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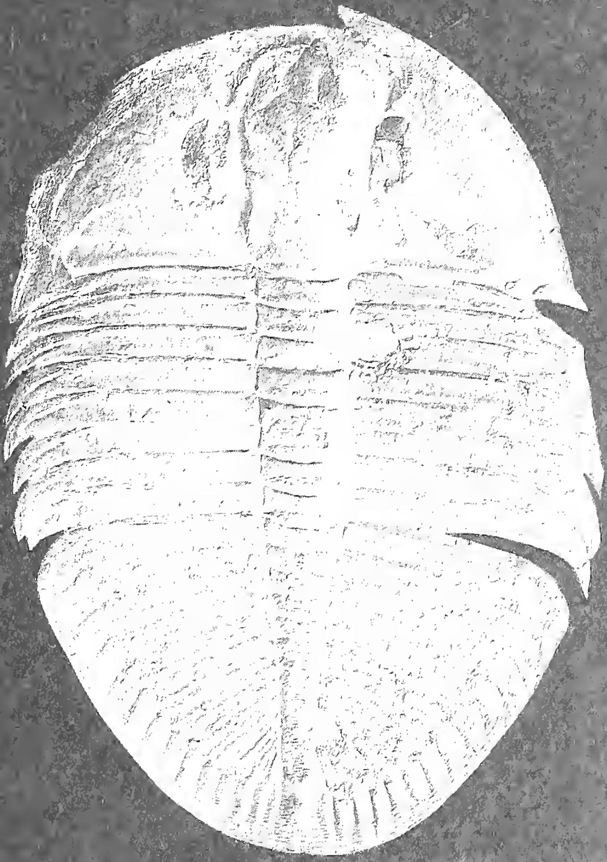

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Cover: The Middle Ordovician trilobite *Ogygiocarella* from Builth was one of the first fossils described from Britain, being figured by Edward Lhwyd in 1698.

RE-EVALUATION OF THE ICHNOGENUS *HELMINTHOPSIS* – A NEW LOOK AT THE TYPE MATERIAL

by ANDREAS WETZEL *and* RICHARD G. BROMLEY

ABSTRACT. The type material of *Helminthopsis* Heer, 1877 has been examined. The ichnospecies established by Heer (1877) are unsuitable for representing this ichnogenus. *Helminthopsis magna* (subsequently designated type ichnospecies by several authors) and *Helminthopsis intermedia* are specimens of *Scolicia* isp. de Quatrefages, 1849, while *Helminthopsis labyrinthica* is a three-dimensionally complex graphoglyptid quite unlike *Helminthopsis* auctt. and very similar to *Spirocosmorhaphe helicoidea* Seilacher, 1989. However, because of its popularity and its distinctive morphology, and in the interests of nomenclatural stability, *Helminthopsis* is retained by erecting a new ichnospecies on the basis of material in Heer's collection. *Helminthopsis hieroglyphica* isp. nov., although never formally published by Heer (only *in litteris*), was labelled as such by him in his collection, and is proposed here as the type ichnospecies. *Helminthopsis* is normally preserved in hyporelief, but seldom in full relief. Trace fossils in full relief preservation having a morphology similar to *Helminthopsis* were grouped into the (ichno)genus *Theobaldia* by Heer (1877). Although *Theobaldia* has page priority over *Helminthopsis*, the name has hardly ever been used and we declare *Theobaldia* an abandoned senior synonym in order to maintain nomenclatural stability.

THE ichnogenus name *Helminthopsis* is very popular among sedimentologists and palaeontologists, and has been in use continuously since its introduction by Heer (1877). The three ichnospecies assigned there by Heer (*H. magna*, *H. intermedia* and *H. labyrinthica*) in fact belong to different ichnogenera and cover a wide range of morphotypes. The choice of *Helminthopsis magna* as the type ichnospecies by Ulrich (1904), Andrews (1955), and Fillion and Pickerill (1990) led to the ichnogenus being interpreted on the basis of Heer's (1877, pl. 47) inadequate illustration; *Helminthopsis* became used for irregularly meandering trace fossils. *Helminthopsis* of authors has thereby become a separate concept from *Helminthopsis* Heer. To overcome this inaccurate usage, many authors gave their own definition of *Helminthopsis* based on their own understanding of the ichnogenus, but not on Heer's. *Helminthopsis* auctt. has come to comprise several elements that are not included in Heer's original diagnosis, for example 'unbranched, irregularly winding or meandering, horizontal burrows or trails that do not touch or cross themselves. Only one order of meandering may be present. Burrow-fill massive' (Fillion and Pickerill 1990, p. 36).

The uncertain use of *Helminthopsis* continued after Książkiewicz (1977) introduced the new ichnospecies *Helminthopsis abeli* and designated it as the type of the ichnogenus. But his lectotype shows narrow meanders (in contrast to his own description) and the specimen is too small to allow the course of the burrow to be evaluated with certainty; the fragment probably belongs to the ichnospecies *Cosmorhaphe* cf. *Cosmorhaphe helminthopsidea* (Sacco, 1888; compare with Seilacher 1977, fig. 3e; see below). The specimen had been figured previously by Abel (1935) without name, and as *Helminthopsis* (without ichnospecies name) by Häntzschel (1962, 1975).

This demonstrable need of a type ichnospecies highlights an unfortunate decision of the ICZN (Ride *et al.* 1985) to provide ichnogenera with genus-group status, whereby they need no type species, a situation that has been deplored by other workers (Kelly 1990; Rindsberg 1990). Herein, we treat *H. hieroglyphica* as the type ichnospecies of *Helminthopsis*. After all, this is not the first time ichnologists have had to take the law into their own hands (Sarjeant 1979; Bromley 1990).

[Palaeontology, Vol. 39, Part 1, 1996, pp. 1–19]

Heer's type material is preserved in the Geological Institute of the ETH, Zürich, and is easily accessible. An examination of this material revealed the true nature of *Helminthopsis* Heer, but resulted in a dilemma; the only valid ichnospecies of *Helminthopsis* is in fact a complex trace fossil which is significantly different in the geometrical pattern from most of the trace fossils for which the name has been applied so far. We attempt to resolve the *Helminthopsis* dilemma by basing the ichnogenus on *H. hieroglyphica*, an ichnospecies named but not published by Heer. Among Heer's collection, material under this name includes specimens that show the morphology of *Helminthopsis* as understood today by authors, as opposed to that of the type material of Heer's published ichnospecies. This rather unusual nomenclatural procedure is necessary to retain the stability of the widely used name *Helminthopsis*.

TAXONOMIC HISTORY

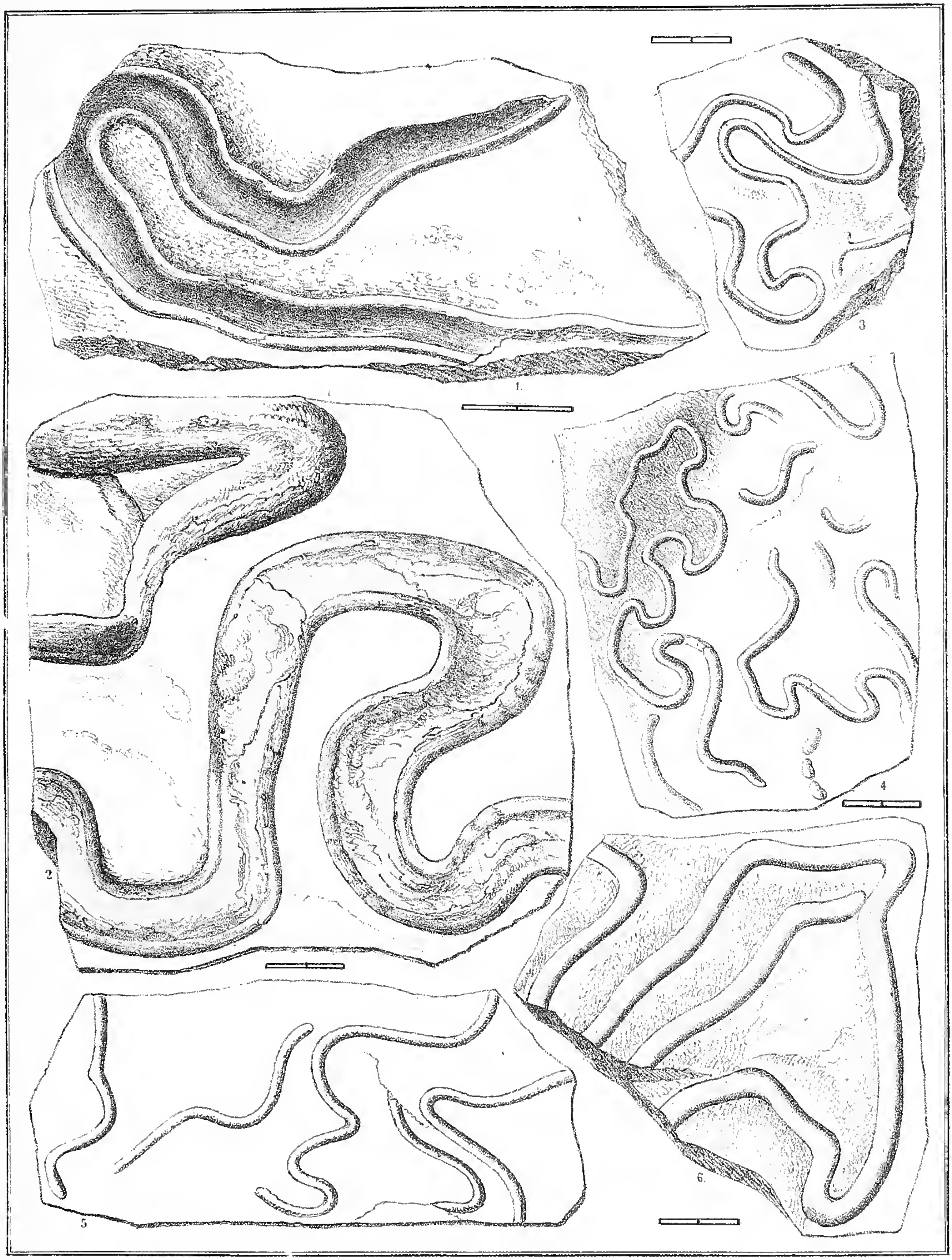
Helminthopsis was erected by Heer (1877) for what he interpreted as a group of fossil algae having a gyrate or curved shape and a diameter ranging from 2 to 20 mm. With respect to the diameter of the fossils and their curvature, Heer defined three different species; *H. magna*, *H. intermedia*, and *H. labyrinthica* (Text-fig. 1). He did not designate a type species, but in his genus description he only referred to *H. magna*, which was therefore later chosen as the lectotype (Ulrich 1904; Andrews 1955; Fillion and Pickerill 1990).

Nathorst (1881) and Maillard (1887) recognized that most of the fossils described as algal remains are in reality trace fossils. When Maillard studied Heer's material, he was informed by Heer about a planned change of the name *Helminthopsis labyrinthica* to *H. hieroglyphica*, to avoid confusion with *Helminthoida labyrinthica*. On the labels of the specimens figured by Heer is written '*Helminthopsis hieroglyphica Helminthopsis labyrinthica in opere*' (*in opere* means 'in the completed work', i.e. Heer 1877). Consequently, Maillard (1887, p. 37) wrote '*Helminthopsis hieroglyphica* Heer (*labyrinthica* dans Heer) mais ce nom fut changé par l'auteur lui-même, pour éviter confusions avec forme du Flysch' (*Helminthopsis hieroglyphica* Heer (*labyrinthica* in Heer), the name has been changed by the author himself to avoid confusion with a[nother trace fossil] form of the Flysch). However, Heer (1877) introduced the name *H. labyrinthica* and never published the change in name in a taxonomically valid way (cf. Wilckens 1947), so the name *H. labyrinthica* has to be retained for the specimens figured by Heer (1877, p. 47, figs 3–5) and covered by his descriptions.

Sacco (1888) examined *Helminthopsis* in more detail and stated on page 174 '...,e non sarebbe improbabile che si trattasse solo di impronte del passagio di animali striscianti' (...it is not unlikely that [these fossils] were produced by crawling animals). He gave an emended taxonomy and pointed out that the 'canal-like forms of *Helminthopsis* must be grouped together with *Taphrhelminthopsis* Sacco'. This is the case for *H. magna*, as he explained in the chapter on *Taphrhelminthopsis*. *Taphrhelminthopsis*, however, is a preservational variant of *Scolicia* (Smith and Crimes 1983). Moreover, Sacco (1888) stated that Heer rejected the ichnospecies *Helminthopsis labyrinthica* because of the similarity in name with *Helminthoida labyrinthica*, but Heer did it invalidly only *in litteris*. Sacco (1888) used *H. hieroglyphyca*, but each time he used a spelling (*hieroglyphyca* (p. 175), *hieroglyfica* (p. 175), *hjeroglyphyca* (p. 192)) which is different from Heer's proposed name. Unaware of Sacco's (1888) work, Ulrich (1904) and Andrews (1955) suggested using *H. magna* as the type ichnospecies. At least since Ulrich (1904), the ichnogenus *Helminthopsis* has been universally used to describe curved, irregularly meandering trace fossils.

Seilacher (1977) reiterated the opinion that *H. magna* is very similar in size and shape to *Scolicia*; Książkiewicz (1977) also agreed with Sacco (1888) that it is *Taphrhelminthopsis*. Later, Fillion and Pickerill (1984) referred to the observation of Sacco (1888) and the suggestion of Książkiewicz (1977). But subsequently, Fillion and Pickerill (1990) gave another emended diagnosis and referred to *H. magna* as type ichnospecies.

Further complications were provided by Häntzschel (1962, 1975) who illustrated *Helminthopsis* in the *Treatise on invertebrate paleontology* (Häntzschel 1962, p. 197, fig. 4*a*; 1975, fig. 44, 2*b*) by



TEXT-FIG. 1. *Helminthopsis*. Material as figured by Heer (1877, pl. 47; scales added by the authors); the drawings do not reflect all details of the original pieces (see Text-figs 2–4). Scale bars represent 20 mm.

a specimen which may be classified as *Cosmorhaphe* Fuchs, 1895. It shows a narrow semi-regular meander pattern and is probably *Cosmorhaphe helminthopsidea* Sacco, 1888; the sample is too small to allow the recognition of second-order meanders, but the trace is nearly identical with respect to meander width, height and radius and tube width to the *C. helminthopsidea* figured by Seilacher (1977, fig. 3*e*). The specimen under discussion was originally figured by Abel (1935, fig. 261B), but without an ichnotaxon. Seilacher's claim (1977, p. 299, paragraph on *Helminthopsis lobata*) that Abel's (1935, fig. 261B) specimen had been originally figured by Ulrich (1904) is an error; Ulrich figured no specimen of *Helminthopsis* sp., and Abel (1935) stated in the caption of figure 261B that his specimen had been found near Vienna (and not in Alaska). Książkiewicz (1977) re-figured Abel's specimen (Książkiewicz 1977, text-fig. 21*d*) and introduced for it the new name *Helminthopsis abeli*. He then suggested establishing *H. abeli* as the type ichnospecies of *Helminthopsis*, although it was not one of Heer's species. Furthermore, he defined the specimen mentioned above as lectotype, but this specimen shows narrow meanders and does not match his ichnospecies description (p. 117) 'loosely winding with a tendency to meandering'. Because of the discrepancies between the description and the lectotype given by Książkiewicz (1977), we suggest abandoning *H. abeli* as type ichnospecies of *Helminthopsis* and that topotype material from Heer's collection should instead be used.

OCCURRENCE

The type material of *Helminthopsis* was found in Ganei (Swiss coordinates 767 660/211 640), at the foot of the Schesaplana in rockfall blocks which probably derived from a location with the coordinates (767 520/212 320). Stratigraphically, Heer (1877) assumed a Jurassic age for the Ganei Shales. The area was first mapped in detail by Trümpy (1916), who found the Ganei Shales in a north-penninic tectonic position, the deposits being flysch, from coarse grained breccia to mud-turbidites. Later Nänny (1948) and Thum and Nabholz (1972) grouped the Ganei Shales into the Ruchberg Serie which has a Palaeocene to early Eocene age. Occurring below a thrust, the strata are strongly compacted and locally sheared. Some of the material described by Heer (1877) was collected by himself, but other specimens had previously been brought to him by G. Theobald (as mentioned by Heer), having been collected at Ganei.

THE MATERIAL COLLECTED BY HEER AND ITS ICHNOTAXONOMY

The description of the genus *Helminthopsis* by Heer (1877, p. 116) is based on the material figured by Heer (1877, pl. 47), shown here in Text-figure 1. The three ichnospecies of *Helminthopsis* Heer belong to different ichnogenera. To clarify the taxonomy we will repeat the original diagnoses and comment on the type material. The original diagnoses are as follows:

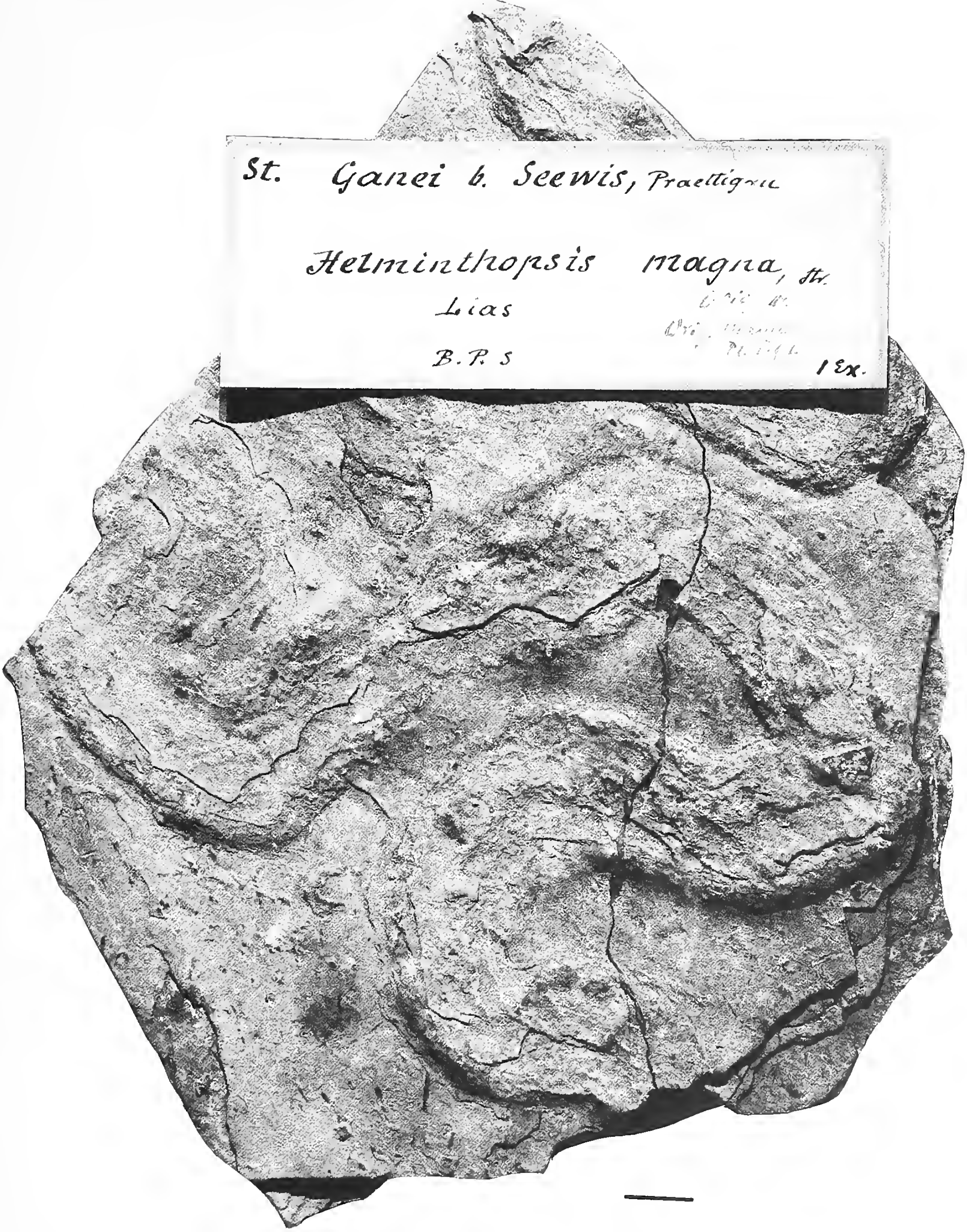
Helminthopsis *Heer, 1877, p. 116*

'Frons simplex, valde elongata, fistulosa, cylindrica, gyrosa.' Simple foliage, very elongate, tubular, cylindrical, gyrate.

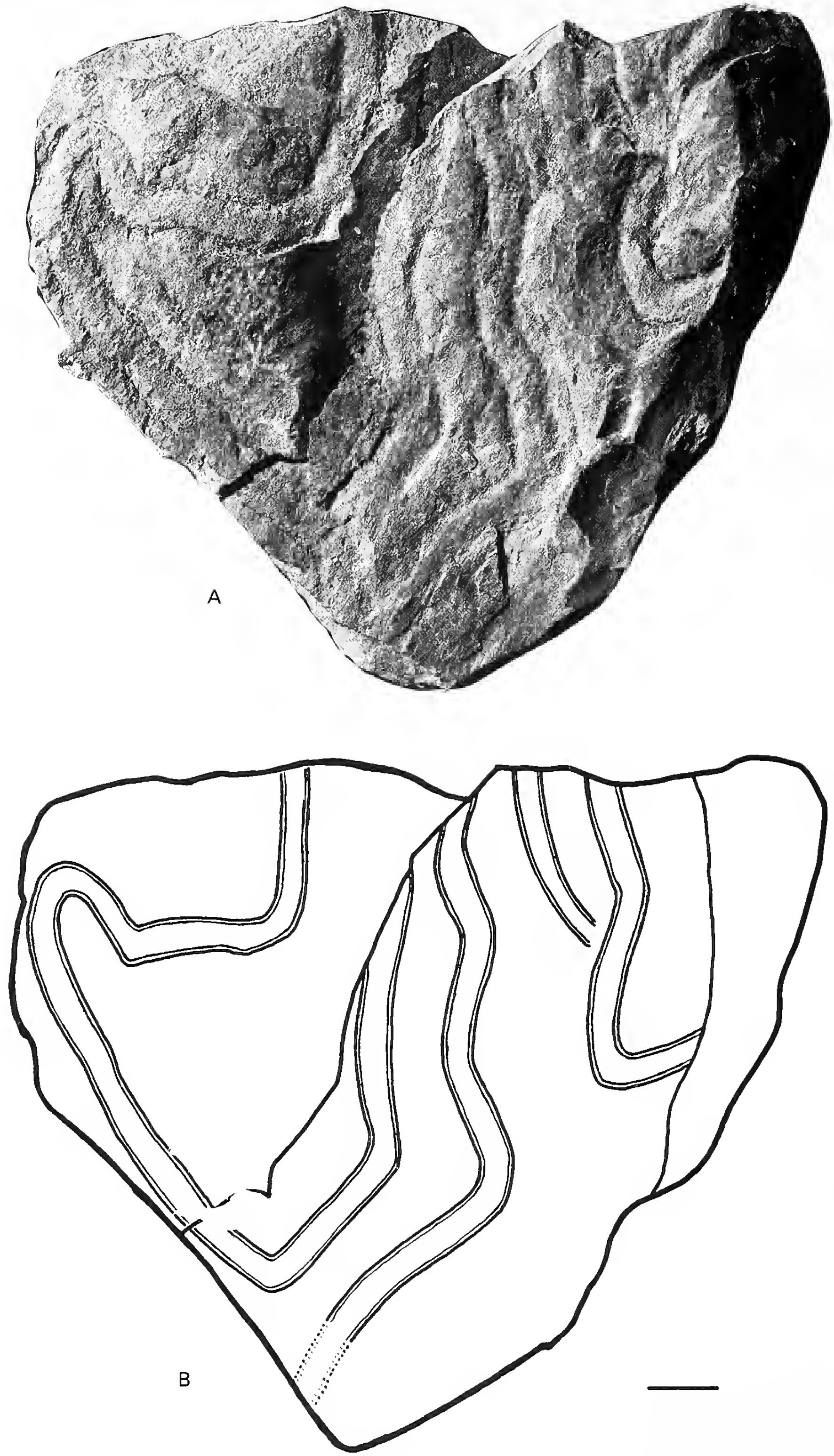
Helminthopsis magna *Heer, 1877, p. 116*

'*Helminthopsis* fronde fistulosa, 15–20 mm. lata, praelonga, valde flexuosa, hippocrepice gyrosa.' *Helminthopsis* having tubular foliage, 15–20 mm wide, very long, with numeous flexures, gyrate like a horseshoe.

The holotype of *H. magna* is a poorly preserved specimen (Text-fig. 2) of *Scolicia* isp. de Quatrefages, 1849. Sacco (1888) also made this observation, and Seilacher (1977, p. 297) stated '...*Helminthopsis*, the type species of which (*Helminthopsis magna* Heer) seems to be a *Scolicia* rather than a graphoglyptid'. Our observations confirm the opinions of Sacco and Seilacher.



TEXT-FIG. 2. *Helminthopsis magna* Heer. Specimen collected by Heer and published in his plate 47 figure 2; this specimen has to be classified as *Scolicia* isp. de Quatrefages, 1849 because of its general geometry, bilobate form, and internal structure. Repository: Geologisches Institut der ETH Zürich, Switzerland; collection of the originals to Heer's book (1876/77) under the given plate and figure numbers. Scale bar represents 10 mm.



TEXT-FIG. 3. For caption see opposite.

Helminthopsis intermedia *Heer, 1877, p. 116*

'*Helminthopsis* fronde cylindrica, 6 mm. lata, elongata.' *Helminthopsis* having cylindrical foliage,' 6 mm wide, elongate.

H. intermedia is represented by a poorly preserved specimen, distorted by tectonic shearing and a small fault. Heer's drawing does not correctly represent the specimen and *H. intermedia* has in fact to be classified as *Scolicia* isp. (Text-fig. 3). Furthermore, because of its infrequent use it can also be regarded as *nomen nullum*.

Helminthopsis labyrinthica *Heer, 1877, p. 116*

'*Helminthopsis* fronde cylindrica, 2–3 mm. lata, valde flexuosa, gyrosa, gyris hippocrepicis.' *Helminthopsis* having cylindrical foliage, 2–3 mm wide, with numerous flexures, curved gyrately, or with horseshoe-like gyres.

H. labyrinthica is the only ichnospecies introduced by Heer (1877) which really justifies the definition of a new ichnogenus. *H. labyrinthica* is a loosely meandering form with horseshoe- or Ω-like turns. Typically, on bedding planes, it is a discontinuously preserved tube with short interruptions, but juxtaposed tubes also occur for short distances (Text-fig. 4). Thus, the producing animal must have left the bedding plane in a vertical direction and so *H. labyrinthica* must be a part of a three-dimensional burrow system. The short interruptions and juxtaposed tubes (observed on a nearly identical specimen) were interpreted by Seilacher (1977) as loops. However, he did not place his material in *H. labyrinthica*, but classified it as new ichnospecies *Cosmorhaphe helicoidea* (Seilacher 1977, p. 298, fig. 3*g*). Seilacher (1989) later introduced the ichnogenus *Spirocosmorhaphe* for this and similar trace fossils. For *Spirocosmorhaphe*, Seilacher (1989) deduced the three-dimensional nature of the burrow (see comment by Pickerill and McCann 1989), gave a satisfying explanation for the behavioural programme, and classified such burrows as belonging to the group of graphoglyptids. In fact *Spirocosmorhaphe helicoidea* is very similar to *H. labyrinthica* in pattern, shape, and size (Text-fig. 4). However, the congeneric nature of both traces could not have been recognized by Seilacher without studying the type material of Heer, because Heer's drawings do not show the kinks at the base of horseshoe-like turns and the occurrence of 'secondary' juxtaposed concave tubes (in plan view) accompanying the convex-shaped tube at the base of the horseshoe-like turns. These elements are particularly important for Seilacher's ichnogenus *Spirocosmorhaphe*.

H. labyrinthica is the only ichnospecies of *Helminthopsis* which has no senior synonym, and hence should be utilized as type ichnospecies. So the congeneric nature of *H. labyrinthica* and *S. helicoidea* produces a real dilemma. If the rules of priority are applied, Seilacher's *S. helicoidea* is a junior synonym of *H. labyrinthica* and can therefore be suppressed. Alternatively, Seilacher's ichnospecies may be renamed as *Spirocosmorhaphe labyrinthica* (Heer), the characteristic geometrical pattern residing in the ichnogenus name. The geometrical pattern is decidedly different from that of most trace fossils to which the name *Helminthopsis* has been applied. In order to provide nomenclatural stability in accordance with ICZN rules (Ride *et al.* 1985), the ichnogenus *Helminthopsis* should retain its present usage.

To solve the evident dilemma, we suggest using topotype material in Heer's collection as a basis for the definition of the ichnogenus *Helminthopsis*, to avoid further confusion with respect to Heer's initial description. The specimen we designate as type ichnospecies covers the present use of the

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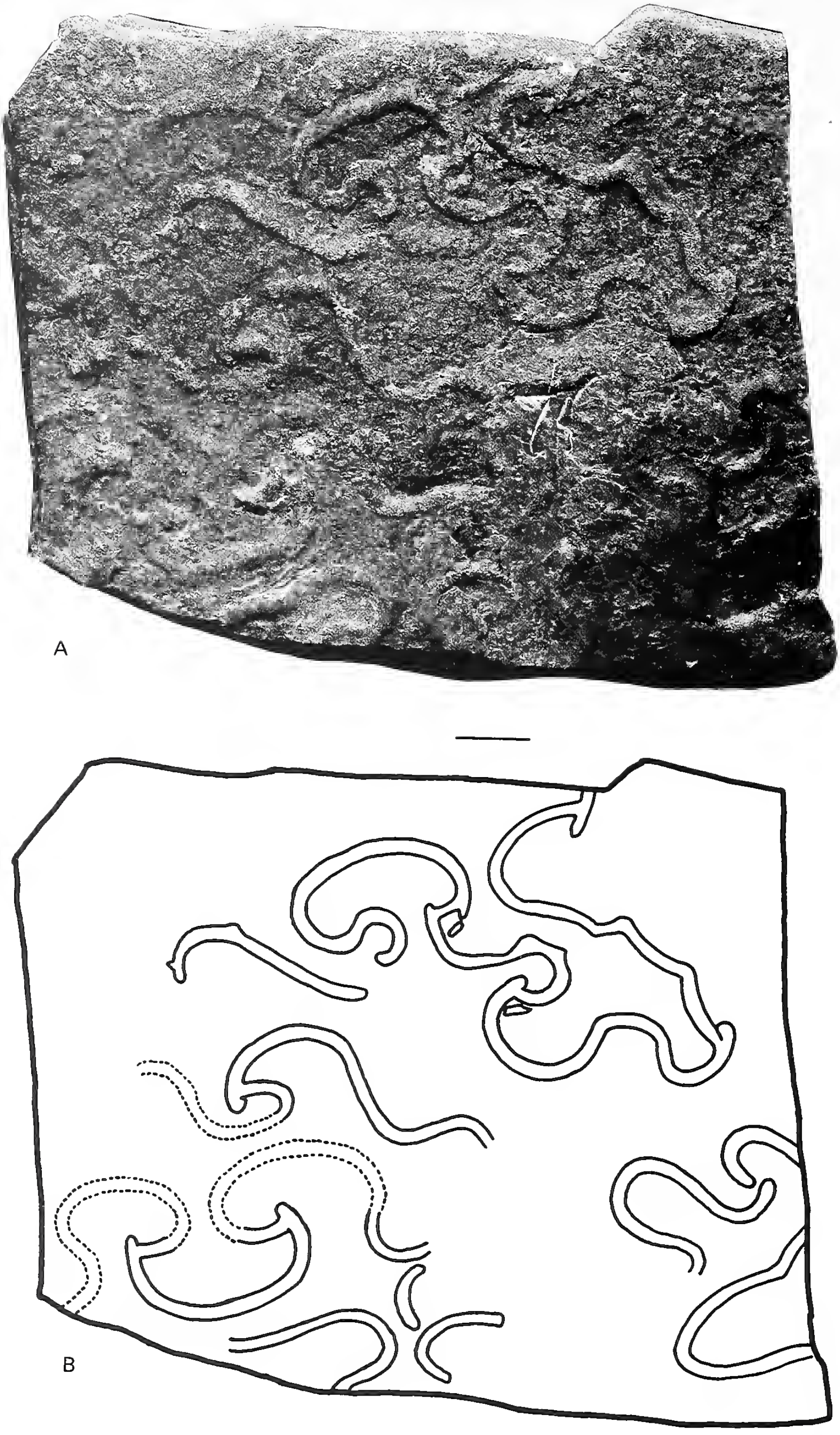
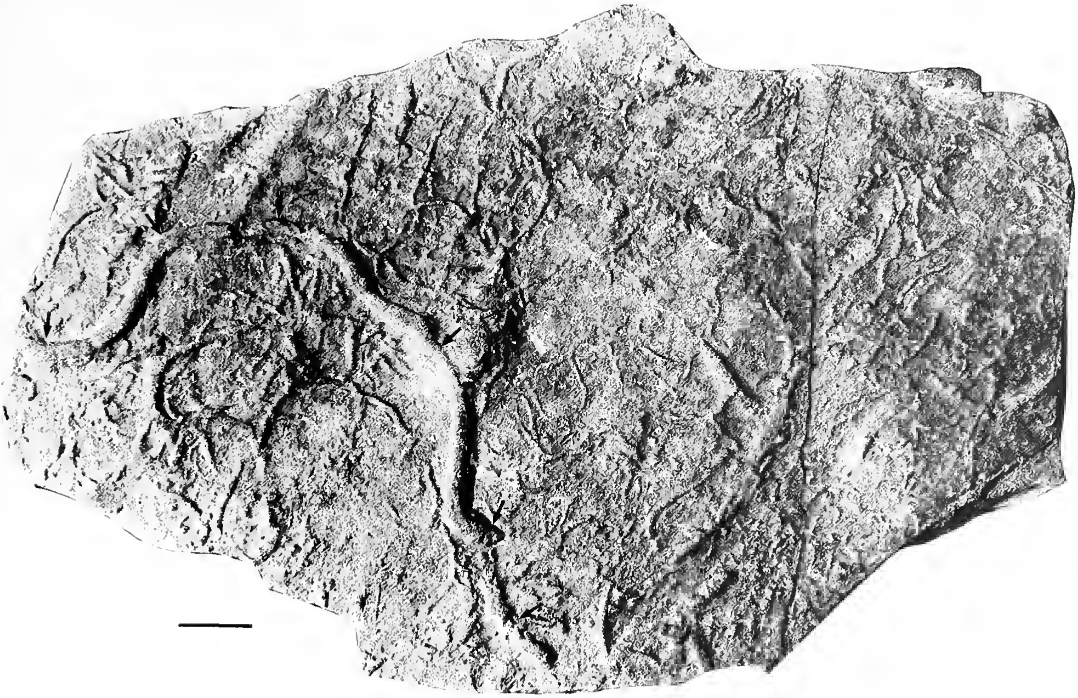
TEXT-FIG. 3. *Helminthopsis intermedia* Heer. A, specimen collected by Heer. B, our interpretation as line drawing which clearly differs from that of Heer (1877, pl. 47, fig. 6; see Text-fig. 1, 6); the specimen is poorly preserved; however, the parallelism of the strings suggests that *H. intermedia* has also to be classified as *Scolicia* isp. in *Subphyllochorda* preservation. Repository: Geologisches Institut der ETH Zürich, Switzerland; collection of the originals to Heer's book (1876/77) under the given plate and figure numbers. Scale bar represents 10 mm.



TEXT-FIG. 4. For caption see opposite.



TEXT-FIG. 5. *Helminthopsis hieroglyphica.* The large, irregularly meandering trace fossil is the designated holotype (arrows); the specimen was first figured by Maillard (1887, pl. 2, fig. 4). The densely packed, small trace fossils are of uncertain taxonomy, we suppose 'mycellia' as described by Wetzel (1983) or juvenile *Helminthopsis*? Repository: Geologisches Institut der ETH Zürich, Switzerland; collection of the originals to Maillard's publication (1887) under the given plate and figure numbers. Scale bar represents 10 mm.

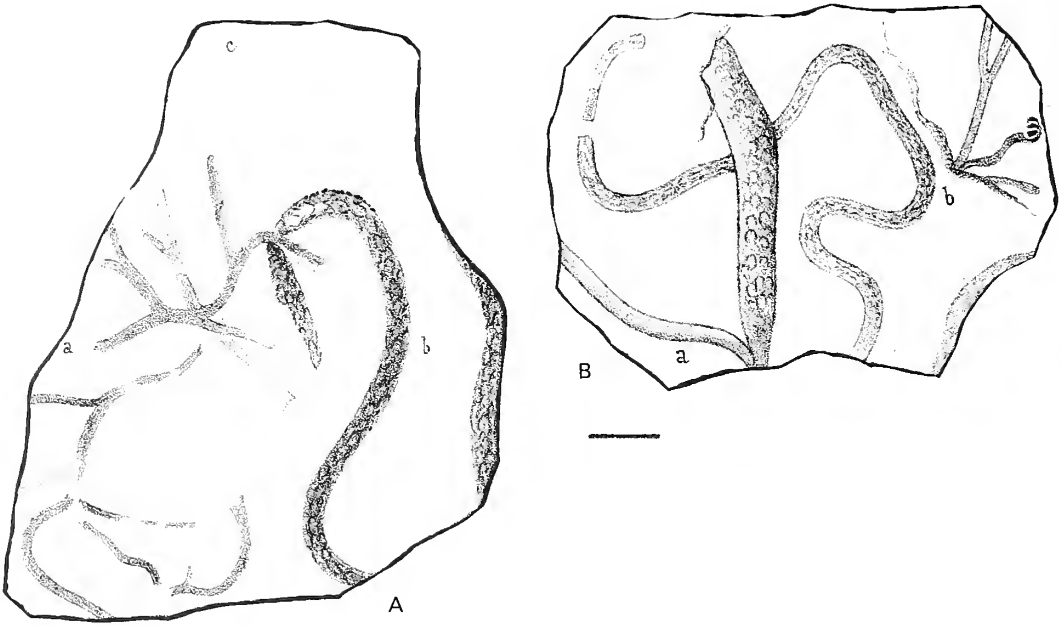
ichnogenus *Helminthopsis.* It was collected by Heer at the type locality and labelled as *Helminthopsis hieroglyphica* (without the comment *Helminthopsis labyrinthica in opere*, see above). This specimen was not figured or described by Heer, but Maillard (1887, pl. 2, fig. 4) subsequently figured it, and briefly described it in the captions as '*Helminthopsis hieroglyphica* which is a slightly curved trace...' (without a comment on a previous name). Because this specimen was not figured by Heer, there is no synonymy or congenerity with the figured *H. labyrinthica* specimens. Therefore we establish this specimen as holotype of *Helminthopsis hieroglyphica*, and propose that ichnospecies as the type for its ichnogenus. Furthermore we suggest (in accordance with ICZN, Article 23b) that the ichnospecies *H. labyrinthica* becomes a senior synonym of *Spirocosmorhaphe helicoidea* as *Spirocosmorhaphe labyrinthica* (Heer). In this way, the ichnogenus *Helminthopsis* Heer can be retained in its present use, and is defined by the ichnospecies *H. hieroglyphica*, collected by Heer at the type locality.

