. Angle between lateral articular fossa and headshield – 30°	22. Angle between spinal and midline of armour – 13°
11. Length of cheek – 40.5 mm	23. Anterior ventrolateral plate length – 44.8 mm
12. Length of postorbital division of cheek – 24.9 mm	24. Length of spinal division of anterior ventrolateral plate – 8.75 mm

TEXT-FIG. 14. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Annular cartilage in A, anterior view; and B, posterior view. Scale bar represents 1 mm.

NEW ANATOMICAL FEATURES FOR ARTHRODIRES

The well-preserved holotype exhibits a number of features never described before in arthrodires or for placoderms in general, or which have only been alluded to in previous descriptions. These include: the first occurrence of annular cartilages; the development of muscle attachment areas for the opercular regions; the presence of bony processes on the suborbital plates; and the presence of additional postocular processes on the visceral surface of the skull roof.

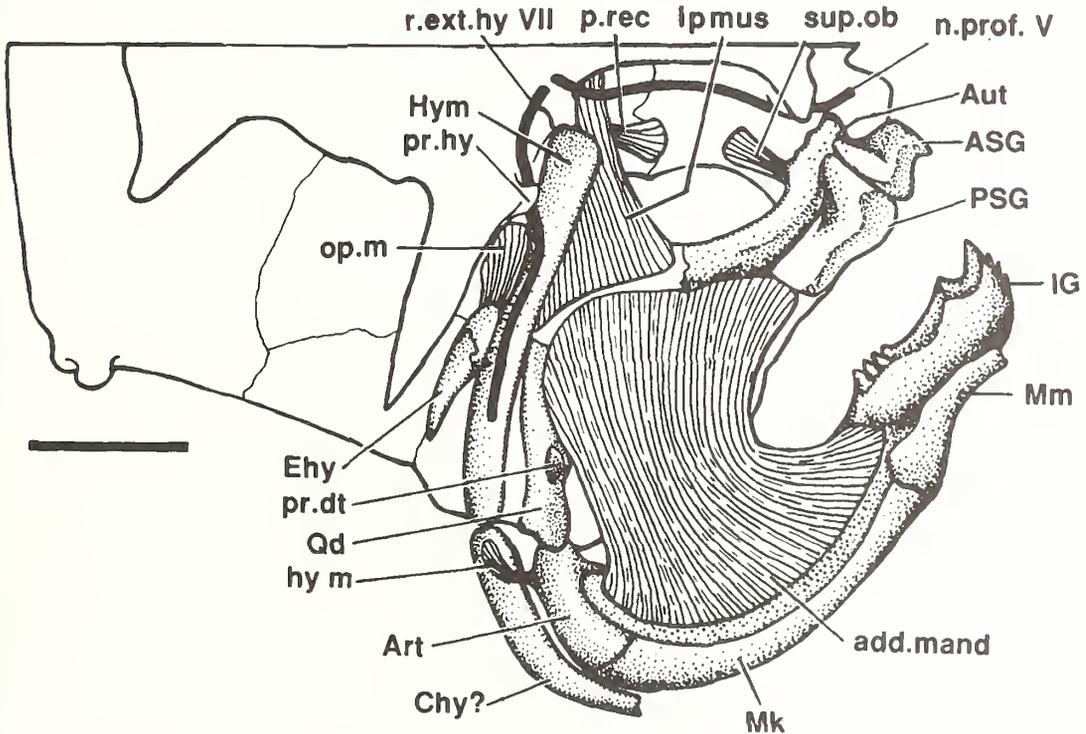
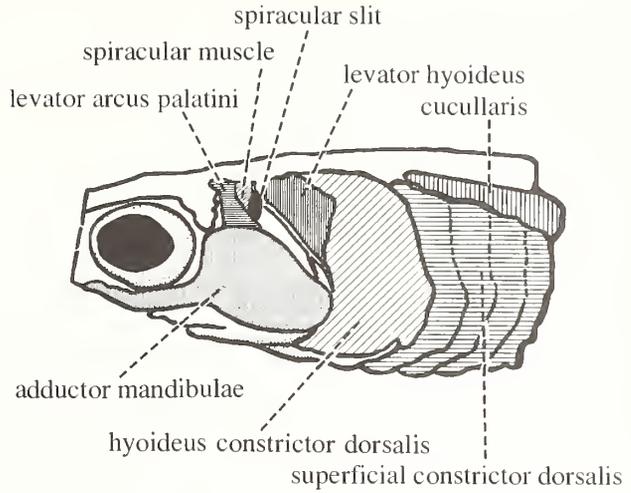
Annular cartilages. The specimen shows preservation of two perichondrally ossified irregular hemispheres (Text-figs 9F-I; 14) which were attached to the front of the snout. As the anterior part of the ethmoid bone was preserved it is possible to fit one of these bones over the front of the cavity for the nasal capsule. The neat fit of the hemispherical bone over the nasal cavity, and the presence of a small slit-like opening for the naris in the bone, suggests that it was an ossified cover to the nasal capsule. In chondrichthyans, an annular cartilage rings the nasal cavity and covers the front of the

nasal capsule (Stensiö 1963). Although Stensiö preferred to restore the annular cartilage in the snouts of arthrodires, there was no fossil evidence for this bone being present in any of the placoderms that he studied. The new Gogo specimen provides the first evidence of an annular cartilage being developed in placoderms. Why only these genera show the feature is not known, but it does not preclude the possibility that it was present as unossified cartilage in other placoderms, and ossified in only a few cases, such as in *Mcnamaraspis*.

In its external shape, viewed anteriorly, the annular cartilage bone is lacrimiform (Text-fig. 14). The external surface is smooth and strongly convex with a small sloping slit, presumably for the incurrent naris (inc.n). The excurrent naris (exc.n) is represented by a notch in the ventral margin of the annular cartilage. This notch is well defined when the bone is fitted over the anterior face of the nasal capsule. The visceral surface (Text-fig. 14B) shows a large cavity around the incurrent naris (cav) and a series of depressions (dep), ridges (ri 1–3) and grooves (gr 1, 2), which in life may have braced a sinuous folded cartilage structure, much like the complex annular cartilage seen in many elasmobranchs (e.g. *Isurus punctatus*; Stensiö 1963, fig. 33). The function of this structure would have been to direct the flow of water from the incurrent naris around the olfactory organ, and out through the excurrent notch. In many sedentary elasmobranchs the annular cartilage is highly specialized, allowing for communication between the nasal openings and the mouth (Bell 1993), and therefore the primitive condition is seen in most free-swimming sharks. *Mcnamaraspis*, having been an active free-swimming predator, also exhibits a simple, unspecialized annular cartilage not too unlike that of modern pelagic sharks such as *Isurus*. As the annular cartilage of *Mcnamaraspis* did not develop nasoral grooves, the flow of water in and around the olfactory organs, situated anterior to the roseate cribrosal bone, was most likely functional purely in olfaction, without any likelihood of involving respiration. It has been suggested that some placoderms, like the antiarch *Bothriolepis*, had paired lung-like structures (Denison 1941) and thus it could be argued the nasal capsules and their surrounding soft tissues may have secondarily developed respiratory specializations, although this has not been alluded to in any descriptions of the rostral bones or preorbital recesses of that genus (e.g. Stensiö 1948; Young 1984).

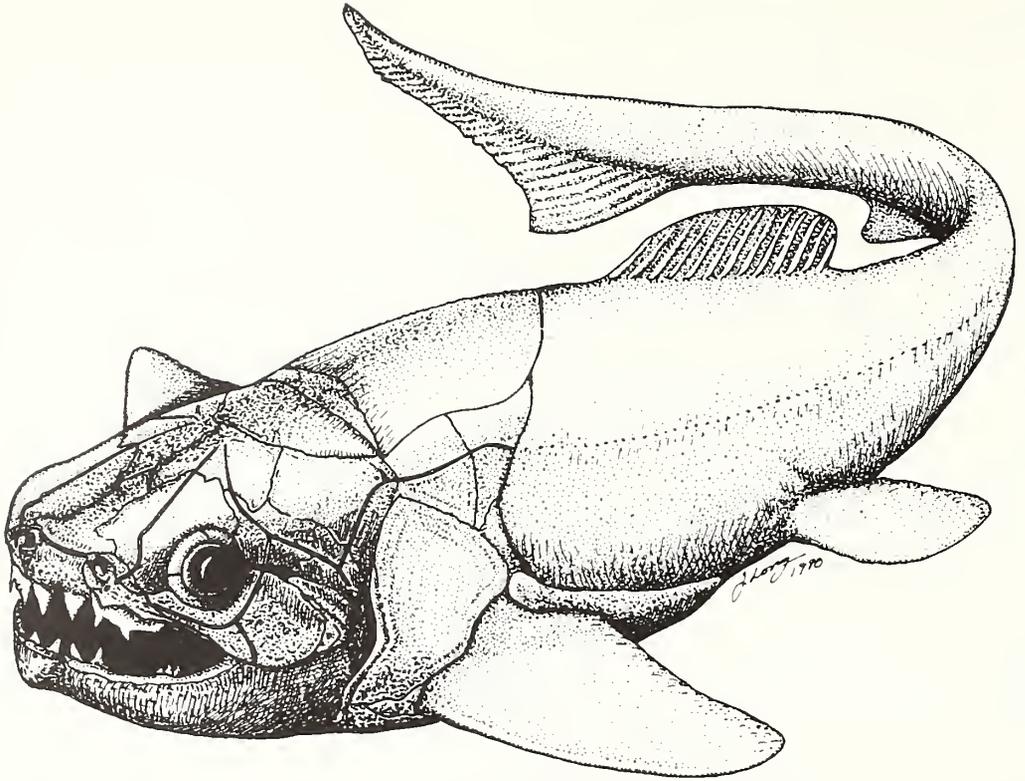
Suborbital bone – orbital autopalatine process. The additional small process found on the inside orbital margin of the suborbital bone in *Mcnamaraspis* (pr, Text-figs 7–8) has also been identified by the author in several other Gogo plourdosteids (*Harrytoombsia*, *Torosteus pulchellus*, *T. tuberculatus*) but is absent from *Eastmanosteus*, *Incoscutum*, all the camuropiscids and the two new, undescribed forms of Gogo ‘coccosteuromorph arthrodires’ currently being studied by workers at the Natural History Museum, London. The process was termed the ‘mesial process’ by Gardiner and Miles (1990) who suggested that it ‘was probably for a branch of the adductor mandibulae muscle’. The process emanates from near the top of the orbital margin of the suborbital plate in *Mcnamaraspis*, and in the middle of the orbital margin in *Torosteus*. The process is situated more ventrally than the dermal articular ridge on the mesial margin of the suborbital plate of *Buchanosteus* (Young 1979, p. 333) and did not take part in any connection with the skull roof. When the cheek unit and jaw cartilages are articulated to the skull roof it is clear that the process aligns well with the posterior margin of the ossified division of the autopalatine and would have most probably have served as a bracing point or attachment point for a lateral ligamentous connection from the autopalatine to the suborbital plate. This is well demonstrated in the holotype of *Torosteus pulchellus* (Gardiner and Miles 1990, fig. 20) where the process can be seen emanating from the suborbital plate lateral to the posterior margin of the autopalatine. The strap-like palatoquadrate would have passed directly lateral to the process, and thus it could not have served as an attachment point for adductor mandibulae muscles. These muscles are here reconstructed as in *Squalus* (Text-fig. 15) inserting dorsally on the ventral concave surface of the palatoquadrate (Text-fig. 16). Thus the small mesial process can be termed ‘an orbital autopalatine process’ of the suborbital bone. This character would appear to be a strong synapomorphy uniting these Gogo taxa, and possibly may characterize the whole plourdosteid group if it can be identified within the other non-Australian genera.

TEXT-FIG. 15. *Squalus acanthias*, outer muscles of the head and pharynx (after Gans and Parsons 1964).



TEXT-FIG. 16. *Mcnamaraspis kaprios* gen. et sp. nov. Attempted reconstruction of soft anatomy of the cheek and jaw regions. Scale bar represents 10 mm.

Reconstructing jaw and opercular musculature. The lateral consolidated area of the skull roof is divided by a ridge (ri, Text-fig. 8) which separates the suborbital vault (suo.v) from a large triangular ventrally facing depression (tri). When the cheek unit is articulated with the skull roof this depression is adjacent to the postsuborbital plate, thus showing that it would have served as an attachment area for musculature that inserted on the visceral surface of the skull roof dorsal to the palatoquadrate. The adductor mandibulae muscles would have passed ventrally from the



TEXT-FIG. 17. *Mcnamaraspis kaprios* gen. et sp. nov. Restoration of living fish, tail based on *Coccosteus cuspidatus* (Miles and Westoll 1968) and *Toroosteus* (WAM 91.4.32).

palatoquadrate to insert along the mesial face of the inferognathal, as is normal of most fishes. Therefore I suggest that the triangular depression on the lateral consolidated area of the skull roof probably served as an attachment site for the levator palatoquadrati muscle (l.p. mus, Text-fig. 16), as occurs in this position in many osteichthyan and elasmobranch fishes (Text-fig. 15; Edgeworth 1935; Gans and Parsons 1964; Lauder and Liem 1983). This muscle would have facilitated movement of the cheek unit for respiration. Immediately posterior to the triangular depression is a smaller, less well-defined area where the lateral consolidated region tapers to the posterolateral corner of the skull roof. This weakly depressed area of dermal bone may have served as an attachment area for the smaller opercular muscle emanating from the perichondral ossification of the submarginal plate, here called an epihyal element. This ossification is only seen in one Gogo specimen, the holotype of *Toroosteus pulchellus* (WAM 88.2.7) and may well be interpreted alternatively as an opercular cartilage as argued by Young (1986, p. 39). If so, the hyomandibular element, not perichondrally ossified in any Gogo arthrodire, would have to be reconstructed between the palatoquadrate and the epihyal/opercular cartilage element. For the purposes of reconstruction here the small ossification of the submarginal seems more likely to be an opercular cartilage, as it is situated adjacent to the weakly depressed area on the skull roof here interpreted as a suitable attachment site for the opercular muscle (Text-fig. 16). However, the true 'epihyal' element may well be situated posteroventral to the opercular cartilage as suggested by Young (1986).

With regard to the adductor mandibulae in arthrodires, the presence of a slender suborbital division of bone on the suborbital plate would suggest that the suborbitalis muscles were well-defined, extending forwards and possibly meeting in a midline raffe. These muscles, along with the

levator palatoquadrati, serve to protract and retract the palatoquadrate in chondrichthyans (Edgeworth 1935), and in arthrodires would have worked with the opercular muscle to move the cheek unit during respiration. Changes in water volume within the buccal cavity may have been regulated by these suggested lateral movements of the dermal cheek unit, forming a simple buccal pump mechanism. This degree of mobility of the cheek unit is not seen in many arthrodires, as several groups have the cheek fixed rigidly to the trunk shield (e.g. camuropiscids, brachydeirids, selenosteids, etc.). In these forms, and other placoderms lacking a separate cheek complex, expulsion of water from the gill chamber would have been achieved by vertical movements of the head shield working in conjunction with gill arch muscles to force water out the branchial opening behind the submarginal plate.

Postocular processes and hyoid process. The robust postocular processes of the plourdosteids are better developed than for any other arthrodire and most probably represent an adaptation for bracing or supporting the cartilaginous endocranium during the powerful bite. In addition to the robust anterior postocular process seen in *Mcnamaraspis*, there are a pair of smaller, delicate processes immediately posterior to the larger postocular processes. These smaller processes I have termed the 'hyoid processes' (pr.hy, Text-figs 7, 16) as they correspond well with the position of the ramus hyoideus nerve emerging from the anterior region of the posterior postorbital process of the braincase (as in *Buchanosteus*; Young 1979), and presumably continuing down to the hyomandibular. These hyoid processes are also observed in *Torosteus* and *Harrytoombsia*. Text-figure 16 shows an attempted reconstruction of some aspects of the soft anatomy of *Mcnamaraspis* based on the new morphological observations discussed above.

Text-figure 17 shows an attempted reconstruction of *Mcnamaraspis* as a living fish with the tail restored after *Coccosteus cuspidatus* (Miles and Westoll 1968). The axial skeleton of the body from the trunk to the anal fin is preserved in one of the Gogo plourdosteids (*Torosteus* sp., WAM 91.4.32) showing these bones to be almost identical with those of *Coccosteus*.

PHYLOGENETIC IMPLICATIONS

Relationships of plourdosteids within the enbrachythoracids. The following discussion of arthrodire interrelationships deals only with the higher eubrachythoracids, defined as a monophyletic group by Lelievre *et al.* (1987), Carr (1991) and Lelievre (1991). The eubrachythoracid arthrodires are defined by having: (1) separate autopalatine and quadrate ossifications of the palatoquadrate; (2) development of a continuous thickening across the posterior margin of the head shield; and (3) the supraorbital vault developed as part of the lateral consolidated arch which is bounded posteriorly by a posterior supraorbital crista (Carr 1991). Lelievre (1991) also used the position of the orbits as lateral on the headshield and the development of a suborbital blade on the suborbital plate, although Carr dismissed these on the grounds that they also occur in more primitive arthrodires such as *Buchanosteus* and to some extent in forms like *Antineosteus*.

Carr (1991) recognized two main subgroups within the eubrachythoracids – coccosteomorphs and pachyosteomorphs. The coccosteomorph arthrodires are defined as monophyletic by sharing: (4) a preorbital plate embayment in the central plate; (5) reduction in medial contact between the preorbital plates; (6) spinous posterior margin on median dorsal plate; (7) posterior lateral plate with well-developed ventral lamina; (8) posterior ventrolateral plate with well-developed postpectoral lamina; (9) parasphenoid perforated by a foramen for the median hypophysial vein. Within the coccosteomorph group I recognize the following monophyletic groups: Incisoscutidae and Camuropiscidae (Denison 1984; Long 1988b, 1994; Carr 1991) and the Plourdosteidae (Vezina 1990; =Torosteidae Gardiner and Miles, 1990). The following synapomorphies define the clade containing the Plourdosteidae + Incisoscutidae + Camuropiscidae: (10) paranuchal sutures with postorbital plate, excluding contact between marginal and central plates; (11) anteroventral wings of the anterior lateral plate in contact with the interlateral plate (Long 1988b, Carr 1991). The Incisoscutidae and Camuropiscidae are united by the following synapomorphies (from Long 1988b,

1994): (12) spindle-shaped ('trullate') body form with elongate head shield; (13) cheek unit attached firmly to lateral margin of skull roof, precluding movement; (14) durophagous dentition; (15) parasphenoid having a rhombic, elongated shape. The plourdosteid group is defined by at least three other synapomorphies discussed in the text: (16) well-developed paired postocular processes; (17) the presence of an orbital autopalatine process on the suborbital bone; (18) a posterior lateral plate that forms part of the margin of the pectoral fenestra and is deeply inserted into the posterior dorsolateral plate. The deep insertion of the posterior lateral plate into the posterior dorsolateral plate was noted by Carr (1991) as a synapomorphy uniting *Eastmanosteus calliaspis* and the dinichthyids, in addition to four other synapomorphies, listed below. As the plourdosteid group is also well-defined by at least three synapomorphies (listed above) it is parsimonious to regard this feature as a parallelism between plourdosteids and the group *Eastmanosteus calliaspis* + dinichthyids.

The interrelationships of the pachyosteorhynchid, dinichthyid and aspinothoracid arthrodires have been discussed in depth by Carr (1991) and Lelievre (1991). Synapomorphies used by Carr to define these groups are as follows. Pachyosteorhynchids share: (19) loss of the paranuchal embayment on the central plate; (20) reduction of contact between the nuchal and central plates; (21) formation of lateral contact between the suborbital and preorbital plates; (22) loss of the groove for the ventral portion of the main lateral line canal on the anterior dorsolateral plate.

Eastmanosteus calliaspis and the dinichthyids (as defined by Carr 1991) are united by the following synapomorphies: (23) position of the posterior margin of pineal plate posterior to orbits; (24) presence of a contact face for the posterior superognathal on the linguiform process of the suborbital plate; (25) presence of a groove for the main lateral line canal on the posterior dorsolateral plate; (26) presence of anterior and lateral cusps on the anterior superognathal. In Carr's analysis *Heintzichthys* and *Gorgonichthys* do not share any derived features with the dinichthyids, and in the light of new descriptions of *Heintzichthys* the analysis of dinichthyid interrelationships by Long (1987) is now redundant. *Heintzichthys* and *Gorgonichthys* share two derived features: (27) an anterior superognathal with an enclosed lateral face; and (28) the loss of adsymphyseal denticles on the inferognathal bone.

The Aspinothoracidi (Stensiö 1959) are defined as a monophyletic group by the following synapomorphies from Carr (1991): (29) reduction of the lateral consolidated part of the head shield; (30) the anterior shift of the junction between the preorbital, central and postorbital plates to a new position over the orbit; (31) loss of the spinal plate; (32) closure of the angle between the postorbital and otic branches of the infraorbital canal, associated with the enlargement of the orbits. Finally, the selenosteids are defined by the presence of: (33) an enlarged orbit; and the following characters defined by Lelievre *et al.* (1987) – (34) denticulated gnathal plates; (35) loss of dorsal process on posterior superognathal plate; and (36) the development of an ethmoid crest.

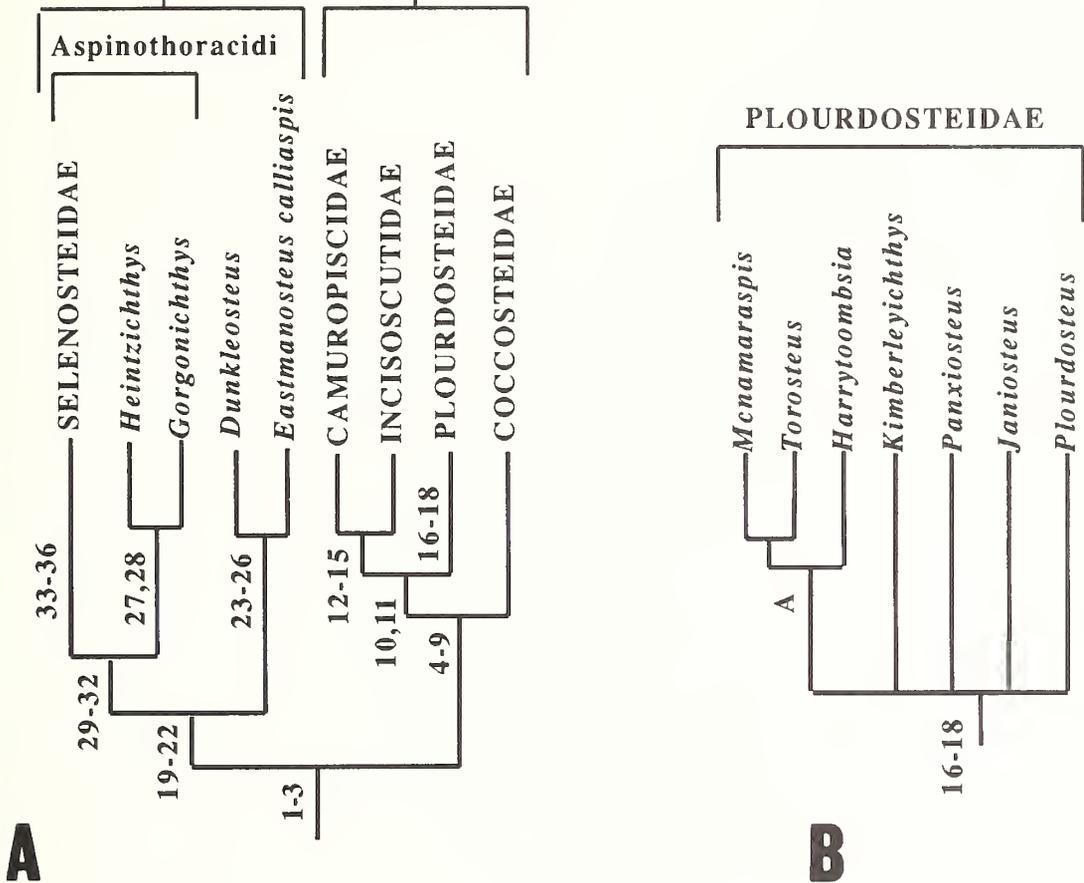
This scheme leaves out many of the poorly known higher eubranchyothoracids which require more complete material before their affinities can be resolved.

Interrelationships of plourdosteids. The taxonomic position of *Mcuamaraspis* as one of the plourdosteids can be demonstrated by the presence of characters (16)–(18) above. Gardiner and Miles (1990) united the Gogo plourdosteids with *Plourdosteus canadensis* on the strength of several general features in their family Torosteidae, but also noted the well-developed postocular processes as a synapomorphy of the group. Well-developed postocular processes are also known in some, but not all, dinichthyids (e.g. present in *Dunkleosteus terrelli*; Heintz 1932; absent in *Eastmanosteus calliaspis* based on observation of Gogo specimens). In this respect they are regarded as a convergent feature in dinichthyids, a monophyletic group, if *Heintzichthys* and *Gorgonichthys* are excluded, as defined by Carr (1991).

Whether an orbital autopalatine process occurs on the suborbital plate of *Plourdosteus* is not yet known, although as similar specializations occur on the inner surface of the skull roof (such as the presence of a well-defined triangular depression mesial to the lateral consolidated area, the development of a hyoid process behind the postocular processes, based on observation of BMNH

PACHYOSTEOMORPHI

COCCOSTEOMORPHI



TEXT-FIG. 18. A, cladogram of higher eubranchyothoracid interrelationships (after Carr 1991). B, cladogram of plourdosteid interrelationships. Synapomorphies are listed in text.

P60583), and the suborbital is of similar robust form, it is predicated that it should also be present in this genus.

Within the plourdosteid group several taxa share a number of derived features with polarity assessed by comparison with the coccosteid and dinichthyid outgroups. For example, the sizes of the marginal and postorbital plates are very similar in coccosteids and dinichthyids, and this is seen also in *Kimberleyichthys*, with increasingly larger postorbitals and smaller marginals in other plourdosteids. Thus the presence of very large postorbital plate relative to the size of the marginal plate may be an autapomorphy of *Panxiosteus*, but is of variable size range in other plourdosteids. The marginal plate is strongly indented into the postorbital plate in all plourdosteids except *Panxiosteus* and *Plourdosteus*, although this character is also of dubious phylogenetic value as it is variable within coccosteids and dinichthyids. The large trilobate centrals of coccosteids and dinichthyids are also present in *Plourdosteus*, *Janiosteus*, *Panxiosteus* and *Kimberleyichthys*, but the posterior lobe is reduced in *Mcnamaraspis*, *Torosteus* and *Harrytoombsia*, here considered to be a synapomorphy (A) uniting these taxa. The parasphenoids are known in the Gogo forms and

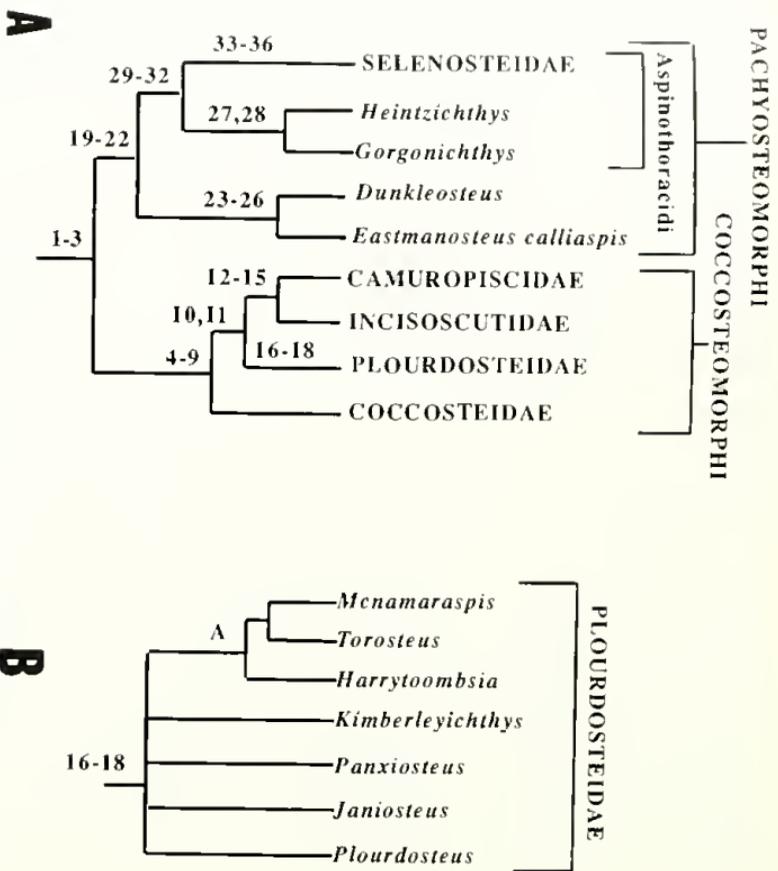


FIG. 18. A, cladogram of higher eubranchyothoracid interrelationships (after Carr 1991). B, cladogram of plourdosteid interrelationships. Synapomorphies are listed in text.

P60S33), and the suborbital is of similar robust form, it is predicated that it should also be present in this genus.

Within the plourdosteid group several taxa share a number of derived features with polarity assessed by comparison with the coccosteid and dimichtyid outgroups. For example, the sizes of the marginal and postorbital plates are very similar in coccosteids and dimichtyids, and this is seen also in *Kimberleyichthys*, with increasingly larger postorbitals and smaller marginals in other plourdosteids. Thus the presence of very large postorbital plate relative to the size of the marginal plate may be an autapomorphy of *Panxiosteus*, but is of variable size range in other plourdosteids. The marginal plate is strongly indented into the postorbital plate in all plourdosteids except *Panxiosteus* and *Plourdosteus*, although this character is also of dubious phylogenetic value as it is variable within coccosteids and dimichtyids. The large trilobate centrals of coccosteids and dimichtyids are also present in *Plourdosteus*, *Janiosteus*, *Panxiosteus* and *Kimberleyichthys*, but the posterior lobe is reduced in *Mcnamaraspis*, *Torosteus* and *Harrytoombsia*, here considered to be a synapomorphy (A) uniting these taxa. The parasphenoids are known in the Gogo forms and

Plourdosteus (Vezina 1990), but are not useful in refinement of plourdosteid relationships as they are of more or less uniform morphology.

The trunk shield is known in all the taxa save *Janiosteus* and only partially in *Pauxiosteus* and *Kiuberleyichthys*. The most variable features are the shape of the posterior lateral plates and the extent of their external ornamentation. The loss of dermal ornamentation on these plates is seen in *Mcnamaraspis*, and to some degree in *Harrytoombsia* and *Torosteus pulchellus*, but the primitive condition of having extensive areas of dermal ornamentation is retained in *Kiuberleyichthys*, *Torosteus tuberculatus* and *Plourdosteus*. In this respect, although the character is quite variable it lends support to the hypothesis that *Mcnamaraspis*, *Torosteus* and *Harrytoombsia* form an apomorphic subgroup within the Plourdosteidae. The extreme reduction of the spinal plate is an autapomorphy of *Mcnamaraspis* within the Plourdosteidae that is paralleled within the Coccosteidae in the similar development of a large pectoral fenestra and short spinal in *Watsouosteus*. Text-figure 18 summarizes the position of the plourdosteids within the higher eubranchyothoracids, and shows an hypothesis of interrelationships of plourdosteids, based on the above discussion.

Placoderm relationships. The presence of annular cartilages in placoderms, based on the single specimen of *Mcnamaraspis*, demonstrates another similarity between placoderms and elasmobranchs, as suggested by Stensiö (1963), although the exact form of the annular cartilages of *Mcnamaraspis* differs in many features from those of elasmobranchs. In elasmobranchs the annular cartilage is a complex folded cartilage of variable morphology that encircles both the incurrent and excurrent nares, whereas in *Mcnamaraspis* it is an ossified single unit with only one narial opening, and thus only borders the space for the excurrent naris.

Non-ossified cartilaginous annular cartilages were probably present in all arthrodires, based on the similar morphology of the cribrosal bones and shapes of the nasal regions (where preserved). The function of the annular cartilage, to divide the incurrent and excurrent nares from the common opening of the nasal capsule, and direct the flow of water around the olfactory organ, appears to be similar in both chondrichthyans and *Mcnamaraspis*. The convoluted folds of bone on the inner surface of the ossified annular cartilages shows clearly the direction of flow from the incurrent naris, around the outer surface of the olfactory organ, and out via the slit in one corner of the cartilage, this being interpreted as the excurrent naris. This character lends weight to the hypothesis of placoderms being more closely related to chondrichthyans (Stensiö 1963; Goujet 1984), rather than being a sister group to osteichthyans (Forey 1980; Gardiner 1984).

Young (1986) reviewed the evidence for placoderm relationships and argued that there was insufficient evidence for direct comparison of osteichthyan skull roof patterns with those of placoderms, and that other listed 'synapomorphies' of placoderms and osteichthyans were often manifestations of a single character, such as the capacity to ossify the perichondrium. Young also preferred new interpretations of placoderm morphology and concluded that placoderms were either the sister group to all gnathostomes, or the sister group to chondrichthyans. The new observations that the arthrodires sometimes possessed an annular cartilage and that the suborbitalis division of the adductor mandibulae was probably developed as in chondrichthyans lend further support to the hypothesis that placoderms and chondrichthyans are sister groups.

Resolution of such higher taxonomic problems will seemingly rest on new discoveries of well-preserved placoderms from sites such as Gogo, where pertinent new anatomical information is coming to light with each season's fieldwork.

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REFERENCES

- BELL, M. A. 1993. Convergent evolution of nasal structure in sedentary elasmobranchs. *Copeia*, **1993**, 144–158.
- CARR, R. H. 1991. Reanalysis of *Heintzichthys gouldii* (Newberry), an aspinothoracid arthrodire (Placodermi) from the Famennian of northern Ohio, with a review of brachythoracid systematics. *Zoological Journal of the Linnean Society*, **103**, 349–90.
- DENISON, R. H. 1941. The soft anatomy of *Bothriolepis*. *Journal of Paleontology*, **15**, 553–561.
- 1978. Placodermi. In SCHULTZE, H-P. (ed.), *Handbook of paleoichthyology*, Vol. 2. Gustav Fischer Verlag, Stuttgart, New York, 128 pp.
- 1984. Further consideration of the phylogeny and classification of the order Arthrodira (Pisces: Placodermi). *Journal of Vertebrate Paleontology*, **4**, 396–412.
- DENNIS, K. D. and MILES, R. S. 1979a. A second eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **67**, 1–29.
- 1979b. Eubrachythoracid arthrodires with tubular rostral plates from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **67**, 297–328.
- 1980. New durophagous arthrodires from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **69**, 43–85.
- 1981. A pachyosteomorph arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **73**, 213–258.
- 1982. A eubrachythoracid arthrodire with a snub-nose from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **75**, 153–166.
- DENNIS-BRYAN, K. 1987. A new species of eastmanosteid arthrodire (Pisces: Placodermi) from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **90**, 1–64.
- and MILES, R. S. 1983. Further eubrachythoracid arthrodires from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **67**, 1–29.
- DINELEY, D. and LOEFFLER, E. 1993. Biostratigraphy of the Silurian and Devonian gnathostomes of the Euramerica Province, 104–138. In LONG, J. A. (ed.), *Palaeozoic vertebrate biostratigraphy and biogeography*. Belhaven Press, London, 369 pp.
- EDGEWORTH, F. H. 1935. *The cranial muscles of vertebrates*. Cambridge University Press, London, 493 pp.
- FOREY, P. L. 1980. *Latimeria*: a paradoxical fish. *Proceedings of the Royal Society of London, Series B*, **208**, 369–384.
- GANS, C. and PARSONS, T. S. 1964. *A photographic atlas of shark anatomy*. Academic Press, New York, London, 106 pp.
- GARDINER, B. G. 1984. The relationships of placoderms. *Journal of Vertebrate Paleontology*, **4**, 379–395.
- and MILES, R. S. 1990. A new genus of eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **99**, 159–204.
- GOUJET, D. 1984. Placoderm interrelationships: a new interpretation, with a short review of placoderm classification. *Proceedings of the Linnean Society of New South Wales*, **107**, 211–243.
- GROSS, W. 1932. Die Arthrodira Wildungen. *Geologische und Paläontologische Abhandlungen*, **19**, 5–61.
- HEINTZ, A. 1932. The structure of *Dinichthys*, a contribution to our knowledge of the Arthrodira. 115–224. *The Bashford Dean Memorial Volume*, Part 1, The American Museum of Natural History, 319 pp.
- IVANOV, A. O. 1988. A new genus of arthrodires from the Upper Devonian of Timan. *Paleontological Journal*, **1988**, 117–120.
- LAUDER, G. V. and LIEM, K. V. 1983. The evolution and interrelationships of the actinopterygian fishes. *Bulletin of the Museum of Comparative Zoology*, **150**, 95–197.
- LELIEVRE, H. 1991. New information on the structure and the systematic position of *Tafilalichthys lavocati* (placoderm, arthrodire) from the Late Devonian of Tafilalt, Morocco. 121–130. In CHANG MEE-MANN, LIU YU-HAI and ZHANG GUO-RUI (eds), *Early vertebrates and related problems of evolutionary biology*. Science Press, Beijing, China, 514 pp.
- LELIEVRE, H. FEIST, R., GOUJET, D. and BLEICK, A. 1987. Les Vertébrés Dévonien de la Montagne Noire (Sud de la France) et leur apport à la phylogénie des Pachyostéomorphes (Placodermes, Arthrodires). *Palaeo-vertebrata*, **17**, 1–26.
- LONG, J. A. 1987. A new dinichthyid fish (Placodermi: Arthrodira) from the Upper Devonian of Western

- Australia, with a discussion of dinichthyid interrelationships. *Records of the Western Australian Museum*, **13**, 515–540.
- LONG, J. A. 1988a. Late Devonian fishes from the Gogo Formation, Western Australia. *National Geographic Research*, **4**, 436–450.
- 1988b. A new camuropiscid arthrodire (Pisces: Placodermi) from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **94**, 233–258.
- 1988c. New information on the Late Devonian arthrodire *Tubonasmus* from Gogo, Western Australia. *Memoirs of the Association of Australasian Palaeontologists*, **7**, 81–85.
- 1990. Two new arthrodires (placoderm fishes) from the Upper Devonian Gogo Formation, Western Australia. *Memoirs of the Queensland Museum*, **28**, 51–63.
- 1991. The long history of Australian fossil fishes. 337–428. In VICKERS-RICH, P., MONAGHAN, J. N., BAIRD, R. F. and RICH, T. H. (eds). *Vertebrate palaeontology in Australasia*. Pioneer Design Studios with Monash University Publications Committee, Melbourne. 1437 pp.
- 1994. A second incisoscutid arthrodire (Pisces, Placodermi) from the Late Devonian Gogo Formation, Western Australia. *Alcheringa*, **18**, 59–69.
- MCCOY, F. 1848. On some new fossil fish from the Carboniferous Period. *Annals and Magazine of Natural History*, **2**, 1–10, 115–133.
- MILES, R. S. 1971. The Holonematidae (placoderm fishes): a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London, Series B*, **263**, 101–234.
- 1977. Dipnoan (lungfish) skulls from the Upper Devonian of Western Australia. *Zoological Journal of the Linnean Society*, **61**, 1–328.
- and DENNIS, K. 1979. A primitive eubrachythoracid arthrodire from Gogo, Western Australia. *Zoological Journal of the Linnean Society*, **66**, 31–62.
- and WESTOLL, T. S. 1968. The placoderm fish *Cocosteus cuspidatus* Miller ex Agassiz from the Middle Old Red Sandstone of Scotland. Part 1. Descriptive morphology. *Transactions of the Royal Society of Edinburgh*, **67**, 373–476.
- and YOUNG, G. C. 1977. Placoderm interrelationships reconsidered in the light of new ptyctodontids from Gogo, Western Australia. In ANDREWS, S. M., MILES, R. S. and WALKER, A. D. (eds). *Problems in vertebrate evolution*. Linnean Society Symposium Series **4**, 123–198.
- STENSIÖ, E. A. 1948. On the Placodermi of the Upper Devonian of East Greenland. 2. Antiarchi: subfamily Bothriolepinae. With an attempt at a revision of the previous described species of that family. *Meddelelser om Grönland* **139**, *Palaeozoologica Groenlandica*, **2**, 1–622.
- 1959. On the pectoral fin and shoulder girdle of the arthrodires. *Kungliga Svenska Vetenskapakademiens Handlingar*, **8**, 1–229.
- 1963. Anatomical studies on the arthrodiran head. Part 1. Preface, geological and geographical distribution, the organisation of the arthrodires, the anatomy of the head in the Dolichothoraci, Cocosteomorphi and Pachyosteomorphi. Taxonomic appendix. *Kungliga Svenska Vetenskapakademiens Handlingar*, **4** (9) 2, 1–419.
- VEZINA, D. 1986. Les plaques gnathales de *Plourdosteus caudensis* (Placodermi, Arthrodira) du Dévonien supérieur du Québec (Canada): remarques sur la croissance dentaire et la mécanique masticatrice. *Bulletin de la Museum National d'Histoire Naturelle, Paris*, 4 ser., **8**, 367–391.
- 1990. Les Plourdosteidae fam. nov. (Placodermi, Arthrodira) et leurs relations phylétiques au sein des Brachythoraci. *Canadian Journal of Earth Sciences*, **27**, 677–683.
- WANG JUN-QING. 1991. A fossil Arthrodira from Panxi, Yunnan. *Vertebrata Palasiatica*, **29**, 264–275.
- WOODWARD, A. S. 1891. *Catalogue of the fossil fishes in the British Museum (Natural History)*, 2. British Museum (Natural History), London, 567 pp., 16 pls.
- 1986. The relationships of the placoderm fishes. *Zoological Journal of the Linnean Society, London*, **88**, 1–57.
- YOUNG, G. C. 1979. New information on the structure and relationships of *Buchanosteus* (Placodermi: Euarthrodira) from the Early Devonian of New South Wales. *Zoological Journal of the Linnean Society*, **66**, 309–352.
- 1984. Reconstruction of the jaws and braincase in the Devonian placoderm fish *Bothriolepis*. *Palaeontology*, **27**, 625–661.

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ABBREVIATIONS USED IN FIGURES

aal	anterior apronic lamina of the interolateral plate	M	marginal plate
acc.PN	accessory postnasal bone	MD	median dorsal plate
add.mand	adductor mandibulae muscle	Mk	Meckel's cartilage
ADL	anterior dorsolateral plate	Mm	mentomeckelian bone
AL	anterior lateral plate	n	notch
AMV	anterior median ventral plate	n.prof.V	profundus nerve (V)
ant.s.a.	anterior smooth area of ventral lamina of interolateral plate	Nu	nuchal plate
ar. Qd	articulation area of quadrate	oa.AVL	area overlapped by AVL
Art	articular bone	occ	occipital sensory-line canal groove
ASG	anterior superognathal	op.m	opercular muscle
Aut	autopalatine bone	orb	orbit
AVL	anterior ventrolateral plate	P	pineal plate
C	central plate	pap	occipital para-articular process
cav	cavity of spinal plate	PDL	posterior dorsolateral plate
ch.pr.sv.	channel for dorsal aspect of supravagal	pi	pineal depression and fossae
Chy	ceratohyal	PL	posterolateral plate
cr.pr	carinal process	pl.pr	posterolateral process on parasphenoid
csc	central sensory canal	PM	postmarginal plate
d.end.c	external opening of endolymphatic duct	pmc	postmarginal sensory-line canal groove
dep	depression	PMV	posterior median ventral plate
dp.m.cu	cucullaris depression	PN	postnasal plate
d.prp	dermal preorbital process of skull-roof formed by preorbital plate	PNu	paranuchal plate
Ehy	epihyal or opercular cartilage	pp	posterior pit-line groove
exc.n	excurrent naris	p.pr	posterior process of nuchal plate
fb.hy	paired buccohypophysial foramen	pr	orbital autopalatine process on suborbital plate
f.pec	pectoral fenestra	pr.dt	detent process of quadrate
gr 1	groove 1	p.rec	posterior rectus muscle
gr 2	groove 2	pr.hy	hyoid process on visceral surface of skull roof
gr.a.com	transverse ventral groove	PrO	preorbital plate
gr. SM	groove on suborbital plate for submarginal plate	PSG	posterior superognathal
Hym	hyomandibular	PSO	postsuborbital plate
hy m	hyoideus muscle	psoc	postsuborbital sensory groove
hypv	foramen for hypophysial vein	PtO	postorbital plate
ifo	infraorbital branch of sensory-like canal groove	pt.o.pr	ventral postocular process
IG	inferognathal	pt.u	paired pits on visceral surface of nuchal plate
IL	interolateral plate	Qd	quadrate bone
inc.n	incurrent naris	R	rostral plate
ioc.pt	supraorbital branch of infraorbital canal	r.ext.hyVII	ramus hyomandibularis VII nerve
ioc.sb	supraorbital branch of infraorbital canal	ri	oblique premedian ridge of head shield
lc	main lateral line canal groove	ri1, ri2 ri3	ridges on visceral surface of annular cartilage
lcp	lateral consolidated area of skull roof	r.pr	depression on visceral surface of rostral plate
lpmus	levator palatoquadrini muscle	sh	prehypophysial shelf on parasphenoid
laf	lateral articular fossa	SM	submarginal plate
ling.pr	linguiform process of suborbital plate	SO	suborbital plate
		soa	subobstantic region of head shield
		soc	supraorbital sensory canal

/sorc	supraoral sensory canal	th.n	nuchal thickening
Sp	spinal plate	th.pre	pre-endolymphatic thickening
spir	spiracular recess	tri	triangular depression on visceral surface of skull roof
subl.pr	sublingual process	vsl	ventral sensory pit-line groove
suo.v	supraorbital vault		
sup.ob	superior obliquus muscle		

DECAPODS IN AMMONITE SHELLS: EXAMPLES OF INQUILINISM FROM THE JURASSIC OF ENGLAND AND GERMANY

by R. FRAAYE and M. JÄGER

ABSTRACT. Inquilinism is that association in which one organism lives within another, using the host as a place of refuge. Four specimens are described from the Jurassic of England and Germany which illustrates ammonite inquilinism by decapods. The inquiline use of ammonite shells in the geological record, and its ecological and taphonomical implications are discussed.

LOBSTERS are heavily armoured decapod crustaceans that generally inhabit holes and crevices of marine rocky and coralline environments. During Mesozoic times ammonites not only provided a food source for decapod crustaceans and other benthic organisms, they were also perfect places of shelter on otherwise fine-grained sea floors. Several fossil groups have been found preserved inside ammonite body chambers. This mode of preservation is referred to as *inquilinism*, a term used to describe those associations in which one animal lives within another, using the host (before or after death) as a place of refuge. Although this mode of preservation has been recorded in the literature, its taphonomic implications have virtually been neglected.

A specimen of the erymid lobster *Palaeastacus?* sp. found in the body chamber of a harpoceratid ammonite from the Lower Toarcian Posidonia Shales of Dotternhausen, southern Germany, is described and illustrated herein. In addition, three specimens of the lobster *Eryma dutertrei* Sauvage, 1891, preserved in the body chambers of large perisphinctid ammonites are recorded from the Portland Limestone Formation (Portlandian) of southern England. The poor record of inquiline preservation of organisms in ammonite body chambers is probably due to the fact that they have not received enough attention rather than because they are rare. The occurrence of ammonite inquilinism in the Posidonia Shales of southern Germany is incompatible with a stagnant basin model, but agrees well with Seilacher's (1990, pp. 123, 126–128) modified model: euxinic stagnant water conditions for most of the time, episodically interrupted by turbidity currents caused by storms. Whereas benthic life was impossible for most organisms during times of stagnant conditions, episodic storm-events brought oxygen down to the sea-floor and made life possible for some months or so. A co-evolutionary relationship between ammonites and the inhabitants of their empty shells is postulated.

AMMONITE BODY CHAMBER CONTENTS

In comparison with many studies of ammonite taphonomy (e.g. Roll 1935; Lehmann 1976; Seilacher *et al.* 1976; Brenner and Seilacher 1978; Seilacher 1982*a*, 1982*b*; Tanabe *et al.* 1984; Maeda 1987, 1991; Neugebauer and Hudson 1987), few studies have dealt with the contents of body chambers. Three types of preservation have been distinguished so far.

(1) Ernst (1967) and Maeda (1991) record post-mortem accumulations of echinoids and small ammonite shells transported into large ammonites.

(2) The preservation of *in situ* ammonite remains. Fossil jaws preserved *in situ* in diagenetically compressed ammonites have been reported (e.g. Lehmann 1976; Morton 1981; Seilacher 1982*a*; Tanabe *et al.* 1984). Fossil crop/stomach remains of ammonites are rare in most deposits and

preserved only in especially favourable environments. Nixon (1988, p. 650) lists only four examples of *in situ* crop/stomach remains in Jurassic ammonites. Riegraf *et al.* (1984, pl. 1, fig. 7) found nearly twenty specimens with crop and/or stomach remains in the Lower Toarcian Posidonia Shales of south west Germany. Recent finds of several compressed harpoceratid ammonites with preserved crop/stomach contents in the Toarcian black shales of southern Germany provide new data on their diet (Jäger 1991; Jäger and Fraaye work in progress). These new observations confirm the convictions of Nixon (1988) and Tshudy *et al.* (1989) that some, if not all, ammonites were potential predators and/or scavengers of decapod crustaceans.

(3) Inquiline preservation. The fossil record of marine Jurassic sediments indicates that enormous numbers of empty ammonite conchs littered former sea floors. These ammonites supplied food for (nekto)benthic scavengers. There is an extensive literature on shell fracturing tentatively ascribed to crustaceans (Boucot 1990, p. 168). Examples of fractures of Jurassic ammonites presumed to have been produced by decapod crustaceans were recorded by, amongst others, Roll (1935), Seilacher and Wiesenauer (1978), Riegraf *et al.* (1984) and Jäger (1991). Lehmann (1976, p. 135) illustrated the lobster *Eryon* breaking up an ammonite conch with its chelae in search of soft parts. Amongst the favourite prey animals of recent and fossil cephalopods are decapod crustaceans (Nixon 1988; Jäger and Fraaye work in progress). Empty ammonite shells have the potential to shelter the small (nekto)benthic animals common on the soft Jurassic sea floors, and as such Jurassic decapod crustaceans may have been, at least in part, dependent on ammonites for food and shelter.

A review of the literature illustrates many examples of inquiline preservation. A fine example is that of Stewart (1990), who recorded several fish genera found preserved in Upper Cretaceous inoceramid bivalves. An example of probably inhabitation of a Cenomanian crab (*Diaulax oweni* Bell *in* Dixon, 1850) with an ammonite was mentioned by Wright and Collins (1972, pl. 10, figs. 1a–b). Unfortunately, the preparation of the crab has destroyed the *in situ* preservation (J. S. H. Collins, pers. comm.). A second example of a decapod crustacean preserved inside an ammonite body chamber was recorded from the Upper Cretaceous Chalk of northern Germany by Ernst (1967). A concretion containing a body chamber of a scaphitid ammonite filled with faecal pellets illustrated by Bishop (1981, p. 390, fig. K) is another example of Cretaceous ammonite inquilinism.

The first example of ammonite inquilinism from the Jurassic was recorded by Krause (1891, pl. 12, figs 1–2), who described a very well-preserved lobster within a large ammonite of the genus *Gravesia* from the Upper Jurassic (Tithonian) of Germany.

Another example of Jurassic ammonite inhabitation was described briefly by Jäger (1990) from the Toarcian Posidonia Shales of Dotternhausen, southern Germany. Inside two compressed body chambers of harpoceratid ammonites fishes assignable to *Pholidophorus* were found.

A further four specimens illustrating Jurassic ammonite inquilinism by decapod crustaceans, in three different types of preservation are described below.

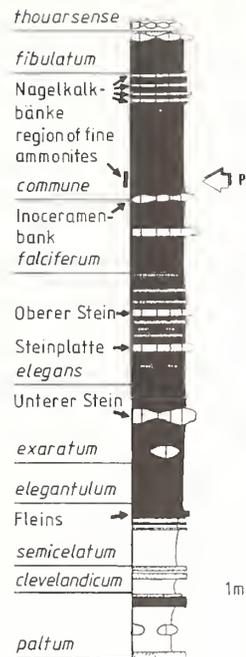
AMMONITE INQUILINISM IN THE LOWER TOARCIAN POSIDONIA SHALE

Geological setting

The bituminous Lower Toarcian Posidonia Shale is well-known for the excellent preservation of marine reptile, fish and crinoid skeletons found within it (Hauff and Hauff 1981). The facies is widespread not only in southern Germany, but also in northern Germany, England, France and Luxemburg (see map in Riegraf *et al.* 1984, p. 26). In Dotternhausen near Balingen, 70 km south-south-west of Stuttgart and 70 km south-west of Holzmaden, the Posidonia Shale (which is around 9 m thick here) is quarried by the Rohrbach Zement factory to produce cement. In Dotternhausen, the range of fossil species and kinds of preservation is nearly the same as at Holzmaden.

The Posidonia Shale is a bituminous shale, compressed to around 5 per cent. of its original thickness, although limestone layers and concretions display little or no compression. The high content of pyrite and of organic hydrocarbon, the fine lamination of the sediment and the poverty of autochthonous benthos are strong arguments for stagnant water conditions during deposition of

TEXT-FIG. 1. Stratigraphical profile, biostratigraphy and lithostratigraphical marker horizons of the Lower Toarcian of Dotternhausen (after Riegraf 1985, text-fig. 4), with the stratigraphical position of *Palaeastacus?* sp. (RZC 0062).



the Posidonia Shale. From the uppermost part of the Semicelatum Subzone till the lower half of the Fibulatum Subzone, benthic life was totally or nearly totally absent in most horizons, although an impoverished fauna is found in several horizons (Riegraf *et al.* 1984). The layers around the 'Inoceramenbank' at the boundary of the Falciferum/Commune Subzone, represent such horizons with a very impoverished, but not totally absent benthic fauna; some foraminiferan and ostracod species are present (Riegraf 1985, p. 45, fig. 22).

In many layers of the Posidonia Shale, epizoans (mostly serpulids and oysters) often are fixed to the ammonite shells and, as the shell is compressed, the epizoans on the opposite side are also visible being distinctly pressed into the periostracum (Seilacher 1982a). From such specimens Kauffman (1978) developed his 'benthic island' model but, according to the results of Riegraf *et al.* (1984), Riegraf (1985) and Seilacher (1990), these findings seem to represent 'islands in time' (periods of sufficient oxygen content at the sea-floor) rather than islands in space.

Many details of ammonite preservation in the Posidonia Shale have been published by Seilacher *et al.* (1976) and Riegraf *et al.* (1984, p. 52). Usually, the phragmocone is compressed to a paper-thin layer, the living chamber often compressed to a thickness of 1–2 mm. The calcareous shell layers are normally dissolved (this is the reason why septa are visible in few specimens only), but the periostracum is beautifully preserved as a golden brown leaf. Some shells are broken into disarticulated pieces (probably by the action of decapods or fish), but in most specimens the whole periostracum is preserved (though often with cracks, formed during compression) including the delicate rostrum of the apertures of *Harpoceras* and *Hildoceras*.

The excellent preservation of many fossils points to rather low water energy, though current-alignment was recognized by Brenner and Seilacher (1978). The siphuncle is often preserved as a whitish band, and in an estimated 25 per cent. of *Harpoceras* and *Hildoceras* specimens' aptychi are still present in the living chamber. Preservation of presumed crop and/or stomach contents is not uncommon (Riegraf *et al.* 1984; Jäger and Fraaye, new data).

Ammonites are present in every horizon of the 9 metre thick Posidonia Shale facies in Dotternhausen. In a section a few decimetres thick in the lowermost part of the Commune Subzone,

between the 'Inoceramenbank' and the 'Nagelkalkbanke' (Text-fig. 1), complete specimens are relatively easy to extract because of the fissility of the shale. Thus in this part of the section ammonites are intensively sampled. Ammonite taxa present (from most to less frequent) are *Dactyloceras commune*, *Harpoceras falciferum* (diameter of adult macroconchs normally 200–300 mm), *Hiodoceras* ex gr. *douvillei/sublevisioni*, *Phylloceras heterophyllum*, *Phymatoceras cf. escheri*.

Material

Decapod crustaceans are rare in the Posidonia Shale except for chelae (propodus plus dactylus) of the swimmer *Uncina posidoniae* Quenstedt 1850 in the 'Fleins' layer and remains of *Coleia?* sp. in the living chamber of ammonites (Jäger and Fraaye, new data) in the lower part of the Commune Subzone. Other remains of decapod crustaceans are rare in the Posidonia Shale of southern Germany, but are found in several horizons. They were described by Beurlen (1928, 1930, 1944), Kuhn (1952) and Hauff and Hauff (1981) and include well-preserved, complete specimens of *Uncina posidoniae*, eight species of *Proeryon*, two *Coleia* species, one *Glyphea*, one *Palaeopagurus* (as *Erymastacus?*), one stomatopode? and one macrure. It is not clear yet how *Proeryon*, which according to its dorsoventrally compressed shape is a typical bottom-dweller, could have managed to live during anoxic conditions, although it may have lived upon floating trunks or have been washed in, although one would expect poorer preservation.

A new specimen (Rohrbach Zement Collection no. 0062) illustrated in Text-figures 2–4 has been determined as *Palaeastacus?* sp. (R. Förster, pers. comm.). According to Förster (1966, p. 126) *Palaeastacus* Bell in Dixon, 1850 is a genus of the family Erymidae. The stratigraphically lowest examples of isolated chelae of *Palaeastacus* are from the lower Sinemurian, while remains of the carapace and more or less complete specimens range from the Upper Jurassic to the Upper Cretaceous.

The new specimen is lying inside the anterior half of the body chamber of an adult macroconch of *Harpoceras falciferum* (Text-fig. 2). The ammonite shell diameter is approximately 270 mm. Though the living chamber is compressed to 1 mm, it is obvious that the crustacean really lies inside the ammonite shell, not at a level above or below. The aptychi are missing. Remains of the siphuncle are preserved. On the ammonite shell at least five oysters (oy.) and four serpulids (serp.) are fixed, probably on both sides of the ammonite, but this is not quite clear. The anterior part of the crustacean is directed towards the aperture of the ammonite, the chelae lying at least 40 mm behind the aperture (which is not preserved). The telson is directed towards the phragmocone. Around the crustacean, and nearly filling the ammonite body chamber, are areas which seem to be composed of masses of elliptical to subspherical bodies. These have an approximate maximum diameter of 1.5–2.0 mm, are compressed and indistinct, and are here interpreted as crustacean coprolites.

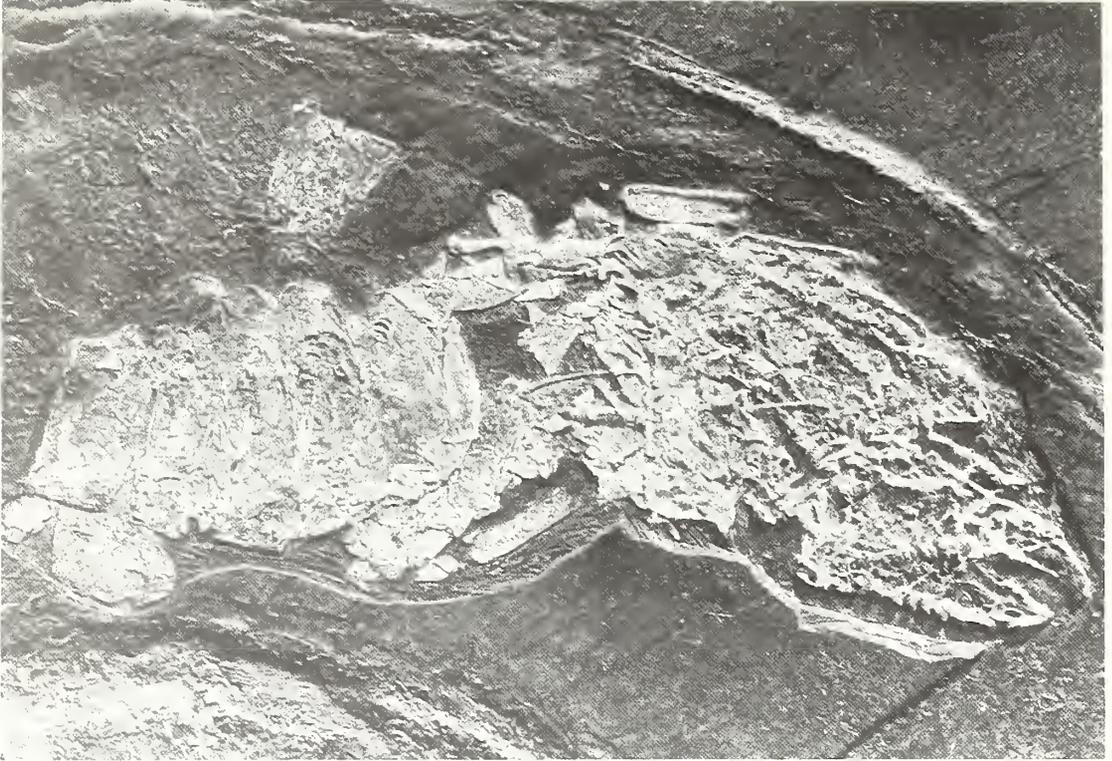
Although the *Palaeastacus?* is almost complete (remains of the chelae, feet, abdomen and telson are visible) and the parts of the skeleton are lying close together, the disarticulation and compression of the skeletal parts makes proper description difficult. The anterior half of the decapod seems to be composed of two chelipeds and a few other fragments, most of them probably fragments of thoracopods. Nothing distinct is visible of the carapace which perhaps is lying underneath the chelipeds ('underneath' is applied according to the present state of the shale slab).

The slab was not found *in situ*, and it is therefore unknown which is the upper and which the lower surface. In both chelipids, dactylus (d), propodus (p) and carpus (c) are lying close together, with only minute traces of disarticulation. One merus (m) is present. The two chelae are lying nearly parallel to each other and close together, with the dactyli touching each other. The chelae are covered with very strong spines, especially at the border. The carpi are triangular and spiny, but the spines are not quite as strong as in the propodi. The meri of the chelipeds are not properly distinguished from the leg fragments (l). Only one slender rectangular remnant seems to be a merus, but it is not clear to which of the chelipeds it belongs. Between the anterior and the posterior half of the crustacean there is an area, approximately 15 mm long, where only few skeletal remains are



TEXT-FIG. 2. *Palaeastacus?* sp. RZC 0062; preserved in body chamber of *Harpoceras falciferum*; large areas with elliptical coprolites indicated with black arrows; Posidonia Shales, Lower Toarcian; Dotternhausen, Germany; $\times 0.88$.

preserved. In the abdomen, five (or perhaps six) of the somites (s) are articulated to each other and clearly visible (Text-fig. 3). Together they are nearly 50 mm long. The telson is disarticulated from the abdomen. After 25 mm of free space, only one large plate of the telson (t) can be identified.



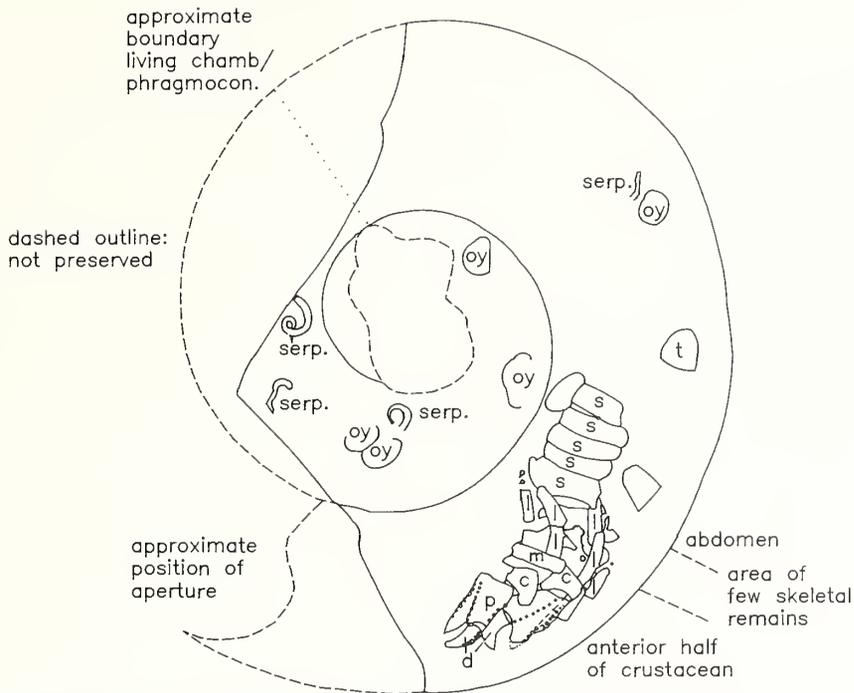
TEXT-FIG. 3. *Palaeastacus?* sp. RZC 0062; preserved in body chamber of *Harpoceras falciferum*, showing details of the spiny chelae and the abdomen; Posidonia Shales, Lower Toarcian; Dotternhausen, Germany; $\times 1.5$.

Ecological interpretation

According to Förster (1966, p. 153) Erymidae preferred muddy soft-bottoms in relatively shallow water near the coast. They probably dug themselves into the mud or hid under stones for resting, for moulting or for protection. Erymidae were probably carnivorous or carrion feeders. Perhaps the fractures in ammonite body chambers, which sometimes look as if they were made by a 'tin-opener' (Riegraf *et al.* 1984, p. 58, fig. 15; Jäger 1991, figs 3–4), were made by the strong chelae of *Palaeastacus?*. However, *Palaeastacus?* is too rare to have been responsible for all such ammonite destruction.

The *Palaeastacus?* is too large and too complete to be the crop and/or stomach contents of the ammonite (as are many specimens of small and disarticulated *Coleia?* sp. to be described in a later paper (Jäger and Fraaye, new data), their interpretation as a moulted skeleton in Jäger (1991, p. 33) probably being wrong). On the other hand the crustacean was not large enough to be able to walk around while within the ammonite shell in the manner of a hermit crab, which, moreover, would have a less calcified abdomen.

Though the skeleton of *Palaeastacus?* should have been sheltered inside the ammonite shell against destruction, disarticulation is more distinct than in specimens found loosely in the sediment. This was the main reason why Jäger (1991, p. 33) interpreted the *Palaeastacus?* as a moult. In fossil crustaceans, moulted skeletons are often recognizable by the splitting of the carapace and by an approximate right angle between the longitudinal axes of the carapace and the abdomen (Förster 1966, p. 154). In the *Palaeastacus?*, however, the carapace is poorly visible, and the right angle may be due to compression. Thus, it cannot be decided if it is a moult or a dead crustacean. The area



TEXT-FIG. 4. *Palaeastacus?* sp. RZC 0062; preserved in body chamber of *Harpoceras falciferum*; outline of skeletal elements partly idealized, because some of the outlines are hardly visible in the original; for explanation of abbreviations see text; Posidonia Shales, Lower Toarcian; Dotternhausen, Germany; $\times 0.33$.

with only few skeletal remains between the anterior half and the abdomen is an argument for breakage between carapace and abdomen during moulting.

Interpreting the small spherical structures as decapod coprolites, the animal must have lived for a relatively long time inside the body chamber (Text-fig. 4). This means that anoxic conditions at the sea-floor must have been interrupted for this period.

AMMONITE INQUILINISM IN THE PORTLAND LIMESTONE FORMATION

Geological setting

The Isle of Portland is a natural peninsula about 6 km long, near Weymouth, on the southern coast of England. The specimens described below were collected in the ARC Broadcraft Quarry, north-east of the village of Easton during a one-week field trip in March 1990.

The Portland Group consists of a lower Portland Sand Formation and an upper Portland Limestone Formation. The Portland Sand Formation grades down into the black shale sequence of the Kimmeridge Clay. The Portland Limestone Formation is overlain by evaporitic limestone-marl sequence known as the Purbeck Group. The Portland Group represents a regressive sequence (Townson 1975). The Portland Sand Formation consists mainly of clay-, silt- and sandstones, accumulated in a marine environment below wave base. The Portland Limestone Formation starts with a 3 m thick Basal Shell Bed. This bed contains a rich biota of mainly bivalves, gastropods and serpulids. The upper 25 m of the Portland Limestone Formation consists of cherty limestones deposited in an open shelf environment that pass up into shallow-water cross-bedded oolitic grainstones.

Some levels within the cherty part of the Portland Limestone Formation are rich in large perisphinctid ammonites whose diameter often exceeds 0.5 m. The grainstones yield numerous

oncolitic algae, bivalves and gastropods. The lower Purbeck Group finally grades through stromatolitic levels with silicified tree trunks into fossil soils and lagoonal limestones.

Two specimens described below were collected from the lower part (*Galbanites* (*Kerberites*) *kerberus* Zone) of the Portland Limestone Formation. The environment was thought by Townson (1975) to have been moderately deep and tranquil marine. A third specimen (Collection Geo Centrum Brabant, no. MAB k. 0049) of a *Glaucolithites* sp. with two partially preserved chelae of *Eryma* sp. coincident with the body chamber was discovered in the Portland Clay Member, a few metres below the Basal Shell Bed, forming the topmost Portland Sand Formation (*Glaucolithites glaucolithus* Zone).

Material

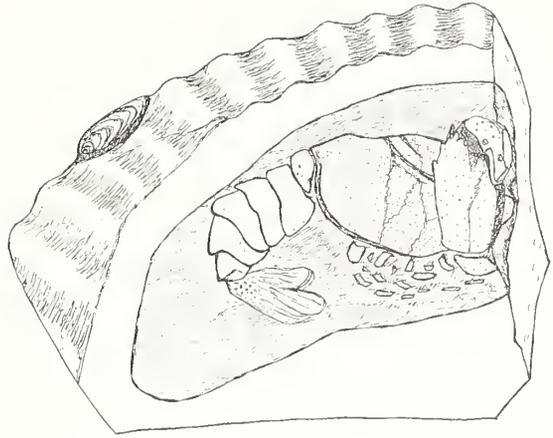
The first specimen (Collection Geo Centrum Brabant, no. MAB K0047) was found in a fragment of an ammonite body chamber 250 mm maximum length, 150 mm maximum width. The preservation of the segments of the lobster is very good. There are no signs of post-mortem transport and only a few compactional cracks are present. The axis of the lobster body runs parallel with the ammonite coiling (Text-figs 5–6). The lobster is embedded within an elongate concretion of slightly banded, light grey chert. This concretion in its turn runs parallel with the outline of the body chamber.

Observations and experimental data from modern marine environments, and from the common Holocene subfossil decapods from concretions along the coasts of south-eastern Asia and northern

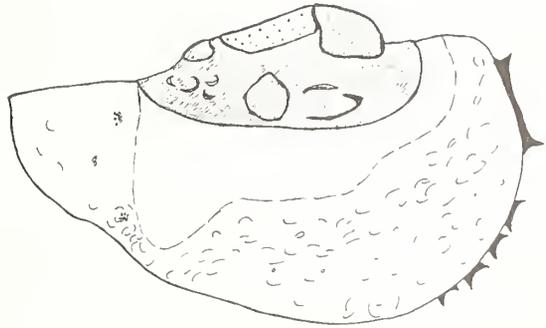


TEXT-FIG. 5. *Eryma dutertrei* Sauvage. MAB K0047; embedded within chert concretion in perisphinctid ammonite body chamber; Portland Limestone Formation, Portlandian; Broadcraft Quarry, Portland, England; $\times 0.8$.

TEXT-FIG. 6. *Eryma dutertrei* Sauvage. MAB K0047; schematic sketch showing chert concretion and preservation of decapod segments in perisphinctid ammonite body chamber; Portland Limestone Formation, Portlandian; Broadcraft Quarry, Portland, England; $\times 0.5$.



TEXT-FIG. 7. *Eryma dutertrei* Sauvage. MAB K0047; schematic sketch of cross section of perisphinctid body chamber, showing position of chert concretion, bioclasts and epibionts; Portland Limestone Formation, Portlandian; Broadcraft Quarry, Portland, England; $\times 0.5$.



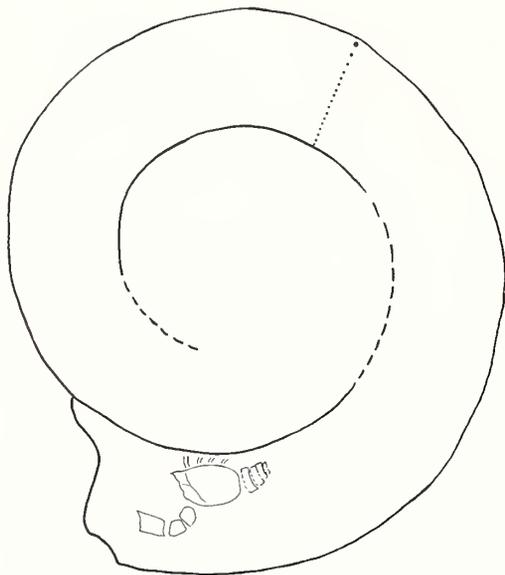
Australia indicate that concretions may form very rapidly around decaying decapod crustaceans (Schäfer 1951; Moore 1969; Plotnick 1986). The process involves locally increased pH, a result of ammonia produced during organic decomposition, and bacterial sulphate reduction. In relatively pure, fine-grained carbonate rocks, chert nodules may develop in or around fossils or burrows, suggesting a possible association with organic micro-environments. The aggregation of silica into nodules apparently takes place during recrystallization of biogenic silica (often sponge spicules). Articulated skeletal remains indicate that the formation of chert concretions was associated with anaerobic decay of organic matter immediately following burial. The field and laboratory studies of Schäfer (1951) and Plotnick (1986) indicate that the decay of soft tissues and the reduction in cuticle rigidity led to the loss of physical integrity of decapod specimens between a few weeks and several months. Size and shape of concretions are strongly influenced by the type of organic remains they grow in or around (Bishop 1981).

The large carapace is covered with fine granules, the density of which decreases towards the rostrum. Unfortunately, most of the cephalic portion is covered by the right cheliped obscuring the cervical, gastro-orbital and hepatic regions. The characteristic intestinal margin is well-preserved. The long branchiocardiac and short postcervical grooves run parallel and are slightly disturbed by compressional cracks. Of the right chela, only the ischium, merus and proximal part of the carpus are visible. The chela is covered with very coarse granules; their density decreases laterally. Some large tubercles appear on the lateral part of the merus and proximal part of the carpus. The long finely granulated and denticulate movable and fixed fingers of both chelipeds are equal in size. Other thoracopods are only partially visible in the chert concretion. The abdomen consists of four more or less equal-sized somites between the considerably smaller first and sixth somites. The posterior margin of each somite overlaps the anterior margin of the adjacent one. The somites are covered with coarsely spaced granules and some tubercles. The tuberculation increases in strength

posteriorly and extends to the telson. The relatively long uropods are faintly striated. The few preserved cuticle fragments show tubercles of various sizes.

The ammonite has only part of its body chamber preserved as a composite mould on which several oysters are attached. The size of the epibiont oysters increases towards the venter of the ammonite (Text-fig. 7). Its body chamber is filled with a bioclastic wackestone, the majority of the bioclasts being small bivalves and serpulids. The body chamber contains the lobster described preserved within a chert concretion.

The second specimen (Collection Geo Centrum Brabant, no. MAB K0048) was found in an almost complete perisphinctid ammonite 380 mm in diameter. The incomplete carapace of the crustacean is split along the dorsal midline. Only the right chela and a few disassociated segments of the abdomen and pereopods are present (Text-fig. 8). The same displacement and splitting of the



TEXT-FIG. 8. *Eryma dutertrei* Sauvage. MAB K0048; schematic sketch showing molting remains in ammonite body chamber; Portland Limestone Formation, Portlandian; Broadcraft Quarry, Portland, England; $\times 1$.

carapace are seen for example, in the Jurassic *Glyphea* and the Cretaceous *Hoploparia* and *Onopareia* and are recognized as indicative of a moulting position. The gastric and antennal regions of the carapace are missing because it was fractured along the cervical groove. The branchiocardiac, postcervical and inferior grooves are distinct and match the description of *Eryma dutertrei* Sauvage, 1891 in Förster's (1966, p. 117) revision of the erymids.

Except for the chert concretion, the infilling of the ammonite body chamber is the same as specimen MAB k0047 except that in this case several little gastropods and some plant remains are also present. The intense upper-side erosion and covering with oysters and other bivalves show that the ammonite acted as a benthic 'island' for a relatively long time.

DISCUSSION

If ammonite inquilinism was a common feature, bite traces on ammonite shells produced by, for example, sharks and reptiles are not necessarily the result of hunting on living ammonites. It is possible that these predators may have hunted the animals which lived, hid or moulted within empty ammonite conchs. By grabbing and shaking, the predators could have forced these inhabitants out of their refuge.

Several groups of organisms develop extreme adaptations to specialized habitats (Boucot 1990). It is likely that, in addition to decapod crustaceans, other (nekto)benthic groups (e.g. fishes, dwarf

ammonites) adapted an ammonite inquiline mode of life, simply because on offshore fine-grained Mesozoic sea floors there were no other suitable hiding places. We therefore concur with Ernst (1967) and Matsumoto and Nihongi (1979), who respectively explained certain accumulations of thin shelled echinoids and small heteromorph ammonites in larger ammonites as *in situ* cave dwellers. Some examples of post-mortem accumulations recorded by Maeda (1991) could also have been ammonite inhabitants. Post-mortem drift is not consistent with the fact that in the same sediments the jaw apparatus of the ammonites are comparatively often preserved within the body chambers (Hirano 1991). Maeda (1991) also recorded considerable amounts of plant remains, disarticulated crinoid stalks and inoceramid shells to have accumulated in body chambers of large ammonites. Lehmann (1975), Lehmann and Weischat (1973) and Riegraf *et al.* (1984) noted accumulations of crinoid ossicles and inoceramid shells within Jurassic ammonites.

There are several modern examples of crustaceans which store pieces of animal material and seagrass leaves in their burrows as bacterial horticultures (Bromley 1990). Were ammonites ideal dining rooms for decapod crustaceans or did the decapods have their own horticultures, or both? And were these horticultures plundered by other (nekto)benthic animals such as fishes and echinoids? Whatever may be the case, the accumulation of organic matter within the ammonite shells certainly increased the preservational potential of the ammonites.

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REFERENCES

- ALDINGER, H. 1965. Zur Ökologie und Stratinomie der Fische des Posidonienschiefers (Lias epsilon). *Senckenbergiana Lethaea*, **46a**, 1–12.
- BEURLEN, K. 1928. Die Decapoden des Schwäbischen Jura mit Ausnahme der aus den oberjurassischen Plattenkalk stammenden. *Palaeontographica, Abteilung A*, **70**, 115–282.
- 1930. Nachträge zur Decapodenfauna des Schwäbischen Jura. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B, Beilagen-Band*, **64**, 219–234.
- 1940. Neue Reste von *Proeryon* (Crustacea, Decapoda, Eryonidae). *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B, Beilagen-Band*, **88**, 374–384.
- BISHOP, G. A. 1981. Occurrence and fossilization of the *Dakoticander* Assemblage, Upper Cretaceous Pierre shale, South Dakota. 383–413. In GRAY, J., BOUCOT, A. J. and BERRY, W. B. N. (eds). *Communities of the past*. Hutchinson Ross, Stroudsburg, 530 pp.
- BOUCOT, A. J. 1990. *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam, 725 pp.
- BRENNER, K. and SEILACHER, A. 1978. New aspects about the origin of the Toarcian Posidonia Shales. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **157**, 11–18.
- BROMLEY, R. G. 1990. *Trace fossils: biology and taphonomy*. Unwin Hyman Ltd., London, 280 pp.
- DIXON, F. 1850. *The geology and fossils of the Tertiary and Cretaceous formations of Sussex*. London, 422 pp.
- ERNST, G. 1967. Über Fossilnester in *Pachydiscus* – Gehäusen und das Lagenvorkommen von Echiniden in der Oberkreide NW-Deutschlands. *Paläontologische Zeitschrift*, **41**, 211–229.
- FÖRSTER, R. 1966. Über die Erymiden, eine alte konservative Familie der mesozoischen Dekapoden. *Palaeontographica, Abteilung A*, **125**, 61–175.
- HAUFF, B. and HAUFF, R. B. 1981. *Das Holzmadenbuch*. Holzmaden, 136 pp.
- HIRANO, H. 1991. Phyletic evolution of desmoceratine ammonoids through OAE at C/T boundary. 14–15. In *The Ammonoidea: evolution and environmental change. Programme with abstracts*. The Systematics Association, London, 80 pp.
- HOUSE, M. 1989. *Geology of the Dorset Coast*. Geologists' Association, London, 162 pp.
- JÄGER, M. 1990. Lias epsilon von Dotternhausen. *Fossilien*, **7**, 274–277.
- 1991. Lias epsilon von Dotternhausen. *Fossilien*, **8**, 33–36.
- KAUFFMAN, E. G. 1978. Benthic environments and paleoecology of the Posidonienschiefer (Toarcien). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **157**, 18–36.

- KRAUSE, P. G. 1891. Die Decapoda des norddeutschen Jura. *Zeitschrift der Deutschen geologischen Gesellschaft*, **43**, 171–225.
- KUHN, O. 1952. Neue Crustacea Decapoda und Insecta aus dem untersten Lias epsilon von Nordfranken. *Palaeontographica, Abteilung A*, **101**, 153–166.
- LEHMANN, U. 1975. Über Nahrung und Ernährungsweise von Ammoniten. *Paläontologische Zeitschrift* **49**, 187–195.
- 1976. *Ammoniten: Ihr Leben und ihre Umwelt*. Enke Verlag, Stuttgart, 171 pp.
- 1979. The jaws and radula of the Jurassic ammonite *Dactyloceras*. *Palaeontology*, **22**, 265–271.
- and WEISCHAT, W. 1973. Zur Anatomie und Ökologie von Ammoniten. Funde von Kropf und Kiemen. *Paläontologische Zeitschrift*, **47**, 69–76.
- MAEDA, H. 1987. Taphonomy of ammonites from the Cretaceous Yezo Group in the Tappu area, northwestern Hokkaido, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, **148**, 285–305.
- 1991. Sheltered preservation: a peculiar mode of ammonite occurrence in the Cretaceous Yezo Group, Hokkaido, north Japan. *Lethaia*, **24**, 69–82.
- MATSUMOTO, T. and NIHONGI, M. 1979. An interesting mode of occurrence of *Polyptychoceras* (Cretaceous heteromorph ammonoid). *Proceedings of the Japan Academy*, **55B**, 115–119.
- MOORE, R. C. (ed.) 1969. *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 651 pp.
- MORTON, N. 1981. Aptychi: the myth of the ammonite operculum. *Lethaia*, **14**, 57–61.
- NEUGEBAUER, J. and HUDSON, J. D. 1978. Neuere Untersuchungen zur Ammonitenerhaltung. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **157**, 188–193.
- NIXON, M. 1988. The feeding mechanism and diets of Cephalopods – living and fossil. 641–652. In WIEDMANN, J. and KULLMANN, J. (eds). *Cephalopods – present and past*. Schweizerbart, Stuttgart, 725 pp.
- PLOTNICK, R. E. 1986. Taphonomy of a modern shrimp: implications for the arthropod fossil record. *Palaeo*, **1**, 286–293.
- QUENSTEDT, F. 1850. Über *Mecochirus* im braunen Jura bei Gammelshausen und einige andere Krebse. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg*, **6**, 186–197.
- RIEGRAF, W. 1985. Mikrofauna, Biostratigraphie und Fazies im Unteren Toarcium Südwestdeutschlands und Vergleiche mit benachbarten Gebieten. *Tübinger Mikropaläontologische Mitteilungen*, **3**, 1–233.
- WERNER, G. and LÖRNER, F. 1984. *Der Posidonienschiefer – Biostratigraphie, Fauna und Fazies des südwestdeutschen Untertoarciums (Lias epsilon)*. Enke, Stuttgart, 195 pp.
- ROLL, A. 1935. Über Frassspuren an Ammonitenschalen. *Zentralblatt für Mineralogie, Geologie und Paläontologie, B*, **1935**, 120–124.
- SAUVAGE, H. 1891. Note sur les Crustacés des terrains jurassiques supérieur du Boulonnais. *Annales des Sciences naturelles Zoologie*, **12**, 83–96.
- SCHÄFER, W. 1951. Fossilisations-Bedingungen brachyurer Krebse. *Senckenbergische Naturforschungs Gesellschaft, Abhandlungen*, **485**, 221–238.
- SEILACHER, A. 1982a. Ammonite shells as habitats in the Posidonia Shales of Holzmaden – floats or benthic islands? *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1982**, 98–114.
- 1982b. Posidonia Shales (Toarcian, S. Germany) – stagnant basin model revalidated. 24–55. In GALLITELLI, E. M. (ed.). *Palaeontology, essential of historical geology*. Modena Press, Venice, 298 pp.
- 1990. Die Holzmadener Posidonienschiefer – Entstehung der Fossilagerstätte und eines Erdölmuttergesteins. 107–131. In WEIDERT, W. K. (ed.) *Klassische Fundstellen der Paläontologie*, **2**, Goldschneck, Korb, 265 pp.
- ANDALIB, F., DIETL, G. and GOCHT, H. 1976. Preservational history of compressed Jurassic ammonites from southern Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **152**, 307–356.
- and WIESENAUER, E. 1978. Preservational and adaptional history of belemnites. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **157**, 145–149.
- STEWART, J. D. 1990. Preliminary account of halecostome-inoceramid commensalism in the Upper Cretaceous of Kansas. 51–57. In BOUCOT, A. J. (ed.). *Evolutionary paleobiology of behavior and coevolution*. Elsevier, Amsterdam, 725 pp.
- TANABE, K., INAZUMI, A., TAMAHAMA, K. and KATSUTA, T. 1984. Taphonomy of half and compressed ammonites from the Lower Jurassic black shales of the Toyora area, west Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **47**, 329–346.
- TOWNSON, W. G. 1975. Lithostratigraphy and deposition of the type Portlandian. *Journal of the Geological Society of London*, **131**, 619–638.

- TSHUDY, D. M., FELDMANN, R. M. and WARD, P. D. 1989. Cephalopods: biasing agents in the preservation of lobsters. *Journal of Paleontology*, **63**, 621–626.
- WRIGHT, C. W. and COLLINS, J. S. H. 1972. British Cretaceous Crabs. *Monograph of the Palaeontographical Society*, **126**, 1–114.

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DISCONTINUITY IN THE PLIO-PLEISTOCENE EURASIAN WATER VOLE LINEAGE

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and T. VAN KOLFSCHOTEN

ABSTRACT. A supposed lineage extending from *Mimomys occitanus* – *M. ostramosensis* to *Arvicola terrestris* through at least seven species has been widely accepted. The early part of the lineage, from *M. occitanus* to *M. ostramosensis*, has been shown mathematically to be a good example of phyletic gradualism. But the transition from *M. ostramosensis* to *M. savini* is somewhat hypothetical. A new morphological analysis of the type population of *M. savini* (West Runton, England) has demonstrated that this species cannot be derived from *M. ostramosensis*, but must stem from another parent species, possibly *M. coelodus* or *Cromeromys irtyschensis*. There are, in fact, two distinct lineages characterized by different *linea sinuosa* and occlusal morphologies, the first corresponding to *M. occitanus* – *M. ostramosensis*, and the second to *Cromeromys savini* – *A. terrestris*. Phyletic gradualism is demonstrated by a new graphic presentation of both lineages. This changed phyletic relationship has no biostratigraphical repercussions.

VOLES (Arvicolidae, Rodentia) figure abundantly in the Plio-Pleistocene fossil record (Chaline 1972, 1987). Among the 140 lineages identified for the period, the Eurasian water vole lineage is of major evolutionary and biostratigraphical interest. This lineage extends from *Mimomys occitanus* – *M. polonicus* – *M. pliocaenicus* – *M. ostramosensis* – *M. savini* to *Arvicola terrestris*. The part of the lineage that runs from *M. occitanus* to *M. ostramosensis* has been used for quantitative testing of phyletic gradualism on a European scale (Chaline and Laurin 1986; Viriot *et al.* 1990; Chaline *et al.* 1993).

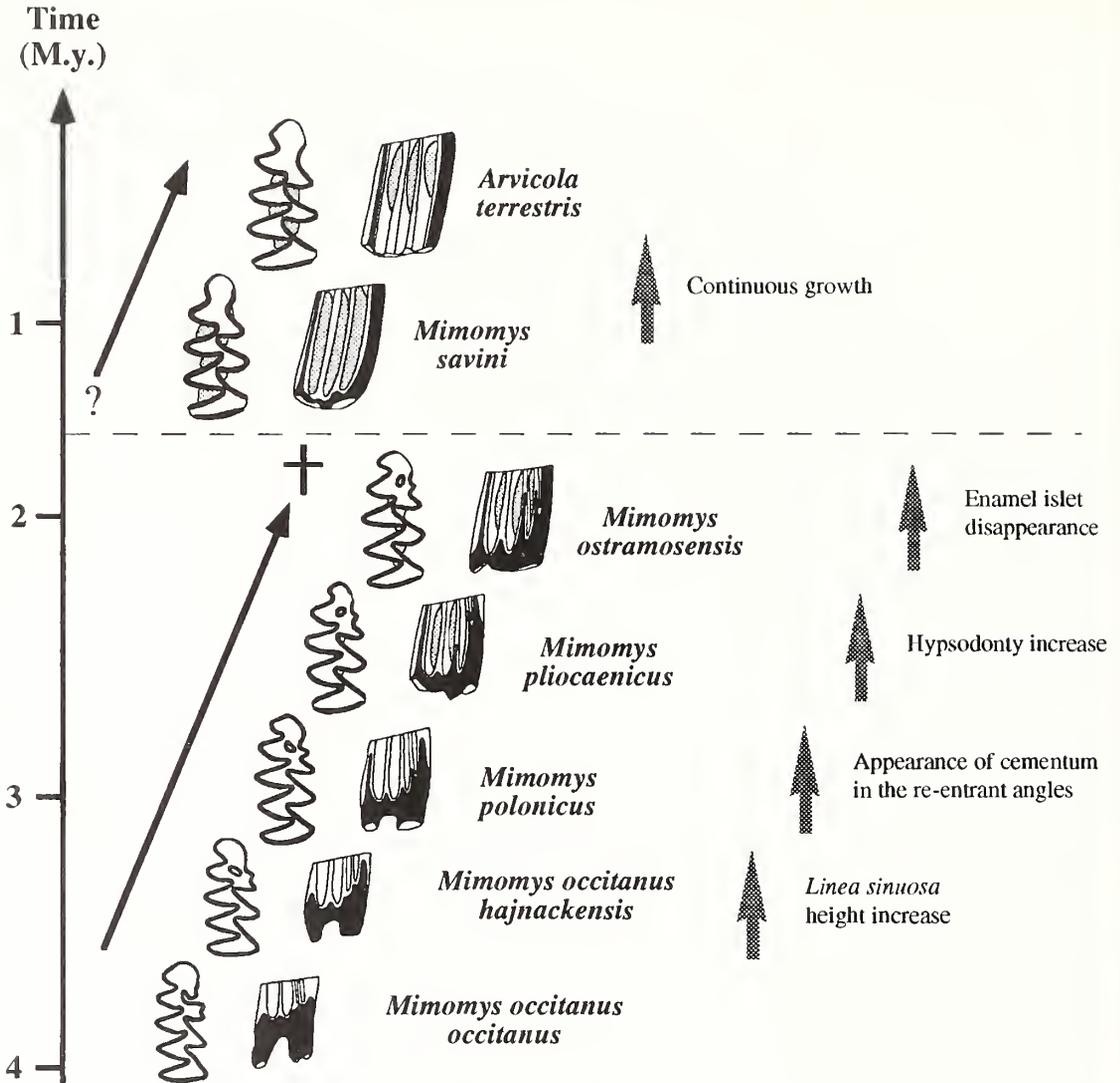
The only remaining hypothetical aspect of the lineage is the transition from *M. ostramosensis* to *M. savini* (Viriot 1989; Kolfschoten 1990*a*, 1993), in part because of the sparse fossil populations. Although the transition seemed plausible in a stratophenetic approach to the development of the lineage, no quantitative test had been made. The purpose of this paper is to carry out this quantitative test, focusing on an abundant and previously unstudied population of *Mimomys savini* from the type locality.

MATERIAL

To test the transition between the *Mimomys occitanus* – *M. ostramosensis* lineage and *M. savini*, the following species and populations have been subjected to morphometric analyses: *Mimomys occitanus occitanus* from Sète (Hérault, France); *Mimomys occitanus hajnackensis* from Wölfersheim (Germany); *Mimomys polonicus* from Rebielice Krolewski 1 and 2 (Poland); *Mimomys polonicus* from Commenailles (Bresse Valley, France); *Mimomys ostramosensis* from Montoussé 5 (Pyrenees, France); *Mimomys savini* from West Runton, Upper Freshwater Bed (England); *Mimomys savini* from Kortchevo (Russia).

THE *M. OCCITANUS* – *M. OSTRAMOSENSIS* CHRONOMORPHOCLINE

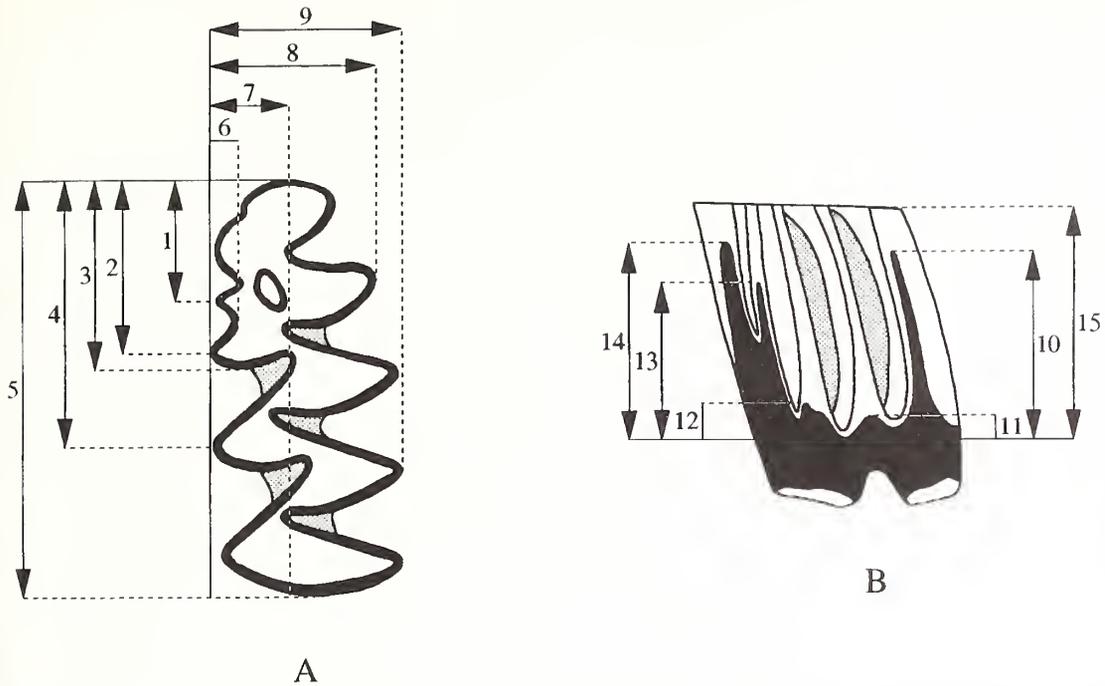
The water vole lineage (Text-fig. 1) was progressively pieced together as new fossil populations were discovered (Hinton 1926; Heim de Balsac and Guislain 1955; Chaline and Michaux 1969, 1974, 1975; Kretzoi 1969; Chaline 1974, 1984; Janossy and Meulen 1975). The first species to be described



TEXT-FIG. 1. Phyletic gradualism in the *Mimomys occitanus* – *M. ostromosensis* lineage, showing the major evolutionary trends: increased hypsodonty related to a higher *linea sinuosa*; appearance of cementum in the re-entrant angles, and disappearance of the enamel islet. Continuous growth only occurs between *Mimomys savini* and *Arvicola terrestris cantiana* (after Chaline 1987, modified).

was *M. pliocaenicus* (Forsyth Major 1902) from Castelfranco in Italy, followed by *M. savini* (Hinton 1926) from West Runton in England and *M. stehlini* (Kormos 1931). The lineage was completed by the description of *M. occitanus* (Thaler 1955), *M. polonicus* (Kowalski 1960), and *M. silasensis* (Janossy 1974), which was shown to be synonymous with *M. occitanus* by Chaline and Laurin (1986). Janossy and Meulen (1975) described an evolved stage of *M. pliocaenicus* under the name of *M. ostromosensis*. Finally, Weerd (1978) rounded off the lineage by describing a primitive *M. occitanus* as *M. davakosi*.

Quantitative analysis, restricted to the *M. occitanus* – *M. ostromosensis* part of the lineage, using morphometric methods (Chaline and Laurin 1986) showed that evolution involved (1) morphological



TEXT-FIG. 2. Nine occlusal measurements (A) and six jugal measurements (B) of the *Mimomys* first lower molar used for multivariate analysis.

changes in the occlusal surface of the first lower molar (*Mimomys* ridge, enamel islet), (2) appearance of cementum in the re-entrant angles, and, above all, (3) a rapid, though irregular, increase in the rate of hypsodonty conveyed by the increased height of the *linea sinuosa* on the crown sides and (4) by the non-appearance of roots (Text-fig. 1). Digital image processing applied to area quantification (Viriot *et al.* 1990), likewise confined to the *M. occitanus* – *M. ostramosensis* part of the lineage, showed that while the anterior part of the occlusal surface was becoming simpler the posterior part was increasing in complexity. The lineage *M. occitanus* – *M. ostramosensis* is a chromomorphocline that stretches from Western Europe (Spain and England) to Siberia and even China (Zheng and Li 1986; unpublished observations by Chaline at the Beijing Institute of Palaeontology and Palaeoanthropology). This vast range means that the lineage is a yardstick in Eurasia for establishing a high-resolution biostratigraphy of the Pliocene and Lower Pleistocene (Chaline 1989; Chaline and Farjanel 1990).

THE *MIMOMYS SAVINI* – *ARVICOLA TERRESTRIS* LINEAGE

Hinton (1926) first suggested the transition from *M. savini* to *Arvicola*. The gradual transition from *M. savini* to *A. terrestris cantiana* and thence to *A. terrestris terrestris* has likewise been demonstrated (Heim de Balsac and Guislain 1955; Koenigswald 1980; Kolfschoten 1990a, 1990b). Zazhigin (1980) described *M. intermedius* (= *M. savini*) under a new genus *Cromeromys*, created for the Siberian species *irtysiensis*.

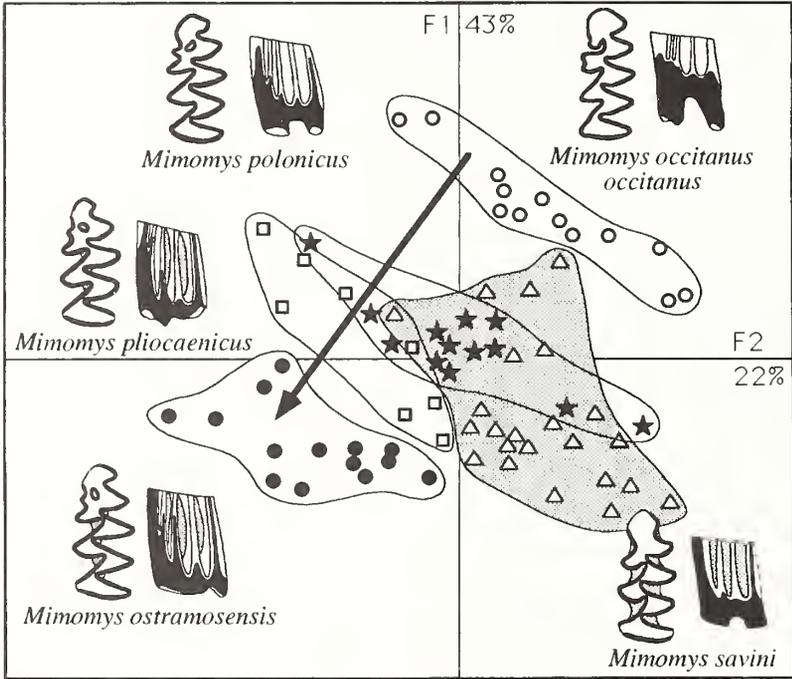
Quantitative studies of the *A. terrestris cantiana* – *A. terrestris terrestris* lineage showed a relative variation in the thickness of the anterior and posterior walls of the tooth triangles (Koenigswald 1980; Heinrich 1982; Kolfschoten 1990a, 1990b, 1992). When converted into index form, this gradual change found an application in quantitative biostratigraphy. Although the evolution is

gradual, it is not always linear, at least not in north-western Europe. The thickness index displays a clinal variation from north to south across Europe, and southern populations have a more primitive appearance with a lower index (Röttger 1986). Where advanced populations became extinct in the north during the late Middle Pleistocene, they were replaced by more primitive populations which migrated from southern areas thus altering the progressive variation over time by a reversal in the thickness index (Kolfshoten 1990a, 1992).

A NEW POPULATION ANALYSIS OF *MIMOMYS SAVINI*

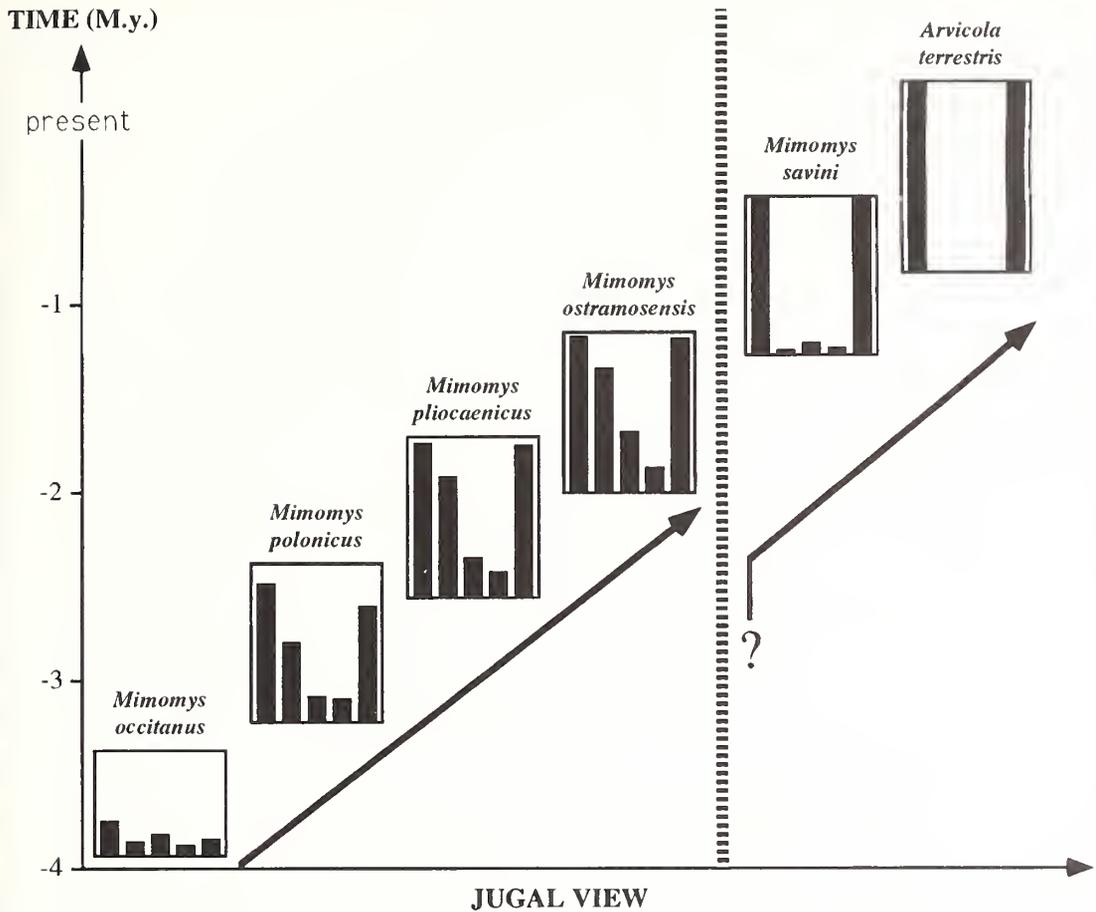
A bivariate study of variability in *M. savini* was conducted independently of the remainder of the lineage (Pasquier 1972). This species supposedly formed a transition with the *Arvicola* genus but had never figured in a general quantified analysis. Analysis of a fairly abundant, previously unstudied population from the type locality of the Freshwater Bed, West Runton, England) provides insight into the question.

A new multivariate analysis was performed using the classic biometric parameters (Text-fig. 2). It clearly shows that there is a trend from *M. occitanus occitanus* to *M. ostramosensis* (Text-fig. 3), and



TEXT-FIG. 3. Multivariate analysis based on Text-figure 2 measurements. The morphological variability of *M. savini* does not fit in with that of *M. ostramosensis* as could have been expected if *M. savini* derived from *M. ostramosensis* and continued the sequence *M. occitanus* – *M. ostramosensis*. Differences concern the anterior complex morphology (parameters 1–3) and the *linea sinuosa* (especially parameters 11–13). There is a clear discontinuity between the two lineages (○, *M. occitanus occitanus*; ★, *M. polonicus*; □, *M. pliocaenicus*; ●, *M. ostramosensis*; △, *M. savini*).

that the morphological variability of *M. savini* (none occlusal and six lateral characters) does not fit in with that of *M. ostramosensis* as could have been expected if *M. savini* were descended from *M. ostramosensis*.



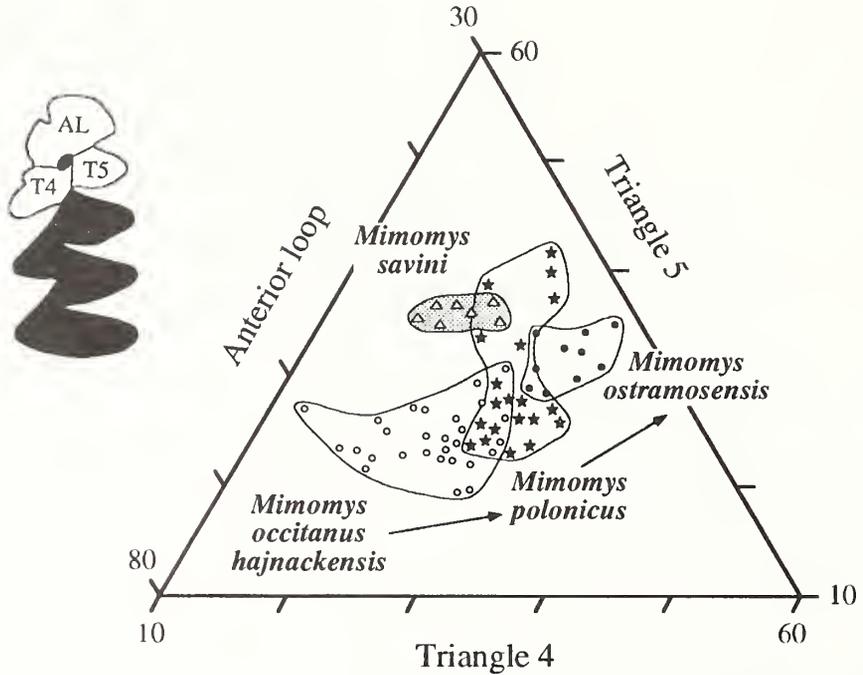
TEXT-FIG. 4. *Linea sinuosa* changes in the *M. occitanus* – *M. ostramosensis* lineage compared with the *M. savini* – *A. terrestris cantiana* sequence. The jugal views correspond to mean values of populations calculated for each species for parameters 10–15. It is clear that the gradual evolution of the *linea sinuosa* in *M. occitanus* – *M. ostramosensis* does not continue in *M. savini*. There is a discontinuity suggesting that *M. savini* derives from another *Mimomys* lineage, perhaps from *M. coelodus*.

The *linea sinuosa* variations observed in jugal view (Text-fig. 4) show that the pattern of change from *M. occitanus* to *M. ostramosensis* involves a distinct upturn of folds 1 and 5 towards the top of the crown and a more limited upward extension of folds 2, 3 and 4 which recede from front to back. This is obviously a gradual evolution.

When these data are compared with *M. savini*, however, a major difference can be seen in the pattern of the *linea sinuosa*. While folds 1 and 5 rise towards the top of the crown, folds 2, 3 and 4 remain very low. *M. savini* does not derive from *M. ostramosensis* but probably from another *Mimomys* lineage.

The occlusal morphology of the anterior complex of *M. occitanus hajnackensis*, *M. polonicus*, *M. ostramosensis* and *M. savini* has been quantified by digital image processing. This computerized technique describes the geometry of objects in a bidimensional space (for details, see Viriot 1989, Viriot *et al.* 1990 and Viriot *et al.* 1993). It is well understood that, in the course of M_1 occlusal evolution in the Eurasian water vole lineage, the greatest changes took place in the anterior

complex. This anterior complex can be broken down into three parts: triangle 4, triangle 5 and the anterior loop. The percentage of the area occupied by these three parts with regard to the total area of the anterior complex can be quantified (Text-fig. 5). From *M. occitanus hajnackensis* to *M.*



TEXT-FIG. 5. Evolutionary trends in the anterior complex of the M_1 from *M. occitanus* to *M. savini* described by digital image processing. Overlapping clouds from *M. occitanus hajnackensis* to *M. ostramosensis* characterized by a decrease in the area occupied by the anterior loop to the profit of triangles 4 and 5. Discontinuity of the *M. savini* plot with an increased area of the anterior loop at the expense of triangle 4 (○, *M. occitanus hajnackensis*; ★, *M. polonicus*; ●, *M. ostramosensis*; △, *M. savini*).

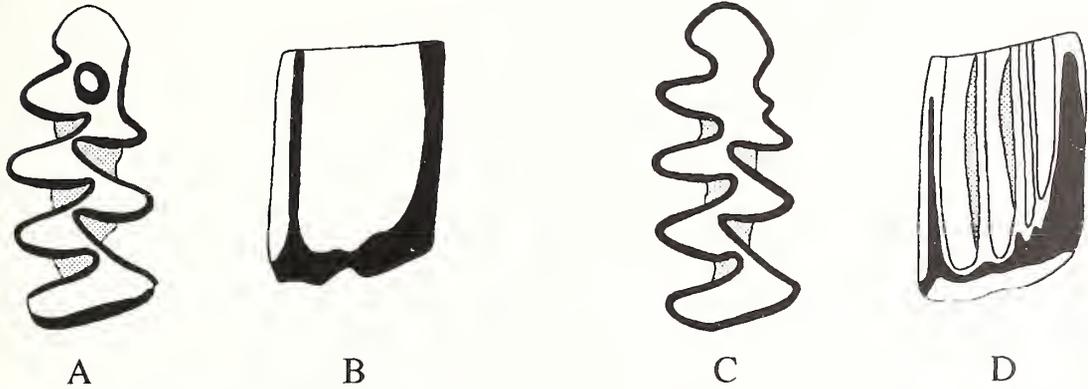
ostramosensis, the area occupied by the anterior loop decreases gradually to the profit of both triangles 4 and 5. Then, if we look at the passage from *M. ostramosensis* to *M. savini*, the process is reversed and the area occupied by the anterior loop increases at the expense of triangle 4 alone. There is a clear discontinuity between the *Mimomys* part of the lineage and the *Arvicola* part, which includes *M. savini*.

THE POSSIBLE ORIGIN OF THE SAVINI LINEAGE

According to the present knowledge of *Mimomys* species, two possible origins can be attributed to the *savini* lineage.

First, Rabeder (1981, text-fig. 81-2b), noticed that the *linea sinuosa* of *Mimomys coelodus* displays only a minor upturn of fold 2 as in some *M. savini*. Moreover, in Zazhigin's figures (Zazhigin's 1980, text-figs 25-8, 9), the *linea sinuosa* of *M. coelodus* has small upturns of the three intermediate folds

as in other *M. savini*. Finally, according to Kretzoi (1954), the holotype of *M. coelodus* coming from the Kislang fauna (Hungary), is closely related to *M. intermedius*, a species previously synonymized with *M. savini*. Therefore, *M. coelodus* is a species with hypsodont molars, with a M_1 displaying a well-developed enamel islet and no *Mimomys* ridge (Text-fig. 6A–B). Therefore, *M. coelodus* is a



TEXT-FIG. 6. Holotypes: A–B, *M. coelodus*; A, occlusal view; B, jugal view (after Rabeder 1981). C–D, *C. irtyshensis*; C, occlusal view; D, jugal view (after Zazhigin 1980).

possible ancestor of *M. savini*. However, the relationship between *M. coelodus* and the larger late Biharian voles has not yet been investigated properly and remains hypothetical, while the taxonomic status of *M. coelodus* is unknown.

The second hypothesis corresponds to Zazhigin's opinion, that *M. savini* should be regarded as part of the *Cromeromys* lineage, known from Late Pliocene deposits from Western Siberia and Transbaikalia, and from Early and Middle Pleistocene deposits from Eurasia. Indeed, the *linea sinuosa* of *Cromeromys irtyshensis*, the type species (Zazhigin 1980, fig. 24-1-8), looks very much like those of *M. coelodus* and *M. savini* (Text-fig. 6C–D). Moreover, the larger voles from West Runton, referred to as *C. intermedius* and related to *C. irtyshensis*, are often assigned to *M. savini* (Kretzoi 1969, Zazhigin 1980), according to their characteristic M^3 .

As *M. savini* can no longer be placed within the lineage of the genus *Mimomys* (type species *Mimomys pliocaenicus*), it must be assigned to *Cromeromys savini* (Hinton, 1910).

In summary, the discontinuity between the lineages *M. occitanus*–*M. ostramosensis* and *C. savini*–*A. terrestris* implies that the first lineage, which displays gradual morphological evolution, ends with *M. ostramosensis*. The lineage is replaced stratigraphically and, it seems, ecologically by that of *C. savini*, which is of uncertain origin, which gradually leads to *A. terrestris cantiana* and which continues to the present day with *A. terrestris terrestris*. This discontinuity between the two lineages was masked by the fact that *C. savini* succeeds *M. ostramosensis* in the same stratigraphical sequences. The phylogenetic re-arrangements introduced here do not change the biostratigraphical significance of *C. savini*.

Acknowledgements. The authors thank the Harrison Zoological Museum of Sevenoaks (Kent) for lending previously unstudied material of the *Mimomys savini* type population, to Dr A. Nadachowski who made it possible for us to obtain the material, to A. Van der Meulen and D. F. Mayhew for useful comments, and to V. Parisot and C. Sutcliffe for translation.

REFERENCES

- CHALINE, J. 1972. Les rongeurs du Pléistocène moyen et supérieur de France. *Cahiers de Paléontologie, CNRS*, Paris, 410 pp.
- 1974. Un nouveau critère d'étude des *Mimomys*, et les rapports de *Mimomys occitanus*, *Mimomys stehlini* et de *Mimomys polonicus* (Arvicolidae, Rodentia). *Acta Zoologica Cracoviensia*, **19**, 337–356.
- 1984. La séquence des rongeurs de Bresse en tant que référence biostratigraphique et climatique. *Géologie de la France, BRGM*, **3**, 251–268.
- 1987. Arvicolid Data (Arvicolidae, Rodentia) and Evolutionary Concepts. *Evolutionary Biology*, **21**, 237–310.
- 1989. Continental faunal units of the Plio-Pleistocene of France. *Mémoire Société Géologique d'Italie*, **31**, 175–183.
- and FARJANEL, G. 1990. Plio-Pleistocene rodent biostratigraphy and palynology of the Bresse Basin, France and correlations within western Europe. *Boreas*, **19**, 69–80.
- and MICHAUX, J. 1969. Evolution et signification stratigraphique des Arvicolidés du genre *Mimomys* dans le Plio-Pléistocène de France. *Comptes Rendus Académie des Sciences*, Paris, **268**, D, 3029–3032.
- 1974. Les micromammifères et la biostratigraphie de la bordure occidentale du remplissage bressan. *Bulletin Scientifique de Bourgogne*, **24**, 55–83.
- 1975. Les rongeurs du Pléistocène de France. *Mémoire du BRGM*, **78**, 89–97.
- and LAURIN, B. 1986. Phyletic gradualism in a European Plio-Pleistocene *Mimomys* lineage (Arvicolidae, Rodentia). *Paleobiology*, **12**, 203–216.
- BRUNET-LECOMTE, P. and VIRIOT, L. 1993. Morphological Trends and Rates of Evolution in Arvicolids (Arvicolidae, Rodentia) at species level: toward a Punctuated Equilibria/Disequilibria Model. In CHALINE, J. and WERDELIN, L. (eds). *Modes and tempos of Evolution in the Quaternary*. *Quaternary International*, **19**, 27–39.
- FORSYTH MAJOR, C. I. 1902. Some jaws and teeth of Pliocene voles (*Mimomys* gen. nov.), from the Norwich Crag at Thorpe, and from the upper Val d'Arno. *Proceedings of the Zoological Society*, London, **1**, 102–107.
- HEIM DE BALSAC, H. and GUISLAIN, R. 1955. Évolution et spéciation des Campagnols du genre *Arvicola* en territoire français. *Mammalia*, **19**, 367–390.
- HEINRICH, W. D. 1982. Ein Evolutionstrend bei *Arvicola* (Rodentia, Mammalia) und seine Bedeutung für die Biostratigraphie im Pleistozän Europas. *Zeitschrift für Geologische Wissenschaften*, Berlin, **6**, 683–735.
- HINTON, M. A. C. 1910. A preliminary account of the British Voles and Lemmings; with some remarks on the Pleistocene climate and geography. *Proceedings of the Geological Association of London*, **21**, 489–507.
- 1926. Monograph of the Voles and Lemmings (Microtidae) living and extinct. *British Museum Natural History*, **1**, 350–383.
- JANOSSY, D. 1974. New 'Middle Pliocene' Microvertebrate fauna from Northern Hungary (Osztramos Loc. 9). *Fragmenta Mineralogia et Paleontologia*, **5**, 17–27.
- and MEULEN, A. J. van der 1975. On *Mimomys* (Rodentia) from Osztramos 3, north Hungary. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B*, **78**, 381–391.
- KOENIGSWALD, W. von 1980. Schmelzstruktur und morphologie in den molaren der Arvicolidae (Rodentia). *Abhandlungen der Senckenberg. Naturforschende Gesellschaft, Frankfurt*, **539**, 1–129.
- KOLFSCHOTEN, T. van 1990a. The evolution of the mammal fauna in the Netherlands and the middle Rhine Area (Western Germany) during the late Middle Pleistocene. *Mededelingen Rijks Geologische Dienst*, **43**, 1–69.
- 1990b. Review of the Pleistocene Arvicolid Faunas from the Netherlands. 255–274. In FEJFAR, O. and HEINRICH, W. D. (eds). *Evolution Phylogeny and Biostratigraphy of Arvicolids*, Praha, 448 pp.
- 1992. Aspect of the migration of mammals to northwestern Europe during the Pleistocene, in particular the reimmigration of *Arvicola terrestris*. *Courrier Forschung. Senckenberg*, **153**, 313–330.
- 1993. On the origin of the Middle Pleistocene larger voles. *Quaternary International*, **19**, 47–50.
- KORMOS, T. 1931. Oberpliozäne Wühlmäuse von Senèze (Haute-Loire) und val d'Arno (Toscana). *Abhandlungen der Schweizerische Paläontologische Gesellschaft*, **51**, 1–14.
- KOWALSKI, K. 1960. Pliocene insectivores and rodents from Rebielice Krolewski (Poland). *Acta Zoologica Cracoviensia*, **5**, 155–201.
- KRETZOI, M. 1954. Bericht über die calabrische villafranchische Fauna von Kisláng, Kom. Fejer. *Jahrbuch Ungarisches Museum Geologisches Anstalt*, **1954**, 213–265.
- 1969. Skizze einer Arvicoliden-Phylogenie-Stand 1969. *Vertebrata Hungarica*, **11**, 1–2, 155–193.
- PASQUIER, L. 1972. Etude d'une population de *Mimomys savini* Hinton, 1910 (Arvicolinae, Rodentia) provenant de l'Upper Freshwater bed (Quaternaire ancien d'Angleterre). *Mammalia*, **36**, 214–225.

- RABEDER, G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Nieder-Osterreich. *Beiträge zur Paläontologie von Österreich*, **8**, 1–373.
- RÖTTGER, U. 1986. Schelzbandbreiten an molaren von Schermäusen (*Arvicola Lacépède*, 1799). *Bommer Zoologische Beiträge*, **38**, 95–105.
- THALER, L. 1955. Sur l'âge pliocène de la faune des grottes du Lazaret (Sète, Hérault). *Comptes Rendus Académie des Sciences*, Paris, **240**, D, 387–398.
- VIRIOT, L. 1989. La lignée évolutive *Mimomys davakosi* – *M. ostramosensis*. Quantification des modifications morphologiques de la surface occlusale à l'aide de l'analyse d'images. Mem. DEA, Université de Bourgogne (unpublished).
- CHALINE, J. and SCHAAF, A. 1990. Quantification du gradualisme phylétique de *Mimomys occitanus* à *Mimomys ostramosensis* (Arvicolidae, Rodentia) à l'aide de l'analyse d'images. *Comptes Rendus Académie des Sciences*, Paris, **310**, D, 1755–1760.
- and LE BOULENGÉ, E. 1993. Ontogenetic change of *Ondatra zibethicus* (Arvicolidae, Rodentia) cheek teeth analyzed by digital image processing. 373–391. In MARTIN, R. A. and BARNOSKY, A. D. (eds). *Morphological change in Quaternary mammals of North America*, Cambridge University Press, 415 pp.
- WEERD, A. van der 1978. Early Ruscianian rodents and lagomorphs (Mammalia) from the lignites near Ptolemais (Macedonia, Greece). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B*, **82**, 127–170.
- ZAZHIGIN, V. S. 1980. *Rodents of the late Pliocene and Anthropogene of the South of Western Siberia*, Nauka, Moscow, 159 pp.
- ZHENG, S. and LI, C. 1986. A Review of Chinese *Mimomys* (Arvicolidae, Rodentia). *Vertebrata Palasiatica*, **24**, 81–109.

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COMPOSITION AND DISTRIBUTION OF THE INOCERAMID BIVALVE GENUS *ANOPAEA*

by J. A. CRAME and S. R. A. KELLY

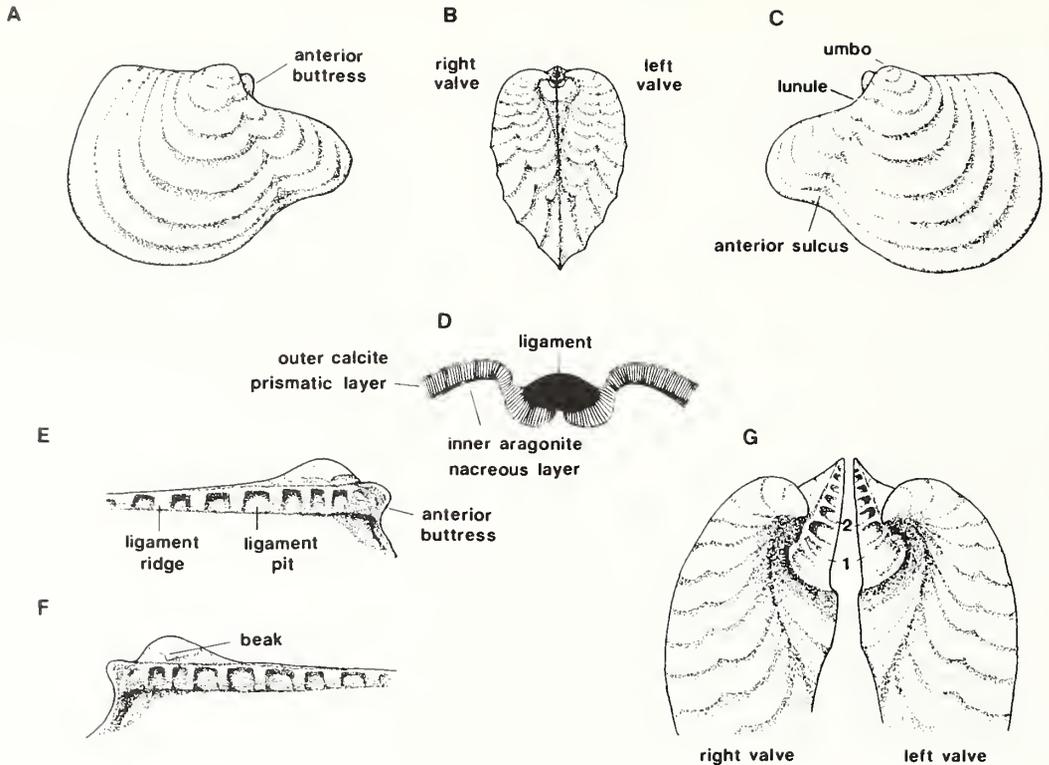
ABSTRACT. *Anopaea* is a distinctive Late Jurassic–Early Cretaceous inoceramid bivalve genus. Traditionally recognized by its elongate-pyriform outline and impressed antero-ventral sulcus, it is now apparent that it also has a distinctive hingeline. In each valve the thickened shell material of the hinge region terminates in a prominent fold, the anterior buttress; this often takes on the appearance of a small anterior ‘ear’. Some fifteen taxa are now assigned to the genus and a further seven are probable members. The bulk of these forms fall within the Late Tithonian–Early Albian. *A. callistoensis* sp. nov., from the Late Tithonian–?Early Berriasian of the Antarctic Peninsula, and a probable new species from the Berriasian of the South Shetland Islands, are described. *Inoceramus constrictus*, from the Early Albian of Queensland Australia, can now be referred to the genus. It can be confirmed that, with only a very small number of exceptions, *Anopaea* was restricted to Late Jurassic–Early Cretaceous extra-Tethyan localities. In this sense it may be regarded as a genuine bipolar taxon, although amphitropical is perhaps a more accurate term.

PROBLEMS of generic discrimination remain at the forefront of taxonomic investigations into the widespread late Palaeozoic–Mesozoic bivalve family Inoceramidae Giebel, 1852. This is particularly so for the prolific Cretaceous representatives and there is currently an urgent need to clarify the definitions and status (i.e. taxonomic rank) of a wide variety of available names. One genus that would appear to be relatively stable is *Anopaea* Eichwald, 1861. Although still poorly known at the time of publication of the *Treatise* (Cox 1969), its status has subsequently been confirmed and its distribution extended to a variety of Late Jurassic–Early Cretaceous extra-Tethyan localities (e.g. Pokhialainen 1974; Crame 1981; Kelly 1984; Dhondt 1992). Its unusual form and essentially bipolar distribution have ensured that it is the focus of continued attention.

Nevertheless, despite the distinctive form of this genus (to be discussed in detail below), instances have been recorded of apparent transitions to the ubiquitous *Inoceramus*. These are perhaps most prevalent in the informal ‘*Inoceramus*’ *anglicus* and ‘*I. neocomiensis*’ groups (e.g. Pokhialainen 1969a, p. 125; Saveliev 1962, pl. 2, fig. 1a; Crame 1985, p. 488). Of equal concern is the fact that some features of the *Anopaea* shell have never been explained satisfactorily. Foremost among these is the ‘concave appendix, similar to the ear-like appendix of *Aucella* [= *Buchia*], situated in front of the beaks’ (Eichwald 1865, p. 481). A similar ‘anterior ear’ was noted by Etheridge, Jr (1901, p. 25) on a specimen of *Inoceramus* [= *Anopaea*] *constrictus*. How could an apparently *bona fide* member of the Inoceramidae have a *Buchia*-like appearance? It is the intention of this study to redefine the diagnostic features of *Anopaea* using new material collected recently from the Antarctic Peninsula region and existing collections from Australia. With a firmer understanding of what constitutes membership of the genus, both its stratigraphical and geographical distribution can be reviewed. This in turn may help to constrain the nature and timing of bipolar events associated with the Jurassic–Cretaceous boundary (Crame 1993).

DISTINGUISHING FEATURES OF *ANOPAEA*

Anopaea is a small to medium sized bivalve (typically 50–80 mm in length) with a distinctive elongate-pyriform (i.e. pear-shaped) outline; the posterior is typically high and rounded, and the

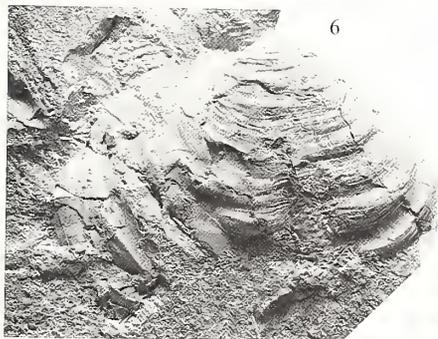
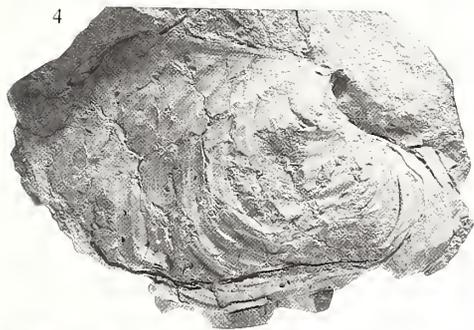
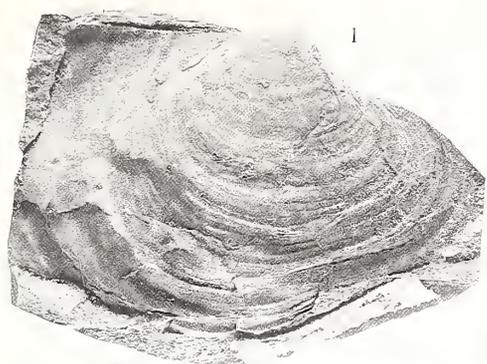


TEXT-FIG. 1. Key morphological features of *Anopaea*. A, external view of a right valve; B, anterior view of a whole specimen; C, external view of a left valve; D, idealised cross-section through the hinge and ligament area (N.B. orientation of prisms in prismatic calcite layer is schematic only); E, left valve hinge area; F, right valve hinge area; G, exploded anterior view to show buttresses at the anterior terminations of the ligament areas.

anterior narrow and pointed (Text-fig. 1). It is equivalve, or very nearly so, and moderately inflated. In front of the prominent beak in each valve there is a deep cordiform lunule and a variably developed anterior sulcus can be traced from the umbonal region to the antero-ventral margin. Here, the latter feature may form a deep embayment which effectively divides the shell into anterior and posterior 'lobes'. Possession of a multivincular ligament, thin prismatic shell layer and regular commarginal ornament provide a ready link to the Inoceramidae. Unfortunately, details of the musculature remain poorly known; general shell form strongly suggests an endobysate mode of life (Crame 1981, fig. 2).

EXPLANATION OF PLATE I

Figs 1-8. *Anopaea callistoensis* sp. nov., Late Tithonian-Early Berriasian?, Fossil Bluff Group, eastern Alexander Island. 1, KG.3404.268, paratype, internal mould of a right valve with traces of shell material, $\times 1.5$. 2, KG.3404.187b, paratype, internal mould of a left valve, $\times 1.5$. 3, KG.3404.435, paratype, internal mould of a juvenile right valve, $\times 1.5$. 4, KG.4209.14, paratype, internal mould of a right valve, $\times 1$. 5, KG.3404.190, paratype, internal mould of a left valve, $\times 1.5$. 6, KG.4209.87, paratype, internal mould of a right valve, $\times 1$. 7, KG.3404.183, holotype, internal mould of a right valve with traces of shell material, $\times 1$. 8, KG.3404.185, paratype, internal mould of a right valve, $\times 1$.



To date, the only region of the *Anopaea* shell which has not been described adequately is the hingeline. Apart from the fact that it seems to be characterized by comparatively small rounded ligament pits, virtually nothing is known about it. However, some recently collected specimens from the Antarctic Peninsula region (described formally below as *Anopaea callistoensis* sp. nov. and *A.* sp. nov?) bear reasonably well preserved hingelines and form the basis, together with a revision of the Australian species *Anopaea constricta* (Etheridge, Jr), of a new reconstruction of this critical region of the shell. The sketches presented in Text-figure 1 are based upon a series of camera lucida drawings of specimens of the two new Antarctic species and the revised Australian form.

Perhaps the most striking feature to emerge from study of this new material is that some specimens do indeed show a small antero-dorsal *Buchia*-like ear (e.g. Text-figs 3A–B, D–E, 5A; Pl. 1, fig. 8). It is present in both left and right valves and takes the form of a rounded, buttress-like fold of shell material that is directed strongly inwards (i.e. towards the plane of commissure; Text-fig. 1). There is no evidence that the buttresses were true ears, in the sense that they are associated with byssal notches, or that they articulated with the other valve. Instead, it would appear that these features represent the anterior termination in each valve of a strip (or shelf) of thickened shell material running along the hingeline. Following the terminology of many Russian workers, such a structure should be referred to as the ligamentat (e.g. Pokhialainen 1969*b*, 1972). On internal moulds this shelf commonly has a shallow, concave cross-profile (Text-figs 1, 3). The net effect of two opposing shelves of thickened shell material would have been to increase the interumbonal distance (Text-fig. 1G). This in turn would have permitted, at least to some extent, the development of more inflated shells; as in endobysate arcids, it may well be that the development of more inflated forms was a strategy to promote greater stability (Savazzi 1987).

It is still unclear whether the material comprising the thickened hingeline is formed consistently from one particular shell layer. Examination of a series of specimens of *A. constricta* (see below) revealed this region to be composed of a thickened prismatic calcite layer (Text-fig. 1D–F; Pl. 2, fig. 6). It would appear that the ligament was mounted directly on this layer, as perhaps it is in most unequivocal members of the Inoceramidae (Crampton 1988). It is also apparent that, as in other true inoceramids, this prismatic calcite layer was in turn superimposed upon a thickened inner aragonitic layer (sheet nacre) which is particularly prominent in the umbonal region (Text-fig. 4A, C). Nevertheless, on one of the two small specimens assigned below to *Anopaea* sp. nov?, it is the inner aragonitic layer, rather than the outer calcitic one, which is considerably thickened in the hinge region (Text-fig. 4A). Although somewhat altered now, this appears to comprise sheet nacre up to 250 μm thick (Text-fig. 4A). Unfortunately, the ligament pits are missing on this specimen, but it cannot be discounted that they were mounted directly upon this aragonitic layer. Resolution of the composition of this important taxonomic feature must await the discovery of well preserved specimens.

Using an amended diagnosis for the genus *Anopaea* (see systematic section below), it has been possible to reassess critically those inoceramids which should be assigned to the taxon. The results of this survey are presented in Table 1, where two main categories are recognized: a group of species which can be assigned with some certainty to the genus, and a group of forms whose status is in some way questionable. Other taxa of less certain affinity are probably best attached with a degree of uncertainty to *Inoceramus*; in particular, the taxonomic position of '*I. deltoides* Crame (1985) and its allies cannot yet be resolved. The two new Antarctic species are described formally in the following systematic section, where the opportunity is also taken of redescribing the Australian Albian form, *A. constricta* (Etheridge, Jr). All the Antarctic material is stored in the collections of the British Antarctic Survey, Cambridge, UK.

TABLE 1. Taxonomic re-appraisal of the genus *Anopaea*. Abbreviations: BAS, British Antarctic Survey, Cambridge; CIRGEO, Centro de Investigaciones en Recursos Geológicos; DVTGU, Dal'nevostochnoye Territorial'noye Geologicheskoye Upravleniye; NHM, Natural History Museum, London; NZGS, New Zealand Geological Survey; SVKNII, Severo-Vostochnogo Kompleksnogo Nauchno-Issledovatel'skogo Instituta.

Taxon	Type material	Range and occurrence	References and notes
1. Valid taxa			
<i>Anopaea brachowi</i> (Rouillier, in Rouillier and Vossinsky, 1849)	The original of <i>I. lobatus</i> Auerbach and Frears (1846, pl. 7, fig. 1) is held in the Museum of A. P. and M. A. Pavlov, Moscow. It is designated herein lectotype of <i>I. lobatus</i> Auerbach and Frears, 1846 and of <i>I. brachowi</i> Rouillier (1849)	Late Volgian, central Russian Platform; Late Volgian and Ryazanian, eastern England	Kelly (1984)
<i>Anopaea sphenoidea</i> Gerasimov (1955)	Holotype: Geological Survey of the Central Areas, Moscow, Gerasimov Collection, No. 1086 (Gerasimov 1955, pl. 20, fig. 2); 3 paratypes (Gerasimov 1955, pl. 20, figs 3–5)	Late Volgian, Russian Platform and eastern England	Kelly (1984)
<i>Anopaea strambergensis</i> (Boehm, 1883)	Holotype: Unnumbered specimen figured by Boehm (1883, pl. 67, figs 1 and 3) is designated herein as the lectotype	Tithonian, Stramberger Schichten, Carpathian Alps	Boehm's (1883, pl. 67, figs 1–3) three specimens almost certainly belong to <i>Anopaea</i> ; however, he noted (Boehm 1883, p. 594) that these specimens are atypical and may have come from elsewhere
<i>Anopaea callistoensis</i> sp. nov.	Holotype: BAS, Cambridge, KG.3404.183; paratypes – as listed in this paper	Late Tithonian–?Early Berriasian, Alexander Island, Antarctica	This paper
<i>Anopaea</i> sp. nov?	(BAS, Cambridge, P.2151.1–3)	Early Berriasian, South Shetland Islands, Antarctica	This paper
<i>Anopaea gerasimovi</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12M/1	Berriasian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)
<i>Anopaea pivanensis</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12/1	Berriasian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)
<i>Anopaea savrasovi</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12/3	Berriasian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)

TABLE 1. (cont.)

Taxon	Type material	Range and occurrence	References and notes
<i>Anopaea stempeli</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12/2	Berriasian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)
<i>Anopaea</i> sp. indet.	(Single right valve, No. 1/11440)	Berriasian, Mangyshlak, Russian Fed.	Bogdanova (1988)
<i>Anopaea amurensis</i> Kapitza (1978)	Holotype: DVTGU, Khabarovsk, No. 12/4	Late Valanginian, Lower Priamur (Primorskiy), Russian Fed.	Kapitza (1978)
<i>Anopaea trapezoidalis</i> (Thomson and Willey, 1972)	Holotype: BAS, Cambridge, KG.18.31a; 4 paratypes, KG.18.31b-c	?Hauterivian-Barremian, Alexander Island, Antarctica	Crame and Howlett (1988)
<i>Anopaea</i> sp. nov. aff. <i>mandibula</i> (Mordvilko, 1949)	(BAS, Cambridge, KG.1682.37)	Albian, Alexander Island, Antarctica	Crame (1985)
<i>Anopaea</i> sp. nov.	(CIRGEO, Buenos Aires, PI 1467)	Early Albian, James Ross Island, Antarctica	Medina and Buatois (1992)
<i>Anopaea constricta</i> (Etheridge, Jr., 1892)	Holotype: Queensland Museum, Brisbane, F17/1241	Early Albian, Queensland, Australia	This paper
2. Taxa of less certain affinity			
<i>Anopaea? stoliczkai</i> (Holdhaus, 1913)	Holotype: unnumbered specimen figured by Holdhaus (1913, pl. 98, fig. 10a); as this now appears to be lost, a neotype may need to be designated from topotypes held in NHM, London (BPM 5051, 7198, ?7198, 7199 and LL 24167)	Tithonian, southern Tibe	Lack of a clearly defined antero-ventral sulcus and more rounded nature of some specimens cast some doubts upon affinity to <i>Anopaea</i> ; Crame (1981)
<i>Anopaea? verbeeki</i> Boehm (1904)	Holotype: unnumbered specimen figured by Boehm (1904, pl. 1, fig. 4a, b), by monotypy	Tithonian, Indonesia	Known from only one incomplete specimen (which may now be lost)
<i>Anopaea? windhouweri</i> Boehm (1904)	Holotype: unnumbered specimen figured by Boehm (1904, pl. 1, fig. 3), by monotypy	Tithonian, Indonesia	Known from only one incomplete specimen (which may now be lost)
<i>Anopaea?</i> sp. nov.	(Three specimens figured by Fleming [1958, figs 12, 14 and 15]; from boulders derived from NZGS locs. S62/523, 525 and 526)	Tithonian, New Zealand	<i>Inoceramus</i> n. sp. A, ?aff. <i>everesti</i> Oppel may be an <i>Anopaea</i> ; <i>Anopaea</i> n. sp. is incomplete; Fleming (1958)

TABLE 1. (cont.)

Taxon	Type material	Range and occurrence	References and notes
<i>Anopaea? mandibula</i> (Mordvilko, 1949)	Holotype: not yet traced	Early Albian, Mangyshlak, Russian Fed.	Although there are indications that this species is close to <i>Anopaea</i> (Saveliev 1962) there are also resemblances to <i>Inoceramus coptensis</i> Casey. The latter form may, in turn, be close to <i>Birostrina salomoni</i> (d'Orbigny) (J. S. Crampton, pers. comm. 1993)
<i>Anopaea?</i> <i>mandibulaformis</i> (Pokhialainen, 1969a)	Holotype: SVKNII, Magadan, No. 289	Late Berriasian–Early Valanginian, Myrgal region, Russian Fed.	By no means an obvious <i>Anopaea</i> ; Pokhialainen (1969a, pl. 3, fig. 3)
<i>Anopaea? attenuata</i> Eichwald (1965)	Holotype: unnumbered specimen figured by Eichwald (1865, pl. 21, fig. 4a), by monotypy	'Neocomian', Russian Platform	Possibly a juvenile; some juveniles of <i>A. callistoensis</i> sp. nov. have this narrow, elongated form

SYSTEMATIC PALAEOONTOLOGY

Order PTERIOIDA Newell, 1965

Family INOCERAMIDAE Giebel, 1852

Genus ANOPAEA Eichwald, 1861

Type species. Inoceramus lobatus Auerbach and Frears, 1846 *non* Münster in Goldfuss and Münster, 1835; subjective synonym of *I. brachowi* Rouillier, 1849.

Emended diagnosis. Small-medium sized, elongate-pyriform inoceramid with deep cordiform lunule; equivalve, or almost so; antero-ventral sulcus usually well developed; opisthodontic hinge based on thickened shell layer (or ligamentat); on internal moulds this thickened layer is represented in each valve by a concave gutter; ligamentat terminates in an anterior, ear-like buttress.

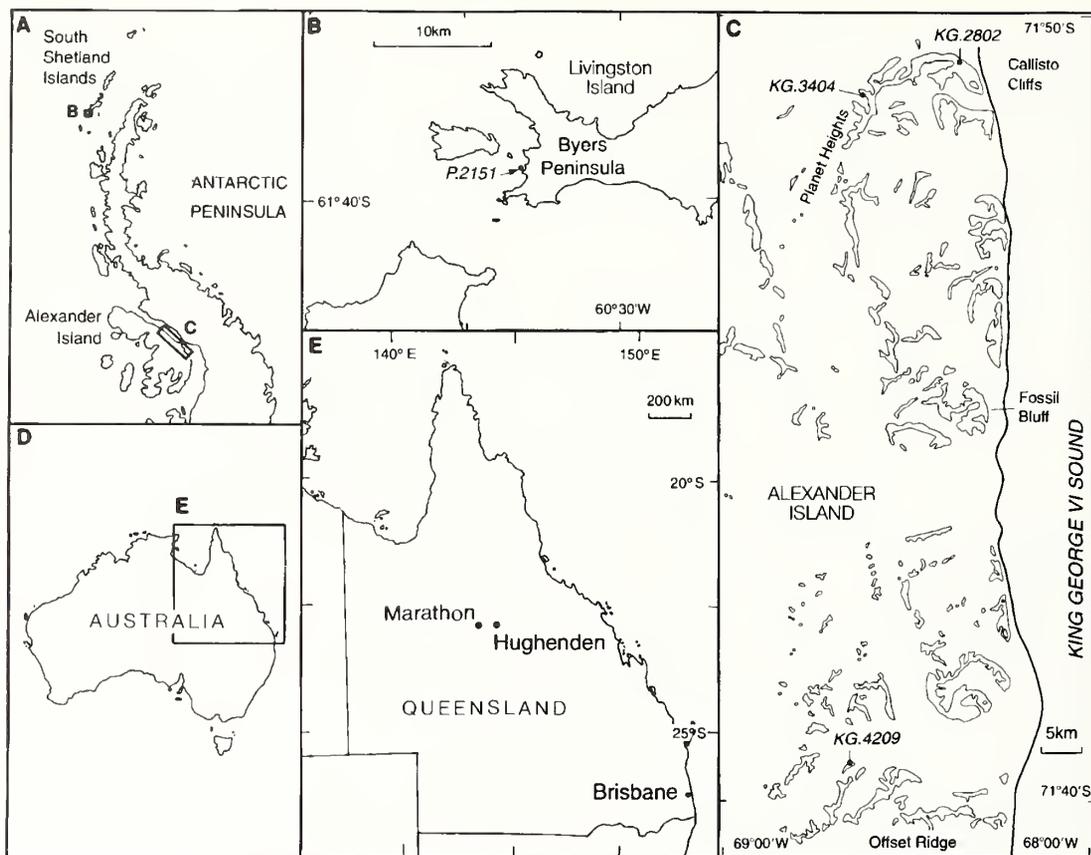
Included species and geographical range. See Table 1.

Age-range. Late Tithonian–Early Albian.

Anopaea callistoensis sp. nov.

Plate 1, figures 1–7; Text-figures 3A–B, D–E, 4B

- v. 1981 *Anopaea* sp. nov.(?) Crame, p. 213, pl. 2, figs e–j [Late Tithonian, Himalia Ridge Formation, Callisto Cliffs, Alexander Island, Antarctica].
- v. 1988 *Anopaea* sp. nov.? Crame and Howlett, p. 15, fig. 6a [Late Tithonian, Himalia Ridge Formation, Planet Heights, Alexander Island, Antarctica].



TEXT-FIG. 2. Locality maps for the Antarctic Peninsula region and Queensland, Australia.

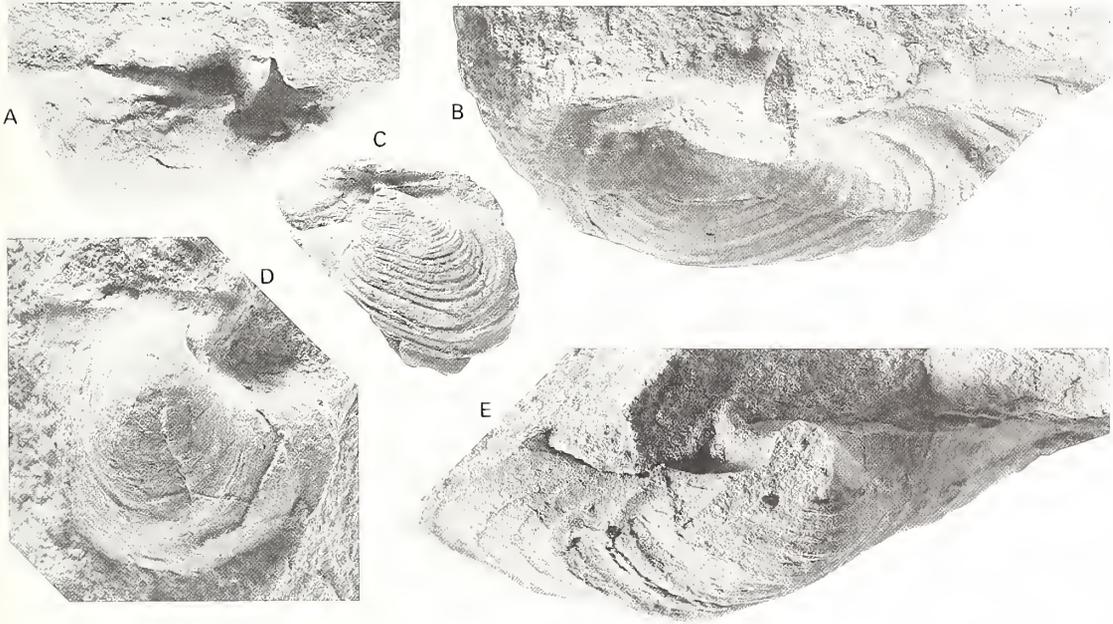
Type material. Holotype: KG.3404.183 (Pl. 1, fig. 7; internal mould RV). Paratypes: KG.2802, 30, 40, 43a, b, 53, 58, KG.3404.162, 167, 178, 183a, b, 184, 185, 186, 187a, 188, 189, 190, 191, 193, 194, 195a, b, 196, 197, 198, 268, 432, 433a, b, 434, 435, KG.4209.12, 13, 14, 19, 38, 39, 40, 42a, 43, 44, 45, 46, 47, 48, 59, 60a, b, 67, 85, 86, 87, 88, 89, 101, 104, 105, 122, 123, 124, 125, 126, 139, 142. All specimens from the Fossil Bluff Group of eastern Alexander Island (Text-fig. 2). At locality KG.2802 (western Callisto Cliffs, $71^{\circ} 01' S$; $68^{\circ} 03' W$), the specimens were obtained from the 91–99 m level in the measured section (Himalia Ridge Formation); at KG.3404 (northern Planet Heights, $71^{\circ} 02' 50'' S$; $68^{\circ} 36' 30'' W$) the specimens were obtained from approx. the 109–118 m level in the measured section (Himalia Ridge Formation); at KG.4209 (central Offset Ridge, $71^{\circ} 38' S$, $68^{\circ} 39' W$) the specimens were obtained from the 132–204 m level in the upper part of the Atoll Nunataks Formation to lower part of the Himalia Ridge Formation.

Occurrence. As for the type material. Associated macrofossils suggest that, at the two more northerly localities (KG.2802 and 3404; Text-fig. 2), the species has a Late Tithonian age (Butterworth *et al.* 1988; Crame and Howlett 1988); at the more southerly locality (KG.4209) it may range into the Early Berriasian. Precise placement of the Jurassic–Cretaceous boundary using macrofossils alone is not yet possible in Antarctica.

Derivation of name. After Callisto Cliffs, eastern Alexander Island.

Diagnosis. Weakly to moderately inflated *Anopaea* with subrectangular posterior and variably developed anterior sulcus; distinctive ornament of fine growth lines superimposed on low, commarginal folds.

Description. This species is equivalve (or very nearly so) and has the typical *Anopaea* outline, as described in the introductory section. Most specimens have the familiar elongate-rectangular form, with the length (L = anterior to posterior extremities) considerably in excess of the height (H = maximum dimension perpendicular to length). A sample of 25 specimens gave the following measurements (in mm): $\times L = 44.72$ (SD = 21.04, range = 16.0–92.0); $\times H = 34.0$ (SD = 11.93, range = 13.0–62.0); $\times H/L = 0.81$ (SD = 0.21, range = 0.52–1.47). A few juveniles have a much more erect profile (e.g. KG.3404.435; Pl. 1, fig. 3), but even in these there are still clear indications of the characteristic high, rounded posterior and narrower, pointed anterior.



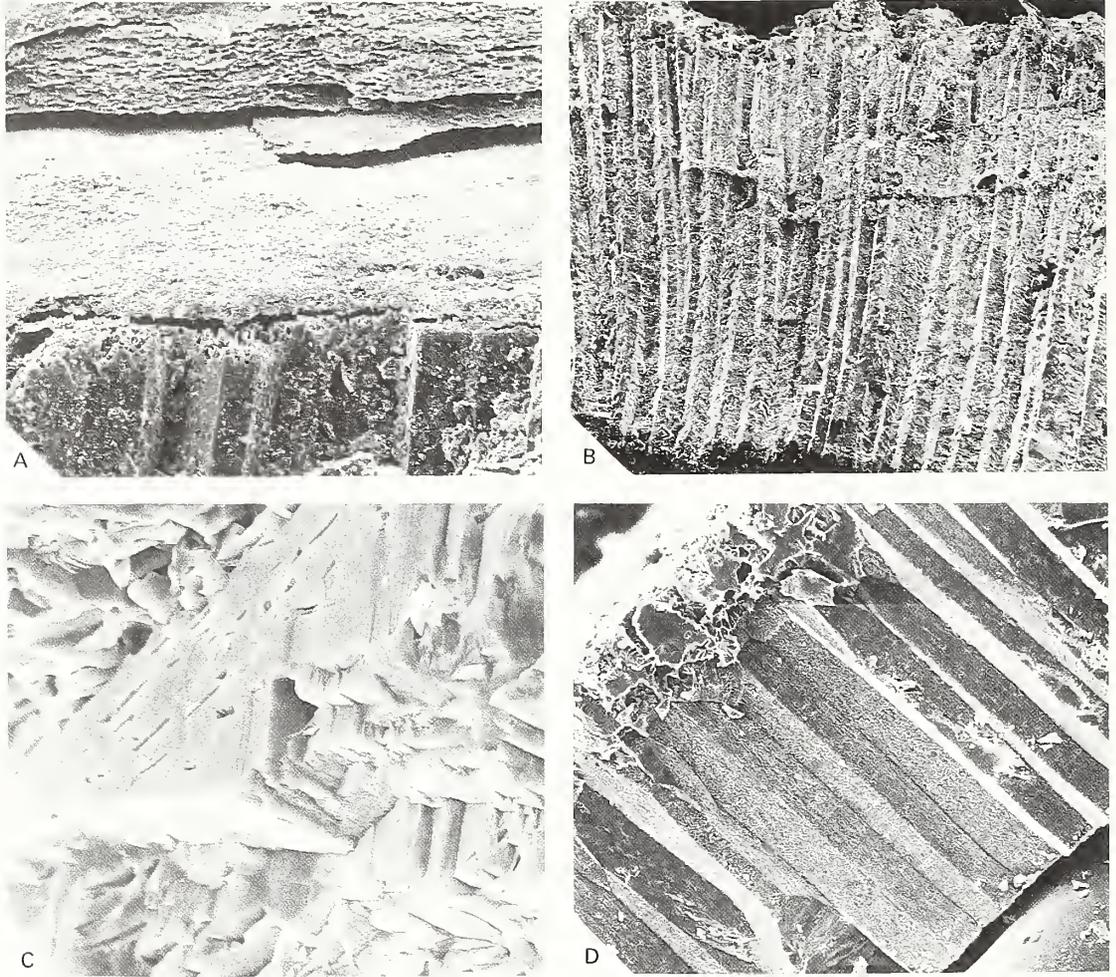
TEXT-FIG. 3. Hinge region and anterior buttress of *Anopaea*. A–B, D–E, *Anopaea callistoensis* sp. nov.; A, KG.3404.193, internal mould of a right valve exhibiting a prominent anterior buttress, $\times 3$; B, KG.3404.191, internal mould of a right valve, showing the concave shelf corresponding to the ligamentat and its abrupt anterior termination in a buttress, $\times 3$; D, KG.3404.434, internal mould of a right valve, showing a concave shelf and anterior buttress overhanging a deep lunule, $\times 3$; E, KG.3404.187b, internal mould of a left valve, showing a prominent anterior buttress, $\times 3$. C, *A. trapezoidalis* (Thomson and Willey), KG.18.31d, internal mould of a bivalved specimen, viewed from the left; the prominent shelf formed by the ligamentat can be seen along the hinge of the right valve, $\times 1$.

The valves are weakly to moderately inflated, with the maximum degree of convexity occurring in the umbonal and central regions; some specimens show a considerable degree of flattening towards the postero-dorsal and ventral margins. The umbones are prominent, prosogyrous and rise slightly above the hingeline. On the antero-dorsal side of the umbo there is a steep descent to the lunule, which is always well developed (Pl. 1, figs 1–8; Text-fig. 3). The antero-ventral sulcus is usually only weakly impressed. It can be traced on the holotype (KG.3404.183; Pl. 1, fig. 7) from the antero-ventral margin to almost the umbo, but on other specimens it is barely more than an indentation on the ventral margin (e.g. Pl. 1, fig. 1).

The best preserved hingelines are straight and a number clearly show the distinctive concave cross-profile (i.e. in dorso-ventral section; Text-fig. 3). The anterior termination of the hingeline in both valves is marked by a small, protruding buttress; on a number of specimens these features have a distinctive 'ear-like' appearance (Pl. 1, fig. 8; Text-fig. 3A–B, D–E). As stated previously, it is believed that the two buttresses simply rested against each other, for neither appears to have crossed the plane of commissure. Nevertheless, on two poorly preserved specimens, which may both have been distorted slightly (KG.3404.196, KG.4209.104), there are

indications that the left buttress rested partly within the right. How widespread a phenomenon this may have been is not known at present.

The ornament on both internal and external moulds comprises a series of prominent commarginal folds with superimposed secondary growth lines (Pl. 1, figs 1–8). The primary folds generally have a wavelength of 2–4 mm, but on the ventral margins of the largest specimens they reach 6–7 mm across; they have acute to well



TEXT-FIG. 4. SEM photomicrographs of the shell structure of *Anopaea*. A, *Anopaea* sp. nov?, P.2151.3, detail from the postero-dorsal region of a right valve from the South Shetland Islands; contact between the inner nacreous (upper two-thirds of photograph) and outer prismatic calcite layer shown, $\times 280$. B, *A. callistoensis* sp. nov., KG.3404.188, outer prismatic calcite shell layer from the postero-dorsal region of a right valve, $\times 90$. C–D, *A. constricta* (Etheridge, Jr, 1901), F.21077. C, inner nacreous shell layer from the umbonal region of a right valve, $\times 2000$; D, F1317, outer prismatic calcite shell layer from the postero-dorsal region of a right valve, $\times 170$. B and D are perpendicular sections, A and C are slightly oblique.

rounded cross-profiles. The secondary growth lines are superimposed across the entire width of the valve but are at their clearest on the primary folds. Here they are regularly and evenly spaced, often on a sub-millimetre scale (Pl. 1, figs 6–7). Traces of a thin, simple prismatic shell layer are found on a number of specimens; in the postero-dorsal region of KG.3404.188 it reaches slightly in excess of 1 mm in thickness (Text-fig. 4B).



TEXT-FIG. 5. *Anopaea* sp. nov?, Berriasian, Byers Group, Livingston Island, South Shetland Islands. A, P.2151.1, internal mould of an incomplete right valve, showing a blunt, rounded anterior buttress overhanging a deep lunule; B, P.2151.2, internal mould of an incomplete right valve. Both $\times 3$.

Remarks. As remarked previously (Crame 1981, p. 213), there is considerable similarity between this taxon and the approximately coeval Russian species, *Anopaea brachowi* (Rouillier) and *A. sphenoidea* (Gerasimov) (Table 1). The resemblance is perhaps strongest with the latter, although *A. callistoensis* sp. nov. can be distinguished by its subrectangular posterior, and less regular commarginal folds. There may also be some overlap with *A. windhouweri* Boehm from the Tithonian of Indonesia (Crame 1981, p. 213). However, this species is based on a single specimen and efforts to trace it have so far proved unsuccessful. The range of Berriasian species described by Kapitza (1978) from the Far East of the Russian Federation (Table 1) is clearly distinct from this new form, as is *A.* sp. nov? from the South Shetland Islands, to be described below.

A specimen of *Anopaea* from Tithonian–Berriasian strata of the Nordenskjöld Formation, northeastern Antarctic Peninsula is not sufficiently well preserved to compare in detail with the Alexander Island material (Kelly and Doyle 1988).

Anopaea sp. nov?

Text-figures 4A, 5A–B

Material. Internal moulds of two small RV (P.2151.1, 2); external mould RV with shell material (P.2151.3, counterpart of P.2151.2). Locality P.2151 is on the northern face of Point Smellie, Byers Peninsula, Livingston Island, South Shetland Islands ($62^{\circ} 38' 55''$ S; $61^{\circ} 09' 15''$ W) (Text-fig. 2). This locality is at approximately the 350 m level in a composite section through the President Beaches Formation of the Byers Group (Crame *et al.* 1993).

Occurrence. As for material. Associated macro- and microfossils indicate a Berriasian age for this locality; dinoflagellate cyst taxa in particular suggest that this can be refined to Early Berriasian (Crame *et al.* 1993).

Description and remarks. These two small right valves are almost certainly juveniles. The ventral regions of both of them are incomplete, but the dimensions can be estimated at 24 mm (L) by 18 mm (H) for P.2151.1, and 19 mm (L) by 13 mm (H) for P.2151.2. Despite their small size, both these forms are quite distinct from the smallest specimens of *A. callistoensis* sp. nov. and would appear to represent the basis of a new taxon. The hinge region of both specimens is well defined, showing the characteristic concave cross-profile (i.e. in a dorso-ventral section) and anterior termination in a distinct buttress (Text-fig. 5). Although there are no indications of an antero-ventral sulcus, it is clear that both specimens have a narrow, pointed anterior region. Traces of regular commarginal ornament characterize P.2151.1, but on P.2151.2 and P.2151.3 the pattern is much more irregular (Text-fig. 5).

Part of the reason for more irregular ornament on the smaller of the two specimens is that it bears traces of a thickened inner shell layer, which is particularly apparent on P.2151.3. This originally aragonitic layer is approximately 250 μm thick, and perhaps more than this in the hinge region where it is especially prominent (see above). It has a distinctive laminated-foliated texture (Text-fig. 4A) but was originally sheet nacre in composition. Although no unequivocal pits can be detected along the hinge of P.2151.3, it would seem possible that this was the layer on which the ligament was mounted. If this observation is correct, it would mean that in some taxa, or possibly the juveniles of some taxa, the ligament was not mounted on the outer prismatic shell layer (see above). The outer prismatic shell layer is far less prominent on specimens P.2152 and P.2151.3.

Anopaea constricta (Etheridge, Jr, 1901)

Plate 2, figs 1–6; Text-figures 4C–D

- v. 1872 *Inoceramus* allied to *I. problematicus* d'Orbigny; Etheridge, p. 344, pl. 22, fig. 4 [refigured here, Pl. 2, fig. 1; QM F1241; anterior missing therefore appears like *Inoceramus*].
- pv. 1878 *Inoceramus carsoni* M'Coy; Etheridge, Jr, p. 109 [Only the reference to *Inoceramus* allied to *I. problematicus* d'Orbigny; see Etheridge, Jr, 1872; i.e. QM F1241].
- vp. 1892 *Inoceramus carsoni* M'Coy; Etheridge, Jr (in Jack and Etheridge, Jr), p. 463 [Only QM F1241].
- v. 1901 *Inoceramus etheridgei* Etheridge; Etheridge, Jr, p. 22 [QM F1241].
- *v. 1901 *Inoceramus constrictus* sp. nov. Etheridge, Jr, p. 24, pl. 2, fig. 7 [GSQ F1317]; pl. 3, fig. 6 [GSQ F1316] [Rolling Downs Formation, Albian; Hughenden and Marathon Stations, Queensland].
- 1928 *Inoceramus constrictus* Etheridge, Jr; Heinz, p. 144 [Rolling Downs Formation, Hughenden and Marathon Stations, Queensland].
- pv. 1966 *Inoceramus sutherlandi* M'Coy; Ludbrook, p. 157 [Only the reference to *Inoceramus* allied to *I. problematicus* d'Orbigny; see Etheridge, Jr, 1872, i.e. QM F1241].
- pv. 1968 *Inoceramus constrictus* Etheridge, Jr; Day, p. 394, pl. 46, figs 1–8 [Ranmoor Member, Early Albian, Queensland].
- 1969 *Inoceramus constrictus* Etheridge, Jr; Day, p. 151 [Tambo fauna, Albian, Queensland].
- 1981 *Inoceramus constrictus* Etheridge, Jr; Crame, p. 216 [Early Albian, Queensland, Australia].
- v. 1990 *Inoceramus* cf. *sutherlandi* M'Coy; Rozefelds *et al.* p. 687 [QM F1241].

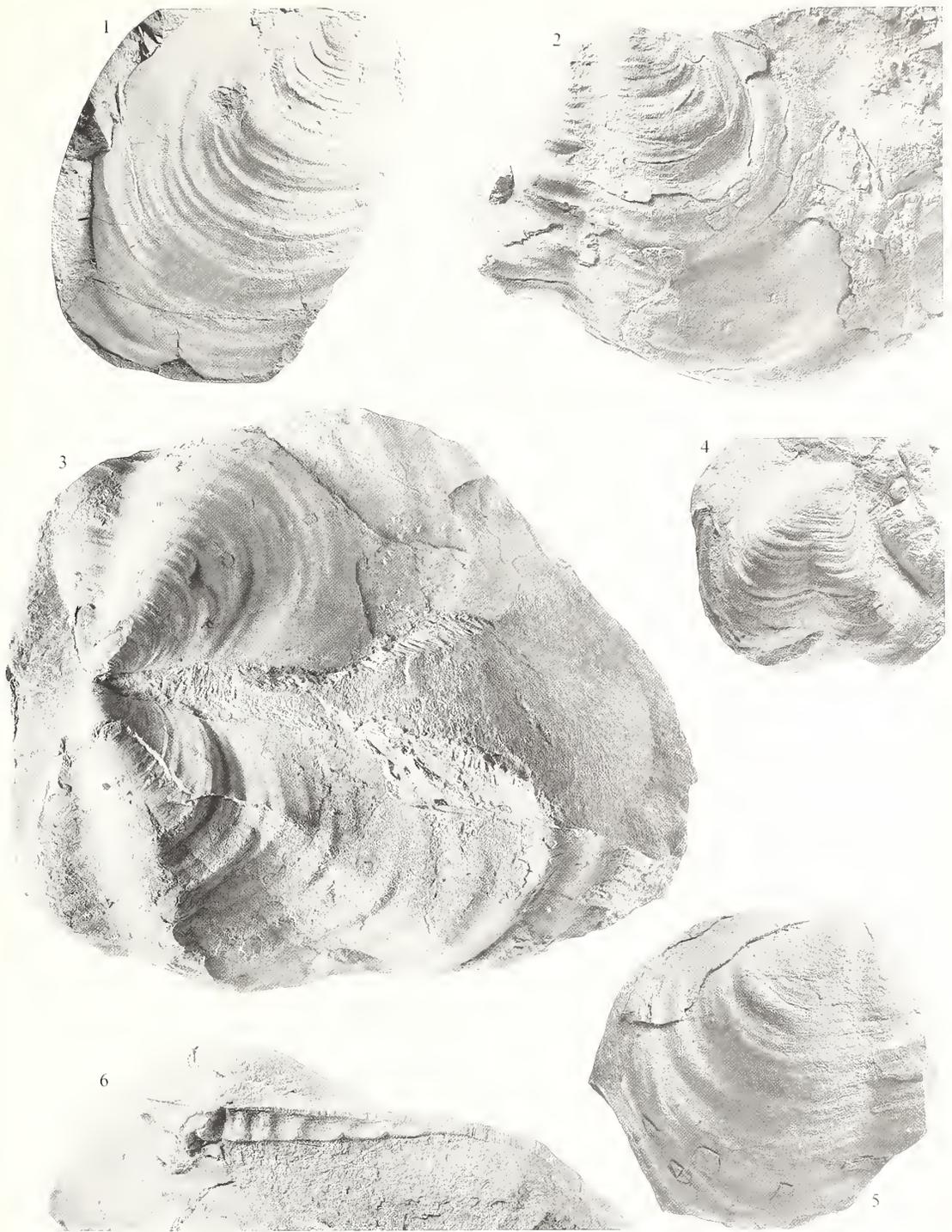
Type and other material. Etheridge, Jr (1901, pl. 2, fig. 7 and pl. 3, fig. 6) figured two syntypes, of which the latter is designated herein as lectotype (= GSQ F1316), and the former as paralectotype (= GSQ F1317). Both specimens are from the Early Albian Ranmoor Member of the Rolling Downs Formation, Queensland; the lectotype is from a locality behind the Hughenden Hotel, Hughenden, Flinders River (Text-fig. 2), and the paralectotype from Marathon Station, Queensland (Day 1968). Other material includes: QM F1241 – originally figured as *Inoceramus* allied to *I. problematicus* d'Orbigny (Etheridge, Jr 1872); QM F16384, F21071, F21072, F21077; as for paralectotype.

Occurrence. As for the type and other material. R. W. Day (pers. comm. 1991) believes that *A. constricta* is associated with *Beudanticeras flindersi* in a level immediately overlying the *Dimitobelus dayi* horizon of the Early Albian of Queensland, Australia.

Diagnosis. Moderately inflated *Anopaea* with well-rounded posterior margin and strongly impressed anterior sulcus.

EXPLANATION OF PLATE 2

Figs. 1–6. *Anopaea constricta* (Etheridge, Jr); Early Albian, Ranmoor Member, Rolling Downs Group, Queensland, Australia. 1, QM F1241, internal mould of a right valve, original of *Inoceramus* allied to *I. problematicus*, d'Orbigny, Etheridge, 1872, p. 344, pl. 22, fig. 4. 2, QM F21072, internal mould of a left valve, with traces of shell material. 3, QM F16384, internal mould of left and right valves in butterfly position. 4, QM F21071, internal mould of a right valve, with traces of shell material. 5–6, GSQ F1317, paralectotype; 5, internal mould of a right valve; 6, the same specimen viewed from the inside and showing detail of the hingeline. Figs 1–5 $\times 1$; Fig. 6 $\times 2$.



CRAME and KELLY, *Anopaea*

Description. The five best preserved specimens (GSQ F1317, QM F16384, F21071, F21072, F21077) show this species to range in length (L) from 50 to 110 mm and height (H) from 39 to 60 mm; mean H/L = 0.734. The same specimens show the typical *Anopaea* form, with perhaps the most striking feature being a deeply impressed antero-ventral sulcus (Pl. 2, figs 2–5); on all specimens this can be traced clearly into the earliest growth stages. As Etheridge, Jr (1901, p. 25) indicated, the maximum degree of inflation occurs immediately posterior to the sulcus, in the central regions of the valve. On the largest specimen (QM F16384), the postero-dorsal region is considerably flattened.

Specimens QM F21071, F21072 and GSQ F1317 display well preserved hingelines. On specimen GSQ F1317, six ligament pits are preserved in a 15 mm strip of hinge immediately posterior to the beak (Pl. 2, fig. 6). Initially, the ligament pits are somewhat narrow and elongate but they broaden posteriorly until the fifth and sixth are comparatively large, oval features measuring 3×1.5 mm. The pits bear fine horizontal striations and are clearly mounted on the prismatic shell layer (Pl. 2, fig. 6). As this ligament surface is inclined at a steep angle to the plane of commissure, it would appear that the ligament must have been partially external (Text-fig. 1D).

On specimen GSQ F1317 (RV), the anterior end of the ligament region terminates in a prominent tongue-like buttress composed of prismatic calcite (Pl. 2, fig. 6). This feature has a length of approximately 4 mm and maximum width (in a dorso-ventral sense and close to its base) of nearly 2 mm; it curves gently towards the left valve but does not appear to have projected across the plane of commissure. The tongue-like appearance is enhanced by a concave upper surface (which is essentially dorsal in aspect) flanked by two sharply defined ridges. There are steep descents on all flanks of the buttress, and on the innermost border there is a small, but distinct, notch. It is unclear at present whether this may represent a point of contact with the left valve buttress.

Traces of a thin (< 1 mm) prismatic shell layer are preserved on the flanks of most specimens and there are also remnants of an altered inner nacreous layer (Text-fig. 4C–D). The ornament pattern on internal moulds is of broad commarginal folds (> 5 mm), with minor folds superimposed (Pl. 2, figs 1–5).

Remarks. Without doubt, this taxon is a *bona fide* member of the genus *Anopaea*. Its general form and style of ornament would seem to set it apart from most other species, although there is perhaps some overlap with *A? mandibula* (Mordvilko) and its allies. *Anopaea* sp. nov. aff. *mandibula* from the Antarctic Peninsula (Table 1) also exhibits a persistent antero-ventral sulcus (Crame 1985, text-fig. 9b), but in general both this form and *A. mandibula sensu stricto* (e.g. Saveliev 1962, pl. 5, figs 1–11) have finer and more closely spaced ornament.

DISTRIBUTION AND PHYLOGENETIC POSITION

Following the taxonomic reappraisal of *Anopaea*, it is possible to review its distribution in both time and space. The first occurrences in the stratigraphical record can now be confirmed as Tithonian (or Volgian in the Boreal realm), and in all probability this can be refined to the Late Tithonian (Table 1). At this time the genus was represented by the very distinctive *A. brachowi* and *A. sphenoides* in localities such as the Russian Platform and eastern England, and the not dissimilar *A. callistoensis* sp. nov. in the Antarctic Peninsula. There are also further probable Tithonian occurrences of *Anopaea* in the Carpathian Mountains, southern Tibet, Indonesia and New Zealand (see below).

New earliest Cretaceous (Berriasian) localities for the genus include the South Shetland Islands, Mangyshlak and the Far East of the Russian Federation (Lower Priamur) (Table 1). In the latter region the genus can also be extended into the succeeding Valanginian stage. Thereafter, however, the Early Cretaceous record of *Anopaea* is somewhat sketchy. *Anopaea trapezoidalis* from the Antarctic Peninsula occurs in strata that are judged to be younger than Valanginian but pre-Aptian in age; nevertheless, no diagnostic Hauterivian or Barremian fossils are yet known from the Fossil Bluff Group of Alexander Island (Crame and Howlett 1988). The next definite datum for the genus is the Albian, with a possible occurrence in Mangyshlak, and definite occurrences in Antarctica (both Alexander Island and James Ross Island) and Queensland, Australia; there is a strong probability that all these occurrences can be referred to the Early Albian.

As has been remarked on previously, it is rather striking how the bulk of these occurrences fall within the Late Jurassic–Early Cretaceous extra-Tethyan regions; *Anopaea* may be said to have had

an essentially bipolar distribution (Crame 1993, and references therein). However, it is necessary to qualify this statement, for a few records may in fact be from Tethyan localities. In particular, *A? straubergeensis* occurs in the Stramberger Schichten in association with a Tethyan fauna, although Boehm (1883, p. 594) noted that the two specimens of this species were of somewhat atypical lithology; they may have originated from another bed, or possibly not from Stramberg at all. The Berriasian Mangyshlak record is also from a region of interdigitating Boreal and Tethyan facies, but it is clear that in this instance the specimen of *Anopaea* sp. indet. occurs in association with a *Buchia* bivalve assemblage (Bogdanova 1988). Lower latitude occurrences of the genus in the Southern Hemisphere include *A? stoliczkai*, if this is indeed a true member of the genus, and *A? verbeeki* and *A? windhouweri* from Indonesia. It can be concluded that, with a small number of exceptions, *Anopaea* had an essentially amphitropical distribution from at least the Late Tithonian to the Early Albian. In this sense it would indeed seem to qualify as a bipolar taxon. What perhaps should also be emphasized here is that new evidence is coming to light which suggests that this was not a deep water inoceramid. Although it was once suggested that *Anopaea* may have achieved widespread distribution via a deep water route (Crame 1981, p. 216), this now seems less likely. *Anopaea callistoensis* sp. nov., for example, is known to occur in association with a molluscan assemblage which suggests comparatively shallow-water, nearshore environments (Crame and Howlett 1988). Similar environments are also indicated for the coeval boreal species, *A. brachowi* and *A. spheoidea* (Kelly 1984).

The combination of features, such as the elongate-pyriform outline, antero-ventral sulcus, cordiform lunule and anterior buttress, serves to distinguish *Anopaea* at least at the generic level. It is becoming increasingly apparent that the latest Jurassic–earliest Cretaceous interval was a time of major turnover in global inoceramid faunas, with the replacement of *Retroceramus*-dominated ones by *Inoceramus sensu lato*-dominated ones (e.g. Pokhialanen 1974; Crame 1985). *Anopaea* flourished briefly in the transitional phase between these two great faunas but appears to have become increasingly rare through the latter part of the Early Cretaceous. Indeed, should *A? maudibula* prove not to be a member of the genus, it may be that, by the early Albian, *Anopaea* was restricted to southern high latitudes.

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REFERENCES

- 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. *Bulleten Moskovskogo obshchestva, Ispytateley Prirody, Otdel Geologicheskij*, **35**, 486–500.
- BOEHM, G. 1883. Die Bivalven des Stramberger Schichten. *Palaeontographica*, Supplement II, Abt. 4, 493–680.
- 1904. Beiträge zur Geologie von Niederländisch-Indien. I. Abt. Die Südküsten der Sula-Inseln Taliabu und Mangoli. I. Abs. Grenzschichten zwischen Jura und Kreide. *Palaeontographica*, **4**, (Supplement), 1–46.
- BOGDANOVA, T. N. 1988. Class Bivalvia. 134–156. In KRIMGOLTS, G. (ed.), *Berriasian of Mangyshlak. Trudy AN SSSR, Mingeo SSSR, stratigraficheskij komitet SSSR*. Nauka, Moscow, 204 pp. [In Russian].
- BUTTERWORTH, P. J., CRAME, J. A., HOWLETT, P. J. and MACDONALD, D. I. M. 1988. Lithostratigraphy of Upper Jurassic–Lower Cretaceous strata of eastern Alexander Island, Antarctica. *Cretaceous Research*, **9**, 249–264.

- COX, L. R. 1969. Family Inoceramidae Giebel, 1852. N314–N321. In MOORE, R. C. (with TEICHERT, C., McCORMICK, L. and WILLIAMS, R. B.) (eds). *Treatise on invertebrate paleontology, Part N, Vol. 1, Mollusca, 6. Bivalvia*. Geological Society of America and University of Kansas Press, Boulder, Colorado, 489 pp.
- CRAME, J. A. 1981. The occurrence of *Anopaea* (Bivalvia: Inoceramidae) in the Antarctic Peninsula. *Journal of Molluscan Studies*, **47**, 206–219.
- 1985. Lower Cretaceous inoceramid bivalves from the Antarctic Peninsula region. *Palaontology*, **28**, 475–525.
- 1993. Bipolar molluscs and their evolutionary implications. *Journal of Biogeography*, **20**, 145–161.
- and HOWLETT, P. J. 1988. Late Jurassic and Early Cretaceous biostratigraphy of the Fossil Bluff Formation, Alexander Island. *Bulletin of the British Antarctic Survey*, **78**, 1–35.
- PIRRIE, D., CRAMPTON, J. S. and DUANE, A. M. 1993. Stratigraphy and regional significance of the Late Jurassic–Early Cretaceous Byers Group, Livingston Island, Antarctica. *Journal of the Geological Society, London*, **150**, 1075–1087.
- CRAMPTON, J. S. 1988. Comparative taxonomy of the bivalve families Isognomonidae, Inoceramidae and Retroceramidae. *Palaontology*, **31**, 965–996.
- DAY, R. W. 1968. Biostratigraphy and taxonomy of Lower Cretaceous molluscan faunas from the Queensland portion of the Great Artesian Basin. Unpublished PhD thesis, Australian National University.
- 1969. The Lower Cretaceous of the Great Artesian Basin. 140–173. In CAMPBELL, K. S. W. (ed.). *Stratigraphy and palaeontology. Essays in honour of Dorothy Hill*. Australian National University Press, Canberra, 390 pp.
- DHONDT, A. V. 1992. Cretaceous inoceramid biogeography: a review. *Palaogeography, Palaeoclimatology, Palaeoecology*, **92**, 217–232.
- EICHWALD, E. 1861. Der Grünsand in der umgegend von Moskwa. *Bulletin de la Société des Naturalistes de Moscou*, **34**, 278–313.
- 1865. *Lethaea Rossica; ou paléontologie de la Russie décrite et figurée. 2. Première section de la période moyenne*. E. Schweizerbart, Stuttgart, 1304 pp.
- ETHERIDGE, R. 1872. Description of the Palaeozoic and Mesozoic fossils of Queensland. In DAINTREE, R. Notes on the geology of the colony of Queensland. *Quarterly Journal of the Geological Society, London*, **28**, 317–350.
- ETHERIDGE, JR., R. 1878. *A catalogue of Australian fossils (including Tasmania and the island of Timor)*. Cambridge University Press, Cambridge, 232 pp.
- 1892. In JACK, R. L. and ETHERIDGE, JR., R. *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, Vol. I, 768 pp., Vol. 2, 68 pls.
- 1901. Additional notes on the palaeontology of Queensland (part 2). *Bulletin of the Geological Survey of Queensland*, **13**, 1–37.
- FLEMING, C. A. 1958. Upper Jurassic fossils and hydrocarbon traces from the Cheviot Hills, North Canterbury. *New Zealand Journal of Geology and Geophysics*, **1**, 375–394.
- GERASIMOV, P. A. 1955. *Rukovodyashchiye iskopayem'ye Mesozoya tsentral'nykh oblastey evropeyskoy chasti SSSR. Chast 1. [Principal Mesozoic fossils of the central regions of the European part of the USSR. Part 1. Lamellibranchiata, Gastropoda, Scaphoda and Brachiopoda of the Jurassic deposits]*. Gosgeoltekhizdat, Moscow, 379 pp. [In Russian].
- GIEBEL, C. G. 1852. *Allgemeine Palaentologie: Entwurf einer systematischen Darstellung der Fauna und Flora der Vorwelt*. Ambrosius Abel, Leipzig, viii + 413 pp.
- GOLDFUSS, A. and MÜNSTER, G. 1835. *Petrefacta Germaniae. Volume 2*, Dusseldorf, 69–140, pls 97–121.
- HEINZ, R. 1928. Über die Kreide-Inoceramen Australiens und ihre Beziehungen zu denen Europas und anderer Gebiete. Beiträge zur Kenntnis der oberkretazischen Inoceramen VIII. *Mitteilungen aus dem mineralogisch-geologischen Staatsinstitut in Hamburg*, **10**, 131–147.
- HOLDHAUS, K. 1913. Fauna of the Spiti Shales (Lamellibranchia and Gastropoda). *Memoirs of the Geological Survey of India Palaontologica Indica*, **4**, 397–456, pls 94–100.
- KAPITZA, A. A. 1978. Novye vidy nizhnemelovykh inotseramid nizhnego priamur'ya [New species of Lower Cretaceous inoceramids from Lower Priamur]. 65–77, pls 4–6. In POYARKOVA, Z. N. (ed.). *Biostratigrafiya yuga dal'nego vostoka (fanerozoj) [Biostratigraphy of the south of the Far East (Phanerozoic)]*. DVNTS AN SSSR, Vladivostok, 139 pp. [In Russian].
- KELLY, S. R. A. 1984. Bivalvia of the Spilsby Sandstone and Sandringham Sands (Late Jurassic–Early Cretaceous) of eastern England. Part 1. *Monograph of the Palaeontographical Society*, **137** (566), 1–94, i–xii, 20 pls.

- and DOYLE, P. 1988. The bivalve *Anlacomyella* from the Early Tithonian (Late Jurassic) of Antarctica. *Antarctic Science*, **3**, 97–107.
- LUDBROOK, N. H. 1966. Cretaceous biostratigraphy of the Great Artesian Basin in South Australia. *Bulletin of the Geological Survey of South Australia*, **40**, 1–223.
- MEDINA, F. A. and BUATOIS, L. A. 1992. Biostratigrafía del Aptiano-Campaniano (Cretácico Superior) en la Isla James Ross. 37–45. In RINALDI, C. A. (ed.). *Geología de la Isla James Ross*. Instituto Antártico Argentino, Buenos Aires, 389 pp.
- MORDVILKO, T. A. 1949. *Atlas rukovodyashchikh form iskopayemykh faun. SSSR, Tom X. Nizhniy mel. Otdel Lamellibranchiata* [Atlas of the index forms of the principal faunas of the USSR. Vol. 10. Lower Cretaceous. Class Lamellibranchiata]. Gostoptekhizdat, Moscow, 120–159. [In Russian].
- NEWELL, N. D. 1965. Classification of the Bivalvia. *American Museum Novitates*, **2206**, 1–25.
- POKHIALAINEN, V. P. 1969a. Neokomskiye inotseramy anadyrskogo-koryakskoy skladchatoy oblasti [Neocomian inoceramids from the Anadyr-Koryak folded region]. In SHILO, N. A. (ed.). *Inotseramy yury i mela severo-vostoka SSSR [Jurassic and Cretaceous inoceramids from the North East USSR]*. *Trudy Severo-Vostoknogo Kompleksnogo Nauchno-Issledovatel'skogo Instituta*, **32**, 124–162. [In Russian].
- 1969b. O kharaktere sochleneniya stvorok u inotseramid neokoma [On the characteristics of valve articulation in Neocomian inoceramids]. In SHILO, N. A. (ed.). *Inotseramy yury i mela severo-vostoka SSSR [Jurassic and Cretaceous inoceramids from the Far East USSR]*. *Trudy Severo-Vostoknogo Kompleksnogo Nauchno-Issledovatel'skogo Instituta*, **32**, 118–123.
- 1972. Sistematicheskoe polazhenie inotseramid neokoma [Systematic position of the inoceramids in the Neocomian]. 57–65. In PERGAMENT, M. A. (ed.). *Trudy Vsesoyuznogo Kollokviuma po Inotseramam* [Transactions of the All-Union Colloquium on inoceramids]. Vol. 1. Academia Nauk SSSR, Geologicheskii Institut, Moscow, 167 pp. [In Russian].
- 1974. Osobennosti rasprostraneniya inotseramid neokoma tikhookeanskoy oblasti [Spreading of the Neocomian Pacific inoceramids]. *Trudy Instituta Geologii i Geofiziki, Sibirskoe Otdelenie*, **80**, 174–187. [In Russian].
- ROUILLIER, C. 1849. In ROUILLIER, C. and VOSSINSKY, A. Études progressives sur la géologie de Moscou; quatrième étude. *Byulleten' Moskovskogo obshchestva, Ispytateley Prirody, Otdel Geologicheskij*, **22**, 337–355.
- ROZEFELDS, A. C., MCKENZIE, E. D. and MOBBS, C. 1990. Type, figured and mentioned fossil invertebrates in the Queensland Museum. *Memoirs of the Queensland Museum*, **28**, 665–713.
- SAVAZZI, E. 1987. Geometric and functional constraints on bivalve shell morphology. *Lethaia*, **20**, 293–306.
- SAVELIEV, A. A. 1962. Al'bskiye inotseramidy Mangyshlaka [Albian inoceramids from Mangyshlak]. In SAVELIEV, A. A. (ed.). *Paleontologicheskij sbornik, 3 [Palaeontological Collection, 3]*. *Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta*, **196**, 219–254 [In Russian].
- THOMSON, M. R. A. and WILLEY, L. E. 1972. Upper Jurassic and Lower Cretaceous *Inoceramus* (Bivalvia) from south-east Alexander Island. *Bulletin of the British Antarctic Survey*, **29**, 1–19.

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DECAY AND FOSSILIZATION OF NON-MINERALIZED TISSUE IN COLEOID CEPHALOPODS

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ABSTRACT. Decay experiments were carried out on three Recent species of coleoid cephalopods (the squids *Alloteuthis subulata* and *Loligo forbesi*, and the sepiolid *Sepiolo atlantica*) over a period of 1 day to 50 weeks. The morphological sequence of degradation and the fate of the more decay resistant organs (beaks, radula, suckers, gladius, statoliths, eye lenses) were recorded. Crystalline magnesium phosphate precipitated, but tissue ultrastructure was not preserved. Sex and stage of maturity may influence rate of degradation. Differences in buoyancy mechanism, physiological changes during reproduction, and post-mortem decay processes affect the highly variable preservation potential of modern coleoids.

Of the six genera (*Belemnotheutis*, *Mastigophora*, *Loligosepia*, *Geopeltis*, *Plesioteuthis* and *Trachyteuthis*) of exceptionally preserved Jurassic fossil coleoids examined for evidence of ultrastructural preservation, *Mastigophora* exhibits a continuous series of tissues from the outer tunic, through the mantle and gladius, to the muscular sheath of the digestive gland. In *Belemnotheutis* and *Mastigophora* the radial and circular muscle, the outer collagenous tunic and the supporting meshwork of intramuscular fibres are all preserved. Longitudinal fibres are evident in the arms and in the mantle of some specimens. The texture of the calcium phosphate replacing the soft-tissue varies even within a specimen. Muscles may be represented by the fibres, or only the sarcolemma. The microspheres of calcium phosphate are 1–2 μm in diameter in the former (perhaps representing the microbes themselves), but only 0.1 μm in the latter (where precipitation is induced by microbial processes). Microspheres in the tunic are 0.5–0.25 μm in diameter. Muscle, tunic, intramuscular fibres and ink are preserved in calcium phosphate. Gladius material is finely banded, with varying proportions of diagenetic calcium phosphate and calcium carbonate in each of the layers in *Geopeltis* from Charmouth. The mantle morphology found in *Mastigophora* and *Belemnotheutis* corresponds with that found in living coleoid cephalopods and indicates that this structure had evolved by the Early Jurassic. This calls into question the systematic position of *Belemnotheutis* as a member of the Belemnitida. It is clear that phosphatization of ultrastructural detail is not confined to a small number of unusual localities. There is considerable potential for histological investigations of the soft-tissues of a range of extinct organisms.

THE Coleoidea, typified by the extant squids, cuttlefish and octopus, rank alongside the Nautiloidea and Ammonoidea as the third major subclass of cephalopods. Whilst the nautiloids and ammonoids have a heavy external shell, most coleoids, with the exception of the living families Sepiidae and Spirulidae and the extinct order Belemnitida, have negligible mineralized tissue and are essentially soft-bodied. Nevertheless the soft tissues of coleoid cephalopods are preserved at a number of Jurassic localities (Table 1), e.g. Holzmaden (Toarcian), Germany; Christian Malford (Callovian), England (Donovan 1983; Allison 1988; Page 1991; Donovan and Crane 1992); Voulte-sur-Rhône (Callovian), France (Fischer and Riou 1982a, b); Solnhofen (Tithonian), Germany (Bandel and Leich 1986; Mehl 1990), as well as in the Cretaceous (Albian) of NW Queensland (Wade 1993), the Carboniferous Mazon Creek biota of Illinois (Allison 1987) and possibly the Devonian (Emsian) Hunsrückschiefer of Germany (Stürmer 1985). Whilst the morphology of a number of coleoids that preserve traces of the soft parts has recently been described in detail from these localities, the mineralization of the soft-tissues has only been subjected to preliminary investigation (Allison 1988; Mehl 1990). The aim of this study is to identify the tissue types preserved in coleoids, to determine the degree of morphological detail preserved, and to interpret this in the light of controlled decay

TABLE 1. Types of soft tissues reported in fossil coleoids. —, feature is not preserved; ?, feature may be preserved; n/a, feature would not normally occur in the coleoids represented in this fauna. Sources of information: Fischer and Riou 1982a; Donovan 1983; Bandel and Leich 1986; Allison 1987, 1988; Mehl 1990; Donovan and Crane 1992.

Locality	Tissue/organ						
	Mantle	Arms	Tentacles	Jaws	Gills	Ink sac	Gladius
Solnhofen	Present	Present	?	Present	Present	Present	Present
Voulte-sur-Rhône	Present	Present	Present	Present	—	Present	Present
Christian Malford	Present	Present	Present	—	—	Present	Present
Holzmaden	Present	—	—	—	—	Present	Present
Lias	—	—	—	—	—	Present	Present
Mazon Creek	—	Present	n/a	Present	—	?	Present

experiments on recent cephalopods. Only when the decay process is understood can fossil tissue be reliably interpreted by comparison with living analogues. This has allowed the evolution of mantle ultrastructure in coleoids to be analyzed. Controls on mineralization were investigated in other experiments using smaller animals (polychaetes and shrimps) which are more easily obtained and processed in the sample sizes required (Briggs and Kear 1993a, 1993b, 1994; Briggs *et al.* 1993).

COLEOID HISTOLOGY AND ULTRASTRUCTURE

Living coleoids have a range of structural tissues of differing composition and resistance to decay (Table 2). The chitin of the buccal mass and digestive system is interconnected and may form a continuous sheet (Kear 1990), starting at the inner surfaces of the lips and encompassing the beaks, hyaline shield of the radula, buccal palp surface and teeth, and oesophageal and stomach lining. Lip chitin has only been reported in adult *Mesonychoteuthis* (Kear 1990). The radular teeth, which originate separately to the hyaline shield (Nixon 1968) and differ in composition, may not be part of this continuum.

Secretion and tanning of the chitin in beaks is carried out by epithelial cells known as beccublasts (Dilly and Nixon 1976), which act as holdfasts for the mandibular muscles (Dilly and Nixon 1976), as well as performing a secretory function. Similar 'chitinoblast' cells are found in association with the radula and hyaline shield (Nixon 1968), buccal palps, oesophagus and possibly the papillary shield (Kear 1990).

The muscular mantle of coleoids is used for both propulsion and respiration. The mantle of the Decapoda (= Decabrachia) (Text-fig. 1) is composed of a thick layer of circular muscle partitioned into bands by thin sheets of radial muscle (Ward and Wainright 1972; Bone *et al.* 1981). Longitudinal muscles have only been observed in *Sepia officinalis* (Bone *et al.* 1981). Layers of parallel collagen fibres (Text-fig. 1) encase the mantle muscle, running around the mantle (the inner and outer tunics) in alternate left and right-handed helices (Ward and Wainright 1972). In addition, there is a network of intramuscular connective tissue within the mantle (Ward and Wainright 1972; Bone *et al.* 1981). This tissue consists of fibres composed of collagen (Bone *et al.* 1981; Gosline and Shadwick 1983) and possibly elastin (Bone *et al.* 1981) and forms a mesh throughout the muscle (Text-fig. 1). The tunics and mesh resist length changes in the mantle during contraction (Ward and Wainright 1972).

Decapod coleoids (Teuthida, Sepiida and Sepiolida) have four pairs of arms and one pair of tentacles; the latter are a specialist prey capture mechanism with suckers present only on the

TABLE 2. Location and composition of the main structural tissues (where present) in living coleoid cephalopods.