TEXT-FIG. 4. *Helminthopsis labyrinthica* Heer. A, specimen collected by Heer. B, line drawing by the authors of the larger specimen figured by Heer (1877, pl. 47 fig. 4; see our Text-fig. 1, 4); note that the drawing by Heer does not show all details of the specimens, especially the sharp kinks and the discontinuity of the tube which provide clear evidence that *H. labyrinthica* is identical to *Spirocosmorhaphe* isp. Seilacher, 1989. Repository: Geologisches Institut der ETH Zürich, Switzerland; collection of the originals to Heer's book (1876/77) under the given plate and figure numbers. Scale bar represents 10 mm.

Książkiewicz (1977) described some trace fossils as *H. hieroglyphica* and referred explicitly to Maillard (1887, pl. 2, fig. 4, and *non* pl. 1, fig. 2) in his description. Later Fillion and Pickerill (1984, 1990) and Crimes and Crossley (1991) ascribed specimens to *H. hieroglyphica*, which are all similar to the specimen collected by Heer and on which we base the new type ichnospecies. In their ichnotaxonomy, these authors referred to *H. hieroglyphica* Heer *in* Maillard (1887) but this ignores the fact that the change in name as mentioned by Maillard is invalid.

The tube of the holotype of *H. hieroglyphica* (Text-fig. 5) is not strictly attached to the bedding plane, which indicates that the trace was produced at varying depths within the sediment. This observation has the important implication that different modes of preservation can occur. In addition to burrows produced shallowly within the sediment and preserved in convex hyporelief (e.g. the type material), a full relief or concave epirelief preservation for deeply emplaced burrows is possible as reported by Chamberlain (1971) and Crimes *et al.* (1981).

With this last implication in mind, we were not surprised to discover in Heer's collection a trace fossil having the geometry and size of *Helminthopsis* in full relief preservation, but named *Theobaldia raetica* (Heer 1877, pl. 44, fig. 15*b*). The type material of *T. raetica* was found at the same locality as *Helminthopsis*, so we cannot leave this discussion without also dealing with *Theobaldia* (Text-fig. 6).



TEXT-FIG. 6. *Theobaldia raetica* Heer, as figured by Heer (1877), the specimens showing all details of *Helminthopsis*, but in full relief preservation. A, *Theobaldia raetica*, shown on plate 44, figure 1, resembles *Helminthopsis hieroglyphica*. B, *Theobaldia raetica*, shown on plate 44, figure 15*b*, resembles *Helminthopsis abeli*. The apparent branching is false. Specimen figured as B is lost, repository for specimen figured as A; Geologisches Institut der ETH Zürich, Switzerland; collection of the originals to Heer's book (1876/77) under the given plate and figure numbers. Scale bar represents 10 mm.

Heer (1877, p. 114) believed that *Theobaldia* was a fossil alga, having stems and leaves; so he included there fossils composed of tubes which he interpreted as stems, and *Chondrites* which he interpreted as leaves (cf. Häntzschel 1965, p. 92). If the *Chondrites* parts are disregarded, the remaining tubes have to be grouped into different ichnogenera.

Theobaldia raetica as shown by Heer (1877, pl. 44, fig. 1) can be classified as *Helminthopsis hieroglyphica* whereas the specimen shown on plate 44, figure 15*b* is similar to *Helminthopsis abeli* (see below).

Theobaldia minor resembles a part of *Nereites* isp. (described as a faecal ribbon form of *Scalarituba* by Chamberlain and Clark 1973, p. 678), but the specimens are too small to evaluate their true taxonomy.

Theobaldia circinalis (pl. 44, figs 7–10, *non* figs 11–14) has to be grouped with *Spirophycus* isp.; for the other specimens (pl. 44, figs 11–14) the taxonomic affinities are unclear, because Heer enhanced the structures on the original (rock) material with black ink.

Although *Theobaldia* has page priority over *Helminthopsis*, the former has been seldom used. The sparse use of these taxa and the doubtful combination of different taxa into one justify the removal of the senior synonym and the retention of the junior synonym.

CONCLUSIONS

1. The three species of *Helminthopsis* defined by Heer belong to two different ichnogenera.
(a) *H. magna* (type ichnospecies of Ulrich 1904; Andrews 1955; Fillion and Pickerill 1990) and *H. intermedia* are junior synonyms of *Scolicia* isp. de Quatrefages, 1849 and should be removed.
(b) *H. labyrinthica* is a senior synonym of *Spirocosmorhaphe helicoidea*, which is a graphoglyptid. To declare *H. labyrinthica* as senior synonym would entirely alter the understanding of the name *Helminthopsis* in its present use. In order to provide nomenclatural stability we would abandon this ichnospecies for *Helminthopsis* and regard it as *Spirocosmorhaphe labyrinthica*.

2. Instead, we define *Helminthopsis* on the basis of *H. hieroglyphica*, a name proposed but never validly introduced by Heer because he did it only *in litteris*. The holotype was collected by Heer at the same locality as yielded the 1877 specimens.

3. *H. hieroglyphica* corresponds closely to *Helminthopsis* auctt., and in choosing it we follow the lead of Fillion and Pickerill (1984, 1990) and Crimes and Crossley (1991).

4. The ichnospecies diagnosis is given below. The introduction of *H. hieroglyphica* as type ichnospecies is necessary because the lectotype of the ichnospecies *Helminthopsis abeli* is problematical.

5. The holotype of *Helminthopsis abeli* Książkiewicz, 1977 does not match the description, which requires irregular widely winding meanders as an important criterion; in fact the holotype shows narrow regular meanders. In our opinion the holotype has to be placed within *Cosmorhaphe* because it is nearly identical with respect to meander width, height and radius and tube width to the *Cosmorhaphe helminthopsidea* figured by Seilacher (1977, fig. 3*e*). However, the specimen is too small to detect a second-order meandering and hence its taxonomy remains uncertain.

6. *H. hieroglyphica* is not strictly attached to the bedding plane and hence various modes of preservation of *Helminthopsis* can occur. Normal preservation is in convex hyporelief (including the topotype material); full relief preservation is also possible.

7. Heer placed full relief preservation in *Theobaldia raetica*. However, *Theobaldia* is a problematical taxon which combines tubular trace fossils (stems) and *Chondrites* (leaves) into alga species. Even if the *Chondrites* elements are disregarded, the ichnospecies of *Theobaldia* belong to different ichnogenera. Although all the ichnospecies of *Theobaldia* are senior synonyms, we suggest declaring them as invalid senior synonyms because they have not been mentioned except by Andrews (1955)

and Häntzschel (1962, 1965, 1975), and are problematical in their combination of two trace fossil ichnogenera.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Helminthopsis* Heer, 1877

non 1851 *Helminthopsis irregularis* (Schafhäutl), pl. 9, fig. 10 [= *Helminthopsis* isp., Schafhäutl, 1851].

non vp 1877 Theobaldia raetica Heer, p. 114, pl. 44, fig. 1 [= *Helminthopsis hieroglyphica* isp. nov.].

non 1877 *Theobaldia raetica* Heer, p. 114, pl. 44, fig. 15*b* [similar to *Helminthopsis abeli*, the specimen is lost].

non v 1877 Helminthopsis magna Heer, p. 116, pl. 47, figs 1–2 [= *Scolicia* isp. de Quatrefages, 1849].

non v 1877 Helminthopsis intermedia Heer, p. 116, pl. 47, fig. 6 [= *Scolicia* isp. de Quatrefages, 1849].

non 1888 *Helminthopsis antiqua* Sacco, p. 175, pl. 2, fig. 10 [probably = *Helminthopsis* isp. Schafhäutl, 1851].

non 1895 *Helminthopsis involuta* de Stefani *in* de Stefani *et al.*, pl. 14, fig. 1 [= *Spirorhaphe involuta* de Stefani, 1895 *in* de Stefani *et al.* 1895].

non 1895 *Helminthopsis barbeyana* de Stefani *in* de Stefani *et al.*, pl. 14, fig. 2 [= *Helminthopsis abeli* Książkiewicz, 1977].

non 1904 *Helminthopsis ?labyrinthica* Ulrich, p. 144, pl. 20, figs 2–3 [= *Cosmorhaphe lobata* Seilacher, 1977].

non 1904 *Helminthopsis magna* Ulrich, p. 144, pl. 21, figs 1–2 [= *Scolicia plana* Książkiewicz, 1970; identified by R. Pickerill, pers. comm. 1994].

non 1933 *Helminthopsis ?concentrica* Azpeitia Moros, p. 46, pl. 12, fig. 23 [= *Spirorhaphe involuta* de Stefani, 1895 *in* de Stefani *et al.* 1895].

non 1933 *Helminthopsis sinuosa* Azpeitia Moros, p. 45, pl. 14, fig. 24B [= *Cosmorhaphe sinuosa* Azpeitia Moros, 1933].

non 1947 *Helminthopsis labyrinthica* Wilckens, pl. 9, fig. 4 [= *Helminthopsis crassa* Schafhäutl, 1851 = *Helminthorhaphe crassa* (Schafhäutl) Seilacher, 1977].

non 1960 *Helminthopsis curvata* Katto, p. 333, pl. 35, fig. 1 [there described as *Tosahelminthes curvata* = *Helminthoida crassa* Schafhäutl, 1851 = *Helminthopsis crassa* (Schafhäutl) Seilacher, 1977].

non 1964 *Helminthopsis toyoensis* Katto, pl. 7, fig. 3 [figured specimen does not allow an exact classification and hence, is regarded as *nomen dubium*; R. Pickerill, pers. comm. 1994].

non 1967 *Helminthopsis* Macsotay, p. 31, fig. 30 [fig. 30 left = *Helminthoida* sp. Schafhäutl, 1851; fig. 30 middle = *Cosmorhaphe helminthopsidea* Sacco, 1888?; fig. 30 right = *Helminthorhaphe japonica* (Tanaka) Seilacher, 1977].

non v 1968 Helminthopsis granulata Książkiewicz, p. 7, pl. 4, fig. 2 [see below].

*v 1968 Helminthopsis tenuis Książkiewicz, p. 7, pl. 4, fig. 1.

non 1971 *Helminthopsis akkesiensis* Tanaka, pl. 2, fig. 2; pl. 3, fig. 4 [previously = *Magarikune akkesiensis* Minato and Suyama, 1949, today = *Cosmorhaphe* isp.; the specimens are too small for an exact taxonomic classification].

non v 1977 Helminthopsis abeli Książkiewicz only text-fig. 21*a*; pl. 12, fig. 5 [= *Cosmorhaphe helminthopsidea* Sacco, 1888].

v 1977 Helminthopsis abeli Książkiewicz, p. 117, text-fig. 21*c*; pl. 12, fig. 5.

non v 1977 Helminthopsis irregularis Książkiewicz, p. 119, text-fig. 22, pl. 12, fig. 2 [= *Helminthoida* isp., Schafhäutl, 1851].

non v 1981 Helminthopsis isp. Wetzel, p. 9, figs 4–5 [= *Phycosiphon incertum*, see Wetzel and Bromley 1994, p. 1400].

non v 1983 Helminthopsis isp. Wetzel, p. 290 [= *Phycosiphon incertum* von Fischer-Ooster, 1858, see Wetzel and Bromley 1994, p. 1400].

non v 1984 Helminthopsis isp. Wetzel, p. 599 [= *Phycosiphon incertum* von Fischer-Ooster, 1858, see Wetzel and Bromley 1994, p. 1400].

non 1986 *Helminthopsis tunluensis* Yang, pl. 1, fig. 5 [= *Helminthoida miocenica* Sacco, 1886].

non 1986 *Helminthopsis yushuensis* Yang, pl. 3, fig. 7 [= *Helminthoida miocenica* Sacco, 1886].

non 1989 *Helminthopsis sigmoideus* Wang, p. 28, fig. 2 [partly preserved specimen; because the exact burrow course cannot be ascertained it is regarded as *nomen dubium*; R. Pickerill, pers. comm. 1994].

non v 1990 Helminthopsis horizontalis (Kern) Bromley, pp. 214, 232, figs 11.20, 12.1, 12.3–12.4, 12.7–12.11 [= *Phycosiphon incertum* von Fischer-Ooster, 1858; see Wetzel and Bromley 1994, p. 1400].

non 1990 *Helminthopsis magna* Dam, p. 130, fig. 7B [probably = *Nereites* MacLeay, 1839, meandering part in faecal string preservation, cf. Chamberlain and Clark 1973, p. 678, pl. 1, fig. 5].

non 1991 *Helminthopsis regularis* Crimes and Crossley, p. 38, figs 4*c–d* and 5*m–n* [= *Cochlichnus anguineus* Hitchcock, 1858].

non 1992 *Helminthopsis* Pattinson, fig. 14A; Pemberton, MacEachern, and Ranger, fig. 7D; Pemberton, Reinson and MacEachern, figs 11D, 12B; Raychaudhuri *et al*., figs 5G–H [= *Phycosiphon incertum* von Fischer-Ooster 1858, see Wetzel and Bromley 1994, p. 1400].

non 1992 *Helminthopsis/Anchonichnus* MacEachern *et al*., figs 9E, H, 10H [= *Phycosiphon incertum* von Fischer-Ooster 1858].

non 1993 *Helminthopsis* isp. Miller, fig. 7B [= *Nereites* MacLeay, 1839 = faecal string preservation of *Scalarituba* Weller, 1899, cf. Chamberlain and Clark 1973, p. 678, pl. 1, fig. 5].

Type ichnospecies. *Helminthopsis hieroglyphica* isp. nov.

Emended diagnosis. Simple, unbranched, elongate, cylindrical tube with curves, windings, or irregular open meanders.

Description. The occurrence of burrow fills that are not strictly attached to the bedding plane indicates varying penetration depth of the burrow producers; shallowly emplaced burrows are normally cast and preserved as convex hyporelief. Crossings have not been observed. Burrow fill cast, seldom revealing faecal pellets, or massive with no indication of an internal structure. In full relief preservation, a subtle lining of fine-grained material can occur.

Remarks. *Helminthopsis* is a feeding burrow produced normally at shallow depth within sediment probably rich in benthic food. With respect to benthic food availability (Carney 1989) a shallow burrow depth is very likely.

In vertical sections the recognition of *Helminthopsis* is difficult, and confusion especially with *Planolites* could easily occur. *Helminthopsis* differs from *Palaeophycus* and *Macaronichnus* by having no distinct lining or mantle. *Gordia* differs from *Helminthopsis* in its looped form, having many level crossings and never showing meanders (cf. Pickerill and Peel 1990, 1991).

We found that the definition of Heer's different ichnospecies of *Helminthopsis* is in principle based on the geometrical pattern of the trace, whereas fill structure, pre- or post-depositional in origin, and width of the tube are subordinate and inconsistently used characteristics. Therefore, we suggest strictly using the geometrical pattern to define the ichnospecies. However, the strict application of geometric pattern as a taxonomic classifier differs from the concept proposed by Han and Pickerill (pers. comm. 1994) who also used ornamentation as a classifying criterion. Han and Pickerill (in litt.) retain three valid ichnospecies, *H. abeli*, *H. granulata*, and *H. hieroglyphica*, incorporating *H. tenuis* into *H. abeli*. For most of the ichnospecies, an irregular geometrical pattern is mentioned in the diagnosis, so we interpret the suggested ichnospecies in a wide sense and do not define new ichnospecies for each small deviation. According to these guidelines, the following ichnospecies should no longer be in use.

1. *Helminthopsis antiqua* Sacco, 1888. The specimen is too small to identify the complete geometrical pattern. Congenerity with other trace fossils is very likely; it probably represents a meandering part of *Helminthoida crassa*.

2. *Helminthopsis granulata* Książkiewicz, 1968. For various specimens a fill with faecal pellets (e.g. Crimes and Crossley 1991) or a granulation of the burrow margin by body appendages (Książkiewicz 1977) has been reported. As the geometrical pattern is used for classification of *Helminthopsis*, we suggest removing this ichnospecies and incorporating the individual specimens into *H. abeli*, *H. hieroglyphica* and *H. tenuis*. If the fill with pellets is believed to represent the taxobase, it should be placed in *Alcyonidiopsis* Massalongo, 1856. Furthermore, preservational effects may have produced the granulation of *Helminthopsis granulata*; in particular, striations produced by body appendages need a certain sediment consistency to be preserved by turbidity

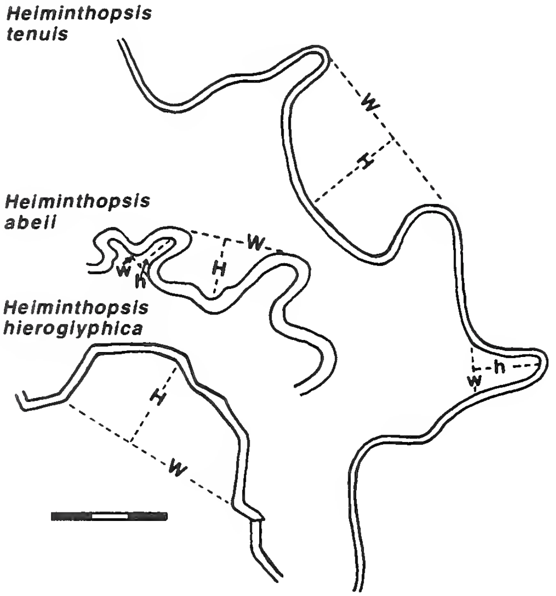
current winnowing and subsequent casting; so the ornamentation of type material of *Helminthopsis granulata* is only preserved on certain parts of the burrow where somewhat protected from the winnowing current.

3. *Helminthopsis irregularis* Schafhäutl, 1851. The tubes are so densely packed that an evaluation of the complete geometrical pattern is difficult, but U-turns and parallel tubes are evident suggesting a congenerity with *Nereites* isp. MacLeay, 1839 (= *Scalarituba* cf. Chamberlain and Clark 1973) or *Helminthoida* cf. *crassa* Schafhäutl, 1851.

4. *Helminthopsis regularis* Crimes and Crossley, 1991. Having regular high-amplitude low-wavelength windings, this should be placed in the ichnogenus *Cochlichnus* which comprises burrows of similar pattern.

5. *Helminthopsis tunluensis* Yang, 1986, and *H. yushuensis* Yang, 1986. Wave-length should not be used as classifying criterion; these specimens should therefore be placed in *Helminthoida* cf. *miocenica*.

6. The following ichnospecies are congeneric with other forms, as explained in the synonymy list: *H. akkesiensis*, *H. barbeyana*, *H. concentrica*?, *H. curvata*, *H. horizontalis*, *H. intermedia*, *H. involuta*, *H. labyrinthica*, *H. magna*, and *H. sinuosa*. Additionally, *H. sigmoideus* and *H. toyoensis* are regarded as *nomina dubia*.



TEXT-FIG. 7. Typical outlines of the valid *Helminthopsis* ichnospecies: *Helminthopsis abeli* (Książkiewicz 1977, text-fig. 21*c*), *Helminthopsis hieroglyphica* (type material) and *Helminthopsis tenuis* (Książkiewicz 1968, pl. 4, fig. 1). Single letters refer to measurements used in Table 1; H, W: height and width of large loops; h, w: height and width of small loops. Scale bar represents 30 mm.

The remaining ichnospecies clearly differ in their geometrical pattern when the type material is compared (Text-fig. 7).

1. *Helminthopsis abeli* Książkiewicz, 1977. This has irregular open meanders and horseshoe-like turns present. After removal of the lectotype (Abel 1935, fig. 261B) we suggest using the co-type (Książkiewicz 1977, pl. 12, fig. 5, no. UJ TF 1321) to define this ichnospecies.

2. *Helminthopsis hieroglyphica* isp. nov. This has irregular low-amplitude windings, partly straight (see below).

3. *Helminthopsis tenuis* Książkiewicz, 1968. This has irregular, high-amplitude windings, but only with U-turns; horseshoe-like turns are not present.

These differences in pattern can be expressed quantitatively (Table 1). It is important, however, to relate the geometrical characteristics of the windings to the tube diameter, otherwise the relationship will become misleading. For instance, if only the curvature of the centre line of the tube

TABLE 1. Geometrical measurements of the three *Helminthopsis* ichnospecies. The tube diameter is related to the body size of the producing animal. Therefore, the measurements of the windings are expressed as multiples of the diameter of the causative tube of the ichnospecies (see Text-fig. 7).

	H. abeli	*H. hieroglyphica*	*H. tenuis*
Small loop		None	
Width	1–2		6–10
Height	2–3		2–5
Wide loop			
Width	4–6	10	20–25
Height	2–4	20	10–15

on an absolute scale is used, *Scolicia* and *Helminthopsis abeli* do not differ. The same is true for *Helminthopsis abeli* and *Helminthopsis tenuis*.

Helminthopsis hieroglyphica isp. nov.

Text-figures 5, 7

v. 1887	Helminthopsis hieroglyphica Maillard, pl. 2, fig. 4.
non v 1887	Helminthopsis hieroglyphica Maillard, only pl. 1, fig. 2 [= *Spirocosmorhaphe helicoidea* Seilacher, 1989].
non 1888	*Helminthopsis hieroglyphyca* Sacco, p. 175, pl. 2, figs 2, 11 [the specimens are too small to identify the complete geometrical pattern; pl. 2, fig. 2 supposedly = *Helminthopsis abeli*; pl. 2, fig. 11 supposedly = *Spirocosmorhaphe helicoidea* Seilacher, 1989].
v. 1977	Helminthopsis hieroglyphica Książkiewicz, p. 119, text-figs 21*i*, *k–o*, pl. 12, fig. 3.
. 1984	Helminthopsis hieroglyphica Fillion and Pickerill, fig. 9*e*.
. 1988	*Helminthopsis hieroglyphica* McCann and Pickerill, p. 337, pl. 4, fig. 3.
. 1990	Helminthopsis hieroglyphica Fillion and Pickerill, p. 37, pl. 8, fig. 12.
. 1991	Helminthopsis hieroglyphica Crimes and Crossley, p. 38, figs 5*j–l*.
. 1992	*Helminthopsis hieroglyphica* Crimes *et al.*, p. 65, fig. 5A.
. 1993	*Helminthopsis hieroglyphica* McCann, p. 45, fig. 4I.

Repository. Collection of the Geological Institute of the ETH Zürich, Maillard 1887 collection (original for pl. 2, fig. 4).

Diagnosis. Strings 5–10 mm in diameter with irregular windings of low amplitude; the windings are composed of low-angle kinks and straight sections giving the trace a box-shaped fold appearance.

Description. The most characteristic features of this ichnospecies are straight element with often kinky curves giving a box-shaped fold appearance. Somewhat similar forms occur in *Helminthopsis tenuis*, but the strings are much thinner and the box-like arrangement is not so well developed.

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NOTE ADDED IN PROOF

While this contribution was in print, Han and Pickerill (1995) published a paper 'Taxonomic review of the ichnogenus *Helminthopsis* Heer 1877 with a statistical analysis of selected ichnospecies'. These authors based their taxonomic evaluation on the statistical method of 'Fourier Transfer Analysis' (FTA) applied to the course of *Helminthopsis* to distinguish the various ichnospecies. It is a fact that FTA can only be performed on uniquely determined and continuous functions (e.g. Bracewell 1978); therefore burrows having a bell-shaped element or other geometrical pattern, which provides in a coordinate system more tha one y-value for one point on the x-axis (i.e. they are not uniquely determined in x), need to be transformed into a uniquely determined and continuous form. Doing this by the method used by Han and Pickerill causes important geometrical information on the burrow course to be lost while all bell-shaped elements become smoothed-out (see their fig. 3). That this transformation procedure is unsuitable can easily be tested; the forward transformation is uniquely determined, while the backward transformation is not (the statement on this point by Han and Pickerill is wrong), because the inverted function allows the production of more than one burrow course. Consequently, the FT analysis is performed on wrongly produced functions and the results are meaningless. In conclusion, the method applied by Han and Pickerill is not suitable for this specific problem and cannot produce significant results. Thus, the ichnotaxonomy based on this type of transformation method is unreliable. So we suggest our revised taxonomy, which is based on the type material (and not on figures in the literature) and which can be easily performed by everybody because it is based on simple geometrical analysis.

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THE JURASSIC *LITHOCODIUM AGGREGATUM-TROGLOTELLA INCRUSTANS* FORAMINIFERAL CONSORTIUM

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ABSTRACT. *Lithocodium aggregatum*, an enigmatic micro-encruster widespread in Mesozoic shallow marine carbonates, was considered to be a codiacean alga but can now be identified from Upper Jurassic examples as loftusiid foraminifer (Order Lituolida, Superfamily Loftusiacea). The microgranular wall may also contain detrital quartz, a feature which excludes any codiacean affinity. The complex, alveolar though imperforate, wall structure is identical to that of other loftusiid foraminifers; the only difference is the encrusting life habit of *Lithocodium*. The foraminifer is coiled in juvenile growth stages but subsequently developed irregular growth, making it possible for it to contribute to the formation of oncoids and reefal biotic crusts. The numerous alveolar structures, which are covered by only a very thin outer wall, suggest that these alveoli were containers for photoautotrophic symbionts. *Lithocodium* and *Bacinella* are not parts of one single organism, although phrenotheca-like structures crossing parts of the chambers partly resemble the latter. In the Upper Jurassic material, nearly every specimen of *Lithocodium* includes bubble-like structures, formerly interpreted as algal sporangia. These structures are identified here as the foraminifer *Troglotella incrustans*. During its later growth, *Troglotella* developed an irregular shape and grew into the alveoli of the *Lithocodium* walls. This may be interpreted as a commensal relationship, with *Troglotella* feeding on the carbohydrates synthesized by the *Lithocodium* symbionts.

THE encrusting microorganism *Lithocodium aggregatum* is widespread in Mesozoic shallow-water carbonates. It was first described from the Cretaceous of Iraq by Elliott (1956) who interpreted it as a codiacean alga, but later regarded it as a form of uncertain affinity ('*Lithocodium-Bacinella*, a very doubtful structure...', Elliott 1978, p. 438), and its systematic position is controversial. The common, though not obligate intergrowth with *Bacinella irregularis*, another enigmatic micro-encruster (Pl. 1, fig. 5), led to the assumption that both taxa represent a tissue differentiation of one single organism (Segonzac and Marin 1972; Banner *et al.* 1990) or different ecological varieties of one organism (Maurin *et al.* 1985), although these interpretations were mostly not followed by other authors. Leinfelder (1986), regarding the form as *incertae sedis*, discussed some similarities with hydrozoans, stromatoporoids or ancestral coralline algae (see below for further discussion). Based on rich new collections of Upper Jurassic material, we will demonstrate that *Lithocodium* shows all the features of a loftusiid foraminifer such as *Pseudocyclammina lituus*.

Lithocodium exhibits a basal cavity which, in the Upper Jurassic material, is often occupied by bubble-like structures (Text-fig. 1). In the algal model, these structures have been interpreted as sporangia (cf. Endo 1961). Leinfelder (1989), Leinfelder *et al.* (1993), and Schmid *et al.* (1993) showed that these bubble-like structures clearly represent a foraminifer (Text-fig. 2) which was provisionally termed *Bullopora* aff. *laevis*. This foraminifer, exhibiting a coelobitic life style, has now been identified as *Troglotella incrustans* Wernli and Fookes, 1992.

In the Triassic as well as in the Cretaceous, *Lithocodium* appears not to be associated with a coelobitic foraminifer. Instead, the basal cavity is empty or commonly occupied by *Bacinella* (Pl. 1, fig. 5), another enigmatic microencruster, in an intimate relationship which occurs only very rarely in the Upper Jurassic material.

Upper Jurassic *Lithocodium* is often a major contributor to the formation of oncoids as well as

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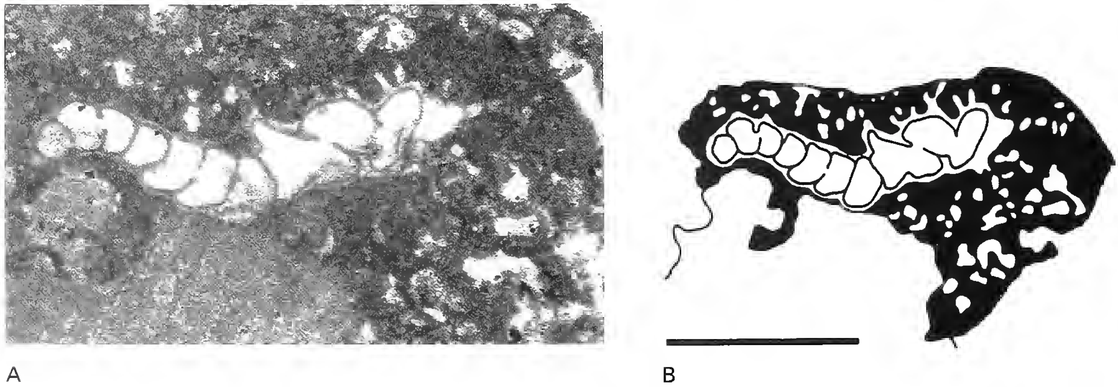
TEXT-FIG. 1. The chambers of *Troglotella* (arrow) have grown into the alveoli of *Lithocodium*. A, thin section 86/28.2.10; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; ×23. B, drawing of the same specimen; scale bar represents 1 mm.



TEXT-FIG. 2. *Troglotella* occupying a chamber of *Lithocodium*. The connections between the chambers of *Troglotella* are partially visible. A, thin section COT IV 15 a; Cabeça beds, late Kimmeridgian; Cotovio near Albufeira, eastern Algarve, Portugal; ×37. B, drawing of the same specimen; scale bar represents 1 mm.

reefal crusts, where it occurs together with *Bacinella*, *Thaumatoporella* and calcareous microbial crusts. This life-style is known from several other foraminifers from other time periods, especially '*Bdelloidina*' *urgonensis* (Wernli and Schulte 1993) and acervulinid foraminifers (see Moussavian and Höfling 1993; Perrin 1994). *Lithocodium*, like some other microencrusters, is nearly always found autochthonous and is of great palaeoecological value (Leinfelder *et al.* 1993), indicating a shallow marine, reefal to lagoonal environment with normal salinity and moderate to elevated water energy. Thus, *Lithocodium* has proven to be a useful environmental indicator in areas where bathymetry is controversial, e.g. the Upper Jurassic of the Swabian Alb (Pl. 1, fig. 4; Leinfelder *et al.* 1994).

MATERIAL

Lithocodium, like most other microproblematica, has been known to date only from thin sections. The material presented here is of Late Jurassic age and consists of numerous thin sections, but also includes a few three-dimensionally preserved specimens. The latter, as well as etched specimens, were examined under the SEM. Most samples are from Portugal (Lusitanian and Algarve Basins); others are from Spain (Celtiberian Basin), Southern Germany (Swabian Alb) and the Czech Republic (Stramberk). Stratigraphically, the samples range from the Oxfordian to the Tithonian. All specimens are in the collection of the Institut für Geologie und Paläontologie, University of Stuttgart.

In the following, locality and stratigraphical details are given for the illustrated material. Further information is in Leinfelder (1986, 1994*a*), Nose (1995), and Schmid and Jonischkeit (1995).

1. Middle Portugal, Lusitanian Basin:

1a. Ota Limestone (reef zone), 'middle' to upper Kimmeridgian: Alenquer (10 km north of Vila Franca de Xira), town quarry. Ota (15 km north of Vila Franca de Xira), valley south of Rio Ota.

1b. Amaral Formation, upper Kimmeridgian: Abadia near Montejunto (12 km north-west of Arruda dos Vinhos), 2·5 km south of the village. Amaral ridge (4·5 km north-east of Arruda dos Vinhos), south-eastern slope. Mata (1·5 km south-west of Arruda dos Vinhos), mountain ridge east of the village. Moinho da Chã (4 km north-west of Arruda dos Vinhos), 0·5 km south-east of the village.

1c. 'Pteroceriano' Formation, lower Tithonian: São Tiago dos Velhos (5 km south-west of Arruda dos Vinhos), 1·2 km south of the village.

2. Southern Portugal, Algarve Basin: Cotovio (3 km north-east of Albufeira), 2 km north of National Street N 125; Cabeça beds, upper Kimmeridgian. São Romão (7 km east of Loulé), 1 km north of the village; São Romão Limestone, lower Kimmeridgian.

3. Southern Germany, Swabian Alb: Wittlingen (4 km south-east of Bad Urach), 'Mockenrain' 1·5 km north-west of the village; coral limestones, lower Tithonian.

SYSTEMATIC PALAEONTOLOGY

In the following we will show that *Lithocodium* is a member of the Cyclamminidae which, according to Loeblich and Tappan (1988), is a group of loftusiid foraminifers. Genera now assigned to the Cyclamminidae or to the Spirocyclinidae were formerly classified as Lituolidae (see Loeblich and Tappan 1964) and therefore were known as lituolid foraminifers. They are now assigned to the Order Lituolida by Loeblich and Tappan (1992).

Class FORAMINIFERA Lee, 1990
Order LITUOLIDA Lankaster, 1885
Superfamily LOFTUSIACEA Brady, 1884
Family CYCLAMMINIDAE Marie, 1941
Subfamily CHOFFATELLINAE Maync, 1958

Genus LITHOCODIUM Elliott, 1956

Diagnosis. As the genus is regarded here as monospecific, its diagnosis is identical to that of the species.

Lithocodium aggregatum Elliott, 1956

Plate 1, figures 1–4; Plate 2, figures 1–6; Text-figures 1–8

1956	*Lithocodium aggregatum* Elliott, p. 331, pl. 1, figs 2, 4 [paratypes], 5 [holotype].
1959	'Problematikum A' Ohlen, p. 73, pl. 10, fig. 1; pl. 17, fig. 3 [quoted from Senowbari-Daryan 1980*b*].
1961	*Lithocodium japonicum* Endo, p. 64, pl. 5, figs 1–3; pl. 15, fig. 2.

1961 *Lithocodium morikawai* Endo, p. 64, pl. 12, figs 1–4; pl. 13, figs 3–4.
non 1964 'Problematikum 3' Flügel, p. 81, pl. 9, figs 1–2, 4 [in pl. 9 termed 'Problematikum 2' by mistake].
1968*a* *Lithocodium* cf. *L. aggregatum* Elliott; Johnson, p. 44, pl. 10, fig. 4.
non 1968*b* *Lithocodium regularis* Johnson, p. 13, pl. 2, fig. 3; pl. 4, figs 6–7.
1969 'Kavernöse Algenkrusten (Problematicum A, Ohlen)'; Zankl, p. 40, text-fig. 41.
1970 '*Lithocodium* Elliott and *Bouenia* [correct name: *Boueina*] Toula'; Bolliger and Burri, p. 38, pl. 9, fig. 2; pl. 11, fig. 1.
1970 *Belzungia* Morellet sp.; Golonka, p. 91, text-fig. 18.
1971 *Lithocodium* Elliott; Barthel *et al.*, p. 13, text-figs 7F, 8A.
non 1971 '*Lithocodium*-artiges Algen-Aggregat'; Barthel *et al.*, p. 15, text-fig. 8D.
non 1971 *Lithocodium aggregatum* Elliott; Basson and Edgell, p. 416, pl. 1, fig. 1.
non 1971 *Lithocodium regulare* Johnson [specific name corrected]; Basson and Edgell, p. 417, pl. 1, figs 2–3.
1971 *Lithocodium aggregatum* Elliott; Ramalho, p. 174, pl. 9. fig. 1; pl. 28, figs 3–5; pl. 29, fig. 1.
1972 *Lithocodium* Elliott/*Bacinella* Radoicic; Segonzac and Marin, pl. 11, figs 1–8.
1979 *Pseudolithocodium carpaticum* Misik, p. 709, pl. 2, figs 2–8.
1981 *Bacinella crispa* Eliasova, p. 30, pl. 2, fig. 3 [*partim*].
1984 *Bacinella morikawai* (Endo); Elias and Eliasova, pl. 1, fig. 4.
1985 *Bacinellacodium calcareus* Dragastan, p. 126, pl. 27, figs 1–3 [each *partim*].
v. 1986 *Lithocodium* Elliott sp.; Leinfelder, p. 60, pl. 12, figs 1–3.
1990 *Lithocodium aggregatum* Elliott; Banner *et al.*, p. 26, pl. 1, ?fig. 1, figs 2–4; ?pl. 2; pl. 3, fig. 1, ?figs 2–4; *non* pl. 4; *non* pl. 5; text-fig. 1. [The authors regard *Lithocodium* and *Bacinella* as synonyms.]
non 1992 *Lithocodium aggregatum* Elliott; Neuweiler and Reitner, pp. 274, 277, pl. 1; pl. 2, figs 1–2; pl. 3, figs 1–6. [The authors regard *Lithocodium* and *Bacinella* as synonyms.]
v. 1993 *Lithocodium* Elliott sp.; Leinfelder *et al.*, p. 202, pl. 42, figs 1–7; text-figs 6–7.
v. 1994*a* *Lithocodium* Elliott sp.; Leinfelder, p. 19, text-fig. 22.

Diagnosis (*emended*). Test multilocular, attached, chambers dome-shaped and roughly planispirally coiled or irregularly arranged in one or more layers; wall microgranular, calcareous and therefore probably a variable mixture of finely agglutinated and secreted calcite, may contain silt- to fine-sand-sized siliciclastic particles; wall dark in transmitted light, with imperforate thin outer layer (epiderm) and thick inner alveolar layer, forming a hypodermal meshwork; alveoli cylindrical, may bi- or trifurcate; attachment surface serving as a basal wall, substrate may be etched; aperture areal and cribrate; occasionally very thin dark lines crossing the chambers of the alveoli can be found, which appear to be phrenotheca-like structures; test commonly exhibiting a brownish coloration in reflected light, rarely white in very pure limestone.

Upper Jurassic specimens are commonly associated with a coelobitic foraminifer, *Troglotella incrustans* Wernli and Fookes (see below), appearing as bubble-like, often irregular structures within the chambers of *Lithocodium*. Outer diameter of chambers 0·8–3 mm; inner diameter of chambers 0·5–2 mm; wall thickness 0·5 mm; thickness of imperforate outer wall layer 8 μm; diameter of cylindrical alveoli 25–90 μm.

Remarks. The original description of Elliott (1956) is still regarded as being valid and is only enlarged and modified terminologically here, since Elliott interpreted *Lithocodium* as a codiacean alga. No significant differences exist between the Jurassic and the Cretaceous specimens described by Elliott, which can be verified best by examination of the paratype figured in his pl. 1, fig. 2.

The bubble-like structures mentioned in the diagnosis, actually representing a coelobitic foraminifer (see below), have been earlier interpreted as sporangia (Endo 1961). The species which have been defined mainly on account of this feature (*L. japonicum* and *L. morikawai*) must therefore be regarded as invalid.

Stratigraphical distribution. Anisian to Cenomanian, ?Turonian. According to Moussavian (1992), the taxon occurs up to the Campanian/?Maastrichtian; but the low magnification of the figures does not allow exact verification.