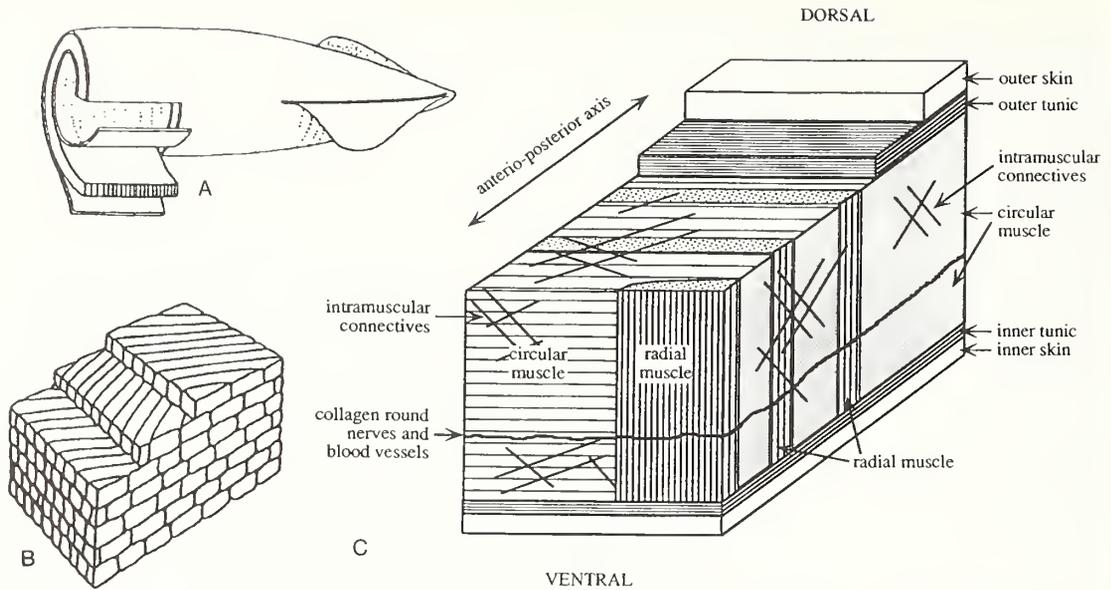
Tissue/organ	Composition	Author
Suckers and/or hooks	β chitin	Hunt and Nixon 1981
Lip lining	Chitin (?type)	Kear 1990
Beaks	α chitin	Hunt and Nixon 1981
Radula	α chitin	Hunt and Nixon 1981
Hyaline shield	chitin (?type)	
Buccal palp teeth	α chitin	Hunt and Nixon 1981
Oesophagus lining	Chitin (?type)	Kear 1990
Stomach lining	γ chitin	Rudall and Kenchington 1973
	α chitin	Rudall and Kenchington 1973; Hunt and Nixon 1981
Brain and nuchal cartilage	Collagen	Nesis 1987
Statoliths	Aragonite	
Eye lenses	Crystallin	
Mantle locking cartilage	Collagen	Nesis 1987
Gladius	β chitin	Rudall and Kenchington 1973; Hunt and Nixon 1981
Internal shell	Calcite and chitin	
Skin tubercles	Collagen	Nesis 1987
Tunics of mantle muscle	Collagen	Ward and Wainright 1972; Bone <i>et al.</i> 1981; Gosline and Shadwick 1983
Intramuscular mesh	Collagen	Bone <i>et al.</i> 1981; Gosline and Shadwick 1983
	Elastin	Bone <i>et al.</i> 1981

terminal portion. In resting position the tentacles are retracted within the cone of the arms, or into special pouches (cuttlefish). Certain species of squid only possess tentacles as juveniles. The musculature of both arms and tentacles is more complex than that of the mantle, consisting of longitudinal, transverse, circular, oblique and helical muscle (Kier 1982, 1988), the last in the tentacles only.

The muscular tissues may undergo substantial morphological changes as a coleoid matures. A number of species resorb their own tissues – particularly mantle, tentacles and arms – to provide energy and resources for gonad growth. This is seen at its most extreme in the squid *Moroteuthis ingens*, in which immature females have thick (up to 10 mm), muscular mantle walls, but mature individuals have a thin, gelatinous mantle (Jackson and Mladenov 1994). Histological examination reveals that the tissue breakdown is due to a loss of muscle, leaving only the intramuscular collagen fibres intact. In spent (i.e. post-spawning) individuals even the collagen breaks down. None of these changes is as extreme in males of the same species (Jackson and Mladenov 1994). In contrast, species which need to retain swimming ability for long migrations to spawning grounds show no loss of mantle integrity with maturation (e.g. *Illex argentinus*; Clarke *et al.* 1994).

There are phylogenetic contrasts as well. In neutrally buoyant families, such as the Architeuthidae and Histioteuthidae, active swimming ability is not needed, and only the fins and tentacles are strongly muscular. Similarly, in some of the oceanic octopods (e.g. Cirroteuthidae, Vitreledonellidae), the ‘muscular’ layer of the mantle is a watery cellular matrix with sparse collagenous and muscle fibres even in juveniles (Nesis 1987). The preservation potential of coleoids therefore varies widely.

Underlying the mantle is the gladius (pen), a chitinous sheet for support and muscle attachment. Muscle and connective tissue surround the digestive gland and other internal organs.



TEXT-FIG. 1. Diagrammatic representation of coleoid mantle and tunic morphology. A, squid body, showing the position of outer tunic, mantle muscle and inner tunic; B, the layered structure of the tunic; C, a section through the skin and upper mantle, showing muscle morphology in relation to the antero-posterior axis of the animal; radial and circular muscle and intramuscular connectives are marked; patterning on the muscle indicates fibre orientation. A–B re-drawn, with permission, from Ward and Wainright (1972).

MATERIALS AND METHODS

Recent coleoid cephalopod material was obtained from the Plymouth Marine Laboratory, UK. The squids *Alloteuthis subulata* and *Loligo forbesi* (Teuthida: Loliginidae) and the cuttlefish *Sepiolo atlantica* (Sepiolida: Sepiolidae) were trawled off Plymouth. The animals used for experiments were those which were brought up dead or dying in the nets, or died overnight in the stock tanks. Only the heads of *Loligo* ($n = 16$: dorsal mantle length 135–295 mm; body weight 111.7–587.9 g) were utilized in experiments. Whole *Alloteuthis* ($n = 16$: dorsal mantle length 60–85 mm) and *Sepiolo* ($n = 4$: dorsal mantle length 15–20 mm) were utilized.

Specimens were placed in 250 ml Kilner jars with 150 ml (*Alloteuthis*, *Sepiolo*) or 200 ml (*Loligo*) of seawater from the Plymouth Marine Laboratory's research circulation (salinity 33.1 ppt; pH 7.63 ± 0.06) and transferred to an incubator at 20 °C within 4 hours. These experiments correspond to the 'slow diffusion' type (1b) of Briggs and Kear (1993a, 1994).

Specimens were inspected/sampled after 1, 2, 3, 4, 7 and 10 days and after 2, 3, 4, 6, 8, 10, 15, 20, 25, 30 and 50 weeks. Morphological changes were recorded without opening the jars or disturbing the carcass. Sampling for analysis involved decanting off the seawater and filtering or sieving the remains. More decay resistant organs (beaks, radula, statoliths, eye lenses, gladius, suckers) were removed and fixed in alcohol. Material was fixed for SEM using the glutaraldehyde-HMDS method (Nation 1983). The remains of the carcass were oven-dried at 105 °C to constant weight. The colour and pH of the seawater within the experimental vessel were noted. Crystalline material was removed from the carcass for analysis with the electron microprobe.

Fossil coleoids which commonly preserve muscle fibres are likely to preserve other soft tissues. Exceptionally preserved material held in the collections of the Natural History Museum (NHM) and Bristol City Museum (BRSMG) was therefore examined (see Appendix). The investigation

TABLE 3. Decay stages in *Alloteuthis* and *Sepiolo*.

After 1 day: Post-mortem

The carcass is firm. The outer layer of mantle skin shows signs of disintegration while the chromatophores of the inner layer contract, giving the animal a pale appearance. The skin shrinks away from the mantle in places, revealing the muscle underneath, which turns opaque white. The ink behaves as a liquid. Some eggs escape down the funnel of a mature female *Sepiolo*.

After 2 days: Osmotic effects

The muscle (arms, funnel, mantle, fins) becomes soft. The arms and mantle may be swollen. The swollen egg mass of mature *Sepiolo* displaces and tears the mantle.

After 3 days: Shrinkage

The arms and eyes, and some of the outer layer of skin, begin to detach from the carcass. Pigment granules are scattered in the water. The muscles disintegrate if disturbed. The body and arms have shrunk, and contraction of the mantle reveals the edge of the ink sac, anus and spermatophoric duct. The gladius of *Alloteuthis* may protrude from the front of the mantle, but is structurally indistinguishable from fresh material (Text-fig. 3D). The gills may be swollen. The muscle of the head has shrunk, making the eyes appear disproportionately large. A bulge in the arm cone may represent the folded tentacles swollen in their "pouch". The chitinous arm suckers may remain in place (*Sepiolo*) (Text-fig. 3E) or be mainly detached due to decay of the attachment muscles (*Alloteuthis*). The ink solidifies.

After 1 week: Disintegration begins

The carcass shrinks further and collapses unless the shape of the mantle is maintained by reproductive material inside (in female *Alloteuthis*). Surviving pigment is very dark. The fins may detach, and the head drifts away from the mantle. The beaks and radula remain in the buccal mass, although the edges of the beaks may have disintegrated. The gladius becomes brittle. Few sucker rings are still attached. Retinal pigment may stain the eye lenses, beaks, and pen. The outer membranes of the ink sac disintegrate, but the ink remains a unit. The digestive gland may still be evident. The spermatophores of *Sepiolo* survive as bunches of transparent tubes, some still containing sperm. The gills of *Alloteuthis* remain evident and possible nidamental glands are visible in females. In places a layer of white crumbly mineralized material is present beneath the pigment layer, but above the mantle muscle. Although the quantity was inadequate for analysis, the crystal form and occurrence are similar to magnesium phosphate that sometimes precipitated in decay experiments on the shrimp *Palaemon* (Briggs and Kear 1994).

After 2 weeks

The carcass has shrunk to several amorphous masses. The outline of the arms and the associated eye lenses remains evident. The ink and remains of mantle may survive as one unit (*Sepiolo*) or the gonad alone is intact and three-dimensional (*Alloteuthis*). Other internal organs have completely decayed or are unrecognizable. Eggs are scattered. The beccublast cells appear white and fibrous and retain their original structure in *Alloteuthis*. A thin membrane peels away from the inner surface of the gladius (Text-fig. 3E). A white coating of mineralized material (probably $MgPO_4$) may be present on the upper surface of gonad and some muscle, as well as on the bottom of the jar. It occurs either as a thin structureless crust or as scattered crystal laths and needles.

After 8–10 weeks

The head and mantle disintegrate further, and muscle peels away from the pen in places. The arms may be recognizable. The eyes are visible as dark purple areas surrounding the lenses. The gonad remains three-dimensional only in *Alloteuthis*.

focused on *Belemnotheutis antiquus* (Belemnitida: Belemnotheutidae) and *Mastigophora brevipinnis* (Teuthida: Mastigophoridae) from Christian Malford, Oxfordshire (Jurassic, Callovian), but material of *Plesiotеuthis prisca* (Teuthida: Plesiotеuthididae) and *Trachyteuthis hastiformis* (Teuthida: Trachyteuthidae) from Solnhofen (Jurassic, Tithonian); *Loligosepia* (= *Geoteuthis*) sp. (Teuthida: Loligosepiidae) from Gloucestershire and Somerset (Jurassic, Upper Lias); and

TABLE 4. Decay stages in *Loligo*.

After 1 week

The head begins to swell. The outer muscle is stained pink. The sucker rings are fragile and detach easily (Text-fig. 3G). The eyes are represented by dark patches and may have separated from the carcass. The lenses remain intact and the brain cartilage is hard. The buccal muscles shrink and lose their shape when disturbed. The beaks pull out with no resistance; lip muscle tissue may remain attached to the lower beak.

After 2 weeks

Gas bubbles are present under the skin. The sucker rings, statoliths and eye lenses are stained pink by retinal pigment. The eyes and tentacles fall off and most of the sucker rings detach. The buccal muscle tissue disintegrates. The brain cartilage becomes soft and spongy and no neural tissue remains.

After 3–4 weeks

The head may float due to the presence of additional gas bubbles. The manus of the tentacles, the eyes and much of the muscle disintegrates. The untanned areas of the beaks are now stained. The anterior of the radula disintegrates. Dark purple-pink crystals of $MgPO_4$ form in the skin of the arms and around the shrinking brain cartilage.

After 6 weeks

The head disintegrates to an amorphous semi-liquid. The beaks disarticulate; some semi-liquid muscle adheres inside the hood area. Only the eyes, brain cartilage and arms are recognizable. Nearly all the sucker rings detach.

After 10 weeks

Only the arms, tentacles, and a few sucker rings are recognizable, but they disintegrate if disturbed. Many doughnut- and spiral-shaped crystals of magnesium phosphate (Table 5) occur loose and on the arms; they form on the sucker rings which may be embedded within them (Text-fig. 3H–I). Their purple colour is derived mainly from the retina, and to a lesser extent from the chromatophores.

After 15–30 weeks

A crumbly, largely amorphous mass containing crystals, either individual or clusters of needles up to 3 mm long, covers the bottom of the experimental vessel. Parts of the arms and tentacles may be recognizable. The brain cartilage has largely disappeared. The edges of the beaks decay. The radula disintegrates if disturbed.

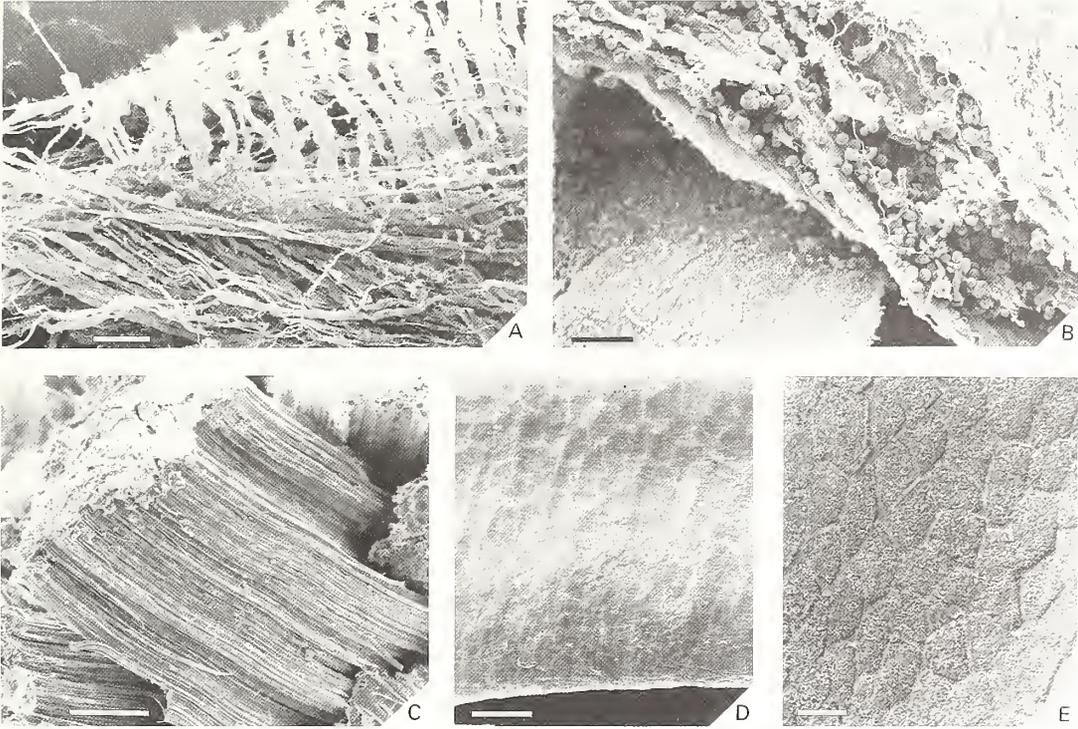
After 50 weeks

The beaks and part of the radula are evident, together with crystals, in a mass of semi-liquid tissue. There is no trace of the suckers.

Geopeltis simplex (Teuthida: Geopeltidae) from Boll, Württemberg, Germany (Jurassic, Upper Lias) was also examined.

Small pieces of phosphatized mantle were removed from specimens of the Christian Malford taxa *Belemniotheutis antiquus* (specimens NHM C.46898 and NHM C.2456) and *Mastigophora brevipinnis* (NHM 31362, NHM 46964 and NHM 62231) for investigation by scanning electron microscopy. Where possible, the orientation of the fragments relative to the antero-posterior axis of the specimens was noted. Muscle fragments from *Mastigophora brevipinnis* (NHM 31362) were analyzed by electron microprobe.

A specimen of *Geopeltis* sp. (University of Bristol, Geology Department, BRSUG 25602) from Black Ven, Charmouth, Dorset (Jurassic, Lower Lias) was sectioned and polished for analysis by light microscopy, SEM and electron microprobe.



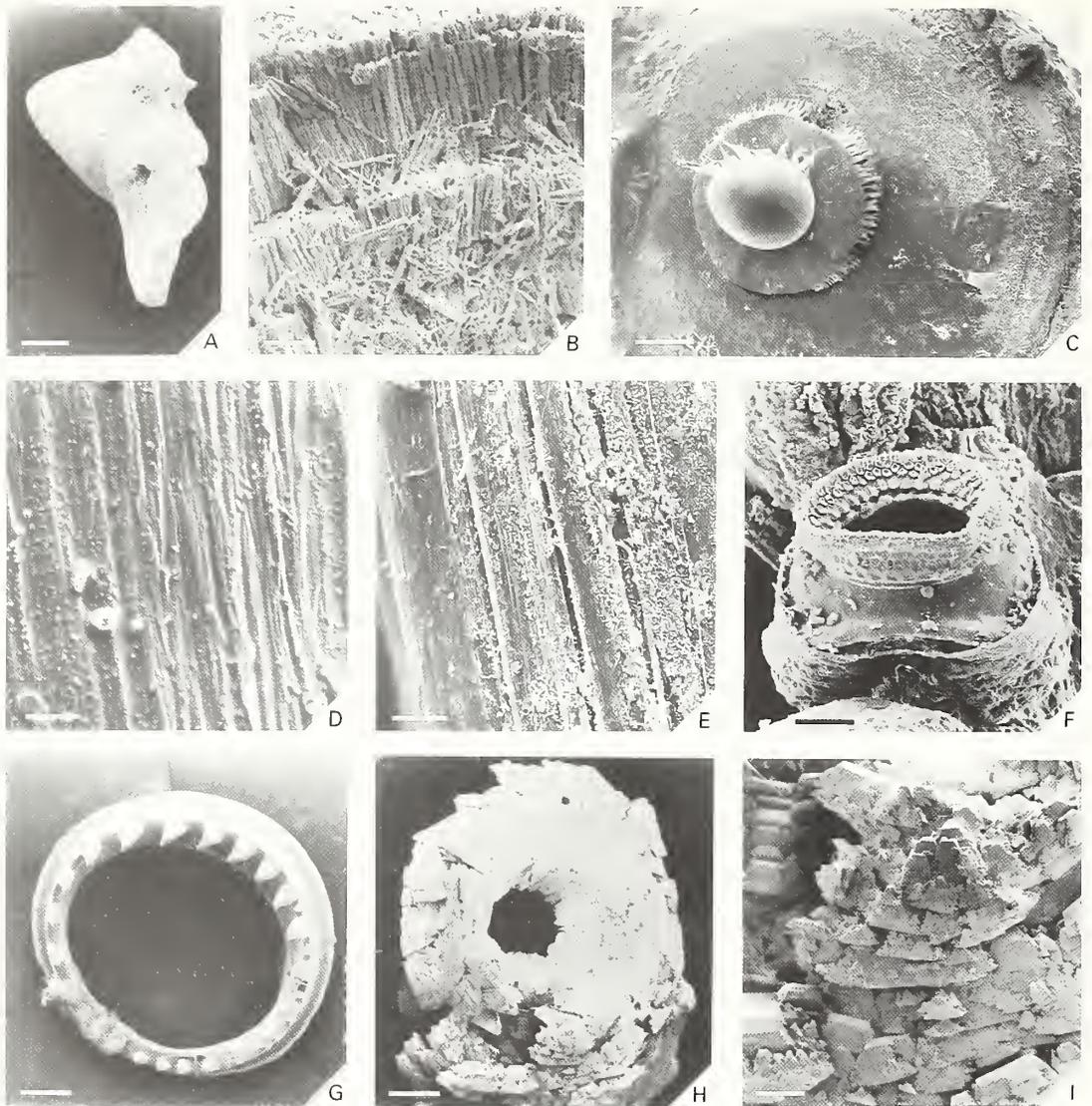
TEXT-FIG. 2. SEM micrographs of soft-tissue decay in slow diffusion conditions. A, *Sepiolo atlantica* mantle at 1.5 days, fixed in HMDS for SEM examination. The muscle has largely decayed away, but collagenous tissues (tunics, intramuscular connectives) remain intact. The fibres in the upper portion of the picture have 'unravell'd' during specimen handling. Scale bar represents 20 μm . B, same specimen as A showing the cut edge of the mantle. Intramuscular connectives are visible, running between the inner and outer tunic layers. The collagen is covered with bacteria of 2–4.5 μm in diameter; compare with phosphate spheres in fossil material in Text-fig. 4. Scale bar represents 20 μm . C, *Alloteuthis subulata* after 4 weeks, oven dried. Fibrillar phase beccublast cells still insert on the upper beak. The fibrils still cluster into hexagonal clumps, which probably represents the original position of the cells. Scale bar represents 40 μm . D, the rear edge of the upper beak crest in *Alloteuthis subulata* after 3 days. The polygonal imprints left by beccublast cells are evident. The chitin of the beak is undecayed at this stage. Scale bar represents 20 μm . E, *Loligo forbesi* sucker surface after 3 weeks. The attachment muscles have decayed away, leaving polygonal imprints of chitinoblast cells similar to the beccublasts in D. Scale bar represents 10 μm .

RECENT COLEOIDS

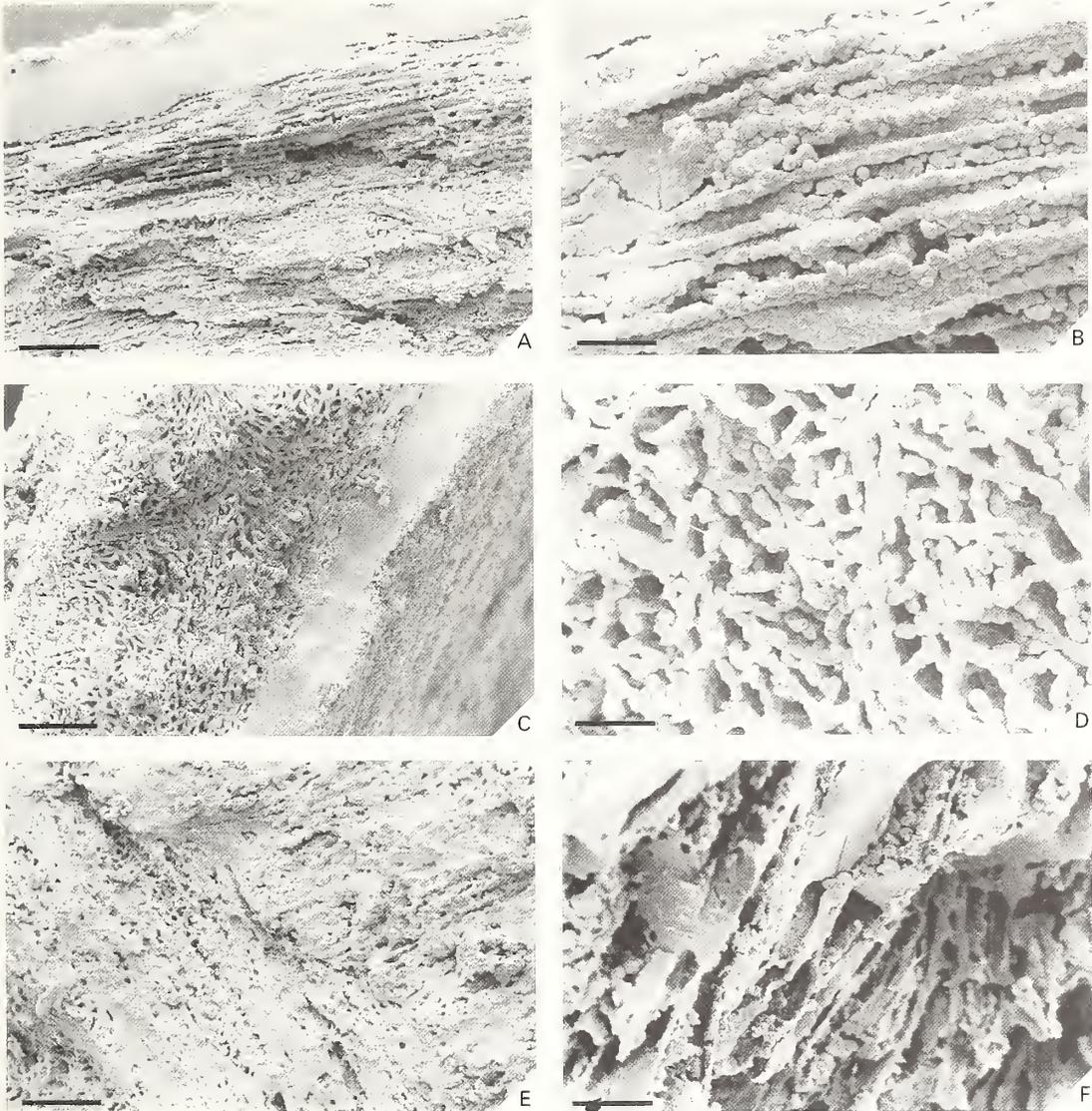
Death and decay stages

In both experimental and aquarium conditions dead and dying *Alloteuthis*, *Sepiolo* and *Loligo* lie on the bottom of the tank. They are ignored by their companions. In contrast, dying *Sepia* float at or near the surface in both aquarium and natural conditions, and are frequently attacked by conspecifics as well as being an easy target for epipelagic and aerial scavengers. Thus, the mode of dying affects the preservation potential of a given taxon.

The tentacles are not normally extended at death and should therefore be concealed in undisturbed carcasses. Any tilting of the carcass head downwards during handling, however, can cause the tentacles to slide from their 'pouch', and they also hang down in this way in anaesthetized and dying *Sepia*.



TEXT-FIG. 3. Decay of structural tissues in recent coleoids under conditions of slow diffusion. A, statolith from an undecayed *Loligo forbesi*. Scale bar represents 400 μm . B, surface of *Loligo* statolith after 4 weeks. The statolith is exfoliating and individual aragonite rhombs are becoming loose. Scale bar represents 10 μm . C, eye lens from *Alloteuthis subulata* after 3 days. The lens has been broken along the natural fracture plane to show the internal structure. Scale bar represents 200 μm . D, ventral side of *Alloteuthis gladius* after 3 days. A membrane covers the surface, obscuring detail of the structure beneath. Scale bar represents 20 μm . E, ventral view of *Alloteuthis gladius* after 1 week. The thin membrane has peeled away and the chitin beneath is splitting along natural growth lines. Bacteria are visible on the gladius surface. Scale bar represents 20 μm . F, sucker *in situ* on the arm of *Sepiolo atlantica* after 1.5 days. The attachment muscles still hold the sucker ring in place. Scale bar represents 40 μm . G, a detached sucker ring from *Loligo* after 1 week. No muscle tissue remains adhering to the chitin. Scale bar represents 400 μm . H, *Loligo* sucker removed from an arm after 10 weeks. The sucker has been overgrown by magnesium phosphate crystals in a spiral pattern. No organic component remains visible. Scale bar represents 400 μm . I, close-up of H to show crystal structure. Scale bar represents 100 μm . Specimens illustrated in C to F were dehydrated in HMDS prior to SEM examination.



TEXT-FIG. 4. SEM of muscle tissue from fossil coleoids. A, transverse section of *Belemnnotheutis antiquus* (NHM C.2456) mantle muscle. Fibrous structure is clearly visible. The massive band at the top of the picture is a layer of varnish. Scale bar represents $40\ \mu\text{m}$. B, close-up of A showing the $1\text{--}2\ \mu\text{m}$ microspheres of calcium phosphate which make up the muscle fibrils. Scale bar represents $10\ \mu\text{m}$. C, longitudinal section of the same specimen with the muscle fibres viewed end on. The massive band on the right is a layer of varnish. Scale bar represents $40\ \mu\text{m}$. D, close-up of C showing microspheres $1\text{--}2\ \mu\text{m}$ in diameter. Scale bar represents $10\ \mu\text{m}$. E, *Belemnnotheutis* (NHM C.46898) mantle with two sets of muscle fibres meeting at 90° . Scale bar represents $40\ \mu\text{m}$. F, *Mastigophora brevipinnis* (NHM 62231) muscle tissue from the digestive gland sheath. The collagenous sarcolemma is preserved but the fibrils themselves have decayed away. Scale bar represents $10\ \mu\text{m}$.

The flesh of *Alloteuthis*, *Sepiolo* and *Loligo* starts to become opaque *before* they stop respiring, indicating that histochemical changes in the mantle can occur prior to actual death. The flesh of *Sepia* is opaque in life.

TABLE 5. Composition of mineral phases in fossil coleoids and decaying *Loligo*. Oxide weights based on electron microprobe analyses (total given as weight per cent. of sample mineralized). Ratio of calcium phosphate to CaCO_3 based on the assumption that all P_2O_5 is incorporated into ideal OH-apatite [$\text{Ca}_5(\text{PO}_4)_3\text{OH}$]. The $\text{CaO}:\text{P}_2\text{O}_5$ ratio is 1:1.32 (based on molecular weights, ignoring H and excess O). The remaining CaO is assumed to form CaCO_3 .

Specimen	% by wt	Na_2O	MgO	SiO_2	Al_2O_3	P_2O_5	SO_3	FO	CaO	CaO in phosphate	Phos:carb (%)
<i>Geopeltis</i>											
Pen layer 1	60.8	0.2	0.6	0.04	—	1.9	0.1	1.0	56.0	2.5	4.5:95.5
Pen layer 2	88.1	2.6	0.3	—	0.05	32.2	1.2	3.2	48.4	42.5	87.8:12.2
Pen layer 3	65.1	0.5	0.7	—	—	11.7	0.4	1.5	49.5	15.4	31.1:68.9
Pen layer 4	88.0	1.3	0.3	—	0.02	31.8	1.0	4.0	49.4	42.0	85.0:15.0
Pen layer 5	70.8	0.7	0.6	—	0.01	16.9	0.7	1.7	49.3	22.3	45.2:54.8
Pen layer 6	95.1	0.8	0.4	—	0.02	33.9	1.4	4.8	53.5	44.7	83.6:16.4
Ink sac	83.2	1.5	0.3	—	0.01	30.4	1.7	3.2	45.8	40.1	87.6:12.4
Rock	56.5	0.3	0.8	2.1	0.83	2.2	0.5	0.2	48.9	2.9	5.9:94.1
<i>Mastigophora</i>											
Radial	86.1	0.9	0.3	—	—	32.5	0.5	1.9	49.6	42.9	86.5:13.5
Circular	85.6	1.0	0.3	—	0.02	32.4	0.4	1.6	49.5	42.8	86.5:13.5
Rock	75.9	0.4	1.7	34.8	17.54	0.8	2.9	—	10.4	1.1	10.6:89.4
<i>Loligo</i> (4w)											
Sucker crystal	58.2	0.1	20.6	—	0.02	37.4	0.1	0.1	0.1	0.1	—

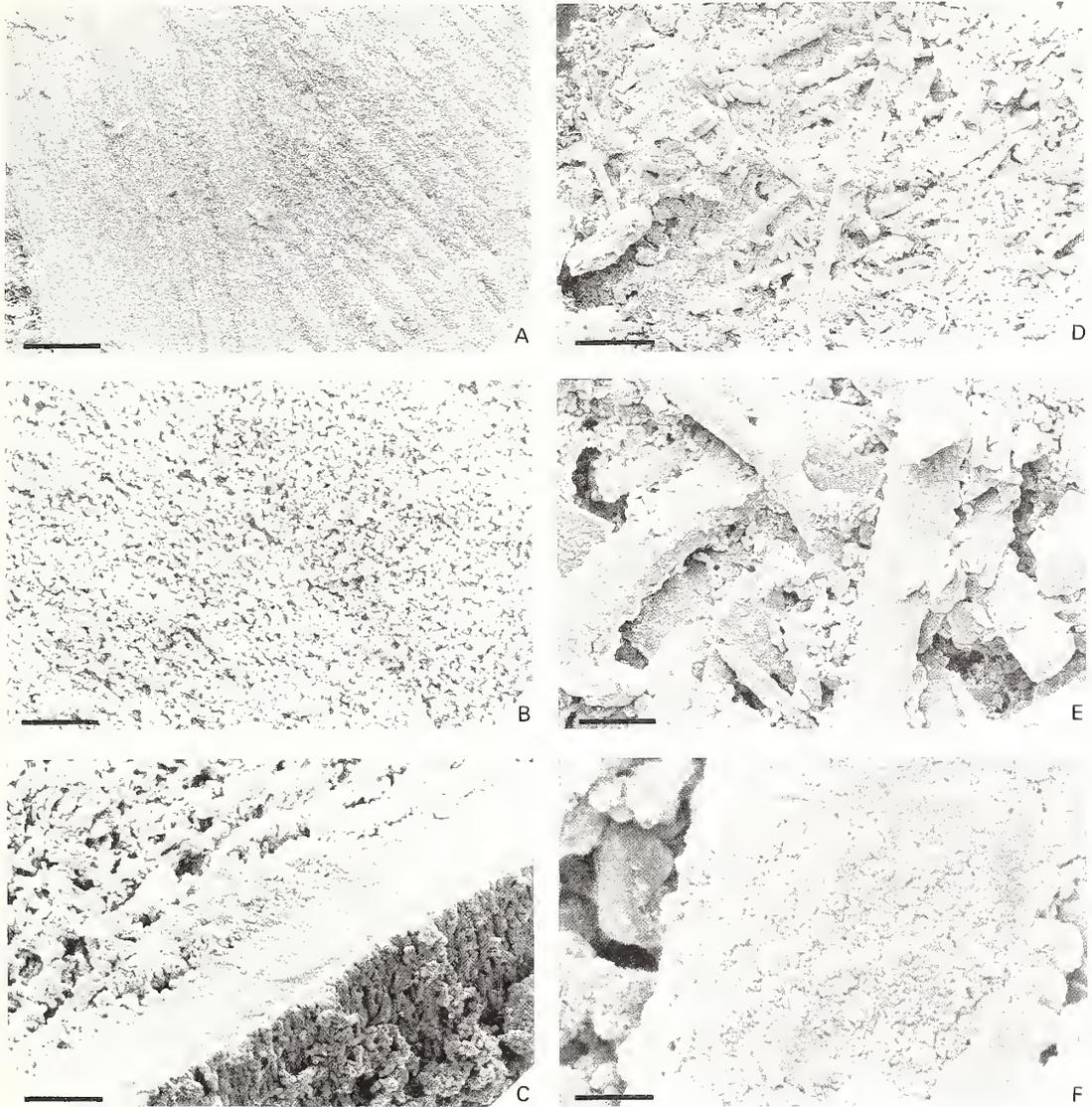
TABLE 6. Ultrastructural features preserved in fossil coleoids examined by light and electron microscopy.

Species	Outer tunic	Inner tunic	Radial muscle	Circular muscle	Intramuscular mesh	Gladius structure
<i>Belemnotheutis</i>	Yes	?	Yes	Yes	Yes	Yes
<i>Geopeltis</i>	?	—	Yes	Yes	—	Yes
<i>Loligosepia</i>	Yes	—	Yes	Yes	—	—
<i>Mastigophora</i>	Yes	Yes	Yes	Yes	Yes	?
<i>Plesiotheutis</i>	Yes	—	Yes	Yes	—	Yes
<i>Trachyteuthis</i>	—	—	?	?	—	Yes

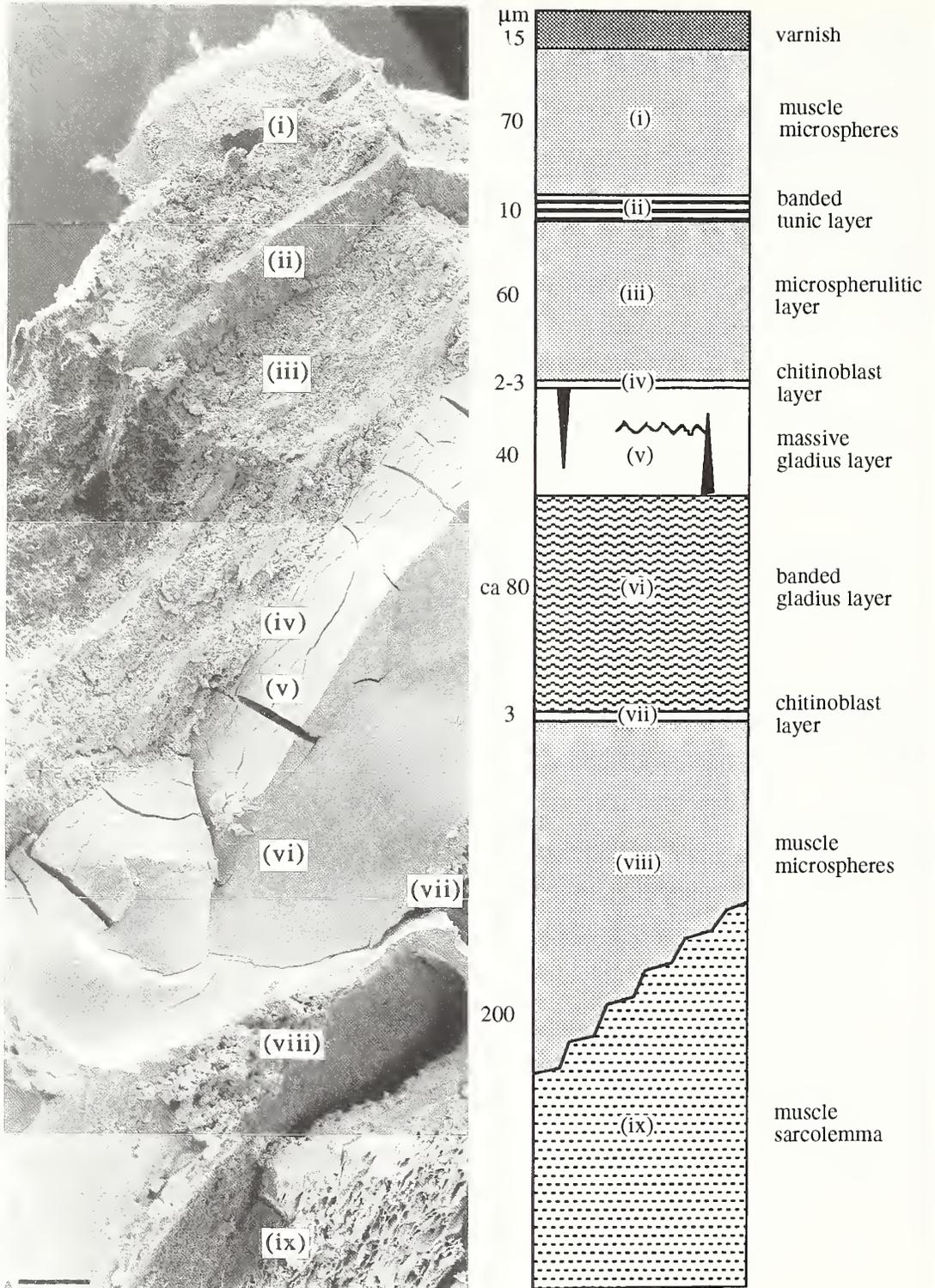
Degradation is very similar in carcasses of *Alloteuthis* and *Sepiolo* (Table 3). Only the head and arm crown portion of *Loligo* were utilized in decay experiments, and studies concentrated on the fate of the structural materials (chitin, collagen, crystalline protein, aragonite) and on the precipitation of minerals in and around the carcass (Table 4).

Ultrastructural decay and preservation

Muscular disintegration is rapid in all three coleoid species and ultrastructural detail is lost in as little as 1.5 days. The collagenous component of the muscle (tunic layers and intramuscular connectives) survives longer than the fibrils themselves (Text-figs 2A, B), and is probably responsible



TEXT-FIG. 5. SEM of collagenous connective tissues from fossil coleoids. A, two outer tunic layers from the ventral surface of *Belemnnotheutis antiquus* (NHM C.2456) (see Text-fig. 1B). The fibres cross at an angle of 30–32°. The axis of the body bisects this angle in living species. Scale bar represents 100 μm . B, close-up of A to show the 0.25–0.5 μm microspheres of which the tunic fibres are composed. Scale bar represents 10 μm . C, section through the inner tunic and overlying mantle muscle in *Mastigophora brevipinnis* (NHM 62231). A number of layers are visible. Scale bar represents 4 μm . D, collapsed intramuscular connective fibres in *Mastigophora* (NHM 31362). The muscle tissue has vanished leaving only the collagenous support structures and scattered 1–2 μm spheres preserved (compare with Text-fig. 2B). Scale bar represents 40 μm . E, close-up of D; some isolated calcium phosphate spheres are visible adhering to the fibres. Scale bar represents 10 μm . F, close-up of surface texture of intramuscular connective fibre from D. The fibre is preserved in clusters of microcrystallites with a framboid-like texture. Scale bar represents 2 μm .



TEXT-FIG. 6. For legend see opposite.

for the mantle and arms retaining their shape when undisturbed. Although no mineral phases were observed in mantle muscle, the structures and bacteria observed resemble those seen in fossil material (compare Text-figs 2B, 4 and 5).

In just two specimens ($n = 19$) of *Alloteuthis* (one each in slow and no diffusion; see Briggs and Kear 1993a, 1994) the cells of the upper beak crest area retained some fine structure even after 4 weeks. A fibrous to 'fluffy' texture was evident under the binocular microscope, remaining white even after oven drying. When viewed with the SEM these fibres appear to insert directly onto the beak (Text-fig. 2c). They are 200 μm in length and seem to clump in distinct hexagons of about 70–100 μm diameter. Within these clumps are smaller bundles, about 10 μm in diameter, which could mimic the pattern of beccublast cell imprint on fresh *Alloteuthis* beaks (Dilly and Nixon 1976). Individual fibrils are about 2 μm in diameter and show no evidence of M or Z bands. They probably represent fibrillar phase beccublast cells (= muscle holdfasts; Dilly and Nixon 1976) rather than mandibular muscle itself. Analysis by electron microprobe revealed these fibres to be primarily organic, with no significant mineral phases. Their survival may reflect their structural nature and the protected position of the buccal mass.

Decay of chitinous tissues

In all taxa the beaks survive throughout the duration of the experiments with little alteration (Tables 3–4). SEM analysis shows that the rear edges of the beaks fracture and disintegrate at 10 weeks.

Preliminary analyses with the electron microprobe demonstrate that fresh beaks (*Eledone*, *Todaropsis*) have high levels of sulphur and calcium, and sometimes high silicon and chlorine. Potassium, magnesium and phosphate are present, but not in substantial quantities. Examination of *Alloteuthis* beak material after 4 weeks decay showed that sulphur, calcium and chlorine remain bound within the chitin of the beaks during this period. Other elements in the analysis (Mg, Si, P) decline. Only potassium increases over the 4 week period.

Polygonal imprints of beccublast cells identical to those reported by Dilly and Nixon (1976) are evident on the outer surface of the beaks when the buccal muscle has decayed away (Text-fig. 2D). In untanned areas this pattern becomes distorted or obscured as decay progresses. Similar polygonal imprints occur on the outer surfaces of the suckers (Text-fig. 2E) presumably representing the imprint of 'chitinoblast' cells, the analogues of beccublasts.

In all taxa examined, the radular ribbon is less decay-resistant than the radular teeth which often remain in place until disturbed. The anterior portion of the radula, which carries the old teeth, disintegrates earlier than the posterior portion with its young and newly formed ribbon and teeth.

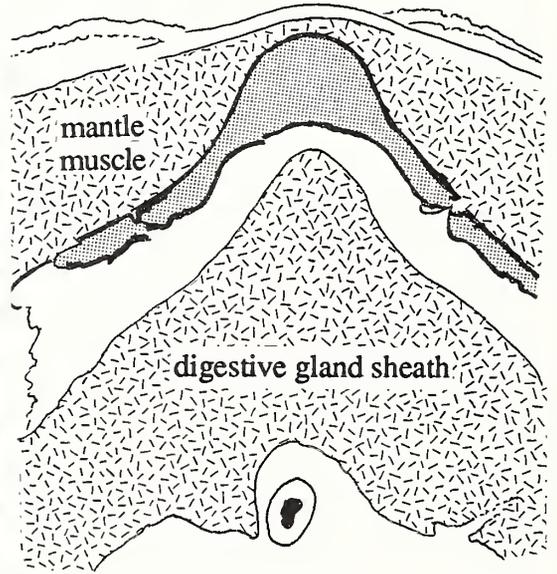
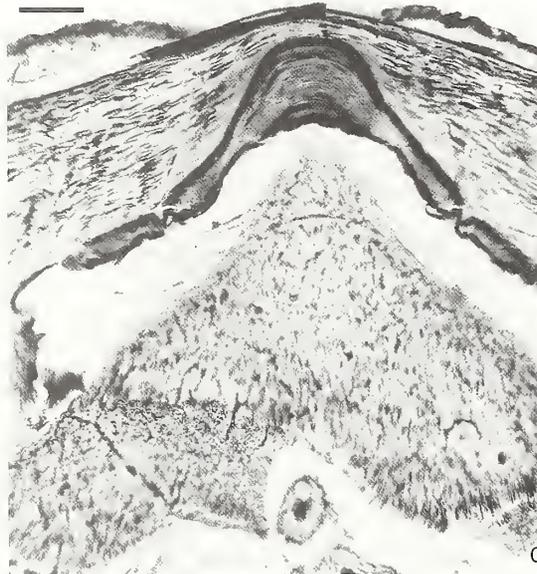
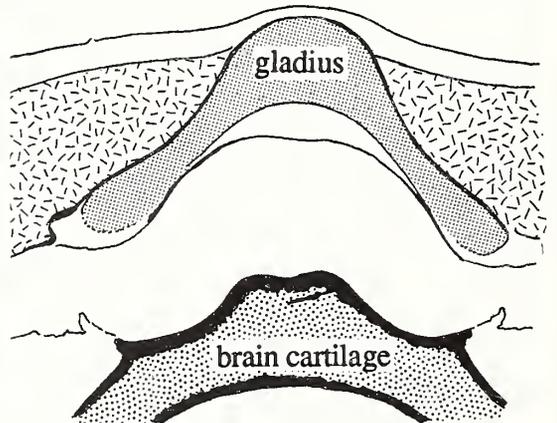
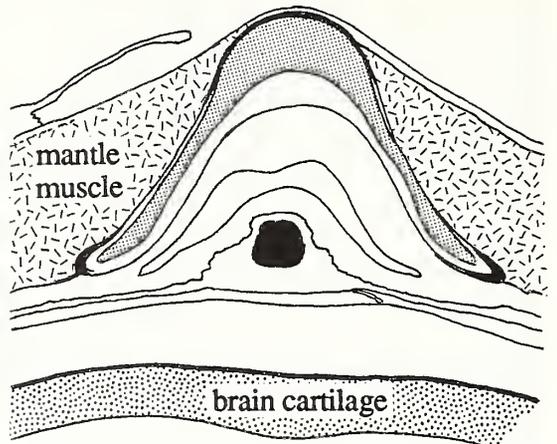
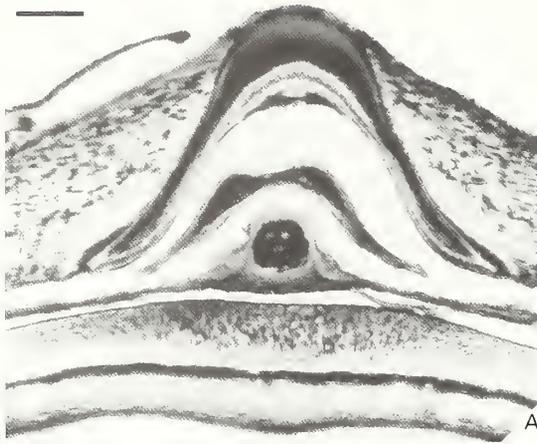
The gladius, despite being untanned, showed little disintegration. No trace was found, however, of the thin chitin of the oesophagus, buccal palps or stomach lining.

Decay of calcareous tissues

Detailed observations of decay were carried out on the statoliths of *Loligo*, as their larger size (1–2 mm) made retrieval and examination feasible (Text-fig. 3A). The statoliths show evidence of surface exfoliation after 1 week under slow diffusion conditions, and there is extensive loss of crystal rhombs in weeks 2–4 (Text-fig. 3B). During decay the statoliths become stained with the pigment released by the carcass, becoming progressively darker.

The statoliths were not recovered beyond week 6. This could be due to their small size which makes them difficult to detect in the disintegrating carcass, their purple-pink colour which makes them impossible to distinguish from the many crystalline fragments which are associated with *Loligo* at this stage, or their complete disintegration or dissolution (vessel pH 7.10–8.46).

TEXT-FIG. 6. A section through the mantle muscle and inner tunic, the underlying gladius, and the muscle forming a sheath around the digestive gland of *Mastigophora brevipinnis*. A, SEM montage of specimen NHM 62231. Scale bar represents 40 μm . B, diagrammatic representation of the section in A. See text for details.



TEXT-FIG. 7. For legend see opposite.

Decay of eye lenses

Initially the eye lenses and surrounding tissues form an intact unit. As early as week 1 the soft tissues have a spongy texture and an imprint is left by forceps tips if they are handled. Soft tissues may remain adhering to the lenses for up to 10 weeks. The eyes remain *in situ* more often in small carcasses (*Alloteuthis*, *Sepiola*) than in the large specimens (*Loligo*), but this is simply because the eyes of the small animals 'rest' on the bottom of the jar and thus have firm support even when the surrounding soft tissue disintegrates. In contrast, *Loligo* eyes are positioned above the substrate at rest, and collapse with decay of the supporting tissues.

The eye lenses themselves cleave along a natural fracture plane (Text-fig. 3c). This can occur as early as week 1 (*Alloteuthis*) or as late as week 50 (*Loligo*). This difference in timing may be a surface area-volume effect. Prior to full cleavage, a fracture is visible running round the lens (day 3 to week 30). Handling of the lenses often causes cleavage along this plane.

FOSSIL COLEOIDS

Musculature

Morphology. Mantle muscle fibres were observed in *Belemnotheutis*, *Mastigophora*, *Geopeltis*, *Loligosepia* and *Plesiotheutis*. Both radial and circular muscle is preserved (Text-fig. 4) but the fibrils or fibres do not always survive. The radial muscles may be represented by raised ridges on the specimens, or they may be missing, leaving a gap between blocks of circular muscle. Where specimens have been conserved by coating in shellac, the varnish fills these gaps and obscures structure. In some specimens (*Belemnotheutis*; BRSMG Ca5242, BRSMG Cd21) the 'muscle' pattern seen is an imprint of the fibres on the surrounding tissues (?tunic).

Longitudinal muscle fibres were observed in *Belemnotheutis* (NHM C.2456), *Mastigophora* (NHM 62231) and *Plesiotheutis* (NHM 83731). In the latter two species these fibres are associated closely with the gladius.

The muscles of the arms or tentacles have preserved fibres only in *Belemnotheutis*, in which they are longitudinal. In one specimen (NHM C.46898) an arm has fractured to reveal longitudinal structure all the way through. The other fibre orientations reported in living coleoids (circular, oblique, helical; Kier 1982, 1988) were not observed.

Ultrastructure. Muscle is preserved in two different forms in material from Christian Malford. The first involves replacement of the muscle by ?sheets of microspheres of 1–2 μm diameter (Text-fig. 4A–E; Allison 1988). The scale of the filaments preserved in this way indicates that they represent muscle fibrils (diameter $1.4 \pm 1.0 \mu\text{m}$; Ward and Wainright 1972) rather than whole fibres (diameter $5.1 \pm 2.1 \mu\text{m}$; Ward and Wainright 1972). This form is well represented in *Belemnotheutis*.

The second way in which muscle tissue is preserved is the 'sarcolemma' form, first described in fish from the Cretaceous Santana Formation of Brazil (Martill 1990). The core of the fibres has vanished, leaving only the outer sheath of the sarcolemma intact (Text-fig. 4F). The 'missing' fibrils

TEXT-FIG. 7. Anterior-posterior histological sections (silver staining) through the front portion of a juvenile *Loligo pealei* to show the gladius and associated tissues. Gaps between tissues are histological artefacts. Slides courtesy of Professor J. Z. Young. A, section through the anterior of the gladius at the rear of the head. The upper skin and tunic meet the central keel of the gladius and only a thin layer covers it. Radial and intramuscular fibres are present in the mantle. The layer of chitinoblast cells surrounding the gladius is clear, particularly ventrally. Scale bar represents 100 μm . B, skin and tunic sit directly on top of the keel of the gladius, which rests directly on the brain cartilage. Chitinoblasts surround the gladius, the ventral cells larger than the dorsal, which may be continuous with the inner tunic. Layering within the gladius is evident. Scale bar represents 100 μm . C, section through the body. The gladius is now embedded within the mantle muscle, and associated with the muscular sheath which surrounds the digestive gland. The chitinoblasts are flattened but still visible in places. Scale bar represents 100 μm .

would have had a diameter of 2–7 μm each. Preservation of the sarcolemma, in the absence of fibrils, has only been observed in *Mastigophora*.

Composition. Analysis of both radial and circular muscle fibres in *Mastigophora* shows them to be calcium phosphate. There is no difference in composition between the two muscle forms (Table 5).

Connective tissue. The three main types of connective tissue associated with the mantle musculature in Recent squid (outer tunic, inner tunic and intramuscular fibres) are all preserved in *Belemnotheutis* and *Mastigophora*. The outer tunic is also preserved in *Plesiotheutis* and *Loligosepia*, and possibly in *Geopeltis* (Table 6).

In *Belemnotheutis* the tunic still preserves the parallel rows of fibres in alternating sheets (Text-fig. 5A, C) which are bisected by the sagittal axis of the specimen at 15–16° (an angle of $27 \pm 1.0^\circ$ is recorded in living *Loligo* and *Lolliguncula*; Ward and Wainright 1972). The fibres in the tunics are preserved as microspheres, 0.25–0.5 μm in diameter (Text-fig. 5B).

The number of sheets in the tunics varies, but at least three are present in *Belemnotheutis*. In *Mastigophora* (NHM 62231) there are four to five in the inner tunic, two to three in a tunic-like layer dorsal to the gladius, and one or two in a similar layer ventral to the gladius (layers ii, iv and vii respectively; Text-fig. 6).

The intramuscular connective tissue fibres are best preserved in *Mastigophora* (Text-fig. 5D–F). These fibres are 5–10 μm in diameter and are fragmented into sections 20–150 μm long. The texture of these fibres is reminiscent of framboids, in that they consist of spheres composed of crystallites of < 0.1 μm (Text-fig. 5F). Ward and Wainright (1972) measured intramuscular connective tissue fibres of diameter $2.6 \pm 0.74 \mu\text{m}$ in living material.

A section through Mastigophora from Christian Malford

In specimen NHM 62231 a section through the gladius and surrounding tissues revealed nine separate layers (Text-fig. 6). These are:

- (i) a muscle layer, about 70 μm thick, composed of microspheres of 1–2 μm diameter, texturally similar to the muscle preserved in other specimens, but with a lower order of information retained;
- (ii) a layer about 10 μm in total thickness, consisting of four to five sheets, representing the inner boundary tunic associated with the muscle layer (i) (Text-fig. 5C);
- (iii) another microspherulitic layer running parallel to the gladius, with a total thickness of about 60 μm , with bands of smoother material within it;
- (iv) a thin (c. 2–3 μm) layer of compacted microcrystallites or spheres similar to those evident in *Belemnotheutis* tunic (Text-fig. 5A–B);
- (v) a massive layer, thickness c. 40 μm , with a fracture reminiscent of the desiccation cracks in dried beak material;
- (vi) a layer about 80 μm thick, with a conchoidal fracture and banded structure. Some of the fractures from layer (v) run parallel to or into this, so it may be a different face of the same material. The bands look like growth lines, with finer lines visible within broad striation. Broad bands are about 1–2 μm and fine bands about 0.3 μm thick. Layers (v) and (vi) represent the gladius.
- (vii) another layer, c. 3 μm thick, of tunic-style microspheres 0.25 to 0.5 μm in diameter;
- (viii) disorganized microspheres of 1–2 μm diameter representing muscle tissue with low order preservation that grades into layer (ix);
- (ix) sarcolemma style preservation. The sarcolemma sheaths appear to have a granular texture, composed of crystallites/grains about 0.1 μm in size (Text-fig. 4F). ‘Muscle’-sized microspheres are scattered around, but not organized into fibres. The hollows in the sarcolemma (= site of fibres) run parallel to the gladius. The combined thickness of layers (viii) and (ix) is about 200 μm .

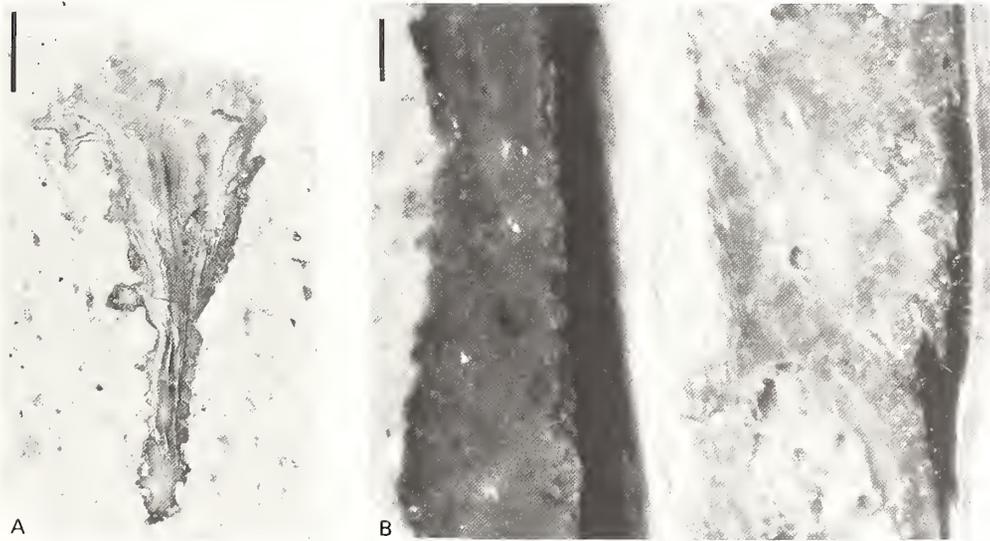
Comparing the structures with living material (see Text-fig. 7), the *Mastigophora* specimen is interpreted as a section from the dorsal mantle to the muscular sheath of the digestive gland. Layers (i), (viii) and (ix) are undoubtedly muscle, the last two representing the digestive gland sheath which sits ventral to the gladius (Text-fig. 7C). The banded structure in layer (ii) is the inner tunic of the mantle muscle.

Layer (iii) does not retain enough structure for a precise interpretation. It may represent either a second muscle band, or epithelial tissue associated with the secretion of the gladius. The mantle muscle is not split into two layers in modern coleoids, so the latter interpretation is more likely. Examination of recent material shows the presence of a layer of epithelial cells surrounding the gladius (Text-fig. 7). Under the light microscope these are similar in morphology to the odontoblasts associated with the radular sac (Nixon 1968), the beccublasts reported by Dilly and Nixon (1976) and the 'chitinoblasts' of Kear (1990). Because of their association with the gladius, layers (iv) and (vi) are suggested to be the remains of these chitinoblast cells. Layers (iii) and (iv), in combination, may be the dorsal chitinoblasts: (iii), responsible for chitin secretion; and (iv), the remains of the fibrillar material which anchors the mantle muscle to the pen.

Complex layering of this type is also preserved in *Belemnotheritis antiquus*. In the tissues dorsal to the gladius of specimen NHM C.2456 twelve layers can be distinguished using the binocular microscope. The topmost two are identifiable as tunic layers (see Text-fig. 5A), and the third as muscle fibres (Text-fig. 4A–D). Layer (viii) shows very fine fibres running at 60° to the orientation of the muscle fibres and may be another tunic type layer. No structure was evident in the other layers.

A section through Geopeltis from Charmouth

An incomplete specimen (BRSUG 25602) of the loligosepiiid *Geopeltis*, preserved in a nodule from the Lower Lias of Black Ven, Charmouth, Dorset, was studied. The form of the gladius identifies the specimen, which preserves the ink sac near the midline.



TEXT-FIG. 8. Polished sections through the gladius and associated soft tissues of *Geopeltis* sp. from Charmouth, Dorset (BRSUG 25602). A, the edge of the rachis of the gladius, with layered structure clearly visible. Sparry calcite is present in the wider portion to the top of the photograph. Scale bar represents 500 μm . B, counterpart of the specimen. The thin layers of the gladius are to the right, with fibrous material overgrown by calcite immediately beneath. The other bands reveal no ultrastructure. Scale bar represents 100 μm .

The broad gladius is about 1 mm in total thickness. A layered structure is evident, with alternating brown and yellow-white bands. At the very edge of the gladius there are eight layers present (Text-fig. 8; compare with the cross sections of modern gladius material in Text-fig. 7). On the counterpart four layers were visible with the binocular microscope, and a further two revealed by the electron microprobe. Fibrous structure is visible within the surface layer (Text-fig. 8B); individual fibres have clearly defined edges with smaller fibrils running obliquely within them. This may represent the original structure of the gladius.

Soft tissues are represented by white to brown material. On the part this 'organic' material appears to be slumped on and around the gladius, with no ultrastructure preserved. Sparry calcite is associated with this material. There appear to be two generations of diagenetic calcite present. On the counterpart there is fibrous structure within the 'organic' material (Text-fig. 8B) and it is layered, different layers showing different degrees of ultrastructural preservation and overgrowth by calcite.

Similar layered structure is preserved in the gladius and muscle tissue of coleoids (*Trachyteuthis hastiformis*, *Plesioeuthis prisca*) from the Solnhofen limestone (NHM 83730 and 83731). Six layers are evident in a section of *Trachyteuthis* under the binocular microscope: five of these are gladius and the sixth possibly mantle muscle. Striations, fibres and sub-layers are evident within the main bands of gladius material. This structure may reflect original morphology. In *Plesioeuthis* six gladius and two possible mantle muscle layers are visible.

Composition of fossil material

Analysis of muscle tissues from *Mastigophora* (Table 5) shows no difference in the composition of radial and circular muscle.

Calcium phosphate and calcium carbonate (Table 5) were present in material from the gladius and ink sac of *Geopeltis*. In the gladius the proportions vary from almost pure fluorapatite (layers 2, 4 and 6), through a phosphate-carbonate mixture (layers 3 and 5), to high carbonate (layer 1). Material from the ink sac is also calcium phosphate (fluorapatite) with some carbonate, and a low organic content (Table 5). These compounds reflect diagenetic mineralization and not original gladius or ink composition. Beyermann and Hasenmaier (1973) demonstrated the presence of melanin in the preserved ink sacs of specimens of *Geoteuthis* from the Posidonienschiefer (Lias) of Germany using infrared spectrometry. The calcium carbonate in the gladius may be the diagenetic sparry calcite abundant elsewhere in the specimen.

Hewitt and Wignall (1988) analysed a specimen of *Trachyteuthis* from the Kimmeridge Clay (Late Jurassic) of England and determined that it was composed of francolite. They interpreted this as implying an originally phosphatic composition, i.e. as a diagenetic replacement of a shell composed of chitin and brushite. Hirschler *et al.* (1990) demonstrated experimentally that aragonite can be replaced by calcium phosphate. Analyses of fossil material (above) and experimental results (Briggs and Kear 1994) confirm that a range of original tissue compositions may be altered to calcium phosphate. Thus the 'shell' of *Trachyteuthis* may have been originally aragonitic in composition.

DISCUSSION

The precipitation of crystals

A striking result of the decay experiments was the precipitation of crystals of magnesium phosphate, particularly in association with *Loligo*. Experiments run under the same conditions of slow diffusion on the crustaceans *Crangon* and *Palaemon* (Briggs and Kear 1994) commonly resulted in the formation of crystal bundles of aragonite. However, laths of magnesium phosphate formed on a *Palaemon* carcass that had decayed under these conditions for 75 weeks. The replication of soft tissue in calcium phosphate was much more prevalent in experiments run under different 'closed' conditions (Briggs and Kear 1994). Whether such soft tissue mineralization can be induced in similar experiments on coleoid cephalopods remains to be investigated.

TABLE 7. Habitat, post-mortem effects and preservation potential of living coleoid families. Data from Schäfer (1972), Clarke *et al.* (1979), Clarke (1985), Nesis (1987), Lipinski and Jackson (1989), Croxall and Prince (1994), Jackson and Mladenov (1994) and this study. * Positive post-mortem buoyancy is assumed where the coleoid is ammoniacal, although data for all families are not available. Classification after Clarke (1988).

		Habitat	Buoyancy		
			Type	Life	Post-mortem*
Sepiida					
Spirulidae	Oceanic	Midwater	Shell	Neutral	
Sepiidae	Shelf	Benthic	Shell	Neutral	Positive
Sepiadariidae	Shelf	Benthic	Shell	Neutral	
Sepiolida					
Sepiolidae	Shelf	Benthic	Muscular	Negative	Negative
Idiosepiidae	Shelf	Benthic	Muscular	Negative	
Teuthida					
Pickfordiateuthidae	Oceanic	Midwater	Muscular	Negative	
Loliginidae	Shelf	Midwater-benthic	Muscular	Negative	Negative
Lycoteuthidae	Shelf-oceanic	Midwater	Ammonia	Neutral	Positive
Enoplateuthidae	Oceanic	Midwater	Ammonia	Negative	
Ancistrocheridae	Oceanic	Midwater-benthic	Ammonia	Neutral	
Pyroteuthidae	Oceanic	Midwater	?	Negative	
Octopoteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Onychoteuthidae	Oceanic	Midwater-benthic	Ammonia	Neutral	Positive
Cycloteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Gonatidae	Oceanic	Midwater-benthic	Oil	Neutral	?Positive
Psychroteuthidae	Oceanic	Midwater	?	?Negative	?Negative
Lepidoteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Pholidoteuthidae	Oceanic	Midwater	?	Negative	
Architeuthidae	Oceanic	Midwater-benthic	Ammonia	Neutral	Positive
Histioteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Neoteuthidae	Oceanic	Midwater	?	Negative	Positive
Bathyteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Ctenopterygidae	Oceanic	Midwater	?	Negative	
Brachyteuthidae	Oceanic	Midwater	?	Negative	
Batoteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Ommastrephidae	Shelf and slope	Midwater-benthic	Muscular	Negative	Both positive and negative records
Thysanoteuthidae	Oceanic	Midwater	Muscular	Negative	
Chiroteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Mastigoteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Promachoteuthidae	Oceanic	Midwater	?	?Negative	
Grimalditeuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Joubiniteuthidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Cranchidae	Oceanic	Midwater	Ammonia	Neutral	Positive
Vampyromorpha					
Vampyroteuthidae	Oceanic	Midwater	Sulphate	Neutral	
Octopoda					
Cirroteuthidae	Oceanic	Benthic	Sulphate	Neutral	
Stauroteuthidae	Oceanic	Benthic	Sulphate	Neutral	
Opistoteuthidae	Oceanic	Benthic	Sulphate	Neutral	
Bolitaenidae	Oceanic	Midwater	Sulphate	Neutral	
Amphitrethidae	Oceanic	Midwater	?	?	
Idioctopodidae	Oceanic	Benthic	?	?	
Vitreledonellidae	Oceanic	Midwater	Sulphate	Neutral	
Octopodidae	Shelf	Benthic	Muscular	Negative	Negative
Tremoctopodidae	Oceanic	Midwater	Muscular	Negative	
Ocythoidae	Oceanic	Midwater	Muscular	Negative	
Argonautidae	Oceanic	Midwater	Muscular	Negative	
Alloposidae	Oceanic	Midwater	Sulphate	Neutral	

Differential survival of chitinous structures

The thick, tanned α chitin of the beaks survived longest and with least damage in the experiments (for 50 weeks in *Loligo*). Buccal masses are routinely allowed to rot for a few days in a jar of sea or tap water to extract beaks for taxonomic purposes because this avoids damaging untanned areas (Clarke 1986; Kear 1990). The tanned portions of the radula (also α chitin; see Table 2) persisted longer than the untanned: the teeth may survive even when the ribbon has disintegrated. The pen (untanned β chitin) also suffered little damage, but the oesophageal cuticle (untanned α) and the stomach lining (untanned γ) do not seem to survive. The suckers (β chitin, untanned) also degenerated quickly but they are preserved in one specimen of *Belemnotherutis* (BRSMG Ca5240) from Christian Malford (Donovan and Crane 1992). Thus thicker, tanned chitinous structures have a higher preservation potential.

Cephalopod beaks are robust as evidenced by their survival in the digestive tract of marine vertebrates (whales, seals, albatrosses). Sperm whales find them indigestible and regurgitate large quantities of beaks, which can be found covering the seafloor at certain localities (Clarke 1962). Aggregations of beaks have not been reported from the fossil record, even though the earliest record of sperm whales (Physeteridae) is lower Miocene (Stucky and McKenna 1993), and earlier marine vertebrates preyed on cephalopods (see e.g. Pollard 1968; Martill 1986). Isolated fossil examples, however, are known (e.g. Dzik 1986).

Other decay resistant structures

Traces of the brain cartilage (collagen) may last up to 20 weeks. As other collagenous tissues (tunics, sarcolemma) preserve well, the brain cartilage would also be expected to survive in fossil material. Fischer and Riou (1982a) interpreted paired structures behind the eyes in *Romanitenthis gevreyi* (Callovian of La Voulte-sur-Rhône) as brain cartilage. In other material, extensive preparation in the head region may be required to reveal the presence of the cartilage.

The statoliths (aragonite) exfoliate during decay and eventually vanish. This disappearance may be real or an artefact of sampling technique. Isolated statoliths are found in the fossil record (Clarke and Fitch 1975; Clarke and Maddock 1988), but none has been reported associated with a body fossil. Possible explanations include: (1) isolated statoliths may have passed through the gut of a predator before reaching the seafloor; (2) exceptionally preserved fossils would need sectioning or extensive preparation to reveal the presence of statoliths within the head; and (3) the statoliths may have recrystallized during diagenesis.

During decay the eye lenses eventually cleave and stain, but seem otherwise undamaged. They are preserved in coleoids from La Voulte-sur-Rhône (Fischer and Riou 1982a, 1982b) but have not been reported from Christian Malford. Eye lenses follow the same pattern of cleavage and are stained orange-brown when they undergo digestion by vertebrates (dogfish and albatross). In addition, digested eyes exfoliate, the various layers of the lens starting to peel away from the centre. This may represent a terminal stage of disintegration not reached during the course of our decay experiments.

The influence of buoyancy on preservation potential

In life, coleoids can be divided into two groups (Table 7): negatively buoyant (14 families; Clarke 1985) and neutrally buoyant (25 families; Clarke 1985). The muscular, active swimmers (Loliginidae, Ommastrephidae) which are the target for commercial squid fisheries are typical examples of negatively buoyant species. Living coleoids achieve neutral buoyancy by four different methods (Clarke *et al.* 1979; Clarke 1985). These are: (a) the use of gas-filled shells in 'true' cuttlefishes and Spirulidae; (b) substitution of sulphate ions by chloride ions within the body tissues of some oceanic octopods, e.g. Cirroteuthidae, and the Vampyroteuthidae; (c) storage of low density fats in the digestive gland in the Gonatidae; and (d) the accumulation of ammonium chloride ions in sixteen families of oceanic squid, e.g. Architeuthidae, Cranchiidae (Table 7).

A freshly dead or dying coleoid may either sink or float. Observations from aquarium animals, decay experiments (Schäfer 1972; Lipinski and Jackson 1989), and the mass mortalities associated with spawning (*Illex illecebrosus* in Newfoundland, *Loligo opalesceus* in California, and *Loligo vulgaris reynaudii* in South Africa) indicate that the majority of negatively buoyant animals remain so at death. Ommastrephids, however, have been observed floating after mass mortalities and stranded on beaches. These events represent death during the migration phase of the life cycle, not post-spawning mortality (M. R. Clarke, pers. comm.).

The normally neutrally buoyant *Sepia*, with its large internal shell, floats in the early stages of decay (Schäfer 1972; Lipinski and Jackson 1989; personal observations), indicating a rapid post-mortem shift to positive buoyancy. This may take place before the animal is dead; morbid animals lose their ability to regulate buoyancy. Subsequent loss of the 'cuttlebone' as *Sepia* decays allows the rest of the carcass to sink (Lipinski and Jackson 1989). Conversely, our experimental observations on *Loligo* heads indicate that negatively buoyant species may be buoyed up by decay gasses after a period on the sea floor (depending on the depth of water: see Allison *et al.* 1991).

Kondakovia longimana is an ammoniacal squid (family Onychoteuthidae). Analysis of its tissues show that it contains almost double the ammonia found in other species which use this buoyancy mechanism (329.4 mm compared with 199.6–206.9 mm in *Moroteuthis* of the same family) and that it has very loosely arranged bundles of muscle fibres, with the ammoniacal fluid filling the 'gaps' (Lu and Williams 1994). This tissue chemistry results in post-mortem positive buoyancy. Most records of *Kondakovia* are from predator stomachs (albatrosses, petrels, whales) and sightings of dead individuals at the sea surface. There are very few records of live captures (Lu and Williams 1994). As albatrosses are incapable of diving to great depths (6–12 m; Croxall and Prince 1994) they are assumed to be scavenging on *Kondakovia* floating at or near the surface (Lu and Williams 1994).

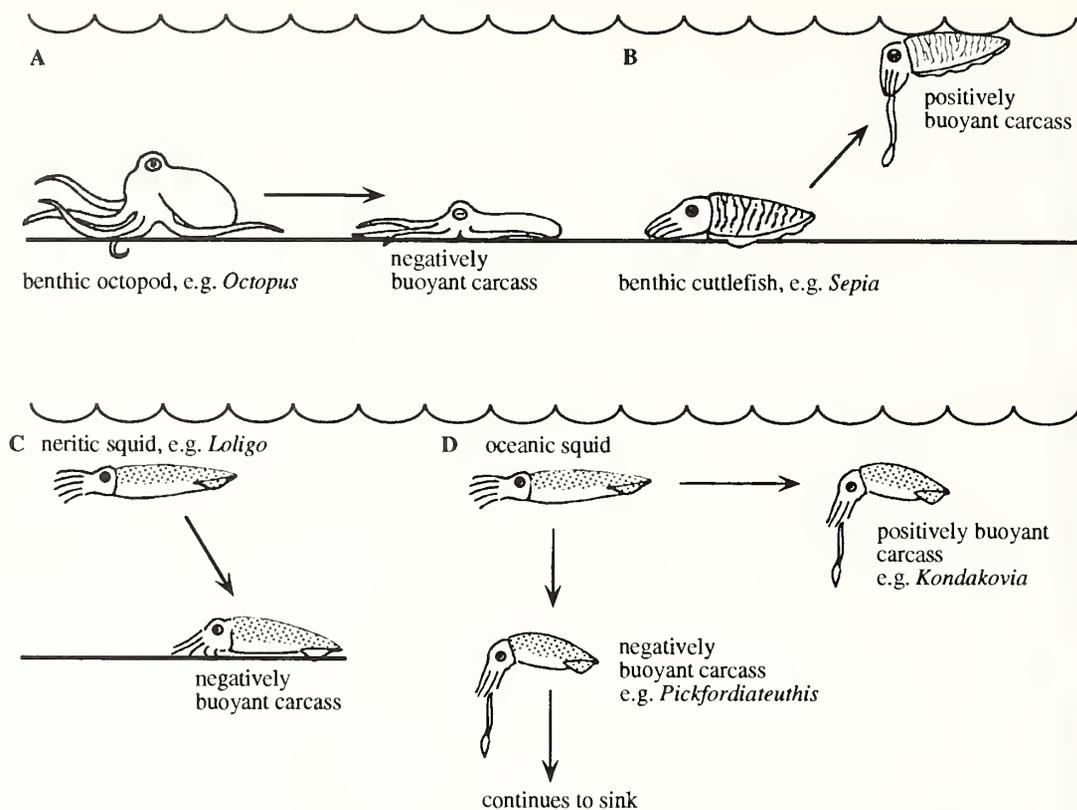
The giant squid *Architeuthis* is occasionally found stranded or floating at the sea surface. Whilst some of these specimens are undoubtedly the regurgitations of sperm whales, several have been reported as still alive (Verrill 1880), showing that the ammoniacal *Architeuthis* was positively buoyant when dying.

In animals that are neutrally buoyant at death and settle rapidly to the sea-floor the tentacles remain concealed within the cone of the arms. By contrast, in morbid and dying *Sepia*, or in carcasses that are handled, the tentacles slip out and hang loose in the water (Text-fig. 9). Hence, an exceptionally preserved animal which only displays four pairs of arms may have the tentacles concealed. Thus *Plesiotenthis* presumably had tentacles even though they have not been recorded.

A morbid animal which floats will be spotted by scavengers (including cannibalistic conspecifics) very easily, and is also unlikely to get buried. In 'sinking' species an annual event such as a spawning mass mortality will attract scavengers in large numbers so carcasses are unlikely to be left undisturbed. Carcasses of *Loligo opalesceus* are rapidly removed from the shelf spawning grounds into deeper water by currents (R. Starr, pers. comm.). A similar process may explain the mass accumulations of belemnite rostra in some localities (Doyle and MacDonald 1993).

Species with the highest potential for fossilization are those benthic shelf species that remain negatively buoyant after death (*Octopus*, *Sepiolo*) or those which spawn in mid-water producing a neutrally buoyant egg mass and a negatively buoyant carcass (e.g. the Ommastrephidae) which may fall into anoxic bottom water. Table 7 categorizes the ecology of modern cephalopods and their post-mortem buoyancy.

Belemniotheutis possessed a phragmocone and might be expected to mimic *Sepia* physiologically and be neutrally buoyant in life and positively buoyant after death. However, the occurrence of exceptionally preserved material seems to indicate that there was little or no positive phase, the carcass reaching the seafloor rapidly after death. The phragmocone may not have represented as large a proportion of the body in *Belemniotheutis* as it does in *Sepia*, so it may not have been capable of refloating the carcass. If the high proportion of living teuthids that become positively buoyant after death (Table 7) is paralleled in extinct genera, it requires an agent such as rapid burial and/or a soupy substrate (Martill 1993) to be invoked where the soft tissues of the fossil forms are preserved (Allison 1988).



TEXT-FIG. 9. Cephalopod habitats and buoyancy (before and after death). A, benthic octopods remain negatively buoyant after death and have a relatively high preservation potential. B, cuttlefish have positive post-mortem buoyancy and a low preservation potential. C, neritic squid have negative post-mortem buoyancy and a high preservation potential. Tentacles do not extend at death. D, oceanic squid families may have either positive or negative post-mortem buoyancy. In negatively buoyant families preservation potential is lower than for their neritic counterparts, and decay will commence before reaching the seafloor. The potential for fossilization is lower still in positively buoyant species. In both cases tentacles will extend during movement of the carcass through the water column.

The influence of sex and maturity on preservation potential

In our experiments the ovary maintained the three dimensional shape of the rear portion of the body, and may be responsible for holding the disintegrating mantle in place. Whilst spermatophores and sperm may survive some time (10 days in *Sepiolo*) they do not show the same cohesion. However, as it is energetically more expensive to produce eggs than sperm, females divert more of their resources to reproduction than males (an extreme case being the disintegration of the mantle in *Moroteuthis ingens*; Jackson and Mladenov 1994). In spent animals, therefore, males are more likely to be preserved than females. A further complication is that eggs, in common with other tissues, swell through osmosis as they decay. In a mature *Sepiolo* carrying large eggs, this process tears the body apart. In *Alloteuthis*, of mid range maturity, the presence of an ovary enhanced the preservation of the body outline (see above). In an immature female (ovary undeveloped) or male, presumably a 'normal' disintegration pattern would be seen.

As determination of sexual maturity or gender in fossil coleoids is problematic (although sexual dimorphs can be recognized, e.g. Doyle 1985), such biases may be difficult to identify.

Phylogenetic implications of ultrastructural preservation

The discovery of a 'modern' mantle structure in Jurassic cephalopods which possessed a phragmocone (*Belemnotherthis*) and in those without (*Geopeltis*, *Loligosepia*, *Mastigophora*, *Plesioteuthis*) is of phylogenetic interest. It supports the view (Donovan 1977; Doyle *et al.* 1994) that the squid grade of organization had already evolved by the Jurassic. Other Jurassic and Cretaceous genera appear to have mantle tissue with a similar structure to that reported here, although they have not been examined using the SEM. They include *Sueviteuthis* (Toarcian), *Teudopsis* (Toarcian), *Kelaeno* (Tithonian), *Leptoteuthis* (Tithonian), *Paraplesioteuthis* (Tithonian), *Trachyteuthis* (Tithonian) and *Dorateuthis?* (Santonian). The Phragmoteuthidae have been regarded as the stem group ancestral to these genera (Donovan 1977). A Toarcian Phragmoteuthid from Holzmaden, Bavaria, (in the Museo Civico di Storia Naturale, Milan) shows what appear to be packets of radial muscle, up to 3 mm long, under the optical microscope, in contrast with the longer bands in other fossil coleoids and in Recent squids. This is tentatively regarded as a more primitive condition.

Squid mantle (Ward and Wainwright 1972) differs from octopus mantle (Gosline and DeMont 1985) in its detailed structure. The system of collagen tunics and intramuscular fibres in squids prevents longitudinal extension of the mantle during contraction of the circular muscles (Wells 1988). In octopods the same function is performed by longitudinal muscles, which are absent from the main part of the squid mantle. The octopod arrangement may permit greater flexibility of the mantle, at the expense of higher energy expenditure (Gosline and DeMont 1985).

The possession of tunics and intramuscular collagen fibres links *Belemnotherthis* and *Mastigophora* to living Decabrachia (Teuthida, Sepiida and Sepiolida) rather than Octobrachia (Cirroctopoda and Octopoda). *Belemnotherthis* and the related *Acanthoteuthis* (Donovan and Crane 1992), both with phragmocone and ten undifferentiated arms, must stand close to the ten-armed forms from which the arm arrangements in living Octobrachia and Decabrachia were derived (Bandel and Boletzky 1988; Boletzky 1992). However, they had already evolved the decabrachia type of mantle. *Mastigophora* (number of arms unknown, without phragmocone) represents a further stage toward modern squids, whether or not it lay on or near the direct line of evolutionary descent.

The presence of squid-type musculature in *Belemnotherthis* calls into question the current systematic placing of the genus in Belemnitida (Jeletzky 1966; Bandel and Kulicki 1988) accepted by Donovan and Crane (1992). The Belemnoidea (Aulacocerida, Belemnitida and Diplobelida) are now considered to have diverged from the ancestors of Phragmoteuthida and modern squids in the Late Palaeozoic (Doyle *et al.* 1994). The structure of the mantle musculature in typical Belemnoidea (i.e. with well-developed rostrum) is unknown. If *Belemnotherthis* is a belemnitid then the squid-type mantle structure had either evolved by the Late Palaeozoic, or evolved independently in Belemnitida and in Loligosepiida (which include Mastigophoridae) subsequently. Both these possibilities are unlikely, and the position of *Belemnotherthis* remains to be resolved.

If the highly specialized mantle structure of squids evolved only once, as seems likely, then the monophyletic group of Recent squids and cuttlefish (Clarke 1988) can be extended back in time to include the fossil forms discussed in this paper. The mantle structure of the Octobrachia may have evolved from that of the squids or, more probably, they represent a separate monophyletic group.

The presence of typical squid mantle structure in the Jurassic suggests that coleoid physiology had evolved by that time. Wells *et al.* (1992) contrasted the physiology of coleoids with that of *Nautilus*, which can survive in conditions of very low oxygen tension, whereas coleoids with their more active life style and high metabolic rate cannot. The fossil record of coleoids, apart from the Aulacocerida, before the Jurassic is almost non-existent, but coleoid organization probably began to evolve in Phragmoteuthida at least as early as the Late Permian, and had given rise to typical squids by the Late Norian (Triassic; Reitner 1978).

CONCLUSIONS

Although the three coleoid species investigated, the squids *Alloteuthis subulata* and *Loligo forbesi*, and the sepiolid *Sepioloatlantica*, degraded in a similar series of stages and at comparable rates under experimental conditions (Tables 3, 4) a range of factors, including habitat and buoyancy (Table 7), will ensure a diversity of preservation potential among coleoids.

The amount of phosphate required for the extensive mineralization of specimens from Christian Malford and other localities must have exceeded that available in the carcass itself. The additional source was presumably phosphate concentrations that built up in the sediment beforehand (Allison 1988; Martill 1988). Some decay is necessary to promote mineralization, and all the fossil specimens show evidence of degradation. The experiments on modern squid show that ultrastructural detail in muscle may be lost in as little as 1.5 days (under conditions of 'slow diffusion': Briggs and Kear 1993a, 1994) although not all the muscle tissue decays at the same time. Experiments on mineralization indicate that the formation of calcium phosphate is more prevalent under 'closed' conditions where it takes some time to initiate after the onset of decay (two weeks in shrimp experiments: Briggs and Kear 1993b, 1994). Precipitation then builds up over a period of weeks.

Detailed documentation of the ultrastructural detail preserved in phosphatized soft tissue (as opposed to the texture of mineralization) has previously been confined to taxa from the Lower Cretaceous Santana Formation of Chapada do Araripe, Brazil (Martill 1988, 1989, 1990; Wilby and Martill 1992) and the Upper Jurassic Cordillera de Domeyko of Chile (Schultze 1989). Coleoid cephalopods have not been reported from the Santana Formation and there are no SEM studies of the rare examples from the Cordillera de Domeyko (Schultze 1989). This investigation therefore demonstrates, for the first time, the range of tissues that may be preserved with ultrastructural detail in phosphatized fossil coleoids. This study emphasizes that this kind of preservation is not confined to a small number of Konservat-Lagerstätten, but is more widespread (see, for example, Briggs *et al.* 1993). It is becoming increasingly clear that there is considerable potential for informative histological studies of the soft tissues of a range of fossil organisms.

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REFERENCES

- ALLISON, P. A. 1987. A new cephalopod with soft parts from the Upper Carboniferous Francis Creek Shale of Illinois, USA. *Lethaia*, **20**, 117–121.
- 1988. Phosphatized soft-bodied squids from the Jurassic Oxford Clay. *Lethaia*, **21**, 403–410.
- SMITH, C. R., KUKERT, H., DEMING, J. W. and BENNETT, B. A. 1991. Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. *Paleobiology*, **17**, 78–89.
- BANDEL, K. and BOLETZKY, S. 1988. Features of development and functional morphology required in the reconstruction of early coleoid cephalopods. 229–246. In WIEDMANN, J. and KULLMAN, J. (eds). *Cephalopods – present and past*. Schweizerbart, Stuttgart, 765 pp.
- and KULICKI, C. 1988. *Belemniten polonica*: a belemnite with an aragonitic rostrum. 303–316. In WIEDMANN, J. and KULLMAN, J. (eds). *Cephalopods – present and past*. Schweizerbart, Stuttgart, 765 pp.
- and LEICH, L. 1986. Jurassic Vampyromorpha (dibranchiate cephalopods). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **1986**, 129–148.

- BEYERMANN, K. and HASENMAIER, D. 1973. Identifizierung 180 Millionen Jahre alten, wahrscheinlich unverändert erhaltenen melanins. *Zeitschrift für Analytische Chemie*, **266**, 202–205.
- BOLETZKY, S. 1992. Evolutionary aspects of development, life style, and reproductive mode in incirrate octopods (Mollusca, Cephalopoda). *Revue suisse de Zoologie*, **99**, 755–770.
- BONE, Q., PULSFORD, A. and CHUBB, A. D. 1981. Squid mantle muscle. *Journal of the Marine Biological Association of the UK*, **61**, 327–342.
- BRIGGS, D. E. G. and KEAR, A. J. 1993a. Decay and preservation of polychaetes: taphonomic thresholds in soft-bodied organisms. *Paleobiology*, **19**, 107–135.
- 1993b. Fossilization of soft-tissue in the laboratory. *Science*, **259**, 1439–1442.
- 1994. Decay and mineralization of shrimps. *Palaïos*, **9**, 431–456.
- MARTILL, D. M. and WILBY, P. R. 1993. Phosphatization of soft-tissue in experiments and fossils. *Journal of the Geological Society, London*, **150**, 1035–1038.
- CLARKE, A., RODHOUSE, P. G. and GORE, D. J. 1994. Biochemical composition in relation to the energetics of growth and sexual maturation in the ommastrephid squid *Illex argentinus*. *Philosophical Transactions of the Royal Society of London*, **B344**, 201–212.
- CLARKE, M. R. 1962. The significance of cephalopod beaks. *Nature*, **193**, 560–561.
- 1985. Cephalopods in the diet of cetaceans and seals. *Rapport et proces-verbaux des rénnions. Commission internationale pour l'exploration scientifique de la Mer Méditerranée*, **29**, 211–219.
- (ed.) 1986. *A handbook for the identification of cephalopod beaks*. Clarendon Press, Oxford, 273 pp.
- 1988. Evolution of recent cephalopods – a brief review. 331–340. In CLARKE, M. R. and TRUEMAN, E. R. (eds). *The mollusca, Vol. 12: Palaeontology and neontology of cephalopods*. Academic Press, London, 355 pp.
- DENTON, E. J. and GILPIN-BROWN, J. B. 1979. On the use of ammonium for buoyancy in squids. *Journal of the Marine Biological Association of the UK*, **59**, 259–276.
- and FITCH, J. E. 1975. First fossil records of cephalopod statoliths. *Nature*, **257**, 380–381.
- and MADDOCK, L. 1988. Statoliths of fossil cephalopods. 153–168. In CLARKE, M. R. and TRUEMAN, E. R. (eds). *The mollusca, Vol. 12: Palaeontology and neontology of cephalopods*. Academic Press, London, 355 pp.
- CROXALL, J. P. and PRINCE, P. A. 1994. Dead or alive, night or day: how do albatrosses catch squid? *Antarctic Science*, **6**, 155–162.
- DILLY, P. N. and NIXON, M. 1976. The cells that secrete the beaks in octopods and squids (Mollusca, Cephalopoda). *Cell and Tissue Research*, **167**, 229–241.
- DONOVAN, D. T. 1977. Evolution of the dibranchiate Cephalopoda. *Symposium of the Zoological Society of London*, **38**, 15–48.
- 1983. *Mastigophora* Owen 1856: a little-known genus of Jurassic coleoids. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **165**, 484–495.
- and CRANE, M. D. 1992. The type material of the Jurassic cephalopod *Belemnotheritis*. *Palaëontology*, **35**, 273–296.
- DOYLE, P. 1985. Sexual dimorphism in the belemnite *Youngibehus* from the Lower Jurassic of Yorkshire. *Palaëontology*, **28**, 133–146.
- DONOVAN, D. T. and NIXON, M. 1994. Phylogeny and systematics of the Coleoidea. *University of Kansas Paleontological Contributions, New Series*, **5**, 1–15.
- and MACDONALD, D. I. M. 1993. Belemnite battlefields. *Lethaia*, **26**, 65–80.
- DZIK, J. 1986. Uncalcified cephalopod jaws from the Middle Jurassic of Poland. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1986**, 405–417.
- FISCHER, J. C. and RIOU, B. 1982a. Les teuthoïdes (Cephalopoda, Dibranchiata) du Callovien Inférieur de la Voulte-sur-Rhône (Ardèche, France). *Annales de Paléontologie (Vert.-Invert.)*, **68**, 295–325.
- 1982b. Le plus ancien Octopode connu (Cephalopoda, Dibranchiata): *Proteroctopms ribeti* nov. gen., nov. sp., du Callovien de l'Ardèche (France). *Comptes rendus Académie Sciences, Paris*, **295**, 277–280.
- GOSLINE, J. M. and DEMONT, M. E. 1985. Jet-propelled swimming in squids. *Scientific American*, **252**, 74–79.
- and SHADWICK, R. E. 1983. Molluscan collagen and its mechanical organisation in squid mantle. 371–398. In HOCHACHKA, P. W. (ed.). *The Mollusca, Vol. 1: Metabolic Biochemistry and Molecular Biomechanics*. Academic Press, London, 510 pp.
- HEWITT, R. A. and WIGNALL, P. B. 1988. Structure and phylogenetic significance of *Trachyteuthis* (Coleoidea) from the Kimmeridge Clay of England. *Proceedings of the Yorkshire Geological Society*, **47**, 149–153.
- HIRSCHLER, A., LUCAS, J. and HUBERT, J.-C. 1990. Apatite genesis: a biologically induced or biologically controlled mineral formation process? *Geomicrobiology Journal*, **8**, 47–57.
- HUNT, S. and NIXON, M. 1981. A comparative study of protein composition in the chitin-protein complexes of

- the beak, pen, sucker disc, radula and oesophageal cuticle of cephalopods. *Comparative Biochemistry and Physiology*, **68B**, 535–546.
- JACKSON, G. D. and MLADENOV, P. 1994. Terminal spawning in the deepwater squid *Moroteuthis ingens* (Cephalopoda: Onychoteuthidae). *Journal of Zoology*, **234**, 189–201.
- JELETZKY, J. A. 1966. Comparative morphology, phylogeny, and classification of fossil Coleoidea. *University of Kansas Paleontological Contributions, Mollusca*, **7**, 1–162.
- KEAR, A. J. 1990. *Feeding mechanisms and diet in cephalopods: special reference to Antarctic mesopelagic squid*. Unpublished PhD thesis, University of Aberdeen.
- KIER, W. M. 1982. The functional morphology of the musculature of squid (Loliginidae) arms and tentacles. *Journal of Morphology*, **172**, 179–192.
- 1988. The arrangement and function of molluscan muscle. 211–252. In TRUEMAN, E. R. and CLARKE, M. R. (eds). *The mollusca, Vol. 11: form and function*. Academic Press, London, 504 pp.
- LIPINSKI, M. R. and JACKSON, S. 1989. Surface feeding on cephalopods by procellariiform seabirds in the southern Benguela region, South Africa. *Journal of Zoology*, **218**, 549–563.
- LU, C. C. and WILLIAMS, R. 1994. *Kondakovia longimana* Filippova, 1972 (Cephalopoda: Onychoteuthidae) from the Indian Ocean sector of the Antarctic Ocean. *Antarctic Science*, **6**, 231–234.
- MARTILL, D. M. 1986. The diet of *Metriorhynchus*, a Mesozoic marine crocodile. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1986**, 621–625.
- 1988. Preservation of fish in the Cretaceous of Brazil. *Palaontology*, **31**, 1–18.
- 1989. The Medusa effect: instantaneous fossilisation. *Geology Today*, **5**, 201–205.
- 1990. Macromolecular resolution of fossilised muscle tissue from an elopomorph fish. *Nature*, **346**, 171–172.
- 1993. Soupy substrates: a medium for the exceptional preservation of ichthyosaurs of the Posidonia Shale (Lower Jurassic) of Germany. *Kaupia: Darmstädter Beiträge zur Naturgeschichte*, **2**, 77–97.
- MEHL, J. 1990. Fossilhaltung von Kiemen bei *Plesiotentis prisca* (Rüppell 1829) (Vampyromorpha, Cephalopoda) aus unter-tithonen Plattenkalcken de Altmühlalb. *Archaeopteryx*, **8**, 77–91.
- NATION, J. L. 1983. A new method using hexamethylidisilazane for preparation of soft-insect tissues for scanning electron microscopy. *Stain Technology*, **58**, 347–351.
- NESES, K. N. 1987. *Cephalopods of the world*. TFH Publications Inc., New Jersey, 351 pp.
- NIXON, M. 1968. *Feeding mechanisms and growth in Octopus vulgaris*. Unpublished PhD thesis, University of London.
- PAGE, K. N. 1991. Nautilid and 'teuthid' cephalopods. 150–162. In MARTILL, D. M. and HUDSON, J. D. (eds). *Fossils of the Oxford clay*. Palaeontological Association, London, 286 pp.
- POLLARD, J. E. 1968. The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset. *Palaontology*, **11**, 376–388.
- REITNER, J. 1978. Ein Teuthiden-Rest aus dem Obernor (Kössener-Schichten) der Lahnewies-Neidernachmulde bei Garmisch-Partenkirchen (Bayern). *Paläontologische Zeitschrift*, **52**, 215–212.
- RUDALL, K. M. and KENCHINGTON, W. 1973. The chitin system. *Biological Reviews*, **48**, 597–636.
- SCHÄFER, W. 1972. *Ecology and palaeoecology of marine environments*. Chicago University Press, 568 pp.
- SCHULTZE, H.-P. 1989. Three-dimensional muscle preservation in Jurassic fishes of Chile. *Revista Geologica de Chile*, **16**, 183–215.
- STUCKY, R. K. and MCKENNA, M. C. 1993. Mammalia. 739–771. In BENTON, M. J. (ed.). *The fossil record*. Chapman and Hall, London, 845 pp.
- STÜRMER, W. 1985. A small coleoid cephalopod with soft parts from the Lower Devonian discovered using radiography. *Nature*, **318**, 53–55.
- VERRILL, A. E. 1880. Cephalopods of the northeastern coast of America. *Transactions of the Connecticut Academy of Arts and Sciences*, **5**, 177–446.
- WADE, M. 1993. New Kelaenida and Vampyromorpha: Cretaceous squid from Queensland. *Memoirs of the Association of Australasian Palaeontologists*, **15**, 353–374.
- WARD, D. A. and WAINWRIGHT, S. A. 1972. Locomotory aspects of squid mantle structure. *Journal of Zoology*, **167**, 437–449.
- WELLS, M. J. 1988. The mantle muscle and mantle cavity of cephalopods. 287–300. In TRUEMAN, E. R. and CLARKE, M. R. (eds). *The mollusca, Vol. 11: form and function*. Academic Press, London, 504 pp.
- WELLS, J. and O'DOR, R. K. 1992. Life at low oxygen tensions: the behaviour and physiology of *Nantilus pompilius* and the biology of extinct forms. *Journal of the Marine Biological Association of the UK*, **72**, 313–328.

WILBY, P. R. and MARTILL, D. M. 1992. Fossil fish stomachs: a microenvironment for exceptional preservation. *Historical Biology*, **6**, 25–36.

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APPENDIX: SPECIMENS EXAMINED FOR THIS STUDY

NHM, Natural History Museum; BRSMG, Bristol City Museum; BRSUG, University of Bristol, Geology Department; *, material removed for examination by scanning electron microscopy; †, material removed for examination by electron microprobe.

Species	Repository	Specimen number	Locality
<i>Belemnotheutis antiquus</i>	NHM	C2456*, C46898*	Christian Malford, Oxfordshire
	BRSMG	Ca 5240 (Lectotype)	Christian Malford, Oxfordshire
	BRSMG	Ca 5242 (Type specimen)	Christian Malford, Oxfordshire
	BRSMG	Cb 7661, Cd 18a, b, Cd 21, Cd 22a, Cd 22b	Christian Malford, Oxfordshire
<i>Geopeltis simplex</i>	NHM	C580	Boll, Wurtemberg, Germany
<i>Geopeltis</i> sp.	BRSUG	25602†	Black Ven, Charmouth, Dorset
<i>Loligosepia</i> (= <i>Geoteuthis</i>)	NHM	C5260	Dumbleton, Gloucestershire
	NHM	C9922	Gloucestershire
	NHM	C12619	Near Ilminster, Somerset
<i>Mastigophora brevipinnis</i>	NHM	31362*†, 46964*, 62231*	Christian Malford, Oxfordshire
	BRSMG	Cd 32, Cd 37, Cd 38a, b, Ce 17967a, b	Christian Malford, Oxfordshire
<i>Plesioteuthis prisca</i>	NHM	83731, 83732, C1046, C46284a, C46847, C46869, C46880, C46886	Solnhofen, Germany
<i>Trachyteuthis hastiformis</i>	NHM	83730	Solnhofen, Germany

A NEW PALAEOONTOLOGICAL TECHNIQUE DESCRIBING TEMPORAL SHAPE VARIATION IN MIOCENE BIVALVES

by TRACY A. GLASSBURN

ABSTRACT. Principal components quantitative shape analysis (PC shape analysis) is demonstrated to be a rapid and effective palaeontological morphometric technique for quantifying shape. It allows easy interpretation, as morphology can be reconstructed from PC scores. Results of PC shape analysis have revealed that temporal patterns of shape variation in four Chesapeake Group (Miocene) taxa from Maryland are not congruent. Whilst there was a significant monotonic trend towards more disc-shaped valves in *Dosinia acetabulum*, there was no significant temporal trend in *Lucina (Stewartia) anodonta* valve shape. Whilst the evolutionary tempo in an *Anadara* lineage was more consistent with punctuated equilibrium, with interspecific changes controlling ultimate shape transformation and reversing intraspecific trends, the *Astarte* lineage had an evolutionary tempo not inconsistent with phyletic gradualism, where intraspecific trends were generally preserved during speciation.

PRESENTLY, no universal method for measuring shape exists. Commonly, morphological techniques utilize measured distances between homologous landmarks as shape variables (reviewed in Bookstein *et al.* 1985). However, if there is a paucity of distinct homologous landmarks (e.g. with simple invertebrates) shape information will be limited. The development of automated image analyzers has led to the creation of better techniques for describing simple invertebrate shape by making use of a nearly continuous representation of an organism's outline. Whilst the outline may not include all critical morphological features, our perception of differences in shape is based largely upon outlines (Scott 1980). Like Fourier (Schwarz and Shane 1969; Ehrlich and Weinberg 1970) and Eigenshape analysis (Lohmann 1983), the PC shape technique (Parks 1983, 1987) has been developed to process the large data sets generated by image analyzers.

The major objective of this study was to develop the PC shape technique as a palaeontological tool for describing temporal variation in bivalve morphology. Miocene bivalve genera from southern Maryland were selected because the stratigraphy and palaeoecology of the Chesapeake Group and the taxonomy, taphonomy and palaeoecology of the genera have been studied extensively. The results are compared with earlier studies which describe evolutionary tempos of the same Chesapeake Group genera from Maryland.

MATERIALS AND METHODS

Study area and bivalve taxonomy

Temporal variation in shape was characterized for eight Early to Late Miocene bivalve species, comprising *Dosinia acetabulum* (Conrad), *Lucina (Stewartia) anodonta* Say, *Anadara subrostrata* (Conrad), *A. staminea* (Say), *A. idonea* (Conrad), *Astarte cuneiformis* Conrad, *A. thisphila* Glenn and *A. perplana* Conrad (Table 1, Text-fig. 1). In a written communication to Kelley (1983a), Blackwelder recognized the congeners of *Anadara* and *Astarte* as being part of lineages with direct ancestor/descendant relationships. Taxonomies are based upon Glenn (1904) with revisions by Vokes (1957), Moore (1969) and Bretsky (1976).

TABLE 1. Number of specimens sampled in each 'zone'.

Taxon	'Zone'						
	10	14	16	17	19	22	24
<i>Anadara</i> sp.							
<i>A. subrostrata</i> (Conrad)	36						
<i>A. staminea</i> (Say)			16	17	37		
<i>A. idonea</i> (Conrad)						60	96
<i>Astarte</i> sp.							
<i>A. cuneiformis</i> Conrad	45	3					
<i>A. thispila</i> Glenn			7	36	3		
<i>A. perplana</i> Conrad							32
<i>Dosinia acetabulum</i> (Conrad)			10	22	6	41	42
<i>Lucina (Stewartia) anodontia</i> Say	39			37	12	9	69

Species were identified and traced in the field in order to preclude the loss of samples through breakage during transport. Whole shells only were collected, and thus the study is biased towards better preserved bivalves. Furthermore, adult specimens within a narrow size range were sampled to limit ontogenetic effects.

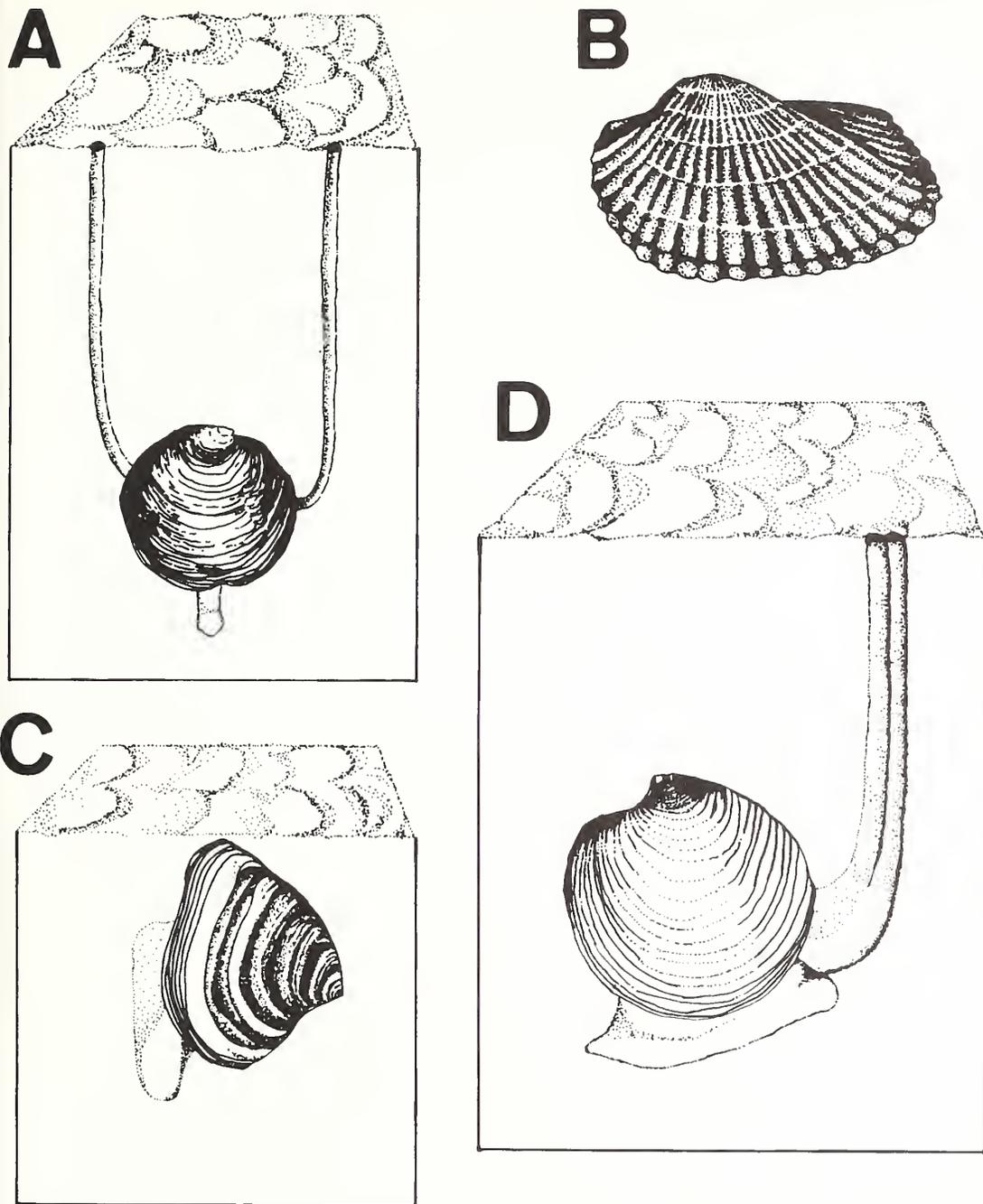
Fossils were collected from fifteen exposures located principally along the western shore of Chesapeake Bay (Text-fig. 2). The strata are part of the Chesapeake Group which is nearly continuously exposed for approximately 60 km, trending north-south, and coinciding roughly with the southerly dip direction of the unconsolidated siliciclastics. The Chesapeake Group in southern Maryland has been divided into three formations, designated the Calvert, Choptank and St Mary's formations (Shattuck 1904; Text-fig. 3). Shattuck (1904) subdivided the formations into twenty-four 'zones' based upon lithology and major shell beds. Difficulties in recognizing formation contacts (Dryden 1930; Gernant 1970; Blackwelder and Ward 1976) and the disputed assumption that all of the 'zones' are laterally continuous and synchronous has led to controversy surrounding the stratigraphical relationships and nomenclature. However, it was not an objective of this study to tackle stratigraphical problems within the Chesapeake Group and therefore, for the purpose of this study, Kidwell's (1988, 1989) classification scheme has been adopted (Text-fig. 3).

The Miocene of southern Maryland records a period of regression during which marine, paralic and non-marine sediments were deposited within the Salisbury embayment (Gibson 1962; Gernant 1970; Kidwell 1988). The Salisbury embayment (which is an extension of the Baltimore Canyon trough) is a structural basin the depth and boundaries of which have varied with changes in tectonic and eustatic controlling factors (Newell and Rader 1982). Basin margin disconformities bracket ten transgressive-regressive cycles which commonly contain major shell beds at their base, representing condensed transgressive lag deposits (Kidwell 1984, 1986).

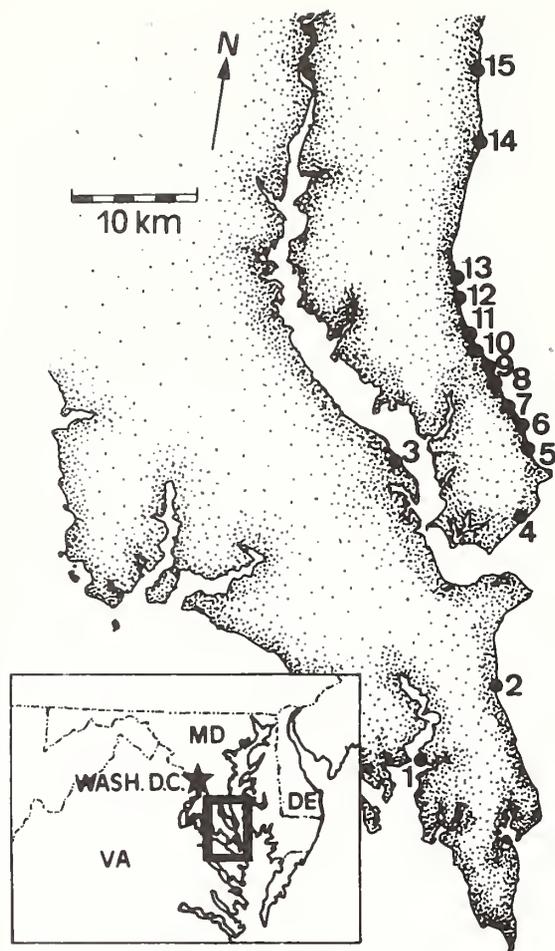
The PC shape technique

Fossil outlines were digitized using a Houston Hipad II digitizing tablet and stylus. Approximately 150-200 data points were recorded for each shell using FORTRAN77 program, DIGITIZE, written by Parks (1983, 1987). Operator error, determined by digitizing the same set of shapes twice, was 0.5 per cent.

Fossil outlines were rotated to a common orientation using one of two FORTRAN77 programs, BINPAXM or MODROT3, developed and written by Parks (1983, 1987). Elongate genera were rotated using BINPAXM which first calculated the principal eigenvector or axis of greatest length, according



TEXT-FIG. 1. A, inferred life position of *Lucina* (*Stewartia*) *anodonta* Say according to Bretsky (1976). B, *Anadara subrostrata* (Conrad). C, inferred life position of *Astarte thisphila* Glenn according to Stanley (1970). D, inferred life position of *Dosinia acetabulum* (Conrad) according to Gernant (1970).

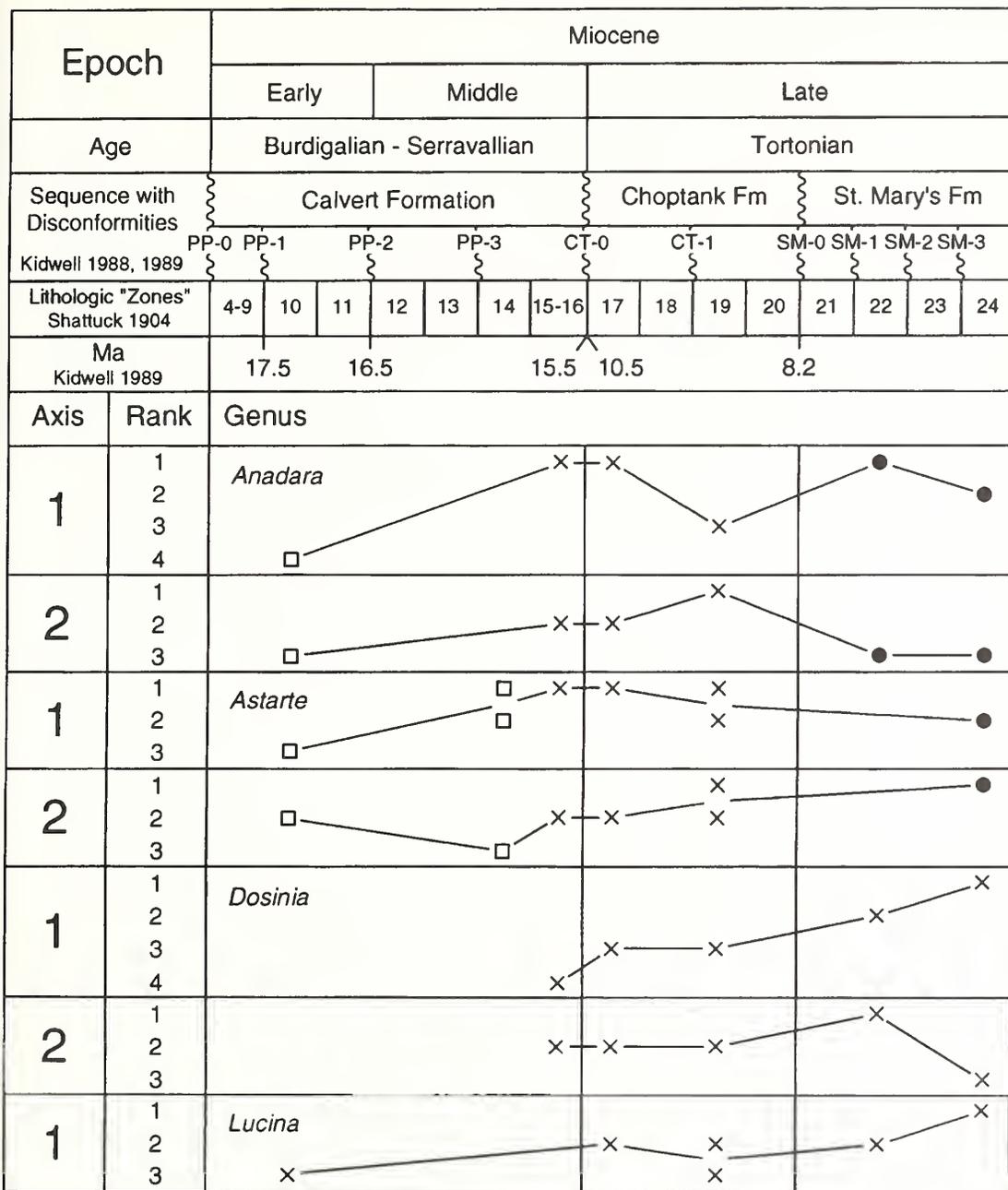


TEXT-FIG. 2. Map of the West Shore of Chesapeake Bay, Maryland with sampling localities: locality 1, Chancellor's Point; 2, Langley's Bluff; 3, Drumcliff; 4, Little Cove Point; 5, Calvert Cliffs State Park; 6, Camp Baybreeze; 7, Rocky Point; 8, Camp Conoy; 9, Flag Ponds Wildlife Reserve; 10, Calvert Beach; 11, Mataoka Cottages; 12, Kenwood Beach; 13, Governor Run Beach; 14, Plum Point; 15, Randle Cliffs Beach.

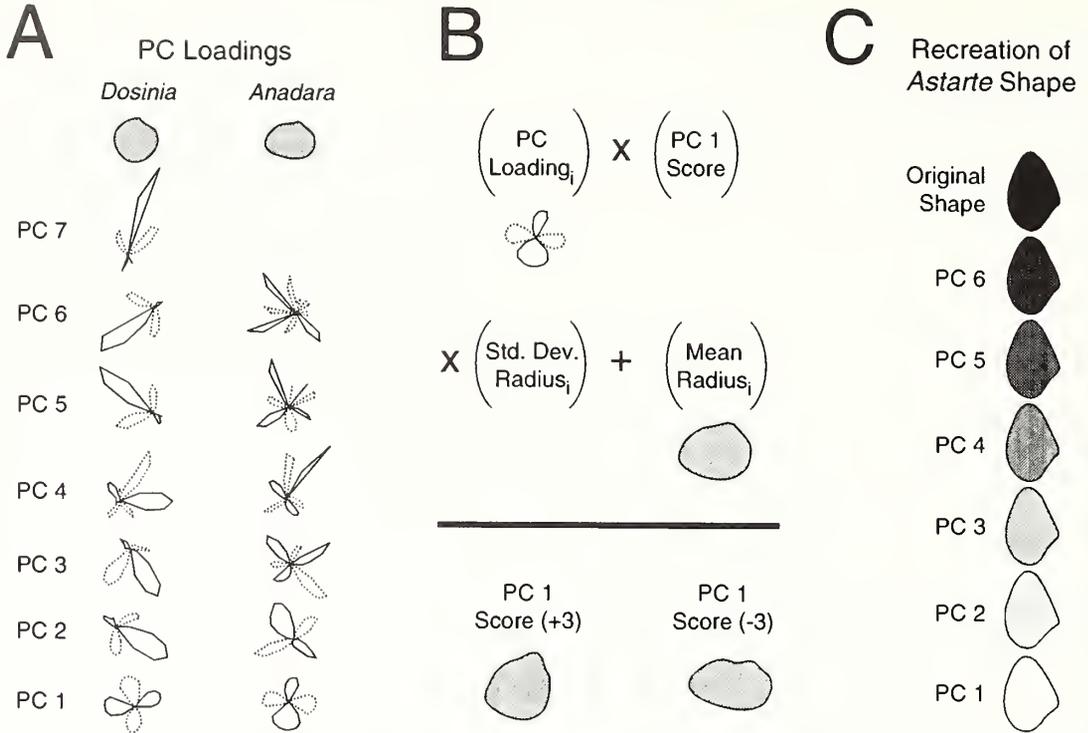
to the method of Tough and Miles (1983), and then positioned the principal axis in a horizontal orientation. This method worked well with elongate genera because the principal eigenvector was consistently orientated with respect to biological landmarks. However, with more rounded genera the principal axis was not consistently orientated. Thus the positioning of biological landmarks varied between specimens. In order to orientate consistently more rounded genera, MODROT3 was used because it rotated outlines to place the beak directly above the calculated centre-of-gravity.

After rotation, thirty-six radial lengths were calculated from the centre-of-gravity to thirty-six points interpolated around the margin at 10° intervals using a cubic curve fit procedure, with the first radial always connecting the tip of the umbo with the centre-of-gravity. The outlines were then rotated around the x and/or y axis according to a best least squares fit to an asymmetrical reference shape. In order to eliminate size effects the data were normalized by dividing an individual's radials by its mean radial length.

A χ^2 test was performed to verify that every variable (radial length) within a data set fitted a normal distribution at the 0.05 significance level. Data matrices containing thirty-six radial lengths of congeners were reduced by principal components analysis (using FORTRAN77 program BMDP4M; Frane *et al.* 1985) to six to seven principal components (PC) each accounting for a variance greater than or equal to one (Table 2). The PCs cumulatively accounted for approximately 90 per cent. of total shape variation which was found to describe shape adequately (Text-fig. 4C).



TEXT-FIG. 3. Stratigraphy and age of Chesapeake Group sequence and homogeneous groups of taxa computed by multiple range analysis using canonical variate 1 (Axis 1) and 2 (Axis 2) scores; in *Anadara* groups - square is *A. subrostrata*, × is *A. staminea* and dot is *A. idonea*; in *Astarte* groups - square is *A. cuneiformis*, × is *A. thisphila* and dot is *A. perplana*.



TEXT-FIG. 4. A, plots of *Dosinia acetabulum* and *Anadara* PC loadings. B, equation used to recreate shape from PC scores and loadings; reconstruction of two specimens of *Anadara* using PC scores +3 and -3. C, reconstruction of an *Astarte* fossil shape by the cumulative addition of PC 1 through PC 6 to average shape.

TABLE 2. Variance explained (expl.) and cumulative per cent. of variance (cum.%) for each PC having a variance ≥ 1 .

Genus:	<i>Anadara</i>		<i>Astarte</i>		<i>Dosinia</i>		<i>Lucina</i>	
	Expl.	Cum.%	Expl.	Cum.%	Expl.	Cum.%	Expl.	Cum.%
PC								
1	19.23	53	18.96	53	14.87	41	13.31	37
2	5.53	69	5.39	68	5.65	57	9.29	63
3	3.12	77	4.59	80	4.24	69	3.73	73
4	1.96	83	1.57	85	2.89	77	2.52	80
5	1.43	87	1.48	89	2.07	83	1.58	85
6	1.19	90	1.15	92	1.45	87	1.33	88
7					1.08	90		

Analysis of evolutionary trends

PC scores for each individual were estimated by post-multiplying its standardized set of thirty-six radial lengths by the matrix of PC loadings. The scores essentially represent the amount of a PC that is contained in a shape. As PC 1 contributed the most to shape variation (Table 2), PC 1 score

frequency histograms at each stratigraphical level were plotted to reveal evolutionary trends in a single species or lineage. The histograms were presented with reconstructed end member shapes to facilitate the interpretation of morphological trends. Within a single lineage, if the direction of an intraspecific shape trend was retained with the transformation of that species into the next, phyletic gradualism was inferred. Morphological change within a lineage would also have to be equally influenced by inter- and intraspecific shape trends. In contrast, if interspecific trends varied markedly in direction from associated intraspecific changes, the punctuational model was implied. In addition, interspecific changes should control the ultimate shape transformation of a lineage. Kruskal–Wallis one-way analysis by ranks was used to determine whether there was a significant difference between PC 1 scores of stratigraphical populations within a genus.

Morphological differences between stratigraphical populations of a genus were quantified using estimated PC scores as input variables in multi-group discriminant analysis (using FORTRAN77 program BMDP7M; Jennrich and Sampson 1985). Mahalanobis distances were computed between stratigraphical population means and between each specimen and its corresponding stratigraphical population centroid. The percentage of individuals in each taxon correctly and incorrectly classified according to 'zones' of occurrence was reported as was the percentage of individuals in each lineage correctly and incorrectly classified according to species. Successful classification of stratigraphical populations and the placement of a high percentage of individuals into stratigraphically proximal 'zones' implied a gradual change, where mixing of individuals from proximal 'zones' was due to the existence of intermediate morphologies.

Canonical variate 1 mean scores of stratigraphical populations, calculated by discriminant analysis, were plotted and the morphological meaning of trends was represented by the shape of individuals with canonical scores most closely approximating group means. Group centroids were used instead of individual canonical variate scores to make trends more easily recognizable. A non-parametric rank correlation technique was used to search through group centroids of all of the canonical variates of a taxa to find significant monotonic trends. Spearman's rank correlation coefficient, C , was calculated to quantify the relationship between temporal order and the order of group centroids along a canonical variate axis. Multiple range tests (STATGRAPHICS software; Statistical Graphics Corporation 1988) were performed using canonical variate 1 and 2 mean scores of stratigraphical populations of congeners. The statistical technique employed least significant difference (LSD) of means at the 95 per cent. confidence level in order to determine the presence of homogeneous stratigraphical populations. The homogeneous groups were plotted against time and associated stratigraphical level in order to show the maximum time interval in which a significant change in canonical variate 1 and 2 score means and, thus, shape occurred.

COMPARISON WITH ALTERNATIVE METHODS OF SHAPE ANALYSIS

The need to quantify shape was recognized by Thompson (1915), who used cartesian coordinates to describe the shape of one organism as the distortion of another. Benson (1981) more recently developed a morphometric technique using a similar approach. However, rather than explaining shape change in terms of homogeneous plane strain, as in Thompson's model, he examined the differential deformation of geometrical representations of homologous parts in relation to overall form. Both methods rely on the recognition of homologous points to compute morphological changes. Point to point measurements have been used widely in biometric studies, probably for reasons of instrumental limitations and past precedents, rather than theoretical considerations (Scott 1980). The development of alternative morphometric techniques to process outline information (e.g. Fourier, Eigenshape and PC shape analysis) has proven to be useful when describing simple invertebrate shape where there are few homologous points along the periphery.

Both Eigenshape (Lohmann 1983) and PC shape analysis use multivariate statistics to reduce orientated fossil outline information to fewer principal components. One difference between PC shape and Eigenshape analysis is the method of representation of an organism's outline. While PC

shape analysis uses equiangular radial lengths about an organism's calculated centre of gravity, Eigenshape analysis uses net angular changes in direction at each step around a perimeter (preferred technique where there are re-entrants along a shape's periphery). Another difference between PC shape and Eigenshape analysis is the calculation of principal components based upon covariances among shapes versus correlations among shapes. Whereas the first principal component in PC shape analysis describes maximum shape variation among organisms, the first Eigenshape describes the average shape of a group of organisms. More recently, users of Eigenshape analysis have started to use covariances among shapes in principal components analysis (e.g. Schweitzer and Lohmann 1990). A strength of multivariate shape methods, such as Eigenshape and PC shape analysis, is that the first k basis vectors (principal components) account for more variation in a data set than the first k basis vectors of other methods, such as the Fourier technique, whose basis vectors are the Fourier harmonics.

The Fourier method characterizes shape using a harmonic Fourier series of the expansion of the radius as a function of the angle about the centre of gravity. The harmonics are computed from:

$$R(\theta) = A_0 + \sum_{n=1}^{\infty} A_n \cos(n\theta - \Phi_n),$$

where R is a radius vector measured from a shape's centre of gravity to a point on the periphery in the polar direction θ , A_0 is the mean radius of the shape, A_n is the amplitude and ϕ_n is the phase angle of the n th term in the series.

Each Fourier harmonic represents a certain shape element, with the lower harmonics describing gross morphology such as elongation (2nd harmonic) and triangular shape (3rd harmonic), and the higher harmonics describing bumps on a shape such as scalloped edges due to ribbing. When the thirty-six radial loadings of each PC (generated by the PC shape technique) are plotted they resemble Fourier harmonic shapes (Text-fig. 4A). There are, however, some profound differences: (1) Fourier harmonics add nodes or loops with an increase in harmonic value while increasing PCs may retain the same number of loops but orientate them differently; thus, PC 1 and 2 might both describe elongation but be offset by 45°; (2) Fourier harmonics have symmetrical loops of equal size, while PC loadings form asymmetrical loops of various sizes.

The significance of the asymmetrical positive and negative loops becomes apparent when PC scores are combined with PC loadings to recreate a shape (Text-fig. 4B). A large negative PC 1 score combined with the PC 1 loadings of the *Anadara* genus creates an elongate shape with a larger length than height, whereas a large positive PC 1 score creates a rounder shape with a roughly equivalent length and height. PC 1 loadings in all of the genera consist of four loops orientated along x (anterior–posterior) and y (dorsal–ventral) axes of elongation, but the orientation of negative and positive loops in the round genera is offset by 90° of the elongate genera (Text-fig. 4A). Elongate species have negative loadings orientated along the anterior–posterior axis, while negative loadings of round species are orientated along the dorsal–ventral axis. Increasingly negative PC 1 scores will generate increasing shell length/height (L/H) ratios in elongate species and decreasing L/H ratios in round species.

PC 1 defines an elliptical component in all of the species. PC 2 also defines an elliptical component but at a different orientation to PC 1. PC 3 and 4 generally represent a triangular component at two different orientations and PC 5 and higher PCs represent more complex shapes. The relative contribution of each PC to shape is presented in Text-figure 4C, where, PC 1 was first added to the average shape of the *Astarte* genus according to the equation in Text-figure 4B, followed by the cumulative addition of increasing PCs. The importance of the contribution of PC 1 in recreating shape is demonstrated by the close approximation of the original morphology. PC 2 and 3 add further detectable shape modifications but are less important than PC 1. Shape modifications added by PC 4 and higher PCs are less discernible.

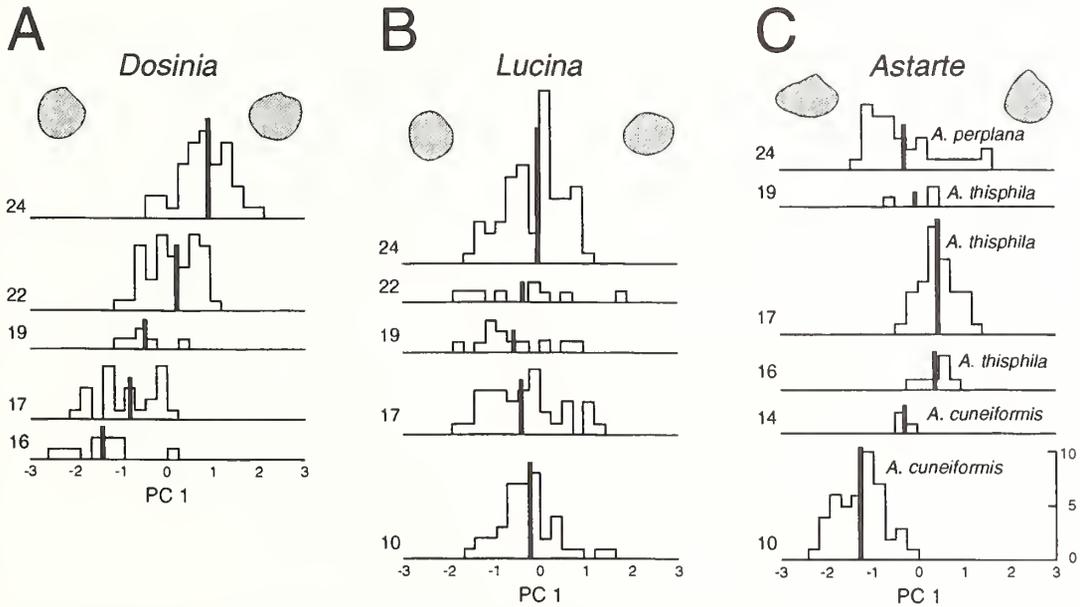
More PCs were required to account for approximately 90 per cent. of total shape variation in the more rounded genera, *Dosinia* and *Lucina*, because PC 1 accounted for less variation in shape than

in the elongate genera, *Anadara* and *Astarte* (Table 2). The greater contribution of PC 1 to the shape of elongate genera is due to the importance of variations in shell length versus height.

TEMPORAL TRENDS IN BIVALVE SHAPE

Dosinia acetabulum (Conrad)

PC 1 frequency histogram plots and the plot of canonical variate 1 group centroids show that valves evolved from elliptical shapes with smaller L/H ratios, reduced posterior regions and shallow gently sloping lunules, to more rounded shapes, with more pronounced anterior and posterior regions and deeper lunules (Text-figs 5A, 6C). Stratigraphical populations had significantly different PC 1 scores

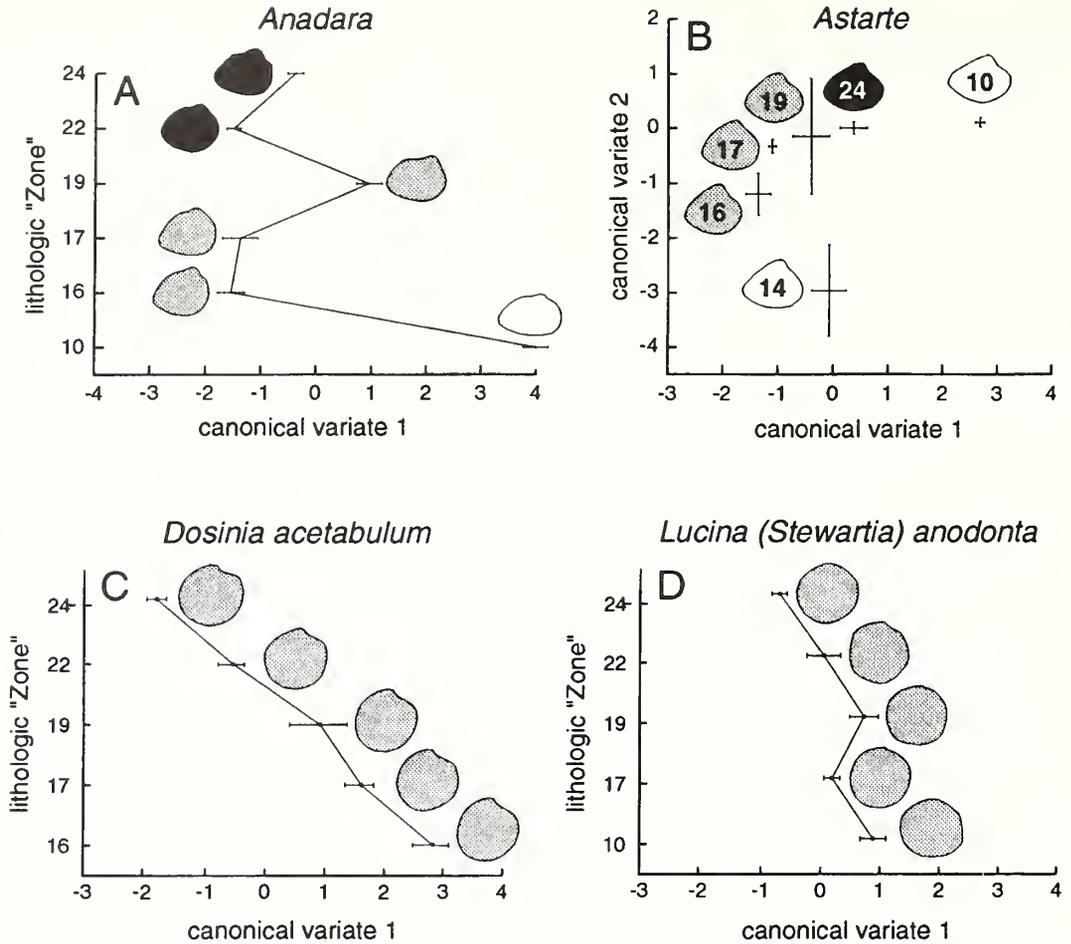


TEXT-FIG. 5. PC 1 score frequency histograms labelled with means and reconstructed end member shapes; C, vertical axis denotes number of individuals which also applies to A and B.

according to Kruskal–Wallis one-way analysis by ranks (Table 3) and the canonical variate 1 monotonic trend was significant according to Spearman's rank correlation analysis (Table 5). Multiple range analysis placed all of the stratigraphical populations into separate groups with the exception of populations from 'zones' 17 and 19, representing a time span of less than 2 million years (Text-fig. 3).

PC 1, accounting for greatest shape variation (Table 2), contributed the most to the canonical variate 1 function (Table 6) and canonical variate 1 accounted for the greatest dispersion between stratigraphical populations (Table 5). Thus temporal shape change made the biggest contribution to total shape variation (Table 6).

Discriminant analysis successfully classified a majority of individuals with their correct stratigraphical level while misclassified specimens were placed predominantly into 'zones' sampled closest to the correct 'zone' (Table 4). The close morphological affinity between adjacent fossiliferous 'zones' suggests that the change from one 'zone' to the next was gradual.



TEXT-FIG. 6. Average canonical variate scores with standard deviation bars and the shape of individuals with scores most closely approximating group centroids; A, white shell is *Anadara subrostrata*, grey shells are *A. staminea* and black shells are *A. idonea*; B, *Astarte* outlines labelled with corresponding 'zones'; white shells are *A. cuneiformis*, grey shells are *A. thisphila* and black shell is *A. perlana*.

Lucina (Stewartia) anodonta Say

No trend is apparent in the PC 1 frequency histograms of stratigraphical populations (Text-fig. 5B). Results of Kruskal-Wallis one-way analysis by ranks revealed that there was less difference between stratigraphical populations of *Lucina (Stewartia) anodonta* than in the other genera studied (Table 3).

Discriminant analysis produced only one canonical variate function and PC 2 was the only PC contributing to canonical variate 1 (Table 6). As PC 2 accounts for only 26 per cent. of total shape variation the discrimination between morphologies of stratigraphical populations is based upon only a quarter of total shape variation; thus three-quarters of shape variation is influenced by factors other than temporal change (Table 2).

Discriminant analysis successfully classified less than 50 per cent. of individuals to their appropriate stratigraphical level, with a larger percentage of incorrectly classified individuals being placed in stratigraphically distant 'zones' versus proximal 'zones' (Table 4). There is no obvious trend apparent in the plot of canonical variate 1 group centroids other than species from 'zone' 24

TABLE 3. Results of Kruskal–Wallis one-way analysis by ranks using PC 1 scores of stratigraphical populations of congeners.

	'Zones'	Ranks		'Zones'	Ranks
<i>Anadara</i>	10	19-46	<i>Dosinia</i>	16	15-10
	16	211-88		17	26-84
	17	184-94		19	35-08
	19	79-15		22	61-80
	22	185-48		24	94-63
	24	138-39			
Test statistic = 153.46			Test statistic = 76.29		
Signif. level = 0			Signif. level = 1.11E-15		
<i>Astarte</i>	10	27-81	<i>Lucina</i>	10	82-82
	14	67-00		17	73-70
	16	101-36		19	56-79
	17	97-74		22	77-00
	19	77-33		24	94-63
	24	66-17			
Test statistic = 82.92			Test statistic = 9.20		
Signif. level = 2.22E-16			Signif. level = 0.06		

TABLE 4. Success of discriminant analysis in classifying individuals to corresponding 'zones'.

Genus	% Classified with correct species	% Specimens classified in		
		Correct 'Zone'	Nearest 'Zone'	Other 'Zone'
<i>Anadara</i> lineage	86.9	66.9	17.5	15.6
<i>A. subrostrata</i>	94.3	94.3	0.0	5.7
<i>A. staminea</i>	80.6	61.1	13.9	25.0
<i>A. idonea</i>	85.9	63.4	23.1	13.5
<i>Astarte</i> lineage	74.7	65.4	16.4	18.2
<i>A. cuneiformis</i>	79.2	79.2	2.0	18.8
<i>A. thisphila</i>	97.9	63.8	34.1	2.1
<i>A. perplana</i>	46.9	46.9	12.5	40.6
<i>Dosinia acetabulum</i>		69.5	26.6	3.9
<i>Lucina (Stewartia) anodonta</i>		42.8	21.7	35.5

are more rounded than earlier species (Text-fig. 6D). The apparent stasis is verified by Spearman's rank correlation analysis which found no significant monotonic trend (Table 5). Multiple range analysis grouped distant stratigraphical populations together, revealing that there was no significant change over more than 9 million years other than the differentiation of 'zone' 24 from earlier stratigraphical populations (Text-fig. 3).

The Astarte lineage

PC 1 accounted for 53 per cent. of total shape variation within the *Astarte* lineage (Table 2). PC 1 frequency histograms reveal that valves evolved from cuneiform to trigonal and then back towards more cuneiform shapes (Text-fig. 5c). Temporal morphological change was significant according to

TABLE 5. Results of non-parametric rank correlation analysis using group centroids for each canonical variate; monotonic trends significant at the 95 per cent. level ($P \leq 0.05$) are denoted by an asterisk.

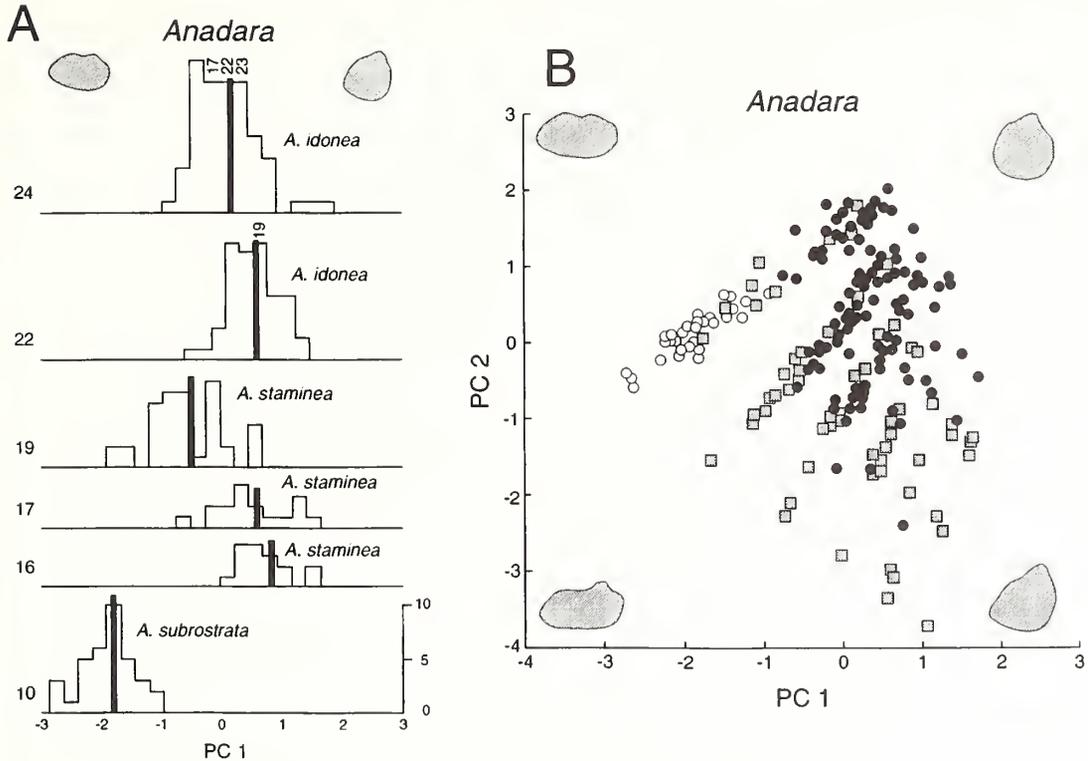
Genus	Canonical variate	% Variation accounted for	Spearman's C	Significance
<i>Anadara</i>	1	71	-0.14	$P = 0.75$
	2	21	-0.09	$P > 0.75$
	3	4	-0.77	$P > 0.075$
	4	2	-0.64	$P > 0.1$
<i>Astarte</i>	1	86	-0.20	$P > 0.5$
	2	8	0.14	$P = 0.75$
	3	5	0.49	$P > 0.25$
	4*	1	-0.89	$P < 0.05$
<i>Dosinia</i>	1*	80	-1.00	$P = 0.00$
	2	17	0.00	$P = 1.00$
	3	2	-0.20	$P < 0.75$
	4	1	0.10	$P > 0.75$
<i>Lucina</i>	1	100	-0.90	$P > 0.05$

TABLE 6. PC coefficients for discriminant functions; canonical variates with significant monotonic trends are marked with an asterisk.

Genus	Axis	PC						
		1	2	3	4	5	6	7
<i>Anadara</i>	1	-2.10	-0.28	0.13	-0.13	0.28	-0.22	
	2	-0.04	0.93	-0.47	-0.71	-0.10	-0.64	
	3	0.02	0.07	-0.06	0.38	0.92	-0.42	
	4	0.13	-0.62	-0.10	-0.77	0.34	-0.04	
<i>Astarte</i>	1	-1.85	-0.35	-0.48		-0.09		
	2	0.17	-0.40	-0.19		-1.00		
	3	-0.02	0.87	-0.54		-0.25		
	4*	0.26	-0.39	-0.80		0.36		
<i>Dosinia</i>	1*	-1.71	0.35		0.38			0.39
	2	0.04	-0.44		1.03			-0.45
	3	0.03	-0.71		0.03			0.74
	4	0.34	0.58		0.47			0.53
<i>Lucina</i>	1		-1.51					

Kruskal-Wallis one-way analysis by ranks (Table 3). The morphological transformation of the youngest species into a shape similar to that of the oldest species was apparent in plots of homogeneous group ranks (Text-fig. 3) and the canonical variate 1 and 2 group centroids of stratigraphical populations (Text-fig. 6B).

Discriminant analysis classified a majority of individuals with their correct 'zones' (Table 4). Discriminant analysis successfully classified 97.9 per cent. of individuals to the *A. thisphila* species while only 46.9 and 79.2 per cent. of individuals were correctly placed into the *A. perplana* and



TEXT-FIG. 7. *Anadara*. A, PC 1 score frequency histograms labelled with means and reconstructed end member shapes; vertical axis denotes number of individuals. B, Plot of PC 1 and 2 scores with reconstructed end member shapes; open circles are *A. subrostrata*, grey squares are *A. staminea* and black circles are *A. idonea*.

A. cuneiformis species, respectively. More incorrectly classified individuals of *A. perplana* and *A. cuneiformis* were placed into stratigraphically distant 'zones' versus levels sampled nearest the correct 'zone'. Mixing of distant stratigraphical populations was due to the transformation of the lineage towards older morphologies. The resemblance between *A. perplana* and *A. cuneiformis* shape was demonstrated by a large percentage of the misclassified individuals being placed in stratigraphical 'zones' corresponding with the other species. The middle species, *A. thisphila*, had a larger percentage of misclassified individuals placed into 'zones' sampled nearest the correct 'zone' suggesting that transformation from the youngest stratigraphical population of *A. cuneiformis*, through all stratigraphical populations of *A. thisphila*, to the single stratigraphical population of *A. perplana* was characterized by mixing of intermediate forms. The presence of intermediate morphologies was further demonstrated with multiple range analysis, which placed the youngest stratigraphical populations of *A. cuneiformis* and *A. thisphila* into two ranks instead of one (Text-fig. 3). Furthermore, PC 1 and canonical variate 1 trends were preserved in succeeding species transformations, which is not inconsistent gradual change. However, it can be argued that the transformation of two homogeneous populations of *A. thisphila* into one population of *A. perplana* resulted from migration of an allopatric *A. thisphila* population into the study area followed by the removal of the earlier population (Text-fig. 3).

Canonical variate 4 had the only significant monotonic trend (Table 5). Canonical variate 4 was most highly influenced by PC 3 (Table 6) having a loading which defined a triangular component of shape (Glassburn 1987, p. 139). The negative Spearman's rank correlation coefficient (Table 5)

indicates that older species have higher canonical variate 4 mean scores and thus, shapes generated by more negative PC 3 scores (because PC 3 has a large negative coefficient in the canonical variate 4 function; Table 6). As more cuneiform shapes would be generated with more negative *Astarte* PC 3 scores (Glassburn 1987, p. 139), the monotonic trend detected by rank correlation analysis of canonical variate 4 was from cuneiform shapes in older species to trigonal shapes in younger species.

The PC which accounted for a majority of total shape variation (PC 1) made the greatest contribution to canonical variate 1, which accounted for 86 per cent. of variation between stratigraphical populations, indicating that temporal shape change had a major influence on overall shape variation. In contrast, canonical variate 4 which accounted for 1 per cent. of variation between stratigraphical populations was influenced predominantly by PC 3 accounting for just 12 per cent. of total shape variation. Thus, the most significant shape trend was from cuneiform to trigonal back to cuneiform shapes. However, there was a small, monotonic trend from cuneiform towards trigonal morphologies.

The Anadara lineage

PC 1 accounted for 53 per cent. of shape variation in the *Anadara* lineage (Table 2). PC 1 frequency histograms showed a dichotomy between inter- and intraspecific shape trends (Text-fig. 7A). Whilst intraspecific trends were from valve shapes with smaller to larger L/H ratios, interspecific trends, which determined the ultimate shape transformation, were from valve shapes with larger to smaller L/H ratios. Temporal shape change was significant according to Kruskal–Wallis one-way analysis by ranks, with the test statistic being nearly double that of the *Astarte* lineage (Table 3).

The plot of PC 1 and 2 scores of the congeners of *Anadara* revealed the presence of at least five different morphological groups (Text-fig. 7B). The odd PC 1 and 2 score pattern was generated with no rotation of the PC loadings matrix. When one of five different rotation methods available in the PC program BMDP4M (Frane *et al.* 1985) was used the pattern was not observed. Thus the appearance of the PC 1 and 2 score pattern may be an artefact of the PC analysis technique. The evolution of all of the *Anadara* morphological groups was from negative PC 1 and 2 scores, generating elongate valves with straight ventral margins to positive PC 1 and 2 scores, generating rounder valves with smaller L/H ratios and curved ventral margins.

Schoonover (1941) noted the presence of different morphological groups of *A. staminea* from different beds at the same locality and between different localities. She observed that variations in shell diameter resulted in variations in valve morphology where specimens with larger diameters had sharper angles at the junction of the anterior and dorsal, dorsal and posterior, and posterior and ventral margins whilst specimens with smaller diameters had outlines less squarely compressed anteriorly and posteriorly. Both Glenn (1904) and Sheldon (1916) noted that some of the variations of *A. staminea* were so distinctive that they had been incorrectly described as separate species. Therefore a preliminary study of geological factors which may have contributed to the presence of the different morphological groups was conducted. When the individual points were labelled according to valve area it was revealed that size did not contribute to the PC 1 and 2 pattern and thus the different morphological groups were not the result of ontogeny (Glassburn 1987, figs 8.37–8.40). Also, the five morphological groups do not represent geographical populations; for instance there were five morphological groups of *A. staminea* from 'zone' 19 sampled at two locations (Calvert Cliffs State Park and Camp Baybreeze; Glassburn 1987, fig. 8.40). Furthermore, the morphological group containing individuals of *A. subrostrata*, *A. staminea* and *A. idonea* had individuals sampled from localities spanning the entire length of the study area from Randle Cliffs Beach to Chancellor's Point (Text-figs 2, 7B). This study cannot clarify whether or not the morphological groups are ecophenotypes, as they might have resulted from differences in local palaeoecology. A more extensive field investigation is required before the PC 1 and 2 pattern can be dismissed as merely an artefact of the shape technique.

Discriminant analysis placed 67.2 per cent. of individuals into the correct stratigraphical level, but was much more successful classifying individuals according to species (Table 4). Thus, there was a

greater distinction between the morphology of species than stratigraphical populations. More incorrectly classified individuals were placed into stratigraphically proximal 'zones' rather than distant 'zones'. However, mixing between proximally sampled stratigraphical populations was predominantly within species with only 2 per cent. of the misclassified individuals being the result of mixing between the youngest population of an ancestor species and the oldest population of its descendant.

Non-parametric rank correlation analyses of canonical variate group centroids revealed no significant monotonic trends (Table 5). Plots of canonical variate 1 group centroids and canonical variate 1 and 2 homogeneous rankings revealed that the direction of species' trends was not preserved with subsequent speciation (Text-figs 3, 6A). Furthermore, a greater amount of change occurred with speciation than with any intraspecific change. The canonical variate 1 plot revealed that overall morphological transformation of the lineage was from species with larger L/H ratios to valves with roughly equivalent lengths and heights. Canonical variate 1, which accounted for 71 per cent. of variation between stratigraphical populations, was most highly influenced by PC 1, which accounted for a majority of total shape variation; thus, variation between stratigraphical populations made the biggest contribution to total shape variation. However, speciation contributed the most to temporal variation.

Comparison with earlier morphometric studies of the Maryland species

The observed lack of congruent temporal patterns between Chesapeake Group bivalves was also noted by Kelley (1984). The morphological variation was probably not the result of shared ecophenotypic responses but the result of genetic variation.

In common with the present study, Kelley (1983a, 1983b, 1984) observed that the *Anadara* lineage had an evolutionary tempo consistent with punctuated equilibrium. The present study found that overall morphological transformation of the lineage was determined by interspecific trends which were from elongate shapes, with straight ventral margins, to rounder shapes, with curved ventral margins. Stanley (1970) describes two life modes for extant *Anadara* species: (1) an infaunal or epifaunal byssally attached life mode which preceded the development of (2) free burrowing forms. Species with byssally attached life modes, such as *Anadara antiquata*, are distinguished from free burrowers, such as *A. ovalis* and *A. chennitzi*, by their more elongate shapes, where an elongate and flattened ventral margin provides a broader means of support for byssal attachment (Stanley 1970). The *Anadara* lineage in this study was composed of elongate forms, especially *A. subrostrata*, suggesting a byssally attached life mode. The supposition that the *Anadara* species in this study were byssally attached is supported by Gernant (1970), who described the *Anadara* species as semi-infaunal suspension feeders. The general transformation of the *Anadara* lineage was from forms more ideally suited to a byssally attached life mode towards shapes more reminiscent of burrowing forms.

As in this study, convergence between youngest and oldest *Astarte* species' morphologies was observed by Kelley (1983a) in seven out of eight measured characters and Schoonover (1941), who noted that *A. perplana* resembled some of the Randle Cliffs Beach *A. cuneiformis* specimens (Text-figs 5c, 6b). Furthermore, Schoonover (1941) observed that *A. perplana* had a smaller L/H ratio, being more trigonal in shape than *A. cuneiformis*, which supports the results of rank correlation analysis which revealed a monotonic trend in canonical variate 4 centroids from cuneiform valve shapes towards more trigonal forms (Table 5). In contrast to the present study, Kelley (1983a, 1983b, 1984) reported an evolutionary tempo of punctuated equilibrium within the *Astarte* lineage. However, morphological intermediates between *Astarte* species were observed by Schoonover (1941) and Kelley (1983a) consistent with gradual change having occurred.

In contrast to this study, Kelley (1983a) observed stasis within *Dosinia acetabulum* (Conrad). Disparities in evolutionary tempos observed between this study and Kelley's (1983a, 1983b, 1984) studies of the *Astarte* lineage and *Dosinia acetabulum* may have been due to differences in the

evolution of valve shape versus biometric parameters measured by Kelley (1983a, 1983b, 1984). Probably, more significant is the difference in the temporal resolution of the two investigators' studies. As results in this study were based upon specimens collected from fewer stratigraphical levels, apparent gradual trends may have resulted from consistent direction in punctuation events or sampling of a zigzagging stasis trend coincidentally resembling unidirectional change.

In contrast to this study, Stanley and Yang (1987) found that stasis best described the evolutionary mode of *Dosinia acetabulum*. Their results were based upon calculations of the area of non-overlap of two populations' first eigenshapes as a percentage of the area of fossil eigenshape. However, discriminant analysis based on twenty-four morphometric variables, including aspects of valve shape, revealed some monotonic trends in *D. acetabulum* (Stanley and Yang 1987, fig. 17).

Stanley and Yang (1987) state that *D. discus*, a US East Coast extant species, arose from *D. acetabulum*. *D. discus* is a rapid burrower preferring sandy substrates and has disc-shaped valves which it uses to slice vertically downward into the substrate (Stanley 1970). While this study reports that *D. acetabulum* valves gradually evolved from oblong to disc-shapes (Test-figs 4A, 5C), Stanley and Yang (1987) found that temporal shape variation in *D. acetabulum* was minor relative to geographical variation and that interspecific change within the 'lineage' containing *D. acetabulum* and *D. discus* was characterized by a speciation event or rapid phyletic change. The present study requires sampling from a wider geographical area and comparison between intra- and interspecific variation within the corresponding 'lineage' of *D. acetabulum* in order to support conclusions concerning evolutionary mode. The monotonic trend observed by the present study may be a minor trend in a larger time frame of zigzagging morphological stasis, or a bend in an anastomosing stream of change in which geographical variability was as great as temporal variability.

Like the present study, Kelley (1984) found that stasis best described temporal shape variation in *Lucina (Stewartia) anodonta* Say. Only individuals of *L. anodonta* from 'zone' 24 could be distinguished from other stratigraphical populations, being smaller and more inflated than the earlier specimens (Schoonover 1941; Kelley 1984). Stasis in *L. anodonta* is supported by the species persistence from the Miocene to the Recent (Bretsky 1976).

DISCUSSION

There were many similarities in results using the PC shape technique and previous studies which used other morphometric techniques to describe temporal shape change within the same bivalve species. Furthermore, many aspects of temporal shape variation highlighted by the PC shape technique were also reported in a thorough study by Schoonover (1941) who made qualitative observations about temporal morphological changes. Although there were some discrepancies between evolutionary tempos and modes reported in this and previous studies the cause was most probably the difference in temporal resolution, where this study sampled from fewer stratigraphical horizons or from a more limited time span and geographical range. Limitations in the sampling scheme notwithstanding the PC shape analysis technique proved to be a fast and simple way to characterize fossil outline shape. Its strength over qualitative assessment of temporal shape change is that it quantifies shape, providing a more objective way to compare shapes of different stratigraphical populations. The advantage of using PC shape analysis versus point-to-point measurement techniques, as with all image analysis techniques, is the speed at which morphological information can be collected.

One doubt concerning the validity of morphometric techniques which process outlines is that comparisons are made between non-homologous points whereas techniques utilizing point-to-point measurements can target homologous points (Bookstein *et al.* 1982; Full and Ehrlich 1986). There are generally few homologous points present on the peripheries of simple invertebrates and outline processing techniques which compare points connected by equiangular radial lengths (e.g. Fourier and PC shape analysis) or equal chord lengths (e.g. Eigenshape analysis) can only be certain of achieving correspondence with respect to one homologous point if it is the initial point.

Although PC shape analysis performed calculations between non-homologous points, the first two PC loadings, accounting for greatest shape variation, were always orientated in relation to morphological landmarks (Text-fig. 4A). PC 1 loadings always contained two pairs of lobes with axes 90° to each other. One axis always connected the umbo with the ventral margin (defining shell height) and the other axis defined shell length. PC 2 loadings always contained two pairs of lobes orientated 45° to the lobes of the PC 1 loadings, with one axis connecting the lunule with the point of intersection between the posterior and ventral regions and the other axis connecting the point of intersection between the posterior and dorsal regions with the point of intersection between the anterior and ventral regions.

Possibly more important than recording changes between limited homologous points present on a bivalve periphery is recording distortions in bivalve shape occurring to accommodate changes in shape or size of soft body parts. An interesting project for the future would be to use PC shape analysis to describe bivalve shape and the shape of muscle scars in order to determine how changes in the shape of the muscle attachment area impacts upon valve shape.

SUMMARY

1. Cubic interpolation reduced 100–200 x - y coordinates of a properly rotated valve periphery to thirty-six radial lengths spaced at equiangular intervals. The thirty-six radial lengths were then used as variables in principal components analysis reducing the original data set to less than eight principal components accounting for approximately 90 per cent. of total shape variation (Table 2). PC scores were used as shape variables in discriminant analysis and non-parametric rank correlation analysis to determine whether significant intra- and interspecific shape trends existed.

2. Original shape was reconstructed by destandardizing results of matrix multiplication of PC scores with PC loadings (Text-fig. 4).

3. Phyletic gradualism was implied in a lineage where the direction of an intraspecific shape trend was retained with the transformation of that species into the next species and total shape change was equally influenced by intra- and interspecific trends.

4. Punctuated equilibrium was implied in a lineage where interspecific trend directions varied markedly from associated intraspecific trends and intraspecific temporal variation contributed much less than speciation to total shape change.

5. Discriminant analysis demonstrated that a species population in one stratigraphical level was measurably different in shape from a population in another stratigraphical level. If a high percentage of misassigned individuals were placed in proximal stratigraphical levels it indicated a mixing of morphological intermediates implying a gradual change.

6. The valves of *Dosinia acetabulum* (Conrad) evolved gradually from oblong to disc shapes (Text-figs 5A, 6C).

7. Stasis best described the temporal shape trend of *Lucina (Stewartia) anodonta* Say (Text-figs 5B, 6D).

8. The *Astarte* lineage evolved gradually from cuneiform to trigonal and back to wedge shapes (Text-figs 5C, 6B).

9. The *Anadara* lineage exhibited an evolutionary mode consistent with punctuated equilibrium. Intraspecific trends were from valves with smaller L/H ratios to more elongate shapes, whilst interspecific changes, controlling ultimate shape transformation in the lineage, were from elongate valves with straight ventral margins to valves with smaller L/H ratios and curved ventral margins (Text-figs 6A, 7).

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REFERENCES

- BENSON, R. H. 1981. Form, function and architecture of ostracode shells. *Annual Review of Earth and Planetary Sciences*, **9**, 59–80.
- BLACKWELDER, B. W. and WARD, L. W. 1976. Stratigraphy of the Chesapeake Group of Maryland and Virginia. *Geological Society of America Southeast Section Field Trip Guidebook*, 1–55.
- BOOKSTEIN, F. L., CHERNOFF, B., ELDER, E. L., HUMPHRIES, J. M., SMITH, G. R. and STRAUSS, R. E. 1985. *Morphometrics in evolutionary biology, Special Publication 15*, Academy of Natural Sciences in Philadelphia, 1–277.
- STRAUSS, R. E., HUMPHRIES, J. M., CHERNOFF, B., ELDER, R. L. and SMITH, G. R. 1982. A comment upon the uses of Fourier methods in systematics. *Systematic Zoology*, **31**, 85–92.
- BRETSKY, S. S. 1976. Evolution and classification of the Lucinidae (Mollusca; Bivalvia). *Palaeontographica Americana, Vol. VIII*, **50**, 219–337.
- DRYDEN, A. L., Jr. 1930. Stratigraphy of the Calvert Formation at Calvert Cliffs, Maryland. Unpublished Ph.D. thesis, Johns Hopkins University.
- EHRlich, R. and WEINBERG, B. 1970. An exact method for characterization of grain shape. *Journal of Sedimentary Petrology*, **40**, 205–212.
- FRANE, J., JENNRICH, R. and SAMPSON, P. 1985. Factor analysis. 480–499. In DIXON, W. J. (ed.). *BMDP Statistical Software*. University of California Press, Berkeley, 733 pp.
- FULL, W. E. and EHRlich, R. 1986. Fundamental problems associated with 'eigenshape analysis' and similar 'factor' analysis procedures. *Mathematical Geology*, **18**, 451–463.
- GERNANT, R. E. 1970. Paleocology of the Choptank Formation (Miocene) of Maryland and Virginia. *Maryland Geological Survey Report on Investigations*, **12**, 1–90.
- GIBSON, T. G. 1962. Benthonic foraminifera and paleocology of the Miocene deposits of the middle Atlantic Coastal Plain. Unpublished Ph.D. thesis, Princeton University, New Jersey.
- GLASSBURN, T. A. 1987. Principal components quantitative shape analysis of Middle Miocene bivalves from Southern Maryland. Unpublished Ph.D. thesis, Lehigh University, Pennsylvania.
- GLENN, L. C. 1904. Systematic paleontology, Miocene Pelecypoda, *Maryland Geological Survey Miocene Volume*, 274–401.
- JENNRICH, R. and SAMPSON, P. 1985. Stepwise discriminant analysis. 519–537. In DIXON, W. J. (ed.). *BMDP Statistical Software*. University of California Press, Berkeley, 733 pp.
- KELLEY, P. H. 1983a. Evolutionary patterns of eight Chesapeake Group molluscs: evidence for the model of punctuated equilibria. *Journal of Paleontology*, **57**, 581–598.
- 1983b. The role of within-species differentiation in macroevolution of Chesapeake Group bivalves. *Paleobiology*, **9**, 261–268.
- 1984. Multivariate analysis of evolutionary patterns of seven Miocene Chesapeake Group molluscs. *Journal of Paleontology*, **58**, 1235–1250.
- KIDWELL, S. M. 1984. Outcrop features and origin of basin margin unconformities, Miocene Lower Chesapeake Group, Atlantic Coastal Plain. *Memoir of the American Association of Petroleum Geologists*, **37**, 37–58.
- 1986. Models for fossil concentrations: paleobiologic implications. *Paleobiology*, **12**, 6–24.
- 1988. Reciprocal sedimentation and noncorrelative hiatuses in marine–paralic siliciclastics: Miocene outcrop evidence. *Geology*, **16**, 609–612.
- 1989. Stratigraphic condensation of marine transgressive records: origin of major shell deposits in the Miocene of Maryland. *The Journal of Geology*, **97**, 1–24.
- LOHMANN, G. P. 1983. Eigenshape analysis of microfossils: a general morphometric procedure for describing changes in shape. *Mathematical Geology*, **15**, 659–672.
- MOORE, R. C. 1969. *Treatise on invertebrate paleontology, Part N, Mollusca 6 (1–2)*. Geological Society of America and University of Kansas Press, Lawrence, Kansas, 951 pp.
- NEWELL, W. L. and RADER, E. K. 1982. Tectonic control of cyclic sedimentation in the Chesapeake Group of Virginia and Maryland. *Geological Society of America Northeastern-Southeastern Section Guidebook Field Trip No. 1*, 1–27.
- PARKS, J. M. 1983. Reference-rotated eigenshape analysis of sands and sandstones. *Bulletin of the American Association of Petroleum Geologists*, **67**, 529.

- 1987. Analysis of two-dimensional shapes by principal components score descriptors: geological interpretations from sand grains, pebbles, benthic foraminifera and bivalve mollusks. *Bulletin of the American Association of Petroleum Geologists*, **71**, 601–602.
- SCHOONOVER, L. M. 1941. A stratigraphic study of the molluscs of the Calvert and Choptank Formations of Southern Maryland. *Bulletin of American Paleontology*, **25**, 169–299.
- SCHWARZ, H. P. and SHANE, K. C. 1969. Measurement of particle shape by Fourier analysis. *Sedimentology*, **13**, 213–231.
- SCHWEITZER, P. N. and LOHMANN, G. P. 1990. Life-history and the evolution of ontogeny in the ostracode genus *Cyprideis*. *Paleobiology*, **16**, 107–125.
- SCOTT, G. H. 1980. The value of outline processing in the biometry and systematics of fossils. *Palaeontology*, **23**, 757–768.
- SHATTUCK, G. B. 1904. Geological and paleontological relations with a review of earlier investigations. *Maryland Geological Survey Miocene Volume*, 33–137.
- SHELDON, P. G. 1916. Atlantic slope *Arcas*. *Palaeontographica Americana. Vol. 1. No. 1*, 1–98.
- STANLEY, S. M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Memoirs of the Geological Society of America*, **125**, 1–199.
- and YANG, X. 1987. Approximate evolutionary stasis for bivalve morphology over millions of years: a multivariate, multilineage study. *Paleobiology*, **13**, 113–139.
- STATISTICAL GRAPHICS CORPORATION 1988. *Statgraphics*. STSC, Inc., 773 pp.
- THOMPSON, D. W. 1915. Morphology and mathematics. *Transactions of the Royal Society of Edinburgh*, **50**, 857–895.
- TOUGH, J. G. and MILES, R. G. 1983. A method for characterizing polygons in terms of the principal axes. *Computer and Geosciences*, **10**, 347–350.
- VOKES, H. E. 1957. Miocene fossils of Maryland. *Department of Geology, Mines and Water Resources Bulletin*, **20**, 1–85.

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THE ULTRASTRUCTURE OF SPORES OF *COOKSONIA PERTONI*

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ABSTRACT. The ultrastructure of spores isolated from sporangia of *Cooksonia pertoni* from Pridoli and Lochkovian rocks of the Welsh Borderland has been elucidated using both scanning and transmission electron microscopy. The Silurian material, attributable to *C. pertoni* subsp. *synorispora*, contains *Synorisporites verrucatus* while the Devonian *C. pertoni* subsp. *apiculispota* yields either *Streelispora newportensis* or *Aneurospora* sp. All three spore taxa show an exospore (\equiv exine) composed of two layers, both of which extend into the murornate and verrucate sculpture in *Synorisporites verrucatus*, into the papillae and proximal folds of *Streelispora newportensis*, and into apertural folds (where observed) in all three taxa. In contrast, only the outer layer occurs in the apiculate sculpture of the Devonian spores. The homology of the layers is briefly discussed in relation to extant vascular cryptogams. Such ultrastructural observations compare favourably with published descriptions of the same taxa recorded from dispersed assemblages using light microscopy. Similar ultrastructure has already been recorded in cf. *Ambitisporites* isolated from Pridoli *Cooksonia pertoni* from Long Mountain, Shropshire, thus providing support for the hypothesis that, while the gross morphology and spore structure of *C. pertoni* remained unchanged from the Silurian into the Devonian, spore sculpture evolved from smooth to verrucate to apiculate.

THE record of early land plants in Silurian and basal Devonian rocks is largely based on small fragmentary coalified fossils of simple morphology and lacking anatomical detail. Studies on the use of *in situ* spores in attempts to deduce relationships and to detect hidden diversity are in their infancy. Thus the morphologically simple taxon *Cooksonia pertoni* Lang has been shown to possess at least three different kinds of spore depending in part on its geological age (Fanning *et al.* 1988). These are the dispersed miospore genera *Ambitisporites*, *Synorisporites* and *Streelispora/Aneurospora*, taxa that are united in their equatorially crassitate structure, but that differ mainly in the nature of their distal exines with sculpture being laevigate, verrucate or apiculate. From the relative ages of the megafossils and data from dispersed spore assemblages, it was inferred that laevigate spores (*Ambitisporites*) represent the ancestral state in *C. pertoni*, that apiculate spores are the most derived, and that the murornate-verrucate sculpture of *Synorisporites verrucatus* possibly represents an intermediate state in the *Ambitisporites-Streelispora/Aneurospora* lineage. *Streelispora/Aneurospora* is so written because limited numbers prevented a study and description of the proximal features of the *in situ* spores in all cases, and it is the presence or absence of proximal folds, that is used to distinguish the two genera in the dispersed record. In more recent work (Edwards *et al.* 1992) we have unequivocal evidence for *in situ Streelispora newportensis* in Lochkovian *C. pertoni*, and, in this study, for papillate apiculate equatorially crassitate spores lacking proximal folds, which can be more confidently assigned to *Aneurospora* than in previous studies, although there remain reservations on identification at specific level. Previous descriptions of the *in situ* spores employed light and scanning electron microscopy. Here we report on ultrastructure as seen in sections viewed by transmission electron microscopy.

LOCALITY DATA, MATERIAL AND TECHNIQUES

All material is housed at the National Museum of Wales, Cardiff (NMW).

Ludford Lane, Shropshire [SO 5122 7412]. Platyschisma Shale Member, Downton Castle Formation; *tripapillatus-spicula* Sporomorph Assemblage Zone; Přídolí Series, Silurian.

Two coalified discoidal sporangia (NMW 93.143G.1 and 2; Pl. 1, figs 1–5) containing *Synorisporites verrucatus* were recovered after bulk maceration, in 40 per cent. hydrofluoric acid, of a fossiliferous siltstone c. 1.6 m above the main bone bed at the famous locality at Ludford Lane Corner. This was the horizon that yielded the earliest terrestrial arthropods and stoma (Jeram *et al.* 1990) and is of early Přídolí age. The discoidal structures resemble *C. pertoni* in shape, with each bearing a centrally placed ridge marking the attachment of the subtended axis. Except at this site and at the periphery, where spores are occasionally visible, the surface of each specimen is covered by an acellular sheet with irregular depressions, interpreted as the remains of the sporangial cuticle. We therefore have neither direct gross morphological nor anatomical evidence for affinity with *C. pertoni*, identification being based on overall shape of the spore-containing region and the fact that *Synorisporites verrucatus* has not to date been found in a sporangium of any other shape.

Brown Clee Hill. Beneath small waterfall in stream section to the north of Brown Clee Hill, Shropshire; Ditton Group; lower middle part of *micromnatus-newportensis* Sporomorph Assemblage Zone; Lochkovian Stage, Lower Devonian.

The sporangia were isolated by disaggregation of the grey siltstone in water and cleaned by brief immersion in 40 per cent. hydrofluoric acid. They come from the upper plant-bearing horizon in the stream (Edwards *et al.* 1994). Dispersed palynomorphs indicate an early Lochkovian age (lower middle *micromnatus-newportensis* Zone). Four samples containing *Streelispora newportensis* were sectioned. Two are unequivocal sporangia. The less compressed one (NMW 93.143G.6) was initially almost intact distally, a fracture near the margin revealing cellular details of the sporangial wall and spores. In the second (NMW 93.143G.5) a short length of the subtending axis remains, but more of the distal wall has disappeared exposing the spores (Pl. 1, fig. 7). The remaining two are more compressed with preservation reminiscent of that in the Silurian examples: NMW 93.143G.3 has an almost circular outline; NMW 93.143G.4 is more fragmentary with an irregular outline (Pl. 1, fig. 6).

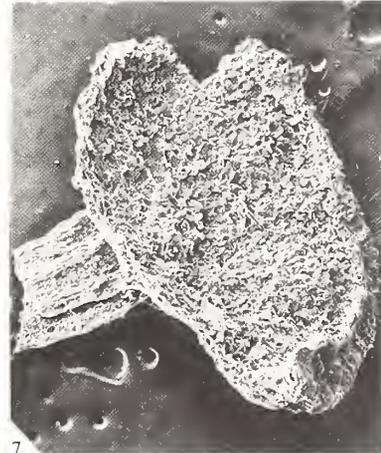
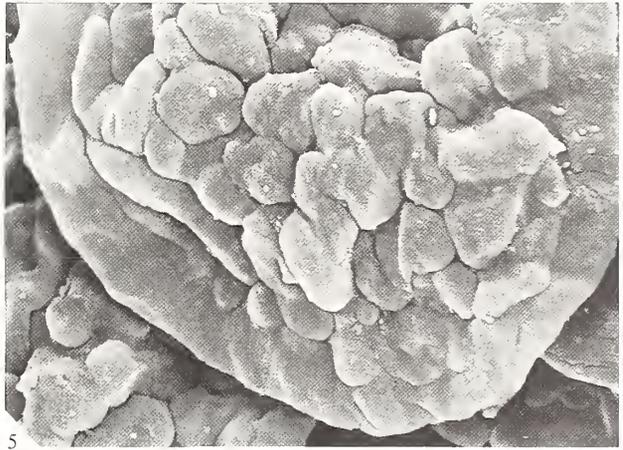
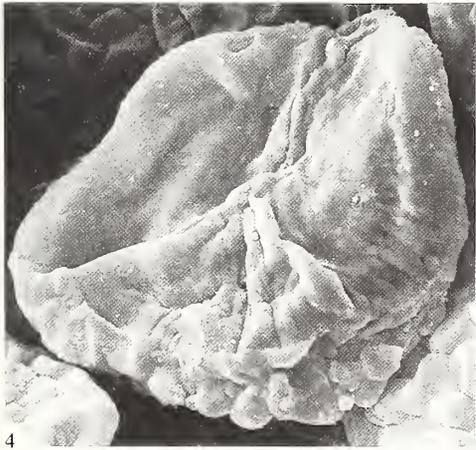
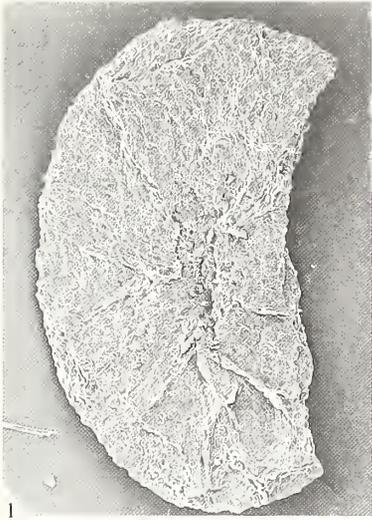
M50 motorway [SO 6650 2658]. Near 29.5 marker post on north side of motorway, Hereford and Worcester; St Maughans Formation; lowest part of *micromnatus-newportensis* Sporomorph Assemblage Zone; Lochkovian Stage, Lower Devonian (details in Edwards and Rose 1984).

The sectioned example (NMW 93.143G.7) was a spore mass, more or less circular in outline (Pl. 2, fig. 3), recovered from bulk maceration of a grey-green shale 2 m above the base of the St Maughans Formation. The distally apiculate, proximally papillate spores (Pl. 2, figs 4–7), lacking any proximal folds, are assigned to *Aneurospora* sp. and are believed to be derived from a *C. pertoni* sporangium since no other Lower Devonian sporangium of this shape has yet been demonstrated to contain *Aneurospora*.

EXPLANATION OF PLATE 1

Figs 1–5. Scanning electron micrographs (SEMs) of *Cooksonia pertoni* subsp. *synorispora*; NMW 93.143G.1; Ludford Lane, Shropshire; Downton Castle Sandstone Formation, Přídolí Series (Upper Silurian). 1, lower side of sporangium showing spores at margins and site of axis attachment; $\times 44$. 2, close up of outer surface of sporangium wall; $\times 210$. 3, spores (*Synorisporites verrucatus*) before acid treatment, with remnants of wall on left; $\times 1000$. 4, proximal surface of spore after acid treatment; $\times 3450$. 5, part of distal surface of spore after nitric acid treatment; $\times 5570$.

Fig 6–8. SEMs of *C. pertoni* subsp. *apiculispora*; north Brown Clee Hill, Shropshire; Ditton Group, Lochkovian (Lower Devonian). 6, NMW 93.143G.4; incomplete sporangium with visible spores and short subtending axis disintegrating on lower surface; $\times 25$. 7, NMW 93.143G.5; sporangium with traces of axis; $\times 55$. 8, NMW 93.143G.3; apiculate sculpture on distal surface of *Streelispora newportensis* after nitric treatment; $\times 3200$.



All specimens were first examined untreated by SEM (Cambridge 360), to allow secure identification. In the early stages of the study, suitable material was then treated with fuming nitric acid to facilitate observations by LM but more importantly to remove pyrite prior to sectioning for TEM. This contrasts with methodology for dispersed spores, where only minimal nitric acid treatment is used to aid clearing. Indeed, our experiences with *Ambitisporites*, from a Pridoli *Cooksonia pertoni* from Long Mountain, Shropshire (Rogerson *et al.* 1993), indicated that valuable information was being destroyed by the concentrated acid treatment and our procedures were subsequently modified to include sectioning of untreated spores and examination by SEM after acid treatment. This was impossible on one of our original specimens (NMW 93.143G.5) where all material had already been used. In this study, therefore, sections were prepared from untreated spores where available and all material was subjected to fuming nitric acid for 30 minutes. Unlike the *Ambitisporites* spore masses from Long Mountain, those treated with nitric acid retained their integrity. Detailed techniques for sectioning for TEM are given in Rogerson *et al.* (1993). Essentially acid-treated and untreated specimens were dehydrated, embedded in Spurr resin, sectioned at 60–90 nm using an LKB Ultratome 8801A and stained with 1 per cent. (w/v) potassium permanganate in 0.1 M phosphate buffer pH 6 followed by 2 per cent. (w/v) uranyl acetate and basic lead citrate. All sections were examined using a JEOL 100S TEM at an accelerating voltage of 80 kV.

TERMINOLOGY

To avoid confusion, particularly with conventional palynological descriptions, the terminology adopted in our ultrastructural studies (Rogerson *et al.* 1993) is repeated. Observations on extant pteridophytes reveal three components of the sporoderm (see e.g. Tryon and Lugardon 1991). These are: *perispore*, the acetolysis-sensitive peripheral envelope; *exospore*, the acetolysis-resistant component largely composed of sporopollenin (exine *sensu* Potonié and Kremp 1954); and the *endospore*, laid down immediately outside the cell membrane and, being composed predominantly of cellulose, considered unlikely to survive taphonomic processes. Similarly the perispore (or perispodium; see Traverse 1988) *sensu stricto* rarely persists in fossils, but the term is sometimes used by palynologists for a loosely attached outer layer showing no infrastructure. In this study, we use the term 'peripheral layer' for extra-exospore coalified material. The trilete mark is usually represented in TEM by a projecting apertural fold, mainly involving the exospore. A superficial suture is rarely visible in SEM. Variations within the exospore such as differences in texture, staining or structure are termed layers.

DESCRIPTIONS OF *IN SITU* SPORES

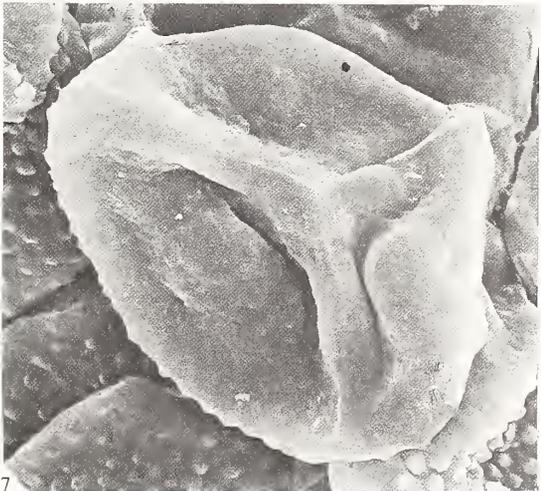
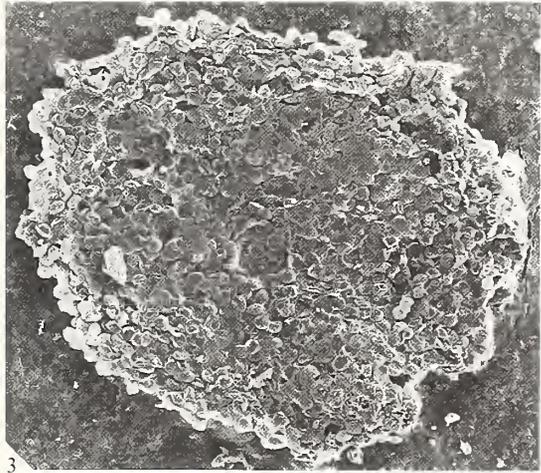
Synorisporites verrucatus Richardson and Lister, 1969

Dimensions, means and sample numbers from the two sporangia are presented in Text-figure 1. A spore mass with abundant *S. verrucatus* recovered on bulk maceration from the type locality of *C. pertoni* at Perton Lane is interpreted as a possible coprolite because of its atypical shape and the

EXPLANATION OF PLATE 2

Figs 1–2. Scanning electron micrographs (SEMs) of *Streelispota newportensis* before acid treatment showing papillae and folds; north Brown Clee Hill, Shropshire; Ditton Group, Lochkovian (Lower Devonian). 1, NMW 93.143G.4; $\times 3000$. 2, NMW 93.143G.3; $\times 2080$.

Figs 3–7. SEMs of spore mass of *C. pertoni* subsp. *apiculispota* shape, containing *Aneurospora* sp. before acid treatment; NMW 93.143G.7; M50 motorway, Hereford and Worcester; St Maughans Group, Lochkovian (Lower Devonian). 3, spore mass; $\times 95$. 4, group of spores; $\times 1575$. 5, sculpture on distal surface; $\times 2650$. 6, close up of proximal face with pitted appearance; $\times 3100$. 7, proximal face with pronounced apertural folds and interradial papillae; $\times 2900$.



CHARACTER			TAXON					
			<i>Synorisporites verrucatus</i>					
			NMW 93.143G.1 ex Ludford Lane			NMW 93.143G.2 ex Ludford Lane		
Dimensions of sporangium (mm)			1.48 x 1.01			0.89 x 0.95		
			min.	mean	max.	min.	mean	max.
Diameter of spore minus acid (μm)			14.00	19.76 (n=23)	22.06	16.80	23.04 (n=5)	27.20
Diameter of spore plus acid (μm)			16.66	20.70 (n=28)	27.27	16.60	24.28 (n=12)	33.30
Width of peripheral layer (μm)			0.025 (n=60)	0.12 [minus acid]	0.33	0.025 (n=27)	0.10 [minus acid]	0.20
Width of outer exospore layer (μm)			0.10	0.27 (n=112)	1.10	0.04	0.05 (n=66)	0.08
Width of inner exospore layer (μm)			0.33	1.15 (n=89)	2.60	0.44	0.96 (n=49)	1.93
Width of dark layer around lumen (μm)			0.030	0.033 (n=47)	0.060	0.020	0.040 (n=40)	0.130
Dimensions of distal sculpture (μm)	TEM data	Height	0.50	1.11 (n=17)	2.00	0.20	0.52 (n=5)	1.00
		Width at base	1.00	2.81 (n=17)	3.66	1.28	1.86 (n=5)	2.62
	SEM data	Height	0.68	1.08 (n=10)	1.59	1.57	1.99 (n=10)	3.15
		Width at base	0.90	1.36 (n=10)	1.59	2.10	2.50 (n=13)	3.15

TEXT-FIG. 1. Quantitative data for *Synorisporites verrucatus*.

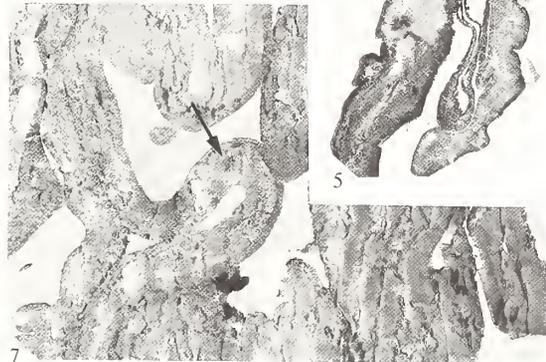
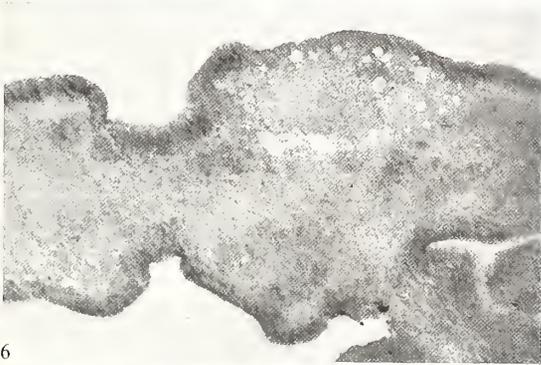
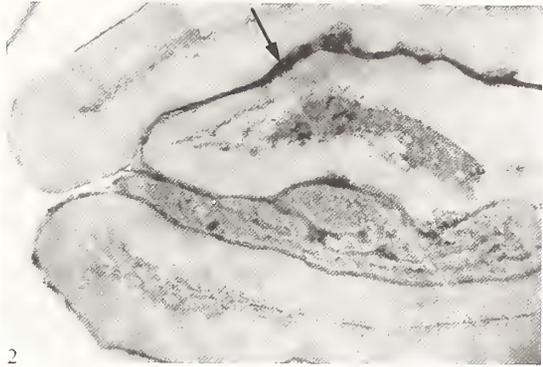
presence of at least two further spore taxa. However, the ultrastructure of unequivocal *S. verrucatus* from the mass is consistent with that in the Ludford Lane samples.

Under the scanning electron microscope, the spores look similar both before and after acid treatment (Pl. 1, figs 3, 5). Untreated examples were usually visible at the edges of the mass, some still as components of tetrads (Pl. 1, fig. 3). Distal surfaces show typical verrucate to murornate

EXPLANATION OF PLATE 3

Figs 1–6. Transmission electron micrographs (TEMs) of sections of *Synorisporites verrucatus*; 1–3, 5–6, NMW 93.143G.1; 4, NMW 93.143G.2; Ludford Lane, Shropshire; Downton Castle Sandstone Formation, Přídolí Series (Upper Silurian). 1, sections through a number of spores, before nitric acid treatment, with extensive darker intersporal material; arrow indicates possible apertural fold; $\times 5840$. 2, as for 1 but with possible aborted spores which are narrower and darker; arrow indicates pronounced black peripheral layer; $\times 9890$. 3, as for 1 and 2 but with well developed black peripheral layer; narrow 'fuzzy' line marks position of lumen; $\times 16690$. 4, narrow innermost layer of exospore following nitric acid treatment adjacent to lumen (light central area); $\times 27360$. 5, remnant of membrane-like material or remains of aborted spores following treatment with nitric acid; $\times 350$. 6, section through both surfaces of single spore after acid treatment, but with lumen barely visible as discontinuous white line; note prominent outer layer of exospore; $\times 9170$.

Figs 7–10. TEMs of sections of *Streelispora newportensis* spores; NMW 93.143G.4; north Brown Cleve Hill, Shropshire; Ditton Group, Lochkovian (Lower Devonian); see Pl. 1, fig. 6, Pl. 2, fig. 1. 7, number of spores before acid treatment; arrow indicates possible apertural fold; $\times 9030$. 8, proximal and distal surface of same spore after acid treatment showing pronounced outer layer of exospore which is thicker and extends into sculpture on distal surface; part of a second spore is seen top right; $\times 14370$. 9, possible detached peripheral layer; $\times 21190$. 10, as for 8 but with dark innermost layer of exospore marking the lumen; $\times 30450$.



sculpture (Pl. 1, fig. 5); the proximal surface is smooth (Pl. 1, fig. 4) as is the equatorial crassitate region. The trilete mark is prominent, each arm being represented by a ridge lacking sutures and extending to the equator. Interradial areas may be folded and always lack papillae (Pl. 1, fig. 4).

In contrast, TEMs look markedly different before and after nitric acid treatment. Untreated spores are tightly adhered in the spore mass (Pl. 3, figs 1–3), but are encompassed by an intersporal matrix, readily distinguished from the very narrow darker region (\equiv peripheral layer of Rogerson *et al.* 1993) immediately surrounding individual spores (Pl. 3, figs 2–3). This intersporal region is more or less homogeneous apart from narrow 'membranous' lines, sometimes describing irregular flattened oval outlines, sometimes disjunct (Pl. 3, fig. 2). These structures usually survive treatment with nitric acid, but the remainder of the intersporal matrix does not (Pl. 3, fig. 5). The peripheral layer, present to varying degrees and of irregular thickness as it 'follows' the contours of the exospore, also disappears on acid treatment. In light microscopy it appears as a coalified layer, obscuring further detail. The wall surviving fuming nitric acid treatment is interpreted as the exospore and, in this state, comprises two or possibly three layers (Pl. 3, figs 4, 6). An outermost dark electron-dense layer of more or less uniform thickness (termed outer exospore) surrounds a wider lighter homogeneous layer (under exospore), both of which are visible in the sculpture (Pl. 3, fig. 6). Groups of circular to oval electron transparent cavities occur largely throughout the homogeneous layer but may extend into the outer exosporal layer (Pl. 3, fig. 6). The innermost narrow dark layer immediately around the lumen is more variable in thickness and sometimes absent (Pl. 3, figs 4, 6). It is more clearly defined and prominent in specimen NMW 93.143G.2 (Pl. 3, fig. 4). In untreated specimens the lumen is represented by a dark line. Acid treatment induces separation of the spore walls so that the lumen becomes visible. The lumen also extends into the apertural fold (Pl. 3, fig. 1), in which all layers of the exospore are visible.

Streelispora newportensis (Chaloner and Strel) Richardson and Lister, 1969

Quantitative data from the four samples, all from north Brown Cleve Hill, are presented in Text-figure 2. Scanning electron micrographs before and after acid treatment look similar. Intersporal variation relates mainly to proximal features; almost all show papillae, but associated folds may be variously orientated, i.e. not consistently periclinal, with additional folding sometimes present (Pl. 2, figs 1–2). Distal ornament of conidia varies only in size (Pl. 1, fig. 8). In all specimens prior to nitric acid treatment, the outlines of individual spores are difficult to observe under TEM since spores are tightly adpressed and consequently difficult to section. Therefore, the existence of a peripheral layer is equivocal. However, less compressed untreated spores were occasionally observed under TEM. Such spores exhibit distinct layering of the exospore (Pl. 3, fig. 7). After exposure to acid the spores separate and the profiles become well-defined. Traces of a thin dark layer (?peripheral layer) remain in one specimen, although this may also be an atypical example of sloughing of the outer exospore (Pl. 3, fig. 9), and there is scant evidence for an intersporal mix. The exospore has two conspicuous layers with a narrow more electron-dense layer surrounding a wider homogeneous one (Pl. 3, fig. 10). Both layers are present in the proximal folds (Pl. 4, figs 1–3), apertural folds and papillae (Pl. 4, fig. 2), but only the outer is seen in the ornament (Pl. 3, fig. 8; Pl. 4, figs 1, 5). A very dark line delimits the lumen (Pl. 3, fig. 10), and may be associated with ovoid electron-dense bodies ($0.66\text{--}2.00\ \mu\text{m} \times 0.50\text{--}0.66\ \mu\text{m}$ diameter). As in *Synorisporites verrucatus*, this line is not visible in all sections and varies in thickness.

Aneurospora sp.