Superfamily HORMOSINACEA Haeckel, 1894
Family TELAMMINIDAE Loeblich and Tappan, 1985

Diagnosis. 'Test attached in the early stage only or throughout growth, consisting of a series of chambers that may be closely appressed or connected by stolonlike tubes; wall agglutinated; no obvious aperture other than the ends of the stolons' (Loeblich and Tappan 1988, p. 56).

Genus TROGLOTELLA Wernli and Fookes, 1992

Diagnosis. As the genus is monospecific, its diagnosis is identical to that of the species.

Troglotella incrustans Wernli and Fookes, 1992

Plate 1, figures 1–4; Plate 2, figures 1–6; Text-figures 1–8

1961 'Sporangia' (within *Lithocodium japonicum*); Endo, p. 64, pl. 5, figs 2–3; pl. 15, fig. 2.
1971 Unnamed structure (within *Lithocodium*); Barthel *et al*., text-figs 7F, 8A.
1971 Unnamed structure (within *Lithocodium*); Ramalho, pl. 9, fig. 1; pl. 28, figs 3–5; pl. 29, fig. 1.
1981 *Bacinella crispa* Eliasova (within *Lithocodium*), p. 30, pl. 2, fig. 3.
1985 *Micrisphaera ovalis* [author = ?] (sporangia within *Lithocodium*); Connally and Scott, text-fig. 9D.
1985 *Bacinella* Radoicic (within *Lithocodium*); Hüssner, pl. 17, fig. 7.
v. 1986 'Sporangia' (within *Lithocodium*); Leinfelder, p. 60, pl. 12, figs 1–2.
1986 'Mikroproblematikum 10' Werner, pl. 16, figs 8–10.
v. 1989 *Bullopora* aff. *laevis* Sollas; Leinfelder, pp. 51, 56, pl. 2, fig. 6; pl. 3, fig. 5; pl. 4, fig. 5.
1991 Unnamed structure (within *Lithocodium*); Darga and Schlagintweit, pl. 2, fig. 6.
1992 'Structures globuleuses'; Bodeur, pl. 18, figs 1–2 [*partim*], 3–4, 11.
1992 *Troglotella incrustans* Wernli and Fookes, p. 97, pls 1–2.
v. 1993 *Bullopora* aff. *laevis* Sollas; Leinfelder *et al*., p. 203, pl. 40, fig. 2; pl. 42, figs 2–7.
v. 1994*a* ?*Bullopora* aff. *laevis* Sollas; Leinfelder, pp. 19, 24, text-figs 22, 25.

Diagnosis (*emended*). The test of *Troglotella incrustans* exhibits two different stages. The juvenile stage is uniserial, slightly curved, consisting of not more than seven or eight chambers and may be situated in a cavity bored by the foraminifer itself, whereas the adult stage encrusted the surface of the substrate. In most cases, *Troglotella incrustans* dwelt in the chambers of the foraminifer *Lithocodium aggregatum* Elliott, 1956, often without boring activity in the juvenile stage. Chamber form in the juvenile stage is spherical to cylindrical, in the adult stage it is commonly irregular or pyriform. Juvenile chambers closely adjacent, later chambers may be separated by stolon-like necks; aperture single, terminal, at the open end of the stoloniferous necks. Wall thin, microgranular, calcareous, imperforate, probably agglutinated; dark in transmitted light. According to the original authors (Wernli and Fookes 1992), short and stocky forms are thought to represent the megalospheric generation, whereas long and slim forms would represent the microspheric generation. The measurements taken from our material are as follows: total length up to 2 mm; diameter of proloculus 50–70 μm (presumed 'microspheric' form); maximum diameter of regular chambers (juvenile stage) 250 μm; maximum diameter of irregular, tube-like chambers 1 mm; number of chambers in juvenile stage not more than seven or eight; length of juvenile part of the test 600–700 μm; total number of chambers 12 to 15; wall thickness 5–10 μm.

Remarks. Our diagnosis contrasts partly with the observations of Wernli and Fookes (1992), who state that the juvenile stage may reach 1·9 mm in length, visible in one specimen (Wernli and Fookes 1992, pl. 1, figs 1, 4). In our opinion, only the first seven to eight chambers, with a maximum length of 700 μm, represent the juvenile stage, characterized by the regular, spherical to cylindrical chamber form (Pl. 1, fig. 1; Text-fig. 6). Later chambers are mostly irregular, but may rarely retain a regular shape. The adult stage of the specimen figured in Wernli and Fookes (1992, pl. 1, fig. 2) is thought to reach 4 mm in diameter, which is not verifiable from the figure itself. Wernli and Fookes (1992) suggested the existence of both microspheric and megalospheric forms. This is plausible and substantiated by their figures. However, due to the irregular morphology of the test and the impossibility of isolating it from the hard calcareous host rocks, thin section material may show all ranges from a very small to a fairly large first chamber. It must be assumed that the proloculus is not always cross-cut at its largest diameter, due to the irregularity of the test, which makes identification of microspheric and megalospheric forms difficult.

Probably, *Troglotella incrustans* was able to branch, although the evidence provided by the present thin section material is equivocal. Branching foraminifers are known particularly among the Telamminidae (see Loeblich and Tappan 1988), but do also occur within several other groups.

Attribution to the Lituolida. The imperforate, microgranular fabric of the wall (pl. 2, fig. 6), which is dark in transmitted light, occurs similarly in miliolids. In reflected light, however, the brownish colour of the test contrasts with the typical bright white coloration of the miliolids, and clearly excludes an attribution to this group. Wernli and Fookes (1992) tentatively attributed the taxon, with some reservations, to the Telamminidae. The features detected in the present material substantiate this interpretation.

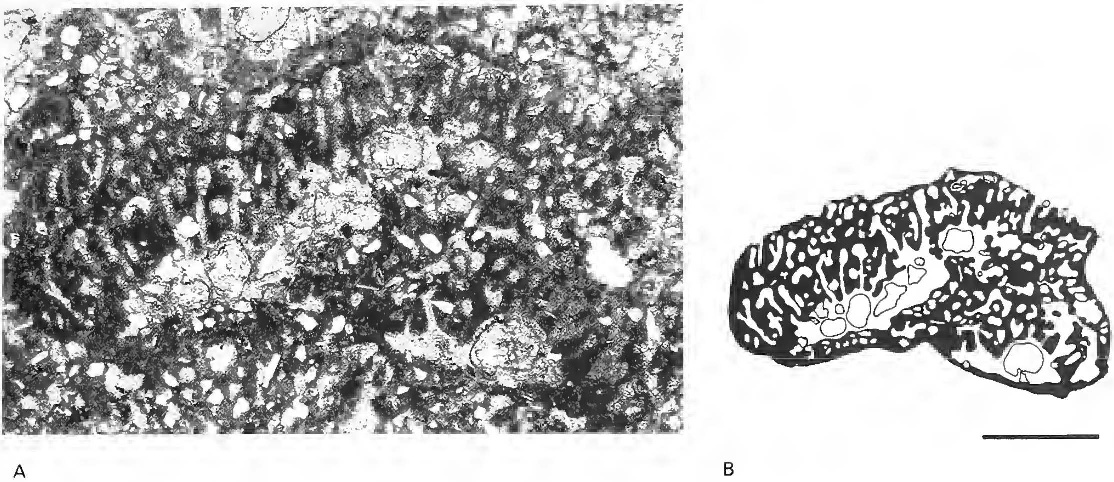
Life habit and association. Troglotella incrustans was a facultative borer in its juvenile stage, boring perpendicularly into its substrate (Pl. 2, fig. 5, Text-fig. 6). Wernli and Fookes (1992), despite clearly figuring boring specimens, alternatively suggested cryptic settlement within pre-existing cavities or borings of other, unknown, organisms (for discussion see below). Other specimens do not exhibit an early boring stage but only inhabited pre-existing cavities. Later growth stages expanded over the substrate, either in an epibenthic fashion or, much more commonly, within pre-existing cavities. In our material, the vast majority of *Troglotella* grew within the chambers of *Lithocodium aggregatum* (Superfamily Loftusiacea), in very shallow, generally wave-agitated settings.

Stratigraphical distribution. Oxfordian to Tithonian.

DETAILED DESCRIPTION OF *LITHOCODIUM* AND DISCUSSION

Wall characteristics

The wall of *Lithocodium* is microgranular, i.e. dense, dark, and therefore probably originally calcitic (Pl. 2, fig. 6). In reflected light, *Lithocodium* shows a brownish to reddish coloration in most samples, which is a typical feature of agglutinating foraminifers (Haynes 1981). Consequently, the microgranular wall structure can be interpreted as finely agglutinated, a feature typical of loftusiid as well as orbitolinid foraminifers and others. Some authors (e.g. Podobina 1990) consider microgranular walls as being secreted in a similar manner to those of the fusulinids. In any case, *Lithocodium* was able to agglutinate detrital particles, which is particularly evident when siliciclastic material is incorporated (Text-fig. 3). Within the loftusiid foraminifers, all transitions from walls composed solely of coarsely agglutinated particles (e.g. *Flabellamminopsis*) to walls with a purely microgranular structure (e.g. *Alveosepta jaccardi*) exist. The tests of *Rectocyclammina* or *Otaina magna*, for example, are composed of both coarse, agglutinated and microgranular material. The amount of coarse particles appears variable (cf. Ramalho 1990), a feature which is consistent with the observations on *Lithocodium*. In *Lithocodium*, incorporation of considerable amounts of silt- to fine-sand-sized siliciclastics (quartz, feldspar, mica; Text-fig. 3) occurs only in terrigeneously contaminated settings; this is similar to the situation in other loftusiid taxa such as *Rectocyclammina*. Despite its rarity, explicable by the strong preference of *Lithocodium* for pure carbonate settings, this is a strong additional argument against the codiacean affinities of *Lithocodium*.



TEXT-FIG. 3. *Lithocodium* nodule containing a high percentage of detrital quartz. The chambers are occupied by *Troglotella*. A, thin section Ab I 7; Amaral Formation, late Kimmeridgian; Abadia near Montejunto, Lusitanian Basin, Portugal; ×26. B, drawing of the same specimen (siliciclastic particles are stippled); scale bar represents 1 mm.

The numerous alveoli in the wall are responsible for the complex labyrinthic wall fabric, a feature typical for all loftusiid and orbitolinid foraminifers. Alveoli of *Lithocodium* can be bi- or trifurcate (Ramalho 1971, p. 174; Text-fig. 1), which makes them appear like algal filaments or cyanobacterial trichomes. However, well preserved material often shows that the alveoli are coated by an outer imperforate layer. The outer layer prevents penetration of sediment even into dead tests, which explains why all cavities are preserved by calcitic spar, unless the test was damaged. Alveoli covered by a thin wall clearly exclude an algal origin but are a typical feature of all loftusiid foraminifers, which are imperforate. In well preserved specimens, where preservational bias can be ruled out, open, spar-filled alveoli are interpreted as representing openings to the adjacent chamber. The generally imperforate nature of *Lithocodium*, as well as the dense, hence probably originally calcitic, structure of its wall has already been noticed by Persoz and Remane (1973, p. 59, pl. 2, fig. 3) who therefore doubted its codiacean nature, without, however, suggesting other explanations.

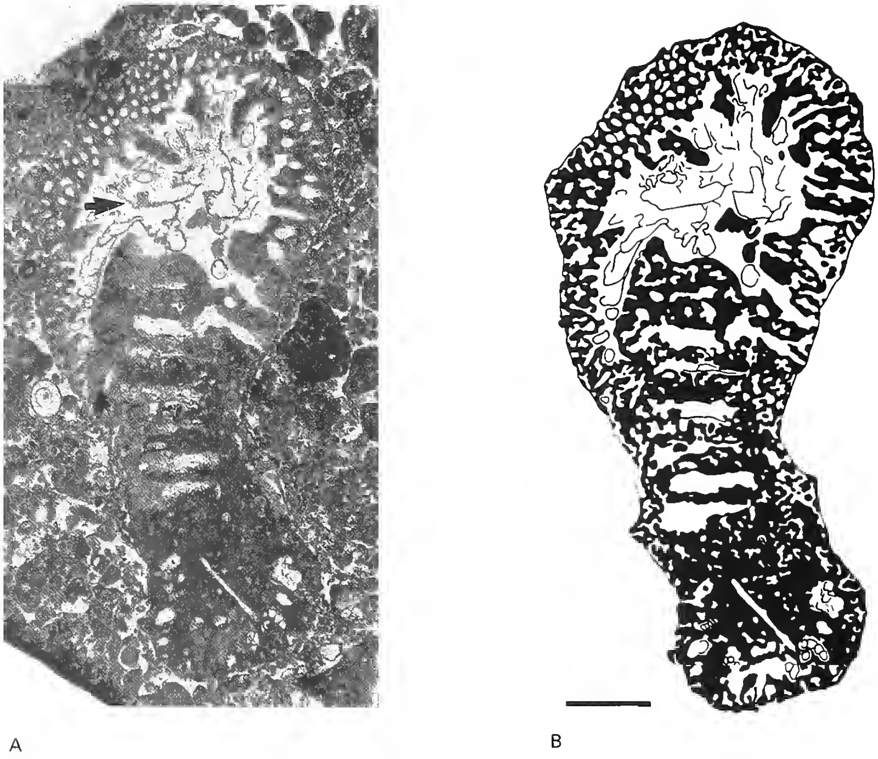
Thin section analysis reveals that these chamber openings of *Lithocodium* are cribrate. The same is assumed for *Paracyclammina* whose openings are also known only from thin sections (Loeblich and Tappan 1988, p. 102).

General growth form and comparison with other loftusiid taxa

An attribution of *Lithocodium* to the Cyclamminidae is not only evident by the labyrinthic, originally calcitic, wall structure but, partly, also by the dimensions and hemispherical shape of the chambers of *Lithocodium*.

Paracyclammina (Loeblich and Tappan 1988, pl. 99, figs 10–13), *Pseudocyclammina* (Loeblich and Tappan 1988, pl. 102, figs 4–6) or *Loftusia* (Loeblich and Tappan 1988, pl. 116, fig. 10) exhibit wall structures virtually identical to those of *Lithocodium*, but differ in dimensions and general growth form. Some cross sections do not allow differentiation between *Lithocodium* and other loftusiid foraminifers. Close similarity exists with *Pseudocyclammina lituus* (cf. Maync 1959, pls 1–6; Hottinger 1967, text-fig. 29*a–b*, pl. 10, figs 11–13), which is particularly similar to *Lithocodium* not only in respect of its wall characteristics, but also regarding its general growth form, although it exhibits smaller chambers. *Pseudocyclammina* tests, though often planispiral, may instead exhibit a streptospiral juvenile growth stage and may become uncoiled in the adult stage (Loeblich and Tappan 1988). Chamber dimensions and the uncoiled adult growth stage of *Rectocyclammina* are also comparable with *Lithocodium*, although the alveolar fabric of the wall differs (Ramalho 1971, pl. 14, fig. 2). This is also true for *Otaina magna*, which may look quite similar to *Lithocodium* in some sections (Pl. 1, fig. 6) but differs from the latter by incorporating coarse bioclasts in its wall (cf. Ramalho 1990). *Loftusia farsensis*, of Maastrichtian age, is almost identical with *Lithocodium* in the structure of its alveolar wall and distinct hemispherical shape of its chambers, and the relation between wall and chamber dimensions (cf. Mehrnusch 1985, text-fig. 2, figs 1–2), but differs from the latter by the smaller dimension of the chambers and by its planispiral growth.

Leinfelder (1989, pl. 4, fig. 5; 1994*a*, text-fig. 2) figured a large, coiled 'lituolid' foraminifer and mentioned close similarities with *Lithocodium* both in the structure of the wall and in the existence of the coelobitic foraminifer '*Bullopora* aff. *laevis*' (identical to *Troglotella incrustans*). Re-examination shows that no differences from *Lithocodium* exist so that the foraminifer is interpreted now as a planispirally coiled specimen of *Lithocodium* (Text-fig. 4). In other thin sections, both the diameter and the alveolar size of subsequent small *Lithocodium* chambers may increase in a regular fashion, which also might indicate a coiled juvenile growth stage (Pl. 2, fig. 2). Moreover, *Lithocodium* specimens in three dimensional preservation show a more or less well developed coiled



TEXT-FIG. 4. Coiled specimen of *Lithocodium*. The chambers are occupied by *Troglotella* (arrow), whose test walls are not completely preserved. A, thin section SOT 1; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; × 12. B, drawing of the same specimen; scale bar represents 1 mm.

chamber arrangement (Text-fig. 5). All these features are also shown in the model of *Lithocodium* (Text-fig. 7), reconstructed from numerous thin sections.

A difference from *Pseudocyclammina* or *Rectocyclammina* is the dominantly encrusting growth of *Lithocodium* during later growth stages. Irregular growth along the substrate is known from *Anchispirocyclina lusitanica*, another large Upper Jurassic/Lower Cretaceous loftusiid foraminifer, which may also bifurcate (cf. Ramalho 1971, p. 148, pl. 15, figs 6–7; pl. 16).

According to Septfontaine's (1980) determination key for imperforate Mesozoic foraminifers, *Lithocodium* falls in 'group C2' (planispirally coiled, later uncoiled and rectilinear, with subepidermal layer without pillars, aperture multiple, test attached) and hence is a close relative of *Pseudocyclammina*, which only differs from the latter in its more irregular growth and larger chambers.

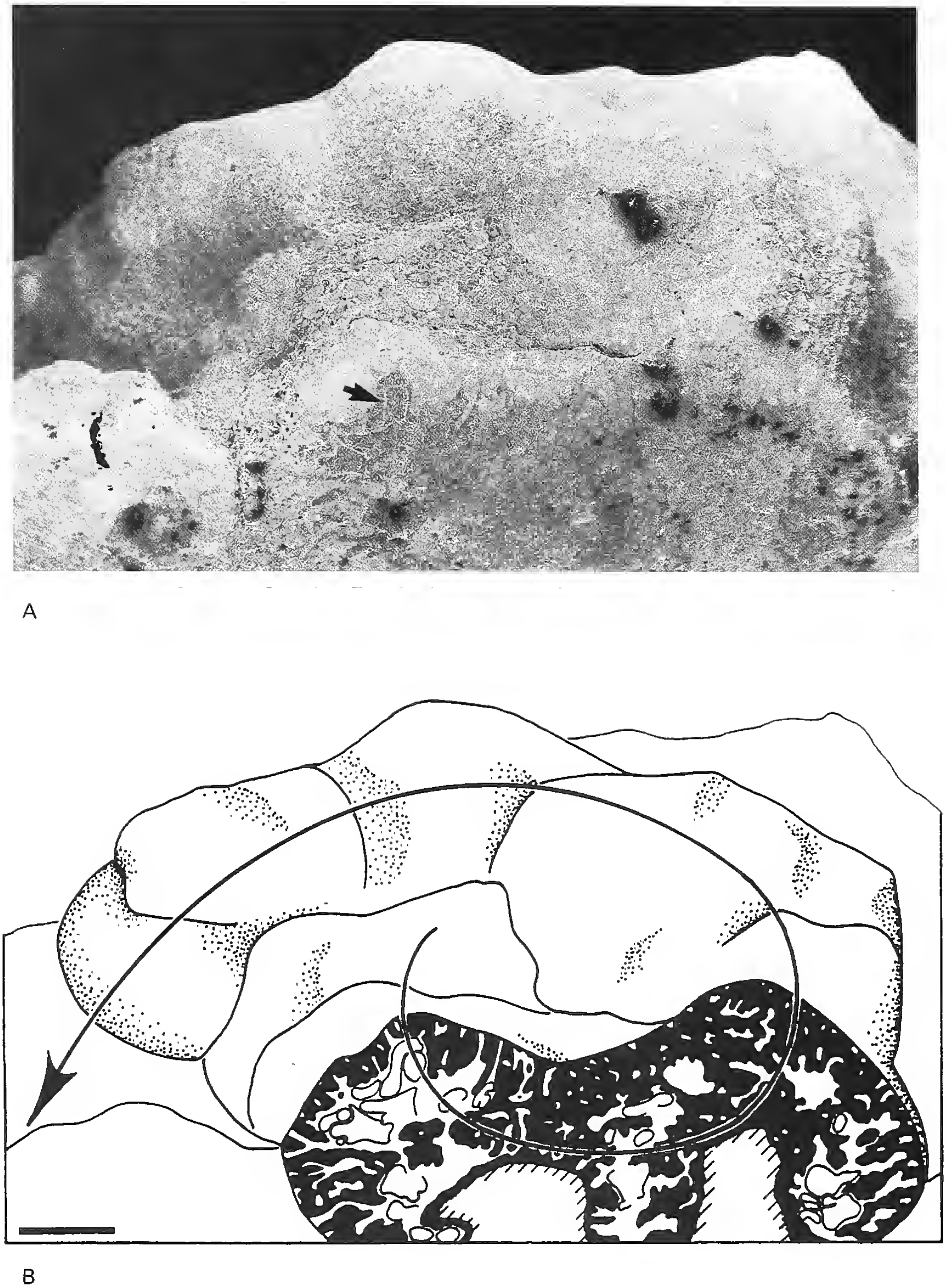
Occasionally, the calcareous substrate of *Lithocodium* shows etching and dissolution features, e.g. thin bivalve shells which are partly dissolved in places where overgrown by *Lithocodium* (Pl. 2, fig. 3). This indicates that *Lithocodium* normally had no basal wall, although in some cases a minute dark basal layer is visible. This is another argument against an interpretation of it as an encrusting alga which normally are attached by a basal skeleton. Sessile foraminifers rarely produce a basal wall below their chambers, since normally (i.e. in coiled forms) the outer walls of preceding chambers serve as substrate. It is known from other encrusting foraminifers, such as the Cretaceous '*Bdelloidina*' *urgonensis* (Wernli and Schulte 1993, pl. 1, figs 5, 8) or the Palaeozoic form *Oxinoxis* (Loeblich and Tappan 1988, p. 64), that the attachment surface may serve as basal wall.

Association with other encrusting organisms

The chambers of Upper Jurassic *Lithocodium* are very commonly occupied by the coelobitic foraminifer *Troglotella incrustans* (see below). *Troglotella incrustans* may also occur outside *Lithocodium*, but never within the test of other foraminifers. *Lithocodium* is furthermore commonly associated with the micro-encrusters *Bacinella* and *Thaumatoporella*, both of which are of uncertain, probably cyanobacterial and algal affinity, respectively. Cayeuxiid cyanobacteria and solenoporacean red algae may co-occur as well. *Lithocodium* is typical of reefal, coral-rich settings as well as non-reefal oncoid environments.

Invalidity of other Lithocodium *species and of the genera* Bacinellacodium *and* Pseudolithocodium

The synonymy list of *Lithocodium aggregatum* presented above shows that we consider all species other than the type species, *L. aggregatum*, as invalid. This is based on the fact that the bubble-like structures present in the chambers of some specimens of *L. aggregatum* (e.g. Pl. 1, fig. 4; Text-figs 3, 7) clearly represent a coelobitic foraminifer (see below) and not calcified sporangia of *Lithocodium*. The latter was assumed by Endo (1961) who separated species with such 'sporangia' from the sporangia-lacking *L. aggregatum*. He established the 'sporangia'-bearing species *L. japonicum* and *L. morikawai* on the basis of the tertiary branching of the filaments (now alveoli) of *L. morikawai*. The present rich material shows that filaments of all sizes and kinds in the range of the above specimens may exist even within one large *Lithocodium* specimen (e.g. Pl. 1, figs 2–3). Differences are due both to variations between juvenile and adult growth stages, and to artificial effects of two-dimensional sampling. All criteria given and figured for the taxa *Pseudolithocodium carpaticum* and *Bacinellacodium calcareus* also fall in the variability of our *Lithocodium aggregatum* material. Consequently, all recorded species of *Lithocodium*, as well as the last two genera, are presumably invalid, although this conclusion is not based on the examination of the original material. *Lithocodium regulare* Johnson is not identical to *Lithocodium aggregatum*, but probably to *Pseudocyclammina* (see below).



TEXT-FIG. 5. Three-dimensionally preserved specimen of *Lithocodium*; the chambers are occupied by *Troglotella* (arrow). A, CHA 1/F, scanning electron micrograph; Amaral Formation, late Kimmeridgian; Moinho da Chã near Arruda dos Vinhos, Lusitanian Basin, Portugal; × 12. B, drawing of the same specimen. The arrow indicates the spiral succession of the *Lithocodium* chambers; scale bar represents 1 mm.

EARLIER INTERPRETATIONS OF *LITHOCODIUM*

Codiacean nature?

Earlier authors attributed *Lithocodium*, partly with reservations, to the codiacean green algae (e.g. Elliott 1956; Ramalho 1971; Jaffrezo 1974). The following features described above argue against this: (1) dark in transmitted light due to the presumed original calcitic fabric; fossil codiaceans, such as *Boueina*, are always light under transmitted light due to the recrystallized character of the original aragonite skeleton; (2) ability to agglutinate siliciclastic particles; (3) encrusting life-style; and (4) clearly to crudely coiled during early growth stages.

A single Lithocodium-Bacinella *organism?*

Parts of structures described as *Bacinella* are identical to *L. aggregatum* (see synonymy list). This confusion is partly a result of considering *Bacinella* (Pl. 1, fig. 5) as the older, valid name for the same organism described as *Lithocodium*. Actually, *Lithocodium* and *Bacinella* are often intimately associated and may commonly overgrow each other. This led to the assumption that the two taxa are parts of one single organism, either representing cortex and medulla, respectively, of a codiacean alga (Banner *et al.* 1990), an organism *incertae sedis* (Segonzac and Marin 1972), or different ecological varieties of an enigmatic organism (Maurin *et al.* 1985; Neuweiler and Reitner 1992). If it is true that *Bacinella* is a microbe (Maurin *et al.* 1985), possibly a cyanobacterium (Schäfer and Senowbari-Daryan 1983), this would imply that *Lithocodium* also represents a different ecological variety of the same cyanobacterium. Agglutination of detrital material, as observed in the present material, would be compatible with a cyanobacterian character. However, the regular growth form and, particularly, the outer imperforate layer clearly exclude a cyanobacterian nature for *Lithocodium*. It should be mentioned that Schäfer and Senowbari-Daryan (1983), though considering *Bacinella* to be a cyanobacterian microbe, did not see any relation to *Lithocodium* which was interpreted as a codiacean alga. Generally, the interpretation of genomic identity of *Bacinella* and *Lithocodium* is not followed by most authors or is clearly rejected (e.g. Conrad 1969, p. 63; Wnendt-Juber 1990, p. 101; Leinfelder *et al.* 1993), based on the fact that both taxa may occur together in the same environment, without overgrowing each other, or simply occur without each other.

Confusion with *Bacinella* has resulted particularly from the occasional occurrence of phrenotheca-like structures which may cross chambers or even alveoli of *Lithocodium* in various places and at various angles (Pl. 2, fig. 1; Text-figs 7–8). They are irregular, thin, dense partitions which may be interconnected and hence appear in a mesh-like, 'bacinellimorph' fashion. Phrenotheca are facultative structures of unknown function which occur in some fusulinids, particularly in *Pseudofusulina* (Loeblich and Tappan 1964, fig. 291; 1988, pl. 283, fig. 8). Similar structures also occur in some loftusiid foraminifers, such as *Valvulina lugeoni* (Septfontaine 1980, pl. 3, fig. 7) as well as in other foraminiferal groups (e.g. *Biokovina*, cf. Loeblich and Tappan 1988, pl. 82, figs 2–4). We also detected them in Portuguese material of *Otaina magna*, although they are not mentioned in the original description by Ramalho (1990, pl. 2, fig. 1; pl. 3, fig. 1).

Phrenotheca-like, 'bacinellimorph' structures are common in Triassic and Cretaceous *Lithocodium* but also occur occasionally in Upper Jurassic material (see below). Confusion of phrenotheca-like foraminiferal structures with *Bacinella irregularis*, an enigmatic organism of unclear systematic position, can be avoided when restricting *Bacinella* to clearly epibenthic meshwork crusts of noticeable thickness and extension.

Attribution to multicellular animals?

Leinfelder (1986) assigned *Lithocodium* to the '*incertae sedis*'. However, he noticed certain similarities to multicellular animals in the complex character of the labyrinthic wall, the detection of occasional cross-partitions within 'filaments' (i.e. alveoli), and the existence of larger cavities.

Hydrozoans and stromatoporoids show similarities in the occurrence of both horizontal and vertical elements. However, the present material shows that cross-partitions are a rare, possibly secondary, feature and the basal cavities of *Lithocodium* cannot represent an astrorhizal system of stromatoporoids but rather are individualized chambers. The character of stacked chambers, as well as the multiporous connections between them, show some similarities with segmented coralline sponges (sphinctozoans). General size, labyrinthic wall structure, the partly coiled nature and the ability to agglutinate detrital particles clearly stands against such an interpretation, although it should be noticed that general morphological similarities between foraminifers and sphinctozoans may exist. An example is the Triassic problematical form *Cheilosporites tirolensis* Wähner which was interpreted as foraminifer by Fischer (1962) and as sphinctozoan sponge with microcrystalline wall structure by Senowbari-Daryan (1980*a*).

Earlier 'near misses' of the foraminiferan character

Interestingly, some earlier interpretations already approached the idea of the foraminiferan character of *Lithocodium*, but the authors failed to recognize it.

Senowbari-Daryan (1980*b*), after a similar suggestion by Schäfer (1979), identified 'Problematicum A' Ohlen (1959) as a younger synonym of *Lithocodium aggregatum*. Some confusion was caused by another similar enigmatic encruster, which had been described by Flügel (1964, p. 81; 1972, p. 966) as 'Problematicum 3'. Flügel interpreted this coarse agglutinating organism as a foraminifer and compared it with 'Problematicum A' Ohlen (i.e. with *Lithocodium* according to Senowbari-Daryan 1980*b*). Zankl (1969, p. 46, text-fig. 57) described the same form, 'Problematicum 3' Flügel (1964) also as a sessile foraminifer. However, Senowbari-Daryan (1980*b*, p. 90) rejected the synonymy of 'Problematicum 3' Flügel with 'Problematicum A' Ohlen/*Lithocodium* but rather noticed similarities of 'Problematicum 3' to the loftusiid foraminifer *Labyrinthina* Weynschenk.

Schäfer (1979) noted that 'Problematicum A' Ohlen/*Lithocodium* could be placed either within the codiaceans or within the foraminifers, but this interpretation is obviously based on the erroneous synonymization of 'Problematicum 3' Flügel and 'Problematicum A' Ohlen (see above).

Johnson (1968*b*) established the species *Lithocodium regularis* (later corrected to *L. regulare* by Basson and Edgell 1971). Originally assuming a codiacean character, Johnson later noticed the foraminiferan character of the form (Johnson 1969, p. 38). In our opinion, it probably represents the genus *Pseudocyclammina*, as the chamber dimensions are too small for *Lithocodium*.

EXPLANATION OF PLATE 1

Fig. 1. *Lithocodium* chamber, occupied by *Troglotella* and overgrown by the stromatoporoid *Burgundia trinorchii*. Acetate peel M I 6; Amaral Formation, late Kimmeridgian; Mata near Arruda dos Vinhos, Lusitanian Basin, Portugal; × 23.

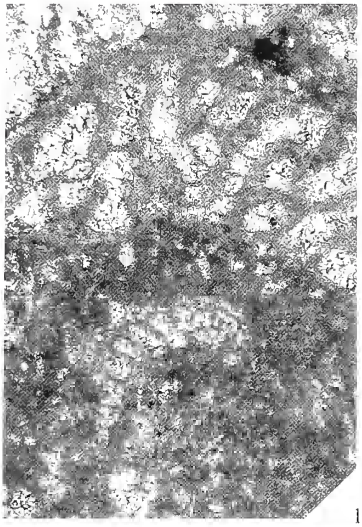
Figs 2–3. 2, Thick *Lithocodium* crust, overgrowing *Marinella lugeoni* (left). Spirally arranged chambers (arrow) indicate a coiled growth stage. All chambers are occupied by *Troglotella*. Thin section SV 26a; 'Pteroceriano' Formation, early Tithonian; São Tiago dos Velhos near Arruda dos Vinhos, Lusitanian Basin, Portugal; × 8. 3, Detail of part of fig. 2 (from right hand side). Chamber formation is progressing from left to right, as shown in Text-fig. 8; × 18.

Fig. 4. *Lithocodium*, overgrowing and overgrown by *Pseudochaetetes polyporus* and an oyster. All chambers are occupied by *Troglotella*. Thin section WIT 1/1; coral limestones, early Tithonian; Wittlingen near Bad Urach, Swabian Alb, Germany; × 15.

Fig. 5. The meshwork structure of *Bacinella irregularis*, an enigmatic microencruster which is commonly, though not necessarily associated with *Lithocodium*. Thin section RO 112; São Romão Limestone, early Kimmeridgian; São Romão near Loulé, eastern Algarve, Portugal; × 12.

Fig. 6. *Otaina magna*, a loftusiid foraminifer with a structure similar to that of *Lithocodium*. Thin section 86/26.2.18; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; × 23.

PLATE 1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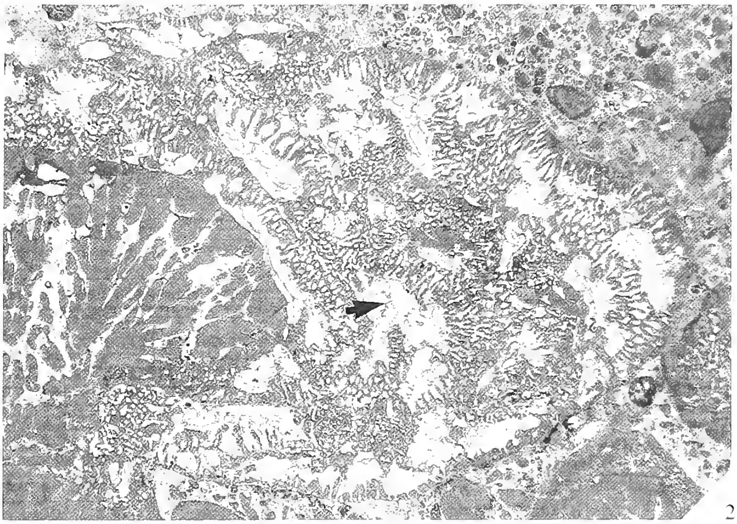
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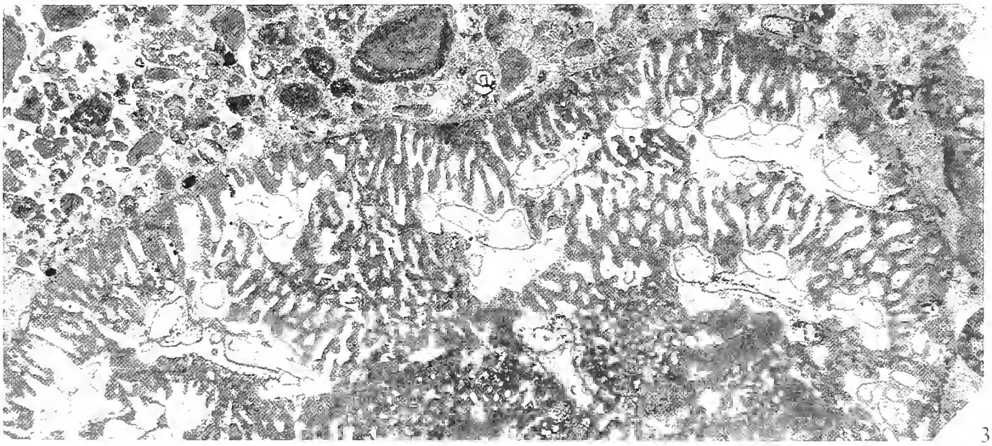
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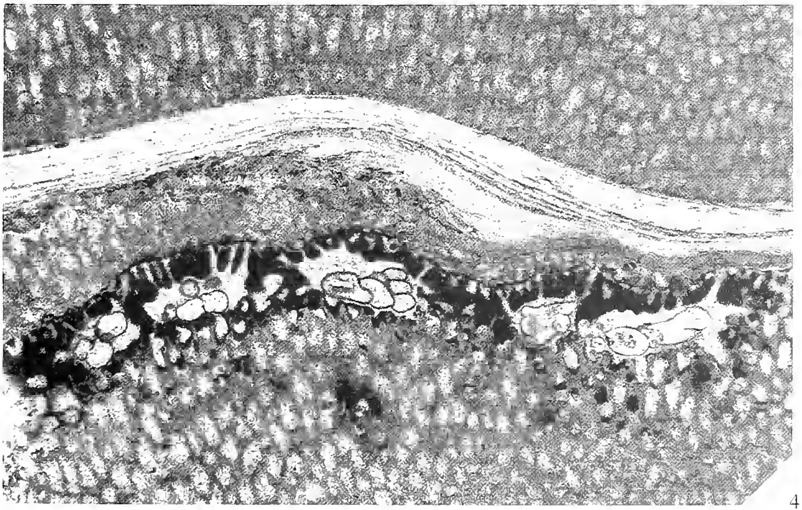
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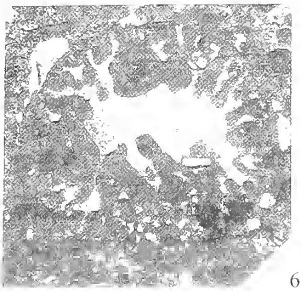
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SCHMID and LEINFELDER. *Lithocodium-Troglotella* foraminiferal consortium

Segonzac and Marin (1972) noticed some similarities to the foraminifer *Coscinophragma* but concluded that other features, particularly the presumed identity with *Bacinella* (see above), were not compatible with a foraminiferan character.

Leinfelder (1989, 1994*a*) described coiled 'lituolid' foraminifers with a close similarity to the *Lithocodium* structure, but did not synonymize both, due to the fact that the figured specimen represented the only known coiled exemplar at that time (see above).

ECOLOGICAL REQUIREMENTS AND LIFE STRATEGY OF *LITHOCODIUM*

Both the association with reefal and non-reefal microbial crusts, and typical shallow-water organisms such as corals, stromatoporoids, dasycladacean algae or red algae show that *Lithocodium* was a fully marine, shallow-water organism (Leinfelder *et al.* 1993). As an encruster, it demanded a low background sedimentation rate and commonly grew alternating with other organisms such as microbial or algal-type organisms (e.g. *Bacinella* or *Thaumatoporella*) or stromatoporoids (particularly *Burgundia*). *Lithocodium* frequently also contributed to the formation of oncoid cortices where it co-occurred with microbial crusts, *Bacinella*, cayeuxiid cyanobacteria, red algae, nubeculariid and placopsilinid foraminifers as well as bryozoans. Besides lagoonal low-energy settings, it more commonly occurred in debris-rich, high-energy reefs (Leinfelder 1992), indicating its tolerance of elevated water energy. Pure carbonate environments were preferred but a certain influx of siliciclastic material could be tolerated, whereby the siliciclastic particles may have become incorporated in the test (see above). Being readily identifiable, *L. aggregatum* is a valuable palaeoecological indicator.