The sporangium of *C. pertoni* shape (Pl. 2, fig. 3) contained proximally tripapillate, equatorially crassitate, apiculate spores (Pl. 2, fig. 7), assigned to *Aneurospora* in that proximal folding is lacking. Dimensions are given in Text-figure 2. A thin, darkly stained peripheral layer is apparent under TEM (Pl. 4, fig. 9) and only partially disappears on exposure to acid (Pl. 4, fig. 6). The exospore itself is two-layered (Pl. 4, figs 6, 10–11) with the outer narrow electron-dense layer contrasting with the wide homogeneous inner, the latter being relatively wider than that in *Streelispora*. Both layers

CHARACTER		TAXON						
		<i>Streelispora newportensis</i>			<i>Aneurospora</i>			
		Pooled data for NMW 93 143G 3-6 ex Brown Clee Hill			NMW 93.143G.7 ex locality DE 98 M50			
Dimensions of sporangium/spore mass (mm)		1.43 x 1.0 (30.1 series) 1.95 x 1.87 (40.1 series) 1.14 x 0.68 (UF1566 series) 0.93 x 0.79 (55.6 series)			0.78 x 0.67			
		min.	mean	max.	min.	mean	max.	
Diameter of spore minus acid (µm)		13.64	21.56	28.38	18.97	24.52	28.00	
		(n=32)			(n=22)			
Diameter of spore plus acid (µm)		15.00	22.81	31.20	-			
		(n=26)						
Width of peripheral layer (µm)		0.12	0.18	0.36	0.03	0.04	0.11	
		(n=5)			(n=34)			
Width of outer exospore layer (µm)		0.06	0.25	0.55	0.03	0.06	0.12	
		(n=273)			(n=42)			
Width of inner exospore layer (µm)		0.16	0.65	1.87	0.40	0.99	1.68	
		(n=205)			(n=42)			
Width of dark layer around lumen (µm)		0.02	0.04	0.12	0.05	0.11	0.35	
		(n=48)			(n=23)			
Dimensions of proximal fold (µm)	Height	0.86	1.44	3.66	-			
	Width at base	0.46	0.73	1.33	-			
	Width at apex	0.33	0.52	0.80	-			
		(n=9)						
		(n=9)						
		(n=5)						
Dimensions of proximal papilla (µm)	Height	1.39	1.98	2.66	1.29	2.17	2.22	
	Width at base	1.25	3.85	6.00	3.22	4.70	5.80	
	Width at apex	0.62	2.87	4.00	-			
		(n=8)			(n=7)			
		(n=8)			(n=7)			
		(n=3)						
Dimensions of distal sculpture (µm)	TEM data	Height	0.33	0.77	1.20	0.25	0.43	0.95
		Width at base	0.73	1.44	2.13	0.25	0.72	0.93
	SEM data	Height	0.45	0.82	0.93	0.51	0.63	1.02
		Width at base	0.69	1.01	1.39	0.51	0.83	1.02
		(n=21)			(n=10)			
		(n=20)			(n=10)			
		(n=20)			(n=10)			
		(n=20)			(n=15)			

TEXT-FIG. 2. Quantitative data for *Streelispora newportensis* and *Aneurospora*.

are present in the apertural fold and papillae (when present) with only the outermost layer in the distal coni (Pl. 4, fig. 11). TEMs reveal that the projecting coni frequently coincide with depressions in the exospore of adjacent spores. It is a possibility that the pitted appearance of the latter when observed under SEM (Pl. 2, fig. 6) is due to the impaction of coni on neighbouring spores during compression, or may merely be due to localized corrosion.

DISCUSSION

Effects of nitric acid treatment

Layering within the exospore. The striking differences noted in cf. *Ambitisporites* spores from *Cooksonia pertoni* sporangia before and after acid treatment allowed interpretation of observed ultrastructure in terms of the original chemistry of the peripheral layer and the exospore. However, it raised the possibility that the layering of the exospore, particularly prominent after staining, is actually produced by acid treatment (Rogerson *et al.* 1993). The same kind of layering, present in all the acid-treated spores in this study, demands similar assessment as a prerequisite for comparisons of exospore structure in extant and extinct embryophytes. Is the nitric acid accentuating original differences in the wall and their affinities for the stain, or is the layering merely reflecting the degree of penetration of the nitric acid (and hence chemical modification) into the spore wall? Evidence for the latter comes from the consistently peripheral position of the staining and its more or less uniform width. It could be argued that the minor variations relate to timing of the various procedures and/or degree of penetration of the resin. On the other hand, again based on a relatively small sample size, for *Streelispora* and *Synorisporites*, the thickness of the outer layer relative to that of the exospore is more or less constant. Further, in considering the apiculate ornament of *Aneurospora* and *Streelispora*, the area of staining is greater than that anticipated from the degree of penetration into the rest of the wall. Perhaps most importantly, the layering is not a feature of all spores treated with nitric acid (see e.g. *Synorisporites downtonensis* illustrated in Text-fig. 3A–B) and is frequently observed in non-treated spores. Further layering has been recorded and illustrated in specimens of *Ambitisporites*, *Synorisporites*, *Streelispora* and *Aneurospora* studied using light microscopy (Richardson and Ioannides 1973, p. 14).

The differing intensity of staining observed between samples and occasional 'reversed staining' effects may well reflect minor differences in procedures, but even where there is little or no contrast between layers, the outer consistently appears smoother and the middle more granular.

EXPLANATION OF PLATE 4

Figs 1–5. Transmission electron micrographs (TEMs) of sections of *Streelispora newportensis* after fuming nitric acid treatment; 1–3, NMW 93.143G.4; 4–5, NMW 93.143G.6; north Brown Clee Hill, Shropshire; Ditton Group, Lochkovian (Lower Devonian). 1, number of spores stacked in sporangium; lumens are not visible, arrow indicates possible proximal fold; $\times 5940$. 2, part of spore with papilla and fold in section on proximal surface and sculpture on distal; lumen is not visible; $\times 10490$. 3, fold on proximal surface and some extraspore material; $\times 20000$. 4, possible equatorial thickening; note differing response of layers of the exospore to sectioning and 'reversed' staining of middle and outer layers; $\times 9200$. 5, sculpture comprising outer layer of exospore; $\times 12400$.

Figs 6–11. TEMs of sections of *Aneurospora* sp. following concentrated nitric acid treatment, all except fig. 9 which is before acid treatment; note outer layer of exospore is here stained lighter than remainder of wall; see NMW 93.143G.7 (Pl. 2); M50 motorway, Hereford and Worcester; St Maughans Group, Lochkovian (Lower Devonian). 6, outer and inner layers, lumen and possible peripheral layer; $\times 20570$. 7, apertural fold, triangular area with extended 'arms' marks lumen; $\times 4360$. 8, poorly developed equatorial thickening; $\times 5960$. 9, distal surface showing sculpture with peripheral layer before acid treatment; $\times 22000$. 10, section through distal and proximal surface with some evidence of innermost exospore layer visible as a dark line around oblique lumen; $\times 22225$. 11, distal surface with sculpture formed from outer layer only; some evidence for a particulate peripheral layer; $\times 27780$.





TEXT-FIG. 3. A, SEM showing tetrads of *Synorisporites downtonensis* (NMW 93.143G.8), Ludford Lane, Přídolí Series, $\times 792$. B, TEM of section of thick-walled spores after nitric acid treatment (NMW 93.143G.8), $\times 3352$.

Assuming then that the nitric acid is revealing information on wall layering, what is the basis for this response? Possibilities include chemical differences relating to polymerization of sporopollenin or physical differences involving variation in the original substructures on which sporopollenin is deposited. The differing responses of the exospore layers of *Aneurospora* and *Streelispora* to the knife may well reflect differences in their physical properties. Thus, the inner layer appears chattered while the outer is unaffected (cf. Pl. 3, fig. 7; Pl. 4, figs 4–5). Whatever the cause, it is likely that differential compaction and homogenization during diagenesis would have obliterated any original fine structure, making comparisons with extant spores of limited value. Nevertheless, there are similarities with certain filicalean ferns, such as zonation with comparable dimensions (Lugardon 1990), and indeed Professor Lugardon, having seen our *Ambitisporites* material, was of the same opinion and wrote 'elles (i.e. the layers) correspondent probablement à des résistances à l'acide en relation avec des variations chimiques, ou physico-chimiques de la sporopollenine à l'intérieur d'une même couche'. He believes that the layers in living ferns correspond to the variation in degrees of polymerization of sporopollenin as layers are deposited during maturation, but which usually, but not consistently, have disappeared in mature spores. Similar atlases are needed for mosses and hepatics. In a brief overview (Brown and Lemmon 1990), two-layered exines are recorded in certain hepatics, hornworts and *Sphagnum* although the bryopsid exine is described as typically homogeneous. Such comparisons made on the 'nearest living match' approach are over simplistic and certainly are not intended to reflect relationship. The likelihood that spore wall ultrastructure has remained static over four hundred million years must be debated. However, surveys of extant filicaleans and a few bryophytes do show that exospore layering is present and that its significance has been addressed in extant cryptogams.

Peripheral layer. Observations by light microscopy in *Ambitisporites* revealed the peripheral layer as an adhering coalified sheet, while its reaction with concentrated nitric acid indicated a different chemistry from the probably sporopollenin-impregnated exospore. Nitric acid had a similar effect

in the present investigations although traces of the enveloping dark layer remain in *Aneurospora* and may be equivalent to a translucent 'structureless' layer sometimes visible in light microscopy.

In contrast to the marked morphological differences noted by SEM in 'before and after' treatments of *in situ* cf. *Ambitisporites*, there is little change in the spores discussed here.

Intersporal matrix. This behaved in similar fashion to the peripheral layer, although traces of 'membranous' sheets remained after concentrated nitric acid treatment in *Synorisporites*.

Size. Although nitric acid is sometimes cited as increasing the size of spores, we have noted only a small increase in maximum diameter (< 5 per cent. in *Synorisporites*, 3 per cent. in *Streelispora*), but the small size sample and difficulties of measurement limit confidence in the data. There are no noticeable changes in wall thickness but, in a number of cases, lumens become apparent as distal and proximal walls separate. There is also the suggestion, particularly from SEMs that the exospore becomes more supple with collapse between unsupported areas, thus enhancing features such as crassitides and apertural folds, although these are also visible on untreated material.

HOMOLOGY OF SPORE LAYERS AND ASSOCIATED STRUCTURES

(Text-figure 4)

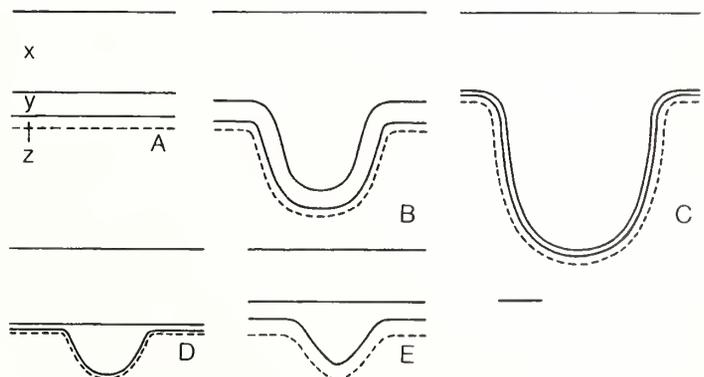
Exospore

The concentrated nitric acid-resilient component is interpreted as exospore. Apart from differences in electron opacity, producing the layering, it is apparently homogeneous, although the possibility that its original structure has been eliminated during diagenesis cannot be discounted. The general appearance is similar to that recorded in cf. *Ambitisporites* (Rogerson *et al.* 1993). The very dark narrow line around the lumen seen in *Aneurospora* and *Synorisporites* is not a consistent feature, but, where present, persists after nitric acid treatment. It might represent the remains of spore contents or even endospore. Layering in an otherwise homogeneous exospore is seen in illustrations of extant ferns (Lugardon's 1990 Filicinées) and articulates and also in liverworts (Brown and Lemmon 1990) where associated with lamellar organization.

A suture on the trilete mark has never been observed in sections of *Ambitisporites*, *Synorisporites verrucatus*, *Streelispora newportensis* and *Aneurospora*. Its apparent presence in preparations viewed by light microscopy may be due to the lumen projecting into the apertural fold.

The electron-transparent circular to oval cavities noted in cf. *Ambitisporites* (Rogerson *et al.* 1993) are common in *Synorisporites verrucatus*, particularly after acid treatment where they may be localized towards the equator, less common in *Streelispora newportensis* and absent from *Aneurospora* sp. They occur in outer and inner layers of the exospore, and occasionally cross the junction between them. Similar structures are present in TEM preparations of *Parka* (Hemsley

TEXT-FIG. 4. Schematic representation of exospore layers in *Ambitisporites* sp. (A), *Synorisporites verrucatus* (B, C), *Aneurospora* sp. (D) and *Streelispora newportensis* (E). x = inner exospore, y = outer exospore, z = peripheral layer. Scale bar represents 0.52 μ m.



1989), and are called 'bubble-like cavities'. It seems likely that they are artefacts of preparation or develop during preservation but we have no explanation for their formation.

Peripheral layer and intersporal matrix

The nature of the acid sensitive layer enveloping the exospore was somewhat inconclusively discussed above in relation to cf. *Ambitisporites* (Rogerson *et al.* 1993). It is comparable in position (Brown and Lemmon 1990) and reaction to concentrated nitric acid with the perispore recorded in mosses, ferns, Lycopodiaceae, and microspores of heterosporous lycophytes (Lugardon 1990) where it is deposited by condensation of tapetal particles onto one or several layers, after completion of the exospore. However, the perispore of extant plants is highly ordered, sometimes with taxon-specific surface patterning and seems to comprise a far more discrete layer than that recorded here. We therefore remain equivocal on the homology of the peripheral layer with the perispore. We are also uncertain of its relationship to the far more extensive intersporal 'matrix' recorded in *Synorisporites* which may be distinguished from the peripheral layers because of its more granular appearance and lighter staining. Like the peripheral layer it disappears on treatment with fuming nitric acid. The membrane-like structures which withstand acid treatment may well be the remains of aborted spores and have outlines consistent with this hypothesis. A further possibility is that they are similar to the ornamented sheets noted between spores of *Uskiella spargeus* (Shute and Edwards 1989) and compare with sheets formed by fusion of Ubisch bodies in spermatophytes. The intersporal matrix may represent the remains of a periplasmodial tapetum, but more probably represents the locular fluid which bathes developing spores. Although a liquid has low fossilization potential, it may have been preserved in this case because of its colloidal or viscous nature, itself possibly due to the presence of more recalcitrant molecules as precursors of sporopollenin.

COMPARISONS WITH RELEVANT DISPERSED SPORE TAXA

It is of some interest to compare the ultrastructural detail presented here with structure recorded in the diagnoses of the dispersed spores which were originally based on light microscope observations. Thus, considering the emended diagnosis of the genus *Streelispora*, Richardson *et al.* (1982) described the exine as 'two-layered (possibly three-layered)' with 'layers closely adpressed over most of the surface' and contact areas 'characterized by tangential folds and small radial folds of the outer thin exo-exinal layer'. For *S. newportensis* the papillate thickenings are considered part of a second and thicker underlying exo-exinal layer. Our observations confirm the layering, our outer and inner exospore being equivalent to the outer thin exo-exinal and underlying thicker exo-exinal layers respectively, but suggest that the inner exo-exinal layer also contributes to the folds (Text-fig. 4). From the nature of the proximal radial and tangential folds, as interpreted by light microscopy, it had been expected that the two layers were loosely attached on the proximal surface. However, none of the sectioned spores illustrated here show separation of the two layers with the outer, forming a fold. The major structural feature, 'the more or less equatorial crassitude', is surprisingly difficult to identify in our TEM sections, although it is present and best developed in spores from specimen NMW 93.143G.6 (Pl. 4, fig. 4). Likewise it is not pronounced in TEMs of *Syurisporites* or *Aueospora*. Indeed in their emended generic diagnosis for the latter, Richardson *et al.* (1982) described a subequatorial region which is 'especially rigid and probably thickened so as to appear like a dark band (equatorial crassitude); the inner limits of it are often ill-defined and its width is also \pm variable even in the same specimen'. This description fits very well with our observations. In all four genera (*Ambitisporites*, *Syurisporites*, *Streelispora* and *Aueospora*), viewed under the light microscope, the equatorial crassitude sometimes appears as more rigid than the adjacent distal area and retains its shape in various compressional states.

In contrast, although, in the original description of *Synorisporites verrucatus* (Richardson and Lister 1969), the exine is described as homogeneous with the equatorial crassitude 2–3 μm wide, in later light microscope descriptions of better preserved *Syurisporites* (*verrucatus* and *tripapillatus*) and *Ambitisporites*, Richardson and Ioannides (1973, p. 277, pl. 5, fig. 5) showed a closely adherent

diaphanous outer layer. This is now thought to be equivalent to the outer exospore seen in our TEM sections.

EVOLUTION IN *COOKSONIA* SPORES

Based on SEM studies and stratigraphical occurrences it was originally suggested that spores of *Cooksonia pertoni* all have a similar structure (i.e. equatorially crassitate) but that sculpture changed in time from smooth to verrucate to apiculate (Fanning *et al.* 1988). These TEM observations support the hypothesis as regards structure, and show how the distribution of the outermost layer varies with change in ornament. There is also a decline in total wall thickness excluding sculpture, although, because of the nature of its ornament, *Synorisporites verrucatus* spores appear to have larger amounts of sporopollenin than *Ambitisporites*. There is no evidence that the ornament in *S. verrucatus*, although superficially sometimes similar to surface wrinkling, was formed by contraction: the muri and verrucae were formed by additional material with resultant increase in surface area even though the actual diameter of the *in situ* spores of *S. verrucatus* is less than that for *Ambitisporites* sp.

Although our *in situ* *Aneurospora* and *Streelispora* came from strata of differing age, their apiculate sculpture is similar and shows little intrasporangial variation. Minor differences in appearance between the two relate to quality of preservation. Considering the dispersed spore record, although the two genera form only a small numerical proportion of assemblages, there is a large number of integradational forms based mainly on the type and distribution of apiculate/granulate sculpture. The various types of sculptural forms and the proportions of the variants present change throughout the Lochkovian, but as yet we have insufficient numbers of megafossils with *in situ* spores to relate this to the evolution of subspecies of *Cooksonia pertoni*.

A similar trend in exine morphology (namely, laevigate–verrucate–apiculate) has been recorded in dispersed spore representatives of a second structurally different miospore morphotype, although as yet the parent plants remain unknown. The trend is further exhibited by cryptospores, probably indicating a convergence in response to common environmental pressures in at least two major groups of land plants (Richardson and Burgess 1988).

Finally, a peripheral layer has been demonstrated in all four taxa, and is most persistent in *Aneurospora*, where traces remain after nitric acid treatment, but is frequently absent in *Streelispora*. This leads to questions relating to the relative maturity of these *in situ* spores and the possibility that *Cooksonia* sporangia containing *Aneurospora* spores with their thinner peripheral layer (specimen NMW 93.143G.7, Pl. 2, figs 3–7) are immature. Against the latter is the common occurrence of *Aneurospora* in the dispersed record.

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REFERENCES

- BROWN, R. C. and LEMMON, B. E. 1990. Sporogenesis in bryophytes. 56–94. In BLACKMORE, S. and KNOX, R. B. (eds). *Microspores: evolution and ontogeny*. Academic Press, London, x + 347 pp.
- EDWARDS, D. and ROSE, V. 1984. Cuticles of *Nematothallus*: a further enigma. *Botanical Journal of the Linnean Society*, **88**, 35–54.
- DAVIES, K. L. and AXE, L. 1992. A vascular conducting strand in the early land plant *Cooksonia*. *Nature*, **357**, 683–685.
- FANNING, U. and RICHARDSON, J. B. 1994. Lower Devonian coalified sporangia from Shropshire: *Salopella* Edwards & Richardson and *Tortilicaulis* Edwards. *Botanical Journal of the Linnean Society*, **16**, 89–110.
- FANNING, U., RICHARDSON, J. B. and EDWARDS, D. 1988. Cryptic evolution in early land plants. *Evolutionary trends in plants*, **2**, 13–24.
- HEMSLEY, A. 1989. The ultrastructure of the spores of the Devonian plant *Parka decipiens*. *Annals of Botany*, **64**, 359–367.

- JERAM, A. J., SELDEN, P. A. and EDWARDS, D. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science*, **250**, 658–661.
- LUGARDON, B. 1990. Pteridophyte sporogenesis: a survey of spore wall ontogeny and fine structure in a polyphyletic plant group. 95–120. In BLACKMORE, S. and KNOX, R. B. (eds). *Microspores: evolution and ontogeny*. Academic Press, London, x+347 pp.
- POTONIÉ, R. and KREMP, G. 1954. Die Gattungen der paläozoischen *Sporae dispersae* und ihre Stratigraphie. *Geologisches Jahrbuch*, **69**, 111–194.
- RICHARDSON, J. B. and BURGESS, N. 1988. Mid-Palaeozoic sporomorph evolution in the Anglo-Welsh area: tempo and parallelism. 7 *International Palynological Congress, Brisbane. Symposium abstracts*, 140.
- and IOANNIDES, N. 1973. Silurian palynomorphs from the Tanezzucht and Acacus Formations, Tripolitania, North Africa. *Micropaleontology*, **19**, 257–307.
- and LISTER, T. R. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology*, **12**, 201–252.
- STREEL, M., HASSAN, A. and STEEMANS, P. 1982. A new spore assemblage to correlate between the Breconian (British Isles) and the Gedinnian (Belgium). *Annales de la Société Géologique de Belgique*, **105**, 135–143.
- ROGERSON, E. C. W., EDWARDS, D., DAVIES, K. L. and RICHARDSON, J. B. 1993. Identification of *in situ* spores in a Silurian *Cooksonia* from the Welsh Borderland. *Special Papers in Palaeontology*, **49**, 17–30.
- SHUTE, C. H. and EDWARDS, D. 1989. A new rhyniopsid with novel sporangium organization from the Lower Devonian of South Wales. *Botanical Journal of the Linnean Society*, **100**, 111–137.
- TRAVERSE, A. 1988. *Paleopalynology*. Unwin Hyman, Boston, xxiii+600 pp.
- TRYON, A. F. and LUGARDON, B. 1991. *Spores of the Pteridophyta: surface, wall structure and diversity based on electron microscope studies*. Springer-Verlag, New York, x+648 pp.

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LOWER DEVONIAN BIOSTRATIGRAPHY AND VERTEBRATES OF THE TONG VAI VALLEY, VIETNAM

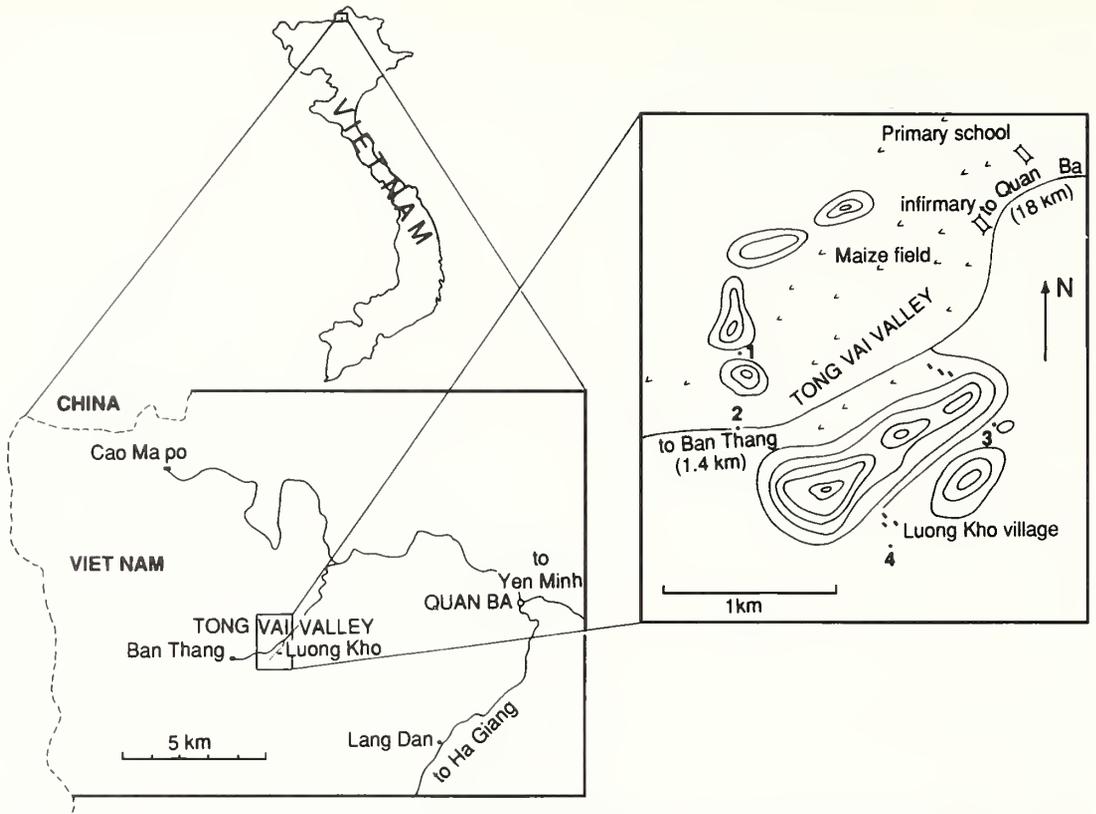
by TONG-DZUY THANH, P. JANVIER, TA HOA PHUONG
and DOAN NHAT TRUONG

ABSTRACT. A new vertebrate assemblage is described from the base of the Khao Loc Formation at Tong Vai, Dong Van district, Ha Giang Province, Vietnam. It includes the galeaspid *Polybranchiaspis liaojaoshanensis*, two acanthothoracid placoderms, and the sarcopterygian *Youngolepis praecursor*. This assemblage is quite similar to that of the Xitun Formation of Yunnan (Late Lianhuashanian to Early Nagaolingian) and can also be correlated with the vertebrate faunas which occur at the base of the Bac Bun Formation of the Bac Bo in Vietnam. New data on the morphology of *P. liaojaoshanensis* are provided on the basis of this material, with special reference to the structure and ornamentation of the exoskeleton.

THE Tong Vai valley is situated near the Chinese–Vietnamese border, west of the Quan Ba hamlet, on the Ha Giang–Yen Minh main road in the Dong Van district (Text-fig. 1). From Quan Ba, the road to Tong Vai runs through a pass in a mountainous area of limestone and sericite-bearing shales. The distance between Quan Ba and the Tong Vai valley is directly about 10 km (18 km by road).

The Palaeozoic rocks of the Tong Vai valley and its surroundings were considered by Deprat (1915) to be Late Cambrian to Early Ordovician in age (see also the geological map of the Ma Li Po area in this work). Vassilevskaya (*in* Dovjikov 1965) regarded the ‘Luong Kho Limestones’ of the Tong Vai valley as Ordovician, on the basis of poorly preserved brachiopods and ostracodes of ‘Ordovician–Silurian aspect’.

In 1973, Ta Thanh Trung and Hoang Anh Truong were the first to collect early Devonian fossils from this area. These included some brachiopods e.g. *Lingulella dussaulti* Patte) and a specimen of the galeaspid fish *Polybranchiaspis* sp. (Ta Thanh Trung 1978). Hoan Xuan Tinh (1976), chief engineer of the Geological Mapping Team for the Bao Lac sheet, correctly described, apart from a few inaccuracies, the stratigraphical sequence of the Early Devonian in the Tong Vai valley, and his description was later referred to in the ‘Stratigraphy of Vietnam’ (Vu Khuc and Bui Phu My 1990). Of the five members he described, the first two may not belong to the Devonian, but rather represent terrigenous beds that Vassilevskaya (*in* Dovjikov 1965) referred to the Late Cambrian, and Deprat (1915) to the Ordovician. The description of the *Polybranchiaspis*-bearing levels in Hoang Xuan Tinh’s (1976) paper is quite different from the one made later by Ta Thanh Trung (1978), who collected the galeaspids from ‘dark grey carbonate-bearing terrigenous deposits’. On the contrary, Hoang Xuan Tinh (1976) depicted his *Polybranchiaspis*-bearing third member of the Lower Devonian as a succession of opalescent, yellowish quartzitic sandstones, siltstones and mudstones, which he referred to as the ‘Bac Bun Suite’. To this author, the ‘Bac Bun Suite’ comprised the Si Ka and Bac Bun formations first described by Deprat (1915) and later reviewed by Tong Dzuy Thanh (1967, 1982) and Tong Dzuy Thanh *et al.* (1986). According to Hoang Xuan Tinh’s description, his third member may be attributed to the Si Ka Formation, although, as will be mentioned below, such coarse terrigenous rocks do not seem to occur in the Lower Devonian of the Tong Vai valley.



TEXT-FIG. 1. Locality Map; 1–4, location of invertebrate and vertebrate-bearing exposures of member 3 of the Tong Vai section.

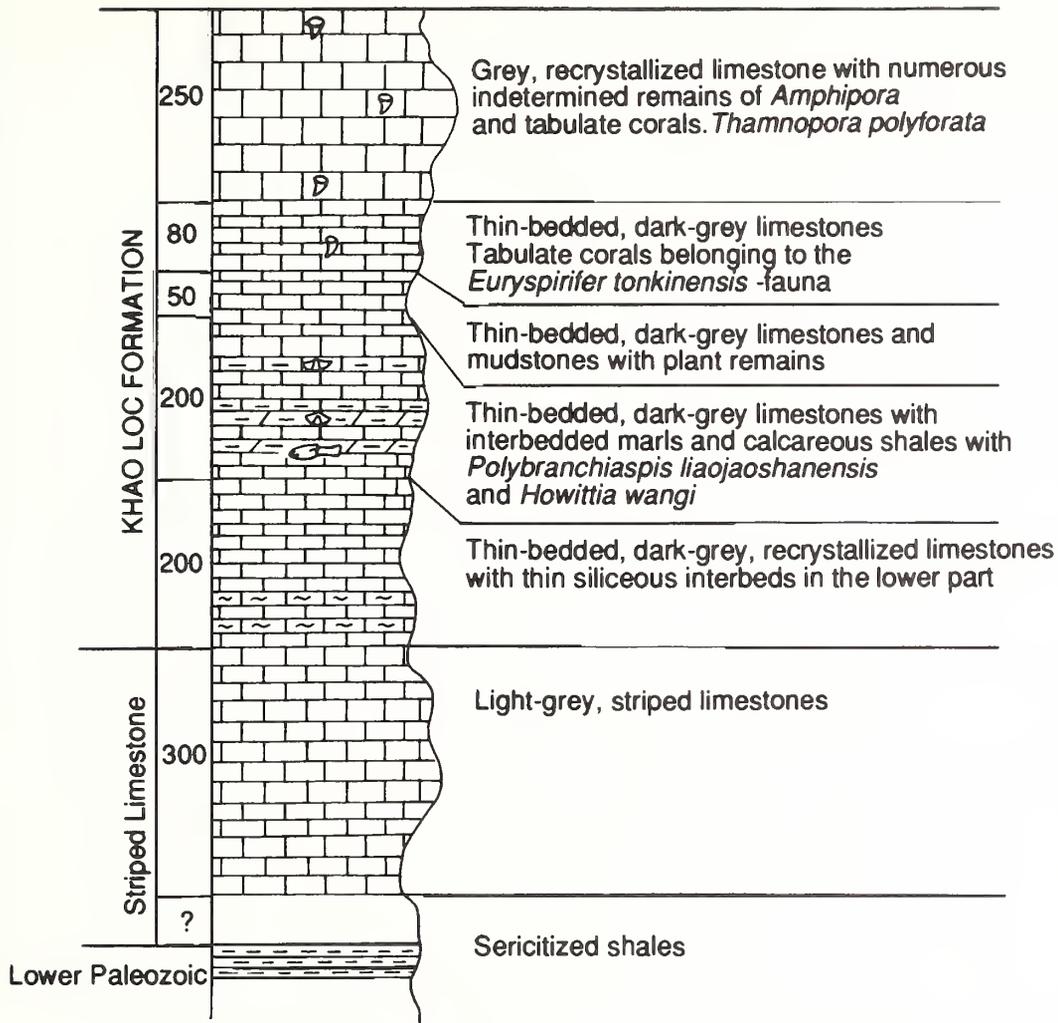
GEOLOGICAL SETTING

In summer 1991, one of us (T. H. P.) made a field trip to the Tong Vai valley and recorded several fossiliferous localities which have since been investigated, in spring 1993, by Tong-Dzuy Thanh, Ta Hoa Phuong and Doan Nhat Truong in the frame of the project KT 04.6.1.1. of the Vietnamese Fundamental Research Program in Natural Sciences.

Description

The eastern slope of the Tong Vai valley consists of sericitized shales and dark grey limestones, dated, with reservations, as Late Cambrian (Dovjikov 1965). The rest of the area consists mainly of limestones and interbedded marls. The complete stratigraphical column in Tong Vai, from the Upper Cambrian to the Devonian, is still unknown because of tectonic complications. However, six successive members can be distinguished in the Devonian, without any breaks (Text-fig. 2). These are, from base to top:

1. The basal member consists of light grey, relatively thin-bedded (200 mm) and sometimes opalescent, striped limestones. They resemble the Upper Palaeozoic limestones widespread in the north of Vietnam. Sometimes, they display a schistosity to various degrees. The contact between these limestones and the underlying Upper Cambrian is not clear and the thickness of this member cannot be estimated precisely. A thickness of only *c.* 300–350 m can be observed, but the sequence may be thicker. They have yielded only scolecodonts and small rounded masses or organic matter (F. Paris, pers. comm.).



TEXT-FIG. 2. Stratigraphical section of the Early Devonian of the Tong Vai valley.

2. The second member begins with cherts and dark-grey, recrystallized limestones and dolomites. Further up, the cherts disappear and the upper part of the member consists only of recrystallized limestones and dolomites. The thickness of this member is *c.* 200 m. It has yielded only scolecodonts (F. Paris, pers. comm.).

3. The third member consists of marls with interbedded dark grey limestone and mudstone layers. Locally, lenses of calcareous shales occur, in particular in the middle part of the member, and these weather to a pink colour. Abundant vertebrate remains occur about 50 m above the base of this member. They are associated with ostracodes and occur in dark grey calcareous siltstones (see below for faunal list).

40 m upwards, on the road from the Tong Vai valley to Ban Thang (1, 2, Text-fig. 1), some brachiopods were collected in marls. They are referred by Duong Xuan Hao and Le Van De (1980) to *Howellella* ex. gr. *crispa* (Hisinger) and *Hysterolites wangiformis* Zuong. The latter species is *Howittia wangi* (*Orientospirifer wangi* Hou of Chinese authors). Other brachiopods occur near the top of this member, on a small hill on the roadside close to Luong Kho village (3, Text-fig. 1) and

were referred by Duong Xuan Hao to *Hysterolites wangiformis* (*Howittia wangi*) and *Tadschikia?* aff. *xuanbaoui* Zuong. The latter is similar to the type material from the lowermost Lower Devonian of the lower Da River basin (northwestern Vietnam). From Ta Thanh Trung's (1978) description, his *Polybranchiaspis* sp. and *Lingulella dussaulti* (Sample 2808/1) were certainly also collected in this member. The total thickness of this third member is *c.* 200 m.

4. The fourth member consists of thin-bedded black limestones intercalated with calcareous shales and mudstones, some of which are coal-bearing. It has yielded some undetermined plant remains which were collected from the mudstones. It is *c.* 50 m thick.

5. The fifth member consists of thin-bedded, dark grey limestones and marl lenses, which contain tabulate corals (in particular, abundant *Favosites kolimaensis* Rukhin) of the *Euryspirifer tonkinensis*-fauna. Its thickness is *c.* 80 m.

6. The uppermost member consists mainly of light grey recrystallized limestones with abundant traces of ramiform stromatoporoids. These limestones are very similar to the Middle Devonian *Amphipora* limestones formerly described by French geologists ('Calcaires à *Amphipora*'; Saurin 1956). The top of member 6 cannot be observed in the area of Tong Vai valley, because of faulting. Its observed thickness is *c.* 250 m.

Discussion

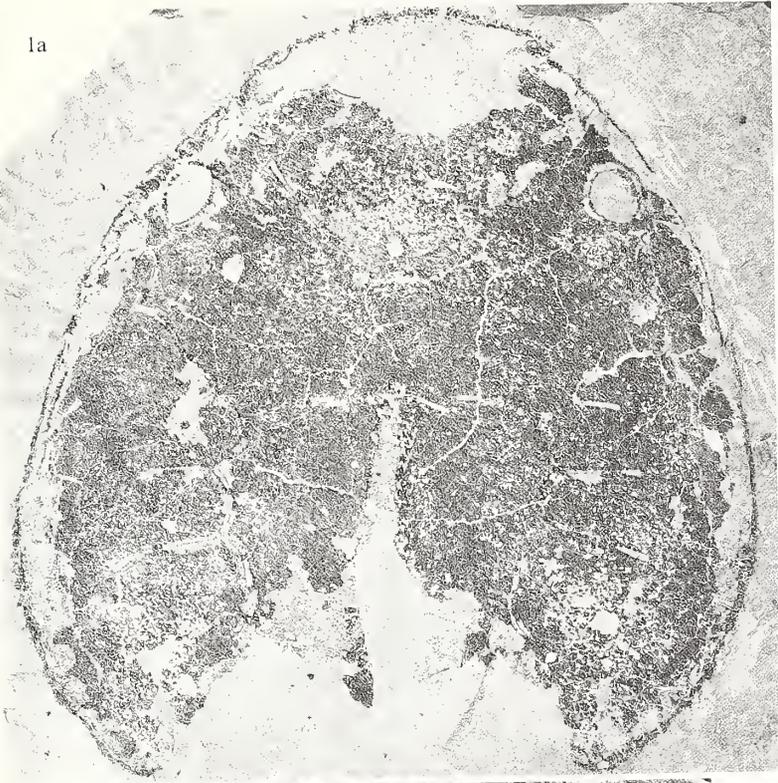
From Hoang Xuan Tinh's (1976) account, one of us (Tong-Dzuy Thanh 1982; Tong-Dzuy Thanh *et al.* 1986) referred the *Polybranchiaspis*-bearing beds of the Tong Vai valley to the Si Ka Formation. The new field observations presented in this paper suggests a reinterpretation of the Devonian of this area. The fauna of the third member unquestionably belongs to the *Howittia wangi* assemblage, which defines the Bacbunian regional stage in the Bac Bo (northern Vietnam, formerly called the Tonkin). Its major representatives are *Howittia wangi* and *Howellella* ex gr. *crispa*, and the vertebrates are quite similar to those in the corresponding stratigraphical level of Dong Mo and Trang Xa (Tong-Dzuy Thanh and Janvier 1990). The only, minor, difference is the presence of the brachiopod *Tadschikia?* aff. *xuanbaoui*, similar to the type material from northwestern Vietnam (Duong Xuan Hao and Le Van De 1980). There is some difference between the Tong Vai vertebrate fauna and that of more southernly localities, such as Trang Xa and Dong Mo (Tong-Dzuy Thanh and Janvier 1987, 1990). Although *Youngolepis* is present in both, no acanthothoracid material has been recorded from the latter two localities. Moreover, there is a marked difference in the structure and ornamentation of the exoskeleton of the galeaspid *Polybranchiaspis* from Tong Vai (see below) and those of the poorly preserved specimens from Dong Mo referred to by Tong-Dzuy Thanh and Janvier (1990, fig. 4) as '*Polybranchiaspis* sp.'. In the latter, the ornamentation consists of simple, rounded tubercles devoid of a basal recess, which are aligned into ridges along the shield margin. Therefore it is probable that the Dong Mo galeaspid, although a polybranchiaspidiform, does not belong to the genus *Polybranchiaspis*, but to a form which is closer to *Bannhuanaspis* (Janvier *et al.* 1993) in exoskeletal structure.

According to the observations of one of us (T. D. T.), the fourth member of the Tong Vai section is quite similar in lithology to the base of the Khao Loc Formation in the Ban Hinh-Khao Loc section, which is situated not far South of Tong Vai. It can thus be suggested that the limestone of

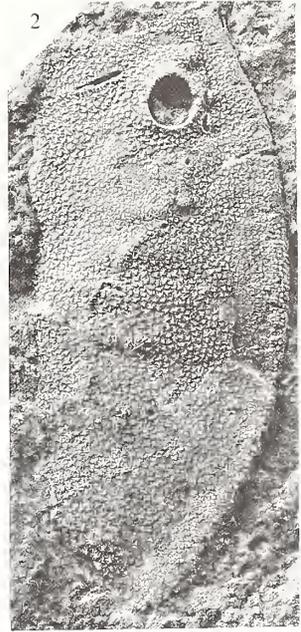
EXPLANATION OF PLATE 1

Figs 1–3. *Polybranchiaspis liaojaoshanensis* Liu, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. 1, BT 170, head shield in dorsal view, photographed in immersion to show the pineal foramen (a) and elastomere cast of its incomplete counterpart (b); note the ostracodes surrounding the specimens. 2, BT 171, right side of a headshield in dorsal view, elastomere cast of natural impression. 3, BT 172, left side of a headshield in internal view, elastomere cast of the internal surface of the exoskeleton and the ornamentation of the posterior wall of the median dorsal duct. All $\times 2$.

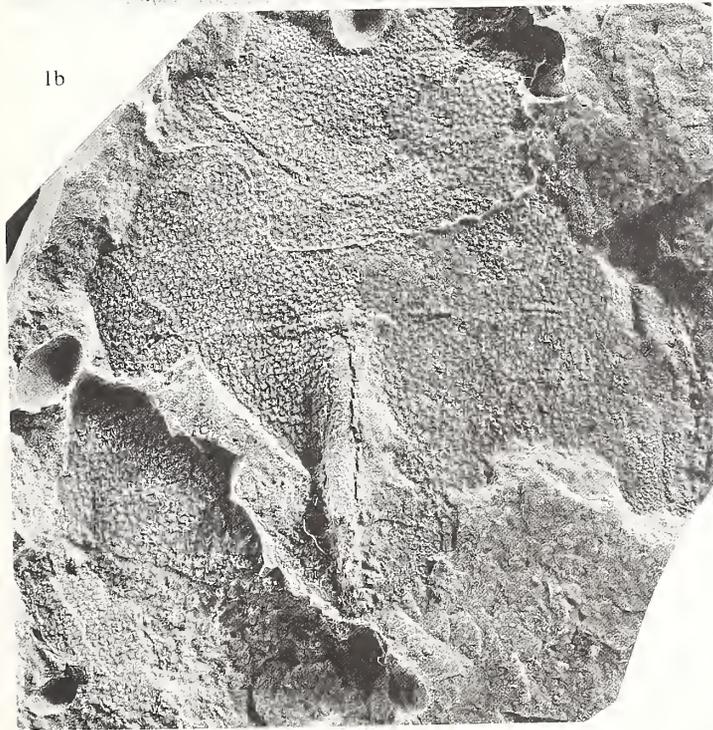
1a



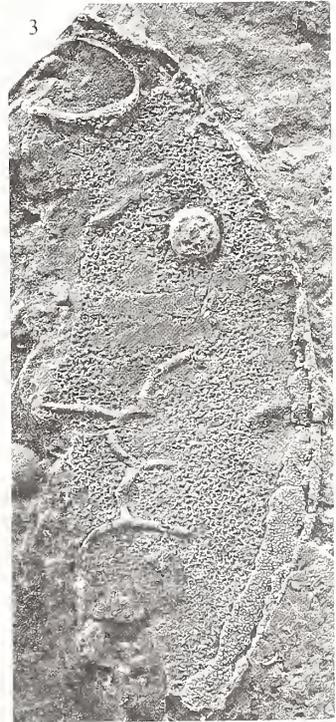
2



1b



3



member 4 and upwards can be attributed to the Khao Loc Formation (Pragian-Givetian), which is widespread in the Northwest of Ha Giang Province (Text-fig. 2). The limestones of the uppermost member of Tong Vai (member 6) can be correlated with the upper part of the Khao Loc Formation and the Ban Pap Formation. The latter formation is widely distributed in the North of Vietnam. This correlation is supported by the abundance of *Amphipora*, a guide fossil for the Middle Devonian limestone in the North of Vietnam.

The red beds of the Si Ka Formation do not occur in the Tong Vai area. Instead, below the Bacbunian faunal assemblage (fishes and *Howittia wangi*), there is a thick series of limestones (members 1 and 2), which are devoid of stratigraphically significant fossils (only scolecodonts are found). They may be a lateral equivalent of the Si Ka Formation.

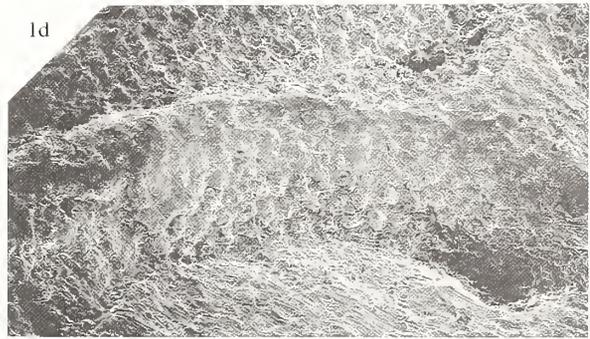
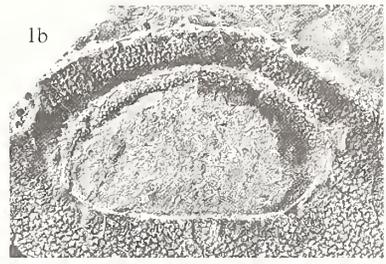
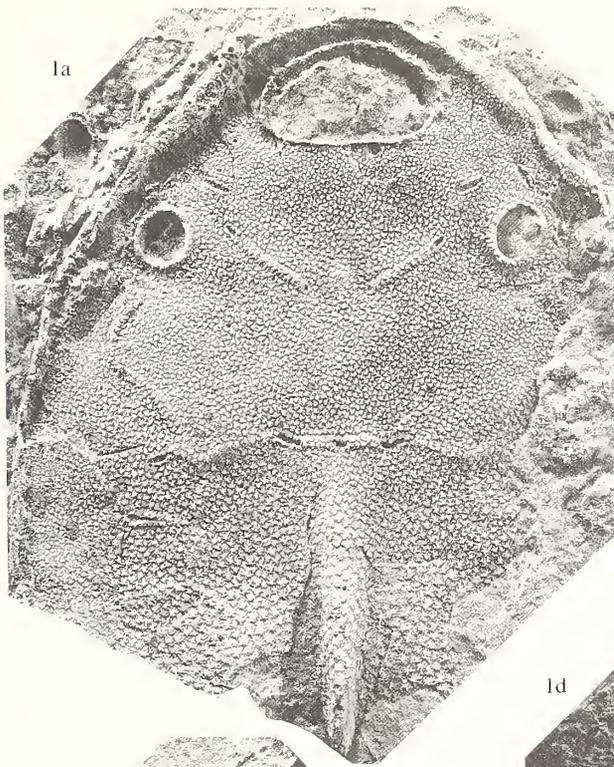
The correlation of the Bac Bun and overlying Mia Le formations of the Bac Bo with the Nakaoling (Nagaoling) and Yukiang formations (or stages) or southern China have been proposed in our former papers (Tong-Dzuy Thanh 1982; Tong-Dzuy Thanh *et al.* 1986, 1988*a, b*; Tong-Dzuy Thanh and Janvier 1987, 1990) on the basis of both vertebrate and invertebrate faunas. It is further supported by the new material described herein.

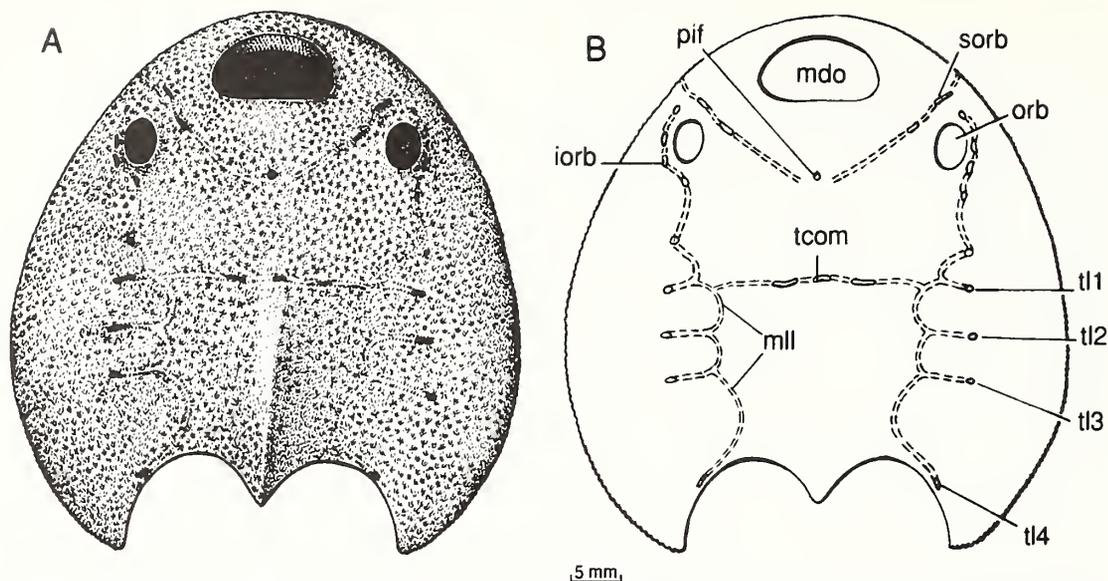
The Bacbunian vertebrates in northeastern Vietnam are frequently found in association with invertebrates of the *Howittia wangi* assemblage or in beds which immediately underlie this assemblage. By comparison with the data provided by S. T. Wang (1991), the Bacbunian vertebrate assemblage (in Dong Mo, Trang Xa, Tong Vai and other Vietnamese localities) is very similar to that of the Xitun Formation of the Cuifengshan Group in eastern Yunnan (China). Moreover, the Lower Devonian succession in the northeastern Bac Bo, from the Sika to Bac Bun and Mia Le formations is closely similar to that from the Lianhuashan to Nakaoling and Yukiang formations of Guangxi, China (Yang *et al.* 1981). This striking resemblance is seen in both the lithology and the faunal assemblages. As a result of the greater faunal diversity in northern Vietnam, these formations can be precisely dated, in particular the Mia Le Formation, which is clearly Pragian in age (Tong-Dzuy Thanh 1982; Tong-Dzuy Thanh *et al.* 1988*a*). This has been recently confirmed by the discovery of dacryoconarids of the *Nowakia zlichovens* and *N. barrandei* zones, and a rich conodont assemblage of the *Perbonus*-zone (determined by Pham Kim Ngan, Hanoi), in the base of the limestones which overlie the Mia Le Formation in the Dong Van – Ma Lu section (Ha Giang Province, near the Chinese–Vietnamese border). Here, in the uppermost beds of the Mia Le Formation, one of us (T.H.P.) discovered new dacryoconarids among which is the well-known Pragian species *Nowakia arcuaria* (H. Lardeux, pers. comm.).

In conclusion, these data suggest that: (1) the Bac Bun Formation, which underlies the Mia Le Formation and contains the vertebrates described below, may be Late Lochkovian to Early Pragian in age; (2) the Bac Bo area of northern Vietnam and the Yunnan–Guangxi areas of southern China belong to the same palaeobasin, characterized by endemic fish faunas; (3) the Bacbunian vertebrate and invertebrate faunas of northern Vietnam display mixed features of the Yunnan and Guangxi assemblages; and (4) they correspond to a foreshore to near-shore palaeoenvironment. Further south, in the Phu Luong and Trang Xa area, the larger amount of detritic sediments in the Sika and Bac Bun Formations suggests an even more near-shore to deltaic type of environment.

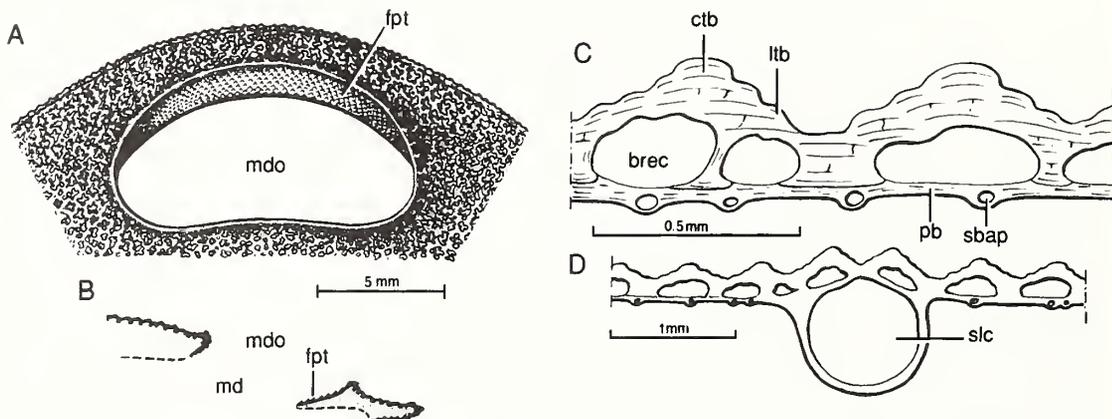
EXPLANATION OF PLATE 2

Figs 1–3. *Polybranchiaspis liaojaoshanensis* Liu, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. 1, BT 173, incomplete headshield in dorsal view, elastomere cast of the specimen (a, $\times 2$), close-up view of the median dorsal opening, lit from the left (b, $\times 3$), and S.E.M. photograph of the elastomere cast of the anterior wall of the median dorsal opening (c, $\times 20$; d, $\times 15$), to show the denticles on the anterior wall of the duct. 2, BT 172 (same specimen as Pl. 1, fig. 3), S.E.M. photograph of an elastomere cast of the ornamentation on the posterior wall of the median duct, partly folded against the internal surface of the exoskeleton, $\times 15$. 3, BT 174, incomplete headshield in ventral view, elastomere cast showing the ventral rim of the dermal headshield and the internal surface of the dorsal exoskeleton, $\times 2$.





TEXT-FIG. 3. *Polybranchiaspis liaojaoshanensis* Liu. A, reconstruction of the headshield in dorsal view (based on several specimens from Tong Vai); B, distribution of the sensory-line canals. Abbreviations: *iorb*, infraorbital canal; *mdo*, median dorsal opening; *mll*, main lateral-line; *orb*, orbit; *pif*, pineal foramen; *sorb*, supraorbital canal; *tcom*, transverse commissural canal; *tl1-4*, transverse lateral canals.

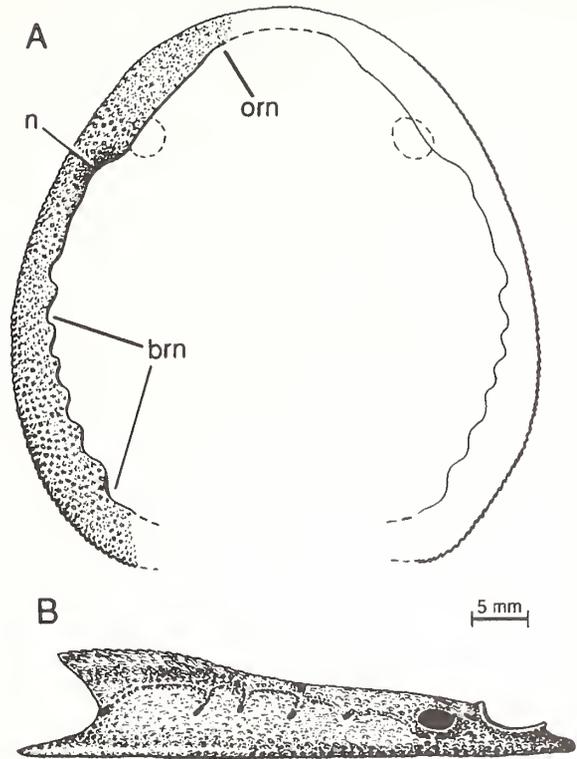


TEXT-FIG. 4. *Polybranchiaspis liaojaoshanensis* Liu. A, reconstruction of the exoskeleton around and inside the median dorsal opening; B, reconstructed sagittal section through the median dorsal opening and duct; C, vertical section through two tubercles of the exoskeleton (combined from several thin sections); D, vertical section through the exoskeleton and a sensory-line canal (combined from several thin sections). Abbreviations: *brec*, basal recess of exoskeleton; *ctb*, central tubercle; *fpt*, forward pointing tubercle of median dorsal duct; *ltb*, lateral, or secondary tubercle; *md*, median dorsal duct; *mdo*, median dorsal opening; *pb*, perichondral bone; *sbap*, subaponeurotic vascular canals; *slc*, sensory-line canal.

SYSTEMATIC PALAEOLOGY

The vertebrate material from the Tong Vai valley consists mainly of well preserved galeaspid headshields, as well as isolated placoderm plates and the cosmine-covered dermal bones and scales of a sarcopterygian. All the specimens come from the marls and shales of member 3, and are associated with smooth-shelled ostracodes. The material described herein is registered in the

TEXT-FIG. 5. *Polybranchiaspis liaojaoshanensis* Liu, reconstruction of the exoskeletal headshield. A, ventral view; B, lateral view. Abbreviations: *brn*, branchial notch; *n*, notch; *orn*, oral notch.



collection of the Geological Museum (Bao Tang Dia Chat, here abbreviated BT), 6 Pham Ngu Lao Str., Hanoi. Casts are deposited in the collection of the Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris).

Class GALEASPIDA Halstead Tarlo, 1967
 Order POLYBRANCHIASPIDIFORMES Liu, 1965
 Family POLYBRANCHIASPIDIDAE Liu, 1965
 Genus POLYBRANCHIASPIS Liu, 1965

The genus *Polybranchiaspis* was erected by Liu (1965) for the species *P. liaojaoshanensis* Liu, 1965 (erroneously spelled as *P. liaojiaoshanensis* by Liu 1975 and several subsequent authors) from the Cuifengshan and Xitun formations of Yunnan (China). *Polybranchiaspis* now comprises nine species (including the type species), all from Yunnan.

Polybranchiaspis liaojaoshanensis Liu, 1965
 Plates 1–2, Plate 3, figures 1, 2; Text-figures 3–5

Type specimen. An almost complete headshield (Institute of Vertebrate Palaeontology and Palaeo-anthropology, Beijing, No. V.3027; Liu 1965, pl. 3, fig. 1), from the Cuifengshan Group at Qujing, Yunnan. A relatively large hypodigm is now also known from this locality. Some other *Polybranchiaspis* species, e.g. *P. gracilis* Cao, 1985, *P. yunnanensis* Cao, 1985, *P. rhombicus* Cao, 1985 and *P. sinensis* Cao, 1985, described from the same locality and formation, are probably reflections of intraspecific variation within *P. liaojaoshanensis*.

Material. The material from Tong Vai consists of five more or less complete headshields (BT 170–175) and numerous exoskeleton fragments (not numbered).

Locality and horizon. All the specimens described are derived from the four fish-bearing exposures of the Tong Vai valley (1–4, Text-fig. 1), which correspond to the same shaly horizon in the basal part of the third member of the Tong Vai section (second member of the Khao Loc Formation proper; Text-fig. 2).

Description. The headshield of the *Polybranchiaspis* species from Tong Vai is indistinguishable from that of *P. liaojaoshanensis* Liu from the Cuifengshan Formation of Yunnan (Liu 1965, 1975). On the basis of the photographs of the incomplete headshields discovered by Ta Thanh Trung (now deposited in the Geological Institute, Beijing), Tong-Dzuy Thanh and Janvier (1987) referred the Vietnamese specimens to *P. cf. gracilis* Cao, recorded from the same formation by Cao (1985). The latter was said to be characterized by posterolateral orientation of the foremost lateral transverse sensory-line canal (*tl*, Text-fig. 3B). However, examination of large populations of *P. liaojaoshanensis* from Yunnan now suggests that *P. gracilis* lies within the range of variation of *P. liaojaoshanensis*.

The exoskeleton of the *Polybranchiaspis* specimens from Tong Vai is well preserved (in contrast to previously described Chinese material) and has yielded new information about its structure and ornamentation. Most of the specimens have been prepared as impressions, by removing the exoskeleton with hydrochloric acid, and making elastomere casts (Pl. 1, figs 1b, 2–3; Pl. 2, fig. 1; Pl. 3, fig. 1).

Ornamentation. In external aspect, the ornamentation of the exoskeleton of *P. liaojaoshanensis* shows relatively large but low, star-shaped tubercles (Pl. 1, figs 1b, 2–3; Pl. 2, fig. 1a; Pl. 3, fig. 1a; Text-figs 3A, 4C–D, 5). These are smaller in the anterior part than in the posterior part of the dorsal surface of the shield. Also, in the posterior part of the shield, particularly on the median dorsal crest and along the lateral margins, they tend to become elongated, and even spine-shaped (Text-figs 3A, 5B). The tubercles on the ventral rim of the shield are very small (Pl. 1, fig. 3; Pl. 2, fig. 3; Text-fig. 5A). They are irregular in shape, with a large median elevation, or central tubercle (*ctb*, Text-fig. 4C), and four or five ‘branches’, each of which is made up by two or three smaller, lateral tubercles (Pl. 3, fig. 1a; *ltb*, Text-fig. 4C). These ‘branches’ may unite one tubercle with neighbouring ones. Although the sensory-line canals are closed over most of their course, their pattern can be traced as a result of the presence of double rows of smaller tubercles (Pl. 1, figs 1b, 2; Pl. 2, fig. 1a; Text-fig. 3A). In internal view, each of these tubercles is followed by a shallow depression, or basal recess (Pl. 1, fig. 3; Pl. 3, fig. 1b; *brec*, Text-fig. 4C), which often leaves a more or less polygonal impression on the surface of the internal natural mould of the exoskeleton. The perichondral layer of the endoskeleton, when still present, closes these polygonal recesses basally (Pl. 1, fig. 3; *pb*, Text-fig. 4C posteriorly to the orbit). This pattern has, for a long time, given the impression that the galeaspid exoskeleton was made up of small tesserae, like that of osteostracans (Halstead *et al.* 1979). Janvier (1981) also regarded this polygonal pattern as evidence for a honeycomb-like structure to the galeaspid exoskeleton, and compared it with the similar structure of the heterostracan exoskeleton. Both interpretations appear now to be incorrect. A vertical thin section through the exoskeleton of *Polybranchiaspis* (Text-fig. 4C–D) displays basically the same histological structure as in the Dong Mo ‘*Polybranchiaspis* sp.’, *Bannhuanaspis* (Tong-Dzuy Thanh and Janvier 1990, pl. 1; Janvier 1990; Janvier *et al.* 1993) and *Xiushuiaspis* (*Changxingaspis*, N. Z. Wang 1991), that is, an acellular, aspidine-like structure with horizontal incremental lines. There is no evidence for any type of dentinous tissue and one cannot distinguish any histological discontinuity between the tubercles. The walls of the basal recesses are made up of the same kind of laminar hard tissue as the tubercles.

The relation of the structure in *Polybranchiaspis* to that in *Bannhuanaspis* (where there is no basal recess and where each tubercle seems to correspond to one exoskeletal unit, in particular in the posterior part of the shield) is unclear. If each of the star-shaped tubercles of *Polybranchiaspis*, with its basal recess, is regarded as a single dermal unit, then it may be regarded primitive, and comparable to, for example, a thelodont scale with its pulp cavity. Conversely, one may consider that the star-shaped tubercles of *Polybranchiaspis* are in fact compounds of much smaller units, represented by the central tubercle and the adjacent cusps on the radiating ridges. Then, each of these ‘primary’ tubercles would correspond to one single unit of *Bannhuanaspis*. The former hypothesis could be supported by the fact that a similar pattern (stellate or costulated tubercles with a large basal recess) occurs also in the Silurian galeaspid *Hanyangaspis* (N. Z. Wang 1986), which was regarded by Janvier (1981) and N. Z. Wang (1991) as the most generalized galeaspid on the basis of several other characters. The latter hypothesis could be supported by the fact that the structure of the exoskeleton of *Bannhuanaspis* is remarkably simple and passes progressively to the body squamation. Also the latter structure (small units, each corresponding to a single, simple tubercle) seems to be that seen in most other galeaspid, in particular the Eugaleaspidiformes. No major conclusions concerning the polarity of the character states in the galeaspid exoskeleton can reasonably be drawn from such sparse data, and a review of the exoskeletal structure in all other galeaspid is urgently needed.

Sensory-line canals. The sensory-line canals of *P. liaojaoshanensis* are remarkably large and form prominent ridges on the internal surface of the exoskeleton, well beyond the base of the walls of the basal recesses (Pl. 1, fig. 3; Pl. 2, fig. 3; *slc*, Text-fig. 4D). The fact that their basal part is often 'unfinished' suggests that they are partly lined by the perichondral bone lamella of the endoskeleton. The cast of the natural impression of the external surface shows that the sensory-line canals were closed over most of their length (Pl. 1, figs 1b, 2; Pl. 2, fig. 1a). The supraorbital and lateral transverse canals were open only distally (Pl. 1, fig. 2; Pl. 2, fig. 1a; *sorb*, *tl1-4*, Text-fig. 3B), and the infraorbital canal opened by only a few broad slits, lateral to the orbits (Pl. 1, fig. 2; Pl. 2, fig. 1a; *iorb*, Text-fig. 3B). In some specimens, the transverse commissural line opens in a few short slits (Pl. 1, fig. 1b; Pl. 2, fig. 1a; *tcom*, Text-fig. 3B). There is no evidence of small sensory-line pores along the canals. This condition differs from that in all other vertebrates, and the function of such, almost entirely closed sensory-line canals remains unexplained.

Subaponeurotic vascular plexus. The presence of a dense subaponeurotic vascular plexus below the exoskeleton of galeaspids has been recorded by Halstead *et al.* (1979) and described by N. Z. Wang (1991) in the Silurian genus *Xiushuiaspis*. It is here shown to be present also in *P. liaojaoshanensis* (Pl. 1, fig. 3; Pl. 3, fig. 2). This network of vascular canals lies between the exoskeleton and the underlying endoskeletal shield, but is lined with perichondral bone (*sbap*, Text-fig. 4C). It is thus situated within or just below the perichondral lamella which closes basally the basal recesses. Its structure is closely similar to that of osteostracans and gnathostomes.

Median dorsal opening. The main defining characteristic of galeaspids is a large median dorsal opening (*mdo*, Text-figs 3B, 4A-B) in the anterior part of the headshield, which is currently interpreted as the external opening of an inhalent duct (*md*, Text-fig. 4B), comparable in function, and perhaps homologous to the nasopharyngeal duct of extant hagfishes (Janvier 1984). The paired olfactory organs open into this duct immediately below its external opening. The duct communicates basally with the gill chamber. This median dorsal opening and its duct are known to be partly lined by a thin layer of exoskeleton (Wang and Wang 1982; Janvier 1984; Liu 1985). Some of the *Polybranchiaspis* specimens from Tong Vai display delicate details of the dermal ornamentation of the duct. In the anterior wall it consists of minute, tilted pyramid-shaped tubercles which point toward the exterior (Pl. 2, fig. 1b-d; *fpt*, Text-fig. 4A-B). The latter are arranged in rows which are parallel to the margin of the median dorsal opening. In contrast, in the posterior wall of the duct, the ornamentation consists of irregularly arranged tubercles which are more similar to those of the external surface of the headshield, and pass posteriorly to small, independent platelets (Pl. 1, fig. 3; Pl. 2, fig. 2). However, even in this part of the duct, the tubercles are tilted toward the exterior.

This new information is of great importance to the understanding of the functional interpretation of the median dorsal opening in galeaspids. It is well known that, in fishes in general, the apertures through which water passes from the exterior to the interior (margin of nasal opening, spiracle, etc.) are lined with minute tubercles or denticles which point toward the exterior, the role of which essentially is to repel ectoparasites (Patterson 1977). The presence of such externally pointing tubercles in galeaspids is thus evidence for an inhalent (and not exhalent, as suggested by Belles-Isles 1985) function of the median dorsal opening, and accords with the position of the olfactory cavities observed in other galeaspids (N. Z. Wang 1991). This condition can be directly compared with the forward-pointing denticles recently discovered inside the snout of some thelodonts, and which have been regarded by Bruggen and Janvier (1993) as evidence for an inhalent nasopharyngeal opening (but in a terminal position) in thelodonts.

In *Polybranchiaspis*, the external margin of the median dorsal opening is lined by a prominent ridge, somewhat accentuated in our specimens by a slight dorsoventral flattening of the rest of the shield (Pl. 2, fig. 1a-b).

Pineal foramen. The pineal foramen seems to be a variable character in galeaspids. Liu (1965) described the pineal opening of *P. liaojaoshanensis* as very small, but Halstead *et al.* (1979) considered that there was no pineal opening, as in heterostracans. The Tong Vai specimens show a very clear, rounded pineal opening, which is variable in size but fairly large (Pl. 1, fig. 1a; Pl. 2, fig. 1a; *pif*, Text-fig. 3B), and surrounded by a crown of small tubercles.

Orbit and orbital cavity. In one specimen from Tong Vai (Pl. 1, fig. 3), the perichondral lining of the orbital cavity is partly preserved and appears almost hemispherical in shape, yet the posterior ventral myodome (or trigeminal chamber) cannot be observed. The orbits are almost circular in shape and protrude slightly above the level of the surrounding exoskeleton (Pl. 1, fig. 2; Pl. 2, fig. 1a). Although the exoskeleton is certainly thicker

around the orbits, there is no major change in the aspect of the ornamentation along the orbital margin, contrary to what is commonly observed in osteostracans.

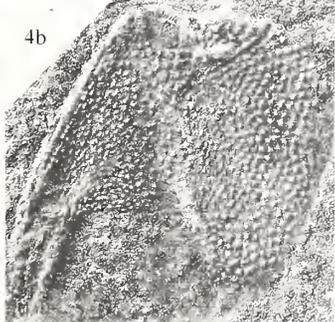
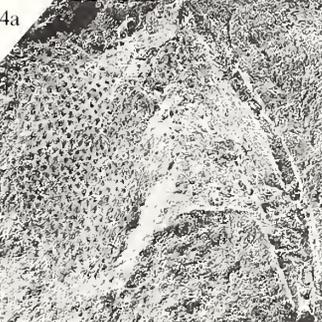
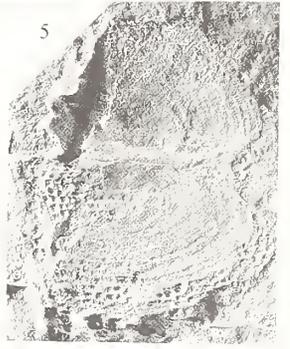
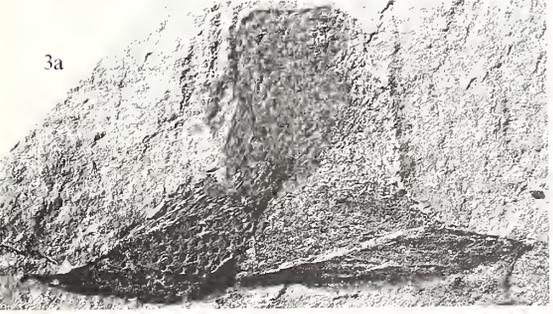
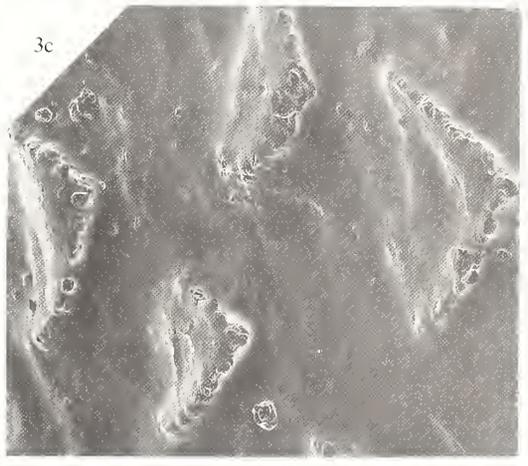
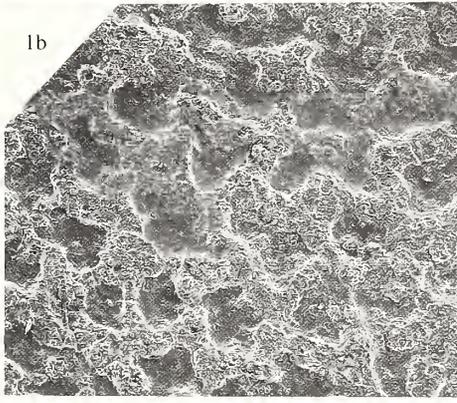
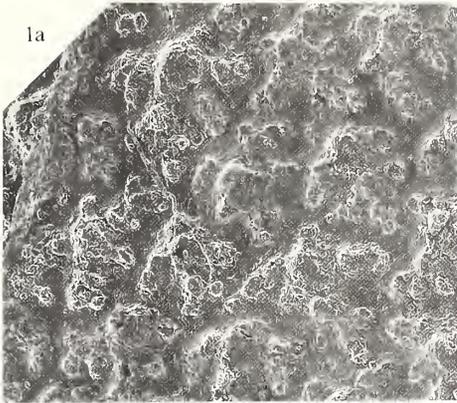
Absence of endolymphatic opening. In spite of the excellent state of preservation of the exoskeleton and ornamentation in our specimens, we have been unable to see any trace of the endolymphatic opening. To date, the latter has been observed only in the Silurian galeaspid *Xiushuiaspis* (N. Z. Wang 1991), where it lies in front of the posterior transverse commissural sensory-line canal (probably homologous to the unique commissural canal of *Polybranchiaspis*). We can thus conclude that there is no endolymphatic opening in *P. liaojaoshanensis*.

Ventral rim. The ventral rim of the headshield is covered with minute stellate tubercles. Along the margin of the oralbranchial fenestra, at least seven branchial notches are visible in one of our specimens (Pl. 2, fig. 3; *brn*, Text-fig. 5A), which is incomplete. Here again, no change in the aspect of the ornamentation is noticeable along the notch margin, and the exoskeleton passes to the smooth surface of the perichondral bone which lines the branchial fossae. Liu (1975) recorded twelve branchial notches in *P. liaojaoshanensis* from Yunnan, where the actual branchial fossae can be observed. It is probable that three or four of the branchial notches in our specimen are less marked, because they lie in the narrowest part of the rim, just behind the level of the orbit. At this level, the rim is recurved dorsally (i.e. toward the oralbranchial cavity), and this does not seem to be due to distortion. This branchial division of the rim ends, immediately behind the level of the orbits, in a well-marked notch (*n*, Text-fig. 5A). Anteriorly, it is much broader, until it reaches the oral region. Only the lateral part of the oral notch is visible in our material (*orn*, Text-fig. 5A). In one specimen (Pl. 1, fig. 2), the external surface of the part of the exoskeleton which extends behind the orbits shows a series of seven or eight 'waves', corresponding to the position of the underlying branchial fossae.

Remarks on galeaspid taphonomy. Owing to their extremely thin exoskeleton (c. 0.1–0.4 mm) and often weakly ossified endoskeleton, complete galeaspid headshields are preserved only in very low energy environments, such as in the third member of the Tong Vai section and at a few Chinese localities. Nevertheless, even in such quiet deposits, some headshields are broken, and seem to have broken always in the same way: the anterior rim of the median dorsal duct, or the lateral parts of the shield are detached from the central part (Pl. 1, figs 2–3; Pl. 2, fig. 1a). This suggests that there are areas of weakness in the headshield, in particular in the epibranchial region, where the roof of the oralbranchial chamber meets the dorsal exoskeleton. This is probably the reason why, in many galeaspid (*Asiaspis*, *Lungmenshanaspis*, *Pentathyraspis*), large fenestrations occur in this particular area, and have been interpreted as either dorsal 'fields' (by reference to those in osteostracans) or dorsal branchial openings (N. Z. Wang 1991; Pan 1992). In some well preserved specimens from Tong Vai, there are often small patches of exoskeleton which are missing in the epibranchial region, and this is presumably due to pre-preservation damage. These fenestrations are thus most probably artefacts of preservation.

EXPLANATION OF PLATE 3

- Figs 1–2. *Polybranchiaspis liaojaoshanensis* Liu, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. 1, S.E.M. photograph of an elastomere cast of the external (a), BT 171, and internal (b), BT 172, surface of the exoskeleton, $\times 45$. 2, BT 175, headshield with exoskeleton removed and photographed in immersion, to show the subaponeurotic vascular plexus (sensory-line canals darker), $\times 5$.
- Fig. 3. *Acanthothoraci* gen. et sp. indet. 1, BT 167, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. Natural cast of the right anterolateral and spinal plates (a, $\times 4$), and S.E.M. photographs of an elastomere cast of the impression, showing a lateral stellate tubercle of the anterolateral plate (b, $\times 150$) and some crescentiform tubercles of the postbranchial lamina (c, $\times 100$).
- Figs 4–5. *Acanthothoraci* gen. et sp. indet. 2, same locality and horizon as Pl. 3, fig. 3. 4, BT 165, natural impression of the right anterior ventrolateral and spinal plates in ventral view (a) and elastomere cast of the latter (b), $\times 4$. 5, BT 168, left anterolateral and anterior ventrolateral plates in lateral view, most of the bone missing, $\times 4$.
- Fig. 6. *Youngolepis praecursor* Zhang and Yu, BT 169, Pragian, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. Right lower jaw in lateral view, $\times 3$.



Superclass GNATHOSTOMATA Cope, 1889

Class PLACODERMI McCoy, 1848

Order ACANTHOTHORACI Stensiö, 1944

The Tong Vai material includes a few placoderm plates which can be referred here to the presumably paraphyletic taxon Acanthothoraci (Goujet 1984), on the basis of their overall morphology and star-shaped ornamentation. They seem to belong to two distinct forms, based on slight differences in the shape of the anterolateral plate. Both forms are probably new, and differ markedly from all previously described acanthothoracids, but we consider that it is preferable to wait for the discovery of cranial material, to ensure a useful systematic analysis, before erecting new species.

ACANTHOTHORACI gen. et sp. indet. 1

Plate 3, figure 3; Text-figure 6A

Material. An anterolateral plate of the right side, associated with the spinal plate (BT 167).

Locality and horizon. Exposure 2 (Text-fig. 1) of the Tong Vai valley, in a thin layer of black shale from the third member of the section (second member of the Khao Loc Formation).

Description. We refer to this first form a complete anterolateral plate, associated with the spinal plate (*AL*, *SP*, Text-fig. 6A), preserved as an impression of its external surface. The dorsal blade of the anterolateral plate is roughly square, and the postbranchial lamina is not clearly distinct from the rest of the plate, yet is covered with crescentiform tubercles (Pl. 3, fig. 3c; *pbrl*, Text-fig. 6A) as in e.g. *Romundina* (Ørvig 1975), *Palaeacanthaspis* and *Kosoraspis* (Stensiö 1944; Denison 1978). The rest of the anterolateral plate is ornamented with large, scattered, star-shaped tubercles (Pl. 3, fig. 3b).

ACANTHOTHORACI gen. et sp. indet. 2

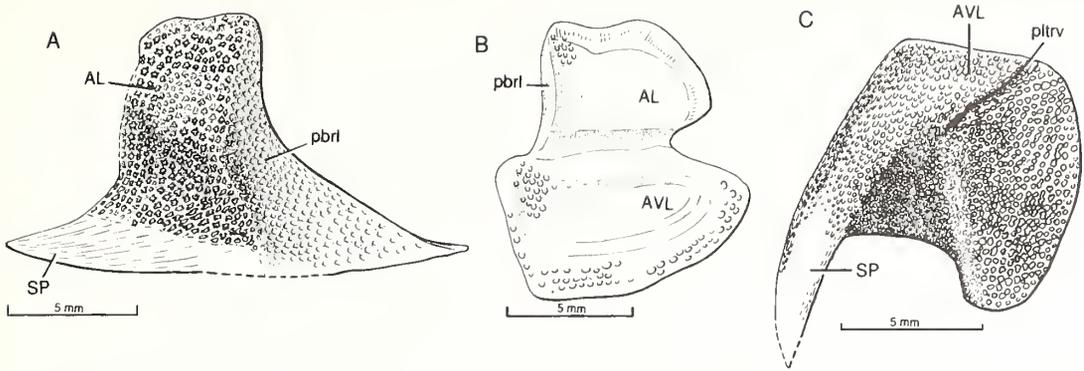
Plate 3, figures 4–5; Text-figure 6B–C

Material. Impression of the anterior ventrolateral and spinal plates of the right side (BT 165); fragmentary impression of an anterior ventrolateral plate of the left side (BT 166); indeterminate plate fragment (BT 164), with the same ornamentation as BT 165; associated anterolateral and anterior ventrolateral plates of left side (BT 168).

Locality and horizon. All specimens referred to this form come from exposure 1 (Text-fig. 1) of the Tong Vai valley and are from the shaly basal part of the third member of the section (second member of the Khao Loc Formation).

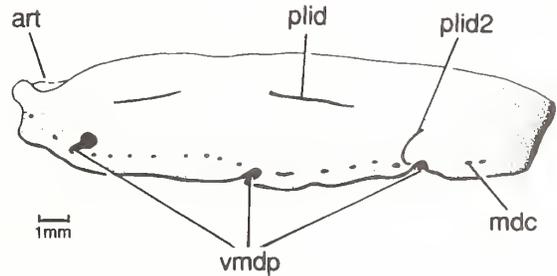
Description. This second form is represented by the external impression of an anterior ventrolateral plate and the associated spinal plate (*AVL*, *SP*, Text-fig. 6C), and two associated anterior ventrolateral and anterolateral plates (*AL*, *AVL*, Text-fig. 6B). They all differ from the preceding form by their larger, more rounded and closely-set tubercles, as well as by the rounded shape of the dorsal blade of the anterolateral plate, and the medially directed postbranchial lamina (*pbrl*, Text-fig. 6B). Since the bone was very thin, the impressions of the internal and external surfaces are somewhat superimposed, and observation of the specimens in immersion reveals traces of the overlap areas. A clear overlap area for the anterior dorsolateral plate, and possibly the posterolateral plate, is visible in the anterolateral plate (Text-fig. 6B). There seems also to be an overlap area for a posterior ventrolateral plate on the anterior ventrolateral plate. In the anterior part of the latter there is an oblique groove for the ventral transverse pit-line (*pltrv*, Text-fig. 6C).

By its broad anterior ventrolateral plate, this form clearly differs from all other acanthothoracids described to date in which this plate is very narrow. However, there is a number of still undescribed forms (e.g. from Siberia and Saudi Arabia) with a similar, broad anterior ventrolateral plate (D. Goujet, pers. comm. 1994). A small acanthothoracid is present in the Cuifengshan Group of Yunnan (Zhu Min, pers. comm. 1994) which



TEXT-FIG. 6. A–C, *Acanthothoraci* gen. et sp. indet., Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. A, *Acanthothoraci* gen. et sp. indet. 1, BT 167, right anterolateral and spinal plates in lateral view, camera lucida drawing of an elastomere cast of a specimen preserved as an impression. B–C, *Acanthothoraci* gen. et sp. indet. 2; B, BT 168, left anterolateral and anterior ventrolateral plates preserved essentially as an impression of the internal surface, with some patches of exoskeleton and external ornamentation, camera lucida drawing; C, BT 165, right anterior ventrolateral plate and spinal plate in ventral view, camera-lucida drawing of an elastomere cast of the specimen preserved as an impression. Abbreviations: *AL*, anterolateral plate; *AVL*, anterior ventrolateral plate; *pbrl*, postbranchial lamina of the anterolateral plate; *pltrv*, transverse ventral pit-line; *SP*, spinal plate.

TEXT-FIG. 7. *Youngolepis praecursor* Zhang and Yu, BT 169, Khao Loc Formation, Tong Vai, Ha Giang Province, Vietnam. Camera-lucida drawing of the right lower jaw in lateral view. Abbreviations: *art*, glenoid articular fossa; *mdc*, pores of the mandibular sensory-line canal; *plid*, horizontal part of infradentary pit-line; *plid2*, vertical pit-line of infradentary 2; *vmdp*, ventral mandibular pits.



seems to be identical to this second form from Tong Vai. All the acanthothoracids known to date are Late Lochkovian to Early Emsian in age.

Class OSTEICHTHYES Huxley, 1880
 Subclass SARCOPTERYGII Romer, 1955
 Infraclass DIPNOMORPHA Ahlberg, 1991
 Genus YOUNGOLEPIS Zhang and Yu, 1981
Youngolepis praecursor Zhang and Yu, 1981

Plate 3, fig. 6; Text-figure 7

Material. A single lower jaw of the right side (BT 169).

Locality and horizon. Exposure 1 (Text-fig. 1) of the Tong Vai valley.

Description. A small right lower jaw of a cosmine-covered sarcopterygian is similar to that of *Youngolepis praecursor*, described by Chang (1991), and shows the characteristic ventral series of large sensory pits (*vmdp*, Text-fig. 7). The pores of the mandibular canal are relatively large (*mdc*, Text-fig. 7), and the horizontal and vertical pit-lines (*plid*, *plid2*, Text-fig. 7) are well marked. The articular area is poorly preserved (*art*, Text-fig.

7). In addition, there are some cosmine-covered dermal bone fragments with very large and closely-set pores, which may belong to a different taxon.

CONCLUSIONS

The vertebrate fauna from Tong Vai accords with the '*Polybranchiaspis liaojaoshanensis* – *Dongfangaspis qujingensis* palaeocommunity' as defined by S. T. Wang (1991) from the base of the Xishancun Formation of the Cuifengshan Group of Qujing, Yunnan. However, *P. liaojaoshanensis* is known to extend into the overlying Xitun Formation, where it occurs in association with *Youngolepis praecursor* (Chang 1982). We would thus be inclined towards correlating the fish horizon in Tong Vai with the Xitun Formation of the Cuifengshan Group of Yunnan which is referred to the Late Lianhuashanian – Early Nagaolingian. Although fragments with a *Polybranchiaspis*-like ornamentation occur also in the more southerly situated Vietnamese localities of Trang Xa and Dong Mo, the material referred to by Tong-Dzuy Thanh and Janvier (1990) as '*Polybranchiaspis* sp.' from Dong Mo probably belongs to a different genus. Its ornamentation of small, isometric and rounded tubercles, and the lack of basal recesses are rather suggestive of *Bannhuanaspis*, yet its size is much smaller than that of the latter. Two forms of acanthothoracid placoderms have been described herein, one of which is unquestionably new. The occurrence of this taxon is consistent with the Pragian age of this locality.

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REFERENCES

- AHLBERG, P. E. 1991. A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zoological Journal of the Linnean Society*, **103**, 241–287.
- BELLES-ISLES, M. 1985. A new interpretation of the medio-dorsal opening in galeaspidomorphs ('Agnatha', Devonian, China). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **7**, 385–394.
- BRUGGHEN, W. van der and JANVIER, P. 1993. Denticles in thelodonts. *Nature*, **364**, 107.
- CAO RENGUAN 1985. Pisces. 106–117. In FANG RUNSEN, JIANG NENREN, FAN JIANCAI, CAO RENGUAN and LI DAIYUN (eds). *The Middle Silurian and Early Devonian Stratigraphy and Palaeontology in Qujing District, Yunnan*, Yunnan Academy of Sciences, Kunming, 167 pp. [In Chinese].
- CHANG MEE-MANN 1982. The braincase of *Youngolepis*, a Lower Devonian crossopterygian from Yunnan, south-western China. Ph.D. thesis, Department of Geology, University of Stockholm, 113 pp.
- 1991. Head skeleton and shoulder girdle of *Youngolepis*. 355–378. In CHANG MEE-MANN, ZHANG GUORUI and LIU YU-YAI (eds). *Early Vertebrates and Related Problems of Evolutionary Biology*. Science Press, Beijing, 514 pp.
- COPE, E. D. 1889. Synopsis of the families of Vertebrata. *American Naturalist*, **23**, 1–29.
- DENISON, R. H. 1978. Placodermi. In SCHULTZE, H.-P. (ed.). *Handbook of Paleichthyology*, vol. 2, Gustav Fischer, Stuttgart, 128 pp.
- DEPRAT, J. 1915. Etudes géologiques sur la région septentrionale du Haut Tonkin (Feuilles de Pa Kha, Ha Giang, Malipo, Yen minh). *Mémoires du Service géologique d'Indochine*, **4**, 1–176.
- DOVJIKOV, A. E. 1965. *Geologia Svernogo V'etnama* [Geology of North Vietnam]. Tong cuc Dia Chat nuoc Viet Nam D.C.C.M., Hanoi, 688 pp. [In Russian].
- DUONG XUAN, H. and LE VAN, D. 1980. 122–126. In DUONG XUAN, H. (ed.). *Hoa thach dac trung o Mien Bac Viet Nam* [Characteristic fossils in the north of Viet Nam]. Nha Xuat ban Khoa hoc va Ky thuat, Hanoi, 600 pp. [In Vietnamese with English summary].
- GOUJET, D. 1984. Placoderm interrelationships: a new interpretation, with a short review of placoderm classifications. *Proceedings of the Linnean Society of New South Wales*, **107**, 211–143.
- HALSTEAD, L. B., LIU YÜ-HAI and P'AN KIANG 1979. Agnathans from the Devonian of China. *Nature*, **282**, 831–833.

- HALSTEAD TARLO, L. B. 1967. Agnatha. 629–636. In HARLAND, W. B., HOLLAND, C. H., HOUSE, M. R., HUGHES, N. F., REYNOLDS, A. B., RUDWICK, M. J. S., SATTERTHWAITE, G. E., TARLO, L. B. H. and WILLEY, E. C. (eds). *The Fossil Record*, Geological Society of London, London, 827 pp.
- HOANG XUAN, T. 1976. Về các trâm tích Devon dưới ở Bao Lạc [On the Lower Devonian deposits in the Bao Lạc sheet]. *Tin Ban do Dia chat [Geological Mapping Information]*, **30**, 20–28 [In Vietnamese].
- HUXLEY, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*, **1880**, 649–662.
- JANVIER, P. 1981. The phylogeny of the Craniata, with particular reference to the significance of fossil 'agnathans'. *Journal of Vertebrate Paleontology*, **1**, 121–159.
- 1984. The relationships of the Osteostraci and Galeaspidia. *Journal of Vertebrate Paleontology*, **4**, 344–358.
- 1990. La structure de l'exosquelette des Galéapides (Vertebrata). *Comptes-Rendus de l'Académie des Sciences, Paris*, **310**, 655–659.
- TONG-DZUY, T. and TA HOA, P. 1993. A new Early Devonian galeaspid from Bac Thai Province, Vietnam. *Palaeontology*, **36**, 297–309.
- LIU YÜ-HAI 1965. New Devonian agnathans of Yunnan. *Vertebrata Palasiatica*, **9**, 125–134. [In Chinese with English summary].
- 1975. Lower Devonian agnathans of Yunnan and Sichuan. *Vertebrata Palasiatica*, **13**, 215–223. [In Chinese with English summary].
- 1985. A galeaspid (Agnatha), *Antiquisagittaspis cornuta* gen. sp. nov., from the Lower Devonian of Guangxi, China. *Vertebrata Palasiatica*, **23**, 247–254. [In Chinese with English abstract].
- M'COY, F. 1848. On some new fossil fish of the Carboniferous period. *Annals and Magazine of Natural History*, (2), **2**, 1–10.
- ORVIG, T. 1975. Description, with special reference to the dermal skeleton, of a new radotinid arthrodire from the Gedinian of Arctic Canada. *Colloques internationaux du Centre national de la Recherche scientifique*, **218**, 41–71.
- PAN JIANG 1992. *New Galeaspid (Agnatha) from the Silurian and Devonian of China*. Geological Publishing House, Beijing, 77 pp.
- PATTERSON, C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. In ANDREWS, S. M., MILES, R. S. and WALKER, A. D. (eds). *Problems in Vertebrate Evolution*. *Linnean Society Symposium Series*, **4**, 77–121.
- ROMER, A. S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? *Nature*, **176**, 126.
- SAURIN, E. 1956. *Lexique stratigraphique international. Asie. 6a, Indochine*. Bureau de Recherches géologiques et minières, Paris, 140 pp.
- STENSIÖ, E. A. 1944. Contributions to the knowledge of the vertebrate fauna of the Silurian and Devonian of Western Podolia. II. Notes on two arthrodires from the Downtonian of Podolia. *Arkiv för Zoologi*, **35**, 1–83.
- TA THANH T. 1978. Trâm tích gọi là Ordovic ở phu doi Khao Loc thuc ra co tuoi Devon som. [The so-called Ordovician deposits in the Khao Loc subzone are in fact Lower Devonian]. *Dia chat [Geology]*, **140**, 20. [In Vietnamese].
- TONG-DZUY (TONG-DUY), T. 1967. Les Coelentérés du Dévonien au Vietnam. Part 1. *Acta scientifica vietnamicarum, section Geology and Geography*, **3**, 304 pp.
- 1982. Biostratigrafiskoe znachenie kompleksov fauny v Devone regiona Bac Bo (Vietnam) [Biostratigraphical significance of the Devonian faunal assemblages of the Bac bo region (Vietnam)]. 90–103. In YUFEREV, O. V. (ed.). *Stratigrafia i Paleontologia Devona i Karbona [Stratigraphy and Paleontology of the Devonian and Carboniferous]*. *Trudy Institut Geologii Geofiziki, Moscow*, **438**. [In Russian].
- DANG TRAN, H., NGUYEN DINH, H., NGUYEN DUC, K., NGUYEN HUU, H., TA HOA, P., NGUYEN THE, D. and PHAM KIM, N. 1986. *He Devon o Viet Nam [The Devonian in Vietnam]*. Nha Xuat ban Khoa hoc va Ky thuat, Hanoi 141 pp. [In Vietnamese].
- NGUYEN THE, D., TA HOA, P., PHAM KIM, N. and DOAN NHAT, T. 1988a. *Stratigrafia i tselenteraty Devona Vietnamia [Devonian stratigraphy and Coelenterata of Vietnam]*. **1**, *Stratigraphy*, Nauka, Siberian Branch, Novosibirsk, 179 pp. [In Russian].
- and JANVIER, P. 1987. Les Vertébrés dévoniens du Viêt Nam. *Annales de Paléontologie*, **73**, 165–194.
- 1990. Les Vertébrés du Dévonien inférieur du Bac Bo oriental (provinces de Bac Thai et Lang Son, Viet Nam). *Bulletin du Muséum national d'Histoire naturelle, Paris*, 4e série, **12**, 143–223.
- NGUYEN DUC, K., KHROMYKH, V. G., NGUYEN HUU, H., NGUYEN THE, D., TA HOA, P. and DOAN NHAT, T. 1988b. *Stratigrafia i tselenteraty Devona Vietnamia. [Devonian stratigraphy and Coelenterata of Vietnam]*. **2**, *Coelenterata*, Nauka, Siberian Branch, Novosibirsk, 248 pp. [In Russian].

- VU KHUC, D. and BUI PHU, M. 1990. *Dia tang Viet Nam [Stratigraphy of Vietnam]*. Nha Xuat ban Khoa hoc va Ky thuat (Scientific and Technical Publishing House), Hanoi, 330 pp. [In Vietnamese].
- WANG NIAN-ZHONG 1986. Notes on two genera of Middle Silurian Agnatha (*Hanyangaspis* and *Latirostraspis*) of China. 49–57. In *Collected Papers of the 13th Annual Conference of the Paleontological Society of China*, Science Press, Beijing. [In Chinese with English abstract].
- 1991. Two new Silurian galeaspids (jawless craniates) from Zhejiang Province, China, with a discussion of galeaspid–gnathostome relationships. 41–65. In CHANG MEE-MANN, ZHANG GUO-RUI and LIU YÜ-HAI (eds). *Early Vertebrates and Related Problems of Evolutionary Biology*. Science Press, Beijing, 514 pp.
- and WANG SHI-TAO 1982. On the polybranchiaspid Agnatha and the phylogenetical position of polybranchiaspiformes. *Vertebrata Palasiatica*, **20**, 99–105. [In Chinese with English summary].
- WANG SHI TAO 1991. Lower Devonian vertebrate paleocommunities from South China. 487–497. In CHANG MEE-MANN, ZHANG GUO-RUI and LIU YÜ-HAI (eds). *Early Vertebrates and Related Problems of Evolutionary Biology*. Science Press, Beijing, 514 pp.
- YANG SHIH-POU, P'AN KIANG and HOU HUNG-FEI 1981. The Devonian System in China. *Geological Magazine*, **117**, 113–138.
- ZHANG MEE-MANN and YU XAOBO 1981. A new crossopterygian, *Youngolepis praecursor*, gen. et sp. nov., from Lower Devonian of E. Yunnan, China. *Scientia Sinica*, **24**, 89–97.

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THE EARLY CRETACEOUS BRACHIOSAURID DINOSAURS *ORNITHOPSIS* AND *EUCAMEROTUS* FROM THE ISLE OF WIGHT, ENGLAND

by WILLIAM T. BLOWS

ABSTRACT. The lectotype of *Ornithopsis* is usually placed within the Brachiosauridae, but is unlike any other material that has been referred to the genus. This referred material is also brachiosaurid but is regarded as belonging to the genus *Eucamerotus* which was originally established without a type species. *Eucamerotus foxi* sp. nov. is erected for this material, and a holotype and five paratypes are designated. *Eucamerotus* is placed within the Brachiosauridae. Several genera of sauropod dinosaurs, previously established from the Lower Cretaceous Wealden formation of the Isle of Wight, are *nomina vana* as they are based on inadequate type material. All described Wealden sauropod material other than dorsal vertebrae should be described as Sauropoda *Incertae Sedis* or Brachiosauridae *Incertae Sedis*.

SEVERAL Lower Cretaceous sauropod genera were established by Owen, Seeley, Hulke and others, mostly based on inadequate material. *Cetiosaurus brevis* Owen, 1842 was founded on some vertebrae from Sussex with other vertebrae also referred to it. These referred specimens were made the type of *Cetiosaurus conybeari* by Melville (1849). A large humerus from Sussex was used by Mantell (1850) to establish the name *Pelorosaurus conybeari*. *Ornithopsis hulkei* Seeley, 1870 was based on two dorsal centra, one from Sussex, the other from the Isle of Wight, both of which were subsequently renamed by Owen (1875): the Sussex specimen as *Bothriospondylus elongatus* and the Isle of Wight specimen as *Bothriospondylus magnus*. Hulke (1870, 1871) described a dorsal neural arch from the Isle of Wight as *Eucamerotus* without giving it a species name. *Chondrosteosaurus gigas* Owen, 1876 and *C. magnus* Owen, 1876 were established for Isle of Wight vertebrae, cervical and dorsal respectively. Owen (1876) also proposed the synonymy of *Chondrosteosaurus magnus* with *Bothriospondylus magnus*. Lydekker proposed the presence of two American genera in the Weald, a new species of *Pleurocoelus* (*P. valdensis* Lydekker, 1889), based on vertebrae, and *Morosaurus* (*Camarasaurus*) (Lydekker, 1892), based on foot bones.

The name *Ornithopsis hulkei* has been much used for sauropod material, both Lower Cretaceous and Upper Jurassic, despite the type specimen being an isolated dorsal centrum, which offers little for comparison with other vertebrate specimens. *Ornithopsis* would be considered as a *nomen vanum* but for the fact that dorsal vertebrae are 'very diagnostic among the sauropods' (Berman and McIntosh 1978, p. 33), and the name remains widely used in dinosaur literature for Wealden sauropods. A brief systematic review and discussion of the species are included here.

Abbreviations. BMNH, Natural History Museum, London; MIWG, Museum of Isle of Wight Geology, Sandown, Isle of Wight.

SYSTEMATIC PALAEOLOGY

Class REPTILIA Linnaeus, 1758
Order SAURISCHIA Seeley, 1888
Suborder SAUROPODOMORPHA Huene, 1932
Infraorder SAUROPODA Marsh, 1878
Family BRACHIOSAURIDAE Riggs, 1904

Diagnosis. Following McIntosh (1990a, 1990b) and Riggs (1904): large sauropods with forelimbs longer than hind limbs; vertebrae with deep, complex pleurocoels; strong opisthocoely

throughout the dorsal series; short simple massive neural spines throughout, tallest over the shoulder region.

Genus ORNITHOPSIS Seeley, 1870

Type species. *O. hulkei* Seeley, 1870

Ornithopsis hulkei Seeley, 1870

Text-figure 1A–B

- 1870 *Ornithopsis hulkei* Seeley, p. 279.
 1875 *Bothriospondylus magnus* Owen, p. 24, pls. 8–9.
 1879 *Ornithopsis* Seeley; Hulke, p. 754.
 1882 *Ornithopsis* Seeley; Hulke, p. 375.

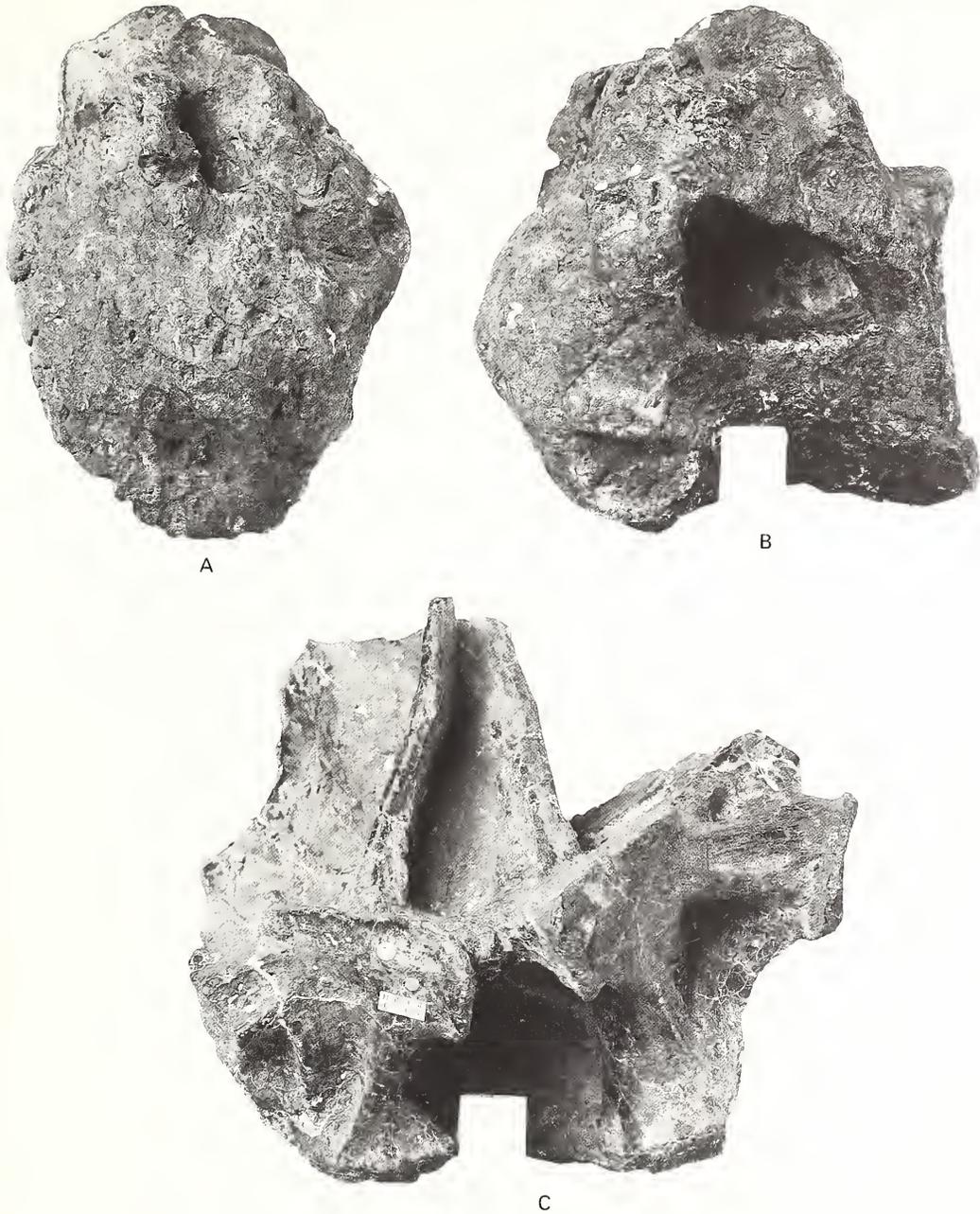
Lectotype. BMNH 28632, posterior dorsal vertebra, chosen from syntypes of Seeley 1870, from Brook, Isle of Wight, England. Figured in Text-figure 1A–B.

Type horizon. Wealden Marls (Wessex Formation) Lower Cretaceous (Barremian).

Diagnosis. Medium-sized brachiosaurid sauropod; posterior dorsal vertebrae are opisthocoelian with tall narrow centra; pleurocoels extend over the posterior two-thirds of the centrum near the base of the neural arch; the centrum has a basal ridge; parapophyses occur high on the neural arch.

Remarks. BMNH 28632 is the lectotype of *Ornithopsis hulkei* (Text fig. 1A–B) and was originally proposed as the syntype together with a vertebra from Sussex (BMNH 2239). There is no justification for linking these two vertebrae together as the syntypes, and Lydekker (1888) noted Seeley's approval for making the Isle of Wight specimen the type of *Ornithopsis hulkei*. The other specimen is here regarded as Sauropoda *Incertae Sedis* and Owen's binomen, *Bothriospondylus elongatus*, is a *nomen vanum* restricted to the type specimen. BMNH 28632 is very different to all other specimens referred to *Ornithopsis hulkei*. On this basis, the binomen can only be retained for this specimen, until such time as new vertebrae referable to *Ornithopsis hulkei* are found in association with other bones.

Since BMNH 28632 is restricted to a centrum only, precise family affinities cannot be established, but the following features are suggestive of a brachiosaurid origin. The centrum is tall and narrow and has a prominently ridged base. The deep pleurocoel is sub-triangular to round, occupying the posterior two-thirds of the centrum close to the neural arch. This is distinct from the other dorsal vertebrae currently referred to *O. hulkei*, where the pleurocoels are more anterior or extend nearly the length of the centrum, and the base is flat. The opisthocoelous nature of the centrum is well developed with a prominent anterior ball, and the parapophyses appear to have been high on the neural arch beyond that portion of the vertebra preserved. The combination of a high parapophysis position with strong opisthocoely suggests that this is a dorsal centrum from the caudal end of the sequence. Strong opisthocoely occurs only in the first four anterior dorsals in diplodocids where the parapophysis is sited on the centrum (dorsals 1–3 in *Diplodocus* and *Apatosaurus excelsus*), the centra becoming more amphiplatyan towards the posterior of the series. Middle and posterior dorsals of brachiosaurids, camarasaurids and titanosaurids have strong opisthocoely. Posterior camarasaurid centra appear short in length relative to height, whilst brachiosaurid centra are more elongate and become progressively more so anteriorly. The increased length of BMNH 28632 relative to height is suggestive of a brachiosaurid origin. The neural and lateral processes are missing, and thus the specimen lacks most of the parts which bear the features cited by McIntosh (1990a) as titanosaurid, except for the pleurocoel which is regular, deep and distinct in the specimen,



TEXT-FIG. 1. A–B, *Ornithopsis hulkei*, lectotype, BMNH 28632, dorsal vertebral centrum. A, anterior view; B, left lateral view. C, *Eucamerotus foxi* sp. nov., holotype, BMNH R2522, neural arch in anterior view. Both from the Lower Cretaceous Wessex Formation of Brook, Isle of Wight. All $\times 0.33$.

not moderate and irregular as in titanosaurids. The internal bone structure incorporates large, coarse cavitations, a brachiosaurid feature, unlike the fine cancellous bone structure of cetiosaurids and other sauropods (J. McIntosh, pers. comm.).

Genus *EUCAMEROTUS* Hulke, 1871

Type species. Eucamerotus foxi sp. nov.

Eucamerotus foxi sp. nov.

Plate 1, figures 1–6; Text-figures 1c, 2, 5

Derivation of name. After William Fox who collected most of the paratypes.

1871 *Eucamerotus* Hulke, p. 36.

Holotype. BMNH R2522, vertebral neural arch, Text-figure 1c.

Type horizon and locality. Wealden Marls (Wessex Formation), Lower Cretaceous (Barremian) of Brook, Isle of Wight, England.

Range. Wealden Marls (Wessex Formation) Lower Cretaceous.

Paratypes. BMNH R89, two dorsal vertebrae; BMNH R90, two dorsal vertebrae; BMNH R2524, juvenile dorsal vertebrae.

Referred specimens. BMNH R91, three dorsal vertebrae; BMNH R2523 (in part), three dorsal vertebrae; BMNH R406, anterior of dorsal centrum; BMNH R708, dorsal centrum; BMNH R94 (in part), dorsal vertebral pieces; MIWG 5314, juvenile dorsal centrum; MIWG 5125, anterior dorsal centrum; MIWG (BP001), new and undescribed partial skeleton.

Diagnosis. Medium-sized sauropod; dorsal vertebrae with broad, rounded centra, flattened bases, strongly opisthocoelean; deep lateral pleurocoels mostly placed anteriorly and becoming shallower posteriorly; shallow depth of bone below pleurocoel; tall neural arch with large anterior and posterior supra-neural concavities; strongly ridged neural and lateral spines; broad termination on the neural spine.

Remarks. The holotype (BMNH R2522, Text-fig. 1c) differs from the lectotype of *Ornithopsis* and cannot be referred to it (as has been the usual practice). The two genera are therefore not synonymous. All the material previously referred to *Ornithopsis* can be referred either to *Eucamerotus* (the dorsal vertebrae listed here) or to Sauropoda *Incertae Sedis*. No species was founded for *Eucamerotus* by Hulke, and *E. foxi* sp. nov. is erected here. Five paratypes, mostly from the Fox collection are also designated. Article 11(c) section (i) of the International Code of Zoological Nomenclature (ICZN 1985) states: 'A work published before 1931 and containing uninominal genus-group names without associated nominal species is accepted as consistent with the Principle of Binominal Nomenclature in the absence of evidence to the contrary'. ICZN Article 12(a) states: 'To be available every new scientific name published before 1931 must satisfy the

EXPLANATION OF PLATE 1

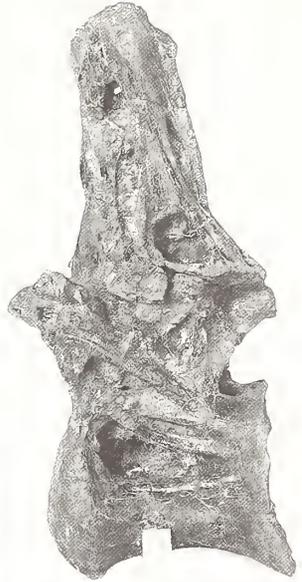
Figs 1–6. *Eucamerotus foxi* sp. nov., paratypes, all are single dorsal vertebrae. 1, anterior view. 2, left lateral view. 3, left lateral view. 4, anterior view. 5, anterior view. 6, left lateral view. All from the Lower Cretaceous Wessex Formation of the Isle of Wight. 1–4 (BMNH R89 in part) are $\times 0.14$; 5 and 6 (BMNH R90 in part) are $\times 0.16$.



1



2



3



4



5



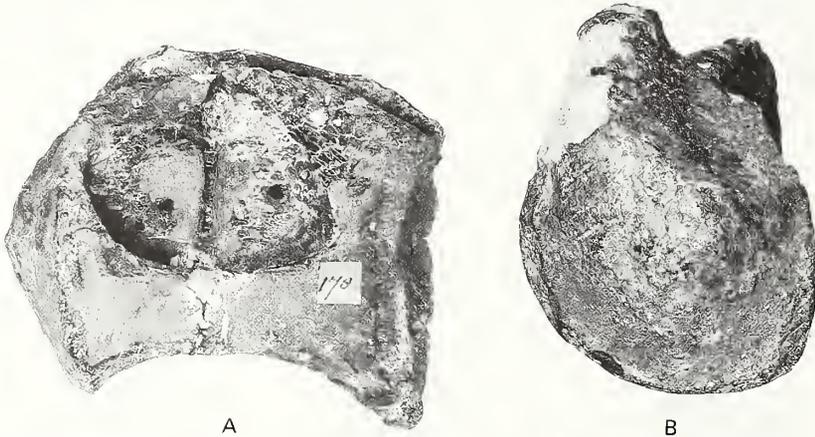
6

BLOWS, *Eucamerotus foxi*

provisions of Article 11 and must have been accompanied by a description or a definition of the taxon that it denotes, or by an indication.' The 'indication' is referred to in ICZN Article 12(b) (7): 'the proposal of a new genus-group name or of a new species-group name in association with an illustration of the taxon being named...even if contained in a work...that is not consistently binominal'.

Four of the new paratypes of *E. foxi* (BMNH R89 and R90) may be part of a single skeleton, perhaps including four cervical vertebrae (BMNH R87, R87a, R173) described by Hulke (1880), although Fox gave no indication of any association (Blows 1983). These cervical vertebrae are regarded as Sauropoda *Incertae Sedis*.

BMNH R89 (Pl. 1, figs 1–4) comprises two dorsal vertebrae, one of which was described and illustrated by Hulke (1880). They are tall with long lateral pleurocoels divided into two or three separate depths, with the deepest cavities being anterior. Large deep supra-neural concavities exist above the neural canals within the neural arch, and the bases of the centra are broad and flat, with less bone below the pleurocoel compared with *Ornithopsis*. BMNH R90 (Pl. 1, figs 5–6; Text-fig. 5A) comprises similar, less complete vertebrae than R89, having lower and longer centra. A juvenile centrum (BMNH R2524, Text-fig. 2) described by Hulke (1879) is also included with the paratypes.



TEXT-FIG. 2. *Eucamerotus foxi* sp. nov., paratype, BMNH R2524, juvenile dorsal vertebra. A, left lateral view; B, anterior view. From the Lower Cretaceous Wessex Formation of the Isle of Wight, $\times 0.5$.

It is similar to the adult forms, being smaller with pleurocoels proportionately larger and deeper, and occupying a larger surface area of the lateral centrum than in the adult. The opisthocoelian nature of the centrum is less well developed than in the adult.

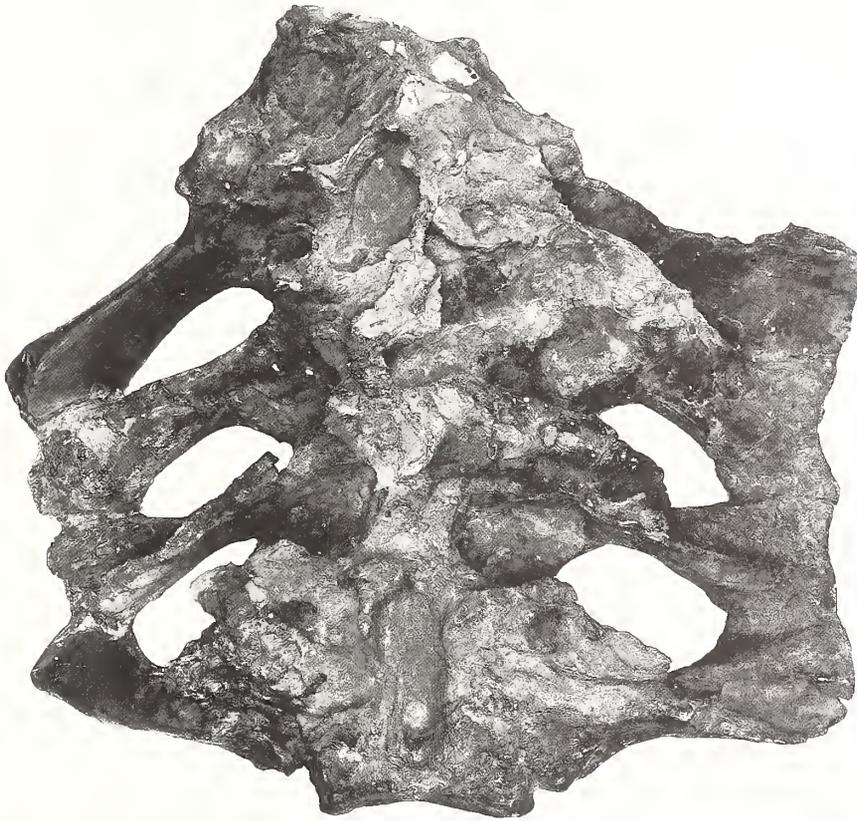
The brachiosaurid dorsal vertebral characteristics described by Riggs (1904) and Bonaparte (1986) are: more than ten vertebrae with simple, non-bifurcated neural spines which increase in length from sacrum to mid-dorsal region; large, elongated centra; axially elongated neural arch and base of spine. To this, McIntosh (1990a, 1990b) has not added familial dorsal vertebral characters, but noted that *Brachiosaurus* shows the highest neural arches and spines over the shoulders and the lowest over the sacrum. This corresponds with limb length. The pleurocoels are deep and clearly defined within a strongly opisthocoelous centrum. In *Eucamerotus*, the dorsals correspond with those features indicated for a single vertebra. The neural arches and spines are tall (especially in R89) which suggests a possible anterior presacral position. If this is correct, the absence of neural spine bifurcation precludes a camarasaurid and diplodocid origin, and the lack of posterior slope

to the neural spine excludes them from a titanosaurid origin. The top of the neural spine expands laterally and has a gently rounded crest, when viewed anteriorly, which is very similar to *Brachiosaurus*.

A newly discovered partial skeleton, currently being prepared at Sandown Museum (MIWG BP001) can be referred to *Eucamerotus foxi* on the basis of the dorsal vertebral morphology, which is identical to that in the paratypes established here. This represents a future opportunity to extend the description of this genus to skeletal elements other than the dorsal vertebrae.

BRACHIOSAURIDAE INCERTAE SEDIS

Parts of a pelvis and sacrum of a large brachiosaurid sauropod from the cliff at Lucombe Chine, Isle of Wight, were briefly described by Swinton (1946) and Stroh (1949). The sacrum (BMNH R12713) comprises four vertebrae (Text-fig. 3), and since most sauropods have five or more, this

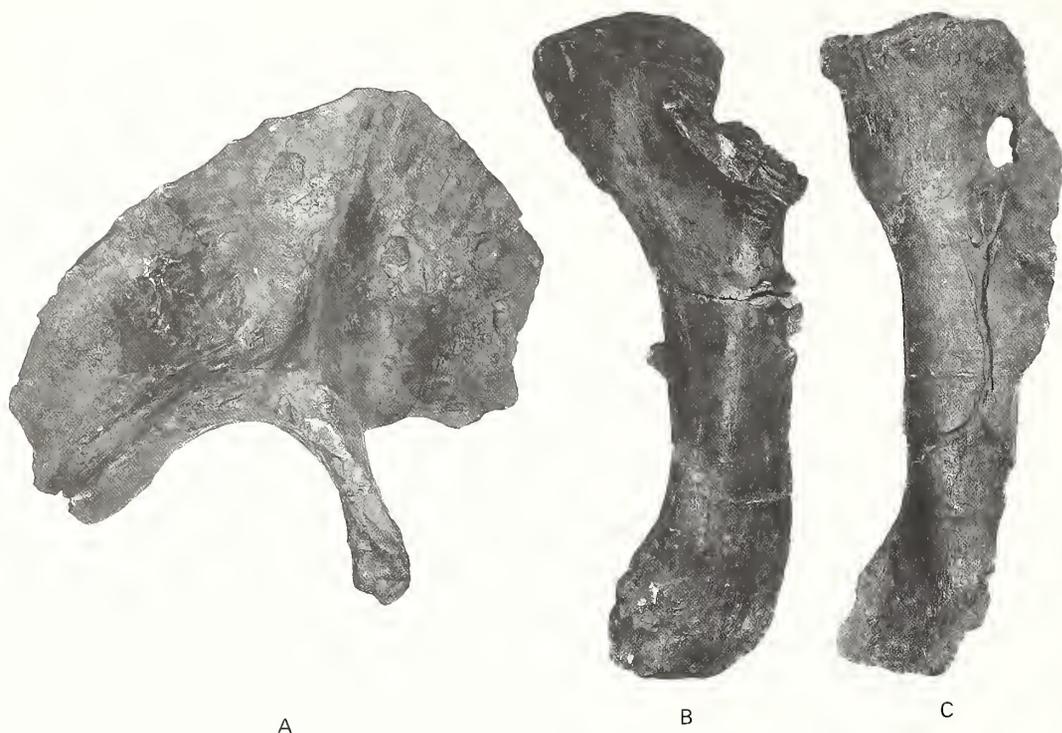


TEXT-FIG. 3. Sauropod sacrum, BMNH R12713, dorsal view, associated with the pelvic bones of Text-fig. 4. From the Cretaceous of Lucombe Chine, Isle of Wight, $\times 0.14$.

suggests that some vertebrae may be lost in this specimen. Four lateral sacral ribs extend from both sides and fuse distally at the ilio-sacral joint, but some of this joint has been artificially replaced.

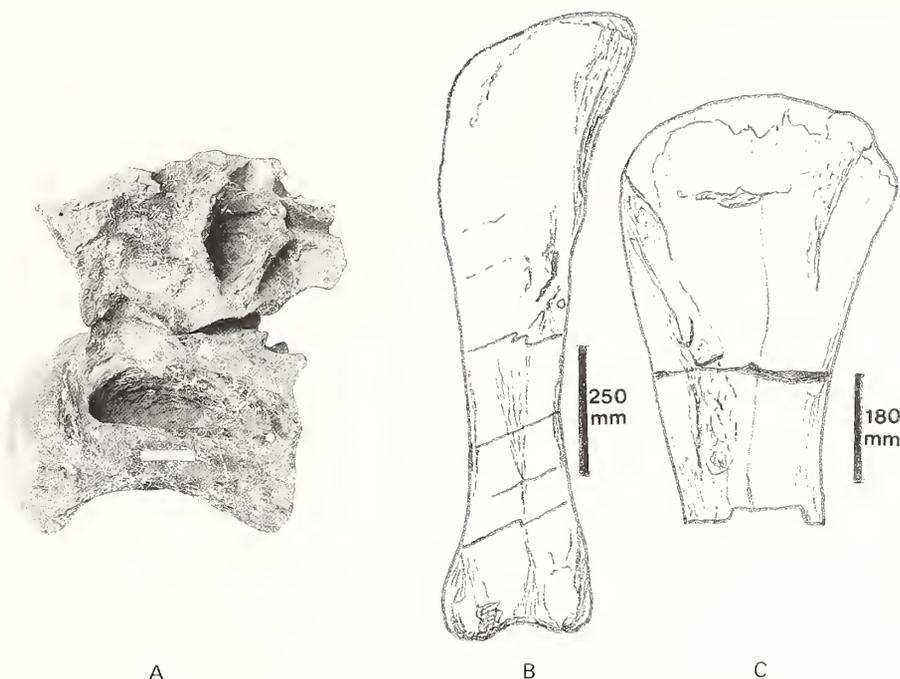
The associated pelvis consists of both ilia and both pubes. The two ilia are nearly complete (Text-fig. 4A) and are about 750 mm long and 630 mm deep. They are concave medially and slightly

convex laterally, with a ridge extending down centrally to the upper margin of the acetabulum. The iliac crest is high as in other brachiosaurid genera. The pubes are long, narrow and flat (Text-fig. 4B-C). Fox found a right ischium and pubis which together were described by Hulke (1882) as the



TEXT-FIG. 4. A, Sauropod right ilium, BMNH R12713, in lateral view; B, associated right pubis in medial view; C, associated left pubis in lateral view. From the Cretaceous of Luccombe Chine, Isle of Wight. All $\times 0.1$.

type specimen of '*Ornithopsis eucamerotus*' (BMNH R97). The pubis is slightly shorter than the Luccombe Chine specimen and is broader with a distinct rounded termination. The ischium, illustrated by Hulke articulated to the pubis, now consists of the proximal half only. I am unable to prove that this pubis and ischium are part of the same pelvis. Although Hulke gave a good description, he did not indicate if they were discovered together, and Fox left no evidence of their association *in situ*. The bones appear to be different in preservation and I consider them to be of separate origin. The addition of a second right ischium to the BMNH R97 assemblage confuses the picture further, and Lydekker (1888) catalogued one ischium as R97a. The name *Ornithopsis eucamerotus*, for which this is the type, is no longer valid, and the specimen is regarded as Brachiosauridae *Incertae Sedis*. A complete left femur (MIWG 6484; Text-fig. 5A) has a long slender shaft that narrows towards the distal epiphysis. The head is inclined obliquely upwards on broad trochanters and merges imperceptibly with the shaft rather than flattening at right angles to the shaft as it does in diplodocids. The fourth trochanter is placed about two-thirds up the length of the bone. It is possible that this femur may be part of the new partial skeleton (MIWG BP001, S. Hutt, pers. comm.). The head of a large right humerus (MIWG 5211; Text-fig. 5B) resembles those of brachiosaurids. It has a well preserved rounded articular end surface with a pronounced deltoid crest.



TEXT-FIG. 5. A, *Eucamerotus foxi* sp. nov. paratype dorsal vertebra, BMNH R90 in part, left lateral view, $\times 0.14$. B–C, Brachiosaurid sauropod; B, left femur, MIWG 6484, in posterior view, $\times 0.07$; C, proximal portion of a humerus, MIWG 5211, in anterior view, $\times 0.83$. All from the Lower Cretaceous of the Isle of Wight.

Taxonomic status of some British sauropods

Jurassic material attributed to the genus Ornithopsis. Delair (1959) indicated that sauropod remains from the Jurassic of Dorset were *Ornithopsis* but gave no supporting evidence for this. However, since the lectotype of *Ornithopsis* is a single dorsal centrum of Lower Cretaceous age and no Jurassic specimens are bones homologous with this lectotype, direct comparison and therefore referral is not possible. The name *Ornithopsis* is therefore confined at present to the Lower Cretaceous and all the Jurassic specimens listed by Delair (1959, pp. 81–83) are regarded as Brachiosauridae *Incertae Sedis* (McIntosh 1990a). These are: '*Ornithopsis humerocristatus*' Hulke, 1874 based on a humerus from the Kimmeridge Clay of Weymouth, Dorset (BMNH 44635); '*Ornithopsis manseli*' Lydekker, 1888 based on a humerus from the Kimmeridge Clay of Dorset (BMNH 41626); and '*Ornithopsis? leedsi*' Hulke, 1887 based on a proximal portion of a pubis from the Kimmeridgian of Weymouth, Dorset (BMNH 49165). '*Ornithopsis sp.*', based on a tooth from the Portland Stone of the Isle of Portland, Dorset (BMNH R5833), is regarded as Sauropoda *Incertae Sedis*.

The status of Pelorosaurus conybeari Mantell, 1850. *Ornithopsis* and *Eucamerotus* have been synonymized with the mainland genus *Pelorosaurus* by several authors (e.g. Romer 1966; Olshevsky 1978). McIntosh (1990a and pers. comm.) tentatively accepted the synonymy of all the English Lower Cretaceous brachiosaurs under *Pelorosaurus conybeari*, which he stated to be close to *Brachiosaurus* in most respects. However, the type of *Pelorosaurus* is a humerus which cannot be compared with dorsal vertebrae, or most of the other bones referred to the Brachiosauridae, and therefore the genera should be regarded as separate. *Pelorosaurus* is from the Tilgate Stone (Grinstead Clay) which is Valanginian and thus earlier than the Wealden Marls (Barremian) of the Isle of Wight. Between these two horizons, a hiatus occurs in the dinosaur faunas (Hauterivian) as

noted for the nodosaurs by Blows (1987). *Pelorosaurus conybeari* is probably best regarded as a *nomen vanum* as the type specimen is undiagnostic.

CONCLUSIONS

1. The binomen *Ornithopsis hulkei* can only be upheld for a single dorsal centrum, the lectotype (BMNH 28632) which is placed within the Brachiosauridae. *Ornithopsis* and *Eucamerotus* are therefore not synonymous.

2. All other specimens labelled as *Ornithopsis* are either 'Sauropoda *Incertae Sedis*' or are referable to the genus *Eucamerotus*. *Pelorosaurus conybeari* cannot safely be synonymized with Isle of Wight specimens.

3. *Eucamerotus* is regarded as brachiosaurid, with *E. foxi* sp. nov. established.

Acknowledgements. I am most grateful to Angela Milner and Sandra Chapman (Natural History Museum, London) and Steven Hutt (Museum of Isle of Wight Geology) for their help with the specimens in their care, to Andrew Milner (Birkbeck College, University of London) for his advice, and to John McIntosh for his comments on sauropods. Photographs are by courtesy of the Photographic Unit of the Natural History Museum, London.

REFERENCES

- BERMAN, D. S. and MCINTOSH, J. 1978. Skull and relationships of the Upper Jurassic sauropod *Apatosaurus* (Reptilia, Saurischia). *Bulletin of the Carnegie Museum of Natural History*, no. 8, 1–35.
- BLOWS, W. T. 1983. William Fox (1813–1881), a neglected dinosaur collector of the Isle of Wight. *Archives of Natural History*, **11**, 299–313.
- 1987. The armoured dinosaur *Polacanthus foxi* from the Lower Cretaceous of the Isle of Wight. *Palaontology*, **30**, 557–580.
- BONAPARTE, J. 1986. The early radiation and phylogenetic relationships of the Jurassic sauropod dinosaurs, based on vertebral anatomy. 247–258. In PADIAN K. (ed.). *The beginning of the age of dinosaurs*. Cambridge University Press, 378 pp.
- DELAIR, J. 1959. Mesozoic reptiles of Dorset. Part 2. *Proceedings of the Dorset Natural History and Archaeological Society*, **80**, 52–90.
- HUENE, F. von. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monographien zur Geologie und Palaentologie* **1**, viii + 1–361.
- HULKE, J. 1870. Note on a new and undescribed Wealden vertebra. *Quarterly Journal of the Geological Society, London*, **26**, 318–324.
- 1871. Appendix to a 'Note on a new and undescribed Wealden vertebra'. *Quarterly Journal of the Geological Society, London*, **28**, 36–37.
- 1874. Note on a very large saurian limb-bone adapted for progression upon land, from the Kimmeridge clay of Weymouth, Dorset. *Quarterly Journal of the Geological Society, London*, **30**, 16–17.
- 1879. Note (3rd) on *Eucamerotus* (Hulke), *Ornithopsis* (Seeley). *Quarterly Journal of the Geological Society, London*, **35**, 752–762.
- 1880. Supplementary note on the vertebra of *Ornithopsis* (Seeley) = *Eucamerotus* (Hulke). *Quarterly Journal of the Geological Society, London*, **36**, 31–34.
- 1882. Note on the os pubis and ischium of *Ornithopsis eucamerotus*. *Quarterly Journal of the Geological Society, London*, **38**, 372–376.
- 1887. Note on some dinosaurian remains in the collection of A. Leeds Esq., of Eyebury, Northamptonshire. Part I. *Ornithopsis leedsii*. *Quarterly Journal of the Geological Society, London*, **42**, 695–699.
- LINNAEUS, C. 1758. *Systema Naturae*. 10th ed. vol. 1. Salvi, Stockholm, 824 pp.
- LYDEKKER, R. 1888. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum. Part I. Containing the orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia and Pterosauria*. British Museum, London, xxviii + 309 pp.
- 1889. Note on some points in nomenclature of fossil reptiles and amphibians with preliminary notices of two new species. *Geological Magazine*, (3), **6**, 325–326.
- 1892. Note on two dinosaurian foot bones from the Wealden. *Quarterly Journal of the Geological Society, London*, **47**, 375–376.

- MANTELL, G. 1850. On the *Pelorosaurus*; an undescribed gigantic terrestrial reptile, whose remains are associated with those of the *Iguanodon* and other saurians in the strata of the Tilgate Forest, in Sussex. *Philosophical Transactions of the Royal Society, London*, **140**, 379–390.
- MARSH, O. C. 1878. Principal characters of American Jurassic dinosaurs. Part 1. *American Journal of Science*, **3**, **16**, 411–416.
- MCINTOSH, J. 1990a. Sauropoda. 345–401. In WEISHAMPEL, D. D., DODSON, P. and OSMOLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, California, 733 pp.
- 1990b. Species determination in sauropod dinosaurs with tentative suggestions for their classification. 53–69. In CARPENTER, K. and CURRIE, P. (eds). *Dinosaur systematics: approaches and perspectives*. Cambridge University Press, 318 pp.
- MELVILLE, A. 1849. Notes on the vertebral column of the *Iguanodon*. *Philosophical Transactions of the Royal Society, London*, **139**, 285–300.
- OLSHEVSKY, G. 1978. The Archosaurian Taxa (excluding the Crocodylia). *Mesozoic Meanderings* **1**, 1–50.
- OWEN, R. 1842. Report on British fossil reptiles. Part II. *Report of the British Association of the Advancement of Science*, XI, 60–204 (1841).
- 1875. Monograph of the Mesozoic Reptilia. Part 2 – *Bothriospondylus magnus*. *Palaeontographical Society Monograph*, **29**, 15–26.
- 1876. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Supplement 7. *Palaeontographical Society Monograph*, **30**, 1–7.
- RIDE, W. D. L., SABROSKY, C. W., BERNARDI, G. and MELVILLE, R. V. 1985. *International code of zoological nomenclature, 3rd edition*. University of California Press, Berkeley, California, 338 pp.
- RIGGS, E. 1904. Structure and Relationships of opisthocoelian dinosaurs. Part 2: the Brachiosauridae. *Field Columbian Museum Publication* 94, *Geological Series*, **2**, 229–248.
- ROMER, A. S. 1966. *Vertebrate paleontology* (3rd edition). University of Chicago Press, 468 pp.
- SEELEY, H. G. 1870. On *Ornithopsis*, a gigantic animal of the Pterodactyl kind from the Wealden. *Annals and Magazine of Natural History*, (4), **5**, 279–283.
- 1888. On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society, London*, **43**, 165–171.
- STROH, F. 1949. An Isle of Wight Dinosaur. *Proceedings of the Isle of Wight Natural History and Archaeological Association*, **4**, 93–94.
- SWINTON, W. 1946. An Isle of Wight Dinosaur. *Illustrated London News*, **209**, 278.

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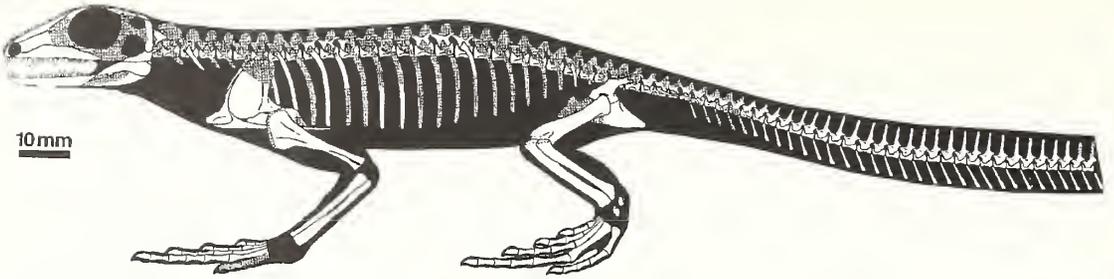
A NEW DIAPSID REPTILE FROM THE UPPERMOST CARBONIFEROUS (STEPHANIAN) OF KANSAS

by MICHAEL deBRAGA and ROBERT R. REISZ

ABSTRACT. Diapsids represent one of the most diverse lineages within Amniota, yet, until recently, their Carboniferous record was restricted to one taxon from a single locality near Garnett, Kansas. Accordingly, diapsids were thought not to have undergone the degree of evolutionary radiation which has been attributed to other Carboniferous amniotes. The description of *Spinoaequalis schultzei* gen. et sp. nov. from Upper Carboniferous deposits at Hamilton Quarry, Kansas, indicates that it is closely related to araeoscelidians and provides the first evidence for the diversification of diapsids within the Carboniferous. In addition, *Spinoaequalis* possesses a suite of autapomorphies, most notably to the tail, which display evidence for the earliest known aquatic specialization among amniotes.

DIAPSIDA is one of the most successful groups of amniotes (Carroll 1988) and includes three of the four orders of extant reptiles (crocodiles, lizards, and snakes), dinosaurs including birds, flying reptiles, many aquatic taxa, and other, lesser known, extinct groups. Although diapsids are represented by a long, rich fossil record, little is known of their early history. Araeoscelidia, universally recognized as containing some of the earliest recognized members within Diapsida (Reisz 1977, 1981; Benton 1985; Carroll 1988; Gauthier *et al.* 1988; Evans 1988; Laurin 1991) is represented by two well known genera *Petrolacosaurus* and *Araeoscelis*, and two poorly known forms *Zarcasaurus* Brinkman *et al.*, 1984 and *Kadliosaurus* Credner, 1889. These taxa are regarded as being representative of the Bauplan from which advanced diapsids evolved (Reisz 1981; Carroll 1988). In addition, due in part to the homogenous morphology of the known members of this clade, it is considered an interesting side branch in diapsid evolution, but one that did not undergo any significant morphological differentiation during its tenure in the Carboniferous. Consequently, increased diapsid diversity is generally thought to coincide only with the appearance of the specialized eosuchians *Claudiosaurus* and *Coelurosauravus* and neodiapsids in the Upper Permian (Laurin 1991).

Reisz (1988) briefly introduced two new diapsids from the Upper Carboniferous Hamilton Quarry of Kansas. He suggested that one of these diapsids may be closely related to araeosceloids (University of Kansas Vertebrate Palaeontology collection KUV 12484), remarking that the limbs possessed similar propodial/epipodial ratios. He chose, however, not to name or classify the specimen formally, but remarked that the unusual caudal anatomy of this amniote was suggestive of aquatic affinities. Further preparation and detailed inspection of its anatomy has permitted a nearly complete skeletal reconstruction (Text-fig. 1). Furthermore, a brief phylogenetic analysis provides strong evidence that this small reptile is indeed a diapsid and the sister taxon to Araeosceloidea. A detailed comparison with later, better known aquatic reptiles (Russell 1967; Currie 1981a; Frey 1982; deBraga and Carroll 1993) has been undertaken to assess its anatomical potential for aquatic propulsion (Hildebrand 1982).



TEXT-FIG. 1. Reconstruction of *Spinoaequalis schultzei* gen. et sp. nov. in lateral view; Hamilton Quarry, Greenwood County, Kansas; Virgilian Series (Stephanian of Europe), Upper Pennsylvanian. Shaded area represents missing data.

SYSTEMATIC PALAEOLOGY

DIAPSIDA Osborn, 1903

ARAEOCELIDIA Williston, 1913

Emended diagnosis. Diapsid reptiles exhibiting long limbs with propodial/epipodial ratios 1:1; anterior margin of scapula slanted posteriorly; and femoral shaft exceeding width of humeral shaft by 50 per cent.

Genus SPINOAEQUALIS gen. nov.

Spinoaequalis schultzei sp. nov.

Text-figures 1-5

Derivation of name. From the Latin *spina* (spine) and *aequalis* (symmetry) referring to the equal length of caudal neural and haemal spines; specific designation in honour of Dr Hans-Peter Schultze, in recognition of his work on Palaeozoic vertebrates.

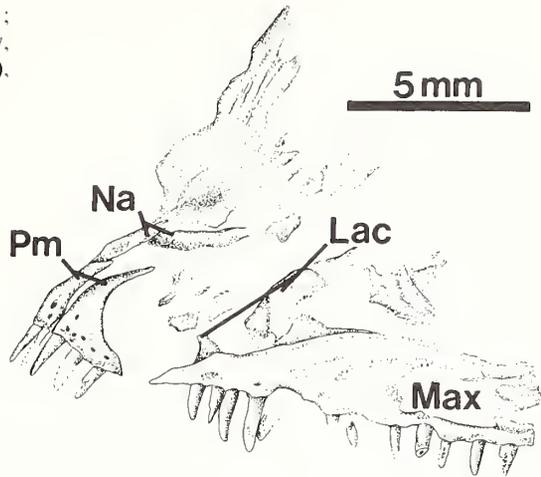
Holotype. KUVF 12484, a nearly complete, articulated, immature individual with a poorly preserved skull, missing the distal portion of the tail. The specimen was collected in three pieces: one containing the snout region, a second containing the rest of the skull and most of the body, and a third piece which contains the hindlimbs, pelvic region, and the preserved portion of the tail.

Type Horizon and Locality. Calhoun Shale, Shawnee Group, Virgilian Series (Stephanian of Europe), Upper Pennsylvanian; Hamilton Quarry near Hamilton, Greenwood County, Kansas.

Diagnosis. A small diapsid reptile distinguished by the following autapomorphies: ventral process of squamosal narrow; trunk ribs holocephalic; caudal neural spines distal to eleventh caudal vertebra elongate, at least 50 per cent. taller than those of proximal caudals; haemal spines are equal in length to the caudal neural spines of same vertebrae; haemal spines increase in length posteriorly; haemal spines with slight distal expansion; caudal centra with a length to height ratio approaching 1:1; caudal neural arches saddle-shaped; transverse processes absent from caudal vertebrae; interclavicle long approaching the length of eight dorsal vertebrae; and acetabulum sub-circular in outline.

Description. The specimen was collected originally as three separate sections, and as a result, it cannot be illustrated as a single figure. Therefore, each block is figured separately (Text-figs 2-4). The smallest piece (Text-fig. 2) contains paired premaxillae, a poorly preserved lacrimal, fragments of what are interpreted as the

TEXT-FIG. 2. *Spinoaequalis schultzei* gen. et sp. nov.; KUVF 12484; Hamilton Quarry, Greenwood County, Kansas; Virgilian series (Stephanian of Europe), Upper Pennsylvanian; anterior portion of snout.



nasals, and the left maxilla. Of the two larger pieces, one (Text-fig. 3) has suffered damage over much of the exposed surface (corresponding to the specimen's dorsal surface) and has, therefore, been embedded in bioplastic and prepared from its ventral side. Most of the palate, the right maxilla in lateral view, and the medial half of the posterior portion of the left maxilla, the left prefrontal, the paired frontals in ventral view, and a portion of the right parietal are all preserved in this piece. In addition, the block contains what is left of the cheek region and portions of both lower jaws as well as most of the remainder of the skeleton. The second large piece (Text-fig. 4) which contains the remains of the pelvis, a complete left hindlimb and foot, the right foot, and the preserved region of the tail was prepared from the left side and presents the opposite view from that of the other large piece containing most of the skeleton.

The premaxilla presents the typical diapsid configuration, as the dorsal processes of both bones, as preserved, are quite slender (Text-fig. 2). This agrees with the configuration in both *Petrolacosaurus* and *Araeoscelis* as well as in eosuchians (personal observation) and probably represents a diapsid synapomorphy. Captorhinids, *Protorothyris* and *Paleothyris* possess a comparably broad premaxillary dorsal process which occupies nearly the entire dorsal surface of the snout tip (Carroll 1969; Clark and Carroll 1973; Heaton 1979). The tooth-bearing portion of the premaxilla has portions of three teeth preserved, of which the first is a simple, slender peg. Five teeth are described in *Petrolacosaurus* (Reisz 1981), *Araeoscelis* (Reisz *et al.* 1984), and *Paleothyris* (Carroll 1969). The reduced number in *Spinoaequalis* may be an autapomorphy of this taxon, but the state of preservation of the tooth-bearing region of the premaxilla is not sufficient to draw a definite conclusion.

The maxilla (Text-figs 2, 5) is similar to the configuration in *Paleothyris* and the araeosceloids *Petrolacosaurus* and *Araeoscelis*. There is a caniniform region, but the caniniform teeth are not much larger than the first premaxillary tooth. The teeth are very slender and are quite similar to those in *Petrolacosaurus*.

The plate-like frontals (Text-fig. 5) have a large orbital margin, and are constricted above the orbits. This latter condition is present in araeosceloid and eosuchian diapsids and represents a synapomorphy of these taxa (Laurin and Reisz 1995).

Much of the posterior half of the cheek (Text-fig. 5) is preserved and the posteroventral border of the lower temporal fenestra is discernible. The configuration differs somewhat from that seen in *Petrolacosaurus* in that the post-temporal bar is composed of a slender ventral process of the squamosal and a shorter dorsal process of the quadratojugal. It appears that the lower temporal fenestra is located farther posteriorly, or is relatively larger in *Spinoaequalis* than in *Petrolacosaurus*. However, the posteroventral margin of the lower temporal fenestra has never been established confidently in *Petrolacosaurus* (Reisz 1981, text-fig. 2).

A sliver of bone, visible directly behind the squamosal, may represent the quadrate. However, the preservation of this region of the skull is poor, and this identification is uncertain.

The palate is only partially exposed. The left pterygoid is visible in ventral aspect and is essentially similar to that of araeosceloids except that the transverse flange is not directed anterolaterally and hence retains the primitive transverse orientation (Text-fig. 5). No other palatal elements are visible except for a small portion of the ectopterygoid. The posterior border of the suborbital fenestra can be detected along the anterolateral edge of the ectopterygoid.



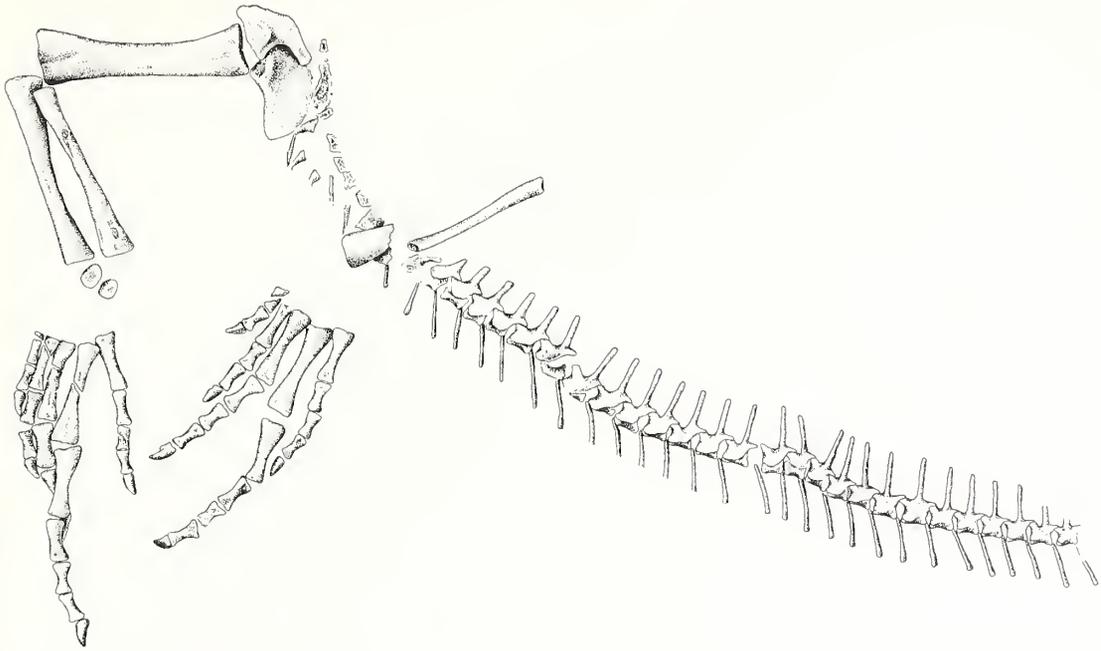
TEXT-FIG. 3. *Spinoaequalis schultzei* gen. et sp. nov.; KUVV 12484; Hamilton Quarry, Greenwood County, Kansas; Virgilian Series (Stephanian of Europe), Upper Pennsylvanian; ventral aspect of skeleton minus caudal region, $\times 1$.

The braincase and occiput are only incompletely preserved. The exoccipitals are preserved, however, and can be seen as isolated elements. The ventral and lateral borders for the foramen magnum can be seen clearly on the left exoccipital. The posterior margin of the parasphenoid lying behind the overlying posterior half of the lower jaw resembles that of the araeosceloid *Petrolacosaurus* in being concave along its posteriomedial margin. This derived condition may suggest an autapomorphy for Araeoscelidia or perhaps a more inclusive diapsid synapomorphy. This concavity of the parasphenoid exposes the basioccipital to a greater degree than that which is seen in *Paleothyris* (see Carroll 1969, text-fig. 4) or other captorhinomorphs (Clark and Carroll 1973). In these taxa a posteriorly directed flange of the parasphenoid overlies the basioccipital ventrally. A small bone, partially covered by the basioccipital, may represent the opisthotic (Text-fig. 5).

The stapes is a small, robust element (Text-fig. 5) that does not differ in any significant way from the stapes of other early amniotes. The perforating foramen is present and the large footplate suggests a supportive rather than an auditory role for this element in *Spinoaequalis*.

The mandibles are partially preserved, with the nearly complete left jaw ramus exposed medially and the posterior half of the right jaw ramus exposed in lateral view. The generally slender configuration of the lower jaw is quite similar to that found in *Petrolacosaurus*. This slender configuration is certainly the primitive condition for Araeoscelidia, and differs from the much more robust jaws found in *Araeoscelis* (Reisz *et al.* 1984).

Twenty-two presacral vertebrae are visible in *Spinoaequalis* (Text-fig. 3). There is room for an additional four vertebrae within the column making the probable count twenty-six. *Petrolacosaurus* is reconstructed as having twenty-six presacrals (Reisz 1981), but *Araeoscelis* has a long presacral series of twenty-nine vertebrae (Reisz *et al.* 1984). Most of the presacral series in *Spinoaequalis* is exposed only in ventral aspect. Although the bases of the arches can be seen in some of the mid-dorsals and on the axis, little detail can be observed.

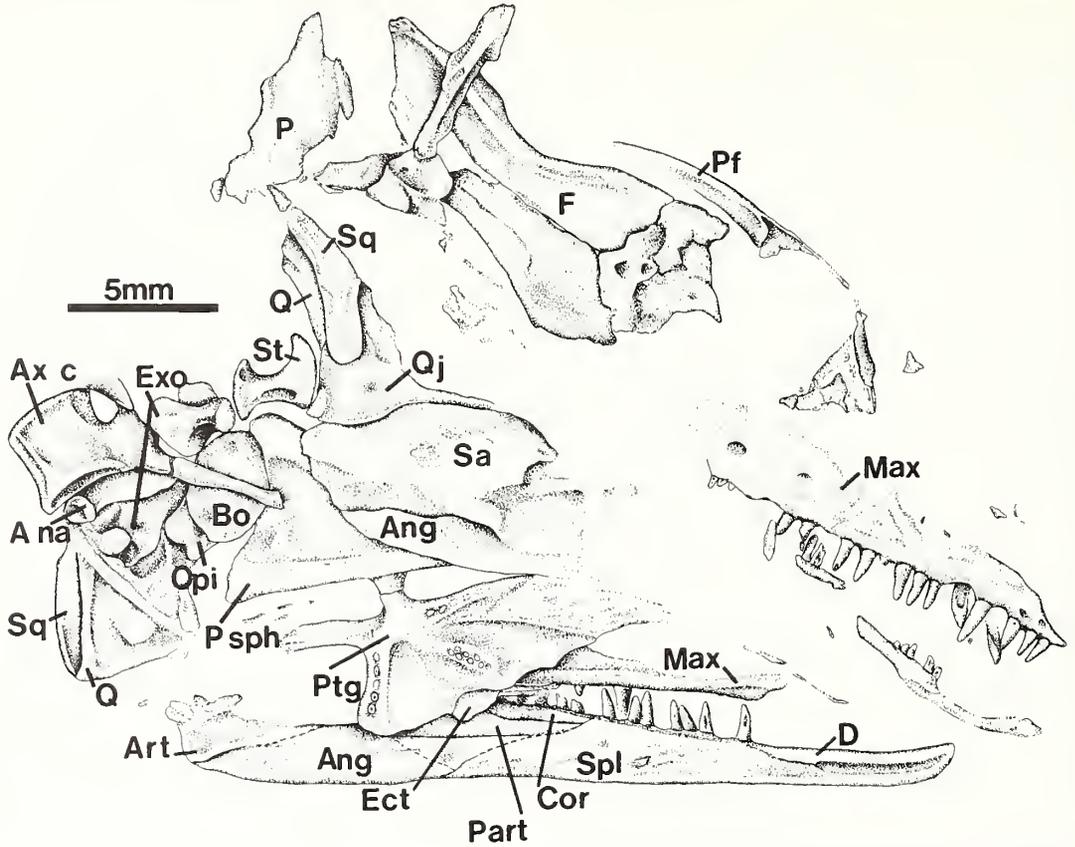


TEXT-FIG. 4. *Spinoaequalis schultzei* gen. sp. nov.; KUPV 12484; Hamilton Quarry, Greenwood County, Kansas; Virgilian Series (Stephanian of Europe), Upper Pennsylvanian; hindlimb and caudal region, $\times 1.3$.

The atlantal neural arch (Text-figs 3, 5) is preserved but can be seen only in partial internal aspect. Except for the neural spine, the axis is well preserved. The axial centrum is keeled ventrally, but the keel is not as strongly pronounced as in araeosceloids. In addition, unlike all other known araeoscelidians, the cervical centra of *Spinoaequalis* are not appreciably longer than those of the dorsal series. Two cervical ribs are preserved and are associated with the axis and third cervical vertebra. Unfortunately these rib heads are too poorly preserved to determine whether they are dichococephalic or holocephalic. Articular surfaces for the trunk ribs appear to be composed of a single facet and are located directly below the anterior zygapophysis on the respective neural arch. Holocephalous trunk rib heads would represent an autapomorphy of *Spinoaequalis*. Intercentra are visible throughout the presacral series as in most early amniote groups.

The sacral series is not preserved and the first eight caudals are very poorly preserved (Text-fig. 4). Beyond this region, twenty-six well exposed caudals are present. The remainder of the tail was lost during excavation. In strong contrast to the condition seen in araeosceloids and most other amniotes, where the caudal neural spines get progressively shorter and eventually virtually disappear, along the length of the tail (Reisz 1981, text-fig. 1), the caudal neural spines of *Spinoaequalis* (Text-figs 1, 4) increase in height posteriorly: the spines increase dramatically in height from the tenth caudal (second vertebrae of the last twenty-six) to about the fifteenth and then remain tall, increasing slightly to the twenty-eighth caudal, beyond which there is no noticeable increase in neural spine height for the remainder of the preserved portion of the tail. In addition, in other Permo-Carboniferous amniotes, the haemal spines are generally quite long at the base of the tail, and decrease rapidly in length posteriorly. In most cases the decrease in length is such that distinct haemal spines are absent by the middle of the caudal series. The opposite occurs in *Spinoaequalis*, where the haemal spines are shortest at the base of the tail, and then steadily increase in length posteriorly, remaining long throughout the preserved portion of the tail and matching the height of the neural spines. The haemal spines are slightly expanded distally, but this expansion is only very weakly developed, and does not in any way approach the condition seen in the eosuchian *Hovasaurus* (Currie 1981a). In most other amniotes, including *Petrolacosaurus*, the haemal spines actually taper distally.

The caudal vertebrae also exhibit well developed neural arches with very tall zygapophyses, together formed into a saddle-shaped structure (Text-fig. 4). This unusual appearance is probably the result of the dorsal expansion of the zygapophyseal articulating facets.



TEXT-FIG. 5. *Spinoaequalis schultzei* gen. et sp. nov.; KUVF 12484; Hamilton Quarry, Greenwood County, Kansas; Virgilian Series (Stephanian of Europe), Upper Pennsylvanian. Magnification of skull region from Text-figure 3.

Transverse processes are absent in *Spinoaequalis* throughout the preserved portion of the tail (ninth to thirty-fourth vertebrae). The combination of rudimentary transverse processes along with tall spines (described above) results in a tail the transverse width of which does not exceed 25 per cent. of its total height.

The caudal centra are unspecialized, but, in combination with the well developed neural arches, result in the combined height of the arch and centrum approaching their antero-posterior length, a condition unknown in any other Carboniferous amniote.

The pectoral components of the appendicular skeleton of *Spinoaequalis* are well preserved (Text-figs 1, 3) and, in most respects, similar to those of araeosceloids. The interclavicle resembles that of *Petrolacosaurus* except that it is relatively longer. Its length occupies seven and one half dorsal vertebrae and is 25 per cent. longer than the humerus. In araeosceloids, such as *Petrolacosaurus* and *Araeoscelis*, the interclavicle is equal to the length of only five and one half dorsal vertebrae and is equal to the humerus in length. The elongate interclavicle may be the result of the juvenile nature of the specimen, for, as demonstrated by Currie (1981a), interclavicular length is negatively allometric relative to dorsal vertebral length.

The clavicles are also preserved and appear unremarkable in comparison with those of other early tetrapods. The scapulocoracoid is ossified as two separate elements. On the left side of the specimen (Text-fig. 3), the anterior-most element supports the glenoid surface along its postero-distal margin. Although the ossification of this region is poor, a large, well developed supraglenoid buttress is visible. This process is similar to that present in araeosceloids and partly conceals the coracoid foramen which lies directly below. The overall size of the scapula (height) is less than that of an araeosceloid of equivalent size. This may be related to its juvenile nature or it may represent an autapomorphy of this taxon. The reconstruction (Text-fig. 1) has been drawn with the scapula possessing typical araeosceloid proportions. Very little else of consequence can be identified,

although the anterior margin of the right scapulocoracoid appears gently convex, so that in a reconstructed individual (Text-fig. 1), this margin would appear to be orientated posteriorly. This configuration is apparent in all araeosceloids (Reisz 1981; Reisz *et al.* 1984) and differs from the tall straight anterior scapular margin present in other Palaeozoic amniotes (Carroll 1969).

The forelimb (Text-fig. 3) is distinguished by its elongate and slender configuration. The distal ends of the limb elements are not preserved and neither are any of the carpal ossifications. An entepicondylar foramen is not visible but a groove located along the postero-distal margin of the humerus presumably represents the proximal limits of this structure. Given the low degree of ossification in other parts of this skeleton, it is likely that the limbs are equally underdeveloped and, therefore, lack ossified ends and their associated structures. The manus is only preserved on the left side and is incomplete, except for the third and fourth digits which have a typically primitive phalangeal count of four and five respectively.

The pelvic girdle has only the right ilium and ischium preserved (Text-fig. 4). The elements are unremarkable and hence differ little from the typical early amniote configuration. The ilium has a strongly developed posteriorly directed iliac blade and contributes to most of the acetabular surface. The ischium forms the remainder of the acetabulum. Unlike *Petrolacosaurus* and other Palaeozoic amniotes, such as *Paleothyris*, the acetabulum is not anteroposteriorly long but nearly circular. This circular configuration was described by Laurin (1991) as an eosuchian synapomorphy. In *Spinoaequalis*, it may simply represent the lack of complete ossification or it may represent a unique condition that may reflect some modification in the motion of the hindlimb.

The hindlimbs are virtually complete, with the right limb best preserved. The femur and crus are nearly equal in length and as such are typical of araeosceloids. The femoral shaft is much more robust (nearly 50 per cent. thicker) than the humeral shaft. This condition is also present in araeosceloids and the eosuchian *Apsisaurus* (Laurin 1991). A robust femur is absent in *Paleothyris* and captorhinids and it may, therefore, represent a diapsid synapomorphy. As in the forelimb, the hindlimb is incompletely ossified. The articulating ends of the limb bones are not preserved and most of the tarsus is missing, with the exception of two small circular structures, best interpreted as the astragalus and calcaneum. The pes is complete and possesses the typically primitive count of 2, 3, 4, 5, 4. As in araeosceloids and unlike other Palaeozoic amniotes, the first metatarsal is much less than half the length of the fourth metatarsal (Text-fig. 3).

DISCUSSION

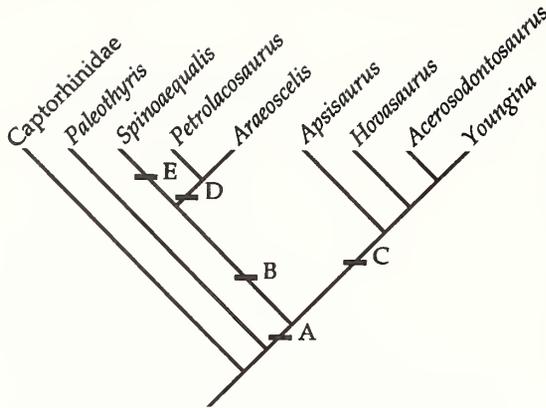
Phylogenetic position

Phylogenetic analysis of *Spinoaequalis* indicates that it is a basal diapsid reptile closely related to the oldest known diapsid, *Petrolacosaurus kansensis*. This phylogenetic interpretation is based on data evaluated below.

A total of nine taxa including two outgroups were used in this analysis. Out-group selection is based on the well established sister-group relationship between captorhinids and *Paleothyris* to Diapsida (Heaton and Reisz 1986; Laurin 1991; Laurin and Reisz 1995). Anatomical data for the out-groups was taken from direct observation and from Carroll (1969) and Heaton (1979). The in-group includes the two best known araeosceloids *Petrolacosaurus* (Reisz 1981) and *Araeoscelis* (Reisz *et al.* 1984), the eosuchians *Apsisaurus* (Laurin 1991) and *Hovasaurus* (Currie 1981a), and the younginiformes *Youngina* (Gow 1975; Carroll 1981; Currie 1981b) and *Acerosodontosaurus* (Currie 1979).

Fifty characters (Appendices 1 and 2) are used in the present analysis, most of which are taken from Laurin (1991) and Laurin and Reisz (1995). However, some of the characters (character numbers below refer to those in Appendices 1 and 2) have been reinterpreted (nos 33, 42) and a few are original (nos 1, 13, 38, 44, 45, 46, 47, 49). The analysis was performed on a Macintosh Quadra 800 computer using the branch-and-bound algorithm of PAUP 3.1.1, which finds the most parsimonious trees (Swofford 1993). All characters were left unordered and subjected to DELTRAN optimization, which tends to minimize synapomorphies at any given node.

Only one most parsimonious tree (Text-fig. 6) was found requiring seventy steps to resolve and with a consistency index of 0.742 excluding uninformative characters. The cladistic analysis supports the monophyly of Diapsida and the nested sister-group relationship between *Spinoaequalis* and Araeosceloidea to Eosuchia (Younginiformes), as most recently defined by Laurin (1991) and



TEXT-FIG. 6. Cladogram of basal diapsid interrelationships. Ambiguous characters are denoted by an asterisk, reversals by a minus sign, and in the case of a multi-state character, the derived state is placed in parentheses. Nodes assigned a letter in the figure are followed here by the character numbers referred to in Appendix 1: Node A (Diapsida) 1, 5, 7, 12, -16*(1), 17, 24, 37 and 41; Node B (Araeoscelidia) 27, 33 and 38*; Node C (Eosuchia) 13, 32 and 39; Node D (Araeosceloidea) 15, 18*, 19, 20, 21*, 22*, 28*, 36* and 40*; and Node E (*Spinoaequalis schultzei*) 11, 23, 25, 35, 44, 45, 46, 47, 48, 49 and 50.

Laurin and Reisz (1995). In addition, the sister-group relationship between *Spinoaequalis* and Araeosceloidea, coupled with their shared derived appendicular anatomy, allows for the re-establishment of the higher taxon Araeoscelidia (Williston 1913) to accommodate these Palaeozoic diapsid taxa.

For brevity we will not discuss all of the character states diagnosing the various nodes, but, as a result of the addition of *Spinoaequalis*, will consider only those changes that have revised the diagnosis or resolved critical issues of ambiguity for Diapsida and Araeosceloidea. Given the highly specialized anatomy of *Spinoaequalis*, a more detailed discussion of the specific autapomorphies diagnosing this taxon will be considered in the section on lifestyle interpretation.

Diapsida is universally recognized as a monophyletic group but some specific issues concerning character optimization have been problematic. Reisz *et al.* (1984) determined that the presence of a lower temporal fenestra was ambiguous for Diapsida and could have evolved twice. This interpretation was based on the absence of a lower temporal fenestra in *Araeoscelis*. However, the presence of a lower temporal fenestra in *Spinoaequalis* confirms, for the first time, the derived character as an unambiguous synapomorphy for Diapsida with a reversal in *Araeoscelis*.

Araeosceloidea, as most recently defined by Laurin (1991), is diagnosed by eight autapomorphies (numbers preceding character refer to character number in Appendix 1): 18 – dorsal and sacral neural arches shallowly excavated; 19 – cervical centra with sharp ventrally placed keel; 20 – cervical centra elongate; 21 – mammillary processes present on dorsal neural spines; 22 – accessory processes on cervical ribs present; 28 – enlarged coracoid process for triceps musculature; 33 – propodial/epipodial ratios 1:1, 36 – paired, large pubic tubercles present. One additional unambiguous autapomorphy has been more recently recorded by Laurin and Reisz (1995): 15 – transverse flange of pterygoid orientated anterolaterally. Therefore, until the present study, a total of nine autapomorphies diagnosed the clade. Of the nine autapomorphies only one (no. 5 above) was ambiguous.

The present analysis supports the monophyly of Araeosceloidea but revises the diagnosis by excluding one character (no. 33) and creating ambiguity for five of the remaining eight characters: nos 18, 21, 22, 28, and 36. This ambiguity arises due to the incomplete preservation of *Spinoaequalis* which precludes character state determination for the five characters. Therefore, from the original literature, only three unambiguous characters (nos 15, 19, and 20) remain to diagnose Araeosceloidea. One additional character (no. 40) is added as a result of this present analysis, but it is ambiguous. The higher level taxon Araeoscelidia, as resurrected here, is now diagnosed by three characters, only one (no. 38) being ambiguous: 27 – scapular blade slanted posteriorly; 33 – propodial/epipodial ratios 1:1; and 38 – femoral shaft width exceeds width of humeral shaft by 50 per cent. The ambiguity for character no. 38 stems from its presence in the derived state in the eosuchian *Apsisaurus*. The character may have arisen independently in araeoscelidians and

Apsisaurus or it may be a diapsid synapomorphy with a reversal in Neodiapsida. Of the three characters, nos 27 and 38 are new to this study and no. 33 is a former araeosceloid synapomorphy.

The confident identification of *Spinoaequalis* as an araeoscelidian has obviously affected the identification, if not the composition, of diapsids and araeoscelidians. In addition, the presence of *Spinoaequalis* along with an additional as yet undescribed diapsid from the same locality (Reisz 1988), suggests that diapsids were more diverse in the Pennsylvanian than was previously believed. These finds alter the prevailing view that diapsids diversified only around the Permo-Triassic boundary. Instead, diapsid evolutionary radiation may have been well under way during the Carboniferous, very soon after the appearance of its first recognized member.

Lifestyle interpretation

The Hamilton quarry of south-eastern Kansas represents a palaeovalley where rapid sediment deposition occurred in a marine setting (Feldman *et al.* 1993). The fauna is dominated by aquatic vertebrates, including hundreds of superbly preserved small acanthodian fish. Only a handful of fully terrestrial amniote specimens have been found, and most of them are fragmentary and disarticulated, suggesting that their presence is the result of postmortem displacement (Feldman *et al.* 1993). In strong contrast, the delicately constructed skeleton of *Spinoaequalis* has been preserved in articulation. The unfinished articulating surfaces of the long bones, the lack of tarsal and carpal ossification, and the exploded nature of the cranium attest to the immaturity and delicacy of this specimen, suggesting that this individual was not subjected to postmortem transport, but may have been a member of this community. Therefore, the possibility that *Spinoaequalis* represents an aquatic, or at the very least a semi-aquatic, amniote must be considered. The juvenile nature of the specimen makes evaluation of certain parts of the skeleton, for example some of the appendicular components, difficult. However, there is extensive evidence for aquatic affinities in the tail: 1, caudal neural and haemal spines increase in length posteriorly; 2, distal expansion of haemal spines, presumably to strengthen and resist tensile forces applied by powerful lateral flexors of tail; 3, loss of transverse processes throughout most of caudal series; 4, saddle-shaped neural arches with tall zygapophyses to restrict dorso-ventral flexion of tail and hence improve its sculling efficiency; and 5, vertebral bodies (centrum and neural arch) anteroposteriorly compressed, resulting in a length to height ratio approaching 1:1. Most of the features described above are common to aquatic diapsids as documented in the available literature (Russell 1967; Currie 1981a; Carroll 1988; Carroll and deBraga 1992; deBraga and Carroll 1993) and will be briefly discussed below.

The unusual configuration of the neural and haemal spines has been alluded to above, but the significance of this arrangement is that, among tetrapods, only aquatic or semi-aquatic organisms possess the characteristic increase in both neural and haemal spine height from base to at least mid-caudal length (deBraga and Carroll 1993). In addition, distal expansion of the haemal spines is also common to taxa that have been interpreted as having an aquatic or semi-aquatic lifestyle including, in addition to the amniote *Hovasaurus*, the anamniote *Archeria* (Holmes 1989). The haemal spine expansion in *Spinoaequalis*, although not as strongly developed as in *Hovasaurus* (Currie 1981a), certainly exhibits an incipient condition that further supports the suggestion that the tail was modified to enable an aquatic existence.

The absence of transverse processes beyond the most proximal portion of the tail (usually around the tenth caudal vertebrae) is well documented for aquatic taxa such as mosasaurs (deBraga and Carroll 1993) and *Hovasaurus* (Currie 1981a). Transverse processes are also absent in *Spinoaequalis*, whereas they remain well developed in non-aquatic amniotes throughout most of the caudal series. The loss of transverse processes is probably the result of the need to compress the tail so that it might function more effectively as a sculling organ.

The unusual saddle-shaped neural arches result from the elaboration of tall zygapophyses. Presumably, this zygapophyseal configuration would tend to resist flexion along the dorso-ventral axis of the tail, thereby improving its effectiveness as a sculling organ. In aquatic taxa, tall, well-developed zygapophyses are generally present only on the anterior-most caudals, where much of the muscular stress would be imparted during lateral flexion of the tail (Russell 1967; Carroll and

deBraga 1992; deBraga and Carroll 1993). In aquatic reptiles, such as *Hovasaurus* (Currie 1981a) and mosasaurs, the absence of well developed zygapophyses beyond the most proximal region of the tail coincides with the presence of anteroposteriorly-expanded neural spine bases. These accessory articulations serve to resist vertebral dislocation in the absence of functional zygapophyses. The absence, in *Spinoequalis*, of accessory articulations may explain the need to maintain well-developed zygapophyses beyond the most proximal region of the tail. As in crocodiles (Frey 1982), it is possible that modifications to the caudal musculature may have also served to stabilize the tail.

The absence of functional zygapophyses may also serve to reduce the transverse width of the tail in many aquatic taxa. Aigialosaurs and mosasaurs lose all functional zygapophyses beyond the pygal series (Russell 1967; Carroll and deBraga 1992; deBraga and Carroll 1993). The retention of zygapophyses in *Spinoequalis* may present a paradox initially, but the configuration of the zygapophyses (transversely narrow) and the absence of transverse processes does not interfere with lateral compression of the tail. As mentioned above, the loss of transverse processes in *Spinoequalis* results in a tail that is only 25 per cent. as wide as it is tall. These ratios are similar to those of other aquatic taxa (personal observation) and differ from the configuration in non-aquatic amniotes where the tail is much broader, with the width approaching 50 per cent. of its height.

The last caudal modification present in *Spinoequalis* is the antero-posterior compression of the caudal centra. The result is a vertebral body which is as tall as it is long. This differs from the pattern in most Palaeozoic amniotes (except in aquatic taxa) where the antero-posterior length of the caudal vertebrae, excluding spines, is always greater than its height (deBraga and Carroll 1993).

There is very little doubt that the tail of *Spinoequalis* possesses all of the necessary refinements required of an aquatic or semi-aquatic animal. However, it is surprising that, unlike most other aquatic amniotes, *Spinoequalis* does not appear to have any significant modifications to the limb girdles and retains typically terrestrial long, slender limbs.

In *Hovasaurus* (Currie 1981a) and other aquatic taxa (Russell 1967; Carroll and deBraga 1992) the scapula has a low aspect. This modification is interpreted as an aid in lowering the centre of gravity in an aquatic animal. This is required so that stability in the water can be maintained. Slight reduction in scapular height has been identified in the lizard *Aigialosaurus* (Carroll and deBraga 1992), although it does not possess any other typically aquatic appendicular characteristics. The poor ossification of the scapular blade in *Spinoequalis* precludes confirmation of whether scapular reduction is an aquatic characteristic or simply an indicator of immaturity.

Some aquatic diapsids do have long limbs, most notably the hindlimbs of *Hovasaurus* (Currie 1981a). However, the limbs of *Hovasaurus* are modified in that the manus, and to an even greater extent the pes, possess digits that are nearly of equal length. This is apparent when comparing digits III–V of *Hovasaurus* with the same digits in *Petrolacosaurus*, *Spinoequalis*, or most other Palaeozoic amniotes. In *Hovasaurus* digit III is 80 per cent. of the length of digit IV. This ratio is only slightly greater than that present in *Petrolacosaurus* and *Spinoequalis*. (75 per cent.). However, the ratio between the fifth digit and the fourth is quite noticeably different when comparing *Hovasaurus* and the latter taxa. In *Hovasaurus*, as in many other aquatic taxa, the hands and feet are modified into paddles and, accordingly, the digits are subequal in length. The fifth digit of the pes in *Hovasaurus* has increased in length to such an extent that it exceeds the length of the third digit and approaches (exceeding 80 per cent.) the total length of the fourth (Currie 1981a). In *Spinoequalis*, the fifth digit retains the characteristic terrestrial ratio where it is always shorter than the third digit and only slightly greater than one-half the length of the fourth digit.

The evidence presented here seems to pose a contradiction. The tail of *Spinoequalis* certainly exhibits typically aquatic features and yet most features of the limbs suggest a fully terrestrial lifestyle. This apparent conflict has been noted also in the Cretaceous lizard *Aigialosaurus* (Carroll and deBraga 1992). This taxon possesses a typically terrestrial morphology with only slight modifications to the tail, most notably compression of the vertebral centra. These modifications are even less striking than those present in *Spinoequalis* (the neural and haemal spines are not greatly elongated in *Aigialosaurus*), yet show a progressive pattern of modification which is only completely

manifested in their fully aquatic relatives the mosasaurs. The modifications present in *Spinoaequalis*, although not convincingly representative of a fully aquatic animal, are certainly incipient for that lifestyle and offer a rare glimpse of a 'transitory' organism.

CONCLUSIONS

The evidence presented above demonstrates that from both phylogenetic and biological points of view, diapsids were diversifying during the Palaeozoic. *Spinoaequalis* clearly represents an initial attempt at occupying an aquatic habitus not expressed by any other known Carboniferous amniote. It is noteworthy to consider that for a very long time aquatic amniotes are represented only by diapsid reptiles. Aquatic turtles do not make their appearance until the Mesozoic and synapsids (whales) do not invade the seas until the Cenozoic. It is likely that some aspect of both the anatomy and the physiology of diapsids imparts to them a selective advantage in invading the aquatic medium. Seymour (1982) demonstrated the energetically efficient means of aquatic locomotion among living diapsid reptiles. The typical sinusoidal motion present in diapsids is advantageous for aquatic locomotion. Diapsids were not only the first amniotes apparently to return to the water, they have continued to do so repeatedly and in greater number.

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REFERENCES

- BENTON, M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, **84**, 97–164.
- BRINKMAN, D. B., BERMAN, D. S. and EBERTH, D. E. 1984. A new araeoscelid reptile, *Zarcasaurus tanyderus*, from the Cutler Formation (Lower Permian) of north-central New Mexico. *New Mexico Geology*, **6**, 34–39.
- CARROLL, R. L. 1969. A Middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *Journal of Paleontology*, **43**, 151–170.
- 1981. Plesiosaur ancestors from the Upper Permian of Madagascar. *Philosophical Transactions of the Royal Society of London, Series B*, **293**, 315–383.
- 1988. *Vertebrate paleontology and evolution*. W. H. Freeman, New York, 698 pp.
- and deBRAGA, M. 1992. Aigialosaurs: mid-Cretaceous varanoid lizards. *Journal of Vertebrate Paleontology*, **12**, 66–86.
- CLARK, J. and CARROLL, R. L. 1973. Romeriid reptiles from the Lower Permian. *Bulletin of the Museum of Comparative Zoology*, **144**, 353–407.
- CREDNER, H. 1889. Die Stegocephalen und Saurier aus dem Rotliegenden des Plauen'schen Grundes bei Dresden. Teil. VIII. *Kadaliosaurus priscus*. *Zeitschrift der Deutschen Geologische Gesellschaft*, **41**, 319–342.
- CURRIE, P. J. 1979. A new younginid (Reptilia: Eosuchia) from the Upper Permian of Madagascar. *Canadian Journal of Earth Sciences* **17**, 500–511.
- 1981a. *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. *Palaeontologia Africana*, **24**, 99–168.
- 1981b. The vertebrae of *Youngina* (Reptilia: Eosuchia). *Canadian Journal of Earth Sciences*, **18**, 815–818.
- deBRAGA, M. and CARROLL, R. L. 1993. The origin of mosasaurs as a model of macroevolutionary patterns and processes. *Evolutionary Biology*, **27**, 245–322.
- EVANS, S. E. 1988. The early history and relationships of the Diapsida. 221–260. In BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods, Volume 1: Amphibians, reptiles, birds*. Clarendon Press, Oxford, 377 pp.
- FELDMAN, H. R., ARCHER, A. W., KVALE, E. P., CUNNINGHAM, C. R., MAPLES, C. G. and WEST, R. R. 1993. A tidal model of Carboniferous Konservat-Lagerstätten Formation. *Palaios*, **8**, 485–498.
- FREY, E. 1982. Ecology, locomotion and tail muscle anatomy of crocodiles. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **164**, 194–199.

- GAUTHIER, J. A., KLUGE, A. G. and ROWE, T. 1988. The early evolution of the Amniota. 103–155. In BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods, Volume 1: Amphibians, reptiles, birds*. Clarendon Press, Oxford, 377 pp.
- GOW, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia Africana*, **18**, 89–131.
- HEATON, M. J. 1979. Cranial anatomy of primitive captorhinid reptiles from the Late Pennsylvanian and Early Permian of Oklahoma and Texas. *Bulletin of the Oklahoma Geological Survey*, **127**, 1–84.
- and REISZ, R. R. 1986. Phylogenetic relationships of captorhinomorph reptiles. *Canadian Journal of Earth Sciences*, **23**, 402–418.
- HILDEBRAND, M. 1982. *Analysis of vertebrate structure*. John Wiley and Sons, New York, 654 pp.
- HOLMES, R. B. 1989. The skull and axial skeleton of the Lower Permian anthracosauroid amphibian *Archeria crassidisca* Cope. *Palaeontographica Abteilung A*, **207**, 161–206.
- LAURIN, M. 1991. The osteology of a Lower Permian eosuchian from Texas and a review of diapsid phylogeny. *Zoological Journal of the Linnean Society*, **101**, 59–95.
- and REISZ, R. R. 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, **113**, 165–223.
- OSBORN, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs from the American Museum of Natural History*, **1**, 265–270.
- REISZ, R. R. 1977. *Petrolacosaurus*, the oldest known diapsid reptile. *Science*, **196**, 1091–1093.
- 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Special Publication of the Museum of Natural History, University of Kansas*, **7**, 1–74.
- 1988. Two small reptiles from a Late Pennsylvanian quarry near Hamilton, Kansas. *Regional geology and paleontology of Upper Paleozoic Hamilton quarry area*. Kansas Geological Survey, Guidebook Series, **6**, 189–194.
- BERMAN, D. S. and SCOTT, D. 1984. The anatomy and relationships of the Lower Permian reptile *Araeoscelis*. *Journal of Vertebrate Paleontology*, **4**, 57–67.
- RUSSELL, D. A. 1967. Systematics and morphology of American mosasaurs. *Bulletin of the Peabody Museum of Natural History*, **23**, 1–237.
- SEYMOUR, R. S. 1982. Physiological adaptations to aquatic life. 1–51. In GANS, C. and POUGH, H. (eds). *Biology of the Reptilia, Volume 13*. Academic Press, New York, 345 pp.
- SWOFFORD, D. L. 1993. *PAUP: Phylogenetic analysis using Parsimony; version 3.1.1*. Champaign: Illinois Natural History Museum.
- WILLISTON, S. W. 1913. An ancestral lizard from the Permian of Texas. *Science*, **38**, 825–826.

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ABBREVIATIONS USED IN THE TEXT-FIGURES

Ana	atlantal neural arch	Na	nasal
Ang	angular	Opi	opisthotic
Art	articular	Psph	parasphenoid
Axc	axial centrum	Part	prearticular
Bo	basioccipital	Pm	premaxilla
Cor	coronoid	Ptg	pterygoid
D	dentary	Q	quadrate
Ect	ectopterygoid	Qj	quadratojugal
Exo	exoccipital	Sa	surangular
F	frontal	Spl	splenic
Lac	lacrimal	St	stapes
Max	maxilla	Sq	squamosal

APPENDIX 1

Description of characters used in the phylogenetic analysis. Characters are ordered anatomically. A zero in parentheses denotes the primitive condition whereas a number one or two in parentheses represents the derived state.

1. Dorsal process of premaxilla broad (0) or narrow (1), resulting in dorsal exposure of external nares.
2. Lacrimal large forming posterior border of external nares (0), or reduced and excluded from narial margin (1).
3. Anterodorsal process of maxilla absent (0) or present (1), reaching nasal and dorsal limit of external nares.
4. Caniniform teeth present (0) or absent (1).
5. Lateral margins of frontals straight resulting in a parallelogram shape (0) or lateral margins constricted above orbit (1) creating an hour-glass shape.
6. Dorso-lateral margins of parietal not excavated (0) or excavated (1) for adductor musculature.
7. Upper temporal fenestra absent (0) or present (1).
8. Posterior process of postorbital short, not reaching posterior limit of upper temporal fenestra (0), or long (1), extending beyond posterior border of fenestra.
9. Occipital flange of squamosal present (0) or absent (1).
10. Quadrate not exposed in lateral aspect behind squamosal (0) or exposed (1).
11. Ventral process of squamosal broad with the distal width approaching total height (0) or slender with width much less than total height (1).
12. Lower temporal fenestra absent (0) or present (1).
13. Posterior process of jugal short and relatively broad (0) not reaching beyond mid-point along ventral margin of lower temporal fenestra or long and slender (1) approaching posterior limit of lower temporal fenestra.
14. Paroccipital process not reaching cheek (0) or well ossified and reaching suspensorium (1).
15. Transverse flange of pterygoid orientated transversely or postero-laterally (0) or oriented antero-laterally (1).
16. Ectopterygoid present and large (0), present but small (1) and restricted to lateral margins of palate, or absent (2).
17. Suborbital fenestra absent (0) or present (1).
18. Neural arches or posterior dorsal and sacral vertebrae not excavated (0) along lateral margins or shallowly excavated (1).
19. Ventral surface of cervical and anterior dorsal centra without sharp keel (0) or strongly keeled (1).
20. Cervical vertebrae and remainder of presacral column subequal (0) or cervical vertebrae elongate (1).
21. Neural spines of dorsal vertebrae without dorsolaterally projecting (mammillary) processes (0) or mammillary processes present (1).
22. Anterior margin of cervical ribs without accessory processes (0) or accessory processes present (1).
23. Trunk rib heads dichoccephalic (0) or holocephalic (1).
24. Sternum not mineralized (0) or mineralized (1).
25. Interclavicle equal to not more than the length of six dorsal vertebrae (0) or interclavicle length equal to eight dorsal vertebrae (1).
26. Interclavicle head diamond shaped (0) or T-shaped (1).
27. Anterior margin of scapula straight (0) or slanted posteriorly (1).
28. Coracoid process for triceps musculature small (0) or large (1).
29. Humeral ends robust exceeding one third of total humeral length (0) or humerus gracile (1) with ends less than one third the total length.
30. Entepicondyle of humerus weakly developed (0) or large and strongly developed (1).
31. Radial shaft straight (0) or twisted (1) along its long axis.
32. Olecranon process on ulna present (0) or absent (1).
33. Propodial/epipodial ratios less than one (0) or equal to one (1).
34. Iliac blade with well-developed postero-distal process (0) or expanded into fan-shaped structure dorsally (1).
35. Acetabulum elongate or oval in configuration (0) or circular (1).
36. Pubic tubercles small (0) or large (1).
37. Adductor crest on femoral shaft present (0) or absent (1).
38. Femoral shaft equal to humeral shaft in diameter (0), exceeding humeral shaft diameter by 50 per cent. (1), or humeral shaft diameter exceeds that of femur by 50 per cent. (2).

39. Femur equal to humerus in length (0) or femur at least 10 per cent. longer than humerus (1).
40. Tibia without distinct ridge (0) for articulation with astragalus or tibia with distinct ridge that fits into astragalar groove (1).
41. Metatarsal I at least 50 per cent. the length of metatarsal IV (0) or less than 50 per cent. the length (1) of metatarsal IV.
42. Manus and pes short and broad (0) or long and slender (1).
43. Metapodials do not overlap proximally (0) or do overlap (1).
44. Neural spines of proximal caudal vertebrae equal or taller than those of distal portion (0) or proximal caudal vertebrae shortest and increasing in height posteriorly (1).
45. Haemal spines longer than neural spines of same caudal vertebrae (0) or neural and haemal spines of equal length (1).
46. Haemal spines tallest at base of tail and decreasing in height posteriorly (0) or haemal spines shortest at base of tail increasing in length posteriorly (1).
47. Haemal spines not expanded distally (0), slightly expanded distally (1), or greatly expanded distally (2).
48. Caudal vertebrae (neural arches and centra) longer than tall (0) or length and height subequal (1).
49. Caudal zygapophyses flat and not expanded dorsally (0), zygapophyses tall (1), or functional zygapophyses absent (2).
50. Transverse processes present throughout most of caudal series (0) or absent on distal caudals (1).

APPENDIX 2

Data matrix for taxa examined in present analysis. Numbers above taxon names refer to character state numbers from Appendix 1. A question mark represents missing data.

	1111111111222222
<u>Taxon</u>	<u>1234567890123456789012345</u>
<i>Captorhinidae</i>	0000000?0000000200000000
<i>Paleothyris</i>	0000000?0000000000000000?
<i>Spinoaequalis</i>	100010????11??011?00??1?1
<i>Petrolacosaurus</i>	1000101000010?111111110?0
<i>Araeoscelis</i>	1000101000000111111111010
<i>Apsisaurus</i>	????????00011??110110?0??
<i>Acerosodontosaurus</i>	?1111?1111111?11000001??
<i>Youngina</i>	1111111111110011000001?0
<i>Hovasaurus</i>	????1111111110??00000110

	222233333333334444444445
<u>Taxon</u>	<u>6789012345678901234567890</u>
<i>Captorhinidae</i>	00001000000000000000000000
<i>Paleothyris</i>	0001000000000000110??000
<i>Spinoaequalis</i>	01?1000101?110?1111111111
<i>Petrolacosaurus</i>	011100010011101111000000
<i>Araeoscelis</i>	011100010011111111000000
<i>Apsisaurus</i>	00010010??0111???????????
<i>Acerosodontosaurus</i>	????111011010?????1???????
<i>Youngina</i>	10001110110101??1?000000
<i>Hovasaurus</i>	10001010000121?1111112121

THE SKULL OF THE HERBIVOROUS SYNAPSID *EDAPHOSAURUS BOANERGES* FROM THE LOWER PERMIAN OF TEXAS

by S. P. MODESTO

ABSTRACT. The cranial anatomy of the Lower Permian synapsid *Edaphosaurus boanerges* is described, based upon well-preserved material from the Geraldine Bonebed (Wichita Group: Nocona Formation) of north-central Texas. Two autapomorphies for this species are identified: (1) 120–150 teeth are present on each palatal tooth plate; and (2) the mandibular symphysis is deeply excavated dorsally. Phylogenetic analysis of the interrelationships of *Edaphosaurus* species supports the hypotheses that the Lower Permian Texan species *E. boanerges*, *E. cruciger*, and *E. pogonias* are a monophyletic group, and *E. boanerges* is excluded from a clade formed by *E. cruciger* and *E. pogonias*. The suite of cranial specializations that characterizes *Edaphosaurus* is interpreted as an adaptation complex towards terrestrial herbivory. Isodonty, the presence of cutting edges on the marginal teeth, the oblique orientation of the cutting edges, and the shouldering of the marginal teeth, indicate that the anterior marginal teeth of *E. boanerges* served to crop bite-sized portions from tough, terrestrial plants. The food was then triturated by the palatal and mandibular tooth plates; minor grinding was provided also by the procumbent posterior teeth of the maxilla and dentary. The morphology of the jaw suspension indicates that the mandible was capable of fore-and-aft translation; the orientation of tooth plate occlusal surfaces and palatal tooth wear in *E. boanerges* indicate that propalinal movement was a major component of the grinding phase during oral food processing. The dual organization of the feeding system in *Edaphosaurus* is the earliest known example of its kind among amniotes.

THE Permo-Carboniferous is arguably one of the most interesting times in amniote evolutionary history, for it was during this time that the first large terrestrial herbivorous and carnivorous vertebrates appeared. The edaphosaurid synapsid genus *Edaphosaurus* was one of the most abundant, widespread and long-lived of the large herbivores.

Edaphosaurus is currently recognized as the oldest known genus of herbivorous amniote (Modesto and Reisz 1992). Recent studies have identified two small faunivorous taxa, *Ianthasaurus* and *Glaucosaurus* (Reisz and Berman 1986; Modesto 1994), as basal edaphosaurids. Accordingly, the presence of both faunivorous and herbivorous taxa within Edaphosauridae makes the family an indispensable component of investigations into the origins of terrestrial vertebrate herbivory (Modesto 1992).

Although *Edaphosaurus* has been known for well over one hundred years, its presence at many edaphosaurid localities is indicated only by fragments of the distinctive neural spines. Most species assigned to *Edaphosaurus* are represented by one or two poorly preserved skeletons, and the occasional tooth plate or isolated appendicular elements. Accordingly, our knowledge of the cranial anatomy of *Edaphosaurus* is imperfect. Most of what is known is based mainly upon descriptions of a single flattened and incomplete skull, the holotype of *Edaphosaurus pogonias* (Case 1906; Broom 1910; Watson 1916; Romer and Price 1940). Romer and Price (1940) were the last workers to describe this specimen. Although their description of the skull is now known to feature several major errors (Brinkman and Eberth 1983), recent studies (e.g. Olson 1986; Reisz 1986; Carroll 1988) continued to refer to it.

Interestingly, exceptionally preserved cranial materials attributed to *E. boanerges* have been available since the publication of Romer and Price's (1940) *Review of the Pelycosauria*. Between

1934 and 1941, an unprecedented amount of edaphosaurid material was recovered from the Geraldine Bonebed in Archer County, Texas (Wichita Group: Nocona Formation) by Harvard and Amherst College field parties. The remains of at least fourteen skeletons of this species were collected, including several complete, articulated skulls (Sander 1987). Accordingly, the material from Geraldine has made *E. boanerges* the best known member of the genus. However, that label does not extend to the cranial morphology, since the original description of *E. boanerges* (Romer and Price 1940) was based upon materials collected by Romer during the 1934 excavation, which apparently produced complete jaws but only a few disarticulated cranial elements. Romer and Price's (1940) reconstruction of the skull of *E. boanerges* appears to be a reworking of their reconstruction of the skull of *E. pogonias*, since most of the sutures are represented by dashed lines. The skulls collected during the 1939 and 1941 excavations were partially prepared, but only to serve as the basis for exhibition models. More recently, these specimens were used in a review of early synapsid phylogeny (Brinkman and Eberth 1983).

The rich assemblage of Geraldine materials provides an opportunity to describe thoroughly the cranial osteology of an edaphosaurid. The exceptional preservation of the tooth-bearing elements of the Geraldine skulls also permits an investigation into the adaptation to herbivory that has long been attributed to *Edaphosaurus*. This hypothesis was prompted by the presence of the large denticulate plates on the palate and the lingual surface of the mandible, and the presence of a large, barrel-shaped body. Most edaphosaurid marginal dentitions that were available to early workers were not well preserved, and accordingly did not figure in their hypotheses concerning diet. The well preserved Geraldine materials shed additional light on edaphosaurid herbivory.

This description and restudy of the skull of *Edaphosaurus boanerges* is essential in the light of recent systematic studies of early amniotes, for much remains to be clarified concerning the relationships of primitive synapsids. The goals of this work are to provide a detailed description of the skull of *Edaphosaurus boanerges*, to determine its probable feeding mechanism, to strengthen the hypothesis of herbivory attributed to this genus using the new cranial data, and to provide a robust phylogeny for *Edaphosaurus*.

Institutional abbreviations. AMNH, American Museum of Natural History, New York; MCZ, Museum of Comparative Zoology, Harvard University; ROM, Royal Ontario Museum, Toronto.

SYSTEMATIC PALAEOLOGY

SYNAPSIDA Osborn, 1903

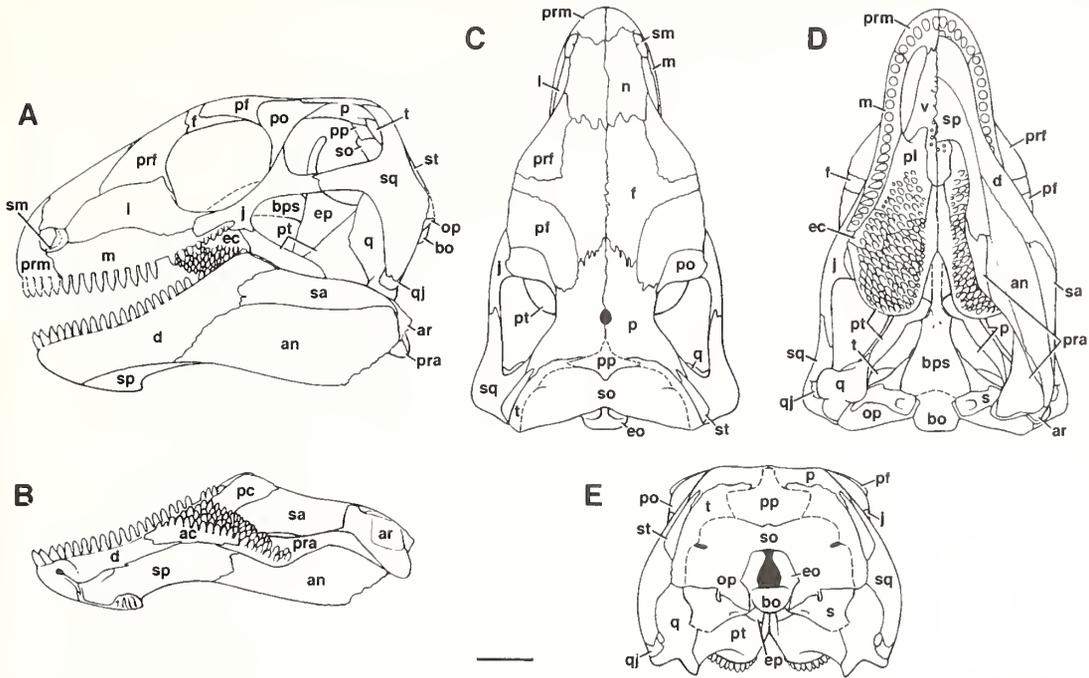
EUPELYCOSAURIA Kemp, 1982

Family EDAPHOSAURIDAE Cope, 1882

Genus EDAPHOSAURUS Cope, 1882

Type species. *Edaphosaurus pogonias* Cope, 1882

Diagnosis. Edaphosaurids (see Modesto and Reisz 1990 for familial diagnosis) with small skulls, approximately equal in length to five dorsal centra; posterior process of the postorbital short, does not extend posterior to the level of the parietal foramen; nasal is approximately three-quarters the length of the frontal; frontal anterior process reduced in antero-posterior length to one-third frontal sagittal length; posterior cheek deeply emarginated; tooth plates are developed on the palate and the inner aspect of the mandible; palatal tooth plates are formed by the palatine, ectopterygoid, and pterygoid; mandibular tooth plates are formed by anterior coronoid, posterior coronoid, and prearticular; marginal teeth are isodont, slightly swollen distally, and feature fine serrated tips that curve slightly backwards; cutting edges of the cheek teeth are inclined obliquely with respect to the axis of the tooth row. Maxillary teeth become increasingly laterally directed posteriorly, while the



TEXT-FIG. 1. *Edaphosaurus boanerges* Romer and Price 1940. Outline guide to skull reconstructions in Text-figures 2–4. A, skull and left mandible in left lateral view; B, right mandible in medial view; C, skull in dorsal view; D, skull and left mandible in ventral view; E, skull in occipital view. Scale bar represents 20 mm.

opposing dentary teeth become increasingly medially directed; neural spines of the sacral and anterior caudal vertebrae are tall and pointed, with longitudinal ridges running along their lateral surfaces; multiple laterae tubercles, when present, are usually arranged horizontally on the neural spines.

Edaphosaurus boanerges Romer and Price, 1940

Text-figures 1–18

1916 *Edaphosaurus* sp., Williston, p. 233, fig. 81.

1940 *Edaphosaurus boanerges*, Romer and Price, p. 48, fig. 6A; p. 66, fig. 8; p. 79, fig. 12F; p. 86, fig. 15C–D; p. 391, fig. 66.

Diagnosis. A medium-sized *Edaphosaurus* characterized by the presence of 120–150 teeth on each palatal tooth plate and a jaw symphysis that is deeply excavated dorsally; distinguished from other edaphosaurids by the following suite of advanced and primitive characters: frontal lateral lappet slender; anterior presacral neural spines slender; and lateral tubercles slender.

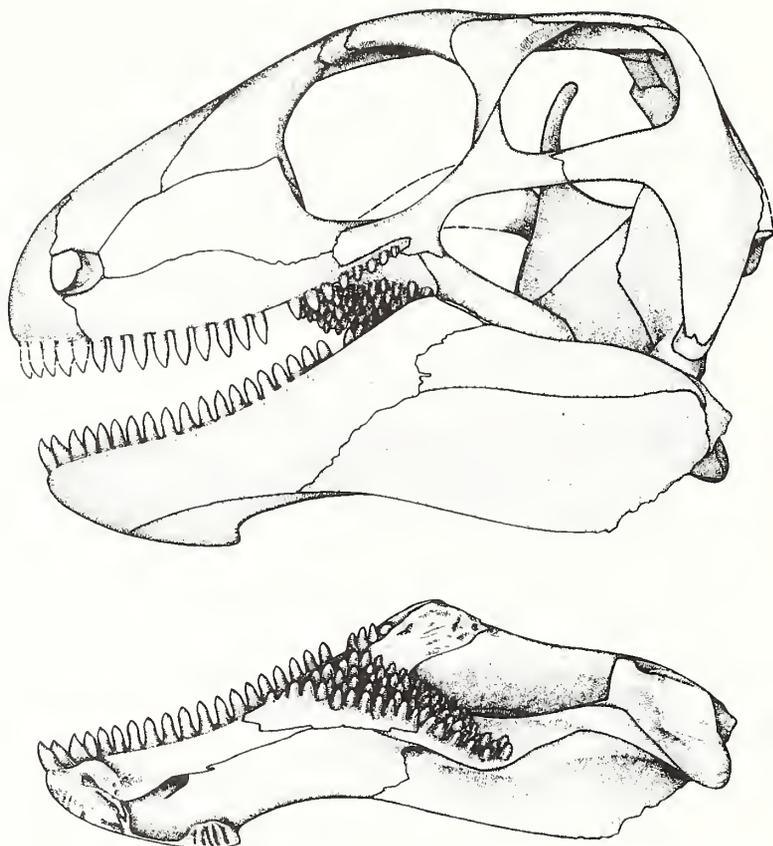
Horizon and Locality. Nocona Formation (formerly Admiral Formation; see Hentz 1988 for stratigraphical review for north-central Texas), Wichita Group, Lower Permian. Study specimens are from the Geraldine Bonebed, approximately 13 km northwest of Archer City, Archer County, Texas.

Holotype. MCZ 1531, a pair of mandibles. According to Romer and Price (1940), this number originally contained ‘the remains of about six individuals’ from Geraldine, with the type jaws forming part of a mounted

MCZ specimen. In the early 1980s all specimens except the type jaws were reassigned to MCZ numbers 4309–4324.

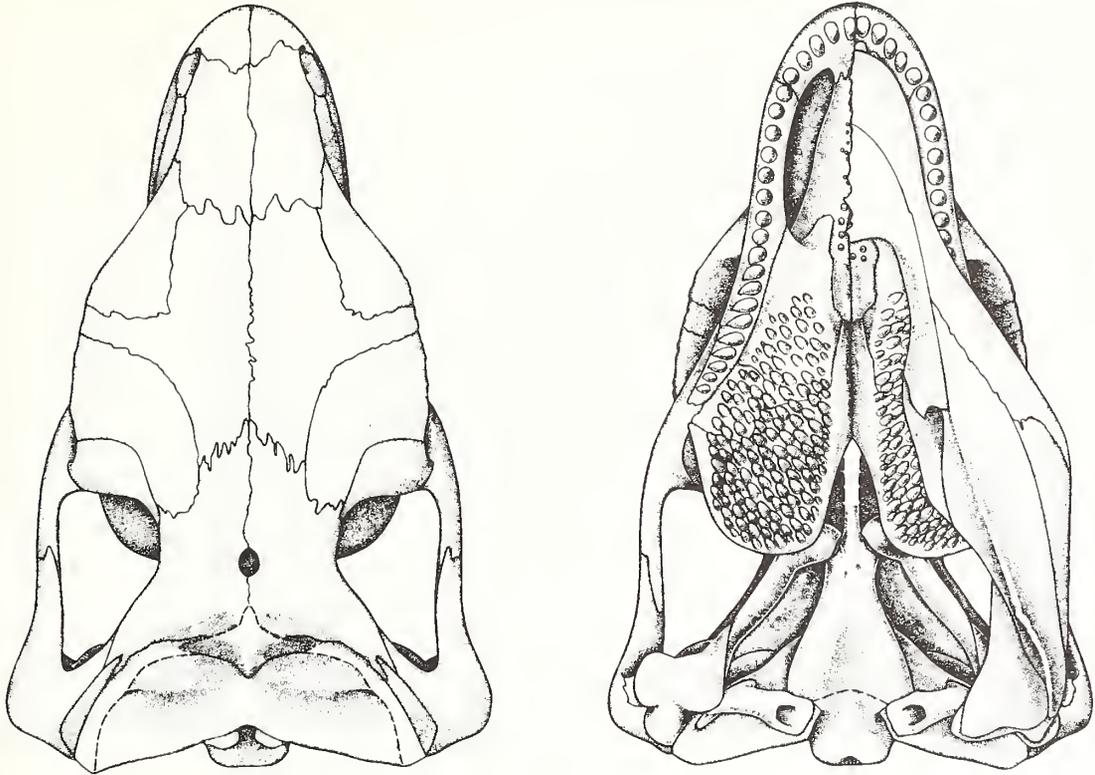
Study material. MCZ 1680, a partial skeleton with an obliquely compressed skull; MCZ 1762, a partial skeleton with fragmentary skull and mandibles; MCZ 1764, a fragmentary skull; MCZ 4309, a partial skull with mandibles (formerly part of MCZ 1531); ROM 37760, a fragmentary left maxilla. This is not an exhaustive list of *Edaphosaurus boanerges* specimens reposit at the MCZ, ROM, or elsewhere, and includes only those specimens examined here.

Description. The Geraldine specimens permit a confident restoration of the skull of *Edaphosaurus boanerges* (Text-figs 1–4). The reconstruction is based mainly upon MCZ 1762, with additional information taken from



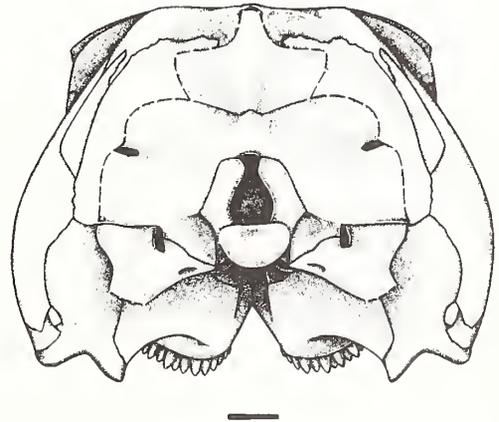
TEXT-FIG. 2. *Edaphosaurus boanerges* Romer and Price 1940. Restoration of skull and left mandible in left lateral view, and right mandible in medial view. Scale bar represents 10 mm.

MCZ 1680, MCZ 1764, and MCZ 4309. The mandible is reconstructed mainly from MCZ 4309, with additional data taken from MCZ 1680 and MCZ 1762. Several features distinguish this genus from other Permo-Carboniferous synapsids. Most significantly, the cheek margin is greatly emarginated, the slender subtemporal bar is displaced dorsally, and the temporal fenestra is enlarged antero-posteriorly. The



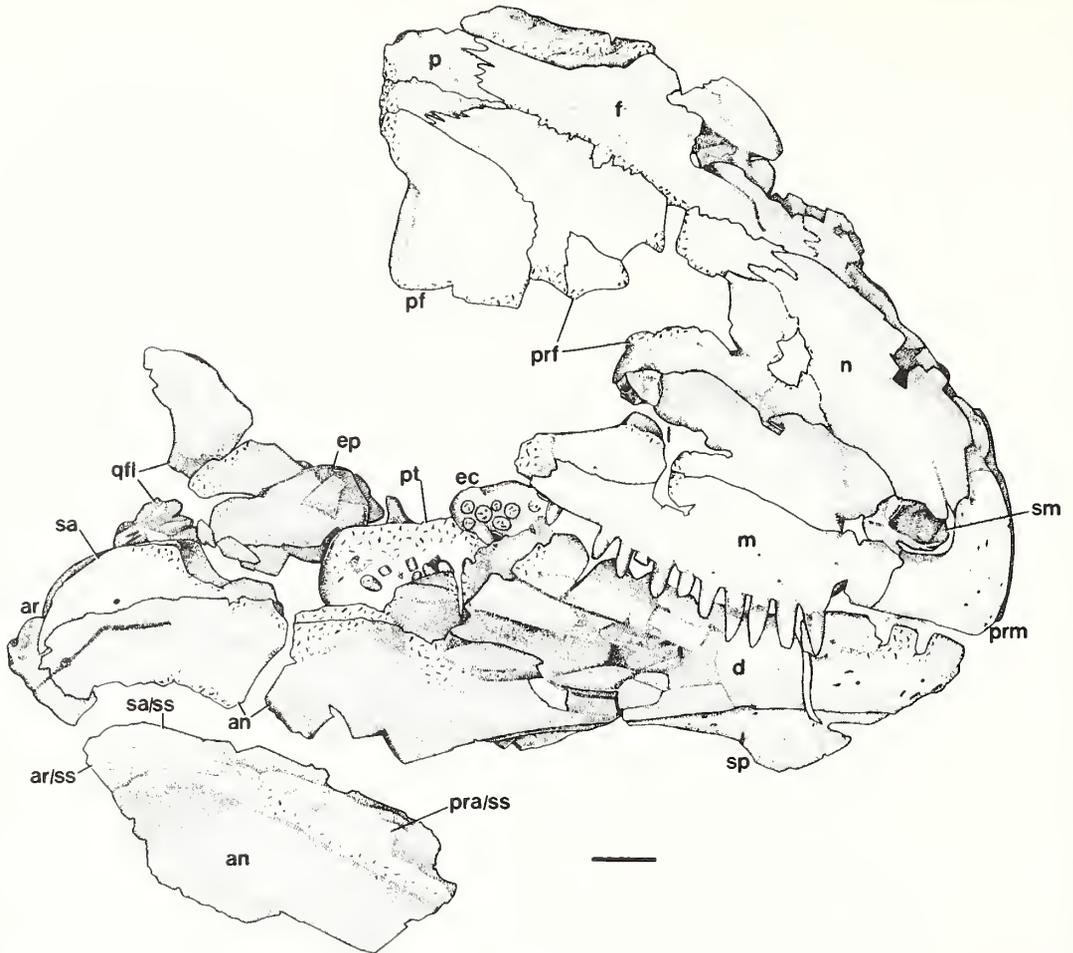
TEXT-FIG. 3. *Edaphosaurus boanerges* Romer and Price 1940. Restoration of skull and left mandible in dorsal and palatal views. Scale bar represents 10 mm.

TEXT-FIG. 4. *Edaphosaurus boanerges* Romer and Price 1940. Restoration of skull in occipital view. Scale bar represents 10 mm.



supraorbital shelf is very deep transversely and conceals the orbits in dorsal view. The posterior maxillary teeth become increasingly laterally directed posteriorly along the marginal tooth row.

Skull. The dorsal process of the premaxilla (Text-fig 5), obliquely elongate in cross section, overlies a broad anterior shelf of the nasal. The vomerine process is not preserved well enough for description. The premaxilla

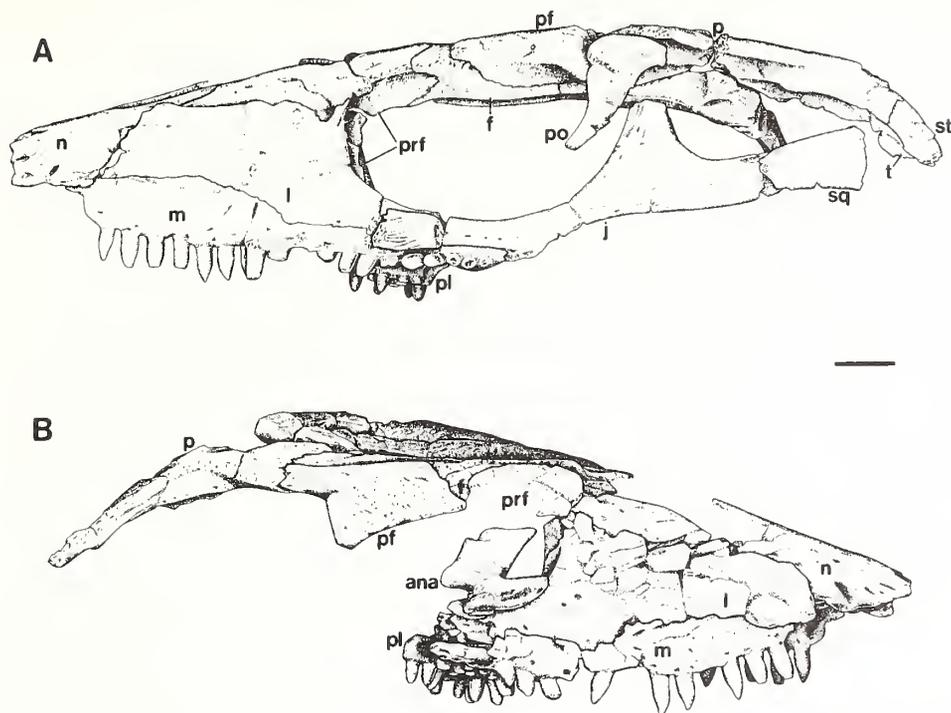


TEXT-FIG. 5. *Edaphosaurus boanerges* Romer and Price 1940; MCZ 1680; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Skull roof and right mandible in right lateral view, and left angular in medial view. Scale bar represents 10 mm.

accommodates five teeth, but none is preserved well enough to determine their length. However, the cross-sectional area of the premaxillary tooth stumps of MCZ 4309 are similar to those of the maxillary dentition, which suggests that the premaxillary teeth probably differed little in size from those of the maxilla.

The septomaxilla (Text-fig. 5) extends the full height of the narial opening, and the medial shelf is large enough to have easily made contact with the nasal septum at the midline. The presence of a posterolateral process on the septomaxilla, seen in spheonacodontids, cannot be determined.

The maxilla (Text-figs 5-7) is a slender rod of bone accommodating 18-21 teeth. All previous descriptions of the marginal dentition of *Edaphosaurus* restored the teeth vertically, as in most other early tetrapods. The well preserved Geraldine materials reveal that the alveolar ridges of the maxillae and dentaries are twisted, such that their posterior teeth become directed laterally and medially, respectively. The lateral edge of the maxillary alveolar ridge becomes disproportionately thinner posteriorly than the medial edge, and the ventral surface of the alveolar portion exhibits a progressive lateral flexure, approximately 13°-16° at the sixteenth tooth position, and roughly 35°-40° at the eighteenth and nineteenth tooth positions. Accordingly, the angle of tooth implantation changes, and the posterior maxillary teeth become increasingly laterally directed. In lateral aspect, the ventral margin of the maxilla is arched weakly, and the lateral edge forms a distinct lip over the tenth



TEXT-FIG. 6. *Edaphosaurus boanerges* Romer and Price 1940; MCZ 1762; Geraldine Bonebed, Lower Permian; Archer Co., Texas. A, left lateral and B, right lateral views of skull. Scale bar represents 10 mm.

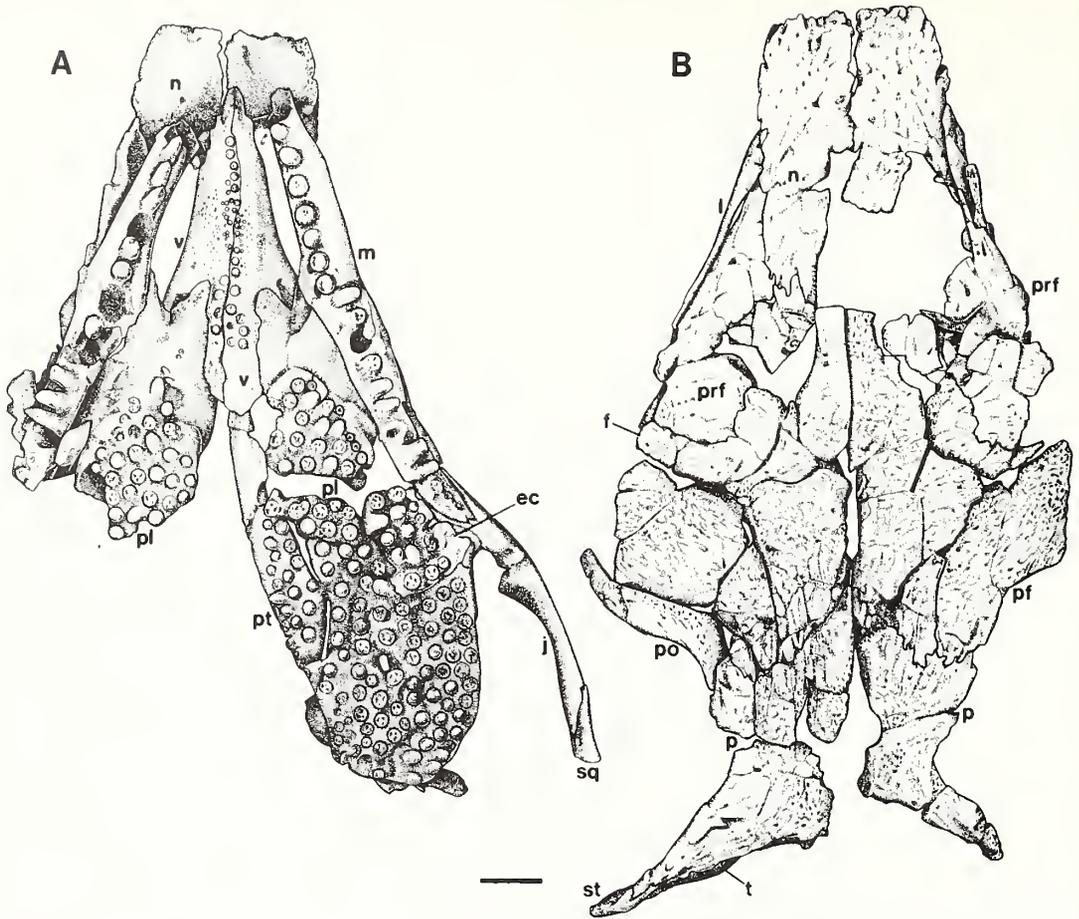
through fifteenth teeth. The implantation of the teeth (Text-fig. 9) is protothecodont. Each tooth bears a perceptible shoulder, beyond which it attenuates to a sharp tip. The tips are compressed slightly transversely and curve slightly posteriorly. Posterior cutting edges are aligned slightly posterolaterally, whereas anterior cutting edges are inclined anteromedially. Many teeth feature extremely fine serrations along their cutting edges, and these are emphasized by short, oblique grooves running inwards from the edge; those teeth lacking serrations presumably lost them from heavy use. Approximately every third tooth in the maxillae of MCZ 1762 is at the same level of development, and there are few natural gaps in the marginal dentition, suggesting that tooth replacement was relatively rapid. Wear is present on several anterior teeth in MCZ 1762, occurring as a planing-off of the lingual surface of the shoulder; the posterior teeth are too damaged to determine true tooth-to-tooth wear. However, examination of ROM 37760 reveals that many of the procumbent posterior teeth display similar wear on their lingual surfaces.

In lateral aspect, the lacrimal (Text-figs 5–6, 10) underlies the dorsal flange of the maxilla anteriorly, but as the lacrimal becomes progressively thicker posteriorly, it comes to overlie the maxilla totally. The medial wall of the lacrimal duct is thicker than the lateral wall, perhaps to strengthen contact with the ventral process of the prefrontal medially. The lacrimal is greatly thickened along the orbital margin and has a well-developed contact with the ventral process of the prefrontal.

Anteriorly, the nasal (Text-figs 5–7) has a strongly scarred shelf for the reception of the premaxilla, and the internasal suture is bevelled and irregular, presumably to strengthen the snout against forces generated during feeding.

The ventral process of the prefrontal (Text-figs 5–7) is transversely thick and is attached solidly to the medial surface of the lacrimal. The transverse width of the ventral process decreases ventrally in direct proportion to a progressive increase in the width of the lacrimal, forming a stout buttress of constant width between the skull roof and palate (Text-fig. 10). The ventral process continues dorsally as a ridge on the ventral surface of the posterodorsal process.

Romer and Price (1940) reconstructed the frontal with a large lateral lappet. However, the lateral lappet of the frontal (Text-figs 5–8) is markedly slender, with a lateral exposure about one-quarter that of the



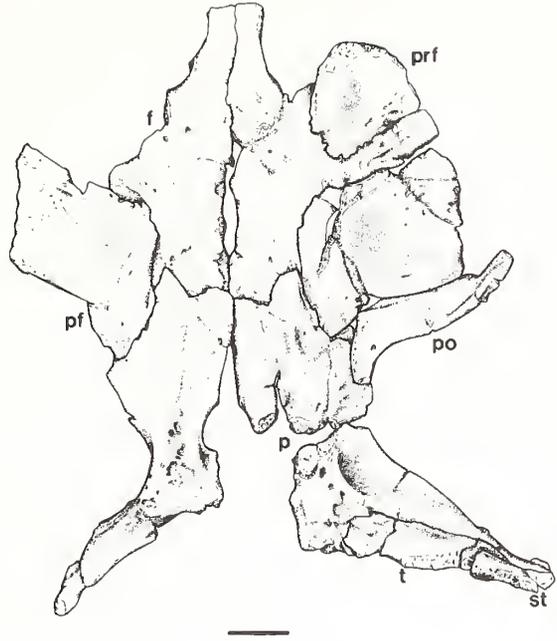
TEXT-FIG. 7. *Edaphosaurus boanerges* Romer and Price 1940; MCZ 1762; Geraldine Bonebed, Lower Permian; Archer Co., Texas. A, palatal and B, dorsal views of skull. Scale bar represents 10 mm.

postfrontal. Posteriorly, the frontal overlies, and has a moderately to deeply serrate suture with, the parietal; a ventral ridge extends anteriorly from this suture to contact and merge with the ventral ridge and ventral process system of the prefrontal.

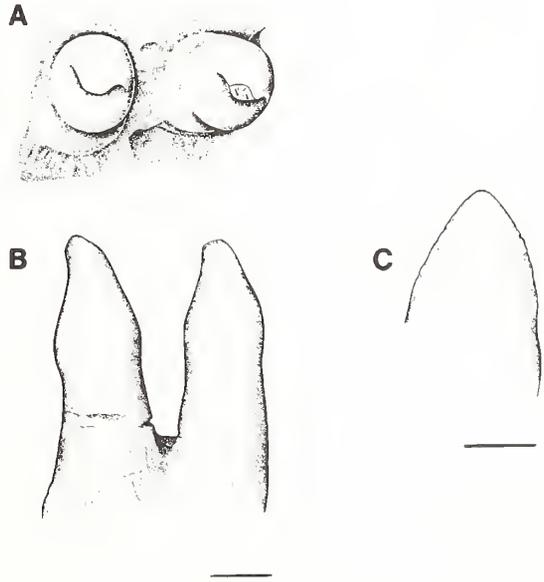
A notable feature of the parietal (Text-figs 6–8) is its concave lateral edge. Contrary to previous interpretations, the lateral edge of the parietal was free and formed the dorsal margin of the temporal fenestra. The medial half of the ventral surface of the bone is dominated by two well-developed parasagittal ridges. The lateral ridge is continuous with the ventral ridge of the frontal, and presumably marks the former contact of the orbital-plate cartilage, whereas the medial ridge arises immediately anterior to the parietal foramen, extends to the posterior edge of the parietal, and overlies an anterodorsal pilaster-like process of the postparietal. Posteriorly, the parietal has a small occipital shelf that contacts the postparietal and the tabular.

The lateral edges of the postparietal (Text-fig. 11) of MCZ 1762 are imperfectly preserved, making it difficult to establish the precise nature of the contact with the tabular and the parietal. However, scars present on the posterior margin of the parietal suggest that the postparietal overlies the occipital flange of the parietal. A pair of pilaster-like projections arise from a point slightly lateral to the centre of the anterior surface and end dorsally as broad-based supports for the medial ventral rugosities of the parietals. These processes lie snugly within the crenels of the dorsal process of the supraoccipital. A small, median process extends anterodorsally from the postparietal to interpose itself between the posterior ends of the parietals; this is inferred by a small, triangular gap which lies sagittally between the ends of the articulated parietals. An anterodorsal process is found also on the postparietal of *Edaphosaurus pogonias* (AMNH 4009).

TEXT-FIG. 8. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Skull table of MCZ 1762 in ventral view. Scale bar represents 10 mm.

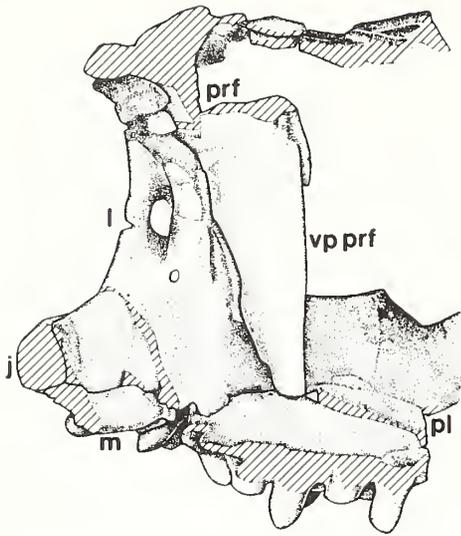


TEXT-FIG. 9. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Maxillary teeth of MCZ 1762. A, occlusal and B, lingual views of 6th and 7th right maxillary teeth; C, lingual view of the tip of unankylosed maxillary tooth, showing serrations. Scale bars represent 1 mm.

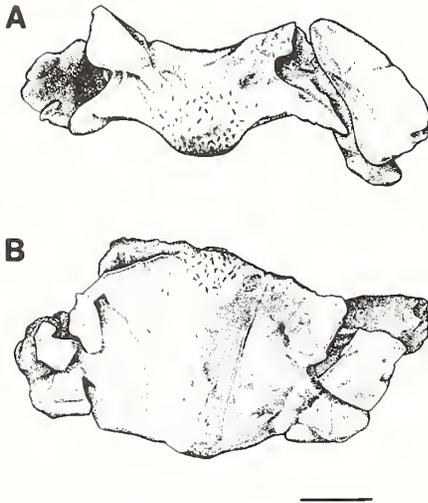


The supratemporal (Text-figs 6-8) is a narrow, gently arched bone with little lateral exposure. The supratemporal of *Edaphosaurus boanerges* differs little from that of *E. pogonias*. The supratemporal of the latter species was reconstructed by Romer and Price (1940) as a large element, but re-examination of the holotype reveals that it, too, is a slender, predominantly occipital element.

The relatively thick dorsal edge of the tabular (Text-figs 6-8) occupies a broad embayment in the posterior edge of the parietal. Though the ventromedial edge of the tabular is not preserved, the preserved parts of the bone rapidly thin inwards from the dorsal edge, suggesting that the ventromedial edge was quite thin. Sutural surfaces on the occipital surfaces of the paroccipital process and lateral process of the supraoccipital mark its ventromedial limits.



TEXT-FIG. 10. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Left antorbital region of MCZ 1762 in posterior view. Hachure indicates broken surface. Scale bar represents 10 mm.



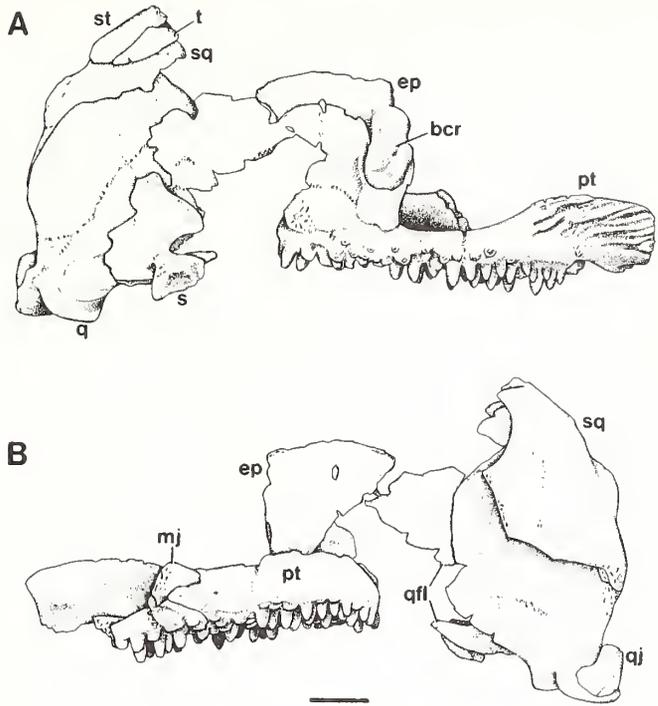
TEXT-FIG. 11. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Postparietal of MCZ 1762. A, dorsal and B, posterior views. Scale bar represents 5 mm.

The postfrontal (Text-figs 5–8) consists of a small but thick posterior process that gives rise to a wedge-shaped anterior flange that forms the posterior half of the supraorbital hood. The sutural surface for the postorbital is twisted: internally and medially the posterior process of the postfrontal overlies the base of the postorbital posterior process, whereas laterally it underlies the postorbital.

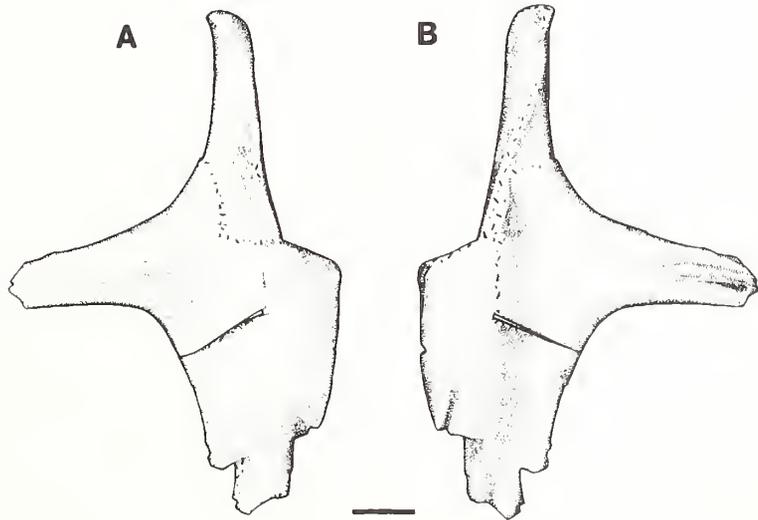
The postorbital (Text-figs 6–8) is a slender, sigmoidal bone. The posterodorsal process does not extend posteriorly beyond the pineal foramen, and it is completely overlain by the parietal. In spite of the fragmentary nature of the available squamosals, it is very unlikely that the postorbital contacted the squamosal. The posterodorsal process does not possess an area that may be interpreted as a sutural surface for the squamosal, nor does the parietal immediately posterior to the postorbital bear any markings for the reception of the squamosal.

The jugal (Text-figs 6–7) is remarkably slender in lateral view, and is laterally compressed for most of its length except for the slightly swollen anterior third. A short protuberance extends medially from the anterior jugal process to contact the palate. The sutural surface for the squamosal is extensive and marked by strong ridges and furrows.

TEXT-FIG. 12. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Palatoquadrate ossifications and associated elements of MCZ 1762. A, medial and B, lateral views. Scale bar represents 10 mm.

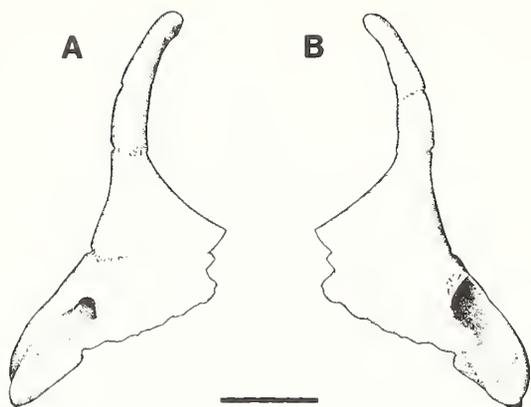


TEXT-FIG. 13. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Left squamosal of MCZ 1680. A, lateral and B, medial views. Scale bar represents 10 mm.



The ventral process of the squamosal (Text-figs 6, 12-13) is well developed. An occipital flange extends medially from the ventral process of the squamosal, and serves as a broad base for the supratemporal and, to a lesser extent, the tabular. A thickened, irregular prominence on the medial edge of the squamosal marks the area receiving the tip of the paroccipital process. The anterior process displays either a slight anteroventral curvature, as in MCZ 1762, or extends forward without arching, as in MCZ 1680.

Despite the absence of well preserved specimens, Romer and Price (1940) described the quadratojugal as extending anteriorly under the postorbital bar. However, the quadratojugal (Text-fig. 12) is antero-posteriorly short and covered laterally by the squamosal, resembling closely those of sphenacodonts.



TEXT-FIG. 14. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Left epipterygoid of MCZ 1764. A, lateral and B, medial views. Scale bar represents 10 mm.

The palate departs from the typical primitive synapsid condition in the possession of a pair of large tooth plates, formed by the palatine, ectopterygoid, and pterygoid. These plates are tilted ventrolaterally, are faintly concave in order to meet more firmly the gently convex tooth plates of the mandible, and accommodate about 120–150 teeth each. The internal nares (Text-fig 3) are more elongate than suggested by Romer and Price (1940), but they are neither as long, nor as transversely constricted, as in carnivorous eupelycosaur. The median longitudinal depression between the tooth plates is deep and compressed transversely, and the post-plate region is significantly more abbreviated than in other genera.

The ventrolateral surface of the vomer (Text-fig. 7) is slightly concave and covered by a shagreen of tiny teeth, which is replaced anteriorly by a smooth surface ingrained by shallow striae. The largest vomerine teeth reach a maximum diameter equal to approximately one-half that of an average-sized plate tooth.

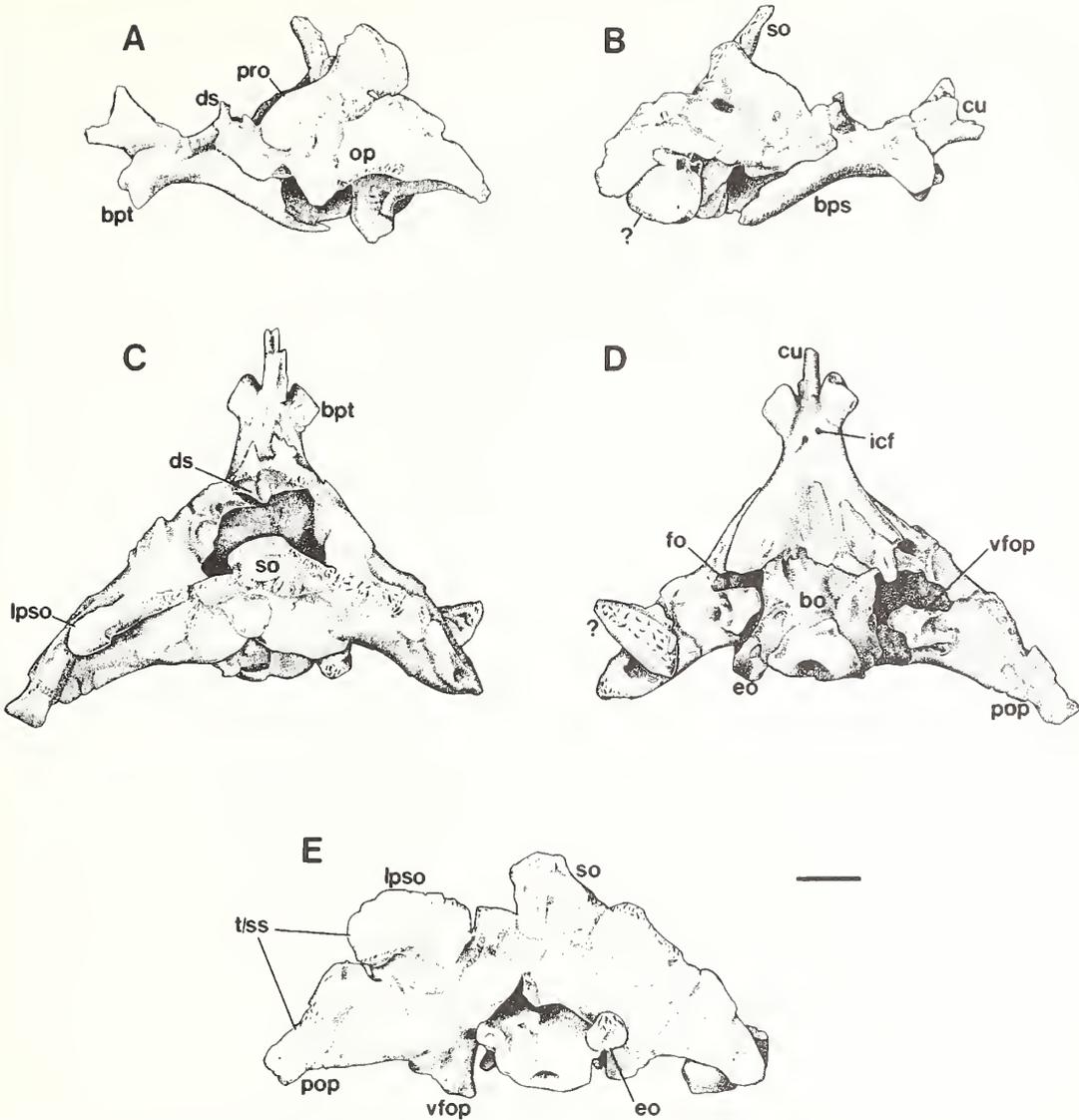
The palatine's (Text-figs 6–7) contribution to the tooth plate is a thick, diamond-shaped structure which bears approximately thirty-two conical teeth. The majority of the teeth are approximately one-half as long and two-thirds the diameter of the maxillary dentition. They are roughly uniform in diameter and are densely packed. Smaller teeth, some approaching the size of the vomerine teeth, occupy the lateral and anterior fringes of the tooth-bearing area. All well-preserved palatal teeth display some degree of wear, which generally takes the form of a planing-off of the tips of the teeth. However, the tips of most teeth appear to have been planed off by previous preparators, making it difficult to identify true tooth wear. A diagonally-orientated orbitonasal ridge arises on the dorsal surface near the lateral edge of the palatine, forms the medial wall of the lateral orbitonasal foramen, and runs anteromedially to the medial orbitonasal foramen. Laterally, the orbitonasal ridge has a small contact with the lacrimal and the ventral process of the prefrontal.

The ectopterygoid (Text-figs 5, 7) is a small element that is almost completely covered ventrally by about fifteen teeth. Laterally, the ectopterygoid has a small contact with the jugal.

The pterygoid (Text-figs 5, 7, 12) is the largest and most complex palatal element. The low dorsal lamina of the pterygoid is scarred medially with numerous longitudinal ridges and grooves, presumably required to withstand the forces generated by the jaw adductor musculature. The ventral surface of the palatal ramus is covered completely by teeth except for the edges bordering the interpterygoid vacuity and the jugal. The tooth plate faces slightly rostrally as well as anterolaterally, and lies well below the level of the cheek in lateral aspect. Nearly 100 teeth are present, and these are set deeply into the alveolus of the tooth plate. The thin quadrate ramus of the pterygoid is similar to those of sphenacodontids, but differs strongly from other eupelycosaur in the elaboration of the region associated with the epipterygoid. The ramus rises directly upwards from the dental plate and wraps around the basicranial process of the epipterygoid. A broad, prominent channel of unknown function issues from the scrolled flange enclosing the basicranial process and ends abruptly on the dorsal surface of the palatal plate.

The basal portion of the epipterygoid (Text-figs 12, 14) overlies the quadrate ramus of the pterygoid in lateral view. The basicranial process extends medially from the basal portion and ends in a tall, screw-shaped recess for the basiptyergoid process of the basiparasphenoid. The ventral half of the recess faces slightly posteriorly as well as medially, whereas the dorsal half faces anteromedially. The basicranial process is held firmly within the anterior fold of the quadrate ramus of the pterygoid. The dorsal columella is a slender, transversely compressed finger of bone that arches posteriorly.

The dorsal and posterior margins of the vertical plate of the quadrate are thickened and flare slightly laterally (Text-fig. 12). The posterior margin has a strong contact with the squamosal and a smaller sutural surface for

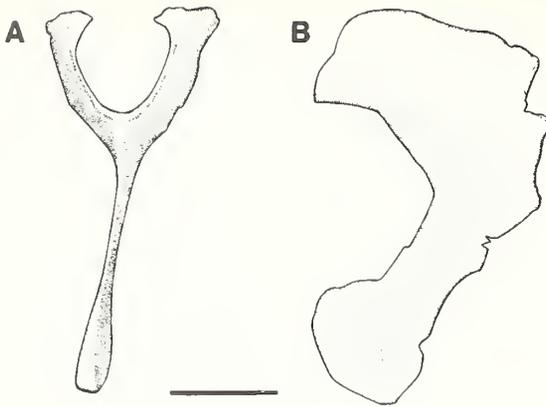


TEXT-FIG. 15. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Braincase of MCZ 1762. A, left lateral, B, right lateral, C, dorsal, D, ventral, and E, occipital views. Scale bar represents 10 mm.

the quadratojugal. A shallow, rounded depression posteromedial to the quadrate foramen probably received the distal end of a cartilaginous extension of the stapes. The two condyles are aligned parasagittally, are separated by a deep notch, and share a single articulating surface.

The braincase (Text-fig. 15) resembles in most respects that of sphenacodontids, but differs in the morphology of the paroccipital processes and the organization of the region formerly surrounding the pituitary body. As in most early synapsids, there is a marked tendency towards fusion of the elements: the parasphenoid and the basisphenoid are united, the supraoccipital is fused to the opisthotics and the prootics, and the basioccipital and exoccipitals are fused.

Because the basisphenoid and its dermal cover, the parasphenoid, are indistinguishably fused, the term basi-parasphenoid is used here when referring to this complex. The cultriform process is poorly known, but



TEXT-FIG. 16. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Sphenethmoid of MCZ 1764. A, posterior and B, right lateral views. Scale bar represents 10 mm.

what is preserved indicates that it projected forward from the anterior end of the bone as a narrow trough. The bifaceted basipterygoid processes extend anterolaterally from the complex. Each has a prominent hourglass-shaped articulating surface, with a dorsal facet directed posterolaterally, and a marginally larger ventral facet orientated anterolaterally. Immediately posterior to the dorsal basipterygoid demi-facets, the lateral walls of the basiparasphenoid of MCZ 1762 have been pushed inwards revealing the underlying vidian canals. Crushing makes it difficult to determine the suture with the proötics. Ventrally, the basal tubera contacted the ventral margins of the proötics and the stapedia footplates.

The longitudinal trough of the sphenethmoid (Text-fig. 16) is open dorsally; the dorsal edges of the trough feature distinct lips that project medially, but these do not appear to have been interconnected by cartilage, as their edges are smoothly finished. The well preserved posterior edge is strongly sigmoidal, as in other forms in which this bone is known. Unfortunately, the anterior portion of the element is missing, and it is impossible to determine how far anteriorly the bone extended.

The proötics (Text-fig. 15) form the relatively gracile dorsum sella. The dorsum sella is poorly preserved in MCZ 1762, but what is present suggests that it resembles a thin, posteriorly-arching wall, which differs significantly from the thick, plate-like structures of other early synapsids. As in sphenacodontids (Romer and Price 1940), the proötic forms the anterolateral wall of the otic capsule, but the free dorsal border is smooth, rounded, and is considerably longer than those described for sphenacodontids (Romer and Price 1940; Eberth 1985).

Each opisthotic (Text-fig. 15) contacts the basiparasphenoid on either side of a deep, ventral emargination representing the lateral margin of the ventral opening of the otic capsule. A ventral flange extends ventrally, abuts the basioccipital tubercle, and marks the posterior edge of the fenestra ovalis. The paroccipital process extends slightly ventrally as well as posterolaterally, and terminates with a blunt, downturned tip. A pronounced ridge at the base of the process on the anteroventral edge abutted the anterior edge of the stapedia dorsal process, and immediately posterior to the ridge lies an elongate scarred area for the reception of the dorsal process of the stapes.

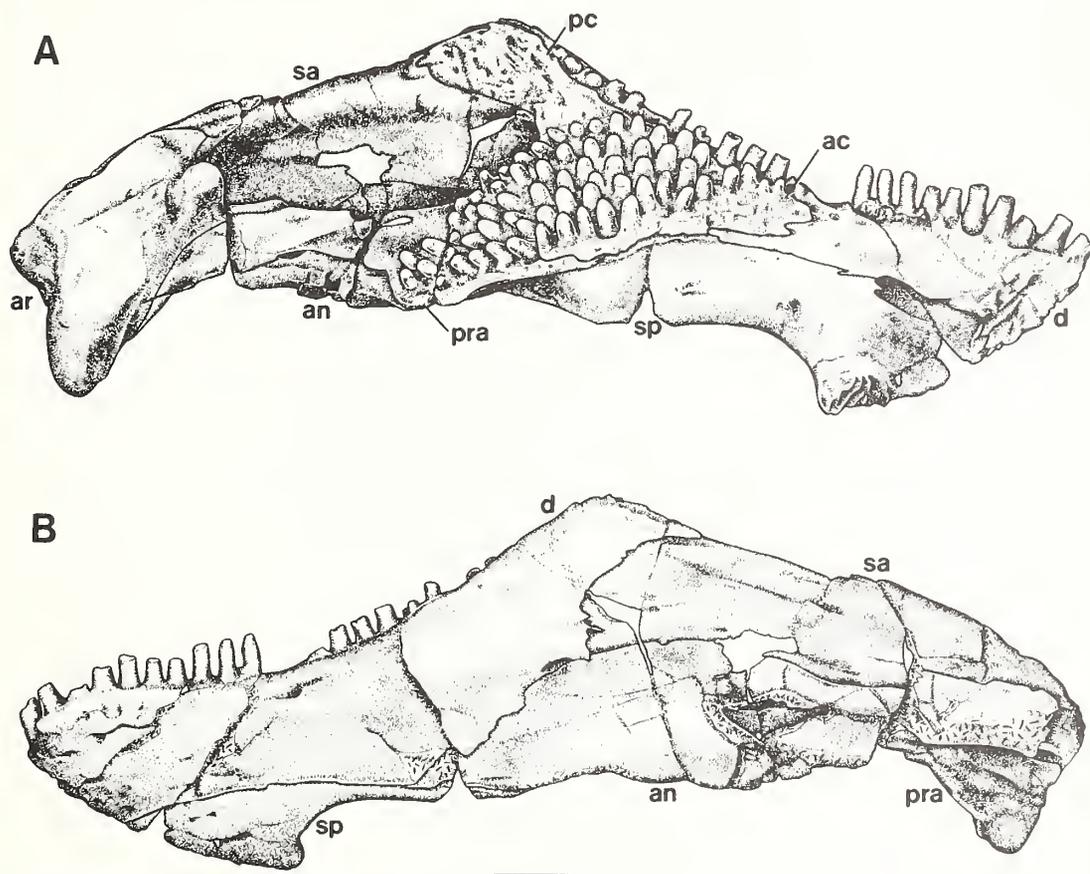
Dorsally, the supraoccipital (Text-fig. 15) lies just below the upper edge of the postparietal, and its unfinished dorsal edge is crenellated for the accommodation of the pilaster-like processes of the latter. Light scarring on the lateral processes marks the sutural surface for the tabular.

The dorsal tips of the exoccipitals constrict slightly the dorsal part of the foramen magnum. The dorsal edge of the shallow notochordal pit on the occipital condyle probably marks the ventral extent of the exoccipitals, and a pronounced median ridge along the floor of the braincase of MCZ 1762, exaggerated by crushing, marks the line of contact between the fused exoccipitals. The basioccipital forms most of the semicircular occipital condyle. The articulating surface of the condyle is separated from its neck by narrow ridges, and a medial ridge, more strongly developed than that seen in sphenacodontids, arises from the ventral lip of the condyle and merges anteriorly with the body of the basioccipital. Paired basioccipital tubera, arched strongly ventrally in parasagittal section, extend laterally to contact the ventral flanges of the opisthotics.

The stapes (Text-fig. 12) is similar to that of sphenacodontids (Romer and Price 1940; Eberth 1985). The dorsal process widens above the footplate, and has a strongly convex lateral margin, which is slightly thinner than the medial edge. The quadrate process is blade-like rather than rod-like as described by Romer and Price (1940). It ends in unfinished bone, and was probably tipped with cartilage. The stapedia foramen is large

relative to the size of the footplate, as two small, thin sheets couple the body to the footplate. The footplate is oval in medial view, with the long diameter aligned parallel to the axis of the stapedial foramen.

Mandible. Relative to its length, the mandible of *Edaphosaurus* (Text-figs 2-3) is much deeper than those of other eupelycosaurian genera. The symphysis can be subdivided into a large, anterodorsal pad and a smaller, posteroventral pad. A large denticulate plate occupies the central third of the lingual surface, and accommodates approximately sixty teeth that are indistinguishable from those of the palatal plates. The tooth plate does not extend as far forward as restored by Romer and Price (1940). The alveolar ridge of the dentary is twisted posteriorly, causing the posteriormost marginal teeth to become medially directed. Except for the vertically aligned angular keel, the jaw leans laterally.



TEXT-FIG. 17. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Left mandible of MCZ 4309. A, medial and B, lateral views. Scale bar represents 10 mm.

The dentary (Text-fig. 17) occupies the anterior 70 per cent. of the mandible in lateral view. It forms most of the anterior symphyseal pad, but makes no contribution to the smaller posterior pad. The anterior pad is incised deeply by an anterior extension of the meckelian canal. Posteriorly, the dentary contacts the angular and surangular with a serrate, overlapping suture, and forms the lateral portion of the angular coronoid eminence. The dentary accommodates about 23 tall, isodont teeth, which, except for their slightly smaller size, resemble those of the upper marginal dentition. The alveolar ridge of the dentary is twisted inwards posteriorly, such that the most posterior marginal teeth lean lingually. Unfortunately, the surfaces of most teeth are damaged, but the orientation of wear present on the labial surfaces of the recumbent teeth suggests that they contacted the upper dentition.

Anteriorly, the splenial (Text-fig. 17) extends downwards and medially as a prominent symphyseal flange, which contacts its fellow at the midline. The anterior half of the symphyseal flange of the splenial is exceedingly thin, such that a pocket lies dorsally between the anterior and posterior symphyseal pads. This condition differs from that seen in *Edaphosaurus pogonias* (AMNH 4009) and *Dimetrodon*, in which the symphyseal area consists of a single large pad. Although the symphyseal flange of the splenial does extend farther ventrally than in other eupelycosaur taxa, it is not as extensive as reconstructed by Romer and Price (1940), as they have apparently restored the mandible vertically. The mandible displays, instead, a strong lateral lean, which foreshortens the lateral exposure of the splenial. Posteriorly, the splenial becomes twisted almost 90° beneath the medially expanded tooth plate, and its posterior edge forms the anterior margin of the caudally-directed inframeckelian foramen.

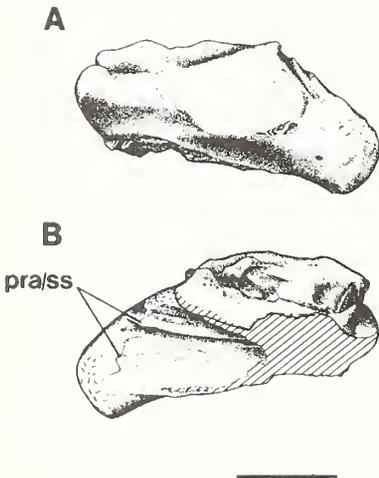
The anterior coronoid (Text-fig. 17) is moderately arched dorsally and accommodates approximately sixteen teeth. Most of the bone overlies the posterior end of the splenial, but anteriorly and posteriorly it has smaller contacts with the dentary and prearticular, respectively. The posterior coronoid (Text-fig. 17) is a typically triradiate structure. The ventral half supports a dense field of about forty isodont, peg-like teeth. The tooth field is approximately four tooth bases wide, but the teeth are not arranged in true rows as in some multiple-tooth rowed captorhinids, as they are irregularly positioned. In ventromedial view, the tooth field is dorsally arched. The tips of several teeth bear oblique facets, which may represent true tooth wear. The superior half of the posterodorsal process is etched deeply by a system of vermiculate grooves, and its dorsal rim bears deep pits and a strong spur, for the insertion of the jaw adductor musculature.

The prearticular (Text-fig. 17) forms most of the floor of the adductor fossa. Its anterior third is expanded medially and accommodates nine teeth. The prearticular overlies a long medial shelf of the angular, but posteriorly this contact becomes attenuated and eventually disappears as the prearticular becomes more closely associated with the articular, where the prearticular becomes exceedingly thin and twisted, and sheathes the ventral face of the pterygoideus process of the articular.

The dorsal margin of the surangular (Text-fig. 17) is moderately arched laterally. It is notably thickened dorsally, but becomes thinner ventrally. Anteriorly, the surangular is sandwiched between the posterodorsal processes of the posterior coronoid and dentary, and the dorsal margin bordering the posterior coronoid is deeply scarred, demonstrating that the *M. adductor mandibulae externus* extended at least this far posteriorly onto the surangular.

The angular (Text-figs 5, 17) is the second largest bone in the mandible. A medially-projecting shelf buttresses the prearticular and forms the ventral margin of the inframeckelian foramen. Ventrally, a deep, vertical keel extends downwards from the body of the angular, and becomes thinner in cross-section distally. The edge of the keel is smoothly finished anteriorly, but the posterior third is thickened and slightly crenulated, which suggests that the edge of the keel may have served as the site of insertion for musculature of uncertain origin. The posterior third of the keel is arched slightly laterally, possibly to allow the pterygoideus musculature to insert on the ventral surface of the pterygoideus process.

The articulating surface for the condyle of the quadrate dominates the dorsal surface of the articular (Text-figs 5, 17-18) and is approximately 50 per cent. longer in antero-posterior dimension than the articulating



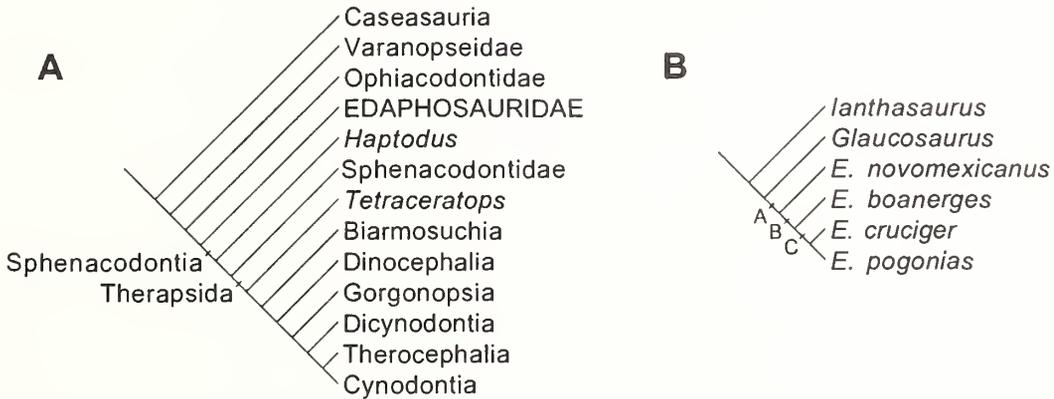
TEXT-FIG. 18. *Edaphosaurus boanerges* Romer and Price 1940; Geraldine Bonebed, Lower Permian; Archer Co., Texas. Right articular of MCZ 1762. A, medial and B, ventrolateral views. Hachure indicates broken surface. Scale bar represents 10 mm.

surface of the opposing quadrate. The inward-tilting surface consists of two main elliptical areas divided by an antero-posteriorly directed ridge which fits into a notch in the quadrate. The ridge continues anteriorly and swells into a large, anterior boss. The anterior process of the articular extends forwards along the floor of the adductor fossa between the surangular and prearticular and narrows anteriorly, ending in unfinished bone that presumably continued forwards as cartilage. A robust retroarticular process projects backwards and bears numerous fine ridges and furrows for attachment of the *M. depressor mandibulae*. In contrast to the reconstruction of the mandible by Romer and Price (1940), the pterygoideus process of the articular projects posteriorly as well as ventromedially. Its posterodorsal surface is marked by pits and grooves, which suggests that the pterygoideus musculature may have inserted at least this far posterodorsally on the process. A longitudinal groove, presumably the chorda tympani canal, traverses the sutural surface for the prearticular (Text-fig. 18).

DISCUSSION

Phylogenetic relationships

The family Edaphosauridae occupies a prominent phylogenetic position among early synapsids as the sister group to Sphenacodontia (*sensu* Reisz *et al.* 1992), the Permo-Carboniferous clade which eventually gave rise to mammals. The relationships of Edaphosauridae to other basal synapsid groups is given in Text-figure 19A.



TEXT-FIG. 19. Phylogenetic trees discussed in the text. A, cladogram showing the phylogenetic position of Edaphosauridae among Palaeozoic Synapsida. Adapted from Rowe (1988), Laurin and Reisz (1990), and Reisz *et al.* (1992). B, cladogram illustrating a hypothesis of edaphosaurid interrelationships. See text for synapomorphies diagnosing nodes A-C.

Edaphosauridae is comprised currently of three genera and nine species from the Permo-Carboniferous of North America and Europe (Reisz 1986; Modesto 1994). Seven edaphosaurid species are assigned to the genus *Edaphosaurus*. However, the assignment of two European species to the genus has been questioned because of the fragmentary nature of their respective holotypes (Reisz and Berman 1986; Modesto and Reisz 1990). Although based upon only fifteen morphological characters, a tentative phylogeny for edaphosaurids presented by Modesto and Reisz (1992) corroborated previous hypotheses concerning interrelationships among the better known species of *Edaphosaurus* (Romer and Price 1940; Reisz and Berman 1986). The Geraldine *E. boanerges* cranial material described here allows for the reinterpretation of the cranial anatomy of other members of the genus. Accordingly, this permits a phylogenetic analysis of *Edaphosaurus* more comprehensive than heretofore possible.

The following edaphosaurid taxa, including *Edaphosaurus boanerges*, form the ingroup: *E. novomexicanus*, from the Permo-Carboniferous of New Mexico, redescribed recently by Modesto and Reisz (1992); the two largest edaphosaurids, *E. cruciger* and *E. pogonias*, from the Lower

Permian of Texas, known adequately from early descriptions (Case 1907; Romer and Price 1940) with both cranial and postcranial material examined by the author. In addition to the cranial information presented in this paper, the postcranial osteology of *E. boanerges* is known from a description by Romer and Price (1940).

Due to their fragmentary nature, three taxa are omitted from the analysis: *Edaphosaurus colohistion*, from the Lower Permian Pittsburgh Formation of West Virginia, excluded as it is known only from a single series of presacral vertebrae and dorsal ribs (Berman 1979); similarly, two small European taxa assigned to the genus (Reisz 1986) are omitted.

The following taxa serve as outgroups: *Ianthosaurus hardestii*, from the Upper Pennsylvanian of Kansas (Reisz and Berman 1986; Modesto and Reisz 1990), and *Glaucosaurus megalops*, from the Lower Permian of Texas and identified recently as an edaphosaurid (Modesto 1994), represent the small, presumably carnivorous, members of the family; *Haptodus garnettensis* (Laurin 1993) and the varanopseid *Mycterosaurus* (Berman and Reisz 1982) serve as more distant outgroups.

Thirty-six characters were used in the analysis. These are described in Appendix 1. Many of these are from the literature (Romer and Price 1940; Brinkman and Eberth 1983; Modesto and Reisz 1992), although a few are new. The analysis was run on a Macintosh Quadra 800 computer using the branch-and-bound algorithm of PAUP 3.1, which is guaranteed to find the most parsimonious trees. Character states were optimized using the delayed transformation (DELTRAN) algorithm and run unordered.

The most parsimonious tree (Text-fig. 19B) requires 38 steps and has a consistency index of 0.973. Synapomorphies are grouped below under the nodes and/or the taxonomic units that they diagnose. Numbers appearing in square brackets refer to character descriptions listed in Appendix 1; multiple character states, indicated as 1 or 2, are encased in parentheses. A negative sign indicates a reversal, and asterisks denote ambiguous characters, which may define more inclusive nodes.

Node A. The following synapomorphies diagnose *Edaphosaurus*: 1. marginal teeth slightly bulbous [1]; 2. alveolar ridges twisted [7]; 3. supraorbital margin expanded laterally [10]; 4. parietal lateral margin deeply concave [11*]; 5. quadrate condylar portion saddle-shaped [14*]; 6. jaw suspension offset ventrally [15*]; 7. skull short [16*]; 8. postorbital and antorbital regions subequal [17*]; 9. tooth plates present [19]; 10. cervical centra short [23*]; 11. neural arches not excavated [-28*]; 12. dorsal vertebrae with elongate transverse processes [29*]; 13. sacral and caudal neural spines with rugose tips [30*]; 14. sacral and caudal neural spines with longitudinal ridges [31*]; 15. caudal neural spine tips expanded sagittally [32*]; 16. caudal neural spines tall and pointed [33*]; 17. dorsal ribs strongly curved [34*]; 18. dorsal rib tubercula greatly reduced [35*].

Node B. These apomorphies diagnose the clade of Texan edaphosaurids, *E. boanerges*, *E. cruciger*, and *E. pogonias*: 1. marginal teeth with cutting edges [2*]; 2. frontal lateral lappet slender [9]; 3. postorbital does not contact squamosal [12*]; 4. mandible short and deep [20*]; 5. splenial lateral exposure enlarged [22*]; 4. ilium with well-developed anterodorsal process [36(2)*].

Node C. These apomorphies diagnose the clade of *E. cruciger* and *E. pogonias*: 1. dentary antero-posterior length equal to or less than two-thirds of mandibular length [21]; 2. swollen-tipped lateral tubercles present [26(2)]; 3. club-shaped anterior presacral neural spines [27].

Eighteen apomorphies diagnose the genus *Edaphosaurus*. Three of these are newly identified *Edaphosaurus* synapomorphies: the twisting of the alveolar ridges [7]; the saddle-shaped quadrate condyle [14]; and the absence of lateral excavations on the neural arches [28]. However, five of the six apomorphies diagnosing the clade of Texan edaphosaurs are ambiguous since they cannot be determined in *E. novomexicanus*, and therefore may represent additional synapomorphies of the genus. Similarly, many of the apomorphies diagnosing *Edaphosaurus* are ambiguous, due to the total absence of postcrania of *Glaucosaurus megalops*. It is possible that analysis of new material attributable to this little edaphosaurid may unite it more strongly to *Edaphosaurus*. The presence of serrations on the marginal teeth, the oblique arrangement of the cutting edges of the marginal teeth, the presence of a medial process on the jugal, the anterior folding of the quadrate flange of

the pterygoid, and the presence of a posterior infra-meckelian foramen, all present in *E. boanerges*, but not currently determinable in other members of the genus, may represent further synapomorphies of *Edaphosaurus*. In the course of compiling the data matrix, two characters used formerly to diagnose this genus were found to be of limited use. The first, reduced marginal dentition (Reisz 1986; Reisz and Berman 1986), is difficult to assess, since eupelycosaurian tooth counts cannot be separated into discrete categories for the purposes of character-state coding. In any event, *Glaucosaurus megalops* possesses fewer marginal teeth than *Edaphosaurus*. The second problematical character, the presence of an ectepicondylar foramen (Romer and Price, 1940; Reisz 1986), can be determined only in *E. boanerges* and *E. pogonias*.

Edaphosaurus boanerges, *E. cruciger*, and *E. pogonias* form a clade, with the latter two species being more closely related to each other than either is to *E. boanerges*. Romer and Price (1940) suggested tentatively that these species may have formed a species phylum, since *E. cruciger* appears to replace *E. boanerges*, and *E. pogonias* in turn appears to replace *E. cruciger* in regular succession in the Wichita and Clear Fork deposits; the sequence would be among the earliest of examples of anagenesis in Amniota. However, the Texan edaphosaurids demonstrably do not form a species phylum, as each possesses at least a single autapomorphy. *Edaphosaurus pogonias* is distinguished among Permo-Carboniferous synspsids in possessing two spade-like dorsal processes on the ilium. Its sister taxon *E. cruciger* is distinguished by one autapomorphy, the anterior margins of the clavicular plate and the clavicular stalk describe a distinct angle in anteroventral view (personal observation of AMNH 4060); the same edges on the clavicles of the other species of *Edaphosaurus* form a continuous, concave margin. *Edaphosaurus boanerges* possesses two autapomorphies: (1) the palatal tooth plates of this species possess 20–50 per cent. more teeth than those of other *Edaphosaurus* species for which tooth-plate tooth counts can be determined; and (2) the jaw symphysis is deeply excavated dorsally. However, these autapomorphies are currently ambiguous, because these characters are indeterminable in the single skull assigned to *E. cruciger*.

Diet and feeding system

The superb quality of the *E. boanerges* cranial material warrants a re-examination of the adaptation to herbivory that has long been attributed to *Edaphosaurus*. Although the genus possesses many features that are shared with other early herbivores, Williston (1914) had misgivings that *Edaphosaurus* was herbivorous, and later postulated a diet of (unspecified) invertebrates (Williston 1916). Case (1918) believed that the morphological evidence available at the time was equivocal, and considered *Edaphosaurus* to have been either exclusively molluscivorous or exclusively herbivorous. Both hypotheses were prompted by the presence of tooth plates on the palate and the inner aspect of the mandible. Romer and Price (1940) concurred with Case's (1918) second hypothesis, remarking that fossils of freshwater molluscs are absent from the terrestrial deposits that have produced *Edaphosaurus* specimens, and added that a large, barrel-shaped rib cage is found only in herbivorous reptiles. However, the adaptation to herbivory in *Edaphosaurus* has been questioned recently (Munk and Sues 1993), and it is therefore necessary to review the evidence supporting the hypothesis of herbivory in this genus.

In addition to the presence of the tooth plate dental batteries and the barrel-shaped body, there are several other, non-dental features mentioned briefly by Romer and Price (1940) and subsequent authors (Olson 1986; Reisz 1986) that lend support to the herbivory hypothesis, largely because they are found also in other herbivorous forms and are not present in carnivorous taxa. These include small skull size, isodonty, reduced marginal tooth number, the abbreviated antorbital region, enlarged temporal fenestrae, the ventral offsetting of the jaw suspension, and antorbital buttressing. The last two features suggest clearly that the preferred food was tougher and more resistant than that utilized by other eupelycosaurian taxa of similar skull size.

With the exception of isodonty, the morphology of the marginal tooth series of *Edaphosaurus* has been ignored completely when the hypothesis of herbivory is considered. Although dental

morphology is the foremost indicator of probable diet in fossil tetrapods, the evidence for edaphosaurid herbivory provided by tooth plate morphology has overshadowed that of the marginal dentition. This is unusual, given that well preserved maxillary teeth from the Briar Creek Bonebed were figured and described briefly by Williston (1916). However, the marginal teeth of *Edaphosaurus* were described by Romer and Price (1940) as slightly bulbous pegs, and hence were considered unremarkable.

The Geraldine material reveals that marginal teeth of *Edaphosaurus* have several features that are consistent with a diet of terrestrial plant foliage. Notably, cutting edges are present on the marginal teeth, and they are inclined obliquely with respect to the long axis of the tooth row. Although this feature is found in some carnivorous reptiles (Molnar and Farlow 1990) as well as in many herbivorous ones, the marginal teeth of *Edaphosaurus* widen slightly before tapering to form distinctive shoulders, a trait that is never observed in the teeth of carnivorous types (Galton 1986). Furthermore, the cutting edges of unworn teeth bear fine, oblique serrations that are emphasized by grooves on the lingual surfaces of the teeth. The oblique orientation of the grooves suggests that the serrations here are strikingly similar to those found in other herbivorous reptiles, which are directed more-or-less apically, rather than those of carnivorous reptiles, which are invariably perpendicular to the cutting edge of the teeth (Galton 1986). Interestingly, many of the mature teeth in *Edaphosaurus* have lost their serrations, which suggests that the preferred food was highly abrasive and possibly siliceous.

The general morphology of the tooth plates is relatively well known (Romer and Price 1940; Modesto and Reisz 1992), and the hypothesis that the plates served to crush food has not been disputed. Romer and Price (1940) observed that the articular facet of the articular was longer antero-posteriorly than that of the quadrate, and suggested that propaliny was probably present. However, they did not elaborate on the subject. The cranial materials described here suggest that propalinal movement of the mandible was a necessary component to the grinding action of the tooth plates. Further evidence for propalinal movement of the jaws comes from additional morphology of the jaw suspension, the orientation of the tooth plates with respect to the jaw suspension, and palatal tooth wear. The strongest evidence for fore-and-aft jaw movement is suggested by the nature of the contact between the quadrate and the articular. The condylar portion of the former is modified from the bicondylar type characteristic of other eupelycosaurs: instead of two parasagittally-aligned, elongate condyles, there is a single, broad, saddle-shaped articulating surface. The trough of the quadrate condyle sat in tongue-and-groove fashion over the antero-posterior ridge that bisects the opposing articulating facet on the articular. As noted by Romer and Price (1940), the articular was clearly capable of antero-posterior translation relative to the quadrate since its articulating facet is approximately 50 per cent. longer antero-posteriorly than that of the quadrate; the overall antero-posterior range of movement appears to have been no more than about 8 mm, or approximately 7 per cent. of the antero-posterior length of the mandible. The long axes of the palatal and mandibular tooth plates are roughly parallel to the plane of articulation between the articular and the quadrate in medial view (Text-figs 2, 17), whereas those of the marginal tooth rows are set at an angle to the axis of translation. This suggests that propaliny was associated with the requirement for an efficient grinding mechanism, and evidence from palatal tooth wear supports this postulate. The tips of most well-preserved tooth plate teeth display oblique bevelling of their lateral and medial surfaces; bevelling of the anterior or posterior surfaces of tooth plate teeth, which would be expected to be equally common if plate occlusion was strictly orthal, is less frequent. An SEM study of tooth plate teeth referable to *E. boanerges* (Olson *et al.* 1991) suggests strongly that the wear was induced by propalinal tooth plate movement. Propalinal jaw action may also have been responsible for the wear seen on the lingual surfaces of the marginal teeth. The bevelling present on the ventral surfaces of the recumbent, posterior maxillary teeth must have resulted from the opposing dentary teeth sliding antero-posteriorly beneath them; it is unlikely that such uniform wear was incurred during orthal occlusion. Since the above-mentioned morphological evidence is identifiable in cranial material of all members of the genus (where preserved), propaliny can be considered an adaptation uniting the species of *Edaphosaurus*.

The jaw musculature must have been arranged appropriately in *Edaphosaurus* in order to effect fore-and-aft movement of the mandibles. The temporal fenestra is antero-posteriorly expanded, suggesting that posterior fibres of the jaw adductor muscles were inclined at roughly 45° relative to the long axis of the mandible, and therefore may have served to draw the mandible posteriorly. The anterior pterygoideus muscle, originating from the dorsal surface of the large palatal tooth plate, probably served to pull the mandible anteriorly. A similar arrangement is hypothesized to power propalinal jaw movement in dicynodonts (Crompton and Hotton 1967; King *et al.* 1989). Interestingly, propalinal jaw movement may have been assisted by a posteriorly-directed muscle attaching to the vertical keel of the angular. The posterior third of the keel is thickened and crenulated, suggesting that it may have served for muscular attachment. The strong evidence for propalinal jaw movement, and its requirement for suitably orientated muscles to power the propalinal jaw stroke, suggests that this may have been the case. Such a peculiar muscular arrangement was suggested also for dinocephalian therapsids, although the hypothetical muscle was considered to assist only in abducting the mandible (Kemp 1982).

Lastly, the peculiar arrangement of the marginal tooth rows, due to the twisting of the alveolar ridges of the maxilla and dentary in all species of *Edaphosaurus*, is an unusual development among Palaeozoic tetrapods; there are no extant analogues that may suggest a reason for such a remarkable condition. What is noteworthy is that the orientation of the marginal teeth alters immediately anterior to the tooth plates, which implies that only the marginal teeth anterior to the tooth plates could function effectively to crop small pieces from food items; the recumbent marginal teeth adjacent to the plates could not take part in cropping actions, as their tips would not be able to slide past their fellows in the opposing dentition. These recumbent maxillary and dentary teeth may have added respectively their lingual and labial surfaces to the total area of the neighbouring tooth plates, as the lingual surfaces of well preserved procumbent marginal teeth display wear suggestive of such contact. However, since the long axes of the marginal tooth rows are positioned at an angle to the axis of propalinal movement, the posterior marginal teeth would only have been able to occlude at the end of the forward translation of the mandible during propalinal jaw movement, as the upper and lower tooth rows would have been drawn apart when the mandible moved posteriorly. Their contribution to the grinding phase of food processing, however, would have been minor compared to that of the tooth plate dentition. Nevertheless, the division in function between the anterior and posterior regions of the marginal tooth rows in this early amniote genus is quite remarkable.

Marginal tooth morphology, tooth plate organization, the evidence for propalinity, and the suite of non-dental features which are shared with known herbivorous reptiles form a character complex that strongly supports the hypothesis of herbivory in *Edaphosaurus*. The feeding system of this genus appears to be the most specialized of the early Permo-Carboniferous synapsids. Food processing appears to have been comprised of two distinct steps: (1) the anterior marginal dentition served to section bite-sized pieces from terrestrial plants; and (2) the tooth plates served to pulverize the food via propalinal jaw action. Grinding presumably prepared the food for fermentative digestion. Among other Palaeozoic tetrapods, compelling evidence for propalinal jaw action has been presented only for dicynodonts, which appear much later in the Upper Permian (King *et al.* 1989). *Edaphosaurus*, therefore, is the oldest amniote known to have been capable of fore-and-aft translation of the mandible. Perhaps more importantly, *Edaphosaurus* is further distinguished as the oldest known amniote to exhibit a dual-purpose, two-step feeding system. Such partitioning of function in the oral region is not seen elsewhere in amniotes until cynodont therapsids appear at the close of the Permian (Kemp 1982).

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REFERENCES

- BERMAN, D. S. 1979. *Edaphosaurus* (Reptilia, Pelycosauria) from the Lower Permian of northeastern United States, with description of a new species. *Annals of the Carnegie Museum*, **48**, 185–202.
- and REISZ, R. R. 1982. Restudy of *Mycterosaurus longiceps* (Reptilia, Pelycosauria) from the Lower Permian of Texas. *Annals of the Carnegie Museum*, **51**, 423–453.
- BRINKMAN, D. B. and EBERTH, D. A. 1983. The interrelationships of pelycosaur. *Breviora*, **473**, 1–35.
- BROOM, R. 1910. A comparison of the Permian reptiles of North America with those of South Africa. *Bulletin of the American Museum of Natural History*, **28**, 197–234.
- CARROLL, R. L. 1988. *Vertebrate paleontology and evolution*. W. H. Freeman and Co., New York, 698 pp.
- CASE, E. C. 1906. On the skull of *Edaphosaurus pogonias* Cope. *Bulletin of the American Museum of Natural History*, **22**, 19–26.
- 1907. Revision of the Pelycosauria of North America. *Carnegie Institution of Washington, Publication*, **55**, 1–176.
- 1918. A mounted skeleton of *Edaphosaurus cruciger* Cope, in the geological collection of the University of Michigan. *Occasional Papers of the Museum of Zoology, University of Michigan*, **62**, 1–8.
- COPE, E. D. 1882. Third Contribution to the history of the Vertebrata of the Permian Formation of Texas. *Proceedings of the American Philosophical Society*, **20**, 447–461.
- CROMPTON, A. W. and HOTTON III, N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). *Postilla*, **109**, 1–51.
- EBERTH, D. A. 1985. The skull of *Sphenacodon ferocious*, and comparisons with other sphenacodontines (Reptilia, Pelycosauria). *Circular of the New Mexico Bureau of Mines and Mineral Resources*, **190**, 1–39.
- GALTON, P. M. 1986. Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs. 203–221. In K. PADIAN (ed.). *The beginning of the age of dinosaurs*. Cambridge University Press, Cambridge, 378 pp.
- HENTZ, T. F. 1988. Lithostratigraphy and paleoenvironments of upper Paleozoic red beds, North-Central Texas: Bowie (new) and Wichita (revised) Groups. *University of Texas, Austin, Bureau of Economic Geology Report of Investigations*, **17**, 1–55.
- KEMP, T. S. 1982. *Mammal-like reptiles and the origin of mammals*. Academic Press, London, 363 pp.
- KING, G. M., OELOFSEN, B. W. and RUBIDGE, B. S. 1989. The evolution of the dicynodont feeding system. *Zoological Journal of the Linnean Society*, **96**, 185–211.
- LAURIN, M. 1993. Anatomy and relationships of *Haptodns garnettensis*, a Pennsylvanian synapsid from Kansas. *Journal of Vertebrate Paleontology*, **13**, 200–229.
- and REISZ, R. R. 1990. *Tetraceratops* is the oldest known therapsid. *Nature*, **345**, 249–250.
- MODESTO, S. P. 1992. Did herbivory foster early amniote diversification? *Journal of Vertebrate Paleontology, Abstracts*, **11**, 49A.
- 1994. The Lower Permian synapsid *Glaucosaurus* from Texas. *Palaontology*, **37**, 51–60.
- and REISZ, R. R. 1990. A new skeleton of *Ianthasaurus hardestii*, a primitive edaphosaur (Synapsida: Pelycosauria) from the Upper Pennsylvanian of Kansas. *Canadian Journal of Earth Sciences*, **27**, 834–844.
- — 1992. Restudy of Permo-Carboniferous synapsid *Edaphosaurus novomexicanus* Williston and Case, the oldest known herbivorous amniote. *Canadian Journal of Earth Sciences*, **29**, 2653–2662.
- MOLNAR, R. E. and FARLOW, J. O. 1990. Carnosaur paleobiology. 210–224. In WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 773 pp.
- MUNK, M. and SUES, H.-D. 1993. Gut contents of *Parasaurus* (Parsiasauria) and *Protorosaurus* (Archosauromorpha) from the Kupferschiefer (Upper Permian) of Hessen, Germany. *Paläontologische Zeitschrift*, **67**, 169–176.
- OLSON, E. C. 1986. Relationships and ecology of the early therapsids and their predecessors. 47–60. In HOTTON III, N., MCLEAN, P. D., ROTH, J. J. and ROTH, E. C. (eds). *The ecology and biology of mammal-like reptiles*. Smithsonian Institution Press, Washington, 326 pp.
- HOTTON III, N. and BEERBOWER, J. R. 1991. Wear of tetrapod teeth as indication of Lower Permian herbivory. *Journal of Vertebrate Paleontology Abstracts*, **11**, 49A.
- OSBORN, H. F. 1903. On the primary division of the Reptilia into two subclasses, Synapsida and Diapsida. *Science*, **17**, 275–276.

- REISZ, R. R. 1986. Pelycosauria. In WELLNHOFER, F. (ed.). *Handbuch der Paläoherpetologie*, Teil 17A. Gustav Fischer Verlag, Stuttgart, 102 pp.
- and BERMAN, D. S. 1986. *Ianthasaurus hardestii* n. sp., a primitive edaphosaur (Reptilia, Pelycosauria) from the Upper Pennsylvanian Rock Lake Shale near Garnett, Kansas. *Canadian Journal of Earth Sciences*, **23**, 77–91.
- and SCOTT, D. 1992. The cranial anatomy of *Secodontosaurus*, an unusual mammal-like reptile (Synapsida: Sphenacodontidae) from the early Permian of Texas. *Zoological Journal of the Linnean Society*, **104**, 127–184.
- ROMER, A. S. and PRICE, L. I. 1940. Review of the Pelycosauria. Geological Society of America, Special Paper, **28**, 1–538.
- ROWE, T. 1988. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology*, **8**, 241–264.
- SANDER, P. M. 1987. Taphonomy of the Lower Permian Geraldine Bonebed in Archer County, Texas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **61**, 221–236.
- WATSON, D. M. S. 1916. Reconstructions of the skulls of three pelycosaurs in the American Museum of Natural History. *Bulletin of the American Museum of Natural History*, **35**, 637–648.
- WILLISTON, S. W. 1914. The osteology of some American Permian vertebrates. 1. *Contributions from Walker Museum*, **1**, 107–162.
- 1916. Synopsis of the American Permo-Carboniferous Tetrapoda. *Contributions from Walker Museum*, **1**, 193–236.

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ABBREVIATIONS USED IN THE TEXT-FIGURES

ac	anterior coronoid	pf	postfrontal
an	angular	pl	palatine
ana	atlantal neural arch	po	postorbital
ar	articular	pop	paroccipital process
ar/ss	sutural surface for articular	pra	prearticular
ber	basicranial recess	pra/ss	sutural surface for prearticular
bo	basioccipital	prf	prefrontal
bpt	basipterygoid process	prm	premaxilla
bps	basiparasphenoid	pro	proötic
cu	cultriform process	pt	pterygoid
d	dentary	q	quadrate
ds	dorsum sella	qfl	quadrate flange of pterygoid
ec	ectopterygoid	qj	quadratojugal
eo	exoccipital	s	stapes
ep	epipterygoid	sa	surangular
f	frontal	sa/ss	sutural surface for surangular
fo	fenestra ovalis	sm	septomaxilla
icf	internal carotid foramen	so	supraoccipital
j	jugal	sp	splénial
l	lacrimal	sq	squamosal
lpso	lateral process of supraoccipital	st	supratemporal
m	maxilla	t	tabular
mj	medial process of jugal	t/ss	sutural surface for tabular
n	nasal	v	vomer
op	opisthotic	vp prf	ventral process of prefrontal
p	parietal	vf op	ventral flange of opisthotic
pc	posterior coronoid		

APPENDIX 1

Description of characters used in the analysis. Characters are listed in order of their location on the skull, the mandible, and the postcranial skeleton.

1. Marginal teeth: taper gradually (0) or are slightly bulbous (1). The marginal teeth of all *Edaphosaurus* species are slightly swollen distally. The teeth of the outgroup taxa taper gradually to their distal tips, and represent the plesiomorphic condition.
2. Marginal teeth: cutting edges are absent (0) or present (1) on mesial and distal surfaces. The marginal teeth of the Texan species of *Edaphosaurus* feature cutting edges on their mesial and distal surfaces. This character is indeterminable in *E. novomexicanus*. No cutting edges are present on the teeth of the outgroup taxa.
3. Premaxillary dentition: larger than (0) or equal to or smaller than (1) the maxillary teeth in basal cross-section. On the basis of basal cross-sectional diameter, the premaxillary teeth are roughly equal to the maxillary teeth in size in both *Glaucosaurus* and *Edaphosaurus*. Because premaxillary teeth are unknown in *Ianthasaurus*, this character may diagnose Edaphosauridae. The presence of premaxillary teeth larger than maxillary teeth (except caniniforms) is primitive for eupelycosaur.
4. Caniniform region: present (0) or absent (1). Neither *Glaucosaurus* nor *Edaphosaurus* possesses a caniniform region. Accordingly, the presence of a caniniform region is the primitive condition.
5. Caniniform tooth: absent (0) or present (1). There is no caniniform tooth in either *Glaucosaurus* or *Edaphosaurus*. The presence of a caniniform represents the primitive condition for edaphosaurids.
6. Maxilla: long, extends past orbit (0) or short, does not extend beyond posterior orbital margin (1). The derived condition diagnoses here the clade of Edaphosauridae plus Sphenacodontia. The long maxilla of *Glaucosaurus* is a reversal (Modesto 1994).
7. Maxillary and dentary alveolar ridges: straight (0) or twisted (1). The alveolar ridges of the maxillae and dentaries of all members of *Edaphosaurus* are twisted such that the orientation of the marginal dentition becomes laterally directed as one progresses posteriorly. The marginal teeth of the outgroup taxa are vertically directed, representing the primitive condition.
8. Prefrontal: ventral process tongue-like (0) or expanded medially (1). In *Glaucosaurus* and *Edaphosaurus* the ventral process of the prefrontal is greatly expanded medially, forming most of the antorbital buttress that characterizes both taxa. The presence of a prefrontal ventral process that is transversely slender is plesiomorphic.
9. Frontal: lateral lappet broad, antero-posterior width no less than one-quarter frontal sagittal length (0) or narrow, antero-posterior width no less than one-ninth frontal sagittal length (1). The lateral lappet of the frontal is remarkably slender in the Texan edaphosaurids, displaying an antero-posterior width approximately one-ninth the sagittal length of the frontal. The lateral lappet of *Haptodus* has an antero-posterior width roughly one-fifth the length of the frontal, whereas the same figure for the edaphosaurids *Edaphosaurus novomexicanus* and *Ianthasaurus* is approximately one-quarter. Although varanopseids are not considered to possess a lateral lappet (Brinkman and Eberth 1983), the frontal of *Mycterosaurus* has a broad contribution to the orbital rim. This character cannot be determined in *Glaucosaurus*.
10. Supraorbital margin: weakly developed, interorbital width less than frontal sagittal length (0) or expanded laterally, interorbital width 50 per cent. greater than frontal sagittal length (1). The supraorbital margin of *Edaphosaurus* is a broad shelf formed by the prefrontal, frontal, and postfrontal. The transverse breadth of the supraorbital margin is roughly 75 per cent. of the antero-posterior length of the frontal, and, accordingly, the orbits are concealed in dorsal view. The supraorbital margins are weakly developed or absent in the other genera, their transverse breadth lying between 26 per cent. and 46 per cent. of the sagittal length of the frontal, and the orbits are clearly visible in dorsal view.
11. Parietal: lateral margin roughly straight or convex (0) or deeply concave (1) in dorsal aspect. The lateral edge of the parietal is deeply bayed in dorsal aspect in all species of *Edaphosaurus*. In *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* the lateral margin of the parietal is straight to markedly convex, interpreted here as a plesiomorphy.
12. Postorbital: contacts (0) or separate from (1) squamosal. The postorbital posterodorsal process in *E. boanerges*, *E. cruciger* and *E. pogonias* is short and does not contact the squamosal. Since the state of this character cannot be determined in either *E. novomexicanus* or *Glaucosaurus*, it may diagnose a more inclusive node with Edaphosauridae. The outgroup taxa are plesiomorphic in that the postorbital contacts the squamosal.

13. Quadratojugal: large and forms ventral margin of posterior cheek (0) or small and covered laterally by squamosal (1). The derived state diagnoses the clade of Edaphosauridae plus Sphenacodontia (*sensu* Reisz *et al.* 1992). This character cannot be determined in *Glaucosaurus*.
14. Quadrate: condyles distinct, separate (0) or confluent, forming a saddle-shaped articulating facet (1). The articulating surface of the quadrate is a single, broad articulating surface that is yoke-shaped in posterior aspect in all *Edaphosaurus* species. Two elongate, rounded ridges present as condyles represents the primitive condition.
15. Jaw suspension: at level of (0) or offset ventrally from (1) maxillary tooth row. In all species of *Edaphosaurus* the jaw suspension is positioned far below the level of the upper tooth row. This is easily demonstrated as a ratio between the distance the jaw suspension lies ventral to the longitudinal axis of the upper marginal tooth row and the length of the cheek (taken along the longitudinal axis of the upper tooth row). In *Edaphosaurus* this figure is approximately 29 per cent. The jaw suspensions of the other genera are primitive in that they lie slightly below the longitudinal axes of their respective upper tooth rows, with a jaw suspension depth falling between 3 per cent. and 12 per cent. of the length of the cheek.
16. Skull: long, eight dorsal centra or more in length (0), or short, five dorsal centra or less in length (1). The skulls of all *Edaphosaurus* species are relatively short, being less than five dorsal centra in length. The skulls of *Ianthasaurus* and the outgroup taxa are at least eight dorsal centra in length; relatively long skulls are therefore primitive.
17. Postorbital region: shorter than (0) or equal to or longer than (1) antorbital region. In all species of *Edaphosaurus*, the antero-posterior length of the postorbital region of the skull is equal to, or even marginally greater than, the antorbital length. The postorbital regions of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are less than half the length of their respective antorbital regions. A postorbital region that is shorter than antorbital length is a plesiomorphy of eupelycosaurs.
18. Pterygoid: transverse flange present (0) or absent (1). A transverse flange is absent from the pterygoid in *Glaucosaurus* and *Edaphosaurus*. Because the palate is unknown for *Ianthasaurus*, this character may diagnose Edaphosauridae. The presence of a transverse pterygoid flange is plesiomorphic for eupelycosaurs.
19. Tooth plates: absent (0) or present (1). *Edaphosaurus novomexicanus* possesses palatal tooth plates that undoubtedly contacted similar plates on the mandibles. Palatal and mandibular tooth plates are present in *E. boanerges*, *E. cruciger*, and *E. pogonias*. The palatal plate is formed by the palatine, ectopterygoid and the pterygoid, whereas the mandibular tooth plate is formed by the anterior and posterior coronoids, and the prearticular. Tooth plates are not present in the outgroup taxa; the absence of tooth plates is the primitive condition for eupelycosaurs.
20. Mandible: dorso-ventral height one-quarter or less (0) or one-third or greater (1) total length. The mandibles of the three Texan edaphosaurs are relatively deep, with a height no less than one-third the total length of the mandible. In contrast, those of *Ianthasaurus*, *Mycterosaurus* and *Haptodus* are relatively slender, with a height equal to or less than one-quarter the total length of the mandible. Since the posterior ends of both the skull and the mandible are absent in *Glaucosaurus*, the character state cannot be determined for this taxon. The mandible is unknown in *E. novomexicanus*.
21. Dentary: comprises 70 per cent. or more (0) or 66 per cent. or less (1) of the mandibular antero-posterior length. The dentaries of *Edaphosaurus cruciger* and *E. pogonias* are 66 per cent. and 63 per cent. of the total length of the mandible, respectively. The dentary of *E. boanerges* is about 70 per cent. of the length of the mandible, and this figure in *Haptodus* and *Mycterosaurus* is roughly 80 per cent. The mandibles of *Ianthasaurus* and *Glaucosaurus* are inadequately known, but resemble more closely those of carnivorous eupelycosaurs. The presence of a dentary that is more than two-thirds the length of the mandible represents the primitive condition for *Edaphosaurus*.
22. Splenial: lateral exposure one-fifth or less (0) or one-third or more (1) the height of the anterior end of the mandible. The splenial is deep and occupies the lower one-third of the anterior end of the mandible in lateral view in those species of *Edaphosaurus* for which mandibular material is available. In contrast, the splenial has only a slender, antero-posteriorly elongate lateral exposure in the outgroup taxa.
23. Cervical centra: equal to or longer than (0) or shorter than (1) mid-dorsal centra. The cervical centra are notably shorter than those of the dorsal centra in *Edaphosaurus*. In contrast, the cervical vertebrae are slightly longer antero-posteriorly than the dorsal vertebrae in *Ianthasaurus* (Reisz and Berman 1986). The cervicals and dorsal are approximately equal in length in *Haptodus* and *Mycterosaurus*. The character state for this and the following characters cannot be determined in *Glaucosaurus*.
24. Presacral neural spines: short (0), or long, more than five times the height of the centrum (1). The presacral neural spines are greatly elongated in all edaphosaurid taxa for which postcrania is available. In the

- outgroup taxa, neural spines are always less than five times the height of the centrum. Other Permian-Carboniferous synapsids feature greatly elongate neural spines, but these have evolved independently (Reisz *et al.* 1992).
25. Presacral neural spines: laterally compressed (0) or subcircular (1) in distal cross section. Except for a short basal portion which is expanded slightly antero-posteriorly, the presacral neural spines of *Ianthasaurus* and *Edaphosaurus* are subcircular in distal cross-section. The presence of blade-like neural spines is primitive for eupelycosaurian synapsids.
 26. Presacral neural spines: lateral tubercles absent (0), present and moderately developed (1), present and gall-like (2). The elongate neural spines of the presacral vertebrae of *Ianthasaurus* and *Edaphosaurus* feature laterally-directed processes. Swollen, gall-like tips are present on many of the tubercles of both *E. cruciger* and *E. pogonias*. The lateral surfaces of the presacral neural spines of the outgroup taxa are devoid of processes, and represent the plesiomorphic condition.
 27. Presacral neural spines: anterior spines are slender (0) or club-shaped (1). The distal ends of the neural spines of the anterior presacral vertebrae of *E. cruciger* and *E. pogonias* are slightly thickened laterally and expanded antero-posteriorly to twice the basal diameter of the subcircular portion of the spine. The expansion is so great that the spines resemble pegged clubs. Romer and Price (1940) report a definite, albeit slight, sagittal expansion of the cervical spines of *E. boanerges*, but clearly not to the extent seen in the other Texan species.
 28. Neural arches: excavated (0) or not excavated (1). The neural arches of all *Edaphosaurus* species do not display the shallow excavations present in those of *Ianthasaurus*, *Haptodus*, or *Mycterosaurus*. The presence of excavations on neural arches is plesiomorphic for eupelycosaurians.
 29. Dorsal vertebrae: transverse processes moderately developed (0) or elongate (1). The transverse processes of the presacral vertebrae of *Edaphosaurus* are elongate. The transverse processes of the outgroup taxa are relatively short transversely, and represent the primitive condition for eupelycosaurians.
 30. Sacral and caudal vertebrae: neural spine tips smoothly finished (0) or rugose (1). The distal tips of the sacral and caudal neural spines in *Edaphosaurus* are roughened with crenulated edges. The tips of the sacral and caudal neural spines in *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are plesiomorphic in that they are smoothly finished.
 31. Sacral and caudal vertebrae: neural spines smooth-sided (0) or with longitudinal ridges (1). The lateral surfaces of the sacral and caudal neural spines of *Edaphosaurus* feature rough, longitudinal ridges. The lateral surfaces of the caudal neural spines of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are plesiomorphic in that they are smoothly finished.
 32. Caudal vertebrae: neural spines are rectangular in lateral aspect (0) or expanded sagittally (1). The distal ends of the caudal neural spines of *Edaphosaurus* are expanded antero-posteriorly. The caudal neural spine tips of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are plesiomorphic in that they are squared in lateral aspect.
 33. Caudal vertebrae: neural spines are short and squared (0) or tall and pointed (1) in lateral aspect. The distal tips of the caudal neural spines of all *Edaphosaurus* species are tall (at least twice the height of the neural arch proper) and taper to pointed tips. The neural spines of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are plesiomorphic in that distally they are squared in lateral aspect, and are never taller than their respective pedicels.
 34. Dorsal ribs: curved proximally only (0) or curved throughout length (1). The dorsal ribs of all species of *Edaphosaurus* are strongly curved throughout their length. Only the proximal regions of the dorsal ribs of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are strongly curved; the distal parts of the ribs are only slightly bowed.
 35. Dorsal ribs: tubercula well developed, flange-like (0) or reduced to low tuberosities (1). The tubercular heads of the dorsal ribs of all species of *Edaphosaurus* are present only as small rugosities. The tubercular heads of the dorsal ribs of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are normally developed as prominent projections of bone, representing the primitive condition for eupelycosaurians.
 36. Ilium: anterodorsal process smaller than posterodorsal process and convex in lateral view (0) or equal to posterodorsal process in size and triangular in lateral view (1). The ilia of the Texan edaphosaurids have triangular, spade-like anterodorsal processes that equal the posterodorsal processes in size. The iliac anterodorsal processes of *Ianthasaurus*, *Haptodus*, and *Mycterosaurus* are low and convex in lateral aspect, and never approach the size of the posterodorsal processes.

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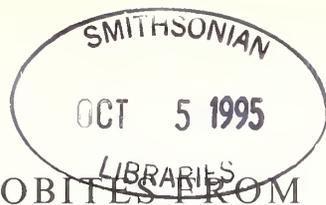
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Cover: This specimen of *Calymene blumenbachii* from the Wenlock of Dudley is mounted in gold, forming the centrepiece of a nineteenth century brooch presented to the Natural History Museum by Miss E. Begg.



LATE CAMBRIAN AGNOSTOID TRILOBITES FROM ARGENTINA

by JOHN H. SHERGOLD, OSVALDO BORDONARO *and* ELADIO LIÑÁN

ABSTRACT. Late Cambrian agnostoid trilobites are described from an *in situ* locality near the base of the El Relincho Formation in Mendoza Province, northwestern Argentina, and from allochthonous blocks in the younger, Ordovician, Empozada and Los Sombreros Formations of Mendoza and neighbouring San Juan Provinces. The faunas of the olistolites fall into three age groups in terms of North American Late Cambrian biochronology: one Trempealeauan and two late Dresbachian assemblages are represented. Species occurring are compared with appropriate taxa from the USA, Canada and Australia. Species of *Lotagnostus* previously described by Rusconi are reassessed on the basis of replicas of the types and the present material.

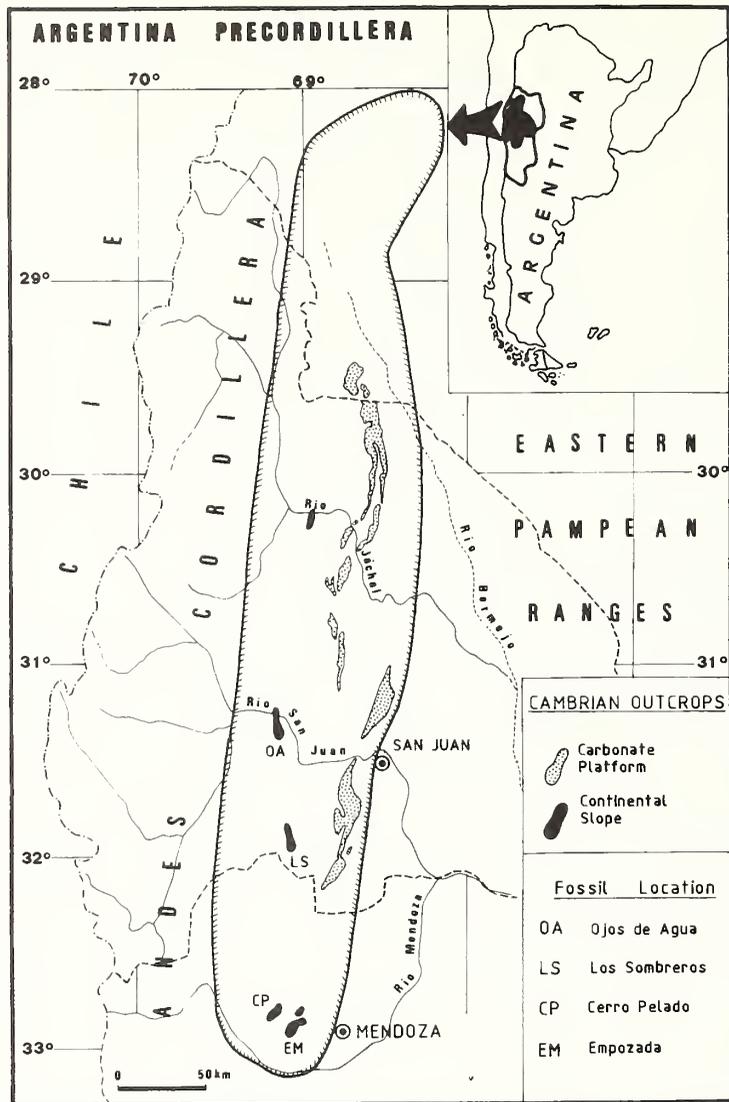
Precordilleran Argentina is a N-S elongated belt about 500 km in length situated between the Pampeanas Ranges to the east and the Cordillera de los Andes to the west. The region contains a fairly complete sequence of Cambrian rocks which have the most abundant and closely investigated trilobite biofacies in South America. These are distributed in two sedimentary environments: carbonate shelf to the east and continental slope to the west (Text-figs 1-2). Cambrian trilobite biofacies follow this distribution: the endemic species inhabited the restricted carbonate shelf whilst the cosmopolitan species are found in the mixed talus facies interdigitating with the open shelf.

STRATIGRAPHY

The stratigraphy of the Cambrian carbonate shelf facies is well known though the work of Baldi and Bordonaro (1985) who studied a continuous sequence from the Lower Cambrian to Lower Ordovician. Currently, the stratigraphy of Cambrian slope facies is not well known because of abrupt facies changes, chaotic sedimentation and relatively poor palaeontological recovery. Text-figure 2 shows a stratigraphical synthesis of the Precordilleran Cambrian rocks. More data can be found in Bordonaro (1992).

Late Cambrian agnostoid trilobites from the Precordillera of Mendoza Province were studied principally by Rusconi (1948, 1950*a*, 1950*b*, 1951*a*, 1951*b*, 1952, 1953, 1954, 1955*a*, 1955*b*, 1955*c*), but many of his determinations are grossly erroneous. Partly as a result of inadequate illustration, much of his work is difficult to interpret. However, the material is extant and revision is possible, so that misleading biostratigraphical conclusions drawn from it may be corrected. Revised generic assignments have been made by Shergold (1977) and Shergold *et al.* (1990). The objective of the present paper is the description of new material from the classic Mendoza locality and from new localities discovered in Mendoza and San Juan. The agnostoids here described are from the Los Sombreros Formation (San Juan Province), Empozada Formation (Mendoza Province), and El Relincho Formation (Mendoza Province).

The Los Sombreros Formation is a sequence of almost one thousand metres thickness cropping out on the eastern flank of the Tontal Range in the western Precordillera of San Juan. It is composed of a talus association of shale and thinly bedded limestone with olistolites, olistostromes, calcareous breccias and channelled conglomerates. The age is not known precisely, but it was probably deposited during the Ordovician, since it is common to find calcareous olistolites containing

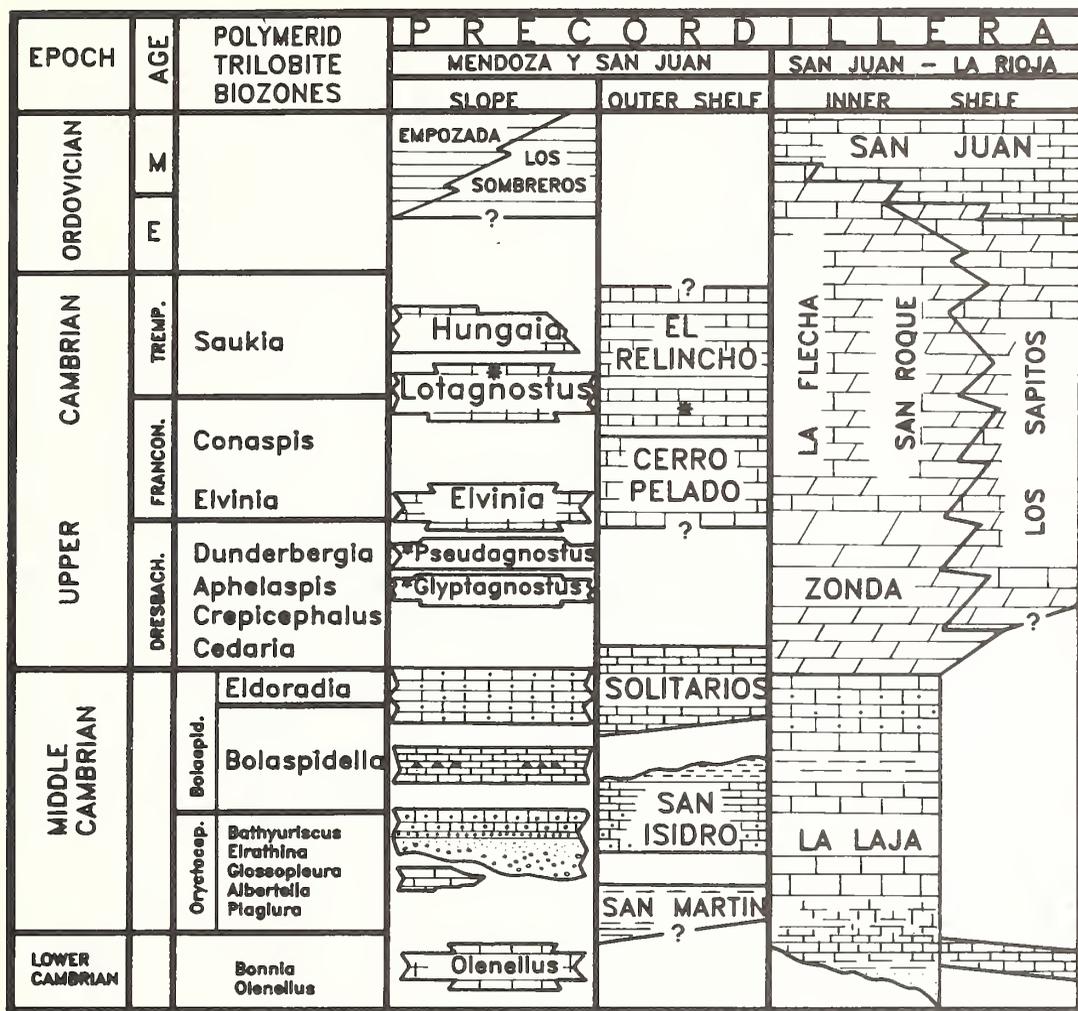


TEXT-FIG. 1. Geographical and geological setting of the Cambrian rocks of Precordilleran Argentina. Material studied here is from localities OA, Ojos de Agua; LS, Los Sombreros; CP, Cerro Pelado; EM, Empozada.

allochthonous Middle and Late Cambrian trilobites, and also autochthonous Early and Middle Ordovician graptolites in dark green shales (Cuerda *et al.* 1983).

The Empozada Formation is about 300 m thick and crops out in the San Isidro area to the west of Mendoza city. It is composed mainly of black shales with abundant calcareous olistolites, breccias and sandstones. It contains allochthonous Late Cambrian trilobites which occur in dispersed calcareous blocks within the lower half of the unit. The age of deposition of the Empozada Formation is at least mid-Ordovician as indicated by the presence of the graptolites *Nemagraptus gracilis* (see Cuerda 1979) and *Glossograptus hincksi*.

The El Relincho Formation is a unit composed mainly of limestone and black shale exposed in Cerro Pelado to the west of Mendoza city. The age of the base of this formation is Late Cambrian



LITHOLOGY

- | | | | | | |
|--|-------------------|--|----------|--|--------------|
| | Limestone | | Marl | | Sandstone |
| | Dolomite | | Limolite | | Conglomerate |
| | Oolitic Limestone | | Shale | | Breccia |

TEXT-FIG. 2. Cambrian stratigraphy of Precordilleran Argentina. In the slope facies of the Los Sombreros Formation, beds containing the names of representative trilobite genera indicate allochthonous blocks. The asterisked names show the biostratigraphical position of the fossils studied against a basically North American timescale.

because conodonts belonging to the *Proconodontus tenuiserratus* Zone have been found (Heredia 1990). The top of the formation is not yet dated.

SYSTEMATIC PALAEOLOGY

All material used in this study is identified as the Bordonaro Collection and is deposited in the collections of the Departamento de Paleontología Invertebrados, Universidad Nacional de San Juan (PIUNSJ), Argentina. Descriptive terminology follows Harrington *et al.* (1959), with additional terms from Öpik (1967), Shergold (1977), and Shergold *et al.* (1990).

- Order AGNOSTIDA Salter, 1864a
- Superfamily AGNOSTOIDEA M'Coy 1849
- Family AGNOSTIDAE, M'Coy, 1849
- Subfamily AGNOSTINAE, M'Coy, 1849
- Genus LOTAGNOSTUS Whitehouse, 1936
- Subgenus LOTAGNOSTUS Whitehouse, 1936

Type species. *Agnostus trisectus* Salter, 1864b, p. 10, by original designation of Whitehouse, 1936, p. 101.

Lotagnostus (Lotagnostus) peladensis (Rusconi, 1951a)

Plate 1, figures 1–9

- v1951 *Homagnostus peladensis* Rusconi, 1951a, p. 2, text-fig. 1.
- v1951 ?*Homagnostus manantialensis* Rusconi, 1951a, p. 2, text-fig. 2.
- v1951 *Triplagnostus pedrensis* Rusconi, 1951b, pl. 7, text-fig. 7.

Material. Many dozens of cephalon and pygidia preserved as calcite exoskeletons, external and internal moulds; studied paradigm PIUNSJ 651–662.

EXPLANATION OF PLATE 1

- Figs 1–9. *Lotagnostus (Lotagnostus) peladensis* (Rusconi, 1951a). 1, PIUNSJ 651; cephalon with exoskeleton mostly preserved; locality CP74, El Relincho Formation, Cerro Pelado, Mendoza; $\times 8$. 2, PIUNSJ 652; laterally compressed cephalon, mostly effaced, showing weak scrobiculation; same locality; $\times 8$. 3, PIUNSJ 653; sagittally compressed cephalon, mostly exfoliated; same locality; $\times 10$. 4, PIUNSJ 654; laterally compressed, mostly exfoliated cephalon, same locality; $\times 8$. 5, PIUNSJ 662; mostly exfoliated cephalon; olistolite LC9, Empozada Formation, San Isidro, west of Mendoza; $\times 8$. 6, PIUNSJ 656; pygidium preserved with thin exoskeletal vestige; locality CP74, El Relincho Formation, Cerro Pelado, Mendoza; $\times 6$. 7, PIUNSJ 657; latex replica of sagittally slightly compressed pygidium; same locality; $\times 6$. 8, PIUNSJ 658; pygidium with exoskeleton preserved, same locality; $\times 6$. 9, PIUNSJ 661; pygidium, largely exfoliated with laterally constricted acrolobe; olistolite LC9, Empozada Formation, San Isidro, west of Mendoza; $\times 10$.
- Figs 10–11. *Lotagnostus (Lotagnostus) attenuatus* (Rusconi, 1955a). 10, MNH Mendoza 18208B; silicone replica of mostly exfoliated, weakly scrobiculate syntype cephalon; 300 m west of San Isidro, Mendoza; $\times 8$. 11, MNH Mendoza 18208A; silicone replica of exfoliated pygidium showing tripartite posterior lobe and faintly constricted, scrobiculate acrolobe; same locality; $\times 8$.
- Fig. 12. *Lotagnostus (Lotagnostus) trisectus* (Salter, 1864). MNH Mendoza 9973; silicone replica of exfoliated strongly scrobiculate cephalon, the original material of *Goniagnostus verrucosus* Rusconi, 1951b; Cerro Pelado, west of Casa de Piedra, Depto de las Heras, Mendoza; $\times 10$.
- Figs 13–15. *Glyptagnostus reticulatus* (Angelin, 1851) *sensu lato*. All material from olistolite LST3, Los Sombreros Formation, Tontal Range, San Juan. 13, PIUNSJ 700; latex replica of sagittally compressed, exfoliated cephalon; $\times 12$. 14, PIUNSJ 699; incomplete, exfoliated cephalon; $\times 8$. 15, PIUNSJ 701; obliquely compressed, exfoliated pygidium; $\times 16$.



Occurrence. Olistolite LC9, Empozada Formation, San Isidro, Mendoza, and locality CP74, at the base of the El Relincho Formation, Cerro Pelado, Mendoza.

Description. Cephalon en grande tenue with non-deliquiate border furrows; acrolobe unconstricted, often very faintly scrobiculate; median preglabellar furrow well-defined; glabella trilobed, with long (sag.) ogival anterior lobe; anterior glabellar furrow well-defined, curved adaxially backwards; anterolateral lobes well-defined, separated by a forward extension of the posterior lobe, constrained posteriorly by prominent lateral furrows at which the glabella is laterally constricted; posterior furrows weakly defined, not transglabellar; posterior lobe elevated, parallel-sided, with angular culmination; axial node placed in anterior half immediately behind the glabellar constriction; basal lobes large, long (exsag.), undivided. Pygidium en grande tenue, quadrangular, with non-deliquiate border furrows; gently constricted, non-scrobiculate acrolobe; axis trilobed, only gently constricted at second lobe; anterior two lobes tricomposite, first axial furrow discontinuous, separated medially by large axial node extending forwards over the two anterior lobes; posterior edges of muscle scar impressions are faintly visible on the second axial lobes of some specimens (Pl. 1, figs 6–7); posterior lobe lanceolate, ending in rounded point and terminal node; minute posterolateral spines situated at level of rear of axis.

Remarks. This species most closely resembles *Lotagnostus (Lotagnostus) hedini* (Troedsson, 1937) because it is essentially non-scrobiculate while remaining en grande tenue. It cannot be synonymized with that species, however, because the anterolateral glabellar lobes are separated by an extension of the median body of the posterior lobe; the basal lobes are longer (exsag.), and in the pygidium the first axial furrow is medially discontinuous. In this last characteristic, *L. (L.) peladensis* resembles *L. (L.) americanus* (Billings, 1860), *L. (L.) asiaticus* Troedsson, 1937 and *L. (L.) punctatus* Lu, 1964.

The synonymy suggested above is based on evaluation of silicone replicas obtained from the Rusconi collection by A. R. Palmer and replicated for Shergold in 1972. Other species of *Lotagnostus* are represented in Rusconi's collections but they differ from the specimens noted above in being more highly scrobiculate. For example, specimens attributed to *Goniagnostus attenuatus* [*sic*] Rusconi (1955c, p. 28, pl. 2, figs 13–14; herein Pl. 1, figs 10–11), which also has a tripartite posterior axial pygidial lobe, *G. rotundatus* Rusconi (1951b, p. 6, text, fig. 6) and *G. verrucosus* Rusconi (1951b, p. 5, text-fig. 5, illustrated as a pygidium; herein Pl. 1, fig. 12) which are based on heavily scrobiculate cephalata. These specimens so closely resemble *L. (L.) trisectus* (Salter, 1864b) that Shergold *et al.* (1990, fig. 9.7a) used the cephalon of *verrucosus* to illustrate the species *trisectus*, thus effectively synonymizing these species (see also Manca 1992, fig. 2).

Age. *L. (L.) peladensis* is associated in olistolite LC9 with the olenid trilobite *Mendoparabolina pirquinensis* Rusconi, 1951a which seems to be a species of *Bienvillia* Clark, 1924 very close to *B. corax* (Billings, 1865). This is known elsewhere from boulders in the Lévis Formation of Quebec (Billings 1865; Rasetti 1944) and Shallow Bay Formation (Cow Head Group) of western Newfoundland (Rasetti 1954; Fortey *et al.* 1982; Ludvigsen *et al.* 1989), and the Gorge Formation of Vermont. In western Newfoundland, *B. corax* is associated with *Lotagnostus (Lotagnostus) hedini* and is representative of the *Keithia schucherti* Fauna, of Sunwaptan age, correlated with the *Saukiella serotina* Subzone of the *Saukia* Zone in continental USA (e.g. Oklahoma) (see Ludvigsen *et al.* 1989). Judging from the morphological similarity of the taxa in LC9, a similar age may be assumed.

Genus ONCAGNOSTUS Whitehouse, 1936
Subgenus ONCAGNOSTUS Whitehouse, 1936

Type species. *Agnostus hoi* Sun, 1924, p. 28; by original designation of Whitehouse 1936, p. 84.

Oncagnostus (Oncagnostus) sp.

Plate 3, figures 13–15

Material. The internal and external moulds of a single cephalon, and the external mould of a pygidium, PIUNSJ 678–679.

Occurrence. Olistolite Em O1, Empozada Formation, San Isidro, Mendoza.

Description. Cephalon en grande tenue, with narrow (sag.) borders and deliquiate border furrows, and weakly scrobiculate, unconstricted acrolobe divided sagittally by median preglabellar furrow; glabella proportionately short (sag.), elevated, with weakly ogival anterior lobe differentiated from posteroglabella by strong, continuous, anterior transglabellar furrow; posteroglabella with prominent lateral notches behind anterolateral lobes and adjacent to front of basal lobes as in some species of *Immitagnostus*; condition of glabellar culmination unknown; axial glabellar node at mid-length of posteroglabella; basal lobes more extensive transversely than exsagittally; short posterolateral spines.

Pygidium en grande tenue, with non-deliquiate border furrows and unconstricted, non-scrobiculate acrolobe, lacking a median post-axial furrow; relatively long (sag.) axis, laterally inflated, constricted where the first segmental furrow intersects the axial furrow; first furrow interrupted medially, defining anterolateral ellipsoidal lobules; second axial furrow interrupted medially by prominent, elongate axial node which extends on to front part of posterior lobe; posterior lobe longer (sag.) than anterior two lobes combined, laterally inflated, posteriorly broadly rounded, bearing nodular lines, but poorly defined terminal node; posterolateral spines prominent, retrally sited across the rear of the pygidial axis.

Remarks. *Oncagnostus* (*Oncagnostus*) was revived by Shergold *et al.* (1990) to include four species previously classified within the closely related *Aagnostus* (*Homagnostus*). The pygidia of the subgenera are similar in that they both develop anterolateral lobules on the pygidial axis and accordingly do not have a continuous transaxial anterior furrow. In general, however, species of *Oncagnostus* have deliquiate border furrows in both cephalon and pygidium, have an often long (sag.) and inflated pygidial axis which is broadly rounded posteriorly, and a relatively broader (tr.) glabella. They often lack a median preglabellar furrow, but not in the presently described species, and they frequently have retral posterolateral pygidial spines lying level (tr.) with the posterior end of the pygidial axis. The pygidium of our species resembles *Homagnostus comptus* Palmer (1962, pl. 1, fig. 13), from Nevada, *H. tumidosus* Hall and Whitfield *sensu* Palmer (1968, pl. 7, fig. 8) from Alaska, *Homagnostus* sp. 2 *sensu* Shergold (1982, pl. 5, fig. 12), from western Queensland, and, to some extent, specimens from southern Alberta referred to *Homagnostus obesus* (Belt) by Westrop (1986, pl. 1, figs 1–3). The cephalon is also not unlike that assigned by Palmer (1962, pl. 1, fig. 12) to *H. comptus*, but the North American specimen lacks a median preglabellar furrow. Most similar is the specimen that Öpik (1963, pl. 2, fig. 12) referred to *Immitagnostus* [*Aagnostus*] *inexpectans* (Kobayashi) which is comparably en grande tenue, weakly scrobiculate and has an identical glabellar format, including the centrally situated axial glabellar node. Species of *Immitagnostus* seemingly are characterized by an axial node located farther towards the anterior of the posteroglabella, and frequently the anterior glabellar lobe is cleft slightly by the median preglabellar furrow. However, this is not always the case, and the possibility of the Argentinian specimen described here representing *Immitagnostus* rather than *Oncagnostus* cannot be dismissed. More material is required to confirm the present determination.

Age. The species mentioned above are from the late Dresbachian of the USA and equivalent Idamean Stage of Australia. The Nevadan and Australian species occur within the *Glyptagnostus reticulatus* Range Zone, but the Alaskan species is associated with *Acmarhachis acuta* (Kobayashi), and is probably representative of the *Dunderbergia* Zone of the Great Basin. The Albertan specimens are slightly younger, occurring in the *Irvingella major* Subzone of the *Elvinia* Zone.

Genus TRILOBAGNOSTUS Harrington, 1938

Type species. *Aagnostus innocens* Clark, 1923, p. 122; by original designation of Harrington, 1938, p. 148.

Trilobagnostus? sp.

Plate 2, figures 1–9

Material. Thirteen cephalata and seven pygidia preserved as calcite exoskeletons, PIUNSJ 663–677.

Occurrence. Olistolite Em O2, Empozada Formation, San Isidro, Mendoza.

Description. Subrectangular cephalon, strongly convex, narrow, non-deliquate border furrow; unconstricted acrolobe, non-scribulate; lacking median preglabellar furrow; glabella essentially bilobed, short, with subspherical frontal lobe; anterior glabellar furrow well defined and weakly curved backward; posterior lobe convex, unfurrowed, with broadly rounded culmination; axial node subcentral; small basal lobes.

Pygidium subrectangular, degree of deliquation of border furrow depending on preservation, internal moulds being deliquate but external moulds being non-deliquate; narrow borders; unconstricted, non-scribulate acrolobe, lacking median post-axial furrow; moderately long axis (sag.), tapering rearwards, posteriorly rounded; anterolateral lobes well defined, as in *Oncagnostus* (*Oncagnostus*) delimited by furrows that are curved forward, not transaxial; second furrow interrupted medially by prominent axial node lapping on to the front of the posterior lobe which narrows rearwards, failing to extend to the posterior border furrow; insignificant terminal node; stout, incurved posterolateral spines retrally sited to the rear of the termination of the axis.

Remarks. Material from Em O2 is compared with the type species of *Trilobagnostus* which has recently been refigured as *Micragnostus innocens* (Clark, 1923) by Ludvigsen *et al.* (1989, p. 12, pl. 1, fig. 25). These authors remark on the length of the pygidial axis and the nature of its anterolateral furrows, and illustrate a similar border furrow and retral posterolateral spines to those described here. Also very similar are the specimens from Jilin Province, China, which Qian (1986, p. 263, pl. 67, figs 1–7) placed in *Geragnostus* (*Micragnostus*) cf. *subobesus* (Kobayashi, 1936), but these are likely to be slightly younger. Shergold *et al.* (1990) noted the apparent similarity of *Trilobagnostus* to the subgenera of *Oncagnostus* as conceived by them (*Oncagnostus*, *Kymagnostus* and *Strictagnostus*) and suggested that it could form a fourth subgenus. There is also great similarity to species of *Eurudagnostus*, especially *E. brevispinus* Lermontova (1951, pl. 2, figs 5–6, non fig. 7) and *Rudagnostus*, which is reflected in the synonymies proposed by Shergold *et al.*, i.e. *Eurudagnostus* [= *Oncagnostus*] and *Rudagnostus* [= *Trilobagnostus*]. However, all the taxa involved require thorough revision and reassessment beyond the scope of this paper. Our present uncertainty is expressed in the question mark and open nomenclature.

Age. The type specimen of *Trilobagnostus innocens* (Clark) is associated with a species of *Lotagnostus* of the *hedini* group. Thus a Late Cambrian, *Saukia* Zone, age is probable for it. By inference, *Trilobagnostus?* sp. may have a similar age, possibly the same as *Lotagnostus* (*Lotagnostus*) *peladensis* (Rusconi).

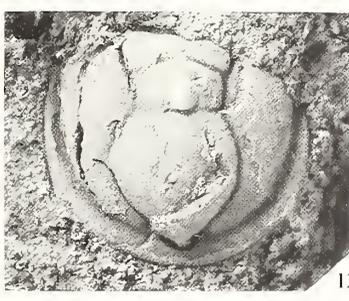
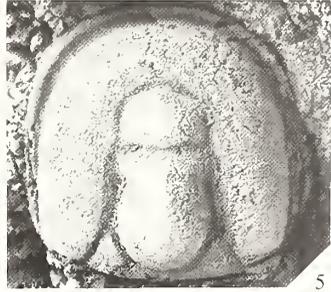
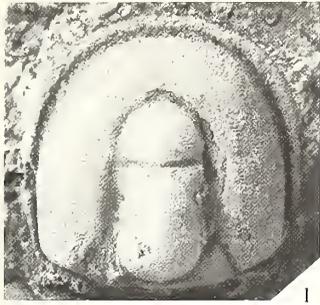
Subfamily GLYPTAGNOSTINAE Whitehouse, 1936

Genus GLYPTAGNOSTUS Whitehouse, 1936

Type species. *Glyptagnostus toreuma* Whitehouse, 1936, p. 101 [= *Aagnostus reticulatus* Angelin, 1851, p. 8].

EXPLANATION OF PLATE 2

Figs 1–9. *Trilobagnostus?* sp. All material from olistolite Em O2, Empozada Formation, San Isidro, west of Mendoza. 1, PIUNSJ 663; cephalic exoskeleton; × 14. 2, PIUNSJ 664; cephalic exoskeleton; × 14. 3, PIUNSJ 665; cephalon with most of exoskeleton preserved; × 10. 4, PIUNSJ 666; latex replica of cephalic exoskeleton; × 12. 5, PIUNSJ 667; latex replica of cephalic exoskeleton; × 14. 6, PIUNSJ 668; latex replica of cephalic exoskeleton; × 12. 7, PIUNSJ 674; latex replica of pygidial internal mould; × 14. 8, PIUNSJ 675; pygidium with exoskeleton largely preserved; × 14. 9, PIUNSJ 676; partly exfoliated pygidium; × 12. Figs 10–14. *Acmarghachis* sp. cf. *A. acuta* (Kobayashi, 1938, *sensu* Rasetti, 1961). All material from olistolite OA2, Los Sombreros Formation, San Juan. 10, PIUNSJ 694a; partly exfoliated cephalon; × 24. 11, PIUNSJ 695; partly exfoliated cephalon; × 16. 12, PIUNSJ 696; largely exfoliated pygidium; × 12. 13, PIUNSJ 697; partly exfoliated pygidium; × 20. 14, PIUNSJ 698; incomplete pygidial exoskeleton; × 16. Fig. 15. *Neoagnostus* (*Neoagnostus*) sp., PIUNSJ 703; internal mould of small pygidium; locality CP74, El Relincho Formation, Cerro Pelado, Mendoza; × 20.



Glyptagnostus reticulatus (Angelin, 1851) *sensu lato*

Plate 1, figures 13–15

Material. Three cephalae and two pygidia preserved as external moulds, PIUNSJ 699–702.*Occurrence.* Olistolite T3, Los Sombreros Formation, Sierra del Tontal, San Juan.*Remarks.* Although very poorly preserved, this material has the typical characteristics of *Glyptagnostus reticulatus* (Angelin), and, eventually, when more material is available it may be possible to refer it to the subspecies *reticulatus reticulatus*. The material illustrated here is the first record of this cosmopolitan species in South America. Essentially comparable material occurs in Australia (Shergold 1982) and the Ellsworth Mountains of West Antarctica (Shergold and Webers 1992).*Age.* All material is representative of the *Glyptagnostus reticulatus* Zone, recognized worldwide (see references in Shergold 1982).

Subfamily INCERTAE SEDIS

Genus ACMARHACHIS Resser, 1938

Type species. *Acmarhachis typicalis* Resser, 1938, p. 47, by original designation.*Acmarhachis* cf. *A. acuta* (Kobayashi, 1938) *sensu* Rasetti, 1961

Plate 2, figures 10–14

cf. 1961 *Acmarhachis acuta* (Kobayashi); Rasetti, p. 109, pl. 23, figs 1–8 (see Pratt, 1992, p. 39 for synonymies).*Material.* Thirteen cephalae and nine pygidia preserved as external moulds and exoskeletons; studied paradigm PIUNSJ 694–698.*Occurrence.* Olistostrome level OA2, Los Sombreros Formation, Sierra del Tontal, San Juan.*Description.* Cephalic border narrow, gently convex; border furrow subdeliquiate, narrow and deep; acrolobe smooth, unstricted, lacking median preglabellar furrow, although some specimens have an incipient furrow in front of the glabella. Glabella long and narrow, with elongate, semicircular anterior lobe; anterior glabellar furrow deep, gently arched forwards; anterolateral furrow shallow and chevronate; the posterior lobe is tumid with elevated culmination, laterally constricted where the chevronate anterolateral furrow intersects the axial furrow; axial glabellar node subcentral on the posterior lobe. Pygidium subrectangular, border narrow and uniform, with diminutive, advanced posterolateral spines; border furrow subdeliquiate, shallow; acrolobe unstricted; axis long and posteriorly ogival; second axial segment subpentagonal and laterally constricted, with a large, prominent axial node; the posterior lobe is lanceolate, its tapered posterior end bearing a terminal node which touches the border furrow. In very small specimens, the posterior lobe is more rounded.*Remarks.* *Acmarhachis* was reappraised by Pratt (1992, p. 38), who considered it to represent a pseudagnostine genus. However, for reasons earlier explained (Shergold 1982; Shergold *et al.* 1990), we prefer to retain *Acmarhachis* within the Agnostidae. Pratt also listed previously described species, grouping most into the American species *A. typicalis* and *A. acuta*. Among the species that he documented, the Argentinian material most closely resembles the former in terms of the diagnostic characteristics of the first segment of the pygidial axis, being laterally undivided. In North America, *A. typicalis* has been described from the North West Territories of Canada (Kobayashi 1938; Pratt 1992), Nevada (Palmer 1962), and Alabama (Resser 1938), where it has an early Dresbachian, *Crepicephalus* Zone, age. However, in terms of furrowing, axial proportions and shape, the Argentinian species clearly most resembles that from Maryland, described by Rasetti (1961) as *Acmarhachis acutus* (Kobayashi, 1938), of late Dresbachian, *Dunderbergia* Zone, age. The

Argentinian species differs from the youngest species so far documented, *A. hybrida* (Shergold, 1980, p. 20, pl. 11, figs 1–6), from western Queensland, in the position of the axial glabellar node. This lies farther forward in the Australian species, which is further distinguished by the presence of a faint median preglabellar furrow.

Age. *Amarhachis acuta* (Kobayashi) reportedly has a long range from late in the Middle Cambrian through to the early part of the Late Cambrian in North America, Siberia, Kazakhstan, south-central China and northern and southeastern Australia. The Argentinian species appears most likely to date from the later part of this range.

Family DIPLAGNOSTIDAE Whitehouse, 1936 emend. Öpik, 1967
Subfamily PSEUDAGNOSTINAE Whitehouse, 1936

Genus PSEUDAGNOSTUS Jaekel, 1909
Subgenus PSEUDAGNOSTUS Jaekel, 1909

Type species. *Agnostus cyclopyge* Tullberg, 1880, p. 26, by original designation of Jaekel 1909, p. 400.

Pseudagnostus (Pseudagnostus) idalis idalis Öpik, 1967

Plate 3, figures 1–6

1982 *Pseudagnostus (Pseudagnostus) idalis idalis* Öpik, 1967; Shergold, p. 26, pl. 2, figs 1–13 [with synonymy].

Material. Six cephalata and two pygidia, preserved as calcitic internal moulds and exoskeletons, PIUNSJ 680–685.

Occurrence. Olistolite Em O1, Empozada Formation, San Isidro, Mendoza.

Description. Cephalon en grande tenue, strongly deliquiate, with unconstricted acrolobe; preglabellar median furrow deeply incised, widening forward; spectaculate, anterior glabellar furrow being gently curved backward. Pygidium en grande tenue, strongly deliquiate, with gently constricted acrolobe, plethoid and ampullate deutero-lobe; retral posterolateral spines sited a little forward of a transverse line drawn across the rear of the deutero-lobe.

Age. According to Shergold (1982), this taxon characterizes the Late Cambrian, Idamean, zones of *Glyptagnostus reticulatus*, *Proceratopyge cryptica* and *Stigmatia diloma* in the Georgina Basin, western Queensland, Australia.

Pseudagnostus (Pseudagnostus) idalis Öpik, 1967 *sensu lato*

Plate 3, figures 7–12

Material. Eight cephalata and twelve pygidia preserved as external moulds and exoskeletons, PIUNSJ 686–693.

Occurrence. Olistostrome level OA2, Los Sombreros Formation, Sierra del Tontal, San Juan.

Remarks. The Pseudagnostidae from the Los Sombreros Formation have morphologies referable to *Pseudagnostus (P.) idalis* Öpik *sensu lato* according to the classification of Shergold (1977). In general, the exoskeleton shows a higher degree of effacement than *Ps. (Ps.) idalis idalis* as described above. However, it cannot be assigned to any known subspecies because of differences in preservation. This taxon differs from *Ps. (Ps.) idalis s. l.* of Shergold (1982, pl. 2, figs 14–15) because its cephalon has substantially less deliquiate border furrows and better defined anterolateral glabellar lobes. Pygidia may be essentially similar, but their varying modes of preservation prevent detailed comparison. Preservation also prevents adequate comparison with *Ps. (Ps.) idalis denisonensis* Jago (1987, p. 210, pl. 24, figs 4–12) from southwestern Tasmania, and *Pseudagnostus* spp. described by Jell *et al.* (1991, p. 463, figs 4–5) from western Tasmania, although the former shares with the Argentinian taxon a similar, subcentrally positioned, axial glabellar node. Also

similar, on some specimens of *Ps. (Ps.) idalis s.l.*, is the sagittally elongated deutero-lobe, which may have a central depression. Such features, however, may be related to preservation. Both of the Tasmanian occurrences are slightly younger than the Idamean as defined by Shergold (1982, 1989, 1993). Specimens with similar morphologies from western Zhejiang Province, China, described by Lu and Lin (1989, p. 232, pl. 14, figs 1–4), are also assigned to *Pseudagnostus (Ps.) idalis* Öpik. These occur in the *Proceratopyge fenghwangensis* Zone, which correlates with the late Idamean of Australia.

Genus NEOAGNOSTUS Kobayashi, 1955
Subgenus NEOAGNOSTUS Kobayashi, 1955

Type species. Neoagnostus aspidoides Kobayashi, 1955, p. 473, by original designation.

Neoagnostus (Neoagnostus) sp.

Material. A single small pygidium measuring (Lp2) 1.9 mm, PIUNSJ 703.

Occurrence. Locality CP74, autochthonous El Relincho Formation, Cerro Pelado, Mendoza Province.

Description. Pygidium with comparatively wide (tr, sag.) borders, non-deliquate border furrows and minute posterolateral spines; rounded and laterally unconstricted acrolobe; axis with effaced anterior transaxial furrow, axial node situated across (sag.) second lobe, defined only posteriorly; effaced accessory furrows; deutero-lobe short (sag.), barely defined but with terminal axial node indicated.

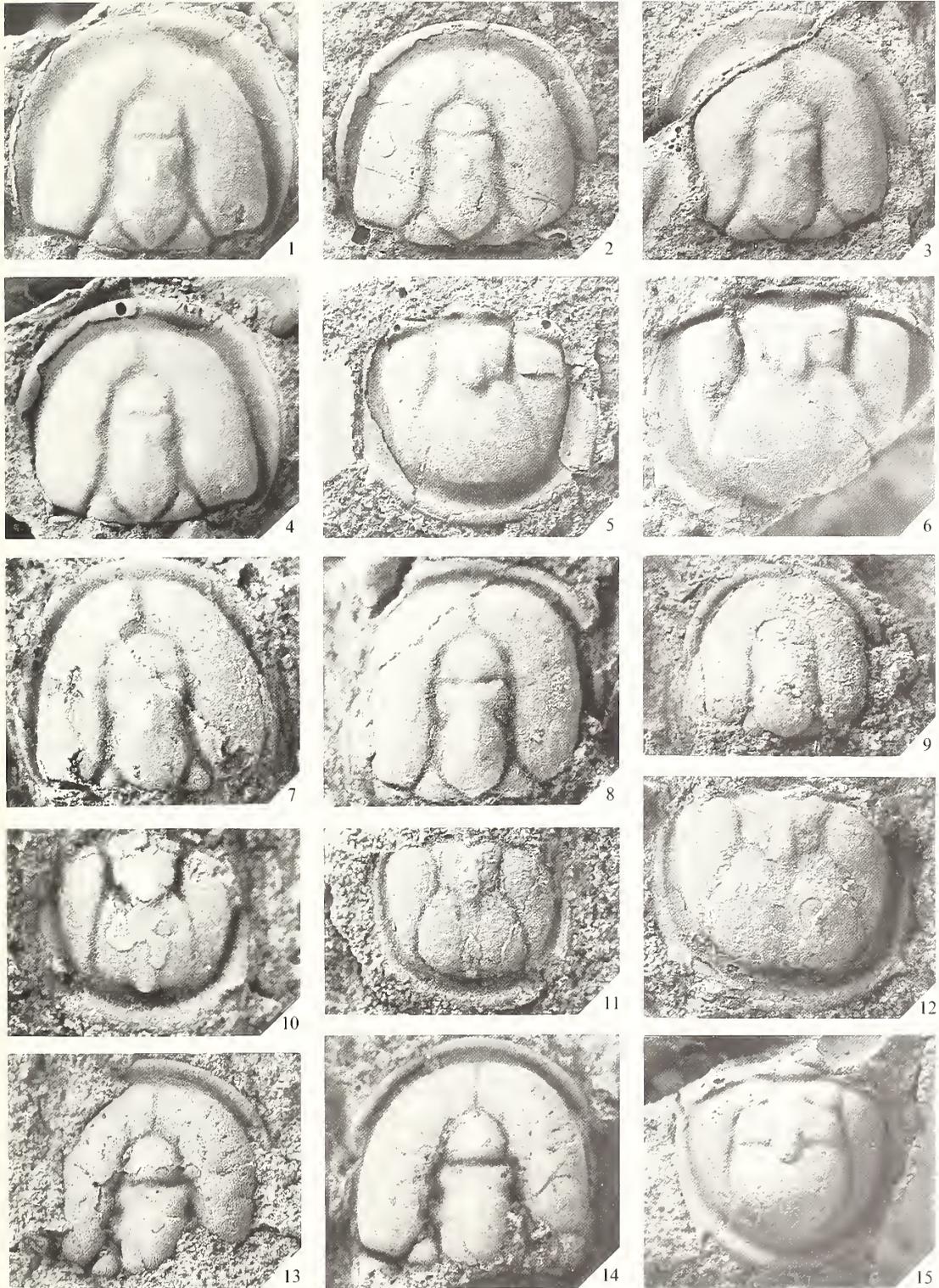
Remarks. The combination of extremely small posterolateral spines, subcircular acrolobe and short (sag.) deutero-lobe permit comparison with previously described material from China, Australia and North America (Vermont). *Neoagnostus (N.) longicollis* (Kobayashi, 1966) *sensu* Zhou and Zhang (1985, p. 68, e.g. pl. 27, fig. 7), from northern Shanxi and southern Jilin, is essentially similar except that it possesses a third pair of axial lobules. *N. (N.) araneavelatus* (Shaw, 1951, especially pl. 24, fig. 15) from Vermont, and *N. (N.) orbiculatus* (Shergold, 1975, particularly pl. 12, fig. 10) from western Queensland, Australia, have more circular acrolobes. *N. (N.) quasibilobus* (Shergold, 1975, see pl. 12, figs 5–7), also from western Queensland, has the most similar acrolobe morphology, but seems to have more prominent posterolateral spines. All of these species have virtually effaced anteroaxes and imperceptible deutero-lobes. All similarly occur in the latest Cambrian: Fengshanian, *Mictosaukia orientalis* Assemblage Zone in Shanxi and *Changia* Assemblage Zone of Jilin in China; Payntonian, *Neoagnostus (N.) quasibilobus*/*Shergoldia nomas* Assemblage Zone in western Queensland; and their equivalents in Vermont.

EXPLANATION OF PLATE 3

Figs 1–6. *Pseudagnostus (Pseudagnostus) idalis idalis* Öpik, 1967. All material from olistolite Em O1, Empozada Formation, San Isidro, west of Mendoza. 1, PIUNSJ 680; internal mould of cephalon; × 10. 2, PIUNSJ 681; latex replica of mostly exfoliated cephalon; × 10. 3, PIUNSJ 682; latex replica of cephalic internal mould; × 10. 4, PIUNSJ 683b; latex replica of cephalic internal mould; × 10. 5, PIUNSJ 685; latex replica of largely exfoliated pygidium; × 12. 6, PIUNSJ 684; internal mould of pygidium; × 10.

Figs 7–12. *Pseudagnostus (Pseudagnostus)* sp. cf. *P. idalis* Öpik, 1967 *sensu lato*. All material from olistolite OA2, Los Sombreros Formation, San Juan. 7, PIUNSJ 686; mostly exfoliated cephalon; × 16. 8, PIUNSJ 687; small cephalic internal mould; × 20. 9, PIUNSJ 688; mostly exfoliated cephalon; × 16. 10, PIUNSJ 689; early holaspide pygidium showing initial development of deutero-lobe; × 24. 11, PIUNSJ 690; internal mould of early holaspide pygidium with fully developed deutero-lobe; × 16. 12, PIUNSJ 691; internal mould of late holaspide pygidium; × 16.

Figs 13–15. *Oncagnostus (Oncagnostus)* sp. All material from olistolite Em O1, Empozada Formation, San Isidro, west of Mendoza. 13, PIUNSJ 678b; latex replica of partly exfoliated, weakly scrobiculate cephalon; × 16. 14, PIUNSJ 678a; counterpart of fig. 13, cephalic exoskeleton; × 16. 15, PIUNSJ 679; latex replica of exfoliated pygidium; × 14.



SUMMARY

Late Cambrian agnostoids have been obtained from the autochthonous El Relincho Formation, and from five olistolites in the Empozada and Los Sombreros Formations (Text-fig. 3). Agnostoids

MENDOZA					SAN JUAN		
Unit	Order of Occurrence of Olistolites	Agnostoids	Autochthonous Unit	Agnostoids	Unit	Order of Occurrence of Olistolites	Agnostoids
EMPOZADA FORMATION	Em 02	→ ? <i>Trilobagnostus</i> sp	EL RELINCHO FORMATION	CP74 → <i>Lotagnostus</i> (L.) <i>peladensis</i> <i>Neoagnostus</i> (N.) sp.	LOS SOMBREROS FORMATION	LST3	→ <i>Glyptagnostus reticulatus</i>
	Em 01	→ <i>Pseudagnostus idalls idalls</i> <i>Oncagnostus</i> (O.) sp.				OA2	→ <i>Pseudagnostus idalls</i> <i>Acmarrhachis</i> cf. <i>acuta</i>
	LC9	→ <i>Lotagnostus</i> (L.) <i>peladensis</i>					
EMPOZADA FORMATION	LC9	→ <i>Lotagnostus</i> (L.) <i>peladensis</i>	EL RELINCHO FORMATION	CP74 → <i>Lotagnostus</i> (L.) <i>peladensis</i> <i>Neoagnostus</i> (N.) sp.	LOS SOMBREROS FORMATION		
	Em 02	→ ? <i>Trilobagnostus</i> sp					
	Em 01	→ <i>Pseudagnostus idalls idalls</i> <i>Oncagnostus</i> (O.) sp.				OA2	→ <i>Pseudagnostus idalls</i> <i>Acmarrhachis</i> cf. <i>acuta</i>
						LST3	→ <i>Glyptagnostus reticulatus</i>

TEXT-FIG. 3. A, Stratigraphical distribution of the olistolites in the Empozada and Los Sombreros Formations; B, their inferred biochronological order. Note that the fauna recorded from the El Relincho Formation at Cerro Pelado is autochthonous, and also the youngest of the faunas described.

identified from them include: CP74, *Lotagnostus (Lotagnostus) peladensis* (Rusconi), *Neoagnostus (Neoagnostus) sp.*; LC9, *Lotagnostus (Lotagnostus) peladensis* (Rusconi); Em O2, *Trilobagnostus?* sp.; Em O1, *Oncagnostus (Oncagnostus) sp.*, *Pseudagnostus (Ps.) idalis idalis* Öpik; OA2, *Acmarhachis cf. A. acuta* (Kobayahsi), *Pseudagnostus (Ps.) idalis* Öpik *sensu lato*; LST3, *Glyptagnostus reticulatus* (Angelin) *sensu lato*. They fall into three zonal groups. In North American terms LC9, CP74 and Em O2 represent the late Dresbachian *Dunderbergia* Zone of the USA, equivalent to the late Idamean *Stigmatoa diloma* Zone of Australia, and correlating with the late Steptoean *Parabolinooides calvilimbatus* Zone of northwestern Canada; LST3 represents the late Dresbachian, early *Aphelaspis* Zone of the USA, early *Glyptagnostus reticulatus* Zone of both Canada and Australia.

REFERENCES

- ANGELIN, N. P. 1851. *Palaeontologica Scandinavica*: Academiae Regiae Scientiarum Suecanae (Holmiae); *Pars 1, Crustacea formationis transitionis*, 1–24, pls 1–24.
- BALDIS, B. and BORDONARO, O. 1985. Variaciones de facies en la cuenca cámbrica de la Precordillera Argentina, y su relación con la génesis del borde continental. *Sexto Congreso Latino-Americano de Geología*, Bogotá, Colombia, **1**, 149–161.
- BILLINGS, E. 1860. On some new species of fossils from the limestone near Point Levis opposite Quebec. *Canadian Naturalist*, **5**, 301–324.
- 1865. *Palaeozoic Fossils, 1. Containing descriptions and figures of new or little known organic remains from the Silurian rocks*. Geological Survey of Canada, Montreal, 326 pp.
- BORDONARO, O. 1992. El Cámbrico de Sudamérica. 69–84. In GUTIÉRREZ-MARCO, J. C., SAAVEDRA, J. and RÁBANO, I. (eds). *Paleozoico inferior de Ibero-América*. Imprime Gráficas Topacio, S.A., Madrid, 630 pp.
- CLARK, T. H. 1923. A group of new species of *Agnostus* from Levis, Quebec. *Canadian Field Naturalist*, **37**, 121–125.
- 1924. The paleontology of the Beekmantown Series at Levis, Quebec. *Bulletins of American Paleontology*, **10**, 1–134.
- CUERDA, A. 1979. El género *Amphigraptus* (graptolítina) en el Ordovícico argentino. *Ameghiniana*, **16**, 1–8.
- CINGOLANI, C. and VARELA, R. 1983. Las graptofaunas de la formación Los Sombreros, Ordovícico inferior, Sierra del Tontal, Precordillera de San Juan. *Ameghiniana*, **20**, 239–260.
- FORTEY, R. A., LANDING, E. and SKEVINGTON, D. 1982. Cambrian-Ordovician boundary sections in the Cow Head Group, western Newfoundland. 95–129. In BASSETT, M. G. and DEAN, W. T. (eds). *The Cambrian-Ordovician boundary: sections, fossil distributions and correlations*. *National Museum of Wales Geological Series*, **3**, National Museum of Wales, Cardiff, 227 pp.
- HARRINGTON, H. J. 1938. Sobre las faunas del Ordoviciano Inferior del Norte Argentino. *Revista del Museo de la Plata, New Series*, **1**, *Paleontología*, **4**, 109–289, 14 pls.
- MOORE, R. C. and STUBBLEFIELD, C. J. 1959. Morphological terms applied to Trilobita. O117–O126. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part O, Arthropoda 1*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, xix + 560 pp.
- HEREDIA, S. 1990. Geología de la cuchilla del cerro Pelado, Precordillera de Mendoza, Argentina. *XI Congreso Geológico Argentino*, **2**, 101–104.
- JAEKEL, O. 1909. Über die Agnostiden. *Zeitschrift der Deutsche Geologische Gesellschaft*, **61**, 380–401.
- JAGO, J. B. 1987. Idamean (Late Cambrian) trilobites from the Denison Range, south-west Tasmania. *Palaentology*, **30**, 207–231, pls 24–27.
- JELL, P. A., HUGHES, N. C. and BROWN, A. V. 1991. Late Cambrian (post-Idamean) trilobites from the Higgins Creek area, western Tasmania. *Memoirs of the Queensland Museum*, **30**, 455–485.
- KOBAYASHI, T. 1936. Cambrian and Lower Ordovician trilobites from northwestern Canada. *Journal of Paleontology*, **10**, 157–167, pl. 21.
- 1938. Upper Cambrian fossils from British Columbia, with a discussion on the isolated occurrence of the so-called 'Olenus' beds of Mount Jubilee. *Japanese Journal of Geology and Geography*, **15**, 149–192.
- 1955. The Ordovician fossils of the McKay Group in British Columbia, western Canada, with a note on the early Ordovician palaeogeography. *Journal of the Faculty of Science, Tokyo University*, [2], **9**, 355–493, pls 1–9.
- 1966. The Cambro-Ordovician formations and faunas of South Korea, part X. Stratigraphy of the Chosen Group in Korea and south Manchuria and its relation to the Cambro-Ordovician formations of other areas.

- Section B. The Chosen Group of North Korea and northern China. *Journal of the Faculty of Science, Tokyo University*, [2], **16**, 209–311.
- LERMONTOVA, E. A. 1951. Upper Cambrian trilobites and brachiopods from Boshche-Kul (northeastern Kazakhstan). *Trudy Vsesoyuzniy Nauchno-issledovatel'skiy Geologicheskiiy Institut (VSEGED)*, 49 pp., 6 pls. [In Russian].
- LU YAN-HAO 1964. Trilobites. 26–39. In ZHU BIAN (ed.). *Handbook of the index fossils of China, Hunan region*. 2nd edn. Geology Press, Beijing, 173 pp., 92 pls. [In Chinese].
- and LIN HUANLING 1989. The Cambrian trilobites of western Zhejiang. *Palaeontologia Sinica*, **178**, [B] **25**, iv + 1–172 [in Chinese], 173–273 [in English], pls 1–28.
- LUDVIGSEN, R., WESTROP, S. R. and KINDLE, C. H. 1989. Sunwaptan (Upper Cambrian) trilobites of the Cow Head Group, western Newfoundland, Canada. *Palaeontographica Canadiana*, **6**, 175 pp., 50 pls.
- M'COY, F. 1849. On the classification of some British fossil Crustacea, with notices of new forms in the University collection at Cambridge. *Annals and Magazine of Natural History*, [2], **4**, 161–179, 392–414.
- MANCA, N. 1992. El género *Lotagnostus* (Trilobita, Agnostida) en la Formación Santa Rosita (Jujuy, Argentina) y su significado cronológico. *Ameghiniana*, **29**, 45–48.
- ÖPIK, A. A. 1963. Early Upper Cambrian fossils from Queensland. *Bulletin of the Bureau of Mineral Resources of Australia*, **64**, 133 pp., 9 pls.
- 1967. The Mindyallan fauna of North Western Queensland. *Bulletin of the Bureau of Mineral Resources of Australia*, **74**, vol. 1, 1–404, vol. 2, 1–167, 67 pls.
- PALMER, A. R. 1962. *Glyptagnostus* and associated trilobites in the United States. *U.S. Geological Survey, Professional Paper*, **374-F**, 49 pp., 6 pls.
- 1968. Cambrian trilobites from east-central Alaska. *U.S. Geological Survey, Professional Paper*, **559-B**, 115 pp., 13 pls.
- PRATT, B. R. 1992. Trilobites of the Marjuman and Steptoean Stages (Upper Cambrian), Rabbitkettle Formation, southern McKenzie Mountains, northwest Canada. *Palaeontographica Canadiana*, **9**, 179 pp., 34 pls.
- QIAN YI-YUAN 1986. Trilobites. 255–313, pls 67–82. In CHEN JUN-YUAN (ed.). *Aspects of the Cambrian-Ordovician Boundary in Dayangcha, China*. China Prospect Publishing House, Beijing, 410 pp., 98 pls.
- RASETTI, F. 1944. Upper Cambrian trilobites from the Levis conglomerate. *Journal of Paleontology*, **18**, 229–258, pls 36–39.
- 1954. Early Ordovician trilobite faunules from Quebec and Newfoundland. *Journal of Paleontology*, **26**, 797–802, pls 60–61.
- 1961. Dresbachian and Franconian trilobites of the Conococheague and Frederick Limestones of the central Appalachians. *Journal of Paleontology*, **35**, 104–124, pls 21–25.
- RESSER, C. E. 1938. Cambrian System (restricted) of the southern Appalachians. *Geological Society of America, Special Papers*, **15**, 140 pp., 16 pls.
- RUSCONI, C. 1948. Apuntes sobre el Triásico y el Ordovicio de el Challao, Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **2**, 165–198, pls 1–4.
- 1950a. Trilobitas y otros organismos del Cámbrico de Canota. *Revista del Museo de Historia Natural de Mendoza*, **4**, 71–84.
- 1950b. Nuevas trilobitas y otros organismos del Cámbrico de Canota. *Revista del Museo de Historia Natural de Mendoza*, **4**, 85–94.
- 1951a. Trilobitas cámbricos del Cerro Pelado (Mendoza). *Boletín Paleontológico de Buenos Aires*, **24**, 4 pp.
- 1951b. Más trilobitas cámbricos de San Isidro, Cerro Pelado y Canota. *Revista del Museo de Historia Natural de Mendoza*, **5**, 3–30.
- 1952. Varias especies de trilobitas del Cámbrico de Canota. *Revista del Museo de Historia Natural de Mendoza*, **6**, 5–17.
- 1953. Nuevos trilobitas cámbricos de la Quebrada de la Cruz. *Boletín Paleontológico de Buenos Aires*, **27**, 8 pp.
- 1954. Trilobitas cámbricos de la Quebradita Oblicua, Sud Cerro Aspero. *Revista del Museo de Historia Natural de Mendoza*, **7**, 3–60, 4 pls.
- 1955a. Más fósiles cámbricos y ordovicios de San Isidro, Mendoza. *Boletín Paleontológico de Buenos Aires*, **31**, 4 pp.
- 1955b. Nota previa sobre organismos ordovicios y cámbricos de San Isidro, Mendoza. *Boletín Paleontológico de Buenos Aires*, **32**, 4 pp.

- 1955c. Fósiles cámbricos y ordovicios al Oeste de San Isidro, Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **8**, 3–64, 5 pls.
- SALTER, J. W. 1864a. A monograph of the British trilobites from the Cambrian, Silurian, and Devonian formations. Part 1. *Monograph of the Palaeontographical Society*, **16** (67), 1–80, pls 1–6.
- 1864b. Figures and descriptions illustrative of British organic remains. Decade 11. *Memoirs of the Geological Survey of the United Kingdom*, 64 pp., 9 pls.
- SHAW, A. B. 1951. Paleontology of northwestern Vermont, 1. New late Cambrian trilobites. *Journal of Paleontology*, **25**, 97–114, pls 21–24.
- SHERGOLD, J. H. 1975. Late Cambrian and early Ordovician trilobites from the Burke River Structural Belt, western Queensland. *Bulletin of the Bureau of Mineral Resources, Australia*, **153**, 251 pp., 58 pls (2 vols).
- 1977. Classification of the trilobite *Pseudagnostus*. *Palaeontology*, **20**, 69–100, pls 15–16.
- 1980. Late Cambrian trilobites from the Chatsworth Limestone, western Queensland. *Bulletin of the Bureau of Mineral Resources of Australia*, **186**, 111 pp., 35 pls.
- 1982. Idamean (Late Cambrian) trilobites, Burke River Structural Belt, western Queensland. *Bulletin of the Bureau of Mineral Resources of Australia*, **187**, 69 pp., 17 pls.
- (compiler) 1989. Australian Phanerozoic Timescales, 1: Cambrian. Australian Cambrian Biochronology: chart and explanatory notes. *Record of the Bureau of Mineral Resources of Australia*, **1989/31**, 25 pp.
- 1993. The Iverian Stage (Late Cambrian) and its subdivision in the Burke River Structural Belt, western Queensland. *BMR Journal of Australian Geology and Geophysics*, **13**, 345–358.
- LAURIE, J. R. and SUN XIAOWEN 1990. Classification and review of the trilobite order Agnostida Salter, 1864: an Australian perspective. *Report of the Bureau of Mineral Resources of Australia*, **266**, 92 pp. 19 figs.
- and WEBERS, G. F. 1993. Late Dresbachian (Idamean) and other trilobite faunas from the Heritage Range, Ellsworth Mountains, West Antarctica. 125–168, 10 pls. In WEBERS, G. F., CRADDOCK, C. and SPLETTSTOESSER, J. F. (eds). *Geology and paleontology of the Ellsworth Mountains, West Antarctica. Memoir of the Geological Society of America*, **170**, 459 pp.
- SUN YUN-CHU 1924. Contribution to the Cambrian faunas of China. *Palaeontologia Sinica*, [B], **II**, Fasc. 4, 109 pp., 5 pls.
- TROEDSSON, G. T. 1937. On the Cambro-Ordovician faunas of western Quruq Tagh, eastern Tien-shan. In Report of the scientific expedition to the northwestern provinces of China under the leadership of Dr Sven Hedin. The Sino-Swedish Expedition Publication 4, V, Invertebrate Palaeontology, 1. *Palaeontologia Sinica, New Series*, [B], **2** (whole series **106**), 74 pp., 10 pls.
- TULLBERG, S. A. 1880. *Agnostus*-arterna i de Kambriska afflagringarne vid Andrarum. *Sveriges Geologiska Undersökning*, [Series C], **42**, 1–37.
- WESTROP, S. R. 1986. Trilobites of the Upper Cambrian Sunwaptan Stage, southern Canadian Rocky Mountains, Alberta. *Palaeontographica Canadiana*, **3**, 179 pp., 41 pls.
- WHITEHOUSE, F. W. 1936. The Cambrian faunas of northeastern Australia. Part 1. Stratigraphic outline. Part 2. Trilobita (Miomera). *Memoirs of the Queensland Museum*, **11**, 59–112, pls 8–10.
- ZHOU ZHI-YI and ZHANG JIN-LIN 1985. Uppermost Cambrian and lowest Ordovician trilobites of North and Northeast China. 63–163, pls 1–29. In NANJING INSTITUTE OF GEOLOGY AND PALAEONTOLOGY, ACADEMIA SINICA (compiler). *Stratigraphy and palaeontology of systemic boundaries in China. Cambrian-Ordovician Boundary 2*. Anhui Science and Technology Publishing House, Beijing, 412 pp.

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TELEPHINID TRILOBITES FROM THE ORDOVICIAN OF SWEDEN

by PER AHLBERG

ABSTRACT. Twelve telephinid trilobite species, all assigned to the genus *Telephina*, from the Middle and Upper Ordovician of Sweden are described or discussed. In Sweden, the genus appears in equivalents of the uppermost *Didymograptus murchisoni* Biozone and ranges into the late Ashgill or Harjuan (Jerrestadian Stage), where only one species, *T. wegelini*, is present. The others are restricted largely to strata belonging to the *Hustedograptus teretiusculus* and *Nemagraptus gracilis* biozones. In Baltoscandia, telephinid trilobites are commonest in fine-grained rocks west of the Central Baltoscandian Confacies Belt, and they seem to have occupied relatively peripheral sites on the continental plate of Baltica.

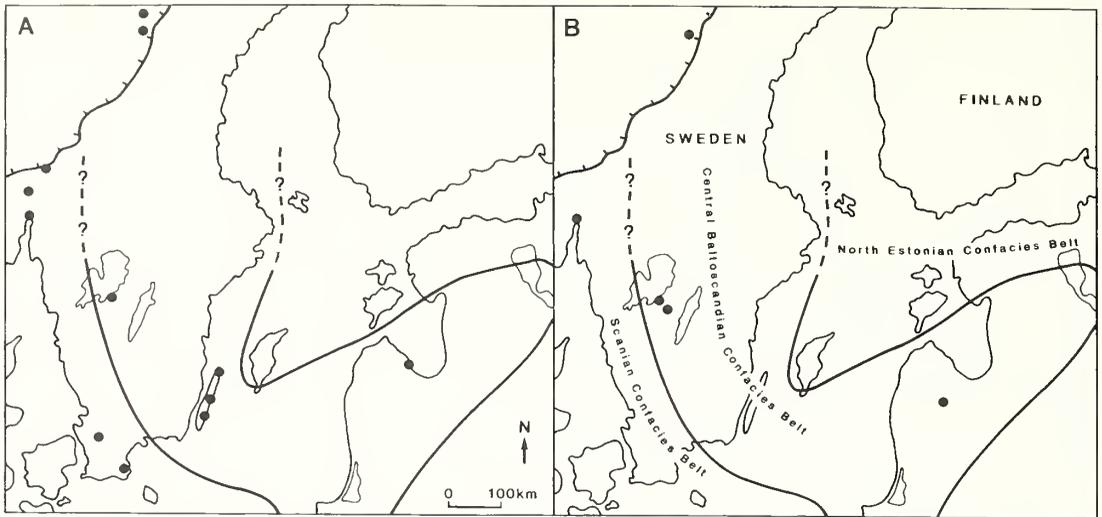
THE Telephinidae Marek, 1952 includes small- to medium-sized, micropygous trilobites with large eyes and short (tr.) pleurae. They are characteristic elements of many Ordovician faunas, and range upwards into the pre-Hirnantian Ashgill. It is generally agreed that they were adapted to a pelagic mode of life (e.g. Fortey 1975, 1981, 1985).

The earliest reference to telephinid trilobites from the Ordovician of Sweden is by Angelin (1854), who described *Telephina wegelini* from the Upper Ordovician of the Siljan district in Dalarna, central Sweden. Subsequently, additional material of this species was described from the Upper Ordovician Fjäckå Shale at various localities in this area (Linnarsson 1871, p. 350; Törnquist 1884, p. 89). During the latter half of the nineteenth century, telephinids were also reported from the island of Öland, southern Sweden, and Jämtland, central Sweden (Linnarsson 1872; Tullberg 1882; Moberg 1890; Wiman 1893; Holm 1897). Later Hadding (1913a) gave a valuable review of *Telephus* Barrande, 1852 (= *Telephina* Marek, 1952) and described all species known at the time, including four from Scandinavia. Subsequently further collecting resulted in an increased number of specimens from various horizons and localities in Sweden (e.g. Funkquist 1919; Warburg 1925; Thorslund 1935, 1948; Asklund 1936; Nilsson 1951; Nikolaisen 1963; Jaanusson 1960, p. 226; 1964, table 3; 1982b, p. 177). This paper focuses on the taxonomy and distribution of telephinids of Sweden, and includes an examination of all available museum material.

GEOLOGICAL SETTING

Ordovician sedimentary rocks are widely distributed in Baltoscandia (see Jaanusson 1976, p. 300, and Bruton *et al.* 1985 for brief reviews). The deposits belong to two distinct tectonic settings: the thick and largely siliciclastic sequences of the allochthonous Caledonides, and the generally much thinner autochthonous platform successions south and south-east of the Caledonides. The platform deposits accumulated in extensive belts, which maintained fairly constant litho- and biofacies characteristics throughout most of the post-Tremadoc Ordovician (Männil 1966; Jaanusson 1973). These distinct, composite belts were termed confacies belts by Jaanusson (1976, p. 308), and their approximate boundaries are shown in Text-figure 1.

The Central Baltoscandian, North Estonian and Lithuanian confacies belts consist predominantly of a variety of limestones with rich shelly faunas, whereas the western belts are developed mainly in graptolitic shale facies (Scanian Confacies Belt) or as mudstone with lenses or beds of limestone and some shale (Oslo belts and Lower Allochthon of Jämtland). Opinions differ as to the depth of deposition within the confacies belts. It is generally agreed, however, that the arrangement of the



TEXT-FIG. 1. Maps of confacies belts in Baltoscandia (after Jaanusson 1976, text-fig. 7; 1982a, fig. 2), and the distribution of telephinid trilobites (black dots) in the uppermost *Didymograptus muchisoni* and *Hustedograptus teretiusculus* biozones (A) and the *Nemagraptus gracilis* Biozone (B). The boundaries between the confacies belts fluctuated to some extent, and the development of calcareous mudstones on Kinnekulle in Västergötland, south-central Sweden, can be regarded as an influence from the prevailing facies in the Oslo Region, Norway. The ticked line indicates the Caledonian Front.

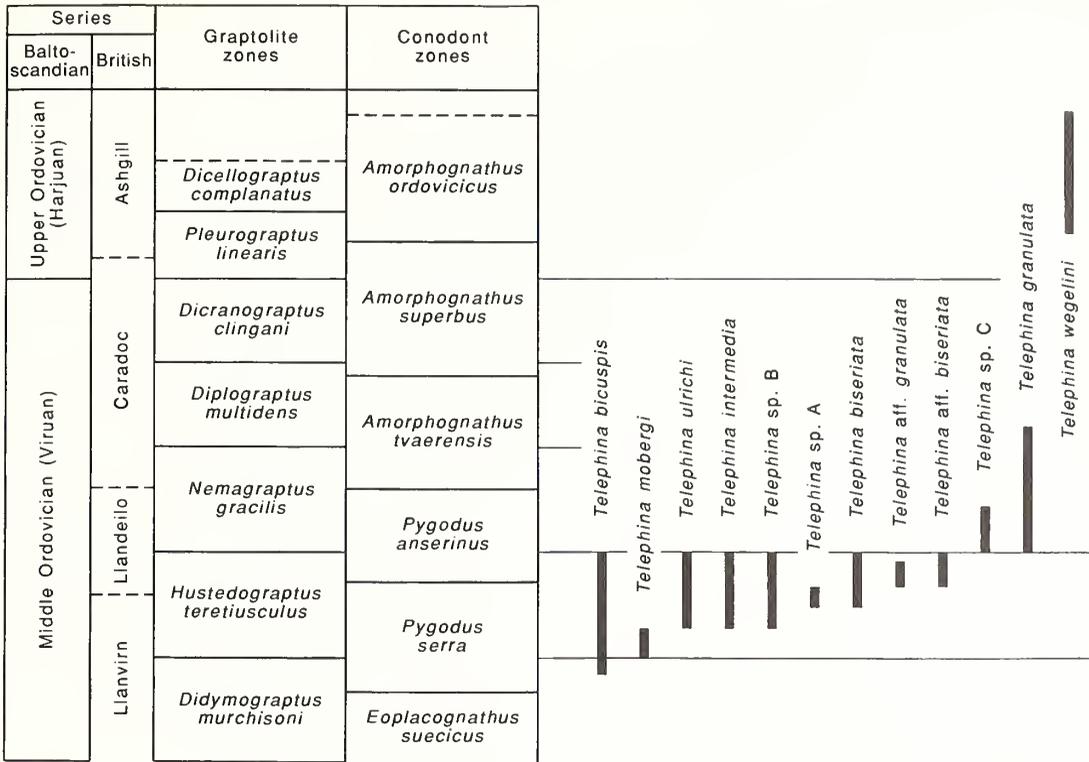
belts reflects an overall westward deepening (Jaanusson 1976, p. 309; Bruton *et al.* 1985, p. 274), but, as noted by Jaanusson (1976), this was not constant.

DISTRIBUTION

The *Telephina* species described herein range from equivalents of the uppermost *Didymograptus muchisoni* Biozone to the late Ashgill or Harjuan (Jerrestadian Stage), where only one, *T. wegelini* (Angelin, 1854), is present. The remainder are restricted largely to strata corresponding to the biozones of *Hustedograptus teretiusculus* or *Nemagraptus gracilis* (Text-fig. 2). These trilobites are confined largely to shales, mudstones, or fine-grained limestones, and they are frequently associated with graptolites. With respect to the distribution in relation to the confacies belts, it is worth noting that they are most common in those west of the Central Baltoscandian Confacies Belt (Text-fig. 1). Thus, telephinid trilobites are also characteristic elements in many Middle Ordovician faunas from the Oslo Region, Norway (see Nikolaisen 1963), and the Lower Allochthon in Jämtland, central Sweden. With respect to biofacies, the Ordovician of the Oslo Region shares several features with the Lower Allochthon in Jämtland, and several species are common to the two areas. These include *Telephina bicuspis* (Angelin, 1854), *T. intermedia* (Thorslund, 1935), *T. mobergi* (Hadding, 1913a), and *T. granulata* (Angelin, 1854).

Rare specimens are also known from Scania (Skåne), southern Sweden, which include an indeterminate specimen (*Telephina* sp. A), from the graptolitic shales (*Hustedograptus teretiusculus* Biozone) at Röstånga in western Scania, and *Telephina* aff. *granulata*, from the Killeröd Formation of southeastern Scania.

Telephinids are generally very rare in the Central Baltoscandian Confacies Belt. A notable exception is the occurrence of *T. bicuspis* in the Middle Ordovician Folkeslunda Limestone of Öland. This unit consists largely of grey calcarenites and is mostly rich in macrofossils (Jaanusson 1960). Telephinids have also been recorded from the Gullhögen, Ryd and Dalby formations in Västergötland in this confacies belt (Jaanusson 1964), where they are restricted largely to fine-



TEXT-FIG. 2. Approximate ranges of telephinid trilobites in the Middle and Upper Ordovician of Sweden. Many specimens in older collections are only vaguely localized with respect to the stratigraphy, and for most species the ranges shown are tentative. Stratigraphy slightly modified after Jaanusson (1982a, fig. 2).

grained limestones or mudstones. The appearance of telephinids in the Middle Ordovician of Västergötland seems to be related to brief eastward shifts of the general facies of the Oslo Region (Jaanusson 1964, p. 53; 1973, p. 21; 1982b, p. 168). Within the Central Baltoscandian Confacies Belt, rare specimens of *Telephina* are also known from drill cores in western Latvia (Männil 1963), and the Pskov district of western Russia. No telephinids are known from the North Estonian and Lithuanian confacies belts.

In North America, *Telephina* species have been recorded only from the Appalachian orogenic belt. The oldest forms are from the Llanvirn of the northern part (western Newfoundland and southern Quebec). In the southern and central Appalachians of the USA, *Telephina* is widely distributed in beds equivalent to the *Hustedograptus teretiusculus* and *Nemagraptus gracilis* biozones. Analysis of the distribution of shelly faunas and conodonts in this area has revealed a differentiation into three Middle Ordovician confacies belts (Jaanusson and Bergström 1980). Ulrich (1930, p. 47) noted that 'in the Appalachian Valley remains of *Telephus* are confined to areas in the eastern half of the valley', that is, to the Blount Confacies Belt of Jaanusson and Bergström (1980), and this is confirmed by the available evidence (V. Jaanusson, pers. comm. June 1993). The faunas of the Blount Belt are closely similar to those of northeastern Ireland and the Girvan district of southwestern Scotland (Jaanusson and Bergström 1980, p. 102). The latter area has also yielded telephinids, such as *Telephina girvanensis* (Reed, 1935) and *T. subsecuta* (Reed, 1944). These species were redescribed by Tripp (1976). In Baltoscandia, the closest equivalent to the Blount Belt is the Central Baltoscandian Confacies Belt, but the Blount Belt also includes analogues of the Oslo belts and the Scanian Confacies Belt (Jaanusson and Bergström 1980, p. 100).

In conclusion, most species of *Telephina* appear to be restricted to sequences situated fairly peripherally on the continental plates, at least in Baltica and in Laurentia. The lack of *Telephina* on the Siberian Platform supports this view.

SYSTEMATIC PALAEOLOGY

The terminology used herein in general follows that of Harrington *et al.* in Moore (1959), except that the terms rachis and dorsal furrow are preferred to axis and axial furrow. The glabella is taken to exclude the occipital ring and furrow. The palpebral area of the fixigena is between the palpebral furrow and the dorsal furrow.

Illustrated and cited specimens are deposited in the type collections of the Geological Survey of Sweden, Uppsala (SGU), the Department of Historical Geology and Palaeontology, University of Lund (LO or LR), the Palaeontological Museum, Oslo (PMO), the Palaeontological Museum, University of Uppsala (PMU), and the Swedish Museum of Natural History, Stockholm (RM). All specimens were painted with matt black opaque and then lightly coated with a sublimate of ammonium chloride prior to being photographed. Dorsal views are shown unless stated otherwise in the captions.

Measurements were made with a micrometer eyepiece fitted in a binocular microscope. All dimensions were measured as straight-line distances. The accuracy of all measurements is to 0.05 mm. Estimated values and transverse measurements arrived at by doubling the width from the sagittal line are indicated with a question mark. The following symbols are used for measured parameters: Lc, length (sag.) of cephalon (excl. occipital spine and anterior pair of spines); G, length (sag.) of glabella; Lo, length (sag.) of occipital spine; Wc, maximum width (tr.) of cranium; Wg, maximum width (tr.) of glabella; Wf, maximum width (tr.) of fixigena (incl. palpebral lobe).

Family TELEPHINIDAE Marek, 1952

Diagnosis. See Fortey 1975, p. 94.

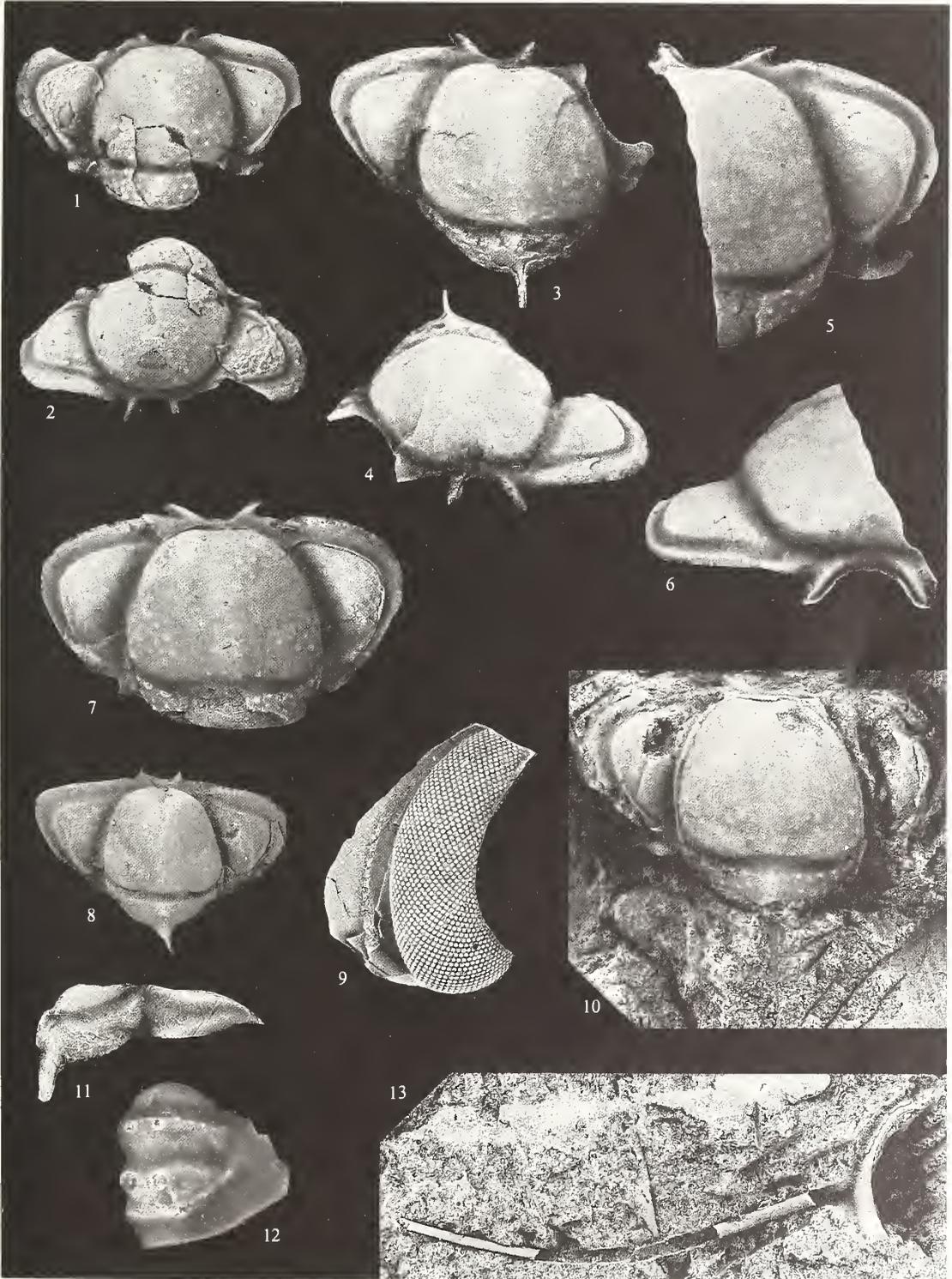
Remarks. The concept of the family Telephinidae was discussed comprehensively by Fortey (1975), and his definition and discussion cover all important aspects.

Genus TELEPHINA Marek, 1952

Type species. *Telephus fractus* Barrande, 1852 (p. 890, pl. 18, figs 30–34), from the Králův Dvůr Formation (Ashgill) at Králův Dvůr, Bohemia; by original designation.

EXPLANATION OF PLATE I

Figs 1–13. *Telephina bicuspis* (Angelin, 1854). All specimens except 1–2 and 13 are from the lower Andersö Shale (*Hustedograptus teretiusculus* Biozone) on the northwestern shore of Andersön, Jämtland (locality 1 of Hadding 1912, pl. 7A, 1913b, fig. 12). 1–2, neotype, RM Ar 37315; dorsal and anterodorsal views; Oslo, Norway; original of Thorslund (1935, pl. 2, figs 1–2); × 8. 3–4, LO 2566t; cranidium in dorsal and anterior views; original of Hadding (1913a, pl. 1, fig. 4); coll. A. Hadding 1912; × 7. 5–6, LO 2544t; cranidium in dorsal and anterior views; original of Hadding (1913a, pl. 1, fig. 1a–d); coll. A. Hadding 1912; × 6. 7, LO 2565t; cranidium; original of Hadding (1913a, pl. 1, fig. 3a–b); coll. A. Hadding 1912; × 7.5. 8, SGU 8637; cranidium; coll. P. Thorslund 1949; × 7. 9, LO 6701t; incomplete librigena; coll. A. Hadding 1912; × 5. 10, LO 2564t; cranidium; original of Hadding (1913a, pl. 1, fig. 2); coll. A. Hadding 1912; × 7.5. 11, LO 2546t; incomplete thoracic tergite; original of Hadding (1913a, pl. 1, fig. 6); coll. A. Hadding 1912; × 7. 12, LO 2547t; incomplete pygidium, latex cast from external mould; original of Hadding (1913a, pl. 1, fig. 7); coll. A. Hadding 1912; × 13. 13, SGU 6687; incomplete librigena in ventral view; Ö. Ottsjön, Föllinge area, Jämtland; original of Thorslund (1935, pl. 2, fig. 6); coll. P. Thorslund 1934; × 5.



AHLBERG, *Telephina bicuspis*

Diagnosis. Telephid trilobites with wide (tr.) glabella, tapering forward and broadly rounded to truncate in front. Cranidial anterior border narrow (tr.), distally turned downward to form a pair of spines; width of anterior border (between lateral extremities of spines) less than half the width (tr.) of occipital ring. Posterior border short (tr.). Librigenae with very large crescentic eyes and generally long genal spines. In addition to genal spines, one or two pairs of marginal librigenal spines may be present. Pygidial rachis with two rings, that may bear paired spines or tubercles, and short (sag.) terminal piece. Dorsal surface generally tuberculate, especially on glabella and occipital ring, and commonly with a pattern of fine, raised lines on the external exoskeletal surface. Glabella with three or four pairs of smooth muscle attachment areas.

Remarks. The earliest representatives of *Telephina* appear near the base of the Llanvirn. The genus underwent prolific radiation during the Middle Ordovician and ranges upwards into the pre-Hirnantian Ashgill. The origin of the genus was discussed by Fortey (1975), who showed that it was probably derived from a species of the early Ordovician genus *Oopsites* Fortey, 1975.

Species attributed to *Telephina* appear to have a distinctive arrangement of the glabellar muscle attachment areas. The posterior pair is generally prominent, transversely elongate, and situated immediately in front of the outer ends of the occipital furrow. The second area is larger, composite, and situated generally at about half the length of the glabella. The anterior sets are generally indistinct, small, and situated fairly close to the dorsal furrows. The inner, posterior part of the fixigena is commonly smooth, kidney-shaped, and slightly vaulted, and this area may also be a muscle attachment area (cf. Whittington 1965, p. 369; Fortey 1975, p. 100).

Nikolaisen (1963) proposed the subgenus *Telephina* (*Telephops*), with *T. grammlata* (Angelin, 1854) as type species, for those species with a pair of spines or horns on the glabella. In most other characters, the type species of this subgenus is like the type and other species of *Telephina* (*Telephina*), and I am inclined to the view that the presence or absence of glabellar spines is not of subgeneric significance, because in many evolving trilobite lineages spines can be ephemeral characters. A metalibrigenal spine appears to be present in most species referable to *Telephina* (*Telephops*). A corresponding spine may, however, also be present in species attributed to *Telephina* (*Telephina*). Thus, I follow Tripp (1976, p. 376) and regard *Telephina* (*Telephops*) as a synonym of *Telephina* (*Telephina*).

Telephina bicuspis (Angelin, 1854)

Plate 1, figures 1–13; Plate 2, figures 1–12

- *1854 *Telephus bicuspis* Angelin, p. 91, pl. 41, figs 22 and 22a.
- v.1882 *Telephus* sp.; Tullberg, p. 233.
- v.1890 *Telephus bicuspis* Ang.; Moberg, p. 16.
- v.1897 *Telephus bicuspis* Ang.; Holm, p. 463 [*partim*].
- v.1913a *Telephus bicuspis* Ang.; Hadding, pp. 33–35, pl. 1, figs 1–7.
- v.1913b *Telephus bicuspis* Ang.; Hadding, pp. 75–76, pl. 8, figs 1–4 [copies of Hadding's (1913a, pl. 1, figs 1a–c, 5b–7) original figures].
- v.1930 *Telephus haddingi* Ulrich, pp. 12–13, pl. 1, figs 11–18 [copies of Hadding's (1913a, pl. 1, figs 2–7) original figures].
- v.1930 *Telephus jamtlandicus* Ulrich, p. 13, pl. 1, figs 8–10 [copies of Hadding's (1913a, pl. 1, fig. 1a–d) original figures].
- .1930 *Telephus bicuspis* Angelin; Ulrich, p. 12, pl. 2, figs 20–21 [copies of Angelin's (1854) original figures].
- v.1935 *Telephus bicuspis* Ang.; Thorslund, pp. 20–21, 60, pl. 2, figs 1–6.
- v.1954 *Telephus bicuspis* Angelin; Kobayashi, pl. 6, fig. 1a–c [drawings of Hadding's (1913a, pl. 1, figs 1, 5–7) specimens].
- .1963 *Telephina* (*Telephina*) *bicuspis* (Angelin, 1854); Nikolaisen, pp. 364–367, pl. 1, figs 1? and 2–10.
- .1963 *Telephina* (*Telephina*) *furnesensis* Nikolaisen, pp. 367–368, pl. 1, fig. 11.
- .1963 *Telephina* (*Telephina*) aff. *furnesensis* Nikolaisen, p. 360, fig. 4.

- .1963 *Telephina (Telephina) norvegica* Nikolaisen, pp. 373–375, pl. 3, figs 1–2.
 1975 *Telephina bicuspis* Hadding; Fortey, p. 95.

Neotype. A nearly complete cranidium (RM Ar37315; Pl. 1, figs 1–2), figured and selected by Thorslund (1935, pl. 2, figs 1–2). The specimen is from Oslo, Norway, and it may be Angelin's (1854) original (cf. Holm 1897, p. 463; Thorslund 1935, p. 21; Nikolaisen 1963, p. 365). The horizon is not precisely known, but it comes probably from the Engervik Member of the Elnes Formation (Ogygiocaris Shale or 4ax₃ of earlier usage).

Additional material. About one hundred cranidia, four eyes, three librigenae, one thoracic tergite, and one pygidium from Jämtland, and fifteen cranidia from Öland.

Emended diagnosis. Cranidium wide (length/width ratio 1.0:1.6–1.8). Glabella and occipital ring distinctly tuberculate. Anterior end of glabella broadly rounded to truncate with a slight backward curvature medially. Fixigenae wide (tr.) and subtriangular. Palpebral area with narrow, raised rim along postero-lateral margin. Anterior border relatively wide (width between lateral extremities of spines 0.4–0.5 times that of occipital ring). Pygidium wide with broadly rounded posterior margin.

Description. Length of cranidium (sag.; excl. occipital spine) 0.55 to 0.65 times the width, and widest along a transverse line passing through the anterior half of the glabella. Glabella highly convex (tr.), tapering forward, broadly rounded to truncate anteriorly (or curved slightly backwards medially), and generally 0.80–0.85 times as long (sag.) as its maximum width. Anterior part of glabella steeply down-sloping to preglabellar furrow, which is tucked beneath the frontal convexity of the glabella. Occipital furrow deep, widest medially, and curved forward abaxially. Occipital ring with moderately long, posteriorly directed spine, and a prominent tubercle antero-medially. Fixigenae wide (tr.) and subtriangular. Palpebral area convex, strongly down-sloping laterally and antero-laterally, and with a narrow, raised rim or ridge postero-laterally. This rim extends parallel to the posterior part of the palpebral furrow. Palpebral lobe anteriorly slightly wider than posteriorly, depressed below the level of the palpebral area and separated from it by a well-defined palpebral furrow. Facial suture running forwards and outwards at about 30° to sagittal line from posterior border furrow, then curving strongly around lateral extremity of palpebral lobe to run inwards and slightly forwards. Anterior border distally turned downward to form a pair of spines, which is generally seen in dorsal view. Width (tr.) of anterior border (between lateral extremities of spines) 0.4 to 0.5 times that of occipital ring.

TABLE 1. Dimensions (in mm) of cranidia of *Telephina bicuspis*.

	Lc	G	Lo	Wc	Wg	Wf
LO 6703t	2.00	1.60	1.00?	3.20	1.55	0.95
RM Ar 37315	3.30	2.35	—	5.55	2.80	1.45
LO 2565t	4.10	3.00	—	7.15	3.90	2.15
LO 2564t	4.35	3.15	3.30?	7.35?	3.75	2.15
SGU 8641	4.50	3.30	—	7.30	3.75	2.15
LO 2566t	4.80	3.55	—	8.65?	4.45	2.55
SGU 8657	5.35	4.00	—	8.70	4.75	2.50
SGU 8658	6.20	4.45	—	11.25	5.55	3.35
SGU 8659	6.65?	4.70	—	10.65	5.60	2.85
LO 2544t	7.30	5.50	—	—	—	3.00
SGU 8642	8.00	5.75	—	13.25	6.60	3.60

Librigena with approximately semi-elliptical outer margin, and with long, slender and gently curved genal spine. Extraocular cheeks narrow, widest (tr.) at genal spine. Eye bounded on outer side by a deep furrow, outside which is a convex border.

Thoracic tergite with pointed pleura. Rachial ring nearly twice as wide (tr.) as the pleura, and with a posteriorly directed spine at posterior margin. Pleural furrows transverse and widest (exsag.) adaxially. Articulating furrow deep and curved backwards medially.

Pygidium semicircular to subtriangular in outline and about 1.6 times wider (tr.) than long (sag.; incl. articulating half-ring). Rachis highly convex (tr.), tapering backwards, and truncate to bluntly rounded posteriorly. Articulating furrow wide (sag.) and deepest laterally. Two rachial rings well defined by a wide and deep ring furrow. Rachial rings bear a prominent pair of tubercles or spines at mid-line. Terminal piece short (sag.) and steeply downsloping to short (sag.) postrachial field. Pleural region with narrow (tr.) horizontal area adaxially, steeply downsloping and concave laterally. Pleural furrows absent. Border very narrow.

The external exoskeletal sculpture consists of relatively widely spaced tubercles on the glabella and on the occipital ring, and a reticulate pattern of raised lines anteriorly and laterally on the palpebral area. Furthermore, well-preserved specimens show a pattern of fine, raised lines on the palpebral lobe and on the glabella. Four pairs of smooth muscle attachment areas are present on the glabella. The posterior pair is transversely elongate and situated immediately in front of the outer ends of the occipital furrow. A second area is considerably larger, composite, diagonally directed, and situated at about half-way along the length of the glabella. The two anterior sets are small and situated close to the dorsal furrows. A smooth, kidney-shaped, and vaulted area is present adaxially on the posterior part of the fixigena, and it may also represent a muscle attachment area.

Remarks. In the wide, arched anterior border and the wide fixigenae, *Telephina bicuspis* closely resembles the early Ordovician genus *Oopsites* Fortey, 1975 (cf. Fortey 1975, p. 95). On the other hand, the short (tr.) posterior border, the presence of an occipital spine and spines or prominent tubercles on the pygidial rachial rings, and the arrangement of the muscle insertion areas, suggest that it is best classified as a species of *Telephina*.

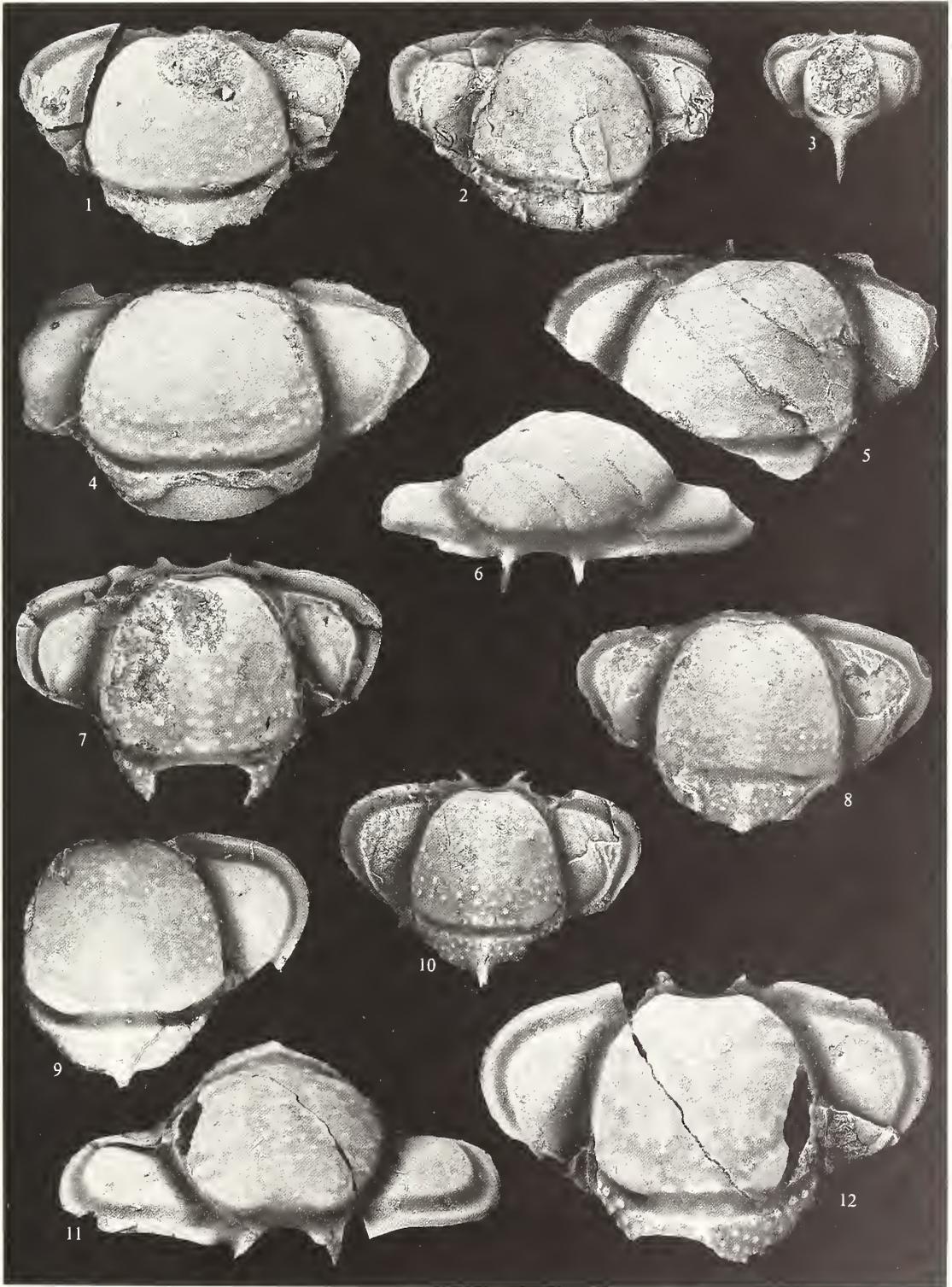
There is considerable variation exhibited by the material. Much of this variation, such as the expression of the tubercles, is due to varying degrees of flattening and to the mode of preservation. The width of the fixigenae and the shape of the glabella can, however, be shown to vary intraspecifically. The fixigena is 0.50 to 0.65 times as wide as the maximum width of the glabella. In dorsal view, the anterior end of the glabella ranges from broadly rounded to truncate with a slight backward curvature medially. In general, the front of the glabella is broadly rounded in juvenile specimens, whereas it tends to be truncate in mature ones. Small specimens also have a pair of shallow lateral depressions on the glabella that disappear during ontogeny, and they are generally effaced in cranidia longer (sag.) than 3.5 mm (cf. Nikolaisen 1963, p. 366). Well-preserved specimens exhibit cephalic muscle insertion areas (Pl. 2, figs 9, 11–12); their arrangement is similar to that of *T. americana* (Billings, 1865) (see Whittington 1965, p. 369, pl. 37, figs 5 and 18).