L. aggregatum commonly occurs in colonies, i.e. various specimens or generations overgrew each other forming flat to domal, crustose colonies which are up to several tens of millimetres thick and broad (Pl. 1, figs 2–3). Pure *Lithocodium* nodules (Pl. 2, fig. 4) and oncoids exist as well. With the additional participation of *Bacinella* and microbial crusts they may attain diameters of up to 100 mm. To a small extent, *Lithocodium* may also have contributed to reef formation, partly acting as a binder but more as a constructor. This is a close analogue of the agglutinating Cretaceous foraminifer '*Bdelloidina*' *urgonensis* (cf. Schulte *et al.* 1993; Wernli and Schulte 1993) and of acervulinid foraminifers, including the formerly supposed red alga *Solenomeris*, from the Tertiary. *Solenomeris* was regarded as a foraminifer by only a few authors, such as Trauth (1918; see Hagn and Wellnhofer 1967), and was identified as a reef-building foraminifer by Perrin (1987; see also Plaziat and Perrin 1992). Moussavian and Höfling (1993) regarded *Solenomeris* as a synonym of *Acervulina*, a view which was rejected by Perrin (1994).

'*Bdelloidina*' and *Solenomeris* show very similar growth form and environmental distribution to *Lithocodium*, except that *Solenomeris* is able to build large biostromes and bioherms up to several metres thick. Recent acervulinid foraminifers such as *Acervulina* also contribute to the formation of oncoids or 'macroids', e.g. in the Red Sea and the Mediterranean Sea (Hottinger 1983). This special life strategy of forming bioconstructions is also known from the miliolid foraminifer *Nubecularia*, which forms, or contributes strongly to the formation of oncoids in the Middle Jurassic of the Paris Basin (e.g. Hilly and Haguenauer 1979) and Lusitanian Basin, Portugal (cf. Leinfelder 1983, pl. 1). Nubeculariid foraminifers are also able to build small bioherms (0·5 m), as known from the Middle Miocene of Bessarabia/Eastern Paratethys (Gillet and Derville 1931) and are also major constituents of the biostromes reported from the Middle Miocene of Austria/Central Paratethys (Friebe 1994). Recent counterparts of *Lithocodium* do not exist among the Lituolida; *Bdelloidina* is the only living larger foraminifer in this group (cf. Loeblich and Tappan 1988). The encrusting life style and the alveolar wall structure of this genus resemble those of *Lithocodium*, but the coarsely agglutinated wall and the apparent absence of algal symbionts represent important differences. The Recent rotaliid genus *Homotrema* is an encrusting foraminifer which very probably harbours algal symbionts (Strathearn 1986) and contributes to reef formation; therefore, it may be compared with *Lithocodium*.

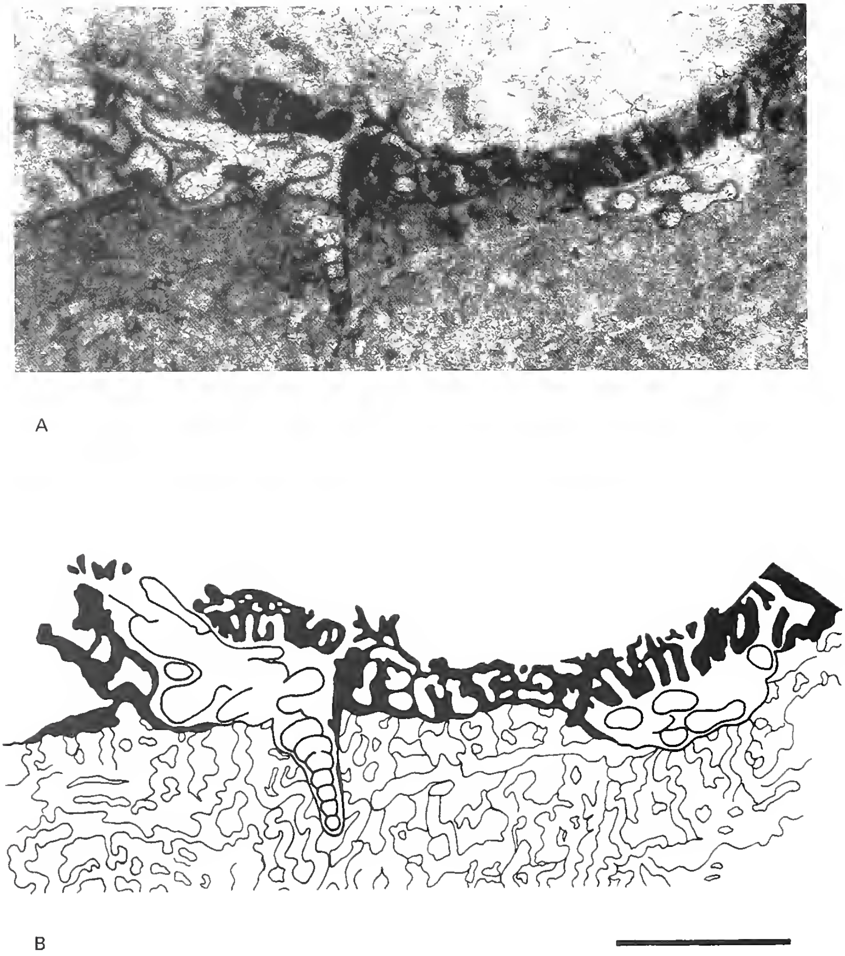
The suggestion seems plausible that the irregular, consistently flat growth form of *Lithocodium*, which spread across the substrate (Pl. 1, fig. 4), was an adaption to shallow marine environments in order to enlarge the surface area in order to receive more light for symbiotic algae (cf. Cowen 1983, p. 450; 1988, text-fig. 2). According to Hallock (1985, p. 205), 'algal symbiont-bearing organisms have tremendous energetic advantage over similar organisms lacking symbionts under nutrient-deficient conditions'. Generally, feeding plays only a minor role in larger symbiont-bearing foraminifers and merely supplies metabolites such as vitamins which are not synthesized within the association (Lee and Anderson 1991, p. 200). Symbiotic unicellular algae (diatoms, dinophyceans, rhodophyceans, chlorophyceans and chloroplasts) are common in miliolid and rotaliid foraminifers, especially in large forms (Röttger 1972; Haynes 1981; Lee and McEnery 1983; Leutenegger 1984; Lee and Anderson 1991; Murray 1991) and have also been recorded from one agglutinated species (Knight and Mantoura 1985, p. 245). Ross (1979, p. 59) stated that, besides the general flattened shape of larger foraminifers, complex wall structures appear also to be adaptations to a symbiotic relationship with algae. According to Leutenegger (1984, p. 33), most symbiont-bearing foraminifers possess pore cups or separated chamber compartments, which serve to stabilize the symbiont's preferred position directly below outer chamber walls, avoiding larger cytoplasmic currents which could carry the algae away. Additionally, Lee and McEnery (1983, p. 57) suggested that this feature could be a mechanism to segregate algal endosymbionts from the digestive vacuoles of the host.

In *Lithocodium*, as well as in other loftusiids, the alveoli in the test wall could be an adaptation to house symbiotic algae. The existence of symbionts in larger agglutinated foraminifers with complex wall structures was also suggested by Hottinger (1984, p. 313). The restriction of *Lithocodium* to shallow marine, mostly reefal (hence nutrient-depleted) environments, their irregular, flat morphology, and their large size, are good arguments for a symbiosis with unicellular algae (see 'check-list' in Cowen 1988, text-fig. 2). Most modern foraminifers with zooxanthellate symbionts show a relatively wide bathymetric distribution, whereas foraminifers with chlorophycean symbionts ('zoochlorellae') are restricted to very shallow water (Leutenegger 1984). The association of *Lithocodium* with distinct shallow-water faunal elements such as reef building corals is indicative of its shallow habitat (Leinfelder *et al.* 1993) and might therefore hint at a chlorophycean nature of the *Lithocodium* symbionts, although some modern zooxanthellate foraminifers (e.g. *Marginopora vertebralis*) are also restricted to very shallow settings (cf. Leutenegger 1984). However, a flat growth form in foraminifers is not an unequivocal indicator for algal symbiosis, since some extant species of larger, flat foraminifers are living without symbionts (see discussion in Cowen 1983, p. 454; Leutenegger 1984; Hallock 1985; Brasier 1986; Murray 1991).

Leutenegger and Hansen (1979) demonstrated that the pores of perforate foraminifers, although covered by a thick organic lining, serve for gas exchange. In non-symbiont bearing species, the pores serve the purpose of oxygen uptake, as indicated by the concentration of mitochondria below the pores, whereas in symbiont-bearing species CO_2 passes inward through the pores when the symbionts are active (Leutenegger and Hansen 1979, p. 15). Hansen and Dalberg (1979) showed that the thin walls of the pseudopores of some miliolid foraminifers permit the passage of CO_2 for use by symbiotic algae, as observed in living *Amphisorus*. They suggested an identical mechanism for other miliolid foraminifers with thin lateral walls. If this is true, the same can be assumed for *Lithocodium*, since its epidermal layer is similarly thin. In addition, Hottinger (1986, p. 226) suggested that the thin outer walls of lituolid and fusulinid foraminifers also probably served for the exchange of small molecules.

DETAILED DESCRIPTION OF *TROGLOTELLA* AND DISCUSSION

Lithocodium was thought to exhibit calcified sporangia (Endo 1961). Leinfelder (1989, p. 51, pl. 3, fig. 5; pl. 4, fig. 5; identical with Leinfelder 1994*a*, text-fig. 22) identified these bubble-like structures within *Lithocodium* cavities as cryptic foraminifers and provisionally attributed them to *Bullopora* aff. *laevis* and ?*Bullopora* aff. *laevis*. Further figuring and a brief description of this foraminifer was



TEXT-FIG. 6. *Troglotella* within *Lithocodium*, clearly boring into a microsolenid coral whose septa are cut. The shape of adult chambers is adapted to the inner surface of the *Lithocodium* chamber. The roof of this chamber was either partially eroded or lifted off by *Troglotella*. A, thin section 7/17.4.18; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; × 23. B, drawing of the same specimen; scale bar represents 1 mm.

later given by Leinfelder (1992) and Leinfelder *et al.* (1993, p. 203; text-figs 6–7; pl. 42, figs 1–7). This foraminifer has now been identified as *Troglotella incrustans* Wernli and Fookes, 1992.

Structure, morphology and function of the test

Lituolid foraminifers with microgranular walls of very minute agglutinated particles or with a dominance of calcitic matrix are common (cf. Hansen and Abd-Elshafy 1988). No pores are visible in thin section and under SEM examination (Pl. 2, fig. 6). Sometimes, poorly preserved specimens show diagenetic crystal enlargement which may result in a partly hyaline, pseudoporous structure. Although originally taken as characteristic for the genus *Bullopora* (see above), the very rich material now available shows that this was a misinterpretation caused by diagenetic alteration of the test.

Juvenile specimens had the ability to bore facultatively into hard substrates. Imperforate walls do not exclude this habit, since most foraminifers are partly surrounded by ectoplasma, and pseudopodia are not necessarily restricted to the area of the opening of the test. The extant facultatively boring foraminifers *Rotaliammina* and *Siphotrochammina* exhibit an agglutinating, non-canaliculate, i.e. imperforate, test (Vénec-Peyré 1987, p. 207; 1988). Other features of these two genera parallel the *Troglotella* example. Compatible are the very thin walls and the reduction of wall formation in juvenile chambers (occasionally resulting in proteinous walls only, cf. Vénec-Peyré 1987; Loeblich and Tappan 1988). *Siphotrochammina* also exhibits a smooth outer surface. In contrast with *Troglotella*, both extant genera exhibit a trochospiral test which is a characteristic feature of the superfamily Trochamminacea.

The fact that *Troglotella* is imperforate may explain why the boring activity of the taxon is restricted to the juvenile stage (Text-figs 6–8; Pl. 2, fig. 5). At later stages the pseudopodia, which are more common around the opening in imperforate foraminifers, may not have reached down to the early ontogenetic chambers and hence could not further enlarge the bore hole, given the elongate shape of *Troglotella*.

The very thin character of the wall may have demanded further protection from enemies and elevated water energy, which may have been achieved either by occupying *Lithocodium* chambers or by a boring life-style. From the modern examples it is known that agglutinating foraminifers with a boring life-style use boring particles for wall formation (Vénec-Peyré 1987, p. 210).

Functional interpretation of morphology in foraminifers is debatable. Protection is certainly important but is only one function of the test. Among other explanations for test formation are the maintenance of protoplasma shape and cell organization without waste of energy (cf. Vogel and Gutmann 1988; Culver 1993). Excretion of calcareous skeletons may also serve to remove the cell toxin calcium (cf. Simkiss 1977). Consequently, test characteristics of boring foraminifers are rather variable. Extant *Planorbulinopsis parasita* (Banner 1971, termed '*P. parasitica*' in Loeblich and Tappan 1988) and some others exhibit thick walls (cf. Smyth 1988), by using drilled particles for test formation. The reason for drilling is, however, normally not to produce particles for test formation, since dissolved calcium carbonate is abundant in warm, shallow marine environments. On the other hand, *Troglotella* might have had problems in calcium carbonate availability within the test of living *Lithocodium* due to lacking direct contact with sea water (see below).

A partial to complete adaptation of the growth form of *Troglotella* to the morphology of *Lithocodium* chambers is apparent in almost all specimens (e.g. Pl. 1, fig. 3; Text-figs 1–2, 6). Particularly characteristic is the irregular growth of *Troglotella* tests towards, and sometimes even into, the alveoli of *Lithocodium* (Pl. 1, fig. 3; Text-fig. 1). Many adult *Troglotella* exhibit a very irregular shape due to decreasing space availability, and completely mimic the internal shape of *Lithocodium* chambers. In one example, the roof of a *Lithocodium* chamber was lifted off, but it is not clear whether this was caused by the growth of *Troglotella* or by external erosion (Text-fig. 6).

Comparison with other fossil organisms

In cases where *Troglotella* developed a very irregular adult growth form, it may show astonishing similarity to the enigmatic organism *Bacinella irregularis* (Pl. 1, fig. 5), which is commonly associated with *Lithocodium*, or with phrenotheca-like structures, respectively (see above). Since, in the Triassic and Cretaceous, and more rarely also in the Upper Jurassic, bacinelloid structures may also occur within the chambers of *Lithocodium*, confusion with very irregular *Troglotella* specimens could occur, particularly if the *Troglotella* is not completely preserved (e.g. Text-fig. 4). However, better preserved *Troglotella* specimens show that there is a clear, unconfusable morphological separation between the two taxa. Diagnostic are micrite threads crossing at right angles, which never occur in *Troglotella*.

The Triassic forms of the fusulinid genus *Endothyranella*, particularly *E. wirzi* (cf. Bucur *et al.* 1994, pl. 14, fig. 2), exhibit close similarities to *Troglotella*, both in their wall structure and general growth form. According to Loeblich and Tappan (1988), the attribution of the Triassic forms to the Carboniferous representatives of the genus is doubtful.

Troglotella shows some similarity to *Cheilosporites tirolensis* Wähner, which, according to Senowbari-Daryan (1980*a*), represents a sphinctozoan coralline sponge, but which also has been interpreted as a foraminifer (Fischer 1962). Similarities comprise general growth form, segmentation into chambers and the partial cryptic life style of *Cheilosporites*. However, differences between the two are more obvious. *Cheilosporites* is ten times larger than *Troglotella* and shows an indistinct central canal which accounts for its attribution to the sphinctozoan sponges.

Substrate relation and the boring activity of Troglotella

The most common occurrence of *Troglotella incrustans*, which is restricted to the Upper Jurassic, is within the chambers of *Lithocodium*. Such specimens of *Troglotella* were facultative borers during the juvenile growth stage when attacking the substrate of *Lithocodium* (Text-fig. 6; Pl. 2, fig. 5), since *Lithocodium* does not form a basal wall. *Lithocodium* is never bored by *Troglotella*. Later growth stages encrust the bottom of the *Lithocodium* chambers, by developing the typical irregular growth. Occasionally, different specimens of *Troglotella* occupied one single *Lithocodium* chamber. Less commonly, *Troglotella* occurs outside *Lithocodium*, where it bored oncoids or bioclastic cortoids, and rarely also corals. In these cases, the last chambers extrude from the borehole and encrust their surface.

Wernli and Fookes (1992) noticed the occurrence of *Troglotella* within perforations, but excluded the idea of boring activity for *Troglotella*, due to the imperforate nature of the test which would prevent ectoplasma reaching the apex of the test where the supposed boring site had to be situated. In our opinion, this is not a sufficient argument since ectoplasmatic pseudopodia of foraminifers may reach lengths of up to three or more times the diameter of the test (Haynes 1981, p. 31), and therefore etching activity leading to boreholes seems not to be a problem even for imperforate foraminifers. This is corroborated by the existence of modern boring imperforate foraminifers (see

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EXPLANATION OF PLATE 2

Fig. 1. *Lithocodium* with chambers of *Troglotella* (left arrow) and phrenotheca-like structures (right arrow). Thin section AM I 2; Amaral Formation, late Kimmeridgian; Amaral ridge near Arruda dos Vinhos, Lusitanian Basin, Portugal; ×23.

Fig. 2. *Lithocodium* specimen in which the diameter of chambers and alveoli is increasing from juvenile chambers (below) to adult chambers (above). The chambers are partly occupied by *Troglotella*. Thin section CH VII 1; Amaral Formation, late Kimmeridgian; Moinho da Chã near Arruda dos Vinhos, Lusitanian Basin, Portugal; ×31.

Fig. 3. A thin bivalve shell is partially dissolved in places where overgrown by *Lithocodium*. Some chambers of *Troglotella* are also visible. Thin section 86/26.2.18; Ota Limestone, 'middle' to late Kimmeridgian; Ota, Lusitanian Basin, Portugal; ×23.

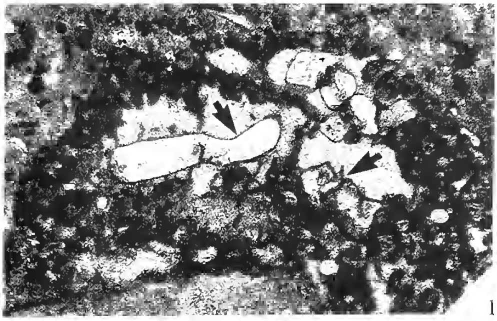
Fig. 4. *Lithocodium* nodule; the chambers are occupied by *Troglotella*. Thin section CH VII 1; locality as in fig. 2; ×26.

Fig. 5. *Troglotella* occupying a chamber of *Lithocodium* (in tangential section), boring in a coral septum during juvenile stage. Thin section ALQ 12; Ota Limestone, 'middle' to late Kimmeridgian; Alenquer, Lusitanian Basin, Portugal; ×23.

Fig. 6. The micrograular and imperforate wall structure of *Troglotella* (lower arrow) and *Lithocodium* (upper arrow). M I 6B, scanning electron micrograph; Amaral Formation, late Kimmeridgian; Mata near Arruda dos Vinhos, Lusitanian Basin, Portugal; ×670.

Fig. 7. A minute cryptic foraminifer with a very thin wall, occupying a chamber of *Alveolina* sp. The latter clearly reacted to the infestation by enlarging the infested chamber. Thin section ALV 1; Alveolinid limestone, middle Eocene; Criales near Villarcayo, Villarcayo Basin, Cantabria, northern Spain; ×50.

PLATE 2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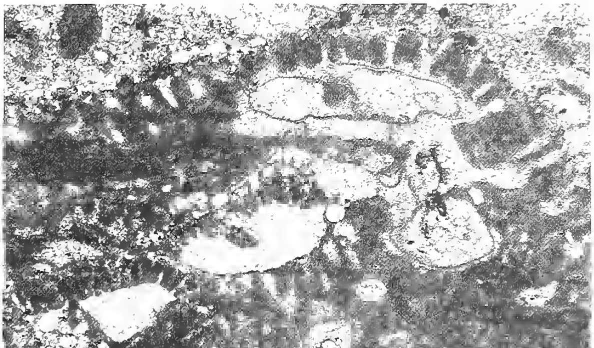
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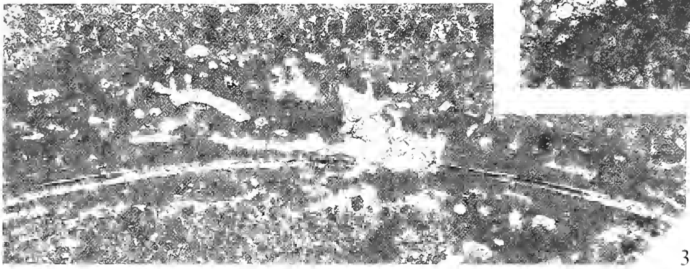
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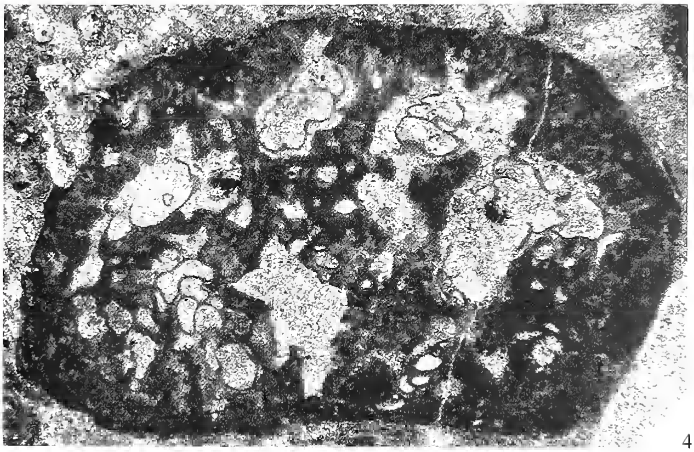
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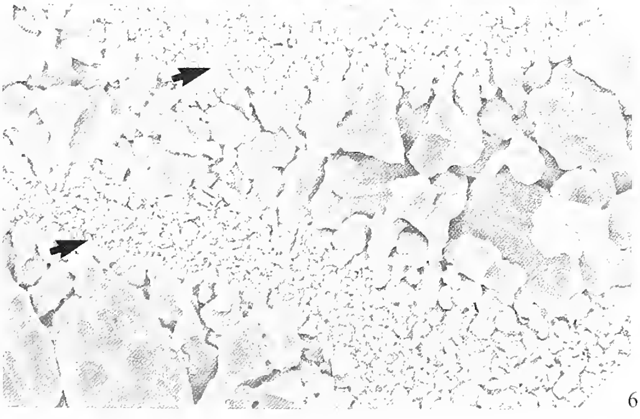
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SCHMID and LEINFELDER. *Lithocodium-Troglotella* foraminiferal consortium below). Given the high tendency of *Troglotella* to exhibit morphological variation, the constant shape of the juvenile stage would be puzzling, if pre-existing cavities were passively occupied. Also, the lack of any space between the borehole and the test, as well as the constancy of the juvenile, seven to eight chamber arrangement, positioned perpendicularly to the substrate, substantiates the idea of the well developed boring abilities of the young foraminifer. The adult foraminifer had to change to a different life-style from the eighth chamber onwards. However, it must be emphasized that boring activity was facultative, and, given suitable shelter in a pre-existing larger cavity (i.e. particularly within a *Lithocodium* chamber) the boring activity was often suppressed.

Boring activity in other foraminifers

The boring activity of both agglutinating and rotaliid foraminifers is described comprehensively by Vénec-Peyré (1987). Other reports of boring foraminifers are from Banner (1971), Matteucci (1974), Baumfalk *et al.* (1982), Alexander and Delaca (1987), Smyth (1988), Cherchi and Schroeder (1991, 1992) and Vénec-Peyré (1993). Todd (1965) and Delaca and Lipps (1972) focused on *Rosalina* which is able to etch its substrate strongly, e.g. bivalve shells. Boring foraminifers generally etch and partly dissolve their calcareous substrate by means of their pseudopodia. Complete dissolution is not necessary, since loosened parts can be mechanically removed or, in the case of agglutinating foraminifers, even incorporated in the test. Pseudopodial etching activity may also cause thin, lateral channels (Banner 1971).

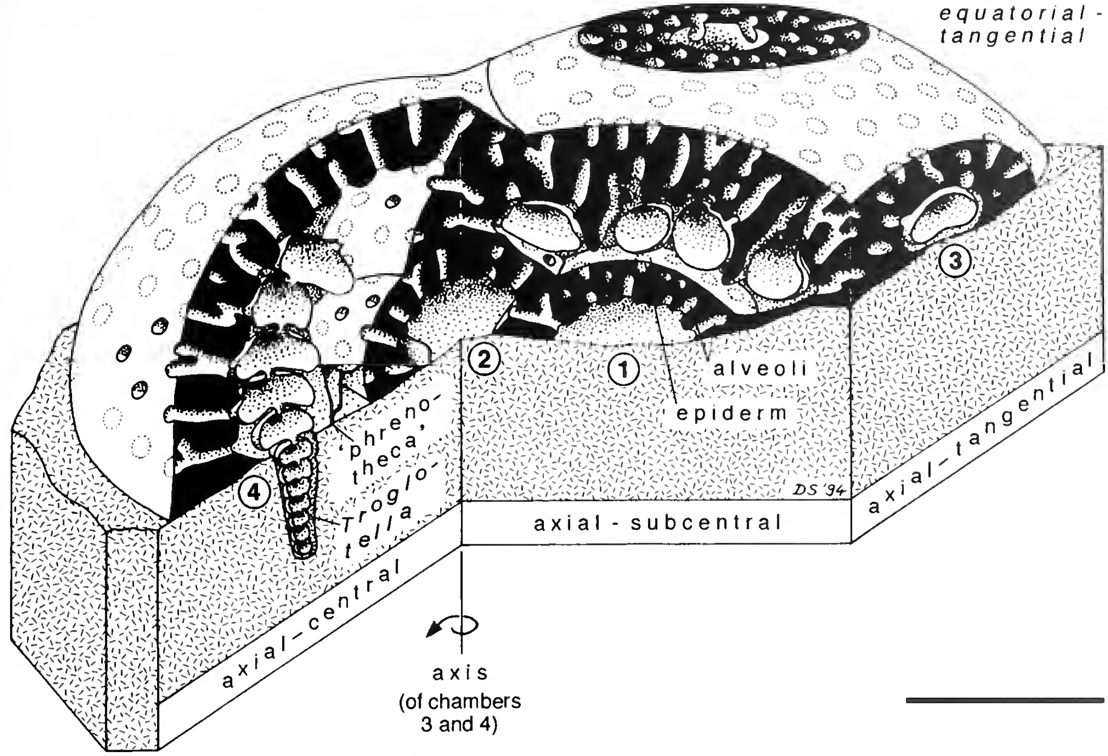
The first boring foraminifer described from the Upper Jurassic is *Troglotella incrustans* (see above) but, recently, another Upper Jurassic boring foraminifer has been described by Plewes *et al.* (1993). The form is known as *Globodendrina monile* and produces a globular hole with a series of radiating etched canals and a small agglutinated chimney rising from the surface around the hole. Therefore, this boring foraminifer differs clearly from *Troglotella*.

Examples of foraminifers boring into other foraminifers are rare. The extant miliolid *Alveolinella* is occasionally bored by the rotaliid *Planorbulinopsis* (Banner 1971). Baumfalk *et al.* (1982) described *Talpinella*, a rotaliid foraminifer from the Cretaceous, boring within tests of *Orbitoides*. *Talpinella* exhibits an early involute growth, whereas chambers increase rapidly in size and become irregular during later growth. This is a clear parallel with *Troglotella*. A major difference is, however, that *Talpinella* destroys the chamber walls of *Orbitoides*, something which has never been noticed in *Troglotella*. Another small foraminifer has been found boring into *Paleodictyoconus*, a Cretaceous foraminifer (Cherchi and Schroeder 1992).

LIFE STRATEGY OF THE *LITHOCODIUM-TROGLOTELLA* CONSORTIUM

The unique relationship between *Lithocodium* and *Troglotella* deserves special attention. In the Upper Jurassic, almost all *Lithocodium* specimens are found infested by *Troglotella*. On the other hand, *Troglotella* may occur rarely without *Lithocodium*.

Interpretation of the Upper Jurassic *Lithocodium-Troglotella* consortium is difficult, since apparently no direct modern counterparts exist. Partial modern analogues are foraminifers housing algal symbionts or parasitic heterotrophs (amongst which even foraminifers are known), commensal foraminifers in sponges, parasitic foraminifers in bivalves, foraminifers boring dead substrates, and foraminifers living cryptically in dead algal filaments as well as in other dead foraminifers. In the following, we will discuss the various possibilities of the heterotypic *Lithocodium-Troglotella* interrelationship and propose the most likely interpretation. The interpretation has to focus particularly on the following features: (1) the early boring stage of *Troglotella*; (2) the later irregular growth form of *Troglotella*, with *Troglotella* chambers normally paralleling the irregular inner surface of *Lithocodium* chambers; (3) the abundance of *Troglotella* within *Lithocodium*; (4) the occasional occurrence of *Troglotella* without *Lithocodium*; (5) the imperforate and multilayered character of *Lithocodium*; and (6) the occurrence of *Lithocodium* without *Troglotella*, particularly in material older or younger than Late Jurassic.



TEXT-FIG. 7. Reconstruction of *Lithocodium*, occupied by some specimens of *Troglotella*. 1–4 = succession of chambers of *Lithocodium*. In subcentral or tangential section, where connections between the chambers of *Troglotella* are not visible, the bubble-like chambers may resemble algal sporangia. Scale bar represents 1 mm.

Exclusion of post-mortem infestation of Lithocodium *by* Troglotella

Dead *Lithocodium* tests would have provided rather large cavities for the settlement of *Troglotella*. *Troglotella*, with its thin, fragile test would be perfectly sheltered and could occupy waters which would be too agitated for a free life style. *Hospitella*, a modern, probably allogromiid, foraminifer with imperforate, chitinous walls lives in the chambers of other, most probably dead foraminifers (cf. Loeblich and Tappan 1988, p. 17, pl. 10, fig. 3). In Upper Jurassic material (Birmensdorf beds, Oxfordian), Gaillard (1983, p. 214, text-fig. 99) identified the foraminifer *Tolypammina vagans* encrusting the inner wall of a chamber of the foraminifer *Bullopora tuberculata*.

As *Lithocodium* represents an imperforate foraminifer, the embryos or zygotes of *Troglotella* could have entered the empty tests only through the cribrate opening of the final chamber or through damaged walls. If *Troglotella* dwelt only occasionally within *Lithocodium*, it could be readily interpreted as post-mortem infestation. However, even in thick, multilayered *Lithocodium* crusts, most or all chambers are occupied by *Troglotella*, which makes post-mortem settlement most unlikely (e.g. Pl. 1, figs 2–3). If infestation had happened after the death of the entire *Lithocodium* crust, both settlement paths and flow of nutrient waters would be strongly hindered. Only if *Troglotella* could feed on decaying *Lithocodium* material, would nutrition appear feasible. However, in this case, the chambers would still be partially blocked and infestation of nearly all *Lithocodium* chambers would not be possible. Only a repetitive process of growth, death and infestment of *Lithocodium* would explain the occurrence of larger *Lithocodium* colonies with *Troglotella* in all chambers, an assumption which is most unlikely. Additionally, there would be no reason for the boring activity of *Troglotella* in its early ontogenetic stages. Moreover, phrenotheca-like structures, crossing the chambers and produced by *Lithocodium* are common in Triassic and Cretaceous

Lithocodium specimens (see below), but much rarer in Upper Jurassic ones. Although formation of phrenotheca-structures was possible in the Late Jurassic, its rarity shows that chambers were occupied by *Troglotella* prior to their possible time of formation, i.e. during the lifetime of *Lithocodium*.

The nature of coeval existence of Lithocodium *and* Troglotella

Although the coexistence of both foraminifers seems plausible, the kind of interrelationship is difficult to interpret.

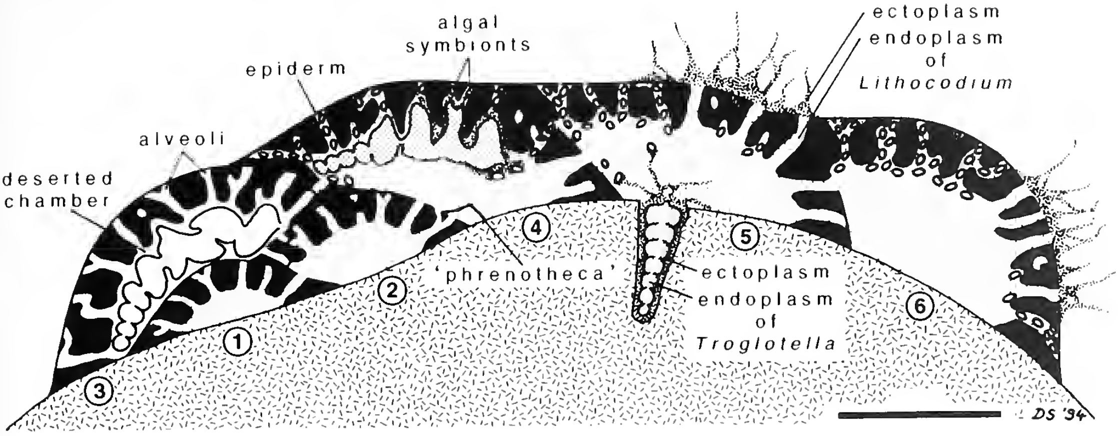
Cibicides refulgens is a modern foraminifer which lives epizoically on bivalves (Alexander and Delaca 1987). It bores the shell in order to obtain nutrition from the mantle cavity and thus exhibits a parasitic mode of life. Similarities with juvenile, boring specimens of *Troglotella* are apparent. Wetzel (1953) described *Bullopora parasitica* from the Middle Jurassic as an endoparasite within bivalves. The modern foraminifer *Planorbulinopsis parasitica* is considered as an endoparasite of another foraminifer (Banner 1971). Unlike *Troglotella*, the modern parasite does not, however, occupy almost the entire chamber space of the host. Loeblich and Tappan (1988, pl. 154, figs 7–8) figured a modern specimen of *Textulariella*, a genus with a wall structure similar to that of the loftusiaceans, in which several chambers are infested by a minute, spirally coiled foraminifer. Although this infestation is not mentioned in the text it might represent commensalism.

In the fossil examples, a parasitic life style for foraminifers living within other foraminifers is indicated either by the severe destruction or by the growth reactions of the host. Some examples for such an interpretation exist. Baumfalk *et al.* (1982) considered the Late Cretaceous boring foraminifer *Talpinella*, which lived within *Orbitoides*, as possibly parasitic. This interpretation was based on the fact that *Talpinella* perforated the chamber walls around the proloculus. According to the authors, there is no obvious penetration of the outer *Orbitoides* chambers and the partial destruction of foraminiferal hardparts excludes a post-mortem or a symbiotic/commensal life-style. A parasitic life-style is, furthermore, substantiated by the fact that *Talpinella* is not known outside *Orbitoides*.

We have detected a second example of a probable foraminiferal parasite living within another foraminifer from the Tertiary of Spain (Pl. 2, fig. 7). Here, a minute cryptic foraminifer with a very thin wall grew in a chamber of *Alveolina* sp. The latter clearly reacted by modifying and enlarging the infested chamber. The supposed endoparasitic foraminifer is involutely, probably planispirally coiled and has a dark, imperforate wall. As, to date, we have only one thin section specimen of this foraminifer, no taxonomic description can yet be given.

No damage or growth reaction related to the infestation by *Troglotella* is obvious in *Lithocodium*. If *Troglotella* was an endoparasite feeding on the *Lithocodium* endoplasma, it should have had severe effects on the host, particularly because almost the entire chamber space of the host would have been occupied, which contrasts with the modern and fossil examples of foraminiferal parasites within foraminifers given above. It may be argued that the large size of *Troglotella* does not unequivocally exclude a parasitic life style, but may have triggered *Lithocodium* to build rapidly new chambers. However, *Troglotella*-hosting *Lithocodium* grew to a considerable size, indicating an extended life time with healthy growth. The association was, moreover, very successful throughout the entire Late Jurassic. Given the generally high repair capacities of foraminifers, it seems unlikely that, for about 20 million years, *Lithocodium* would not have developed protective mechanisms, such as shutting-off infested chambers by closure of connective pores or formation of additional walls such as phrenotheca or the ability to digest the intruder, if *Troglotella* was a dangerous parasite. In fact, phrenotheca are tentatively interpreted in Text-figure 8 to have served partly to shut off chambers which had been deserted by *Lithocodium* for some reason, but this method was obviously not meant to prevent infestation by *Troglotella* generally.

On the other hand, virtually no evidence exists to suggest a symbiotic relationship between the two foraminifers. A variety of advantages is obvious for *Troglotella* when it lives within *Lithocodium* (see below), but no apparent advantages exist for *Lithocodium*. Theoretically, the



TEXT-FIG. 8. Reconstruction of the living *Lithocodium-Troglotella* consortium (axial section; algal symbionts not to scale). 1–6 = succession of chambers of *Lithocodium*. Phrenotheca-like structures are interpreted in this figure to have served partly to shut off chambers deserted by *Lithocodium* protoplasm. Scale bar represents 1 mm.

autotrophic symbionts of *Lithocodium* could have produced too much oxygen, endangering oxidation of plasma which could be neutralized by oxygen uptake of *Troglotella*. However, more plausible in this case would be that *Lithocodium* controlled the degree of oxygen production by partial ejection of symbionts, whereas direct digestion of surplus symbionts is thought to be rare (Murray 1991, p. 11). Symbiotic relationships between modern foraminifers and unicellular algae (symbiotic dinophyceans = 'zooxanthellae', symbiotic chlorophyceans = 'zoochlorellae', diatoms or rhodophyceans) are common (for comprehensive reports see Leutenegger 1984; Lee and Anderson 1991; Murray 1991).

Obviously, the infestation of *Lithocodium* by *Troglotella* did not greatly bother the host. Hence, the most likely interrelationship between *Troglotella* and *Lithocodium* was commensal, possibly with only a slightly parasitic effect. Text-figure 8 gives an interpretation of the relationship between both foraminifers. The following stages in the life cycle of *Troglotella* are thought to have occurred.

1. Infestation of *Lithocodium*. Probably by chemotaxis, sexually produced gametes settled on the ectoplasma of *Lithocodium* and were transported into the endoplasma. According to Kremer (1994), potential algal symbionts are generally recognized by their hosts by means of signal molecules and surface features, thus preventing digestion. The same mechanism may have prevented digestion of *Troglotella*.
2. Early growth stages. *Troglotella* attached itself to the floor of the *Lithocodium* chamber (i.e. normally the roof of the underlying chamber, or the *Lithocodium* substrate). If settling on the substrate, it commonly exhibited an early boring stage, either to produce material for test formation, to obtain nutrients from the substrate, to anchor itself within the flowing cytoplasma, or to create additional space (or a combination thereof).
3. Later growth stages. If *Troglotella* fed on the endoplasma of *Lithocodium*, it would not have been necessary for it to develop the irregular form of its adult stage. The rapid growth of *Troglotella*, particularly into the thin-walled alveoli of *Lithocodium* (i.e. into the presumed site of accumulation of autotrophic symbionts), rather suggests that *Troglotella* fed directly on these symbionts or their synthesized products. According to Lipps (1983, p. 339), permanently attached foraminifers, like *Troglotella*, are passive herbivores, which feed on bacteria and algae. In modern foraminifers, symbiotic algae may appear in great numbers. This explains why *Lithocodium* had only minor

disadvantages and could flourish despite the *Troglotella* infestation. The *Lithocodium* endoplasma was successively displaced by the growth of *Troglotella*, urging *Lithocodium* to form a new chamber. Probably, this lack of space was not too precarious, as Severin and Lipps (1989) were able to show that the living large foraminifer *Alveolinella quoyi* can only fill an average of 39 per cent. of its chamber space with protoplasm.

4. Reproduction. During asexual reproduction of *Lithocodium*, *Troglotella* embryos or gametes possibly already infested *Lithocodium* embryos and thus propagated. This would be the same mechanism which symbiotic algae use to pass over from parent individuals to new foraminifers (Röttger 1972; Hottinger 1982). Symbionts and, presumably, commensals cannot be passed over during sexual reproduction of gametes due to the very small size of the gametes (Leutenegger 1984). The products of sexual reproduction have to acquire their symbionts anew. This is one reason why large, symbiotic foraminifers largely reduced sexual reproduction in favour of the dominating asexual reproduction (cf. Röttger and Schmaljohann 1976; Hottinger 1983, text-fig. 3; Murray 1991, p. 11).

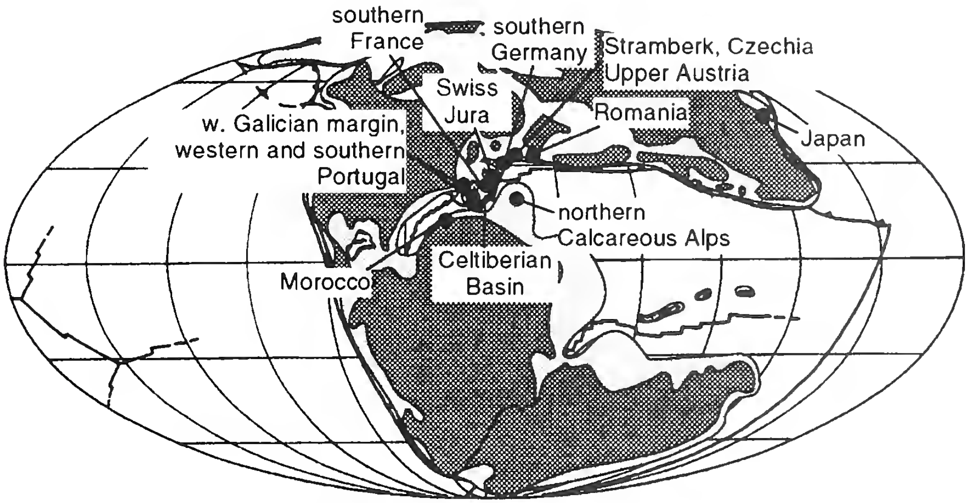
Reports on commensal foraminifers are rare. Voigt and Bromley (1974) describe a commensal association between agglutinating foraminifers (*Placopsilina* and *Bdelloidina*) and the papillae of clionid boring sponges from modern and Cretaceous examples. Probably, the foraminifers took advantage of the nutrient current produced by the propelling activity of the choanocyte flagellae. To our present knowledge, there are no modern examples of commensal foraminifers living within other foraminifers, although Le Calvez (1947) reported a partly comparable example in the case of the foraminifer *Fissurina*, which captures granules from the pseudopodial network of *Discorbis* for its own nutrition. On the other hand, looking at a totally different group such as the ants, numerous examples of symbiotic, commensal and parasitic relationships with various other insects have been identified (cf. Dumpert 1978), seemingly even more astonishing than the one recorded here.

Troglotella occurs occasionally without *Lithocodium*, though it has to be taken into account that *Lithocodium* may still be present, but remains unrecognized (in tangential sections where the typical alveolar structure is barely visible). This does not exclude a commensal life of *Troglotella* inside *Lithocodium*, since even symbionts within foraminifers may also occur free-living. For instance, actively swimming dinoflagellates can apparently be attracted by foraminifers and used as symbionts by them (Ross 1972). However, the interpretation that *Troglotella* fed on autotrophic symbionts of *Lithocodium* or their products raises the question as to the nutrition of the occasional *Troglotella* specimens living outside *Lithocodium*. As has been mentioned above, these specimens always exhibit an early boring stage. In most cases, they attacked oncoidal nodules formed by cyanobacteria. They were also observed to have attacked solenoporacean red algae or *Marinella lugeoni*, a close relative of the coralline red algae (Leinfelder and Werner 1993). In the cases of attacks on bioclasts or corals, these specimens always exhibit a micritic rim caused by microbial borers, including cyanobacteria. This leads to the assumption that *Troglotella* outside *Lithocodium* may also have fed on autotrophic organisms or their products. The boring stage of these specimens can be interpreted as the result of the need for better protection, while the more regular, thicker chambers of the late, adult growth stage show that in cryptic specimens a more irregular, thin-walled, often barely visible, chamber clearly is the result of cavity outlines and the better protection available. Therefore, it must be concluded that there were not two different species or subspecies of *Troglotella*, but rather, that *Troglotella incrustans* exhibited wide intraspecific, ecological growth variation.

COMPARISON WITH *LITHOCODIUM* FROM OTHER STRATIGRAPHICAL LEVELS

Our description, taxonomic attribution and interpretation of the life habit of *Lithocodium aggregatum* is based on rich Upper Jurassic material. However, all figured Cretaceous specimens, including the original material of Elliott (1956), appear to be identical with the Upper Jurassic material. Judging from figured Triassic specimens, again, no apparent differences exist. Therefore, we synonymize the entire material from *Lithocodium aggregatum*, although a re-study of the very widely distributed Triassic and Cretaceous material was not performed. However, in particular the original material of Elliott is abundantly figured, so that our conclusion seems to be substantiated at least for the Cretaceous forms.

All *Lithocodium* occurrences are clearly from warm, shallow, tropical to arid low-latitudes, exclusively from coral reef and lagoonal settings. The earliest occurrences are known from the Anisian of the Southern Alps (Bechstädt and Brandner *in* Senowbari-Daryan *et al.* 1993, p. 230). Particularly widespread in the Northern Calcareous Alps are Norian to Rhaetian occurrences (e.g. Zankl 1969; Flügel 1972; Kuss 1983; Matzner 1986). South Alpine (Lakew 1990) and Greek occurrences (Schäfer and Senowbari-Daryan 1983) of the same age are known as well. To our present knowledge, no forms of Early and Middle Jurassic age are recorded, which partly appears to be an effect of the lower abundance of reefs at this time (cf. Stanley 1988; Leinfelder 1994*b*), and partly due also to lack of investigation. It was particularly the Late Jurassic which brought an enormous spreading of *Lithocodium*, from the Atlantic to central and southern Europe, Northern Africa, and Japan (Text-fig. 9, also for references).



TEXT-FIG. 9. The distribution of *Lithocodium* during the late Jurassic, extending from Morocco (Hüssner 1985), the western Galician margin (Dupeuble *et al.* 1987), western and southern Portugal (Lusitanian Basin: Ramalho 1971; Leinfelder 1989; Algarve Basin: Leinfelder *et al.* 1993), the Celtiberian Basin (Fezer 1988; Wnendt-Juber 1990), southern France (Bouroullec and Deloffre 1968; Bernier 1984; Bodeur 1992), the Swiss Jura (Bolliger and Burri 1970), Southern Germany (Swabian Alb: Leinfelder *et al.* 1994, Franconian Alb: Barthel *et al.* 1971), Stramberk/Czechia (Eliasova 1981), Upper Austria (Hofmann 1993), Romania (Herrmann *in* Leinfelder *et al.* 1994) and the northern Calcareous Alps (Steiger and Wurm 1980; Darga and Schlagintweit 1991) to Japan (Endo 1961). World map from Scotese *et al.* (in press), simplified.

Cretaceous forms are also widely distributed in areas where reef or platform growth persisted, e.g. Texas (Johnson 1968*a*), Spain (Cherchi and Schroeder 1985), France (Jaffrezo 1974), Italy (Praturlon 1964), the Middle East (Elliott 1956; Saint-Marc 1970; Connally and Scott 1985; Alsharhan 1987) and the Far East (Endo 1961; Mu 1986; Moussavian 1992).

The *Lithocodium-Troglotella* consortium does not occur throughout the long range of *Lithocodium*. Chambers of all *Lithocodium* outside the Upper Jurassic either are empty (i.e. spar-filled) or are crossed by irregular, bacinelloid phrenotheca-like structures. Although these latter structures may rarely occur within the Upper Jurassic material as well, the vast majority of chambers is occupied by the endocommensal foraminifer *Troglotella incrustans*. Since infestation of

Troglotella did not really complicate life for *Lithocodium*, except possibly in speeding up chamber development, it took from the middle Oxfordian to the late Tithonian (*c.* 20 My) for the commensal form to disappear. It remains unclear as to whether *Lithocodium* developed a defense mechanism or *Troglotella* became extinct through other processes.

CONCLUSIONS

Lithocodium aggregatum Elliott is a loftusiid foraminifer with an encrusting life habit, not a codiacean alga. Features diagnostic for its foraminiferan nature are partial coiling of the test, microgranular, imperforate wall with alveoli, ability to agglutinate particles and facultative occurrence of phrenotheca-like structures. This reinterpretation is based on Upper Jurassic material, but no obvious differences exist in the Triassic and Cretaceous material.

Lithocodium is a typical shallow-water organism from lagoonal and reefal, high energy marine settings. It contributes considerably to the formation of oncoids and microbial-biotic crusts. The strong dependence on shallow, hence illuminated, water and the ability to create up to 0·1 m large, several millimetre thick, intensively calcified crusts suggests, but does not prove, the existence of photoautotrophic symbionts. This is also supported by the existence of common alveoli which may have been the site for such possible endosymbionts. The fact that light enhances the calcification rates of symbiont-bearing foraminifers has been observed by several authors (Lee and Anderson 1991, p. 199).

In the Late Jurassic, *Lithocodium* chambers are almost always occupied by the cryptic, telamminid foraminifer *Troglotella incrustans* Wernli and Fookes. *Troglotella* is interpreted here as a facultative borer during its juvenile stage. This stage is represented by regular growth of seven to eight chambers, completely filling the borehole. Later growth stages may become very irregular and may occupy a large proportion of *Lithocodium* chambers.

Cross sections of adult *Troglotella* chambers within *Lithocodium* may appear subcircular or tube-like and were previously mistaken for calcified sporangia of the *Lithocodium*-'alga'. These were used, among other criteria, to establish the species *Lithocodium morikawai* Endo and *L. japonicum* Endo, which are consequently invalid. *Lithocodium* appears to represent a monospecific genus.

The almost exclusive occurrence of *Troglotella* within *Lithocodium*, as well as the occupation of all *Lithocodium* chambers even within thick crusts, together with the imperforate nature of the *Lithocodium* wall, excludes post-mortem settlement. A parasitic life habit for *Troglotella* is unlikely because of its large size and the lack of growth reactions of *Lithocodium*, which seems unaffected by the infestation of *Troglotella*. A commensal association is indicated by the fact that adult *Troglotella* chambers have a strong tendency to grow into the alveoli of the host. This may indicate that *Troglotella* fed on the supposed photoautotrophic symbionts of *Lithocodium* or their synthesized products. Such an interpretation is compatible with the rare occurrences of *Troglotella* outside *Lithocodium* chambers where it occurs with algal or cyanobacterial crusts. The boring stage of *Troglotella* outside *Lithocodium* is always developed which reflects the need for better protection and anchoring.

The foraminifer *Lithocodium aggregatum* and the enigmatic *Bacinella irregularis* are two clearly different taxa. They have similar environmental demands and may overgrow each other, but also occur independently. This precludes them being two different ecological varieties, or different tissue parts, of one single organism, as suggested by some authors. However, *Lithocodium* may develop phrenotheca-like partitions irregularly subdividing its chambers. These structures are 'bacinellimorph' and may in part account for the confusion of *Bacinella* with *Lithocodium*.

The reinterpretation of *Lithocodium* as a loftusiid foraminifer is another example of microproblematical forms being attributed to an alga simply to avoid dealing with a problem, as already stated by Babcock (1986). A similar case is represented by the well known, enigmatic '*Tubiphytes*' *morronensis*, occurring in the Jurassic and Cretaceous, which is interpreted by Schmid (1995) as a probably symbiont-bearing miliolid foraminifer with a two-fold test.

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A REVIEW OF THE MORPHOLOGICAL FEATURES AFFECTING THE CLASSIFICATION OF CLITAMBONITIDINE BRACHIOPODS

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Abstract. It is difficult to provide a monothetic diagnosis of a clitambonitidine brachiopod, as any important feature (chilidium, deltidium, spondylium, etc.) of a 'standard' genus such as *Vellamo* may be absent from another stock that is nevertheless a quite acceptable member of the suborder. Critical examination is made of the morphological structures, particularly those associated with the vital functions of maintaining position relative to the substrate and of feeding. The pedicle foramen became sealed in numerous stocks; a sequence of stages from an open delthyrium via deltidial plates to a complete plate confirms a deltidium rather than a pseudodeltidium; the chilidium likewise varies from a large structure, the outer growing surface of which lies within the conch, to a more modest normal arrangement, a pair of chilidial plates or an open notothyrium. The spondylium supporting the ventral muscle field is variously modified or may only be simulated by a pseudospondylium; the dorsal muscle field is disported in various ways and, with other variable structures normally accorded taxonomic status like the ancillary cardinal process ridges and the presence of aditicules, illustrates the fundamental taxonomic tenet of features unstable in one group becoming stable and of taxonomic importance in another.

The clitambonitidines form a distinctive group of articulate brachiopods which lived throughout the Ordovician and, although achieving world-wide distribution in the shallow seas of the time, are particularly associated with the Baltic faunas of Estonia and western Russia (Ingria), from which species were first described by von Schlotheim (1822). The outstanding study of the group was the very thorough review of these excellently preserved east Baltic brachiopods by Öpik (1934), which still stands as the leading research contribution; but a useful and easily accessible review is the contribution to the brachiopod *Treatise* volume by Williams (1965). The present article arises from our researches in preparation for the forthcoming revision of that *Treatise*. These highlighted the need for a critical review of the shell morphology, its understanding and interpretation especially with regard to classification within the group. In a further study, we are formally revising the classification of the group utilizing a cladistical approach and incorporating the morphological developments here recorded.

Williams (1965, p. H346) pointed out that although the clitambonitidines possess a unique assemblage of characters, the individual features themselves are typical of other contemporaneous groups and accordingly make the origin of the group uncertain. Thus there is little difficulty in recognizing a 'standard' clitambonitidine, such as the ubiquitous *Vellamo* (Text-fig. 1) with its wide hinge, ventri-biconvex profile and costellate exterior, long ventral interarea with convex deltidium perforated by a large foramen and a strong spondylium internally; the short dorsal interarea with well developed chilidium, and internally with a simple ridge-like cardinal process and laterally directed socket ridges. But within the accepted umbrella of the suborder, the morphologies stray far from this standard picture through the not uncommon absence of one or more of the definitive features, and the relationships of those early Ordovician stocks from Laurentia which lack a spondylium to those of Baltica with a strong spondylium are by no means certain.

The vital functions of any brachiopod are (1), to be able to open its valves to feed and (2), to maintain a life position on the sea floor, initially achieved by attachment to the substrate via the

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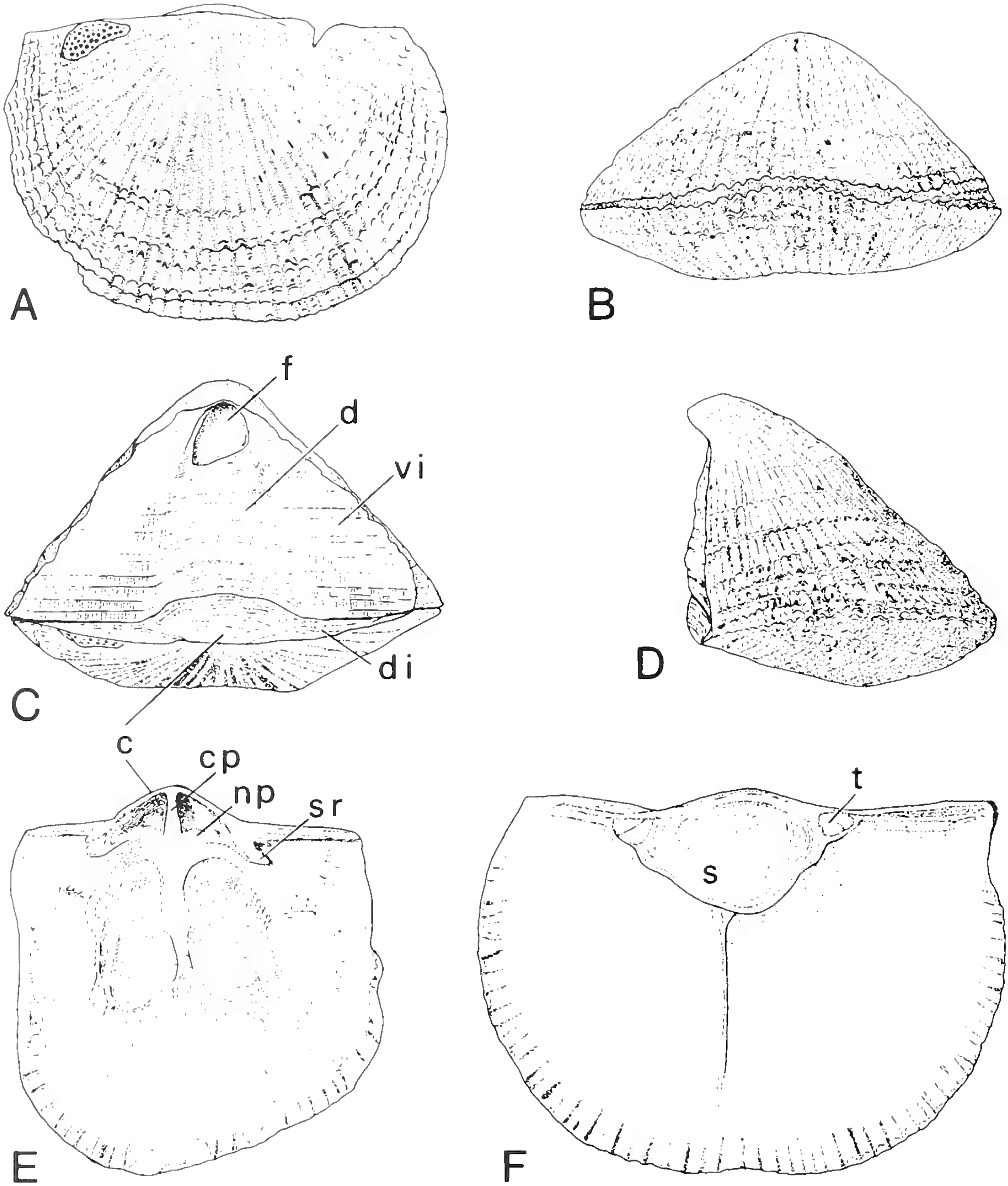

TEXT-FIG. 1. The basic morphology of a 'standard' clitambonitidine, based on specimens of *Vellamo oandoensis* Öpik. A–D, dorsal, anterior, posterior and lateral views of conjoined valves, ventral valve uppermost; E, dorsal valve interior with quadripartite adductor scars and some vascular markings preserved; F, ventral valve interior. The predominantly intercalated costellae of the dorsal valve are reflected as branching ribs on the ventral valve. c – chilidium; cp – cardinal process; d – deltidium; di – dorsal interarea; f – foramen; np – notothyrial platform; s – spondylium; sr – socket ridge; t – hingetooth; vi – ventral interarea. × 3 approx.

pedicle. It would seem reasonable that structures associated with these functions are likely to be the more important in morphological diversification and that the systematics should be based on this. In the case of the clitambonitidines, the delthyrium and notothyrium are typically closed by convex plates (e.g. *Vellamo*), although these are unknown in some stocks (*Oslogonites*), which are presumed to have had open delthyria and notothyria. Other stocks, like *Atelelasma*, in which the delthyrium is largely open, developed incomplete plates along its margins. The entire plate in the delthyrium of the ventral valve has variously been called a deltidium (e.g. Wright 1964; Harper 1989) or pseudodeltidium (e.g. Öpik 1934; Williams 1965) and, if this plate is incomplete along the anterior margin of the pedicle foramen, the parts have been termed lateral plates (Cooper 1956). According to Williams (1965, p. H346), the pedicle remained functional throughout the life of most clitambonitidines. Although there is no doubt that the collar-like extension of the pedicle foramen in *Kullervo* (Wright 1964, pl. 10, figs 19–20) indicates a functional pedicle throughout life in this case, despite its distortions (Wiman 1907, pl. 1, figs 1–4), the plugging of the pedicle foramen in adult shells is not uncommon, and certainly is not restricted to *Antigonambonites* as implied by Williams (1965, p. H346) but occurs variably in other genera such as *Clitambonites* itself (Pl. 4, fig. 6), *Clinambon*, *Estlandia* and *Raunites*. Study of the developmental stages of sealing of the foramen in these forms together with the pattern of the growth lines in specimens of *Vellamo* shows how the plates accreted and indicates the nature of the plate. The difference between deltidium and pseudodeltidium is not one of semantics, but is of fundamental importance in any attempt to ascertain the affinities of the stocks.

THE DELTIDIUM

According to the glossary of morphological terms in the *Treatise* (Williams and Rowell 1965), a deltidium (p. H143) is defined as the 'cover of the delthyrium formed by conjunct deltidial plates, line of junction of plates visible'. Where the deltidial plates are fused, and the median line of junction is lacking, the term 'symphytium' is used (p. H154), but this is fundamentally the same structure. A pseudodeltidium (p. H151) is defined as a 'single, convex or flat plate affording variably complete cover of delthyrium but *invariably* closing apical angle when foramen is supra-apical or absent and *always* dorsally enclosing apical foramen' (our italics). The significance of this is discussed by Williams and Rowell (1965, p. H88), but morphologically the pseudodeltidium always isolated the pedicle from the dorsal valve, and either occurs or does not occur; by contrast, a deltidium grew by increments gradually to fill the delthyrium in front of the pedicle.

In essence then, to recognize a pseudodeltidium we need to be able to confirm the presence of a strip of pseudodeltidium separating the foramen from the remainder of the delthyrium. Accepting that preservation commonly leaves something to be desired so that it has not been possible to study the plate in all genera, and that *Antigonambonites* remains problematical, the available evidence noted below all indicates the plate to be a deltidium.

In some clitambonitidines, such as the Atelelasmatinae and Anomalorthinae, the delthyrium is open or with only selvages of shell along the lateral margins. Williams (1965, p. H346) interpreted this state as probably indicating that the pseudodeltidium failed to develop 'during the differentiation of the young shell'. But this growth pattern is typical of a deltidium, not of a pseudodeltidium which, as noted, always defines the front of a pedicle foramen. The absence of a delthyrial cover is also noted by Williams (*in* Whittington and Williams 1955, p. 412) in at least some young specimens of a species of the more standard *Kullervo*.

Vellamo is a genus with a large foramen extending anteriorly from the apex of the delthyrium where the spondylium may or may not show the scar of a pedicle callist. The foramen has a somewhat variable degree of regularity in its outline, and small forms may lack the standard deltidium. The type specimen of *Vellamo parva* Öpik, 1934 is one such small form, 14 mm wide, in which the usual large foramen of the genus is not enclosed at the front by the deltidium which is present only as a pair of plates along the lateral margins of the delthyrium. A specimen of *Vellamo* *simplex* (Pl. 1, fig. 7) shows well preserved growth lines on the deltidium which illustrate how the deltidial plates developed, initially as small plates occupying the antero-lateral corners of the delthyrium. The growth lines show the addition of increments extended further towards the midline until the plates abutted; subsequently secretion took the form of continuous convex strips of calcite arching across the width of the delthyrium to form a deltidium, the growth lines of which are continuous with those across the adjacent interarea. The form of the growth lines makes it quite clear that the structure could not have been produced by resorption of continuous strips of a deltidium, but that it gradually accreted as indicated. Many specimens of *Vellamo* in the Öpik (1934) collection in Tallinn illustrate this growth pattern, which has also been observed in *Clitambonites*. The deltidium of *Clinambon anomalis* (Pl. 1, fig. 8) again shows how the deltidial plates accreted before joining at the front with continuous strips across the deltidium, but this specimen also shows well the gradual sealing of the foramen within the deltidium; the secretion to the posterior of the foramen additionally confirms that the direct contact of the pedicle with the apex in the manner of a strophomenid pseudodeltidium was lacking. The mode of sealing of the foramen at the posterior of the deltidium in a specimen of *Estlandia* (Pl. 2, fig. 4) is less obvious. The sealed posterior part, presumably where the foramen was originally situated, is depressed relative to the frontal portion; across its middle is a topographically higher arcuate band of shell. Internally this part is smooth, lacking any indication of the presence of a foramen in the young stages.

Kullervo displays varying stages of a deltidium. Cooper (1956, p. 528) noted the presence of a vestige in the apex of a delthyrium which is figured by him (1956, pl. 80, figs 2, 7–8; pl. 99, fig. 45), and a similar vestige is also present in figures of Williams (*in* Whittington and Williams 1955, pl. 39, figs 58–59). This apical vestige is also present in shells with a well defined foramen and deltidium as figured by Öpik (1934, pl. 35, fig. 4*a*; text-fig. 39) and Wright (1964, pl. 10, figs 16, 19). In other specimens the foramen would appear to reach the extreme apex (Wright 1964, pl. 10, fig. 4) and may be sealed (Öpik 1934, pl. 35, fig. 6).

Thus it is easy to see how the delthyrial structure in *Apomatella*, with small deltidial plates, could evolve into that of *Clitambonites*, *Clinambon*, *Vellamo*, etc., with their fully fledged deltidia. Where evidence is currently lacking is in forms like *Antigonambonites* and *Raunites*, which simulate the strophomenids in their resupinate profiles and in having a commonly minute foramen situated close to the apex of the valve which became sealed early; the chances of obtaining the necessary very earliest stages to study early growth in such forms are currently remote.

VALVE HINGING

While the delthyrium is concerned primarily with the pedicle and relations with the substrate, it is in direct contact with the hinge line about which the valves open to feed, and moreover is located in the middle of the ventral area which records the growth of the hinge line. Externally, the clitambonitidines are strophic, wide-hinged forms with interareas well developed on both valves; that of the ventral valve is commonly long and varies in attitude from apsacline to procline. The

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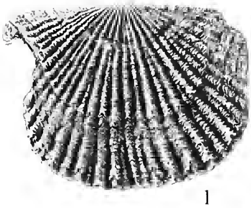
EXPLANATION OF PLATE 1

Figs 1–6. *Kullervo panderi* (Öpik). Two valves showing relationships of aditicules between interior and exterior shell surfaces. 1–3, RMS Br136961; Kohtla-Järve, Estonia; Ordovician (Llandeilo), Kukruse Stage (CII); 1–2, exterior and interior of dorsal valve; ×3; 3, enlarged tilted view to show details near the anterior margin; ×6. 4–6, QUB 26139; Küttejõu, Estonia; Kukruse Stage (CII); anterior, ventral and postero-dorsal views of ventral valve; all ×6.

Fig. 7. *Vellamo simplex* Öpik; IGT Br511; Kohtla, Estonia; Ordovician (Llandeilo), Kukruse Stage (CII); posterior view of conjoined valves showing detail of areas, including growth of deltidium; ×6.

Fig. 8. *Clinambon anomalus* (Schlotheim); IGT Br524; Rakvere, Estonia; Ordovician (Caradoc), Keila Stage (DII); posterior view of conjoined valves showing detail of areas, including sealing of foramen; ×6.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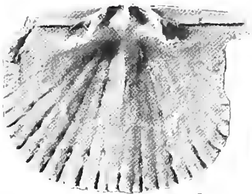
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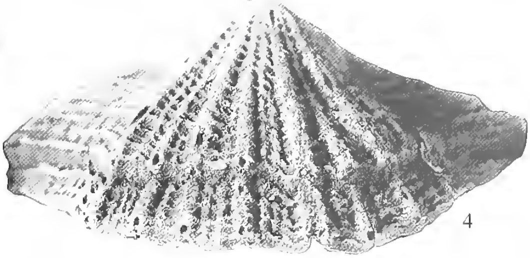
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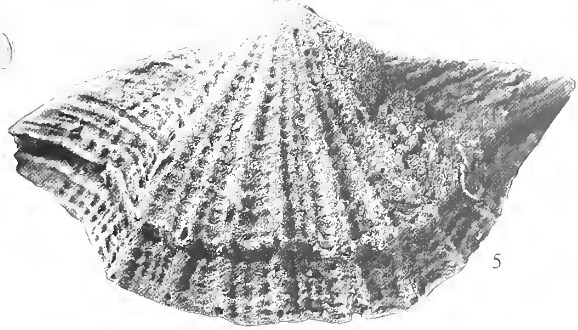
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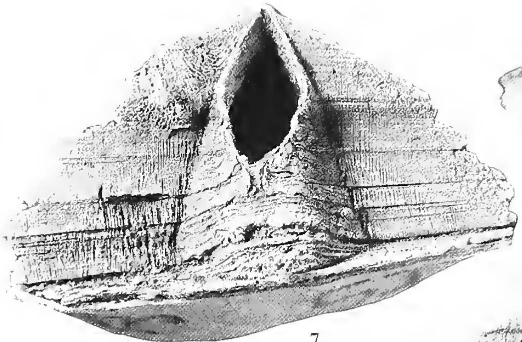
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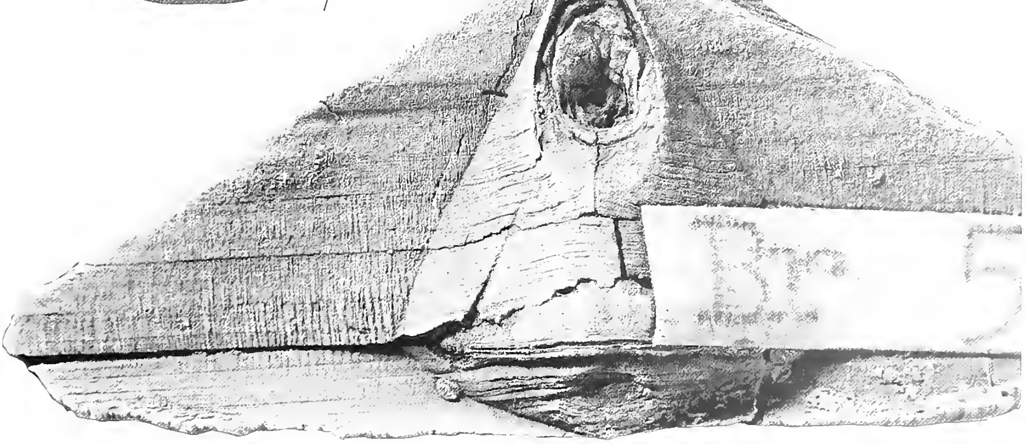
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WRIGHT and RUBEL, *Kullervo*, *Vellamo*, *Clinambon* surface of the areas shows growth lines parallel to the hinge, tracks perpendicular to this and, less commonly, oblique grooves radiating from the apex like the margins of the delthyrium, as in *Antigonambonites* (see Pl. 3, fig. 6 and Öpik 1934, pl. 31, fig. 3*c*) and *Tritoechia* (Ulrich and Cooper 1938, pl. 33, fig. 24). In well preserved material, this surface detail on the ventral valve is commonly more strongly developed in the sector closer to the delthyrium (Pl. 1, figs 7–8) in a manner reminiscent of the perideltidial areas of the orthotetidines. As with the deltidium, a strong chilidium is typically developed in the 'standard' forms; the variations in this stucture are discussed below (p. 63). In the figure of *Clinambon* (Pl. 1, fig. 8) the margin of the deltidium is seen overlying the large chilidium so that when the valves opened, the chilidium would have slid further beneath the deltidium. The shallow grooves near the lateral edges of the chilidium are matched by corresponding grooves in the deltidium, demonstrating that the two structures may reflect each other closely, as has been noted for *Vellamo* and other groups of brachiopods (Wright 1981, p. 349).

Teeth and spondylium

The teeth of clitambonitidines are deltidiodont (Jaanusson 1971, p. 35; pl. 1, fig. 5). In this context the specimen of *Estlandia* (Pl. 2, figs 2–4) is of interest. The teeth, emerging from beneath the interarea, are double structures in this genus. The inner part, along the lateral edge of the deltidium, stands high at the hinge-line and is separated from the main part of the tooth by a groove, essentially corresponding to the delthyrial margin on the surface of the interarea, and which runs down the inner surface of the tooth to mark the crural fossette. The antero-dorsal edge of the tooth curves dorsally, so that the distal end stands above the projected continuation of the interarea. The significance of this is that for growth to take place in such a structure resorption of the proximal part of the tooth is necessary. Thus although basically a deltidiodont tooth, the need to resorb the proximal part of the tooth as it grew would make it more akin to the hook-like type of cyrtomatodont tooth that characterizes the Spiriferacea (Jaanusson 1971, p. 35). This pattern Wright (1979) felt was closer to a deltidiodont tooth than to the knob-like cyrtomatodont tooth of the terebratulides and rhynchonellides, and suggested 'advanced deltidiodont' for what he regarded as a deltidiodont tooth with resorption, a phenomenon which characterizes the dorsal structures in deltidiodont orthides like *Dicoelosia* and *Rhipidomella*. Professor Jaanusson (pers. comm.) has also observed the hook-like growth of the teeth on *Estlandia* shells, but only in older shells; he interprets this as meaning that the interarea would have ceased growing by this stage and accordingly it would not be necessary for resorption in the manner of the Spiriferacea.

Internally the teeth of the hinge are supported by a spondylium in a 'standard' clitambonitidine (Text-fig. 1F). The muscle scars of the ventral valve are located on this spondylium, radially disposed, with the median adductors commonly separated by a clear break from the flanking diductors with the adjustors next to the line of the teeth at the lateral margins (Pl. 3, fig. 1). The principal modifications to the muscle surface are best seen in *Clinambon* and *Kullervo* and relate to the breaks in slope along the outer edges of the adductor scar. In *Clinambon* (Pl. 4, fig. 8) a sharp crest, which may even be acute in profile, separates the essentially V-shaped spondylium from a deep

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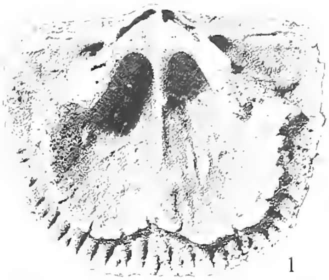
EXPLANATION OF PLATE 2

Figs 1–8. *Estlandia marginata* (Pahlen). 1, RMS Br68369; Türisalu, Estonia; Ordovician (Llandeilo), Kukruse Stage (CII); interior of dorsal valve showing strong subperipheral rim and *vascula terminalia*; × 3. 2–4, IGT Br553; Kohtla, Estonia; Kukruse Stage (CII); anterior, dorsal and posterior views of incomplete ventral valve to show mantle canals, double tooth, spondylium and deltidium; all × 3. 5–8, RMS Br68368; Türisalu, Estonia; Kukruse Stage (CII). 5, dorsal valve showing detail of surface ornament, × 10; 6, exterior, and 7, interior of valve; both × 2; 8, details of cardinalia and the granular internal surface; × 6.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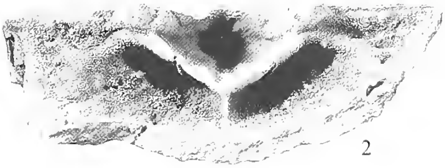
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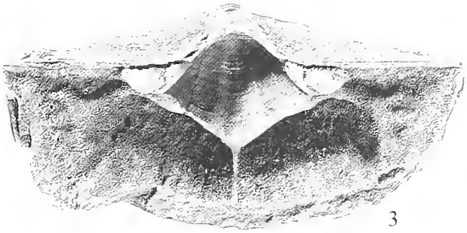
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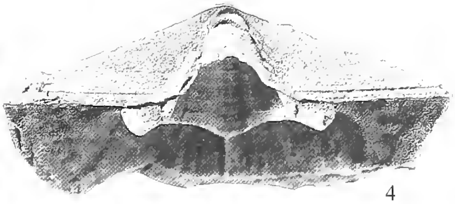
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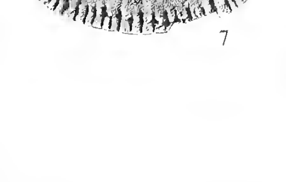
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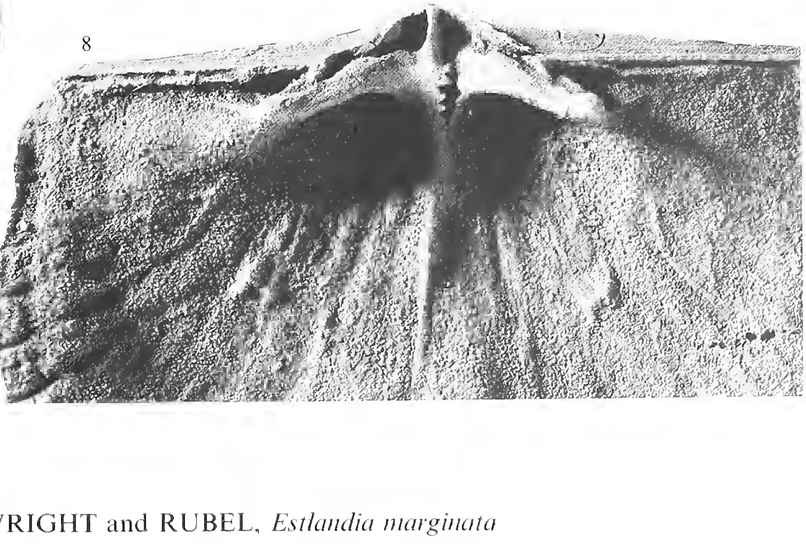
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WRIGHT and RUBEL, *Estlandia marginata*

subelliptical median portion bearing the adductor scars. A similar but less exaggerated pattern is found in *Ilmarinia*, and it may be that the deep median depression is a reflection of the procline interareas which characterize these two genera. The condition in *Kullervo* (Pl. 3, fig. 5) is quite distinct and was referred to by Öpik (1934, p. 162) as a hemisyrinx. Here the median adductor scars are almost roofed over by a pair of plates to form a chamber (hemisyrinx). Although easily damaged, the plates are separated by only a narrow slit for two-thirds or so of the spondylium, with wider access to the chamber only at the front. Presumably therefore the adductor muscles only extended from the front of the chamber across the body cavity to the dorsal valve. It is difficult to interpret any function for the upper surface of the plates apart from serving as an additional attachment surface for diductor muscles which would then have extended almost to the median line.