T. furnesensis Nikolaisen, 1963 and *T. norvegica* Nikolaisen, 1963, both from the middle Elnes Formation in the Mjösa area of Norway, agree in all essential features with *T. bicuspis* as described herein. Therefore, I regard them as subjective junior synonyms of *T. bicuspis*.

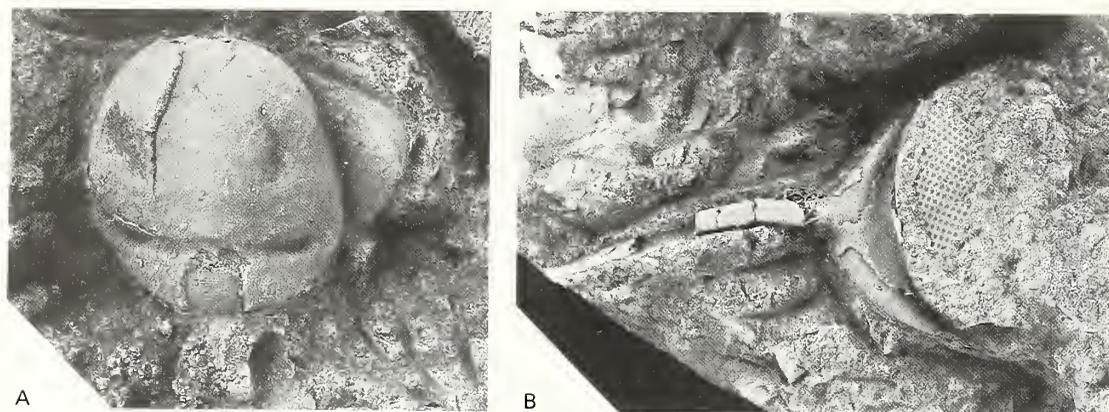
Occurrence. In Scandinavia, this species is known from the middle Elnes Formation ($4a\alpha_{1-2}$ and $4a\alpha_3$ of earlier usage; Owen *et al.* 1990) in the Oslo Region (Nikolaisen 1963, p. 366; Wandås 1984, p. 217), the lower Andersö Shale (Uhakuan Stage) in Jämtland, and the Folkeslunda Limestone (Lasnamaegian Stage) on Öland.

EXPLANATION OF PLATE 2

Figs 1–12. *Telephina bicuspis* (Angelin, 1854). Lower Andersö Shale, section in Raftan rivulet, Föllinge area, Jämtland (1, 5–6), lower Andersö Shale on the northwestern shore of Andersön, Jämtland (2–4), and the Folkeslunda Limestone of Öland (7–12). 1, SGU 6684; cranidium; original of Thorslund (1935, pl. 2, fig. 3); coll. P. Thorslund 1934; $\times 7$. 2, LO 6702t; cranidium, latex cast from external mould; coll. A. Hadding 1912; $\times 7$. 3, LO 6703t; small cranidium; coll. A. Hadding 1912; $\times 7.5$. 4, LO 6704t; cranidium; $\times 7.5$. 5–6, SGU 8638; cranidium in dorsal and anterior views; coll. P. Thorslund 1937; $\times 6$. 7, SGU 8639; cranidium; Lerkaka, central Öland; coll. G. C. von Schmalensee 1881; $\times 6$. 8, SGU 8640; cranidium; Slagerstad, southern Öland; coll. J. C. Moberg 1887; $\times 6$. 9, RM Ar 23864; cranidium; Slagerstad, southern Öland; coll. J. G. Andersson 1892; $\times 5$. 10, SGU 8641; cranidium; Lerkaka, central Öland; coll. G. C. von Schmalensee 1881; $\times 6.5$. 11–12, SGU 8642; cranidium in dorsal and anterior views; Slagerstad, southern Öland; coll. J. C. Moberg 1887; $\times 5.5$.



AHLBERG, *Telephina bicuspis*



TEXT-FIG. 3. *Telephina intermedia* (Thorslund, 1935). Lower Andersö Shale; *Hustedograptus teretiusculus* Biozone; Raftan rivulet, Föllinge area, Jämtland; coll. P. Thorslund 1934. A, holotype, an incomplete cranidium; original of Thorslund (1935, pl. 2, fig. 7) and Nikolaisen (1963, pl. 2, fig. 1); SGU 6688. B, nearly complete librigena; original of Thorslund (1935, pl. 2, fig. 8); SGU 6689. Both $\times 7.5$.

In Jämtland, it is widely distributed in the lower Andersö Shale (*Hustedograptus teretiusculus* Biozone) and it has been collected from a large number of localities. These include, among others: (1) Ö. Ottsjön and a stream section of the Raftan rivulet in the Föllinge area (sections described by Thorslund 1935, pp. 6–9); (2) Andersön in the central Storsjön area (locality 1 of Hadding 1912, pl. 7A; 1913b, fig. 12); (3) the northern shore of Norderön in the central Storsjön area (see Thorslund and Jaanusson 1960, fig. 22); (4) Mellersta Utön in the central Storsjön area; (5) east of Övre Måläng, about 11 km SE of Sunne; (6) a road section (temporary exposure) at Borgen, 2–3 km NW of Oviken; and (7) a stream section 600 m NW of Abbåsen, about 4 km NNW of Oviken.

On Öland, the species is known from the Folkeslunda Limestone ('Centaurus limestone'; Moberg 1890) at: (1) Skärlöv, south of Hulterstad, southern Öland; (2) Slagerstad, south of Stenåsa, southern Öland; (3) Brunneby (drainage ditch east of the main road), north of Stenåsa, southern Öland; (4) Lerkaka, north of Runsten, central Öland; and (5) from a loose boulder at Stora Mossen, NNW of Böda, northern Öland.

A nearly complete cephalon of *T. bicuspis* is known from the lowermost Uhaku Stage in the Engure drill core (depth: 966.00 m) of western Latvia.

Telephina ulrichi (Thorslund, 1935)

Plate 3, figures 1–2

v*1935 *Telephus ulrichi* Thorslund, pp. 21–22, 60–61, pl. 2, figs 9–10.

Holotype. An internal mould of a nearly complete cranidium (SGU 6691; Pl. 3, fig. 1), illustrated by Thorslund (1935, pl. 2, fig. 10), from the lower Andersö ('Ogygiocarid') Shale, *Hustedograptus teretiusculus* Biozone, associated with *Botrioides efflorescens* (Hadding, 1913b), Ö. Ottsjön, Föllinge area, Jämtland (see Thorslund 1935, p. 6 for locality data).

Additional material. A largely exfoliated cranidium (SGU 6690; Pl. 3, fig. 2), illustrated by Thorslund (1935, pl. 2, fig. 9).

Dimensions of holotype (mm). Lc = 3.85; G = 2.75; Lo = 3.00; Wc = 5.00; Wg = 2.85; Wf = 1.35.

Diagnosis. See Thorslund (1935, pp. 21–22 and 60–61).

Remarks. *Telephina ulrichi* is closely comparable with *T. bicuspis* but differs in having a proportionately narrower and longer glabella, and narrower (tr.) fixigenae. Although the width of

TABLE 2. Dimensions (in mm) of cranidia of *Telephina mobergi*.

	Lc	G	Lo	Wc	Wg	Wf
LR 1	1.95	1.35	—	3.25	1.70	1.15
SGU 8643	2.60	1.85	1.35	4.90?	2.75	1.40
LO 2569t	3.20	2.25	—	5.10	3.05	1.45
LO 6705t	3.40	2.35	—	5.70?	3.50	1.50
SGU 8645	4.15	2.80	—	8.35	4.85	2.35
LO 2549t	5.40	3.85	—	—	5.15	—
LO 2568T	6.10	4.20	—	10.50?	6.75	2.80

the fixigenae is a variable feature in most species of *Telephina*, their width in *T. ulrichi* seems to fall outside the range of variation seen in *T. bicuspis*, and I regard them as two separate species. The glabella of *T. ulrichi* is subequal in length and width, whereas it is considerably wider than long in *T. bicuspis*. The occipital ring of *T. ulrichi* is comparatively long (sag.) with a long occipital spine. Tubercles are faintly indicated on the occipital ring and along the sagittal line of the glabella.

Occurrence. In addition to the type locality, known from the lower Andersö Shale in a section in the Raftan rivulet, Föllinge area, Jämtland (see Thorslund 1935, p. 7 for a locality description).

Telephina intermedia (Thorslund, 1935)

Text-figure 3

v*1935 *Telephus intermedius* Thorslund, pp. 22 and 61, pl. 2, figs 7–8.

1963 *Telephina (Telephina) intermedia* (Thorslund, 1935); Nikolaisen, pp. 369–370, pl. 2, figs 1–5.

Holotype. An incomplete cranidium (SGU 6688; Text-fig. 3A), illustrated by Thorslund (1935, pl. 2, fig. 7) and Nikolaisen (1963, pl. 2, fig. 1), lower Andersö ('Ogygiocaris') Shale, *Hustedograptus teretiusculus* Biozone, section in Raftan rivulet, Föllinge area, Jämtland (see Thorslund 1935, p. 7 for locality data).

Additional material. An incomplete librigena (SGU 6689; Text-fig. 3B), illustrated by Thorslund (1935, pl. 2, fig. 8).

Dimensions of holotype (mm). Lc = 5.10; G = 3.65; Wg = 4.70; Wf = 1.70?.

Diagnosis. See Thorslund (1935, pp. 22 and 61).

Remarks. In the outline and proportions of the individual parts of the cranidium, *Telephina intermedia* bears a strong similarity to *T. bicuspis*. The only difference observed is that *T. intermedia* has a pair of distinct depressions on the glabella. It is doubtful whether this is of specific significance, because such depressions are present in juvenile specimens of *T. bicuspis*, and may also be faintly indicated in adult specimens. Hence, *T. intermedia* may eventually prove to be a junior subjective synonym of *T. bicuspis*. For the time being, however, I treat it as a distinct species.

Occurrence. Outside the type locality, this species has been described from the middle–upper Elnes Formation in the Oslo Region of Norway (Nikolaisen 1963, p. 369).

Telephina mobergi (Hadding, 1913a)

Plate 3, figures 3–14

v*1913a *Telephus mobergi* Hadding, pp. 37–38, pl. 2, figs 12–17.

- v.1913b *Telephus mobergi* Hadding; Hadding, p. 76, pl. 8, figs 6–8 [copies of Hadding's (1913a) original figures].
- v.1917 *Telephus mobergi* Hdg; Isberg, pp. 593–596, pl. 6, figs 1–3.
- v.1930 *Telephus mobergi* Hadding; Ulrich, pp. 14–15, pl. 2, figs 1–9 [copies of Hadding's (1913a) original figures].
- .1963 *Telephina (Telephina) mobergi* (Hadding, 1913); Nikolaisen, pp. 371–373, pl. 2, figs 6–12.

Lectotype. An incomplete cranidium (LO 2568T; Pl. 3, fig. 7) figured by Hadding (1913a, pl. 2, fig. 13), selected and refigured by Nikolaisen (1963, pl. 2, fig. 6), lowermost Andersö ('Ogygiocaris') Shale, lower *Hustedograptus teretiusculus* Biozone, Andersön, Jämtland (locality 1 of Hadding 1912, pl. 7A, 1913b, fig. 12).

Additional material. Thirty-three cranidia, seven librigenae, ten fragmentary eyes, and five thoracic tergites. The specimens are preserved in a dark grey limestone or calcareous siltstone, and in general they are slightly compressed.

Emended diagnosis. Cranidium subrectangular in outline and wide (length/width ratio 1.0:1.6–2.0). Glabella strongly tapered forward, slightly pear-shaped in dorsal view, and with a pair of distinct, longitudinally elongated depressions. Glabella smooth. Anterior part of palpebral lobe wide, and directed along a nearly transverse line passing just in front of the glabella.

Description. Cranidium subrectangular in outline, about three-fifths as long as it is wide, and widest along a transverse line passing through the anterior part of the glabella. Glabella moderately convex, strongly tapered forward, broadly rounded anteriorly, slightly pear-shaped in dorsal view, and 0.6–0.8 times as long (sag.) as its maximum width (Table 2). Slightly posterior to the mid-length of glabella there is a pair of distinct, longitudinally elongated depressions. Occipital furrow moderately deep and wide, curved forward abaxially. Occipital ring bears a moderately long, slender spine, posteriorly directed and with circular cross section. Fixigenae subtriangular and wide (tr.). Palpebral area convex and strongly downsloping anteriorly and laterally. It is widest (tr.) anteriorly, gradually narrowing backwards. Palpebral lobe widest anteriorly and directed forward and slightly outward from the posterior border furrow, then curved abruptly inward along a transverse line passing just in front of the glabella.

Librigena fairly wide with semicircular outer margin and very long spine, directed laterally. Extraocular cheeks and border widest at librigenal spine. Border convex (tr.).

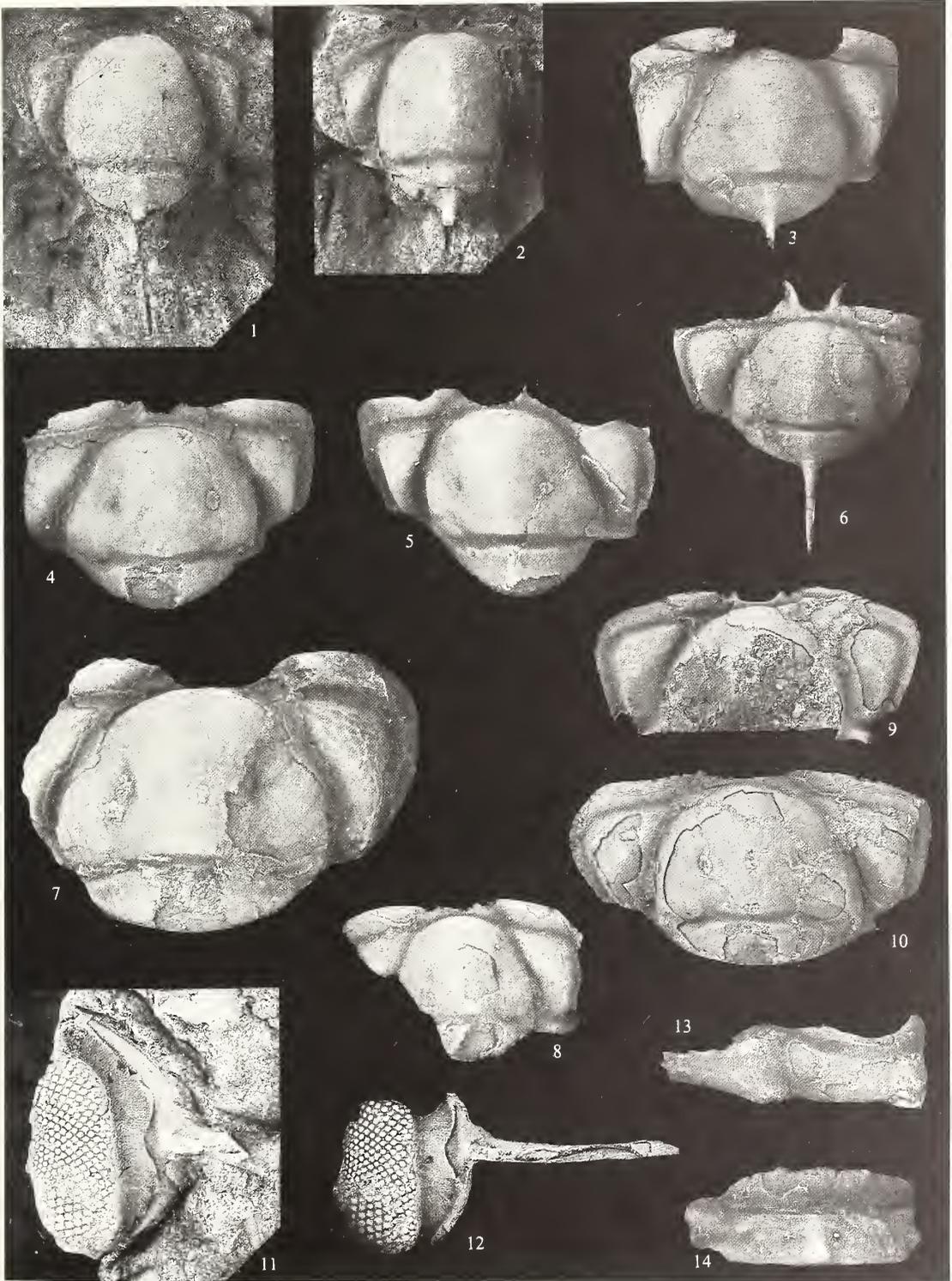
Thoracic tergites with short (tr.), pointed pleurae. Pleural furrows transverse and widest (exsag.) adaxially. Rachial ring nearly twice as wide (tr.) as the pleura, and with a posteriorly directed spine at posterior margin.

Surface sculpture poorly known but appears to be smooth except for granules on the occipital ring and the thoracic rachial rings. In addition, a reticulate pattern of raised lines is present laterally and antero-laterally

EXPLANATION OF PLATE 3

Figs 1–2. *Telephina ulrichi* (Thorslund, 1935); lower Andersö Shale; *Hustedograptus teretiusculus* Biozone; Jämtland; coll. P. Thorslund 1934. 1, holotype, SGU 6691; a nearly complete cranidium; original of Thorslund (1935, pl. 2, fig. 10); Ö. Ottsjön, Föllinge area; 2, SGU 6690; cranidium, internal mould; original of Thorslund (1935, pl. 2, fig. 9); Raftan rivulet, Föllinge area. Both $\times 7$.

Figs 3–14. *Telephina mobergi* (Hadding, 1913a); lowermost Andersö Shale; lower *Hustedograptus teretiusculus* Biozone; northwestern shore of Andersön, Jämtland (3–5, 7–8, 11–14; coll. A. Hadding 1912), and Fagerdal, Jämtland (6, 9–10; coll. P. Thorslund and R. Skoglund 1961). 3, LO 2569t; cranidium; original of Hadding (1913a, pl. 2, fig. 14); $\times 8$. 4, LO 6705t; cranidium; $\times 8$. 5, LO 6706t; cranidium; $\times 8$. 6, SGU 8643; cranidium; $\times 9$. 7, lectotype, LO 2568T; an incomplete cranidium; original of Hadding (1913a, pl. 2, fig. 13) and Nikolaisen (1963, pl. 2, fig. 6); $\times 6$. 8, LO 6707t; cranidium; $\times 8$. 9, SGU 8644; cranidium; $\times 7$. 10, SGU 8645; cranidium; $\times 7$. 11, LO 2570t; incomplete librigena; original of Hadding (1913a, pl. 2, fig. 16), Isberg (1917, pl. 6, figs 2–3), and Nikolaisen (1963, pl. 2, fig. 8); $\times 6$. 12, same librigena, latex cast from external mould; $\times 6$. 13, LO 2550t; incomplete thoracic tergite; original of Hadding (1913a, pl. 2, fig. 17); $\times 8$. 14, LO 6708t; incomplete thoracic tergite; $\times 8$.



AHLBERG, *Telephina*

on the palpebral area, and transversely arranged terrace lines occur on the doublure of the occipital ring. Rare specimens exhibit a pattern of fine raised lines on the external exoskeletal surface and transversely elongate muscle attachment areas immediately in front of the outer part of the occipital furrow.

Pygidium not known.

Remarks. *Telephina mobergi* most closely resembles *T. sulcata* Nikolaisen, 1963, from the basal Elnes Formation (Helskjer Member; Owen *et al.* 1990, p. 17) in the Mjösa area, Norway, but *T. sulcata* has a considerably less tapered and nearly subrectangular glabella, and shorter (exsag.) lateral glabellar depressions (furrows).

T. bipunctata (Ulrich, 1930), from the Botetourt Formation (Caradoc; *Baltoniodus gerdae* Subzone; S. M. Bergström, pers. comm. 1992) of the southern Appalachians (Virginia), also invites comparison. In the proportions of the individual parts of the cranidium it is closely comparable with *T. mobergi*, but has deeper and more distinct lateral glabellar depressions, a strongly curved genal spine, and the external surface has a distinct pattern of raised lines and a more conspicuous muscle attachment area immediately in front of the occipital furrow. It must be emphasized, however, that the majority of the specimens ascribed to *T. mobergi* are largely exfoliated and the surface sculpture is poorly known.

Isberg (1917) described damaged and irregularly regenerated lenses in the eyes of *T. mobergi*.

Occurrence. In Sweden this species is known with certainty only from the type stratum and type locality, and from the lower Andersö Shale at Fagerdal (temporary exposure in the northern part of the village), about 8 km north of Hammerdal, Jämtland. Outside Sweden, the species has been described from the upper Elnes Formation (formerly Ogygiocaris Shale or 4a₃) in the Oslo Region of Norway (Nikolaisen 1963, p. 371).

Telephina wegelini (Angelin, 1854)

Plate 4, figures 1–9

- *1854 *Telephus wegelini* Angelin, p. 91, pl. 41, fig. 23.
- v.1884 *Telephus fractus* Barr.; Törnquist, pp. 89–90 [remarks].
- v.1913a *Telephus wegelini* Ang.; Hadding, pp. 40–41, pl. 2, figs 18–19.
- v.1925 *Telephus wegelini* Angelin; Warburg, pp. 90–92, pl. 1, figs 16–18.
- .1930 *Telephus wegelini* Angelin; Ulrich, pp. 13–14, pl. 2, figs 10–12 [copies of Angelin's (1854, pl. 41, fig. 23) and Hadding's (1913a, pl. 2, figs 18–19) original figures].
- v.1930 *Telephus linnarssoni* Ulrich, pp. 15–17, pl. 2, figs 15–17 [copies of Warburg's (1925, pl. 1, figs 16–18) original figures].
- ?1963 *Telephina* (*Telephina*) *wegelini* (Angelin, 1854); Nikolaisen, pp. 383–384.
- non 1971 *Telephina* cf. *linnarssoni* (Ulrich); Dean, pp. 46–48, pl. 22, figs 1–2, 11.
- ?1979 *Telephina* sp.; Bruton and Owen, fig. 6.
- ?1980 *Telephina* sp.; Owen and Bruton, p. 11, pl. 1, fig. 9.

Type data. The holotype by monotypy (Angelin 1854, pl. 41, fig. 23) cannot be traced, and is considered lost. A nearly complete but flattened cranidium (LO 2571T; Pl. 4, fig. 5), figured by Hadding (1913a, pl. 2, fig. 18), is here selected as neotype. It was collected by S. L. Törnquist from the Fjäckå Shale (formerly black Tretaspis or Trinucleus shale; lower Ashgill) at Vikarbyn in the Siljan district, Dalarna (see Törnquist 1883, p. 58 for locality data).

Material. Fourteen cranidia from the Fjäckå Shale, and one cranidium from the Boda Limestone.

Remarks. Only cranidia of this species are known, and they show considerable variation due to varying degrees of flattening. For instance, the anterior border is clearly visible in dorsal view in strongly flattened specimens (Pl. 4, fig. 7), whereas it is tucked beneath the frontal lobe of the glabella in specimens retaining more of their original convexity (Pl. 4, fig. 8).

To the detailed description given by Warburg (1925, p. 90) it can be added that the occipital spine is long with a circular cross section (Pl. 4, fig. 2), and the posterior part of the palpebral area has

a distinct, kidney-shaped muscle insertion area. Furthermore, there is a narrow, raised ridge or rim along the postero-lateral margin of the palpebral area.

TABLE 3. Dimensions (in mm) of cranidia of *Telephina wegelini*. An asterisk indicates that the specimen is strongly flattened.

	Lc	G	Lo	Wc	Wg	Wf
LO 6709t	3.40	2.65	—	5.25	2.80	1.50
LR 2*	3.40?	2.65?	—	5.95	3.50	1.30
SGU 8646*	4.15	3.15	—	6.50	4.35	1.35
LO 6710t*	4.35	3.20	—	5.75	3.75	1.30
SGU 4106	4.55	3.35	—	7.00?	4.20	1.50
LO 2571T	4.60	3.70	2.40	6.60	4.25	1.80
LO 2572t*	4.70	3.70	2.75	7.25	4.70	1.80

Warburg's (1925) description of *T. wegelini* is based on a fairly well-preserved cranidium (SGU 4106; Pl. 4, figs 8–9) from the Boda Limestone in the Siljan district. It differs in some minor respects from the neotype and other specimens from the Fjäckå Shale, and Ulrich (1930, p. 15) assigned it to a new species, *T. linnarssoni*. This specimen is, however, uncompressed, and the differences pointed out by Ulrich (1930) can largely be attributed to the flattening of the specimens from the Fjäckå Shale. Hence, I concur with Nikolaisen (1963, p. 383) and regard *T. linnarssoni* as a junior subjective synonym of *T. wegelini*.

A fragmentary cranidium from the Chair of Kildare Limestone (Ashgill) of eastern Ireland was described by Dean (1971, p. 46) as *T. cf. linnarssoni* (Ulrich). The poor preservation makes evaluation difficult, but it differs from *T. wegelini* in having a proportionately wider (tr.) glabella, which is strongly tapered forwards and less broadly rounded in front.

T. wegelini is closely comparable with the type species, *T. fracta* from the Ashgill of Bohemia, and the two species are distinguishable only on the basis of minor characters. I have examined the type specimen of *T. fracta* (see Horný and Bastl 1970, pl. 4, fig. 11), and it differs from *T. wegelini* mainly in that the anterior part of the palpebral lobe is narrower, and the palpebral area lacks a raised rim along the postero-lateral margin. Moreover, there is no indication of muscle insertion areas on the palpebral areas, but this may be due to the mode of preservation.

Occurrence. Upper Ordovician (Harjuan Series) in the Siljan district, Dalarna. One specimen (SGU 4106; Pl. 4, figs 8–9) is from the Boda Limestone at Boda; the remaining ones are from the Fjäckå Shale (*Pleurograptus linearis* Biozone) at Vikarbyn, Amtjärn, Enån, and Skattungbyn. In addition, specimens questionably assigned to the species are known from the upper Solvang Formation (lowermost Ashgill) in the Oslo Region of Norway (Nikolaisen 1963, p. 383; Owen and Bruton 1980, p. 11).

Telephina granulata (Angelin, 1854)

Plate 4, figures 13–14; Plate 5, figures 1–11; Plate 6, figures 1–3

- *1854 *Telephus granulatus* Angelin, p. 91, pl. 41, fig. 21.
- v.1875 *Bohemilla(?) denticulata* Linnarsson, pp. 495–497, pl. 22, figs 4–5.
- .1897 *Aeglina denticulata* (Linnr.); Holm, p. 461.
- v.1897 *Telephus bicuspis* Ang.; Holm, p. 463 [*partim*].
- v.1913a *Telephus granulatus* Ang.; Hadding, pp. 35–37, pl. 1, figs 8–10.
- v.1913b *Telephus granulatus* Ang.; Hadding, p. 76, pl. 8, figs 9–10 [copies of Hadding's (1913a, pl. 1, figs 8, 10) original figures].
- v.1930 *Telephus granulatus* Angelin; Ulrich, p. 11, pl. 1, figs 19–23 [copies of Hadding's (1913a, pl. 1, figs 8–10) original figures].

- v.1936 *Telephus granulatus* Ang.; Asklund, pp. 9–10, pl. 2, figs 1–7.
 non 1963 *Telephina (Telephops) granulata* (Angelin, 1854); Nikolaisen, pp. 386–387, text-fig. 5, pl. 4, fig. 13.
 v.1963 *Telephina (Telephops) bos* Nikolaisen, pp. 389–391, pl. 4, figs 4–9.
 v.1982b *Telephina* sp.; Jaanusson, p. 177.

Type data. The specimen figured by Angelin (1854, locality given as 'Norvegiæ') cannot be located and is considered lost. No other possible syntypes can be traced, and as neotype I select a cranidium (PMO 72698; Pl. 5, fig. 1) from the Vollen Formation (formerly Ampyx Limestone or 4a β ; Owen *et al.* 1990) on the western side of Bygdøy in Oslo, Norway. It was illustrated by Nikolaisen (1963, pl. 4, fig. 8), who assigned it to a new species, *T. bos*.

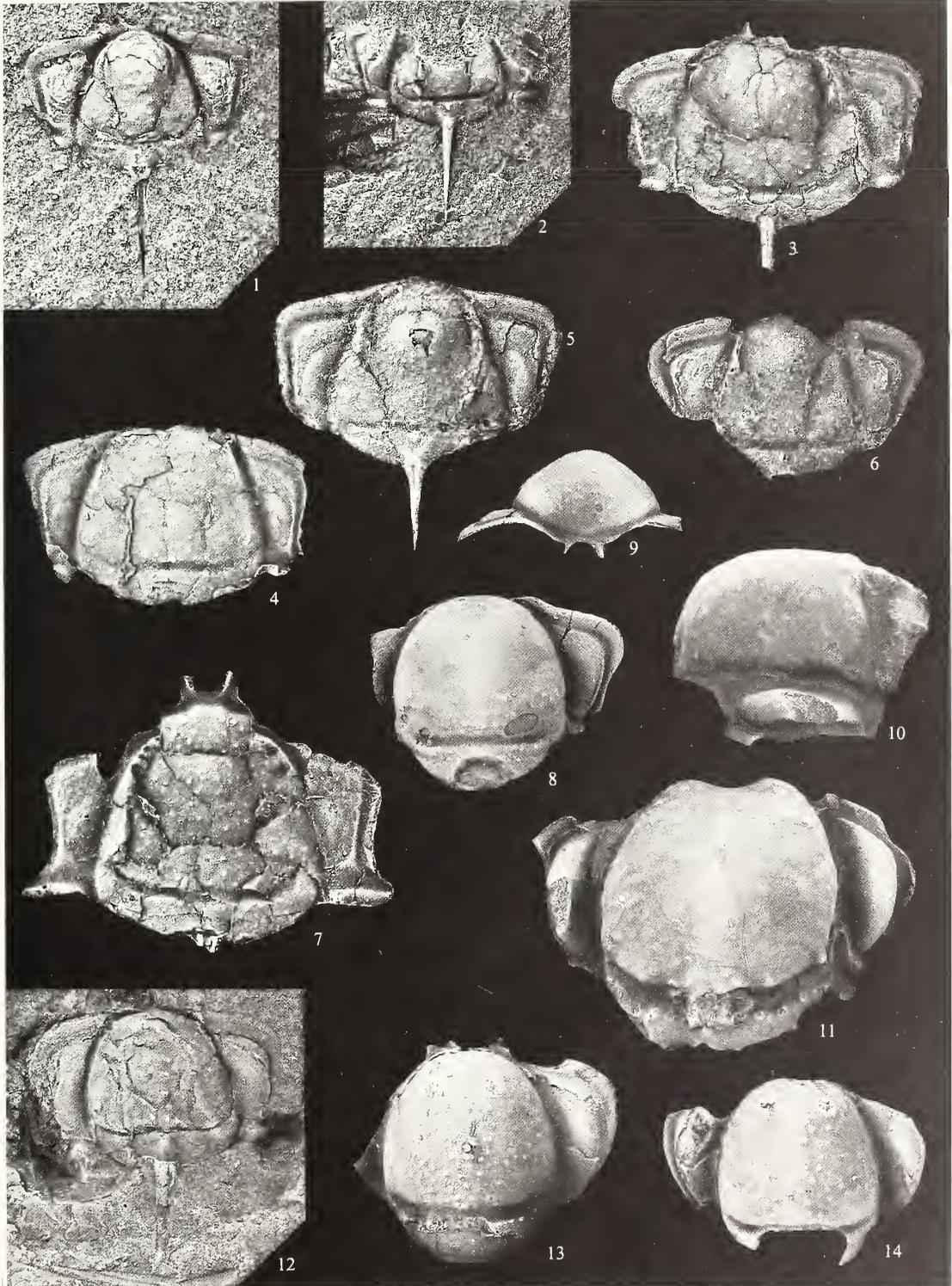
Angelin's illustration (1854, pl. 41, fig. 21) is of a tuberculate cranidium with fairly narrow (tr.) fixigenae and a pair of spines (broken) at the anterior end of the glabella. For a long time, however, the concept of *T. granulata* has been based on Hadding's (1913a) fairly detailed description, which is based on material from Jämtland. It would have been preferable to choose one of Hadding's (1913a) specimens as neotype, but this is not possible because Angelin's missing specimen was from Norway (precise locality not known). *T. bos* Nikolaisen, 1963 from Norway agrees in all essential features with *T. granulata sensu* Hadding, 1913a, and I regard them as conspecific. To retain stability, a neotype was therefore chosen among specimens described as *T. bos* by Nikolaisen (1963). In this context, it is worth noting that the specimens described as *T. granulata* by Nikolaisen (1963, p. 386) differ in some respects from *T. granulata sensu* Hadding, 1913a, and seem to represent a different species.

Material. Fourteen nearly complete cranidia, six fragmentary cranidia, four librigenae, two incomplete thoracic tergites, and two pygidia (SGU 3954 and 6721). The specimens are generally preserved as internal moulds.

Description. Length of cranidium (sag.; excl. occipital spine) about 0.7 times the width. Glabella highly convex (tr.), widest adjacent to or slightly in front of the occipital furrow, tapering forward (more rapidly in the anterior part), broadly rounded anteriorly, and generally about 0.9 times as long (sag.) as its maximum width. Preglabellar furrow tucked beneath the frontal convexity of the glabella. A pair of horns or spines is present at the top of the frontal slope of the glabella. These spines are situated far apart from each other and project obliquely forward, outward, and upward from the antero-lateral parts of the glabella. Occipital ring with a moderately long and slender spine, posteriorly directed and with circular cross section. Palpebral area

EXPLANATION OF PLATE 4

- Figs 1–9. *Telephina wegelini* (Angelin, 1854). All specimens except 8–9 are from the Fjäcka Shale (*Pleurograptus linearis* Biozone) at Amtjärn (1–3; coll. C. Wiman 1906), Enån (4), and Vikarbyn (5–7; coll. S. L. Törnquist) in the Siljan district, Dalarna. 1, PMU D2148; flattened cranidium; $\times 8$. 2, PMU D2146; flattened cranidium with complete occipital spine; $\times 6$. 3, PMU D2147; flattened cranidium; $\times 6$. 4, SGU 8646; flattened cranidium; $\times 6$. 5, neotype, LO 2571T; a nearly complete cranidium; original of Hadding (1913a, pl. 18); $\times 6$. 6, LO 6709t; flattened cranidium; latex cast from external mould; $\times 8$. 7, LO 6710t; flattened cranidium; $\times 8$. 8–9, SGU 4106; cranidium in dorsal and anterior views; original of Warburg (1925, pl. 1, figs 16–18); Boda Limestone at Boda, Siljan district, Dalarna; coll. G. Linnarsson; $\times 6.5$.
- Figs 10–11. *Telephina* sp. B. SGU 8647; cranidium in left lateral and dorsal views; Andersö Shale, Mellersta Utön, central Storsjön area, Jämtland; $\times 6$.
- Fig. 12. *Telephina* sp. A. LO 2548t; flattened cranidium; original of Hadding (1913a, pl. 2, fig. 24); Lower Dichellograptus Shale, Kyrkbäken rivulet in Röstånga, Scania; $\times 8$.
- Figs 13–14. *Telephina granulata* (Angelin, 1854); upper Andersö Shale (*Nemagraptus gracilis* Biozone), Andersön, central Storsjön area, Jämtland. 13, SGU 8648; cranidium; locality 2 of Hadding (1912, pl. 7A; 1913b, fig. 12); coll. P. Thorslund 1956; $\times 8$. 14, LO 2567t; cranidium with glabellar muscle attachment areas; original of Hadding (1913a, pl. 1, fig. 9); locality 5 of Hadding (1912, pl. 7A; 1913b, fig. 12); coll. A. Hadding 1912; $\times 7$.



crenate and moderately wide (tr.). Palpebral lobe slightly wider anteriorly than posteriorly. Width (tr.) of anterior border (between lateral extremities of spines) about one-third that of occipital ring.

Librigena with approximately semi-elliptical outer margin and extremely long genal spine, which is directed laterally to postero-laterally. Extraocular cheeks narrow and occupied mainly by a convex border, which is strongly downslowing laterally. A distinct, postero-laterally directed metalibriginal spine is present. Extraocular cheeks widest (tr.) at genal spine. Visual surface bounded on outer side by a deep furrow.

Thoracic rachial rings highly convex (tr.) and with a posteriorly directed spine at posterior margin. Pleurae not known.

Pygidium subtriangular in outline and slightly wider than long (length/width ratio about 1.0:1.3). Rachis highly convex (tr.), tapering backwards, and occupying slightly more than half of the maximum pygidial width at its anterior end. Terminal piece small, poorly defined, and fused with the posterior rachial ring. Rachial rings bear a pair of spines or prominent tubercles very close together at mid-line. Posterior end of rachis truncate and sloping down almost vertically to the short (sag.) post-rachial field. Pleural region narrow, steeply downslowing laterally, and with a narrow, convex border. Anterior margin of pleural region a narrow, raised rim. Antero-lateral corners of pygidium pointed or with a short spine. Pleural furrows not apparent.

Surface sculpture consists of fairly widely spaced tubercles on the glabella, the occipital ring and the thoracic rachial rings. In addition, transversely arranged terrace lines are present on the ventral surface of the occipital ring, and the external exoskeletal surface of the pygidial pleural region exhibits fine, raised lines arranged in a Bertillon pattern. At least two pairs of smooth muscle attachment areas appear to be present on the glabella. The posterior pair is transversely elongate and situated immediately in front of the outer parts of the occipital furrow. The anterior pair is larger, composite, diagonally directed, and situated at about half-way along the length of the glabella.

Remarks. The material of *T. granulata* displays considerable morphological variation. Much of this variability is due to variation in the width and shape of the fixigenae, and in the curvature of the palpebral lobe. Modest variation in the shape of the glabella and in the position of the glabellar spines can also be observed.

The holotype of *T. bos* Nikolaisen, 1963 (PMO 72701) differs from *T. granulata* in having wider fixigenae and a proportionately wider and shorter glabella. It may well be sagittally compressed, however, and is considered a junior synonym (see above).

The specimens described by Nikolaisen (1963, p. 386) as *T. granulata* are from the upper Elnes Formation (probably *Hustedograptus teretiusculus* Biozone) in the Oslo Region, Norway. The small cranidium figured in Nikolaisen's text-fig. 5 differs from *T. granulata* as described herein in having wider (tr.) fixigenae and the glabellar spines close together in a fairly posterior position. In the position of the glabellar spines, it approaches *T. biseriata* (Asklund, 1936), but the wide fixigenae (closely resembling those of *T. bicuspis*) indicate that it cannot be assigned to that species. The narrow palpebral lobe and the extremely long and stout occipital spine distinguishes the cranidium figured in Nikolaisen's pl. 4, fig. 13 from those of *T. granulata*. In addition, it has the glabellar spines fairly close together, and the palpebral lobe is more evenly curved than in most specimens referred to *T. granulata*. Hence, I conclude that the specimens described as *T. granulata* by Nikolaisen (1963) do not belong to that species.

T. bicornis (Ulrich, 1930), from the Effna Limestone (Caradoc; *Prioniodus variabilis* Subzone; S. M. Bergström, pers. comm. 1992) of the southern Appalachians (Virginia), is very similar to *T. granulata*. However, I hesitate to regard them as conspecific because there appear to be slight differences. For instance, the fixigenae are consistently somewhat wider (tr.) and the tubercles are larger and more conspicuous in *T. bicornis*, which in addition, has the short metalibriginal spine situated much closer to the genal spine. Ulrich (1930, p. 25) emphasized that the glabellar spines are in a more posterior position in *T. bicornis*, but this is a variable feature (compare the cranidia figured by Ulrich 1930, pl. 4, figs 6 and 8).

A fragmentary cranidium from the Brickworks Quarry Shales Member, Knockerk Formation (Caradoc), of eastern Ireland was illustrated and described by Brenchley *et al.* (1967, p. 302, pl. 7, figs 7-8) as *T. cf. bos* Nikolaisen. It is closely comparable with *T. granulata*, but differs in having slightly wider (tr.) fixigenae and a less broadly rounded glabellar front. In these respects the Irish specimen is more like *T. bicornis*, and it probably represents that species (cf. Romano 1980, p. 68).

TABLE 4. Dimensions (in mm) of cranidia of *Telephina granulata*.

	Lc	G	Lo	Wc	Wg	Wf
LO 2567t	3.95?	2.95	—	5.45?	3.20	1.30
SGU 8648	4.25	3.10	—	6.15?	3.55	1.50
SGU 8651	4.90	3.75	—	6.70?	3.90	1.60
SGU 8660	5.00?	3.90	—	6.85	4.15	1.65
PMO 72698	5.35	4.00	—	7.10?	4.00	1.65
LO 6712t	5.95	4.45	—	7.75	4.85	1.85
SGU 6427	7.00	5.25	—	9.50	5.80	2.00

Additional material from the Brickworks Quarry Shales was described by Romano and Owen (1993), who reassigned the Irish form to *T. cf. bicornis*.

Occurrence. In Jämtland, this species has been collected from limestones in the *Nemagraptus gracilis* Biozone on Andersön (localities 2 and 5 of Hadding 1912, pl. 7A; 1913b, fig. 12), on the southwestern shore of Bynäset, Frösön, at Hara about 9 km south of Sunne (see Thorlund 1937, p. 11 for locality data), at Digernäs about 4 km north-east of Sunne, and at Ytterhallen in the Hallen area (loose boulder).

In Västergötland, *T. granulata* is known from an argillaceous limestone in the lowermost part of the upper Dalby Limestone in the Gullhögen quarry on the southeastern slope of northern Billingen (see Jaanusson 1982b, p. 176 and Holmer 1989, p. 6 for locality data and stratigraphy). In terms of the graptolite biozonation, the Västergötland specimens were recovered from strata corresponding with the uppermost *Nemagraptus gracilis* Biozone or, more probably, the lowermost *Diplograptus multidentis* Biozone.

A nearly complete cephalon is known from the Kukruse Stage in the Blidene drill core (depth 910-85 m) in western Latvia, and a cephalon tentatively assigned to the species has been recorded from the uppermost Uhaku Stage in the Lopatovo-8 drill core (depth 456-30 m) in the Pskov district of western Russia.

Telephina aff. granulata (Angelin, 1854)

Plate 6, figures 4-8

v.1919 *Telephus granulatus* Ang.; Funkquist, p. 39, pl. 2, fig. 9.

v.1951 *Telephus granulatus* Ang.; Nilsson, pp. 684, 688.

Material. One nearly complete cranidium (LO 6714t) and two incomplete cranidia (LO 2966t and 6713t).

Dimensions (mm).

	Lc	G	Lo	Wc	Wg	Wf
LO 6714t	5.65	4.15	—	7.50?	4.35	2.00

Remarks. The cranidia are very like those of *T. granulata* but differ in having a slightly longer glabella, which is truncate in front. In addition, the spines on the glabella are in a slightly posterior position and closer to the mid-line than in *T. granulata*, especially in the specimen figured on Plate 6, figures 7-8.

Occurrence. Killeröd Formation ('*bronnii* beds'; equivalent to part of the upper *Hustedograptus teretiusculus* Biozone according to Bergström 1973, p. 15) at Killeröd in south-east Scania (locality 2 of Regnéll 1960, fig. 4; section described by Nilsson 1951, p. 683). It is also known from a loose boulder at Rödmölla in the Tosterup area, south-east Scania (cf. Funkquist 1919, p. 42).

Telephina biseriata (Asklund, 1936)

Plate 6, figures 9-13

v*1936 *Telephus biseriatatus* Asklund, pp. 11-12, pl. 1, figs 9-11.

Type data. The holotype by monotypy is a nearly complete cranidium (SGU 6714; Pl. 6, fig. 9), illustrated by Asklund (1936, pl. 1, figs 9–11). It was collected by G. Linnarsson in 1871 from a shore section on northwestern Andersön in the central Storsjön area, Jämtland. Its stratigraphical position is not known precisely, but it was probably collected from a dark grey limestone in the middle–upper part of the *Hustedograptus teretiusculus* Biozone (middle Andersö Shale).

Material. In addition to the holotype, six cranidia, one incomplete pygidium, and fragments of the eyes. The majority of the specimens are preserved as internal moulds in a dark grey limestone and seem to retain their original convexity.

Description. Glabella subequal in length (sag.) and maximum width or slightly wider than long. A pair of horns or spines, situated very close together, is present at 0.6–0.7 of the glabellar length from its posterior end. Occipital spine probably present but not preserved. Anterior border narrow (sag.) with the spines situated very close together (width between lateral extremities of spines one-quarter to one-third that of occipital ring). Thorax and extraocular librigenae not known (Table 5).

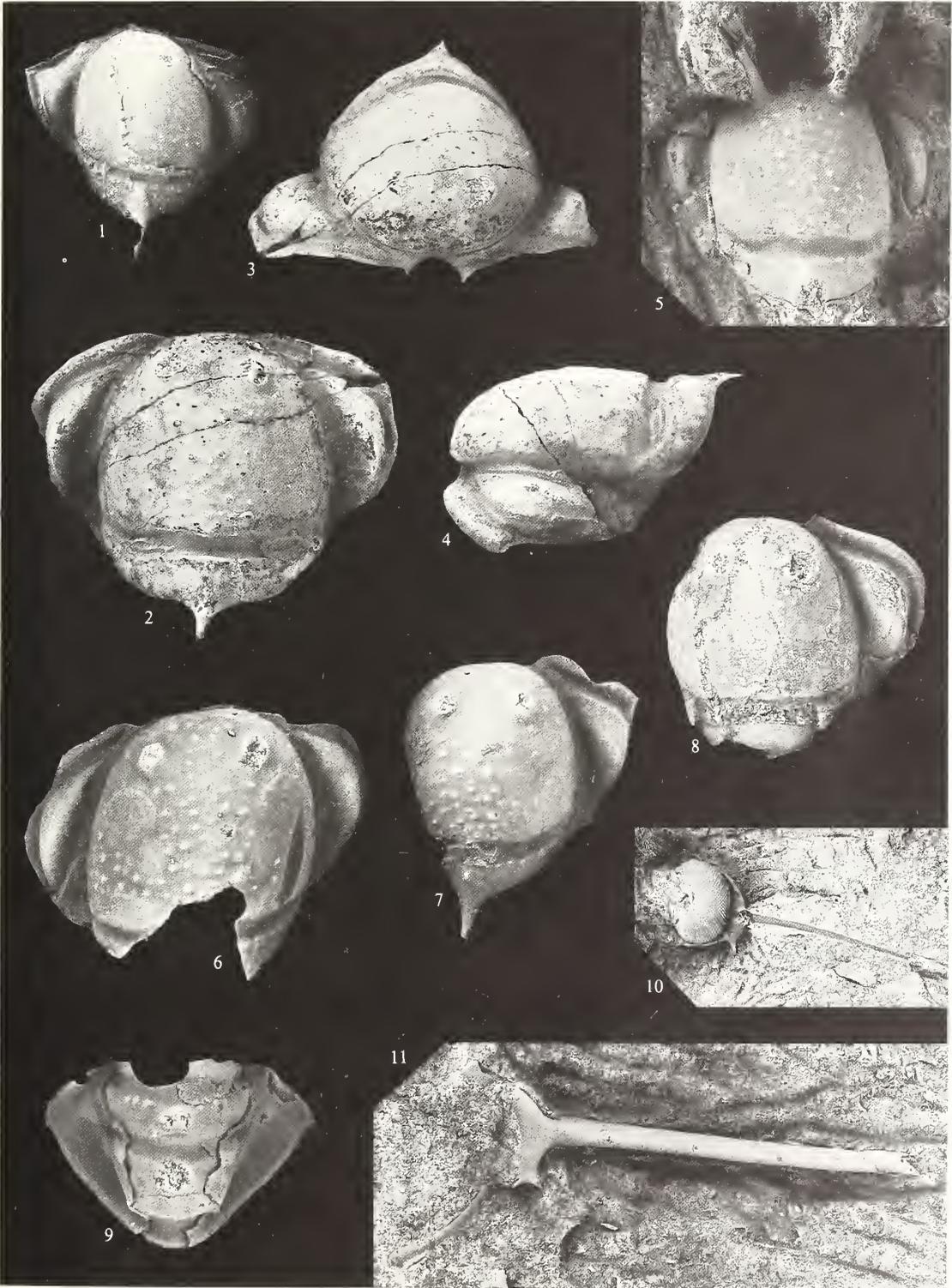
Surface sculpture consists of fairly widely spaced tubercles on the glabella and the occipital ring, and terrace lines occur on the ventral surface of occipital ring. The tubercles are most prominent along the mid-line of the glabella. The fixigenae and the pygidium appear to be smooth, except for indistinct ‘wrinkles’ anterolaterally on the palpebral area.

Remarks. This species is distinctive and differs from *T. granulata* in that the glabellar spines are situated very close together in a posterior position. It is worth noting, however, that the position of the spines is a variable feature. In the holotype (Pl. 6, fig. 9), for instance, they are in an extremely posterior position, whereas they are more anteriorly placed in the cranidium figured on Plate 6, figures 11–12. The expression of the tubercles varies in strength, but this can be attributed probably to the mode of preservation. The glabella is generally subequal in length and maximum width, and comparatively longer than in *T. granulata*. The pygidium is slightly wider than long and very similar to that of *T. granulata*.

Occurrence. Middle Andersö Shale (middle–upper *Hustedograptus teretiusculus* Biozone) on the northwestern and northern shore of Andersön (cf. Thorslund 1937, p. 10), the northern shore of Norderön (see Thorslund and Jaanusson 1960, fig. 22), and 0.5 km E of Lövtorpet on Frösön in the central Storsjön area, Jämtland. In addition, a few cranidia are known from coeval strata at Önsvedsbäcken south of Sunne, Jämtland (see Hadding 1912 for locality data). The majority of the specimens are from a dark grey, bedded limestone generally referred to as the Biseriata Limestone (‘*Telephina biseriata* beds’ of Thorslund and Jaanusson 1960). Conodonts recovered from this limestone are indicative of the *Eoplacognathus lindstroemi* Sub-biozone and the lower

EXPLANATION OF PLATE 5

Figs 1–11. *Telephina granulata* (Angelin, 1854). All specimens except 1 are from the upper Andersö Shale (*Nemagraptus gracilis* Biozone), central Storsjön area, Jämtland. 1, neotype, PMO 72698; a nearly complete cranidium; original of Nikolaisen (1963, pl. 4, fig. 8); Vollen Formation, western side of Bygdøy in Oslo, Norway; coll. F. Nikolaisen 1958; × 5.5. 2–4, SGU 6427; cranidium in dorsal, anterior, and left lateral views; original of Hadding (1913a, pl. 1, fig. 8a–c); Hara south of Sunne; coll. G. C. von Schmalensee 1884; × 6. 5, RM Ar 9897a; cranidium with glabellar spines; original of Asklund (1936, pl. 2, fig. 2); Ytterhallen, Hallen area (loose boulder); coll. G. C. von Schmalensee; × 6. 6, SGU 8649; cranidium with glabellar muscle attachment areas; Hara south of Sunne; coll. G. C. von Schmalensee 1884; × 7. 7, SGU 8650; cranidium; Hara south of Sunne; coll. G. C. von Schmalensee 1884; × 7. 8, SGU 8651; cranidium; Hara south of Sunne; coll. P. Thorslund 1936; × 7.5. 9, SGU 6721; nearly complete pygidium; original of Asklund (1936, pl. 2, fig. 7); Bynäset, Frösön; × 9. 10, RM Ar 9899; nearly complete librigena; original of Asklund (1936, pl. 2, fig. 4); Ytterhallen, Hallen area (loose boulder); coll. G. C. von Schmalensee 1885; × 2.5. 11, RM Ar 9897b; incomplete librigena in ventral view; Ytterhallen, Hallen area (loose boulder); coll. G. C. von Schmalensee; × 6.



AHLBERG, *Telephina granulata*

Pygodus anserinus Biozone (Bergström *et al.* 1974, table 10), and, in terms of the graptolite biozonation, the Biseriata Limestone seems to represent the middle–upper part of the *H. teretiusculus* Biozone.

Telephina aff. *biseriata* (Asklund, 1936)

Plate 6, figure 14

Material. An incomplete cranidium (SGU 8656), largely exfoliated, collected by P. Thorslund in 1937.

Dimensions (mm). G = 4.20; Wg = 5.00; Wf = 1.60.

Remarks. The cranidium resembles that of *T. biseriata* in having the glabellar spines situated close together, but they are in a more anterior position (at about 0.9 of the glabellar length from its posterior end). In addition, it has a proportionately wider glabella (length/width ratio 1:1.2) and considerably narrower (tr.) fixigenae with the facial suture curved more evenly around the lateral extremity of the palpebral lobe. It seems to represent a new, undescribed species, but with the limited material at hand it is left under open nomenclature.

The glabellar surface sculpture consists of fairly widely spaced tubercles, except for two pairs of large, smooth muscle attachment areas. The posterior pair is transversely elongate and situated immediately in front of the outer parts of the occipital furrow. The anterior pair is larger and situated about half way along the glabella.

Occurrence. Dark grey limestone in the middle Andersö Shale (probably upper *Hustedograptus teretiusculus* Biozone) on the northwestern shore of Andersön, Jämtland (locality 1 of Hadding 1912, pl. 7A; 1913b, fig. 12).

Telephina sp. A

Plate 4, figure 12

v.1913a *Telephus* sp.; Hadding, p. 42, pl. 2, fig. 24.

v.1913b *Telephus* sp.; Hadding, p. 76, pl. 8, fig. 5 [copy of Hadding's (1913a, pl. 2, fig. 24) original figure].

v.1930 *Telephus* species undetermined; Ulrich, pl. 1, fig. 2 [copy of Hadding's (1913a, pl. 2, fig. 24) original figure].

Material. An internal mould of a flattened cranidium (LO 2548t), collected by A. Hadding in 1911.

Dimensions (mm). Lc = 3.40?; G = 2.50; Lo = 2.25?; Wc = 5.25; Wg = 3.00; Wf = 1.35.

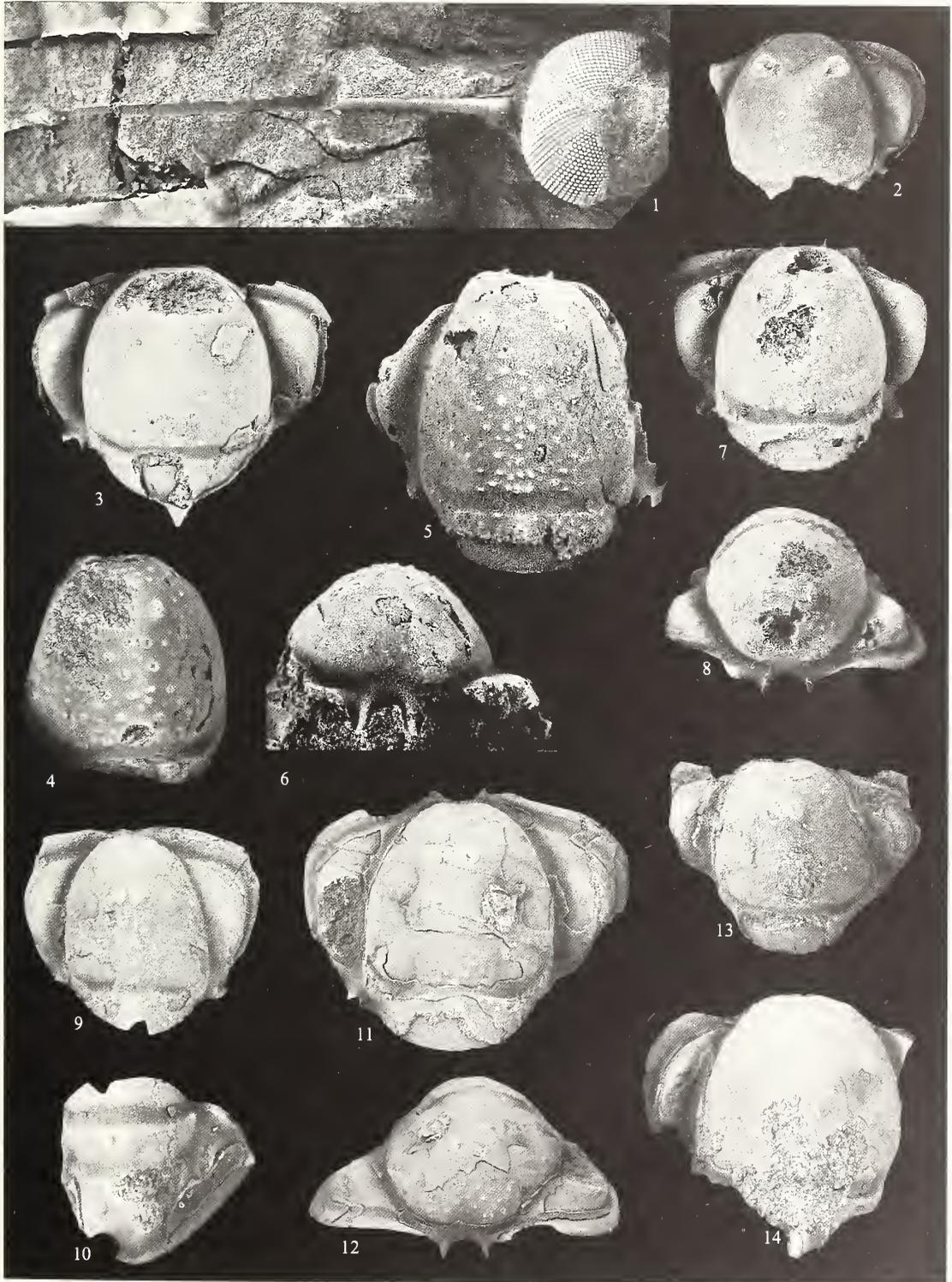
EXPLANATION OF PLATE 6

Figs 1–3. *Telephina granulata* (Angelin, 1854). 1, SGU 8652; incomplete librigena; upper Andersö Shale (*Nemagraptus gracilis* Biozone) at Hara south of Sunne, Jämtland; coll. P. Thorslund 1936; $\times 6$. 2–3, cranidia; upper Dalby Limestone, Gullhögen quarry, Billingen, Västergötland; coll. J. Johansson. 2, LO 6711t. 3, LO 6712t. Both $\times 6$.

Figs 4–8. *Telephina* aff. *granulata* (Angelin, 1854). Killeröd Formation at Rödmölla, Tosterup area (4; coll. K. A. Grönwall) and at Killeröd (5–8; coll. R. Nilsson 1943), south-east Scania. 4, LO 2966t; fragmentary cranidium; original of Funkquist (1919, pl. 2, fig. 9). 5–6, LO 6713t; incomplete cranidium in dorsal and anterior views. 7–8, LO 6714t; nearly complete cranidium in dorsal and anterior views. All $\times 6$.

Figs 9–13. *Telephina biseriata* (Asklund, 1936). Middle Andersö Shale (middle–upper *Hustedograptus teretiusculus* Biozone) on Andersön (9, 11–12) and Norderön (10), central Storsjön area, and at Önsvedsbäcken (13) south of Sunne, Jämtland. 9, holotype, SGU 6714; a nearly complete cranidium; original of Asklund (1936, pl 1, figs 9–11); $\times 8$. 10, SGU 8653; incomplete pygidium; coll. P. Thorslund 1950; $\times 9.5$. 11–12, SGU 8654; nearly complete cranidium in dorsal and anterior views; coll. P. Thorslund 1950; $\times 7.5$. 13, SGU 8655; cranidium; coll. P. Thorslund 1950; $\times 7$.

Fig. 14. *Telephina* aff. *biseriata* (Asklund, 1936). SGU 8656; Middle Andersö Shale, northwestern shore of Andersön, Jämtland (locality 1 of Hadding 1912, pl. 7A, 1913b, fig. 12); $\times 6$.



AHLBERG, *Telephina*

TABLE 5. Dimensions (in mm) of crania of *Telephina biseriata*.

	Lc	G	Lo	Wc	Wg	Wf
SGU 6714	3.55	2.65	—	4.35	2.55	1.20
SGU 8655	4.45	3.40	—	6.00?	3.55	1.30?
SGU 8654	5.20	3.70	—	6.70	4.00	1.65

Remarks. The specimen is strongly flattened and imperfectly preserved. A comparison with named taxa is therefore difficult. The overall shape of the cranium and the glabella is similar to that of *T. bicuspis* and it may belong to that species. It differs, however, in having a stouter occipital spine, narrower (tr.) fixigenae, and less strongly curved palpebral lobes. The posterior part of the palpebral area is fairly wide (tr.), and in this respect it is similar to flattened specimens of *T. wegelini*.

Occurrence. Lower Dicollograptus Shale (probably middle part of the *Hustedograptus teretiusculus* Biozone) at the Kyrkbäcken rivulet in Röstänga, Scania, southern Sweden (locality IIIb of Moberg 1910, p. 114, pl. 3; section III:3 of Hadding 1913b, p. 19).

Telephina sp. B

Plate 4, figures 10–11

Material. An internal mould of a nearly complete cranium (SGU 8647), collected by G. Linnarsson in 1871.

Dimensions (mm). Lc = 7.60; G = 5.00; Wc = 10.00?; Wg = 5.85; Wf = 2.25?.

Remarks. The cranium slopes down steeply anteriorly and differs from those of most other species of *Telephina* in having a strongly convex glabella and extremely convex palpebral areas, which are steeply downsloping laterally. The fixigenae are narrow (tr.) with a crescentic and ridge-like palpebral area. The dorsal and palpebral furrows are wide and deeply incised. The glabella is tapered forwards and steeply downsloping anteriorly. The glabellar frontal lobe is truncate and distinctly arched backwards medially. The occipital furrow is very wide (sag.) and deep. Tubercles are present on the glabella and the occipital ring.

A broadly similar form from the Engervik Member of the Elnes Formation at Huk in Oslo, Norway, was described and figured by Nikolaisen (1963, p. 384, pl. 3, figs 15–16) as *Telephina* sp. no. 2.

Occurrence. Andersö Shale (probably lower part; *Hustedograptus teretiusculus* Biozone) on Mellersta Utön in the central Storsjön area, Jämtland.

Telephina sp. C

(not figured)

v.1948 *Telephus* sp.; Thorslund, p. 362, pl. 11, fig. 10.

v.1964 *Telephina* sp.; Jaanusson, p. 17.

Material. A flattened and poorly preserved cranium (PMU Vg 37), about 1.3 mm long (sag.; excl. occipital spine).

Remarks. The poor preservation makes evaluation difficult, but the specimen shows the following: the glabella is tapered forward, rounded in front, and subequal in length and maximum width; the occipital ring is fairly long (sag.) with a stout and broad-based occipital spine, and the fixigenae are wide (tr.).

Occurrence. Lower Dalby Limestone in the Kullatorp drill core, Kinnekulle, Västergötland (depth 86.50–86.52 m). In terms of the graptolite biozonation, it was probably recovered from strata corresponding to the *Nemagraptus gracilis* Biozone (e.g. Jaanusson 1964, table 1, 1982a, fig. 4).

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REFERENCES

- ANGELIN, N. P. 1854. *Palaeontologia Scandinavica. I: Crustacea formationis transitionis*. Fasc. 2, 21–92, pls 25–41, Leipzig, Lund.
- ASKLUND, B. 1936. Zur Kenntnis der jämtländischen Ogygiocaris-fauna. *Sveriges Geologiska Undersökning, Series C*, **395**, 1–12, pls 1–2.
- BARRANDE, J. 1852. *Système Silurien du centre de la Bohême. 1^{ère} partie: Recherches paléontologiques, I. Crustacés: Trilobites*. Prague and Paris, xxx+935 pp, 50 pls.
- BERGSTRÖM, S. M. 1973. Correlation of the late Lasnamägian Stage (Middle Ordovician) with the graptolite succession. *Geologiska Föreningens i Stockholm Förhandlingar*, **95**, 9–18.
- RIVA, J. and KAY, M. 1974. Significance of conodonts, graptolites, and shelly faunas from the Ordovician of western and north-central Newfoundland. *Canadian Journal of Earth Sciences*, **11**, 1625–1660.
- BILLINGS, E. 1861–1865. *Palaeozoic fossils, Vol. 1*. Geological Survey of Canada, Montreal, 426 pp.
- BRENCHLEY, P. J., HARPER, J. C., ROMANO, M. and SKEVINGTON, D. 1967. New Ordovician faunas from Grangegeeth, Co. Meath. *Proceedings of the Royal Irish Academy, Series B*, **65**(11), 297–304.
- BRUTON, D. L., LINDSTRÖM, M. and OWEN, A. W. 1985. The Ordovician of Scandinavia. 273–282. In GEE, D. G. and STURT, B. A. (eds). *The Caledonide Orogen – Scandinavia and related areas*. John Wiley and Sons Ltd, Chichester, 1266 pp.
- and OWEN, A. W. 1979. Late Caradoc–early Ashgill trilobite distribution in the central Oslo Region, Norway. *Norsk Geologisk Tidsskrift*, **59**, 213–222.
- DEAN, W. T. 1971. The trilobites of the Chair of Kildare Limestone (Upper Ordovician) of eastern Ireland. Part 1. *Monograph of the Palaeontographical Society*, **125** (531), 1–60, 25 pls.
- FORTEY, R. A. 1975. The Ordovician trilobites of Spitsbergen. II. Asaphidae, Nileidae, Raphiophoridae and Telephinidae of the Valhallaformation. *Skrifter Norsk Polarinstiutt*, **162**, 1–125, pls 1–41.
- 1981. *Prospectatrix genatenta* (Stubblefield) and the trilobite superfamily Cyclopygacea. *Geological Magazine*, **118**, 603–614.
- 1985. Pelagic trilobites as an example of deducing the life habits of extinct arthropods. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 219–230.
- FUNKQUIST, H. P. A. 1919. Asaphusregionens omfattning i sydöstra Skåne och på Bornholm. *Lunds Universitets Årsskrift, NF 2*, **16** (1), 1–55, pls 1–2.
- HADDING, A. 1912. Några iakttagelser från Jämtlands ordovicium. *Geologiska Föreningens i Stockholm Förhandlingar*, **34**, 589–602.
- 1913a. Släktet *Telephus* Barr. *Geologiska Föreningens i Stockholm Förhandlingar*, **35**, 25–50, pls 1–2.
- 1913b. Undre Dichellograptusskiffern i Skåne jämte några därmed ekvivalenta bildningar. *Lunds Universitets Årsskrift, NF 2*, **9** (15), 1–91, pls 1–8.
- HOLM, G. 1897. Om *Bohemilla*(?) *denticulata* Linrs. och *Remopleurides microphthalmus* Linrs. *Geologiska Föreningens i Stockholm Förhandlingar*, **19**, 457–480.
- HOLMER, L. 1989. Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. *Fossils and Strata*, **26**, 1–172.
- HORNÝ, R. and BASTL, F. 1970. *Type specimens of fossils in the National Museum Prague. Volume 1: Trilobita*. National Museum, Prague, 354 pp., 20 pls.
- ISBERG, O. 1917. Ein regeneriertes Trilobitenauge. *Geologiska Föreningens i Stockholm Förhandlingar*, **39**, 593–596.
- JAAUSSON, V. 1960. The Viruan (Middle Ordovician) of Öland. *Bulletin of the Geological Institutions of the University of Uppsala*, **37**, 207–288, pls 1–5.

- JAANUSSON, V. 1964. The Viruan (Middle Ordovician) of Kinnekulle and northern Billingen, Västergötland. *Bulletin of the Geological Institutions of the University of Uppsala*, **43**, 1–73.
- 1973. Aspects of carbonate sedimentation in the Ordovician of Baltoscandia. *Lethaia*, **6**, 11–34.
- 1976. Faunal dynamics in the Middle Ordovician (Viruan) of Balto-Scandia. 301–326. In BASSETT, M. G. (ed.), *The Ordovician System*. University of Wales Press and National Museum of Wales, Cardiff, 696 pp.
- 1982a. Introduction to the Ordovician of Sweden. 1–9. In BRUTON, D. L. and WILLIAMS, S. H. (eds). Field excursion guide. IV International Symposium on the Ordovician System. *Paleontological Contributions from the University of Oslo*, **279**, 1–217.
- 1982b. Ordovician in Västergötland. 164–183. In BRUTON, D. L. and WILLIAMS, S. H. (eds). Field excursion guide. IV International Symposium on the Ordovician System. *Paleontological Contributions from the University of Oslo*, **279**, 1–217.
- and BERGSTRÖM, S. M. 1980. Middle Ordovician faunal spatial differentiation in Baltoscandia and the Appalachians. *Alcheringa*, **4**, 89–110.
- KOBAYASHI, T. 1954. On the Komaspidae. *Japanese Journal of Geology and Geography*, **24**, 23–44.
- LINNARSSON, J. G. O. 1871. Jemförelse mellan de siluriska aflagingarna i Dalarne och i Västergötland. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, **1871** (3), 339–354.
- 1872. Anteckningar om den kambrisk-siluriska lagerserien i Jemtland. *Geologiska Föreningens i Stockholm Förhandlingar*, **1**, 34–47.
- 1875. En egendomlig trilobitfauna från Jemtland. *Geologiska Föreningens i Stockholm Förhandlingar*, **2**, 491–497.
- MÄNNIL, R. 1963. Biostratigrafisches obosnovanie raschleneniya ordovikskikh otlozhenij zapadnoj Latvii. [The biostratigraphical subdivision of the Ordovician strata in Latvia.] *Eesti NSV Teaduste Akadeemia Geoloogia Instituudi Uurimused*, **13**, 41–74. [In Russian with English summary].
- 1966. *Istoriya razvitiya Baltijskogo basseyna v ordovike*. [Evolution of the Baltic Basin during the Ordovician.] Eesti NSV Teaduste Akadeemia Geoloogia Instituudi, Tallinn, 200 pp. [In Russian with English summary].
- MAREK, L. 1952. Příspěvek ke stratigrafii a fauně nejvyšší části břidli c kralodvorských (dč.). *Sborník Ústředního ústavu geologického, paleontologického*, **19**, 429–455, pls 1–2. [In Czech with English summary 449–455].
- MOBERG, J. C. 1890. Anteckningar om Ölands ortoceralk. *Sveriges Geologiska Undersökning, Series C*, **109**, 11–22.
- 1910. Guide for the principal Silurian districts of Scania (with notes on some localities of Mesozoic beds). *Geologiska Föreningens i Stockholm Förhandlingar*, **32**, 45–194, pls 1–5.
- MOORE, R. C. (ed.) 1959. *Treatise on invertebrate paleontology. Part O. Arthropoda 1*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 560 pp.
- NIKOLAISEN, F. 1963. The Middle Ordovician of the Oslo Region. 14. The trilobite family Telephiniidae. *Norsk Geologisk Tidsskrift*, **43**, 345–399, pls 1–4.
- NILSSON, R. 1951. Till kännedom om ordovicium i sydöstra Skåne. *Geologiska Föreningens i Stockholm Förhandlingar*, **73**, 682–694.
- OWEN, A. W. and BRUTON, D. L. 1980. Late Caradoc-early Ashgill trilobites of the central Oslo Region, Norway. *Paleontological Contributions from the University of Oslo*, **245**, 1–63.
- — BOCKELIE, J. F. and BOCKELIE, T. G. 1990. The Ordovician successions of the Oslo Region, Norway. *Norges Geologiske Undersøkelse, Special Publication*, **4**, 1–54.
- REED, F. R. C. 1935. The Lower Palaeozoic trilobites of Girvan. Supplement No. 3. *Monograph of the Palaeontographical Society*, **88** (400), 1–64, 4 pls.
- 1944. Five new Ordovician trilobites. *Geological Magazine*, **81**, 58–64.
- REGNÉLL, G. 1960. The Lower Palaeozoic of Scania. 3–43. In REGNÉLL, G. and HEDE, J. E. The Lower Palaeozoic of Scania; the Silurian of Gotland. *International Geological Congress XXI Session, Norden 1960, Guide-book Sweden d*. Geological Survey of Sweden, Stockholm, 89 pp.
- ROMANO, M. 1980. The stratigraphy of the Ordovician rocks between Slane (County Meath) and Collon (County Louth), eastern Ireland. *Journal of Earth Sciences, Royal Dublin Society*, **3**, 53–79.
- and OWEN, A. W. 1993. Early Caradoc trilobites of eastern Ireland and their palaeogeographical significance. *Palaentology*, **36**, 681–720.
- THORSLUND, P. 1935. Paleontologisk-stratigrafisk undersökning. 5–23. In THORSLUND, P. and ASKLUND, B. Stratigrafiska och tektoniska studier inom Föllingeområdet i Jämtland. *Sveriges Geologiska Undersökning, Series C*, **388**, 1–61, pls 1–3.
- 1937. Kvartsiter, sandstenar och tektonik inom Sunneområdet i Jämtland. *Sveriges Geologiska Undersökning, Series C*, **409**, 1–30.

- 1948. The Chasmops Series of the Kullatorp core. 343–373. In WÆRN, B., THORSLUND, P. and HENNINGSMOEN, G. Deep boring through Ordovician and Silurian strata at Kinnekulle, Vestergötland. *Bulletin of the Geological Institutions of the University of Uppsala*, **32**, 337–474.
- and JAANUSSON, V. 1960. The Cambrian, Ordovician, and Silurian in Västergötland, Närke, Dalarna, and Jämtland, central Sweden. *International Geological Congress XXI Session, Norden 1960, Guide-book Sweden e.* Geological Survey of Sweden, Stockholm, 51 pp.
- TÖRNQUIST, S. L. 1883. Öfversigt öfver bergbyggnaden inom Siljansområdet i Dalarna, med hänsyn företrädesvis fäst vid dess paleozoiska lag. *Sveriges Geologiska Undersökning, Series C*, **57**, 1–59.
- 1884. Undersökningar öfver Siljansområdets trilobitfauna. *Sveriges Geologiska Undersökning, Series C*, **66**, 1–101, pls 1–3.
- TRIPP, R. P. 1976. Trilobites from the basal *superstes* Mudstones (Ordovician) at Aldons Quarry, near Girvan, Ayrshire. *Transactions of the Royal Society of Edinburgh*, **69**, 369–423.
- TULLBERG, S. A. 1882. Förelöpande redogörelse för geologiska resor på Öland. *Geologiska Föreningens i Stockholm Förhandlingar*, **6**, 220–236.
- ULRICH, E. O. 1930. Ordovician trilobites of the family Telephidae and concerned stratigraphic correlations. *Proceedings of the United States National Museum*, **76**, 1–101, pls 1–8.
- WANDÅS, B. T. G. 1984. The Middle Ordovician of the Oslo Region, Norway, 33. Trilobites from the lowermost part of the Ogygiocaris Series. *Norsk Geologisk Tidsskrift*, **63**, 211–267.
- WARBURG, E. 1925. The trilobites of the Leptaena Limestone in Dalarna. *Bulletin of the Geological Institutions of the University of Uppsala*, **17**, 1–446, pls 1–11.
- WHITTINGTON, H. B. 1965. Trilobites of the Ordovician Table Head Formation, western Newfoundland. *Bulletin of the Museum of Comparative Zoology*, **132**, 275–442, pls 1–68.
- WIMAN, C. 1893. Ueber die Silurformation in Jemtland. *Bulletin of the Geological Institutions of the University of Uppsala*, **1** (2), 256–276.

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THE RESPIRATORY ORGANS OF EURYPTERIDS

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ABSTRACT. Cuticle fragments from the upper Silurian (Prídolí Series) of south Shropshire, England, are described and interpreted as the respiratory organs of eurypterids. These fragments, combined with whole body evidence, suggest a dual respiratory system: lamellate book-gills, homologous with those of modern xiphosurans and arachnid book lungs, and an additional Kiemenplatten on the true sternite, the roof the branchial chamber. Kiemenplatten is used in preference to gill-tract, because it is a more 'neutral' term, without functional implications. Eurypterids may have been partially terrestrial: the Kiemenplatten is interpreted as an accessory aerial respiratory organ, most closely analogous to the branchial 'lungs' of certain terrestrial crabs. Cuticular projections from the Kiemenplatten are interpreted as having held a layer of water to keep the structure moist during excursions onto land. A new reconstruction of the eurypterid respiratory system is presented.

EURYPTERID respiratory organs were first described by Laurie (1893) from a specimen of *Slimonia* as 'branchial lamellae,' and were interpreted as being located on the dorsal surface of the abdominal plates (Blatfüsse). The Blatfüsse consist of five pairs of plate-like appendages (Clarke and Ruedemann 1912, pl. 26, fig. 2; Waterston 1975, fig. 4a) which are ventral to the true sternites (ventral body wall) of the opisthosoma, and they enclose a series of five pairs of branchial chambers (Waterston 1975) between themselves and the true sternites. It is these branchial chambers which contain the respiratory organs, which were described subsequently from *Baltoeurypterus* as five pairs of oval respiratory areas termed 'Kiemenplatten' (Holm 1898); these are areas of raised, conical 'spinules' covered in microscopic cuticular projections, arranged hexagonally as 'rosettes' (Holm 1898; Wills 1965). They were later re-interpreted as being on the ventral surface of the true sternite (the roof of the branchial chamber), not on the Blatfüsse (Moore 1941), and were subsequently renamed 'gill tracts' (Wills 1965). Their position within the branchial chamber of *Tarsoptereella* was reconstructed in detail by Waterston (1975).

Some eurypterids may have been capable of terrestrial activity (Størmer 1976; Rolfe 1980) and the Kiemenplatten (gill tracts) have been interpreted variously as having aquatic and/or aerial respiratory functions (Størmer 1976; Rolfe 1980; Selden 1985), comparable with isopod pseudotracheae (Størmer 1976). A possible osmoregulatory function was suggested by Waterston (1979) and by Selden (1985), and plastron respiration by Rolfe (1980), with the microscopic cuticular projections acting like plastron hairs. Palaeophysiological calculations suggested that the respiratory surface area (RSA) alone of the gill tract was inadequate to supply a eurypterid's energy requirements (Selden 1985). From this, it was inferred that the gill tract acted primarily as an accessory aerial 'lung', and that eurypterids possessed additional true gills which had yet to be found (Selden 1985).

Taugourdeau (1967) figured gill tract material from the Sahara in micropalaeontological preparations, but did not recognize its significance. During an investigation into the earliest demonstrably terrestrial biota, from the late Silurian of Ludford Lane (Jeram *et al.* 1990), a number of unusual fragments of arthropod cuticle were recovered. These authors figured gill tract material and interpreted it as the posterior end of an unknown arthropod. New discoveries of these cuticle fragments are described here, and interpreted as representing fragments of the respiratory organs of eurypterids.

GEOLOGICAL SETTING

The fossils came from the Platyschisma Shale Member of the Downton Castle Sandstone Formation, above the Ludlow Bone Bed at its type locality in Ludford Lane, Ludlow, Shropshire (SO 5116 7413), and are of late Silurian (Přidolí Epoch) age (see Bassett *et al.* 1982 for details). This sequence is interpreted as a nearshore deposit (Smith and Ainsworth 1989), and work by one of us (PLM, unpublished) and by Maquaker (1994) suggests that the Ludlow Bone Bed represents a deepening event, with the overlying Platyschisma Shale Member being deposits reworked in a shallowing sequence. The best preserved material was collected from organic-rich horizons within the Platyschisma Shale Member, capping reworked, storm-generated deposits, which are characterized by hummocky cross-stratification. These organic-rich horizons are probably the result of the argillaceous and organic elements of the sediment load settling out after a severe storm. The high quality of preservation of these delicate arthropod fragments may be related to the small grain size of the sediments.

Schmitz (1992) recognized within the Ludlow Bone Bed a high concentration of iridium (0.49 ppb) compared with background (0.040 ppb), which he suggested was precipitated from sea water. Although he did not exclude a relation of the anomaly initially with an asteroid impact event, there is little evidence (such as tektites and shocked quartz) for this at the time of deposition of the Ludlow Bone Bed, and Antia (1979) suggested a volcanic origin for some of its constituents. The evidence for such an origin for part of the bone bed is supported by the high percentage of quartz grains which have highly patchy extinction patterns and contain abundant inclusions (Schmitz 1992). We suggest that the high concentrations of iridium (Schmitz 1992) relate directly to the sedimentary environments prevailing at the time of deposition (Manning 1993; Maquaker 1994). The deepening event, which resulted in sediment by-pass and the subsequent build-up of vertebrate sands, would also allow a concentration of iridium to accumulate, precipitated from the sea water.

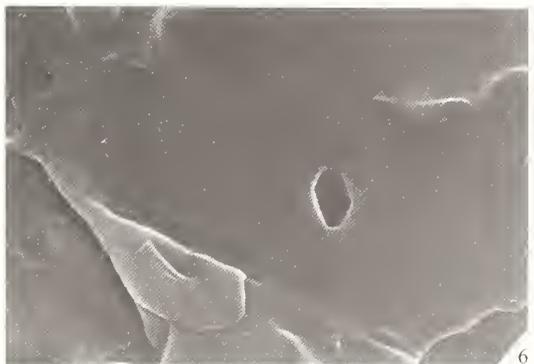
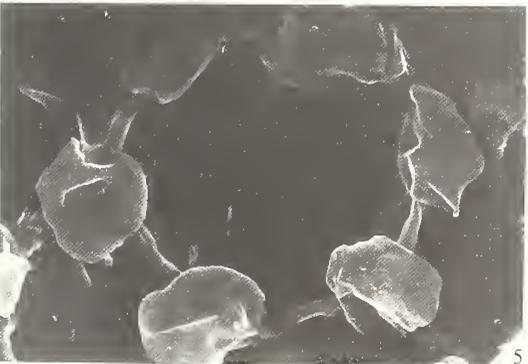
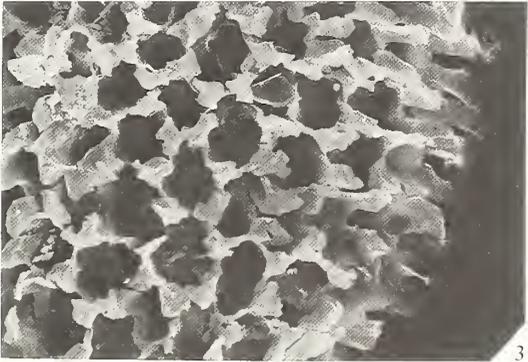
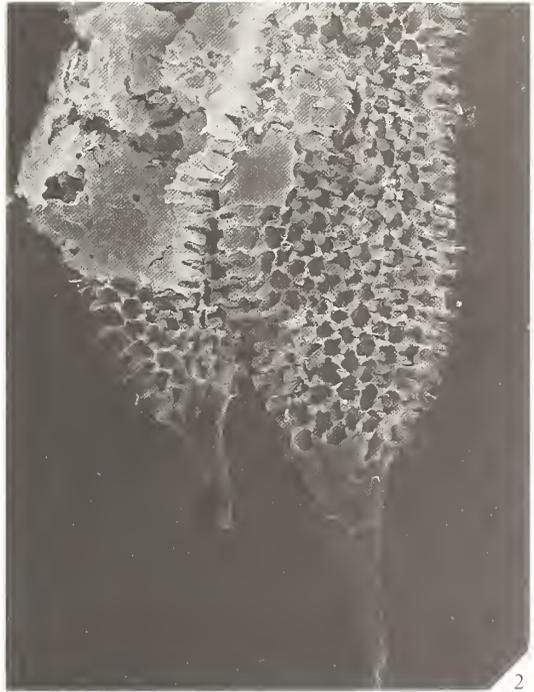
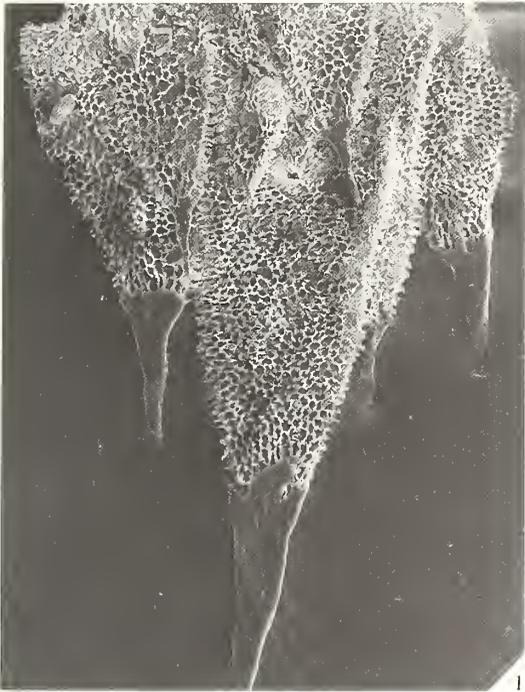
The uncertain report of the crustacean *Ceratiocaris* sp. from this sequence (Bassett *et al.* 1982, fig. 6, p. 13) could not be substantiated in this present study. The eurypterids which have been recognized from it by the senior author are as follows: *Pterygotus* sp; *Pterygotus* (*Pterygotus*) *denticulatus*; *Eurypterus* sp; *Eurypterus cephalaspis*; *Hughmilleria* sp; *Hughmilleria banksi*; *Nanalughmilleria* sp; *Parahughmilleria* sp; *Erretopterus* (*Truncatiramus*) *gigas gigas* and *Stylonurus* sp. The respiratory material described here is too fragmentary to ascribe to any of these taxa.

MATERIALS AND METHODS

Fragments of arthropod and plant cuticle were recovered by hydrofluoric acid (60 per cent.) maceration of samples of sediment following the method of Shear *et al.* (1987). The resulting

EXPLANATION OF PLATE 1

Figs 1–6. Scanning electron micrographs of cuticular material which represents fragments of eurypterid Kiemenplatten; Upper Silurian (Přidolí), Ludford Lane, Shropshire. 1, LL1119.1; group of seven spinules in assumed life orientation, showing the basic conical shape, terminal spine, surface sculpture and size variation; $\times 170$. 2, LL1119.2; pair of spinules, showing the shape, sculpture and the smooth inner surface where the cuticle is folded over (at the top left); $\times 350$. 3, LL1119.2; detail of cuticular projections ornamenting the spinules, showing the polygonal arrangement extending out from the surface; $\times 790$. 4, LL1121; detail of the cuticular projections, here more densely packed and no longer polygonally oriented; $\times 1200$. 5, LL1117; detail of a single regular 'rosette' of projections from the surface of the Kiemenplatten, showing their approximately circular cross-sectional area; $\times 4500$. 6, LL1117; detail of Kiemenplatten near the base of the spinules, where the cuticular projections have merged into smooth cuticle and which shows a single pore of approximately $1.0 \mu\text{m}$ in diameter; $\times 5000$.



MANNING and DUNLOP, Eurypterid Kiemenplatten

residues were picked for cuticle under both transmitted and incident light. Eurypterid cuticle represents the most common arthropod fragments and was identified by its distinctive morphology and ornamentation (Tollerton 1989; Manning 1993). Material interpreted as eurypterid respiratory organs was dried, mounted on aluminium stubs and gold-coated. It was examined using a Jeol 2020 scanning electron microscope (SEM). All figured material is held in the Department of Geology, Manchester Museum, University of Manchester, numbers LL1117–LL1123. A specimen of a eurypterid, *Rhenopterus?* sp. (Hunterian Museum, Glasgow, no. A23113), believed to show respiratory structures (Selden 1985, p. 223, who referred to it by its Hunterian Museum loan number, G807), was studied under incident light. Preserved specimens of the extant xiphosuran *Limulus polyphemus* were examined for comparative purposes.

RESULTS

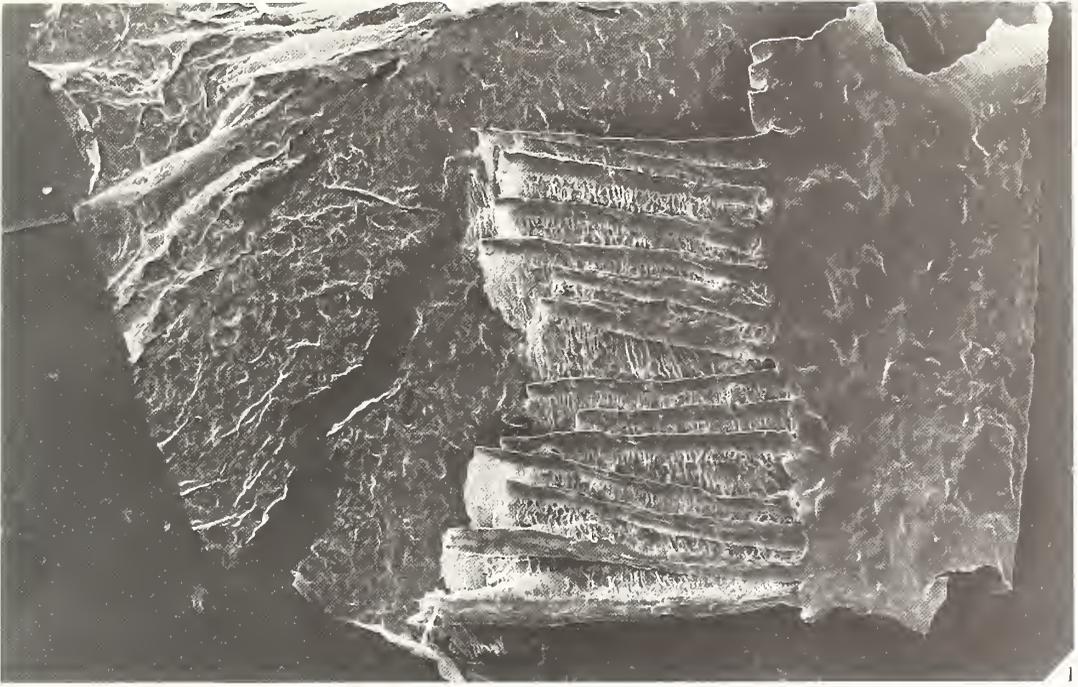
Kiemenplatten (gill tract)

The material includes highly ornamented, conical, cuticular structures (Pl. 1, figs 1–2). These are sometimes found isolated, sometimes grouped, and occasionally attached to larger sheets of cuticle. These cones have a total length of 0.5–2.0 mm and have a basal width of 50–200 μm . The tips of the cones are drawn out into long, tapering spines, typically between 30–150 μm long, which have no surface sculpture (Pl. 1, figs 1–2). The rest of each cone has a dense sculpture of microscopic cuticular projections which stand proud of the surface by approximately 10–15 μm (Pl. 1, figs 3–4). These projections are 2–3 μm wide and give the impression of originally having been cylindrical, and perhaps hollow, but having subsequently become compressed (Pl. 1, fig. 4). However, the internal surface of the *Kiemenplatten*, where visible (Pl. 1, fig. 2), does not show corresponding pores leading into these cuticular projections, suggesting that they may be composed of solid cuticle.

When compared with the material figured by Holm (1898) and Wills (1965) it is clear that these conical structures represent eurypterid *Kiemenplatten*. The latter term is used in preference to gill tract as discussed below. The term spinule was introduced by Wills (1965) for the cones (conical structures) covering the surface of the *Kiemenplatten*. When examined in detail, the polygonal arrangement of the cuticular projections noted by the previous authors is apparent (Pl. 1, fig. 3) including the ‘rosettes’ (Pl. 1, fig. 5) of Wills (1965), which have a diameter of approximately 20 μm , with the cuticular projections spaced approximately 2 μm apart. However, these projections are less regular and more densely distributed closer to the tip of the spinule, where they lose the ‘rosette’ arrangement (Pl. 1, fig. 4). Pores were found sparsely distributed in the cuticle between these projections, especially close to the base of the spinules where the projections are less dense (Pl. 1, fig. 6). These pores have smooth margins, which suggests that they are not artefacts, and have a consistent diameter of between 0.5–1.0 μm .

EXPLANATION OF PLATE 2

Figs 1–5. Scanning electron micrographs of lamellate cuticular material interpreted as fragments of eurypterid book-gills, from Ludford Lane, Shropshire. 1, LL1118; parts of eighteen lamellae attached to a large fragment of cuticle, which may represent the dorsal surface of the Blatfuss; $\times 115$. 2, LL1118; detail of lamella from figure 1 showing the thickened supporting bar with the ribbed surfaces of the lamella hanging from and continuous with it; $\times 490$. 3, LL1118; detail of lamellae from figure 1 showing them overlapping like the lamellae of modern *Limulus* book gills; $\times 230$. 4, LL1123; fragment of a single lamella, showing a wider, ribbed surface; $\times 230$. 5, LL1122; fragment of a single lamella, showing a broken edge revealing the cross sectional shape of the supporting bar and the two sheets of the lamellae hanging from it, and the smooth inner surface of the lamellae; $\times 230$.



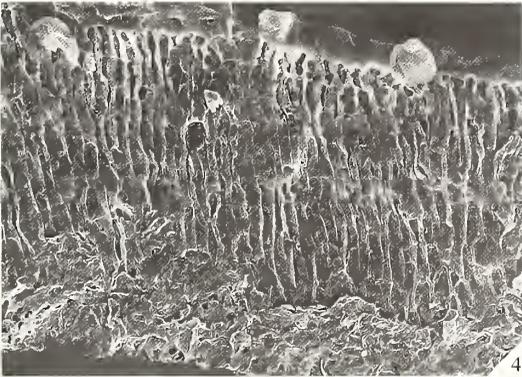
1



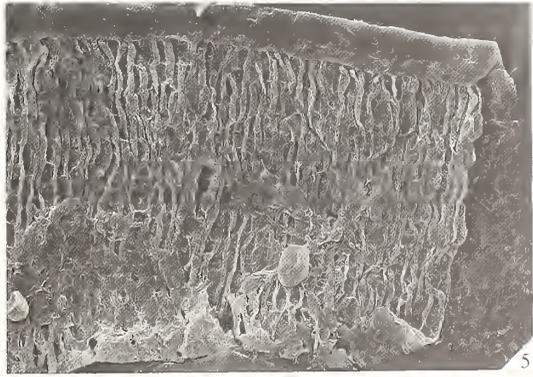
2



3



4



5

Lamellate gills

Other fragments recovered consist of small thickened cuticular bars (Pl. 2, figs 1–5) up to 7 mm long and approximately 20 μm wide. These bars are ovate in cross section, but with a concave interior surface and support two sheets of thin cuticle (Pl. 2, fig. 5). These cuticle sheets are estimated to have been 20 μm apart, and less than 0.5 μm thick where there is no surface sculpture. The cuticle sheets are fragmentary, at most 3 mm wide but usually much narrower. The two sheets suggest that they once formed an enclosed structure with a smooth interior surface and an exterior surface ornamented with a series of solid, cuticular ‘ribs’ lying perpendicular to the supporting bar (Pl. 2, figs 1–3). These ribs are approximately 2–3 μm wide, with a spacing of 2–5 μm and stand proud of the surface by approximately 5 μm . There are cross-bars, approximately 0.1–0.5 μm wide, between the cuticular ribs (Pl. 2, figs 1–5) which do not appear to be artefacts. The spacing of these cross-bars is irregular and they occur more commonly towards the thickened cuticular bars.

These supporting bars and their cuticle sheets are usually found isolated, but occasionally up to eighteen overlapping sheets, connected to fragmentary sheets of cuticle (Pl. 2, fig. 1), are found. These structures are interpreted as fragments of the marginal edges of lamellate gills, using the book-gills of *Limulus* as a comparison. Longer fragments show that the supporting bars were curved, suggesting that the whole structure may have been semicircular in life, as are the gill lamellae of *Limulus*.



TEXT-FIG. 1. Phosphatized eurypterid in ventral view. *Rhenopterus?* sp., Lower Carboniferous, Montagne Noire region, France; HM A23113; $\times 1.5$. Specimen interpreted as showing book-gills (arrowed) in life position, consisting of stacked, overlapping lamellae within a branchial chamber.

Whole body evidence

An undescribed specimen of *Rhenopterus?* sp. (Text-fig. 1) is interpreted as showing a single, open branchial chamber which contains at least seven phosphatized, overlapping, lamellate structures. These structures are interpreted as the gills of a single branchial chamber approximately in life position. This specimen provides strong supportive evidence for the presence of lamellate gills in

eurypterids and further suggests that the individual lamellae have an approximately semicircular shape and also that they attach obliquely, close to the midline of the body as in *Limulus*.

DISCUSSION

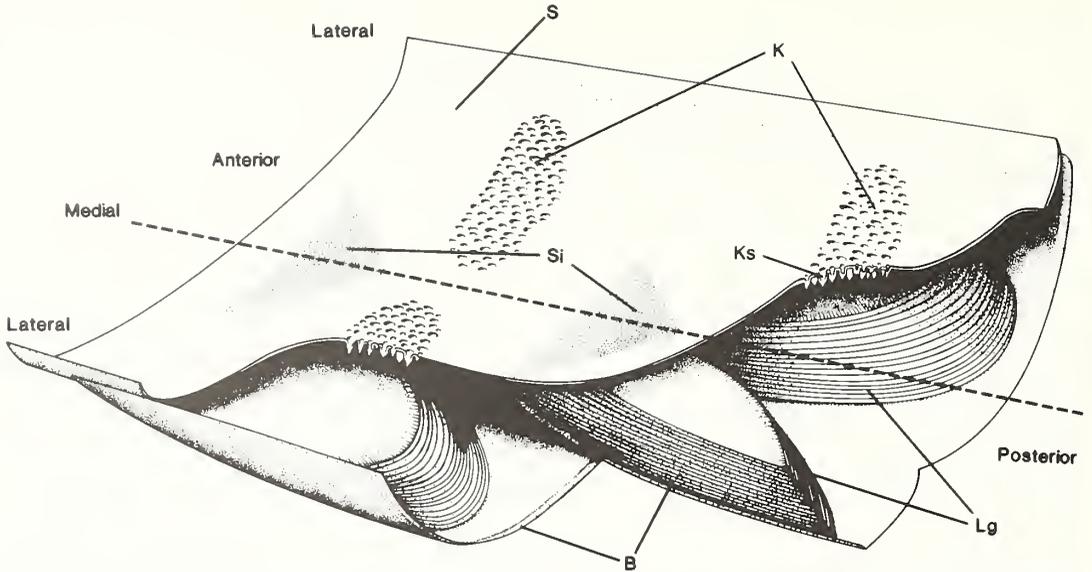
Interpretation of the Kiemenplatten (gill tract)

We are confident that these dissociated fragments of Kiemenplatten belong to eurypterids because their structure matches the material described and figured by Holm (1898) and Wills (1965) from whole body specimens. Also, some fragments show the margins of the Kiemenplatten where it merges with sternite cuticle which matches recognizable fragments of eurypterid cuticle (see Manning 1993 for a discussion of cuticle form and structure). Kiemenplatten material is reasonably common in macerates containing large quantities of eurypterid fragments, and has not been demonstrated to occur in any other arthropod group. Material superficially similar to the spinules described here, but lacking obvious cuticular projections arranged in 'rosettes', has been described as scorpion gill tract from the Upper Carboniferous (Kjellesvig-Waering 1986). This interpretation is probably incorrect because these structures originate from the scorpion abdominal plate, not from the true sternite (A. Jeram, pers. comm.). The fragments recovered during this study can be regarded as being part of a larger, oval area of Kiemenplatten, as noted by previous authors (e.g. Holm 1898). In fragments attached to sternite cuticle the spinules tend to be small, suggesting that the Kiemenplatten is most developed in its centre. The fragmentary nature of this material does not allow the size of the whole Kiemenplatten area to be determined.

The Kiemenplatten bears all the hallmarks of a respiratory structure with its increased surface area formed by the spinules (Pl. 1, figs 1–2). If the projections from the spinules (Pl. 1, figs 3–5) were hollow, this would also increase the respiratory surface area (RSA). It seems likely that the cuticle of the spinules was backed by a blood sinus and provided a surface for gas exchange. There seems no reason to doubt that the Kiemenplatten could have functioned as an accessory 'gill' in water, but what is more interesting is the suggestion that it is a structure which evolved primarily for respiration in air. The structure of the Kiemenplatten suggests that the downward-hanging spinules (Pl. 1, figs 1–2) would not have collapsed in air, leading to a reduction in RSA, in the same way as a lamellate gill. The presence of downward projecting Kiemenplatten spinules could also have maintained a cavity above the lamellae by preventing them from being compressed against the roof of the branchial chamber (A. Jeram, pers. comm.). The suggested primary respiratory function of the highly vascularized regions of the eurypterid sternite, is contradicted by the use of the term gill tract (Wills 1965). Because of its functional implications the term gill tract is rejected and the term Kiemenplatten (Holm 1898) is preferred here as a more 'neutral' term.

The overall morphology of the eurypterids shows that they were clearly primarily aquatic animals (Selden 1985). However, by closing the Blatfüsse during excursions onto land they could have reduced water loss over the gills, in the same way that a narrow book-lung spiracle prevents water loss in arachnids, while relying on gas exchange with air over the gill tract. Since air has a higher partial pressure of oxygen than water, the RSA of the Kiemenplatten may not have needed to be as great as that of the lamellate gills in order to support metabolically the animal in air. The respiratory evidence therefore suggests that at least some eurypterids could have ventured onto land, but the degree to which these animals could have been terrestrial can only be answered in a fuller account of Kiemenplatten palaeophysiology and corroborative evidence from eurypterid palaeoecology.

The small pores described in the Kiemenplatten (Pl. 1, fig. 6) could be interpreted as spiracles leading into some sort of tracheal system (as the figures of Stormer 1976 appear to suggest), but no such tracheae backing them were observed in any of the specimens. An alternative hypothesis is that they were backed by osmoregulatory cells, although this is mere conjecture at this stage. The spines at the tips of the spinules (Pl. 1, figs 1–2) could possibly have been a protective device against haematophagous parasites.



TEXT-FIG. 2. Interpretative reconstruction of two branchial chambers of a generalized eurypterid. The lamellate book-gills (Lg) originate from the dorsal surface of the Blatfüsse (B) and occupy most of the branchial chamber. Blood entered a Blatfuss from a hypothetical blood sinus (Si) and from here entered the lamellae, probably by tidal flow. The Kiemenplatten (K) is a well vascularized oval area of the sternite (S), comprising a series of spinules (Ks) and located above the lamellae within the branchial chamber.

Kiemenplatten have also been found in association with eurypterid fragments in macerates from older horizons at Monterrey, Virginia (Silurian, Llandovery) and younger ones at Hudwick Dingle, Shropshire (Devonian, Lochkovian) and Gilboa, New York (Devonian, Givetian) (unpublished observations). Initial examination of this material suggests some minor, but potentially significant differences, from the material described here.

Interpretation of the lamellate gills

We are confident that these lamellate structures belong to eurypterids and are not the gills of xiphosurans or crustaceans since, like the Kiemenplatten, the lamellae are occasionally found attached to recognizable eurypterid cuticle (Manning 1993). Xiphosurans and non-ostracode crustaceans were not found in the Ludford sequence either as recognizable fragments in macerates, macrospecimens or trace fossils. Also, the lamellae are reasonably common in macerates containing large amounts of eurypterid fragments. Scorpion cuticle fragments have been recorded, and these lamellae could represent the gills of aquatic forms; however scorpion cuticle was rare, rarer even than the lamellate structures within the macerates.

Comb-like structures have been described as the pectinated appendages of the eurypterid *Cyrtoctenus* (Stormer and Waterston 1968). These were subsequently interpreted as modified spines of the distal limb podomeres with a sweep-feeding function (Waterston *et al.* 1985). Detailed examination of the lamellate structures found in this present study has shown that they display two ribbed surfaces, not individual filaments attached to a supporting bar as in *Cyrtoctenus*. Based on these characters we are confident that the lamellate structures from Ludford Corner are not appendicular sweep-feeding devices.

The eurypterid book-gills resemble those of *Limulus* in having a marginal thickening (Pl. 2, figs 1–5), but differ from those of living xiphosurans in having the ribs on the surface of the lamellae (Pl. 2, figs 1–4). These ribs may have strengthened and supported the lamellae, but the fragmentary

evidence does not show if the whole lamella was ribbed or only the margins, which have therefore been preferentially preserved. All the fragments of lamellae found in this study were ribbed, regardless of size. The ribs are not obviously homologous, or functionally analogous, with the struts separating the air spaces between the lamellae of arachnid book lungs (e.g. Reisinger *et al.* 1990), so that the lamellae would probably have collapsed in air. However, it is worth noting that certain extant terrestrial crabs, e.g. *Cardisoma* and *Geograspus* (Mill 1972; Farelly and Greenaway 1992), have reduced lamellate gills with thickened and stiffened lamellae which help support the structure in air and allow effective ventilation and draining of the gills when the crab comes onto land. The total number of lamellae comprising any particular eurypterid gill found in this study, and the shape and variation in shape of the entire lamellae, cannot be determined for this fragmentary material. The *Rhenopterus?* specimen (Text-fig. 1) and comparisons with *Limulus* suggests that the lamellae were quite large, occupying most of the space in the branchial chamber.

The dorsal surface of the eurypterid Blatfüsse has not been described satisfactorily (Selden 1985). We speculate that, as in *Limulus*, where the gills attach to the gill operculum, the dorsal surface of the homologous eurypterid Blatfüsse is the attachment site of their lamellae. The large fragments of cuticle attached to some specimens (Pl. 2, fig. 1) may represent part of this dorsal surface. The Blatfüsse appear to have served the dual purpose of attachment area and protection for the lamellate gill. If the animal did come onto land, the lamellate gills would probably have collapsed onto the dorsal surface of the Blatfüsse without the support of water. A collapsed gill would probably have been ineffective for aerial respiration and this could explain the need to evolve an accessory aerial respiratory organ in a partially terrestrial animal.

Reconstruction of the eurypterid respiratory system

While Kiemenplatten and lamellate gills have not been recorded from a single specimen to date, we have no evidence that the two structures belong to two different taxa. On this basis the eurypterid respiratory system is reconstructed as possibly comprising two elements (Text-fig. 2), as suggested by Selden (1985): lamellate book-gills and the accessory Kiemenplatten. The multiple lamellae of the book-gills were probably attached to the dorsal surface of the Blatfüsse and were presumably the principal means of aquatic respiration. By analogy with *Limulus*, the Blatfüsse and their gills would have connected to a blood sinus towards the midline of the animal and there would have been a tidal flow of haemolymph in and out of the lamellae. The Kiemenplatten hung above the gills within the branchial chamber and was probably also backed by a blood sinus, gas exchange occurring with the haemolymph in this sinus.

The 'branchial hung' model of Kiemenplatten function

The eurypterid Kiemenplatten has no counterpart in any other chelicerate group and thus represents a previously unknown respiratory system in arthropods. The pseudotracheal model for the Kiemenplatten proposed by Stormer (1976) appears inappropriate. Isopod pseudotracheae are invaginated cutaneous tubules lying within the blood sinus of an appendage (Snodgrass 1952), whereas the eurypterid Kiemenplatten is interpreted as a vascularized region of evaginations of the body wall (Pl. 1, figs 1–2). The plastron model of Kiemenplatten function (Rolfe 1980) was rejected by Selden (1985) because the cuticular projections were claimed to be too widely spaced to hold a meniscus. This study suggests that cuticular projections on the Kiemenplatten (Pl. 1, figs 3–5) are over twice as long and wide as typical hydrofuge plastron hairs. There is no evidence that the Kiemenplatten projections were water repellent or that they had linkages between the tops of the projections (Pl. 1, figs 4–5) to provide an incompressible air space as in a plastron (Mill 1972). More significantly, a plastron is a secondarily aquatic-adapted respiratory mechanism originally of terrestrial arthropod lineages, whereas eurypterids are suggested as having been primarily aquatic animals attempting terrestrialization (Selden 1985).

The closest arthropod analogues to eurypterid Kiemenplatten are the cutaneous brachial lungs of certain terrestrial crabs, e.g. *Ocypode* and *Pseudothelphusa* (Mill 1972; Little 1990), formed from

highly vascularized regions of the branchial chamber wall (i.e. not the gills, as in *Cardisoma*) and which act as osmoregulatory and aerial respiratory organs. However, it is worth comparing the apparent strengthening structures both on eurypterid and crab gill lamellae, which may suggest that the eurypterid lamellae had some terrestrial adaptations. Terrestrial crabs must still keep their gills or branchial lungs moist (Mill 1972), presumably to avoid desiccation. The cuticular projections on the eurypterid Kiemenplatten may have served principally to trap a fine meniscus of water, in order to keep the area moist, a requirement of all respiratory surfaces (Hill and Wyse 1989), and functioning longer on land. This is similar to a plastron, except that, rather than trapping air as the animal enters water, and then holding a meniscus of water away from a tract as in the hydrofuge hairs of a plastron, these projections may have held a meniscus of water next to the Kiemenplatten. It is worth noting that, when removed from water and dried on SEM stubs, the fragments of Kiemenplatten took longer to dry than comparable cuticular fragments.

It is interesting to observe that recent crabs attempt terrestrialization in two ways: adapting their gills directly into lamellate 'lungs' (Mill 1972; Little 1990; Farrelly and Greenaway 1992), as has occurred with the arachnid book-lungs (Selden and Jeram 1989); and, alternatively by vascularization of the branchial chamber wall (Mill 1972; Little 1990), which is apparently analogous to the eurypterid Kiemenplatten. Different eurypterid taxa may similarly have used different strategies for aerial respiration, i.e. Kiemenplatten or strengthened book-gills, but we have no evidence for this dual adaptation at present, and we favour the model proposed in Text-figure 2. Eurypterids, however, appear ultimately to have failed to colonize land and this may be the result, in part, of their reliance on the Kiemenplatten, whereas the successful terrestrial chelicerates transformed their lamellate book-gills directly into lamellate book-lungs.

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REFERENCES

- ANTIA, D. D. J. 1979. Bone-beds: a review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering, and microbiotas. *Mercian Geologist*, **7**, 93–174.
- BASSETT, M. G., LAWSON, J. D. and WHITE, D. E. 1982. The Downton Series as the fourth Series of the Silurian System. *Lethaia*, **15**, 1–24.
- CLARKE, J. M. and RUEDEMANN, R. 1912. The Eurypterida of New York. *Memoir of the New York State Museum*, **14**, (2 vols), 1–439, pls 1–88.
- FARRELLY, C. A. and GREENAWAY, P. 1992. Morphology and ultrastructure of the gills of the terrestrial crabs, Crustacea, Gecarcinidae and Grapsidae: adaptations for air-breathing. *Zoomorphology*, **112**, 39–49.
- HILL, R. W. and WYSE, G. A. 1989. *Animal physiology*. 2nd Edition. Harper and Row, New York, 656 pp.
- HOLM, G. 1898. Über die Organisation des *Eurypterus fischeri* Eichw. *Memoirs of the Academy of Science, St. Petersburg*, **8**, 1–57.
- JERAM, A. J., SELDEN, P. A. and EDWARDS, D. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science*, **250**, 658–661.
- KJELLESVIG-WAERING, E. N. 1986. A restudy of the Fossil Scorpionida of the world. *Palaentographica Americana*, **55**, 1–287.
- LAURIE, M. 1893. The anatomy and relations of the Eurypteridae. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **37**, 509–528.
- LITTLE, C. 1990. *The terrestrial invasion: an ecophysiological approach to the origins of land animals*. Cambridge Studies in Ecology, Cambridge University Press, Cambridge, 304 pp.
- MANNING, P. L. 1993. Palaeoecology of the eurypterids of the Upper Silurian of the Welsh Borderland. Unpublished M.Sc. thesis, University of Manchester.
- MAQUAKER, J. H. S. 1994. Palaeoenvironmental significance of bone-beds in organic-rich mudstone successions: an example from the Upper Triassic of South West Britain. *Zoological Journal of the Linnean Society, London*, **112**, 285–308.

- MILL, P. J. 1972. *Respiration in the invertebrates*. Macmillan Press, London, 212 pp.
- MOORE, P. F. 1941. On gill like structures in the Eurypteridae. *Geological Magazine*, **78**, 62–70.
- REISINGER, P. W. M., FOCKE, P. and LINZEN, B. 1990. Lung morphology of the tarantula, *Eurypelma californicum* Ausserer, 1871 (Aranae: Theraphosidae). *Bulletin of the British Arachnological Society*, **8**, 165–170.
- ROLFE, W. D. I. 1980. Early invertebrate faunas. 117–157. In PANCHEN, A. L. (ed.). *The terrestrial environment and the origin of land vertebrates*. Academic Press, London and New York, 633 pp.
- SELDEN, P. A. 1985. Eurypterid respiration. 209–226. In CHALLONER, W. G. and LAWSON, J. D. (eds). *Evolution and environment in the Late Silurian and Early Devonian*. *Philosophical Transactions of the Royal Society of London, Series B*, **309**, 342 pp.
- and JERAM, A. J. 1989. Palaeophysiology of terrestrialisation in the Chelicerata. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **80**, 303–310.
- SHEAR, W. A., SELDEN, P. A., ROLFE, W. D. I., BONAMO, P. M. and GRIERSON, J. D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbitida). *American Museum Novitates*, **2901**, 1–74.
- SCHMITZ, B. 1992. An iridium anomaly in the Ludlow Bone Bed from the Upper Silurian, England. *Geological Magazine*, **129**, 359–362.
- SMITH, R. D. A. and AINSWORTH, R. B. 1989. Hummocky cross-stratification in the Downton of the Welsh Borderland. *Journal of the Geological Society, London*, **146**, 897–900.
- SNODGRASS, R. E. 1952. *Textbook of arthropod anatomy*. Cornell University Press, New York, 363 pp.
- STORMER, L. 1976. Arthropods from the Lower Devonian (Lower Emsian) of Alken-an-der-Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks and problems regarding invasion of land by arthropods. *Senckenbergiana Lethaea*, **57**, 87–183.
- and WATERSTON, C. D. 1968. *Cyrtoctenus* gen. nov., a large Palaeozoic arthropod with pectinate appendages. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **68**, 63–104.
- TAUGOURDEAU, P. 1967. Débris microscopiques d'euryptéridés du Paléozoïque saharien. *Revue de Micropaléontologie*, **10**, 119–127.
- TOLLERTON, V. P. 1989. Morphology, taxonomy and classification of the Order Eurypterida, Burmeister 1843. *Journal of Paleontology*, **63**, 642–657.
- WATERSTON, C. D. 1975. Gill structure in the Lower Devonian eurypterid *Tarsopteryella scotica*. *Fossils and Strata*, **4**, 241–254.
- 1979. Problems of functional morphology and classification in stylonurid eurypterids, Chelicerata, Merostomata, with observations on the Scottish Silurian Stylonuroidea. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **70**, 251–322.
- OELOFSEN, B. W. and OOSTHUIZEN, R. D. F. 1985. *Cyrtoctenus witterbergensis* sp. nov. Chelicerata: Eurypterida, a large sweep feeder from the Carboniferous of South Africa. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 339–358.
- WILLS, L. J. 1965. A supplement to Gerhard Holm's 'Über die Organisation des *Eurypterus fisheri* Eichw.' with special reference to the organs of sight, respiration and reproduction. *Archiv für Zoologie*, **18**, 93–145.

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OCCURRENCE OF THE BIVALVE GENUS *MANTICULA* IN THE EARLY CRETACEOUS OF ANTARCTICA

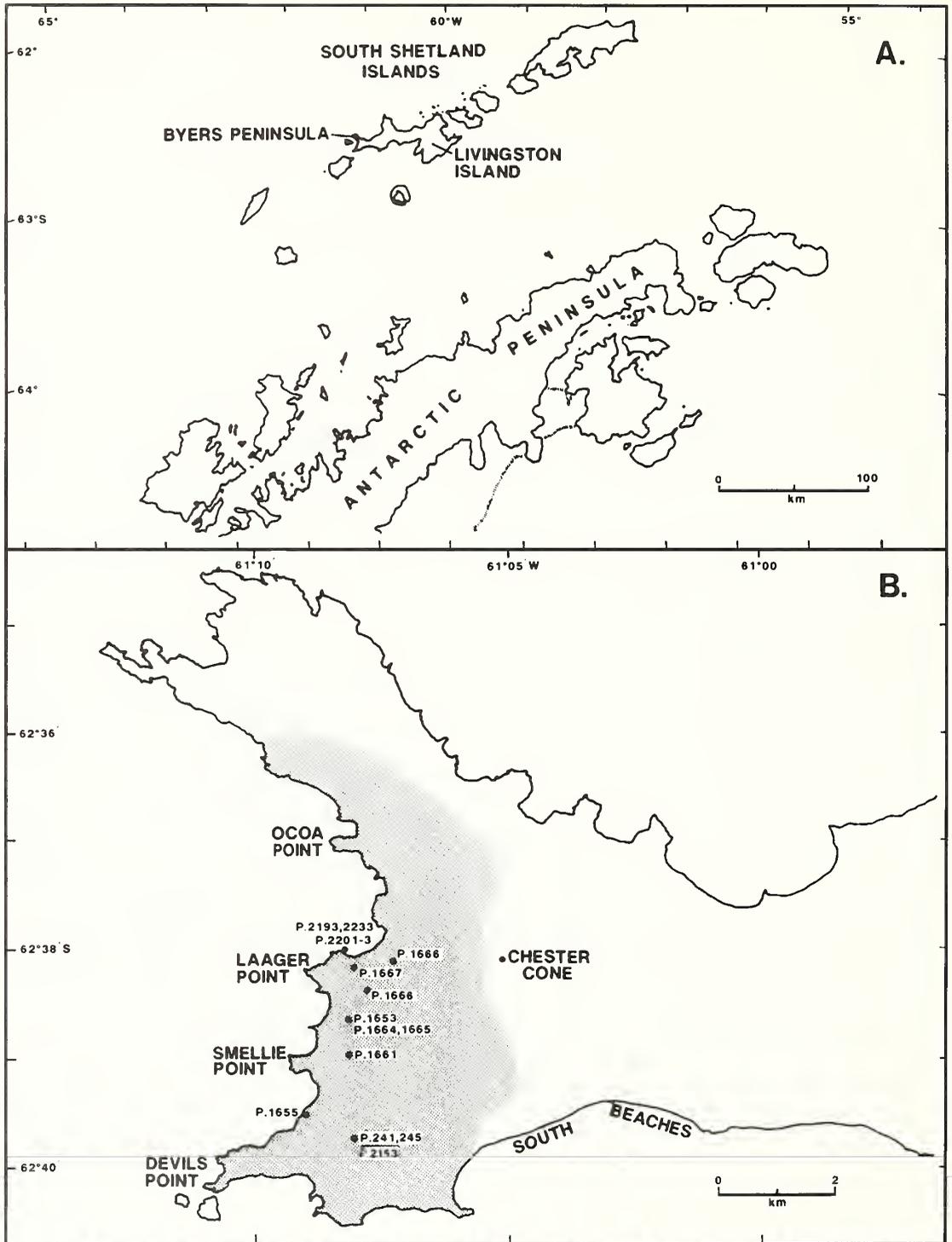
by J. A. CRAME

ABSTRACT. A new occurrence of a pergamidiid bivalve genus, which can probably be assigned to *Manticula* Waterhouse, 1960, is established within the Early Cretaceous (Berriasian) of Antarctica. Such a record is of particular interest as this taxon was only known previously from the Late Triassic of New Zealand and New Caledonia. The Antarctic material is contained within a new species, *M. complanata*, which is shown to be somewhat smaller and less inflated than the genotypic *M. problematica* (Zittel). There are indications from the Antarctic species that, at least in juvenile specimens, the hinge region of the left valve is characterized by a prominent saddle-shaped fold (or tooth) and a triangular resilifer. Using features such as these and details of the shell structure, it is possible to establish close links between *Manticula* and the pergamidiid genus *Krumbeckiella* on the one hand, and the eurydesmid genus *Eurydesma* on the other. The eurydesmid-pergamidiid group is essentially a Southern Hemisphere one with high-latitude origins in the Early Permian. Following a phase of expansion through the Triassic, it would appear to have retracted to the single Antarctic occurrence of *Manticula* in the Early Cretaceous.

DURING the course of systematic geological surveys, a thick sequence of Late Jurassic–Early Cretaceous marine clastic rocks was discovered on Byers Peninsula, western Livingston Island, South Shetland Islands (62° 38' S; 61° 04' W) (Smellie *et al.* 1980, 1984) (Text-fig. 1). This sequence is in places highly fossiliferous, and a variety of ammonite and belemnite types has been used to establish an age-range of at least Kimmeridgian–Valanginian (Smellie *et al.* 1980). Further field studies have recently been completed and an estimated 1 km thickness of mudstone-dominated lithologies has been combined into the new Byers Group. It is envisaged that these sediments accumulated in a marginal fore-arc setting (Crame *et al.* 1993).

Bivalves form a prominent component of the marine invertebrate macrofaunal assemblage from the lower levels of the Byers Group (principally the President Beaches Formation; Crame *et al.* 1993). Epifaunal types present include retroceramids, inoceramids, various oxytomids, occasional entoliids and several types of oyster; infaunal and semi-infaunal groups include nuculids, nuculanids, grammatodontids, trigoniids, astartids and other small heterodonts. An initial study (Crame 1984) identified a number of distinctive elements within this bivalve fauna, with perhaps the most unusual one being a small-medium, mytiliform and almost smooth taxon with superficial similarities to both the Buchiidae and Inoceramidae. Nevertheless, subsequent detailed examination revealed that it clearly could not be assigned to either of these families; it would seem, instead, to be referable to one of the lesser-known pteriomorph groups, the Pergamidiidae Cox, 1969.

The smooth, mytiliform Byers Peninsula taxon can probably be referred to the pergamidiid genus *Manticula* Waterhouse, 1960. Such a determination is of immediate biostratigraphical and biogeographical interest, for *Manticula* has hitherto been recorded from only the Late Triassic (Carnian–Norian) of New Zealand and New Caledonia; indeed, the stratigraphical range of the entire Pergamidiidae is only Upper Triassic–Lower Jurassic (Cox 1969). As the Byers Peninsula material is dated unequivocally as earliest Cretaceous (Berriasian; Crame *et al.* 1993), it would



TEXT-FIG. 1. Locality map for Byers Peninsula, western Livingston Island. A, The northern Antarctic Peninsula region. B, Byers Peninsula – showing localities at which *Manticula* has been collected and the outcrop of the lower part of the Byers Group (shaded). A more detailed geological map is given in Crame *et al.* (1993, fig. 1).

appear that *Manticula* might be a Lazarus Taxon (*sensu* Jablonski 1986), with no known Jurassic representative, and Antarctica serving as a last refuge for this formerly more widespread family.

SYSTEMATIC PALAEOONTOLOGY

Order PTERIOIDA Newell, 1965
 Suborder PTERIINA Newell, 1965
 Superfamily AMBONYCHIOIDEA Miller, 1877?
 Family PERGAMIDIIDAE Cox, 1969
 Genus MANTICULA Waterhouse, 1960

Type species. *Mytilus problematicus* Zittel (1864); by original designation.

Diagnosis. Small–medium (and occasionally large) mytiliform bivalves; prominent, pointed beaks; generally smooth but can exhibit low concentric folds and fine radial striae; largest forms may develop bizarre gibbous shape in ?RV; thickened, striated hinge region bears oblique, ridge-like fold or ‘tooth’ – this feature may become overthickened and obscured in large specimens; thickened shell largely calcitic – predominantly crossed-foliated?

Storage of Material: All Antarctic specimens (prefixed by P.) are housed in the collections of the British Antarctic Survey, Cambridge, UK. New Zealand specimens from the C. T. Trechmann Collection are housed in the Department of Palaeontology, Natural History Museum, London (NHM); specimens prefixed TM are located in the reference collections of the Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand.

Manticula complanata sp. nov.

Plate 1, figures 1–10; Plate 2, figures 1–2; Text-figure 2

Type material. Holotype: P. 241.9 (internal mould LV). Paratypes: P. 241.8, 10, 18, P. 245.10–12, P. 1667.1, 6–9, 11–18, 20, 21, 23–25, P. 1653.3, 4, P. 1655.9–11, P. 1661.16, P. 1664.21, P. 1665.8, 9, 12, 14, 15, P. 1666.1–4, P. 1668.3–10, P. 2193.83–85, 90–95, P. 2201.6, 7, 9, 11, 13–15, 17, 18, 20–22, P. 2202.19, P. 2203.1, P. 2153.80–82, P. 2233.4–12, 16, 17, 19. All the specimens were obtained from the President Beaches Formation, the principal lithostratigraphical unit within the lower Byers Group, western Byers Peninsula (Text-fig. 1).

Occurrence. As for the type material. Associated macrofossils date the President Beaches Formation as Berriasian (Smellie *et al.* 1980), and there are some indications that at least the lowest 360 m may be assignable to the Early Berriasian (Crame *et al.* 1993).

Derivation of name. Latin ‘*complanata*’, flattened; referring to the non-inflated form of this species.

Diagnosis. A small *Manticula* which does not exhibit any grossly over-inflated valves.

Description. A small–medium sized, elongate–rounded and almost smooth bivalve which tapers dorsally into a finely pointed umbo and expands ventrally to become well rounded; a number of specimens give a superficial impression of bilateral symmetry. This species is equivalve, or very nearly so (see possible minor differences, below), with no statistically significant differences between the mean lengths and widths of the best preserved left and right valves (Student’s *t*-test, $P < 0.001$).

Measurements taken on some 60 specimens indicate a mean length (L) of 35.73 mm (s.d. = 14.38, range = 12–64 mm), mean width (W) of 25.22 mm (s.d. = 9.37, range = 9–44 mm) and mean W/L of 0.712 (s.d. =

0·069, range = 0·48–0·83). There is a spectrum from more or less bilaterally symmetrical specimens (e.g. Pl. 1, fig. 2) to obviously obliquely elongated ones (e.g. Pl. 1, fig. 7). In the latter there are clear traces of a short, straight posterodorsal hinge, together with a variably-developed radial, posterodorsal furrow. It is just possible that this feature is more deeply impressed in left than right valves (Pl. 1, figs 7–10). In a typical specimen, the outline in the posterodorsal region is very slightly more angular than in the corresponding anterodorsal region; the ventral margin is always well rounded. The poorly defined umbonal region terminates in a sharply pointed beak. This feature rises just above the hingeline and varies from slightly prosogyrous to slightly opisthogyrous (Pl. 1, figs 1–10).

Both left and right valves are weakly inflated, with the maximum degree of inflation occurring in the umbonal and central regions of the valve. In specimens preserved in fine- to medium-grained sandstone, the principal ornament pattern comprises very fine concentric growth lines with superimposed radial growth threads. The latter can be traced from the umbo to the ventral margin, where they may become somewhat erratic in their course (e.g. Pl. 1, figs 5, 9). Some specimens preserved in mudstone reveal slightly coarser concentric ornament, which may be described as wrinkles. They also show, especially in the central regions of the valve, more pronounced radial ornament (Pl. 1, figs 1–3).

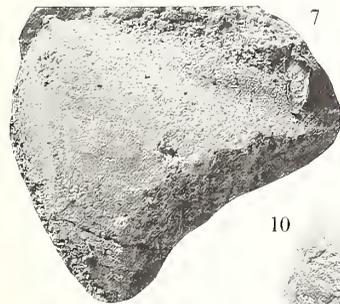
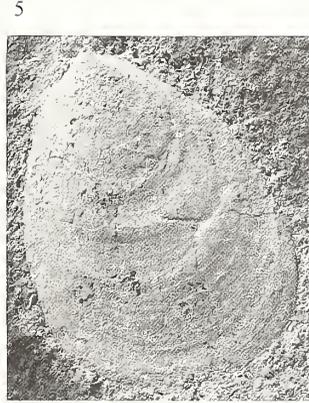
A few specimens exhibit a very clearly delimited larval shell (or prodissoconch). On P. 2201.16 (Pl. 2, fig. 1), this takes the form of a smooth, inflated, cap-like structure bordered by an annular sulcus. In its longest dimension it measures approximately 430 μ m and towards the outer borders there are traces of a shallow depression which may mark the separation of Prodissococonch I from Prodissococonch II. In any event, it would appear that the former of these two subdivisions must have been comparatively large and this may be taken as evidence of nonplanktotrophic or even brooded larval development (Jablonski and Lutz 1980). The first 1–2 mm growth of the dissoconch proper is characterized by acute, regularly spaced, radial ribs which are crossed by faint concentric riblets (e.g. Pl. 2, fig. 1). This initial cancellate pattern is stronger than anything seen on the adult shell.

Details of the hingeline and immediately adjacent areas are particularly well preserved on three small, juvenile specimens: the internal moulds of two left valves (P. 2201.16, P. 2233.5; Pl. 2, figs 1–2) and the external mould of a right (P. 241.8). All three specimens show the hinge to be a comparatively broad, complex structure whose principal features are picked out by very fine, regular growth lines. In particular, directly beneath the beak (marked by the prodissococonch) these lines pick out a prominent ridge-like fold which is broadly analogous to a tooth. In specimen P. 2201.16 (Pl. 2, fig. 1) this ridge can be seen to slant obliquely forwards and span the whole width of the hinge area. It falls away steeply on both flanks from a comparatively sharp crest, and indications that it is hollow in the centre are confirmed by examination of P. 2233.5 (Pl. 2, fig. 2). Anterior to the tooth-like ridge, in both left and right valves, the hinge appears to be simple, straight and marked by sub-parallel growth lines (Pl. 2, figs 1–2). However, immediately in front of the 'tooth' in both specimens, P. 241.8 and P. 2201.16 (Pl. 2, fig. 1), there are traces of a shallow, transverse depression which may mark the line of a narrow byssal notch.

Immediately posterior to the tooth-like ridge there are traces of a deeply impressed ligament pit. This feature is clearest in specimen P. 2201.16 (Pl. 2, fig. 1), where it has an oblique, triangular outline and can be seen to be firmly recessed into the space directly beneath the umbo. The floor of the pit is covered by fine, sub-horizontal growth lines. In specimen P. 2233.5 the form of the ligament pit is less obvious (Pl. 2, fig. 2), but in P. 241.8 it is again obliquely triangular. In all three specimens the posterior segment of the hinge seems to be composed of an irregular set of elongate grooves and ridges. These features are perhaps clearest on specimen P. 2233.5 (Pl. 2, fig. 2).

EXPLANATION OF PLATE 1

Figs 1–10. *Manticula complanata* sp. nov.; Berriasian; Byers Group; Livingston Island, Antarctica. 1, paratype, P. 1667.6; internal mould of a probable right valve. 2, paratype, P. 1667.20; internal mould of a right valve. 3, paratype, P. 1667.12; internal mould of a right valve. 4, paratype, P. 2203.1; internal mould of a left valve. 5, holotype, P. 241.9; internal mould of a left valve. 6, paratype, P. 2153.80; internal mould of a probable right valve. 7, paratype, P. 1668.3; internal mould of an incomplete left valve. 8, paratype, P. 1668.4; internal mould of an incomplete right valve. 9, paratype, P. 241.8; internal mould of an incomplete probable right valve. 10, paratype, P. 2233.17; internal mould of a left valve. Specimens 1–3 are preserved in mudstone, and 4–10 in fine sandstone. All are $\times 1$.





TEXT-FIG. 2. Scanning electron micrograph of crossed-foliated shell structure in the hinge region of a probable right valve of *Manticula complanata* sp. nov. (P. 2233.6); $\times 1560$.

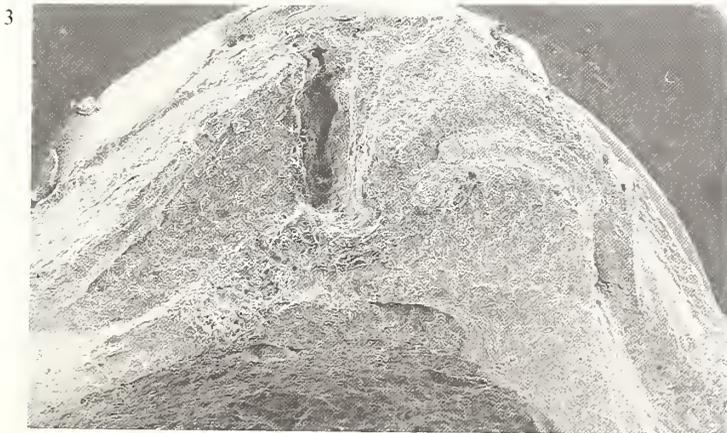
Only thin (< 1 mm) remnants of shell material are preserved on any specimen. As far as can be determined, these are nearly always calcitic in nature and crossed-foliated in structure (Text-fig. 2). This type of shell material has been detected in several parts of both left and right valves (including both hinge regions). Although nearly always showing signs of alteration, it can be seen to comprise at least two orders of obliquely orientated lamellae which intersect at a low angle (Text-fig. 2). Occasionally, this foliated layer passes into a fine grained homogeneous zone which may represent an altered inner aragonitic layer. It is noticeable too, how a few mudstone moulds have an iridescent, nacreous sheen. A band of prismatic shell material in the central region of specimen P. 2233.6 is taken to represent a myostracal shell layer.

Discussion. The material described here bears a striking resemblance to the smallest specimens of *Manticula problematica* (Zittel), the type species of the genus from the Late Triassic (Carnian–Norian) of New Zealand and New Caledonia (e.g. Pl. 3, figs 1–4). There is a considerable degree of overlap in both overall valve outlines and the form of the narrow, pointed beaks; in addition, at least some small specimens of *M. problematica* possess a radial, posterodorsal depression (e.g. Wilckens 1927, pl. 2, fig. 6). However, some of the prolific New Zealand material exhibits rather straighter anterior margins and there is an impression of a slightly more prominent umbonal region than in the Antarctic species (Pl. 3, figs 1–4).

The most obvious difference between *Manticula complanata* sp. nov. and *M. problematica* is in their respective maximum sizes. Whereas the former reaches no more than 64 mm in length, the latter can be in excess of 110 mm. The larger New Zealand and New Caledonian forms are obviously more inflated, with some specimens exhibiting a dramatic expansion of the ventral margins to produce a bizarre, gibbous shape (Pl. 3, figs 5–6). Such specimens were the basis of Trechmann's (1917) new species, *Mytilus mirabilis* (= *Mytilus trechmanni* Waterhouse, 1960), but it is now apparent that there is every gradation between the most flattened forms of *Manticula problematica* and the grossly inflated *M. trechmanni*; the two species have thus been synonymized (Waterhouse 1960). Although it has been claimed that the gibbous form is a feature of the right

EXPLANATION OF PLATE 2

Figs 1–3. Scanning electron micrographs of the hinge region of *Manticula*. 1, P. 2201.16; beak and central hinge region of a juvenile left valve of *M. complanata* sp. nov.; further details of the slanting, tooth-like ridge, triangular ligament pit and cap-like prodissoconch are given in the text; $\times 60$. 2, P. 2233.5; beak and central hinge region of a juvenile left valve of *M. complanata* sp. nov.; slanting, tooth-like ridge and ligament pit partially eroded; $\times 20$. 3, TM 7672; locality GS14977; rubber peel from an internal mould of a left valve of *M. problematica* (Zittel); behind a blunt, rounded anterior lobe (right hand side) is a deeply impressed subcentral resilifer; further details given in the text; $\times 12$.



valve only (Waterhouse 1960), it would seem that in a number of instances it is genuinely difficult to distinguish left from right (e.g. see Avias 1953, pl. 24, figs 1–3). It is unclear whether two gibbous valves would have been in juxtaposition, or whether one was always paired with a flatter, lid-like valve.

It is apparent that the largest New Zealand specimens have greatly thickened shells, with thicknesses of 6–7 mm being recorded in the hinge region (Waterhouse 1960). Much of this is due to very prominent outer calcitic layers in which irregular to branching crossed-foliated structures predominate (Waterhouse 1960; Carter 1990*a, b*). The innermost, aragonitic layers apparently have a crossed-lamellar structure.

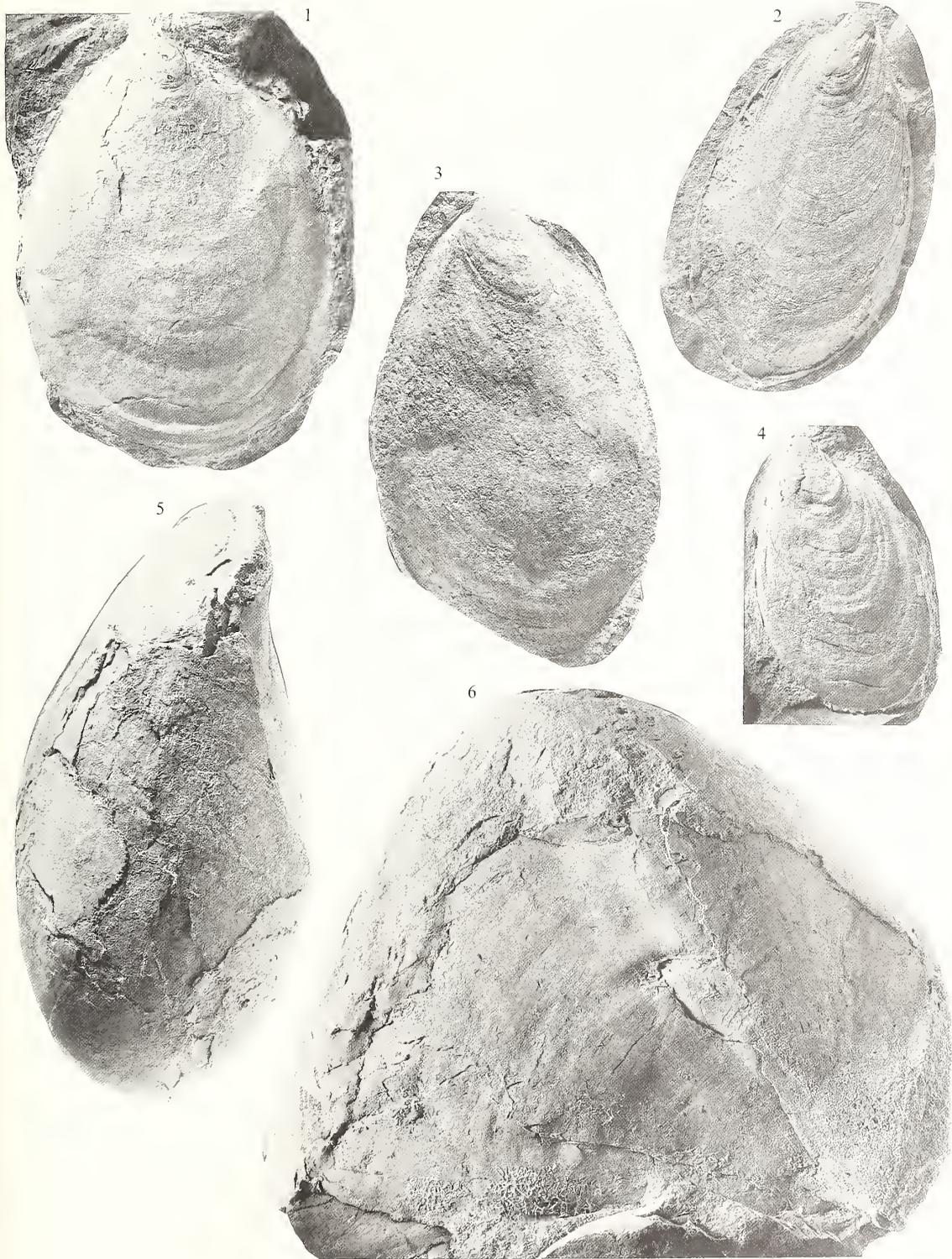
Despite the large number of specimens that have been collected, our knowledge of the hinge area of *M. problematica* is still incomplete. There has been a general recognition that it is comparatively broad, striated by growth lines and edentulous, but only very rarely is it preserved in its entirety (Trechmann 1917; Wilckens 1927; Marwick 1953; Waterhouse 1960, 1979). In the specimens described by Waterhouse (1960), the ligament appears to have been mounted in the right valve on a small striated plate (or septum) which overlies an umbonal cavity. This plate has a triangular form and terminates abruptly anteriorly against the thickened margin of the shell (Waterhouse 1960, pl. 20, fig. 3). In the adult left valve, there are again impressions of a comparatively small, triangular ligament area, but the specimen illustrated by Waterhouse (1960, pl. 21, fig. 4) is partially distorted. Examination of further adult specimens of *M. problematica* from locality GS14977, Eighty-Eight Valley, Nelson, New Zealand, has confirmed that the crucial central region is rarely preserved in its entirety. This is probably because of its location on a septal plate which overlies a deep umbonal cavity. Nevertheless, several specimens indicate that there has been a considerable degree of thickening in this region in both left and right valves, with distinct traces of an anterior blunt, rounded, tooth-like fold. This is most apparent in specimen TM 7672, where it is situated in front of what is taken to be a deeply impressed elongate-triangular resilifer (Pl. 2, fig. 3).

There is now some evidence to suggest that, as the hinge region of *Manticula* develops, it becomes considerably thickened and simplified in form. Certainly in the left valve, it would appear that the anterior, narrow, tooth-like ridge may have become transformed into a much blunter, lobe-like feature (Pl. 2, figs 1–3). In addition, it may also be that a sub-central, oblique, triangular resilifer is a consistent feature of the genus. Quite how the two valves would have articulated is not known for certain; were the tooth-like ridges in close juxtaposition or was one set slightly in front of the other? Whereas some specimens might suggest the presence of a resting groove (or socket) directly in front of the tooth, others show no sign of it. As suggested previously by Trechmann (1917, p. 201), it is more likely that this was the position of a shallow byssal sinus (e.g. Pl. 2, figs 1–2).

The presence of a thickened, striated hinge region bearing a prominent, tooth-like fold undoubtedly links this material to the Pergamidiidae; no other pteriomorph bivalve family possesses such an arrangement (see further discussion, below). Within this taxon there is a particularly close resemblance externally to small forms of *Manticula*, and this would appear to be the best genus for the new Antarctic specimens. Of course, it could be argued that lack of large, gibbous forms in the Antarctic collections, together with uncertainty about the nature of the hinge in New Zealand specimens, casts some doubt upon this assignment. Nevertheless, it is felt that, at

EXPLANATION OF PLATE 3

Figs 1–6. *Manticula problematica* (Zittel), Carnian–Norian; Eighty-Eight Valley, Nelson, New Zealand. 1, NHM L.51985; internal mould of a probable left valve. 2, TM 7673; locality GS14977; rubber peel from an external mould of a right valve. 3, TM 7674; same locality as 2; internal mould of an indeterminate valve. 4, NHM L.41262; internal mould of a probable left valve; figured previously by Trechmann (1917, pl. 20, fig. 8). 5, NHM L.41266, holotype of *Mytilus mirabilis* Trechmann, 1917 (= *Mytilus trechmanni* Waterhouse, 1960, a subjective synonym of *Manticula problematica*; Waterhouse 1960, p. 426). 6, the same specimen as 5, viewed from the anterior; figured previously by Trechmann (1917, pl. 20, fig. 9a). All are $\times 1$.



CROME, *Manticula problematica*

the present state of our knowledge, it is better to place the Antarctic material within *Mantidula* rather than create a new genus.

RELATIONSHIPS AND DISTRIBUTION OF *MANTIDULA*

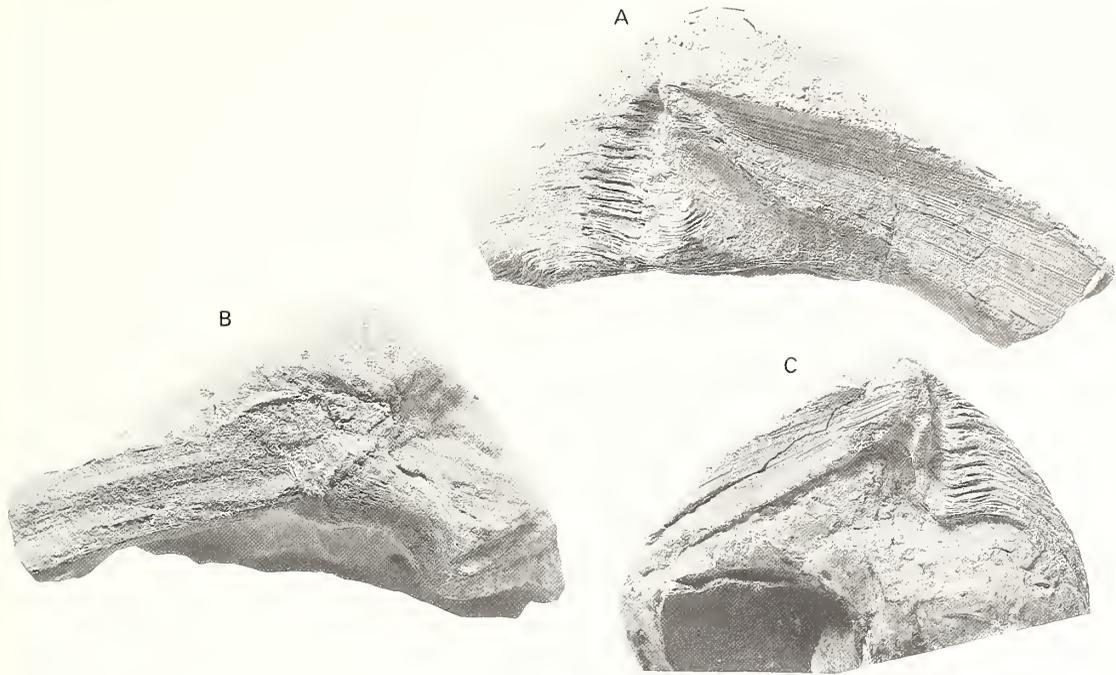
In early studies of the genus, opinion varied as to whether *Mantidula* should be classified within the Mytilidae Rafinesque, 1815 or the Myalinidae Frech, 1891 (Trechmann 1917; Wilckens 1927; Avias 1953; Marwick 1953). Even when more material became available for study, Waterhouse (1960) was unable to differentiate with certainty between these two categories. In the *Treatise on invertebrate paleontology*, Cox (1969) placed *Mantidula* within the Pergamidiidae, a new family situated close to the Inoceramidae, within the superfamily Pteriacea Gray, 1847. This taxon comprised four genera with a combined stratigraphical range of Upper Triassic–Lower Jurassic. They are distinguished collectively by their weakly ornamented mytiliform and sub-mytiliform shapes, although it should be emphasized that the genus *Pergamidia* Bittner, 1891 has an atypical anterior ear and some unusual antero-ventral radial ornament (Cox 1969, fig. C44). The sole Lower Jurassic representative, *Semuridia* Melville, 1956, may be distinguishable by its nacreous inner shell layers (Carter 1990a), but its anatomy is still far from being fully understood.

The two most prolific pergamidiid genera, *Mantidula* and *Krumbeckiella* Ichikawa, 1958, are characterized by thickened, striated hinge regions which bear a distinctive saddle-shaped fold beneath the beak; this is perhaps best described as a tooth (or tooth-like ridge) in juvenile specimens of *Mantidula* and an 'ear' in *Krumbeckiella* (Pl. 2, figs 1–3; Text-fig. 3C). The ligament area in both genera is essentially opisthodetic, and contains a variably developed central resilifer.

Krumbeckiella is a similar-sized genus to *Mantidula* but can be distinguished externally by its more oblique outline and protruding anterior margin (e.g. Krumbeck 1924, pl. 195, figs 6, 8, 9a); in some extreme forms the outline is almost quadrate (e.g. Krumbeck 1924, pl. 196, figs 6a, 7a). From the inside, the anterior ear can be seen to overhang an anterior depression which takes the form of a small lunule in the right valve and a byssal slit in the left (Text-fig. 3C; Krumbeck 1924, pl. 195, figs 3b, 9b). Such is the deeply impressed nature of the latter feature in some specimens that the anterior ear is clearly visible from the outside (Krumbeck 1924, pl. 195, figs 12b, c).

One of the most closely related genera to both *Mantidula* and *Krumbeckiella* may be the Early Permian austral taxon *Eurydesma* Morris, 1845. Although considerably larger and thicker-shelled (some forms reach 160 mm in length), it is characterized by a striated hinge region which bears a prominent saddle-shaped fold (or ear; see Waterhouse and Gupta 1982) directly beneath the beak (Text-fig. 3A–B). Such folds are particularly evident in juveniles and smaller species such as *Eurydesma playfordi* Dickins and *E. cordata* Morris (Dickins 1957; Runnegar 1970). In large, adult specimens of *Eurydesma*, the opisthodetic ligament is mounted on a broad platform which occasionally bears traces of a shallow resilifer (e.g. Waterhouse 1980, fig. 6); otherwise, the ligament surface exhibits subparallel growth striae (Text-fig. 3A–B). The shell structure of *Eurydesma* is still not known for certain, but it would appear that the greatly thickened outer calcitic layers have a predominantly foliated structure, with some minor homogeneous and simple prismatic material (Runnegar 1970, 1979; Carter 1990a, b). In this respect there would appear to be a very close correspondence with *Mantidula*; a right valve of *M. problematica* examined by Carter (1990a) was found to be almost identical in shell structure to *Eurydesma playfordi*.

There is probably a direct line of descent from *Eurydesma* to the genus *Glendella* Runnegar, 1970, which has so far only been described from the early Middle Permian of Queensland, Australia (Runnegar 1970). Also globular in shape and almost smooth, *Glendella* possesses a comparatively broad hinge along which an acute fold in the growth lines picks out a structure analogous to the *Eurydesma* 'ear'. However, it is apparent that *Glendella* is strongly inequivalve, with a large, inflated left valve and smaller, flatter right valve. There are some indications that the ligament area of this right valve is carried more on its dorsal surface and it also possesses a narrow, slit-like byssal notch (Runnegar 1970, pl. 18, fig. 4). Although the correspondence is not exact, there are a number of



TEXT-FIG. 3. The hinge region of *Eurydesma* and *Krumbeckiella*. A–B, *Eurydesma cordata* Morris. A, NHM PL4043; right valve showing prominent, subcentral tooth slanting obliquely forwards; the crest of the tooth bears a shallow depression which marks the point of articulation with the left valve tooth; prominent byssal notch lies immediately in front of the tooth; broad ligament area with fine, subparallel growth striae lies behind it; $\times 1.5$. B, NHM 8-12-5; left valve showing broad, subcentral tooth with narrow crest; $\times 1.5$. C, *Krumbeckiella subtimorensis* (Krumbeck). Mineralogisch-Geologisch Museum, Delft, No. 12933; left valve, a subcentral, ridge-like fold forms the basis of an anterior 'ear' (N.B. the crest is slightly eroded in this specimen); immediately in front of the 'ear' there is a narrow but deep byssal notch and immediately behind it a broad, flat ligament area bears traces of a shallowly impressed, triangular pit; the obliquely sloping anterior margin of this pit is clearly seen; $\times 1.5$; figured previously by Krumbeck (1924, pl. 17, fig. 9b).

points of similarity between *Glendella* and *Manticula*. These include: their inequivalve nature (at least in certain adult forms), possession of a thick crossed-foliated outer shell layer, and similar hinge regions (Runnegar 1977; Waterhouse 1980). Because of features such as its globular, strongly inequivalve form and its primitive ear and notch in the right valve, it has also been suggested that *Glendella* may be the earliest representative of the widespread monotoidean family, Buchiidae Cox, 1953 (hitherto Triassic–Cretaceous; Waterhouse 1980; Waterhouse and Gupta 1982).

It is accepted generally now that *Eurydesma* should be classified within its own family, the Eurydesmidae Reed, 1932 (e.g. Runnegar 1979). Because of overall similarities to Late Palaeozoic taxa such as *Posidoniella* Koninck (Ambonychiidae) and *Atomodesma* Beyrich (Inoceramidae), most authorities have in turn assigned the Eurydesmidae to the superfamily Ambonychioidea Miller, 1877 (Kaufmann and Runnegar 1975; Dickins 1983); this is probably the best category for the Pergamidiidae too (Carter 1990a). Nevertheless, the presence of a distinct right valve byssal notch suggests at least some pectinoid affinities for *Eurydesma* (Runnegar 1970; Carter 1990a), and whether *Glendella* is best assigned to the Eurydesmidae or Buchiidae is, perhaps, still a moot point (Runnegar 1979; Waterhouse 1980). Possible phylogenetic links between the pteroid superfamily Ambonychioidea and the pectinoid Monotoidea need to be investigated further. Waterhouse and

Gupta (1982), for example, have gone so far as to suggest that the Eurydesmidae, Pergamidiidae and Buchiidae may collectively be distinct enough to comprise a separate superfamily (the Eurydesmatoidea Reed, 1932).

Eurydesma is a consistent component of Permian cool-temperate marine invertebrate assemblages throughout Gondwana. It has been recorded from both eastern and Western Australia, India (various localities), South Africa and Argentina (Runnegar 1979, fig. 2). As stated previously, *Glendella* is known only from the Middle Permian of eastern Australia and *Manticula* occurs in the Late Triassic (Carnian–Norian) of both New Zealand and New Caledonia. *Krumbeckiella* is prolific in the Late Triassic (Norian) of Timor in a palaeoenvironmental setting which is judged to have been close to the southern margins of the Tethyan Ocean (Audley-Charles 1988). At this locality it co-occurred with *Pergamidia*, which is known from Turkey, and possibly other Tethyan Triassic localities too (Cox 1969).

Thus it is possible to conclude that the group of taxa represented by *Eurydesma*, *Glendella*, *Manticula* and *Krumbeckiella* is essentially a southern one with high-latitude, cool-temperate origins in the Early Permian. The group may well have spread subsequently so that by the Late Triassic it came to occupy marginal-Tethyan environments. Indeed, if *Pergamidia* is a valid further member of the group, it may well have disseminated through the Tethyan realm proper. Thereafter, however, the story would appear to be one of dramatic range retraction, for there may well be no true Jurassic representatives of either the Eurydesmidae or Pergamidiidae. The sole further stratigraphical record is now established for *Manticula* in the Early Cretaceous of Antarctica. Such an occurrence may well indicate that this genus became a relict in a high-latitude refugium. It may also be that it can be regarded as a Late Triassic (Carnian–Norian)–Early Cretaceous (Berriasian) Lazarus Taxon (Jablonski 1986), with no known Jurassic records. However, it is apparent that *Manticula* is still known from comparatively few stratigraphical levels in New Zealand and New Caledonia, and application of 95 per cent. confidence intervals to its Triassic range (*sensu* Marshall 1990) could see an extension into the Cretaceous. Precise stratigraphical occurrences of *Manticula* are currently being reinvestigated.

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REFERENCES

- AUDLEY-CHARLES, M. G. 1988. Evolution of the southern margin of Tethys (North Australian region) from the early Permian to late Cretaceous. In AUDLEY-CHARLES, M. G. and HALLAM, A. (eds). *Gondwana and Tethys*. Geological Society, London, Special Publication, No. 37, 79–100.
- AVIAS, J. 1953. Contribution à l'étude stratigraphique et paléontologique de la Nouvelle-Calédonie centrale. *Sciences Terre*, **1**, 1–276.
- BITTNER, A. 1891. Triaspetre-fakten aus Balia in Kleinasien. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt*, **41**, 97–116, pls 1–3.
- CARTER, J. G. 1990a. Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorpha and Isofilibranchia (Bivalvia: Mollusca). 135–296. In CARTER, J. G. (ed.). *Skeletal biomineralization: patterns, processes and evolutionary trends. Volume 1*. Van Nostrand Reinhold, New York, 832 pp.
- 1990b. Shell microstructural data for the Bivalvia. 297–411. In CARTER, J. G. (ed.). *Skeletal biomineralization: patterns, processes and evolutionary trends. Volume 1*. Van Nostrand Reinhold, New York, 832 pp.

- COX, L. R. 1953. Lower Cretaceous Gastropoda, Lamellibranchia and Annelida from Alexander I Land (Falkland Islands Dependencies). *Falkland Islands Dependencies Survey Scientific Reports*, No. 4, 14 pp., pls 1–2.
- 1969. Family Pergamidiidae Cox, new family. N313–N314. In MOORE, R. C. and TEICHERT, C. (eds). *Treatise on invertebrate paleontology. Part N. Mollusca 6(1). Bivalvia*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 489 pp.
- CRAME, J. A. 1984. Preliminary bivalve zonation of the Jurassic-Cretaceous boundary in Antarctica. 242–254. In PERILLIAT, M. de C. (ed.). *Memoria, III congreso Latinoamericano de Paleontología, Mexico, 1984*. Universidad Nacional Autónoma de México, Instituto de Geología, México City, 661 pp.
- PIRRIE, D., CRAMPTON, J. S. and DUANE, A. M. 1993. Stratigraphy and regional significance of the Upper Jurassic–Lower Cretaceous Byers Group, Livingston Island, Antarctica. *Journal of the Geological Society, London*, **150**, 1075–1087.
- DICKINS, J. M. 1957. Lower Permian pelecypods and gastropods from the Carnarvon Basin, Western Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, No. 41, 55 pp.
- 1983. *Posidoniella*, *Atomodesma*, the origin of the Eurydesmidae, and the development of the pelecypod ligament. *Bulletin of the Bureau of Mineral Resources, Australia*, No. 217, 59–65.
- FRECH, F. 1891. Die devonischen Aviculiden Deutschlands, ein Beitrag zur Systematik und Stammesgeschichte der Zweischaler. *Abhandlungen zur Geologischen Specialkarte von Preussen und den Thüringischen Staaten*, **9**, 253 pp., 5 pls; atlas of 18 pls.
- GRAY, J. E. 1847. A list of the genera of Recent Mollusca, their synonyms and types. *Proceedings of the Zoological Society of London*, **15**, 129–219.
- ICHIKAWA, K. 1958. Zur taxonomie und phylogenie der Triadischen 'Pteriidae' (Lamellibranch.) mit besonderer berücksichtigung der gattungen *Claraia*, *Ennorphotis*, *Oxytoma* und *Monotis*. *Palaontographica, Series A*, **3**, 131–212.
- JABLONSKI, D. 1986. Causes and consequences of mass extinctions: a comparative approach. 183–229. In ELLIOT, D. K. (ed.). *Dynamics of extinction*. John Wiley, New York, 294 pp.
- and LUTZ, R. A. 1980. Larval shell morphology: ecological and paleontological implications. 323–377. In RHOADS, D. C. and LUTZ, R. A. (eds). *Skeletal growth of aquatic organisms*. Plenum, New York, 750 pp.
- KAUFFMAN, E. G. and RUNNEGAR, B. 1975. *Atomodesma* (Bivalvia) and Permian species of the United States. *Journal of Paleontology*, **49**, 23–51.
- KRUMBECK, L. 1924. Die Brachipoden, Lamellibranchiaten, und Gastropoden der Trias von Timor, 2. *Paläontologie von Timor*, No. 13, 275 pp., 20 pls.
- MARSHALL, C. R. 1990. Confidence intervals on stratigraphic ranges. *Paleobiology*, **16**, 1–10.
- MARWICK, J. 1953. Divisions and faunas of the Hokonui System (Triassic and Jurassic). *Palaontological Bulletin. New Zealand Geological Survey*, No. 21, 141 pp.
- MELVILLE, R. V. 1956. Stratigraphical palaeontology, ammonites excluded, of the Stowell Park Borehole. *Bulletin of the Geological Survey of Great Britain*, **11**, 67–139.
- MILLER, S. A. 1877. *The American Paleozoic fossils; a catalogue of the genera and species, etc.* Published by the author, Cincinnati, Ohio, 334 pp.
- MORRIS, J. 1845. Descriptions of fossils. 270–291. In STRZELECKI, P. E. de. *Physical description of New South Wales and Van Diemen's Land*. Longman, Brown, Green and Longmans, London, 469 pp.
- NEWELL, N. D. 1965. Classification of the Bivalvia. *American Museum Novitates*, No. 2206, 25 pp.
- RAFINESQUE, C. S. 1815. *Analyse de la nature*. Published by the author, Palermo, 225 pp.
- REED, F. R. C. 1932. New fossils from the Agglomeratic Slate of Kashmir. *Memoirs of the Geological Survey of India, Palaontologia Indica*, **20**, 1–79.
- RUNNEGAR, B. 1970. *Eurydesma* and *Glendella* gen. nov. (Bivalvia) in the Permian of eastern Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics*, No. 116, 106 pp.
- 1977. Marine fossil invertebrates of Gondwanaland: palaeogeographic implications. 144–159. In LASKAR, B. and RAJA RAO, C. S. (eds). *Fourth International Gondwana Symposium: Papers (Volume 1)*. Hindustan Publishing Corporation (India), Delhi, 384 pp.
- 1979. Ecology of *Eurydesma* and the *Eurydesma* fauna, Permian of eastern Australia. *Alcheringa*, **3**, 261–285.
- 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. *Bulletin of the British Antarctic Survey*, No. 50, 55–76.
- PANKHURST, R. J., THOMSON, M. R. A. and DAVIES, R. E. S. 1984. The geology of the South Shetland Islands. VI. Stratigraphy, geochemistry and evolution. *British Antarctic Survey Scientific Reports*, No. 87, 85 pp.

- TRECHMANN, C. T. 1917. The Trias of New Zealand. *Quarterly Journal of the Geological Society, London*, **73**, 165–246.
- WATERHOUSE, J. B. 1960. Some Carnian pelecypods from New Zealand. *Transactions of the Royal Society of New Zealand*, **88**, 425–442.
- 1979. The Upper Triassic bivalve *Oretia* Marwick 1953 (Note). *New Zealand Journal of Geology and Geophysics*, **22**, 621–625.
- 1980. A new bivalve species (Buchiidae) from the Early Triassic of New Zealand. *Alcheringa*, **4**, 1–10.
- and GUPTA, V. J. 1982. Palaeoecology and evolution of the Permian bivalve genus *Eurydesma* Morris. *Bulletin of the Indian Geologists' Association*, **15**, 1–19.
- WILCKENS, O. 1927. Palaeontology of the New Zealand Trias. *Palaeontological Bulletin, New Zealand Geological Survey*, No. 12, 59 pp.
- ZITTEL, K. A. 1864. Fossile Mollusken und Echinodermen aus Neu-Seeland. *Novara Expedition, Geologische Teil*, **1**, 17–68.

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CHIGUTISAURID TEMNOSPONDYLS FROM THE LATE TRIASSIC OF INDIA AND A REVIEW OF THE FAMILY CHIGUTISAURIDAE

by DHURJATI P. SENGUPTA

ABSTRACT. Two chigutisaurids (Amphibia, Temnospondyli), *Compsocerops cosgriffi* gen. et sp. nov. and *Kuttycephalus triangularis* gen. et sp. nov., from the Late Triassic Maleri Formation, Pranhita–Godavari valley, Deccan, India are described. In the past, the only known chigutisaurids have been two genera from Australia and probably two from South America. Relationships within the family are analysed and two groups are recognized. They possess marked differences in their palate and dentition. The Late Triassic beds of the Pranhita–Godavari valley exhibit a rapid faunal change. Two faunal zones are present in the Maleri Formation. The age of the lower zone is possibly Late Carnian and the upper is Early Norian. Chigutisaurids are present in the upper faunal zone only.

Two new taxa of the family Chigutisauridae, a rare group of temnospondyl amphibians, previously known only from South America and Australia, have been recovered from Late Triassic continental red beds of the Maleri Formation of the Pranhita–Godavari valley, Deccan, India (Text-fig. 1). During the last decade or so, the chigutisaurids have attracted the attention of palaeontologists, as they are known to have crossed the Triassic–Jurassic boundary (Warren and Hutchinson 1983). The new taxa from India have been discovered at a juncture when more information is needed to bridge the geographical gap between the South American and the Australian chigutisaurids. Against this background, the new chigutisaurids seem to be of extreme importance.

The appearance of the chigutisaurids in India is accompanied by the disappearance of the metoposaurids and some reptilian forms. The present work suggests that this change possibly indicates the Carnian–Norian faunal turnover. The discovery of the new chigutisaurids thus adds valuable knowledge not only about this group but also about the Indian Late Triassic.

SYSTEMATIC PALAEOONTOLOGY

Order TEMNOSPONDYLI Zittel, 1888

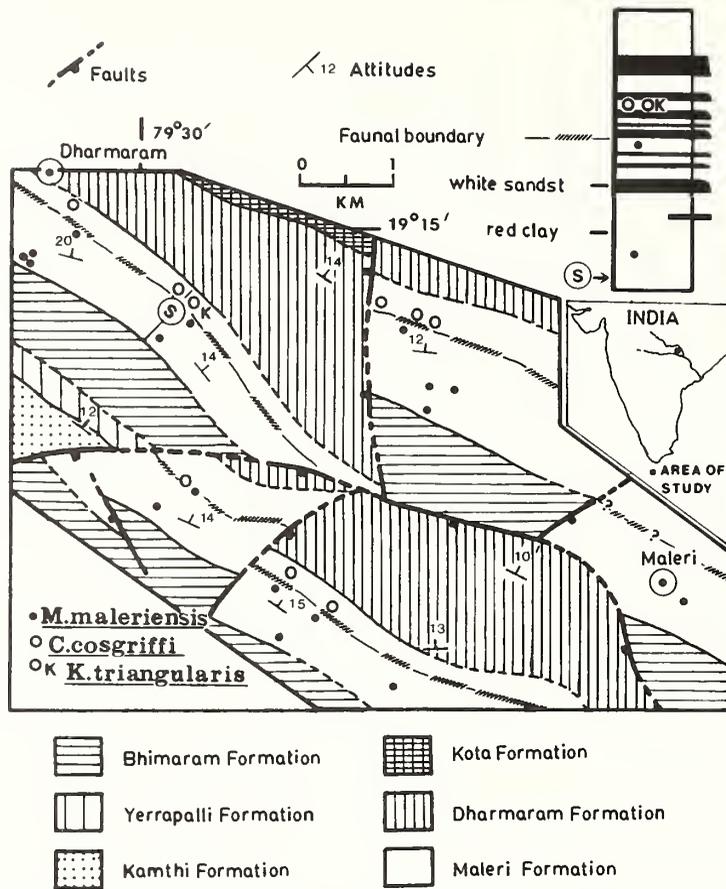
Superfamily BRACHYOPOIDEA Säve-Söderbergh, 1935

Family CHIGUTISAURIDAE Rusconi, 1951

Genus COMPSOCEROPS gen. nov.

Derivation of name. From the Greek *compso* (beautiful), *ceros* (horn) and *ops* (face), alluding to an animal with beautiful horns/projections on the skull.

Diagnosis. Large chigutisaurid with parabolic skull, anteriorly placed orbits and a pair of tabular horns; pair of projections present on postparietals, squamosals and quadratojugals; lacrimal absent; pineal foramen anteriorly placed; cultriform process of parasphenoid long and narrow; dentigerous area restricted to anterior region of the skull and lower jaw; complete row of teeth on vomer, palatine and ectopterygoid bones; palatal tooth row separated from marginal row by a



TEXT-FIG. 1. Geological map of area between Dharmaram and Maleri, with significant temnospondyl localities. A schematic section along 'S' is shown at top right. Inset indicates the location of the area studied.

conspicuous groove; dorsal process of clavicle unusually long; pleurocentrum and intercentrum fused in some vertebrae.

Compsoceros cosgriffi sp. nov.

Text-figures 2-14

Derivation of name. The species is named after the late Dr John W. Cosgriff, who first identified as brachyopoids some jaw fragments collected from the Maleri Formation.

Holotype. ISI A 33, an almost complete skull with attached mandibles, in the collection of the Geological Museum of the Indian Statistical Institute (ISI), Calcutta, India.

Referred specimens. ISI A 24-27 and ISI A 34-49

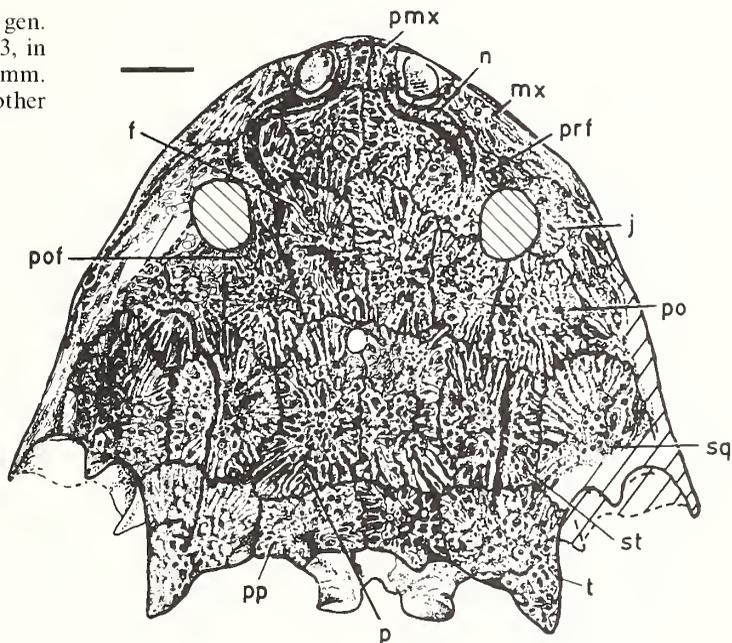
Diagnosis. As for the genus.

Horizon and age. All the material described here was collected from the upper part of the Maleri Formation. The type skull was collected from a red clay horizon near Rechni village (Text-fig. 1). An Early Norian age has been assigned to the Upper Maleri fauna in the present work.

Description

Nature of preservation and reconstruction. The type skull is nearly complete with most of the sutures and ornamentation of the skull roof intact (Text-fig. 2). The mandibles were attached to the skull (Text-fig. 3). The

TEXT-FIG. 2. *Compsocerops cosgriffi* gen. et sp. nov. Holotype skull, ISI A 33, in dorsal view. Scale bar represents 50 mm. For abbreviations for this and all other Text-figures, see list on p. 339.



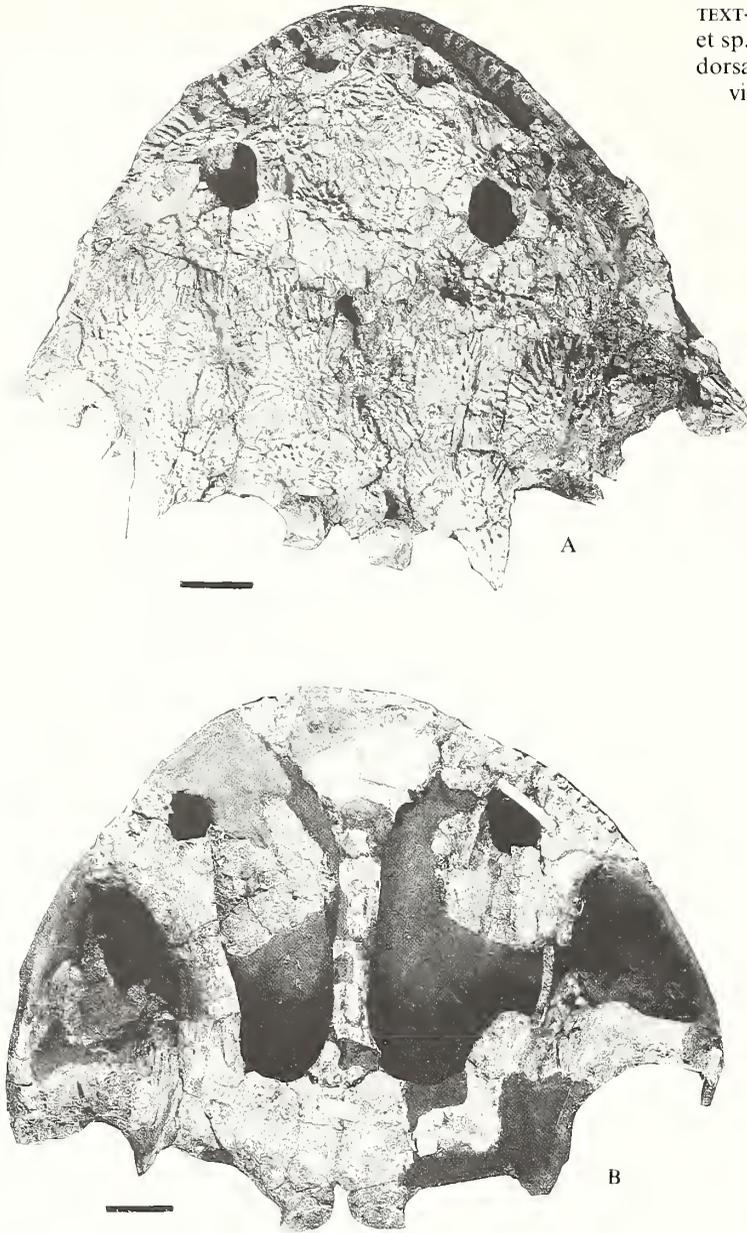
occiput has been flattened. The palate along with the dentition (Text-figs 3-4) is very well preserved in ISI A 34.

A complete left mandible and another fragmentary specimen have been studied, in addition to the mandibles with ISI A 33. A number of postcranial elements have been recovered both from clay and sandstone. Characteristic skull roof bones or vertebrae are always found in association. A list of specimens studied is given in Table 1.

Dorsal surface of the skull (Text-fig. 5). The skull is large and parabolic with conspicuous tabular horns and anteriorly placed dorsolateral orbits. The skull roof is 300 mm long and 400 mm wide with the posterior margin about 170 mm from the rear of the skull roof. A projection is present on the postparietal, squamosal and quadratojugal. The skull is relatively deep (Text-fig. 5B). The skull roof bones show the usual chigutisaurid arrangement. The anterior part of the skull is rounded with the premaxilla at the anteriormost tip. The nasal is broad, expanded anteriorly and strongly ornamented. The frontal is almost rectangular. The parietal is large, rectangular, and shorter than the postparietal. Thicknesses of the bones are at a minimum around the pineal foramen which is relatively anteriorly placed almost at the suture between the parietal and the frontal. The posterior region of the skull is wide and stout and appears to have been the active zone of intensive growth. The tabular horn projects posteriorly. The posterior part of the horn remains unsupported from below as the descending (paroccipital) process of the tabular does not extend posteriorly beneath the horn. The otic notch is marked.

The subcircular orbit is formed by the prefrontal, jugal, postfrontal and postorbital. These bones have fainter sculpturing compared with the posterior skull roof bones. The external naris is elliptical and faces anterodorsally. The unusually deep lateral line canal around the posterolateral border of the naris causes the rim of the naris to be raised except anteriorly, where it is confluent with the skull roof. The rim is conspicuous.

TEXT-FIG. 3. *Compsoceros cosgriffi* gen. et sp. nov. A, holotype skull, ISI A 33, in dorsal view. B, skull, ISI A34, in ventral view. Scale bar represents 50 mm.



The ornamentation on the skull roof has numerous pits at the centre of each bone and radiating ridges near the edges. Narrow U-shaped grooves between the ridges gradually widen towards the periphery of each bone. In places, these ridges bear small uneven pustules. The grooves are very coarse on the tabular horns, while the ridges are longest at the posterior of the quadratojugals.

Ventral surface of the skull roof (Text-fig. 6). On the ventral face of the tabular, the descending process starts with a thinning fan of bone which divides the ventral side of the unsupported part of the tabular into two deep

TEXT-FIG. 4. *Compsoceros cosgriffi* gen. et sp. nov. Skull, ISI A 34, in ventral view. Scale bar represents 50 mm.

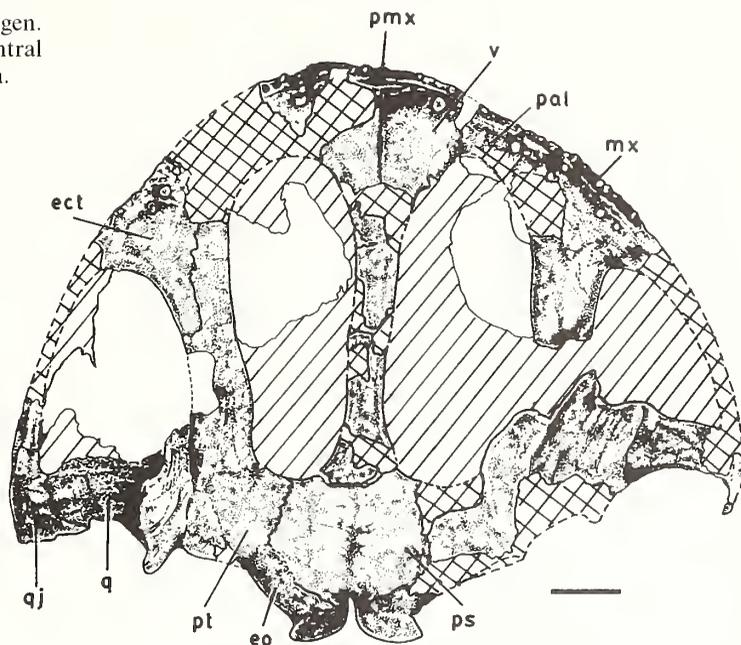
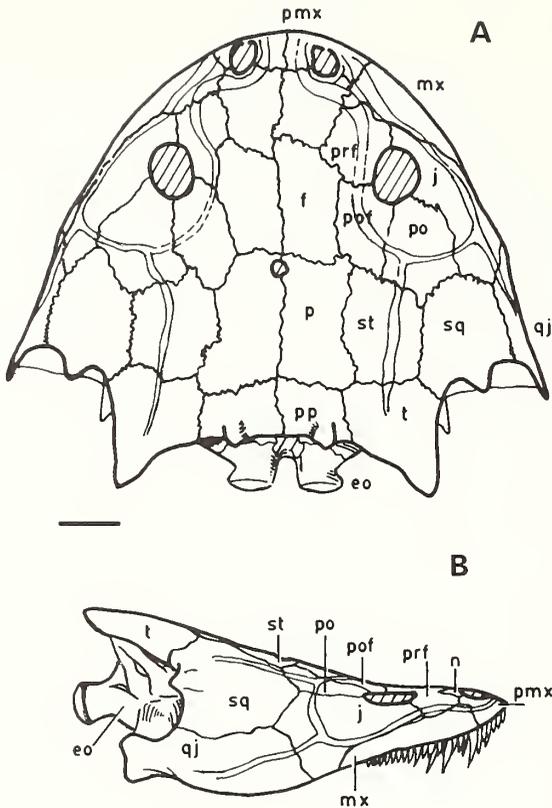


TABLE 1. List of specimens studied.

Material	Specimen no.
<i>Compsoceros cosgriffi</i>	
Parts of vertebra	ISI A 22
Parts of vertebra	ISI A 24
Right ilium	ISI A 25
An isolated occipital condyle (left) with part of the basal plate of the parasphenoid	ISI A 26
A broken interclavicle	ISI A 27
A complete skull with both mandibles attached	ISI A 33
A mostly complete skull with one side of the palate intact	ISI A 34
Right side of a skull roof	ISI A 35
A complete left mandible	ISI A 36
Left posterior portion of a skull roof with tabular and post-parietal only	ISI A 37
A nearly complete clavicle	ISI A 38
Parts of two vertebrae	
(i) One intercentrum and pleurocentrum fused together	ISI A 39
(ii) One intercentrum	ISI A 40
Parts of humerus	ISI A 41
Parts of neural spines	ISI A 43 to ISI A 49
<i>Kuttycephalus triangularis</i>	
A complete skull with left lower jaw	ISI A 50
Skull fragments	ISI A 51 ISI A 52

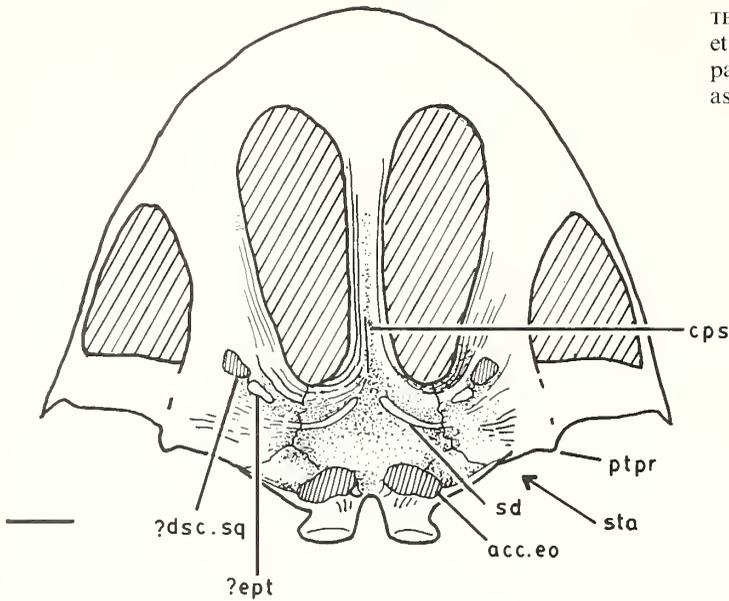


TEXT-FIG. 5. *Compsoceros cosgriffi* gen. et sp. nov. A, reconstruction of the skull in dorsal view. B, reconstruction of the skull in lateral view. Scale bar represents 50 mm.

elliptical scars of the internal and external *tabularis*. Beneath the supratemporal, a semicircular ridge of bone may represent the remains of the ascending ramus of the pterygoid. Near the anterior border of the orbit, on the ventral side of the prefrontal, is a small prominence (Text-fig. 6). This type of prominence in this position has not been reported from any other chigutisaurid. It may indicate the presence of a muscular connection between the roof and the more anterior parts of the palate. It is interesting to note that *Benthosuctus sushkini* has a pair of projections, the '*spina lachrymalis*' (Bystrow and Efremov 1940), on the dorsal side of the palatines.

Ventral surface of the palate (Text-fig. 7A). Posteriorly, the palate is essentially a parallel-sided longitudinal vault with a flat roof. The vertical lateral wall of the pterygoid projects posteriorly as far as the occipital condyle with an exceptionally deep development of the pterygoid.

Although the suture is not preserved completely, the posterior parts of the vomers appear to include the anterior tongue of the cultriform process of the parasphenoid, slightly posterior to the level of the anterior borders of the interpterygoid vacuities. The anterior margin of the vomers forms the border of the transversely lenticular anterior palatal vacuity. On the ventral surface of the palate, along the anterior margin of this vacuity, at least two irregular ridges of bone are present. The dentigerous area is restricted to the anterior region of the palate leaving a larger posterior portion, with big subtemporal vacuities, which extends anterior to the centre of the interpterygoid vacuities. The parasphenoid has a large subcircular base and a long and narrow cultriform process with a low ridge-like elevation along its ventral margin at the axis of curvature. The exoccipitals suture with the posterior margin of the body of the parasphenoid. More laterally, the quadrate is exposed between the pterygoid ramus and a flat posterior projection of the quadratejugal. The quadrate condyle is positioned well anterior to the occipital condyle. The quadrate-ptyerygoid suture is present on the outer side of the downturned wall of the pterygoid.



TEXT-FIG. 8. *Compsoceros cosgriffi* gen. et sp. nov.; ISI A 34; the base of the parasphenoid and the braincase and associated features in dorsal view. Scale bar represents 50 mm.

Dorsal surface of the palate (Text-fig. 8). The cultriform process forms an elongate canal-like depression. This depression gradually flattens on to the basal plate of the parasphenoid as a pair of shallow depressions which fan out symmetrically. They lead to two crescentic canals for the internal carotid arteries within the base of the parasphenoid (Text-fig. 8).

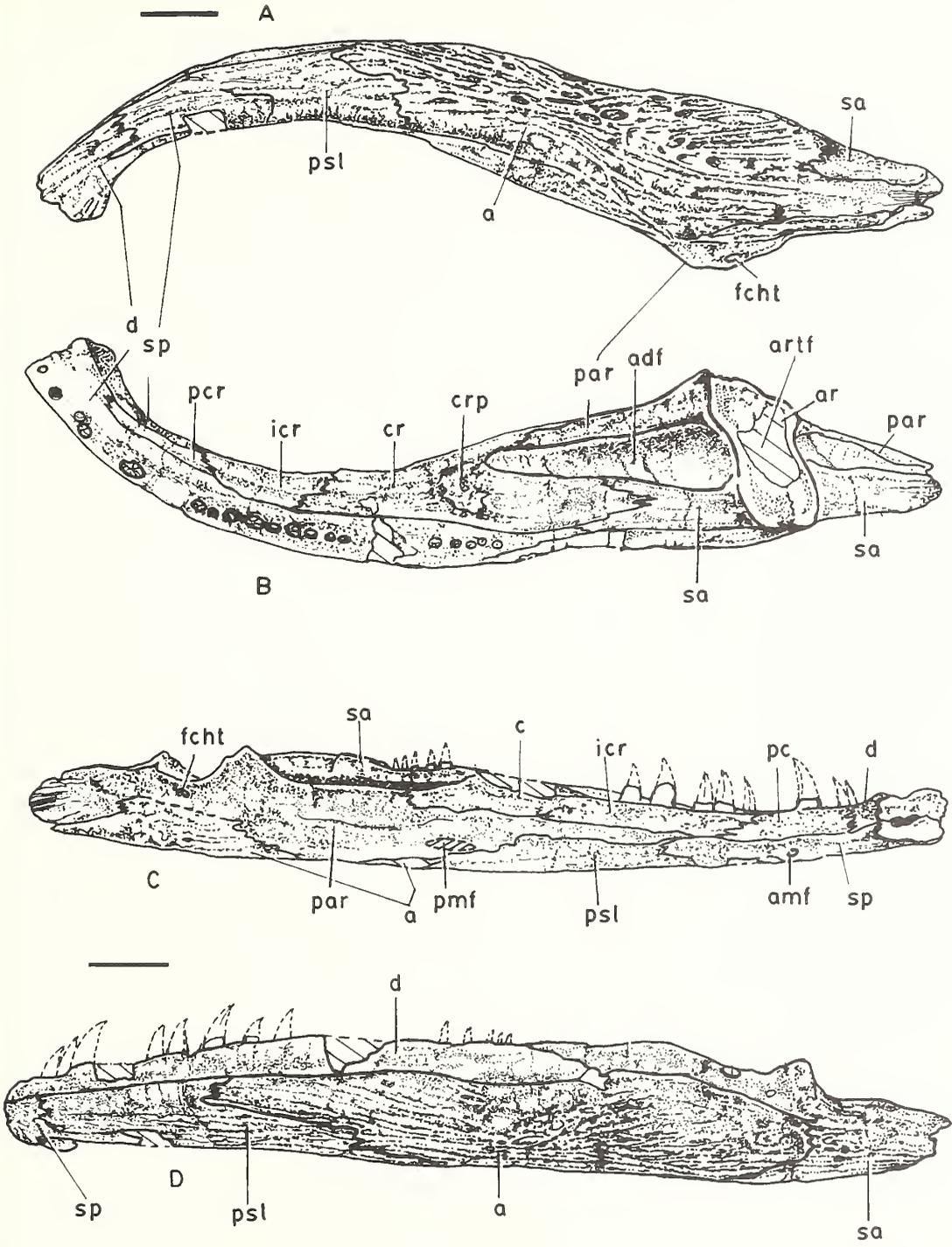
On the dorsal surface of the pterygoid, the base of the ascending process of the pterygoid is preserved. Anterior to this, another lateral canal runs towards the carotid canals. However, it cannot be determined whether an ascending column of the pterygoid (Warren and Hutchinson 1983) was present on the medial margin of this process. It appears that the braincase may have been relatively wide, anteriorly expanded and low.

Occiput (Text-fig. 7B). The occiput is an inverted U-shaped structure with the skull roof and the palate present as a flat table in the middle and flanged by two large squamosal-quadratojugal troughs. The inverted U is formed by the downturned quadrate rami of the pterygoids.

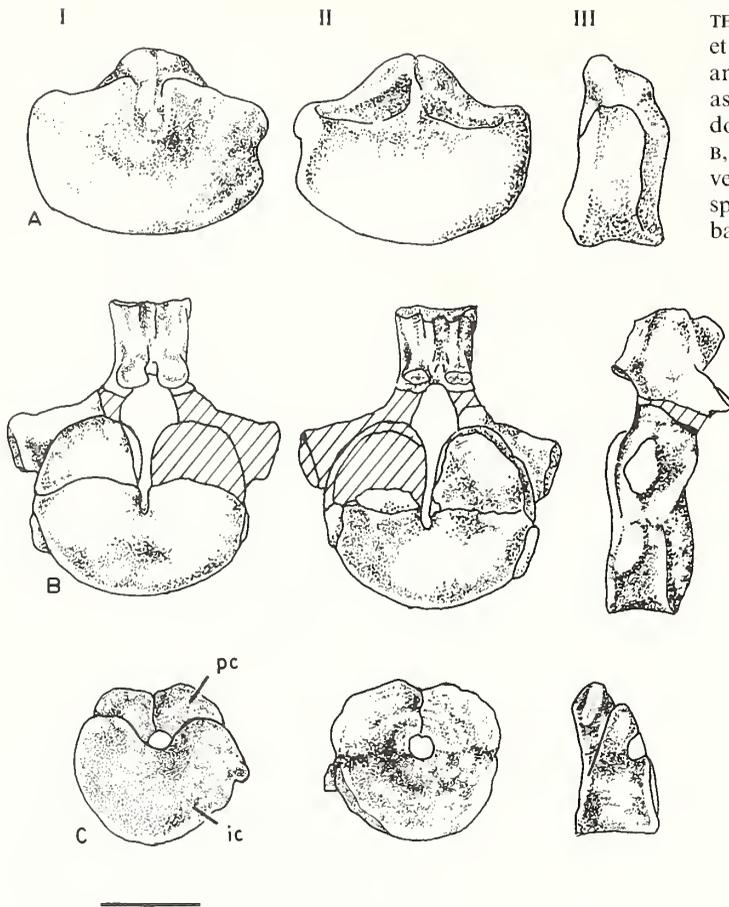
The exoccipitals form the posteriorly directed condyles. They have quite long necks. The columnar part of the ascending process of the exoccipital is flat and inclined, and meets the descending process of the postparietal and the tabular. Ventrally the exoccipital continues up to the pterygoid, forming a plate which is curved inwards. The exoccipital bears a large oval foramen for nerve (x) just at the point where the process of the exoccipital starts ascending. The otic recess is extremely large and so is the otic notch. No stapes is preserved.

At the posterior end, where the quadrate ramus of the pterygoid turns ventrally, a marked posterior projection of the pterygoid is present. Pronounced muscle attachment scars are present on the transverse edge of the postparietal and tabular which are very conspicuous in the occipital view. As mentioned above, a large rectangular trough, formed by the squamosal, quadratojugal and quadrate, is present in *C. cosgriffi*. The trough has its lower part almost infolded, creating a depression at the bottom. This may represent the origin of the *depressor mandibuli* muscle (Welles and Estes 1969). A circular paraquadrate foramen is present on the quadratojugal. The quadrate is seen in occipital view, separating the quadratojugal and the downturned pterygoid. The dorsal part of the quadrate-ptyergoid suture extends laterally onto the squamosal-quadratojugal trough, whereas more ventrally this suture runs down the medial wall of the trough.

Mandible (Text-fig. 9A-D). The mandible has the characteristic chigutisaurid shape, as described by Jupp and Warren (1986). In cross-section it is elliptical with a flat top. The dentition is restricted to the anterior half. The ornamentation in the posterior part consists essentially of large elliptical grooves walled by coarse ridges.



TEXT-FIG. 9. *Compsoceroops cosgriffi* gen. et. sp. nov., ISI A 36, left mandible in A, ventral view; B, dorsal view; C, lingual view; D, labial view. Scale bars represent 50 mm.



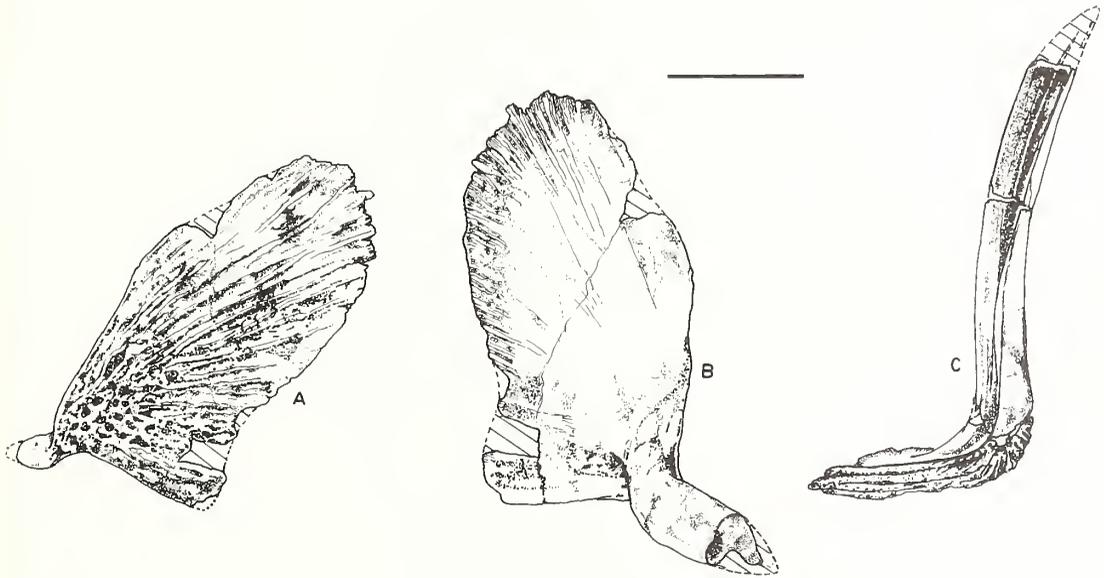
TEXT-FIG. 10. *Compsocerops cosgriffi* gen. et sp. nov. Presacral vertebrae in I, anterior, II, posterior and III, left lateral aspects. A, parts of pseudostereospondyl dorsal vertebra as preserved in ISI A 39. B, composite reconstruction of a dorsal vertebra based on ISI A 43-47 (neural spine) and ISI A 24 (centra). C, axis based on ISI A 22. Scale bar represents 50 mm.

Anteriorly, the ornament consists of anastomosing ridges on the splenial and postsplenial. The articular is exposed on the dorsal surface of the postglenoid area as a triangular bone between the surangular and the prearticular. The posteriormost part of the postglenoid area is pointed but without any marked retroarticular process. Lingually, a small foramen, possibly for the *chorda tympani*, is present in the prearticular. Two openings for the anterior meckelian foramen and a third, opening a little anterior to it, are visible in the splenial. Three coronoids also appear on the lingual surface and a conspicuous coronoid process is present at the posterior coronoid. Dorsally, the dentary has a thin posterior extension. It increases in width anteriorly. The large adductor fossa is pointed near its anterior tip. The articular fossa is bilobed. The symphysis is formed largely by the dentary, with a small ventral inclusion of the anterior splenial.