Williams (1965, p. H346) regarded the development of the spondylium as being 'related as it is in its forward extension to the exaggerated growth of the ventral interarea' but this very plausible explanation is somewhat of an oversimplification. Amongst other brachiopods, forms with exceptionally long interareas like *Terebrirostra* and *Onchotreta* do not have spondylia; those orthotetidines with long interareas may have well developed dental plates (*Meekella*) or a spondylium (*Geyerella*) or they may not (*Diplanus*, *Tropidolasma*, *Goniarina*); and, conversely, forms with well developed spondylia commonly do not have long interareas (as in *Stenocisma* and some Palaeozoic rhynchonellides like *Camerophorina*, in addition to most pentamerides). One is back here to the fundamental of opening and closing the valves and thus the relative positions of especially the diductor muscles for leverage purposes; if the interarea is long, reflecting a particular relationship with the substrate, raising the ventral muscle field on a spondylium is only one method of bringing the ventral attachment of the diductors closer to the cardinal process. An alternative, as seen for example in *Tropidolasma*, is to carry the dorsal seat of diductor attachment up into the extended ventral umbo on an elongated cardinal process. There are no suggestions that the function of a spondylium was other than to bear the muscles in a raised position off the floor of the valve and closer to the fulcrum along the hinge line in a relatively deep ventral valve. As an adaptation to valve articulation, the structure arose independently in various brachiopod stocks. In the 'standard' clitambonitidine, the structure is a spondylium simplex, formed from union of the dental plates fused on to a single median septum. This is modified in the gonambonitaceans into a spondylium triplex, with a pair of lateral septa extending from below the spondylium towards the valve floor on either side of the median septum. In *Antigonambonites*, with its closely opposed valves and spondylium lying close to or sessile on the valve floor, the lateral septa are quite prominent (Pl. 3, fig. 4), while the medium septum may be poorly developed or even absent. In *Estlandia* and *Kullervo*, with their deeper ventral valves and well developed median septum, the lateral septa are present only as low ridges on the underside of the spondylium (Pl. 2, fig. 2; Pl. 3, figs 1–2) with the lateral septa only reaching the valve floor in the umbonal region (Öpik 1934). The spondylium in

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EXPLANATION OF PLATE 3

Figs 1–2. *Estlandia pyron* (Eichwald) *silicificata* Öpik; NHM BB5234; Aluvere, Estonia; Ordovician (Caradoc), Jõhvi Stage (DI). 1, direct and 2, anterior, views of a silicified ventral valve interior showing the pedicle callist and the lateral septa of the spondylium triplex; × 2.

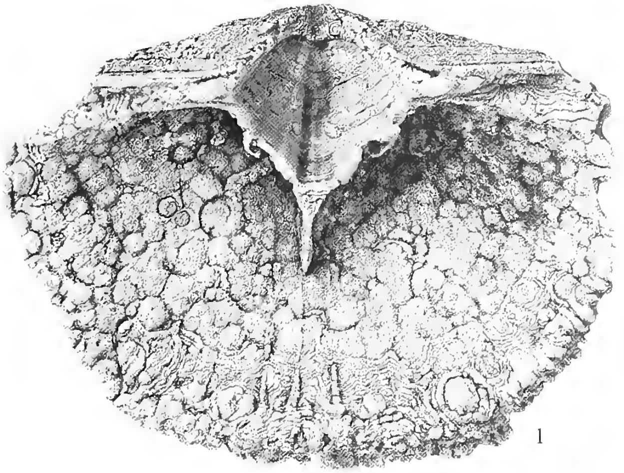
Figs 3, 7. *Lacunarites ilmatar* Öpik; IGT Br605; Paldiski, Estonia; Ordovician (Llanvirn), Kunda Stage (BIII). 3, ventral valve exterior, × 3; 7, detail showing fila and aditicules; × 10.

Figs 4, 6. *Antigonambonites planus* (Pander); River Lava, Vassilkovo, Ingria, Russia; Ordovician (Arenig), Volkhov Stage (BII). 4, IGT Br982; ventral valve interior; showing sessile spondylium triplex; × 2. 6, IGT Br983; posterior view of conjoined valves showing features of the interareas; × 3.

Fig. 5. *Kullervo lacunata* Öpik; Kohtla, Estonia; Ordovician (Llandeilo), Kukruse Stage (CII); IGT Br598; ventral valve interior showing spondylium with hemisyrinx; × 3.

Fig. 8. *Ladogiella imbricata* Öpik; Vassilikovo, Ingria, Russia; Ordovician (Llanvirn), Kunda Stage (BIII); IGT Br464; ventral valve exterior, × 5.

PLATE 3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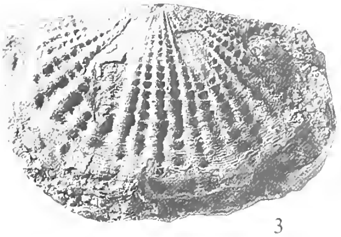
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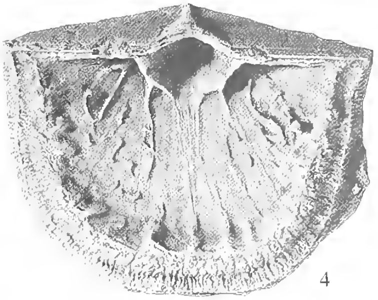
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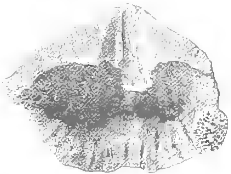
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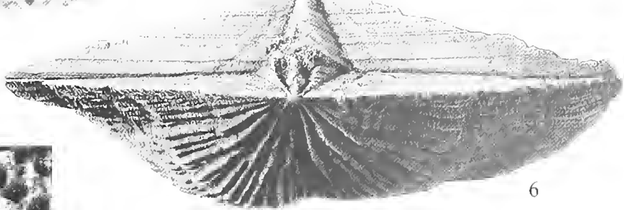
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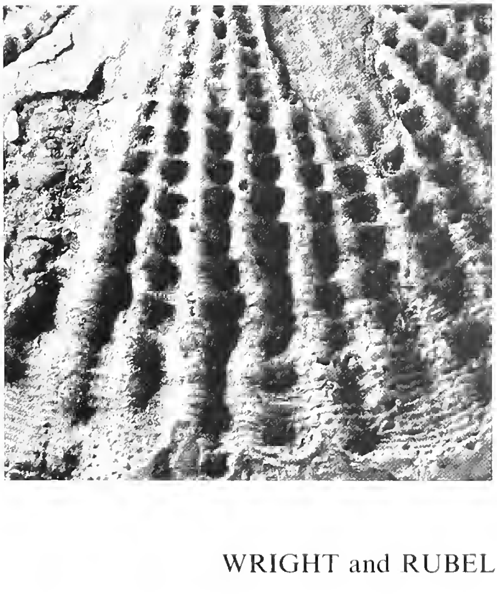
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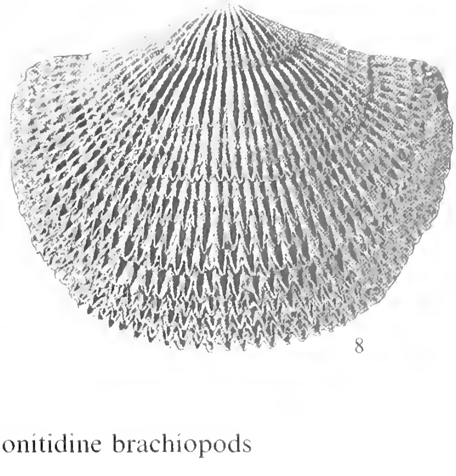
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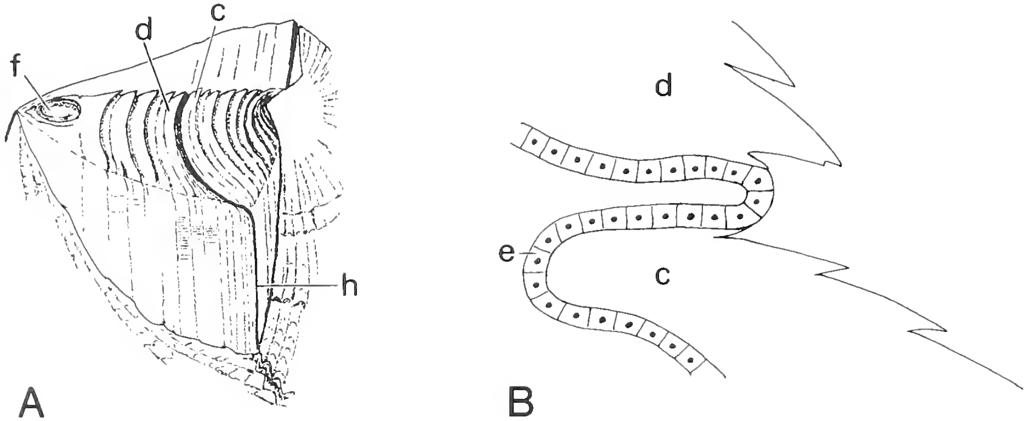
WRIGHT and RUBEL, clitambonitidine brachiopods

Anomalorthis is sessile; according to Williams (1965, p. H347), the structure in the Polytoechiidae is a pseudospondylium, differing in that the dental plates do not unite, but extend directly to the valve floor with the muscle field between built up by shell thickening. In *Polytoechia* itself, the structure, with median septum and dental plates continuous to the valve floor, strongly simulates a spondylium triplex. But the opposite is also true: a well developed spondylium triplex, with its lateral septa reaching the valve floor, strongly simulates a pseudospondylium. Öpik (1934, p. 28) regarded *Polytoechia* as having a true spondylium triplex, and suggested (p. 29) that the spondylium may have originated independently in different brachiopod stocks, a view borne out by the diverse forms, even including a lingulate (*Spondylotreta*), which possess this structure.

The cardinalia

The clitambonitidine cardinalia typically forms an anchor-shaped structure (Pl. 5, fig. 2) comprising the chilidium, socket ridges and sockets, and notothyrial platform, with a posteriorly directed plate-like cardinal process and an anteriorly directed median septum that together form the shaft of the 'anchor'.

Chilidium. A chilidium is usual; in *Clinambon* it is particularly strong, this being a reflection of its association with an unusually long dorsal interarea. *Clitambonites* itself has a large, high, semicircular chilidium with flattened lateral margins, well demarcated from the dorsal interarea (Pl. 5, fig. 1). The imbricate nature of the main shell surface is reflected in that of the chilidium, which is intriguing as its surface laminae are undercut *towards* the umbo and away from the hinge line. Thus the impression is of younger shall having been laid down on the external surface of the earlier shell. The deltidium of *Clitambonites* has its shell layers undercut away from the umbo and towards the hinge line as would be expected. In other words, the lamellose arrangement of the deltidium is stacked in the same direction as that of the chilidium. The latter is tucked in below the front of the deltidium (Text-fig. 2), so that in life the part of the chilidium currently being secreted was *within* the conch and with the shell-secreting outer epithelium lining what would subsequently become an external surface. The outer epithelia of the ventral and dorsal valves are fused in this area, but only as far as the edges of the notothyrium/delthyrium in these protremate shells. Lateral to the



TEXT-FIG. 2. Sketches of (A) the postero-median part of the hinge region of *Clitambonites* to show the orientation of the growth laminae on the deltidium and chilidium, and (B) a longitudinal section showing the envisaged relationships of the shell secreting outer epithelium to the edges of the deltidium and chilidium during growth. c – chilidium; d – deltidium; e – epithelium; f – foramen; h – hinge line.

chilidium, the lamellae pass into the non-lamellose growth lines of the interarea; this in life was underlain by mantle (Wright 1994). The same type of stacking on the chilidia is present, but not so pronounced, in forms like *Clinambon* and *Ilmarinia*. Some specimens of *Vellamo* show the feature but in many it is difficult to observe more than the general presence of growth lines.

Other clitambonitidines, such as *Antigonambonites* and *Estlandia*, possess smaller, less pronounced and more triangular chilidia on which the growth lines are undercut on the side of the hinge line (in those specimens where preservation is sufficient to allow the direction to be determined). In these cases the growing edges would have been external, i.e. not concealed within the conch by the deltidium, and lined internally by outer epithelium in the usual way.

In addition to these two arrangements of the chilidia, in other clitambonitidines the notothyrium was either flanked by chilidial plates as in *Tritoechia* or, as with *Oslogonites*, completely lacking any calcareous plates within an open notothyrium. The various forms of the structure have accordingly been used as a basis for differentiating stocks.

Socket ridges. The socket ridges extend latero-anteriorly from within the limits of the notothyrium (Pl. 5, fig. 1), coming away from the underside of the chilidium and forming a ridge lying along the lateral extensions of the notothyrial platform, defining the sockets medianly and commonly culminating in a small ventrally projecting process. The amount of associated shell deposition may produce a quite different appearance as seen in the contrasting cardinalia of the two specimens of *Estlandia marginata* figured as Plate 2, figures 1 and 7. The heavy ridges seen in figure 1 coupled with the strong subperipheral rim suggest that this is gerontic specimen. This must remain a possibility, but from the viewpoint of size rather than presumed age the specimen of figure 7, with its more slender socket ridges and barely developed subperipheral rim, is clearly the larger of the two, being nearly 4 mm the wider.

Notothyrial platforms. The notothyrial platform in a standard clitambonitidine is well developed. At the front it is undercut, apart from in the middle sector where it passes anteriorly into a strong median ridge to produce the characteristic anchor-shaped cardinalia (Pl. 5, fig. 2). But there is considerable variability. In species of *Vellamo* the undercutting may or may not occur. In *Oslogonites* and *Progonambonites* the notothyrial platform is short, barely extending beyond the hinge line, is concave forward and sharply truncated anteriorly, with any low median ridge between the adductor pairs rising anterior to, and not continuous with, the platform (Rubel 1963, pl. 1, fig. 2; pl, 3, fig. 1). Despite the variation, what does appear valid is that, while in most forms the platform is built up to be almost flush with the dorsal interarea, in *Polytoechia* and its allies the platform is only weakly developed or, at best, depressed well below the interarea. It may not be coincidence that the polytoechiids also lack the generally strong chilidium of the other clitambonitidines.

Cardinal process. The cardinal process is a simple, generally narrow and prominent ridge in the centre of the notothyrial platform which extends towards, and may fuse with, the inner surface of the chilidium. The cardinal process is not always present, but its absence as a generic character is unreliable. For example, its use as a feature separating *Oslogonites* from *Progonambonites* (Williams 1965, p. H355) is not valid, for although the latter genus does have a cardinal process, *Oslogonites* is described by Rubel (1963, p. 92) as being either with or without a weak cardinal process. Again, the cardinal process in some specimens within the *Hemipronites*-*Ladogiella* complex may be absent, yet it is present in others, and cannot therefore be used as a means of differentiating the two genera. This situation resembles that of the punctate orthide *Paurorthis*, another example of an early stock which lacks the stable development of a cardinal process so that its presence or absence is of little taxonomic significance.

Taxonomic use has also been made of the presence of subsidiary or ancillary cardinal process ridges which flank cardinal process in some forms, so that they are said to characterize specific genera. Thus, for example, in the subfamily Clitambonitinae (Williams 1965, p. H348) they form part of the diagnoses of *Clinambon*, *Iru* and *Ladogiella*, while, by contrast, *Vellamo* is diagnosed as having a simple cardinal process. However, the recognition of these ridges, termed *Seitenleiste* by Öpik (1934, p. 213), appears simply to reflect their degree of development, and even within a population they may be strongly or imperceptibly developed, as may readily be seen by comparing the two specimens of *Ilmarinia dimorpha* illustrated in Plate 4, figures 1–4. Regarding the specific case of *Vellamo*, ancillary ridges are clearly visible on many species of the genus in the Öpik (1934) collection, and indeed are apparent from his figures (e.g. 1934, pl. 13, figs 1, 5). The structures were also clearly figured for *V. sulculata* by Wright (1964, pl. 10, figs 2, 5), who specifically noted the presence of two muscle scars on either side of the cardinal process for which he suggested (p. 236) that the inner pair (which extend up on to the side of the cardinal process) were for attachment of the diductor muscles and the outer pair for the accessory diductor or possibly dorsal adjustor muscles. The division of the notothyrial platform into three areas on either side of the median cardinal process in the figured specimen of *Ilmarinia* (Pl. 4, fig. 2), *Iru* (Öpik 1934, pl. 4, fig. 3) and other forms suggests that in fact all three muscles may be sited on the notothyrial platform. The delimitation of the various scars by ridges would appear to be dependent on the amount of differential secretion beneath the muscle and at its lateral margins. In gerontic valves this difference could be expected to be greater, but other morphological factors affecting the function of the diductors, such as a procline interarea, may also be contributory to the relative amounts of shell secretion and hence the relative emphasis of the ancillary ridges.

Thus we have serious misgivings about the taxonomic value of these ridges which display a high degree of variability that is shared also with other internal structures currently accepted as characterizing different genera. To evaluate the taxonomic significance of such variable features will require the future statistical treatment of large samples.

Adductor field

The dorsal adductor field in genera such as *Clitambonites*, *Ilmarinia*, *Clinambon* and *Ladogiella* is typically quadripartite, with the anterior and posterior pairs being separated by a clearly defined ridge perpendicular to the median ridge. But, because of variability, the scars of some specimens of such genera take on a different aspect caused by strong radial ridges traversing the scars, so that the appearance is of a posterior pair disposed lateral to the anterior pair (compare *Ilmarinia* of Öpik 1934, pl. 19, fig. 3 with fig. 4 or pl. 18, fig. 2; and *Ladogiella* in pl. 42, fig. 1 with fig. 2). These radial ridges occur commonly external to the muscle field in well preserved and particularly gerontic specimens and characterize the pinnate mantle canal system. Their presence across the muscle scars in some specimens may reflect their earlier strong development on the floor of the mantle cavity before the body cavity with the muscle scars advanced over it. The significance of this is that in some clitambonitidines, such as *Kullervo*, the adductor scars do appear to be arranged radially (Öpik 1934, pl. 35, figs 1–2) and have been described as subpetaloid. But in such valves the posterior part

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EXPLANATION OF PLATE 4

Figs 1–4. *Ilmarinia dimorpha* Öpik; Üksnurme, Estonia; Ordovician (Caradoc), Oandu Stage (DIII); detail of cardinalia of two dorsal valves to show variation in development of ancillary ridges. 1–2, QUB 26137. 1, valve interior; × 1·5; 2, details of the cardinalia; × 5. 3–4, QUB 26138; 3, valve interior; × 1·5; 4, tilted to show details of the cardinalia; × 5.

Figs 5–7. *Clitambonites squamatus* (Pahlen); NHM BB68557; N Estonia; Ordovician, ?Kukruse Stage (CII). 5, ventral valve interior; × 2; 6, interarea viewed from exterior to show sealed foramen; × 4; 7, internal view of spondylium and deltidium showing smooth surface lacking any trace of foramen of young stages; × 4.

Fig. 8. *Clinambon anomalus* (Schlotheim); NHM B5858, Davidson collection; 'Reval, Russia. Ordovician'; [?Keila Stage (DII), Caradoc, N Estonia]. Ventral valve, view of interior to show spondylium; × 1·5.

PLATE 4

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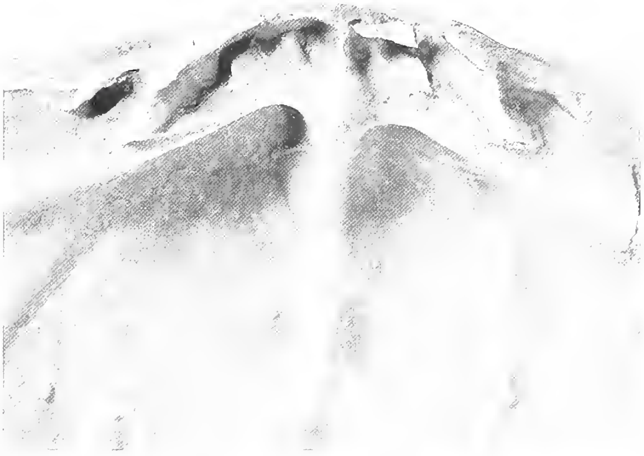

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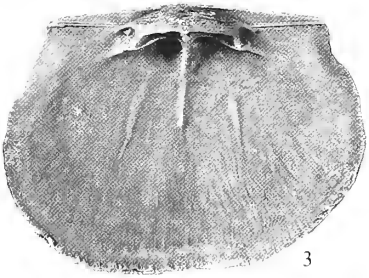

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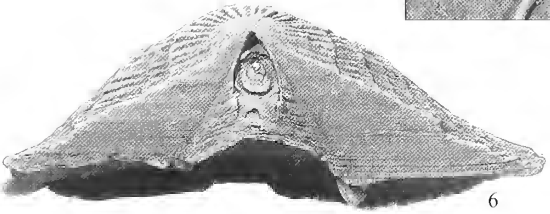

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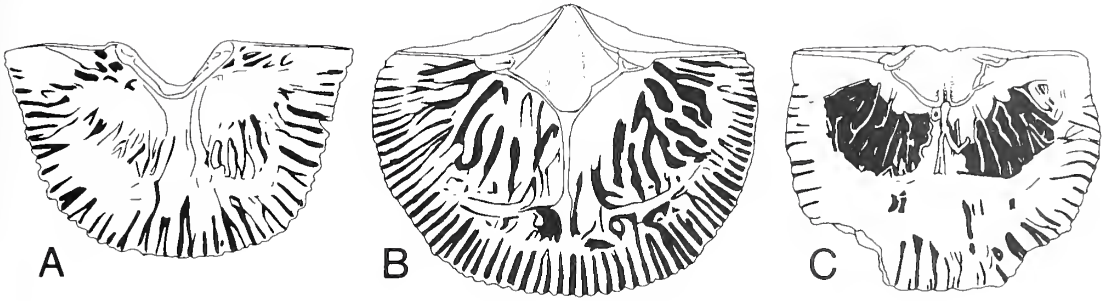
WRIGHT and RUBEL, *Ilmarinia*, *Clitambonites*, *Clinambon* of the scar shows no clear traces at all, and the figure of a different species (Öpik 1934, pl. 36, fig. 2) shows a pattern tending towards quadripartite, although the ridges separating anterior from posterior scars still have a basically radial disposition, being oriented antero-laterally in a manner developed to a certain extent in some *Vellamo* (Öpik 1934, pl. 12, fig. 7). In the more radial disposition as figured for *Kullervo* by Öpik (1934, text-fig. 52) the anterior pair is apparently larger than the posterior pair. The posterior scars appear as long narrow tracks, whilst the medianly situated anterior scars are tear-shaped. However, if the latter reflects the movement of an advancing muscle attachment, it may be that it is the smaller scar. The gonambonitids and the polytoechiids also have radially arranged adductor scars and in these cases the anterior pair is smaller than the posterior pair. This relative length of the adductor scar pairs has been used as a taxonomic character and, unlike members of these two families, *Clitambonites* and the majority of clitambonitidine genera have a posterior adductor pair which is shorter than the anterior pair. Nevertheless, the size difference is not always clear-cut and some stocks, such as *Vellamo*, are variable in this character both between and within species.

This emphasizes what appears to be a well-known tenet of taxonomy; that a feature variable in one group and therefore of little use in classification becomes consistent in another stock, when it provides that certainty for identification and also for classification.

MANTLE CANALS

The mantle canals, well known for the clitambonitidines as a result of the classic work of Öpik (1934), are characterized by displaying the pinnate pattern of Williams (1956). This was further emphasized by Williams (1965, p. H132), when he described them as being 'decisively' pinnate. It is therefore somewhat surprising to find that the overall pattern in the ventral valves of at least *Apomatella*, *Ladogiella* and *Neumania* is apparently saccate, with faintly developed vascula media sweeping around laterally in an arc to contain the gonocoeles. The *Ladogiella* specimen (IGT Br464) figured by Wright (1994, fig. 1F) is the same as that illustrated by Öpik (1934) as his plate 43, figure 1*b* and diagrammatically in his text-figure 13. In the text-figure description, Öpik stated that the bow-shaped vascula arcuata and ovarian markings were completely missing, and the radiating canals are depicted as being strong and continuous. This continuity is not, however, seen in his photograph, where the canals of the central areas fade across an ill-defined band before reaching the vascula terminalia. A different conclusion is reached from Wright's photograph, where the zone of uncertainty is seen as arcuate ridges, interpreted as arcuate vascula media, behind which terminate the canals of the central areas, interpreted as the site of gonocoeles. In the postero-lateral areas, certainly on the left-hand side of this specimen, the canals do radiate directly into the vascula terminalia so that the arcuate vascula media do not extend as far as these parts of the valve. Text-figure 3B is drawn from Wright 1994, figure 1F. Likewise, the photograph of *Apomatella* figured in the same paper as figure 1C again shows clearly, albeit faintly, arcuate vascula media enclosing ovarian markings; the vascular markings of this specimen (RMS Br74575) are drawn here as Text-figure 3A. Additional support for the presence of the saccate condition in the ventral valves of *Apomatella* and *Neumania* is seen in the figures of these genera illustrated by Rubel and Popov (1994). *Apomatella* again shows strong vascula media curving away at the front of the spondylial septum, although they fade and are difficult to trace laterally (Rubel and Popov 1994, pl. 1, figs 5, 16). Nevertheless, the clear, irregular ridges of the ovarian scars do not cross their smooth lateral continuation to reach the vascula terminalia, which is suggestive of the presence of arcuate vascula media along these smooth areas. The gonocoele areas in *Neumania* again stop against somewhat more clearly defined smooth arcuate vascula media, sketched in Text-figure 3C (based on the Rubel and Popov figure of IGT Br968; 1994, pl. 2, fig. 8). A form closely related to *Apomatella* is *Atelelasma*. Cooper (1956) figured the impression of a ventral valve interior which he identified as *Atelelasma* aff. *A. perfectum* Cooper (pl. 79, fig. 3), and although he makes no comment on the mantle canals, this figure clearly shows the saccate arrangement with arcuate vascula media which

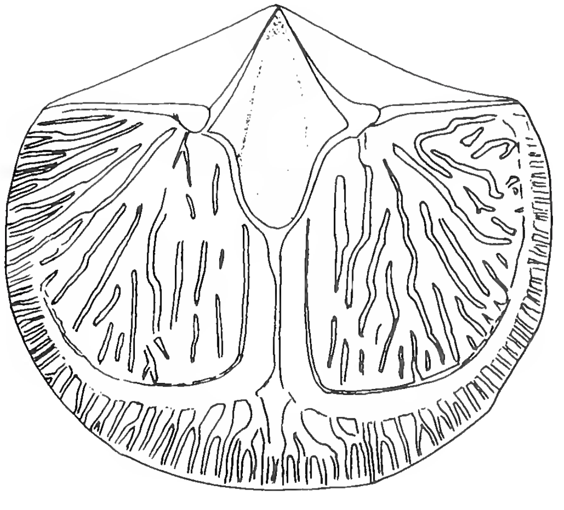


TEXT-FIG. 3. The mantle canal systems in the ventral valves of *Apomatella*, *Ladogiella* and *Neumania*, interpreted as indicating the saccate condition. Uncoloured areas are topographically positive or poorly preserved; black areas are topographically negative. A, *Apomatella ingrica* (Pahlen), based on Wright 1994, fig. 1C; B, *Ladogiella imbricata* Öpik, based on Wright 1994, fig. 1F; C, *Neumania erecta* (Pander), based on Rubel and Popov 1994, pl. 2, fig. 8.

appear to be directed laterally towards the antero-lateral margin. The saccate condition is also to be seen in the specimen of *Hemipronites tumidus* figured by Schuchert and Cooper (1932, pl. 8, fig. 10), who further drew attention to the similarity of the ovarian impressions to those of *Orthis*, etc. in their description. It is now clear that along with *Ladogiella* and *Hemipronites* (which we find hard to differentiate generically) the Atelelasmatinae are characterized by a saccate mantle canal system in the ventral valve (Text-fig. 4) in which arcuate vascula media confine the gonocoeles anteriorly and anterolaterally but which do not appear to confine them posterolaterally, where the radiating canals pass directly into the vascula terminalia, thus suggesting the onset of the pinnate pattern which characterizes the bulk of the clitambonitidine genera.

More fundamental to the understanding of the soft tissue distribution in extinct brachiopods generally and in protremates in particular has been the discovery of mantle canals lining the internal surface of the interareas in the procline clitambonitidines *Apomatella*, *Clinambon* and *Ilmarinia*. This demonstrated that the interareas of these strophic shells was lined with mantle and thus that the fusion of the mantle lobes and the start of the body cavity occurred not at the ends of the hinge

TEXT-FIG. 4. Generalized diagram to show the disposition of the mantle canals in those clitambonitidines which possess a saccate pattern in the ventral valve. The arcuate vascula media fade posterolaterally and the evidence so far available suggests that these may either break down laterally, with a pinnate pattern developing in the posterolateral angles (left-hand side), or may narrow but continue to the posterior margin (right-hand side). It may well be that both arrangements occur.



lines, as in extant telotremates, but at the edge of the delthyrium (Wright 1994). The problems of finding mantle canals beneath apsacline interareas were discussed in that paper, so that it is interesting to note their occurrence in a specimen of *Estlandia* (Pl. 2, fig. 2). Coming out from below the teeth at the lateral edges of the spondylium in this specimen are a pair of strongly developed mantle canals which extend across the valve floor in the usual way. The posterior branches of these canals, however, extend to the inner surface of the interarea which is marked by a series of nodes close to the hinge line. Though less impressive than the above noted mantle canals recorded from the procline areas of *Apomatella* and *Ilmarinia* (Wright 1994, fig. 1C–D, I–J), these impressions on apsacline shells confirm that, as predicted, the interareas of these strophic shells were also lined with mantle from the extremities of the hinge line medianly to the teeth and it is the teeth therefore which mark the lateral edges of the body cavity. Indeed, once pointed out, it is fairly obvious from the main canal system across the valve floors in these shells that the body cavity in the ventral valve must have been defined laterally by the position of the teeth and anteriorly by the edge of the spondylium.

ORNAMENTATION AND HOLLOW COSTELLAE

At present, there are no known smooth-shelled clitambonitidines, and apart from a single costate species, *Neumania costata* (Pander, 1830), the entire order possesses a costellate shell. The costellae arise by either branching or intercalation, or both; while their coarseness varies from the fine strophomenoid-like ribbing of *Raunites* (Pl. 5, fig. 5) to the coarse ribbing of *Vellamo*. The concentric ornament, by contrast, is highly variable (e.g. Pl. 2, fig. 5; Pl. 5, fig. 6), so that in addition to fine growth lines, there may be regular or irregular fila, and/or lamellae and imbrications. In combination with the radial ornament, a reticulate pattern may develop, as in *Kullervo* (Pl. 1, fig. 5) or *Lacunarites* (Pl. 3, fig. 3), or spines, as in some *Progonambonites* (Öpik 1934, pl. 24, fig. 5) and *Estlandia*. It has, however, not been possible to verify the record of the presence of occasional rugae in *Raunites* in any specimen seen by us. The radial ribs are commonly described as hollow; this is a term which needs some clarification.

All ribs are initially 'hollow' in that they represent the external expression of ridge-like undulations of the mantle edge which housed setae along the internal concave surfaces. Along the internal edge of the valves the marginal crenulations reflect the ribs and intercostal spaces, with the setae located in the follicular embayments of Williams and Wright (1963). In most brachiopods these marginal crenulations fade away from the margin as they become concealed by continued secondary shell deposition and, as the shell grows, the modification of this inner surface by differential secretion below the mantle canals and areas of muscle insertion.

However, the term 'hollow ribs' is usually understood to indicate the presence of holes along the length of ribs which are not related to the punctae (endopunctation) and from which they are defined as differing by not passing through the shell to the inner surface, hence the term exopunctation. Although there is a variety of form in external pitting, the larger, forwardly directed, shallow-angled aditicules (Wright 1981, p. 472), which are the most obvious kind of perforations associated with 'hollow ribs', do in fact pass through the entire shell but normally only at or near

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EXPLANATION OF PLATE 5

Figs 1–4. *Clitambonites schmidti* (Pahlen); NHM BB68553; N Estonia; Ordovician, ?Kukruse Stage (CII). 1, detail of chilidium and interarea of dorsal valve; × 6; 2, dorsal valve interior; × 1·5; 3, dorsal valve exterior; × 1·5; 4, oblique view of exterior, showing detail of ornamentation; × 10.

Fig. 5. *Raunites venusta* (Öpik); Vassilkovo, Ingria, Russia; Ordovician (Arenig), Volkov Stage (BII); figure from Öpik 1934, pl. 25, fig. 1*b*, showing nature of ribbing and concentric corrugated fila; × 5.

Fig. 6. *Clitambonites schmidti* (Pahlen) *epigonus* Öpik; Aluvere, Estonia; Ordovician (Lower Caradoc), Johvi Stage (DI); figure from Öpik 1934, pl. 8, fig. 1, showing strongly developed concentric fila and imbrications; × 6.

PLATE 5


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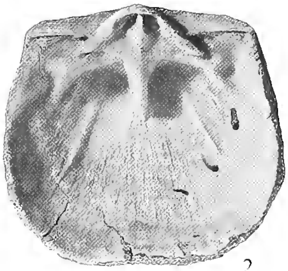
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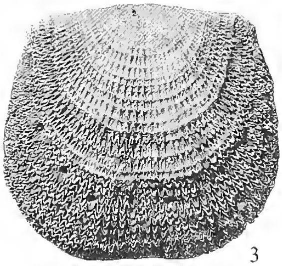
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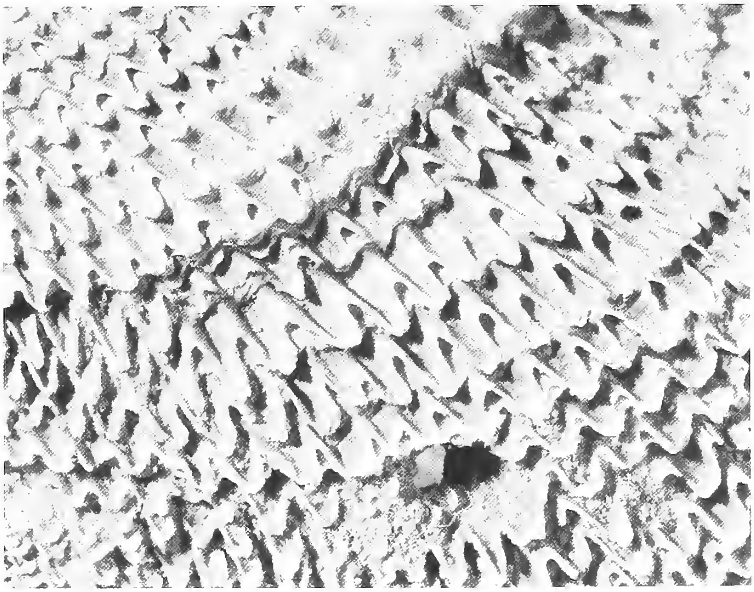
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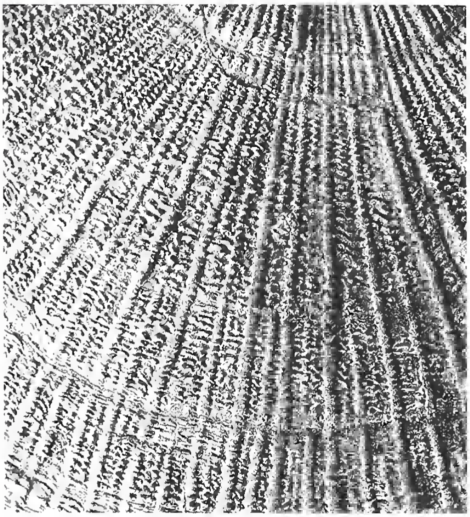
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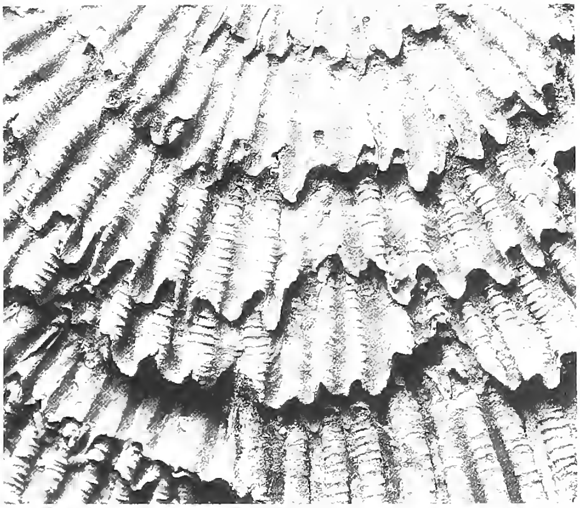
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WRIGHT and RUBEL, *Clitambonites*, *Raunites* to the shell margin where they are formed; thereafter they are sealed within shell and only have an expression on the external surface. The origin of these aditicules has been demonstrated in *Doleroides* and particularly *Rhipidomella* where the presumed setal-bearing follicular embayments can be observed in various degrees of incorporation into the shell (Wright 1981, p. 466), so that in life the setae would have become sealed into the shell as it grew, with a new seta arising along the line of the re-developing rib.

Aditicules are not uncommon in the clitambonitidines, and in fact have already been figured as such on the exterior of *Kullervo lacunata* (Wright 1981, pl. 66, fig. 8). A well preserved dorsal valve of *Kullervo panderi* collected by Professor Jaanusson (from the lowermost Kukruse Stage (CII) at Kohtla-Järve) and a ventral valve of the same species collected by Professor Rõõmusoks (from the Kukruse Stage (CII) at Küttejõu) are figured here (Pl. 1, figs 1–6). Both show even more convincingly than the silicified *Rhipidomella* the relationship between the deep follicular embayments and the external apertures of the aditicules, with some aditicules unusual in maintaining contact with the mantle through a tube-like perforation well to the posterior of the shell margin. This evidence, if any were needed, confirms the previous conviction (Wright 1981) that it is difficult to postulate any other realistic function for aditicules other than the accommodation of setal bristles within the shell surface; any speculation must start with the potential functions of these incorporated bristles. It is noteworthy that both the ventral and the dorsal valves of *Kullervo* show a similar scattering of the aditicules; this is in marked contrast to *Doleroides* and *Rhipidomella*, in which the arrangement differs on the two valves (Wright 1981).

Aditicules have not been observed in all clitambonitidines. Indeed, the absence of hollow ribs is used as a generic character in *Apomatella*; but occasional aditicules occur sporadically in many genera such as *Pahlenella*, *Raunites*, *Vellamo* and even *Lacunarites* (Pl. 3, fig. 7), a form which is more obviously characterized by strong intercostal pitting. In strongly imbricate stocks like *Ladogiella* and *Clitambonites* the aditicules occur largely in concentric rows associated with the anterior edges of the imbrications, while the extreme development is represented by *Estlandia*. A ventral exterior of *Ladogiella imbricata* is figured in Plate 3, figure 8. The young stages of this well preserved shell show 13 initial costae with very fine concentric filose growth lines (20 per mm) and only two weak imbrications prior to a well marked imbrication at 2·0 mm by which stage there are 27 ribs, the additional costellae apparently all arising by branching. This pattern is essentially repeated to the next well-marked imbricate growth stage at 3·8 mm (47 ribs here, with additional costellae arising on the downslope side of existing ribs). At the weak imbrications the ribs simply step down, as at any accentuated growth line, with, for the most part, little space at the crest of a rib for the incorporation of a seta as a bristle within the shell. Continued growth resulted in increasingly strong imbrications developing at about every half mm; when forward growth stopped temporarily at an imbrication, the valve would have had a scalloped margin, with the crests of the ribs marking embayments. Renewed growth along the line of the ribs produced a flat floor, partly arched over by the sides of the ribs along the embayments to give a cave-like effect, before the rib again developed at about half the length of the invagination. This morphology indicates that a seta could have projected from such a site, but the fact that other ribs appear to have developed very tightly against the rib of the previous imbrication, and commonly so along particular imbrications, indicates that any such incorporated setae would not have been uniformly developed across the shell, although potential setal sites increase in number in the later imbrications. The scalloped margins in life would not have been as exaggerated as they now appear. Where the shell is well preserved, the concentric fila can be traced down off the rib and across the intercostal spaces where they advance modestly, and postero-laterally such fila correspond with the shell edge of the time. But where the scalloping is well displayed, although the fila at the front of the rib crest can be traced, again advancing slightly, across the intercostal space, the fila parallel to them along the sides of the ribs terminate abruptly against the outside edge (as illustrated for *Clitambonites* in Pl. 5, fig. 4), i.e. they do not follow the line of the embayment. Whilst it is possible that the shell was resorbed medianly, it seems more probable that, protruding away from the surface, the fragile edge of the imbrication was simply abraded.

In *Clitambonites* the imbrications are more exaggerated (Öpik 1934, pl. 8, fig. 1, reproduced here as Pl. 5, fig. 6). The radial ornament consists of costellae, which arose by intercalation or branching, that show clear, sharp-crested concentric fila with a density of about 5 per mm. The shell growth is interrupted by a small number of strongly defined imbrications, typically *c.* 2·5 mm apart, which reflect marked pauses in anterior growth. Öpik's figure shows ribs with the crests withdrawn from the margin of the earliest imbrication shown, sometimes with a clear 'cave' proximally. But these are not widely present, and the appearance of these ribs would appear to result again from abrasion of the crests of the ribs along the edge of the imbrication, a view supported by the variably frayed margins of the other imbrications as well as the pattern of the concentric fila crossing the rib without any inflexion that would correspond to an invagination along the rib crest. In the specimen of *C. schmidti* (Pl. 5, fig. 4) the margin of the imbrication has a modest scalloping compared with that of the rib and intercostal groove. Again the fila along the advancing edges of the rib are truncated and suggest abrasion of the rib crest. At the same time, the revealed forward-pointing apertures (aditicules) strongly suggest an array of setae incorporated all along the imbrication.

Because of the delicate nature of lamellose structures and the possibility that damage has occurred during extraction from the matrix, a ventral valve of *C. schmidti* with adherent matrix was embedded in resin and sectioned longitudinally (Text-fig. 5). This shows the extended nature of the imbricated rib beyond the underlying step, which must make it prone to breakage. Internal to a rib there is a groove, interpreted as being the site of a seta. This groove swells at the proximal end into a slender bulb, so that the overall shape corresponds to that of a setal follicle in an extant brachiopod. The younger shell below an imbrication shows the pronounced step before the shell advanced again, just as in shells manually freed from their matrix; but what has not been observed in such shells are the small lamellose extensions on this step, which indicate a series of anteriorly directed growth layers which built up the shell thickness before the shell finally advanced to form the succeeding imbrication.

TEXT-FIG. 5. Longitudinal section through a ventral valve of *Clitambonites schmidti* (Pahlen) with the exterior embedded in matrix (stippled) to show a series of surface imbrications (i) underlain by a setal groove terminating proximally in a bulb (b) interpreted as containing a setal follicle. The succeeding step (s) shows fine laminae, not preserved in matrix-free shells, representing minor oscillations in the mantle edge before the growth of the succeeding imbrication. RMS Br92111; Kukruse Stage (CII); Kohtla, Estonia; × 10.

The ornament of *Estlandia* (Pl. 2, fig. 5) appears to be peculiar to this genus. The costellae arise largely by intercalation on this dorsal valve, and the regular, straightish concentric fila of the intercostal spaces (*c.* 8 per mm) cut back across the ribs, where their topographic development varies. Some cross the ribs simply as strong fila; with growth, an increasing number become lamellose with the posterior side curving away from the valve surface to form an arch over a pit, the attitude of which varies from being directed anteriorly to almost perpendicular to the surface.

When developed evenly over the whole length of a rib such lamellae strongly resemble the overlapping hip tiles along roof angles but with pits between; other lamellae which are directed upwards away from the shell surface may have the sides joined beneath to form a hollow spine in the manner of *Spinorthis* (Wright 1964). The arched pits and hollow spines of these tubulose ribs are all interpreted as aditicules each of which contained a seta embedded in the shell. Around the internal margin, outside the subperipheral rim, deep follicular embayments with pits or, posterolaterally, just single pits, remain as evidence of the connection of the aditicule to the internal valve margin.

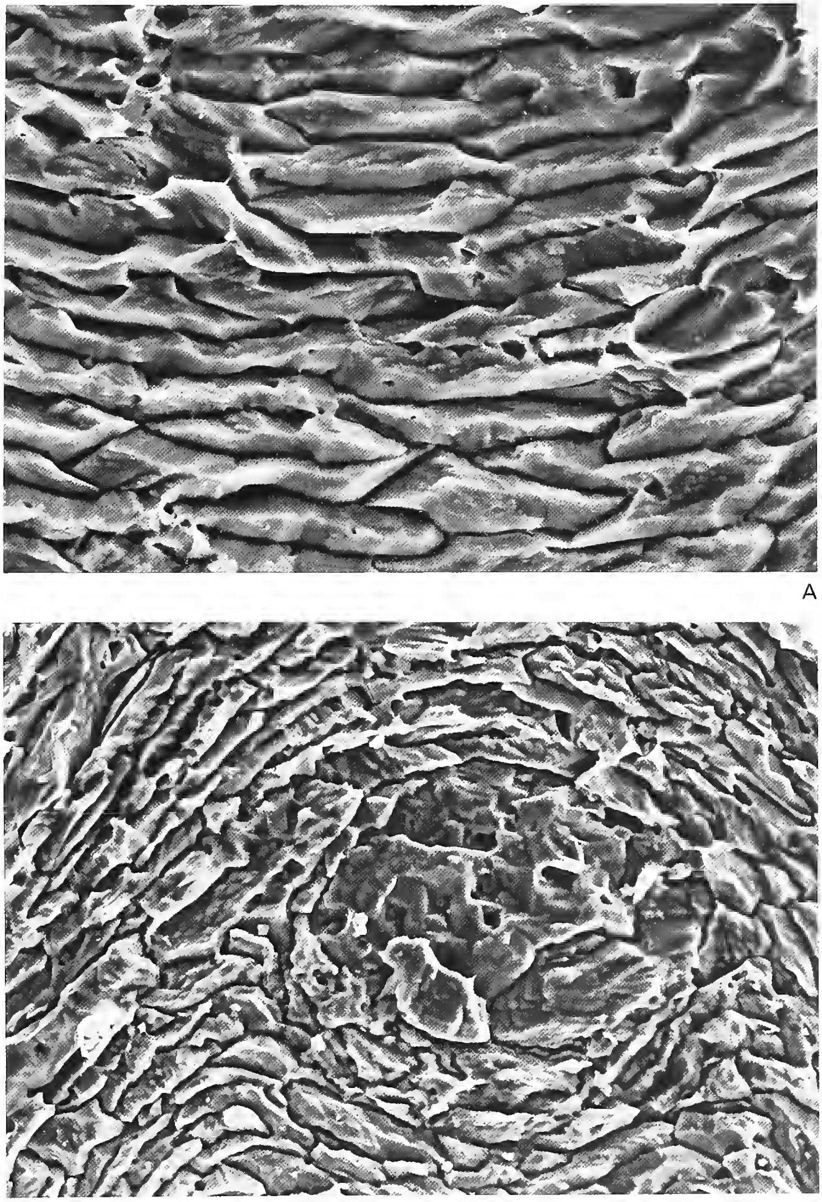
In the Polytoechiidae, *Tritoechia* is a form which shows well developed aditicules along the rib crests. *Acanthotoechia* appears to be unique in this family in developing rows of spines along the ribs peripherally. Their distribution on the differentiated ribs is detailed by Williams and Curry (1985, p. 224) and is characterized by the coarser primary ribs bearing two rows of laterally inclined fine cylindrical spines with the finer intermediary ribs bearing a single row of hollow erect spines. The paired spines are clearly not situated centrally along the rib as are aditicules and, moreover, there is a tendency for those of the single rows to zig-zag, so that their distribution is closely comparable to these features as displayed by arrugiae and not aditicules (Wright 1981, p. 476). A second feature of significance of these pits is their size; the diameter of the largest aperture figured by Williams and Curry (1985, fig. 159*b*) is 0·04 mm; this compares well with the diameter of 0·04 mm for the arrugiae but not with that of 0·18 mm for the aditicules on the *Doleroides* illustrated by Wright (1981, pl. 70, fig. 2). This again supports the interpretation of the *Acanthotoechia* perforations as being comparable to arrugiae and not aditicules.

SHELL SUBSTANCE

The shell substance of the clitambonitidines had been regarded as being impunctate until Öpik (1932) established the presence of pseudopunctae in the shell of stocks such as *Estlandia* and *Kullervo*. Williams (1968, p. 35), in his review of the shell structure of the articulate brachiopods as revealed by transmission electron microscopy, reported the presence of a fibrous secondary layer in *Vellamo*, *Eremotoechia* and *Antigonambonites*. These genera represent the broad spread of the clitambonitidines, covering both impunctate and pseudopunctate stocks. The fibres were well illustrated by Williams for *Vellamo* (1968, pl. 18, fig. 6).

Within the clitambonitidines, it is the Superfamily Gonambonitacea which is characterized by the presence of pseudopunctae. This shell modification is strikingly obvious in most genera ascribed to the superfamily, with the associated granular internal surface being visible at relatively low magnifications, e.g. in *Estlandia* (Pl. 2, fig. 8). The exception to this dense granulation is *Anomalorthis*, which was reported by Ulrich and Cooper (1938, p. 127) as having 'scattered pseudopunctae like those occurring in the Strophomenacea'. The mixture of clitambonitid and orthid characters in these enigmatic shells resulted in Ulrich and Cooper placing the family on balance in the Orthacea. Williams (1965, p. H353) judged it best to assign the stock to the Gonambonitidae.

The thin section of *Anomalorthis oklahomensis* figured by Ulrich and Cooper (1938, pl. 22, fig. 6) has been examined for the present study, and the small dots visible in that figure are certainly the right diameter for pseudopunctae although the usual swirling of the shell about such structures was not seen. A small piece of shell, 3·7 mm wide, was kindly made available from the Ulrich and Cooper Collection by the Smithsonian Institution for examination under SEM. This was cut transverse to the growth direction, etched, coated and the surface examined; then reground, polished and the examination repeated. These examinations established the fibrous nature of the shell (Text-fig. 6A), but only one pseudopuncta was observed in the two operations (Text-fig. 6B). The confirmed scattered and sporadic nature of the pseudopunctae does not match their distribution in the other members of the family. Accordingly, the contribution of the shell substance to its systematic position remains ambiguous. In our opinion, little systematic significance can be placed on the occasional presence of pseudopunctae in *Anomalorthis*, any more than it can on the presence of pseudopunctae in the Triplesiacea, where they also occur only rarely in some species of



TEXT-FIG. 6. Scanning electron micrographs of a tranverse section of a ventral valve fragment of *Anomalorthis oklahomensis* Ulrich and Cooper; USNM 91293; Oil Creek Limestone; Falls Creek, Oklahoma. A, stacked fibres, ×2500; B, pseudopuncta, ×1300. Exterior of shell uppermost.

Ogmoplecia (Wright 1970). Again, the Orthotetidina have long been known to have impunctate shells in the earlier stocks, with pseudopunctae developing only in the later forms. *Anomalorthis* is accordingly here considered probably better placed as an aberrant orthidine.

CONCLUSIONS

1. While a widely distributed clitambonitidine like *Vellamo* is well recognized by its assemblage of characters, when these characters are examined for the whole group of genera currently assigned to the Suborder Clitambonitidina, the variation is such that it is difficult to arrive at a clear-cut diagnosis of a clitambonitidine.

(a) Shell. The secondary shell substance is fibrous, but may be impunctate or pseudopunctate.

(b) Attachment. The means of attachment to the substrate, the pedicle, may have functioned throughout life but in many stocks became atrophied with progressive sealing of the foramen. The delthyrial cover may be entire, partial, or absent altogether. The notothyrial cover may be large and semicircular, with a different growth arrangement to one which is small and triangular; or may only be partial, or absent altogether.

(c) Shell opening. The valve consistently opened about a strophic hinge with a deltidiodont dentition. But the ventral muscles were located on a spondylium which is typically simplex, may be triplex or be merely a pseudospondylium. The dorsal adductor scars may be quadripartite or radially arranged; in either case the anterior pair may or may not be larger, a character which may or may not vary within a genus. The cardinal process, typically a strong ridge separating the diductor scars, may not be developed; while the ancillary ridges appear to reflect differential shell secretion in different individuals rather than to have any taxonomic value.

2. Shape, profile, proportions and ornamentation, useful taxonomically at generic level, can be expected to, and indeed do, show considerable variation from the typical ventribiconvex shells with a moderately long apsacline ventral interarea and, although costellate ribbing is almost universal, the concentric ornament varies from the almost imperceptible to grossly exaggerated frills and imbrications, surface pitting and even spines.

3. The ribs commonly may be perforated by aditicules, numerous or sparse, initially passing through to the inner shell surface and interpreted as the site of setae; rarely by finer and differently disposed arrugiae; or lacking any form of exopunctae.

4. Evidence of the growth of the delthyrial cover, not available to Williams and Rowell (1965, p. H88) when they assumed the structure to be a pseudodeltidium, shows a series of stages of development indicating it to be a deltidium.

5. The recently discovered mantle canals lining the ventral interareas of certain procline clitambonitids, important for their soft tissue implications (Wright 1994), are now recorded for the apsacline *Estlandia*.

6. After re-examination, the aberrant *Anomalorthis*, which lacks many 'typical' morphological features of the clitambonitidines, is here considered rather to be an aberrant orthidine, with little taxonomic weight being ascribed to the presence of scattered and sporadic pseudopunctae.

Repositories. The institutional abbreviations for the repositories of the specimens illustrated in this paper are: IGT, Institute of Geology, Tallinn; NHM, The Natural History Museum, London; QUB, Department of Geology, Queen's University of Belfast; RMS, Riksmuseum, Stockholm; USNM, National Museum of Natural History, Smithsonian Institute, Washington DC.

Acknowledgements. We are grateful for financial support from the Royal Society for study visits by MR to London and Belfast, and from the Natural Environment Research Council, through Sir Alwyn Williams, for ADW visits to Stockholm, Tallinn and Tartu. We are indebted to Dr Robin Cocks, The Natural History Museum, London, and Professors Valdar Jaanusson and Jan Bergström, Riksmuseum, Stockholm, for facilitating our work in their institutions and, along with the late Dr Richard Grant, Smithsonian Institution, Washington, DC, for arranging for the loan of specimens from the collections in their care.

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SIRENID SALAMANDERS AND A GYMNOPHIONAN AMPHIBIAN FROM THE CRETACEOUS OF THE SUDAN

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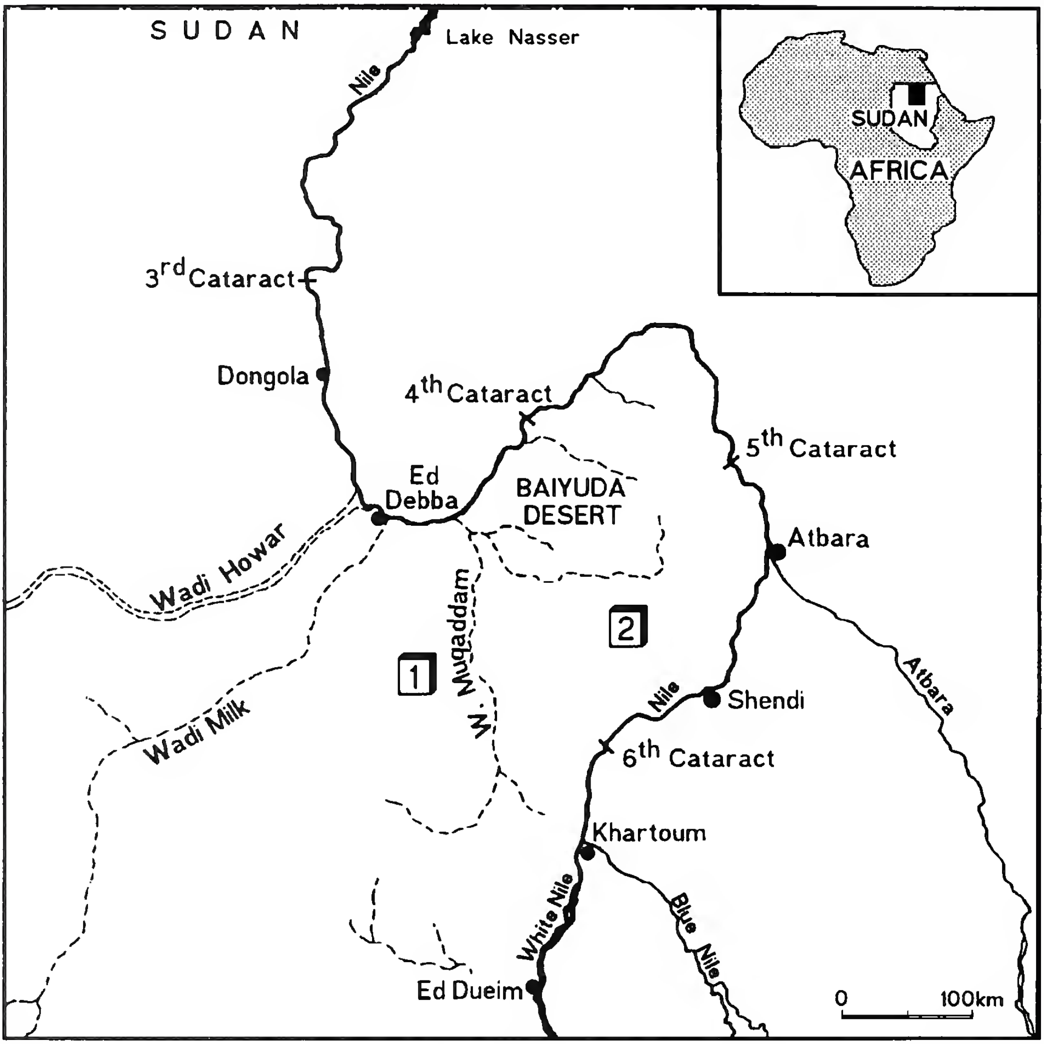
ABSTRACT. A vertebrate assemblage from the Cenomanian of Wadi Milk, northern Sudan, includes material of all three major groups of lissamphibian, namely frogs, salamanders and gymnophionans, of which the latter two groups are described in this work. The productive horizons in the Wadi Milk Formation are lacustrine and the vertebrates are represented by isolated elements. The salamander material is described as *Kababisha humarensis* gen. et sp. nov. and *Kababisha sudanensis* gen. et sp. nov. and is referred to the family Sirenidae. *Kababisha* is the earliest sirenid genus, the first sirenid to be recognized outside North America, and is only the second fossil salamander genus to be reported from the African Plate, *Ramonellus* from Israel being the first. It is suggested that the recently described *Noterpeton*, from the Maastrichtian of Bolivia, is also a sirenid and that the Noterpetontidae is a junior synonym of the Sirenidae. The gymnophionan is represented by four trunk vertebrae and is strictly indeterminate within the Gymnophiona, although the vertebrae bear a non-derived resemblance to those of the dermophine Caeciliidae found in Africa. It is the oldest gymnophionan material from Gondwana, the first fossil gymnophionan from Africa and the earliest gymnophionan with holospondylous vertebrae.

THE Mesozoic record of lissamphibians (frogs, salamanders and gymnophionans) from the African Plate is extremely limited. The Lower Cretaceous (Hauterivian–Barremian; Buffetaut and Rage 1993) of Israel has produced assemblages of pipid frogs (Nevo 1968), pipid tadpoles (Estes *et al.* 1978), and an enigmatic salamander, *Ramonellus* (Nevo and Estes 1969). Four frog taxa, as yet undescribed, have been reported from the Lower Cretaceous of Cameroon (Brunet *et al.* 1988), and two anuran skulls, also undescribed, have been found in the Lower Cretaceous of Malawi (Jacobs *et al.* 1990). The Upper Cretaceous (Coniacian/Santonian; Moody and Sutcliffe 1991) of Niger has yielded two pipid frogs (de Broin *et al.* 1974; Báez and Rage 1988). A second Gondwanan salamander has been reported from this locality (de Broin *et al.* 1974) and a vertebra figured (Rage *et al.* 1993) but has not been fully described. Most recently, a diverse amphibian assemblage (including gymnophionans, salamanders and frogs) has been recovered from the lower Upper Cretaceous (Cenomanian) of the Sudan (Werner 1993*a*, 1993*b*, 1994*a*, 1994*b*). The frog material is being studied separately by Dr A. Báez and one of the authors (CW) and will be described elsewhere. The salamander and gymnophionan material provides an important contribution to our knowledge of the Cretaceous faunas of Gondwana and is described here.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The amphibian fossils described here were collected from the Wadi Milk Formation, which is widespread in the northern Sudan. The Wadi Milk Formation is dominated by deposits of braided river and sandy braided-meandering river systems, which interfinger locally with sediments of meandering rivers, flood plains and lakes (Bussert 1993*a*, 1993*b*). The vertebrate-bearing locality is situated 200 km north-west of Khartoum (Text-fig. 1) and lies at the base of the exposed part of the Wadi Milk Formation. The fossil-bearing horizons consist of fine-grained smectite-rich layers. They were deposited in a fluvio-lacustrine environment and overprinted by soil formation processes

[Palaeontology, Vol. 39, Part 1, 1996, pp. 77–95]



TEXT-FIG. 1. Map of the Sudan showing the position of the vertebrate-bearing localities referred to in this work.

reflecting a warm climate with seasonal rainfall patterns (Bussert 1993*a*, 1993*b*). In these layers, continental vertebrate remains occur in abundance as scales, teeth and disarticulated skeletal elements. A rich fish fauna is present, collected material including the freshwater shark *Asteracanthus aegyptiacus*, a new rajiform batoid (one tooth), polypterids, lepisosteids, osteoglossids (represented by many scales), characiforms (represented by teeth) and the lungfish *Protopterus humei*, *P. protopteroides*, *P.* sp. nov. and *Neoceratodus tuberculatus* (represented by toothplates; Werner 1993*b*). The tetrapod assemblage includes amphibians (pipid frogs, and the salamander and gymnophionan material described here), testudinates (at least three erymnochelyines represented by carapace and vertebral fragments; Werner 1993*b*), snakes (at least seven species, represented by vertebrae; Werner and Rage 1994), lizards (rare elements), crocodiles (long- and medium-snouted species of mesosuchian; Werner 1993*b*) and dinosaurs (vertebrae and teeth of sauropods, ornithopods and theropods; Werner 1994*a*). The assemblage is dominated by freshwater fish, aquatic amphibians and amphibious reptiles, reflecting the lacustrine facies from which it was collected. Terrestrial elements, such as lizards and dinosaurs, are rare, and no mammalian material has been recovered.

A combination of palaeobotanical (Lejal-Nicol 1987), palynological (Schrank 1990; Schrank and Awad 1990) and lithological correlation (Wycisk 1991) indicates an Albian to Cenomanian age for the Wadi Milk Formation. The vertebrate assemblage resembles the Cenomanian assemblage from Bahariya Oasis in Egypt (Werner 1991) and is closely similar to that from the later, Coniacian/Santonian Ibeceten Formation of Niger (Moody and Sutcliffe 1991). This tends to support a Cenomanian rather than an Albian age for the basal layers of the exposed part of the Wadi Milk Formation.

To date, only two salamander atlantes, Vb-820–Vb-821, and other fragmentary vertebrae (uncatalogued) have been recovered from the neighbouring Shendi Formation, which represents a lateral time equivalent of the Wadi Milk Formation. In this fluvial-dominated sequence, which crops out west of the Nile town of Shendi (Text-fig. 1), vertebrate-bearing channel deposits occur locally. The new fossils of the Shendi Formation have yet to be studied in detail, but a preliminary report on its vertebrate content has been given by Werner (1993*b*).

MATERIAL

Most of the amphibian material was obtained by screening the residue of about seven tons of sediment from the Wadi Milk Formation. The technique of collection of Sudanese microvertebrates was described in detail by Werner (1994*a*). Only a few amphibian specimens were collected by eye from the weathered surface of the vertebrate-bearing horizons.

All amphibian bones are preserved as isolated, and often fragmentary, elements. The Sudanese specimens described and figured here are stored in the collection of the Special Research Project 69 of the Technical University of Berlin (TUB-SFB-69) catalogued as Vb-659 to Vb-661, Vb-781 to Vb-809 and Vb-813 to Vb-821.

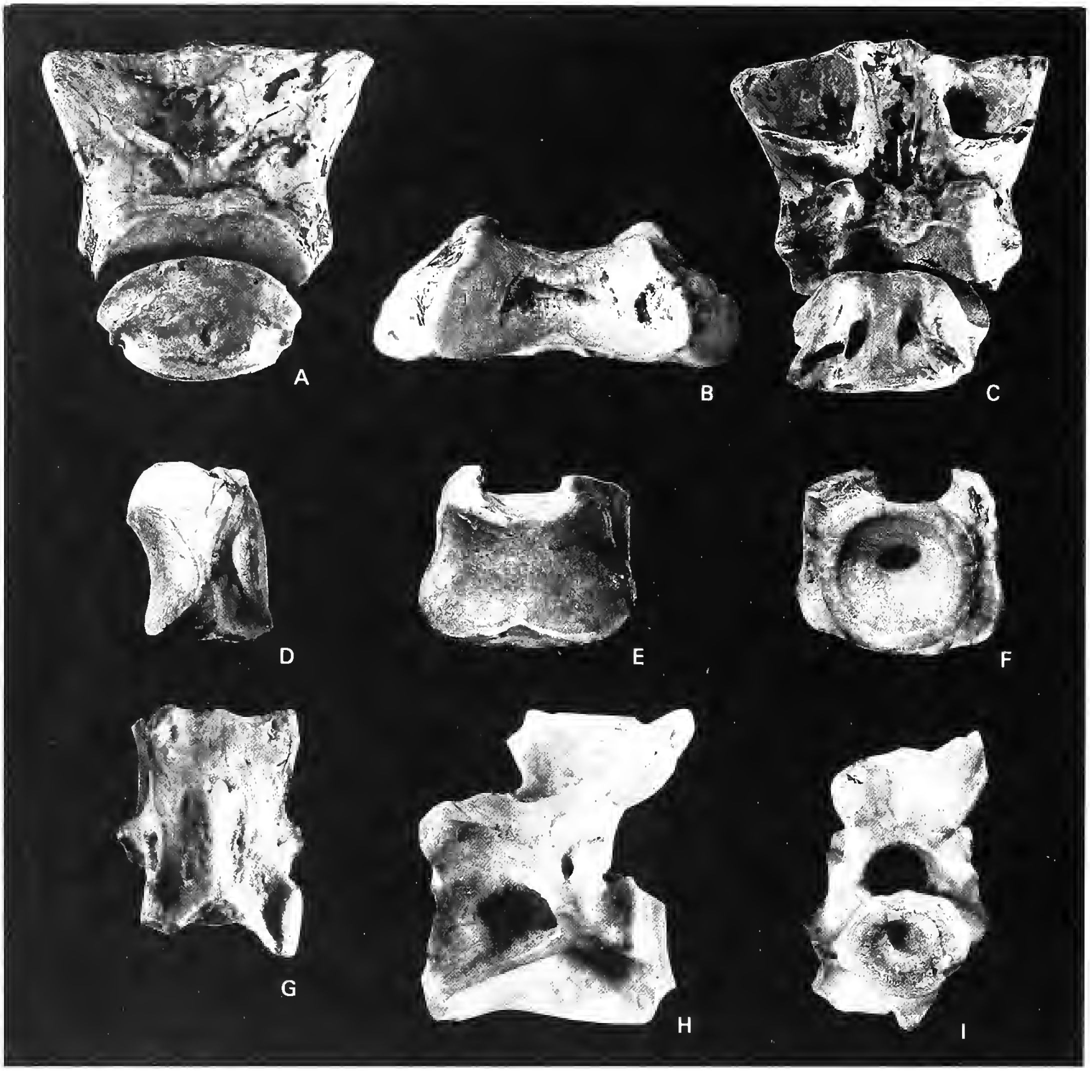
SYSTEMATIC PALAEONTOLOGY

LISSAMPHIBIA Haeckel, 1866
CAUDATA Scopoli, 1777
Family SIRENIDAE Gray, 1825
Genus KABABISHA gen. nov.

Type species. Kababisha humarensis sp. nov.

Derivation of name. The generic name *Kababisha* refers to the nomadic people, the Kababish, who occupy the Northern region of the Sudan.

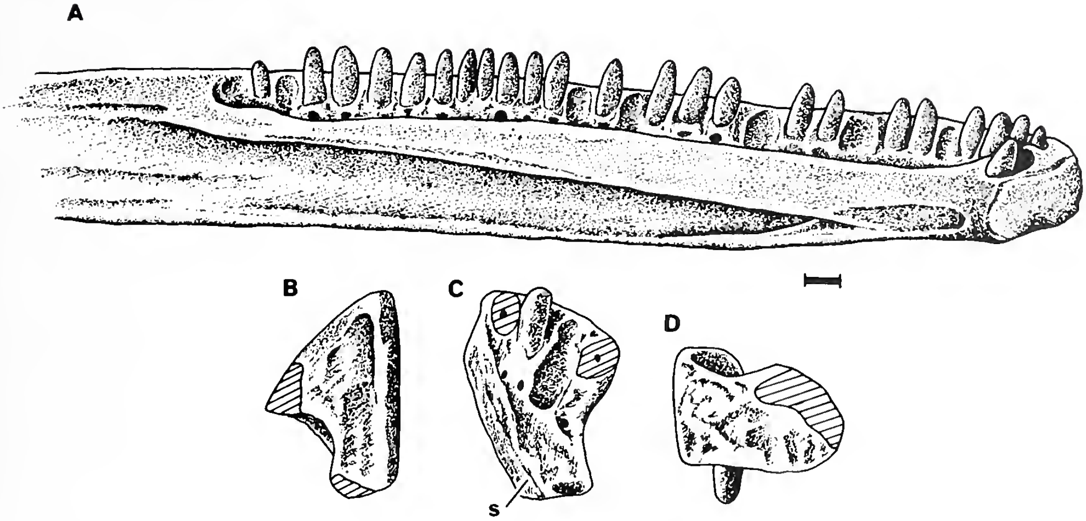
Diagnosis. Neotenous sirenid salamanders ranging in size from estimated skull lengths of less than 10 mm up to over 100 mm. Teeth non-pedicellate, thick-walled, conical (tips not preserved), showing 'zahnreihc'-type replacement. Dentary elongate, extending well beyond tooth row; deep subdental ridge faceted posteriorly for angulosplenial (or splenial if separate); lateral groove deepening posteriorly; lateral sensory nerve foramina absent; symphysial surface compressed dorso-ventrally; symphysial tooth position lying lingual to main tooth row. Premaxilla narrow, lacking alary process. Exoccipitals and parasphenoid fused into a composite structure; continuous, strap-like, U-shaped occipital surface; dorsal concavities for ear capsule; vagus foramina large. Atlas anteroposteriorly short but deep; no tuberculum interglenoideum; cotyles fused to form a smooth continuous, dorsoventrally concave surface closely complementing the occipital surface (Text-fig. 2B, E); strong neural spine; posterodorsal spinal nerve foramina present, posteroventral vascular pits present. Trunk vertebrae typically without spinal nerve foramina; parallel-sided neural arches bearing woven sculpture, steeply inclined zygapophyses and low neural spines; small aliform



TEXT-FIG. 2. *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. A, C, fused basicranial-exoccipital element, Vb-788, and holotype atlas centrum, Vb-791, in A, dorsal; and C, ventral views; × 1·5. B, fused basicranial-exoccipital element, Vb-788, in posterior view; × 2. D–F, holotype atlas centrum, Vb-791, in D, left lateral; E, anterior; and F, posterior views, × 2. G–I, trunk centrum, Vb-802, in G, dorsal; H, left lateral; and I, posterior views; × 2·5.

processes visible on some vertebrae; rib bearers absent, transverse processes flange-like lacking rib facets and supported by accessory flanges; deep anterolateral fossae; vertebrarterial canal piercing the transverse process in an anteroventral direction; neural canal relatively small; midventral keel. Caudal vertebrae elongate, most bearing double ventral keel; narrow centrum; reduced transverse processes with faceted triangular surface; some (probably all) caudals with posterior spinal nerve foramina.

Remarks. The atlas and trunk central are present as two morphological types, treated here as two species. In *Kababisha humarensis*, represented mostly by large specimens, the vertebral centra are



TEXT-FIG. 3. *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. A, reconstruction of left dentary ramus in medial view based largely on Vb-782, Vb-784 and Vb-785. B–D, Vb-787, left premaxilla in B, dorsal; C, ventromedial; and D, anterior views. Abbreviation: s, sutural surface. Scale bar represents 1 mm.

amphicoelous, with a deep anterior cotyle and a shallower posterior cotyle which is infilled to a varying degree by what appears to be a layer of calcified material. In this form, the calcified layer always lies within the posterior cotyle. It does not bulge backwards except in some posterior trunk vertebrae. However, in *Kababisha sudanensis*, mostly represented by small specimens, the infilling layer typically forms a thick bulging rim which forms a partial condyle (with a pit at the centre). These vertebrae are thus functionally procoelous, a very unusual condition in salamanders, which typically have either opisthocoelous or amphicoelous centra (for further discussion of the significance, see below). In the tail, all vertebrae show this procoelous condition and are not determinate at specific level.

We cannot be absolutely certain that the two morphologies represent two species. *K. sudanensis* rarely attains the size of *K. humarensis*, but the vertebrae are more heavily ossified in the smaller form and the atlas vertebrae of both forms are distinct over a range of sizes. These features suggest that the former is not simply an ontogenetic stage of the latter, but might be a progenetic dwarf species. Nevertheless the two morphologies might represent two morphs (sexual or paedomorphic/non-paedomorphic) within a single species, although we know of no present-day analogy for this.

Kababisha humarensis sp. nov.

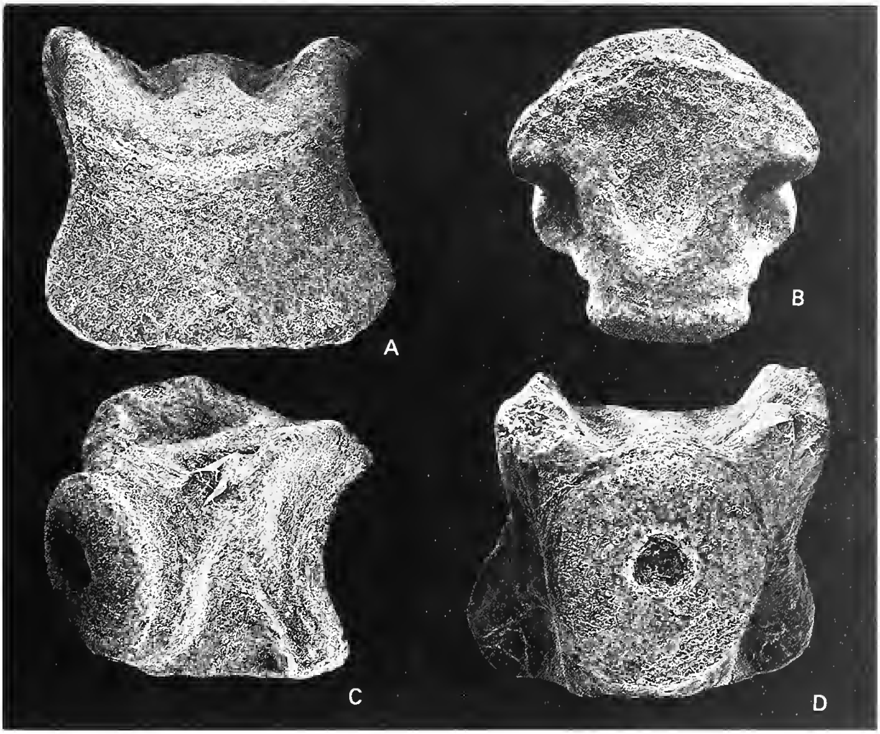
Text-figures 2–3, 4A–E, 6F–J, 7A, C, 8A–G, 9A–C, E–F

Holotype. TUB-SFB-69 Vb-791, an atlas centrum (Text-fig. 2A, C–F).

Derivation of specific name. The specific epithet relates to Humar Hill (549 m) which is situated 25 km south-east of the vertebrate-bearing locality.

Diagnosis. Large (skull length up to at least 100 mm) *Kababisha* with amphicoelous presacral vetebrae in which the depth of the posterior cotyle is only slightly reduced by calcified infilling. In ventral aspect, the atlas centrum has a width:length ratio of 1·5 and there is only a faint suggestion of a three-lobed structure to the ventral surface.

TEXT-FIG. 4. *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. A–C, left dentary, Vb-782, in A, occlusal; B, lingual; and C, labial views; A, × 9; B–C, × 7·5. D, dorsal surface of neural arch of trunk vertebra, Vb-806, showing characteristic sculpturing; × 8·5. E, atlas neural arch, Vb-800, in left lateral view; × 5·5. F–G, *Kababisha* sp. indet. Wadi Milk Formation, Sudan. Caudal vertebra, Vb-808, in F, ventral and G, left ventrolateral view; × 10.



TEXT-FIG. 5. *Kababisha sudanensis* sp. nov.; Wadi Milk Formation, Sudan. A–D, Vb-801, atlas centrum in A, anterior, ×23; B, ventral, ×22; C, right posterolateral, ×21; and D, posterior view, ×25.

Type horizon and locality. Wadi Abu Hashim member of the Wadi Milk Formation at Wadi Abu Hashim, *c.* 200 km north-west of Khartoum, Sudan. Map reference: 31° 8·7′ E, 16° 41·7′ N. The stratigraphical position of this exposure within the Wadi Milk Formation is yet to be established. The Wadi Milk Formation is assigned to the Cenomanian.

Paratypes. Vb-782, left dentary (Text-fig. 4A–C); Vb-788, fused basicranial-exoccipital element (Text-fig. 2A–C); Vb-800, atlas vertebra; Vb-802 (Text-figs 2G–I, 9A–C), Vb-803 (Text-fig. 7F–G), Vb-813 (Text-fig. 8A–E) trunk vertebrae; Vb-806, trunk neural arch (Text-fig. 4E).