In the upper jaw, two tooth rows, marginal and palatal are embedded in narrow ridges with a narrow groove in between them. This groove is prominent at the ectopterygoid-maxillary junction. In the maxillary row, the teeth are larger anteriorly and are of uniform shape. All the teeth, including the tusks, are curved lingually. The curvature is probably maximal near the tip.

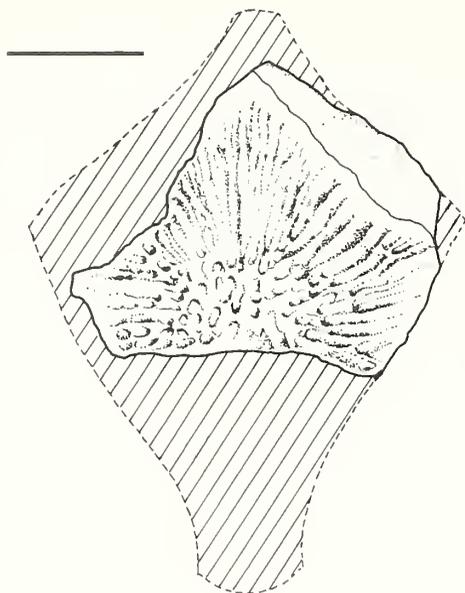
Dentition. A single row of teeth is present in the anterior half of the mandible. No symphyseal row is preserved. An indication that a large tusk pit is present near the mandibular symphysis is seen in one specimen, but not in another. The teeth are largest midway along each ramus. At the ectopterygoid-palatine contact, the bite may have been most severe with larger teeth located there. Sixty-four teeth are estimated to have been present in the mandible of ISI A 33.

Vertebrae (Text-fig. 10A–C). All the vertebral elements collected are presacral, but their exact position is difficult to determine. In at least one element, the pleurocentra are fused with the intercentrum to give a pseudo-stereospondyl appearance (Text-fig. 10c). From anterior to posterior the convexity of the intercentra decreases. The pleurocentra are two symmetrical, small, roughly spindle-shaped, bones. Possibly they met to form the floor of the neural canal. Anteriorly, they are fused with the intercentrum, so that a notochordal canal is formed near the centre of each vertebral unit. The canal is U-shaped, with the long arm in the axis, and becomes circular posteriorly. The pleurocentra also become curved posteriorly and, while joined with crescentic intercentra, they become almost spool-shaped. This type of vertebra is known only from a few vertebral elements of *Metoposaurus ouazzoui* and, to some extent, in the entire vertebral column of the almasaurids (Dutuit 1976). The former vertebrae resemble those of *C. cosgriffi*, but the latter look different. The axis is rectangular in shape. It appears that, more posteriorly, the intercentra become heart-shaped. All of them have strong parapophyses. The neural arch is small and blunt. The neural spines are thick, moderately high, and have two symmetrically disposed posterior and anterior zygapophyses. The anterior side of each spine is marked by two thin symmetrical ridges. The neural arches appear to have been intervertebrally placed.

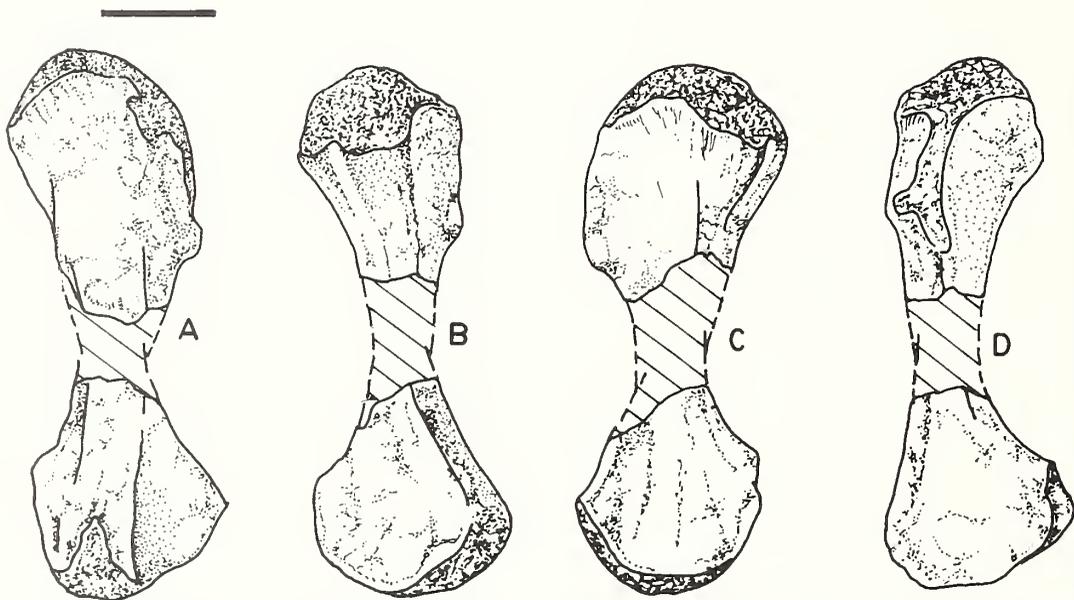


TEXT-FIG. 11. *Compsocerops cosgriffi* gen. et sp. nov. ISI A 38, right clavicle in A, ventral view; B, dorsal view; C, posterior view. Scale bar represents 50 mm.

Appendicular skeleton (Text-figs 11–14). The preserved appendicular elements of *Compsocerops* resemble their counterparts in *Siderops*. The clavicle bears an unusually long cleithral process which begins abruptly and becomes narrow dorsally (Text-fig. 11A–C). Posteriorly, the process is deeply grooved for the cleithrum. The groove continues onto the flat plate of the clavicle where it dies out. The incomplete interclavicle has been reconstructed as a diamond-shaped plate (Text-fig. 12). The clavicle and the interclavicle are very similar to those of *Siderops*. The humerus is also slender and lacks extensive projections. The angle of torsion is almost 90 degrees (Text-fig. 13A–D). The distal articulation is rounded and knob-like in the ectepicondylar region. This was probably the area for the insertion of muscles like the *trochlea* and *capitellum*. The entepicondylar side is somewhat flattened. Both condyles are sharp and pointed. The ectepicondyle merges with the supinator process. There is also a well developed furrow for the supinator muscle. The proximal articulation is thinner on the deltopectoral side. The deltopectoral crest is relatively blunt. The area of attachment of the *pectoralis*



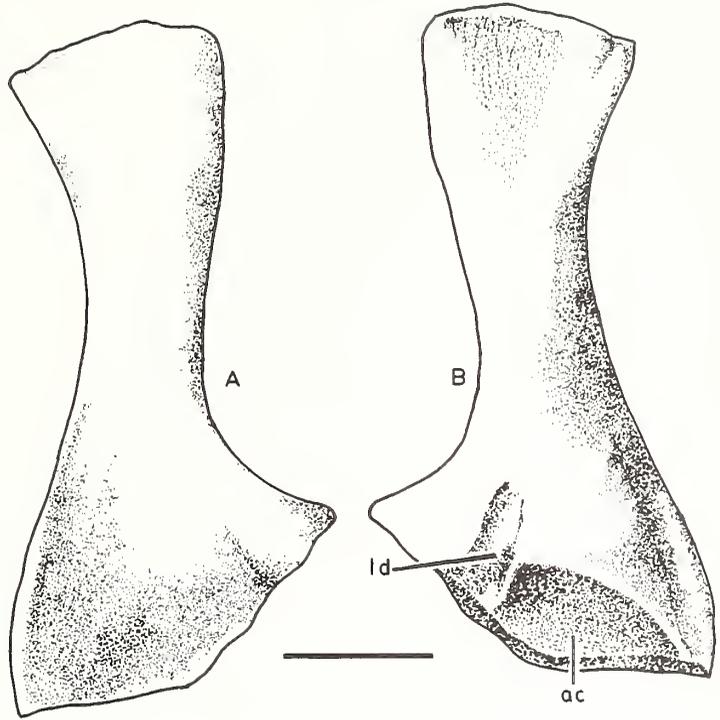
TEXT-FIG. 12. *Compsocerops cosgriffi* gen. et sp. nov. ISI A 27, interclavicle in ventral view. Scale bar represents 50 mm.



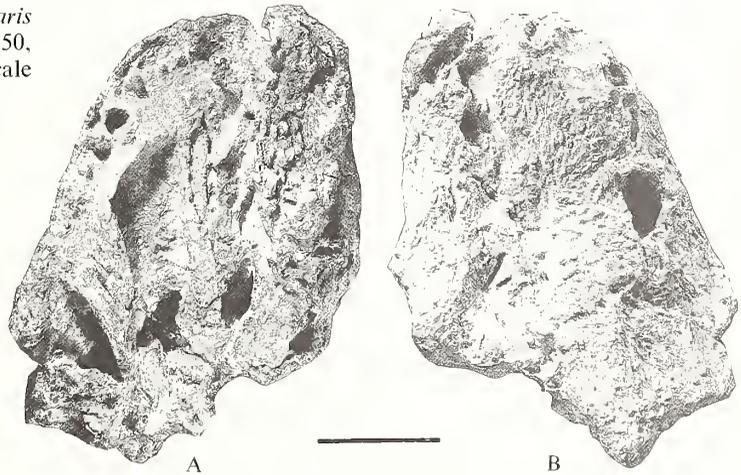
TEXT-FIG. 13. *Compsocerops cosgriffi* gen. et sp. nov. Right humerus in A, anterior view; B, dorsal view; C, posterior view; D, ventral view; based on ISI A 41 and A 42. Scale bar represents 50 mm.

muscle is very distinct as are the attachments for the deltoid muscle. Attachment for the medial head of the *triceps* is also very prominent. The ilium is thin and elongate with prominent ridges dorsally on the external surface (Text-fig. 14A-B). Deep furrows are present on both sides of the dorsal edge of the acetabulum. The acetabulum is a comparatively large knob-like structure with a deep fossa.

TEXT-FIG. 14. *Compsocerops cosgriffi* gen. et sp. nov., ISI A 25, right ilium in A, medial view; B, lateral view. Scale bar represents 50 mm.



TEXT-FIG. 15. *Kuttycephalus triangularis* gen. et sp. nov., holotype skull, ISI A 50, in A, ventral view; B, dorsal view. Scale bar represents 50 mm.

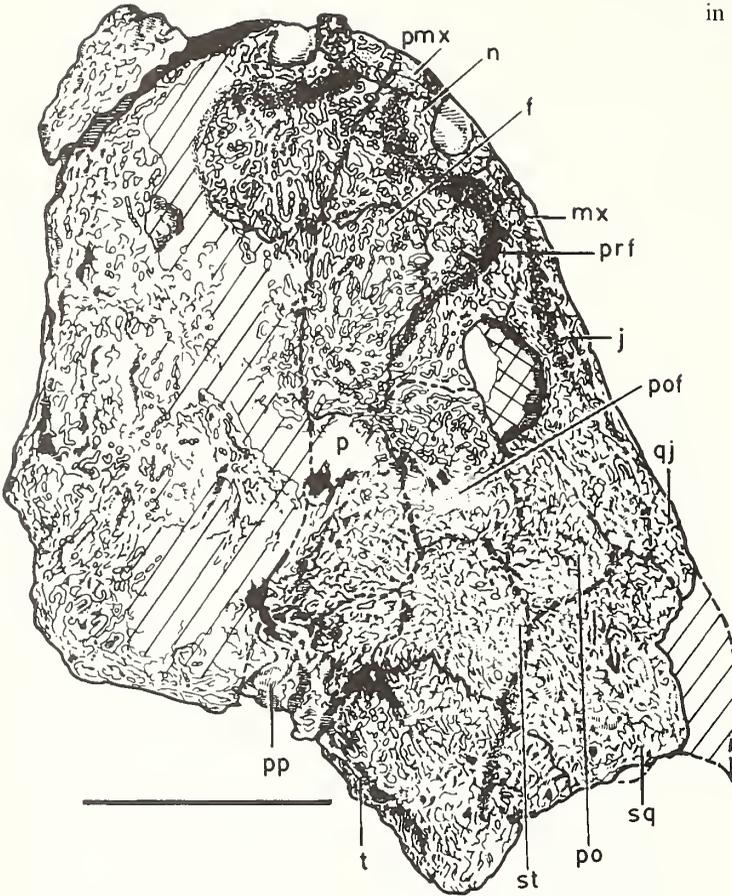


Genus KUTTYCEPHALUS gen. nov.

Derivation of name. The genus is named after Mr T. S. Kutty of the Geological Studies Unit, Indian Statistical Institute, who discovered most of the material, including the skull.

Diagnosis. Chigutisaurid with relatively triangular skull and fine, reticulate ornamentation; pair of projections on the squamosals and quadratejugsals together with tabular horns; postparietal

TEXT-FIG. 16. *Kuttycephalus triangularis* gen. et sp. nov., holotype skull, ISI A 50, in dorsal view. Scale bar represents 50 mm.



projections are absent; dentigerous area of the upper jaw and palate extends to the posterior half of the skull; cultriform process of the parasphenoid broad; anterior tip of the subtemporal vacuity not reaching level of centre of interpterygoid vacuities; numerous small marginal teeth present.

Kuttycephalus triangularis sp. nov.

Text-figures 15–18

Derivation of name. The specific name highlights the triangular shape of the skull.

Holotype. ISI A 50. A complete skull with left lower jaw in the collection of the Geological Museum of the Indian Statistical Institute, Calcutta, India.

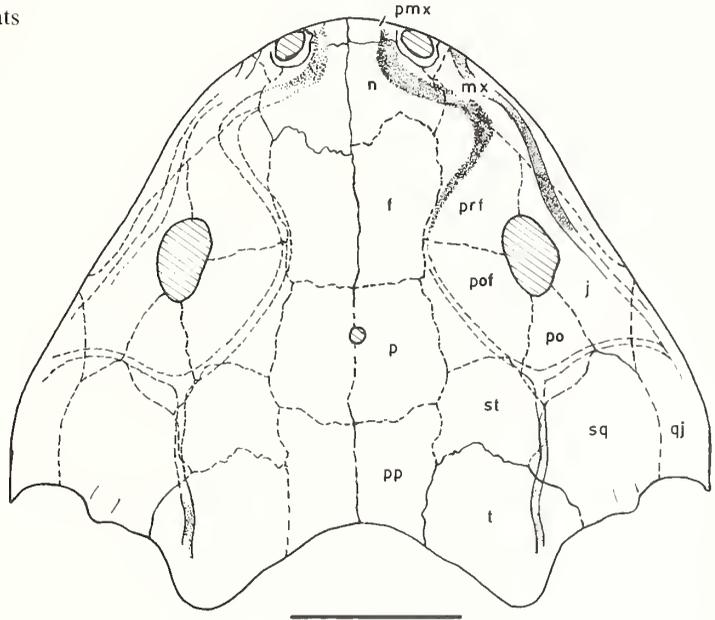
Referred specimens. ISI A 51, 52.

Diagnosis. As for genus.

Horizon and Age. A surface find from a clay bed in the upper part of the Maleri Formation, assigned to the Early Norian.

Description of the skull (Text-figs 15–18). The nearly complete skull is distorted and had calcareous encrustation on the bone surface. The left mandible is attached to the skull (Text-figs 17–18). Part of the left side of the skull, along with the mandible, is strongly infolded and rides over the palate. The left side of the skull is more complete.

TEXT-FIG. 17. *Kuttycephalus triangularis* gen. et sp. nov. Reconstruction of skull in dorsal view. Scale bar represents 50 mm.



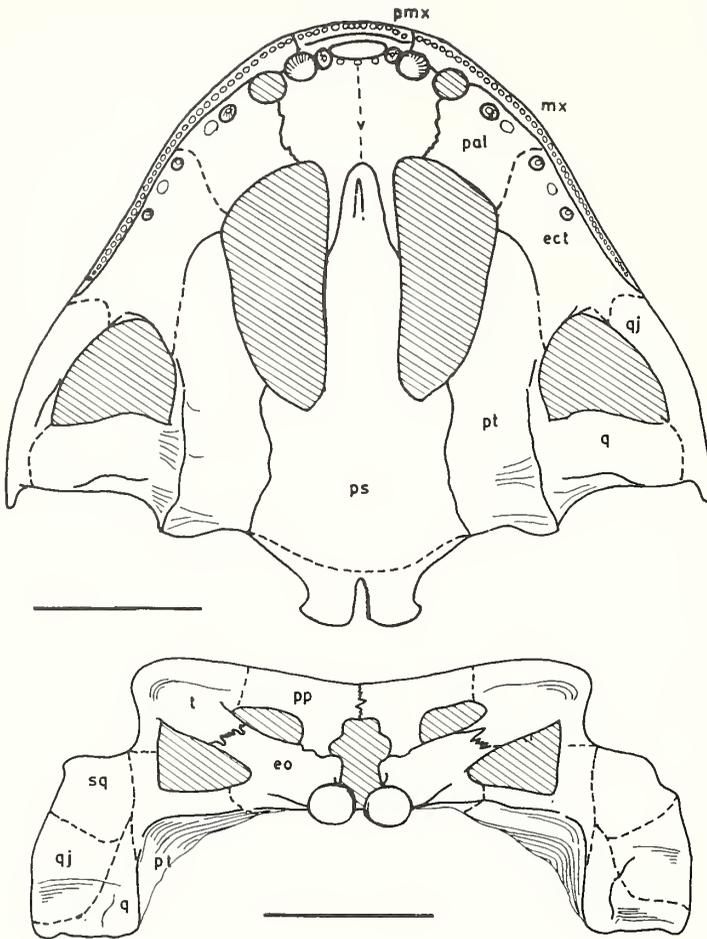
It appears that the skull was distorted by forces acting in more than one direction. The skull roof appears to be shorter and narrower than in other chigutisaurids and, in this, it bears resemblance to a rhytidosteid skull. The skull is 145 mm long and nearly 220 mm wide. The reconstructions of the skull roof, palate and occiput are shown in Text-figures 17–18. The skull shows the usual chigutisaurid bone arrangement. The tabular has a stout large unsupported horn typical of the chigutisaurids. The ornament of *K. triangularis* is composed of fine ridges and wide grooves branching out rapidly in a reticulate pattern. The ridges are markedly thin (less than 0.5 mm in places). The tabular horns and the quadratojugal and squamosal projections look similar to those observed in *C. cosgriffi*. The parietal foramen is more anterior than in other chigutisaurids except *C. cosgriffi*. The border of the naris stands out as a conspicuous rim, as in *C. cosgriffi*. The lacrimal appears to be absent. The postparietal projections are absent. The pterygoid is vaulted as in other chigutisaurids. The vaulting begins more posteriorly than in *C. cosgriffi*.

The cultriform process of the parasphenoid is wider than other chigutisaurids. In ISI A 50 the process is partly folded, the original width having been greater. The anterior tip of the process extends anterior to the interpterygoid vacuities, and becomes spatulate at the anterior end which is enclosed by the vomers. Unlike the situation in *C. cosgriffi*, the anterior palatal vacuity is a single elliptical depression. The anterior tip of the subtemporal vacuity does not extend forward beyond the central portion of the interpterygoid vacuity.

The upper jaw is characterized by numerous, small, uniform marginal teeth which extend posterior to the centre of the interpterygoid vacuity. The palatal tusks and tusk pits are marked. Thus, unlike *C. cosgriffi*, no tooth row is present on the palatine and ectopterygoid apart from the tusks. The vomer bears a pair of tusks and tusk pits along with three other smaller teeth at the border of the posterior edge of the anterior palatal vacuity. The tusk pits are shallow, large and circular. The palatine and ectopterygoid also bear smaller tusks.

The occiput is typically chigutisaurid with deep vaulting of the palate, and the quadratojugal–squamosal flange opens up into a wide trough on two sides. The quadrate ramus of the pterygoid in the angle between

TEXT-FIG. 18. *Kuttycephalus triangularis* gen. et sp. nov. Reconstruction of skull in ventral view and occipital view. Scale bars represent 50 mm.



its horizontal and vertical portion forms a sharp pointed posterior projection as in *C. cosgriffi*. The ascending ramus of the pterygoid is not very well preserved. The otic recess is large.

DISCUSSION

The family Chigutisauridae

The family Chigutisauridae was erected by Rusconi (1951) to include several short-faced Triassic temnospondyls from Argentina. The first chigutisaurid, *Pelorocephalus mendozensis*, was described by Cabrera (1944) from the upper part of the Cacheuta Formation. It was initially placed in the Family Brachyopidae by Romer (1947, 1966). However, Welles and Estes (1969) excluded *Pelorocephalus* from the family Brachyopidae revalidating the distinctiveness of the chigutisaurids. Rusconi (1948) described another chigutisaurid, *Chigutisaurus tunuyanensis*. Subsequently he also described *C. tenax* (Rusconi 1949) and *C. cachentensis* (Rusconi 1953) as well as a number of other genera and species (see Rusconi 1950, 1951). Bonaparte (1975) recognized another species from the Ischigualasto Formation (Late Triassic) of Argentina and named it *P. ischigualastensis*. Later, Bonaparte (1978) synonymized all Argentinian chigutisaurids with *P. mendozensis*. Recently

Marsicano (1993) has undertaken a revision of the Argentinian chigutisaurids and recognized the presence of more than one taxon. However, the present discussion is based on the assumption that there are two valid genera of Argentinian chigutisaurids, *Pelorocephalus* and *Chigutisaurus*.

Warren (1981) described a chigutisaurid *Keratobrachyops australis* from the Arcadia Formation (Early Triassic) of the Rewan Group of Australia. Subsequently Warren and Hutchinson (1983) described another large chigutisaurid, *Siderops kehli*, from the Evergreen Formation (Early Jurassic) of south-west Queensland, Australia.

Chigutisaurids have been considered as active predators and agile swimmers by Cosgriff (1984). DeFauw (1989) considered chigutisaurids as semiaquatic forms. Warren and Hutchinson (1983) defined the chigutisaurids as having a parabolic skull with anteriorly placed orbits, a deeply vaulted palate, a pair of occipital condyles positioned much posterior to the quadrate condyles, a complete inner row of palatal teeth, an ascending column of the pterygoid and a pair of tabular horns. The lacrimal is absent.

Relationships within the Chigutisauridae

The following discussion is intended to bring out some salient features of the two new chigutisaurid genera and species erected in the present work. The characters chosen for detailed analysis are those which have been thought to distinguish chigutisaurid genera. Some of them are argued to be derived and shared by different chigutisaurids, while a few characters, treated as significant by Coldiron (1978) and Warren and Hutchinson (1983), are also discussed. Several projections of the skull roof seem to be of particular systematic value and are discussed first.

Tabular horn. Chigutisaurids are distinguished from brachyopids by the presence of a tabular horn and a deep otic notch. Brachyopids, plagiosaurids and some members of the Rhytidosteidae lack tabular horns, and usually possess a small horn with a shallow otic notch. Warren and Black (1985) noticed that, in the 'Capitosaurians', the otic notch is usually deeply incised almost always with a tabular horn. In this group, the tabular horns are always supported from below but in the chigutisaurids they are not similarly supported. The tabular horn is present in almost all chigutisaurids. It is partly preserved in *Keratobrachyops* (Warren 1981) but not preserved in *Siderops* (Warren and Hutchinson 1983). The tabular horn and the posterior part of the skull, consisting of the tabular and the postparietal, are similar in the Argentinian and Indian genera in many respects. Their postparietal and tabular form a flat bony plate which projects out from the squamosal. The deep otic embayment is responsible for this. The lateral side of the tabular horn is long and straight running parallel to the midline. The tip of the tabular horn is always pointed in the Argentinian and Indian genera. The posterior margin of the plate, formed by tabular and postparietal, is concave anteriorly. *Keratobrachyops* also has the latter character. The angle of the horn with the skull margin, the nature of the posterior boundary of tabular and postparietal and also the shape of the otic embayment of *Siderops* were probably like other chigutisaurids, rather as reconstructed by Warren and Hutchinson (1983).

Postparietal projection. As already mentioned, *Compsoceroops* is characterized by a postparietal projection. This is a narrow, symmetrical, elongate ridge with pointed ends, concave towards the midline and extending a little beyond the posterior margin of the skull roof. The functional significance of this projection is not clear. Somewhat irregular dermal projections are also present in the zatrachydids. They also have a raised ridge at the posterior mid-skull (Langston 1953). *Acanthostomatops vorax*, considered to be the most primitive zatrachyd, has no postparietal projections. Other members of the family Zatrachydidae have them, and hence the origin of those projections is thought to be within this family (Boy 1989). *Keratobrachyops* and the Argentinian forms do not have this projection (though Bonaparte's 1975 reconstruction of *Pelorocephalus ischigualastensis* depicts a depressed area in the posterior part of the skull at the midline flanged by two raised portions of the postparietal bones). Shishkin (1987) also mentioned that all chigutisaurids have postparietal projections. However, the postparietal horn is absent in *Kuttycephalus*. Outside

the Chigutisauridae, postparietal lappets are known in *Cochleosaurus* (Steen 1938; Rieppel 1980) and have also been reported by Warren (pers. comm.) in *Parotosuchus rewanensis* (a capitosaurid) and in two rhytidosteids (*Arcadia myriadens*; Warren and Black 1985; and in an undescribed juvenile). Rieppel (1980) differentiated *Cochleosaurus florensis* from *C. bohemicus* by the size of the postparietal lappets. In the present work the postparietal projection is noted as a derived character in *Compsocerops cosgriffi* (as the size, shape and position of the horn is different from that present in the zatrachydiids, *Cochleosaurus* or in other Australian temnospondyls) and is used here as an autapomorphy (*sensu* Eldredge and Cracraft 1980) for the genus. Steen (1938, fig. 32) noticed that the postparietal lappets of *Cochleosaurus* show allometric growth during ontogeny. *Compsocerops*, however, does not display this. In the present work no taxonomic significance, above generic level, has been assigned to the postparietal projections.

Squamosal projection. A squamosal projection is present in *Compsocerops*, *Kuttycephalus*, *Pelorocephalus* and *Chigutisaurus*. The former two genera have spatulate, blunt projections at the posterior border of the squamosal. In *Compsocerops*, the projection is more conspicuous than in *Kuttycephalus* and is present in all individuals where the squamosal is preserved. The squamosal projection in *Compsocerops* does not show any definite pattern of growth.

The squamosal projection has not been observed in any other Triassic temnospondyls. It is not present in zatrachydiids. This is basically a chigutisaurid character though not present in *Keratobrachyops*. It is not preserved in *Siderops*.

Quadratojugal projection. A quadratojugal projection is present in the Indian and Argentinian genera. In *Siderops* this region is not preserved. *Keratobrachyops* does not have any quadratojugal projection. The quadratojugal projection is most conspicuous in *Chigutisaurus* and *Compsocerops*. At the posteriormost tip of the quadratojugal, a squarish lappet, with coarse ridges, projects out posteriorly in the latter genus from the squamosal-quadratojugal trough. This projection is also visible in *Kuttycephalus*.

Dentition. The basic dentition is similar in all chigutisaurid genera. A row of small marginal teeth and another row of palatal teeth are present in all genera. A similar sized double row of teeth aligned in parallel is present in the maxilla-ectopterygoid of *Compsocerops* and *Siderops*. In *Pelorocephalus*, *Keratobrachyops*, *Kuttycephalus* and in the various species of *Chigutisaurus*, the double row is present but they are not parallel. Nor are the maxillary and ectopterygoid teeth embedded in narrow ridges as they are in *Compsocerops* and *Siderops*. This character is used here as an apomorphy linking these two genera. In *Siderops* and *Compsocerops* the dentition of the palate and the upper jaw is restricted to the anterior half of the skull. In *Pelorocephalus*, the dentigerous area of the upper jaw and palate is positioned further anteriorly. In the lower jaw, the teeth are usually larger and curved lingually.

Mandible. The features of the mandible of *Compsocerops*, as discussed earlier, confirm Jupp and Warren's (1986) character assignments for previously known chigutisaurid mandibles. In all chigutisaurids, the adductor fossa is large and deep while the articular fossa is shallow, feebly bilobed and lingually widening. The postglenoid ridge is not very high in any chigutisaurid. The postglenoid area is relatively longer in all chigutisaurids though the ratio of the total mandibular length and the length of the postglenoid area may vary from genus to genus. This ratio is highest in *Chigutisaurus tunuyanensis* (2.8) and lowest in *Siderops kehli* (1.5). In *Compsocerops cosgriffi* the ratio is 1.8 and in *Keratobrachyops australis* it is 1.76. A distinct coronoid process is present in the lower jaw of *Compsocerops* as well as in *Siderops* and *Keratobrachyops*. Following Warren and Hutchinson (1983), this is thought to be a derived character.

Cultriform process of the parasphenoid. The width of the cultriform process of the parasphenoid was taken as an important apomorphy by Coldiron (1978) for some temnospondyls. This process is

generally believed to be narrower in the chigutisaurids. Among the Indian forms, *Kuttycephalus* has a wide cultriform process similar to that of *Keratobrachyops*. Warren and Hutchinson (1983) noted that only *Keratobrachyops* has the anterior border of the interpterygoid vacuities placed posterior to the anteriormost tip of the cultriform processes among all the chigutisaurids. *Kuttycephalus* has this character and it also shows the inverted 'V'-like grooves running parallel to the vomer-parasphenoid suture as in *Keratobrachyops*. The comparatively narrow cultriform processes of *Siderops*, *Compsoceros* and *Pelorocephalus* are similar on the other hand. The position of the suture between vomer and parasphenoid, as present in *Keratobrachyops* and *Kuttycephalus*, is considered in the present work to be a derived character. The wide cultriform process of *Kuttycephalus* and *Keratobrachyops* is also used in the phylogenetic reconstruction.

Palatal vacuities. Two major palatal vacuities, the subtemporal vacuity and the interpterygoid vacuity, vary both in shape and size among the chigutisaurid genera. The subtemporal vacuity in *Keratobrachyops*, *Chigutisaurus* and *Kuttycephalus* is less than half of the length of the interpterygoid vacuity. *Compsoceros*, *Siderops* and *Pelorocephalus* have subtemporal vacuities with anterior tips extending beyond the centre of the interpterygoid vacuity. This is considered here to be a derived character.

Postcranial elements. Postcranial elements are known only in *Siderops*, *Compsoceros* and *Chigutisaurus*. The clavicle-interclavicle complex and the humerus of the first two are very similar. *Compsoceros* has fused inter- and pleurocentrum to give the vertebrae a pseudostereospondyl appearance. This is unique within the family. The long dorsal process of the clavicle is a derived character, shared by *Compsoceros* and *Siderops*.

There are some other characters which have either been thought by earlier authors as important for construction of relationships or show some variations. These characters are discussed below. The polarities of some of these characters are uncertain.

Parietal-postparietal ratio. Triassic temnospondyls commonly have the postparietal shorter than the parietal. Metoposaurids, brachyopids, rhytidosteids, capitosaurids and plagiosaurids all have shorter postparietals. Warren and Hutchinson (1983) claimed that this condition prevailed in *Keratobrachyops* and *Siderops* but not in *Pelorocephalus*. *Compsoceros* and *Kuttycephalus* also have shorter postparietals. There is no clear indication in Warren and Hutchinson's work whether the postparietal of *Pelorocephalus* is equal to its parietal or longer. All available drawings and photographs of *Chigutisaurus* and *Pelorocephalus* show that the parietal is roughly equal in length to the postparietal. Warren and Hutchinson's cladogram, however, depends heavily on the parietal-postparietal ratio for splitting the Australian and Argentinian genera.

Anterior palatal vacuity. The shape and size of the anterior palatal vacuity vary widely among chigutisaurids. Coldiron (1978) used the bilobed anterior palatal vacuity as an apomorphy. He considered the single lobed anterior palatal vacuity of the brachyopids as a primitive condition or a secondary development for that group. Chigutisaurids also have an unpaired anterior palatal vacuity. The type of *Pelorocephalus* (Cabrera 1944) shows a feebly bipartite anterior palatal vacuity (see Bonaparte 1978). The presence of two deeper depressions at two ends gives rise to this type of structure which is visible also in *Kuttycephalus*. The anterior palatal vacuity of *Compsoceros* is a complicated structure with ridges and grooves running parallel to both anterior and posterior borders of the vacuity. The shape of the vacuity in *Compsoceros* is also lenticular.

Ornamentation. The ornament of *Compsoceros* and *Siderops* is strikingly similar. Both have circular pits present at the centre of ossification and elongate ridges radiating away from the centre. There are grooves between two ridges which widen towards the margin of the bones. The ridges anastomose locally. The ridges do not have symmetrical cross sections. *Kuttycephalus*, in contrast, has finer straight ridges with close reticulations. This type of ornamentation resembles that in

TABLE 2. Derived characters used to construct the relationships of the chigutisaurid genera (Text-fig. 19); characters 1 to 11 after Warren and Hutchinson (1983).

-
- (1) Short, broad, parabolic skull
 - (2) Zones of intensive growth in cheek region only
 - (3) Lacrimal absent
 - (4) Basicranial joint firmly sutured
 - (5) Pterygoid with a deep vertical ventrally-directed plate forming an inverted 'U'-shaped palate; quadrate condyles well below the level of the occipital condyles
 - (6) Squamosal-quadratojugal trough lateral to occiput
 - (7) Retroarticular process long
 - (8) Posterior meckelian foramen and angular-prearticular suture on the ventral surface or very low on lingual surface of lower jaw
 - (9) Articular exposed on dorsal surface of the retroarticular process
 - (10) Quadrate condyles anterior to the occipital condyles
 - (11) Ascending column of pterygoid present
 - (12) Complete row of small marginal palatal teeth present
 - (13) Suture between the cultriform process of the parasphenoid and the vomer situated anterior to the anterior borders of the interpterygoid vacuities
 - (14) Paraquadrate foramen on the quadrate-quadratojugal suture
 - (15) The ratio of maximum palatal width to that of the cultriform process of the parasphenoid very low (10:50)
 - (16) Presence of tabular horns and squamosal and quadratojugal projections in the posterior part of the skull
 - (17) Cultriform process of the parasphenoid long, narrow
 - (18) The anterior tip of the subtemporal vacuity positioned anterior to the centre of interpterygoid vacuity
 - (19) A similar-sized double row of teeth embedded on narrow ridges particularly in the ectopterygoid-maxilla
 - (20) Lower jaw with coronoid process
 - (21) Exceptionally long dorsal process of the clavicle
 - (22) Presence of a pair of projections on the postparietals
 - (23) Posteriorly placed pineal foramen
-

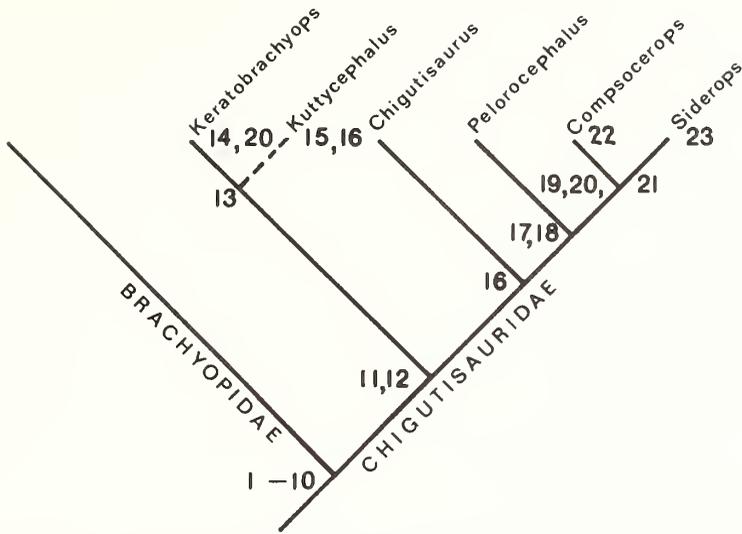
Keratobrachyops (Warren 1981). The ornamentation of *Chigutisaurus* appears to be similar to the *Kuttycephalus-Keratobrachyops* type. The ornament of the Argentinian chigutisaurids, however, has not been described adequately.

Vomerine pit and shagreen. Only *Siderops* has a vomerine pit. *Chigutisaurus tenax* also has a vomerine shagreen (Rusconi 1951).

Quadrate condyles. Quadrate condyles placed anterior to and well below the level of the occipital condyles vary within the family. *Chigutisaurus* and *Pelorocephalus* illustrate this variation among the Argentinian forms. The latter and *Compsocerops* have long cylindrical quadrate condyles. In *Siderops* and, to some extent, in *Chigutisaurus*, the condyles appears to have a screw-like appearance (see Howie 1970 for details of this character in capitosaurids). In *Kuttycephalus* the quadrate condyles are not well preserved.

Orbits. The orbit of *Chigutisaurus* is placed slightly dorsally relative to other genera. In *Compsocerops* the orbit always remains anterior and lateral. *Keratobrachyops*, has comparatively larger orbits.

Occiput. In the occiput, the height of the skull and the angle of the vaulting of the pterygoid vary from genus to genus. These parameters seem to be highly susceptible to deformation because the combination of the heavy squamosal-quadratojugal flanges with the thinner skull table and basal



TEXT-FIG. 19. Cladogram depicting relationships of chigutisaurids. Characters used are listed in Table 2.

plate of the parasphenoid in between, created a situation in which pressure from above or from the sides may have changed the height of the skull. Minor variations in these characters are not suitable for phylogenetic consideration.

The vacuities of the occiput also show some variation. The descending plate of the tabular (posterior to the slender process which comes to the exoccipital) descends down on the dorsal surface of the pterygoid, just at the line of its vaulting in *Compsocerops*. This plate is wide and thin in *Compsocerops*, *Kuttycephalus*, *Pelorocephalus* and *Chigutisaurus*. The paraquadrate foramen is housed in the quadratojugal, near its suture with the squamosal, in all the chigutisaurids except *Keratobrachyops*, where the foramen is on the quadrate-quadratojugal suture.

From the above discussion, several apomorphies have been noted for different chigutisaurid genera (Table 2). Some are thought to be typical brachyopid characters (Watson 1956; Cosgriff 1969, 1974; Chernin 1977), shared by chigutisaurids (Warren and Hutchinson 1983). Others are exclusively chigutisaurid characters. A cladogram (Text-fig. 19) has been constructed to depict the relationships of the chigutisaurid genera.

It is important to note here that some authors prefer to include *Siderops* in the family Brachyopidae (Carroll 1987; Morales 1990; Shishkin 1990). The tabular horn is not preserved in *Siderops* which seems to be the root of the confusion. Shishkin (1990), however, mentioned the absence of other chigutisaurid characters in *Siderops*, such as the axial trough of the skull. Axial troughs are present in the Indian taxa but not yet noted in the Argentinian ones. Similarly, a keel at the ventral surface of the cultriform process of the parasphenoid has been noted by Marsicano (1990) in the type specimen of *Pelorocephalus*. This feature is not present in any other chigutisaurid genera. *Siderops* has all the chigutisaurid characters identified in the present work. Moreover, *Siderops* has a substantial similarity to *Compsocerops*, and the presence of the tabular, squamosal and quadratojugal projections is predicted in *Siderops*. Similarly, the presence of a firmly sutured basicranial joint and the ascending column of pterygoid cannot be verified in the Indian genera. The relevant areas are not well preserved.

In several characters, such as orbit size and position of the paraquadrate foramen, *Keratobrachyops* seems to be distinct from other chigutisaurids. In the shape of the skull and in several palatal characteristics, it resembles *Kuttycephalus* and *Chigutisaurus*. All three have a wide

TABLE 3. The Gondwana succession of the Northern Pranhita–Godavari valley (after Kutty and Sengupta 1989).

Formation	Main lithologies	Important fossils	Age
Deccan traps			Late Cretaceous and Early Tertiary
Chikiala	Highly ferruginous sandstones and conglomerates	?	? = Gangapur Formation
Gangapur	Coarse gritty sandstones; grey white to pinkish mudstones with interbedded ferruginous sandstones and concretions	<i>Gleichenia</i> <i>Pagiophyllum</i> <i>Ptilophyllum</i> <i>Elatocladus</i>	Early Cretaceous
Kota	Sandstones, siltstones and clays with limestone bands	Holostean fish Sauropods Pterosaurs early mammals	Early Jurassic
Dharmaram	Coarse sandstones and red clays	Prosauropods (small and large) Sphenosuchid	Late Late Triassic
Maleri	Red clays, fine to medium sandstones and peloidal calcirudites/calcarenites	Chigutisaurids Metoposaurid Rhynchosaurs Phytosaurs Aetosaurs	Early Late Triassic
Bhimaram	Medium to coarse and fine sandstones, calcareous above and ferruginous below; some red clays	Labyrinthodont Dicynodont	? Late Middle Triassic
Yerrapalli	Red and violet clays; sandstones; calcirudites/calcarenites	Stahleckeriid and Kannemeyeriid dicynodonts Capitosaurid	Early Middle Triassic
Kamthi	Ferruginous nonfeldspathic or slightly feldspathic sandstones and purplish siltstones	Dicynodont from basal beds	Late Late Permian to Early Triassic
Infra-Kamthi	Sandstone, carbonaceous and red mudstones; limonitic shales	Endothiodontid Cistecephalid (from lithozone 3)	Late Permian
Barakar	Feldspathic sandstones, carbonaceous shales and coal	<i>Glossopteris</i> flora	Late Early Permian
Talchir	Tillites, greenish shales and sandstones		Early Early Permian

cultriform process of the parasphenoid (widest in *Kuttycephalus*; see character 15, Table 2), with more posteriorly positioned dentition. The parasphenoid–vomer suture in *Keratobrachyops* and *Kuttycephalus* is positioned anterior to the interpterygoid vacuities. This character is not observed in *Chigutisaurus*. The ornament of the skull roof and the proportions of the subtemporal vacuity

are also similar. The early separation of *Keratobrachyops* (Early Triassic) thus seems to be significant. On the other hand, *Pelorocephalus*, *Siderops* and *Compsocerops* are more similar. The cladogram clearly depicts the two different types of chigutisaurid palate. The *Keratobrachyops*, *Kuttycephalus* and *Chigutisaurus* palate differs from the *Siderops*, *Pelorocephalus* and *Compsocerops* palate by the posteriorly extended dentigerous area. The latter type has the anterior tip of the subtemporal vacuities positioned anterior to the centre of the interpterygoid vacuities (which makes the palate more capacious) and a long, narrow cultriform process of the parasphenoid. *Keratobrachyops*, however, has a coronoid process like that of *Compsocerops* and *Siderops*, while *Kuttycephalus*, unlike *Keratobrachyops*, has posterior projections on the squamosal and quadratojugal. Representatives of the two types of chigutisaurids are found together in one horizon in India and in Argentina. These two types possibly had differences in feeding style and occupied separate niches, as the pattern of dentition and the structure of the palate are different. This may explain the co-existence of these two chigutisaurid morphs in the upper parts of the Maleri and in the Cacheuta formations where no other temnospondyl has so far been reported.

Vertebrates and the age of the Maleri Formation

The Pranhita-Godavari valley of Deccan, India provides a relatively complete succession of Late Triassic continental strata rich in fossil vertebrates (Table 3). The Maleri Formation consists essentially of elongate sandstone ridges and clay valleys. The fossils collected from successive clay valleys have greatly helped the recognition of the faunal change from the base to the top (Text-fig. 1). There are two faunal zones present in the Maleri Formation. Kutty and Sengupta (1989) argued that the age of the lower fauna is Late Carnian and the upper fauna, Early Norian.

The lower Maleri fauna includes the metoposaurid *Metoposaurus maleriensis*, the rhynchosaur *Paradapedon huxleyi*, and the phytosaur *Parasuchus hislopi*. Two species of dipnoan, *Ceratodus hunterianus* and *C. virapa*, are also common. A cynodont, *Exaeretodon statisticae*, an eosuchian, *Malerisaurus robinsonae*, and a small coelurosaur, *Walkeria maleriensis*, are restricted to the lower Maleri fauna. An aetosaur similar to *Typothorax* (Huene 1940), a prosauropod and a dicynodont are also believed to be present. In the upper Maleri fauna, the first three elements of the lower fauna are absent. A different species of *Ceratodus*, *C. nageswari* Shah and Satsangi, 1970, is present. Two chigutisaurids, *Compsocerops cosgriffi* and *Kuttycephalus triangularis*, appear in place of the metoposaurids. Among the phytosaurs, instead of *Parasuchus hislopi*, a long-snouted primitive form and an advanced *Rutiodon*-like form have been noticed. Dicynodonts and aetosaurs are still present.

A comparison of these two faunas indicates that the lower fauna has metoposaurids while the chigutisaurids are restricted to the upper fauna. In North America and Europe, metoposaurids continued up to the Norian (Roychowdhury 1965; Benton 1986; Chatterjee 1986; Long and Padian 1986; Murry 1986; Hunt and Lucas 1990). In Morocco the picture is not clear as no temnospondyls, except almasaurids and metoposaurids, are found there. On the other hand, chigutisaurids are noted in the Gondwanas and are known from the upper part of the Late Triassic Maleri Formation of the Pranhita-Godavari valley, India, the Late Triassic Cacheuta and Ischigualasto Formations of the Mendoza Province, South America (Bonaparte 1982) and the Early Triassic Arcadia Formation (Rewan Group) and Early Jurassic Evergreen Formation of Queensland, Australia. Though the metoposaurids and the chigutisaurids help to distinguish the lower and upper fauna of the Maleri Formation, their stratigraphical ranges do not help to fix the age of boundary between the two faunas. India is the only country where both metoposaurids and chigutisaurids have been found so far.

Apart from the appearance of chigutisaurids, two other events also occurred in the interval between the two Maleri faunas. The rhynchosaurs are absent from the upper fauna and their disappearance may indicate the end of the Carnian (Chatterjee 1974; Tucker and Benton 1982; Benton 1983; Hunt and Lucas 1991). The phytosaurs evolved into advanced forms, evidence of which is very conspicuous in the successive clay valleys of Maleri (T. S. Kutty, pers. comm.).

The demise of the rhynchosaurs at the end of Carnian is also noted in Wyoming, Arizona and Texas and in Argentina and Scotland. The progressive change in the phytosaurs, as noted in Maleri, has been described from several parts of the world. Kutty and Sengupta (1989) noted that the lower Maleri fauna has the primitive *Parasuchus* (= *Paleorhinus*, see Chatterjee 1978) while the upper Maleri fauna has a primitive as well as a specialized *Rutiodon*-like form, and the immediately overlying lower Dharmaram Formation has only the advanced *Nicrosaurus*. They noted that, on the basis of the phytosaurs, the lower Maleri can be correlated with the lower part of the Dockum and Chinle formations while the upper Maleri can be equated with the middle part of these formations. The *Nicrosaurus*-bearing lower Dharmaram Formation can similarly be equated with the upper parts of the Dockum and Chinle formations.

The fauna of the Petrified Forest National Park, Arizona and in the Chinle Formation has been described by Murry and Long (1989). They considered the Norian *Nicrosaurus* to be an advanced phytosaur and *Rutiodon* to be primitive. In the Placerias and Downs quarries of the St John's area, Arizona, they found *Rutiodon* and *Paleorhinus* together with *Metoposaurus*. Elsewhere, either *Metoposaurus*, or *Anaschisma*, or both, are present with *Rutiodon* and the age of the assemblage has been considered to be Late Carnian. *Nicrosaurus* and *Rutiodon*-like forms have not been found to occur together. The faunal assemblages of the Dockum Formation, characterized by *Rutiodon*, *Nicrosaurus* and *Metoposaurus perfecta*, were thought to be of a later age than the *Paleorhinus*-bearing fauna (Gregory 1972). The fauna found at Otis Chalk, Howard County, in the lower Dockum Formation (see Murry 1989) has similarities with the lower Maleri fauna. It contains both *Metoposaurus* and *Laticopus* (not found in Maleri), and also *Paleorhinus*, *Angiostorhinus*, *Rhynchosaurus* and protorosaurids like *Malerisaurus*. If the lower Maleri fauna is thought of as Late Carnian, that would corroborate its correlation with the basal part of the Chinle and Dockum formations. So far, no vertebrates have been collected from the lower Maleri inconsistent with that age. The upper Maleri, with advanced phytosaurs, could be Early Norian (Kutty and Sengupta 1989).

As noted by Chatterjee (1974), Chatterjee and Roychowdhury (1974) and Kutty and Sengupta (1989), the correlation of the Maleri faunas with those of the German Keuper is not very straightforward. The last-named authors placed the *Franchosuchus*-bearing Buntemergel in equivalence with the lower Maleri, because *Franchosuchus* and *Parasuchus* were considered by Chatterjee (1978) to be synonyms. The Stubensandstein, on the other hand, contains advanced *Mystriosuchus*, *Nicrosaurus* and *Rutiodon* (Chatterjee 1986).

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REFERENCES

- BENTON, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, Series B*, **302**, 605–720.
- 1986. The Late Triassic tetrapod extinction events. 303–320. In PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic-Jurassic boundary*. Cambridge University Press, 378 pp.
- BONAPARTE, J. F. 1975. Sobre la presencia del laberintodonte *Pelorocephalus* en la Formacion de Ischigualasto y su significado estratigrafico. *Actas I Congress Argentinoda Paleontologia y Biostratigrafica, Tucuman*, **1**, 537–544.

- 1978. El Mesozoico de America del Sur y sus tetrapodos. *Tucuman: Fundacion Miguel Lillo, Opera Lilloana*, **26**, 596 pp.
- 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology*, **2**, 362–371.
- BOY, J. A. 1989. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europäischen Rotliegend (?hochstes Oberkarbon–Perm) 2. *Acanthostomatops*. *Paläontologische Zeitschrift*, **63**, 133–151.
- BYSTROW, A. P. and EFREMOV, J. A. 1940. *Benthosuchus sushkini* Efr. a labyrinthodont from the Eotriassic at Sharzhenga river. *Travaux de l'Institut Paléontologique*, **10**, 1–152. [In Russian with extended English summary].
- CABRERA, A. 1944. Sobre un estegocephalo de la Provincia de Mendoza. *Notas del Museo de La Plata*, **9**(69), 421–429.
- CARROLL, R. L. 1987. *Vertebrate paleontology and evolution*. W. H. Freeman and Company, New York, 698 pp.
- CHATTERJEE, S. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London, Series B*, **267**, 209–261.
- 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. *Palaeontology*, **21**, 83–127.
- 1986. The Late Triassic Dockum vertebrates: their stratigraphic and paleobiogeographic significance. 139–150. In PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, 378 pp.
- and ROY-CHOWDHURY, T. 1974. Triassic Gondwana vertebrates from India. *Indian Journal of Earth Sciences*, **1**, 96–112.
- CHERNIN, S. 1977. A new brachyopid, *Batrachosuchus concordi* sp. nov., from the Upper Luangwa valley, Zambia with a recapitulation of *Batrachosuchus browni* Broom, 1903. *Palaeontologia Africana*, **20**, 87–109.
- COLDIRON, R. W. 1978. *Acroplops vorax* Hotton (Amphibia, Saurerpetontidae) restudied in the light of new material. *American Museum Novitates*, **2662**, 1–27.
- COSGRIFF, J. W. 1969. *Blinasaurus*, a brachyopid genus from Western Australia and New South Wales. *Proceedings of The Royal Society of Western Australia*, **52**, 65–88.
- 1974. Lower Triassic Temnospondyli of Tasmania. *Geological Society of America Special Papers*, **149**, 1–134.
- 1984. The temnospondyl labyrinthodonts of the earliest Triassic. *Journal of Vertebrate Paleontology*, **4**, 30–46.
- DEFAUW, S. 1989. Temnospondyl amphibians: a new perspective on the last phases in the evolution of Labyrinthodontia. *Michigan Academician*, **21**, 7–32.
- DUTUIT, J. M. 1976. Introduction à l'étude paléontologique du Trias continental marocain. Description des premiers stégocéphales recueillis dans le couloir d'Argana (Atlas Occidental). *Mémoires du Muséum National d'Histoire Naturelle, New Series C*, **36**, 1–255.
- ELDREDGE, N. and CRACRAFT, J. 1980. *Phylogenetic pattern and evolutionary process*. Columbia University Press, 349 pp.
- GREGORY, J. T. 1972. Vertebrate faunas of the Dockum Group, Triassic, Eastern New Mexico and West Texas. *New Mexico Geological Society Guidebook, 23 Field Conference*, 120–123.
- HOWIE, A. A. 1970. A new capitosaurid labyrinthodont from East Africa. *Palaeontology*, **13**, 210–253.
- HUENE, F. von, 1940. The tetrapod fauna of the Upper Triassic Maleri beds. *Palaeontologia Indica, New Series*, **32**, 1–42.
- HUNT, A. P. and LUCAS, S. G. 1990. The status of 'Jurassic' metoposaurs in the American South West. *Stegocephalian Newsletter*, **1**, 16.
- 1991. A new rhynchosaur from the upper Triassic of West Texas and the biochronology of Late Triassic rhynchosaurs. *Palaeontology*, **34**, 927–938.
- JUPP, R. and WARREN, A. A. 1986. The mandible of the Triassic temnospondyl amphibians. *Acheringa*, **10**, 99–124.
- KUTTY, T. S. and SENGUPTA, D. P. 1989. Late Triassic formations of the Pranhita–Godavari valley and their vertebrate faunal sequence – a reappraisal. *Indian Journal of Earth Science*, **16**, 189–206.
- LANGSTON, W. 1953. Permian amphibians from New Mexico. *University of California Publications in Geological Sciences*, **29**, 344–416.
- LONG, R. A. and PADIAN, K. 1986. Vertebrate biostratigraphy of the Late Triassic Chinle Formation, Petrified Forest National Park, Arizona: preliminary result. 161–169. In PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, 378 pp.

- MARSICANO, C. M. A. 1990. Redescription del craneo del holotipo de *Pelorocephalus mendozensis* Cabrera 1944 (Amphibia, Temnospondyli) de Triasico del Cerro Bayo, Provincia de Mendoza. *Ameghiniana*, **27**, 39–44.
- 1993. Evolutionary relationships in the Triassic Gondwana family Chigutisauridae (Amphibia, Temnospondyli). *Journal of Vertebrate Paleontology*, **13** (3 Supplement), 48A.
- MORALES, M. 1988. A brief review of post Triassic labyrinthodonts. *Journal of Vertebrate Paleontology*, **10** (3 Supplement), 36 A.
- MURRY, P. A. 1986. Vertebrate paleontology of the Dockum Group, Western Texas and Eastern New Mexico. 109–137. In PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, 378 pp.
- 1989. Geology and paleontology of the Dockum Formation (Upper Triassic), West Texas and Eastern New Mexico. 102–145. In LUCAS, S. G. and HUNT, P. H. (eds). *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, 414 pp.
- and LONG, A. R. 1989. Geology and paleontology of the Chinle Formation, Petrified Forest National Park and vicinity, Arizona and a discussion of vertebrate fossils of the Southwestern Upper Triassic. 29–65. In LUCAS, S. G. and HUNT, P. H. (eds). *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, 414 pp.
- RIEPPPEL, O. 1980. The edopoid amphibian *Cochleosaurus* from the Middle Pennsylvanian of Nova Scotia. *Palaentology*, **23**, 143–149.
- ROMER, A. S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard*, **99**, 1–352.
- 1966. *Vertebrate paleontology*. 3rd ed. Chicago University Press, Chicago and London, 468 pp.
- ROYCHOWDHURY, T. 1965. A new metoposaurid amphibian from the Upper Triassic Maleri Formation of Central India. *Philosophical Transaction of the Royal Society of London, Series B*, **250**, 1–52.
- RUSCONI, C. 1948. Nuevos laberintodontes del Triasico de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **2**, 225–229.
- 1949. I. Presencia de ictiosaurios en el liasico de San Juan. II. Otra especie de la laberintodonte triasico de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **3**, 89–94.
- 1950. Presencia de laberintodontes en varias regiones de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **4**, 3–8.
- 1951. Laberintodontes Triasicos y Permicos de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **5**, 33–158.
- 1953. Nuevo laberintodonte de Mendoza Nova Presia. *Boletin Paleontológico de Buenos Aires*, **26**, 1.
- SÄVE-SÖDERBERGH, G. 1935. On the dermal bones of the head in labyrinthodont Stegocephalians and primitive reptilia with special reference to Eotriassic Stegocephalians from East Greenland. *Meddelser om Gronland*, **98**, 1–211.
- SHAH, S. C. and SATSANGI, P. P. 1970. A *Ceratodus nageswari* sp. nov. from Kota–Maleri beds of Andhrapradesh. *Records of the Geological Survey of India*, **98**, 751–752.
- SHISHKIN, M. A. 1987. *Evolution of the fossil amphibians Plagiosauroida*. Nauka, Moscow, 142 pp. [In Russian].
- 1990. A labyrinthodont from the Jurassic of Mongolia. *Paleontologicheskii Zhurnal*, **1**, 78–91. [In Russian].
- STEEN, M. C. 1938. On fossil Amphibia from the Gas Coal of Nýřany and other deposits in Czechoslovakia. *Proceedings of the Zoological Society of London, Series B*, **108**, 205–283.
- TUCKER, M. E. and BENTON, M. J. 1982. Triassic environments, climates and reptile evolution. *Palaeoecology, Palaeoclimatology, Palaeoecology*, **40**, 361–379.
- WARREN, A. A. 1981. A horned member of the labyrinthodont Superfamily Brachyopoidea from the Early Triassic of Queensland. *Alcheringa*, **5**, 273–288.
- and BLACK, T. D. 1985. A new rhytidosteid (Amphibia, Labyrinthodontia) from the Early Triassic Arcadia Formation of Queensland, Australia and a consideration of the relationships of Triassic temnospondyls. *Journal of Vertebrate Paleontology*, **5**, 303–327.
- and HUTCHINSON, M. N. 1983. The last labyrinthodont? A brachyopid (Amphibia, Temnospondyli) from the Early Jurassic Evergreen Formation of Queensland, Australia. *Philosophical Transaction of the Royal Society of London, Series B*, **303**, 1–62.
- WATSON, D. M. S. 1956. The brachyopid labyrinthodonts. *Bulletin of the British Museum (Natural History), Geology Series*, **2**, 317–391.
- WELLES, S. P. and ESTES, R. 1969. *Hadrokkosaurus bradyi* from the Upper Moenkopi Formation of Arizona. *University of California Publications in Geological Sciences*, **84**, 1–56.

ZITTEL, K. von, 1888. *Handbuch der Paläontologie Abteilung 1. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. R. Oldenbourg, Munich and Leipzig, 900 pp.

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ABBREVIATIONS USED IN THE FIGURES

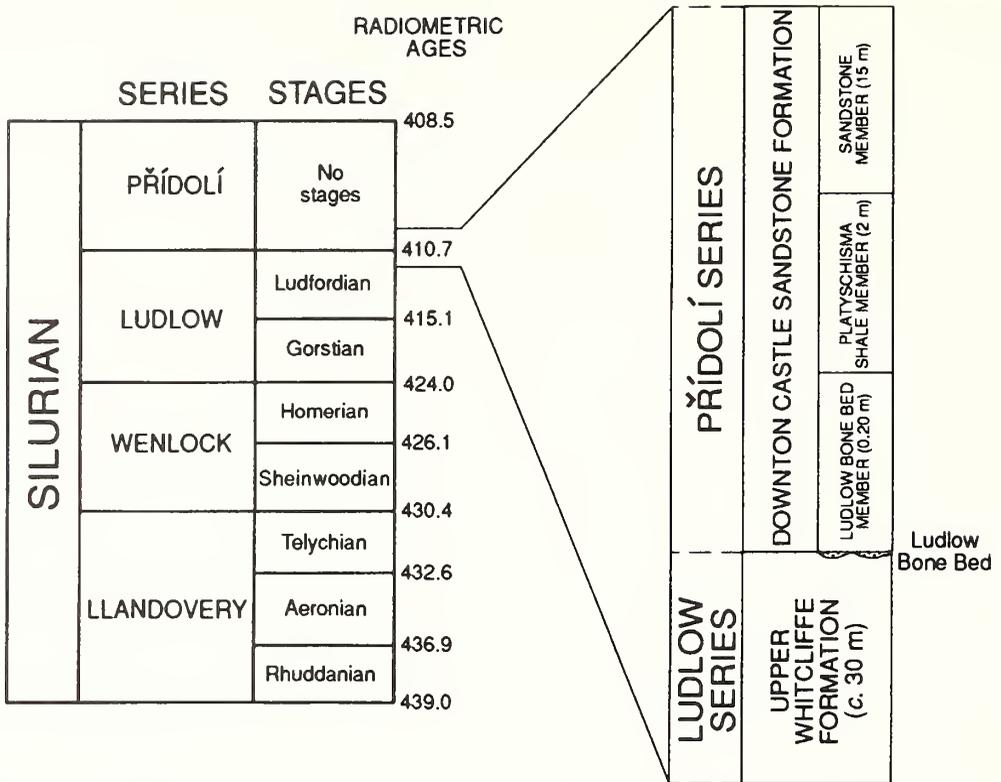
a	angular	p	parietal
ac	acetabulum	pal	palatine
acr	ascending ramus of the pterygoid	par	prearticular
adf	adductor fossa	pc	pleurocentrum
amf	anterior meckelian foramen	pcr	precoronoid
ar	articular	pmf	posterior meckelian foramen
artf	articular fossa	pmx	premaxilla
acc. eo	ascending process of the exoccipital	po	postorbital
cr	coronoid	pof	postfrontal
crp	coronoid process	pp	postparietal
cps	canal on the dorsal side of the cultriform process of the parasphenoid	prf	prefrontal
d	dentary	ps	parasphenoid
dsc, sq	descending process of the squamosal	psl	postsplenial
ect	ectopterygoid	pt	pterygoid
eo	exoccipital	ptr	posterior projection of the pterygoid
ept	epipterygoid	q	quadrate
f	frontal	qj	quadratojugal
fcht	chorda tympanic foramen	sa	surangular
ic	intercentrum	sd	semicircular depression on the dorsal surface of the base of the parasphenoid
icr	intercoronoid	sp	splenial
j	jugal	sq	squamosal
ld	lateral depression	st	supratemporal
mx	maxilla	t	tabular
n	nasal	v	vomer

OSTRACODE AND CONODONT DISTRIBUTION ACROSS THE LUDLOW/PŘÍDOLÍ BOUNDARY OF WALES AND THE WELSH BORDERLAND

by C. G. MILLER

ABSTRACT. The ostracodes and conodonts of the Silurian Ludlow/Přídolí Series boundary are documented in detail at Ludlow, and described from across Wales and the Welsh Borderland. The Upper Whitcliffe Formation and its lateral equivalents are characterized by the ostracode *Calcaribeyrichia torosa* and the conodonts *Ozarkodina confluens*, *O. excavata*, *Panderodus serratus* and *Coryssognathus dubius*. The Downton Castle Sandstone Formation and its lateral equivalents are characterized by the ostracodes *Frostiella groenvalliana*, *Londinia arisaigensis*, *L. fissurata* and *Nodibeyrichia verrucosa*. Conodont faunal trends across the Welsh Borderland reflect an increasingly turbulent environment towards the top of the Ludlow Series. The sudden ostracode faunal change at the base of the Downton Castle Sandstone at Ludlow (shelf) contrasts with a gradual change at Long Mountain (basin) and parallels shelf–basin palynofacies. Ostracode faunal variations in the Downton Castle Sandstone Formation at Ludlow coincide with minor lithofacies variations. Local variations in ostracode and land plant spore frequency may be related to proximal channels that delivered sediment off an irregularly prograding shoreline. Ostracodes correlate the base of the Downton Castle Sandstone across the Welsh Borderland to localities in east central Wales where bone beds are absent. Combined conodont and ostracode evidence suggests that the base of the Přídolí Series is at the base of the Downton Castle Sandstone Formation in Britain.

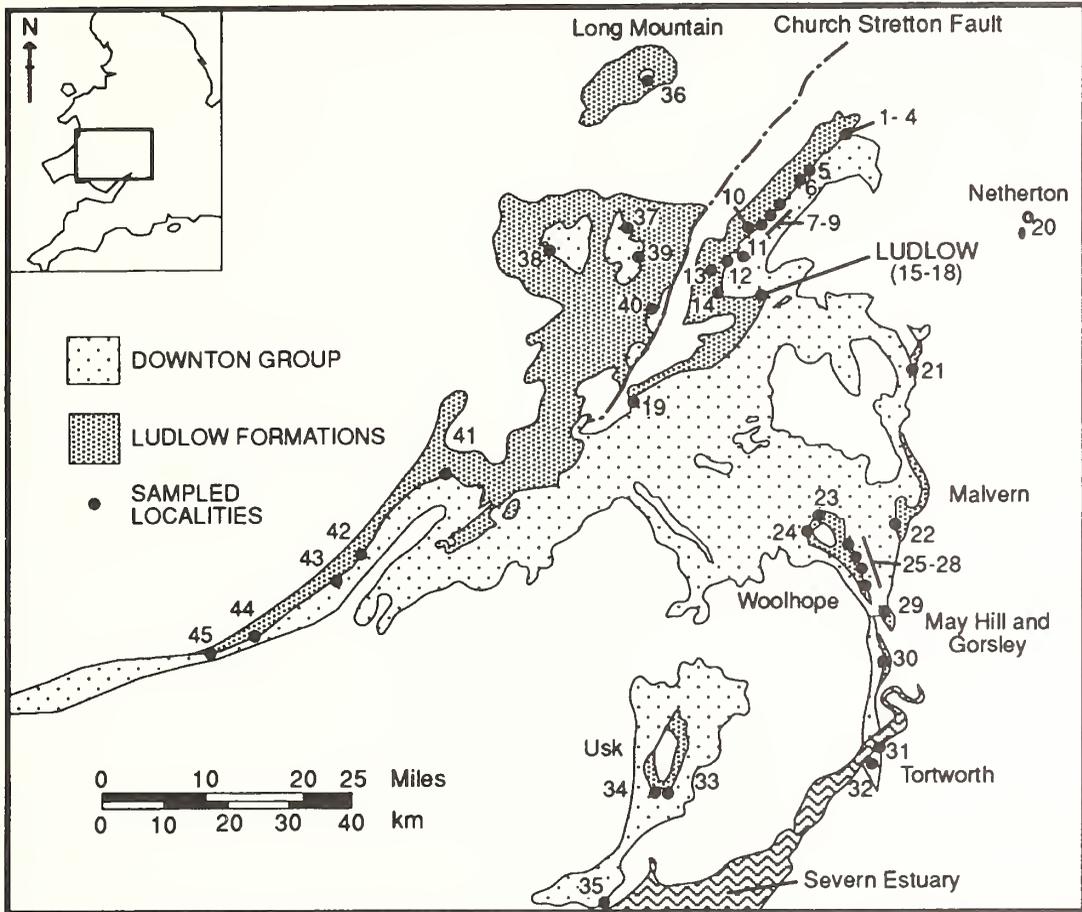
‘So brilliantly black are many of the organic fragments, that when discovered, this bed conveyed the impression that it enclosed a triturated heap of black beetles cemented in a rusty ferruginous paste’ (Murchison 1839, p. 198). This is the first description of the bed which was first mentioned by Murchison (1834), later described in detail (Murchison 1852) and named the Ludlow Bone Bed (Murchison 1854). Murchison (1839, p. 198) also noted that, ‘this bone bed is not merely local, since fragments having the same structure, but of greater thickness than any of Ludford, have been found near Richard’s Castle; and there is every reason to believe that it extends through various parts of the Ludlow promontory.’ The Ludlow Bone Bed, which consists essentially of acanthodian remains and thelodont dermal denticles, is the lowest of several bone beds in the Ludlow Bone Bed Member at Ludford Corner, Ludlow (Holland *et al.* 1963; Antia 1979a, 1980). For the purpose of the present study, other bone beds, either higher in the section at Ludlow or at any other locality in the Welsh Borderland, will be referred to simply as a bone bed, thus implying no correlative significance with the Ludlow Bone Bed itself. Murchison never stated that the Ludlow Bone Bed defined the upper limit of the Silurian System. French workers (Dorlodot 1912; Barrois *et al.* 1918, 1922) mis-translated Murchison (1842, p. 648) and considered the Ludlow Bone Bed as the Siluro-Devonian boundary (White 1950). The Ludlow Bone Bed was then accepted (Stamp 1920, 1923; and subsequent workers) as the base of the Devonian System. The suggestion that the Siluro-Devonian boundary be raised to be coincident with the base of the *Monograptus uniformis* Zone (Holland 1965), led to abandonment of the Welsh Borderland as a standard for the Siluro-Devonian boundary (McLaren 1977). The Siluro-Devonian boundary is now defined at a level coincident with the base of the *M. uniformis* Biozone, within Bed 20 at Klonk in the Czech Republic (Chlupáč 1972; McLaren 1977). This is stratigraphically higher than the Ludlow Bone Bed. To accommodate the strata between these two stratigraphical markers a fourth and youngest series of the Silurian had



TEXT-FIG. 1. Chronostratigraphy of the Silurian (radiometric dates after Harland *et al.* 1990) and lithostratigraphy of the Upper Whitcliffe and Downton Castle Sandstone formations (after Bassett *et al.* 1982) at the type locality for the Ludlow Bone Bed Member at Ludford Corner, Ludlow, Shropshire (loc. 18).

to be established (Text-fig. 1). The base of the Downton Group at Ludlow (the base of the Ludlow Bone Bed) was a prime contender for the basal stratotype for this series (Bassett *et al.* 1982), as was the base of the Skala Series in Podolia, and the Přídolí Series of the Barrandian area (Prague Basin). There was little support for the Skala section as 'at this level cyclic dolomites dominate the sequence and correlation with the base of the corresponding Downton and Přídolí sequences could be achieved only with the use of limited ostracodal evidence' (Holland 1989, p. 18). Even though the base of the Downton Group could be correlated with graptolitic facies via a complex chain of correlation (Bassett *et al.* 1982), the marine Přídolí succession was eventually confirmed as the fourth series of the Silurian (Bassett 1985). The basal boundary stratotype was designated at Požáry near Prague with the base at a level coincident with the base of the *Monograptus parultimus* Biozone (Kříž *et al.* 1986; Kříž 1989, 1992).

In the Welsh Basin the lithostratigraphical boundary between the Upper Whitcliffe Formation and the Downton Castle Sandstone Formation, corresponds to the base of the Ludlow Bone Bed at Ludford Corner, Ludlow, Shropshire (Text-fig. 1). Ostracodes correlate the base of the Downton Castle Sandstone Formation, via Baltic marine sequences, approximately with the base of the Přídolí Series at the stratotype in the Czech Republic (Siveter 1978, 1989; Bassett *et al.* 1982; Siveter *et al.* 1989; Hansch *et al.* 1991). Conodont evidence has suggested that the base of the Přídolí may be slightly higher than the base of the Downton Castle Sandstone Formation at Ludlow (Schönlaub 1986; Aldridge and Schönlaub 1989). The aims of this paper are:



TEXT-FIG. 2. Outcrop of the Downton Group and Ludlow formations in Wales and the Welsh Borderland (after Bassett *et al.* 1982) showing localities sampled by Miller (1993).

1. To document the detailed distribution of ostracodes and conodonts across the base of the Downton Castle Sandstone Formation at Ludlow and its lateral equivalents, throughout the Welsh Basin.
2. To use conodont and ostracode faunas to test the correlation of the base of the Downton Castle Sandstone Formation across the Welsh Basin.
3. To integrate the results with published palynofacies (Richardson and Rasul 1990) and sedimentological studies at coeval sections.
4. To investigate the correlation of the base of the Přídolí Series, as defined in the Czech Republic, with the base of the Downton Castle Sandstone Formation within the Welsh Basin.

METHODS OF STUDY

Fieldwork. Slightly calcareous lithologies, bone beds and horizons with decalcified macrofauna or ostracode moulds were sampled from localities across Wales and the Welsh Borderland (Text-fig. 2) covering the lateral equivalents of the base of the Downton Castle Sandstone Formation. The local lithostratigraphical units of Cocks *et al.* (1992, figs 3–4) are followed unless stated. Some localities exposing strata immediately above or below this level were also sampled. Detailed sedimentary logs were measured at prolific localities with sampling interval dictated by the presence of calcareous horizons or ostracode moulds. For each sample the minimum

practical thickness of strata was collected (0.01–0.1 m) and, where possible, approximately 2 kg of sample. However, sample size was often dictated by unstable overhanging strata or vertical cliff exposures. Additional material has been obtained from a number of sources: British Geological Survey (BGS), Dr R. J. Aldridge (RJA), and Dr David J. Siveter (DJS). Dr Aldridge's samples are suffixed by an asterisk and the original locality numbers retained as they have been used in previous publications (Aldridge 1985; Miller and Aldridge 1993) and the numbers are to be published in a monograph on British Silurian conodonts.

Acid preparation. To recover conodonts and other phosphatic microfossils, slightly calcareous lithologies and bone beds were disaggregated in 10 per cent. acetic acid and, if the acid had little or no effect, crushed in a fly press. All residues were sieved at 75 μm and separated into heavy and light fractions using an aqueous solution of sodium polytungstate (manufactured by Sometu, Berlin) at a specific gravity of 2.80. Each heavy residue was picked completely for conodonts. The dry weight of each sample was taken initially and after treatment, to enable numbers of conodont elements per gram to be calculated.

Ostracode mould fauna preparation. Samples containing ostracode moulds were split in the laboratory, with care taken to keep part and counterpart together. An approximate calculation of ostracode abundance for each bed was obtained by dividing the total number of ostracode valves and carapaces for each bed by the total surface area viewed. Ostracodes with well preserved external moulds were prepared and cast using silicone rubber (manufactured by Ambersil Ltd., Basingstoke) by the method described by Siveter (1982).

LOCALITIES AND HORIZONS

1. Callaughton Mill: roadside exposure, 2.5 km SW of Much Wenlock, Shropshire; SO 6198 9746 (Robertson 1927, p. 86); Whitcliffe Formation, Downton Castle Sandstone Formation with bone bed at base; (BGS 18–151).
2. Willey: quarry behind stables, Willey Estate, Willey, 5 km ESE of Much Wenlock, Shropshire; SO 6731 9912 (White and Coppack 1978, text-fig. 1); Whitcliffe Formation, Downton Castle Sandstone Formation with bone bed at base and 3 m above base; (BGS and CGM).
3. Linley: 6.5 km E of Much Wenlock, Shropshire (White and Coppack 1978, text-fig. 3).
- 3a. Road from Linley Hall to Linley Brook, E of Linley Bridge; SO 6870 9817 (Robertson 1927, loc. L17); Downton Castle Sandstone; (BGS 18–84).
- 3b. Linley Brook, 90 m E of Hem Farm; SO 6920 9820 (Robertson 1927, loc. L18); Downton Castle Sandstone Formation; (CGM and BGS 18–85).
- 3c. Tributary to Linley Brook 1 km E of Linley Bridge; SO 6940 9815 (Robertson 1927, p. 87, loc. L19); Downton Castle Sandstone Formation with bone bed; (BGS 18–85).
4. Dean Brook: tributary to R. Severn 6.5 km E of Much Wenlock, Shropshire (White and Coppack 1978, text-fig. 3).
- 4a. Left bank of Dean Brook at mouth of small dry stream; SO 6955 9915 (Robertson 1927, locs L13 and 14); Downton Castle Sandstone Formation; (BGS 18–92).
- 4b. 40 m N of 4a; SO 6875 9955 (Robertson 1927, loc. L16); Downton Castle Sandstone Formation; (BGS 17–123).
5. Brockton: on B4378, 6.5 km SW of Much Wenlock, Shropshire.
- 5a. Stream section opposite Ivy Cottage, Brockton, Corve Dale, Shropshire; SO 5755 9388. Whitcliffe Formation; (BGS 54–267).
- 5b. Road cutting 150 m NE of Brockton cross roads on B4378; SO 579 939; Whitcliffe Formation, Downton Castle Sandstone Formation with bone bed at base; (BGS 19–152).
- 5c. Old quarry behind old school house, Brockton; SO 5765 9400; Whitcliffe Formation; (RJA).
6. Shipton: junction of B4368 and B4378 on Corve Dale, 9 km SW of Much Wenlock, Shropshire.
- 6a. Pathside exposure, 30 m SE of B4368; SO 5634 9186; Whitcliffe Formation; (CGM).
- 6b. Old quarry in farmyard, 150 m at 26° from NE end of St. James Church; SO 5625 9194; Whitcliffe Formation and Downton Castle Sandstone Formation with bone bed at base; (BGS 54–271).
- 6c. Laneside section, 155 m at 125° from SW end of St. James Church; SO 5629 9169; Whitcliffe Formation and Downton Castle Sandstone Formation with bone bed at base; (CGM and BGS 54–271).
7. Aston Munslow: Corve Dale, 10 km NE of Craven Arms, Shropshire.
- 7a. Swan Inn car park; SO 5124 8658; Whitcliffe Formation and Downton Castle Sandstone Formation with bone bed at base; (BGS 54–120, CGM and RJA).

- 7b. Roadside exposure, 120 m NW of 7a; SO 5113 8671; Whitcliffe Formation; (CGM and RJA).
8. Diddlebury: roadside exposure on Middlehope road, Diddlebury, Corve Dale, Shropshire; SO 503 858; Whitcliffe Formation; (CGM and RJA).
9. Corfton: roadside cutting, 55 m SE of Sun Inn, Corfton, c. 7 km ENE of Craven Arms, Corve Dale, Shropshire; SO 497 846; Downton Castle Sandstone Formation; (CGM and BGS 54–124).
10. Siefert: c. 5 km E of Craven Arms, Shropshire.
- 10a. Quarry in Siefert Batch, 1 km NW of B4368, Corve Dale, Shropshire; SO 4770 8475; Whitcliffe Formation; (CGM).
- 10b. Temporary roadside trench; SO 475 833 to 478 835 (Antia 1979b); Whitcliffe Formation and Downton Castle Sandstone Formation.
11. Culmington: old quarry S of new house near Culmington, Shropshire; SO 4745 8150; Downton Castle Sandstone Formation with bone bed at base (BGS records); (CGM and BGS 66–101).
12. Onibury: 4 km SSE of Craven Arms, Shropshire.
- 12a. Farmyard exposure, 3 km WNW of Onibury Church; SO 425 796; Upper Whitcliffe Formation; (BGS 54–198).
- 12b. Norton road section, NNE of Onibury; SO 4575 7982 (Shaw 1969); Temeside Bone Bed, Temeside Shales, Downton Group; (DJS).
- 12c. Locality not constrained, on road from Onibury to Norton; Tilestones (Downtown Group); BGS 22–140).
13. Clungunford: 5 km SW of Craven Arms, Shropshire.
- 13a. Lane in wood, 3.2 km E of Clungunford; SO 434 789; Whitcliffe Formation; (BGS 54–196).
- 13b. Old quarry, 150 m E of Brandhill Farm, 2 km E of Clungunford; SO 4236 7883; Whitcliffe Formation; (CGM and BGS 54–197).
14. Downton Estate: area around Downton Castle, c. 6 km W of Ludlow, Shropshire.
- 14a. Bank to SE of Downton Bridge, Downton Estate; SO 4449 7427 (Whitaker 1962); Upper Whitcliffe Formation, Ludlow Bone Bed Member with bone bed at base and Platyschisma Shale Member of Downton Castle Sandstone Formation; (DJS).
- 14b. Weir Quarry, NW bank of the River Teme, c. 275 m NE of Bringewood Forge Bridge, Downton Estate; SO 4560 7525 (Shaw 1969; Richardson and Rasul 1990, loc. 1); Upper Whitcliffe Formation, Ludlow Bone Bed Member with bone bed at base, Platyschisma Shale Member and Sandstone Member of Downton Castle Sandstone Formation; (CGM).
- 14c. Track section in field to S of Downton Castle Bridge; SO 4442 7402 (Whitaker 1962); Platyschisma Shale Member (including Downton Bone Bed) and Sandstone Member of Downton Castle Sandstone Formation; (collected in 1968 by Dr L. Jeppsson, University of Lund, Sweden).
15. Whitcliffe Quarry: S bank of the River Teme, Ludlow, Shropshire.
- 15a. 250 m W of Ludford Bridge; SO 5098 7414 (Siveter *et al.* 1989, loc. 3.1f); boundary between Lower Whitcliffe Formation and Upper Whitcliffe Formation at top to convoluted bedding; (CGM and RJA).
- 15b. 40 m W of 15a; SO 5096 7414; same strata exposed as at 15a; (CGM).
- 15c. 60 m W of 15a; SO 5092 7415; possible boundary between Lower and Upper Whitcliffe formations marked by similar convoluted bedding to 15a; (CGM and RJA).
- 15d. 120 m W of 15a; SO 5089 7416; Lower and Upper Whitcliffe formations; (CGM and RJA).
16. Whitcliffe: car park to Charlton Arms Hotel, near Ludford Bridge, Ludlow, Shropshire; SO 5116 7416; Upper Whitcliffe Formation, c. 10 m below Ludlow Bone Bed; (RJA).
17. Ludford Lane: N side of Whitcliffe Road (formerly Ludford Lane), Ludlow, Shropshire.
- 17a. Next to road sign 90 m W of junction with A49; SO 5116 7413 (Siveter *et al.* 1989, loc. 3.2b); Upper Whitcliffe Formation, Ludlow Bone Bed Member with multiple bone beds and Platyschisma Shale Member, Downton Castle Sandstone Formation; (CGM, DJS, RJA and BGS).
- 17b. 80 m W of junction with A49; SO 5117 7413; strata sampled as for 17a.
- 17c. 70 m W of junction with A49; SO 5118 7413; strata exposed as for 17a, b, Upper Whitcliffe Formation only sampled.
18. Ludford Corner: at junction of A49 with Ludford Lane, Ludlow, Shropshire; SO 5124 7413 (Siveter *et al.* 1989, loc. 3.2a); Upper Whitcliffe Formation§, Ludlow Bone Bed Member§ with multiple bone beds, Platyschisma Shale Member and Sandstone Member of Downton Castle Sandstone Formation; only units suffixed by § and the lowermost 0.07 m of the Platyschisma Shale Member sampled.
19. Kington: Hereford and Worcester town c. 25 km SW of Ludlow.

- 19a. Section on N side of Kington by-pass; SO 2998 5706 (Holland and Williams 1985, loc. 5); Upper Whitcliffe Formation, multiple bone beds in Ludlow Bone Bed Member, Platyschisma Shale Member, Sandstone Member of Downton Castle Sandstone Formation.
- 19b. Lane-side exposures on Newton Lane; SO 2902 5716 (Holland and Williams 1985, loc. 3); Upper Whitcliffe Formation, multiple bone beds in Ludlow Bone Bed Member and Platyschisma Shale Member of Downton Castle Sandstone Formation.
20. Netherton: old tramway, SW side of reservoir, Salt Wells Nature Reserve, Primrose Hill, Netherton, Birmingham; SO 9358 8732 (King and Lewis 1912; Ball 1951); Whitcliffe Formation, Ludlow Bone Bed Member of Downton Castle Sandstone Formation; (CGM, RJA and DJS).
21. Abberley: village c. 15 km NW of Worcester, Hereford and Worcester.
- 21a. Small quarry 50 m S of Abberley Hall; SO 745 663; Whitcliffe Flags Member, Upper Ludlow Formation; (BGS 32–28).
- 21b. Old quarry to E of road 100 m SE of Camp Farm, Great Whitley, near Abberley; SO 7405 6505; Whitcliffe Flags Member, Upper Ludlow Formation; (BGS 28–212).
- 21c. Woodbury (working) Quarry, 1500 m at 33° from church at Shelsey Beauchamp, Worcestershire; SO 743 637 (Mitchell *et al.* 1962; Phipps and Reeve 1967); Whitcliffe Flags Member, Upper Ludlow Formation; (BGS 28–215 and 59–146).
- 21d. Small quarry 100 m SW of Rodge Hill Farm, Shelsey Beauchamp, Worcestershire; SO 746 622; Whitcliffe Flags Member, Upper Ludlow Formation; (BGS 28–207).
22. Brockhill Quarry: 250 m NNE of Brockhill Farm, Colwall, near Malvern Wells, Hereford and Worcester; SO 7568 4394 (Penn and French 1971, loc. 38); Whitcliffe Flags Member, Upper Ludlow Formation, Downton Castle Sandstone Formation with bone bed at base; (CGM, RJA and BGS 28–281).
23. Perton Lane: exposures to the E of Perton Lane, Perton, 5 km NNW of Woolhope, Hereford and Worcester.
- 23a. 20 m S of 3-way road junction at Perton; SO 5971 4035 (Squirrell and Tucker 1960, text-fig. 2, loc. F); Upper Perton and Rushall beds; (CGM, DJS and RJA).
- 23b. 20 m S of 23a at base of cliff section; SO 5969 4031 (Squirrell and Tucker 1967, text-fig. 5, loc. 2); Upper Perton Beds; (CGM and RJA).
24. Prior's Frome: exposures opposite Yew Tree Inn, Prior's Frome, Woolhope c. 5 km ESE of Hereford, Hereford and Worcester; SO 5662 3901 (Gardiner 1927, text-fig. 4; Squirrell and Tucker 1982; Brandon 1989).
- 24a. Old quarry face; Upper Perton Beds; (CGM and RJA).
- 24b. To S of old overgrown path; Rushall Beds with bone bed at base; (CGM, RJA and BGS 59–235).
25. Caerswell Farm: 3.5 km SW of Woolhope, Hereford and Worcester; SO 6440 3380; Upper Perton Beds and Rushall Beds with bone bed at base; (CGM and BGS 59–147).
26. Whittock's End Farm: 550 m W of Whittock's End Farm, 3 km S of Much Marcle, Hereford and Worcester; SO 6540 2990; Rushall Beds with bone bed at base; (BGS 59–147).
27. Rushall: Roadside exposure at Rushall, 3 km ESE of Woolhope, Hereford and Worcester; SO 6410 3481 (Squirrell and Tucker 1967, loc. 18); Upper Perton Beds, Rushall Beds with bone bed at base; (CGM).
28. Bodenham Farm: small quarry immediately to N of Bodenham Farm, 5.5 km SE of Woolhope, Hereford and Worcester; SO 6524 3201 (Squirrell and Tucker 1967, loc. 19); Lower Perton Beds and Upper Perton Beds with bone bed at base.
29. Gorsley: Linton Quarry, 4 km W of Newent, Gloucestershire; SO 6770 2570 (see Lawson (1954) for local lithostratigraphical names); Wenlock Limestone, unconformity, Upper Blaisdon Beds, unconformity, Upper Longhope Beds with phosphatic pebble bed at base, Cliffords Mesne Sandstone with phosphatic pebble bed at base.
30. Longhope: exposures around Longhope Village, Mayhill, Gloucestershire.
- 30a. Exposure behind Longhope railway station; SO 6910 1901 (Lawson 1955, 1967, 1982); Upper Longhope Beds, Cliffords Mesne Sandstone with phosphatic pebble bed at base.
- 30b. Road cutting on A4136, Longhope Village by-pass; SO 692 186 (Lawson 1982, loc. 19); same strata as for 30a; (RJA).
- 30c. Stream section at Wood Green; SO 6930 1670 (Lawson 1955, text-fig. 1, loc. C); Upper Longhope Beds, Cliffords Mesne Sandstone with phosphatic pebble bed at base.
31. Tite's Point: exposures on S bank of Severn Estuary near Berkeley Arms, Purton, Gloucestershire.
- 31a. Ditch to S of tow path of Purton-Gloucester canal, 180 m at 244° from the Berkeley Arms; SO 6897 0438 (Cave and White 1971); Whitcliffe Formation; (BGS 62–254).

- 31b. Foreshore of Severn Estuary, 250 m W of Berkeley Arms, Tite's Point; SO 688 046 (Cave and White 1971, text-fig. 2; Curtis 1982); Upper Leintwardine Formation, Whitcliffe Formation, and Downton Castle Sandstone Formation with bone bed at base; (CGM and RJA).
32. Brookend Borehole: Vine Farm, 3 km N of Berkeley, Gloucestershire; SO 6877 0230 (Cave and White 1968, 1978); Elton/Bringewood Beds, Leintwardine Beds, Whitcliffe Formation, Downton Castle Sandstone Formation and Thornbury Beds.
33. Brook House: exposure on W bank of Cwm-ffrwd Brook near Brook Cottage, c. 2 km WSW of Llangybi, Usk Valley, Gwent; SN 356 957 (Walmsley 1959, text-fig. 7, 1982); Upper Llangibby Beds and Speckled Grit Beds with bone bed at base; (CGM).
34. Usk: exposures around the town of Usk, Gwent (Walmsley 1959); Speckled Grit Beds with fragmentary fish remains.
- 34a. A few metres below the wall in Llandegveth church yard, Llandegveth, 6.5 km SW of Usk; SN 338 957.
- 34b. Old quarry 400 m SW of Llangybi Castle; SN 365 972.
- 34c. Dingle immediately N of Granary Farm; SN 322 968.
- 34d. Stream section 500 m N of Llanddewi Court; SN 316 982.
35. Rumney Borehole: E of R. Rhymney, c. 1.5 km W of Rumney, Cardiff; ST 2108 7925 (Waters and White 1978); Wenlock Series extending through Ludlow Series including Llanedeyrn Formation, overlain by Raglan Mudstone Formation with fragmentary fish remains at base.
36. Long Mountain: exposures around the Long Mountain, NW Shropshire, c. 8 km W of Welshpool, Powys.
- 36a. Wallop Hall: exposure under trees near ruins of Wallop Hall, Lower Wallop, 2.7 km SW of Westbury, Long Mountain, Shropshire; SJ 3150 0725 (Richardson and Rasul 1990, loc. 5); Wallop Hall Member of Causemountain Formation with bone bed.
- 36b. 800 m WSW of March Manor Farm; SN 330 103; Causemountain Formation; (BGS 17-40).
37. Nantyrhynau Quarry: exposure behind barn, 5 km NNW of Felindre, Powys; SO 1602 8588; Cefn Einion and Clun Forest formations; (CGM and BGS 143-1776).
38. Felindre: village of Felindre, Powys; SO 1698 8110, c. 13 km W of Clun, Shropshire.
- 38a. Medwaled Brook: dry stream bed, c. 3 km NNW of Felindre, Powys; SO 1534 8391 to SO 1568 8389 (Earp 1938, p. 138); discontinuous exposures showing general succession through uppermost Cefn Einion Formation into Clun Forest Formation.
- 38b. Stonehouse Dingle: 1 km SE of Felindre, Powys; SO 1712 7983 to 1757 8016 (Earp 1940, p. 7); same strata as for 38a.
- 38c. Hendre Farm: trackside exposure, 1.7 km NW of Felindre, Powys; SO 1538 8220; Cefn Einion Formation; (CGM).
39. Clun: c. 20 m NNW of Ludlow, Shropshire (Earp 1940).
- 39a. Within's Wood: cutting for new forestry path near Within's Wood, Clun Forest, Shropshire; SO 317 836; Clun Forest Formation with one well-developed bone bed and a succession of thin bone beds. (CGM).
- 39b. Clun Forest: floor of forestry track, near Lydbury North, Shropshire; SO 3176 8317; similar to Green Downton Formation of Holland (1959); (CGM and BGS).
- 39c. Roadside exposure at Bryn, 1.2 km SE of Cefn Einion, Shropshire; SO 2951 8535; Cefn Einion Formation; (BGS).
- 39d. Hurst Mill: exposure next to forestry track in Radnor Wood, c. 1.5 km ENE of Clun, Shropshire; SO 3162 8128; Cefn Einion Formation; (CGM and BGS).
- 39e. Five Turnings Outlier: old quarry, 280 m E of Black Garn Farm; SO 297 759 (Stamp 1918, p. 237); Cefn Einion Formation with an exposure gap followed by lowest Clun Forest Formation.
40. Knighton: town c. 23 km W of Ludlow, Shropshire.
- 40a. Old quarry immediately W of bridge on Gwernaffel Estate; SO 273 706 (Holland 1959, p. 462, 1988; Richardson and Rasul 1990, loc. 6); Upper Llan-wen Hill and *Platyschisma helicites* beds.
- 40b. Stream section SSE of Middle Pitts Cottages; SO 3120 7176 (Holland 1959, p. 463); Upper Llan-wen Hill and *Platyschisma helicites* beds; (DJS).
- 40c. Meeting House Lane: discontinuous track and trackside exposures on steep track from Meeting House Farm to Llan-wen Hill; SO 3023 6940 (Holland 1959; Allender *et al.* 1960); Upper Llan-wen Hill Beds, *Platyschisma helicites* Beds (including small bone bed), Green Downton and Yellow Downton formations; (DJS).
41. Builth Wells: NW of Gwenddwr, on bank of Nant Gwenddwr, 5 km SW of Builth Wells, Powys; SO 061 436 (Straw 1930, p. 84; 1937); *Holopella conica* Beds and Green Marls.

42. Cwm Graig Ddu: valley WSW of Builth Wells, 4 km SSE of Garth; SN 968 465 (Straw 1953, p. 217); *Holopella conica* Beds overlain by Long Quarry Formation (formerly Tilestones) with junction marked by line of quarry workings.
43. Capel Horeb: N side of A 40, 5.5 km ESE of Llandovery; SN 8445 3234 (Cwm Dwr section of Potter and Price 1965; Siveter *et al.* 1989, loc. 5.8); Upper Roman Camp Formation (= Lower Whitcliffe Formation) unconformably overlain by Long Quarry Formation and Raglan Marls Group; (CGM, RJA and BGS).
44. Sawdde Gorge: river valley c. 10 km SW of Llandovery, Dyfed.
- 44a. Exposure in stream bed NW of main bridge over R. Sawdde at Pont-ar-llechau; SN 7280 2447; Lower Roman Camp Formation (= Upper Leintwardine Formation), Long Quarry Formation.
- 44b. Small quarry behind Three Horseshoes Inn, Pont-ar-llechau; SN 7279 2446, (Bassett 1982, text-fig. 2, loc. 6); Long Quarry Formation.
- 44c. Exposure next to forestry track; SN 7372 2418 (Bassett 1982, text-fig. 2, loc. 7G; Siveter *et al.* 1989, loc. 5.5i); Long Quarry Formation.
45. Cennen Valley: 4 km SSW of Llandeilo, Dyfed.
- 45a. Cutting W of A476; SN 6100 1908 to 6102 1902 (Siveter *et al.* 1989, loc. 5.6e); Cennen Formation (= possible uppermost Ludlow Series) and Long Quarry Formation; (BGS and RJA).
- 45b. Small quarry above A483, S of Llandeilo; SN 6145 1915 (Siveter *et al.* 1989, loc. 5.7); Long Quarry Formation.

REPOSITORIES

Illustrated material with the prefix PM is deposited in the Natural History Museum (London) and with the prefix BGS is deposited at the British Geological Survey (Keyworth). A representative suite of specimens (LEIUG 14555–14566) collected by Miller (1993) is held at the Department of Geology, University of Leicester. Tables of data have been deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14045 (17 pp.).

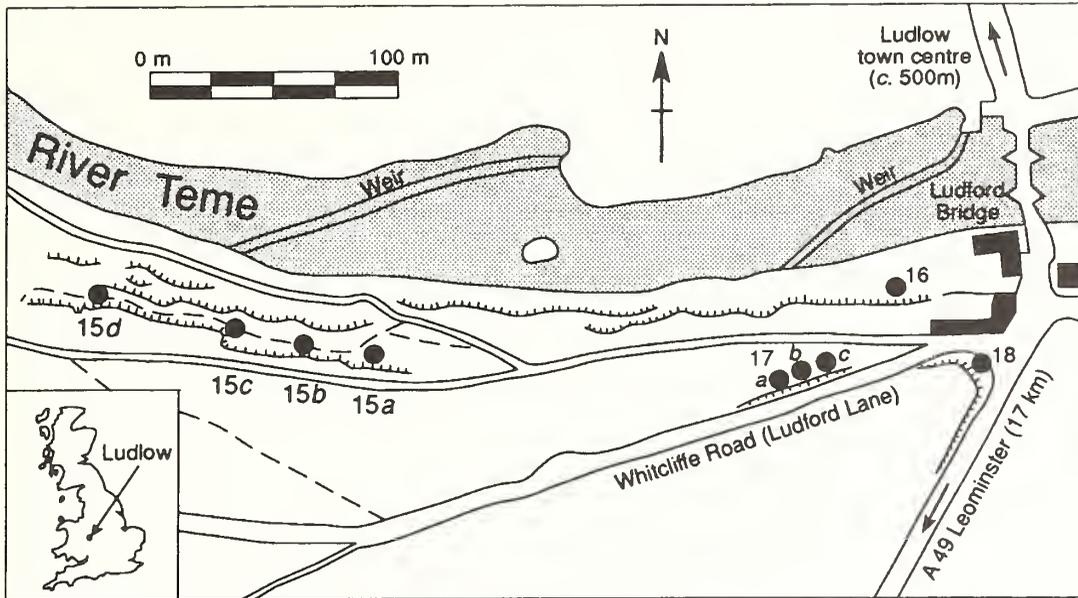
SECTIONS AT LUDLOW, SHROPSHIRE

Upper Whitcliffe Formation

The base of the Upper Whitcliffe Formation is defined (Holland *et al.* 1963, p. 123) at the base of the bed above a convoluted horizon at the disused Whitcliffe Quarry (loc. 15a, Text-figs 3–4). Convoluted bedding is well developed at the ‘dog-leg’ of the exposure at 15c and for the purposes of this study has been taken as the topmost bed of the Lower Whitcliffe Formation, although the section is faulted and the convoluted bed is considerably thicker at 15c than at 15a (Text-fig. 4). As there are no continuous exposures through the Upper Whitcliffe Formation at Ludlow, the sampling interval throughout the formation is irregular and ranges from 0.05 m to approximately 10 m. Localities 15 and 16 are cliff exposures and give an almost complete coverage of the formation (Text-fig. 5). The top of the Upper Whitcliffe Formation is at the base of the Ludlow Bone Bed Member at localities 18 (Text-figs 1, 3, 6), and the formation is approximately 32 m thick at Ludlow (Siveter *et al.* 1989, text-fig. 30).

Conodont distribution. Conodonts were recovered from calcareous to slightly calcareous lithologies which occur sporadically throughout the Upper Whitcliffe Formation. Elements are well preserved and pale amber in colour although some specimens are fragmentary, particularly those from the slightly calcareous lithologies which required crushing to extract the fauna. More than 1800 specimens belonging to nine multielement species were extracted and examined from localities 15 to 18. Conodont-bearing samples contain from twenty to 1056 conodont elements per kg (Text-fig. 7).

Conodont faunas from the topmost Lower Whitcliffe Formation and lowermost 5 m of the Upper Whitcliffe Formation (Text-fig. 7) consist dominantly of *Ozarkodina excavata* and *Coryssognathus dubius* elements with minor numbers of *Panderodus serratus* and *O. confluens*. Other less common species include *O. remscheidensis eosteinhornensis*, *O. remscheidensis* ssp. nov. Aldridge, 1985, *O. snajdri* and *O. wimani* (Pl. 1). At the top of the Upper Whitcliffe Formation these less common species become more frequent and the fauna becomes dominated by *C. dubius* and *O. snajdri* with minor numbers of *remscheidensis* subspecies (notably *O. r. eosteinhornensis*) and *O. cf. crispa*; the latter only in strata 0.15–0.3 m below the top of the formation. In the



TEXT-FIG. 3. Locations of sampled exposures on the Whitcliffe at Ludlow, Shropshire (after Holland *et al.* 1963, and Siveter *et al.* 1989).

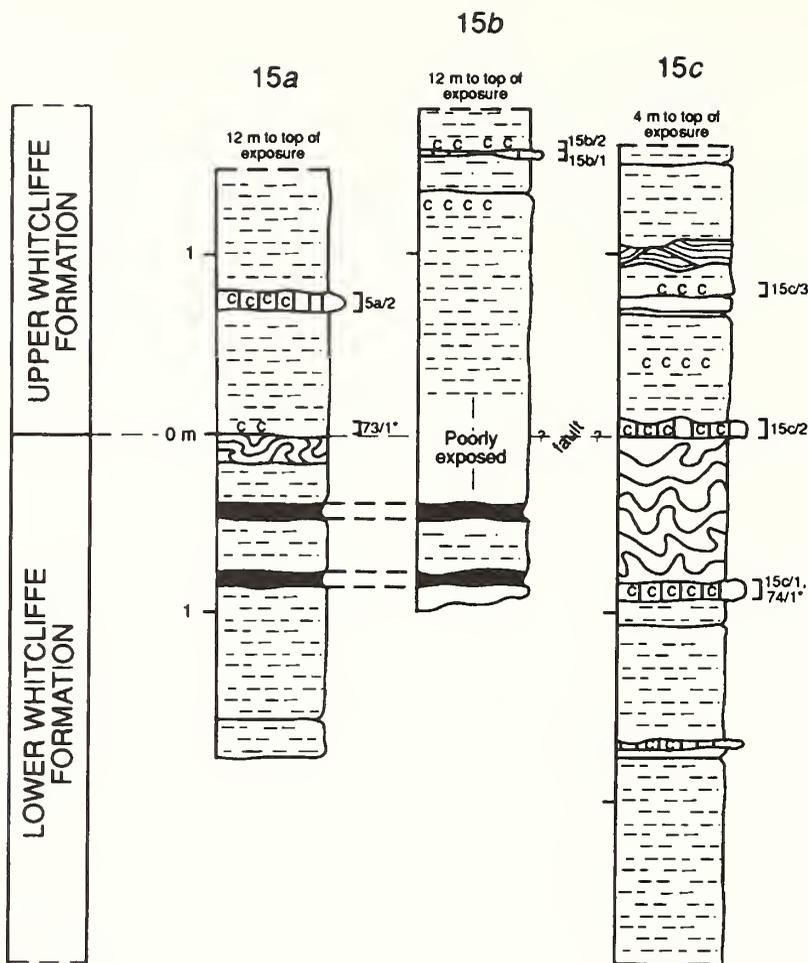
topmost 0.3 m of the Upper Whitcliffe Formation *O. excavata* is much less abundant, *O. confluens* becomes more abundant and *P. serratus* is no longer present. Relative proportions of the individual elements from the apparatus of *O. excavata*, calculated for samples that contain more than fifty elements of *O. excavata*, show insignificant variation in relative percentages of elements (Text-fig. 8).

Ostracode distribution. The Upper Whitcliffe Formation has a virtually monospecific ostracode fauna of *Calcaribeyrichia torosa* (Pl. 2, figs 9–12). This species has been found throughout the Upper Whitcliffe Formation (loc. 17a and in samples 15b/2, 15c/3, 17c/1, 18/1) and is mostly confined to decalcified brachiopod coquinas. At localities 17a–c and 18, where the uppermost 0.5 m of the Upper Whitcliffe Formation has been sampled 'bed by bed', only a few isolated specimens of *C. torosa* have been recovered (samples 17c/1, 18/1, and specimen BGS DEY 3653). *C. torosa* has been reported from both the Lower Whitcliffe and Upper Whitcliffe formations (Siveter 1974). An internal mould of *Hemsiella cf. maccoyiana* has been recovered from 0.15 m below the top of the Upper Whitcliffe Formation at Ludford Corner (loc. 18).

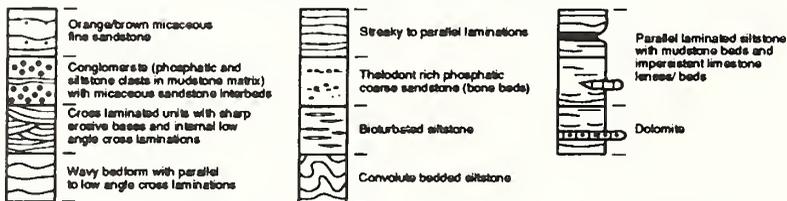
Downtown Castle Sandstone Formation

The base of the Downtown Castle Sandstone Formation is defined at locality 18 at the base of the Ludlow Bone Bed (Holland *et al.* 1963). The Downtown Castle Sandstone Formation has three members (Text-fig. 1) and has been described in detail by Bassett *et al.* (1982, pp. 6, 14) and Smith and Ainsworth (1989). The upper limit of the Ludlow Bone Bed Member is defined at the top of three closely spaced, millimetre scale, bone beds 0.21 m above its base (Bassett *et al.* 1982, p. 14). These bone beds are discontinuous and the top of the member has not been located accurately at Ludford Lane (locs 17a–b). Only a single bone bed has been located at the same level at locality 18 (Text-fig. 6). The Sandstone Member was not sampled for the present study.

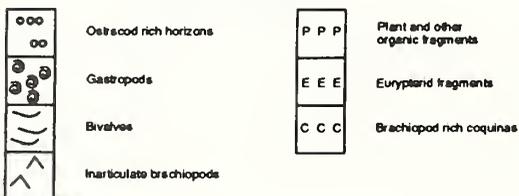
Conodont distribution. Conodonts are very rare in the Downtown Castle Sandstone Formation, samples containing six to 105 conodont elements per kg, but generally fewer than twenty per kg (Text-fig. 7). Conodont elements have been obtained from bone beds within the Ludlow Bone Bed Member, but elements are extremely fragmentary and abraded making identification difficult (Pl. 1, fig. 11). Only fragments of Pa elements of *O. confluens* and Sa/Sb elements of *C. dubius* have been identified with any certainty (Miller and Aldridge 1993;



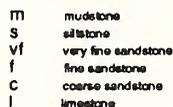
SEDIMENTS AND SEDIMENTARY STRUCTURES



FLORAS AND FAUNAS

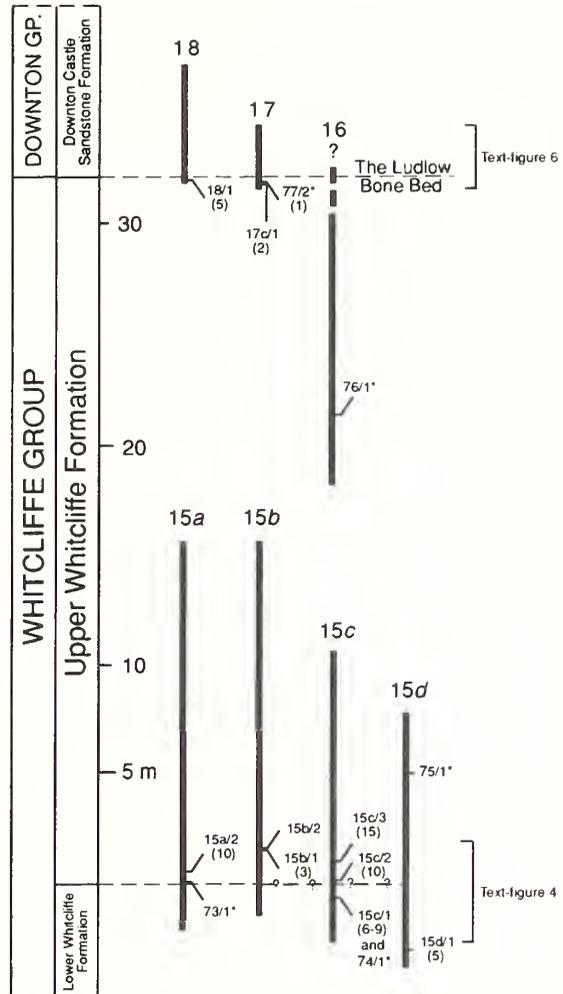


GRAIN SIZE ABBREVIATIONS



TEXT-FIG. 4. Measured logs across the boundary between the Lower and Upper Whitcliffe Formations at Whitcliffe Quarry, Ludlow (locs 15a-c) showing sampled horizons. Log at Locality 15a after Holland *et al.* (1963, text-fig. 6). The key represents all measured logs for the present study.

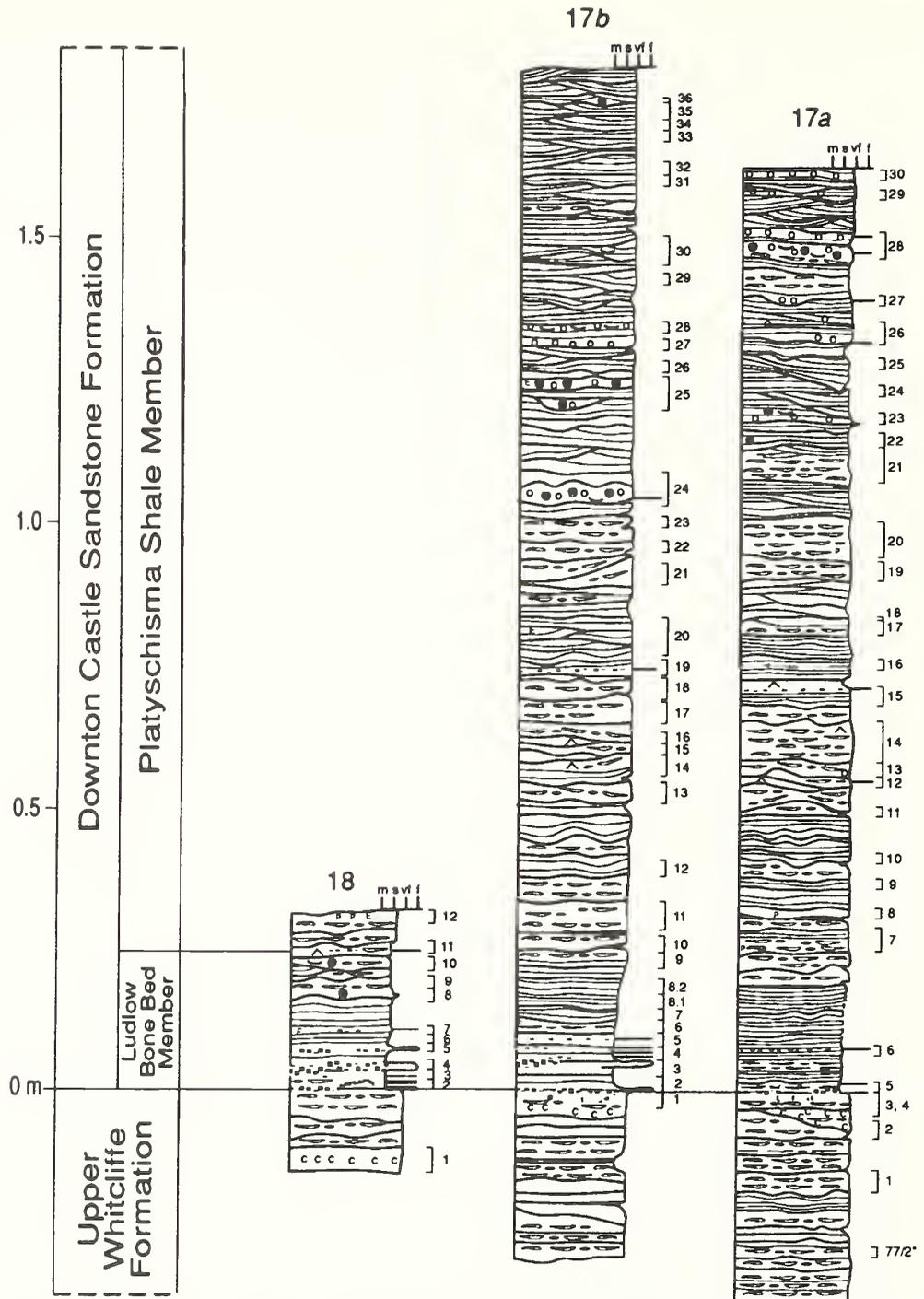
TEXT-FIG. 5. Approximate stratigraphical position of sections (thick black lines) and horizons sampled for conodonts and ostracodes through the Lower and Upper Whitcliffe formations on the Whitcliffe at Ludlow, Shropshire. Total thickness 32 m (Siveter *et al.* 1989, text-fig. 30). Bed thicknesses given in brackets if known. For detailed sedimentary logs see Text-figures 4 and 6.



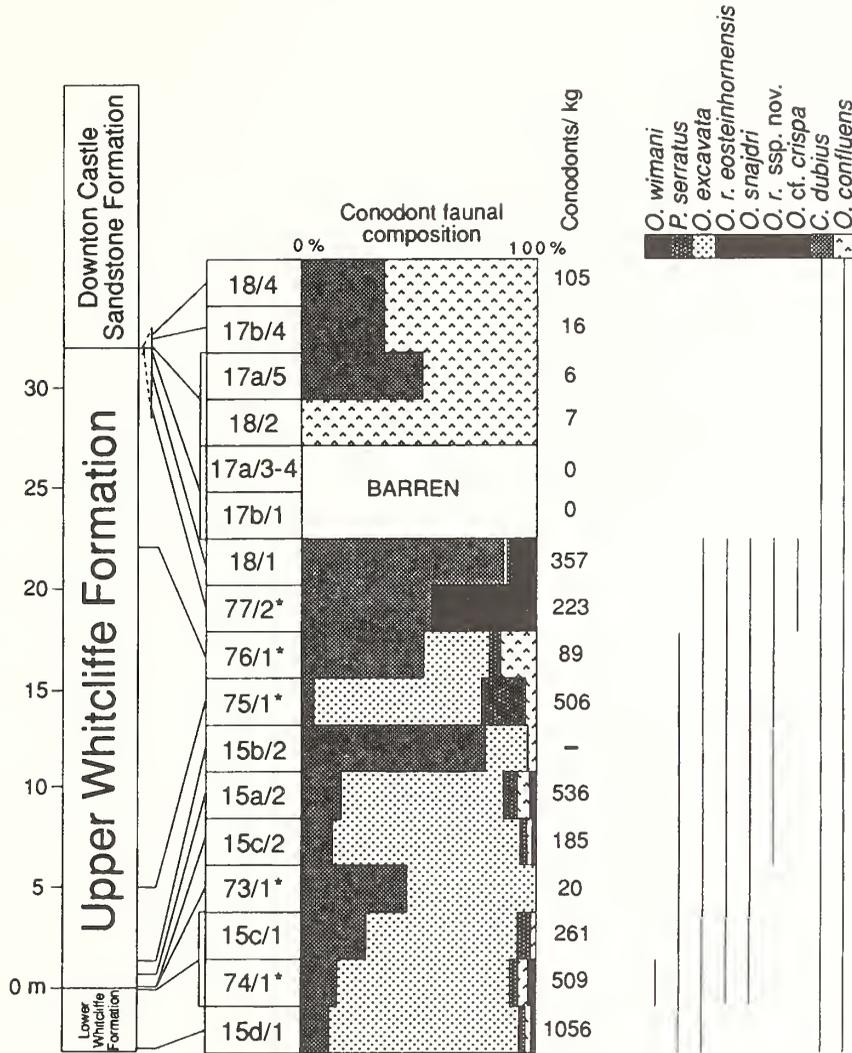
this study). Harley (1861) figured a similar fauna; Aldridge and Smith (1985) also reported fragments of *O. excavata* and Walliser (1966) recorded *O. r. eosteinhornensis* from the Ludlow Bone Bed Member.

Ostracode distribution. A total of 2145 individual ostracode valves and twenty-three specimens of carapaces with co-joined valves has been recovered from the Downton Castle Sandstone Formation at localities 17 and 18 (Text-fig. 9). Individual (mould) specimens are often incomplete and therefore identifiable only to generic level. Relative generic proportions for each bed containing more than ten identifiable ostracodes have been plotted (Text-fig. 9), with ostracode frequency and percentage of carapaces against valves plotted for every bed in the section (Text-fig. 10).

The ostracode fauna shows a similar trend in the two parallel sections 10 m apart (locs 17a–17b) and also at locality 18. The lowest bed in the Ludlow Bone Bed Member at all three sections contains *Frostiella groenvalliana*, *Londinia arisaigensis*, *L. fissurata*, and *Nodibeyrichia verrucosa* (Pl. 2) in similar relative proportions (Text-fig. 9). In the present study *C. torosa* has not been found above the Upper Whitcliffe Formation, but Bassett *et al.* (1982, text-fig. 6) recorded *C. torosa* within the Ludlow Bone Bed Member at locality 17a. This specimen (BGS MR DEY 3694) has been examined by the author and confirms the occurrence of *C. torosa* (with coeval *F. groenvalliana*) at a level 0.08 m above the base of the Ludlow Bone Bed Member.



TEXT-FIG. 6. Measured logs across the boundary between the Upper Whitcliffe and Downton Castle Sandstone Formations at Ludford Corner and Ludford Lane (locs 17-18), showing sampled horizons.

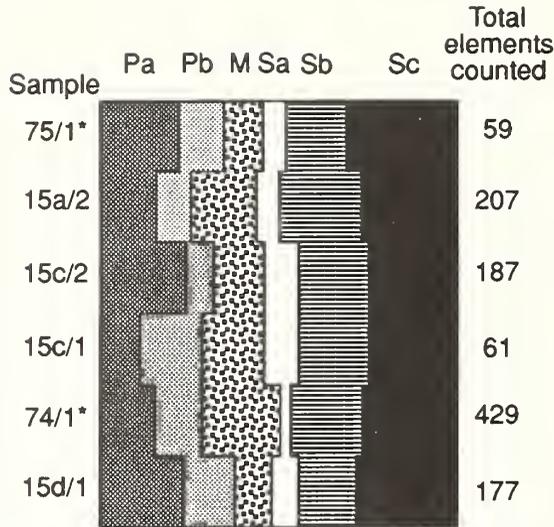


TEXT-FIG. 7. Conodont ranges and compositions of conodont faunas from the Lower Whitcliffe, Upper Whitcliffe and Downton Castle Sandstone Formations at Ludlow, Shropshire (locs 15-18). Positions marked on the lithostratigraphical column are given to the centre of the bed sampled. Bed thicknesses are given in Text-figures 4-6.

The coarsening upwards of the sediments in the Ludlow Bone Bed Member and lowermost 0.15 m of the *Platyschisma* Shale Member corresponds with an increase in the proportion of *Frostiella* and a parallel decrease in the proportion of *Londinia*. Frequency is relatively high and carapaces are most commonly preserved in these strata reaching a maximum of 15 per cent. with respect to the number of valves in sample 17b/10.

The last occurrence of *N. verrucosa* and the occurrence of bioturbated, synaeresis-cracked siltstones 0.34 m above the base of the *Platyschisma* Shale Member corresponds to a horizon above which ostracode frequency becomes very low ($< 0.1 \text{ ostracode m}^2 \times 10^4$) but carapaces are still preserved.

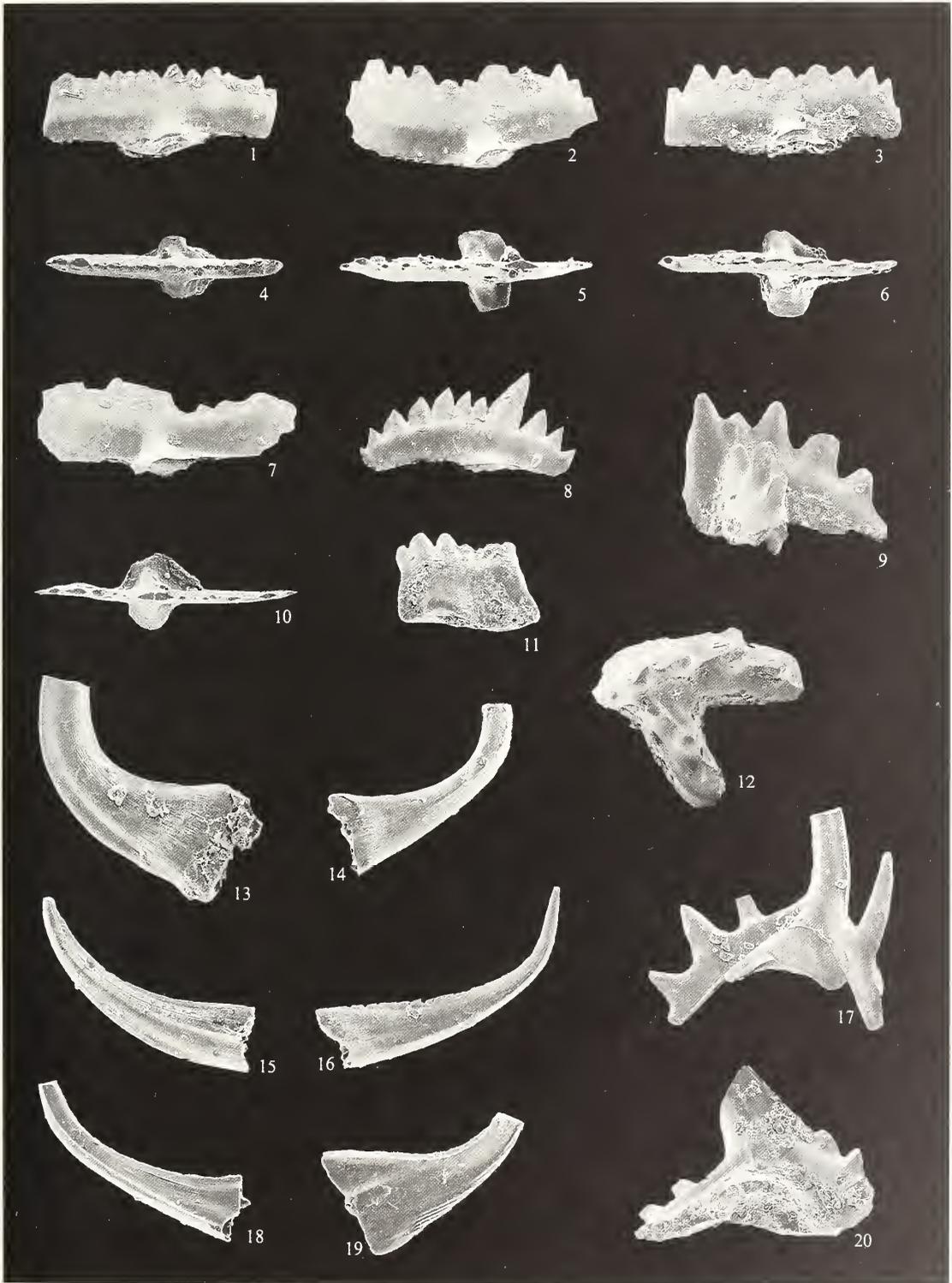
The onset of cross laminated units with sharp erosive bases corresponds to high frequency ostracode faunas (maximum of $2.0 \text{ ostracodes m}^2 \times 10^4$) dominated by *Frostiella* and non-palaeocopes, with *Londinia* very rare



TEXT-FIG. 8. Relative proportions of *O. excavata* elements from the Whitcliffe Group at Whitcliffe Quarry (loc. 15). Samples are arranged in stratigraphical order with the oldest at the base. Sample positions are given in Text-figures 4–5.

EXPLANATION OF PLATE I

- Figs 1, 4. *Ozarkodina remscheidensis easteinhornensis* (Walliser, 1964). PM X 1164; loc. 8, sample 8/1, Diddlebury, Shropshire; Whitcliffe Formation; Pa element; 1, lateral, and 4, oral views; $\times 30$.
- Figs 2, 5. *Ozarkodina remscheidensis remscheidensis* (Ziegler, 1960). PM X 1277; loc. 31b, sample 31b/3, Tite's Point, Gloucestershire; Whitcliffe Formation; Pa element; 2, lateral, and 5, oral views; $\times 45$.
- Figs 3, 6. *Ozarkodina remscheidensis* ssp. nov. Aldridge, 1985. PM X 1156; loc. 7a, sample 78/1*, Aston Munslow, Shropshire; Whitcliffe Formation; Pa element; 3, lateral, and 6, oral views; $\times 45$.
- Figs 7, 10. *Ozarkodina winani* (Jeppsson, 1974). PM X 1184; loc. 15c, sample 74/1*, Whitcliffe Quarry, Ludlow, Shropshire; Upper Whitcliffe Formation; Pa element; 7, lateral, and 10, oral views; $\times 85$.
- Fig. 8. *Ozarkodina excavata* (Branson and Mehl, 1933). PM X 1193; loc. 20, sample 20/1a, Netherton, West Midlands; Upper Whitcliffe Formation; Pa element; lateral view; $\times 50$.
- Figs 9, 12. *Coryssognathus dubius* (Rhodes, 1953). PM X 1162; loc. 7a, sample 39/1*, Aston Munslow, Shropshire; Whitcliffe Formation; Pa element; 9, lateral, and 12, oral views; $\times 34$.
- Fig. 11. *Ozarkodina confluens* (Branson and Mehl, 1933). PM X 1188; loc. 17a, sample 17a/5, Ludford Lane, Ludlow, Shropshire; Ludlow Bone Bed Member, Downton Castle Sandstone Formation; fragment of Pa element; lateral view; $\times 22$.
- Figs 13–14. *Panderodus recurvatus* (Rhodes, 1953). 13, PM X 1170; loc. 10, sample 10/1, Siefton, Shropshire; Whitcliffe Formation; falciform element; unfurrowed lateral face; $\times 110$. 14, PM X 1214; loc. 20, sample 20/1a, Netherton, West Midlands; Upper Whitcliffe Formation; similiform element; unfurrowed lateral face; $\times 85$.
- Figs 15–16. *Panderodus serratus* (Rexroad, 1967). 15, PM X 1199; loc. 20, sample 20/1b, Netherton, West Midlands; Upper Whitcliffe Formation; falciform element; furrowed lateral face; $\times 50$. 16, PM X 1178; loc. 15a, sample 15a/2, Whitcliffe Quarry, Ludlow, Shropshire; Upper Whitcliffe Formation; arcuatiform element; unfurrowed lateral face; $\times 80$.
- Figs 17, 20. *Oulodus* sp. 17, PM X 1266; loc. 24a, sample 162/2*, Prior's Frome, Hereford and Worcester; Upper Perton Beds; Sb element; lateral; $\times 45$. 20, PM X 1280; loc. 31b, sample 31b/3, foreshore of Severn Estuary, Tite's Point, Gloucestershire; Whitcliffe Formation; Pb element; lateral; $\times 30$.
- Fig. 18. *Walliserodus* cf. *sancticlairi*. PM X 1223; loc. 20, sample 20/1b, Netherton, West Midlands; Upper Whitcliffe Formation; symmetrical element; lateral; $\times 100$.
- Fig. 19. *Dapsilodus obliquicostatus* (Branson and Mehl, 1933). PM X 1172; loc. 10, sample 10/1, Siefton, Shropshire; Whitcliffe Formation; symmetrical element; lateral; $\times 100$.



MILLER, Silurian conodonts

(0–7 per cent.). Ostracodes are concentrated as lags at the bases of beds (Text-fig. 6). Carapaces are no longer preserved.

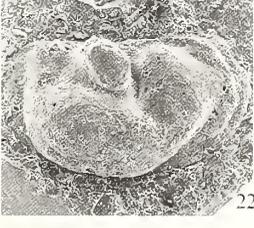
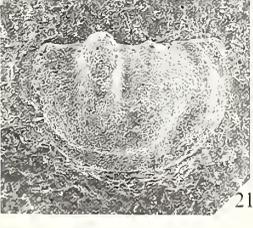
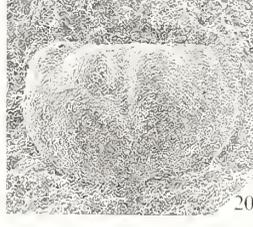
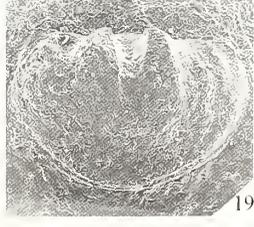
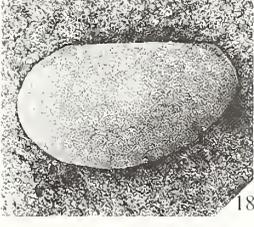
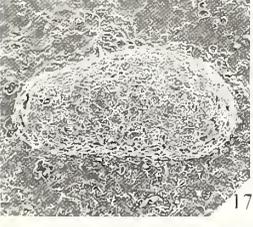
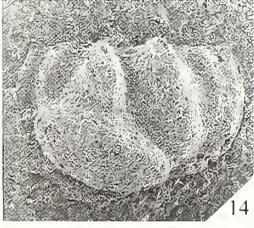
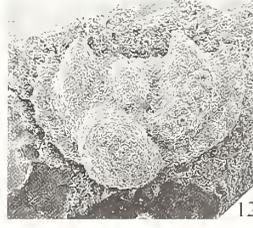
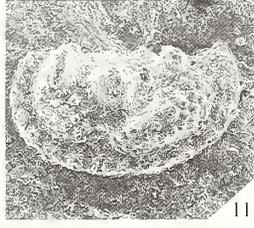
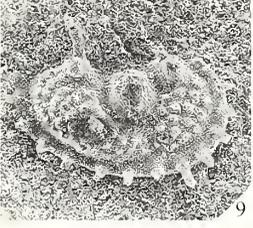
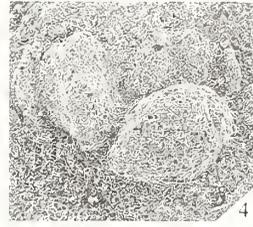
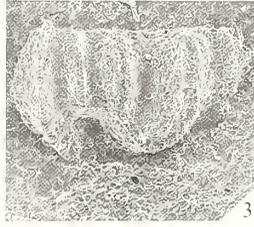
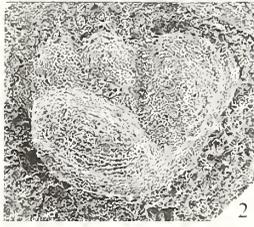
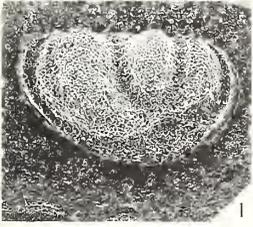
THE LUDLOW ANTICLINE AND SURROUNDING AREA

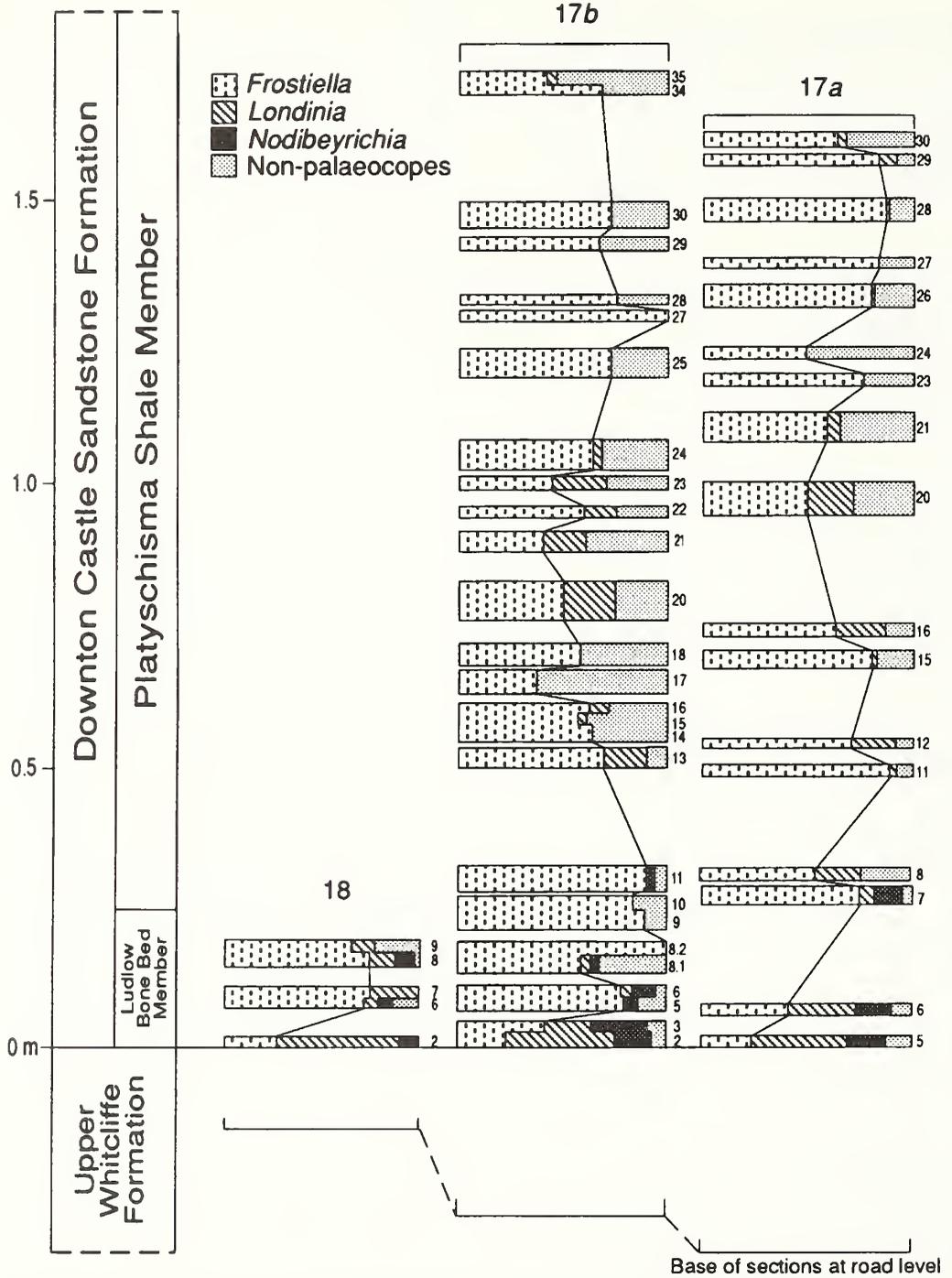
The Much Wenlock area

Localities in this area have not yielded abundant conodont or ostracode faunas in this study. White and Coppack (1978) recorded the ostracode *F. groenvalliana* at the base of the Downton Castle Sandstone Formation, from a horizon marked at Willey (loc. 2) by a bone bed. Their collections (BGS) have been

EXPLANATION OF PLATE 2

- All specimens are SEM illustrations of silicone rubber casts of external moulds in lateral view, unless stated.
- Figs 1–2. *Hemsiella* cf. *maccoyiana*. 1, PM OS 14146; loc. 38c, Felindre, Powys; Cefn Einion Formation; tecnomorphic right valve; $\times 19$. 2, PM OS 14093; loc. 14b, sample 14b/1, Weir Quarry, Downton, Shropshire; Upper Whitcliffe Formation; heteromorphic left valve; $\times 22$.
- Figs 3–4. *Lophoctenella* cf. *scanensis*. 3, BGS RT 336; loc. 4b, Dean Brook, Much Wenlock, Shropshire; Whitcliffe Formation; tecnomorphic left valve; $\times 18$. 4, PM OS 14136; loc. 36a, sample 36a/k, Wallop Hall, Long Mountain, Powys; Causemountain Formation; heteromorphic right valve; $\times 18$.
- Figs 5–8. *Nodibeyrichia verrucosa* Shaw, 1969. 5, PM OS 14123; loc. 18, sample 18/2, Ludford Corner, Ludlow Corner, Ludlow, Shropshire; Ludlow Bone Bed Member, Downton Castle Sandstone Formation; tecnomorphic right valve; $\times 17$. 6, BGS SH 3685; loc. 3b, Linley Brook, Much Wenlock, Shropshire; Downton Castle Sandstone Formation; heteromorphic left valve; $\times 14$. 7, PM OS 14119; loc. 17b, sample 17b/3a, Ludford Lane, Ludlow, Shropshire; Ludlow Bone Bed Member, Downton Castle Sandstone Formation; tecnomorphic left valve; $\times 35$. 8, PM OS 14138; loc. 36a, sample 36a/M2, Wallop Hall, Long Mountain, Powys; Causemountain Formation; heteromorphic left valve; $\times 23$.
- Figs 9–12. *Calcaribeyrichia torosa* (Jones, 1855). 9, PM OS 14150; loc. 39d, Radnor Wood, Clun, Shropshire; Cefn Einion Formation; tecnomorphic right valve; $\times 27$. 10, PM OS 14094; loc. 15b, sample 15c/3a, Whitcliffe Quarry, Ludlow, Shropshire; Upper Whitcliffe Formation; heteromorphic left valve; $\times 11$. 11, BGS DEY 3653; loc. 17a, Ludford Lane, Ludlow, Shropshire; Upper Whitcliffe Formation; tecnomorphic left valve; $\times 12$. 12, PM OS 6584; loc. 39e, Five Turnings outlier, Clun, Shropshire; Cefn Einion Formation; heteromorphic left valve; $\times 11$.
- Figs 13–14. *Londinia arisaigensis* Copeland, 1964. Loc. 18, from loose material dumped after the excavation of Ludford Corner, Ludlow, Shropshire in 1988; Downton Castle Sandstone Formation. 13, PM OS 14125; tecnomorphic right valve; $\times 13$. 14, PM OS 14128; heteromorphic left valve; $\times 12$.
- Figs 15–16. *Londinia fissurata* Shaw, 1969. 15, PM OS 14098; loc. 17a, sample 17a/5s, Ludford Lane, Ludlow, Shropshire; Ludlow Bone Bed Member, Downton Castle Sandstone Formation; internal mould of an open tecnomorphic carapace; $\times 15$. 16, PM OS 14112; loc. 17a, sample 17a/12d, Ludford Lane, Ludlow, Shropshire; Platyschisma Shale Member, Downton Castle Sandstone Formation; heteromorphic right valve; $\times 15$.
- Fig. 17. Non-palaeocene ostracode. PM OS 14120; loc. 17b, sample 17b/12a, Ludford Lane, Ludlow, Shropshire; Platyschisma Shale Member, Downton Castle Sandstone Formation; $\times 27$.
- Fig. 18. *Leperditia* sp. PM OS 14641; loc. 17, from loose material from landslide on Ludford Lane, Ludlow, Shropshire in 1993; Platyschisma Shale Member, Downton Castle Sandstone Formation; $\times 43$.
- Figs 19–20. *Londinia kiesowi* (Krause, 1891). 19, PM OS 14135; loc. 36a, sample 36a/L, Wallop Hall, Long Mountain; Causemountain Formation; tecnomorphic right valve; $\times 15$. 20, BGS SH 3685; loc. 3b, Linley Brook, Much Wenlock, Shropshire; Downton Castle Sandstone Formation; heteromorphic left valve; $\times 15$.
- Figs 21–24. *Frostiella groenvalliana* Martinsson, 1963. 21, PM OS 14113; loc. 17a, sample 17a/26a, Ludford Lane, Ludlow, Shropshire; Platyschisma Shale Member, Downton Castle Sandstone Formation; tecnomorphic left valve; $\times 13$. 22, PM OS 14124; loc. 18, Ludford Corner, Ludlow, Shropshire; Platyschisma Shale Member, Downton Castle Sandstone Formation; heteromorphic left valve; $\times 13$. 23, PM OS 14111; loc. 17a, sample 17a/14a, Ludford Lane, Ludlow, Shropshire; Platyschisma Shale Member, Downton Castle Sandstone Formation; tecnomorphic carapace with open valves; $\times 9$. 24, PM OS 13922; loc. 18, from loose material dumped after the excavation of Ludford Corner, Ludlow, Shropshire in 1988; Downton Castle Sandstone Formation; tecnomorphic left valve; $\times 17$.





TEXT-FIG. 9. Ostracode faunal composition from the Downton Castle Sandstone Formation at Ludford Lane and Ludford Corner (locs 17a-b and 18). The height of each bar corresponds to the relative thickness of beds from which more than ten identifiable ostracodes were collected. The positions of numbered samples are given in Text-figure 6.

examined by the author and identifications confirmed. Two abraded Pa element fragments of *O. confluens* have been recovered from this horizon. *F. groenvalliana* and *L. fissurata* are recorded from the Downton Castle Sandstone Formation at Callaughton (loc. 1) and Dean Brook (loc. 4b) (Robertson, 1927; White and Coppack 1978, p. 28). White and Coppack (1978, p. 29) reported similar ostracode faunas from Linley (locs 3a–b), remarking that they closely resemble faunas from the old quarry at Willey (loc. 2). The Downton Castle Sandstone Formation at Linley Brook (loc. 3b), has been sampled by the author and contains abundant *F. groenvalliana* associated with the gastropod *Turbocheilus helicites* (J. de C. Sowerby). In one individual calcareous bed at Linley Brook these taxa retain their original calcareous carapaces. The bed has also yielded whole, unabraded conodont specimens of *O. confluens* and *Oulodus* sp. Specimens of similar limestone beds from the Downton Castle Sandstone Formation at Dean Brook (loc. 4) are held at the BGS (Keyworth). Ostracode faunas from the Upper Whitcliffe Formation in the Much Wenlock area are dominated by *C. torosa*, with minor occurrences of *H. cf. maccoyiana* and *Lophoctenella cf. scanensis* (Pl. 2, fig. 3). The ostracode fauna of the Downton Castle Sandstone Formation is dominated by *F. groenvalliana* with minor occurrences of *L. fissurata*, *L. arisaigensis* and a single specimen of *Londinia kiesowi* (Pl. 2, fig. 20).

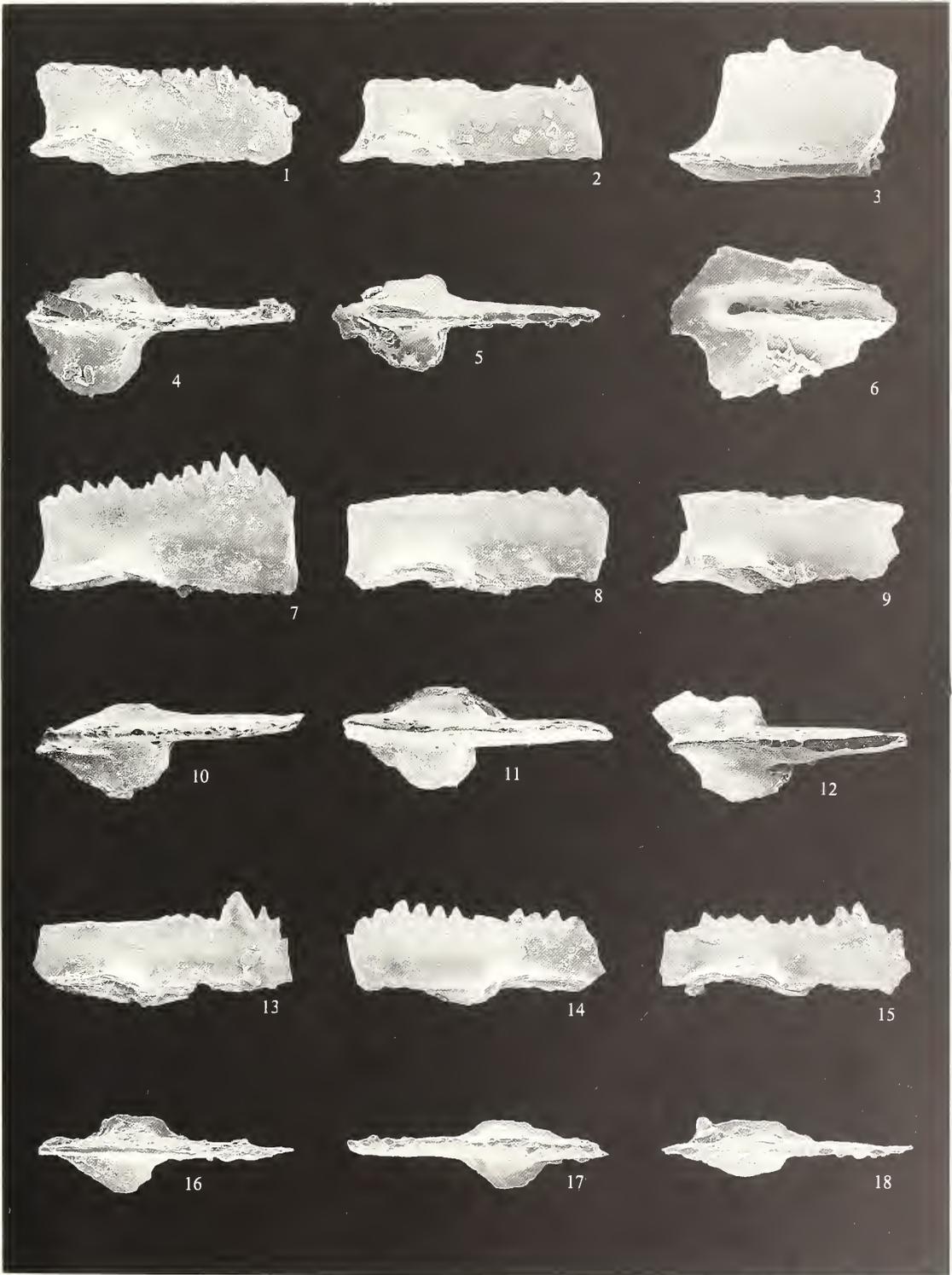
Corve Dale

At Brockton (loc. 5b), Shipton (locs 6a–c), and Culmington (loc. 11) bone beds have been reported at the base of the Downton Castle Sandstone Formation (BGS records; Turner 1973; Antia 1979a), but are no longer exposed. Ostracode faunas from the Whitcliffe Formation at Brockton (locs 5a–b) and Shipton (loc. 6a) contain only *C. torosa*, while those from the Downton Castle Sandstone Formation are almost exclusively dominated by *F. groenvalliana* with minor proportions of *L. arisaigensis*, *L. fissurata* and non-palaeocene ostracodes. *F. groenvalliana*, although confined to the Downton Castle Sandstone Formation, is not present immediately at the base of the Downton Castle Sandstone Formation at any locality on Corve Dale.

Aston Munslow. Two well preserved specimens of *C. torosa* have been recovered from a bed 0–0.02 m below the top of the Whitcliffe Formation at locality 7a. A single conodont sample from locality 7b (3 m below the top of the formation) is dominated by the conodont *O. excavata* with *O. confluens*, *C. dubius* and minor *P. serratus*. The two faunas from locality 7a are very similar to each other, dominated by *C. dubius* with minor *O. confluens*, *O. snajdri* and elements from the *remscheidensis* plexus. The topmost bed of the Whitcliffe Formation has yielded *O. cf. crispa* (Pl. 3, fig. 8). 1.63 m of the Downton Castle Sandstone Formation is exposed at locality 7a, yielding two poorly preserved specimens of *F. cf. groenvalliana* and *L. cf. arisaigensis*. *O. confluens* (Pa and Pb elements) and *C. dubius* are present in a laterally discontinuous bone bed up to 0.05 m thick at the base of the Downton Castle Sandstone Formation which has produced 122 conodont elements per kg.

EXPLANATION OF PLATE 3

- Figs 1–2, 4–5. *Ozarkodina crispa* (Walliser, 1964). 1, 4, PM X 1276; loc. 31b sample 31b/7, foreshore of Severn Estuary, Tite's Point, Gloucestershire; Whitcliffe Formation; Pa element; 1, lateral, and 4, oral views; $\times 60$. 2, 5, PM X 1263; loc. 24a, sample 162/2*, Prior's Frome, Hereford and Worcester, Upper Perton Beds; Pa element; 2, lateral, and 5, oral views; $\times 45$.
- Figs 3, 6–12. *Ozarkodina cf. crispa*. 3, 6, PM X 1187; loc. 17a, sample 77/2*, Ludford Lane, Ludlow, Shropshire; Upper Whitcliffe Formation; fragment showing cavity and posterior termination of Pa element; 3, lateral, and 6, oral views; $\times 120$. 7, 10, PM X 1244; loc. 24a, sample 24a/2a, Prior's Frome, Hereford and Worcester; Upper Perton Beds; Pa element; 7, lateral, and 10, oral views; $\times 50$. 8, 11, PM X 1160; loc. 7a, sample 7a/4, Aston Munslow, Shropshire; uppermost bed of Whitcliffe Formation; Pa element; 8, lateral, and 11, oral views; $\times 40$. 9, 12, PM X 1189; loc. 18, sample 18/1, Ludford Corner, Ludlow, Shropshire; Upper Whitcliffe Formation; Pa element; 9, lateral, and 12, oral views; $\times 40$.
- Figs 13, 16. *Ozarkodina cf. snajdri*. PM X 1189; loc. 7a, sample 7a/1, Aston Munslow, Shropshire; Whitcliffe Formation; Pa element; 13, lateral, and 16, oral views; $\times 40$.
- Figs 14–15, 17–18. *Ozarkodina snajdri* (Walliser, 1964). 14, 17, PM X 1190; loc. 24a, sample 24a/2a, Prior's Frome, Hereford and Worcester; Upper Perton Beds; Pa element; 14, lateral, and 17, oral views; $\times 50$. 15, 18, PM X 1191; loc. 33, sample 33/3, Brook House, Usk, Gwent; Upper Llangibby Beds; Pa element; 15, lateral, and 18, oral views; $\times 60$.



Downton to Onibury area

The Downton Bridge locality (14a) is no longer exposed, but collections made by Dr David J. Siveter in 1982 include *F. groenvalliana*, *L. arisaigensis* and non-palaeocene ostracodes from a bed immediately above the base of the Downton Castle Sandstone Formation. Like the basal bed of the Ludlow Bone Bed Member at Ludlow, carapaces of *F. groenvalliana* are present, although *N. verrucosa* is absent. The Downton Bone Bed (loc. 14c) within the Platyschisma Shale Member (Whitaker 1962) has yielded abraded conodonts, dominantly Pa elements of *O. confluens*, also elements of *C. dubius* with minor *O. excavata*, *O. r. eosteinhornensis* and *Oulodus* sp. At Onibury (loc. 12a) and Clungunford (locs 13a, 13b) *C. torosa* has been found in the Upper Whitcliffe Formation. Locality 12b at Onibury has yielded *L. fissurata* from the Downton Castle Sandstone Formation.

Weir Quarry, Downton. The ostracode fauna from the Upper Whitcliffe Formation is very sparse with only *H. cf. maccoyiana* and *C. torosa* present. No conodonts have been recovered. Ostracode faunas of the Downton Castle Sandstone Formation are very sparse reaching a maximum frequency of 0.2 ostracodes $m^2 \times 10^4$ but generally fewer than 0.1 ostracodes $m^2 \times 10^4$. Only three beds yielded more than ten ostracodes and these had very similar faunas of dominant *F. groenvalliana*, with rare specimens of *L. arisaigensis*, *L. fissurata* and non palaeocene ostracodes. The basal bone bed yielded a conodont fauna dominated by Pa elements of *O. confluens* with *C. dubius*, fragments of *Oulodus* sp. and two Pa elements of *O. excavata*.

Other localities

The base of the Downton Castle Sandstone Formation has been recognized at Kington (locs 19a–b) where multiple bone beds are developed in the Ludlow Bone Bed Member (Holland and Williams 1985). No conodonts and only a single specimen of *H. cf. maccoyiana* has been collected from the uppermost Upper Whitcliffe Formation (loc. 19a). A distinctive bed of limestone nodules in the Upper Whitcliffe Formation at Netherton (loc. 20) contains abundant *P. serratus*, *C. dubius*, *O. excavata*, *O. confluens*, a minor proportion of *P. recurvatus* and single specimens of *O. r. eosteinhornensis* and *Walliserodus cf. sancticlairei* (Pl. 1, fig. 18). The bed at the top of the formation contains *P. serratus*, *O. excavata* and large, abraded specimens of *O. confluens*. Only 0.32 m of the Downton Castle Sandstone Formation is exposed at Netherton and has yielded conodont collections consisting almost exclusively of *C. dubius* elements and a single Pa element of *O. confluens*. A single ostracode specimen of *F. cf. groenvalliana* has been collected by Dr David J. Siveter from the lowermost Downton Castle Sandstone Formation (Siveter 1989; Hansch *et al.* 1991).

SOUTHERN WELSH BORDERLAND INLIERS

Abberley and the Malverns

No localities in this area yielded abundant conodont or ostracode faunas in the present study. Material (BGS collections) has been examined and includes abundant examples of *C. torosa* from the Upper Ludlow Formation at Woodbury Quarry (loc. 21c). There are no examples of the *H. maccoyiana* material that Mitchell *et al.* (1962) indicated to be present. Exposures of the Whitcliffe Flags Member of the Upper Ludlow Formation around the village of Abberley (locs 21a–b, d) have also yielded specimens of *C. torosa*. At Brockhill Quarry (loc. 22), a single conodont sample from the Whitcliffe Flags Member yielded *O. excavata*, *C. dubius* and *O. confluens* in ascending order of abundance.

Woolhope inlier

Perton Lane. Non-palaeocene ostracodes have been recovered from the topmost Upper Perton Beds and a single specimen of *H. cf. maccoyiana* recovered from a coquina 0.06 m below the top of the beds. Two samples from locality 23b, 4 m below the top of the Upper Perton Beds contain *O. excavata*, *C. dubius*, *O. confluens* and *P. serratus*, also rare examples of *O. wimani*, *O. r. eosteinhornensis* and *O. snajdri* (Pl. 1). A sample 0.15 m below the top of the Upper Perton Beds contains only *C. dubius*, *O. confluens* and *O. excavata*.

Ostracode moulds from the Rushall Beds are stained rusty brown, occur almost exclusively in the coarse bases of fining-upwards beds and are poorly preserved due to the coarse nature of the sediment. Plant and eurypterid fragments are commonly associated and ostracode frequency is low, ranging from 0.02–0.18 $m^2 \times 10^4$. The lowermost 0.5 m of the Rushall Beds contains a relatively consistent ostracode fauna dominated by non-palaeocopes, together with approximately equal proportions of *Londinia* and *Frostiella*.

F. groenvalliana, *L. arisaigensis* and *L. fissurata* are present, with a specimen of *Nodibeyrichia* sp. recovered from a sample 0.15 m above the base of the Rushall Beds. 1.10 m above the base of the Rushall Beds the fauna is dominated by non-palaeocopes, with minor proportions (< 15 per cent.) of *Londinia* and *Frostiella*. Approximately 1.5 m above the base of the Rushall Beds the fauna consists of equal proportions of *Frostiella*, *Londinia*, and non-palaeocope ostracodes. The only carapace recovered from this section is that of *L. fissurata* from 1.5 m above the base of the Rushall Beds.

Prior's Frome. An old quarry face (loc. 24a) exposes 2.96 m of the Upper Perton Beds. Conodont faunas from the lower metre of the exposure are characterized by *O. excavata*, *C. dubius*, *O. confluens*, *P. serratus* and *P. recurvatus* in ascending order of abundance. A limestone bed 0.1 m thick, near the base of the exposure has also yielded *O. r. eosteinhornensis*, *O. r.* ssp. nov., *O. wimani*, and *O. crispa* (Pl. 3, fig. 5). Samples from the upper 2 m of the Upper Perton Beds contain an abundance of *Panderodus* elements, together with *C. dubius*, *O. excavata* and *O. confluens*. A single internal mould of *C. torosa* has been recovered from approximately 0.8 m below the top of the Upper Perton Beds. The junction between the Rushall Beds and the underlying Upper Perton Beds is no longer exposed; the present exposure gap of 0.5 m has been estimated using a published photograph of the section (Gardiner 1927, pl. 39, text-fig. 2). Conodonts obtained from the Rushall Beds are fragmentary, abraded and consist dominantly of *C. dubius*; *O. confluens* is less common and *O. excavata*, *P. recurvatus* and *O. cf. snajdri* are rare.

Other localities. The BGS record bone beds from the base of the Rushall Beds, on the eastern margin of the Woolhope inlier at Caerswell Farm (loc. 25), Whittock's End Farm (loc. 26) and Rushall (loc. 27). *Calcaribeyrichia torosa* and non-palaeocopes have been recovered from the uppermost Upper Perton Beds at Rushall (loc. 27).

May Hill inlier

Localities in this area have not yielded abundant ostracode and conodont faunas for the present study. A single conodont sample from the Upper Longhope Beds of the Longhope by-pass road cut (loc. 30b) is dominated by Pa elements of *O. confluens*, together with elements of *O. excavata*, *C. dubius* and small numbers of *P. serratus* and *Oulodus* sp.

Tortworth inlier

Tite's Point. The Whitcliffe Formation directly overlies the Upper Leintwardine Formation and is marked at the base by an intraformational conglomerate. Only poorly preserved, often abraded and fragmentary conodont specimens have been recovered from the Whitcliffe Formation, ranging in frequency from sixty-one to 6961 elements per kg. The percentage of *C. dubius* elements gradually increases upwards through the formation; the percentage of *O. confluens* and *O. excavata* fluctuate greatly throughout the formation and show no regular pattern. All samples contain a predominance of Pa elements of *O. confluens* compared with other elements in its apparatus. One sample contains only the Pa elements of *O. confluens* and another contains twice as many Pa elements of *O. confluens* as the total of all the other elements of its apparatus. *Panderodus* elements are last present 7.5 m below the top of the Whitcliffe Formation. Rare taxa include *O. crispa*, which was found only in a sample 17 m below the top of the Whitcliffe Formation (Pl. 3, fig. 1). There are rare occurrences of *O. snajdri*, *O. r.* ssp. nov. and *O. r. remscheidensis*. Only 1.7 m of the Downton Castle Sandstone is exposed at Tite's Point, and has not yielded conodonts or ostracodes for the present study.

Other localities. The Brookend Borehole (loc. 32) covered the base of the Downton Castle Sandstone Formation (Cave and White 1968, 1978) but has not been sampled for the present study.

Usk inlier

The Upper Llangibby Beds and Speckled Grit Beds of the Usk area are distinct lithologically from the Upper Whitcliffe Formation and Downton Castle Sandstone Formation, respectively. The original lithostratigraphy of Walmsley (1959) has, therefore, been used for the present study rather than the mixture of lithostratigraphical units from Walmsley (1959) and from the Ludlow area (Bassett *et al.* 1982) as used by Barclay (1989) and Cocks *et al.* (1992).

Brook House. Three phosphatized internal moulds of the ostracode *H. cf. maccoyiana* have been recovered from conodont preparations from the Upper Llangibby Beds (loc. 33) and external moulds of *C. torosa* and *H. cf. maccoyiana* recovered by members of the Ludlow Research Group in 1992. Conodonts from the Upper Llangibby Beds are small, fragmentary and range in frequency from thirty-five to 236 elements per kg. Collections from the lower, more calcareous part of the exposure have similar faunas characterized by *C. dubius*, *O. confluens* and *O. excavata*. Less common species, also confined to the base of exposure, include *Oulodus* sp., *O. r.* ssp. nov. and *O. snajdri* (Pl. 3, fig. 15). The highest sample collected from approximately 3.5 m below the top of the Upper Llangibby Beds, contains only *C. dubius* and *O. confluens*. Approximately 0.4 m of the Speckled Grit Beds, exposed in a small overgrown bank on the south side of the lane to the west of the bridge, have yielded *O. confluens* and *C. dubius*.

Other localities. Localities at Llandegveth Church (loc. 34a), Llangybi Castle (loc. 34b), Granary Farm (loc. 34c) and Llanddewi Court (loc. 34d) previously displayed Speckled Grit Beds with fragmentary fish remains (Walmsley 1959) but none of these is now exposed. The base of the Raglan Mudstone Formation in the Rumney Borehole (loc. 35) is marked by a 0.06 m bed containing abundant fish remains and shell fragments, a level taken to correlate with the Ludlow Bone Bed (Waters and White 1978).

EAST CENTRAL AND SOUTHWEST WALES

Long Mountain

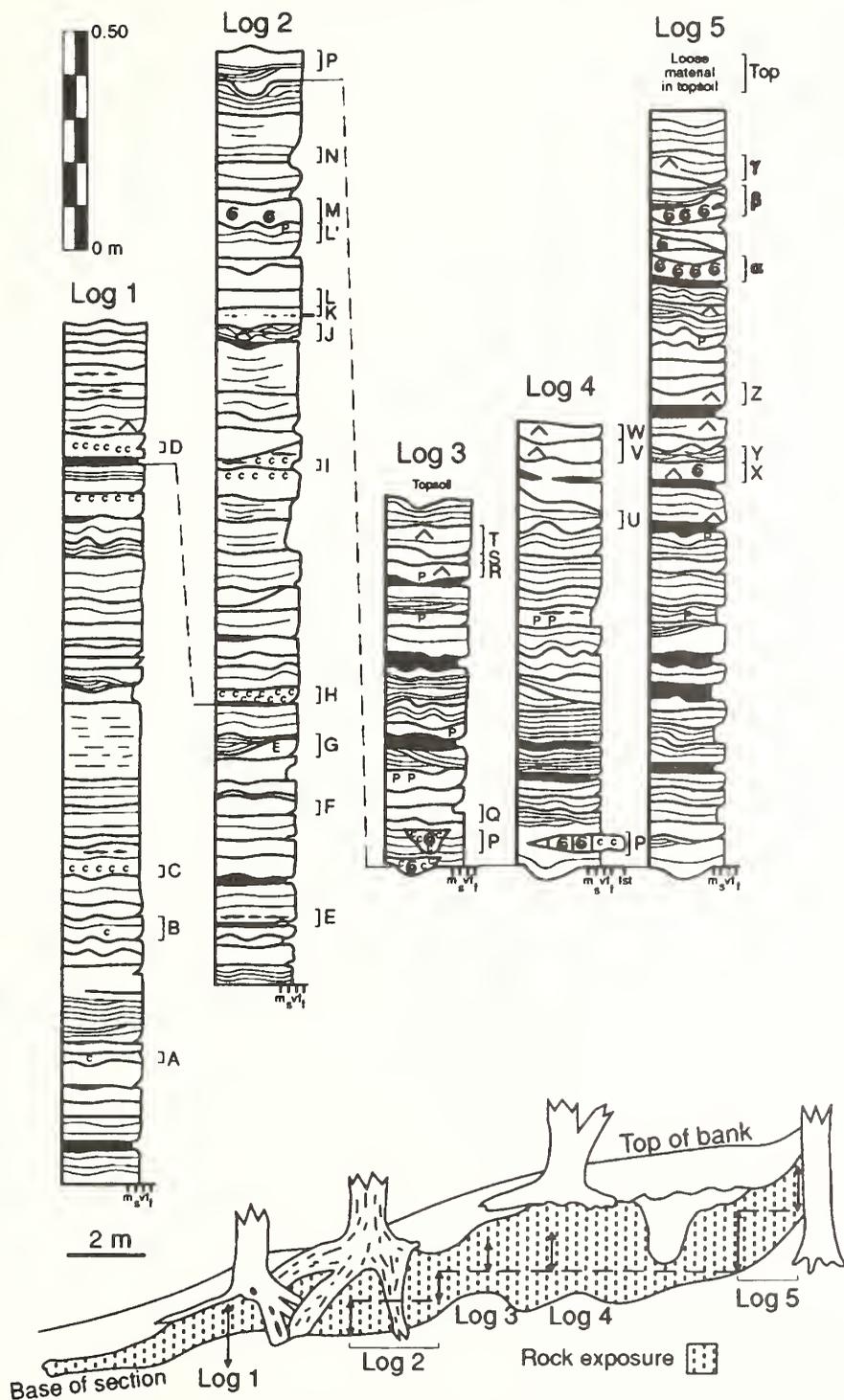
In the Long Mountain area the base of the Downton Castle Sandstone Formation cannot be distinguished lithologically, but correlates with a level within the upper part of the Wallop Hall Member of the Causemountain Formation (Palmer 1970, 1973).

Wallop Hall. 4.75 m of the Wallop Hall Member, Causemountain Formation are exposed, showing a gradual transition in macrofauna from parallel laminated siltstones, rich in articulate brachiopods, below a thin bone bed (bed K) to very fine sandstones characterized by gastropods, inarticulate brachiopods and plant fragments above the bone bed (Text-fig. 11). Ostracodes, preserved only as moulds of disarticulated valves, range in frequency from 0.01 to 1.35 ostracodes $m^2 \times 10^4$ (Text-fig. 12). Most ostracode specimens have been collected above the bone bed (bed K); faunas below that level are sparse (Text-fig. 12). Ostracode specimens below the bone bed are predominantly *C. torosa* with rare *H. cf. maccoyiana* and *L. cf. scanensis*; all three species are also present above the bone bed, and last appear within bed M (Text-fig. 12). *Londinia arisaigensis* and *L. fissurata* first occur just below the bone bed. On the bedding plane surface of the bone bed (Bed K), *C. torosa*, *Lophoctenella* sp., *N. verrucosa*, *L. arisaigensis*, *L. fissurata*, *F. groenvalliana*, and non-palaeocope ostracodes are present. 0–0.25 m above the bone bed the fauna is dominated by *Londinia* with minor proportions of *Nodibeyrichia*, *Frostiella* and non-palaeocopes. Beds 3P and 3Q contain abundant *Londinia*, but the other ostracode collections from beds more than 0.25 m above the bone bed are dominated by non-palaeocopes with minor *Londinia*, *Nodibeyrichia* and *Frostiella*. Eight well-preserved *C. dubius* conodont elements have been recovered from bed K.

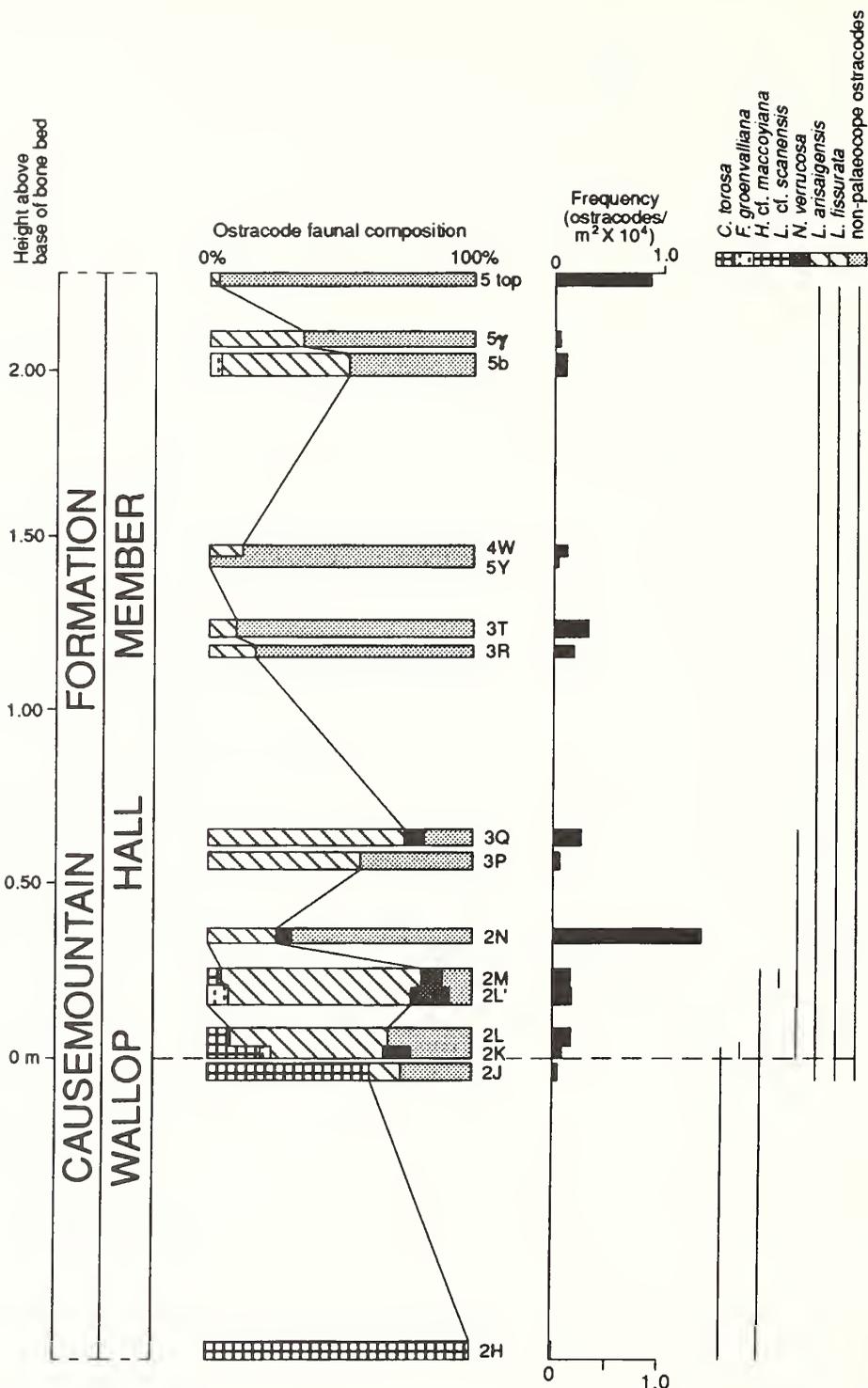
Clun to Felindre area

Nantyrhynau Quarry. This locality (loc. 37) was discovered in 1986 by the BGS during field mapping for the Montgomery Sheet. The field report stated that the boundary between the Cefn Einion and Clun Forest formations was exposed within the quarry, at the base of a calcareous bed approximately 2.5 m below the top of the section. The calcareous bed yielded two *O. excavata* Pa elements and the ostracodes *C. torosa*, *H. cf. maccoyiana*, *Lophoctenella* sp., *L. arisaigensis*, *L. fissurata* and *Frostiella* sp.

Other localities. A section through the Clun Forest Formation was recently exposed when a new forestry path was cut at Within's Wood (loc. 39a). A well developed bone bed is present and is followed by a succession of eight, one millimetre thick bone beds. *F. groenvalliana*, non-palaeocope ostracodes and a specimen of *Londinia* sp. have been recovered from a rottenstone below the level of the bone beds. Abraded conodont elements of *O. confluens* and *C. dubius* have been recovered from the well developed bone bed which yielded 216 conodont elements per kg. Localities in the vicinity of Felindre at Medwaledd Brook (loc. 38a) and Stonehouse Dingle (loc. 38b), provide discontinuous exposures through the uppermost Cefn Einion Formation and the lowermost Clun Forest Formation (Earp 1938, 1940), but provided no conodont or ostracode material for the present



TEXT-FIG. 11. Measured logs of the Wallop Hall Member, Causemountain Formation at Wallop Hall, Long Mountain (loc. 36a), showing sampled horizons (A-Z, α - γ) and sketch of the exposure showing position of logged sections.



TEXT-FIG. 12. Ostracode faunal composition, frequency and ranges of species from the Wallop Hall Member, Causemountain Formation at Wallop Hall, Long Mountain (loc. 36a). Only samples with ten or more valves present are included.

study. A locality at Hendre Farm (loc. 38*c*) has yielded *H. cf. maccoyiana* (Pl. 2, fig. 1) and *L. arisaigensis* from the Cefn Einion Formation. A forestry cutting in the Clun Forest (loc. 39*b*) has yielded *L. arisaigensis*, *L. fissurata*, non-palaeocene ostracodes, and *Leperditia* sp. from a lithology similar to the Green Downton Formation of Holland (1959). *Calcaribeyrichia torosa* has been recovered from the Cefn Einion Formation at Bryn (loc. 39*c*) and Hurst Mill (loc. 39*d*).

Knighton

Meeting House Lane. Collections made by Dr David J. Siveter from the *Platyschisma helicites* Beds are described herein as the locality (40*c*) is no longer exposed. No conodont or ostracode faunas have been found from the Llan-wen Hill Beds at this locality. The lowermost bed of the *Platyschisma helicites* Beds contains *C. torosa*, *H. cf. maccoyiana*, *L. arisaigensis*, *L. fissurata* and abundant non-palaeocene ostracodes. Higher in the *P. helicites* Beds, *L. arisaigensis*, *L. fissurata*, and two specimens of *Frostiella* sp. have been obtained. The Green Downton Formation contains *L. arisaigensis* and *L. fissurata*.

Other localities. Collections made by Dr David J. Siveter from the now overgrown *P. helicites* Beds at Middle Pitts Cottages (loc. 40*b*) include *L. arisaigensis*, *N. verrucosa*, and non-palaeocene ostracodes.

Southwest Wales

The unconformable base of the Downton Group, progressively oversteps older and more deformed rocks in a westerly direction, until west of Llandeilo the Downton Group overlies Ordovician strata (Potter and Price 1965; Squirrell and White 1978; Bassett 1982). Localities reported to expose this unconformity at Builth Wells (loc. 41), Cwm Graig Ddu (loc. 42) and the Sawdde Gorge area (locs 44*a-c*) have yielded no conodont or ostracode faunas for the present study.

Capel Horeb Quarry. No conodont or ostracode specimens have been recovered from the Upper Roman Camp Formation, a correlative of the Lower Whitcliffe Formation (Potter and Price 1965). *F. groenvalliana* and non-palaeocene ostracodes have been recovered from the Long Quarry Formation. The conodont specimen reported by Aldridge (1985) as *O. r. eosteinhornensis* has been re-examined and identified by the present author as a fragment of *O. confluens*. *Coryssognathus dubius*, *O. excavata*, and *P. serratus* also occur in the same sample.

Cennen Valley. In the road cut (loc. 45*a*), the Long Quarry Formation overlies unconformably the Cennen Formation (Potter and Price 1965; Squirrell and White 1978, text-fig. 2*b*; Bassett 1982; Siveter *et al.* 1989), but the section is now completely overgrown. Authors have used differing lithostratigraphical nomenclature, but the stratigraphy employed by Siveter *et al.* (1989) is adopted herein. A thickness of 3.55 m of the Cennen Formation rests unconformably on the older Trichrûg Formation (a full list of macrofauna is given in Squirrell and White 1978, table 3). Ostracodes were identified by the author (BGS collections) as *F. cf. groenvalliana*, *L. cf. scanensis*, and *C. torosa*. Conodont samples collected by Dr R. J. Aldridge when the section was fully exposed, proved to be barren. *F. groenvalliana* and *H. cf. maccoyiana* have been recorded 9.83 m above the base of the overlying Long Quarry Formation (Squirrell and White 1978, table 3).

PALAEOENVIRONMENTS

Upper Whitcliffe Formation and lateral equivalents

Watkins (1979) and Bassett *et al.* (1982) interpreted deposition as subtidal on a proximal shelf, mostly within wave base, shallowing towards the top of the formation with coquinas representing storm events. Allen (1985, p. 90) also recognized storm-related planar to hummocky lamination, cross-lamination and current ripples. Conversely, Richardson and Rasul (1990) proposed a deepening towards the end of deposition of the Upper Whitcliffe Formation at Downton (loc. 14*b*), based on palynofacies. The thickness of upper Ludlow strata is much greater in east central Wales

than on the shelf and probably reflects subsidence of the outer shelf and shelf margin of the Welsh Basin (Bassett *et al.* 1982). Palynofacies at Downton, Long Mountain and at Knighton all show a change towards more open sea floras towards the top of the Ludlow Series (Richardson and Rasul 1990). Sedimentological evidence suggests a shallowing stratigraphically upwards through the Llanwen Hill Beds at Knighton (Holland 1959, p. 475). The Ludlow Series in south-west Wales, traditionally regarded as part of the basinal facies of the Welsh Basin (Holland 1962, text-fig. 1), has also been described as a sandy shelf facies (Potter and Price 1965). A proximal land area probably existed to the south during deposition of the Upper Roman Camp Formation at Capel Horeb, from which plant debris drifted into a shallow sea (Siveter *et al.* 1989, p. 97). The depositional environment of the Cennen Formation near Llandeilo has been interpreted as very shallow marine (Squirrell and White 1978). Breaks in the succession occur near the top of the Ludlow Series in the Cennen Valley, but the succession is continuous at the Sawdde Gorge (Squirrell and White 1978). The apparent 'early' occurrence of *F. groenvalliana* in the Cennen Formation of the Cennen Valley was attributed to 'occurrence in this area in late Ludlow times of a lithofacies comparable with that of the Downton Series' (Squirrell and White 1978, p. 9).

The composition of conodont samples that have undergone significant post-mortem sorting reflect the hydrodynamic regime, rather than the original faunal composition (McGoff 1991). It seems unlikely that samples from the base of the Upper Whitcliffe Formation at Ludlow (loc. 15) have undergone significant post-mortem sorting, as elements are well preserved and relative proportions of individual elements of *O. excavata* remain almost constant, thus reflecting original apparatus composition (Text-fig. 8). Elements from the uppermost metre of the Upper Whitcliffe Formation contain a dominance of *C. dubius* and *O. confluens*, often present almost exclusively as abraded specimens of Sa/Sb and Pa elements respectively. Post-mortem sorting seems to have significantly affected these samples as the Sa/Sb and Pa elements of the respective species are the most robust in the apparatus and therefore most likely to withstand the abrasion associated with sorting. Conodont faunal variations (Text-fig. 7) probably reflect a combination of changes in faunal abundances and hydrodynamic regimes. The preservation of the conodont fauna indicates a more turbulent environment towards the top of the Upper Whitcliffe Formation compared with the basal 5 m. This increased turbulence could be associated with the shallowing interpreted by Watkins (1979) and Bassett *et al.* (1982). General trends in conodont faunal composition towards the top of the Ludlow Series are similar at Aston Munslow (loc. 7a), Woolhope (locs 23–24) and Usk (loc. 33) and may also indicate shallowing. The fauna from the topmost bed of the Whitcliffe Formation at Aston Munslow, dominated by *C. dubius* with minor proportions of *O. confluens*, *O. snajdri*, and *O. cf. crispera*, is almost directly comparable with that from sample 18/1, 0.1–0.15 m below the top of the Upper Whitcliffe Formation at Ludford Corner, Ludlow (loc. 18), differing only in the absence of *remscheidensis* plexus elements.

Conodont elements from the Upper Longhope Beds at Longhope (loc. 30b) and throughout the Whitcliffe Formation at Tite's Point (loc. 31b) have probably undergone significant sorting; the collections are dominated by abraded Pa elements of *O. confluens*. Abrasion and winnowing indicate that, compared with the rest of the shelf, a more turbulent environment existed in this area during deposition of the Whitcliffe Formation.

Downton Castle Sandstone Formation

The marked sedimentological, macro- and microfaunal change at the base of the Ludlow Bone Bed Member has been explained by a sudden regression and subsequent transgression (Allen and Tarlo 1963; Allen 1974; Antia and Whitaker 1978; Antia 1979a, 1980; Bassett *et al.* 1982; Richardson and Rasul 1990). Smith and Ainsworth (1989, p. 898) explained the deposition of the Ludlow Bone Bed Member by 'repeated storm reworking during a period of reduced sediment supply, probably associated with a raised sea level'. Hummocky cross-stratification has been documented from the Sandstone Member at Ludford Corner and suggests shallow deposition (water depths of a few

metres), possibly in a shoreface environment dominated by storms (Siveter *et al.* 1989; Smith and Ainsworth 1989). Richardson and Rasul (1990) stated that the lowermost Downton Castle Sandstone Formation at Ludlow contains a greater proportion of land-derived sporomorphs than the coeval section at Weir Quarry, Downton, although Ainsworth (1991) noted that these differences could be explained by preferential winnowing of the smaller acritarchs from the larger spores. Richardson and Rasul (1990, p. 681) suggested that distribution patterns could have been affected by a 'pattern of distributionary channels delivering high concentrations of land-derived sporomorphs in a non-uniform fashion along an irregularly prograding shoreline'. Ainsworth (1991) questioned Richardson and Rasul's (1990) palynofacies interpretations suggesting that more recent sedimentological interpretations (Smith and Ainsworth 1989) indicated storm dominated environments in which onshore and offshore sediment movements probably influenced proportions of microplankton and spores. Jeram *et al.* (1990) documented trigonotarbid arachnids from the Ludlow Bone Bed Member at Ludford Corner (loc. 18), which are the earliest reported undoubted land animals and indicate a proximal land area. Localized variations of lithofacies at the base of the Rushall Beds in the Woolhope inlier have been proposed to indicate shoals in a shallow sea (Gardiner 1927). The bone bed at the base of the Rushall Beds has been interpreted as a lag concentrate formed during marine regression, and the Rushall Beds interpreted as a marginal marine deposit on a prograding sandy shore which is succeeded by subtidal mud flats (Allen 1985; Brandon 1989). The *Platyschisma helicitis* Beds in the basin at Knighton have no basal bone bed and are thicker than the equivalent Platyschisma Shale Member on the shelf at Ludlow, suggesting continuous deposition in the basinal region (Bassett *et al.* 1982; Allen 1985). Palynofacies variations at Wallop Hall (loc. 36a) indicate a gradual change to more inshore environments between the late Ludlow and the early Přídolí, followed by a gradual change to a more offshore setting and a subsequent return of more onshore conditions (Richardson and Rasul 1990). A similar but less pronounced palynofacies curve has been documented at Knighton (Richardson and Rasul 1990). Concentrations of the inarticulate brachiopod *C. implicata* at the top of the Upper Llan-wen Hill Beds at Knighton (locs 40a, c), also provide an environmental link with similar beds in the uppermost Upper Whitcliffe Formation at Downton (loc. 14a) and Kington (locs 19a, b) (Holland 1962, 1988).

By the end of the Silurian, 'ostracodes had occupied most of the marine environments and taken up most of the life-styles known from modern ostracodes' (Siveter 1984, p. 71). Based on evidence from elsewhere in Europe and also in North America, Siveter (1984, p. 73) suggested that in the marine to restricted marine transition of the British Downton Group that ostracodes 'for the first time began adapting to salinity changes that included reduced salinity, brackish water, and hypersaline conditions'. The species present in the Upper Whitcliffe and Downton Castle Sandstone formations cannot be directly compared taxonomically with Recent ostracodes. However, to assess their palaeoenvironmental and biostratigraphical potential, one can compare other reported occurrences of the same late Silurian species.

Frostiella groenvalliana has been reported in a wide range of environments (Hansch *et al.* 1991), from the deeper water, outer shelf areas of the Łeba elevation, Poland (Tomczykowa and Witwicka 1974) and the Kaliningrad region, Estonia (Kaljo and Sarv 1976) to fully marine carbonate facies of Scånia, Sweden (Martinsson 1962, 1963, 1967). Sarv (1968, 1971) and Kaljo and Sarv (1966) demonstrated the incoming of *F. groenvalliana* within a fully marine succession in the east Baltic. *F. groenvalliana* has been reported from basal part of the Downton Castle Sandstone Formation in the basinal area of the Welsh Basin at Clun, Knighton and Long Mountain (Shaw 1969; present study), across the 'shelf' area of Shropshire (Shaw 1969; Siveter 1974, 1978, 1988, 1989; White and Coppack 1978; Hansch *et al.* 1991; present study), at Woolhope and Capel Horeb, Llandoverly (present study) and in the Scout Hill Flags of the Lake District (Shaw 1971). Because of its apparently wide facies tolerance, the sudden appearance of *F. groenvalliana* at the base of the Ludlow Bone Bed Member is therefore unlikely to be influenced entirely by a marked facies change at that level.

Londinia arisaigensis has been reported from Arisaig, Nova Scotia from both limestones and

shales (Copeland 1960, 1964). In the Welsh Basin *L. arisaigensis* has been recovered from the Downton Castle Sandstone Formation and its lateral equivalents across the 'shelf' area throughout Shropshire and at Woolhope and from the 'basinal' area at Long Mountain and Knighton (Shaw 1969; Siveter 1974, 1978, 1989; present study). The same species has been recovered also from the Cefn Einion Formation at Clun (present study) and the Causemountain Formation at Long Mountain (Shaw 1969), and therefore appears to have been tolerant of a wide range of environments. *L. fissurata* has been reported only from the Welsh Basin (Shaw 1969; Siveter 1974, 1978, 1989) commonly associated with *L. arisaigensis* (present study).

Nodibeyrichia verrucosa is considered by Hansch and Siveter (1994) to be conspecific with *Nodibeyrichia jurassica* (Gailite, 1967) the index species for the late Pridoli Ohessare 'Stage' of Saaremaa, Estonia; it is commonly found in faunally rich and diverse open shelf, marine environments (Sarv 1968, 1971; Kaljo 1970; Meidla and Sarv 1990; Nestor 1990; Hansch and Siveter 1994). In the Welsh Borderland, *N. verrucosa* is restricted to the Much Wenlock, Ludlow, Downton, Knighton and Long Mountain areas (Shaw 1969; Siveter 1974, 1978; present study), areas which embrace both the shelf and basin areas of the Welsh Borderland.

Calcaribeyrichia torosa, the characteristic ostracode of the Upper Whitcliffe Formation in the Welsh Borderland, is found in the lateral equivalent to the Downton Castle Sandstone Formation at Long Mountain (Shaw 1969; present study) and on the shelf at Ludlow (Bassett *et al.* 1982). It is also present in the Underbarrow, Kirkby Moor, and Scout Hill Flags of Cumbria (Shaw 1971). *Beyrichia cuspidata* (Grönwall, 1867), a species characteristic of the marine upper Ludlow of Scania, has been noted as a possible synonym for *C. torosa* (Siveter 1989).

The ostracode taxa characteristic of the Upper Whitcliffe and Downton Castle Sandstone formations appear to be tolerant across a wide range of environments; the marked turnover in ostracode faunas at the base of the Ludlow Bone Bed Member is, therefore, unlikely to be entirely facies related. In the more offshore basinal area of the Welsh Borderland at Long Mountain, the ostracode faunal change is not as sudden as at Ludlow (Shaw 1969; Text-fig. 12). This gradual ostracode faunal change is consistent with coeval gradual palynofacies changes (Richardson and Rasul 1990). The abundance of some ostracode taxa, for example *C. torosa*, therefore appears to be partly environmentally controlled. Changes in ostracode frequencies, preservation, and faunal compositions (Text-figs 9–10) are coeval with fine scale sedimentological changes in the Ludford Lane section, and these factors are possibly related.

The ostracode faunas from the Rushall Beds at Perton Lane (loc. 23a) are concentrated in the coarse bases to fining upwards units. Smith and Ainsworth (1989) proposed that similar beds in the basal metre of the Platyschisma Shale Member at Ludlow were the products of storms; therefore, it is possible that the ostracodes at Perton were selectively winnowed and concentrated by storm action.

Local factors also appear to affect the presence and frequency of ostracode faunas in the Downton Castle Sandstone Formation, which at Downton (loc. 14b) contains a very sparse ostracode fauna compared with Ludford Corner, only 5.5 km to the east, when sedimentological evidence (present study) does not suggest vast differences in lithofacies. The sedimentology of the Downton Castle Sandstone Formation, which yields very few ostracodes, at Aston Munslow is distinct from coeval levels at Ludford Lane, as the sediment coarsens upwards much more rapidly, and lacks multiple bone beds in the lowermost 0.3 m. The Rushall Beds at Perton Lane (loc. 23) are characterized by plant-rich fine sandstones and siltstones with ostracodes, while at Prior's Frome (loc. 24), only 2.5 km to the SE, they comprise conglomerates, very fine sandstones and mudstones but lack ostracodes. Ostracodes are common at localities characterized by an abundance of land plant fragments and/or land derived sporomorphs, for example the Rushall Beds at Perton (loc. 23a) and the Downton Castle Sandstone Formation at Ludford Lane (loc. 17). This may explain why the Downton Castle Sandstone Formation at Downton (loc. 14b), with a lower percentage of land derived sporomorphs compared with Ludford Lane (Richardson and Rasul 1990) also contains a rather sparse ostracode fauna. It is, therefore, possible that high percentages of palynomorphs, land plant fragments, and ostracodes are related phenomena. High frequencies

of land-derived sporomorphs could have been the result of proximal distributary channels delivering sediment along an irregularly prograding shoreline (Richardson and Rasul 1990).

Ostracode faunas recovered from a limestone bed at Linley Brook (loc. 3*b*) are very similar to faunas from beds 17*a*/28 and 17*b*/24 in the Platyschisma Shale Member at Ludlow (Text-figs 9–10). Ostracode collections from these limestone beds are also similar to collections from the Downton Castle Sandstone Formation at Willey (White and Coppack 1978). It is, therefore, possible that the Much Wenlock and Ludlow areas experienced similar environmental conditions at the time of deposition of the Downton Castle Sandstone Formation. However, unabraded conodont specimens recovered from one of these limestone beds at Linley Brook (loc. 3*b*) are unusual, as conodont specimens recovered from the Downton Castle Sandstone Formation across the Welsh Borderland are usually heavily abraded (Pl. 1, fig. 11); the possibility that these abraded specimens have been transported or reworked from older strata cannot be discounted. These calcareous beds with well preserved conodont elements suggest a marine environment in the Much Wenlock area in which conodonts of the genera *Oulodus* and *Ozarkodina* existed during deposition of the Downton Castle Sandstone Formation. Original calcareous ostracode valves obtained from these beds are unusual as ostracodes are only present at these levels elsewhere in the Welsh Borderland as decalcified moulds.

Leperditiid ostracodes are often regarded as shallow water restricted forms (Siveter 1984). *Leperditia* sp. occurs within the Green Downton Formation at Clun (loc. 39*b*) and in a glacial erratic from the Vale of Wigmore, which suggests that by late Downton times the Welsh Basin had become so restricted that only leperditiid ostracodes together with inarticulate brachiopods such as *Lingula* sp. could exist. A single specimen of *Leperditia* sp. has been recovered from loose material from the Platyschisma Shale Member of the Downton Castle Sandstone Formation at Ludford Lane (Pl. 2, fig. 18).

CORRELATION

Britain

The base of the Ludlow Bone Bed at Ludford Corner (loc. 18) defines the base of the Downton Group (Holland *et al.* 1963), formerly regarded as the base of the Downtonian Stage. At the stratotype section (loc. 18) this horizon is marked by the onset of vertebrate sand deposition which has been used to correlate this lithostratigraphical level across the Welsh Borderland to Much Wenlock (Robertson 1927; White and Coppack 1978), Corve Dale (Shergold and Shirley 1968), Downton (Whitaker 1962), Netherton (Stamp 1923; Ball 1951), Kington (Holland and Williams 1985), the Malvern-Abberley Hills (Phipps and Reeve 1967), Woolhope (Squirrell and Tucker 1960), May Hill and Gorsley (Lawson 1954, 1955), Tite's Point (Cave and White 1971), Usk (Walmsley 1959) and Cardiff (Waters and White 1978). Bone beds are developed within the Platyschisma Shale Member of the Downton Castle Sandstone Formation, at Weir Quarry Downton (loc. 14*b*) and Ludford Lane (Text-fig. 6); although they are not as well developed as the Downton Bone Bed (loc. 14*c*; Whitaker 1962), they are possible correlatives. In the absence of a basal bone bed, Antia (1979*b*) used the first occurrence of *F. groenvalliana* and the disappearance of distinctive Upper Whitcliffe brachiopods to indicate the local base of the Downton Castle Sandstone Formation at Siefton (loc. 10*b*). Bone beds at the base of the Downton Castle Sandstone Formation and its lateral equivalents across the shelf area rarely extend laterally into coeval successions in east central Wales (Straw 1930). Only at Wallop Hall, Long Mountain (loc. 36*a*) is a thin bone bed developed at a comparable level within the Causemountain Formation (Palmer 1973). The ostracode succession of *Neobeyrichia lauensis* (Kiesow, 1888) – *C. torosa* – *F. groenvalliana* – *Leperditia* sp. has been recognized in the Ludlow and Přídolí Series of Shropshire and east central Wales, and used for correlation (Straw 1930; Shaw 1969; Siveter 1978, 1989). Other correlations of the base of the Downton Castle Sandstone Formation into east central Wales are based on macrofaunas. For example, the basal *Platyschisma helicitis* Beds at Knighton (the local equivalent to the Downton Castle Sandstone Formation) have a similar lithology to the underlying Upper Llan-wen Hill Beds, but can still be identified on the basis of a faunal change from articulate

brachiopod-dominated faunas to gastropod, bivalve and inarticulate brachiopod faunas (Holland 1959, 1962). Similar faunal successions have been described from the area around Clun and Kerry (Earp 1938, 1940).

The base of the Downton Castle Sandstone Formation at Ludlow is coincident with changes in the macro- and microfaunas (Bassett *et al.* 1982, text-fig. 6). The microfaunal changes displayed by the ostracode faunas offer a potential for biostratigraphical correlation of the base of the Downton Group in Britain. As discussed above, this changeover in ostracode fauna is unlikely to be entirely due to the facies change at this level as these species are known elsewhere in a wide range of environments.

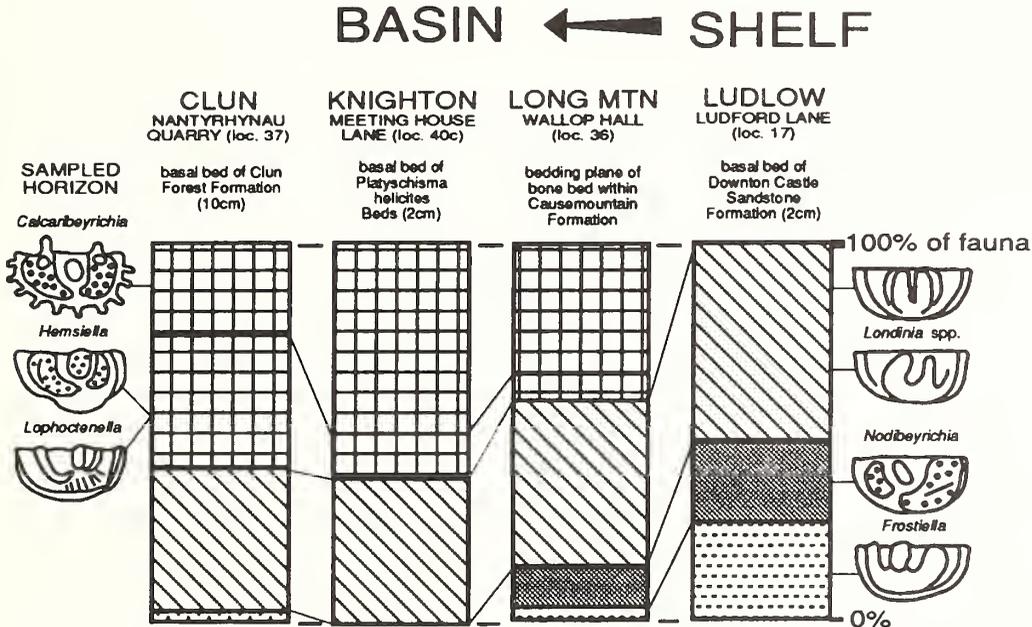
Calcaribeyrichia torosa appears to be environmentally controlled (see above) and it cannot be used as a definitive indicator of Ludlow strata within Britain. *L. arisaigensis*, although common in the Downton Castle Sandstone Formation, has been recovered at Clun and Long Mountain during the present study from levels taken by Cocks *et al.* (1992) to correlate with the Upper Whitcliffe Formation, and thus possibly has only limited correlation potential. *L. fissurata* is confined to the Downton Castle Sandstone Formation (and its lateral equivalents) and could prove biostratigraphically useful. *Nodibeyrichia verrucosa* is restricted to the lowermost 0.34 m of the Downton Castle Sandstone Formation at Ludlow, and therefore has potential for correlation with other areas of the Welsh Borderland. *F. groenvalliana* is more abundant than *N. verrucosa* and is geographically more widespread. In Britain it is widespread at the base of the Downton Castle Sandstone Formation and its lateral equivalents (see above) and can, therefore, be used to indicate basal Downton strata across the Welsh Borderland and into the Lake District.

The only potential anomaly in an otherwise consistent scheme in Britain is the reported occurrence of *F. groenvalliana* in the Cennen Beds (?uppermost Ludlow) of the Cennen Valley, Wales (Squirrell and White 1978; Bassett *et al.* 1982; Siveter 1989). The presumed Ludlow age for the Cennen Formation is based on the occurrence of the characteristic Ludlow trilobite *Calymene neointermedia* and the brachiopod *Sphaerirhynchia* cf. *wilsoni* in the lower part of the Cennen Beds (Squirrell and White 1978). However, most species in the Cennen Formation, including the characteristic Upper Leintwardine brachiopod *Hyattidina canalis*, also occur in the Tilestones (Long Quarry Formation) (Squirrell and White 1978, table 3). The Cennen Valley section is no longer exposed, although the author has examined material at the BGS (Keyworth). The specimens of *Frostiella* are not well preserved and are almost exclusively internal moulds. Well preserved external moulds are needed for positive identification and the specimens are here considered to be best referred to *F.* cf. *groenvalliana*. The species itself is not lithofacies related, so it is unlikely that a lithofacies comparable with the Downton Group could account for the occurrence of it in the Cennen Formation of the Cennen Valley in late Ludlow times (cf. Squirrell and White 1978, p. 9). The ostracodes *Lophoctenella* cf. *scanensis* and *C. torosa* are also present but do not unequivocally indicate a Ludlow age (see earlier discussion). The uppermost Ludlow age for the Cennen Beds is therefore unproven, and *F. groenvalliana* is here considered restricted to the Downton Group of Britain until the Cennen Beds can be shown to be unequivocally Ludlow in age. The upper and lower contacts of the Cennen Formation are uncomfortable, and it is possible that it is a local unit at the base of the Downton Group.

Frostiella groenvalliana does not always occur immediately at the base of the Downton Castle Sandstone Formation as at Linley (locs 3a-c), Brockton (loc. 5), Culmington (loc. 11), Downton (loc. 14b), Clun (loc. 39a) and Llandovery (loc. 43). Without detailed bed by bed collections, the assumption that the base of the Downton Castle Sandstone Formation is at the level of the first occurrence of *F. groenvalliana* at Siefton (Antia 1979b) is therefore unsubstantiated. 'The fauna below does contain some species (e.g. *Lingula minima* and *L. kiesowi*) which are commonly found in the Downtonian' (Antia 1979b, p. 127) which suggests that the base of the Downton Castle Sandstone Formation at Siefton is possibly at a level below the first occurrence of *F. groenvalliana*.

The first occurrence of *F. groenvalliana* at Wallop Hall is coincident with a thin (1 mm) bone bed within the Causemountain Formation (Text-figs 11-12). Closely spaced ostracode samples across this level show a gradual change from a fauna similar to that of the Upper Whitcliffe Formation

at Ludlow to a fauna comparable with that of the Downton Castle Sandstone Formation (Text-fig. 9). *Nodibeyrichia verrucosa* is confined to the lowermost 0.34 m of the Downton Castle Sandstone Formation at Ludlow and first occurs (with *F. groenvalliana*) at the base of bed K, at Wallop Hall (Text-fig. 12). On this basis, the base of the Downton Castle Sandstone Formation should be correlated with the base of bed K within the Causemountain Formation at Wallop Hall (loc. 36a). Similar ostracode faunas from assumed basal Přídolí horizons at Knighton (locs 40b–c), and Nantyrhynau Quarry, Clun (loc. 37) offer potential for correlation of the base of the Downton Castle Sandstone Formation from the shelf at Ludlow to the westernmost part of the Ludlow outcrop (Text-fig. 13).



TEXT-FIG. 13. Comparison of ostracode faunas from individual beds at assumed basal Přídolí horizons along a shelf-basin transect of the Welsh Basin.

The bone beds at Within's Wood (loc. 39c) occur above the first occurrence of *F. groenvalliana*, indicating that these bone beds correlate above the base of the Downton Group and within the Clun Forest Formation. The bone beds are possible correlatives of similar bone beds in the Clun Forest Formation at Bishop's Castle (Allender 1958; Allender *et al.* 1960), the *Platyschisma helicites* Beds at Meeting House Lane at Knighton (loc. 40c), and the *Platyschisma* Shale Member at Downton (loc. 14c). Conodonts recovered from the lowermost bone bed at Within's Wood (loc. 39c) are also similar to conodont collections from the Downton Bone Bed (loc. 14c).

International correlation

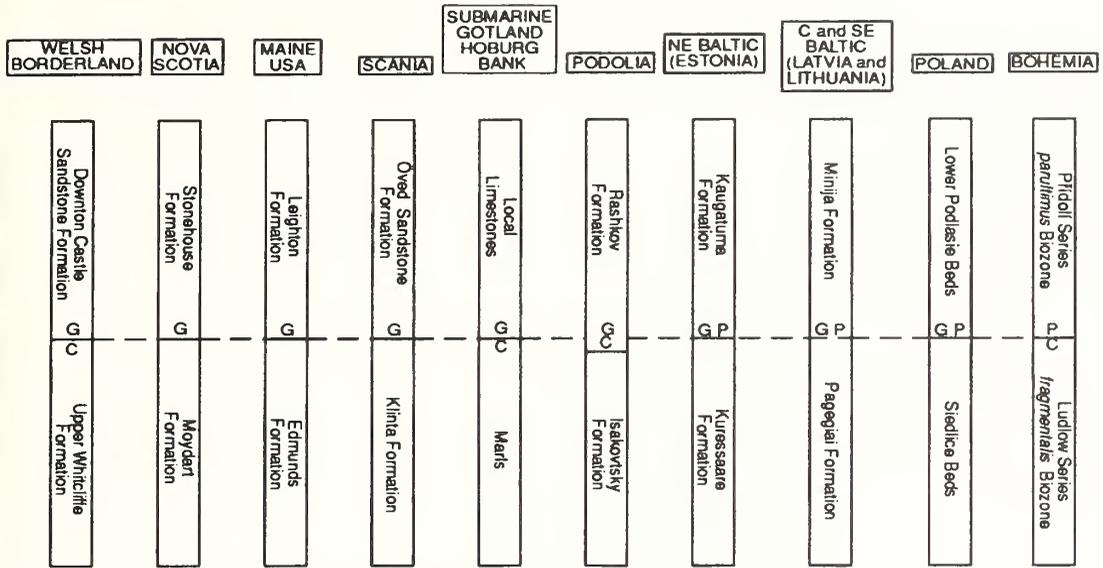
The base of the Přídolí Series is defined at Požáry near Prague (Bassett 1985), within bed 96 at a level coincident with the first occurrence of *Monograptus parultimus* (the base of the *parultimus* Biozone). The stratotype section has been sampled in detail for graptolites, chitinozoans, conodonts, trilobites, bivalves and brachiopods (Jaeger *et al.* 1981; Paris 1981; Kříž *et al.* 1983,

1986; Paris and Kříž 1984; Kříž 1989, 1992). Graptolites are the most important biozonal fossil group for the type Přídolí and allow detailed correlation of the Přídolí Series throughout the Prague Basin.

Conodonts. The stratigraphically important conodont taxa *O. r. eosteinhornensis* and *O. crispera* have been recovered from the section at Požáry. *O. r. eosteinhornensis* ranges from c. 2 m below the base of the Přídolí Series at Požáry, to a level above the top of the Přídolí Series (Chlupáč *et al.* 1980; Kříž *et al.* 1983). *O. crispera* is stratigraphically restricted to the uppermost Ludlow Series at Požáry, appearing only in beds 87–91, and last occurs at a level 0.5 m below the base of the Přídolí Series (Kříž 1989, text-fig. 67). There is a similar situation throughout the Barrandian Basin: *O. crispera* last occurs just below the base of the *parultimus* Biozone at Lochof Marble Quarry, Lochof Cephalopod Quarry, Hvíždalka, Koledník Quarry and at Kosov (Kříž *et al.* 1986; Kříž 1992).

Conodonts from the Upper Whitcliffe Formation at Ludlow offer a direction correlation between the Welsh and Prague basins. Rare specimens of *O. r. eosteinhornensis* occur in collections from the uppermost Ludlow Series at Ludlow and at other localities across the Welsh Borderland (Collinson and Druce 1966; Aldridge 1975, 1985; Aldridge *et al.* 1980; Aldridge and Schönlaub 1989; present study); the subspecies has also been recovered from the Ludlow Bone Bed Member at Ludlow (Walliser 1966). The stratigraphical ranges of *O. cf. crispera* and *O. r. eosteinhornensis* overlap at the top of the Ludlow Series at Ludlow (Text-fig. 7). However, *O. crispera* has a much shorter stratigraphical range in both the Welsh and Prague basins, and therefore has greater correlative potential. Until the present study, only one reported occurrence of *O. cf. crispera* (Pl. 3, fig. 3) had been documented from Britain, 0.3 m below the Ludlow Bone Bed at Ludford Lane, Ludlow (Aldridge and Smith 1985; Aldridge and Schönlaub 1989). This occurrence marked the first (and last) occurrence of *O. crispera* in the Welsh Basin and therefore could be correlated only with the first occurrence of *O. crispera* at Požáry, at a level 2.75 m below the top of the Ludlow Series. Consequently it has been suggested (Schönlaub 1986; Aldridge and Schönlaub 1989), that the base of the Přídolí Series at Ludlow occurs at a level above the Ludlow Bone Bed. Two specimens of *O. crispera* have been recovered from the Upper Whitcliffe Formation as part of the present study, one at Tite's Point, Severn Estuary (Pl. 3, fig. 1) and another at Prior's Frome in the Woolhope inlier (Pl. 3, fig. 2). A broken specimen of *O. cf. crispera* (Pl. 3, fig. 9) has been recovered from sample 18/1 at Ludford Corner (loc. 18), and a specimen of *O. cf. crispera* recovered from the topmost bed of the Upper Whitcliffe Formation at Aston Munslow, Shropshire (Pl. 3, fig. 8). This latter specimen has similar dentition, cavity shape and outline to unequivocal specimens of *O. crispera*, although the curved posterior termination to the element is not well developed (Pl. 3, fig. 8). These new occurrences confirm the presence of *O. crispera* in the Welsh Basin towards the end of deposition of the Upper Whitcliffe Formation, and more importantly provide a range for *O. cf. crispera* at Ludford Corner and Ludford Lane. *O. cf. crispera* can now be shown to range from 0.15–0.3 m below the base of the Downton Castle Sandstone Formation at Ludlow (Text-fig. 7). This new conodont evidence from Ludlow and other localities in the Welsh Borderland, confirms that base of the Přídolí Series in Britain is very close to the level of the base of the Downton Castle Sandstone Formation. Taken in isolation, the occurrence of *O. cf. crispera* in the topmost bed of the Upper Whitcliffe Formation at Aston Munslow indicates that the base of the Přídolí Series is at least as high as the base of the Downton Castle Sandstone Formation and possibly at a level above its base. In the latter case, without the key graptolite *M. parultimus* it would not be possible to pinpoint the level of the base of the Přídolí Series in Britain.

O. crispera follows *O. snajdri* stratigraphically and is thought to be a direct phylogenetic descendant (Aldridge and Schönlaub 1989). *O. snajdri* is considered to be restricted to the Ludlow Series (Aldridge and Schönlaub 1989, text-fig. 172), even though *Spathognathodus* aff. *snajdri* has been recovered from the Äigu Member of the Kaugatuma Formation of Estonia (Viira 1982). The base of the Kaugatuma Formation is considered coincident with the base of the Přídolí Series, as *M. ultimus* occurs at the base of the formation in the south-east Baltic (Kaljo 1990). Viira (1982) was not able to distinguish *S. snajdri* from *S. crispera*. However, *O. crispera* is now regarded as confined to



TEXT-FIG. 14. Correlation of the base of the Downton Castle Sandstone Formation through Europe and eastern North America using ostracode, graptolite and conodont faunas. The correlations of the local lithostratigraphical units are based on Bassett *et al.* (1982; 1989) and Siveter (1989). G, refers to the occurrence of the key ostracode *F. groenvalliana* within a formation; P, denotes the presence of the graptolite *M. parultimus*; C, indicates the presence of the conodont *O. crista*. The symbols are not intended to indicate exact stratigraphical positions and the columns are not drawn to scale.

the Ludlow Series of the Baltic (Männik and Viira 1990); thus the material that Viira (1982) identified as *Spathognathodus* aff. *snajdri* probably includes specimens of *O. snajdri* from the Prídolí Series.

If *O. snajdri* is considered to be a predecessor to *O. crista*, the occurrence of *O. cf. snajdri* above the base of the Rushall Beds at Prior's Frome suggests that there the base of the Prídolí Series should be at least as high as the last occurrence of *O. snajdri*. Conodont faunas from the Barrandian Basin (Schönlaub 1986) indicate that *O. snajdri* and *O. crista* occur together. *Ozarkodina snajdri* also occurs higher than *O. crista* in the Whitcliffe Formation at Tite's Point and the Upper Perton Beds at Prior's Frome. In the Welsh Basin the first appearance of *O. crista* stratigraphically follows that of *O. snajdri*, though their stratigraphical ranges overlap, and *O. snajdri* continues into the Prídolí Series. It must also be noted that the specimens of *O. cf. snajdri* in the Rushall Beds at Prior's Frome are abraded and the possibility that the specimens have been reworked cannot be discounted. The occurrence of *O. cf. snajdri* above the base of the Rushall Beds cannot, therefore, be taken as an indication that the base of the Prídolí Series should be placed above the base of the Rushall Beds at Prior's Frome.

Ostracodes. The ostracodes in the type section for the base of the Prídolí Series in the Barrandian area are provincial and in need of further study (Kříž 1989; Siveter 1989; Hansch 1993); therefore, direct correlation with British ostracode faunas cannot be made. Using the ostracode *F. groenvalliana* and graptolites, the base of the Downton Castle Sandstone Formation can be correlated to Maine, Nova Scotia, Podolia, Scania, Gotland, the Baltic, Poland and Bohemia (Martinsson 1967; Siveter 1978, 1989, text-fig. 164, and references therein; Bassett *et al.* 1982). Text-figure 14 summarizes the chain of correlation based on Bassett *et al.* (1982, text-fig. 7; 1989) and Siveter (1989, text-fig. 164), including conodont data and recent information from Podolia.

The correlative link between ostracode and graptolite faunas occurs in the Kaliningrad region of the Baltic which then provides a link with the graptolite biozonal schemes of Polish and hence,

Bohemian successions. *F. groenvalliana* and the key graptolite *M. parultimus* occur together only in the Kaliningrad region, but at separate stratigraphical levels in the Dubovskoe borehole; the first occurrence of the former occurs 68 m higher than the first occurrence of the latter (Kaljo and Sarv 1976, text-fig. 1; Hansch *et al.* 1991). The first occurrence of *F. groenvalliana* has been recognized within the fully marine Äigu Member of the Kaugatuma Formation of Estonia (Kaljo and Sarv 1966; Sarv 1968, 1971). At Ohesaare on Saaremaa, where the base of the Kaugatuma Formation is shown as coincident with the base of the *parultimus* Biozone, *F. groenvalliana* has also been reported 8 m above the base of the formation (Bassett *et al.* 1989, text-fig. 123). In Lithuania the first occurrence of *F. groenvalliana* coincides with the lowest sample taken within the Kaugatuma Regional Stage (4 m above its base) in the Stoniskiai borehole (Sarv 1977, text-fig. 7). In the Pajevonis 13 borehole of Lithuania, *M. parultimus* is reported at the base of the Minija Formation (Paškevičius 1979). Accepting the correlation of the base of the Minija Formation with the base of the Kaugatuma Stage (Bassett *et al.* 1989, text-fig. 118), this indicates that *F. groenvalliana* and *M. parultimus* first appear at approximately the same level in Lithuania.

Martinsson (1964) reported *Frostiella lebiensis* at a restricted range of 681.75–694.40 m in the Leba 1 borehole in northern Poland. *F. lebiensis* is now recognized as a synonym of *F. groenvalliana* (Hansch *et al.* 1991); the species occurs within the Lower Podlasie Beds of Poland (Text-fig. 14). Tomczyk (1968) recorded graptolites from Polish boreholes including the Lebork Borehole where *M. ultimus* directly follows *M. formosus*. Recovery from most of the Polish boreholes is incomplete, except for the Lebork borehole where it is almost complete. Tomczyk (1968) used the upper limit of *M. formosus* to define the boundary between the Ludlow and the Podlasie Beds. The correlation chart for the Polish Silurian (Tomczykowa and Witwicka 1974, text-fig. 2) based on ostracode, graptolite, and trilobite evidence, places the last occurrence of *M. formosus* in the Leba 1 borehole at a level between 800 and 850 m, at least 230 m below the occurrences of *F. groenvalliana* (*lebiensis*) reported by Martinsson (1964). The first occurrence of *F. groenvalliana* is therefore consistently above the level of the base of the *parultimus* Biozone, most notably at Kaliningrad which is the only locality where the two species occur in the same section.

Since Bassett *et al.* (1982) outlined the correlation of the base of the Downton Castle Sandstone Formation across Europe, further information has become available on the distribution of the ostracode *F. groenvalliana* and the resolution of graptolite biozonal schemes has been increased. A number of potential problems regarding the correlation noted by Bassett *et al.* (1982) can now be addressed.

1. 'There is currently some discrepancy in the interpretation of the ranges of graptolites associated with the lowest Downton ostracode assemblages in Poland' (Bassett *et al.* 1982, p. 18). Ostracode assemblages from the Lower Podlasie Beds in Poland correlate within the *ultimus* Biozone but occur above horizons containing *M. formosus* (Tomczyk 1968, 1970; Tomczykowa and Witwicka 1974). Levels with *M. formosus* were formerly regarded as being within the *ultimus* Biozone, although the taxonomy of the *formosus* group was poorly known (Teller 1969; Jaeger 1977). The graptolite biozonation for the Přídolí in the Prague Basin (Jaeger 1986) shows that the range of *M. formosus* spans the Upper Ludlow *fragmentalis* Biozone and the Přídolí *parultimus* and *ultimus* biozones. The *ultimus* Biozone has now been subdivided into a (lower) *parultimus* Biozone and (upper) *ultimus* Biozone, as *M. parultimus* and *M. ultimus* are almost certainly successive members of a lineage (Jaeger 1986). Occurrence of the ostracode *F. groenvalliana* above levels containing *M. formosus* is not therefore inconsistent with the occurrence of *F. groenvalliana* above the base of the *parultimus* Biozone.
2. Various reviews of the correlation of the Silurian of the East Baltic (Kaljo and Sarv 1966; Kaljo 1970, 1978) have expressed differing opinions as to the correlation of the base of the Downton Group with the Kaugatuma and underlying Kuressaare beds (Bassett *et al.* 1982, p. 18). Kaljo (1979) correlated the base of the Kuressaare Beds with the base of a broad *formosus-ultimus* graptolite interval, with *F. groenvalliana* entering slightly higher in the succession (at the base of the Kaugatuma Beds), suggesting that the base of the Kaugatuma Beds is approximately coincident with the base of the *ultimus* graptolite Biozone (Bassett *et al.* 1982). The latest correlative schemes

for the Silurian of the Baltic place the Kuressaare Formation at the top of the uppermost Ludlow *formosus* Biozone and the base of the Kaugatuma Formation coincident with the base of the *parultimus* Biozone (Bassett *et al.* 1989, text-fig. 118; Kaljo 1990, text-fig. 2).

3. The position of the base of the Minija Formation in the East Baltic is marked as uncertain (Bassett *et al.* 1982, text-fig. 7) and possibly at a level below the base of the *ultimus* Biozone. Bassett *et al.* (1982, p. 17) reported that the basal 'Downton' ostracode fauna in Latvia and Lithuania entered at or closely above the base of the Minija Formation, but it is unclear from what authority this has been cited. Paškevičius (1982) and Sidaravičienė (1986) confirmed that *F. groenvalliana* is present at the base of the Minija Formation in the Stoniskiai, Vidukle and no. 110 (Arjogal profile) boreholes of Lithuania. If the base of the Minija Formation is below the base of the *parultimus* Biozone (see Bassett *et al.* 1982, text-fig. 7) then the correlation using *F. groenvalliana* is wrong. The latest published correlation chart for the Silurian of the Baltic (Bassett *et al.* 1989, text-fig. 118) places the base of the Minija Formation coincident with the base of the *parultimus* Biozone, but a dotted line is used as there is still a degree of uncertainty concerning the exact position of the base of the formation.

Dr David J. Siveter (pers. comm.) has examined material from Podolia and considers *F. modesta* Abushik, 1971, conspecific with *F. groenvalliana*. This further extends the geographical distribution of the species to Podolia where it occurs 17 m above the base of the Rashkov Formation (Abushik *et al.* 1985; Koren' *et al.* 1989). *Ozarkodina crispa* last occurs 5 m above the base of the Rashkov Formation in Podolia (Abushik *et al.* 1985; Koren' *et al.* 1989, text-fig. 105). Conodont evidence therefore suggests that the base of the Přídolí Series is at a level at least 5 m above the base of the Rashkov Formation. This provides an additional example of *F. groenvalliana* closely stratigraphically following *O. crispa*, but with no overlap in their ranges (cf. Ludford Corner, Ludlow). According to Viira (1982) and Schönlaub (1986) it is possible that *O. crispa* ranges into the lowermost Kaugatuma Formation of the east Baltic and, therefore, occurs above levels containing *F. groenvalliana*. As discussed above, *O. crispa* is now considered to be confined to the Upper Paadle Formation, at a level below the Kaugatuma Formation (Männik and Viira 1990).

Frostiella groenvalliana is not always present at the base of the lithostratigraphical units shown in Text-figure 14. However, the distribution is remarkably consistent across the whole of Europe, with *F. groenvalliana* always occurring above the base of the *parultimus* Biozone and occurrences of *O. crispa* and never below these levels. The evidence currently available therefore suggests that *F. groenvalliana* is restricted to the Přídolí Series. The correlation of the base of the Downton Castle Sandstone Formation in the Welsh Borderland with the base of the Přídolí Series in the Czech Republic using the ostracode *F. groenvalliana* is regarded as approximate in terms of the detailed stratigraphical resolution of the present study. The correlation is indirect as the two key species are both present only at Kaliningrad, and then at different stratigraphical levels (see above; Kaljo and Sarv 1976). Lithostratigraphical correlation between local units has to be used to provide the link between ostracode and graptolite faunas. Often there is a degree of uncertainty regarding these correlations, for example with the position of the base of the Minija Formation in western Latvia and western Lithuania. Sampling in Baltic, Scanian, Polish and North American sections has not been carried out to the same high resolution as at the stratotype for the base of the Přídolí Series at Požáry, or at Ludlow in the present study. More detailed sampling is therefore needed on and around the stratigraphical level at the base of the *parultimus* Biozone to recover more detailed records of *F. groenvalliana* and to enable occurrences to be more accurately tied in with the base of the *parultimus* Biozone. With only a limited sample size, borehole data does not often permit detailed studies of these faunas. Borehole recovery is seldom complete, and important faunas may have been lost.

Indirect and approximate correlation using ostracodes and graptolites (Text-fig. 14) suggests that the base of the Přídolí Series in Britain is coincident with the base of the Downton Castle Sandstone Formation. Conodont faunas from the uppermost Upper Whitcliffe Formation at Ludlow and across the Welsh Borderland offer a direct correlation with the Barrandian Basin and suggest that the base of the Přídolí Series in Britain is at least as high as the base of the Downton Castle

Sandstone Formation and possibly a little higher than this. At present, the exact position of the base of the Přídolí Series in Britain cannot be demonstrated because of the absence of the key graptolite species *M. parultimus*; the current state of knowledge on British, European and North American conodont, ostracode and graptolite correlations suggests that the base is coincident with the base of the Downton Castle Sandstone Formation at Ludlow.

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REFERENCES

- ABUSHIK, A. F. 1971. [Ostracoda from the Silurian-Lower Devonian key sections of Podolia.] 7–133. In ABUSHIK, A. F., GUSSEVA, E. A. and ZANINA, I. E. (eds). [*Palaeozoic ostracodes from key sections in the European part of the USSR*], Nauka, Moscow, 248 pp. [In Russian].
- BERGER, A. YA., KOREN', T. N., MODZALEVSKAYA, T. L., NIKIFOROVA, O. I. and PREDTECHENSKY, N. N. 1985. The fourth series of the Silurian in Podolia. *Lethaia*, **18**, 125–146.
- AINSWORTH, R. B. 1991. Discussion on palynofacies in a Late Silurian regressive sequence in the Welsh Borderland and Wales; reply by RICHARDSON, J. B. and RASUL, S. M. *Journal of the Geological Society, London*, **148**, 781–784.
- ALDRIDGE, R. J. 1975. The stratigraphic distribution of conodonts in the British Silurian. *Journal of the Geological Society, London*, **131**, 607–618.
- 1985. Conodonts of the Silurian System from the British Isles. 68–92. In HIGGINS, A. C. and AUSTIN, R. L. (eds). *A stratigraphical index of British conodonts*. Ellis Horwood, Chichester, 263 pp.
- and SMITH, M. P. 1985. Lower Palaeozoic succession of the Welsh Borderland. *Fourth European Conodont Symposium (ECOS IV) Field Excursion B, Guidebook*, 39 pp.
- and SCHÖNLAUB, H.-P. 1989. Conodonts. 274–279. In HOLLAND, C. H. and BASSETT, M. G. (eds). *A global standard for the Silurian System, National Museum of Wales Geological Series No. 9*, National Museum of Wales, Cardiff, 325 pp.
- DORNING, K. J., HILL, P. J., RICHARDSON, J. B. and SIVETER, D. J. 1980. Microfossil distribution in the Silurian of Britain and Ireland. 433–438. In HARRIS, A. L., HOLLAND, C. H. and LEAKE, B. E. (eds). *The Caledonides of the British Isles – reviewed. Special Publication of the Geological Society, London*, **8**. Scottish Academic Press, Edinburgh, 768 pp.
- ALLEN, J. R. L. 1974. Sedimentology of the Old Red Sandstone (Siluro-Devonian) in the Cleve Hills area, Shropshire, England. *Sedimentary Geology*, **12**, 73–167.
- 1985. Marine to fresh water: the sedimentology of the interrupted environmental transition (Ludlow-Siegenian) in the Anglo-Welsh region. *Philosophical Transactions of the Royal Society, London, Series B*, **309**, 85–104.
- and TARLO, L. B. 1963. The Downtonian and Dittonian facies of the Welsh Borderland. *Geological Magazine*, **100**, 129–155.
- ALLENDER, R. 1958. On the stratigraphy and structure of an area of Ludlovian and lower Downtonian rocks near Bishops Castle, Shropshire. Unpublished Ph.D. thesis, University of Wales.
- HOLLAND, C. H., LAWSON, J. D. and WALMSLEY, V. G. 1960. Summer field meeting at Ludlow. *Proceedings of the Geologists' Association*, **71**, 209–232.
- ANTIA, D. D. J. 1979a. Bone Beds: a review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering and microbios. *Mercian Geologist*, **7**, 93–174.
- 1979b. Comments on the environments and faunas across the Ludlovian-Downtonian boundary (upper Silurian) at Siefton, Salop. *Geological Journal*, **14**, 127–134.

- 1980. Sedimentology of the type section of the Upper Silurian Ludlow-Downton Series boundary at Ludlow, Salop, England. *Mercian Geologist*, **7**, 291–321.
- and WHITAKER, J. H. McD. 1978. Scanning electron microscope study of the genesis of the Upper Silurian Ludlow Bone Bed. 119–136. In WHALLEY, W. B. (ed.). *Scanning electron microscopy in the study of sediments*. Geo Abstracts, Norwich, 414 pp.
- BALL, H. W. 1951. The Silurian and Devonian rocks of Turner's Hill and Gornal, south Staffordshire. *Proceedings of the Geologists' Association*, **61**, 225–236.
- BARCLAY, W. J. 1989. Geology of the South Wales coalfield; Part II, the country around Abergavenny (third edition). *Memoir of the Geological Survey of Great Britain for Sheet 232*. Her Majesty's Stationery Office, London, 147 pp.
- BARROIS, C., PRUVOST, P. and DUBOIS, C. 1918. Sur les couches de passage du Silurien au Dévonien dans le bassin houiller du Pas-de-Calais. *Comptes Rendu de l'Académie de Sciences, Paris*, **167**, 705–710.
- — — — 1922. Considérations générales sur les couches siluro-devoniennes de l'Artois. *Mémoires de la Société Géologique du Nord*, **6**, 165–225.
- BASSETT, M. G. 1982. Ordovician and Silurian sections in the Llandagog-Llandeilo area. 271–287. In BASSETT, M. G. (ed.). *Geological excursions in Dyfed, south-west Wales*. National Museum of Wales Geological Series, No. 2. National Museum of Wales, Cardiff, 327 pp.
- 1985. Towards a common language in stratigraphy. *Episodes*, **8**, 87–92.
- LAWSON, J. D. and WHITE, D. E. 1982. The Downton Series as the fourth Series of the Silurian. *Lethaia*, **15**, 1–24.
- KALJO, D. and TELLER, L. 1989. The Baltic. 158–170. In HOLLAND, C. H. and BASSETT, M. G. (eds). *A global standard for the Silurian System*. National Museum of Wales Geological Series No. 9, National Museum of Wales, Cardiff, 325 pp.
- BRANDON, A. 1989. Geology of the country between Hereford and Leominster. *Memoir of the Geological Survey of Great Britain for Sheet 198*. Her Majesty's Stationery Office, London, 62 pp.
- BRANSON, E. B. and MEHL, M. G. 1933. Conodonts from the Bainbridge (Silurian) of Missouri. *University of Missouri Studies*, **8**, 39–52, 69–70.
- CAVE, R. and WHITE, D. E. 1968. Brookend Borehole. *Report of the Institute of Geological Science for 1967*, 75–76.
- — — — 1971. The exposures of Ludlow rocks and associated beds at Tite's Point and near Newnham, Gloucestershire. *Geological Journal*, **7**, 239–254.
- — — — 1978. Stratigraphy of the Brookend Borehole (Vine Farm). *Bulletin of the Ludlow Research Group*, **25**, 44–45.
- CHLUPÁČ, I. 1972. The Siluro-Devonian boundary in the Barrandian. *Bulletin of Canadian Petroleum Geologists*, **20**, 104–174.
- KRÍŽ, J. and SCHÖNLAUB, H.-P. 1980. Field Trip E: Silurian and Devonian conodont localities of the Barrandian. *Abhandlungen der Geologischen Bundesanstalt*, **35**, 147–180.
- COCKS, L. R. M., HOLLAND, C. H. and RICKARDS, R. B. 1992. A revised correlation of Silurian rocks in the British Isles. *Special Report of the Geological Society, London*, **12**, 1–33.
- COLLISON, C. W. and DRUCE, E. C. 1966. Upper Silurian conodonts from the Welsh Borderlands. *Bulletin of the American Association of Petroleum Geologists*, **50**, 608.
- COPELAND, M. J. 1960. Ostracoda from the Upper Silurian Stonehouse Formation, Arisaig, Nova Scotia, Canada. *Palaeontology*, **3**, 92–103.
- 1964. Stratigraphic distribution of Upper Silurian Ostracoda, Stonehouse Formation, Nova Scotia. *Bulletin of the Geological Survey of Canada*, **117**, 1–13.
- CURTIS, M. L. K. 1982. The Tortworth inlier. 27–32. In LAWSON, J. D., CURTIS, M. L. K., SQUIRRELL, H. C., TUCKER, E. V. and WALMSLEY, V. G. 1982. *The Silurian inliers of the south-eastern Welsh Borderland (second edition)*. *Geologists' Association Guide*, **5**, 33 pp.
- DORLODOT, H. de 1912. Le système Dévonien et sa limite inférieure. *Annuaire Société Géologique de Belge*, **39**, M291–371.
- EARP, J. R. 1938. The higher Silurian rocks of the Kerry district, Montgomeryshire. *Quarterly Journal of the Geological Society, London*, **94**, 125–160.
- 1940. The geology of the south-western part of the Clun Forest. *Quarterly Journal of the Geological Society, London*, **96**, 1–11.
- GAILITE, L. K. 1967. [Ostracodes]. 90–168. In GAILITE, L. K., RYBNIKOVA, M. B. and ULST, R. Z. (eds). [The stratigraphy, fauna and conditions of deposition of the Silurian rocks of the East Baltic Republics]. Ministry of Geology of the USSR, Institute of Geology, Riga, 304 pp. [In Russian].

- GARDINER, C. I. 1927. The Silurian inlier of Woolhope (Herefordshire). *Quarterly Journal of the Geological Society, London*, **83**, 501–550.
- GRÖNWALL, K. A. 1867. Översikt af Skånes yngre öfversiluriska bildningar. *Sveriges Geologiska Undersökning*, **19**, 5–39.
- HARSCH, W. 1993. The distribution of ostracodes in the Přídolí, upper Silurian, of the Prague Basin, Czechoslovakia. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung*, **187**, 183–198.
- and SIVETER, DAVID, J. 1994. 'Nodibeyrichia jurassica' and associated beyrichiacean ostracode species and their significance for the correlation of late Silurian strata in the Baltic and Britain. *Journal of Micropalaeontology*, **13**, 81–91.
- and MILLER, C. G. 1991. On *Frostiella groenvalliana* Martinsson. *Stereo-Atlas of Ostracod Shells*, **18**, 125–134.
- HARLAND, W. B., ARMSTRONG, R. L., COX, A. V., CRAIG, A. G., SMITH, A. G. and SMITH, D. G. 1990. *A geologic time scale 1989*. Cambridge University Press, 263 pp.
- HARLEY, J. 1861. On the Ludlow Bone-Bed and its crustacean remains. *Quarterly Journal of the Geological Society, London*, **17**, 542–552.
- HOLLAND, C. H. 1959. The Ludlovian and Downtonian rocks of the Knighton district, Radnorshire. *Quarterly Journal of the Geological Society, London*, **114**, 449–482.
- 1962. The Ludlovian-Downtonian succession in central Wales and the central Welsh Borderland. 87–94. In ERBEN H. K. (ed.). *Symposiums-Band der 2 Internationalen Arbeitstagung über die Silur-Devon-Grenze und die stratigraphie der Silur und Devon, Bonn-Bruxelles 1960*. E. Schweizerbart'sche Verlagsbuchhandlung (Nägele und Obermiller), Stuttgart, 315 pp.
- 1965. The Siluro-Devonian Boundary. *Geological Magazine*, **102**, 213–221.
- 1988. Concentration of the inarticulate brachiopod *Craniops* near the top of the Ludlow Series in the central Welsh Borderland. 189–193. In WOLBERG, D. L. (ed.). *Contributions to Palaeozoic Palaeontology and Stratigraphy in honor of Rousseau H. Flower. Memoir of the New Mexico Bureau of Mines and Mineral Resources*, **44**.
- 1989. Principles, history and classification. 7–26. In HOLLAND, C. H. and BASSETT, M. G. (eds). *A global standard for the Silurian System. National Museum of Wales Geological Series No. 9*. National Museum of Wales, Cardiff, 325 pp.
- and WILLIAMS, E. M. 1985. The Ludlow-Downton transition at Kington, Herefordshire. *Geological Journal*, **20**, 21–31.
- LAWSON, J. D. and WALMSLEY, V. D. 1963. The Silurian rocks of the Ludlow district, Shropshire. *Bulletin of the British Museum (Natural History), Geology Series*, **8**, 95–171.
- JAEGER, H. 1977. Graptolites. 337–345. In MARTINSSON, A. (ed.). *The Siluro-Devonian boundary*. IUGS, Series A, **5**. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 349 pp.
- 1986. Graptolithina. 312–334. In KRÍŽ, J., JAEGER, H., PARIS, P. and SCHÖNLAUB, H. P. (eds). *Přídolí – the fourth subdivision of the Silurian. Jahrbuch der Geologische Bundesanstalt*, **129**, 291–360.
- KRÍŽ, J. and SCHÖNLAUB, H.-P. 1981. *The Přídolí Series as the fourth Series of the Silurian System*. A submission to the Subcommittee on Silurian Stratigraphy, May 1981. International Commission on Stratigraphy, Subcommittee on Silurian Stratigraphy, 41 pp.
- JEPSSON, L. 1974. Aspects of Late Silurian conodonts. *Fossils and Strata*, **6**, 1–54.
- JERAM, A., SELDEN, P. A. and EDWARDS, D. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science*, **250**, 658–661.
- JONES, T. R. 1855. Notes on the Palaeozoic bivalved Entomostraca, no. 1. Some species of *Beyrichia* from the Upper Silurian limestones of Scandinavia. *Annals and Magazine of Natural History*, **16**, 80–92.
- KALJO, D. L. (ed.). 1970. [*The Silurian of Estonia*]. Eesti NSV Teaduste Akadeemia Geoloogia Instituut Valgus, Tallinn, 344 pp. [In Russian].
- 1978. The Downtonian or Přídolian from the point of view of the Baltic Silurian. *Eesti NSV Teaduste Akadeemia Toimetised Geologija Serija*, **27**, 5–10.
- 1979. [On the Silurian stratigraphy of the Baltic republics and the relationships of different types of stratigraphic units]. *Izvestiia Akadeemia nauk kazakhstan SSR*, **4–5**, 107–115. [In Russian].
- 1990. The Silurian of Estonia. 21–26. In KALJO, D. and NESTOR, H. (eds). *Field meeting Estonia, 1990*. Institute of Geology, Estonian Academy of Sciences, Subcommittee on Ordovician Stratigraphy, IUGS, Subcommittee on Silurian Stratigraphy, IUGS, Project 'Global Bioevents' IGCP, Tallinn, 209 pp.
- and SARV, L. 1966. [On the correlation of the Baltic upper Silurian]. *Eesti NSV Teaduste Akadeemia Toimetised Tehnikateaduste Fisika Matematika Serija*, **15**, 277–288. [In Russian].

- . 1976. [Stratigraphy of the upper Silurian section of the Dubovskoye boring (Kaliningrad region)]. *Eesti NSV Teaduste Akadeemia Toimetised Geologija Serija*, **25**, 325–333. [In Russian].
- KIESOW, J. 1888. Über Gotländischen Beyrichien. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **40**, 1–16.
- KING, W. W. and LEWIS, W. J. 1912. The uppermost Silurian and Old Red Sandstone of south Staffordshire. *Geological Magazine*, **19**, 437–443, 481–484.
- KOREN¹, T. N., ABUSHIK, A. F., MODZALEVSKAYA, T. L. and PREDTECHENSKY, N. N. 1989. Podolia. 141–149. In HOLLAND, C. H. and BASSETT, M. G. (eds). *A global standard for the Silurian System. National Museum of Wales Geological Series No. 9*. National Museum of Wales, Cardiff, 325 pp.
- KRAUSE, A. 1891. Beitrag zur Kenntnis der Ostracoden-fauna in silurischen Diluvialgeschieben. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **43**, 488–521.
- KŘÍŽ, J. 1989. The Přídolí Series in the Prague Basin (Barrandian area, Bohemia). 90–100. In HOLLAND, C. H. and BASSETT, M. G. (eds). *A global standard for the Silurian System. National Museum of Wales Geological Series No. 9*. National Museum of Wales, Cardiff, 325 pp.
- . 1992. Silurian field excursions: Prague Basin (Barrandian), Bohemia. *National Museum of Wales Geological Series No. 13*. National Museum of Wales, Cardiff, 111 pp.
- and twelve others. 1983. *The Přídolí Series as the fourth Series of the Silurian System*. A supplementary submission to the Subcommittee on Silurian Stratigraphy, March 1983, International Commission on Stratigraphy, Subcommittee on Silurian Stratigraphy, 59 pp.
- JAEGER, H., PARIS, F. and SCHÖNLAUB, H.-P. (eds). 1986. Přídolí – the fourth subdivision of the Silurian. *Jahrbuch der Geologische Bundesanstalt*, **129**, 291–360.
- LAWSON, J. D. 1954. The Silurian succession at Gorsley (Herefordshire). *Geological Magazine*, **91**, 227–237.
- . 1955. The geology of the May Hill inlier. *Quarterly Journal of the Geological Society, London*, **111**, 84–116.
- . 1967. The May Hill inlier. 22–27. In LAWSON, J. D., CURTIS, M. L. K., SQUIRRELL, H. C., TUCKER, E. V. and WALMSLEY, V. G. *The Silurian inliers of the south-eastern Welsh Borderland (first edition)*. *Geologists' Association Guide*, **5**, 33 pp.
- . 1982. The May Hill inlier. 17–27. In LAWSON, J. D., CURTIS, M. L. K., SQUIRRELL, H. C., TUCKER, E. V. and WALMSLEY, V. G. *The Silurian inliers of the south-eastern Welsh Borderland (second edition)*. *Geologists' Association Guide*, **5**, 33 pp.
- McGOFF, H. J. 1991. The hydrodynamics of conodont elements. *Lethaia*, **24**, 235–247.
- McLAREN, D. J. 1977. The Siluro-Devonian Boundary Committee – a final report. 21–34. In MARTINSSON, A. (ed.). *The Siluro-Devonian boundary*. IUGS, Series A, No. 5. E. Schweitzerbart'sche Verlagsbuchhandlung, Stuttgart, 349 pp.
- MÄNNIK, P. and VIIRA, V. 1990. Conodonts. 84–89. In KALJO, D. and NESTOR, H. (eds). *Field Meeting Estonia, 1990*. Institute of Geology, Estonian Academy of Sciences, Subcommittee on Ordovician Stratigraphy, IUGS, Subcommittee on Silurian Stratigraphy, IUGS, Project 'Global Bioevents' IGCP, Tallinn, 209 pp.
- MARTINSSON, A. 1962. Ostracodes of the family Beyrichiidae from the Silurian of Gotland. *Bulletin of the Geological Institutions of the University of Uppsala*, **41**, 1–369.
- . 1963. The concealed Silurian of the Baltic area. *Geologiska Föreningens i Stockholm Förhandlingar*, **84**, 539–541.
- . 1964. Palaeocene ostracodes from the well Leba 1 in Pomerania. *Geologiska Föreningens i Stockholm Förhandlingar*, **86**, 125–161.
- . 1967. The succession and correlation of faunas from the Silurian of Gotland. *Geologiska Föreningens i Stockholm Förhandlingar*, **89**, 350–386.
- MEIDLA, T. and SARV, L. 1990. Ostracodes. 68–71. In KALJO, D. and NESTOR, H. (eds). *Field meeting Estonia, 1990*. Institute of Geology, Estonian Academy of Sciences, Subcommittee on Ordovician Stratigraphy, IUGS, Subcommittee on Silurian Stratigraphy, IUGS, Project 'Global Bioevents' IGCP, Tallinn, 209 pp.
- MILLER, C. G. 1993. Micropalaeontology (Conodonts, Ostracoda) across the Ludlow/Přídolí series boundary (Silurian) of Wales and the Welsh Borderland. Unpublished Ph.D. thesis, University of Leicester, U.K.
- and ALDRIDGE, R. J. 1993. The taxonomy and apparatus structure of the Silurian distomodontid conodont *Coryssognathus Link and Druce*, 1972. *Journal of Micropalaeontology*, **12**, 241–255.
- MITCHELL, G. H., POCOCK, R. W. and TAYLOR, J. H. 1962. Geology of the country around Droitwich, Abberley and Kidderminster (explanation of sheet 182). *Memoirs of the Geological Survey of Great Britain, England and Wales*. Her Majesty's Stationery Office, London, 137 pp.
- MURCHISON, R. I. 1834. On the structure and classification of the Transition Rocks of Shropshire, Herefordshire and part of Wales. *Proceedings of the Geological Society, London*, **2**, 13–18.
- . 1839. *The Silurian System*. John Murray, London, 768 pp.

- MURCHISON, R. I. 1842. Anniversary address of the President. *Proceedings of the Geological Society, London*, **3**, 637–687.
- 1852. On some of the remains in the bone-bed of the Upper Ludlow Rock. *Quarterly Journal of the Geological Society, London*, **9**, 16–17.
- 1854. *Siluria*. John Murray, London, 523 pp.
- NESTOR, H. 1990. Ohesaare Cliff. 175–178. In KALJO, D. and NESTOR, H. (eds). *Field meeting Estonia, 1990*. Institute of Geology, Estonian Academy of Sciences, Subcommittee on Ordovician Stratigraphy, IUGS, Subcommittee on Silurian Stratigraphy, IUGS, Project 'Global Bioevents' IGCP, Tallinn, 209 pp.
- PALMER, D. C. 1970. A stratigraphical synopsis of the Long Mountain, Montgomeryshire and Shropshire. *Proceedings of the Geological Society, London*, **1660**, 341–346.
- 1973. The geology of the Long Mountain, Montgomeryshire and Shropshire. Unpublished Ph.D. thesis, Trinity College, Dublin.
- PARIS, F. 1981. Les chitinozoaires dans le Paléozoïque du sud-ouest de l'Europe. *Mémoires de la Société Géologique et Minéralogique de Bretagne*, **26**, 1–412.
- and KRÍŽ, J. 1984. Nouvelles espèces de chitinozoaires à la limite Ludlow – Přídolí en Tchécoslovaquie. *Review of Palaeobotany and Palynology*, **43**, 155–177.
- PAŠKEVIČIUS, I. J. 1979. [*Biostratigraphy and graptolites of the Lithuanian Silurian*]. Mokslas Publishers, Vilnius, 268 pp. [In Russian with English summary].
- 1982. [Problems of distribution of conditions of deposition and correlation of Silurian fauna in Lithuania and neighbouring region]. *Geologija*, **3**, 17–51. [In Lithuanian with English summary].
- PENN, J. S. W. and FRENCH, J. 1971. *The Malvern Hills. Geologists' Association Guide*, **4**, 36 pp.
- PHIPPS, C. B. and REEVE, F. A. E. 1967. Stratigraphy and geological history of the Malvern, Abberley and Ledbury Hills. *Geological Journal*, **5**, 339–368.
- POTTER, J. F. and PRICE, J. H. 1965. Comparative sections through rocks of Ludlovian–Downtonian age in the Llandovery and Llandeilo districts. *Proceedings of the Geologists' Association*, **76**, 379–402.
- REXRoad, C. B. 1967. Stratigraphy and conodont paleontology of the Brassfield (Silurian) in the Cincinnati Arch area. *Bulletin of the Indiana Geological Survey*, **36**, 1–64.
- RHODES, F. H. T. 1953. Some British lower Palaeozoic conodont faunas. *Philosophical Transactions of the Royal Society, Series B*, **237**, 261–334.
- RICHARDSON, J. B. and RASUL, S. M. 1990. Palynofacies in a late Silurian regressive sequence in the Welsh Borderland and Wales. *Journal of the Geological Society, London*, **147**, 675–686.
- ROBERTSON, T. 1927. The highest Silurian rocks of the Wenlock district. *Memoir of the Geological Survey of Great Britain, Summary of the Program for 1926*, 80–97.
- SARV, L. 1968. [*Ostracod Families Craspedobolbinidae, Beyrichiidae and Primitiopsidae in the Silurian of Estonia*]. Eesti NSV Teaduste Akadeemia Geoloogia Institut, Tallinn, 104 pp. [In Russian].
- 1971. [Silurian ostracodes from the Ohesaare boring]. *Eesti NSV Akadeemia Toimetised, Keemia, Geoloogia*, **20**, 349–355. [In Russian].
- 1977. [On the Upper Silurian ostracode stratigraphy in the middle and south-east Baltic area]. 159–178. In KALJO, D. L. (ed.). *Facies and fauna of the Baltic Silurian*. Academy of Sciences of the Estonian SSR, Institute of Geology, Tallinn, 286 pp. [In Russian].
- SCHÖNLAUB, H.-P. 1986. Conodonts. 334–337. In KRÍŽ, J., JAEGER, H., PARIS, F. and SCHÖNLAUB, H.-P. (eds). *Přídolí – the fourth subdivision of the Silurian. Jahrbuch der Geologische Bundesanstalt*, **129**, 291–360.
- SHAW, R. W. L. 1969. Beyrichiacean ostracodes from the Downtonian of Shropshire. *Geologiska Föreningens i Stockholm Förhandlingar*, **91**, 52–72.
- 1971. Ostracoda from the Underbarrow, Kirkby Moor and Scout Hill Flags (Silurian) near Kendal, Westmorland. *Palaeontology*, **14**, 595–611.
- SHERGOLD, J. H. and SHIRLEY, J. 1968. Faunal stratigraphy of the Ludlovian rocks between Craven Arms and Bourton near Much Wenlock, Shropshire. *Geological Journal*, **6**, 119–138.
- SIDARAVICIENE, N. V. 1986. [Distribution of ostracodes in different Přídolian facies of Lithuania.] 116–126. In KALJO, D. L. and KLAAMANN, E. (eds). *Theory and practice of ecostratigraphy*. Institute of Geology, Estonian Academy of Sciences, Tallinn, Valgus, 295 pp. [In Russian].
- SIVETER, DAVID, J. 1974. The Superfamily Beyrichiacea (Ostracoda) from the Silurian and Devonian Systems of Britain. Unpublished Ph.D. thesis, University of Leicester.
- 1978. The Silurian. 57–100. In BATE, R. H. and ROBINSON, E. (eds). A stratigraphical index of British Ostracoda. *Geological Journal, Special Issue*, **8**, 538 pp.
- 1982. Casts illustrating fine ornament of a Silurian ostracode. 105–122. In BATE, R. H., ROBINSON, E. and SHEPPARD, L. M. (eds). *Fossil and Recent ostracods*. Ellis Horwood, Chichester, 493 pp.

- 1984. Habits and modes of life of Silurian ostracodes. 71–85. In BASSETT, M. G. and LAWSON, J. D. (eds). *Autecology of Silurian organisms. Special Paper in Palaeontology*, **32**, 1–295.
- 1988. The lower Palaeozoic of the northern Welsh Borderland and south Wales. *British Micropalaeontological Society Field Guide*, **2**, 47 pp.
- 1989. Ostracodes. 252–264. In HOLLAND, C. H. and BASSETT, M. G. (eds). *A global standard for the Silurian System. National Museum of Wales Geological Series No. 9*. National Museum of Wales, Cardiff, 325 pp.
- OWENS, R. M. and THOMAS, A. T. 1989. *Silurian field excursions: a geotraverse across Wales and the Welsh Borderland. National Museum of Wales Geological Series No. 10*. National Museum of Wales, Cardiff, 133 pp.
- SMITH, R. D. A. and AINSWORTH, R. B. 1989. Hummocky cross-stratification in the Downton of the Welsh Borderland. *Journal of the Geological Society, London*, **146**, 897–900.
- SQUIRRELL, H. C. and TUCKER, E. V. 1960. The geology of the Woolhope inlier (Herefordshire). *Quarterly Journal of the Geological Society, London*, **116**, 139–180.
- 1967. Woolhope and Gorsley. 9–17. In LAWSON, J. D., CURTIS, M. L. K., SQUIRRELL, H. C., TUCKER, E. V. and WALMSLEY, V. G. *The Silurian inliers of the south-eastern Welsh Borderland (first edition). Geologists' Association Guide*, **5**, 33 pp.
- 1982. Woolhope and Gorsley. 9–17. In LAWSON, J. D., CURTIS, M. L. K., SQUIRRELL, H. C., TUCKER, E. V. and WALMSLEY, V. G. *The Silurian inliers of the south-eastern Welsh Borderland (second edition). Geologists' Association Guide*, **5**, 33 pp.
- and WHITE, D. E. 1978. Stratigraphy of the Silurian and Old Red Sandstone of the Cennen Valley and adjacent areas, south-east Dyfed, Wales. *Report of the Institute of Geological Sciences*, **78/6**, 45 pp.
- STAMP, L. D. 1918. The highest Silurian rocks of the Clun Forest district. *Quarterly Journal of the Geological Society, London*, **74**, 221–246.
- 1920. Note on the determination of the limit between the Silurian and Devonian Systems. *Geological Magazine*, **57**, 164–171.
- 1923. The base of the Devonian with special reference to the Welsh Borderland. *Geological Magazine*, **60**, 276–282, 331–336, 367–372, 385–410.
- STRAW, S. H. 1930. The Siluro-Devonian boundary in south central Wales. *Journal of the Manchester Geological Association*, **1**, 257–264. [for 1929].
- 1953. The Silurian succession at Cwm Graig Ddu (Breconshire). *Liverpool and Manchester Geological Journal*, **1**, 208–219.
- TELLER, L. 1969. The biostratigraphy of Poland based on graptolites. *Acta Geologica Polonica*, **19**, 393–501.
- TOMCZYK, H. 1968. Silurian stratigraphy in the Peribaltic areas of Poland based on drilling data. *Zwart Geologica*, **12**, 15–36.
- 1970. The Silurian. 237–319. In SOKOLOWSKI, S. (ed.). *Geology of Poland, volume 1. Stratigraphy, part 1. Pre-Cambrian and Palaeozoic*. Geological Institute, Publishing House Wydawnictwa Geologiczne, Warsaw, 651 pp. [Translation of Polish Edition 1968].
- TOMCZYKOWA, E. and WITWICKA, E. 1974. Stratigraphic correlation of Podlasian deposits on the basis of trilobites and ostracods in the peri-Baltic area of Poland (upper Silurian). *Instytut Geologiczny Biuletyn*, **276**, 55–84.
- TURNER, S. 1973. Siluro-Devonian thelodonts from the Welsh Borderland. *Journal of the Geological Society, London*, **188**, 319–351.
- VIIRA, V. 1982. Late Silurian shallow and deep water conodonts of the east Baltic. 79–88. In KALJO, D. and KLAAMANN, E. (eds). *Ecostratigraphy of the east Baltic Silurian*. Institute of Geology, Estonian Academy of Sciences, Tallinn, 295 pp.
- WALLISER, O. 1964. Conodonten des Silurs. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, **41**.
- 1966. Die Silur-Devon Grenze. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **125**, 235–246.
- WALMSLEY, V. G. 1959. The geology of the Usk inlier (Monmouthshire). *Quarterly Journal of the Geological Society, London*, **114**, 483–521.
- 1982. The Usk inlier. 4–9. In LAWSON, J. D., CURTIS, M. L. K., SQUIRRELL, H. C., TUCKER, E. V. and WALMSLEY, V. G. *The Silurian inliers of the south-eastern Welsh Borderland (second edition). Geologists' Association Guide*, **5**, 33 pp.
- WATERS, R. A. and WHITE, D. E. 1978. The Rumney borehole. *Report of the Institute of Geological Science*, **79**, 10–11.
- WATKINS, R. 1979. Benthic community organisation in the Ludlow Series of the Welsh Borderland. *Bulletin of the British Museum (Natural History), Geology Series*, **31**, 175–280.

- WHITAKER, J. H. McD. 1962. The geology of the area around Leintwardine, Herefordshire. *Quarterly Journal of the Geological Society, London*, **118**, 319–351.
- WHITE, D. E. and COPPACK, B. C. 1978. A new section showing the junction between the Ludlow and Downton series in the Much Wenlock area, Shropshire. *Bulletin of the Geological Survey of Great Britain*, **62**, 25–32.
- WHITE, E. I. 1950. The vertebrate faunas of the Lower Old Red Sandstone of the Welsh Borders. *Bulletin of the British Museum (Natural History), Geology Series*, **1**, 49–67.
- ZIEGLER, W. 1960. Conodonten aus dem Rheinischen Unterdevon (Gedinnium) des Remscheider Sattels (Rheinisches Schiefergebirge). *Paläontologische Zeitschrift*, **34**, 169–201.

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THE TYPE SPECIES OF THE BRACHIOPOD *YUNNANELLINA* FROM THE DEVONIAN OF SOUTH CHINA

by MA XUEPING

ABSTRACT. *Yunnanellina hanburyi*, the type species of the genus, is widely distributed in South China. Study of the external and internal features of abundant specimens from three sections in central Hunan indicates that other previously described nominal species and subspecies of *Yunnanellina* from the Upper Devonian of South China, are junior synonyms of the type species. *Y. hanburyi* is very varied in both external form and internal structures. Internally, the septalium may be open, or covered anteriorly by a connectivum. This connectivum shows a systematic change with time and, on this basis, three morphotypes have been established which comprise the *Y. hanburyi* lineage. The stratigraphical range of the lineage can be correlated with the upper *crepida* Zone (Early Famennian).

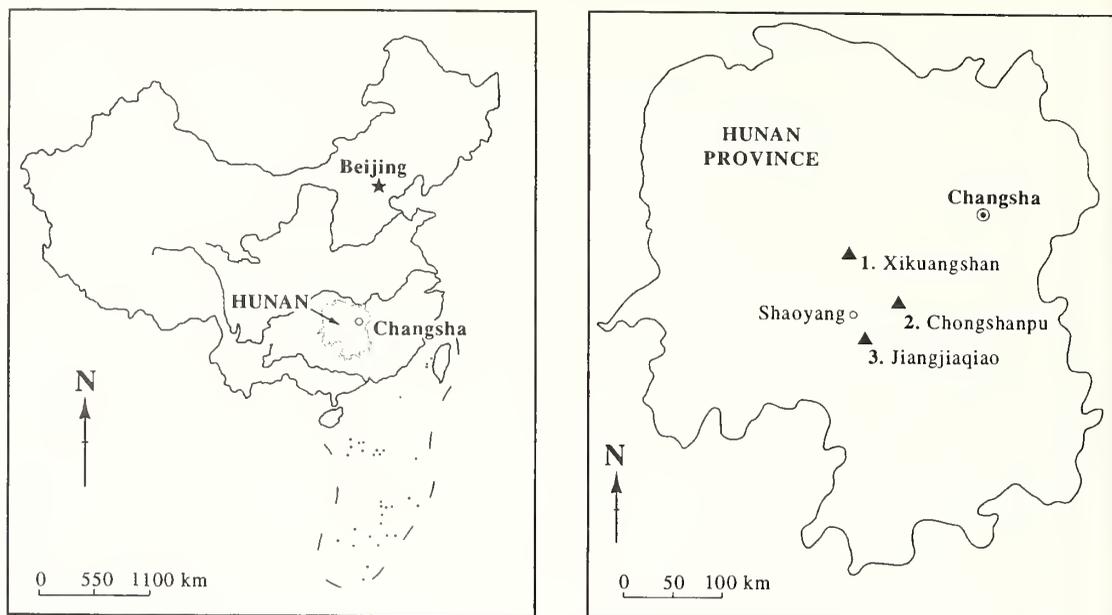
RHYNCHONELLA hanburyi Davidson, 1853, the type species of *Yunnanellina* Grabau, 1931, is widely distributed in South China. Davidson's original material includes only five specimens, four of which possess two plications in the sulcus, with one, a juvenile, too immature to have developed a sulcus or fold. Kayser (1883) noticed some uniplicate specimens and correctly assigned them to Davidson's species as a varietal form. But since 1931, more species and subspecies, some of which have been introduced in the literature as mutations or varieties, have been described from the Upper Devonian of South China. These are *Yunnanellina hanburyi* mut. *lata* Grabau, 1931; *Y. uniplicata* Grabau, 1931; *Y. triplicata* Grabau, 1931; *Y. hanburyi* mut. *sublata* Tien, 1938; *Y. triplicata* var. *latiformis* Tien, 1938; *Y. obesa* Tien, 1938; *Y. heyuanzhaiensis* Fang in Fang and Zhu, 1974 (= *Y. xintianensis* Zhao in Yang et al. 1977); *Y. uniplicata mesosulcata* Liu in Liu et al. 1982 and *Y. undatussulcus* Li, 1987. All the above nominal species or subspecies were established solely on different external features, especially the number of sinial plications and general outline. The validity of these taxa has not as yet been tested. Nevertheless, the binomials *Yunnanellina hanburyi*, *Y. uniplicata* and *Y. triplicata* have frequently appeared in the Chinese literature.

Sartenaer (1971) gave a fairly thorough treatment of *Yunnanellina* and discussed forms labelled *Yunnanellina* from most parts of the world. He redescribed the type species based chiefly on the type material deposited in the Natural History Museum in London, and material in the United States National Museum in Washington, D.C. This redescription was largely based on external characters. Regarding the internal structure, Sartenaer pointed out (p. 204) that the 'septalium [was] short, deep, wide, amphora-shaped and uncovered'. This description was based on only one sectioned specimen and as such can not be taken as definitive.

Xu (1979) discussed the stratigraphical distribution of the genus and gave a Famennian age for the *Yunnanellina*-*Yunnanella* fauna. The present study is an attempt to clarify the taxonomy of *Yunnanellina hanburyi* and related forms from South China and to demonstrate its intraspecific and stratigraphical variations in internal morphology.

MATERIAL AND METHODS

Yunnanellina is very abundant in Hunan, especially in the centre of the province, where Upper Devonian strata with abundant benthic fossils are well developed, making it the most important



TEXT-FIG. 1. Location map of the study area. 1, Xikuangshan section (samples beginning with the letter L). 2, Chongshanpu section (T). 3, Jiangjiaqiao section (C).

area for research into the Upper Devonian of China. Numerous specimens of *Yunnanellina*, most of which are well preserved, have been collected from three sections in central Hunan (Text-fig. 1). Thirty-six specimens were sectioned, of which twenty-two have been serially sectioned to reveal the systematic change in internal structure. Most of the sections were recorded as acetate peels. The distance between each adjacent peel was usually taken at *c.* 0.3 mm. Detailed microstructure was added to the camera lucida drawings of the outline of the internal structure through examination of the peels under a microscope. The illustrated acetate peels were selected to show significant changes in the internal structure. The thirty-six sectioned specimens include twelve of '*Y. uniplicata*', eighteen of '*Y. hanburyi*', and six of '*Y. triplicata*'. In the following text, these three 'species' are expressed as uniplicate, biplicate and triplicate forms, respectively. All specimens illustrated in the text-figures and plates are deposited in the Department of Geology, Peking University.

TAXONOMIC DISCUSSION OF *YUNNANELLINA* FROM SOUTH CHINA

Ten species and subspecies of *Yunnanellina* have been described from the Upper Devonian of South China. The following list gives the features by which they were distinguished.

1. *Y. hanburyi* (Davidson, 1853): with two plications in the sulcus.
2. *Y. h. mut. lata* Grabau, 1931: with flatter shell than *Y. hanburyi*.
3. *Y. h. mut. sublata* Tien, 1938: similar to *Y. h. mut. lata*, but smaller.
4. *Y. uniplicata* Grabau, 1931: one plication in the sulcus.
5. *Y. u. mesosulcata* Liu in Liu *et al.*, 1982: with a furrow on the sinial plica and correspondingly a small median plica present in the interspace on the fold.
6. *Y. triplicata* Grabau, 1931: with three plications in the sulcus.
7. *Y. t. var. latiformis* Tien, 1938: with a flatter shell than *Y. triplicata*.
8. *Y. obesa* Tien, 1938: a rather broader obese form with three plications in the sulcus.

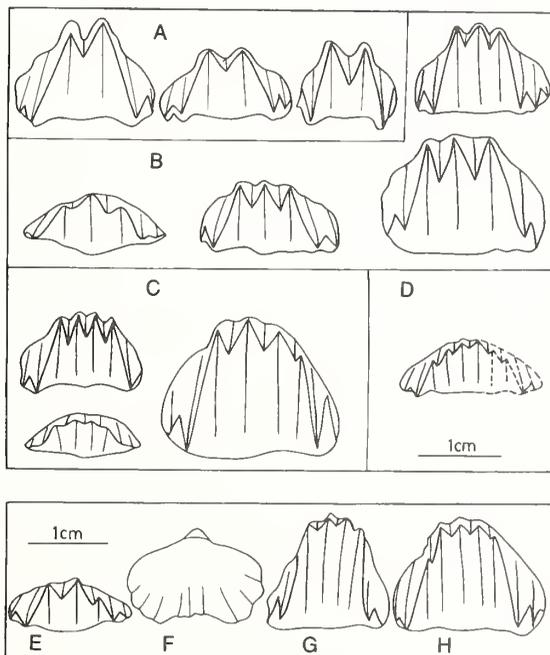
9. *Y. heyuanzhaiensis* Fang in Fang and Zhu, 1974 (= *Y. xintianensis* Zhao in Yang *et al.* 1977?): with four plications in the sulcus.
10. *Y. undatussulcus* Li, 1987: with two or three plications in the sulcus, which is concave in the middle part.

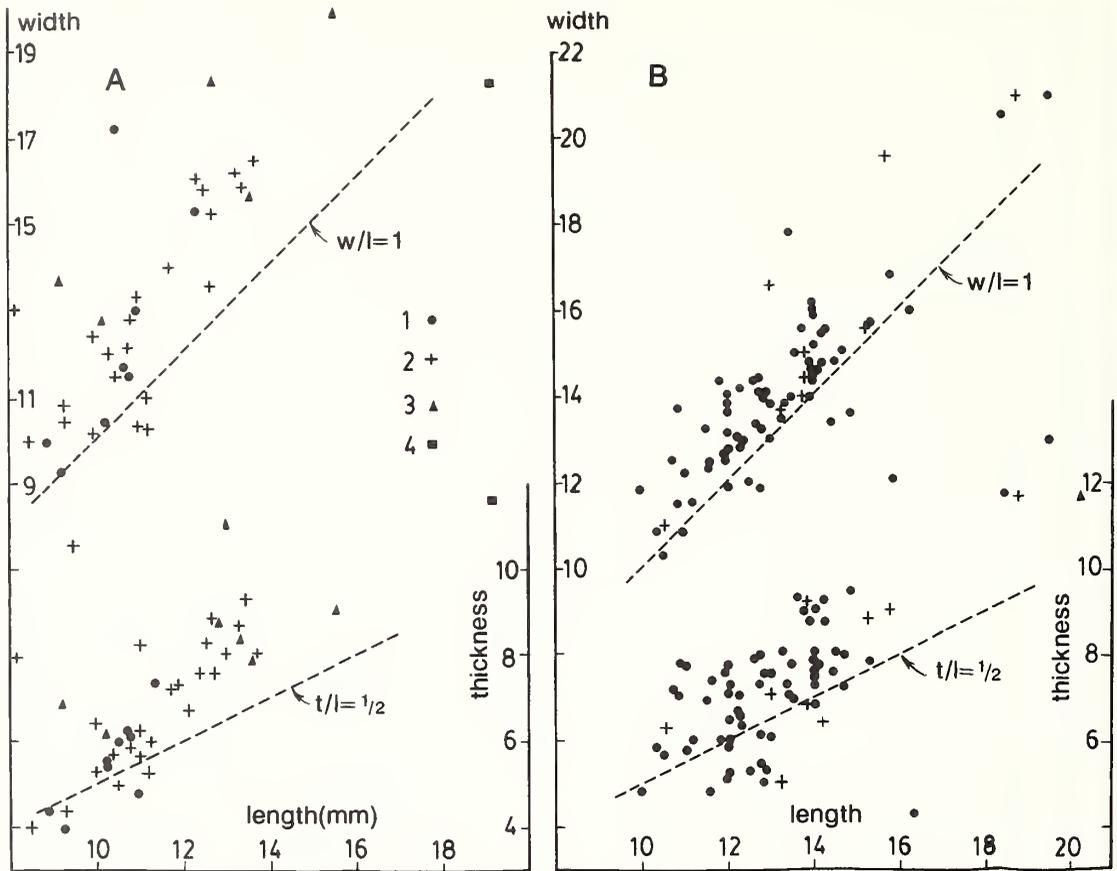
Most of the above species or subspecies were originally defined on the basis of only a few or even a single specimen. Davidson's original material was purchased from a Chinese drugstore, and the original locality and stratum can not be determined. It is questionable that the material is from Guangxi Province. Grabau's material, which also has questionable provenance, was used by him to establish two new species and a subspecies chiefly based on differences in the number of the sinal plications. Most subsequent Chinese workers followed this example and named species and subspecies based on minor differences in external morphology.

The present study shows that all the above species and subspecies belong to the type species, *Y. hanburyi*. However, this idea is not new. Kayser (1883) included his uniplicate form in *Y. hanburyi* (Davidson). Tien (1938, p. 46) considered that his *Y. cf. triplicata* Grabau (based on one specimen) 'is not only a direct derivative of the biplicate form – *Y. hanburyi*, but also foreshadows the quadruplicate form. If we could prove this in the future when more materials are available, I would prefer to regard all them as varieties of *Y. hanburyi* because they are all essentially identical, apart from the number of the plicae in the sinus and on the fold' (quoted from Tien's original English text). Sartenaer (1971) did not consider the species *Y. triplicata* and *Y. uniplicate* to be valid as they entered the range of variability of *Y. hanburyi*, but this was not discussed in depth. I have the following evidence to reject the other species and subspecies.

1. Specimens from the same sample show different shapes and possess different numbers of plications in the sulcus. If the number of sinal plications and general shape of a shell is taken as the most important criterion for species recognition, this would lead to many 'species' and 'subspecies' in a given sample, which is unlikely according to modern concepts in biology. This is demonstrated by sample C–C, for example (Text-fig. 2A–D). Uniplicate, biplicate and triplicate forms are present, and one specimen shows five plications in the sulcus. This would require the erection of four

TEXT-FIG. 2. Variation in external morphology. A–D, sample C–C; all anterior views of uniplicate (A), biplicate (B), triplicate (C) and pentaplicate (D) specimens (PUM92032–42). E, sample C–D; PUM92043, showing a parietal plica on the right slope. F–G, sample L–D3xt; showing transverse shell (PUM92044) and high sinal tongue (PUM92045). H, sample L17; PUM92046, with two strong central plicae and a faint plica on each side, of which the plica on the left may be considered as a parietal one.





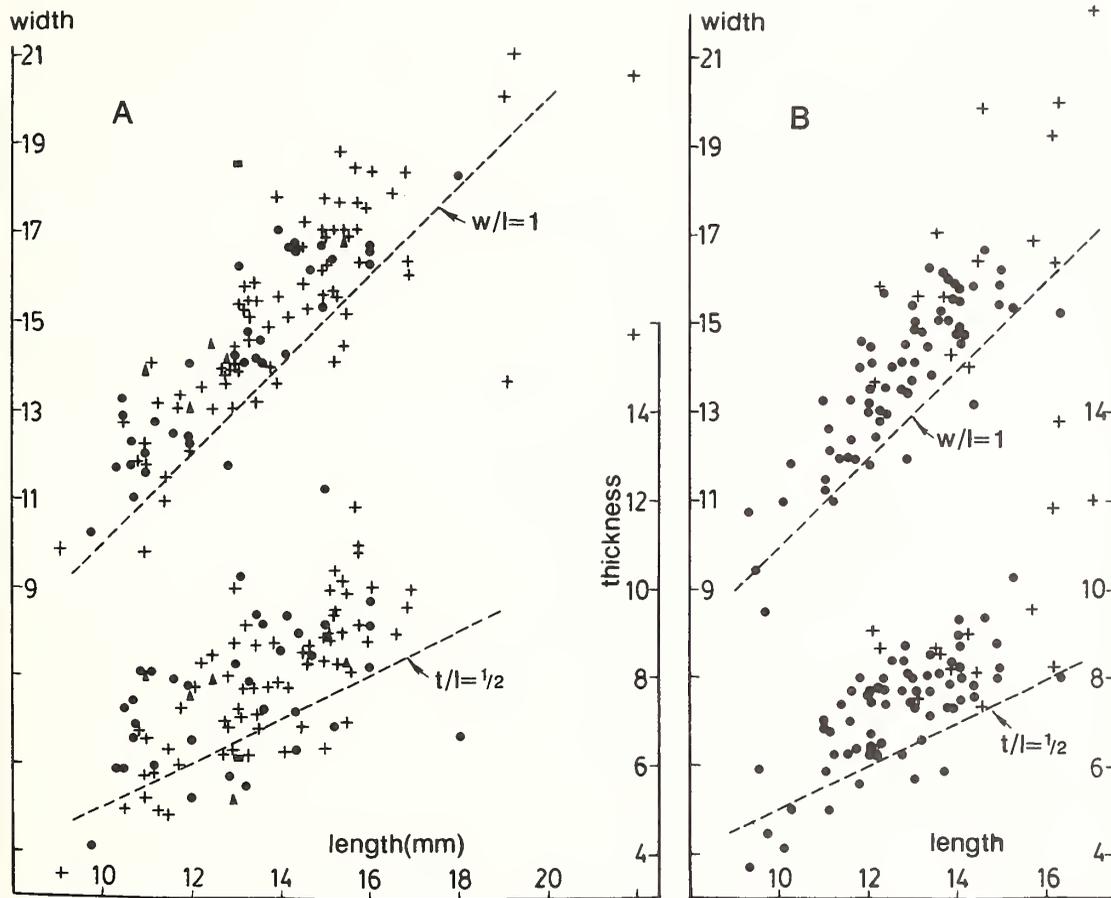
TEXT-FIG. 3. Scatter diagram showing length-width and length-thickness relationship. Legends 1-4 refer to uniplicate, biplicate, triplicate and quadriplicate specimens, respectively. Reference lines (dashed) are drawn for comparison of different samples. A, sample L17. B, sample C-H.

'species' on account of the number of sinal plications. But, only the rarity of specimens would preclude the quadriplicate or pentaplicate forms from being a separate species because they are basically identical with the uni-, bi- and triplicate forms. Secondly, different shapes are present in the uni-, bi-, and triplicate forms. In the biplicate form, '*Y. hanburyi*', '*Y. h. mut. lata*' and '*Y. h. mut. sublata*' can be recognized; in addition, there is still a globose form similar to '*Y. obesa*' in general shape, but different from it in the number of sinal plications (this again would be a new 'species'). A similar case is for the triplicate form including '*Y. triplicata*', '*Y. t. var. latiformis*' and '*Y. obesa*'. Actually flat forms ('*lata*', '*sublata*' and '*latiformis*') are composed of most immature specimens. Certainly, some flat specimens could be adults because their frontal commissure is highly elevated by plications, a feature of maturation (see section on General Morphology).

2. Occasionally in a sample, one or two specimens of bizarre morphology may be present. I have observed specimens with the sulcus protruding to a high tongue, or with a transverse or very globose shell, or with parietal plications, which are normally absent (Text-fig 2E-H). Several more examples of abnormal growth are shown in Plate 1, figures 7-8, 21-22. The specimens in Plate 1, figures 7-8 would represent '*Y. uniplicata mesosulcata*' Liu with a furrow on the strong sinal plica and, correspondingly, a small median plica present in the interspace on the fold. The specimens in Plate

1, figures 21–22 show a similar case with, in addition, the right plica on the fold (or left plica in sulcus) bifurcating anteriorly.

3. The growth curve shows basically the same pattern for specimens of uniplicate, biplicate and triplicate forms in the same sample (Text-figs 3–4).



TEXT-FIG. 4. Scatter diagram showing L-W and L-T relationship. Legend as for Text-figure 3. A, sample C-C. B, sample C-D.

4. Like external features, internal structures also vary between specimens in a single sample, e.g. sample C-H. In this sample in the uniplicate form, the connectivum (i.e. cover plate over the septalium; see Sartenaer 1969) may appear when the septalium disappears in some specimens; in others it may cover the septalium and persist in front of the septalium; other specimens may not have a connectivum or may just possess a semiconnectivum (see below). In the biplicate form, the connectivum is not present. The internal characters, like the external morphology, are therefore quite varied. These internal variations apparently do not represent separate species or subspecies, otherwise the uniplicate form with similar general shape in one sample (as in sample C-H) would have to be further subdivided into 'species' or 'subspecies'.

In conclusion, the *Yunnanellina* specimens from the Upper Devonian of South China appear to belong in the same species *Y. hanburyi*. Such species as *Pugnax utah* (Marcou), *P. postmodica-*

formis, *P. hunanensis* and *P. chaoi* described from Shaoyang by Ozaki (1939) probably also belong to the type species. This is especially the case if Ozaki's (1939) specimens are confirmed to be Famennian in age, rather than Viséan as was originally reported (see Yang *et al.* 1977, p. 389).

GENERAL MORPHOLOGY OF *YUNNANELLINA HANBURYI*

External morphology

The external structure of *Yunnanellina hanburyi* has been extensively described by many previous workers (Grabau 1931; Tien 1938; Wang *et al.* 1964; Sartenaer 1971). However, these authors have concentrated chiefly in describing the ornament. Here I present a brief description of other aspects.

Shape and growth. *Y. hanburyi* is usually dorsibiconvex, but the ventral valve is more convex at the umbo. The general outline is triangular. Width, length and thickness dimensions of *Yunnanellina* are characterized by simple linear growth (Text-figs 3–4). In young shells width and length are seen to be nearly equal. When the shell is very small, length is even greater than width, but in adult forms width increased more rapidly than length. The greatest thickness is at the frontal commissure because it is highly elevated there by plications. This feature is a reflection of growth stage (Text-fig. 5). In the young stage, the shell is much flatter; the plications are not present, with only numerous striae covering the whole shell surface; the greatest thickness is not at the frontal commissure, but near the mid-length. Because of the influence of the growth pattern, the thickness of specimens in a sample is very variable, making this character poorly correlated with length or width.

Beak and pedicle opening. *Yunnanellina hanburyi* possesses deltidial plates and a small palintrope (Text-fig. 6). The pedicle opening is oval. The beak is usually slightly incurved.

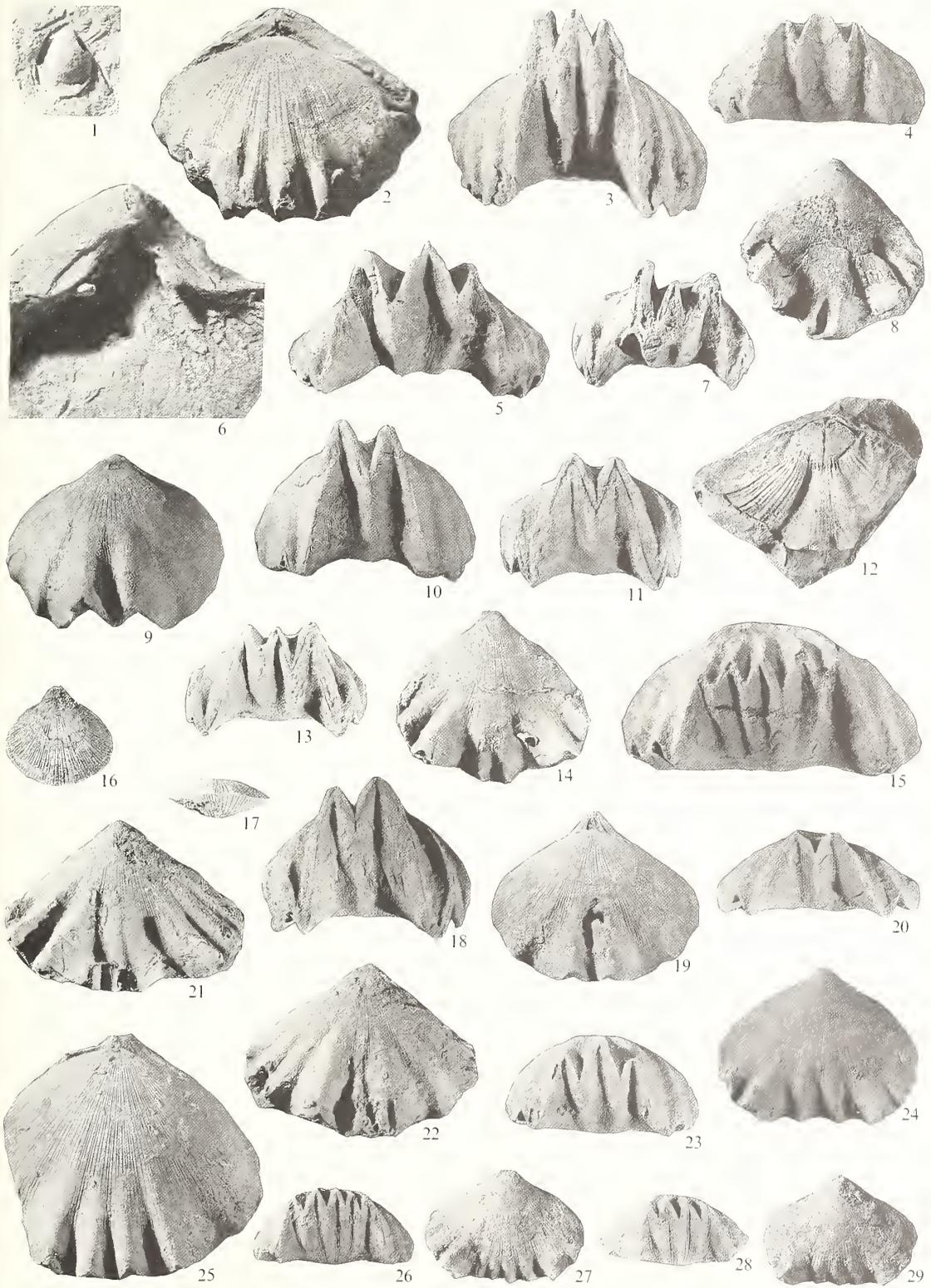
EXPLANATION OF PLATE I

Figs 1–15. *Yunnanellina hanburyi* Morphotype 1. 1, sample L12/0-7-0-8; ventral view of a juvenile specimen (PUM92080) showing greater length than width. 2–5, sample L12/0-0-1; dorsal view of a triplicate specimen (PUM92063), anterior views of biplicate specimens (PUM92081–83); note the variation. 6, sample L12/0-4-0-5; showing teeth of a biplicate specimen (PUM92084). 7–8, sample C–H; anterior and ventral views of PUM92085 showing the presence of a small central plication on the fold and corresponding anterior furrow on the sinial plication. 9–10, sample L12/0-7-0-8; dorsal and anterior views of a uniplicate specimen (PUM92086). 11, sample C–H; anterior view of a uniplicate specimen (PUM92087). 12, sample L12/0-7-0-8; internal mould of brachial valve of a uniplicate specimen (PUM92088) showing adductor muscle scars. 13–14, sample C–H; anterior and ventral views of biplicate specimen (PUM92089). 15, sample C7–2; anterior view of a large quadriplicate specimen (PUM92090).

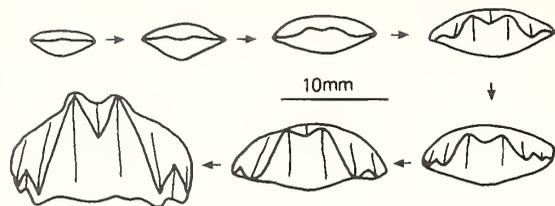
Figs 16–25. *Yunnanellina hanburyi* Morphotype 2. 16–17, sample C–E; dorsal and anterior views of a juvenile specimen (PUM92091). 18, sample C–C; anterior view of PUM92092. 19–20, sample C–D; dorsal and anterior views of immature specimen (PUM92093). 21–22, sample C–G, PUM92094; ventral and dorsal views showing abnormal growth of sinial plications; note a faint median furrow present in the sulcus and small median plica in the interspace on the fold; one lateral plica bifurcates at the front into two weak ones. 23–24, sample L19/0; anterior and ventral views of a biplicate specimen (PUM92095). 25, sample L19/0; dorsal view of a triplicate specimen (PUM92096) showing pattern of striation.

Figs 26–29. *Yunnanellina hanburyi* Morphotype 3. Sample L–D3xt; anterior and ventral views of quadriplicate and triplicate specimens (PUM92097–98).

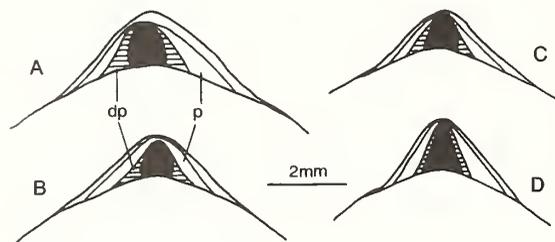
All figures $\times 2$, except fig. 1, $\times 3$ and fig. 6, $\times 4$.



MA XUEPING, *Yunnanellina*



TEXT-FIG. 5. Growth stages as reflected by the outline of the frontal commissure. Drawn from specimens PUM92047-53 from the same sample (C-D).



TEXT-FIG. 6. Pedicle opening and related structures from juvenile (D) to adult (A) stages. dp = deltidial plate; p = palintrope. A, sample C-E, PUM92054. B, sample L17, PUM92055. C, sample C-C, PUM92056. D, sample C-D, PUM92057. Specimens of A and B uniplicate, whereas in the latter two, the sulcus has not developed and sinal plication cannot be defined.

TABLE 1. Relative proportion of various forms of *Y. hanburyi* in different samples (arranged in stratigraphical order).

Sample	N	Uniplicate		Biplicate		Triplicate		Morphotypes
		N ₁	%	N ₂	%	N ₃	%	
L-D3xt	20	—	—	6	30.0	13	65.0	Morphotype 3
C-A	11	—	—	7	63.6	4	36.4	
C-C	116	35	30.2	75	64.7	5	4.3	Morphotype 2
C-D	83	67	80.7	16	19.3	—	—	
C-E	63	53	84.1	9	14.3	—	—	
L17	45	10	22.2	26	57.8	8	17.8	
C-G	18	7	38.9	9	50.0	2	11.1	
C-H	76	65	85.5	10	13.2	1	1.3	Morphotype 1

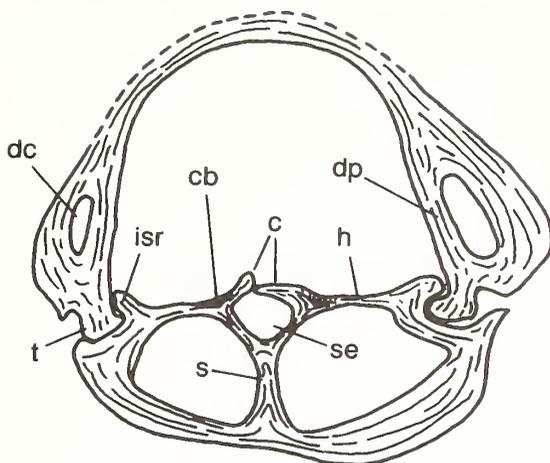
Plications. One to five plications may be present in the sulcus of *Yunnanellina hanburyi*. Specimens with one to three sinal plications are most common. However, in a given sample, usually only one of the three forms is predominant (Table 1). Specimens with four or five sinal plications are very rare. There are, on average, two plications on each side in the uniplicate, biplicate, or triplicate form. This character does not seem to vary stratigraphically.

Internal structure

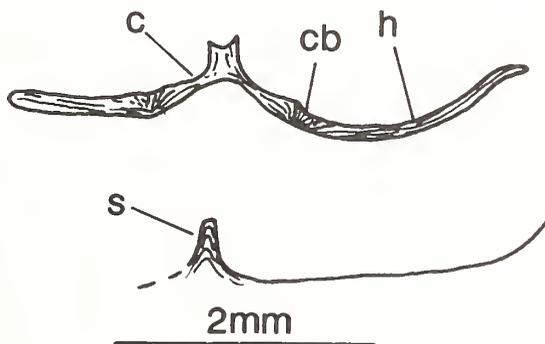
Nomenclature used for the description of the internal structure in serial sections is shown in Text-figure 7.

Cardinalia. Teeth are supported by a pair of dental plates. The dental cavity is variable in size. This feature does not show any systematic change with time, but in '*Y. uniplicata*', the dental plates seem nearly consolidated with the shell wall. The inner socket ridge is more prominent than the outer.

TEXT-FIG. 7. Nomenclature for the internal structure in transverse serial sections. cb = crural base; c = connectivum; dc = dental cavity; dp = dental plate; h = hinge plate; isr = inner socket ridge; s = septum; se = septalium; t = tooth.



TEXT-FIG. 8. The herringbone-shaped connectivum with a divided crest. See also Plate 2, figure 8.

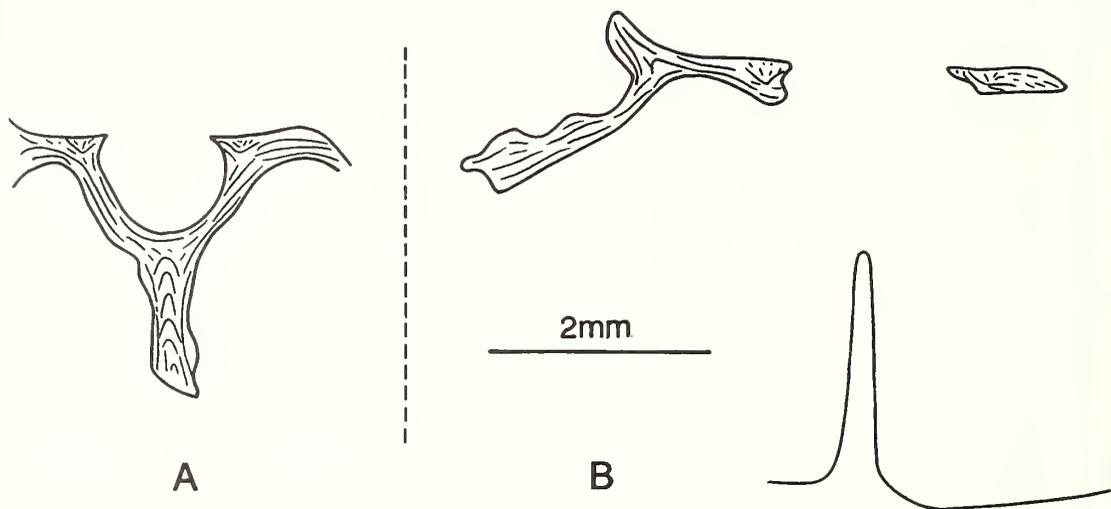
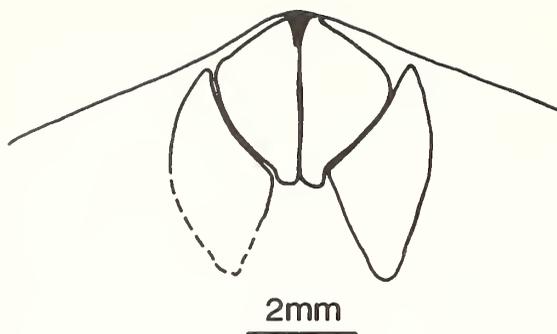


The latter is low, its inner face being crenulated. The hinge plates are horizontal, divided by the septalium. The septalium may be wide or narrow. Stratigraphically lower specimens usually show a wide septalium, while those from upper levels have a narrow one. The septalium is usually open posteriorly, being uncovered or covered anteriorly by a connectivum. This is the first record of a connectivum in *Yunnanellina*. In some specimens this structure may be just an extension halfway to the midline from each of the hinge plates, here called a *semiconnectivum*; in others, it may not be present. The connectivum is actually a joint plate resulting from further development of the semiconnectivum. The unification makes it appear slightly concave, planar, or herringbone-shaped. In the latter form, a divided crest may exist (Text-fig. 8).

Lophophore support. Crural bases are located at the junction of the hinge plates and the septalium. They begin at the posterior end of the hinge plates, and extend anteriorly giving rise to the freely projecting crura. Crural bases, which are usually clearly defined, are triangular, point downward, and have, in cross-section, a tail extended horizontally outward.

Muscle attachment. *Yunnanellina* does not possess a cardinal process. Adductor muscle scars in the brachial valve are well impressed in a mould specimen (Text-fig. 9). Posterior adductors are heart-shaped, separated by a low, rounded septum. Anterior adductors are horn-shaped.

TEXT-FIG. 9. Adductor muscle scars in the brachial valve (see Pl. 1, fig. 12).

TEXT-FIG. 10. Transverse peels of *Y. hanburyi* Morphotype 1, showing broad septalium (A) and the absence of connectivum (B). Sample T12, a biplicate specimen (PUM92058).

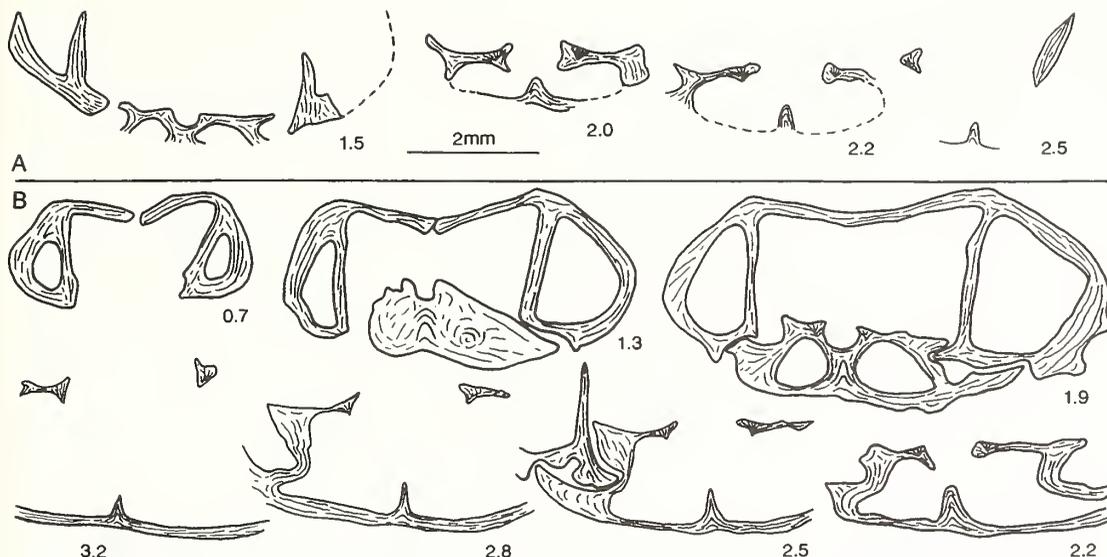
SYSTEMATIC PALAEOLOGY

Order RHYNCHONELLIDA Kuhn, 1949

Family YUNNANELLIDAE Rzhonsnitskaya, 1956

Genus YUNNANELLINA Grabau, 1931

Type species. *Rhynchonella hanburyi* Davidson, 1853, p. 356, pl. 15, figs 10–11.*Range.* Famennian. Rare occurrences of Frasnian (Yang *et al.* 1977) and Viséan (Ozaki 1939) ages have been reported, but these need confirmation.*Distribution.* South China (abundant), Northwest China (rare), ?Kazakhstan, ?Novaya Zemlya (Russia).*Remarks.* The combination *Yunnanella hanburyi* was first utilized by Grabau (1923–24, p. 195). However, the genus *Yunnanella* was neither described nor given a type species in this paper (contrary to Tien 1938, p. 48). It was only in 1931 that Grabau thoroughly described the genus



TEXT-FIG. 11. Transverse serial sections of biplicate *Y. hanburyi* Morphotype 1. Numbers refer to distance in mm from ventral apex. A, sample C-H, PUM92059. B, sample L12/0-0-1, PUM92060 (shell compressed).

Yunnanella and designated *Y. synplicata* Grabau as the type species of *Yunnanella*. *Yunnanellina* was proposed as a subgenus of *Yunnanella*, with *Rhynchonella hanburyi* Davidson as the type species (Grabau 1931). Subsequently both *Yunnanella* and *Yunnanellina* have become two well-used names in the Chinese literature, because they are very abundant and good markers of Famennian strata in South China. However, in the *Treatise* (McLaren in Moore 1965) *Yunnanella* and *Yunnanellina* are listed as junior synonyms of *Nayunnella* Sartenaer, 1961 and *Yunnanella* Grabau, 1923, respectively, a proposal which I do not support.

Yunnanellina Grabau, 1931 can be easily distinguished on superficial evidence from *Yunnanella* Grabau, 1931 by the presence of its finer striae arising independently and continuing over the plications. In the latter, the plicae are formed anteriorly by a single enlarged stria, or two or more united striae. In addition, the striae of *Yunnanellina* increase in number chiefly by multibifurcations and cover more densely the shell surface. In *Yunnanella*, however, the shell surface is covered by relatively coarse and sparse striae characterized by both bifurcation and intercalation. The internal structure of the latter needs detailed study before comparisons can be made with the former.

Stratigraphically this species can be divided into three chronological morphotypes based on the variation pattern of the connectivum, especially in the biplicate form, and in the septalium.

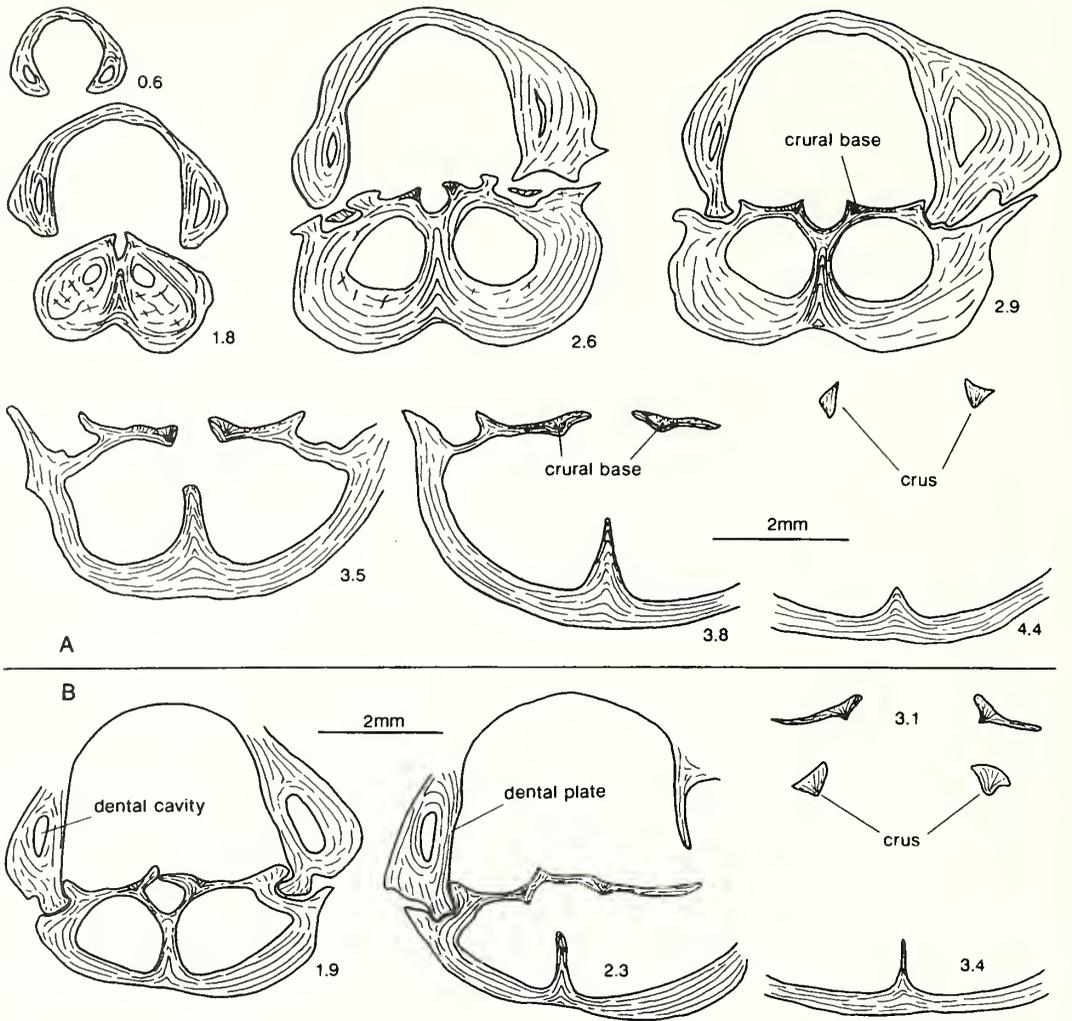
Yunnanellina hanburyi Morphotype 1

Plate 1, figures 1-15; Plate 2, figures 1-3, 7; Text-figures 10-13

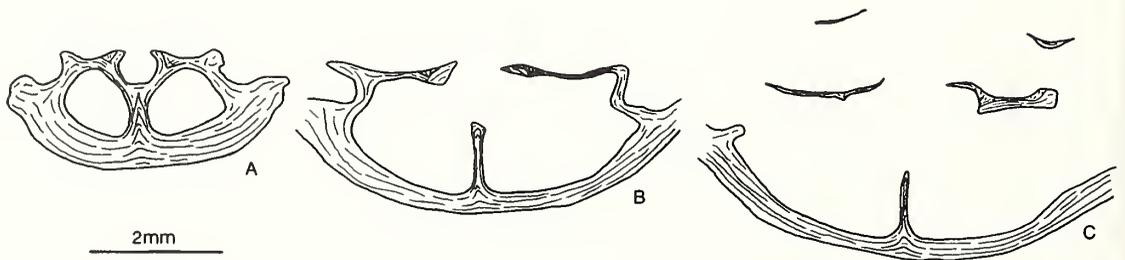
Diagnosis. Specimens of *Yunnanellina hanburyi* in which the biplicate form does not possess a connectivum. The septalium of all specimens is broad and rounded.

Description. In the biplicate form, dental plates are well developed. Dental cavities are large, oval in shape. In the brachial valve, hinge plates are usually horizontal, separated by the septalium. Crural bases are small, not well-defined. The most important feature is the absence of a connectivum anteriorly over the septalium.

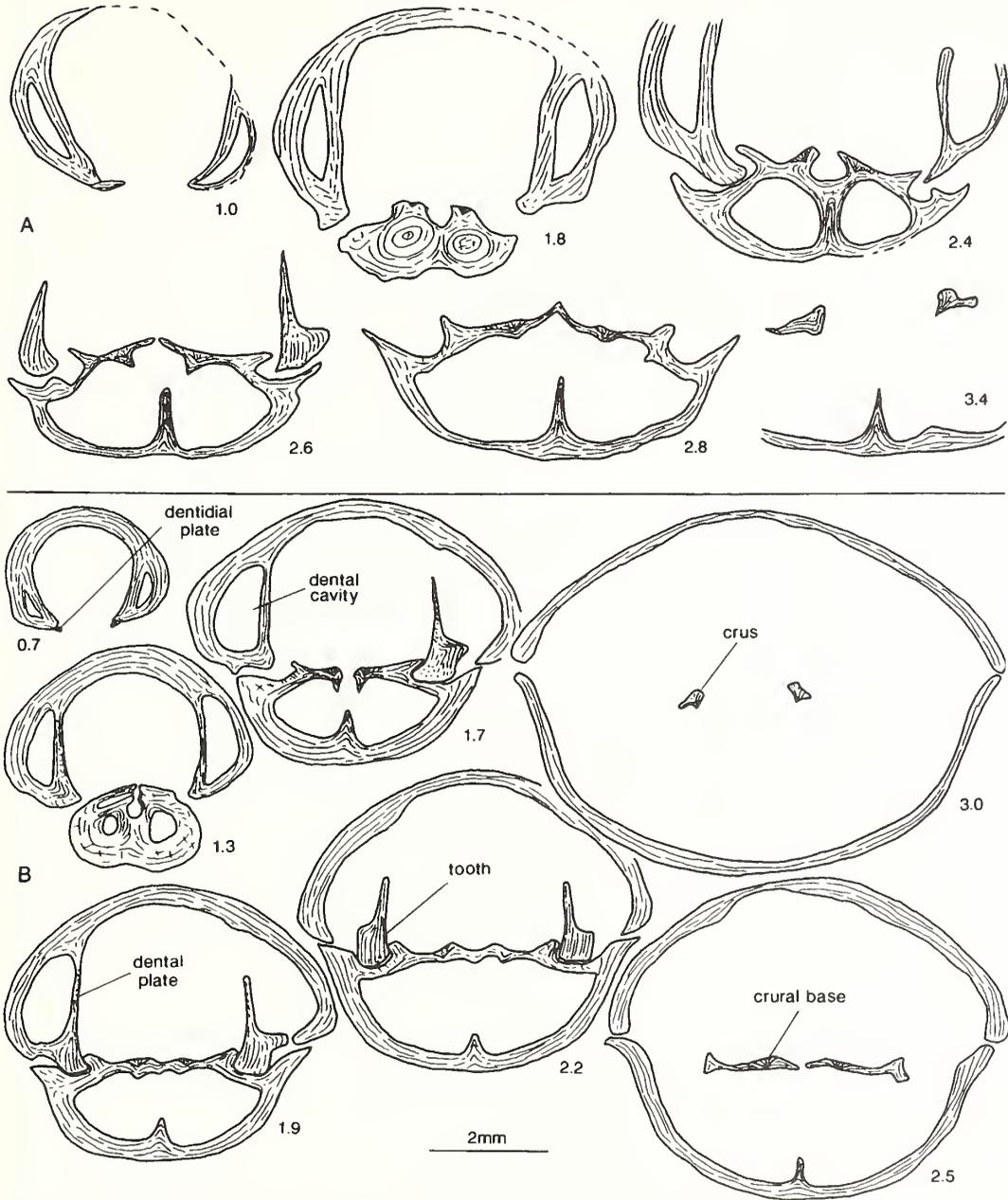
In the uniplicate form, the shell is strong. Dental plates are thick, more or less consolidated with the shell wall, leaving the dental cavities very narrow, small, or even slit-like. The septalium is still broad and rounded, but posteriorly it becomes very narrow. Crural bases are usually well-defined; in some specimens, they may



TEXT-FIG. 12. Transverse serial sections of uniplicate *Y. hanburyi* Morphotype 1. Note the small size of the dental cavity. Sample C-H. A, PUM92061. B, PUM92062. Compare with Plate 2, figure 7.



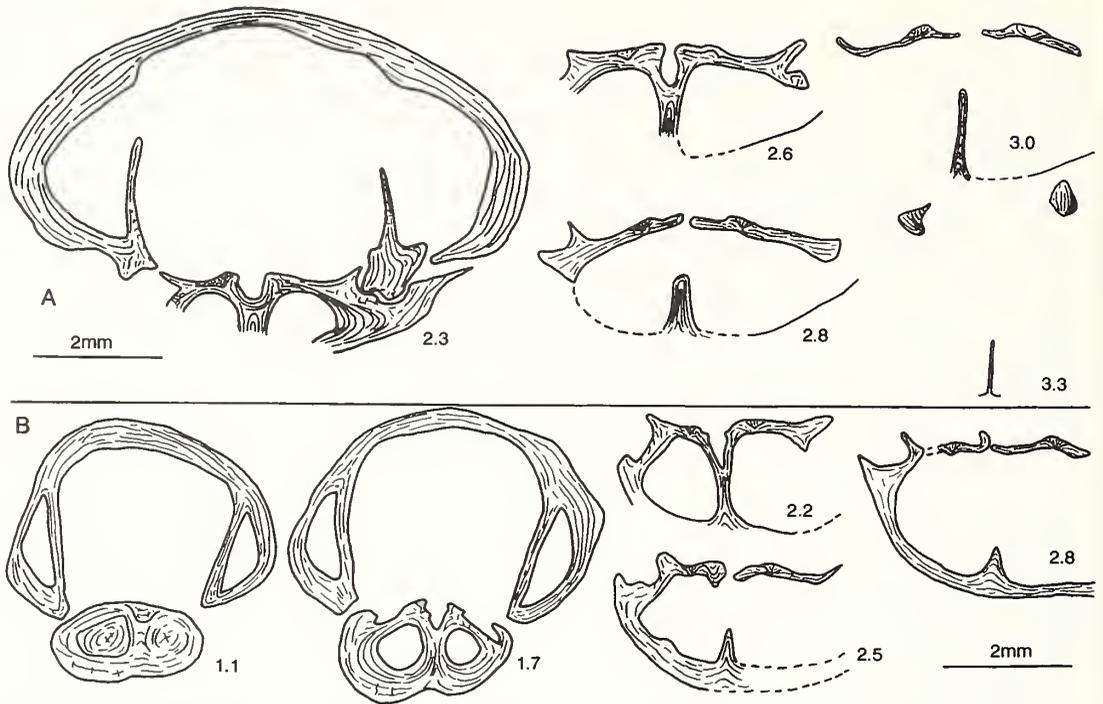
TEXT-FIG. 13. Three serial sections of triplicate *Y. hanburyi* Morphotype 1. Sample L12/0-0-1, PUM92063. (Also shown in Pl. 1, fig. 2; Pl. 2, fig. 2).



TEXT-FIG. 14. Transverse serial sections of uniplicate *Y. hanburyi* Morphotype 2. A, sample C-C, PUM92064. B sample L19/0, PUM92065.

extend for a short distance laterally. The connectivum is present in some specimens, but in others it may be just a semiconnectivum. The connectivum may cover the septalium exactly or stretch farther forward than the septalium. The crus is triangular, point down in cross section, pointing ventrally and slightly anteriorly.

In the triplicate form, a semiconnectivum is present. It seems that the end of the crura are curved ventroposteriorly so that the crura and the hinge plates with crural bases are shown in the same section.



TEXT-FIG. 15. Transverse serial sections of biplicate *Y. hanburyi* Morphotype 2. Note the narrowness of the septalium. A, sample C-C, PUM92066. B, sample L19/0-2-0-4, PUM92067.

Material. Over 145 specimens: from the middle part of the Chang lungchich Shale, near Laojiangchong village, Xikuangshan area: L10/7-9 (one specimen); L11 (fragments); L12 (1.7 m thick, over fifty specimens, some of which are in good state of preservation; the biplicate form is predominant); from the lower part of the Famennian, near Tingziling, about 4 km east of Chongshanpu: T12 (two specimens); T13 (two specimens); from the lower part of the Famennian, near Chenjiayuan, about 4 km east of Jiangjiaqiao: C7-2 (two specimens); C-H (eighty-five specimens).

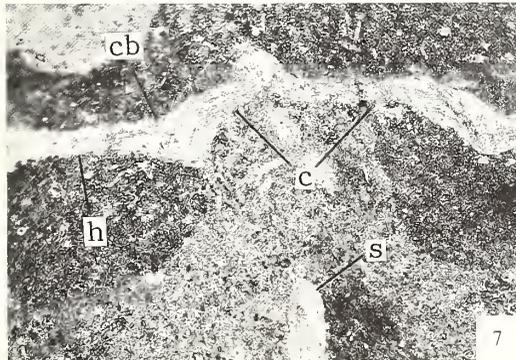
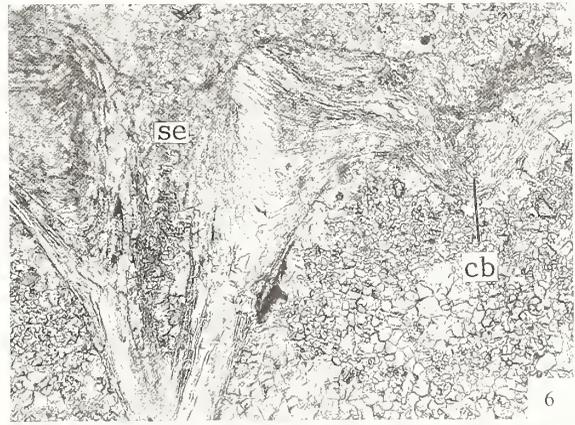
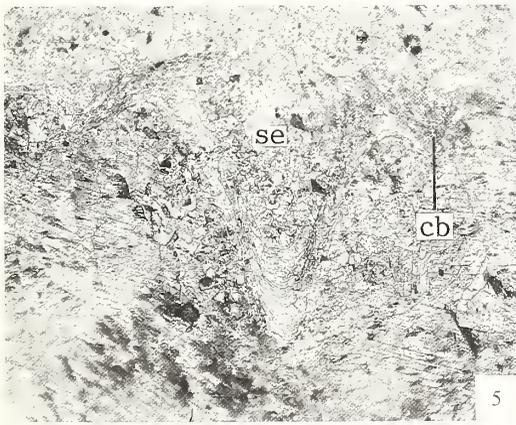
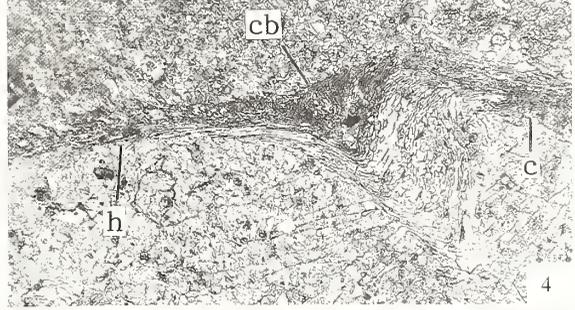
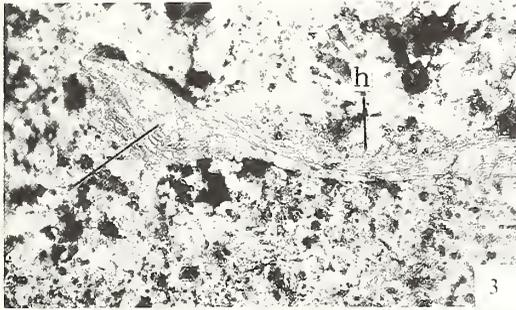
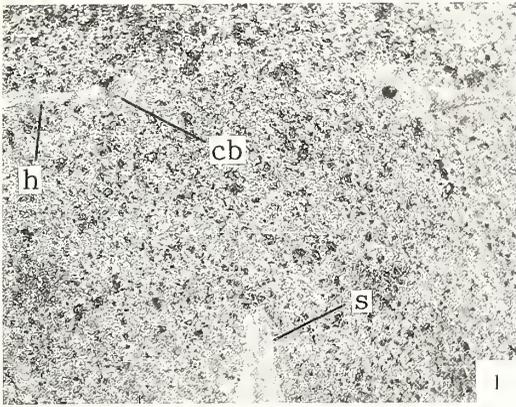
EXPLANATION OF PLATE 2

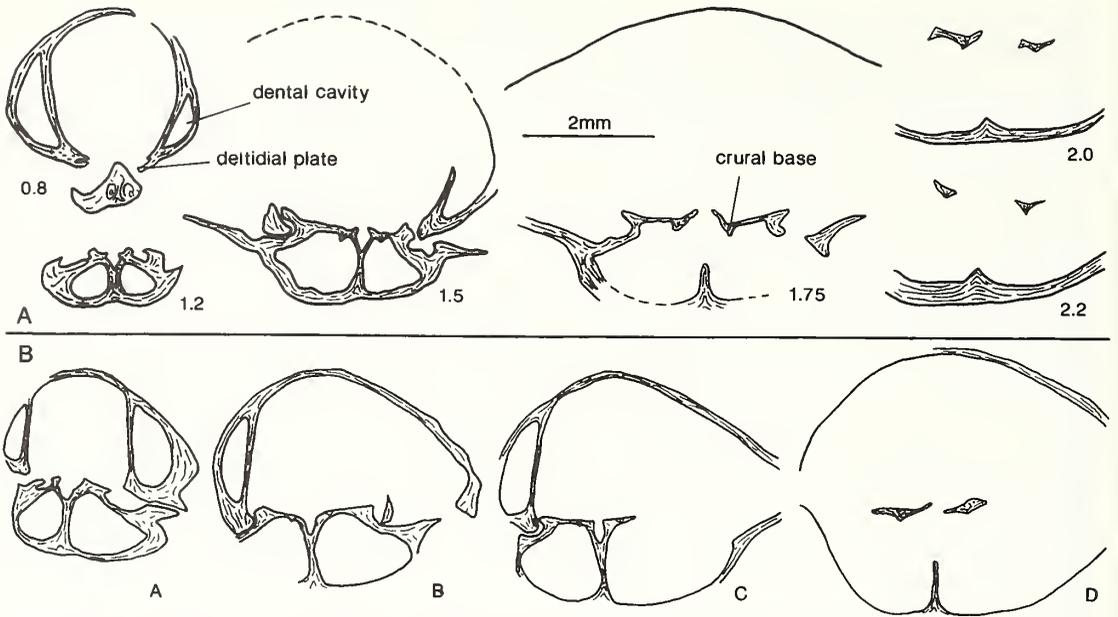
Figs 1-3, 7. *Yunnanellina hanburyi* Morphotype 1. 1, sample L12/0-0-1; showing the absence of connectivum of a biplicate specimen (PUM92060). 2, same specimen as Pl. 1, fig. 2; showing broad and rounded septalium. 3, sample L12/0-6; a biplicate specimen (PUM92077) showing right hand hinge plate and crural base, but without connectivum medially (towards the left on photograph). 7, sample C-H; showing a uniplicate specimen (PUM92062) with connectivum.

Figs 4, 6, 8. *Yunnanellina hanburyi* Morphotype 2, 4, sample C-D; showing a biplicate specimen (PUM92078) with the connectivum. 6, sample L17; showing a triplicate specimen (PUM92072) with very narrow septalium; note that the position of the crural base is on the hinge plate and not at the junction of the hinge plate and the septalium. 8, sample C-E; showing a uniplicate specimen (PUM92079) with a herringbone-shaped connectivum; note the divided crest.

Fig. 5. *Yunnanellina hanburyi* Morphotype 3. Sample L-D3xt; a triplicate specimen (PUM92068) with V-shaped septalium and outward disposition of the crural base.

All figures $\times 75$, except figs 1 and 7, $\times 30$; c = connectivum; cb = crural base; h = hinge plate; s = septum; se = septalium.





TEXT-FIG. 16. Transverse serial sections of triplicate (A) and biplicate (B) *Y. hanburyi* Morphotype 3. Sample L-D3xt. A, PUM92068, also partly shown in Plate 2, figure 5. B, PUM92069.

Yunnanellina hanburyi Morphotype 2

Plate 1, figures 16–25; Plate 2, figures 4, 6, 8; Text-figures 14–15

Diagnosis. *Yunnanellina* in which all specimens possess a connectivum. A narrow and deep septalium is common.

Description. In this morphotype, the uni- and biplicate specimens are predominant. In the uniplicate form, the dental cavity is larger than that in Morphotype 1. Dental plates are well developed in all forms. The septalium is usually narrow and deep, V-shaped or vase-shaped. In this case, crural bases are usually not located at the junction of the septalium and the hinge plates but lie outward in the hinge plates. Some specimens from sample C-C may show a broad and rounded septalium.

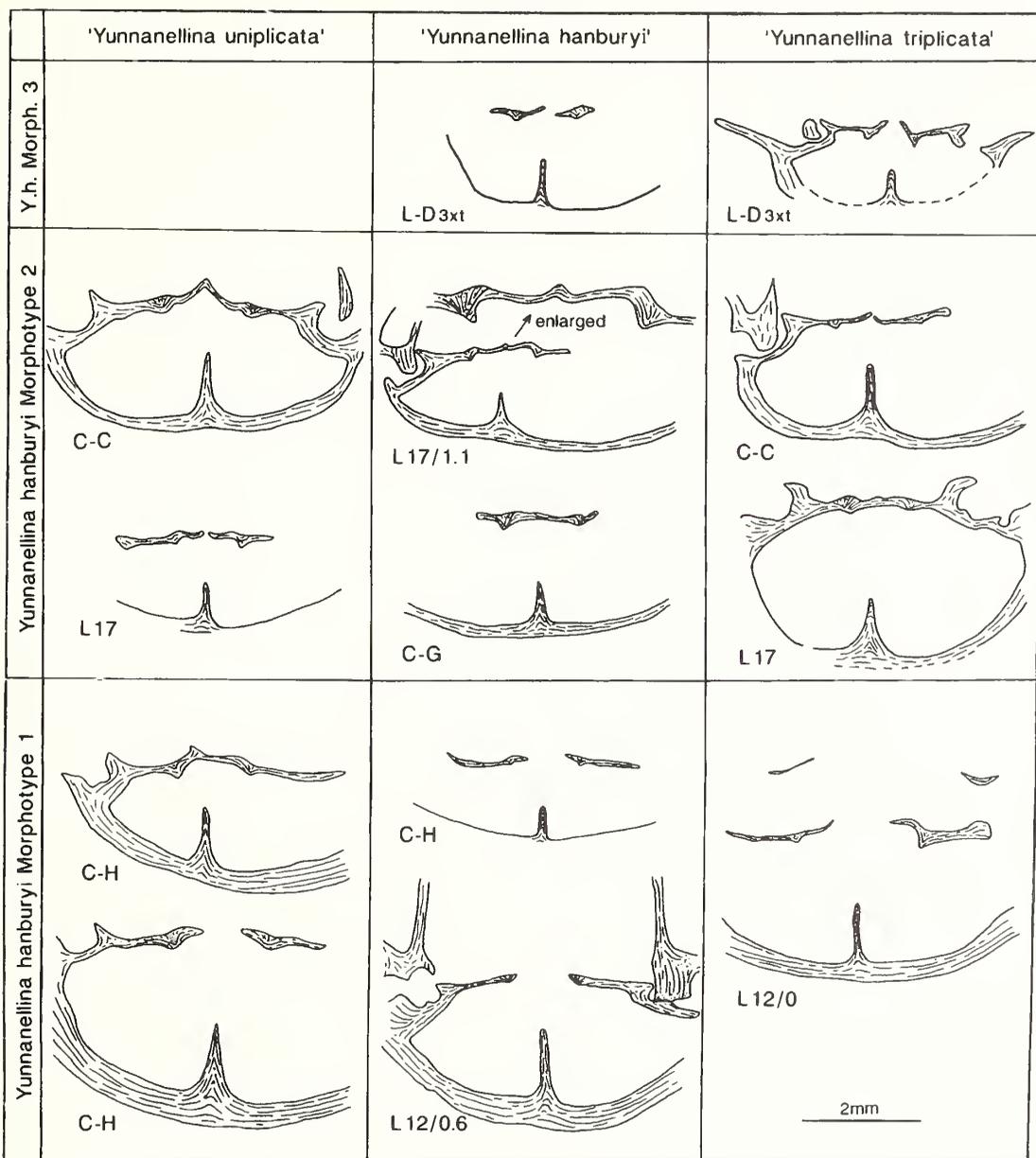
A connectivum is present in all forms. In the uniplicate form, the connectivum may be herringbone-shaped in stratigraphically higher specimens; it may be plane or slightly concave in stratigraphically lower specimens.

Material. In total about 400 specimens, most of which are in a good state of preservation: upper part of the Changlungchich Shale, near Laojiangchong village: L15/0.55 (one specimen); L15/1.7 (three specimens); L17 (about forty specimens); L17/1.1 (about ten specimens on slab); L19/0 (seventeen specimens); L19/0.0.2 (nine specimens); L19/0.2–0.4 (thirty specimens); L19/0.35 (three specimens); L19/0.4–0.6 (three specimens); L20/1.7–2.0 (two specimens); near Chenjiayuan village: C-G (eighteen specimens); C-E (sixty-eight specimens); C-D (ninety specimens); C-C (one hundred and twenty specimens).

Yunnanellina hanburyi Morphotype 3

Plate 1, figures 26–29; Plate 2, figure 5; Text-figure 16

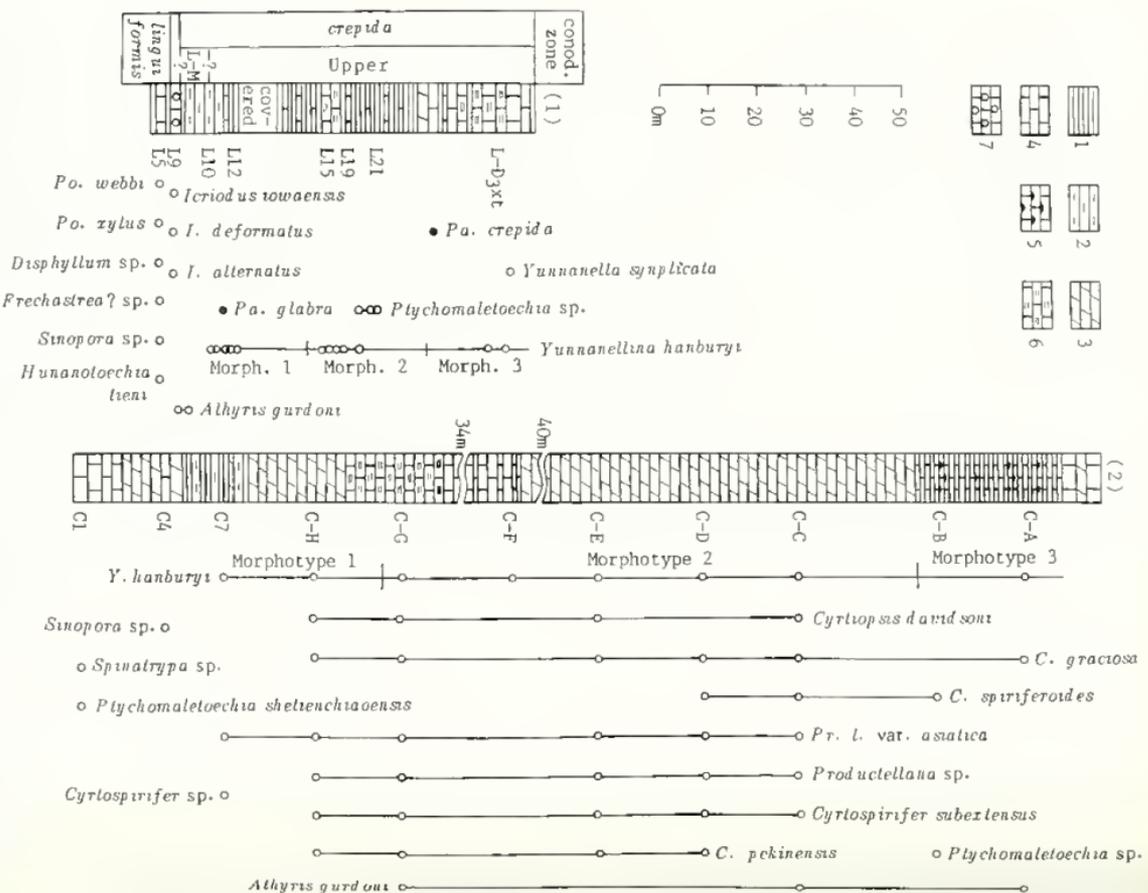
- 1938 *Yunnanellina hanburyi* mut. *sublata* Tien, pp. 45–46, pl. 6, figs 3–5.
- 1938 *Yunnanellina* cf. *triplicata* Grabau; Tien, p. 46, pl. 6, fig. 8.
- 1938 *Yunnanellina triplicata* var. *latiformis* Tien, p. 47, pl. 6, fig. 6.
- 1938 *Yunnanellina obesa* Tien, p. 48, pl. 6, fig. 7.



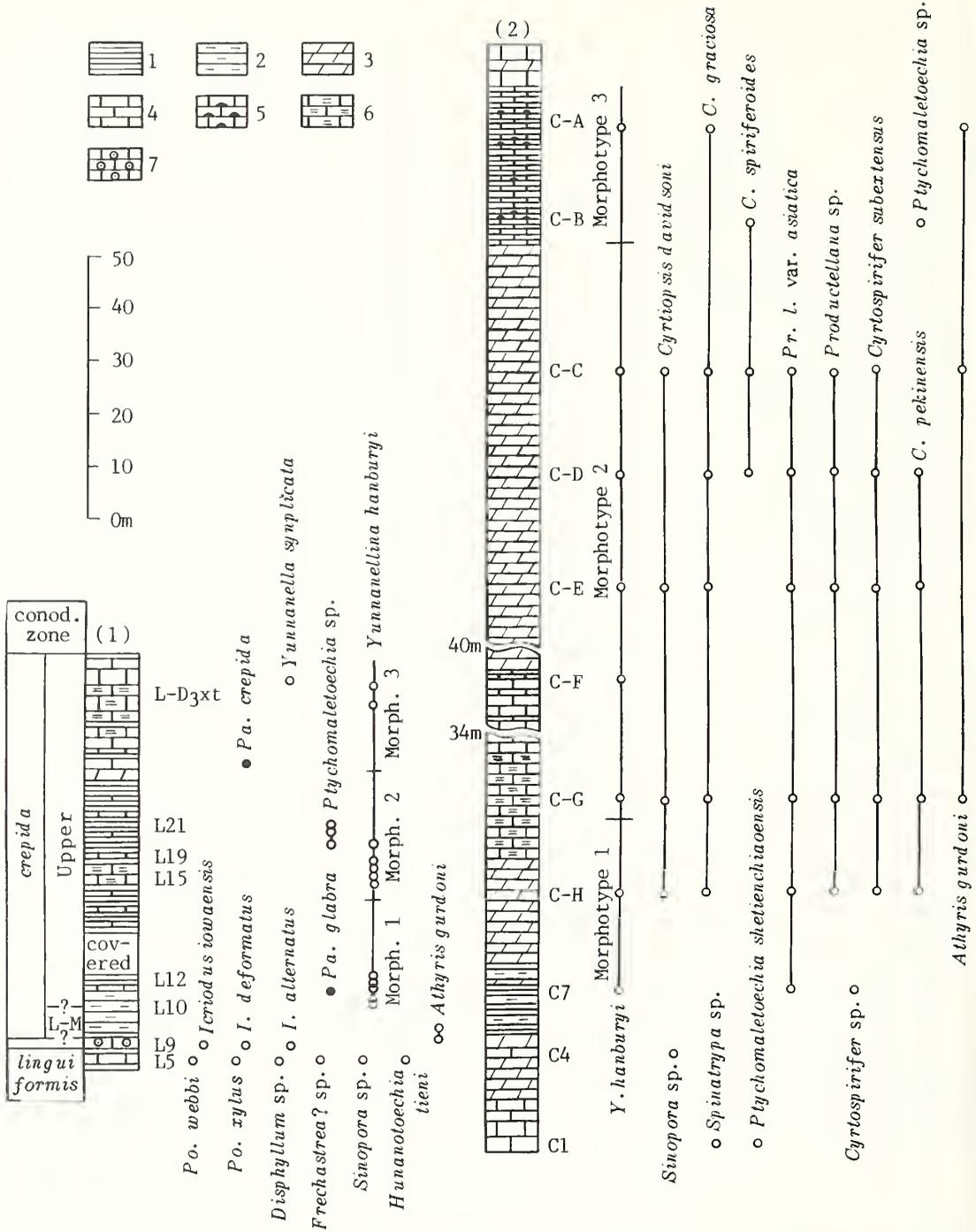
TEXT-FIG. 17. Variation of connectivum in the brachial valve of *Y. hanburyi* with time. Most line drawings are selected from text-figures and plates of serial sections of different specimens shown in the text. Others are from L17, uniplicate (PUM92070) and triplicate (PUM92071); L17/1.1 (PUM92073); C-G (PUM92074); C-H, biplicate (PUM92075) and C-C, triplicate (PUM92076).

Diagnosis. Specimens of *Y. hanburyi* with a semiconnectivum and usually a narrow and deep septalium.

Description. Shell usually small. All specimens so far found are bi- and triplicate. Internal structure is weak. Dental plates are well developed. Septalium is usually narrow and deep. A semiconnectivum is present in all forms.



TEXT-FIG. 18. Stratigraphical distribution of *Y. hanburyi* and correlation of the Xikangshan (1) and Jiangquaqiao (2) sections. Data of black dots are adopted from Hou *et al.* (1988). Legend: 1, shale; 2, mudstone; 3, marl; 4, limestone; 5, nodular limestone; 6, limestone with argillaceous bands; 7, oolitic limestone.



TEXT-FIG. 18. Stratigraphical distribution of *Y. hanburyi* and correlation of the Xikuangshan (1) and Jiangjiaqiao (2) sections. Data of black dots are adopted from Hou *et al.* (1988). Legend: 1, shale; 2, mudstone; 3, marl; 4, limestone; 5, nodular limestone; 6, limestone with argillaceous bands; 7, oolitic limestone.

Material. Thirty-one specimens from the Tutzutang Member, near Laojiangchong village: L-D3xt (twenty specimens); and from near Chenjiayuan village: C-A (eleven specimens).

VARIATION IN THE CONNECTIVUM AND SEPTALIUM WITH TIME

Morphotype 1. In the biplicate form, the connectivum is not present, or it occurs as a very short inward extension from the hinge-plate. This has been verified in the five sectioned specimens from the three stratigraphical sections (Text-fig. 17). In the uniplicate form, the connectivum is very varied, as discussed above for sample C-H. The only sectioned triplicate specimen possesses a semiconnectivum. The septalium in all the forms is broad and rounded.

Morphotype 2. The connectivum is present in all the specimens. It is usually planar in the biplicate and triplicate forms. The uniplicate form of this morphotype may be further subdivided into two varieties. The stratigraphically lower variety is characterized by a planar connectivum as seen in specimens from both the Xikuangshan and Chongshanpu sections. The stratigraphically higher variety is characterized by a herringbone-shaped connectivum. The septalium of this morphotype is usually narrow and deep in the lower part, but becomes broader higher up the stratigraphical section.

Morphotype 3. This morphotype possesses a semiconnectivum. The septalium is variable in shape, usually V- to U-shaped in cross-section.

STRATIGRAPHY AND DISTRIBUTION OF *Y. HANBURYI*

In central Hunan, the Upper Devonian includes the Shetianqiao and the Xikuangshan formations. The Xikuangshan Formation is composed of three members (Tien 1938). The lower member is the Chang lungchieh Shale, about 100 m thick, which consists of grey-green shales, thinly-bedded marls and minor limestones. The lower part possesses abundant corals and a common rhynchonellid, *Hunanotoechia tieni* (Ma, 1993), of late Frasnian age. The upper part (about 50 m thick) hosts abundant *Yunnanellina hanburyi* and cyrtospiriferids. The overlying member is the Tutzutang Limestone (about 20–40 m thick), in which *Y. hanburyi* is present in its lower part. The uppermost member is the Makunao Limestone (about 200 m thick), which is rich in brachiopods, including cyrtospiriferids and *Yunnanella*. It is separated from the Tutzutang Limestone by the thin Nitangli iron ore bed (1–2 m thick).

Yunnanellina hanburyi first occurs about ten metres above the Frasnian/Famennian boundary as found in the Xikuangshan, Jiangjiaqiao and Chongshanpu sections (Text-fig. 18). The boundary can be recognized from the first occurrence of *Icriodus deformatus* Han, a conodont which is present in the lower *triangularis* Zone in South China (Jia *et al.* 1988). But, at the Xikuangshan section, it is associated with *I. iowaensis*, a species beginning to occur in the middle *triangularis* Zone in South China (Bai Shunliang, oral communication). The occurrence of *Palmatolepis glabra* in bed L11 (Hou *et al.* 1988) may indicate the upper *crepida* Zone. The upper occurrence of *Y. hanburyi* probably still lies within the upper *crepida* Zone because of the presence of this zonal species at the base of the Tutzutang Member (Hou *et al.* 1988). This is further supported by data from the Qidong section in Hunan Province, where the *Yunnanellina* fauna is displaced by the *Yunnanella* fauna at the top of the *crepida* Zone (Wang and Bai 1988). Therefore, the entire range of *Y. hanburyi* may well coincide with the upper *crepida* Zone.

At the Jiangjiaqiao section, no conodont data are available, but there are abundant brachiopods, including *Y. hanburyi*, cyrtospiriferids and productids. Using the three morphotypes of *Y. hanburyi*, it is possible to correlate this section with the Xikuangshan section. Obviously, the rate of sedimentation in the Jiangjiaqiao area was much higher than that in the Xikuangshan area because the former sequence is much thicker.

CONCLUSIONS

The variations in both external and internal structures of *Yunnanellina hanburyi* (Davidson, 1853) have been thoroughly described based on abundant specimens collected from central Hunan. It is concluded that the other nominal species and subspecies founded later from South China are all junior synonyms of *Y. hanburyi*. This demonstrates that care must be taken in using external features alone to establish new species, especially when few specimens are to hand. Internal structure is usually considered to be reliable feature for taxonomy, but some species, like *Yunnanellina hanburyi*, may show a wide range of variations in the internal structure, even in specimens from the same sample. Better understanding of this kind of species (variable in both external and internal structure) can only be achieved through the study of numerous specimens whose locality and stratum are clearly known. When the morphology of a brachiopod is well understood, it could, potentially, enable finer subdivision of its stratigraphical range.

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REFERENCES

- DAVIDSON, T. 1853. On some fossil brachiopods, of the Devonian age, from China. *Quarterly Journal of the Geological Society, London*, **9**, 353–359.
- FANG YUNSEN and ZHU XIANGSHUI 1974. Brachiopoda. 287–479. In GEOLOGICAL BUREAU OF YUNNAN PROVINCE (ed.). *Fossil Atlas of Yunnan*. Yunnan People's Press, Vol. 1, 864 pp.; Vol. 2, 296 pls. [In Chinese].
- GRABAU, A. W. 1923–24. *Stratigraphy of China, Part I, Palaeozoic and older*. Geological Survey of China, 528 pp.
- 1931. Devonian Brachiopoda of China. *Palaentologia Sinica, Series B*, **3**, 1–454.
- HOU HONG-FEI, JI QIANG and WANG JINXING 1988. Preliminary report on Frasnian–Famennian events in South China. 63–69. In McMILLAN, N. J., EMBRY, A. F. and GLASS, D. J. (eds). Devonian of the World. *Memoirs of the Canadian Society of Petroleum Geologists*, **14** (3).
- JIA HUI-CHEN, XIAN SI-YUAN, YANG DE-LI, ZHOU HUAI-LIN, HAN YING-JIAN, CHEN ZHEN-HUAN, WANG JIN-XING, WANG RUI-GANG, WANG SHI-TAO, ZHANG ZHEN-XIAN and WEI MING 1988. An ideal Frasnian/Famennian boundary in Ma-an-shan, Zhongping, Xiangzhou, Guangxi, South China. 79–92. In McMILLAN, N. J., EMBRY, A. F. and GLASS, D. J. (eds). Devonian of the World. *Memoirs of the Canadian Society of Petroleum Geologists*, **14** (3).
- KAYSER, E. 1883. Devonische Versteinerungen aus dem sudwestlichen China. 75–102. In RICHTHOFEN, F. P. W. von. *China, Volume 4*. D. Reimer, Berlin, 288 pp.
- KUHN, O. 1949. *Lehrbuch der Palaeozoologie*. E. Schweizerbartsche, Stuttgart, v+326 pp.
- LI YOU-XIN 1987. A new species of Genus *Yunnanellina* from Upper Devonian of Lingling, Hunan. *Acta Palaentologia Sinica*, **26**, 323–325. [In Chinese with English summary].
- LIU ZU-HAN, TAN ZHENG-XIU and DING YA-LING 1982. Brachiopoda. 172–216. In HUNAN GEOLOGICAL BUREAU (ed.) *Palaentological Atlas of Hunan*. Geological Publishing House, Beijing, 997 pp. [In Chinese].
- MA XUE-PING 1993. *Hunanotoechia*: a new Late Devonian rhynchonellid brachiopod from Xikuangshan, Hunan, China. *Acta Palaentologica Sinica*, **32**, 716–724. [In Chinese with English summary].
- MOORE, R. C. (ed.) 1965. *Treatise on invertebrate paleontology. Part H. Brachiopoda*. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, 927 pp.
- OZAKI, K. 1939. Some Lower Carboniferous brachiopod fossils from central Hunan, China. *Institute of Natural Science of Shanghai, Memoir* **2**, 225–252.
- RZHONSNITSKAYA, M. A. 1956. Semeystvo Pentameridae i sem. Camarotoechiidae. *Materiaty po Paleologii Novy Semeystva i Rody, Novaya Seriya*, **12**, 49–50, 53–55. [In Russian].

- SARTENAER, P. 1969. Late Upper Devonian (Famennian) rhynchonellid brachiopods from western Canada. *Bulletin of the Geological Survey of Canada*, **169**, 1–269.
- 1971. Redescription of the brachiopod genus *Yunnanella* Grabau, 1923 (Rhynchonellida). *Smithsonian Contributions to Paleobiology*, **3**, 203–218.
- TIEN, C. C. 1938. Devonian Brachiopoda of Hunan. *Palaeontologia Sinica, New Series B*, **4**, 1–192.
- WANG K. and BAI SHUNLIANG 1988. Faunal changes and events near the Frasnian–Famennian boundary of South China. In McMILLAN, N. J., EMBRY, A. F. and GLASS, D. J. (eds). 71–78. Devonian of the World. *Memoirs of the Canadian Society of Petroleum Geologists*, **14** (3).
- WANG Y., JIN Y. G. and FANG D. W. (eds). 1964. *Brachiopod fossils of China*. Science Press, Beijing, 777 pp., 136 pls. [In Chinese].
- XU HAN-KUI 1979. The brachiopod *Yunnanella-Yunnanellina* fauna from the Upper Devonian of Hunan. *Acta Stratigraphica Sinica*, **3**, 123–126. [In Chinese].
- YANG DE-LI, NI SHI-ZHAO, CHANG MEI-LI and ZHAO RU-XUAN 1977. Brachiopoda. 303–470. In HUBEI INSTITUTE OF GEOSCIENCES ET AL. (eds). *Palaeontological Atlas of Central-Southern China*. Geological Publishing House, Beijing, 856 pp. [In Chinese].

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CHAROPHYTE BIOSTRATIGRAPHY OF THE PURBECK AND WEALDEN OF SOUTHERN ENGLAND

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ABSTRACT. The distribution of charophyte assemblages in the Purbeck and Wealden sequence of southern England has been established from borehole samples from the Weald and from outcrop material collected in Dorset, Wiltshire and on the Isle of Wight. Of the twenty-one taxa represented, three are new: *Globator rectispirale*, *Clypeator britannicus* and *Sphaerochara andersonii*; three new combinations are proposed: *Globator praecursor*, *Globator protoincrassatus* and *Atopochara triquetra*. The Chinese Valanginian species *Flabellochara xiangyumuensis* is recognized for the first time in Europe. In the context of the phylogeny of the Family Clavatoraceae, *G. rectispirale* represents the Jurassic ancestor of the *Globator* lineage and a separate origin is suggested for both *Flabellochara* and *Clypeator*. The correlations established with the Tethyan realm locate the Jurassic–Cretaceous boundary within the Lulworth Formation of the Purbeck Limestone Group; in this context, the whole ‘Purbeck’ sequence of Swindon (Wiltshire) is attributed to the Upper Tithonian. The distribution of Clavatoraceae indirectly confirms the contemporaneity of the Boreal *Galbanites kerberus* and *Titanites anguiformis* with the Tethyan ‘*Durangites*’ ammonite zones. For the Wealden Supergroup, the charophyte data affirm the Hauterivian–Barremian boundary at the base of the upper division of the Weald Clay and the Upper Barremian is identified at the base of the Vectis Formation of the Isle of Wight.

THE charophytes of the Purbeck and Wealden successions of southern England have received little attention since they were first recognized by Forbes (1851) in the Purbeck Beds of Mupe Bay (Dorset). A preliminary report on the Purbeck Beds Characeae was published by Reid and Groves (1916), who established the genus *Clavator*, subsequently discussed by Groves (1924). The only detailed study of Purbeck charophytes to date has been by Harris (1939) who reviewed previous work and provided descriptions of assemblages from the Dorset coast and inland sections, as well as from the Vale of Wardour and quarries at Swindon (Wiltshire). More recently, Barker *et al.* (1975) discussed the depositional environment of the Charophyte Chert at the base of the Great Dirt Bed, 4 m above the base of the Purbeck Beds at Portesham Quarry (Dorset) and described the supposed new species *Clavator westii* from indeterminate Clavatoracean material. Harris (1939), on the basis of studying ‘Middle’ and ‘Upper’ Purbeck charophyte associations, stated that they did not exhibit major evolutionary changes and concluded that ‘these beautiful little fossils [gyrogonites] are likely, in general, to have only slight stratigraphic value’. In contrast to this view, further research on charophyte gyrogonites, following the pioneer work of Peck (1957) and Grambast (1972, 1974), has revealed their stratigraphical importance for dating and correlating Cretaceous and Palaeogene non-marine deposits.

Preliminary studies of charophytes recovered from cored boreholes in the Weald showed that part of the Purbeck sequence could be attributed to the Berriasian Stage and that the upper part of the Weald Clay of the Wealden Supergroup belonged to the Barremian Stage (Feist *in* Lake *et al.* 1987). In this paper we present the results of our research to date on the charophyte biostratigraphy of the Purbeck and Wealden outcrop and subcrop successions of southern England. These results have been directly integrated with the ostracod zonal and faunicycle scheme of Anderson (1985), as charophytes and ostracods are commonly found associated in the same sample. We also review evolutionary trends among the charophyte family Clavatoraceae.

MATERIALS

The greater part of the charophyte specimens was separated from the residues of microsamples taken from cored boreholes in the Weald; most were taken from the ostracod collection of the late Dr F. W. Anderson at the British Geological Survey. For the Dorset, Isle of Wight and Swindon localities, new material collected by M. Feist from exposure has been studied, in addition to specimens from the Natural History Museum (London) and Senckenberg Museum (Frankfurt am Main, Germany). The borehole material from the Weald, the types of the new taxa described herein and the specimens figured in Plate 1, figures 1–2 and 4–8 are housed at the British Geological Survey, Keyworth, UK; the specimens figured in Plate 1, figures 16–17 at the Natural History Museum, London, UK; and the specimen figured in Plate 1, figure 9 at the Senckenberg Museum, Frankfurt am Main, Germany. The other samples are deposited at the Laboratoire de Paléobotanique, Université de Montpellier II, France, under the symbol CF.

EVOLUTIONARY TRENDS AMONG THE CLAVATORACEAE

The Clavatoraceae is a Mesozoic charophyte family characterized by the gyrogonite having a supplementary calcified cover of vegetative elements, known as the utricle. As shown by Grambast (1974) in his analysis of three phylogenetic lineages through the Cretaceous, it is the utricle that underwent evolutionary change. These lineages represent such remarkable examples of progressive evolution that they have been interpreted by Martin-Closas and Serra-Kiel (1991) as 'evolutionary species' (*sensu* Wiley 1978). However, this concept has no formal taxonomic status and is not appropriate to biostratigraphical studies.

The Clavatoraceae are subdivided into three subfamilies, according to the wall structure and the symmetry of the utricle. In the Echinocharoideae and Atopocharoideae, the utricle wall is composed of only one layer of three symmetrically arranged cells. In the former subfamily, the utricle comprises unjoined cells, whereas in the latter the cells are coalescent and entirely cover the gyrogonite inside. Our material comprises three representatives of the Atopocharoideae: the genera *Globator*, *Perimneste* and *Atopochara*. The Clavatoroideae differ from the two former subfamilies by the complexity of the utricle wall, which comprises two layers, with internal canals in the most evolved species, and by a bilateral symmetry. A three-fold symmetry can become superimposed secondarily, as in *Triclypella*. Most Clavatoraceae from southern England belong to this subfamily, namely *Nodosoclavator*, *Clavator*, *Flabellochara*, *Clypeator*, *Triclypella* and *Ascidella*.

The new data from the Purbeck charophyte floras of southern England complement existing data on the *Globator* lineage, and allow us to propose a separate origin for the two genera of the *Flabellochara*–*Clypeator* lineage (Grambast 1970, 1974). Our new data for *P. horrida* and *A. triquetra* do not modify the evolutionary succession outlined by Grambast (1967) for the *Perimneste*–*Atopochara* lineage, and so will not be discussed in this section.

Globator lineage

This series shows the evolution from the Tithonian *Globator rectispirale* to the Barremian *G. trochiliscoides* by reduction in the number of utricle cells and by progressive acquisition of spiralling (Pl. 1, figs 1–8). Only the oldest forms have so far been found in southern England.

G. rectispirale sp. nov. is the oldest and most primitive representative of the *Globator* lineage; each utricle comprises twenty-four vertical cells, without any indication of spiralling, when viewed both laterally and apically (Pl. 1, figs 1, 5). It is found in the Fairlight Borehole at 317.6–317.9 m. As reported below, the occurrences of this form outside the British Isles, have all been attributed to the Upper Tithonian.

G. praecursor (Mojon) comb. nov. occurs at 296.0–296.3 m in the Fairlight Borehole, and equivalent beds in the Warlingham, Broadoak and Brightling boreholes. It has the same utricle structure with twenty-four cells, but the upper elongated cells have begun to spiral (Pl. 1, figs 2, 6).

This form has been dated as Lower Berriasian in the Goldberg Formation in the Jura Mountains, where it is the index species of Mojon's Zone M1. Accordingly, the Jurassic–Cretaceous boundary can be recognized in southern England between the beds with *G. rectispirale* and with *G. praecursor*, near to the base of the Purbeck sequence.

G. protoincrassatus (Mojon) nov. comb. occurs at 293.2–293.5 m in the Fairlight Borehole, as well as in Bed 70 of Clements (*in Cope et al.* 1969) of the higher part of the Soft Cockle Member of the Lulworth Formation of Dorset. The utricle is still composed of twenty-four cells, but the three basal cells are shorter and the upper ones have become even more strongly spiralled (Pl. 1, figs 4, 8). This taxon is the index-species of Mojon's Zone M2, considered to be Lower Berriasian.

The subsequent stages of the *Globator* lineage, which have been reported from Spain (Grambast 1966, 1974; Martin-Closas and Grambast-Fessard 1986) and North America (Peck 1957) are missing in the Purbeck–Wealden succession of the British Isles; this absence may be explained by a local excess in salinity and lack of calcium carbonate in Hastings Beds and Weald Clay times.

Flabellochara and *Clypeator* lineages

The subdivision of the *Flabellochara*–*Clypeator* lineage proposed here differs from Grambast's phylogeny, in that *Clypeator* is not considered to be a descendant of *Flabellochara* because at various localities it has been found that *Flabellochara* appeared later than *Clypeator*. However, the main phylogenetic tendencies are the same as those demonstrated by Grambast (1970).

In the oldest of the Clavatoraceae, *Nodosoclavator* sp., only the internal layer of the utricle is developed, and is composed of nodules covering the spiral cells of the gyrogonite. *Nodosoclavator* appeared in the Oxfordian (Feist and Schudack 1991) and persisted until the Barremian.

In the Upper Tithonian, *Clypeator* (*C. discordis*) appeared. In this genus, the central basal cell of each side of the utricle is subdivided and the lateral pore occupies a central position (Pl. 2, figs 5–6). The evolutionary trend continued by lengthening and spiralling of the upper basal cells, from the late Tithonian, when *C. discordis* appeared, to the Albian *C. caperatus* and *C. lusitanicus*. *Triclypella* (Pl. 2, figs 1–3) represents a side branch of *Clypeator* (Grambast 1970). In the present state of knowledge of the few documented Upper Jurassic charophyte floras, the only possible transitional form between *Nodosoclavator* and *Clypeator* would be *Echinochara peckii*. However, the latter differs fundamentally from *Clypeator* in its utricle structure, built on a six-rayed mode of symmetry (Peck 1957; Grambast 1974), instead of the bilateral symmetry of *Clypeator*, and devoid of a nodular internal layer. The *Clypeator* and *Clavator*–*Flabellochara* lineages seem to have derived from an as yet undiscovered common Late Jurassic ancestor.

The *Clavator*–*Flabellochara* lineage starts with *Clavator* aff. *reidii*, found in the Upper Tithonian; 'aff.' indicates that the utricle is not yet completely constituted (Pl. 1, figs 9–10); the vegetative cells do not reach the apex of the 'nodosoclavatoroid gyrogonite' (*sensu* Schudack 1990, for *Nodosoclavator*).

In the Lower Berriasian *Clavator reidii*, the two-layered utricle is attained; it consists of vertical cells originating from a basal very short cell and joining themselves at the apex (Pl. 1, figs 11–13). Within populations of *C. reidii*, incompletely constituted utricles morphologically similar to *C. aff. reidii* are commonly found. However, these morphotypes do not represent the Tithonian species, because, in the latter, the utricle never reaches the apex of the gyrogonite, whereas, in the Berriasian, populations of *Clavator* generally include typical specimens with complete utricles. Such populations are found notably in the Hils Serpult of north-western Germany (Feist and Schudack 1991). The immature morphotypes can be regarded as reminiscent of the ancestral Tithonian stage. *Flabellochara* was derived from *Clavator* by addition of two cells on each adaxial side of the utricle and by the development of radiating, instead of vertical, upper cells. In *Flabellochara* (Pl. 1, figs 14–21), the small cells surrounding the lateral pores always remain small, unlike in *Clypeator*.

SYSTEMATIC PALAEONTOLOGY

The three families in existence during Late Jurassic to Early Cretaceous times are all represented. As commonly found for this time, Clavatoraceae are dominant, both in number of species and abundance, the Porocharaceae and Characeae remaining small and unornamented forms. Overall, twenty-one species have been identified in our material.

Family POROCHARACEAE Grambast, 1962
Subfamily POROCHAROIDEAE Grambast, 1961

Genus POROCHARA Mädlar, 1955

Porochara maxima (Donze) Donze, 1958

Plate 2, figure 21

1955 *Aclistochara maxima* Donze, p. 289, pl. 13, figs 6–7.

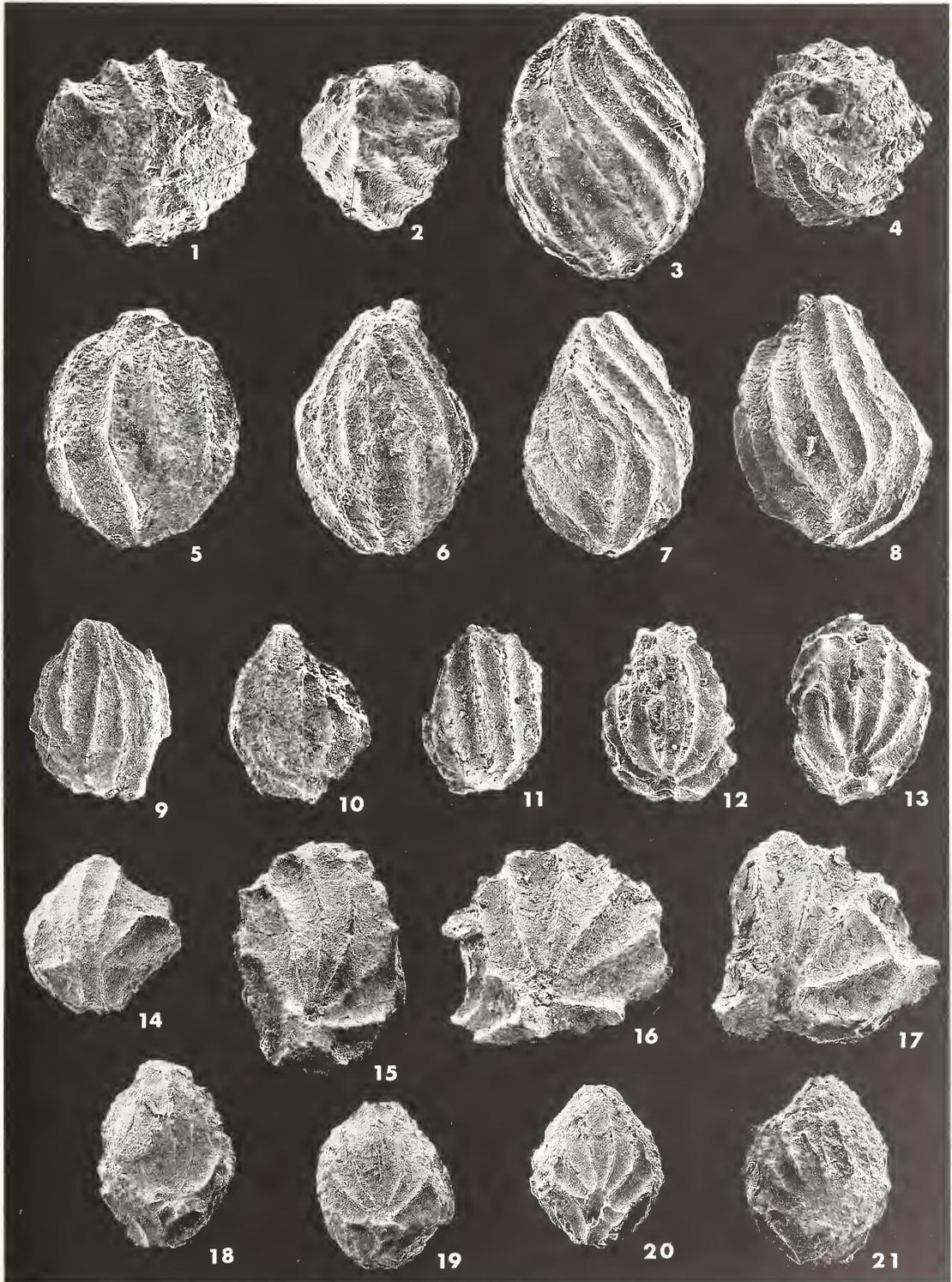
1958 *Porochara maxima* Donze, p. 180.

Distribution and range in southern England. Weald: Warlingham Borehole (612.1 m), upper part of the Broadoak Calcareous Member, Lulworth Formation. This level was referred to the Netherfield ostracod faunicle (Anderson *in* Worssam and Ivimey-Cook 1971; Anderson 1985). The Berriasian age of this horizon is deduced from records of the species from other areas.

Other occurrences. Berriasian of the Jura (Donze 1955; Mojon 1989), Spain (Brenner 1976; Schudack 1987a) and Sardinia (*Musacchiella maxima*) of Colin *et al.* (1985).

EXPLANATION OF PLATE I

- Figs 1, 5. *Globator rectispirale* sp. nov. Fairlight Borehole, Sussex, 317.6–317.9 m; Broadoak Calcareous Member. 1, MPK 8888, paratype; apical view. 5, MPK 8919, holotype; lateral view.
- Figs 2, 6–7. *G. praecursor* (Mojon) comb. nov. Fairlight Borehole, Sussex; Broadoak Calcareous Member. 2, MPK 8889; depth 296.0–296.3 m; apical view. 6, MPK 8920; depth 296.0–296.3 m; lateral view. 7, MPK 8891; depth 293.2–293.5 m; lateral view.
- Figs 3–4, 8. *G. protoincrassatus* (Mojon) comb. nov. 3, CF 2911-1; Swanage, Dorset; upper Soft Cockle Member; lateral view. 4, 8, Fairlight Borehole, Sussex, 293.2–293.5 m; Broadoak Calcareous Member. 4, MPK 8890; apical view. 8, MPK 8921; lateral view.
- Figs 9–10. *Clavator* aff. *reidi* Groves. Exposure III, Town Gardens Quarry, Swindon, Wiltshire; Chara Marls; lateral views; 9, SMF 44798. 10, CF 2791b-1.
- Figs 11–13. *Clavator reidi* Groves. Fairlight Borehole, Sussex, 280.1–280.4 m; Broadoak Calcareous Member; lateral views. 11, MPK 8892. 12, MPK 8895. 13, MPK 8896.
- Figs 14–15. *Flabellochara grovesi* (Harris). Lulworth Formation, Plant and Bone Beds Member; lateral views. 14, MPK 8893; Fairlight Borehole, Sussex, 273.4 m. 15, MPK 8894; Broadoak Borehole, Sussex, 71.50–72.00 m.
- Figs 16–17. *Flabellochara grovesi* (Harris). NHM V 26181-3 and NHM V 26181-4; Poxwell Road cutting, Dorset; Bed 33; lateral views.
- Figs 18–21. *Flabellochara xiangyunensis* Wang *et al.* Wadhurst Clay; lateral views. 18–19, Wadhurst Park No. 3 Borehole. 18, MPK 8897; 7.3–7.6 m. 19, MPK 8898; 6.7–7.0 m. 20, MPK 8899; Glynleigh Borehole, 59.00–59.50 m. 21, MPK 8900; stream section near Warninglid.
- All × 45, except figs 14, 19 and 20, × 48, and fig. 18, × 43.



Family CLAVATORACEAE Pia, 1927
 Subfamily ATOPOCHAROIDEAE Peck, 1938, emend. Grambast, 1969

Genus GLOBATOR Grambast, 1966

Globator rectispirale Feist, sp. nov.

Plate 1, figures 1–5

- 1971 *Globator maillardi* (Saporta); Ramalho, pl. 32, fig. 7.
 1981 *Globator maillardi* Saporta; Benest, p. 1288.
 1985 *Globator* cf. *maillardi* De Saporta; Benest, p. 363.
 1989 *Globator maillardi praecursor* Mojon, *pars*; Mojon in Détraz and Mojon, p. 54, lines 8–9.

Holotype. MPK 8919, British Geological Survey, Keyworth (Pl. 1, fig. 5).

Paratype. MPK 8888 (Pl. 1, fig. 1).

Type horizon and locality. Lulworth Formation, Broadoak Calcareous Member, Fairlight Borehole, Sussex, 317.6–317.9 m.

Derivation of name. From the shape of the upper cells of the utricle, which are quite straight in the new species, but always spiral to some extent in other *Globator* representatives.

Diagnosis. Utricle of *Globator* composed of three units, each comprised of one central basal cell, bearing three upper cells, flanked by two lateral basal cells each bearing an upper cell. Length of the central basal cells equal to 50–52 per cent. of the utricle length. Upper cells straight, and do not reach the apex. General shape globular to ovoid. Dimensions: 775–1025 μm long, 675–825 μm wide; L/W ratio varying from 1.1 to 1.4.

Remarks. This Tithonian species of *Globator* differs from other representatives of the genus by its utricle with very large basal cells and completely straight upper cells. It represents the most primitive grade of the *Globator* lineage.

Distribution and range in southern England. Weald: Fairlight Borehole (317.6–317.9 m), Broadoak Calcareous Member, Lulworth Formation, below the correlative of the Mountfield Adit Limestone. Mojon's identified ostracods in the associated residue (*Cypridea dunkeri papulata* (aberrant), *Damonella pygmaea*, *Fabanella boloniensis*, *Mantelliana purbeckensis* and *Rhinocypris jurassica*) indicate Ostracod Assemblage 1 of Anderson (1985). Only known record to date.

Other occurrences. Algeria: Chellala Mountains, Mahjouba Formation (Tithonian), from 50–60 m below beds with an A2/A3 calpionellid subzonal assemblage (Benest 1981, 1985).

Southwest Portugal: Brouco section, Sintra area, 'Infravalanginian' beds with *Anchispirocyclus* (Ramalho 1971). These beds were referred to the Lower Cretaceous on ostracod evidence; however, *Mantelliana purbeckensis*, the species on which this correlation is based (Rey *et al.* 1968), appeared in the Weald in the ostracod assemblage of the Gypsiferous Beds (Anderson 1985). The former beds are now considered to be Upper Jurassic (Rey, pers. comm. 1991), which agrees with the presence of Upper Tithonian calpionellids in the lower *Anchispirocyclus* beds in the Algarve (Rey 1982, 1983).

Globator praecursor (Mojon) comb. nov.

Plate 1, figures 2, 6–7

- 1987 *Globator maillardi* (Saporta); Feist in Lake *et al.*, p. 14.

- 1989 *Globator maillardi praecursor*; Mojon in Détraz and Mojon, p. 53, figs 5M–5R, non p. 54, lines 8–9.
 1991 *Globator maillardi praecursor*; Feist and Schudack, p. 502.

Holotype. Détraz and Mojon (1989, fig. 5M).

Emended diagnosis. Utricle of *Globator* composed of three units each comprised of one central basal cell, bearing three upper cells, flanked by two lateral basal cells each bearing an upper cell. Length of central basal cells equal to 33–34 per cent. of the utricle length. Upper cells oblique, slightly curved and reaching the apex. General shape ovoid. Dimensions: 850–1000 μm long, 600–700 μm wide. L/W ratio varying from 1.4 to 1.8.

Remarks. This form is remarkably stable in its different morphological characters in localities as distant as Jura, north-west Germany and southern England. A combination of this wide geographical distribution and a very short stratigraphical range makes *G. praecursor* a charophyte index for the basal Berriasian. These factors combine to justify raising this form to specific rank.

Distribution and range in southern England. Weald: Warlingham Borehole (625.1 m), Fairlight Borehole (296.0–296.3 m), Broadoak Borehole (111.50–112.00 m) and Brightling No. 27 Borehole (270.6 m). All occurrences were in the Broadoak Calcareous Member, Lulworth Formation; in the Broadoak Borehole they were from immediately above the Mountfield Adit Limestone. Mojon's identifications of the ostracods in the Fairlight Borehole sample include *Cypridea dunkeri inversa* and *Fabanella boloniensis*, indicating Ostracod Assemblage 2.

Other occurrences. French and Swiss Jura: *G. praecursor* is the index species of the Lower Berriasian M1 charophyte Zone of Mojon (in Détraz and Mojon 1989), the base of which yields the Lower Berriasian marine ostracod *Protocythere revili* and palynofloras of Berriasian affinities.

Germany, Lower Saxony Basin: lower part of the Serpulit (Feist and Schudack 1991).

Globator protoincrassatus (Mojon) comb. nov.

Plate 1, figures 3–4, 8

- 1989 *Globator maillardi protoincrassatus* Mojon in Détraz and Mojon, p. 55, figs 5E–5L.
 1991 *Globator maillardi protoincrassatus*; Mojon *et al.*, p. 502.

Holotype. Détraz and Mojon (1989, fig. 5E).

Emended diagnosis. Utricle of *Globator* composed of three units each comprised of one central basal cell, bearing three upper cells, flanked by two lateral basal cells each bearing an upper cell. Length of central basal cells equal to 29–30 per cent. of the utricle length. Upper cells slightly spiral, joining at the apex. Dimensions: 850–1150 μm long, 600–850 μm width. L/W ratio varying from 1.1 to 1.7.

Remarks. This form differs from *G. praecursor* by its shorter basal cells and more acute curvature of its upper cells, and from *G. maillardi* (Saporta) Grambast, by its larger basal cells and more twisted upper cells. The range of the new species is restricted to the Lower (not basal) Berriasian. The distinctive morphology and short stratigraphical range of Mojon's subspecies support it being raised to specific rank.

Distribution and range in southern England. Weald: Fairlight Borehole (293.2–293.5 m), Broadoak Calcareous Member, Lulworth Formation. Mojon identified *Cypridea dunkeri inversa* and *Fabanella boloniensis* from the same residue, indicating Ostracod Assemblage 2.

Dorset: Swanage, upper Soft Cockle Member, bed 70 of Clements (in Cope *et al.* 1969).

Other occurrences. French Jura: *G. protoincrassatus* is the index species of the Lower Berriasian M2 charophyte Zone of Mojon (in Détraz and Mojon 1989), dated by ammonites (in a marine intercalation) to the *Pseudosubplanites grandis* Zone, *P. grandis* Subzone (Clavel *et al.* 1986; Hoedemaeker 1991).

Germany: Lower Saxony Basin, upper part of the Serpulit (Feist and Schudack 1991).

Genus PERIMNESTE Harris, 1939

Perimneste horrida Harris, 1939

1939 *Perimneste horrida* Harris, p. 54, pls 13–15; pl. 16, figs 6, 8–9.

Distribution and range in southern England. According to Harris (1939) the species is common in the 'Middle' and 'Upper Purbeck Beds' of Dorset. The material of this species published by Harris and preserved at the Natural History Museum, London, comprises predominantly vegetative remains. Utricles are present at Durdle Door and Moigne Down.

Other occurrences. This species is common in the Berriasian of the Jura Mountains (Donze 1958; Mojon and Strasser 1987), Spain (Brenner 1976; Schudack 1987a) and Germany (Schudack 1990; Feist and Schudack 1991). It is unknown outside Europe.

Genus ATOPOCHARA Peck, 1938, emend. Peck, 1941

Atopochara triquetra (Grambast) comb. nov.

Plate 2, figure 9

- 1967 *Atopochara trivolvis* Peck, *pars*; Grambast, pl. 3, fig. 14.
 1968 *Atopochara trivolvis triquetra* Grambast, p. 8, pl. 3, fig. 16.
 1981 *Atopochara trivolvis* Peck *triquetra* Grambast; Musacchio, p. 474, pl. 5, fig. 9.
 1981 *Atopochara trivolvis triquetra* Grambast; Zhang *et al.*, p. 153, pl. 1, figs 1–6.
 1982 *Atopochara trivolvis triquetra* Grambast; Wang and Lu, p. 94, pl. 2, figs 9–13.
 1982 *Atopochara trivolvis* Peck *ssp.*; Feist in Huckriede, p. 187, pl. 6, fig. 4.
 1983 *Clypeator europeus* Grambast, *pars*; Kampmann, pl. 18, fig. 1a.
 1985 *Atopochara trivolvis triquetra* Grambast; Jiang *et al.*, p. 166, pl. 1, fig. 1a–c
 1986 *Atopochara trivolvis* subsp. *triquetra* Grambast; Martin-Closas and Grambast-Fessard, p. 38, pl. 8, figs 7–12.
 1987a *Atopochara trivolvis triquetra* Grambast; Schudack, p. 135, pl. 6, figs 1–4.
 1987b *Atopochara trivolvis triquetra* Grambast; Schudack, p. 16, pl. 2, figs 1–5.
 1987 *Atopochara trivolvis* subsp. *triquetra* Grambast; Martin-Closas and Peybernes, p. 699, fig. 2: 5–6.
 1988 *Atopochara trivolvis triquetra* (Peck) Grambast; Mojon, pl. 2, figs a–c.
 1989 *Atopochara trivolvis triquetra* Grambast; Schudack, p. 415, pl. 2, figs 1–6.
 1991 *Atopochara trivolvis triquetra* Grambast; Lu and Yuan, p. 377, pl. 1, figs 3–6.

Holotype. C.633.16, Montpellier University (Grambast 1968, pl. 3, fig. 16).

Diagnosis. Utricle of *Atopochara*, composed of three basal cells, the two left hand ones bearing three upper cells and the right hand one bearing two upper cells and, in most cases, a slight antheridial cast. Upper cells twisted. Utricle subsurface visible between cells. Utricle showing a triangular and irregular outline when seen from apex or base. Dimensions of paratypes: utricle length, 656–924 μm ; utricle width 632–973 μm ; average cell number, 33; average antheridia number, 3; antheridium diameter, 73–218 μm .

Remarks. This form represents an evolutionary grade of the *Perimneste*–*Atopochara* lineage. During the sixty million years from the Berriasian to the Campanian, this lineage shows progressive

evolution of the utricle with the condensation of the primarily ramified basal cells, the spiralization of the upper cells, and the regression and eventual disappearance of the antheridial casts, which are exceptionally preserved in *Perimneste*. *A. triquetra* is characterized by rather distinct basal branching (portions of the underlying layer being apparent), well spiralized upper cells, and a vestigial antheridial cell persisting in one branch. Two forms can be recognized. In the primitive form, the primary basal cells may be present and the characteristic antheridial sculpture still persistent; in the advanced form, the primary basal cells have disappeared and the ancestral antheridia are represented only by short sterile cells with a smooth surface (Grambast 1967, 1974). In *A. trivolvis*, the utricle structure is quite condensed (the subsurface is no longer visible) and the lower right hand fork still shows a vestigial antheridium, but reduced to a spot without any structure. *A. triquetra* is a species with world-wide occurrences, ranging from Lower to Upper Barremian, *A. trivolvis* from Upper Barremian to Lower Aptian. It seems justified to raise *A. trivolvis triquetra*, which differs from *A. trivolvis* by distinct characters as well as by its range, to species rank.

Distribution and range in southern England (primitive form). Weald: Warlingham Borehole (430.0 m), lower part of the upper division of the Weald Clay, above Bed 3, associated with *Asciidiella iberica* and therefore considered to be Lower Barremian (see above; Feist and Grambast-Fessard 1991, p. 194, fig. 3b).

Distribution and range in southern England (advanced form). Isle of Wight: Cowleaze Chine, basal part of the Vectis Formation, attributed to the Upper Barremian.

Other occurrences (primitive form). Spain: Upper Hauterivian–Lower Barremian of Maestrazgo (Grambast 1968, 1974; Martin-Closas and Grambast-Fessard 1986; Martin-Closas and Salas 1988, 1989) and Cameros Basin (Schudack 1987a). The attribution to the Barremian is based on correlations of marginal non-marine Tethyan sequences with distal marine deposits dated by ammonites, nannofossils and planktonic foraminifers (Martin-Closas and Salas 1989).

Switzerland: a similar dating, based on palynology, was given by Mojon and Médus (1990) for specimens of *A. triquetra* primitive forms, albeit identified from thin sections in which the distinctive characteristics of the species do not appear clearly (cf. Mojon 1988, pl. 1, figs G–H).

Other occurrences (advanced form). Southern Jura: a recent report of this form in the succession of La Ruchère, dated by orbitoline foraminifers and palynofloras (Mojon 1988; Mojon and Médus 1990) is a new and important record, extending the known range of the San Carlos charophyte Zone of Grambast (1974), previously restricted to the Upper Barremian, into the Lower Aptian.

Spain: Maestrazgo, Upper Barremian–Aptian (Martin-Closas and Grambast-Fessard 1986; Martin-Closas and Salas 1989).

Other occurrences (evolutionary stage not recorded). Barremian of Germany (Schudack 1987b), Spain (Schudack 1987a, 1989), Argentina (Musacchio 1971, 1979) and China (Wang and Lu 1982; Jiang *et al.* 1985).

Subfamily CLAVATOROIDEAE Pia, 1927, emend. Grambast, 1969

Genus CLAVATOR Reid and Groves, 1916, emend. Harris, 1939

Clavator reidi Groves, 1924

Plate 1, figures 9–13

1916 *Clavator* Reid and Groves, p. 253, pl. 18.

1924 *Clavator reidi* Groves, p. 116.

Remarks. This species is well represented in the Purbeck Group of southern England. Among the Clavatoraceae, it represents an early stage of the *Flabellochara–Clypeator* lineage, first described by

Grambast (1974). *C. reidi* seems to be derived from *Nodosoclavator* by the intermediate of *C. aff. reidi*, the utricles of which present a bilateral symmetry but are not completely closed at the apex.

Distribution and range in southern England. Weald: Warlingham Borehole (612.3–614.8 m), Fairlight Borehole (273.7–274.0 m, 280.1–280.4 m and 281.0–281.3 m; *C. aff. reidi* at 296.0–296.3 m) and Broadoak Borehole (71.5–72.0 m). All occurrences in the upper part of the Broadoak Calcareous Member, Lulworth Formation.

Dorset: Durdle Door, just below the Cinder Bed Member, Lulworth Formation; Worbarrow Tout, just above the Cinder Bed, Durlston Formation; Swanage, Mammal Bed to 5 m above the Cinder Bed; Poxwell Road Cutting (NHM material).

Wiltshire: (identified with 'aff.') Swindon, exposure III of Sylvester-Bradley (1941); 'Swindon Series', Cythere Marls and Chara Marls.

Other occurrences. Switzerland: Bienne (Jura), Lower Berriasian Goldberg Formation (Häfeli 1966; Mojon and Strasser 1987).

France: Saint-Claude (Jura) and Marseille region, Purbeck Beds attributed to the Berriasian on ostracod evidence (Mojon 1989).

Spain: Maestrazgo, Berriasian beds dated by dasyclads (Canérot 1979).

Northern Portugal: ('*Clavator cf. reidi*'), Lower Cretaceous (Rey *et al.* 1968; Ramalho 1971).

Germany: Lower Saxony Basin, upper part of the Serpultit (Feist and Schudack 1991), attributed to the Berriasian by correlations with the M1b charophyte zone established in the French and Swiss Jura; these correlations are supported by ostracod and miospore evidence (Dörhöfer and Norris 1977; Détraz and Mojon 1989; Feist and Schudack, 1991).

Genus FLABELLOCHARA Grambast, 1959

Flabellochara grovesi (Harris) Grambast, 1962

Plate 1, figures 15–17

1939 *Clavator grovesi* Harris, p. 46, pl. 10, figs 1–12; pls 11–12; pl. 17, figs 8–13.

1962 *Flabellochara grovesi* (Harris) Grambast, p. 69.

Remarks. The specimens from Brouco (Portugal) attributed to *F. grovesi* (Ramalho 1971, pl. 33, fig. 6) have been reinterpreted by Schudack (1990) as *Clypeator discordis*, which co-occurs with *Globator rectispirale*. The beds in question, previously considered to be Lower Cretaceous, are now assigned to the Jurassic (Upper Tithonian). *F. grovesi* has not so far been recorded from Germany; published records of this species refer to *Clypeator discordis*.

Distribution and range in southern England. Weald: Fairlight Borehole (273.4–273.7 m and 280.1–280.4 m). The lowest occurrence is in the Robertsbridge faunicycle ('Lower' Purbeck), but nine faunicycles above the upper limit of *Cypridea dunkeri papulata*.

Dorset: 'Middle' and 'Upper Purbeck Beds' of Durdle Door, Worbarrow Tout, Mupe Bay and Poxwell Road Cutting (see Appendix 2).

Other occurrences. This species occurs in most of the classic 'Purbeck' successions attributed to the Berriasian. The species is restricted to the lower and middle Berriasian (Détraz and Mojon 1989).

Jura (France and Switzerland): Goldberg Formation and Mergel-und-Kalk-Zone (Häfeli 1966; Grambast 1970; Mojon and Strasser 1987; Détraz and Mojon 1989).

Spain: various areas and localities (Brenner 1976; Martin-Closas and Grambast-Fessard 1986; Schudack 1987a).

Sardinia: La Cala d'Inferno, Purbeck beds (Pecorini 1969; Colin *et al.* 1985).

Flabellochara xiangyimensis Wang *et al.*, 1976

Plate 1, figures 18–21

1976 *Flabellochara xiangyimensis* Wang *et al.*, p. 68, pl. 1, fig. 1

Remarks. This species has not previously been recorded outside China. Such wide distribution is not rare in charophytes, and other wide-ranging forms include the genera *Atopochara* (*A. trivolis*, *A. triquetra*), *Peckisphaera* (*P. verticillata*) and *Clypeator* (*C. discordis*).

Distribution and range in southern England. Weald: Wadhurst Park No. 3 Borehole (6.7–7.6 m), Glynleigh Borehole (59.0–59.5 m) and Kitchenham Dam Borehole (281.3 m). All occurrences are in the Wadhurst Clay.

Other occurrences. Yunnan Province, China: Valanginian (Wang *et al.* 1976; Wang and Lu 1982).

Genus *CLYPEATOR* Grambast, 1962, emend., 1970

Clypeator combei Grambast, 1970

Plate 2, figure 4

1970 *Clypeator combei* Grambast, p. 1967, pl. 3, figs 1–5.

Remarks. From the records presented here, the range of *C. combei*, previously reported only from the Lower Barremian, extends from Upper Hauterivian into the Upper Barremian.

Distribution and range in southern England. Weald: Warlingham (430.4 m), Ripe (159.5–160.0 m) and Hailsham (29.5–30.0 m) boreholes. This species occurs in the beds above the main occurrences of Small-*Paludina*, below (Ripe, Hailsham) and above (Warlingham) Bed 3 of the Weald Clay (Lake and Young 1978; Worsam 1978). The borehole records range from Upper Hauterivian to Lower Barremian.

Isle of Wight: Cowleaze Chine, in the basal part of the Vectis Formation (Upper Barremian).

Other occurrences. Spain: Maestrazgo, 'Lower Barremian' (Grambast 1970, 1974; Martin-Closas and Salas 1989). The attribution to Lower Barremian was by Grambast (1974), probably on the basis of charophyte evolutionary stages.

Clypeator britannicus sp. nov.

Plate 2, figures 7–8

Holotype. MPK 8906, British Geological Survey, Keyworth (Pl. 2, fig. 8).

Paratype. MPK 8905 (Pl. 2, fig. 7).

Type horizon and locality. Grinstead Clay (Valanginian), Kingsclere Borehole, Hampshire; 306.6 m (holotype) and 305.7 m (paratype).

Diagnosis. Utricle of *Clypeator* characterized by the position of the lateral pores in the lower third of the utricle length, the lateral shields being composed of ten to eleven triangular cells radiating from the lateral pores. Dimensions: length varying from 475 to 625 μm , width from 500 to 625 μm . L/W ratio varying from 0.9 to 1.1.

Remarks. The *Clypeator* phylogenetic lineage (Grambast 1970) is characterized by the development of intermediate cells between the basal and upper cells. The new species represents a new grade, intermediate between the Berriasian *Clypeator discordis* and the Hauterivian–Barremian *C. combei*. In the new species, the lateral pores are in the lower third of the length of the utricle, as they are in *C. discordis*, but in the latter the intermediate and basal cells are approximately of the same size and rectangular shape. In contrast, *C. britannicus* has intermediate cells which resemble the upper ones, and which are elongated and slightly undulated. By this character, the new species resembles *C. combei*, but differs from it in the low position of the lateral pores.

Distribution and range in southern England. Hampshire: so far recognized only from its type locality (see above).

Clypeator discordis Shaikin, 1976

Plate 2, figures 5–6

1970 *Clypeator* sp. Grambast, p. 1965, pl. 1, fig. 3.1976 *Clypeator discordis* Shaikin, p. 82, figs 9–10.

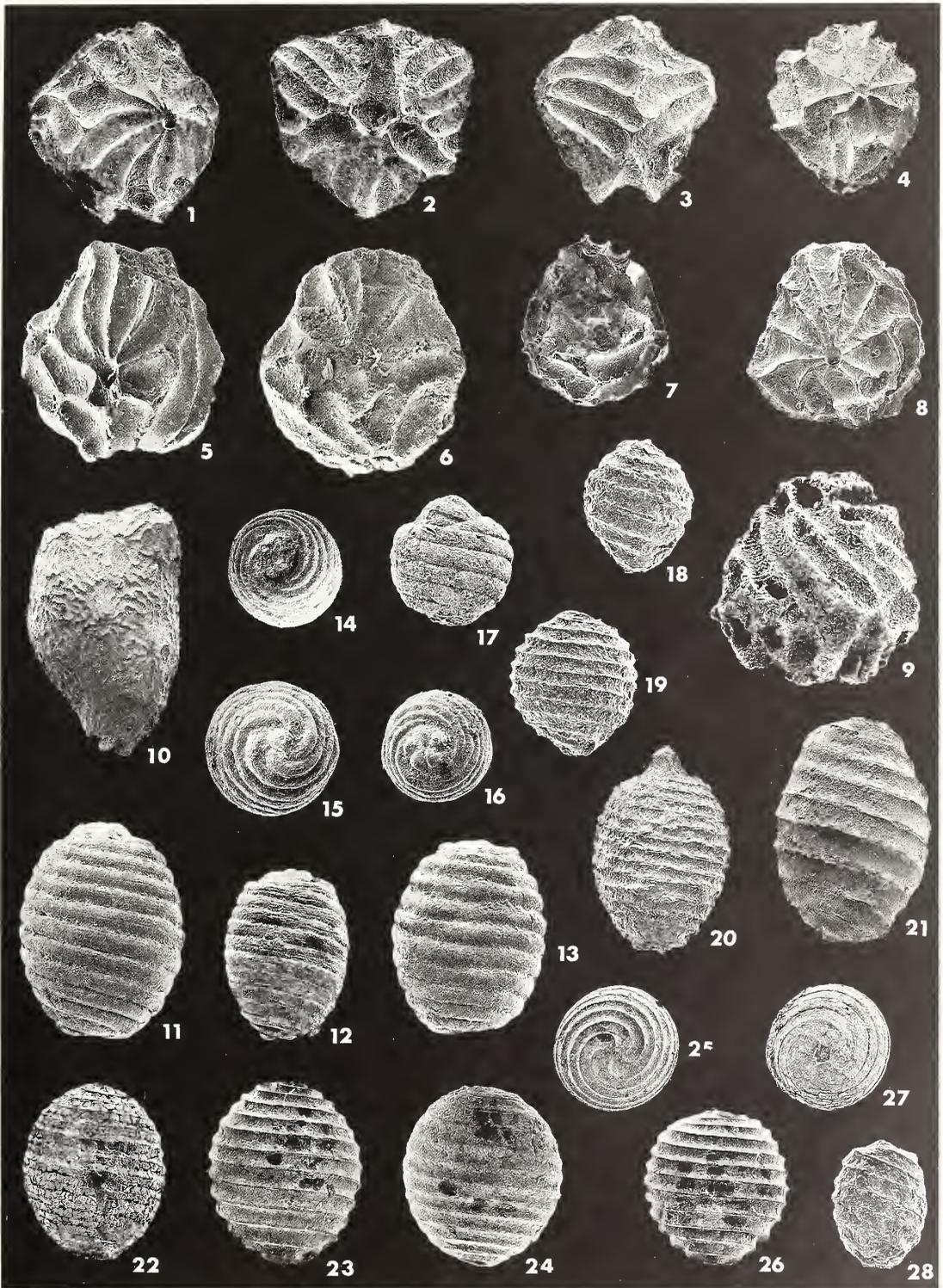
Distribution and range in southern England. Wiltshire: Town Gardens Quarry, Swindon. In the succession established by Sylvester-Bradley (1941), the species ranges through the major part of the Purbeck sequence; in its lowest occurrence, in the Lower Pebbly Beds, it is associated with ostracods of the Quainton–Stair faunicycles (I. P. Wilkinson in litt. 1991). Using Anderson's (1985) ostracod evidence, these faunicycles, which constitute ostracod Assemblage 1, are older than the Swindon faunicycle which, in the Fairlight Borehole, contains the (inferred) Tithonian *Globator rectispirale*. *C. discordis* thus appears in the Upper Jurassic.

Other occurrences. Portugal: Brouco section. The specimen, named *Flabellochara grovesi* and figured by Ramalho (1971, pl. 33, fig. 6), has been re-identified as *Clypeator discordis* (Schudack 1990). The attribution of the Brouco section to the Tithonian on the occurrence of *Globator rectispirale* (see above) confirms that the first appearance of *C. discordis* is in the Upper Jurassic.

This species is common in the Berriasian of Europe (see Schudack 1987a, 1990; Feist and Schudack 1991). It has also been reported from the Valanginian of Sichuan Province, China (Huang 1985) and from the Hauterivian and Barremian of the Pre-Dobrogean Depression in Ukraine (Shaikin 1976).

EXPLANATION OF PLATE 2

- Figs 1–3. *Triclypella calcitrapa* Grambast. Ripe Borehole, Sussex, 154.00–154.50 m; Weald Clay. 1, MPK 8901; lateral view, showing one of the three faces with central pore. 2, MPK 8922; basal view, showing the triradiate symmetry of the utricle. 3, MPK 8923; dorsal (adaxial) face, showing the high position of the lateral pores. All $\times 45$.
- Fig. 4. *Clypeator combei* Grambast. MPK 8902; Ripe Borehole, 154.00–154.50 m; Weald Clay; lateral view, showing one of the two faces of the utricle; $\times 45$.
- Figs 5–6. *Clypeator discordis* Shaikin. Town Garden Quarry, Swindon; Lower Pebbly Beds; lateral views, showing the basal cell subdivided; $\times 60$.
- Figs 7–8. *C. britannicus* sp. nov. Kingsclere Borehole, Hampshire, 306.6 m; ?Grinstead Clay equivalent. 7, MPK 8905, paratype; dorsal view, showing the low position of the lateral pores; $\times 45$. 8, MPK 8906, holotype; lateral view, showing lateral pore and short basal cell; $\times 48$.
- Fig. 9. *Atopochara triquetra* Grambast, advanced form. CF 2777a-7; Cowleaze Chine, Isle of Wight; lower Vectis Formation; $\times 43$.
- Fig. 10. *Asciadiella iberica* Grambast. MPK 8907; Warlingham Borehole, Sussex, 430.0 m; Weald Clay, upper part; lateral view; $\times 25$.
- Figs 11–16. *Sphaerochara andersoni* sp. nov. Ripe Borehole, Sussex, 154.00–154.50 m; Weald Clay. 11, MPK 8908, holotype; lateral view; $\times 60$. 12, MPK 8909, paratype; lateral view; $\times 48$. 13, MPK 8910, paratype; lateral view; $\times 45$. 14, MPK 8911, paratype; apical view of a germinated specimen; $\times 45$. 15, MPK 8912, paratype; basal view; $\times 42$. 16, MPK 8913, paratype; apical view; $\times 45$.
- Fig. 17. *Latochara* sp. A. CF 2792b-1; Town Gardens Quarry, Swindon; Upper Marlstones; lateral view; $\times 45$.
- Figs 18–19. *Mesochara* sp. A. Fairlight Borehole, Sussex, 281.0–281.3 m; Broadoak Calcareous Member; lateral views. 18, MPK 8914. 19, MPK 8915. Both $\times 70$.
- Fig. 20. *Latochara* sp. B. MPK 8916; Warlingham Borehole, Sussex, 581.7 m; Greys Limestones Member; lateral view; $\times 66$.
- Fig. 21. *Porochara maxima* Donze. MPK 8917; Warlingham Borehole, Sussex, 612.1 m; Arenaceous Beds Member; lateral view; $\times 48$.
- Figs 22–27. *Peckispharea verticillata* Peck. Cowleaze Chine, Isle of Wight; lower Vectis Formation. 22–24, 26, CF 2777a 1 to a3, a4; lateral views; 25, CF 2777a-5; apical view. 27, CF 2777a-6; basal view. All $\times 45$.
- Fig. 28. *Aclistochara* sp. A. MPK 8918; Warlingham Borehole, Sussex, 614.2 m; Broadoak Calcareous Member, lateral view; $\times 70$.



Genus TRICLYPELLA Grambast, 1969

Triclypella calcitraba Grambast, 1969

Plate 2, figures 1–3

1969 *Triclypella calcitraba* Grambast, p. 881, pl. 1, figs 1–7.

Distribution and range in southern England. Weald: this species is commonly associated with *C. combei* in the beds above the Small-‘*Paludina*’ Limestone beds of the Weald Clay of the Weald. In the Ripe Borehole, the species occurs in beds at 154.0 to 154.5 m, dated palynologically as Hauterivian (Feist and Batten 1990). It also occurs in equivalent beds in the Hailsham Borehole (Text-fig. 2). In the Warlingham Borehole, it occurs at 430.0–430.7 m; in the sample from 430.0 m, it co-occurs with *Asciidiella iberica*, which is considered to be lower Barremian. The species has not been recorded from the topmost Wealden Beds Vectis Formation of the Isle of Wight; its range thus seems restricted to the highest Hauterivian–Lower Barremian.

Other occurrences. Spain: north-central and eastern Spain, ‘Lower’ (but not ‘basal’) Barremian (Grambast 1970, 1974; Schudack 1987a; Martin-Closas and Salas 1989). The species ranges from the Hauterivian to the Barremian (Wang and Lu 1982).

Genus ASCIDIELLA Grambast, 1966

Asciidiella iberica Grambast, 1966

Plate 2, figure 10

1966 *Asciidiella iberica* Grambast, p. 2210, pl. 1, figs 1–6.

Distribution and range in southern England. Weald: the species was found only in the Warlingham Borehole (430.0 m), in a sample from above Bed 3 of the Weald Clay, which is considered to be Lower Barremian from its position 1.4 m above the lowest horizon dated by angiosperm pollen (Hughes and McDougall 1990, fig. 3) and dinocysts (Harding 1990) as Barremian.

Other occurrences. Spain: eastern Maestrazgo (Combes *et al.* 1966), above beds containing Hauterivian–Barremian foraminifers; Cameros Basin (Schudack 1987a), above beds with ostracods indicating the same age. Although considered to be of early Barremian age, it is therefore possible that the species ranges down into the upper Hauterivian.

Family CHARACEAE, Agardh, 1824

Subfamily CHAROIDEAE Al. Braun *apud* Migula, 1897

Genus PECKISPHAERA Grambast, 1962

Peckisphaera verticillata (Peck) Grambast, 1962

Plate 2, figures 22–27

1937 *Chara verticillata* Peck, p. 84, pl. 14, figs 30–331962 *Peckisphaera verticillata* (Peck) Grambast, p. 78.

Distribution and range in southern England. Isle of Wight; Cowleaze Chine, the fossiliferous bed at the base of the Vectis Formation (attributed to the Upper Barremian – see below).

Other occurrences. USA: Rocky Mountains, common in the Upper Jurassic and Lower Cretaceous (Peck 1957).

East Asia: China, Triassic (Jiang *et al.* 1985; Lu and Luo 1990); Mongolia, Upper Cretaceous (Karczewska and Ziembinska-Tworzydło 1970).

Spain: Barremian (Schudack 1987a, 1990).

Subfamily NITELLOIDEAE Al. Braun *apud* Migula, 1897

Genus SPHAEROCHARA Mädlér, 1952, emend. Horn af Rantzien and Grambast, 1962

Sphaerochara andersoni sp. nov.

Plate 2, figures 11–16

Holotype. MPK 8908, British Geological Survey, Keyworth (Pl. 2, fig. 11).*Paratypes*. MPK 8909–8913 (Pl. 2, figs 12–16).*Type horizon and locality*. Weald Clay, Hauterivian, Ripe Borehole, Sussex, 154.0–154.5 m.*Derivation of name*. The species is dedicated to the late Dr F. W. Anderson, in token of gratitude for having preserved numerous charophyte specimens during his work on the Purbeck and Wealden ostracods of southern England.*Diagnosis*. Gyrogonite of *Sphaerochara*, characterized by its ellipsoid to cylindroid shape, the length–width ratio varying from 1.1 to 1.5. Lower part of the basal plate superficial, bearing a central nodule. Dimensions: length 425–600 μm , width 375–525 μm . Eleven to twelve circumvolutions seen in lateral views.*Remarks*. By its prominent apical rosette and its thick basal plate, superficial at the basal pore level, the new species clearly belongs to *Sphaerochara*. It differs from other species assigned to that genus by its elongated, instead of, the more common, spherical shape. In this character, *S. andersoni* resembles *S. bicarinata* Yang from the Minhe Formation of north-west China (Hao *et al.* 1983), but this latter species is significantly smaller.*Distribution and range in southern England*. Weald: Warlingham Borehole (430.0 m, 430.4 m and 430.7 m), Ripe Borehole (154.0–154.5 m) and Hailsham Borehole (16.50–17.99 m). All these occurrences are in the lower portion of the upper Weald Clay. Forms resembling *S. andersoni* (assigned here to *S. aff. andersoni*) but with a more globular shape, are present in the Wadhurst Clay, in the Wadhurst Park No. 3 Borehole (59.0–59.5 m), and the Robertsbridge Borehole, Sussex (12.2–12.3 m).

Hampshire: Kingsclere Borehole (306.6 m), Grinstead Clay.

SUCCESSION OF THE CHAROPHYTE ASSEMBLAGES AND
BIOSTRATIGRAPHICAL IMPLICATIONS

Charophytes occur intermittently in the Purbeck and Wealden successions of southern England; on the whole, each standard stage can be characterized by a particular assemblage, but abundance, preservation and diversity vary throughout the succession. The abundant and diverse Purbeck floras enable a biozonation to be established for the Jurassic–Cretaceous transition but other intervals, such as the detritic, and/or marine and weakly calcareous deposits either do not contain charophytes or contain only poorly calcified specimens without stratigraphical significance. We have considered as undefined zones, or as interregna, these intervals which, however, are well documented elsewhere and thus permit an appraisal of the entire Upper Jurassic–Lower Cretaceous charophyte zonation. The local charophyte zones introduced here are based on the first occurrences of successive index-species in the succession. The index species are chosen from the best dated and most widely distributed species of the assemblages. An 'interregnum' represents the time-interval between the last occurrence of the index species of the previous zone and the first occurrence of the index species of the following one.

PURBECK LIMESTONE GROUP

Stratigraphy

The Purbeck Limestone Group of southern England constitutes a predominantly non-marine succession of limestones and mudstones spanning the Jurassic–Cretaceous boundary. This sequence rests on marine sediments (Portland Group) of late, but not latest, Jurassic age. It is found in two main depositional areas, a Western or Wessex Basin to the west of the Portsdown structure and an Eastern or Wealden Basin to the east of this structure (Anderson 1985, fig. 1).

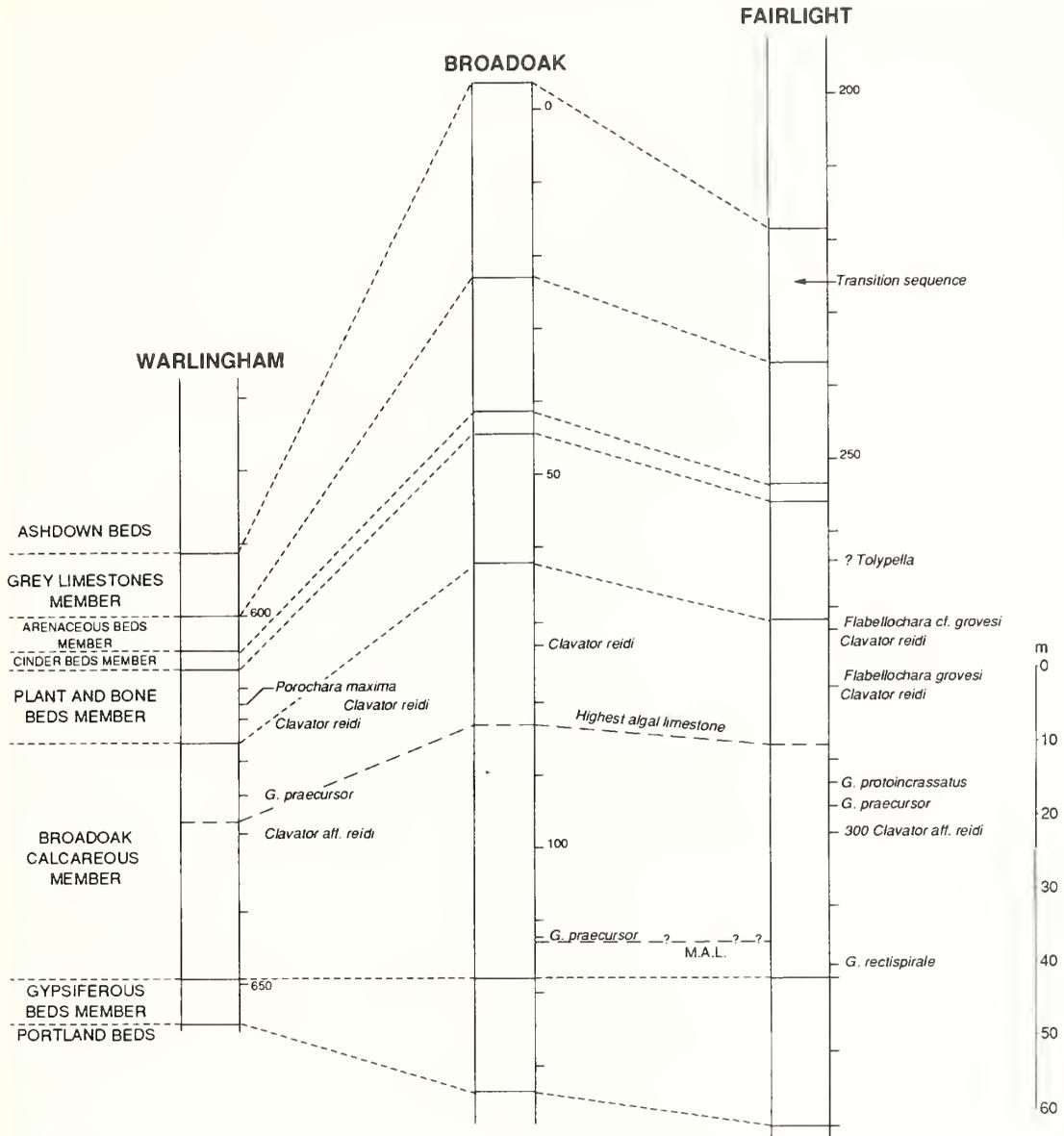
Wessex Basin. The stratotype is the section in Durlston Bay, Swanage (Melville and Freshney 1982, fig. 16), where the group attains its maximum thickness (House 1989, table 7) and, except for the basal and topmost beds, is superbly exposed (for section details see Clements *in Cope et al.* 1969; Clements 1993). The junction in the Isle of Purbeck between the ‘Purbeck Beds’ as originally defined and the overlying Wealden Beds (Supergroup) is gradational (Strahan 1898; Arkell 1947a, p. 148); recent research has shown that the base of the type Wealden Beds as recognized in the Wealden Basin must be located *within* rather than at the top of the Purbeck sequence (Morter 1984; Lake and Shephard-Thorn 1987).

Following Clements (1993) and standard British Geological Survey (BGS) practice, two formations are recognized in the stratotype Purbeck Limestone Group in this paper, the Lulworth and Durlston formations (Townson 1975) in ascending order, with the base of the latter being taken at the base of the near-marine Cinder Bed Member. The succession was earlier divided informally into the now redundant lower, middle and upper Purbeck Beds (Forbes 1851), which were used, extensively, both in this country and abroad, until comparatively recently (e.g. Anderson 1985).

Within each of the original three subdivisions, distinctive groups of beds were recognized and named, based on a combination of their lithological character and fossil content. These groups of beds have member status (Clements 1993) within the two component formations. The Cherty Freshwater Member near the top of the Lulworth Formation is the source of much of the well-preserved Purbeck charophyte material described by Harris (1939), notably *Flabellochara grovesi* and *Perinneste horrida*.

Wealden Basin. In the Wealden Basin, the Purbeck strata crop out in three faulted inliers, where the gypsiferous basal beds have been exploited for gypsum; they have also been penetrated by several deep cored boreholes (for details see Lake and Shephard-Thorn 1987). The occurrence of a shell-rich unit (Cinder Bed Member, Text-Fig. 1), characterized by oysters, and the near-marine ‘*Protocardia*’ major molluscan association (Morter 1984) allows the succession to be subdivided into the same two formations (Lulworth and Durlston) recognized in the Wessex Basin, although the member nomenclature adopted is different (Lake and Shephard-Thorn 1987, table 3). Charophytes indicating a Berriasian age for the Broadoak Calcareous Member of the Lulworth Formation have already been reported by Feist (*in* Lake *et al.* 1987) and are further discussed later in this paper. Near the base of this member there is a marker horizon of local importance, the Mountfield Adit Limestone, also referred to later in the text.

The succession of lithologies and inferred depositional environments of the Purbeck Group in the Wealden Basin, however defined, is essentially comparable with that found in the Wessex Basin (Worssam and Ivimey-Cook 1984 and references therein; Anderson 1985, p. 3, fig. 5). The two successions are generally held to be at least broadly correlative and contemporaneous, despite somewhat controversial palynological evidence to the contrary (Wimbledon and Hunt 1983; Hunt 1985, 1987; Norris 1985), which suggests that the base of the Purbeck succession is significantly younger in the southern Weald (Brightling Mine, Fairlight Borehole) than it is in Dorset. Batten (*pers. comm.* 1992) emphasizes the geographical proximity between Dorset and the Weald at the time, and also the fact that there is good evidence for a more or less synchronous climatic change from arid to humid throughout that part of Europe. He considers that the differences in palynological assemblages between apparently lithostratigraphically correlative successions may



TEXT-FIG. 1. Lithofacies correlation between Warlingham, Broadoak and Fairlight boreholes, modified after Morter (1984), showing key charophyte records. M.A.L., tentative position of Mountfield Adit Limestone.

result from a more hostile environment in Dorset compared with the Weald. Allen and Wimbledon (1991) noted that the same sequence of events (*Classopollis* pollen decline, *Cypridea posticalis* occurrence, quasi-marine Cinder Bed and percentage increase in the kaolinite component of the clay mineral assemblages) can be recognized in both areas, which suggests that the base of the Purbeck is not diachronous.

Marginal areas. Purbeck strata are also found in marginal areas relative to the two main depositional basins, namely in Wiltshire in the Vale of Wardour and in three outliers near Swindon

(Sylvester-Bradley 1941; Arkell 1947*a*, 1947*b*, 1948; Wimbledon 1976), as well as in outliers in Oxfordshire and near Aylesbury, Buckinghamshire (Barker 1966; Bristow 1968; Wimbledon 1980; Radley 1992). The correlation between the Swindon and Aylesbury successions and the Dorset stratotype remains uncertain (see Barker *et al.* 1975; Morter 1984), but Anderson (*in* Worssam and Ivimey-Cook 1971) considered that at least the lower part of the Swindon Purbeck succession predates the Purbeck stratotype and correlates with the higher part of the Portland Stone Formation. Of the marginal localities, only the Swindon succession is considered in this paper. The Purbeck succession cored in the Kingsclere Borehole in the western part of the Wealden Basin exhibits a succession intermediate between that of the Dorset stratotype and that of the marginal developments near Aylesbury.

The Purbeck Limestone Formation succession at Swindon. In the classic Great (now Town Gardens) Quarry near Swindon, a complex succession of marls, limestones and pebble-beds (including at least one limestone with marine fossils), the so-called 'Swindon Series' (Keeping 1883), rests with an erosional contact on the Swindon Sand and Stone Member of the Portland Stone Formation. Stratigraphical details of the sections then exposed, together with an extensive review of previous measured sections, were given by Sylvester-Bradley (1941) and later summarized by Arkell (1947*b*, 1948). The bed nomenclature used in this paper follows that introduced by Sylvester-Bradley, his bed numbers being given in parentheses after the bed names.

The basal 2 m of the 'Swindon Series', comprising a basal pebble bed [Lower Pebble Bed (2)], a marlstone unit [Lower Marlstones (3)], an ostracod-rich marl [Cythere Marl (4)] and terminating in a limestone with marine bivalves and gastropods [Swindon Roach (5)] were separated by Wimbledon (1976) as the Town Gardens Member and assigned to the top of the Portland Stone Formation. The overlying 10 m succession was assigned to the Purbeck Limestone Formation. This succession comprises two units of marlstones [Middle (6) and Upper (8) Marlstones] alternating with units of sandy marls with well-preserved freshwater ostracods and reworked limestone pebbles [Middle Pebbly Bed (7) and Upper Pebbly Beds (9)], these being overlain by two limestones [Boxy Tufa (10) and Swindon Flags (12)] with an intercalated unit of earthy marls [Chara Marls (11)] containing abundant ostracods and charophytes. Arkell (1948, p. 202) recorded an additional unit overlying the Swindon Flags consisting of marl with limestone rubble, which had not been noted previously.

In the present study, charophyte assemblages have been examined from the Lower Pebbly Bed, Cythere Marl, Middle Pebbly Bed, Upper Pebbly Beds and Chara Marls. The identification of the taxa present and the biostratigraphical interpretations arising therefrom differ significantly from those published by Harris (1939; *in* Sylvester-Bradley 1941).

Charophyte succession

The most representative succession of charophyte occurrences was found in borehole samples from the Weald. In contrast, on the Dorset coast, only the beds of the uppermost Lulworth Formation to the lowest Durlston Formation have yielded charophytes.

In the Fairlight Borehole, the Broadoak Calcareous Member can be subdivided into three local zones, based on the first occurrences of the successive chronological species of *Globator*; the succeeding beds are referred to a fourth zone. As discussed below, the Jurassic-Cretaceous boundary lies between local charophyte zones 1 and 2.

Zone 1. This is defined as the interval between the first occurrences of *Globator rectispinale* and *G. praecursor*; the zone is represented in the lowest part of the Broadoak Calcareous Member (Lake and Holliday 1978) which appears in the Fairlight Borehole and may be provisionally interpolated in the Warlingham and Broadoak boreholes, below the occurrences of *G. praecursor*. The only

occurrence of *G. rectispirale* is at 317.6–317.9 m in the Fairlight Borehole. An important additional species is *Clavator* aff. *reidi* (utricles incompletely constituted).

By direct correlation, Zone 1 (as recognized in the Fairlight Borehole) corresponds to the lower part of the Swindon ostracod faunicycle of Assemblage 2 of Anderson (1975). The Swindon succession, which is referable to the underlying Assemblage 1, is provisionally included in the charophyte Zone 1, albeit in the absence of *Globator praecursor* (see below).

Outside southern England, the zone is identifiable by the occurrence of *G. rectispirale* in the Seba Mahjouba Formation of the Chellala Mountains (Algeria), 50 m below beds referred to the Upper Tithonian A2–A3 calpionellid Zone (Benest 1981), which is correlated with the Late Tithonian 'Durangites' ammonite Zone. The lower part of the Portuguese 'Infravalanginian' (Rey *et al.* 1968; Ramalho 1971) which has yielded *G. rectispirale* and *Clypeator discordis* may be equivalent to this zone. Rey (in litt. 1991) considers that these beds should now be attributed to the Upper Jurassic (Tithonian).

In terms of ammonite zones, the basal part of the Broadoak Calcareous Member, which is the stratotype of the charophyte local Zone 1, has been inferred to correlate with the *Titanites anguiformis* Zone (Wimbledon 1980 and this paper). Charophytes thus indirectly confirm the Boreal–Tethyan correlations of the *anguiformis* and 'Durangites' ammonite zones.

Zone 2. This is defined as the interval between the first occurrences of *Globator praecursor* and *G. protoincrassatus*; the zone is found represented in the lower–middle part of the Broadoak Calcareous Member. The lowest occurrences of *G. praecursor* are at 296.0–296.3 m in the Fairlight Borehole, at 625.3 m in the Warlingham Borehole, at 111.50–112.00 m in the Broadoak Borehole and at 270.6 m in the Brightling No. 27 Borehole. An important additional species is *Clavator reidi*.

By direct correlation, Zone 2 (as recognized in the Fairlight Borehole) corresponds to the ostracod faunicycles between Swindon (*pars*) and the upper part of the Lower Soft Cockle (Anderson 1975). Outside the British Isles, Zone 2 corresponds approximately to the M1 charophyte Zone defined by Détraz and Mojon (1989) in the Jura Mountains and referred to the basal Berriasian. Zone 2 is also identifiable in the lower part of the Serpulit of the Lower Saxony Basin (Schudack 1991; Feist and Schudack 1991).

Zone 3. This is defined as the interval between the first occurrences of *Globator protoincrassatus* and *Flabellochara grovesi*; the zone is identified in the upper part of the Broadoak Calcareous Member (Lake and Holliday 1978); the former species occurs in the Fairlight Borehole at 293.2–293.5 m depth. An important additional species is *Clavator reidi* (primitive and advanced forms).

Zone 3 is directly correlated with the Lower Soft Cockle (upper part), Upper Soft Cockle, Penshurst and Ringstead ostracod faunicycles. The zone is recognized by the occurrence of *G. protoincrassatus* in the topmost Soft Cockle Member of Dorset (Bed 70 of Clements in Cope *et al.* 1969; Clements 1993). Outside southern England, Zone 3 corresponds to the Lower Berriasian M2 charophyte zone defined by Détraz and Mojon (1989) in Switzerland, dated by ammonites of the *Pseudosubplanites grandis* Zone (Clavel *et al.* 1986; Hoedemaeker 1991). Zone 3 is also identifiable in the upper part of the Serpulit of the Lower Saxony Basin (Feist and Schudack 1991).

Zone 4. This is defined as the interval between the first occurrence of *Flabellochara grovesi* and the last occurrence of *Clavator reidi*. The zone spans the highest Broadoak Calcareous Member, the Plant and Bone Beds, Cinder Bed, Arenaceous Beds and Greys Limestones members (Lake and Holliday 1978). The lowest record of *Flabellochara grovesi* is at 281.0–281.3 m in the Fairlight Borehole. Important additional species are *Porochara maxima*, *Perinneste horrida* and *Clavator reidi*.

The base of Zone 4 in the Fairlight Borehole is directly correlatable with the Robertsbridge ostracod faunicycle of Anderson (1975). In Dorset, the lowest occurrence of this zone is identifiable in the Cherty Freshwater Member; its upper part includes the Cinder Bed [Member] which is correlated with the *Praetollia runctoni* ammonite Zone (Casey 1973).

WEALDEN SUPERGROUP

Stratigraphy

The Wealden Supergroup (Series) in the type area consists of two broad subdivisions, the Hastings Beds below and the Weald Clay above. The former comprises an alternating sequence of formations (and locally members) which are dominantly argillaceous or of variable grain-size but with a significant arenaceous content (Ashdown Beds–Upper Tunbridge Wells Sand; cf. Text-Fig. 3). Whilst the clay subdivisions are thought to represent lacustrine/lagoonal environments, the intervening ‘sands’ show fluvial/alluvial associations. In the Hastings Beds, important transgressive events are recognized at the bases of the Wadhurst Clay and the Grinstead Clay and the major facies-change below the Weald Clay may reflect another of more regional significance (Allen and Wimbledon 1991).

The Wealden Group of the Wessex Basin is generally poorly understood. The Wessex Formation, of alluvial/fluvial facies with few known lithostratigraphical or faunal markers, comprises sandstones and variegated mudstones (Hesselbo and Allen 1991). The Hauterivian–Barremian boundary has been placed approximately at the levels of the ‘Pine Raft’ of the Isle of Wight and of the ‘Coarse Quartz Grit’ of Dorset, on palynological evidence (Hughes and McDougall 1989). On the Isle of Wight, the Wessex Formation is succeeded by the lagoonal Vectis Formation, grey shelly mudstones, which has been correlated with the upper part of the Weald Clay (Anderson 1967; Stewart 1981).

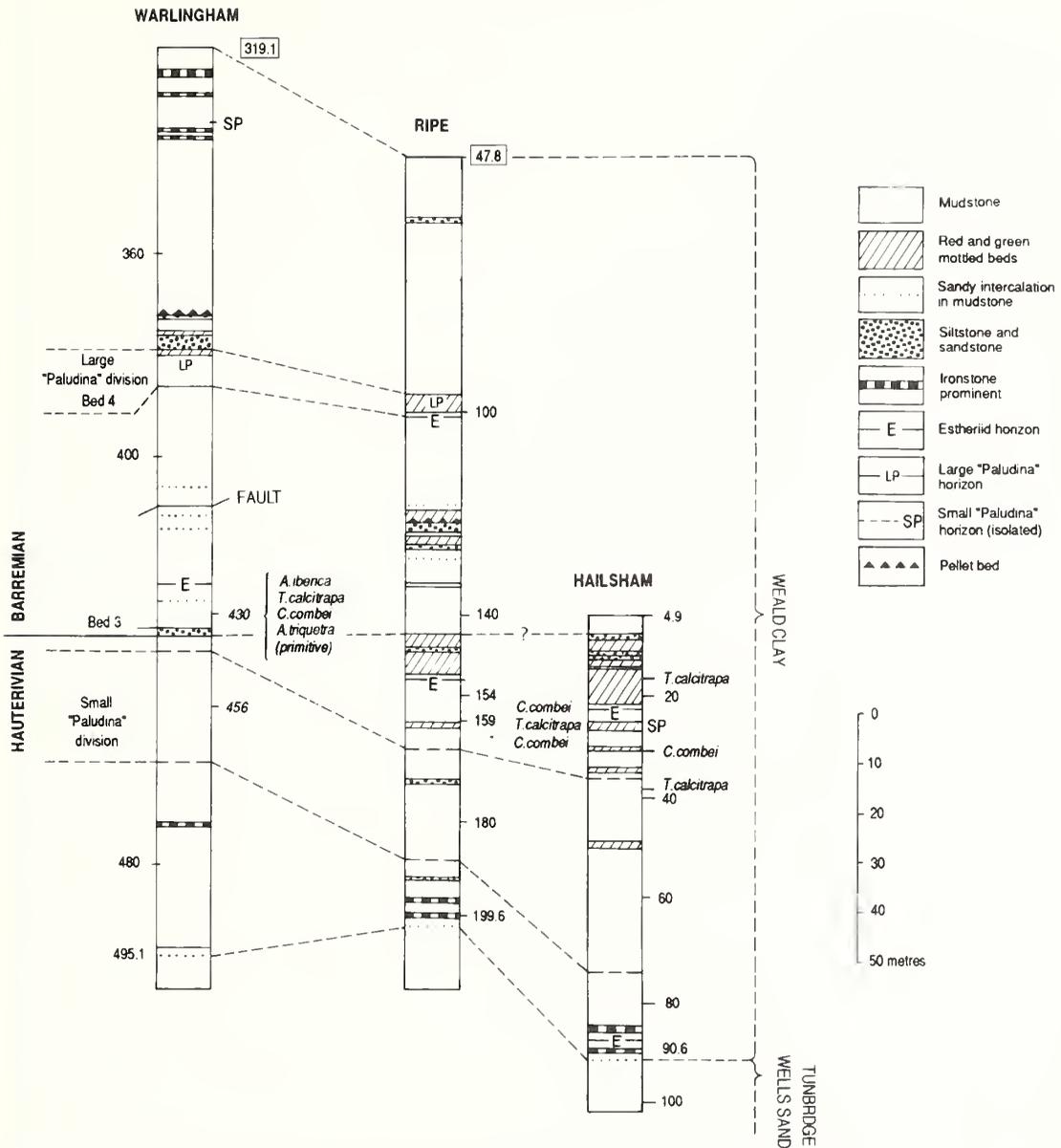
The Kingsclere (Hants) Borehole (National Grid Reference SU 4984 5820) (discussed later) apparently encountered red mottled beds of Wessex Formation facies overlying grey beds of Wealden aspect, but the effect of the sub-Aptian unconformity above is unclear. One possibility is that the variegated beds may reflect an expansion of those seen in the highest Hastings Beds and Weald Clay at outcrop (mid-Tunbridge Wells Sand-equivalent and above). Hughes *et al.* (1979) recognized Barremian palynomorphs in the highest part of the sequence at Kingsclere.

Subdivision of the Weald Clay

The scheme of subdivision adopted here follows that developed in the southern outcrop (Lake and Young 1978; Lake *et al.* 1987; Young and Lake 1988), following the work of Topley (1875, p. 102) and Thurrell *et al.* (1968, p. 24). The lithological marker horizons recognized within the dominantly clay sequence are as follows:

- 7 Sandstone(s)
- 6 Large-‘*Paludina*’ limestone
- 5 Sandstone(s)
- 4 Large-‘*Paludina*’ limestone
- 3 Sandstone(s)
- 2 Small-‘*Paludina*’ limestones and ‘*Cyrena*’ limestones
- 1 Horsham Stone

The Large-‘*Paludina*’ limestone units are individually restricted in vertical range, but the other horizons may comprise more than one intercalation within the sequence. For example, Bed 2 (clays with Small-‘*Paludina*’ limestones and ‘*Cyrena*’ limestones) was found to have only a broad ‘zonal’ equivalence (Text-Fig. 2). Bed 4 (the lower of two commonly occurring Large-‘*Paludina*’ limestones) was, however, shown to be characterized by the ostracod *Cypridea bogdenensis* in the Gillmans faunicycle and therefore forms a useful marker horizon. In the Warlingham Borehole, Worsam and Ivimey-Cook (1971) attributed to ‘Topley’s Bed 5’ a complex tripartite succession comprising, in ascending order: (a) 2.1 m of glauconitic sandstones with a brackish-marine molluscan fauna; (b) 0.8 m of shaly mudstones containing a bed of glauconitic sand with quartz pebbles; (c) 4.3 m of sediments of terrestrial to freshwater aspect containing, in the basal metre, rootlet beds, *Unio* and charophytes. A sample (431.4 m) from above the pebble bed in unit b yielded Barremian angiosperm pollen (Hughes and MacDougall 1990) and dinocysts (Harding 1990); the



TEXT-FIG. 2. Lithofacies correlation between the Warlingham, Ripe and Hailsham boreholes in the Weald Clay, modified after Lake and Young (1978), showing key charophyte records.

charophytes at the base of unit c are thus demonstrably Barremian. The Hauterivian–Barremian boundary falls in the interval between this sample and a sample from near the base of the sandstones (433.8 m) which gave a Hauterivian date (Hughes and MacDougall 1990).

In this paper we specifically restrict 'Topley's Bed 5' to the glauconitic sandstones between 431.8 m and 433.9 m. Moreover, it is evident that this bed underlies Topley's Bed 4 as defined above (Bed 6 in the original borehole classification) and should more properly be numbered 'Bed 3'; albeit

FORMATIONS	Charophyte species													Charophyte Zones southern England	Ostracod faunal Assemblages	Stages					
	<i>Clypeator discoidis</i>	<i>Globator rectispirale</i>	<i>Clavator aff. raidi</i>	<i>Clavator raidi</i>	<i>Globator praecursor</i>	<i>Globator protoincrassatus</i>	<i>Flabellochara grovesi</i>	<i>Perimmesite horrida</i>	<i>Porochara maxima</i>	<i>Sphaerochara andersoni</i>	<i>Flabellochara xiangyunensis</i>	<i>Clypeator britannicus</i>	<i>Clypeator combei</i>				<i>Triclypella calcitrata</i>	<i>Ascidiella iberica</i>	<i>Atopochara triquetra (primitive)</i>	<i>Atopochara triquetra (advanced)</i>	<i>Packisphaera varicillata</i>
Vectis Formation equivalent to topmost Weald Clay																		Atopochara triquetra (advanced)	11	15 (pars)	Late Barremian
Weald Clay above Bed 3																		Ascidiella iberica	10	14 - 15	Early Barremian
Weald Clay above Bed 2																		Triclypella calcitrata	9	13	Hauterivian
Upper Tunbridge Wells Sand and lowest Weald Clay																		Interregnum 7 - 9	8	10 - 12	
Grinstead Clay and ? Lower Tunbridge Wells Sand																		Clypeator britannicus	7	9 (pars)	
Wadhurst Clay																		Flabellochara xiangyunensis	6	8 - 9	Valanginian
Ashdown Beds																		Interregnum 4 - 6	5	5 - 7	
Durleston Beds																		Flabellochara grovesi	4	3 - 4	
Lulworth Beds																		Globator protoincrassatus	3	2 - 3	Berriasian
																		Globator praecursor	2	2 (pars)	
																		Globator rectispirale	1	1 - 2	Late Tithonian

TEXT-FIG. 3. Charophyte succession in the Purbeck and Wealden beds of southern England and correlation with the ostracod Assemblages of Anderson (1985). Dashed lines refer to related unspecified forms.

there is a thin sand at the top of unit c. The transition from brackish-marine to freshwater conditions above this bed clearly marks a significant event at or about the Hauterivian-Barremian boundary (Allen 1989; Allen and Wimbledon 1991). This amendment to the classification of the Warlingham sequence invites reassessment of the correlation with other occurrences of Bed 3 (and subordinate units) which show brackish influences at outcrop in the Weald (Worssam and Ivimey-Cook 1971, p. 29; Worssam 1978, p. 8).

Charophyte succession (Hastings Beds and equivalent strata)

Above the Cinder Bed Member, there are large gaps in the charophyte succession. The Ashdown Beds, as well as the Lower and Upper Tunbridge Wells Sands, have yielded only insignificant charophyte material.

Undefined Zone 5 = Interregnum 4–6. This corresponds to the interval between the last occurrence of *Clavator reidi* and the first occurrence of *Flabellochara xiangyunensis* in the Wadhurst Clay of the Weald. This Zone has not yet been recognized in Dorset. The interval represented by Zone 5 corresponds to the highest part of the Durlston Formation and to the Ashdown Beds, which are interpreted as fluvial deposits (Allen 1989), not favourable to the preservation of charophytes. Taxa identified from this zone comprise *Tolypella* sp., *Peckisphaera knowltoni* (Seward) Schudack, and incompletely calcified utricles of *Flabellochara* (see Appendix 1 for sample location). The Ashdown Beds are currently dated as Berriasian–early Valanginian on palynological evidence (Allen and Wimbledon 1991).

Zone 6. This is defined as the interval between the first occurrence of *Flabellochara xiangyunensis* in the Wadhurst Clay of the Weald and that of *Clypeator britannicus*. The lowest occurrence of *F. xiangyunensis* is at 59.00–59.50 m depth in the Glynleigh Borehole. An important additional species is *Sphaerochara* aff. *andersoni*.

Zone 6 has been identified in Wadhurst Park No. 3 Borehole at an horizon in the upper part of the Wadhurst Clay corresponding to the Hawkhurst ostracod faunicycle. On the basis of the occurrence of *Flabellochara xiangyunensis*, Zone 6 can be broadly correlated with the Valanginian *F. xiangyunensis*–*Clypeator zongjiangensis* Zone established by Wang and Lu (1982) in China. With regard to the European biozonation, Zone 6 seems to correspond to the *Embergerella stellata* Zone, defined by the first occurrence of this species in the Lower Valanginian of Maestrazgo (north-east Spain), dated by orbitoline foraminifers (Martin-Closas and Salas 1988). This dating is compatible with the age attributed to the Wadhurst Clay by Allen and Wimbledon (1991).

Zone 7. This is defined as the interval corresponding to the range of *Clypeator britannicus*, recorded in the Kingsclere Borehole from 305.7–306.6 m; this is above beds between 311.8–354.8 m with ostracod assemblages which indicate a correlation with the whole of the Wadhurst Clay (Anderson and Shephard-Horn 1967). Because this taxon has not been recognized elsewhere, only the evolutionary stage reached enables its occurrence to be dated tentatively. Apparently transitional between the Berriasian, *Clypeator discordis* and the upper Hauterivian–Barremian, *C. combei*, *C. britannicus* can be inferred to be of Valanginian–early Hauterivian age. A probable Valanginian age is, however, only compatible with its occurrences in the Kingsclere Borehole, taking the tentative classification of the beds in question as equivalent to the Grinstead Clay (cf. Lees and Taitt 1945; Anderson 1985).

Undefined Zone 8 = Interregnum 7–9. This corresponds to the interval between the last occurrence of *C. britannicus* and the first occurrence of *Tricyclpella calcitrata* in the middle part of the Weald Clay in the Weald (Warlingham Borehole). This interval is provisionally inferred to equate with the Upper Tunbridge Wells Sand and much of the lower part of the Weald Clay, which have not yielded charophytes.

Following the current dating of the various lithological subdivisions of the Wealden Beds (Allen and Wimbledon 1991), this interval may include the upper part of the Valanginian *Embergerella stellata* Zone and the Upper Hauterivian *Globator trochiliscoides* (primitive form) Zone defined in the Tethyan areas (Martin-Closas and Salas 1989).

Charophyte succession (Weald Clay and equivalent strata)

Charophytes of zonal significance occur above Bed 2 and its correlatives in the Weald Clay of the Weald and also at the base of the Vectis Formation, in the Isle of Wight, the latter representing the highest occurrence of charophytes in the Mesozoic of southern England.

Zone 9. This is defined as the interval between the first occurrence of *Triclypella calcitrata* and the first and only occurrence of *Asciadiella iberica* in the Weald (Warlingham Borehole, 430.0 m). The zone is present in beds immediately below and above the top of the Small-*Paludina* Beds, including Bed 3. Important species are *Clypeator combei* and *Sphaerochara andersoni*.

Zone 9 has been identified in the Warlingham, Ripe and Hailsham boreholes, near the base of the upper part of the Weald Clay. Palynofloras from the Ripe Borehole (Feist and Batten 1990) and from the Warlingham Borehole (Hughes and McDougall 1989) indicate that this zone may straddle the Hauterivian-Barremian boundary.

Zone 10. This is defined as the interval between the first and only occurrence of *Asciadiella iberica* and that of *Atopochara triquetra* (advanced) in southern England. The zone is present, in the lower part of the upper division of the Weald Clay, in beds above the equivalent of Bed 3 in the Warlingham Borehole, where *A. iberica* occurs at 430.0 m. The base of Zone 10 can be dated imprecisely (as late Hauterivian/early Barremian) from records of the index species in Spanish localities. The occurrence of *A. iberica* in the Warlingham Borehole indicates an early Barremian age. Important species are *Atopochara triquetra* (primitive), *Clypeator combei*, *Triclypella calcitrata* and *Sphaerochara andersoni*.

Zone 10 corresponds to the El Mangraner charophyte Zone of Grambast (1974), defined in north-east Spain and also identifiable in the Pre-Dobrogean Depression, Ukraine (Shaikin 1976). The El Mangraner Zone ranges from the Lower Barremian to possibly the Upper Hauterivian from foraminifer evidence (Martin-Closas and Peybernes 1987; Martin-Closas and Salas 1989).

Zone 11. This is defined as the interval based on the range of *Atopochara triquetra* (advanced). The zone is represented in the Cowleaze Chine Member at the base of the Vectis Formation, in the Isle of Wight. Important additional species are *Clypeator combei*, *Triclypella calcitrata* and *Peckisphaera verticillata*.

Zone 11 corresponds to the late Barremian San Carlos charophyte Zone of Grambast (1974) and is identifiable in the La Ruchère section in the Jura (Mojon 1988) dated by foraminifers (Schroeder in Mojon 1988) as Early Aptian.

The occurrence of advanced forms of *A. triquetra* is considered as more significant than that of the persistent accompanying species *C. combei*, previous records of which limited its range to the lower Barremian (Grambast 1970; Martin-Closas and Salas 1989). This interpretation fits with palynofloras characterizing the upper Barremian (Feist and Batten 1990).

THE PURBECK GROUP AND THE PROBLEM OF THE JURASSIC-CRETACEOUS BOUNDARY

The most complete charophyte succession in the Purbeck Group has been found in the boreholes from the Weald. In Dorset, only the sequences from the upper Soft Cackle to the Intermarine members have yielded charophytes so far, well above the level where the base of the Berriasian has been placed (Allen and Wimbledon 1991).

Weald

The Purbeck strata of the Weald rest on marine Portlandian, but the age, based on ammonite data, of the highest marine sediments below the contact varies throughout the basin. In the Fairlight Borehole and in the gypsum mines in the southern Weald, the Gypsiferous Beds rest, locally with

erosional contact (Brightling Mine), on sandstones of the *Glaucolithites glaucolithus* Zone, i.e. equivalent to the middle part of the Portland Sand Formation of Dorset. By contrast, in the Warlingham Borehole (northern Weald), the Gypsiferous Beds rest on the lower part of the Portland Stone Formation, *Galbanites (Kerberites) kerberus* Zone; it has been suggested (Wimbledon 1980) that there was no hiatus between the highest marine Portlandian and the onset of Purbeck facies sedimentation, implying that the lower part of the Purbeck Beds in this area correlated with the *Titanites anguiformis* Zone Portland Freestone of Dorset. Although these data could be taken to demonstrate that the onset of Purbeck facies was diachronous within the Wealden basin, Worssam and Ivimey-Cook (1984) argued that this apparent diachroneity might have resulted from a non-sequence in the southern part of the area caused by intra-Portlandian movement of the Portsdown–Paris Plage Swell and that the beginning of Purbeck-type sedimentation (as distinct from the date of the highest underlying marine Portlandian) might be essentially synchronous throughout the basin.

The Broadoak Calcareous Member of the Lulworth Formation can be subdivided biostratigraphically by means of three successive species of the *Globator* lineage. The inferred Tithonian local charophyte Zone 1 is recognized by the presence of *G. rectispirale* in the basal part of the Member in the Fairlight Borehole, while the Lower Berriasian local charophyte Zone 2, characterized by *G. praecursor*, is represented in four boreholes: Fairlight, Warlingham, Broadoak and Brightling (see Appendix 1). The boundary between zones 1 and 2 appears to occur at about the level of the Mountfield Adit Limestone (Lake and Holliday 1978, fig. 3), i.e. near the base of the Broadoak Calcareous Member and a short distance above the Gypsiferous Beds Member. *G. protoincrassatus*, which succeeds *G. praecursor* in the lower part of the Lower Berriasian, has also been found in the Weald, but only in the Fairlight Borehole.

The fact that charophyte Zone 1 was recognized only in the Fairlight Borehole does not seem sufficient evidence to demonstrate that Purbeck sedimentation began earlier in the southern Weald; the beds spanned by local charophyte Zone 2 in the Warlingham Borehole, in the northern Weald, are situated 30 m above the marine Portland Beds and this interval has yielded ostracods belonging to Assemblage 1 of Anderson (1985) as in the basal Purbeck beds of the Fairlight Borehole, corresponding to local charophyte Zone 1.

Dorset

The dating, in terms of both Tethyan and Boreal ammonite biostratigraphy, of the onset of non-marine (Purbeck facies) sedimentation and of the various members comprising the Purbeck Group remains unresolved. Recent interpretations of the possible correlations between the marine and non-marine successions are based on global sea-level changes (Hoedemaeker 1991, fig. 1), but some additional evidence is provided by palynomorphs and magnetostratigraphy.

Hunt (1985) drew the base of the *Apiculatisporis verbitskayae* miospore Biozone near the top of a group of thin limestones at an horizon only 3 m above the base of the Cypris Freestones Member. In a subsequent paper (Hunt 1987, fig. 11.2), he took this floral change to mark the base of the Berriasian. It is possible that these limestones approximate to the level of the Mountfield Adit Limestone of the Weald, which marks the boundary between local charophyte zones 1 and 2 and the inferred position of the Tithonian–Berriasian boundary (see above). It is noteworthy that a significant change in the miospore assemblage in Purbeck appears to coincide with a change in the charophytes in the Weald. However, the Cypris Freestones palynomorphs and the overlying ostracods are stated to permit correlation with the *Pseudosubplanites grandis* ammonite Subzone of the Berriasian stratotype (Allen and Wimbledon 1991; Wimbledon, pers. comm. 1994), implying that the base of the Berriasian as understood here (i.e. the base of the underlying *Berriassella jacobii* ammonite Subzone) lies below the Cypris Freestones and possibly approximates to the base of the Purbeck Limestone Group. This latter interpretation is supported by preliminary magnetostratigraphical studies of the Purbeck stratotype (Ogg *et al.* 1991), but does not agree with the

correlations of Hoedemaeker (1991, fig. 1), who equated the greater part of the basal Purbeck succession below the Cypris Freestones with the terminal Tithonian 'Durangites' ammonite Zone.

In Dorset, samples collected from the lower part of the Lulworth Formation were barren of charophytes and there is therefore no direct evidence for the recognition of the Jurassic–Cretaceous boundary. The type material of the supposed new taxon *Clavator westi* Costin (*in Barker et al.* 1975) from the Charophyte Chert, near the base of the Lulworth Formation at Portesham Quarry, is indeterminate (see discussion in Appendix 2). The lowest occurrence of determinable charophytes is in the upper part of the Soft Cockle Member at Durlston Bay; Bed DB70 (Clements, *in Cope et al.* 1969; Clements 1993) has yielded *Globator protoincrassatus*, which is the index of local charophyte Zone 3 and of Mojon's Zone M2 in the Jura, and is lower (but not basal) Berriasian and equivalent to the *Pseudosubplanites grandis* Subzone of the *grandis* ammonite Zone. This dating is supported by early Berriasian miospores and dinoflagellates in a sample from the top of Bed 43 in the lower part of the Soft Cockle Member (Batten *et al. in* Lord and Bown 1987).

Charophyte Zone 4 covers the interval from the Cherty Freshwater Member to the Intermarine Member. The charophyte assemblage, with *Flabellochara grovesi*, is that studied by Harris (1939).

By comparison with the Jura and north-western Germany, the Dorset succession from the Soft Cockle to the Intermarine members is attributable to the Lower, not basal, Berriasian.

Wiltshire

The dating of the 'Swindon Series' has always been a matter of controversy (Sylvester-Bradley 1941, 1942; Arkell 1942). Wimbledon (1980, fig. 15) showed the Town Gardens Member divided between the *kerberus* and *anguiformis* zones (by implication assigning the Swindon Roach to the latter zone), with the overlying Purbeck Limestone Formation also placed in the *anguiformis* Zone, but there is no hard evidence for this interpretation (Wimbledon, pers. comm. 1992). The marine Swindon Roach, despite its general lithological and faunal similarity to the *anguiformis* Zone Roach of the Isle of Portland (particularly in the occurrence of the 'Portland screw' *Aptyxiella portlandica*) has so far yielded no ammonites.

Arkell (1942) considered that the 'Swindon Series' equated with the 'Middle Purbeck' by reference to the charophytes, which he noted were particularly characteristic of and common in the 'Middle Purbeck' of Dorset, but which he mistakenly stated were not found below in the 'Lower Purbeck'. However, Sylvester-Bradley (1942) and all subsequent workers (see above) have emphasized that the ostracods point unequivocally to a correlation between the 'Swindon Series' and the basal Purbeck of Dorset, whilst not excluding the possibility of the Swindon succession being a Purbeck-facies equivalent of the highest Portland Beds. The entire succession, which contains *Cypridea dunkeri papulata* throughout, belongs to the lowest Lower Purbeck ostracod assemblage (Assemblage 1), comprising the Quainton, Warren, Ridgeway and Stair faunicycles in ascending order (Anderson 1985, fig. 5), of which the first three were recognized at Swindon by Anderson. The absence of any members of the *Cypridea granulosa granulosa*–*C. granulosa fasciculata* lineage in the higher part of the 'Swindon Series' rules out any correlation of these beds, particularly the Chara Marls, with the charophyte-rich higher part of the Lulworth Formation.

The general consensus is to correlate the entire 'Swindon Series' with the uppermost member (Portland Freestone) of the Portland Stone Formation of the Dorset coast, together with the basal beds of the Dorset Purbeck sequence (Caps, Dirt Beds and Broken Beds). This means that the charophyte assemblages at Swindon are *older* than any other charophytes discussed here from the British Purbeck, with the possible exception of the largely indeterminate material described from the Charophyte Chert of Portesham Quarry (Barker *et al.* 1975; and this paper).

The Town Gardens Quarry at Swindon provides the northernmost exposure of Purbeck strata in Britain that yields charophytes. A preliminary study of the charophyte floras (Harris *in* Sylvester-Bradley 1941) identified *Flabellochara grovesi* and *Clavator reidi*, indicating a broad correlation with the 'Middle Purbeck Beds' of Dorset. Re-evaluation of the charophytes has now shown that the entire succession is characterized by *Clypeator discordis* and the primitive form *Clavator aff. reidi*,

all specimens formerly attributed to *Flabellochara grovesi* having been misidentified. By extrapolation from the Brouco section, Portugal, where *Clavator discordis* co-occurs with *Globator rectispirale*, and on the basis of the occurrence of *Clavator* aff. *reidi*, the Swindon succession, including the Chara Marls near the top, is tentatively assigned to the Tithonian local charophyte Zone 1, albeit in the absence of the zonal index. This new interpretation is supported by the ostracod evidence, which places the Swindon succession in ostracod Assemblage 1, i.e. equivalent to the basal stratotype Purbeck succession below the Cypris Freestones. It also agrees with the correlation scheme presented by Hoedemaeker (1991, fig. 1), in which the three ostracod faunicycles (Quainton, Warren and Ridgeway) recognized by Anderson (1985) at Swindon are equated with the terminal Tithonian 'Durangites' ammonite Zone. There is no evidence at Swindon for the Lower Berriasian local charophyte Zone 2.

CONCLUSIONS

For the first time, a stratigraphical study based on charophytes has been undertaken of the whole of the Purbeck and Wealden sequence of southern England. In contrast with previous views, this group provides a useful tool for subdividing and correlating the non-marine sequences between the Portland Stone and the base of the Lower Greensand. We have subdivided the succession into eleven local charophyte zones, of which two (zones 5 and 8) must remain uncharacterized intervals at present. This new zonal scheme provides useful correlations between successions in the Weald, Dorset and Wiltshire. Because of the wide distribution of most species at this time, direct correlations can be established between the Boreal and Tethyan realms. The Upper Tithonian local charophyte Zone 1 and the Lower Berriasian local charophyte zones 2, 3 and 4 established here can also be recognized in the Tethyan Realm.

Two key indirect correlations can be made between the charophyte local zonal scheme for the Purbeck Limestone Group and marine successions in the Tethyan and Boreal Realms. The zonal index of the *Globator rectispirale* local charophyte Zone 1 can be recognized in Algeria below beds with an A2/A3 calpionellid assemblage, correlated with the Upper Tithonian 'Durangites' ammonite Zone of the Tethyan Realm. The *Flabellochara grovesi* local charophyte Zone 4 embraces the Cinder Beds Member at the base of the Durlston Formation. This bed is taken to correlate with the *Praetollia runctoni* ammonite Zone at the base of the Ryazanian Stage of the Boreal Realm and has been equated approximately with the base of the *Stranbergella occitanica* ammonite Zone of the Tethyan Realm.

The Jurassic–Cretaceous boundary can be inferred on charophyte occurrences (the boundary between local charophyte zones 1 and 2) to be located near the base of the Broadoak Calcareous Member of the Lulworth Formation of the Purbeck Limestone Group of the Weald. The boundary is situated at about the level of the Mountfield Adit Limestone, which may approximate to the basal group of limestones of the Cypris Freestones Member of the stratotype Purbeck Group succession in Dorset and the base of the *Apiculatisporis verbitskayae* miospore Zone. The Jurassic–Cretaceous boundary is understood here as the base of the Berriasian Stage of the Tethyan Realm, i.e. (following Anon. 1975) the base of the *Berriasella jacobi* Subzone of the *Pseudosubplanites grandis* ammonite Zone.

If the base of the Berriasian approximates to the base of the Cypris Freestones, the new charophyte data accord with Hoedemaeker's (1991, fig. 1) correlation diagram. Thus, the gypsiferous basal beds could represent the Tithonian 'Durangites' Zone (Tidalites de Vouglans of the Jura) and the base of the Cypris freestones could equate with the base of the (Berriasian) Goldberg Formation, within which the *Globator* lineage was first recognized.

The charophyte biostratigraphy supports the previous ostracod-based correlations between the Purbeck and Wealden successions of Dorset and the Weald respectively. A reassessment of the charophyte and ostracod data from the Town Gardens Quarry, Swindon, allows this succession to be attributed tentatively to the Upper Tithonian local charophyte Zone 1 and equated indirectly with the 'Durangites' ammonite Zone of the Tethyan Realm. This succession is divided between the *Galbanites kerberus* and *Titanites anguiformis* ammonite zones (Wimbledon 1980); the charophytes

thus provide indirect evidence of the contemporaneity of these boreal ammonite zones with the Tethyan 'Durangites' Zone.

For the Wealden Supergroup, the charophyte data, supported by preliminary palynological indications from Professor D. J. Batten, allow us to locate the Hauterivian–Barremian boundary near the base of the upper division of the Weald Clay in the Weald. The Upper Barremian is identified in an equivalent of the topmost Weald Clay, at the base of the Vectis Formation of the Isle of Wight.

In addition to these stratigraphical results, the work has provided new data on charophyte evolution. The oldest and most primitive representative of the *Globator* lineage has been found in the Fairlight Borehole. On the other hand, correlations establish the presence of the genus *Clypeator* in the Upper Jurassic; this supports the views of Martin-Closas and Serra-Kiel (1991), who considered the Upper Jurassic to be a period of charophyte diversification. The appearance of *Clypeator* before *Flabellochara* suggests that the two genera have a separate origin.

The study of Jurassic–Cretaceous charophytes from southern England is far from complete and the local zonal scheme presented here must be regarded as provisional. Further collecting from the incompletely sampled Purbeck Limestone Group of Dorset should lead to refinements of the zonal scheme for this part of the succession. Future investigations could examine the extent to which changes in taxonomic diversity and degree of calcification are controlled by palaeoenvironmental changes.

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REFERENCES

- AGARDH, C. A. 1824. *Systema Algarum*. Lund, xxxviii + 312 pp.
- ALLEN, P. 1989. Wealden research – ways ahead. *Proceedings of the Geologists' Association*, **100**, 529–564.
- and WIMBLEDON, W. A. 1991. Correlation of NW European Purbeck–Wealden (non-marine Lower Cretaceous) as seen from the English type-area. *Cretaceous Research*, **12**, 511–526.
- ANDERSON, F. W. 1967. Ostracods of the Weald Clay of England. *Bulletin of the Geological Survey of Great Britain*, **27**, 237–269.
- 1975. The Fairlight Borehole: Purbeck faunicycles. Unpublished Internal Report, Institute of Geological Sciences, London.
- 1985. Ostracod faunas in the Purbeck and Wealden of England. *Journal of Micropalaeontology*, **4**, 1–68.
- and BAZLEY, R. A. B. 1971. The Purbeck Beds of the Weald (England). *Bulletin of the Geological Survey of Great Britain*, **34**, 1–173.
- and SHEPHARD-THORN, E. R. 1967. The sedimentary and faunal sequence of the Wadhurst Clay (Wealden) in boreholes at Wadhurst Park, Sussex. *Bulletin of the Geological Survey of Great Britain*, **27**, 1–235.
- ANON. 1975. Colloque sur la limite Jurassique–Crétacé. *Mémoires du Bureau de Recherches Géologiques et Minières*, **86**, 379–393.
- ARKELL, W. J. 1942. Notes on the age of the Swindon Purbeck Beds. *Proceedings of the Geologists' Association*, **51**, 321–324.
- 1947a. The geology of the country around Weymouth, Swanage, Corfe and Lulworth. *Memoirs of the Geological Survey of Great Britain, England and Wales*, 1–386.
- 1947b. *The geology of Oxford*. Clarendon Press, Oxford, 267 pp.
- 1948. A geological map of Swindon. *Wiltshire Archaeological and Natural History Magazine*, **52**, 195–212.
- BARKER, D. 1966. Ostracods from the Portland and Purbeck Beds of the Aylesbury district. *Bulletin of the British Museum (Natural History), Geology Series*, **11**, 459–487.

- BROWN, C. G., BUGG, S. C. and COSTIN, J. 1975. Ostracods, land plants and Charales from the basal Purbeck Beds of Portesham Quarry, Dorset. *Palaeontology*, **18**, 419–436.
- BENEST, M. 1981. Intercalations de faciès à Calpionelles dans des dépôts rythmiques à indices de dessalure: exemple du Tithonique supérieur carbonaté des Monts de Chellala (avant pays Tellien de L'Ouest algérien). *Comptes Rendus de l'Académie des Sciences, Paris, Série II*, **292**, 1287–1292.
- 1985. Evolution de la plateforme de l'ouest algérien et du nord-est marocain au cours du Jurassique supérieur et au début du Crétacé: stratigraphie, milieu de dépôt et dynamique sédimentaire. *Documents du Laboratoire de Géologie, Faculté des Sciences, Lyon*, **95**(1–2), 1–581.
- BRENNER, P. 1976. Ostracoden und Charophyten des nordspanischen Wealden. *Palaeontographica, Abteilung A*, **152**, 113–201.
- BRISTOW, C. R. 1968. Portland and Purbeck Beds. 300–311. In SYLVESTER-BRADLEY, P. C. and FORD, T. D. (eds). *The geology of the East Midlands*. Leicester University Press, 400 pp.
- CANÉROT, J. 1979. Les algues et leur environnement dans le Crétacé inférieur des Chaînes ibérique et catalane (Espagne). *Centre de Recherches, d'Exploration et Production, Elf-Aquitaine*, **3**, 505–518.
- CASEY, R. 1973. The ammonite succession at the Jurassic–Cretaceous boundary in eastern England. *Geological Journal, Special Issue*, **5**, 193–266.
- CLAVEL, B., CHAROLLAIS, J., BUSNARDO, R. and HEGARAT, G. le 1986. Précisions stratigraphiques sur le Crétacé inférieur basal du Jura méridional. *Eclogae Geologicae Helvetiae*, **79**, 319–341.
- CLEMENTS, R. G. 1993. Type-section of the Purbeck Limestone Group, Durlston Bay, Swanage, Dorset. *Proceedings of the Dorset Natural History and Archaeological Society*, **114**, 181–206.
- COLIN, J.-P., FEIST, M., GRAMBAST-FESSARD, N., CHERCHI, A. and SCHROEDER, R. 1985. Charophytes and ostracods from the Berriasian (Purbeckian facies) of Cala d'Inferno (Nurra region, NW-Sardinia). *Bolletina della Società palaeontologica Italiana*, **23**, 345–354.
- COMBES, P. J., GLAÇON, G. and GRAMBAST, L. 1966. Observations stratigraphiques et paléontologiques sur le Crétacé inférieur du Nord-Est du Maestrazgo (Espagne). *Compte Rendu Sommaire de la Société Géologique de France*, **10**, 390–391.
- COPE, J. C. W., HALLAM, A. and TORRENS, H. S. 1969. *Guide for Dorset and south Somerset. International Field Symposium on the British Jurassic*. Geology Department, University of Keele, 71 pp.
- DÉTRAZ, H. and MOJON, P.-O. 1989. Evolution paléogéographique de la Marge jurassienne de la Tethys du Tithonique–Portlandien au Valanginien: corrélations biostratigraphique et séquentielle des faciès marins à continentaux. *Eclogae Geologicae Helvetiae*, **82**, 37–112.
- DONZE, P. 1955. Nouvelles espèces de charophytes de la limite jurassico–crétacée du Jura, des Alpes-Maritimes et de la Provence. *Bulletin de la Société Géologique de France*, **6**, 287–290.
- 1958. Les couches de passage du Jurassique au Crétacé dans le Jura français et sur les pourtours de la fosse 'Vocontienne'. *Travaux du Laboratoire de Géologie, Lyon, Nouvelle Série*, **3**, 5–221.
- DÖRHÖFER, G. and NORRIS, G. 1977. Discrimination and correlation of highest Jurassic and lowest Cretaceous terrestrial palynofloras in North-West Europe. *Palynology*, **1**, 79–94.
- EL-SHAHAT, A. and WEST, I. 1983. Early and late lithification of aragonitic bivalve beds in the Purbeck Formation (Upper Jurassic–Lower Cretaceous) of southern England. *Sedimentary Geology*, **33**, 15–41.
- ENSOP, P. C. 1985. An annotated section of the Purbeck Limestone Formation at Worbarrow Tout, Dorset. *Proceedings of the Dorset Natural History and Archaeological Society*, **106**, 87–91.
- FEIST, M. and BATTEN, D. 1990. Comparative charophyte and palynofloral biozonation of the British Purbeck and Wealden succession of southern England. 17–18. In *Proceedings of the International Symposium of the IGCP-245, Nonmarine Cretaceous Correlations*. Alma-Ata, 72 pp.
- and GRAMBAST-FESSARD, N. 1991. The genus concept in Charophyta. Evidence from Palaeozoic to Recent. 189–203. In RIDING, R. (ed.). *Calcareous algae and stromatolites*. Springer Verlag, München, 571 pp.
- and SCHUDACK, M. 1991. Correlation of charophyte assemblages from the non-marine Jurassic–Cretaceous transition of NW Germany. *Cretaceous Research*, **12**, 495–510.
- FORBES, E. 1851. On the succession of strata and distribution of organic remains in the Dorsetshire Purbecks. *Report of the British Association for the Advancement of Science (1850), Abstracts*, 58 pp.
- GRAMBAST, L. 1959. Tendances évolutives dans le phylum des Charophytes. *Comptes Rendus de l'Académie des Sciences, Paris, Série D*, **249**, 557–559.
- 1961. Remarques sur la systématique et la répartition stratigraphique des Characeae pré-tertiaires. *Compte Rendu Sommaire des Séances de la Société Géologique de France*, **7**, 200–201.
- 1962. Classification de l'embranchement des Charophytes. *Naturalia Monspeliensia, Série Botanique*, **14**, 63–86.

- GRAMBAST, L. 1966. Un nouveau type structural chez les Clavatoracées; son intérêt phylogénétique et stratigraphique. *Comptes Rendus de l'Académie des Sciences, Paris, Série D*, **262**, 1929–1932.
- 1967. La série évolutive *Perinneste-Atopochara* (Charophytes). *Comptes Rendus de l'Académie des Sciences, Paris, Série D*, **264**, 581–584.
- 1968. Evolution of the utricle in the Charophyte genera *Perinneste* Harris and *Atopochara* Peck. *Journal of the Linnean Society, Botany*, **61**, 5–11.
- 1969. La symétrie de l'utricule chez les Clavatoracées et sa signification phylogénétique. *Comptes Rendus de l'Académie des Sciences, Paris, Série D*, **269**, 878–881.
- 1970. Origine et évolution des *Clypeator* (Charophytes). *Comptes Rendus de l'Académie des Sciences, Paris, Série D*, **271**, 1964–1967.
- 1972. Principes de l'utilisation stratigraphique des charophytes. Applications au Paléogène d'Europe occidentale. *Mémoires du Bureau de Recherches Géologiques et Minières*, **77**, 319–328.
- 1974. Phylogeny of the Charophyta. *Taxon*, **23**, 463–481.
- GROVES, J. 1924. A sketch of the geological history of the Charophyta. 72–90. In GROVES, J. and BULLOCK-WEBSTER, G. R. *The British Charophyta*, 2. Ray Society, London, 129 pp.
- HÄFELI, C. 1966. Die Jura/Kreide-Grenzsichten im Bielerseegebiet (Kt. Bern). Inaugural Dissertation. *Eclogae Geologicae Helvetiae*, **59/2**, Special volume, 695 pp.
- HAO YICHUN, RUAN PEIHUA, ZHOU XIUGAO, SONG QISHAN, YANG GUODONG, CHENG SHUWEI and WEI ZHENXIN 1983. Middle Jurassic–Tertiary deposits and ostracod-charophyta fossil assemblages of Xining and Minhe Basins. *Earth Science Journal of the Wuhan College of Geology*, **23**, 1–210.
- HARDING, I. C. 1990. A dinocyst calibration of the European boreal Barremian. *Palaeontographica, Abteilung B*, **218**, 1–76.
- HARRIS, T. M. 1939. British Purbeck Charophyta. *Memoirs of the British Museum (Natural History)*, 83 pp.
- HESSELBO, S. P. and ALLEN, P. A. 1991. Major erosion surfaces in the basal Wealden Beds, Lower Cretaceous, south Dorset. *Journal of the Geological Society, London*, **148**, 105–113.
- HOEDEMAEKER, P. J. 1991. Tethyan–Boreal Correlations and the Jurassic–Cretaceous Boundary. *Newsletters on Stratigraphy*, **25**, 37–60.
- HOLLIDAY, D. W. and SHEPHARD-THORN, E. R. 1974. Basal Purbeck evaporites of the Fairlight Borehole, Sussex. *Report of the Institute of Geological Sciences*, **74/4**, 1–14.
- HORN AF RANTZIEN, H. and GRAMBAST, L. 1962. Some questions concerning Recent and fossil charophyte morphology and nomenclature. *Stockholm Contributions in Geology, Series 9*, **3**, 135–144.
- HOUSE, M. R. 1989. *Geology of the Dorset Coast*. Geologists' Association, London, 163 pp.
- HUAN REN-JIN 1985. Cretaceous and Early Tertiary charophytes from Sichuan. *Acta Micropalaeontologica Sinica*, **2**, 7–89.
- HUCKRIEDE, R. 1982. Die unterkretazische Karsthöhlen-Füllung von Nehden im Sauerland. 1. Geologische, paläozoologische und paläobotanische Befunde und Datierung. *Geologia and Palaeontologica*, **16**, 183–192.
- HUGHES, N. F., DREWRY, G. E. and LAING, J. F. 1979. Barremian earliest angiosperm pollen. *Palaeontology*, **22**, 513–535.
- and McDUGALL, A. B. 1990. New Wealden correlation for the Wessex Basin. *Proceedings of the Geologists' Association*, **101**, 85–90.
- HUNT, C. O. 1985. Miospores from the Portland Stone Formation and the lower part of the Purbeck Formation (Upper Jurassic Lower Cretaceous) from Dorset, England. *Pollen et Spores*, **27**, 419–451.
- 1987. Dinoflagellate cyst and acritarch assemblages in shallow marine and marginal marine carbonates; the Portland Sand, Portland Stone and Purbeck Formations (Upper Jurassic–Lower Cretaceous) of southern England and northern France. 208–225. In HART, M. B. (ed.). *Micropalaeontology of carbonate environments*. Ellis Horwood, Chichester, 296 pp.
- JIANG YUAN, ZHANG ZE-RUN and MENG XIANG-SONG 1985. Early Cretaceous charophyte flora from Southern Henan and its stratigraphical significance. *Acta Micropalaeontologica Sinica*, **2**, 161–167.
- KAMPMANN, H. 1983. Microfossilien, Hölzer, Zapfen und Pflanzenreste aus der unterkretazischen Sauriergrube bei Brilon-Nehden. *Geologie und Paläontologie in Westfalen*, **1**, 53–59.
- KARCZEWSKA, J. and ZIEMBIKA-TWORDZYDLO, M. 1970. Upper Cretaceous Charophyta from the Nemegt Basin, Gobi Desert. *Palaeontologia Polonica*, **21**, 121–144.
- KEEPING, W. 1883. *The fossils and palaeontological affinities of the Neocomian deposits of Upware and Brickhill*. Sedgwick Prize Essay for 1879, Cambridge, 167 pp.
- LAKE, R. D. and HOLLIDAY, D. W. 1978. Purbeck Beds of the Broadoak Borehole, Sussex. *Report of the Institute of Geological Sciences*, **78/3**, 1–28.

- and SHEPHARD-THORN, E. R. 1987. Geology of the Country around Hastings and Dungeness. *Memoir of the British Geological Survey*, 81 pp.
- and YOUNG, B. 1978. Boreholes in the Wealden Beds of the Hailsham area, Sussex. *Report of the Institute of Geological Sciences*, **78/23**, 1–22.
- YOUNG, G. B., WOOD, C. J. and MORTIMORE, R. N. 1987. Geology of the country around Lewes. *Memoir of the British Geological Survey*, 117 pp.
- LEES, G. M. and TAITT, A. H. 1945. The geological results of the search for oilfields in Great Britain. *Quarterly Journal of the Geological Society, London*, **101**, 255–317.
- LORD, A. R. and BOWN, P. R. (eds). 1987. Mesozoic and Cenozoic stratigraphical micropalaeontology of the Dorset coast and Isle of Wight, southern England. *British Micropalaeontological Society Guidebook*, **1**, 183 pp.
- LU HUI-NAN and LUO QI-XIN 1990. *Fossil charophytes from the Tarim Basin, Xinjiang*. Scientific and Technical Documents Publishing House, Beijing, 261 pp.
- and YUAN KIAOQI 1991. Jurassic and Early Cretaceous charophytes from the Bayanhot Basin and its neighbourhood. *Acta Micropalaeontologica Sinica*, **8**, 373–394. [In Chinese with English summary].
- MÄDLER, K. 1952. Charophyten aus dem nordwestdeutschen Kimmeridge. *Geologisches Jahrbuch*, **67**, 1–46.
- 1955. Zur Taxonomie der tertiären Charophyten. *Geologisches Jahrbuch*, **70**, 265–328.
- MARTIN-CLOSAS, C. and GRAMBAST-FESSARD, N. 1986. Les Charophytes du Crétacé inférieur de la région du Maestrat (Chaîne ibérique – Catalanides, Espagne). *Paléobiologie continentale*, **15**, 1–66.
- and PEYBERNES, M. 1987. Datation de la transgression éocétacée dans les Pyrénées basco-béarnaises à l'aide des charophytes. *Géobios*, **20**, 695–700.
- and SALAS, R. 1988. Corrélations de la biozonation des charophytes avec celle des foraminifères (Orbitolinidés) dans le Valanginien inférieur du Bassin du Maestrat (Castello, Espagne). *Géobios*, **21**, 645–650.
- 1989. Nouvelles données stratigraphiques et biostratigraphiques (Charophyta) sur le passage Jurassique–Crétacé dans le Bassin du Maestrat (Chaîne Ibérique orientale). 77–95. In ASSOCIACIÓN DE GÉOLOGOS Y GEOFÍSICOS ESPAÑOLES DEL PETRÓLEO (eds). *Libro Homenaje a Rafael Soler*. Madrid, 132 pp.
- and SERRA-KIEL, J. 1991. Evolutionary patterns of Clavatoraceae (Charophyta) in the Mesogean Basins analysed according to environmental change during Malm and Lower Cretaceous. *Historical Biology*, **5**, 291–307.
- MELVILLE, R. V. and FRESHNEY, E. C. 1982. *British regional geology. The Hampshire Basin and adjoining areas*. Fourth edition. HMSO, London, 146 pp.
- MIGULA, W. 1897. *Kryptogamen-Flora von Deutschland, Oesterreichs und der Schweiz. Die Characeen, Band 5*. Leipzig, 765 pp.
- MOJON, P.-O. 1988. Les dépôts émergifs des faciès urgoniens (Hauterivien–Aptien inférieur) dans le Jura méridional (Ain, France) et les Chaînes subalpines septentrionales (Haute-Savoie, Savoie et Isère, France). *Archives des Sciences*, **41**, 409–417.
- 1989. *Cetacella eocretacas* et *Cypridea mirabilis*, deux nouveaux ostracodes lacustres des faciès purbeckiens (Berriasien inférieur) du Jura franco-Suisse. *Archives des Sciences*, **42**, 499–508.
- and MEDUS, J. 1990. Précisions biostratigraphiques sur l'Urgonien' des Chaînes subalpines septentrionales du sud-est de la France et mise en évidence de *Cypridea gigantissima*, un nouvel ostracode lacustre de l'Aptien inférieur. *Archives des Sciences*, **43**, 429–452.
- and STRASSER, A. 1987. Microfaciès, sédimentologie et micropaléontologie du Purbeckien de Bienne (Jura suisse occidentale). *Eclogae Geologicae Helvetiae*, **80**, 37–58.
- MORTER, A. A. 1984. Wealden Mollusca and their relationship to ostracod biostratigraphy, stratigraphical correlation and palaeoecology in the Weald and adjacent areas. *Proceedings of the Geologists' Association*, **95**, 217–234.
- MUSACCHIO, E. A. 1971. Charophytas de la Formacion La Amarga (Cretacico inferior), Provinica de Neuquen, Argentina. *Revista del Museo de La Plata, Nueva Seria, Paleontologia*, **37**, 19–38.
- 1979. Datos paleobiogeograficos de algunas asociaciones de foraminiferos, ostracodos y carofitas del Jurassico medio y el Cretacico inferior de Argentina. *Ameghiana*, **26**, 247–271.
- 1981. South American Jurassic and Cretaceous foraminifera, ostracoda and charophyta of Andean and Sub-Andean regions. 461–498. In *Cuencas sedimentariás del Jurásico y Cretácico de America del Sur, vol. 2*. Buenos Aires.
- NORRIS, G. 1985. Palynology and British Purbeck facies. *Geological Magazine*, **122**, 187–190.
- OGG, J. G., HASENYAGER, R. W., WIMBLEDON, W. A., CHANNELL, J. E. T. and BRALOWER, T. J. 1991. Magnetostratigraphy of the Jurassic–Cretaceous interval. *Cretaceous Research*, **12**, 455–482.

- PECK, R. E. 1937. Morrison Charophyta from Wyoming. *Journal of Paleontology*, **11**, 83–90.
- 1938. A new family of Charophyta from the Lower Cretaceous of Texas. *Journal of Paleontology*, **12**, 173–176.
- 1941. Lower Cretaceous Rocky Mountain non-marine microfossils. *Journal of Paleontology*, **15**, 285–304.
- 1957. North American Mesozoic Charophyta. *Professional Paper of the United States Geological Survey*, **294-A**, 1–44.
- PECORINI, G. 1969. Le Clavatoraceae del 'Purbeckiano' di Cala d'Inferno nella Nurra di Alghero (Sardegna nord-occidentale). *Bollettino della Società Sarda di Scienze Naturali*, **5**, 1–14.
- PIA, J. 1927. Thallophyta. 31–136. In HIRMER, M. *Handbuch der Paläobotanik*, I. München, Berlin, 708 pp.
- RADLEY, J. D. 1992. Palaeoecology and deposition of Portlandian (Upper Jurassic) strata at the Bugle Pit, Hartwell, Buckinghamshire. *Proceedings of the Geologists' Association*, **102**, 241–249.
- RAMALHO, M. 1971. Contribution à l'étude micropaléontologique et stratigraphique du Jurassique supérieur et du Crétacé inférieur des environs de Lisbonne (Portugal). *Memorias dos Serviços Geológicos de Portugal, Nova Serie*, **19**, 1–212.
- REID, C. and GROVES, J. 1916. Preliminary report on the Purbeck Characeae. *Proceedings of the Royal Society of London, Series B*, **89**, 252–256.
- REY, J. 1982. Le Crétacé dans la région de Faro (Algarve, Portugal). *Comissao do Serviço Geologico de Portugal*, **68**, 225–236.
- 1983. Le Crétacé de l'Algarve: Essai de Synthèse. *Comissao do Serviço Geologico de Portugal*, **69**, 87–101.
- GRAMBAST, L., OERTLI, H. J. and RAMALHO, M. 1968. Les couches de passage du Jurassique au Crétacé au nord du Tage (Portugal). *Compte Rendu Sommaire de la Société Géologique de France*, **5**, 153–154.
- SCHUDACK, M. 1987a. Charophytenflora und fazielle Entwicklung der Grenzschichten mariner Jura/Wealden in den Nordwestlichen Iberischen Ketten (mit Vergleichen zu Asturien und Kantabrien). *Palaeontographica, Abteilung B*, **204**, 1–180.
- 1987b. Charophytenflora und Alter der unterkretazischen Karsthöhlenfüllung von Nehden (NE Sauerland). *Geologie und Paläontologie in Westfalen*, **10**, 7–44.
- 1989. Charophytenfloren aus den unterkretazischen Vertebraten-Fundschichten bei Galve und Uña (Ostspanien). *Berliner Geowissenschaftliche, Abhandlungen A*, **106**, 409–443.
- 1990. Bestandaufnahme und Lokalzonierung der Charophyten aus Oberjura und Unterkreide des Nordwestdeutschen Beckens. *Berliner Geowissenschaftliche, Abhandlungen A*, **124**, 209–245.
- 1991. Eine Charophyten-Biozonierung für den Zeitraum Oberjura bis Berriasium in Westeuropa und ihr Vergleich mit Sequenzstratigraphie und eustatischer Meeresspiegelkurve. *Berliner Geowissenschaftliche, Abhandlungen A*, **134**, 311–332.
- SHAIKIN, I. M. 1976. New data on the biostratigraphy of the Jurassic and Cretaceous deposits of the pre-Dobrogean depression. *Geologicheskii Zhurnal*, **36**, 77–86. [In Russian].
- STEWART, D. J. 1981. A field guide to the Wealden Group of the Hastings area and the Isle of Wight. *Proceedings of the Second International Conference on Fluvial Sediments, University of Keele*, **3**, 1–35.
- STRAHAN, A. 1898. Geology of the Isle of Purbeck and Weymouth. *Memoirs of the Geological Survey of Great Britain*, 278 pp.
- SYLVESTER-BRADLEY, P. C. 1941. The Purbeck Beds of Swindon. *Proceedings of the Geologists' Association*, **50**, 349–372.
- 1942. Notes on the age of the Swindon Purbeck Beds. *Proceedings of the Geologists' Association*, **51**, 325–327.
- 1949. The ostracod genus *Cypridea* and the zones of the Upper and Middle Purbeckian. *Proceedings of the Geologists' Association*, **60**, 125–153.
- THURRELL, R. G., WORSSAM, B. C. and EDMONDS, E. A. 1968. Geology of the country around Haslemere. *Memoirs of the Geological Survey of the United Kingdom*, 169 pp.
- TOPLEY, W. 1875. The geology of the Weald. *Memoirs of the Geological Survey of England and Wales*, 503 pp.
- TOWNSON, W. G. 1975. Lithostratigraphy and deposition of the type Portlandian. *Journal of the Geological Society, London*, **131**, 619–638.
- WANG ZHEN, HUANG RENJIN and WANG SHUI 1976. Mesozoic and Cenozoic Charophyta from Yunnan Province. 65–86. In *Mesozoic fossils of Yunnan*, **1**, 388 pp.
- and LU HUINAN 1982. Classification and evolution of Clavatoraceae, with notes on their distribution in China. *Bulletin of the Nanjing Institute of Geology and Palaeontology*, **4**, 77–108.
- WILEY, E. O. 1978. The evolutionary species concept reconsidered. *Systematic Zoology*, **27**, 17–26.
- WIMBLEDON, W. A. 1976. The Portland Beds (Upper Jurassic) of Wiltshire. *Wiltshire Archaeology and Natural History Magazine*, **71**, 3–11.

- 1980. Portlandian correlation chart. 85–93. In COPE J. C. W., DUFF, K. L., PARSONS, C. F., TORRENS, H. S., WIMBLETON, W. A. and WRIGHT, J. K. Middle and Upper Jurassic. *Geological Society of London, Special Report*, **15**, 1–109.
- and HUNT, C. O. 1983. The Portland–Purbeck junction (Portlandian–Berriasian) in the Weald and correlation of latest Jurassic–early Cretaceous rocks in southern England. *Geological Magazine*, **120**, 267–280.
- WORSSAM, B. C. 1978. The stratigraphy of the Weald Clay. *Report of the Institute of Geological Sciences*, **78/11**, 1–23.
- and IVIMEY-COOK, H. C. 1971. The stratigraphy of the Geological Survey Borehole at Warlingham, Surrey. *Bulletin of the Geological Survey of Great Britain*, **36**, 1–178.
- 1984. Comments on the paper 'The Portland–Purbeck junction (Portlandian–Berriasian) in the Weald and the correlation of latest Jurassic–early Cretaceous rocks in southern England', by W. A. Wimbledon and C. O. Hunt. *Geological Magazine*, **121**, 651–652.
- YOUNG, B. and LAKE, R. D. 1988. Geology of the country around Brighton and Worthing. *Memoir of the British Geological Survey*, 115 pp.

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APPENDIX 1—DISTRIBUTION OF CHAROPHYTES IN BOREHOLES IN THE PURBECK AND WEALDEN OF SOUTHERN ENGLAND

The distribution of charophyte species found in borehole material is described in descending order. Sample numbers with the prefix Mik(M), MPA and SAM refer to the British Geological Survey collections at Keyworth, NHM numbers to the National History Museum, London, SWF to the Senckenberg Museum, Frankfurt, and CF to the Laboratoire de Paléobotanique, Université de Montpellier.

Warlingham Borehole, Surrey (Worssam and Ivimey-Cook 1971)

This includes the most complete succession of charophyte floras and is taken as a reference section, supplemented by data from the Purbeck Group in the Fairlight Borehole.

Weald Clay, lower portion of the upper part

430.0 m. Samples Mik(M) 1068 and SAM 884: *Asciidiella iberica*, *Atopochara triquetra* (primitive), *Triclypella calcitraba*, *Sphaerochara andersoni*.

430.4 m. Sample Mik(M) 2493: *Clypeator combei*, *T. calcitraba*, *S. andersoni*, stems.

430.7 m. Sample Mik(M) 1074 and SAM 886: *T. calcitraba*, *S. andersoni*.

Ashdown Beds

573.6 m. Sample Mik(M) 1545: Small-sized gyrogonites of Characeae, *Tolypella?*

581.7 m. Sample Mik(M) 1558: Characeae genus et species indet.

Purbeck Group (all samples from the Lulworth Formation)

612.1 m. Sample Mik(M) 1758 and SAM 1346 (ex Bp 4971): *Porochara maxima*, Clavatoraceae gen. et sp. indet., stems.

612.3–612.4 m. Sample Mik(M) 1759: *Clavator reidi* (one utricle, with slightly spiralized cells), *Porochara maxima*, stems.

614.2–614.4 m. Sample Mik(M) 1760: *Latochara* sp., *C. reidi* (utricles with well spiralized cells), *Aclistochara* sp., stems.

614.8 m. Sample Mik(M) 1775 and SAM 1360 (ex Bp 5012): *C. reidi* (utricles with spiralized cells).

625.3 m. Sample Mik(M) 1856 and SAM 1403: *Globator praecursor*, *Clavator* aff. *reidi*.

631.9 m. Sample SAM 1424: *C.* aff. *reidi*.

Ripe Borehole, Sussex (Lake and Young 1978)

Weald Clay

154.00–154.50 m. Sample Mik(M) 3927 and MPA 25418: *Triclypella calcitraba*, *Sphaerochara andersoni*, *Clypeator combei*.

159.50–160.00 m. Sample Mik(M) 3935 and MPA 25419: *Clypeator combei*.

Hailsham Borehole, Sussex (Lake and Young 1978)

Weald Clay

16.50–17.00 m. Sample Mik(M) 3736: *T. calcitraba*, *S. andersoni*.

29.50–30.00 m. Sample Mik(M) 3780: *C. combei*.

38.00–38.50 m. Sample Mik(M) 3790: *T. calcitraba*.

Wadhurst Park No. 3 Borehole, Sussex (Anderson and Shephard-Thorn 1967)

Wadhurst Clay

6.7–7.0 m. Sample Mik(M) 1987 and SAM 3779: *Flabellochara xiangyuenensis*, *Sphaerochara* aff. *andersoni*.

7.3–7.6 m. Sample Mik(M) 1993 and SAM 3781: *Flabellochara xiangyuenensis*.

16.8–17.0 m. Sample Mik(M) 2026: *Flabellochara* sp. indet.

Glynleigh Borehole, Sussex (Lake and Young 1978)

Wadhurst Clay

59.00–59.50 m. Sample Mik(M) 3697: *Flabellochara xiangyuenensis*, *Sphaerochara* aff. *andersoni*.

Kingsclere Borehole, Hampshire (Lees and Taitt 1945)

?Grinstead Clay (equivalent)

305.7 m. Sample Mik(M) 2489, ex. Mik(M) 301: *Clypeator britannicus*.

306.6 m. Sample Mik(M) 2490, ex. Mik(M) 327–9: *Clypeator britannicus*, *Sphaerochara* aff. *andersoni*.

Robertsbridge Bypass No. 15 Borehole, Sussex (OS TQ 7391 2523)

Wadhurst Clay

2.9–3.0 m. Sample 15/6, University of Brighton, CF 2773b. Stiff olive-grey, slightly shaly clay: *Flabellochara* sp. (incompletely calcified utricles), *Sphaerochara* aff. *andersoni*.

12.2–12.3 m. Sample 15/18, University of Brighton, CF 2773a. Dark greenish shaly clay with fossil shell fragments: *Sphaerochara* aff. *andersoni*.

Kitchenham Dam Borehole No. K4, Sussex (OS TQ 6816 1313)

Wadhurst Clay

28.30 m. Sample per University of Brighton, CF 2774/1. Light greenish grey, partly friable clay: *Flabellochara xiangyuenensis*.

Fairlight Borehole, Sussex (Holliday and Shephard-Thorn 1974)

Purbeck Group (Plant and Bone Beds Member)

263.3–263.7 m. Sample Mik(M) 4159: ?*Tolypella*.

Purbeck Group (Broadoak Calcareous Member)

273.4–273.7 m. Sample Mik(M) 4192: *Flabellochara* cf. *grovesi*.

273.7–274.0 m. Sample MPA 25422: *Clavator reidi* (with vertical cells), *Flabellochara grovesi*.

280.1–280.4 m: *Flabellochara grovesi*, *Clavator reidi* (spiralized).

281.0–281.3 m: *F. grovesi*, *C. reidi*, small-sized Characeae, oospores.

293.2–293.5 m. Sample MPA 25425: *Globator protoincrassatus*.

296.0–296.3 m. Sample MPA 25426: *G. praecursor*, *Clavator* aff. *reidi*.

317.6–317.9 m: *Globator rectispirale*, nodosoclavatoroid utricles.

Broadoak Borehole, Sussex (Lake and Holliday 1978)
 Purbeck Group (Broadoak Calcareous Member)
 71·50–72·00 m. Sample Mik(M) 4333: *Clavator reidi* (vertical cells).
 111·50–112·00 m. Sample Mik(M) 4296: *Globator praecursor*.

Brightling No. 27 Borehole, Sussex (Anderson and Bazley 1971)
 Purbeck Group (Broadoak Calcareous Member)
 270·6 m. Sample Mik(M) 2651: *G. praecursor*.

APPENDIX 2 – DISTRIBUTION OF CHAROPHYTES IN PURBECK AND WEALDEN OUTCROPS IN SOUTHERN ENGLAND

For the Purbeck Limestone Group, specimens were collected by MF in the classic sections along the Dorset coast and at two localities in the Swindon Marshes: Town Garden Quarry, Swindon and the Upwey section. Sediments collected in the basal Purbeck beds of the Isle of Portland did not yield any charophytes. MF has also revised the specimens from the same areas that are housed in the Natural History Museum (specimen numbers prefixed BMNH-V), notably the important material studied by Harris (1939). Wealden charophyte floras have been collected from a quarry near Capel, Surrey, and on the south-west coast of the Isle of Wight (specimens CF, charophyte collections, University of Montpellier). The distribution of charophyte floras found at outcrop is given below.

Wealden Supergroup

Cowleaze Chine. South-west coast of the Isle of Wight (OS SZ 444 801). There are three levels with charophytes, at the base of the Vectis Formation (Stewart 1981).

CF 2777b. 170 m west of Cowleaze Chine; dark grey marls: *Atopochara triquetra* (advanced), *Clypeator combei*, *Peckisphaera verticillata*.

CF 2777a. 150 m west of Cowleaze Chine; dark grey marls below a bed of light grey sands 0·3 m thick: charophyte flora as above.

CF 2776. 0·1 m above the sand bed; dark grey marls, with white mollusc shells and fish teeth: *C. combei*.

Butterley Brickworks Pit (formerly Clock House Pit). Capel, Surrey (Worssam 1978) (OS TQ 175 384).

CF 2771. Weald Clay, below Bed 3, bed 33 in Worssam (1978, p. 16). Charophytes were collected in 1986 from a shaly clay below a sandstone with *Ophiomorpha: Sphaerochara* sp.

Stream section, 500 m east of Freechase. Near Warninglid, Sussex (OS TQ 2442 2518).

E276, British Geological Survey, Keyworth. Wadhurst Clay, sample of purple shales from beds high in the formation: *Flabellochara xiangyimensis*.

Fairlight section. Sussex.

Hastings Beds, 'Fairlight Clay', Sample BMNH-V1070: *Peckisphaera knowltoni* (Seward) Schudack; internal mould of a ?Characeae.

Purbeck Limestone Group of Dorset

Durdle Door.

CF 2781a–b. Lulworth Formation: Broken Beds and Caps: ostracods. No charophyte seen.

Harris (1939): Below chert: *Perimneste horrida*.

CF 2781. Just below the Cinder Bed [Member], in the Lulworth Formation. Marl with gypsum.

CF 2781c: *Flabellochara grovesi*, *Clavator reidi*.

CF 2781d: *Flabellochara grovesi*.

Durlston Bay, Swanage. (OS SZ 040 786).

Neale and Mojon sample. Higher part of Soft Cockle Member, Lulworth Formation: Bed DB 70 of Clements (in Cope et al. 1969; Clements 1993): *Globator protoincrassatus*.

Worbarrow Tout. See Ensom (1985).

CF 2783. Above the Cinder Bed [Member], in the Durlston Formation: *Porochara* sp., *Clavator reidi*.

Mupe Bay. See Arkell (1947a).

Harris (1939) reported *Perimueste horrida* from this locality, probably from the Charophyte Chert, Cherty Freshwater Member, Lulworth Formation.

CF 2785. 0.8 m above the chert, and below the Cinder Bed [Member]: *Flabellochara grovesi*.

Durlston Bay. Swanage (Clements in Cope *et al.* 1969; Clements 1993; El Shahat and West 1983).

CF 2779a–b. Mammal Bed, in the Marly Freshwater Member, Lulworth Formation: *Porochara* sp., *Clavator reidi*.

CF 2780b. Above the Cinder Bed, in the Durlston Formation: *Porochara* sp., *Clavator reidi*.

Portesham Quarry. Near Abbotsbury (OS SY 611 859).

Harris (1939) reported *Perimueste horrida*, *Clavator reidi* and *C.* (i.e. *Flabellochara*) *grovesi* (holotype) in 'Portesham or near Portesham', from Reid and Groves collection. Portesham Quarry is the type locality of *Clavator westi* (Barker *et al.*, 1975). The type material of this supposed new taxon comprises nodosoclavatoroid utricles and vegetative fragments which could correspond to any Clavatoroideae: '*C. westi*' cannot therefore be considered as a species in the traditional sense of charophyte taxonomy (Feist and Grambast-Fessard 1991).

Sample BMNH-V26280, Reid and Groves Collection: *Clavator reidi*.

Poxwell Road cutting. Dorset.

Bed 33 of Sylvester-Bradley (1949). BMNH-V26181: *Flabellochara grovesi*.

Purbeck Limestone Group of Swindon Marshes

Towu Gardens Quarry. Swindon, Wiltshire. Section after Sylvester-Bradley (1941).

CF 2789a. 'Lower Purbeck Beds'. Exposure II. Lower Pebbly Beds (base): *Clypeator discordis*. Ostracoda:

Cypridea dunkeri papulata. Foraminifera: *Lenticulina muensteri*.

CF 2789b. 0.3 m above: *Clavator* aff. *reidi*.

CF 2790. Cythere Marl: *Clypeator discordis*.

'Middle to Upper Purbeck Beds'. Exposure IV. Middle Pebbly Bed. Sample TCQ-IV, collected by Dr H. Malz, Senckenberg Museum, Frankfurt a. Main and sample CF 2792: *Latochara* aff. *bitruncata*, nodosoclavatoroid utricles, *Clypeator discordis*.

Exposure III. Chara Marls. Sample TGQ-III of H. Malz and sample CF 2791a, at the base of the marls: *Clypeator discordis*, *Clavator* aff. *reidi* (with vertical and slightly spiralized cells).

Sample CF 2791b–c (laterally, at the top of the marls): *Clypeator discordis*, *Clavator* aff. *reidi*, nodosoclavatoroid utricles.

Purbeck Limestone Group of the Vale of Wardour, Wiltshire (see Harris 1939).

Chicksgrave quarry, near Tisbury. Sample CF 2788, grey shaly marls, 1 m above the Portland Stone: *Latochara* aff. *bitruncata*, Clavatoraceae gen. et sp. indet.

LOWER CAMBRIAN REEFAL CRYPTIC COMMUNITIES

by ANDREY YU. ZHURAVLEV and RACHEL WOOD

ABSTRACT. Phanerozoic reefs were differentiated into distinctive open surface and cryptic communities from their first appearance. During the Lower Cambrian, cryptic communities were surprisingly diverse with small, solitary chambered archaeocyath sponges, calcified cyanobacteria and a microburrowing (?)metazoan being the most ubiquitous and abundant elements. Putative primitive cnidarians, spiculate sponges and various problematica were also common crypt dwellers. Several species of archaeocyath sponge, as well as cribricyaths, the calcified cyanobacteria *Chabakovia* spp. and possibly boring sponges, were obligate cryptobionts.

Lower Cambrian crypts offered a habitat of reduced environmental stress, and they housed a substantial proportion of the total biotic diversity of early reefs. Cryptic communities were composed of solitary, pioneering organisms and displayed no succession. Lower Cambrian crypts were small, short-lived structures compared with most modern reefal crypts, and were sites of extensive syn-sedimentary cementation supporting the conjecture that crypts did not remain open for long before partial or total occlusion. There is ample evidence, however, of a soft-bodied cryptos and of intense competition for space, as organisms commonly form multiple overgrowths or chains of individuals.

On a sub-zonal scale, the vast majority of archaeocyath species appear simultaneously in both open surface and cryptic niches, suggesting that Lower Cambrian crypts did not serve either as 'safe-havens' harbouring formerly open surface inhabitants or as 'brood-pouches' of evolutionary innovation.

ONE of the most striking aspects of modern coralgall reefs is their differentiation into distinctive open surface and cryptic communities (Jackson and Buss 1975; Jackson 1977; Jackson and Winston 1982; Choi and Ginsburg 1983; Choi 1984; Kobluk 1988). Whilst phototrophic organisms dominate on exposed, open surfaces, filter and suspension-feeding organisms flourish within hidden, or cryptic niches. Of these, encrusting sponges and ectoprocts are particularly abundant as they appear to be the best overgrowth competitors (Jackson and Winston 1982), but solitary organisms such as serpulids, foraminiferans and brachiopods are also conspicuous, even though they occupy little space (Jackson 1977).

Any association of aggregating skeletal organisms will form cavities or crypts within its framework, as well as generating abundant debris which present attractive undersurfaces for colonization. Such primary crypts provide relatively well-protected niches shielded from direct exposure to local environmental pressures, such as wave scour, irradiation and predation. Unoccupied substratum is rare in crypts and overgrowths are common, suggesting that, as at the open surface, competition for space is intense. Nutrient supply and oxygen availability (provided by sufficient water flow) are critically important to modern cryptic communities (Kobluk and James 1979; Choi and Ginsburg 1983), with competition for food and competitive networking being the principal determinants which maintain high diversity (Jackson and Buss 1975).

Cryptic niches are extremely important within modern reef ecosystems, as many organisms are far more abundant in crypts than on open surfaces and some may be obligate cryptobionts. Crypts can thus house a significant proportion of the total biotic diversity of a reef. In addition, modern reefal caves and grottoes have attracted a celebrated status for the ancient affinities of their biotas (Jackson *et al.* 1971). These crypts house putative relict communities of Mesozoic reef-building calcified demosponges ('sclerosponges') and thecidoid brachiopods (Jackson *et al.* 1971; Wood 1990). Such large cryptic niches have been suggested to be refugia or 'safe havens' to which once-

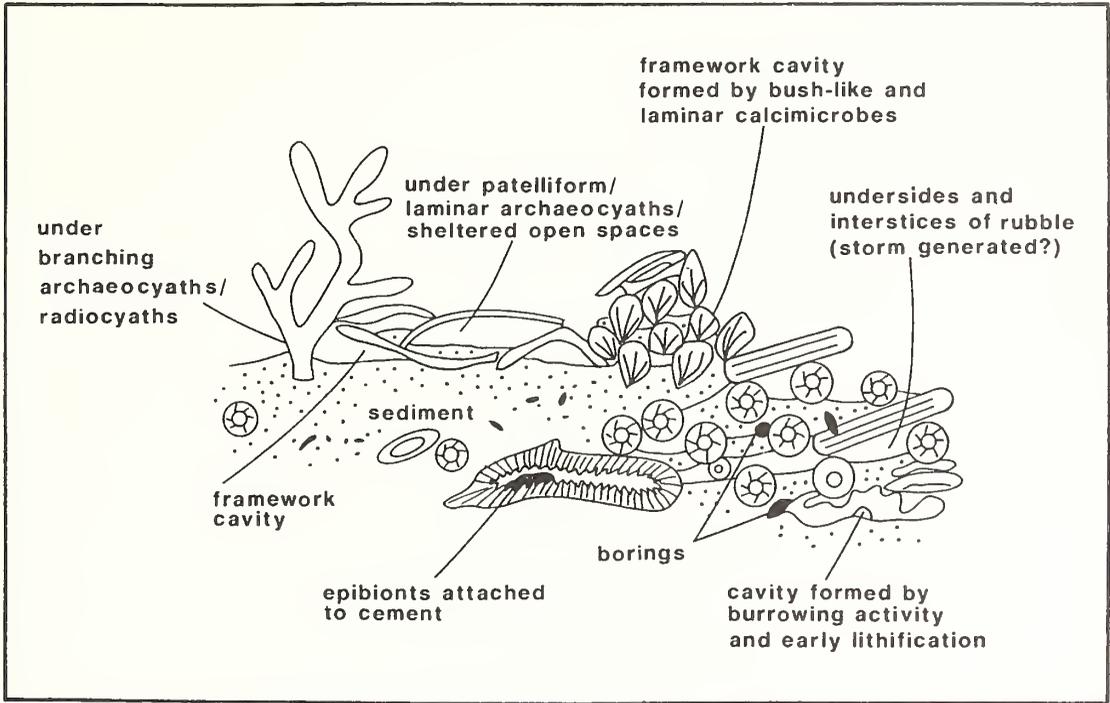
widespread organisms have retreated in the face of new competition (Jackson *et al.* 1971; Vermeij 1985). Others have suggested that crypts may be the crucibles or 'brood-pouches' of evolutionary innovation which spawn new forms that subsequently colonize the open surface (Kobluk and James 1979).

Despite their acknowledged importance in modern reefs, cryptic biotas within fossil reefal buildups have been the subject of limited study (see summaries in Kobluk 1981*b*, 1988). Cryptic communities often go unrecognized in palaeoecological analyses. Although isolated communities have been well documented, it has not yet been established when a distinctive cryptos first developed within reef ecosystems. Nor have any studies been devoted to detailing patterns of temporal development within the cryptos as distinct from open surface communities. Here, we have attempted to describe the cryptos in the earliest known Phanerozoic reefs and to document its development.

The oldest Phanerozoic reefs known are from the 'Nemakit-Daldynian' (= Manykaian; earliest Cambrian; some 544 Ma according to Bowring *et al.* 1993) and were pure calcified cyanobacterial mounds. The first metazoan reefs formed with the appearance of archaeocyath sponges within calcified cyanobacterial communities at the base of the Tommotian (530 Ma; Bowring *et al.* 1993). This consortium was joined later in the Lower Cambrian by other calcified heterotrophs such as radiocyaths and coralomorphs. Lower Cambrian reefal communities usually developed as a series of bioherms in fairly energetic shallow shelf seas (Wood *et al.* 1992*a*), and showed no succession apart from initial stabilization of substrates by the growth of calcified cyanobacteria (Hart 1992) or a consortium of pioneer archaeocyaths and calcified cyanobacteria (Kruse *et al.* in press). Where archaeocyaths were present, bioherms were often dominated by only one or two modular, branching species, implying the rapid colonization and subsequent growth of only a limited number of larval spat falls (Wood *et al.* 1992*a*, 1993). These bioherms were essentially soft-substrate communities, with few massive or encrusting organisms. Early reef communities persisted until the virtual demise of the archaeocyaths at the end of the Toyonian, some 520 Ma (Bowring *et al.* 1993), although calcified cyanobacteria continued to build reefs for the remainder of the Cambrian. Reefs known from the base of the 'Nemakit-Daldynian' to the end of the Toyonian, a period of approximately 25 million years, thus present a coherent ecosystem in which to study the temporal development of cryptic communities.

Crypts are known to have been exploited early in the history of reefs: organic-walled microfossils (*Huroniospera* sp. and *Gunflintia* sp.) and haematitic problematica (*Frutexitis* sp.) have been noted from crypts within lithified algal mat sequences from the Early Proterozoic Odjick Formation, Canada (Hofmann and Grotzinger 1985), and Turner *et al.* (1993) noted *Renalcis*-like cryptobionts in the pre-Vendian Neoproterozoic reefs of the Little Dal Group in northwestern Canada. The first Phanerozoic cryptic communities are documented from the middle Lower Cambrian (Kobluk and James 1979; Kobluk 1981*c*, 1985; Rees *et al.* 1989; James and Gravestock 1990; Fröhler and Bechstädt 1992; Wood *et al.* 1993). These cryptic biotas show, however, marked differences in composition. The cryptos described from the Botomian Poleta Formation in Nevada (Kobluk 1981*a*), the early Toyonian Forteau Formation in Labrador and Newfoundland (Kobluk and James 1979) and the Upper Shady Dolomite in Virginia (Kobluk 1985) have only rare, if any, recorded archaeocyath sponges, even though they have revealed otherwise diverse and unique biotas. In contrast, late Atdabanian cryptic biotas from the Flinders Ranges, South Australia (James and Gravestock 1990) and Zuune Arts, Mongolia (Wood *et al.* 1993) contain abundant archaeocyath sponges, as well as calcified cyanobacteria, putative primitive cnidarians and various problematic forms. Additionally, reported total cryptobiontic diversity and abundance is very variable. These isolated descriptions suggest that cryptic communities were common and well differentiated in Lower Cambrian reefs and deserve systematic study.

Here, we have examined representative reefal communities from throughout the Lower Cambrian. Early cryptic communities were surprisingly well developed, and show biotic and ecological features quite distinct from contemporary open surface communities. We have attempted to highlight these ecological differences by considering differences in morphology and in systematic



TEXT-FIG. 1. Schematic diagram of different cryptic niche types determined within Lower Cambrian reefal buildups.

distribution. In addition, we present quantitative data to test between the competing hypotheses of cryptic niches as 'safe havens' for relict faunas, or as 'brood pouches' of evolutionary innovation.

METHODS

This study is the result of the examination of over 1500 oriented thin-sections from 38 localities embracing 'Nemakit-Daldynian' to middle Toyonian bioherms from the Siberian Platform, South Urals, Altay Sayan Fold Belt, Mongolia, South Australia, Antarctica and North America (see Appendix: Localities 1–38).

We have documented only demonstrably *in situ* elements of the cryptic biota. Although sediment infills within crypts often contain bioclastic debris (such as small shelly fossils, trilobite fragments, brachiopod valves, sponge spicules and echinoderm ossicles), this material is often equally abundant in the non-crypt micrite and interbiohermal sediments of reefal sequences. We have excluded such skeletal material from our analyses except where preferential enrichment within crypts is evident.

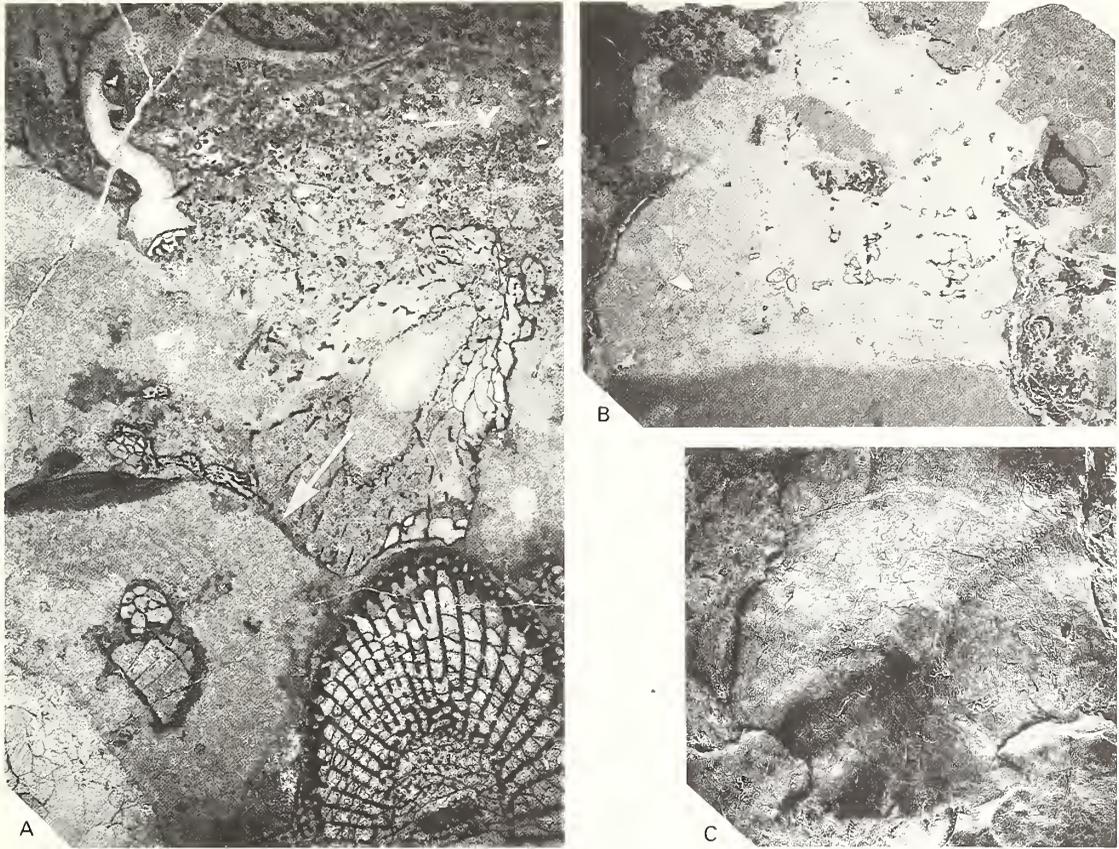
We follow the terminology outlined by Kobluk (1988) and the biostratigraphy of Mansy *et al.* (1993) given in Table 1. Most of the material described herein is housed in the Palaeontological Institute, Russian Academy of Sciences, Moscow (PIN) with supplementary material from the Northern Territory Geological Survey, Darwin, Australia (NTGS), the Sedgwick Museum, Cambridge (SM), and the National Museum of Wales, Cardiff (NMW).

VARIETY AND FORM OF CRYPTS

A surprising variety of cryptic niches was present within Lower Cambrian buildups (Text-fig. 1), whose size ranged from a few millimetres in diameter to several decimetres in some cases. Many

TABLE 1. Biostratigraphy and correlation of Lower Cambrian (Tommotian to Toyonian) in the studied localities studied using archaeocyath zonation (modified from Mansey *et al.* 1993)

Stage	Zone	Siberian Platform	Altay-Sayan	Australia	Mongolia	North America
		Zhuravleva <i>et al.</i> 1969, 1976 (revised)	Osadchaya <i>et al.</i> 1979	Zhuravlev and Gravestock in press	Voronin <i>et al.</i> 1982	Mansy <i>et al.</i> 1993
Toyonian	3		<i>Erbocyathus heterovallum</i> <i>Tegerocyathus edelsteini</i>			
	2	<i>Irinaeyathus shabanovi</i> <i>Archaeocyathus okulitchi</i> Beds	<i>Irinaeyathus ratus</i> <i>Archaeocyathus kusmini</i>	<i>Archaeocyathus abacus</i> Beds		<i>Tegerocyathus greenlandensis</i> <i>Pycnoidocyathus pearylandicus</i> Beds
	1		' <i>Claruscyathus solidus</i> '			<i>Archaeocyathus atlanticus</i> Beds
Botomian	3		<i>Syringocyathus aspectabilis</i>	<i>Syrinocnema favus</i> Beds		<i>Pycnoidocoscinus serratus</i> <i>Tabulacoccus kordeae</i>
		Not established			Not established	<i>Claruscoccus fritzi</i> <i>Metacyathellus caribouensis</i>
	2		<i>Terycyathellus altaicus</i>			<i>Etlunophylthum whitneyi</i> <i>Sekwicyathus nahanneinsis</i>
1		<i>Rozanovicyathus alexi</i> Beds	<i>Clathricoscinus</i>	Not established		
		<i>Carinacyathus squamosus</i> <i>Botomocyathus zelenovi</i>				
Ardabanian	4	<i>Fansicyathus lermontovae</i>	<i>Arturocyathus borisovi</i>	<i>Jugalcycyathus tardus</i>	<i>Alataucyathus jaroshevitschi</i> <i>Tabulacyathellus bidzhaensis</i> <i>Pretiosocyathus subtilus</i> Beds	Not established
	3	<i>Nochoroicyathus kokouhni</i>	<i>Nahivkinicyathus cyroflexus</i>	<i>Spirillicyathus tenuis</i>		
				<i>Warriootacyathus wilkawillinensis</i>		
	2	<i>Carinacyathus pinus</i>	<i>Gordonicyathus howelli</i>			
1	<i>Retecoscinus zegebarti</i>	<i>Nochoroicyathus marinskii</i>				
Tommotian	4	<i>Dokidocyathus lenaicus</i> <i>Tumuliolynthus primigenius</i>				
	3	<i>Dokidocyathus regularis</i>				
	2					
	1	<i>Nochoroicyathus sumnagicus</i>				



TEXT-FIG. 2. A SM X25956; transversely folded cup of *Pycnoidocyathus latiloculatus* (Hill) with rich cryptic fauna of *Tumuliolynthus irregularis* (Bedford and Bedford) (top), *Archaeopharetra* sp. (centre) and *Metaldetes lairdi* (Hill) (bottom). The development of syndimentary cement (lower left) has distorted the growth of *Archaeopharetra* sp. (arrowed) and the cement has also served as a substrate for an encrusting *Khasaktia*-like organism and later generations of irregular archaeocyaths; Locality 32 (Botomian 3); $\times 5$. B, NMW 95.2G.1; probable boring excavations of the ceiling of a crypt, showing scalloped edges. The crypt is formed by *Cambroclyathellus ichuranicus*, Zhuravleva and has been subsequently colonized by *Archaeolynthus polaris* (Vologdin) and *Renalcis jacuticus*, Korde; Locality 2 (Tommotian 1); $\times 6$. C, PIN 3848/701; fungal hyphae on the undersurface of *Okulitchicyathus discoformis* (Zhuravleva); Locality 3 (Tommotian 2); $\times 0.3$.

primary growth framework crypts were formed by upright solitary, branching or laminar reef-building organisms, such as archaeocyath sponges (Pl. 1, fig. 1), radiocyaths (Pl. 1, fig. 5), coralomorphs (Pl. 1, fig. 6) and calcified cyanobacteria (Pl. 1, fig. 3). Areas beneath toppled or reworked skeletal debris also provided shelter crypts (Pl. 1, fig. 4). Selective removal of pockets of sediment by currents or storms within accumulations of reefal debris also formed secondary crypts by early lithification of the remaining sediment. Such crypts may have initiated as open burrow systems (Pl. 1, fig. 2). No crevice crypts have been noted, but this may be due their small size and difficulty of recognition. Peculiar sheet-like cracks have, however, been noted within the 'Nemakit-Daldynian' stromatolites of the Chapel Island Formation in southeastern Newfoundland (Myrow and Coniglio 1991).

The lower parts of crypts were often infilled with homogenous or finely laminated micrite, together

with minor amounts of terrigenous material and variable quantities of bioclastic debris. Sediment infills, which may postdate some cement generations, were commonly microburrowed (Pl. 1, figs 1 and 4), and may be layered and graded indicating episodic sedimentation. The upper parts of crypts may be filled with further generations of early and late cements. The presence of a variety of cements indicates that crypts developed in well-oxygenated and agitated conditions (James *et al.* 1976). Early cements were a ubiquitous feature of Lower Cambrian crypts, with microcrystalline and fibrous rimming cements being especially common (Pl. 1, fig. 1; Text-fig. 2A). The *in situ* skeletal cryptobionta was attached to the walls and ceilings of the crypts, and encrusted framebuilders, other cryptobionts or the surfaces of symsedimentary cements (Text-fig. 3).

LOWER CAMBRIAN CRYPTOBIANTS AND THEIR DISTRIBUTION

Sessile cryptos

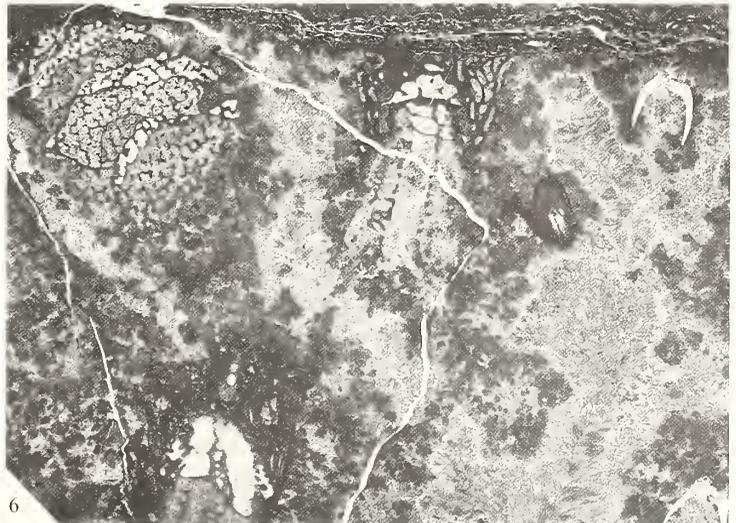
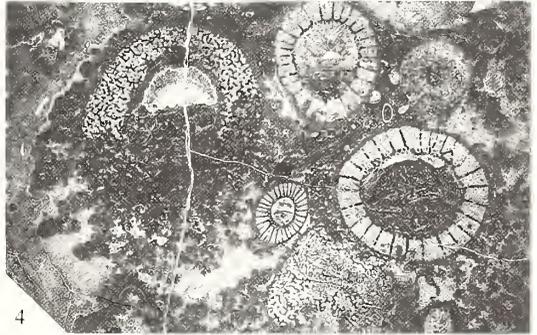
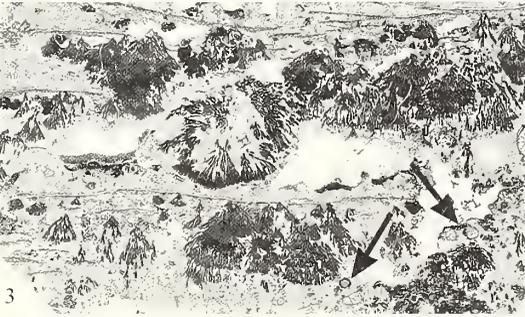
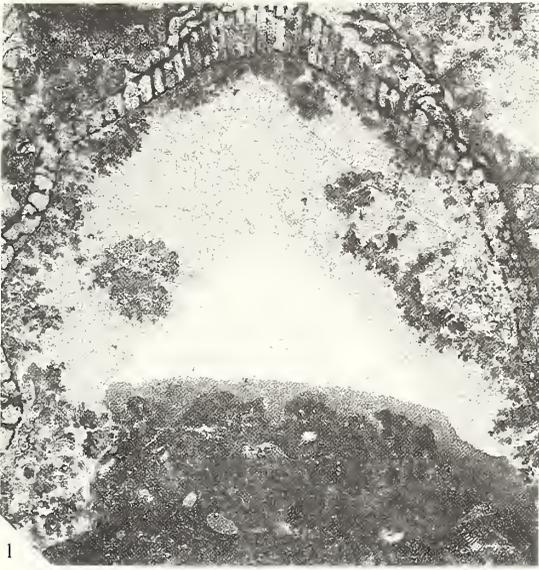
Archaeocyaths. Archaeocyaths were aspiculate calcified sponges, which formed a high-Mg calcite skeleton via calcification of a collagenous template (Zhuravlev 1989; Wood 1990). They were probably closely related to demosponges (Debrenne and Zhuravlev 1992). Archaeocyaths displayed a variety of growth forms although solitary and low integration branching forms were by far the most common (Wood *et al.* 1992a). They appeared at the base of the Tommotian on the Siberian platform, after which they diversified rapidly to reach an acme in the Botomian. During the late Botomian–early Toyonian their diversity plummeted and only two species are known from the post Lower Cambrian (Wood *et al.* 1992b).

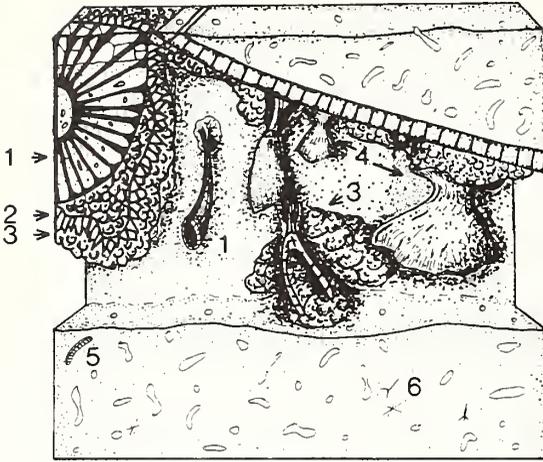
Archaeocyaths were a common to abundant faunal element in Lower Cambrian reefs, forming

EXPLANATION OF PLATE I

Types of Lower Cambrian reefal crypt

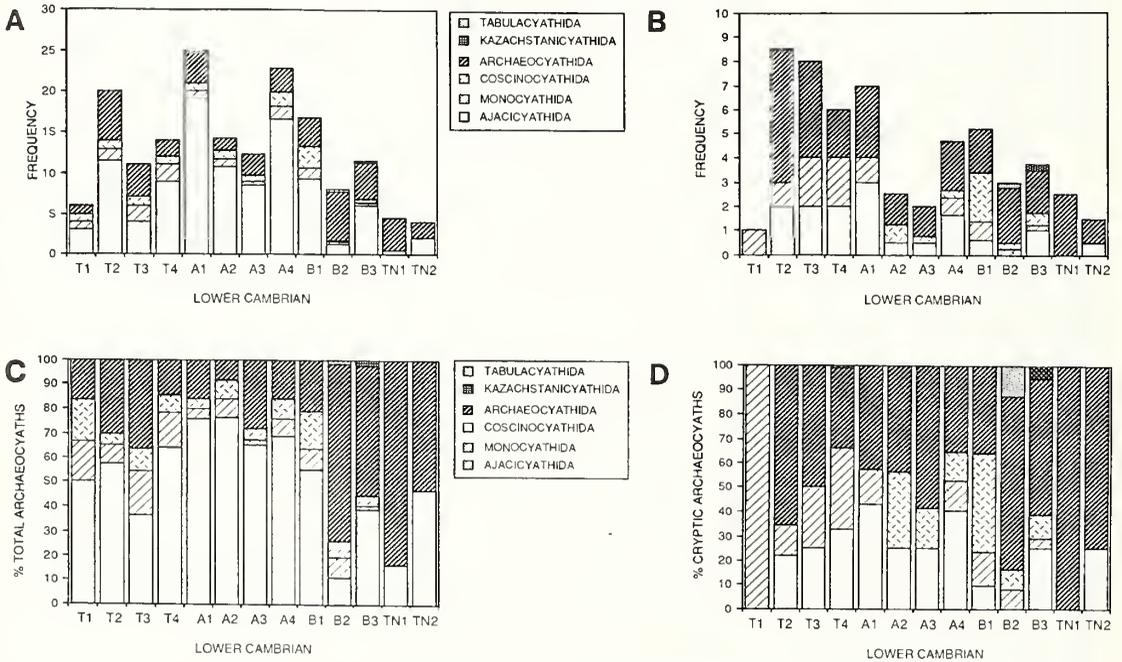
- Fig. 1. NTGS 810028; a domal cup of *Sakhacyathus subatus* (Zhuravleva) forming a crypt colonized by *Renalcis jacuticus* Korde; the first generation of geopetal micrite infill is burrowed and followed by a second layer; all sediment infill postdates *R. jacuticus* encrustation and the precipitation of fibrous calcite; the remaining pore-space is filled with sparry calcite; Locality 3 (Tommotian 2); $\times 5$.
- Fig. 2. NTGS 810038; self-supporting cavity-system formed by symsedimentary lithification of a burrow system, possibly further enhanced by scour; parts of the crypt wall have been colonized by *Renalcis jacuticus* Korde (arrowed); Locality 5 (Tommotian 3); $\times 6$.
- Fig. 3. PIN 4451/90; crypt ceilings formed by rafts of the calcified cyanobacteria *Razumovskia uralica* Vologdin; the resultant crypts were colonized by pendent colonies of *Epiphyton fruticosum* Vologdin and juvenile individuals of the archaeocyath *Spiroclyathella kyzylartauense* Vologdin (arrowed); Locality 25 (Botomian 1); $\times 7$.
- Fig. 4. PIN 3848/702; shelter crypts formed by toppled cups of the archaeocyaths *Dictyocyathus bobrovi* Korshunov (top left), *Nochoroicyathus anabarensis* (Vologdin) (top centre and right) and *Heckericyathus heckeri* (Zhuravleva) (centre); crypts have been colonized by *Renalcis jacuticus* Korde, *Archaeolythus polaris* (Vologdin) (lower centre), and *Dictyocyathus bobrovi* Korshunov; the geopetal micrite infills within the toppled archaeocyath cups have been extensively microburrowed; Locality 7 (Atdabanian 1); $\times 4$.
- Fig. 5. PIN 3482/401; chain of pendent solitary archaeocyath individuals (*Nochoroicyathus changaiensis* (Vologdin) (upper right), *Cambrocyathellus pannonicus* (Fonin) (centre) and *Ajacyathina* gen. et sp. indet. (bottom) forming under the skeleton of the branching radiocyath *Gurphanovella georgensis* (Rozev); several individuals of the cribricyath *Striatocyathus sajanensis* Vologdin and *Jankauskas* are also present; Locality 19 (Atdabanian 4); $\times 5$.
- Fig. 6. PIN 3848/703; framework crypt formed by the encrusting coralomorph *Khasaktia vesicularis* Sayutina; cryptobionts include pendent archaeocyaths *Neoloculicyathus sibiricus* (Sundukov) (centre and lower left), *Dictyocyathus bobrovi* Korshunov (upper left), the coralomorph *Hydrocoelus* sp. (upper and lower left); this cryptic fauna was subsequently encrusted by the calcified cyanobacterium *Renalcis jacuticus* Korde; Locality 7 (Atdabanian 1); $\times 10$.





TEXT-FIG. 3. Schematic block diagram of a typical Lower Cambrian crypt. 1, archaeocyaths; 2, synsedimentary cements; 3, calcified cyanobacteria; 4, coralomorphs; 5, microburrowing metazoan; 6, bioclastic debris, including sponge spicules.

up to 50 per cent. of the total rock volume of some bioherms. Most were attached by an epitheca to hard substrates, such as calcified cyanobacteria or archaeocyath, radiocyath and coralomorph skeletons. Some large solitary, regular individuals, although initiating upon small ephemeral hard substrates, may have been rooted in lime mud. Many had abundant exocyathoid buttresses which served for both stabilization and binding and as competitive exclusion structures (Brasier 1976; Debrenne and Zhuravlev 1992; Wood *et al.* 1992a). Most irregular forms tend to be in growth



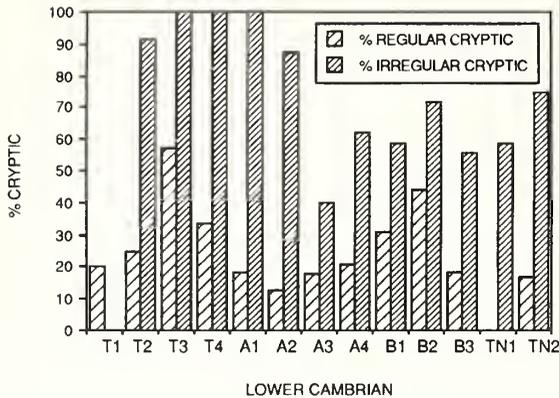
TEXT-FIG. 4. Total number of archaeocyath species within each order in A, total bioherm community, B, cryptic communities only. C, percentage of each order within total communities. D, percentage of each order within cryptic communities only. Community proportions are averaged for each stage.

TABLE 2. Distribution of cryptobionts through the Lower Cambrian. X marks the certain occurrence of cryptic forms. ? marks the probable first appearance. * refer to James and Gravestock (1990) for detailed descriptions.

Cryptobionts	'Nemakit-Daldynian'	Tommotian				Atdabanian				Botomian			Toyonian					
		1	2	3	4	1	2	3	4	1	2	3	1	2	3			
Non-calcified bacteria		<-----																
Calcified cyanobacteria		-----																
<i>Korilophyton</i>	X	----- X																
<i>Angulocehlularia</i>	X	-----																
<i>Botominella</i>		?	-----													X		
<i>Renalcis</i>	X	-----																
<i>Tarthinia</i>	X	-----																
<i>Girvanella</i>	?	-----											X	-----				
<i>Obruchevelia</i>	?	-----												X	-----			
<i>Epiphyton</i>		X	-----															
<i>Tubomorphophyton</i>			?	-----											X	-----		
<i>Gordonophyton</i>			?	-----											X	-----		
<i>Kordephyton</i>			?	-----											X	-----		
<i>Bija</i>													X	-----				
<i>Chabakovia</i>													X	-----				
<i>Wetheredella</i>															X			
'Encrusting microfossils'*								X	-----		X	-----						
'Calcareous microspheres'*								X	-----		X	-----						
Fungi		X-----																
Archaeocyaths:		-----																
<i>Monocyathida</i>	X	-----													X			
<i>Ajaciocyathida</i>	X	-----																
<i>Archaeocyathida</i>	X	-----																
<i>Kazachstaniocyathida</i>															X			
<i>Coscinoocyathida</i>						X	-----					X	-----					
<i>Tabulacyathida</i>												X	--	X	-----			
<i>Cribriocyaths</i>						X	-----								X	-----		
Coralomorphs:		-----																
<i>Cysticyathus</i>		X	--	X	-----													
<i>Hydroconus</i>				X	-----								X	-----				
<i>Khasaktia</i>				X	-----							X	-----					
<i>Rackovskia</i>								X	-----									
<i>Aploconus</i>										X	--	X	-----					
<i>Tabulaconus</i>												X	--	X	-----			
<i>Labyrinthus</i>														X	--	X		
Microburrowers	X	-----																
Siliceous sponges		X	-----															
Calcarean sponges			X	-----														
Stenothecoids						?	-----		X	-----								
<i>Archaeotrypa</i>														X	-----			
Pellets			X	-----														
Unidentified borings	X	-----																
Grazers														X	-----			
Microborings									X	-----								

position, where branching individuals were often bound together to form bafflestones and laminar forms bindstones. Reworked archaeocyath skeletal debris was also a common component of inter-biohermal sediment.

Contrary to previous accounts (Kobluk and James 1979; Kobluk 1981a, 1985), archaeocyaths were abundant cryptobionts; in most communities studied between 20–60 per cent. of the species represented were cryptic (Text-fig. 4). Monocyathid archaeocyaths appeared as an element in



TEXT-FIG. 5. Percentage of cryptic regular and irregular species as a proportion of the total numbers of regulars and irregulars within individual bioherm communities. Community proportions are averaged for each stage.

cryptic faunas in the Tommotian 1, with regular (Ajacicyathida) and irregular forms (Archaeocyathida) following in the Tommotian 2 (Table 2). Representatives from all six archaeocyathan orders (*sensu* Debrenne and Zhuravlev 1992) were present in crypts, but in markedly different proportions. Irregular archaeocyaths (Archaeocyathida, Kazachstanicyathida) formed between 7–80 per cent. (averaging approx. 35 per cent.) of the total bioherm community (Text-fig. 4C), yet between 30–100 per cent. (averaging approx. 55 per cent.) of the cryptic community (Text-fig. 4D). A far greater proportion of the irregular order Archaeocyathida and the regular orders Monocyathida and Coscinyathida are represented in any one cryptic community than members of the regular orders Ajacicyathida and Tabulacyathida (Text-fig. 4A–B). During the early Lower Cambrian often all irregular archaeocyaths (archaeocyathids) present in any one community were both open surface and crypt dwellers (Text-fig. 5). Ajacicyathids were only a minor component of the crypts, even though they were the most species-rich order in open surface communities (Text-fig.

TABLE 3. Differences in morphology and abundance between organisms which occur as both open surface inhabitants and cryptobionts.

Biota	Open surface	Crypt
Archaeocyaths	Reef-builders predominantly modular irregulars + large regulars	Small, solitary irregulars and thalimid regulars Abundant exothecal tissue
<i>Renalcis</i> and <i>Epiphyton</i> -groups	Globular, compact	Delicate branching, arborescent
<i>Chabakovia</i>	Absent	Present
<i>Khasaktia</i>	Sheath-like, encrusting	Conical, small attachment site
Microburrowing (?)metazoan	Rare	Abundant
Cribricyaths	Absent	Abundant
Hydroconozoans, <i>Labyrinthus</i> and <i>Rackovskia</i>	Rare	Common
<i>Archaeotrypa</i>	?	Present
<i>Wetheredella</i>	?	Present

4B, D). We have noted only one occurrence of a tabulacyathid: *Putapacyathus regularis* Bedford and Bedford, which occurs in both the open surface and cryptic community (Locality 30; Botomian 3). For all communities where sufficient data is available, the Fisher Exact Test shows statistically significant underrepresentation of ajacicyathids, and significant enrichment of archaeocyathids within crypts at the 5 per cent. level.

The diversity of archaeocyaths within Lower Cambrian cryptic communities was highly variable. Some communities show no cryptic archaeocyaths (localities 12 (Atdabanian 3) and 18 (Atdabanian 4)) whereas others were almost entirely cryptic, e.g. locality 22 (Botomian 1). Here, of the seven cryptic species, five were coscinocyathids (Pl. 2, fig. 5). Although this community has yielded a total fauna of seventeen species, many of these forms were uncommon.

In addition to differences in systematic distribution, cryptic archaeocyaths display distinct morphological differences from those typical of open surface, frame-building communities (Table 3). Firstly, all cryptic archaeocyaths have porous septa. Savarese (1992) argues that such forms were adapted hydrodynamically to low turbulence conditions, which is supported by the fact that modern cryptic niches generally create lower energy settings than the open environment. Secondly, Kobluk and James (1979, p. 203) noted that the rare archaeocyaths found in the lower Toyonian reefs of Labrador (Locality 36) were small and 'poorly organized'. We note too that cryptic forms were often small, but have detected no evidence for any differences in their rate of growth compared with open surface conspecifics. Their small size appears to result from their reduced longevity, i.e. many were young individuals. Most interesting, however, is that those archaeocyath species which possessed both modular and solitary phenotypes, consistently displayed modular forms on open surfaces but solitary organizations in crypts (see Appendix for specific details). The only exception to this is *Cambrocyathellus proximus*, which was present in a modular state in both open surface and cryptic niches within the Tommotian 2 and Tommotian 3 reefs of Siberia. The encrusting, modular species *Altaicyathus notabilis* (Pl. 2, fig. 6), *Dictyofavus araneosus* (Pl. 2, fig. 2) and *Zmyicyathus* sp., however, appear to be obligate cryptobionts together with the chambered, encrusting forms *Polythalamia americana* and *P. perforata* Debrenne and Wood (Pl. 2, fig. 3). When present, these forms were very abundant.

Many cryptic archaeocyaths (both regulars and irregulars) show abundant exothecal tissue (epithecium and buttresses), which was probably necessary to secure firm attachment to the ceiling or walls of a crypt (Pl. 1, fig. 6; Pl. 2, figs 1–2). The pronounced ability to produce abundant exothecal tissue in the orders Monocyathida and Archaeocyathida might thus explain their preferential occupation of crypts.

Archaeocyaths clearly preferred attachment to hard substrates, and pendent chains of individuals have been noted in larger crypts (Pl. 1, fig. 5). Some archaeocyath individuals also show growth in a series of distinct morphological phases, where each phase appears as rapid growth followed by complete cessation (Pl. 3, fig. 4). This might be related to periodic, possibly seasonal, environmental fluctuations.

Calcified cyanobacteria. Calcified cyanobacteria were abundant in many Cambrian platform carbonates, and constructed reefal buildups throughout this period even after the extinction of the majority of archaeocyaths (Rees *et al.* 1989; James and Gravestock 1990; Wood *et al.* 1992a). They were often associated with micrite, and may form a substrate for the attachment of other organisms. James and Gravestock (1990) have suggested that the micrite between *Renalcis* colonies was originally a cement similar to modern sea-floor cements.

Calcified cyanobacteria occurred as framework constructors in the form of substantial upright bushes or rafts, as encrustations around reef dwellers and as pendent colonies in crypts. All forms may have trapped sediment and many were common as facultative cryptobionts (e.g. Pl. 1, figs 1–3). *Renalcis*, *Angulocellularia*, *Chabakovia*, *Gordonophyton* and *Epiiphyton* were especially abundant in crypts, but only *Chabakovia* was a preferential cryptobiont.

Renalcis and *Tarthinia* had a botryoidal external form, consisting of rounded compartments with micritic, fibrous or peloidal walls. Individual colonies are difficult to discern but all these forms

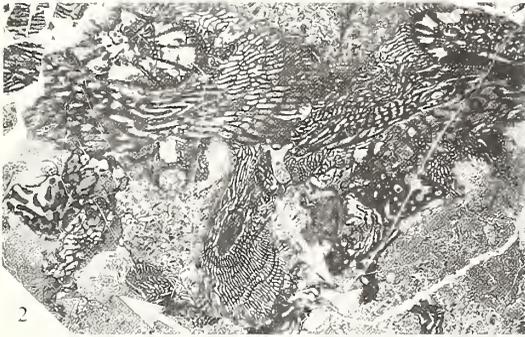
produced dense accumulations or crusts up to 5 mm thick. *Girvanella* formed encrusting sheets or rafts of intertwined microtubules. *Korilophyton*, *Angulocellularia*, *Chabakovia*, *Gordonophyton*, *Epiphyton* and *Tubomorphophyton* all formed dendritic colonies with bifurcating branches and micritic walls. Of these, *Gordonophyton* and *Chabakovia* were the most volumetrically important constituent in crypts (Pl. 2, fig. 4). *Epiphyton*, with short, compact branches (Pl. 1, fig. 3), and *Tubomorphophyton*, with hollow branches, were also common in crypts, whilst *Kordephyton*, which formed branches of radiating fine tubes, inhabited crypts but was generally a relatively uncommon component in Lower Cambrian bioherms.

The previously problematic form *Wetheredella*, noted in the Toyonian reefs of Labrador (Kobluk and James 1979), was suggested by Riding (1991) to be a calcified cyanobacterium. This has been confirmed by the finding of Recent analogues in the mildly alkaline crater lakes of Indonesia, where an identical form grows in crypts and crevices between foliaceous calcified red algae (Kaźmierczak and Kempe 1992). Other Lower Cambrian calcimicrobes noted to be cryptic have probably been misidentified. The calcimicrobe named *Serligia* noted in crypts from the Toyonian of Labrador (Kobluk and James 1979) is probably a fragment of *Botominella*. Likewise, the form *Cavifera* of Kobluk (1985) probably represents a coiled tube of *Obruchevella* sp. The form described by Myrow and Coniglio (1991) as *Frutexitis* sp. is referable to *Angulocellularia*, and was probably a weakly calcified cyanobacterium.

Kobluk and James (1979) noted that *Renalcis* and *Epiphyton*-group calcified cyanobacteria exhibited phenotypy, showing globular and compact morphologies when growing upright on open surfaces, but delicate branches in an arborescent mode in crypts (Table 3). We confirm this observation.

EXPLANATION OF PLATE 2

- Fig. 1. PIN 3848/704; a rich cryptic community within a crypt formed by the calcified cyanobacteria *Renalcis jacuticus* Korde (upper left) and *Epiphyton scapulum* Korde (upper right); the cyanobacterial shrubs have been encrusted by the coralomorph *Khasaktia vesicularis* Sayutina, and the archaeocyaths *Neoloculicyathus sibiricus* (Sundukov), *Dictyocyathus bobrovi* Korshunov, and *Erismacoscinus oymuranensis* A. Zhuravlev; pockets of micrite within the crypt have been extensively microburrowed; Locality 7 (Atdabanian 1); $\times 4$.
- Fig. 2. PIN 4221/51; cavity created by the abundant secondary skeleton of the archaeocyath *Anaptyctocyathus oppositus* (Gravestock) and encrusted by the same species, as well as *Dictyofavus araneosus* (Gravestock) and the calcarean sponge *Dodecaactinella cynodontota* Bengtson and Runnegar (arrowed); these cryptic forms were subsequently engulfed by the secondary skeleton of *A. oppositus*; Locality 14 (Atdabanian 3); $\times 5$.
- Fig. 3. PIN 4451/69; crypt formed under a calcified cyanobacterial colony encrusted by the chambered archaeocyath *Polythalamia perforata* (Vologdin), which was subsequently completely overgrown by *Clathricoscinus popovi* Vlasov; Cryptic *Cribricyathus* sp. is also present (right); Locality 22 (Botomian 1); $\times 10$.
- Fig. 4. PIN 3848/705; crypts formed by the calcified cyanobacterium *Gordonophyton durum* (Korde) encrusted by the archaeocyaths *Dictyocyathus bobrovi* Korshunov, *Ajacyathina* gen. et sp. indet. and the calcified cyanobacterium *Renalcis jacuticus* Korde; Locality 7 (Atdabanian 1); $\times 12$.
- Fig. 5. PIN 4451/91; a cryptic community of the chambered archaeocyaths *Capsulocyathus irregularis* (Zhuravleva), *Tylocyathus bullatus* (Zhuravleva), *Clathricoscinus popovi* Vlasov the cribricyath *Cribricyathus* sp. (top left and bottom right) and the calcified cyanobacterium *Tubomorphophyton* sp.; Locality 22 (Botomian 1); $\times 5$.
- Fig. 6. PIN 4451/92; small crypts within a cyanobacterial bioherm, colonized by tiny individuals of the archaeocyath *Altaicyathus notabilis* Vologdin (arrowed), a weakly calcified coralomorph (lower right), and *Epiphyton* sp. and *Renalcis* sp.; Locality 34 (Botomian 3); $\times 10$.
- Fig. 7. SM X24900; a cryptic individual of the coralomorph *Khasaktia intermedia* Sayutina, with an attached cryptic archaeocyath fauna of small individuals of *Alatacyathus jaroshevitschi* Zhuravleva (left), *Nochorocyathus changaiensis* (Vologdin) (centre) and juvenile cups of *Cambrocyathellus tuberculatus* (Vologdin); Locality 20 (Atdabanian 4); $\times 3$.



Coralomorphs. Early Cambrian calcified putative cnidarians, known as coralomorphs (Jell 1984), are represented by slender, irregular polygonal tubes or open cups and may occur as solitary individuals or small modular colonies (Zhuravlev *et al.* 1993). All forms were encrusting and many had extensive attachment areas.

Of the ten early Cambrian coralomorph genera, at least seven were known from crypts (Table 2). Five were solitary forms (*Cysticyathus*, *Khasaktia*, *Hydrocoonus*, *Aploconus* and *Tabulaconus*), with *Rackovskia* and *Labyrinthus* bearing a modular habit, although the biological affinity of the latter is uncertain (Kobluk 1979). The earliest coralomorph, *Cysticyathus*, was cryptic and appeared in the lower Tommotian. *Hydrocoonus* (appearing in the Tommotian 4), the branching form *Rackovskia* (Atdabanian 4) and *Labyrinthus* (Toyonian 1) were commonly cryptic, whereas *Khasaktia*, *Aploconus* and *Tabulaconus* were both open surface and cryptic dwellers (Pl. 2, fig. 7; Pl. 3, figs 1, 6).

Khasaktia is the only coralomorph to show phenotypy (Table 3). On open surfaces, it forms an extensive encrusting sheet, whereas in crypts it forms a conical, open cup originating from a small attachment site (Pl. 3, fig. 1).

Cribricyaths. Cribricyaths were simple, usually solitary, narrow, conical or horn-shaped calcareous tubes with a bilaterally symmetrical cross-section. Although common in Lower Cambrian reefal sequences they remain largely problematic (Jankauskas 1972). Cribricyaths were obligate and abundant cryptobionts (Pl. 1, fig. 5; Pl. 2, fig. 5), appearing first in the Atdabanian 1 and disappearing from the record in the Toyonian 1 (Table 2).

Siliceous sponges. Siliceous spicules of hexactinellid sponges first appeared in the Tommotian 1. Such spicules were common components of Lower Cambrian reefal sediments, and some crypts appear to be particularly enriched, perhaps representing disaggregated cryptobiontic sponges.

Calcarean sponges. Tor Herm, in the Australian Flinders Ranges (Locality 16; Atdabanian 4) yields an abundant encrusting sponge, described by Reitner (1992) as a pharetronid calcarean named *Gravestockia pharetroniensis*. The skeleton of this sponge, however, consists of triradiate spicules corresponding with the well known Cambrian form *Dodecaactinella*. This form is a common cryptobiont and often grew attached to the holdfast structures of cryptic archaeocyaths (Pl. 2, fig. 2; Pl. 3, fig. 2).

Problematica. Various Lower Cambrian problematica are known only from reefal crypts (Table 2) and many are described from only one locality. These include 'spherical algae' (Kobluk 1985), 'encrusting microfossils' and 'calcareous microspheres' (James and Gravestock 1990), *Archaeotrypa* (Kobluk 1984) and stenotheccoids.

Stenotheccoids became common in bioherms from the early Atdabanian onwards. They were asymmetrical, bivalved organisms with a sinuous alimentary canal, and may represent a separate phylum (Rozov 1984). Most of the brachiopods and brachiopod-like forms noted from Lower Cambrian crypts (Kobluk and James 1979; Kobluk 1985) are stenotheccoids, although brachiopods are indeed also rarely present. The 'globular foraminifera' identified by Kobluk (1985) are probably compartments of *Tarthinia*.

Uncalcified biota. There is evidence for the presence of soft-bodied, encrusting organisms within Lower Cambrian crypts. Distorted areas on the undersurfaces of archaeocyath skeletons are noted, but in the absence of any preserved attached biota (Pl. 3, fig. 3). These areas were subsequently bioimmured by calcified cryptobionts.

In addition, in Locality 19 (Atdabanian 4), cryptobionts are frequently surrounded by an extensive crystalline area which may represent the remains of uncalcified microbial or bacterial encrustations.

Vagrant cryptos

Microburrowing (?)metazoan. Developments of spar-filled tubular or fenestrate fabric which branch at irregular intervals with numerous blind side branches are extremely common within pockets of micrite in Lower Cambrian reefs, especially within crypts (Pl. 1, fig. 4; Pl. 2, fig. 1). The diameter of the tubes is 100–500 μm , and the burrows extend within archaeocyath intervalla and pore-spaces. These forms first appeared in the 'Nemakit-Daldynian' (R. A. Wood and P. D. Kruse, pers. obs.) and continued to be abundant throughout the Lower Cambrian (Table 2).

Similar fabrics have been described from syndepositional crypts in the Lower Cambrian bioherms of the Forteau Formation of Labrador (Kobluk and James 1979), from late Atdabanian buildups of western Mongolia (Wood *et al.* 1993) and from mid-Ordovician bioherms of the Chazy Group of eastern Canada (Pratt 1982; Desrochers and James 1989). Kobluk and James (1979) and Wood *et al.* (1993) suggested them to be the traces of deposit-feeding worms.

The presence of deposit feeders in crypts indicates, as noted by Kobluk and James (1979), that the crypt-infills were soft and that sediment accumulated while the crypts were still able to support life.

Macroburrows. Macroburrows developed in some micrite crypt infills, often beneath the attached cryptos, and may contain pockets packed with consolidated and cylindrical faecal pellets (Pl. 3, fig. 1). These burrows and pellets first appear in the Tommotian 2 (Table 2). Passive stowage of pellets within vacated regions of a burrow system is well known from the Recent and is generally attributed to the activity of infaunal worms (Schafer 1972). *Planolites*, *Torrowangea*, *Teichichnus*, *Paleophycus* and three unidentified traces have also been noted (Kobluk and James 1979) from the crypts of the Toyonian 1 bioherms of Labrador (Locality 36).

Endolithic cryptos

Borers. Kobluk (1981c) and Kobluk and James (1979) noted that although micro- and macroborers were present by the late Lower Cambrian (Toyonian 1), they had not invaded the cryptic habitat. In this study we have found possible evidence of bioerosion in the lowermost Tommotian reefs of Ulakhan-Sulugur (Locality 2). Here, probable borings are present on the walls and ceilings of crypts, and excavate lithified micrite as well as the cryptic biota of *Renaleis jacuticus* and *Archaeolynthus polaris* (Text-fig. 2B). The borings appear to have scalloped edges similar to modern sponge borings, but no excavated chips have been noted. Similar structures have been noted from Atdabanian 2 crypts (Locality 16), where the secondary skeleton of pendent archaeocyaths has been bioeroded (Pl. 3, fig. 5). This style of bioerosion has only been noted in crypts, and was clearly present in metazoan reefs from their inception.

Kobluk (1985) described sinuous microborings (14–20 μm diameter) from the Upper Shady Dolomite, Virginia. These borings show no evidence of branching, reproductive bodies or septation. Similar microborings have been ascribed to the endolithic cyanobacterium *Endoconchia* by Bengtson *et al.* (1990).

Fungi. The first cryptic fungi are noted in the Tommotian 2 (Locality 3), where a dense, cotton-like mass of long, slender, branched tubes (0.3–1.0 mm diameter) covers the undersurfaces of the disc-shaped archaeocyath *Okulitchicyathus discoformis* (Text-fig. 2C). The relatively large size and flattened morphology of these tubes exclude them from being boring bacteria. Their size and distinct septation suggest them to be the hyphae of fungi (ascomycetes or oomycetes).

ECOLOGY OF LOWER CAMBRIAN CRYPTS

Competition for space in Lower Cambrian reefs must have been severe to produce differentiated and distinct open surface and cryptic communities. This is confirmed by the observation that

cryptobionts commonly formed multiple overgrowths or chains of individuals in crypts (Pl. 1, fig. 5; Pl. 2, fig. 1), indicating that much of the crypt surface was covered with both calcified and non-calcified organisms. The small patches of hard substrate provided by pendent archaeocyaths may have been the only areas available for colonization by later generations of cryptobionts.

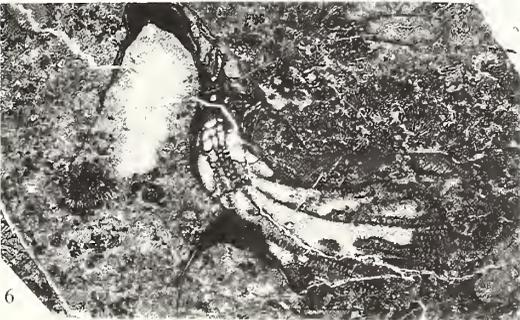
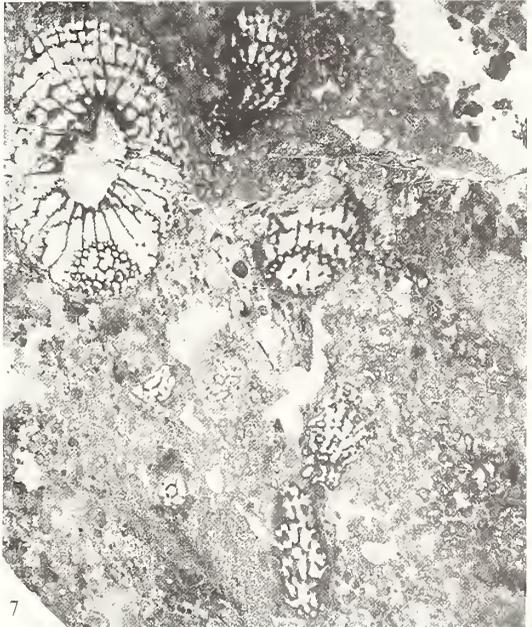
There is also evidence for encrustation of crypt-forming archaeocyaths during their life, as their calcareous skeletons show evidence of distortion in response to attached calcified and non-calcified cryptobionts (Pl. 3, fig. 3). The development of the cryptos was thus contemporary with framebuilder growth, and chains of pendent cryptobionts are also noted to have grown synchronously (Pl. 3, fig. 6).

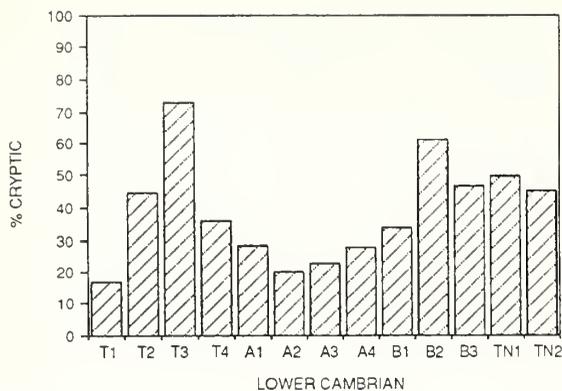
The apparent diversity and abundance of life in any one crypt appears to have been a function of overall community diversity, the size of the crypt and the length of time crypts were available for colonization. The zone-averaged diversity of archaeocyath species within the cryptos through the Lower Cambrian shows a marked decline from the Tommotian 2 onwards (Text-fig. 4B). When analysed, however, as a percentage of total community diversity, no such trend is apparent (Text-fig. 6); crypt diversity, at least as reflected by the richness of the archaeocyath fauna, appears to be broadly a function of overall community diversity.

Yet individual Lower Cambrian communities show a tremendous range of cryptobiont diversity, both within and between different communities. For example, the very dense bioherms formed by the calcified cyanobacterium *Razumovskia* in Eastern Sayan (Localities 11, 12 and 18) possess extremely small cryptic niches, and except for calcified cyanobacteria a cryptic biota was absent in spite of a rich open surface community of 20–45 archaeocyath species. In contrast, the large crypts formed during the mid–late Tommotian of Siberia (localities 3–5) housed a diverse and abundant cryptos. Although this phenomenon is difficult to quantify, large cavities contain more abundant biotas with higher diversities, and also show more examples of multiple overgrowths and chains of individuals (e.g. Pl. 1, fig. 5; Pl. 2, fig. 1).

EXPLANATION OF PLATE 3

- Fig. 1. PIN 3848/706; a secondary crypt formed by a cryptic individual of the coralomorph *Khasaktia vesicularis* Sayutina, which has been colonized by a further individual of the same coralomorph; the crypt was later infilled with micrite, which has subsequently been burrowed; some burrows show the stowage of faecal pellets; Locality 8 (Atdabanian 2); $\times 5$.
- Fig. 2. PIN 4221/52; a cryptic individual of the encrusting calcarean sponge *Dodecaactinella cynodontota* Bengtson and Runnegar forming a further crypt colonized by pendent *Ajacyathina* gen. et sp. indet. (left) and *Archaeocyathina* gen. et sp. indet. (right); the archaeocyath *Metaldetes ferulae* Gravestock and the calcified cyanobacterium *Chabakovia?* sp. are attached to the cup of *Archaeocyathina*; Locality 15 (Atdabanian 3); $\times 7$.
- Fig. 3. PIN 3848/707; distortions caused by the attachment of *Hydroconus* sp. (right) and uncalcified biota (arrowed) to the undersurface of the archaeocyath *Dictyosycon gravis* Zhuravleva; this fauna developed underneath the toppled cup of *Arturocyathus varlamovi* A. Zhuravlev and *Renalcis jacuticus* Korde; Locality 7 (Atdabanian 1); $\times 15$.
- Fig. 4. PIN 3848/708; a succession of cryptic, encrusting archaeocyath individuals *Neolocucyathus sibiricus* (Sundukov), and *Ajacyathina* gen. et sp. indet. (bottom), encrusted by the calcified cyanobacterium *Gordonophyton durum* (Korde) and *Renalcis jacuticus* Korde; Locality 7 (Atdabanian 1); $\times 15$.
- Fig. 5. PIN 4221/53; probable borings with scalloped edges, within a spicule-rich mud-infilled crypt inhabited by the archaeocyaths *Rozanovicoscinus stellatus* Gravestock and *Ajacyathina* gen. et sp. indet.; the boring has excavated both lithified micrite and the secondary skeleton of a pendent archaeocyath; Locality 16 (Atdabanian 4); $\times 12$.
- Fig. 6. PIN 4451/93; interacting cryptic growth of two cups of *Hydroconus* sp. and a solitary individual of the archaeocyath *Locucyathus tolli* Vologdin; Locality 23 (Botomian 1); $\times 5$.
- Fig. 7. PIN 3848/709; abundant individuals of the chambered form *Cellicyathus* sp. within an individual crypt; Locality 33 (Botomian 3); $\times 10$.





TEXT-FIG. 6. The percentage of cryptic species within the total bioherm community through the Lower Cambrian. Community proportions are averaged for each stage.

Although the total diversity of cryptic archaeocyaths may be high for any one community, individual crypts, especially those of limited size, were often dominated by a limited number of species (e.g. Pl. 3, fig. 7). This suggests that, as on open surfaces, crypts were colonized rapidly by a limited number of larval spat falls.

On modern hard substrates, solitary organisms are poor space competitors as they generally have small areas of attachment and lack specific competition mechanisms (Jackson 1977, 1985; Hughes 1989). They appear to be more dependent upon disturbance processes to provide suitable sites for settlement and growth than modular organisms. Small size, rapid growth rates and short generation times favour generalist, opportunist or fugitive life strategies (Jackson 1977). However, many solitary species occur throughout a wide range of modern cryptic habitats, whereas most modular forms, especially the best competitors for space, are more limited in the range of depths and substrates that they occupy (Jackson 1977).

In Jamaica, modern foliaceous coral undersurfaces routinely survive tens to hundreds of years (Hughes and Jackson 1980) and are dominated by dense growths of clonal animals and plants (Jackson 1977; Jackson and Winston, 1982). In contrast, shorter-lived substrates, such as *Pinna* shells, are sparsely colonized by scattered serpulids and bryozoans. Jackson (1985) thus proposed that the ratio of modular to solitary species is a function of substrate longevity and, indeed, studies on community development in modern reefal crypts (e.g. Choi 1984) demonstrate that over time an ecological succession takes place from solitary, generalist forms to modular, encrusting organisms.

No such succession has been noted in Lower Cambrian crypts. Lower Cambrian cryptic systems seem to have been dominated by organisms with solitary organizations, be they archaeocyaths, cribriocyaths or coralomorphs, often together with multiple generations of calcified cyanobacterial colonization. Solitary archaeocyaths, which were out-competed by the larger, branching forms on the open surface, were competitively superior in crypts. Although the modular species *Altaicyathus notabilis*, *Dictyofavus araneosus* and *Zunyicyathus* sp. can be abundant in crypts, they were often engulfed by the extensive growth of the secondary tissue of solitary forms (Pl. 2, fig. 2). Modular soft-bodied forms such as siliceous sponges may, however, have been very important competitors in Lower Cambrian crypts.

The continued dominance of solitary archaeocyaths within crypts throughout the Lower Cambrian is especially noteworthy as modular archaeocyaths became increasingly available during this period (Wood *et al.* 1992a). This, together with the limited number of species present within any one crypt, might suggest that Lower Cambrian crypts were short-lived structures compared with modern reefal crypts, and may have suffered frequent disturbance.

These ecological observations are supported by the fact that cryptobionts are noted to grow against and be distorted by the precipitation of syndimentary cements (Text-fig. 2A). Such cements would have grown rapidly, and would have reduced markedly the size of the cavities as well as leading eventually to the total occlusion of crypt openings.

Although it is difficult to quantify the longevity of individual Lower Cambrian bioherms and their crypts, the small size and dominant solitary to low integration organizations of the framebuilding metazoans (archaeocyaths, radiocyaths and coralomorphs) also suggests that they were relatively short-lived communities (Wood *et al.* 1993). Both Lower Cambrian crypts and their occupants were small compared with modern examples. Modern reef cavities may be vast, and will contain cryptobionts exhibiting a considerable range of sizes. The Lower Cambrian reef ecosystem was thus markedly different from its modern counterpart, with the rapid establishment of an aggregating open surface community of heterotrophs and phototrophs and an attendant cryptos with short generation times, in areas of relative environmental instability (Wood *et al.* 1992a; Wood 1993).

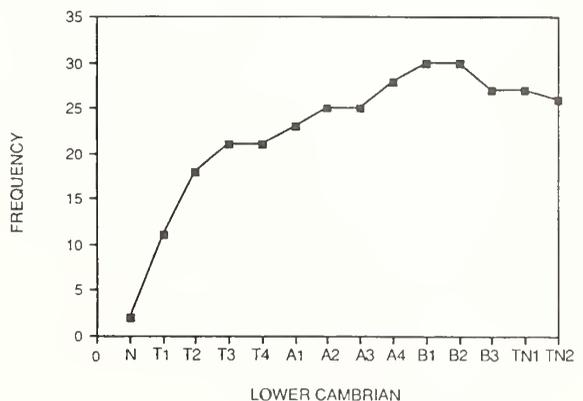
DEVELOPMENT OF THE CRYPTOS THROUGH THE LOWER CAMBRIAN

As predicted by Kobluk and James (1979) cryptobionts were present in the earliest Phanerozoic reefs, in buildups from the 'Nemakit-Daldynian'. In these bioherms, the calcified cyanobacteria *Korilophyton* was present as both upright bushes and as pendent, cryptic colonies. *Angulocellularia* is also known from crypts within stromatolites of this age. Other cryptobiontic calcified cyanobacteria appeared at various times during the Lower Cambrian (Table 2). The first appearance of many of these forms in crypts probably coincides with their first occurrence in the fossil record.

The first probable Phanerozoic cryptic metazoan was a microburrowing organism, which appeared in the 'Nemakit-Daldynian' (R. A. Wood and P. D. Kruse, pers. obs.). Unidentified probable boring organisms and archaeocyath sponges appeared in cryptic niches in the Tommotian 1, and continued to be present throughout the Lower Cambrian (Table 2 and Appendix). All communities studied show irregular archaeocyathids to be proportionally more represented in crypts than regular ajacicyathids (Text-figs 4–5). Phenotypic differentiation occurred in the Tommotian 3–4, when solitary *Archaeolyntus polaris* occupied crypts but a modular phenotype inhabited open surfaces. With the exception of the unidentified borer, obligate cryptobionts did not appear until later in the Lower Cambrian. Cribricyaths appeared in the Atdabanian 1, and obligate cryptic archaeocyaths appeared from the Atbadanian 4 to Botomian 1. All obligate archaeocyaths, including the chambered archaeocyaths, *Polythalamia* spp., possessed encrusting morphologies with large attachment sites.

All large Lower Cambrian cryptic niches were constructed by calcified metazoans, so the appearance of archaeocyaths at the base of the Tommotian vastly increased the size of cryptic niches within reefal buildups. The total diversity of the cryptos follows that of most Lower Cambrian reef-dwelling groups, echoing the general increase in diversity from the Tommotian until the mid-late Botomian mass extinction, and the subsequent decline thereafter (Text-fig. 7). Cribricyaths,

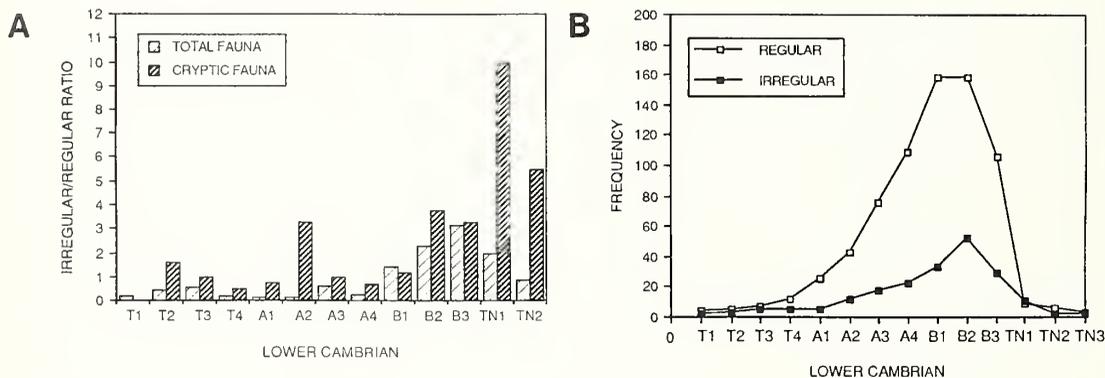
TEXT-FIG. 7. Diversity of cryptobionts through the Lower Cambrian.



together with many coralomorphs (*Khasaktia*, *Hydroconus*, *Rackovskia*, *Aploconus* and *Tabulaconus*) and archaeocyath orders (Monocyathida, Khasachstanicyathida, Coscinocyathida and Tabulacyathida), were lost during this extinction event, suggesting a major community reorganization after this time. Indeed, only calcified cyanobacteria, together with archaeocyathid and ajacicyathid archaeocyaths survived to populate Toyonian crypts.

As a function of total community diversity, the number of cryptic archaeocyath species is relatively constant through much of the Lower Cambrian (Text-fig. 6), but is noticeably low during the middle-late Toyonian. This might be explained by the increased proportion of large, branching, open surface-dwelling archaeocyaths (Wood *et al.* 1992a) and the reduction of coscinocyathids during this interval. In addition, there was a proliferation of dense *Epiphyton/Gordonophyton* bioherms which did not generally provide large crypts. The Toyonian 1 bioherms of Labrador (Locality 36) were an exception to this, as they were built mainly by *Angulocellularia* and *Renalcis* cyanobacteria. These reefs contained large primary crypts, where a rich cryptobionta with four archaeocyath species has been noted.

Interestingly, the proportion of regular to irregular cryptic species, whilst low for most of the lower Cambrian, increased during the Botomian to reach a peak in Botomian 3 (Text-fig. 8A). This



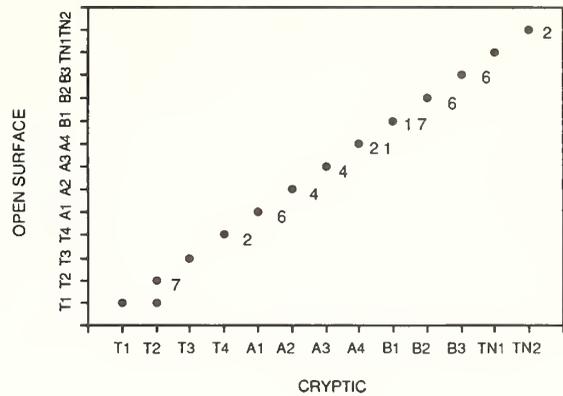
TEXT-FIG. 8. A, Proportion of irregular:regular archaeocyath species present in cryptos of any one bioherm community, through the Lower Cambrian. Community proportions are averaged for each stage. B, Diversity of regulars and irregular archaeocyath genera through the Lower Cambrian (modified from Wood *et al.* 1992a).

reflects the marked increase in global diversity of regulars at that time (Text-fig. 8B). Likewise, the proportion of cryptic irregulars increased markedly in the middle-late Toyonian, following the rapid decline of regulars but continued survival of irregular forms.

TIMING OF CRYPTIC NICHE INVASION

To test the competing hypotheses of cryptic niches as 'safe havens' or 'brood pouches', we have determined the timing to the nearest sub-zone of the first appearance of archaeocyath species in open surface and in cryptic niches (Text-fig. 9). When the first appearance of cryptic species is compared with their first known occurrence, it is clear that, at this temporal resolution, the vast majority of forms appeared simultaneously in both habitats. Many organisms in the Lower

TEXT-FIG. 9. The timing of first appearance of cryptic archaeocyath species on open surface and in cryptic niches. Numbers indicate the number of data points.



Cambrian, however, appeared first in and remained unique to crypts, and there is no evidence of subsequent radiation to the open surface.

If Lower Cambrian reefal communities and hence crypts were short-lived, they offer scant comparison with the long-lived modern reefal caves and grottoes which are known to house organisms up to 1000 years old (Willenz and Hartman 1987). Although few data are yet available, it appears that some of those modern calcified demosponges currently found in crypts have always occupied such niches, and that it is their open surface-dwelling relatives which have been preferentially removed during extinction events (Reitner and Engeser 1987; Wood 1990). There may have been no migration from the open surface to crypts.

Occupation of cryptic niches certainly did not appear to confer preferential survival upon Lower Cambrian cryptobionts. Many common and obligate cryptobiontic metazoans (cribricyaths, some archaeocyaths, and many coralomorphs) perished during the Botomian extinction event (Table 2).

DISCUSSION

The Lower Cambrian reefal cryptos was well developed, and contained a diverse and distinct biota. Apart from a surprising number of obligate cryptobionts (e.g. *Chabakovia*, cribricyaths, some archaeocyaths, infaunal worms and various problematica), one of the most species-rich Lower Cambrian groups, the Archaeocyatha, differentiated early in its history into systematically and ecologically distinctive open surface and cryptic communities. Whilst open surface framebuilders were predominantly branching, irregular forms (Wood *et al.* 1992a), small, solitary irregular archaeocyaths and regulars with chambered (thalamid) organizations were abundant cryptobionts. Like modular forms, only archaeocyaths with porous septa occurred as cryptobionts. Competition for space was intense in Lower Cambrian reefal ecosystems, and crypts housed much of the total reefal diversity.

Cryptic niches offered an alternative habitat of reduced environmental stress. Irradiation and predation do not appear to have been important factors in the Cambrian as they are in Recent reefal crypts. Calcified cyanobacteria were equally abundant in both open surface and cryptic niches, and likewise, except for boring, no evidence of predation of the calcified benthos has been noted in Lower Cambrian reef ecosystems. Reduced hydrodynamic energy would also appear to have characterized the Lower Cambrian crypt.

Lower Cambrian reefs were probably short-lived communities which had little inherent stability without extensive early lithification (Wood *et al.* 1993). The volume of cryptic surface area was variable in Lower Cambrian reefs, and was determined by the individual size of the dominant framebuilders. The size of framebuilders not only determined the size of the crypts, but also the

length of time the crypts were available for colonization; large, relatively stable and long-lived calcified metazoans such as radiocyaths display noticeably more diverse and abundant cryptic biotas than niches formed under small, more fragile forms. Lower Cambrian crypts and their occupants, however, were far smaller than modern examples.

The short-lived nature of many Lower Cambrian crypts compared with modern reefs may explain the dominance of a fauna where solitary organizations were favoured, with often a limited number of species within individual crypts. The rapid growth of synsedimentary cements in crypts may have further reduced the time available for both colonization and growth of the cryptos. Crypts are dominated by rapidly establishing organisms, often with small attachment areas. Solitary forms dominated throughout the Lower Cambrian, which is especially noteworthy within the Archaeocyatha as modular forms became increasingly available (Wood *et al.* 1992a). Forms with encrusting bases appeared in the mid-Lower Cambrian, and several are noted to be obligate cryptobionts.

Chambered sponges appear to have inhabited commonly a cryptic niche through the Palaeozoic. We note that Ordovician sphinctozoans from Koryakia in Russia, and some Silurian aphrosalpingids (which resemble chambered archaeocyaths) from Alaska and the Urals, were common cryptobionts. In addition, Permian sphinctozoans from the Capitan Reef, Texas and New Mexico occupied more commonly cryptic niches than open surface habitats (Wood *et al.* 1994). This hints that several groups of Palaeozoic chambered calcified sponges, previously interpreted as erect reef framebuilders, may in fact have been preferential cryptic dwellers for much of their long history. Chambered calcified sponges exhibit predominantly solitary and low integration, branching morphologies with small attachment sites. Such organizations conferred better competitive abilities within crypts than on open surfaces, where they would have been out-competed by high integration, encrusting organisms with an ability to occupy and cover rapidly new substrate.

CONCLUSIONS

1. Lower Cambrian reefal cryptic communities were surprisingly diverse with archaeocyath sponges, calcified cyanobacteria and a microburrowing (?)metazoan being the most ubiquitous and abundant elements. Putative primitive cnidarians, spiculate sponges and various problematica were also common crypt dwellers.
2. Archaeocyaths differentiated in the late Tommotian into distinct open surface and crypt dwellers. Open surfaces were dominated by solitary ajacicyathids and irregulars with modular, branching organizations, crypts preferentially housed solitary irregulars (archaeocyathids) and solitary chambered forms (coscincyathids and kazachstanicyathids).
3. *Zunyicyathus* sp., *Dictyofavus* spp., *Altaicyathus notabilis*, *Polythalamia americana* and *P. perforata* were obligate cryptobionts, as were the calcified cyanobacteria *Chabakovia* spp. and all cribricyaths. Infaunal deposit-feeding (?)worms and probable borings, possibly made by sponges, have also been noted only in crypts and were present in metazoan reefs from their inception.
4. Lower Cambrian crypts housed a substantial proportion of the total biotic diversity of early reefs. Cryptic communities were composed of solitary, pioneering organisms and unlike modern reefs displayed no evidence of succession. This may be a result of the small size and short-lived nature of both the crypts and their occupants. Lower Cambrian crypts were the sites of extensive synsedimentary cementation, supporting the conjecture that crypts did not remain open for long before partial or total occlusion. Small, solitary archaeocyaths dominated crypts throughout the Lower Cambrian, even though modular forms became increasingly available during this period.
5. There is ample evidence of a soft-bodied cryptos and of intense competition for space, as organisms commonly form multiple overgrowths or chains of individuals.
6. On a sub-zone scale, the vast majority of archaeocyath species appeared simultaneously in both open surface and cryptic niches, suggesting that Lower Cambrian crypts did not serve either as 'safe havens' harbouring formerly open surface inhabitants or as 'brood pouches' of evolutionary innovation.

7. Several groups of Palaeozoic chambered calcified sponges, previously interpreted as erect reef framebuilders, may in fact have been preferential cryptic dwellers for much of their long history.

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REFERENCES

- BENGTSON, S., CONWAY MORRIS, S., COOPER, B. J., JELL, P. A. and RUNNEGAR, B. N. 1990. Early Cambrian fossils from South Australia. *Memoirs of the Association of Australasian Palaeontologists*, **9**, 1–364.
- BOWRING, S. A., GROTZINGER, J. P., ISACHSEN, C. E., KNOLL, A. H., PELECHATY, S. M. and KOLOSOV, P. 1993. Calibrating rates of early Cambrian evolution. *Science*, **261**, 1293–1298.
- BRASIER, M. D. 1976. Early Cambrian intergrowth of archaeocyathids, *Renalcis*, and pseudostromatolites from South Australia. *Palaeontology*, **19**, 233–345.
- CHOI, D. R. 1984. Ecological succession of reef-cavity dwellers (coelobites) in coral rubble. *Bulletin of Marine Science*, **35**, 72–79.
- and GINSBURG, R. N. 1983. Distribution of coelobites (cavity-dwellers) in coral rubble across the Florida reef tract. *Coral Reefs*, **2**, 165–172.
- DEBRENNE, F. and ZHURAVLEV, A. Yu. 1992. *Irregular archaeocyaths: morphology, ontogeny, systematics, biostratigraphy, palaeoecology*. Cahiers de Paléontologie. CNRS Editions, Paris, 212 pp.
- DESROCHERS, A. and JAMES, N. P. 1989. Middle Ordovician (Chazyan) bioherms and biostromes of the Mingan Islands, Quebec. 183–191. In GELDSETZER, H. H., JAMES, N. P. and TEBBUTT, G. E. (eds). *Reefs, Canada and adjacent area. Memoirs of the Canadian Society of Petroleum Geologists*, **13**, 1–775.
- FRÖHLER, M. and BECHSTÄDT, T. 1992. Calcimicrobial-archaeocyathan buildups at the instable northwestern platform margin of the Lower Cambrian Gonnesa Formation, SW-Sardinia (Italy), *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte*, **1992**, 267–278.
- HART, S. F. 1992. Archaeocyath paleoecology. 122. In LIDGARD, S. and CRANE, P. R. (eds). Fifth North American Paleontological Convention, Abstracts and Program. *Paleontological Society Special Volume*, **6**, 1–329.
- HOFMANN, H. J. and GROTZINGER, J. P. 1985. Shelf-facies microbiotas from the Odjick and Rocknest formations (Epworth Group: 1.89 Ga), northwestern Canada. *Canadian Journal of Earth Sciences*, **22**, 1781–1792.
- HUGHES, R. N. 1989. *A functional biology of clonal animals*. Chapman and Hall, London and New York, 331 pp.
- HUGHES, T. P. and JACKSON, J. B. C. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission and fusion. *Science*, **209**, 713–715.
- JACKSON, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *American Naturalist*, **111**, 743–767.
- 1985. Distribution and ecology of clonal and aclonal benthic invertebrates. 297–355. In JACKSON, J. B. C., BUSS, L. W. and COOK, R. E. (eds). *Population biology and evolution of clonal organisms*. Yale University Press, New Haven, 530 pp.
- and BUSS, L. 1975. Allelopathy and spatial competition among coral reef invertebrates. *Proceedings of the National Academy of Science*, **72**, 5160–5163.
- GOREAU, T. F. and HARTMAN, W. D. 1971. Recent brachiopod coralline sponge communities and their paleontological significance. *Science*, **173**, 623–625.
- and WINSTON, J. E. 1982. Ecology of cryptic coral reef communities. 1. Distribution and abundance of major groups of encrusting organisms. *Journal of Experimental Marine Biology and Ecology*, **57**, 135–147.
- JAMES, N. P., GINSBURG, R. N., MARSZALEK, D. S. and CHOQUETTE, P. W. 1976. Facies and fabric specificity of early subsea cements in shallow Belize (British Honduras) reefs. *Journal of Sedimentary Petrology*, **46**, 523–544.
- and GRAVESTOCK, D. I. 1990. Lower Cambrian shelf and shelf-margin buildups, Flinders Ranges, South Australia. *Sedimentology*, **37**, 455–480.

- JANKAUSKAS, T. V. 1972. Cribricyaths of the Lower Cambrian of Siberia. 161–183. In ZHURAVLEVA, I. T. (ed.). *Problems of Lower Cambrian biostratigraphy and palaeontology of Siberia*. Nauka, Moscow, 292 pp. [In Russian].
- JELL, J. S. 1984. Cambrian cnidarians with mineralized skeletons. 105–109. In OLIVER, W. A., JR, SANDO, W. J., CAIRNS, S. D., COATES, A. G., MACINTYRE, I. G., BAYER, F. M. and SORAUF, J. E. (eds). Recent advances in the paleobiology and geology of the Cnidaria. *Paleontographica Americana*, **54**, 557 pp.
- KAZMIERCZAK, J. and KEMPE, S. 1992. Recent cyanobacterial counterparts of Palaeozoic *Wetheredella* and related problematic fossils. *Palaios*, **7**, 294–304.
- KOBLUK, D. R. 1979. A new and unusual skeletal organism from the Lower Cambrian of Labrador. *Canadian Journal of Earth Sciences*, **16**, 2040–2045.
- 1981a. The record of cavity-dwelling (coelobiontic) organisms in the Paleozoic. *Canadian Journal of Earth Sciences*, **18**, 181–190.
- 1981b. Earliest cavity-dwelling organisms (coelobionts), Lower Cambrian Poleta Formation, Nevada. *Canadian Journal of Earth Sciences*, **18**, 669–679.
- 1981c. Lower Cambrian cavity-dwelling endolithic (boring) sponges. *Canadian Journal of Earth Sciences*, **18**, 972–980.
- 1984. *Archaeotrypa* Fritz, 1947 (Cambrian, Problematica) reinterpreted. *Canadian Journal of Earth Sciences*, **21**, 1343–1348.
- 1985. Biota preserved within cavities in Cambrian *Epiphyton* mounds, Upper Shady Dolomite, southwestern Virginia. *Journal of Paleontology*, **59**, 1158–1172.
- 1988. Cryptic fauna in reefs: ecology and geologic importance. *Palaios*, **3**, 379–390.
- and JAMES, N. P. 1979. Lower Cambrian cavity-dwelling organisms in archaeocyathid patch reefs from southern Labrador. *Lethaia*, **12**, 193–218.
- KRUSE, P. D., ZHURAVLEV, A. Yu. and JAMES, N. P. in press. Primordial metazoan and calcimicrobe reefs: Tommotian (early Cambrian) of the Siberian Platform. *Palaios*.
- MANSY, J.-L., DEBRENNE, F. and ZHURAVLEV, A. Yu. 1993. Calcaires à archéocyathes du Cambrien inférieur du Nord de la Colombie britannique (Canada). Implications paléogéographiques et précisions sur l'extension du continent Américano-Koryakien. *Géobios*, **26**, 643–683.
- MYROW, P. M. and CONIGLIO, M. 1991. Origin and diagenesis of cryptobiontic *Frutexites* in the Chapel Island Formation (Vendian to Early Cambrian) of southeast Newfoundland, Canada. *Palaios*, **6**, 572–585.
- OSADCHAJA, D. V., KASHINA, L. N., ZHURAVLEVA, I. T. and BORODINA, N. P. 1979. *Stratigrafiya i arkheotsiati nizhnego kembriya Altae-Sayanskoy skladchatoy oblasti*. [Stratigraphy and archaeocyaths of the Lower Cambrian of the Altay-Sayan Fold Belt]. Nauka, Moscow, 216 pp. [In Russian].
- PRATT, B. R. 1982. Stromatolite framework of carbonate mud mounds. *Journal of Sedimentary Petrology*, **52**, 1203–1227.
- REES, M. N., PRATT, B. R. and ROWELL, A. J. 1989. Early Cambrian reef complexes and associated lithofacies of the Shackleton Limestone, Transantarctic Mountains. *Sedimentology*, **36**, 341–361.
- REITNER, J. 1992. "Coralline Spongien" Der Versuch einer phylogenetisch-taxonomischen Analyse. *Berliner Geowissenschaft Abhandlungen Series E*, **1**, 1–352.
- REITNER, J. and ENGESER, T. 1987. Skeletal structure and habitats of Recent and fossil *Acanthochaetetes* (Sclerospongiae, subclass Tetractinomorpha). *Coral Reefs*, **6**, 151–157.
- RIDING, R. 1991. Cambrian calcareous cyanobacteria and algae. 305–334. In RIDING, R. (ed.). *Calcareous algae and stromatolites*. Springer-Verlag, Berlin, 571 pp.
- ROZOV, S. N. 1984. Morphology, terminology and systematic affinity of stenothecoids. 117–133. In SOKOLOV, B. S. (ed.). *Problematics of the Palaeozoic and the Mesozoic*. Trudy Instituta geologii i geofiz Sibirsk ot Akademii nauk SSSR, 160 pp. [In Russian].
- SAVARESE, M. 1992. Functional analysis of archaeocyathan skeletal morphology and its paleobiological implications. *Paleobiology*, **18**, 464–480.
- SCHAFFER, W. 1972. *Ecology and paleoecology of marine environments*. University of Chicago Press, Chicago, 568 pp.
- TURNER, E. C., NARBONNE, G. M. and JAMES, N. P. 1993. Neoproterozoic reef microstructures from the Little Dal Group, northwestern Canada. *Geology*, **21**, 259–262.
- VERMEIJ, G. J. 1987. *Evolution and escalation*. Princeton University Press, Princeton, 527 pp.
- VORONIN, Yu. I., VORONOVA, L. G., GRIGOR'eva, N. V., DROZDOVA, N. A., ZHEGALLO, E. A., ZHURAVLEV, A. Yu., RAGOZINA, A. L., ROZANOV, A. Yu., SAYUTINA, T. A., SYSOEV, V. A. and FONIN, V. D. 1982. Granitsa dokembriya i kembriya v geosinklinal'nykh oblastyakh (opornyy razrez Salany-Gol, MNR). [The Precambrian/

- Cambrian boundary in the geosynclinal areas (the reference section of Salany-Gol, MPR)]. *Transactions of the Joint Soviet-Mongolian Palaeontological Expedition*, **18**, 152 pp. [In Russian].
- WILLENZ, F. and HARTMAN, W. D. 1987. Calcification rate of *Ceratoporella nicholsoni* (Porifera: Sclerospongiae): an *in situ* study with calceine. *Proceedings of the Fifth International Coral Reef Congress*, **5**, 113–118.
- WOOD, R. 1990. Reef-building sponges. *American Scientist*, **78**, 224–235.
- ZHURAVLEV, A. Yu. and DEBRENNE, F. 1992a. Functional biology and ecology of Archaeocyatha. *Palaios*, **7**, 131–156.
- EVANS, K. R. and ZHURAVLEV, A. Yu. 1992b. A new post early-Cambrian archaeocyath from Antarctica. *Geological Magazine*, **129**, 491–495.
- ZHURAVLEV, A. Yu. and TSEREN, ANAAZ, C. 1993. The ecology of Lower Cambrian buildups from Zuune Arts, Mongolia: implications for early metazoan reef evolution. *Sedimentology*, **40**, 829–858.
- WOOD, R., DICKSON, J. A. D. and KIRKLAND-GEORGE, B. 1994. Turning the Capitan reef upside down: a new appraisal of the ecology of the Permian Capitan Reef, Guadalupe Mountains, Texas and New Mexico. *Palaios*, **9**, 422–427.
- ZHURAVLEV, A. Yu. 1989. Poriferan aspects of archaeocyathan skeletal function. *Memoirs of the Association of Australasian Palaeontologists*, **8**, 387–399.
- DEBRENNE, F. and LAFUSTE, J. 1993. Early Cambrian microstructural diversification of Cnidaria. *Courier Forschungsinstitut Senckenberg*, **164**, 365–372.
- and GRAVESTOCK, D. I. 1994. Archaeocyaths from Yorke Peninsula, South Australia, and archaeocyathan early Cambrian zonation. *Alcheringa*, **18**, 1–54.
- ZHURAVLEVA, I. T., KORSHUNOV, V. I. and ROZANOV, A. Yu. 1969. Atdabanskiy yarus i ego obosnovanie po arkhheotsiatam v stratotipicheskom razreze. [The Atdabanian stage and its archaeocyathan framework in the stratotype section]. 5–59. In ZHURAVLEVA, I. T. (ed.). *Biostratigrafiya i paleontologiya nizhuego keubriya Sibiri i Dal'nego Vostoka*. Nauka, Moscow, 228 pp. [In Russian].
- MESHKOVA, N. P. and REPINA, L. N. 1976. Kembriy Sibiri i smezhnykh regionov. [Cambrian of Siberia and adjacent regions]. 19–30. In SOKOLOV, B. S. and ELKIN, V. A. (eds). *Dokembriy i paleozoy Sibiri i smezhnykh regionov*. Institut Geologii i Geofiziki, Sibirskoe Otdelenie, AN SSR, Novosibirsk, 40 pp. [In Russian].

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APPENDIX

Lower Cambrian reef communities studied, together with a listing of those archaeocyath species which appear in cryptic niches. The timing of their first appearance in the geological record is given: T: Tommotian; A: Atdabanian; B: Botomian; TN: Toyonian. Forms which are modular on the open surface and solitary in crypts are indicated by S, those which are modular in both niches are indicated by M, and those which bear only a modular phenotype are followed by MM. Obligate cryptobionts are shown in bold. (Aj): Ajacicyathida; (M): Monocyathida; (C): Coscinocyathida; (Ar): Archaeocyathida; (K): Kazachstaniyathida; (T): Tabulacyathida.

- | | |
|---|---|
| 1. Nemakit-Daldyn, Siberian Platform, Russia.
Age: Manykaian
no archaeocyaths | Age: T1, <i>sumnaginicus</i> Zone
T1 <i>Archaeolynthus polaris</i> (Vologdin) (M) |
| 2. Ulakhan-Sulugur, middle Aldan River, Siberian Platform, Russia. | 3. Titirikteekh Creek, middle Lena River, Siberian Platform, Russia.
Age: T2, <i>regularis</i> Zone, lower subzone |

- T1 *Cambrocyathellus tchuranicus* Zhuravleva S (Ar)
 T1 *Archaeolynthus polaris* (Vologdin) (M)
Nochoroicyathus spp. (2) (Aj)
 T2 *Cambrocyathellus proximus* (Fonin) M (Ar)
 T2 *Sakhacyathus subartus* (Zhuravleva) S (Ar)
 T2 *Dictyocyathus translucidus* Zhuravleva S (Ar)
 T2 *Spinocyathus maslemikova* Zhuravleva S (Ar)
4. Zhurinsky Mys, middle Lena River, Siberian Platform, Russia.
 Age: T2, *regularis* Zone, lower subzone
 T1 *Cambrocyathellus tchuranicus* Zhuravleva S (Ar)
 T1 *Archaeolynthus polaris* (Vologdin) S (M)
 T2 *Nochoroicyathus aldanicus* Zhuravleva (Aj)
Nochoroicyathus sp. (Aj)
 T2 *Rotundocyathus spinosus* (Zhuravleva) (Aj)
 T2 *Cambrocyathellus proximus* (Fonin) M (Ar)
 T2 *Sakhacyathus subartus* (Zhuravleva) S (Ar)
 T2 *Dictyocyathus translucidus* Zhuravleva S (Ar)
 T2 *Spinocyathus maslennikovae* Zhuravleva S (Ar)
 T2 *Okulitchicyathus discoformis* (Zhuravleva) (Ar)
5. Byd'yangaya Creek, middle Lena River, Siberian Platform, Russia.
 Age: T3, *regularis* Zone, upper subzone
 T1 *Cambrocyathellus tchuranicus* Zhuravleva S (Ar)
 T1 *Archaeolynthus polaris* (Vologdin) (M)
 T3 *Tumuliolynthus primigenius* Zhuravleva (M)
Nochoroicyathus sp. (Aj)
 T2 *Rotundocyathus spinosus* (Zhuravleva) (Ar)
 T2 *Sakhacyathus subartus* (Zhuravleva) S (Ar)
 T2 *Okulitchicyathus discoformis* (Zhuravleva) (Ar)
 T2 *Dictyocyathus translucidus* Zhuravleva S (Ar)
6. Byd'yangaya Creek, middle Lena River, Siberian Platform, Russia.
 Age: T4, *lenaicus-primigenius* Zone
 T1 *Archaeolynthus polaris* (Vologdin) (M)
 T3 *Tumuliolynthus primigenius* Zhuravleva (M)
 T4 *Nochoroicyathus mirabilis* Zhuravleva (Aj)
 T4 *Nochoroicyathus ridiculus* Rozanov (Aj)
 T2 *Okulitchicyathus discoformis* (Zhuravleva) (Ar)
 T2 *Dictyocyathus translucidus* Zhuravleva S (Ar)
7. Oymuran village, middle Lena River, Siberian Platform, Russia.
 Age: A1, *zegebarti* Zone
 T1 *Archaeolynthus polaris* (Vologdin) (M)
 A1 *Nochoroicyathus anabarensis* (Vologdin) (Aj)
- A1 *Rotundocyathus biohermicus* (Zhuravleva) (Aj)
 A1 *Erisnacoscinus oymuranensis* A. Zhuravlev (Aj)
 A1 *Dictyocyathus bobrovi* Korshunov S (Ar)
 A1 *Dictyosycon gravis* Zhuravleva (Ar)
 A1 *Neoloculicyathus sibiricus* (Sundukov) (Ar)
8. Zhurinsky Mys, middle Lena River, Siberian Platform, Russia.
 Age: A2, *pinus* Zone
 A1 *Dictyocyathus bobrovi* Korshunov S (Ar)
 A1 *Neoloculicyathus sibiricus* (Sundukov) (Ar)
9. Achchagy-Kyyry-Taas, middle Lena River, Siberian Platform, Russia.
 Age: A2, *pinus* Zone
 A2 *Geocyathus latini* (Zhuravleva) (Aj)
 A2 *Coscinoicyathus isointervallumus* Zhuravleva (C)
10. Achchagy-Tuoydakh, middle Lena River, Siberian Platform, Russia.
 Age: A2, *pinus* Zone
 A2 *Fansyicyathus lemontovae* Korshunov and Rozanov (Aj)
 A2 *Coscinoicyathus isointervallumus* Zhuravleva (C)
11. Bazaikha River, Eastern Sayan, Russia.
 Age: A2, *howelli* Zone
Neoloculicyathus sp. (Ar)
Dictyocyathus sp. (Ar)
Archaeopharetra sp. (Ar)
Capsulocyathus sp. (C)
12. Bazaikha River, Eastern Sayan, Russia.
 Age: A3, *cyroflexus* Zone
 no archaeocyaths
13. Bachyk Creek, middle Lena River, Siberian Platform, Russia.
 Age: A3, *kokoulini* Zone
 A2 *Geocyathus latini* (Zhuravleva) (Aj)
 A2 *Coscinoicyathus isointervallumus* Zhuravleva (C)
14. Horse Gully, Yorke Peninsula, Australia.
 Age: A3, *tenius* Zone
 A3 *Anaptyctocyathus oppositus* (Gravestock) (Ar)
 A3 *Dictyofavus araneosus* Gravestock MM (Ar)
15. Section G, Wilkawillina Gorge, Flinders Ranges, Australia.
 Age: A3, *tenius* Zone
 A3 *Dictyofavus araneosus* (Gravestock) MM (Ar)

- A3 *Metaldetes fernlae* Gravestock S (Ar)
Ajacicathida gen. and sp. indet. (Aj)
Archaeocyathida gen. and sp. indet. (Ar)
16. Tor Herm, Section N, Mount Scott Range, Australia.
Age: A4, *tardus* Zone
A4 *Metaldetes gracilis* Gravestock S (Ar)
A4 *Erugatocyathus tatei* Gravestock (Aj)
A4 *Gordonicyathus levis* Gravestock (Aj)
A4 *Rozanovicoscinus stellatus* Gravestock (Aj)
A4 *Okulitchicyathus ?amplis* (Gravestock) (Aj)
17. Bachyk Creek, middle Lena River, Siberian Platform, Russia.
Age: A4, *lemontovae* Zone
A3 *Geocyathus latini* (Zhuravleva) (Aj)
A4 *Coscinoocyathus marocanoides* Zhuravleva (C)
18. Bazaikha River, Eastern Sayan, Russia.
Age: A4, *borisovi* Zone
no archaeocyaths
19. Zuune Arts Mount, Tsagaan Olom Depression, Mongolia.
Age: A4, *jaroshevitschi-bidzhaensis-subtilis* Beds
A4 *Nochoroicyathus changaiensis* (Vologdin) (Aj)
A4 *Rotundocyathus levigatus* (Vologdin) (Aj)
A4 *Cambrocyathellus tuberculatus* (Vologdin) S (Ar)
A4 *Cambrocyathellus pannonicus* (Fonin) S (Ar)
Okulitchicyathus sp. (Ar)
Archaeopharetra sp. S (Ar)
20. Salaany Gol, Tsagaan Olom Depression, Mongolia.
Age: A4, *jaroshevitschi-bidzhaensis-subtilis* Beds
A4 *Archaeolynthus solidimurus* (Vologdin) (M)
A4 *Nochoroicyathus changaiensis* (Vologdin) (Aj)
A4 *Nochoroicyathus howelli* (Vologdin) (Aj)
A4 *Cambrocyathellus tuberculatus* (Vologdin) M (Ar)
A4 *Cambrocyathellus pannonicus* (Fonin) S (Ar)
A4 *Archaeopharetra marginata* (Fonin) S (Ar)
A4 *Tabulacyathellus bidzhaensis* Missarzhevsky (Ar)
A4 *Alataucyathus jaroshevitchi* Zhuravleva (C)
A4 *Chouberticyathus lepidus* (Fonin) S (Ar)
A4 *Tumuliolynthus karakolensis* Zhuravleva (M)
21. Sukhie Solontsi Valley, Azyrtal Ridge, Kuznetsky Alatau, Russia.
Age: A4, *borisovi* Zone
A4 *Archaeolynthus aequiporosus* (Vologdin) (M)
A4 *Erismaoscinnus* sp. (Aj)
A4 *Tumuliolynthus antiquus* (Vologdin) (Ar)
- A4 *Tabulacyathellus bidzhaensis* Missarzhevsky (M)
A4 *Nochoroicyathus certus* (Voronin) (C)
22. Sukhie Solontsi Valley, Azyrtal Ridge, Kuznetsky Alatau, Russia.
Age: B1, *Clathricoscinus* Zone
B1 *Capsulocyathus irregularis* (Zhuravleva) (C)
B1 *Clathricoscinus popovi* Vlasov (C)
B1 *Polythalamia perforata* (Vologdin) (C)
Coscinoocyathus sp. (C)
B1 *Loculicyathus tolli* Vologdin (Ar)
B1 *Archaeolynthus cipis* (Vologdin) (M)
B1 *Tylocyathus bullatus* (Zhuravleva) (C)
23. Bazaikha River, Eastern Sayan, Russia.
Age: B1, *Clathricoscinus* Zone
B1 *Capsulocyathus subcallosus* Zhuravleva (C)
B1 *Loculicyathus tolli* Vologdin (Ar)
24. Seer'Nuur Lake, Ozernaya Province, Mongolia.
Age: B2, (2038–2043)
B1 *Archaeolynthus solidimurus* (Vologdin) (M)
B1 *Capsulocyathus subcallosus* Zhuravleva (C)
B1 *Clathricoscinus dentatus* (Vologdin) (C)
Archaeopharetra? sp. (Ar)
25. Kuragan-Sakmara Province, South Urals, Russia.
Age: B1
Tumuliolynthus sp. (M)
Dokidocyathus sp. (Aj)
Chouberticyathus sp. (Ar)
B1 *Erismaoscinnus bedfordi* (Vologdin) (Aj)
B1 *Capsulocyathus nalivkini* (Vologdin) (C)
B1 *Spirocyathella kyzylartauense* Vologdin (Ar)
26. Section 24b, Mackenzie Mountains, Canada.
Age: B1, *whitneyi-nahanniensis* Zone
B1 *Robertiolynthus handfieldi* A. Zhuravlev (M)
B1 *Sekwicyathus nahanniensis* Handfield (Aj)
B1 *Acanthopyrgus yukonesis* Handfield (C)
B1 *Protopharetra jimensis* A. Zhuravlev S (Ar)
B1 *Fenestrocyathus complexus* Handfield (Ar)
B1 *Archaeosycon pustulatus* (Debrenne and Gangloff) S (Ar)
Zunyicyathus? sp. MM (Ar)
27. Section 24b, Mackenzie Mountains, Canada.
Age: B2, *fritzi-caribouensis* Zone
B2 *Clarusoscinnus fritzi* (Handfield) S (Ar)
B2 *Markocyathus clementensis* Debrenne (Ar)
Zunyicyathus? sp. MM (Ar)
B2 *Archaeocyathus arborensis* Okulitch S (Ar)
28. GSC 91690, Mackenzie Mountains, Canada.
Age: B2, *fritzi-caribouensis* Zone
B1 *Robertiolynthus handfieldi* A. Zhuravlev (M)

- B1 *Fenestrocycyathus complexus* Handfield (Ar)
 B2 *Clathricoscinus fritzi* (Handfield) S (Ar)
29. Nevada, USA.
 Age: B2, *fritzi-caribouensis* Zone
 B2 *Keriocycyathus arachnais* Debrenne and Gangloff (Ar)
 B2 *Arrhythmocricus macdamensis* (Handfield) S (Ar)
 B2 *Polythalamia americana* Debrenne and Wood (C)
30. Wirrealpa Mine, Flinders Range, Australia.
 Age: B2
 B2 *Putapacyathus regularis* Bedford and Bedford (T)
 B2 *Metaldetes retesepta* (Taylor) S (Ar)
31. Section 25/7, Mackenzie Mountains, Canada.
 Age: B3, *serratus-kordeae* Zone
 B3 *Plicocycyathus rozanovi* (Handfield) (Aj)
 B3 *Protopharetra junensis* A. Zhuravlev S (Ar)
32. King George Island, Antarctica.
 Age: B3, *favus* Beds
 B3 *Tumuliolythus irregularis* (Bedford and Bedford) (M)
Dokidocyathus sp. (Aj)
Ladaecycyathus sp. (Aj)
 B3 *Bractocycyathus labiosus* Kruse (Aj)
 B3 *Metaldetes lairdi* (Hill) S (Ar)
 B3 *Kruseicnema gracilis* (Gordon) (Ar)
33. Olekma River, Siberian Platform, Russia.
 Age: B3
Cellicyathus sp. nov. S (Ar)
Archaeocycyathus sp. S (Ar)
34. Sanashtykgol Creek, Western Sayan, Russia.
 Age: B3
 B1 *Polythalamia perforata* (C)
 B3 *Clathricoscinus spatiosus* (Vologdin) (C)
Loculicyathus sp. (Ar)
Molybdocyathus sp. S (Ar)
 B3 *Altaicyathus notabilis* Vologdin MM (K)
35. Ynyrga River, Mountain Altay, Russia.
 Age: TN1, '*Claruscycyathus solidus*' Zone
 TN1 *Archaeocycyathus cumfundus* (Vologdin) S (Ar)
36. L'Anse au Loupe, Labrador, Canada.
 Age: TN1, *Archaeocycyathus atlanticus* Zone
 TN1 *Metaldetes profundus* (Billings) S (Ar)
 TN1 *Archaeosycon billingsi* (Walcott) S (Ar)
 TN1 *Arrhythmocricus kobluki* Debrenne and James (Ar)
 TN1 *Archaeocycyathus atlanticus* Billings S (Ar)
37. Sukhie Solontsy Valley, Azyrtal Ridge, Kuznetsky Alatau, Russia.
 Age: TN2, *ratus-kusmini* Zone
 TN2 *Tegerocycyathus edelsteini* (Vologdin) S (Ar)
 TN2 *Archaeocycyathus cumfundus* (Vologdin) S (Ar)
38. Malyy Aim River, Siberian Platform, Russia.
 Age: TN2, '*grandiperforatus*' Zone
 TN2 *Archaeocycyathus okulitchi* (Zhuravleva) (Ar)

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 4. (1991): Fossils of the Oxford Clay, *edited by* D. M. MARTILL *and* J. D. HUDSON. 286 *pp.*, 44 *plates*. Price £15 (U.S. \$30) (Members £12 or U.S. \$24).
 5. (1993): Fossils of the Santana and Crato Formations, Brazil, *by* D. M. MARTILL. 159 *pp.*, 24 *plates*. Price £10 (U.S. \$20) (Members £7.50 or U.S. \$15).
 6. (1994): Plant fossils of the British Coal Measures, *by* C. J. CLEAL *and* B. A. THOMAS. 222 *pp.*, 29 *plates*. Price £12 (U.S. \$24) (Members £9 or U.S. \$18).
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.

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