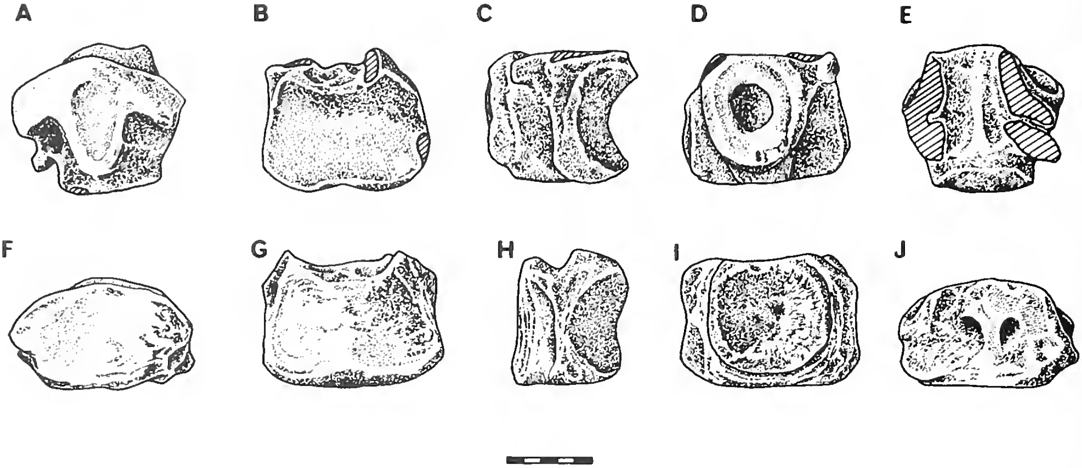
Referred material. Vb-783, Vb-785–Vb-786, posterior regions of right dentaries; Vb-784, middle region of a small left dentary; Vb-787, left premaxilla (Text-fig. 3B–D); Vb-789–Vb-790, fused basicranial-exoccipital elements; Vb-792 (Text-fig. 6F–J), Vb-794, Vb-795 (Text-fig. 7A, C), Vb-796, atlas vertebrae; Vb-804, large trunk vertebra; Vb-807, trunk vertebra. In addition, there are further uncatalogued specimens of most elements in the collections of the TUB-SFB-69.

Description

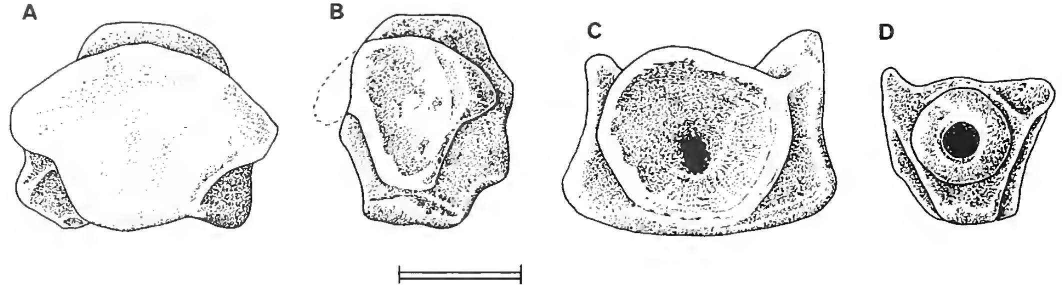
Kababisha humarensis is represented principally by dentaries, fused basicranial-exoccipital elements and vertebrae, which are the commonest lissamphibian remains in the Wadi Milk microvertebrate assemblage. The atlas and trunk vertebrae are diagnostic, the fused basicranial-exoccipital elements are associated by fit with the atlas centra and the other cranial elements are associated on the basis of size.

Premaxilla. One specimen of a left premaxilla, Vb-787 (Text-fig. 3B–D), is associated tentatively with *Kababisha* on the basis of size, tooth structure and implantation. It bears four teeth, one of which is almost complete (no tip) and has a slender conical form. There is a strong midline symphysis, but no alary process. The dorsal surface is concave but the medial border is upturned so that together the united premaxillae formed a low ridge between the two nares.

Braincase and occiput. The exoccipitals are fused into a single median structure which almost certainly incorporates part of the parasphenoid (a similar, but usually still tripartite, structure is found in the living *Cryptobranchus* and *Necturus* and is formed in this way; a comparable fused structure in gymnophionans is termed the os basale). The bone is unusual, however, in that the occipital surfaces have merged across the midline to form a single, strap-like, dorsoventrally compressed surface (Text-fig. 2B) which fits closely against a corresponding surface on the atlas (Text-fig. 2E). The dorsal surface contains a pair of deep anterodorsal depressions which probably housed part of the ear capsule, and is notched posterolaterally by the vagus foramina. Only large specimens of this element have been found (i.e. belonging to *K. humarensis*). By comparison with skulls of extant sirenids, the smallest specimen, Vb-789, belonged to a skull of about 50 mm length; the largest, Vb-790, to a skull closer to 120 mm long.



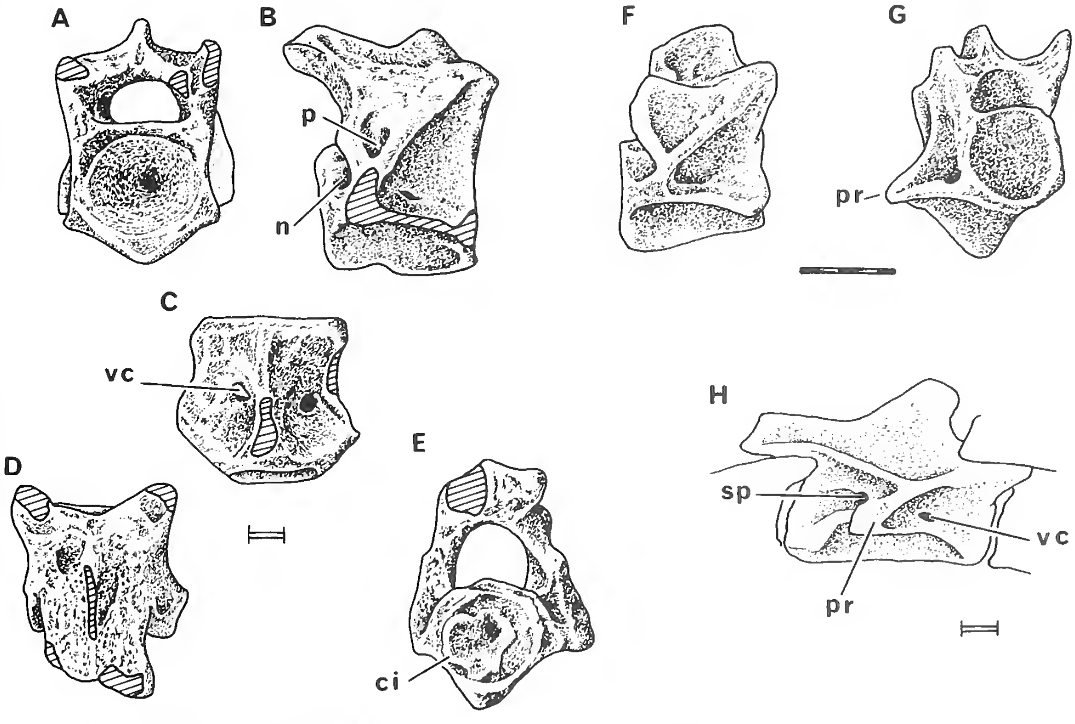
TEXT-FIG. 6. *Kababisha* spp.; Wadi Milk Formation, Sudan. A–E, Vb-793, a large atlas of *Kababisha sudanensis* sp. nov. For comparison with F–J, Vb-792, a large atlas of *Kababisha humarensis* gen. et sp. nov. A, F, ventral; B, G, anterior; C, H, right lateral; D, I, posterior; and E, J, dorsal views. Scale bar represents 5 mm.



TEXT-FIG. 7. *Kababisha* spp.; Wadi Milk Formation, Sudan. A, C, Vb-795, a small atlas of *Kababisha humarensis* gen. et sp. nov. For comparison with B, D, Vb-799, a small atlas of *Kababisha sudanensis* sp. nov. A–B, ventral; C–D, posterior views. Scale bar represents 1 mm.

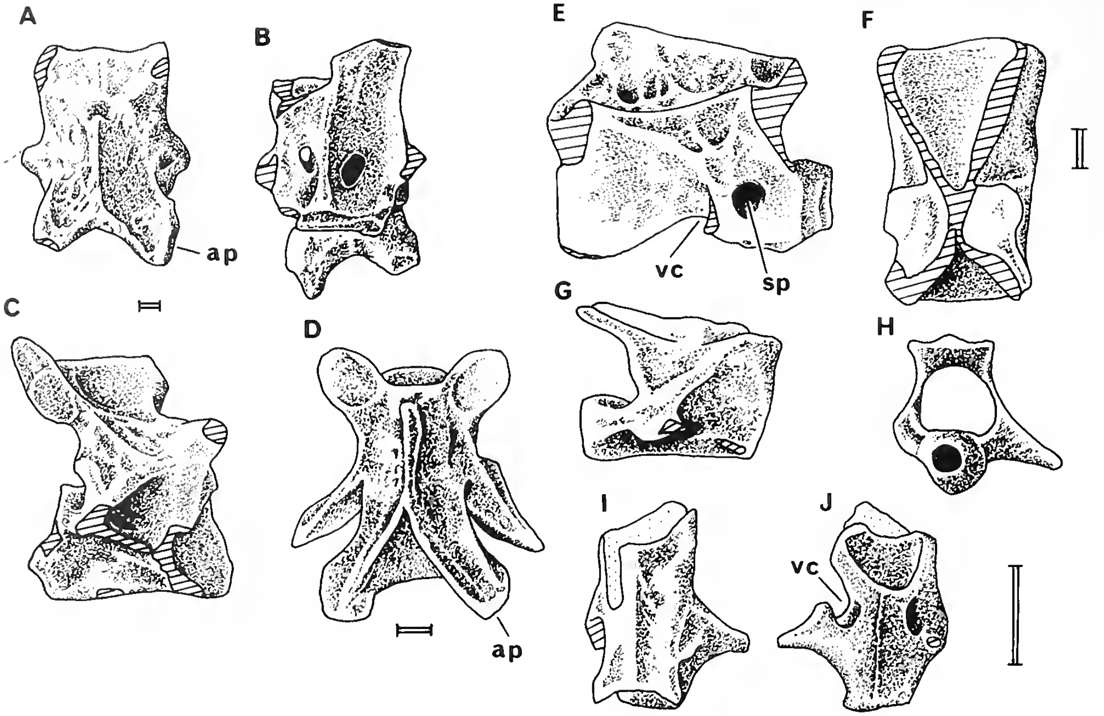
Dentary. The dentaries are mostly large and robust (Text-figs 3A, 4A–C). The symphysis is broad and dorsoventrally compressed. Behind it, the ramus of the dentary constricts slightly before widening again, so creating a waisted effect. The subdental ridge deepens anteriorly. Posteriorly, it bears a ventral facet for either a splenial or an angulosplenial (the condition of these elements, whether separate or combined, is unknown); anteriorly it constricts the Meckelian groove and then closes it for a short distance immediately next to the symphysis. The teeth are robust, thick-walled and show no sign of pedicely; the crowns are broken. Gaps in the tooth row suggest a primitive tetrapod 'zahnreihe' pattern of replacement. Behind the symphysis, and set anteromedial to the tooth row, there are one or two tooth positions (of which only one is filled by a mature tooth). This is a constant feature of all dentaries and suggests the presence of an anterior enlarged symphysial tooth on each ramus. The dentary continues for some distance beyond the tooth row with no step in the upper border; the shape of the posteroventral border is unclear. The lateral surface of the jaw is smooth (no sensory nerve foramina) except for a broad groove which begins as a shallow feature a short distance from the symphysis but deepens posteriorly into a distinct channel.

Atlas. The atlas is short by comparison with subsequent vertebrae. In *K. humarensis*, the atlas is very short, the anteroposterior length of the centrum being about two-thirds of its width. The anterior face is deep with a confluent articular surface which wraps around it. There is thus no interglenoid tubercle. The posterior surface contains a deep notochordal pit with a thick rim. The ventral surface is flat with a slight trefoil structure (Text-fig. 6F) which is more pronounced in small specimens (Text-fig. 7A); the dorsal surface bears deep vascular foramina. The largest atlantes average 10–12 mm in cotyle diameter. There are, however, small atlantes of *K. humarensis* (e.g. Vb-795, Text-fig. 7A, C; Vb-796) with a cotyle diameter of 2 mm.



TEXT-FIG. 8. A–G, *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. Vb-813, anterior presacral vertebra in A, anterior, B, right lateral, C, ventral, D, dorsal and E, posterior views; Vb-803, anterior presacral vertebra in F, right lateral and G, oblique anterolateral views. H, *Siren lacertina*, Recent, North America; UCL Zoology W10, posterior trunk vertebra in right lateral view for comparison with B and F. Abbreviations: ci, calcified infilling; n, notch for spinal nerve exit; p, pit; pr, lateral process; sp, spinal nerve foramen; vc, vertebrarterial canal. Scale bars represent 1 mm (A–E, H) and 5 mm (F–G).

One atlas of *K. humarensis*, Vb-800 (Text-fig. 4E), has part of the neural arch preserved. The neural canal is subtriangular with a tall broad spine. Posterolaterally, the arch is perforated on each side by a spinal nerve foramen for the second spinal nerve; ventrally there are vascular pits.



TEXT-FIG. 9. A–C, *Kababisha humarensis* gen. et sp. nov.; Wadi Milk Formation, Sudan. Vb-802, posterior trunk vertebra in A, dorsal; B, ventral; and C, right lateral views. D, *Siren lacertina*, Recent, North America; UCL Zoology W10; trunk vertebra in dorsal view for comparison with A. E–F, *Kababisha* sp. indet.; Wadi Milk Formation, Sudan. Vb-805; incomplete anterior caudal vertebra bearing spinal nerve foramen in E, left lateral and F, ventral views showing natural fracture of the centrum, demonstrating the notochordal canal and the posterior position of the constriction. G–J, *Kababisha sudanensis* sp. nov.; Wadi Milk Formation, Sudan. Vb-815, immature trunk vertebra in G, right lateral; H, posterior; I, dorsal, and J, ventral views. Abbreviations: ap, aliform process; sp, spinal nerve foramen; vc, vertebrarterial canal. All scale bars represent 1 mm.

Trunk vertebrae. A series of trunk vertebrae is associated with the atlantes on the basis of size, bone type and the detailed structure of the centra. Like the atlas elements, the vertebrae vary in size in broad but not exact correspondence to that of the two species. They are notochordal with a constriction posterior to the midpoint of the centrum, and are essentially amphicoelous. The anterior cotyle is deep in all specimens. In *K. humarensis*, the posterior cotyle is made shallower by a variable amount of calcified material (Text-figs 2I, 8E) but is almost always a cotyle although the rim may bulge slightly in some posterior trunk vertebrae (Vb-802).

The vertebrae bear flange-like transverse processes which vary in size from small flanges to more distinct processes but were not rib-bearing (no articular surfaces). However, few of the transverse processes are complete and it is possible that ribs were borne on a few vertebrae at the anterior end of the column. Each process is supported by accessory crests which run obliquely from the anterior and posterior zygapophyses (Text-figs 2H, 8B, 9C). This arrangement creates deep anterolateral and smaller posterolateral fossae. An anteroventral vertebrarterial canal perforates the transverse process. The neural spines are low but the zygapophyses are steeply angled. In some vertebrae (e.g. Vb-802, Text-fig. 9A–C), small aliform processes extend the arch beyond the posterior zygapophyses. The centra bear strong ventral keels. Well-preserved specimens often show a woven bone pattern on the neural arch (Text-fig. 4D).

Typical trunk vertebrae do not bear spinal nerve foramina. The smaller posterolateral fossa usually has a pit at its base, but these pits do not communicate with the spinal canal in the trunk region (but see below). Notches at the back of the neural arch pedicel suggest that the nerves exited intervertebrally.

Kababisha sudanensis sp. nov.

Text-figures 5, 6A–E, 7B, D, 9G–J

Holotype. TUB-SFB-69 VB-793, an atlas centrum (Text-fig. 6A–E).

Derivation of specific name. From Sudan, the country of origin.

Diagnosis. Small *Kababisha* with functionally procoelous presacral vertebrae in which there is a posterior condyle produced by extreme calcification of the rim of the posterior cotyle. In ventral view, the atlas has a length:width ratio of about 1·0 and bears a pronounced trefoil-shaped ridge pattern on its ventral surface.

Type horizon and locality. Wadi Abu Hashim member of the Wadi Milk Formation at Wadi Abu Hashim, *c*. 200 km north-west of Khartoum, Sudan. Map reference: 31° 8·7′ E, 16° 41·7′ N. The stratigraphical position of this exposure within the Wadi Milk Formation has yet to be established. The Wadi Milk Formation is assigned to the Cenomanian.

Referred material. Vb-797, Vb-798, Vb-799 (Text-fig. 7B, D), Vb-801 (Text-fig. 5), atlas vertebrae; Vb-815 (Text-fig. 9G–J), Vb-816, trunk vertebrae.

Description

Atlas. The atlas is short by comparison with subsequent vertebrae, but the centrum has a length roughly equal to its width, so appearing roughly square in ventral aspect. As in *K. humarensis*, the anterior face is deep with a confluent articular surface which wraps around it. There is thus no interglenoid tubercle. The centrum is proportionally slightly longer than in *K. humarensis*, and at the posterior end, the infilling and rim development of the notochordal pit has increased to the extent that it bulges from the back of the centrum to give the appearance of a posterior condyle. The ventral trefoil pattern is also more marked and has a central concavity (Text-figs 5B, 6A, 7B). The size difference between *K. humarensis* and *K. sudanensis* is, for the most part, extreme. The largest *K. humarensis* atlantes average 10–12 mm in cotyle diameter while the largest atlas of *K. sudanensis* (Vb-793, Text-fig. 6A–E) has a cotyle diameter of only 7 mm, most being much smaller.

Trunk vertebrae. The trunk vertebrae are notochordal with a constriction posterior to the midpoint of the centrum. The anterior cotyle is deep in all specimens. In *K. sudanensis*, the calcified infilling bulges out of the posterior cotyle to form a thickened rim. The notochordal canal remains open but is restricted. The effect, in the small vertebrae of *K. sudanensis* is to produce a posterior condyle (procoely), an almost unique condition in salamanders where vertebral centra are either opisthocoelous or amphicoelous. However, the condition in the large specimens of *K. humarensis* suggests that the procoely of the generally smaller *K. sudanensis* is simply a modification of amphicoely rather than a fundamentally different vertebral type. Naylor (1978) described some species of *Ambystoma* as being 'pseudoprocoelous', with the posterior cotyle smaller in diameter (i.e. with more infilling) than the anterior one. Given that the vertebrae from Wadi Milk are much larger than those from some living *Ambystoma* it seems likely that the condition in *K. sudanensis* is merely an exaggerated type of 'pseudoprocoely'. In all other significant respects they resemble those of *K. humarensis*.

Vb-815 is a small trunk vertebra (Text-fig. 9G–J), almost certainly from an immature animal. It resembles typical vertebrae of *Kababisha* in the presence of wing-like lateral processes and vertebrarterial foramina, but differs in the complete absence of a neural spine and the weak zygapophyses. Like the vertebrae of *K. sudanensis*, however, the posterior cotyle of the notochordal canal is restricted by a bulging rim.

Kababisha sp. indet.

Text-figures 4F–G, 9E–F

Material. Vb-805 (Text-fig. 9E–F) and Vb-814, anterior caudal vertebrae with spinal nerve foramen; Vb-808 (Text-fig. 4F–G) and Vb-809, caudal vertebrae.

Description

Caudal vertebrae. Typical caudal vertebrae are smaller than trunk vertebrae with a narrow centrum and a longer neural spine. The ventral surface of the centrum bears paired flanges. In all collected caudal vertebrae (mostly small), the condition of the centrum is like that of the procoelous trunk centrum in *K. sudanensis*, with a perforated posterior condyle. The flange-like transverse process remains, but the accessory crests are weaker. The tips of the transverse processes appear faceted, presumably in relation to muscle attachment. The few identified caudal vertebrae have spinal foramina (e.g. Vb-805, Vb-808 and Vb-814), but the distribution of these within the caudal series is unknown. The spinal nerve foramen opens through the pit at the base of the posterolateral fossa and it is possible that secondary closure has occurred in the presacral series. The presence of a procoelous condition in all caudal vertebrae implies three possibilities.

1. That all collected caudal centra belong to *K. sudanensis* which has similarly procoelous trunk vertebrae. This would be morphologically tidy, but unusual in that all other elements of *K. sudanensis* are much rarer than those of *K. humarensis* in this assemblage.
2. That the caudals belong to the commoner *K. humarensis* which would thus have procoelous caudals in contrast to its amphicoelous trunk vertebrae. This would imply that the procoely arose in the caudals of this genus and extended to the trunk in the more derived *K. sudanensis*.
3. That the caudal vertebrae belong to both taxa and are indistinguishable, with the same general conclusion as alternative 2. Alternatives 2 and 3 receive some support from the observation that some posterior trunk vertebrae of *K. humarensis* (Text-fig. 9A–C) show slight development of the rim of the posterior condyle. These alternatives cannot be resolved with the material to hand so the caudal vertebrae are treated as entirely indeterminate within the genus.

SYSTEMATIC POSITION OF *KABABISHA*

Kababisha exhibits an unusual combination of characters, a mixture of sirenid, unique and primitive character-states.

Character-states supporting relationship to the Sirenidae

1. Non-pedicellate teeth: not found in most adult salamanders but widespread in caudate larvae and persist in the paedomorphic adults of the families Proteidae and Sirenidae (Means 1972) and the extinct family Batrachosauroididae (Estes 1981).
2. Dentary without lateral sensory foramina but with deep lateral groove: occurs in *Habrosaurus* (Estes 1964, fig. 34 and p. 78) and *Siren* (pers. obs.).
3. Interglenoid tubercle reduced to absent (in the fossil sirenid *Habrosaurus* Estes 1964, fig. 37, the cotyles are also confluent, although the condition is less specialized than that of *Kababisha*).
4. Vertebrae with vertebrarterial canals including a dorsoventral passage, accessory anterior and posterior crests, and deep anterolateral fossae: configuration characteristic of at least some vertebrae in *Siren* (pers. obs.).
5. Trunk vertebrae with strong ventral keels: occurs in *Siren* and *Habrosaurus* (Estes 1964, fig. 37) but also in the Batrachosauroididae (e.g. *Opisthotriton* Estes 1964, fig. 38) and may be a widespread primitive feature.
6. Anterior presacral zygapophyses steeply inclined: occurs in all vertebrae of *Kababisha* and in some anterior trunk vertebrae of later sirenids (Naylor 1978) but not most vertebrae.
7. Relatively small spinal canal in trunk: occurs in *Siren* (pers. obs.) and *Habrosaurus* (Estes 1964, fig. 37c).
8. Transverse vertebral processes not rib-bearing on most if not all trunk vertebrae. In the extant eel-like Sirenidae and Amphiumidae, bicipital ribs are present on only a few anterior vertebrae. In sirenids, only presacrals 2–9, sometimes termed the 'cervicals' have rib-bearers (*Habrosaurus* in Estes 1964, *Pseudobranchus* in Goin and Auffenberg 1955, p. 508, *Siren* in Goin and Auffenberg 1955, fig. 3B and in Holman 1985, fig. 1). The remaining vertebrae lack any trace of rib-bearers (e.g. *Siren* and *Pseudobranchus* spp. in Goin and Auffenberg 1955, figs 1–2, C). Other salamanders have rib-bearers on all the post-atlas trunk vertebrae.
9. Caudal transverse processes with faceted tips: occurs in *Siren* (pers. obs.).

10. Paired tall crests on ventral surface of caudal vertebrae: occurs in *Habrosaurus* (Estes 1964, fig. 37B) and *Siren* (pers. obs.).

11. Caudal vertebrae small in relation to trunk vertebrae: occurs in *Habrosaurus* (Estes 1964, fig. 37) and *Siren* (pers. obs.).

12. In some vertebrae, the neural spine is weakly bifurcated posteriorly to give small aliform processes posteriorly. This bifurcation can be seen as a weak expression of the characteristic configuration of *Habrosaurus*, *Siren* and *Pseudobranchus* in which the neural spine is strongly bifurcated.

Character-states apparently unique to Kababisha *within the Caudata*

13. The sculpture on the neural arches. We have seen this in no other salamander.

14. Confluence of occipital condyles (in the living *Siren lacertina*, there is a near contact of the condyles).

Primitive character-state

15. The form of the premaxilla. Extant sirenids have a long slender lateral nasal process. There is no evidence of this in *Kababisha*.

Ambiguous character-states

16. The presence of symphysial teeth. This is typical characteristic of temnospondyl amphibians and stem-tetrapods, but has not previously been reported in any salamander, living or extinct. This could be argued to be a retention of a primitive character lost in all other salamanders including stem-salamanders, other sirenids and more derived salamanders. Such teeth are unknown in any lissamphibian, so if the Lissamphibia are accepted as monophyletic in relation to archaic amphibians, it might be argued that the loss of symphysial teeth occurred at the base of the Lissamphibia and that this presence represents a derived reversal and hence an autapomorphy for *Kababisha*.

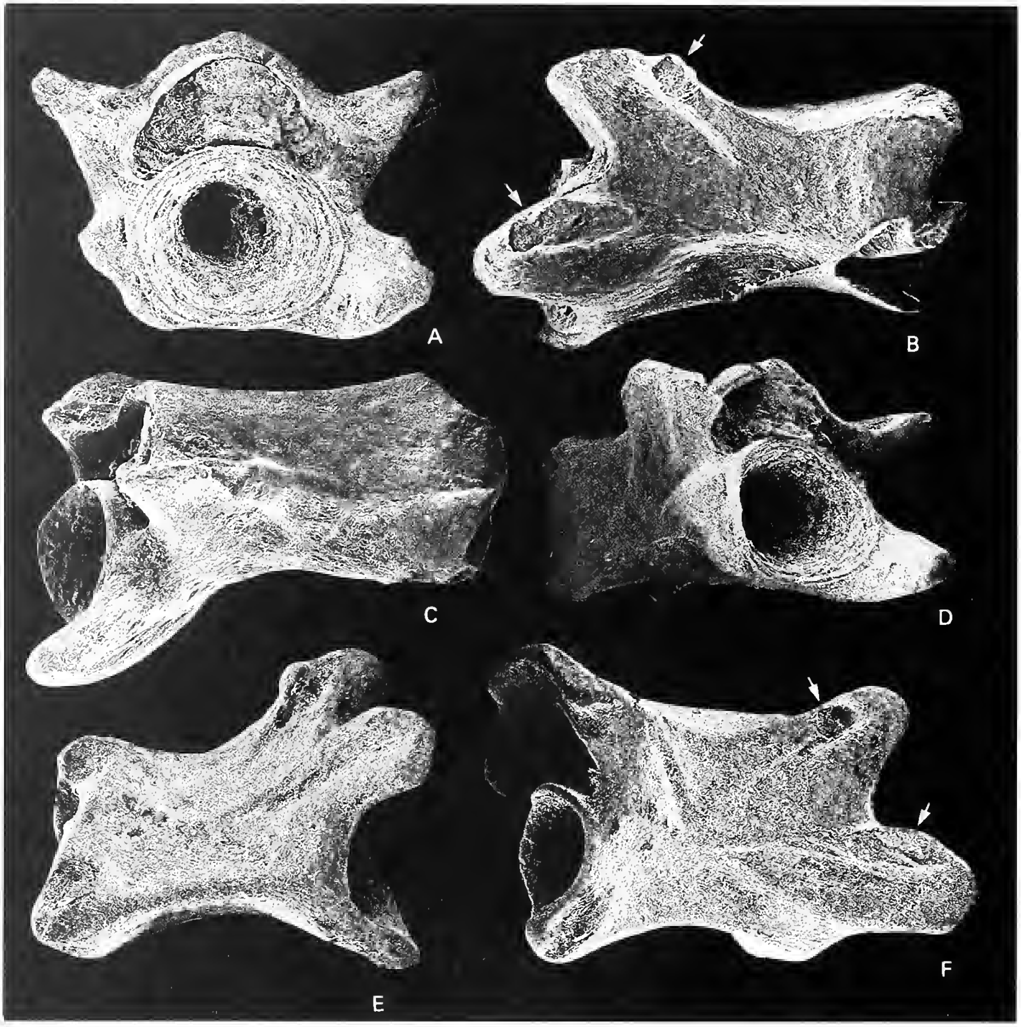
17. Vertebrae primitively amphicoelous (with the assumption that the functional procoely in *K. sudanensis* is a derived condition and an exaggeration of the slight calcification in *K. humarensis*.

18. Except for the atlas and some or all of the tail, all spinal nerves exit intervertebrally. This may be a result of secondary closure. This is more primitive than the condition in the extant sirenids, in which intravertebral foramina occur on all vertebrae except the second (Edwards 1976). This is generally accepted to be convergent with the condition in salamandrids, and implies a separate history of transition from the primitive absence of post-atlas intravertebral foramina to the modern sirenid condition, within the Sirenidae. The condition in *Kababisha* can be argued to be a transitional condition between the primitive urodele condition and that of modern sirenids. It supports the interpretation of *Kababisha* as a primitive sirenid but does occur convergently elsewhere in the Caudata. In *Siren*, the foramina are small and open from the vertebral arterial canal. This is not the case in *Kababisha*.

Characters 1–12 suggest that *Kababisha* is a member of the family Sirenidae. Not all are unique to the Sirenidae but several appear to be. Characters 13–14 are unique specializations of the genus and Character 15 is a primitive feature which other sirenids lack. Characters 16–18 are characters in which there are problems of convergence or polarity interpretation. *Kababisha* thus appears to be a primitive offshoot of the Sirenidae which has acquired some unique specializations.

SYSTEMATIC POSITION OF *NOTERPETON BOLIVIANUM*

Rage *et al.* (1993) described a new and unusual salamander, *Noterpeton bolivianum*, from the Upper Cretaceous (Maastrichtian) of Bolivia. Like the small *Kababisha sudanensis*, *Noterpeton* has procoelous vertebrae with a posterior condyle and all the vertebrae have this construction. Since this



TEXT-FIG. 10. Gymnophiona *incertae sedis*; Wadi Milk Formation, Sudan. A–D, Vb-659; trunk vertebra in A, anterior, × 36; B, left lateral, × 30; C, left dorsolateral, × 33; D, right anterolateral views, × 30. E–F, Vb-660; trunk vertebra in E, right ventrolateral; and F, right posterolateral views, × 30.

is such an unusual condition in salamanders, Rage *et al.* (1993) created a new family of Gondwanan salamanders, the Noterpetontidae, based on *Noterpeton*. To this family, they tentatively referred several poorly preserved vertebrae from the Cretaceous (Coniacian/Santonian) of Niger. They noted that, in other respects, noterpetontid vertebrae were sirenid-like.

The condition of the vertebral centra in the two species of *Kababisha* suggests that *Noterpeton* is a more derived form of the same lineage and should be accommodated within Sirenidae. In *Kababisha humarensis*, the atlas and trunk vertebrae are typically amphicoelous with only a slight thickening of the rim of the posterior cotyle. This is more pronounced in very large specimens and suggests a progressive calcification of this cotyle in this species. In the otherwise similar *Kababisha sudanensis*, the atlas and trunk vertebrae show a highly exaggerated development of the same phenomenon, with the calcification of the rim of the posterior cotyle producing a protruding condyle even in small specimens. This suggests that this type of procoely can develop differentially in otherwise similar forms and is not such a profoundly different condition from amphicoely as to merit family-level separation. Naylor (1978) named a similar phenomenon 'pseudoprocoely' in *Ambystoma*, in which he found it occurring in some species of that genus but not others. We suggest that the procoelous condition in *Noterpeton bolivianum* is not a profound feature meriting family-level separation of this form, but is simply a derived development of the procoely produced by calcification seen in *Kababisha sudanensis*. We suggest therefore that *K. humarensis*, *K. sudanensis* and *N. bolivianum* form a Gondwanan subset of the Sirenidae showing progressive development of procoely. Consequently, *Noterpeton bolivianum* should be transferred to the Sirenidae, and the Noterpetontidae treated as a junior synonym of the Sirenidae. The relationship of *Kababisha* to the somewhat younger salamander from Niger has yet to be determined but they appear to be extremely similar.

GYMNOPHIONA Rafinesque, 1814
Family *Incertae sedis*

Text-figure 10

Material. Four trunk vertebrae: Vb-659 (Text-fig. 10A–D and previously figured by Werner 1994*b*, fig. 2); Vb-660 (Text-fig. 10E–F), Vb-661 and Vb-781.

Horizon and locality. Wadi Abu Hashim Member of the Wadi Milk Formation at Wadi Abu Hashim, *c*. 200 km north-west of Khartoum, Sudan. Map reference: 31° 8·7′ E, 16° 41·7′ N. The Wadi Milk Formation is assigned to the Cenomanian.

Description. The vertebrae are about 2 mm in length, amphicoelous and elongated with a low spineless neural arch, midventral keel and strong anteroventral parapophyses. The prezygapophyses are widely spaced with nearly horizontal facets: the postzygapophyses are broken away in most specimens. The rib facets are double, with one lying below the prezygapophysis and one flush on the shoulder of the parapophysis (Text-fig. 10B, F).

Systematic position. Three of these vertebrae (Vb-659–661) were reported briefly and one figured by Werner (1994*b*, fig. 2) in which they were identified simply as gymnophionan vertebrae. Unfortunately, more detailed comparative study with the vertebrae of living forms has not permitted more precise identification although one constraint can be put on the identity of the material.

The living African gymnophionans are placed in two families, the highly derived monophyletic family Scolecomorphidae, found only in Africa, and the probably paraphyletic Dermophinae, a subfamily of the Caeciliidae, found in Africa and South America. The dermophines probably represent a middle grade of organization within the Gymnophiona and are not characterized by unique features. The Wadi Milk gymnophionan could, in principle, belong to either group or to some other lineage no longer found in Africa. Unfortunately, this small sample of gymnophionan material includes only trunk vertebrae. Taylor (1977) has shown the atlas and anterior trunk vertebrae of gymnophionans to be of some taxonomic value but these are not represented here. However, a limited survey of caecilian trunk vertebrae in the collections of The Natural History Museum, London, suggests that the Scolecomorphidae possess a derived character lacking in caeciliids and in the Wadi Milk material. In *Scolecomorphus kirki* (BMNH 93.10.26.97), each trunk vertebra parapophysis bears a posteriorly directed process to which the head of the rib attaches. In all other gymnophionans examined, the ventral rib head meets a facet which lies along the side of the parapophysis. The latter condition is also the condition in the Wadi Milk vertebrae and may be seen in Vb-659 (Text-fig. 10B) and Vb-660 (Text-fig. 10F). If the extended process proves to be a consistent feature for all scolecomorphids, then its absence would tend to exclude the Wadi Milk caecilian from the Scolecomorphidae, or at least the crown-group Scolecomorphidae. The Wadi Milk vertebrae show no features which would exclude them from the Dermophinae.

DISCUSSION

The microvertebrate assemblage from the Cenomanian Wadi Milk Formation of the Sudan contains representatives of all three lissamphibian groups, namely frogs, salamanders and gymnophionans.

Anura

The anuran material from the Wadi Milk Formation will be described elsewhere (Báez and Werner in prep.) but appears to comprise two types of frog, one of which is a pipid. The anuran family Pipidae is known only from the African Plate (including Israel) and South America (Buffetaut and Rage 1993). The earliest known pipids are from the Lower Cretaceous of Israel (*Cordicephalus* and *Thoraciliacus*, Nevo 1968; and *Shomronella*, Estes *et al.* 1978). Pipids are also known from the Upper Cretaceous of both Argentina and Niger (*Saltenia*; Báez 1981). The pipids from Wadi Milk may be closely related to the slightly younger frogs from Niger, but detailed comparison is needed.

Caudata

The salamander family Sirenidae is represented by two extant genera, *Siren* and *Pseudobranchus*, and, until now, by one extinct genus, *Habrosaurus*. Living sirenids are restricted to south-eastern and central North America and north-eastern Mexico. *Siren* first appears in the Middle Eocene of Wyoming and has thus been more widespread over North America than it is now. Fossil *Pseudobranchus* is known certainly only from the Plio-Pleistocene of Florida although *Siren miotexana* from the Miocene of Texas may also be a *Pseudobranchus* (Estes 1981). *Habrosaurus* occurs in deposits of Campanian to Upper Palaeocene age (Estes 1981) in Montana and Wyoming and was, until the recognition of the African material, the oldest recorded sirenid. Yadagiri (1986) reported sirenid material amongst an assemblage of microvertebrate material from the Lower Jurassic Kota Formation of India, but the figured fragments are not diagnostically urodelan.

Thus, the recognition of *Kababisha* as a sirenid not only extends the stratigraphical range of the group back to the Cenomanian but also extends the geographical range to Africa, and more generally, to Gondwana. Furthermore, the vertebral structure of *Kababisha* suggests that the Bolivian genus *Noterpeton* and the undescribed Niger material (Rage *et al.* 1993) are also *Kababisha*-like sirenids.

The systematic position of sirenids in relation to other salamanders has long been debated. Most recent analyses (e.g. Milner 1983; Duellman and Trueb 1986; Larson and Dimmick 1993), suggest that the sirenids are the sister-taxon to all other living salamanders and represent the most primitive surviving salamander lineage. As pointed out by Milner (1983), this implies that they diverged from the other salamanders prior to the cryptobranchoid-neocaudate dichotomy corresponding with the late Jurassic separation of Laurasia into Euramerica and East Asia by the Turgai Straits. Milner argued that the sirenid stem must have been present from the Mid Jurassic prior to the major subdivision of Pangaea, and hence that early sirenids could be expected to be more widespread than the Cenozoic and living forms and might be expected across Laurasia. A range extension southwards into Gondwana was less to be expected. The fundamentally Laurasian distribution of the living and fossil Caudata (with the well-documented exceptions of the South American bolitoglossine plethodontids and the North Africa salamandrids), still indicates that the group arose and diversified in Laurasia in the mid-Mesozoic as argued by Milner (1983). The presence of the sirenids *Kababisha* and *Noterpeton* and the enigmatic *Ramonellus* in Gondwana in the Mesozoic shows that one or two lineages underwent temporary range extensions into Gondwana in the mid-Mesozoic and that a subclade of sirenids (*Kababisha* and *Noterpeton*) diversified there with the development of procoelous vertebrae as one visible trend within the group. The alternative hypothesis, that sirenids were initially Gondwanan and only later extended their range into North America, implies that the stem lineage of the Caudata was Gondwanan, and there is no supporting evidence for this, all stem-caudates being known from the Mesozoic of Laurasia (Evans and Milner in prep.).

Gymnophiona

The four gymnophionan vertebrae provide the earliest record of this group in Gondwana, the earliest record of gymnophionan vertebrae of modern aspect, and the first record of a fossil gymnophionan from Africa. The only older gymnophionan material is the stem-gymnophionan *Eocaecilia* from the Lower Jurassic Kayenta Formation of Arizona (Jenkins and Walsh 1993), which has more primitive vertebrae with distinct pleurocentrum and intercentrum. The only other records of fossil gymnophionans are single vertebrae from the Palaeocene of Brazil (Estes and Wake 1972) and of Bolivia (Rage 1991). The presence of living Gymnophiona across South America, Africa, the Seychelles and India suggests that they were widespread by the late Jurassic–early Cretaceous prior to the break-up of Gondwana (Duellman and Trueb 1986, p. 485) and so their presence in Africa in the Cenomanian had been theorized.

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LATEST TOARCIAN AMMONOIDS FROM THE NORTH AMERICAN CORDILLERA

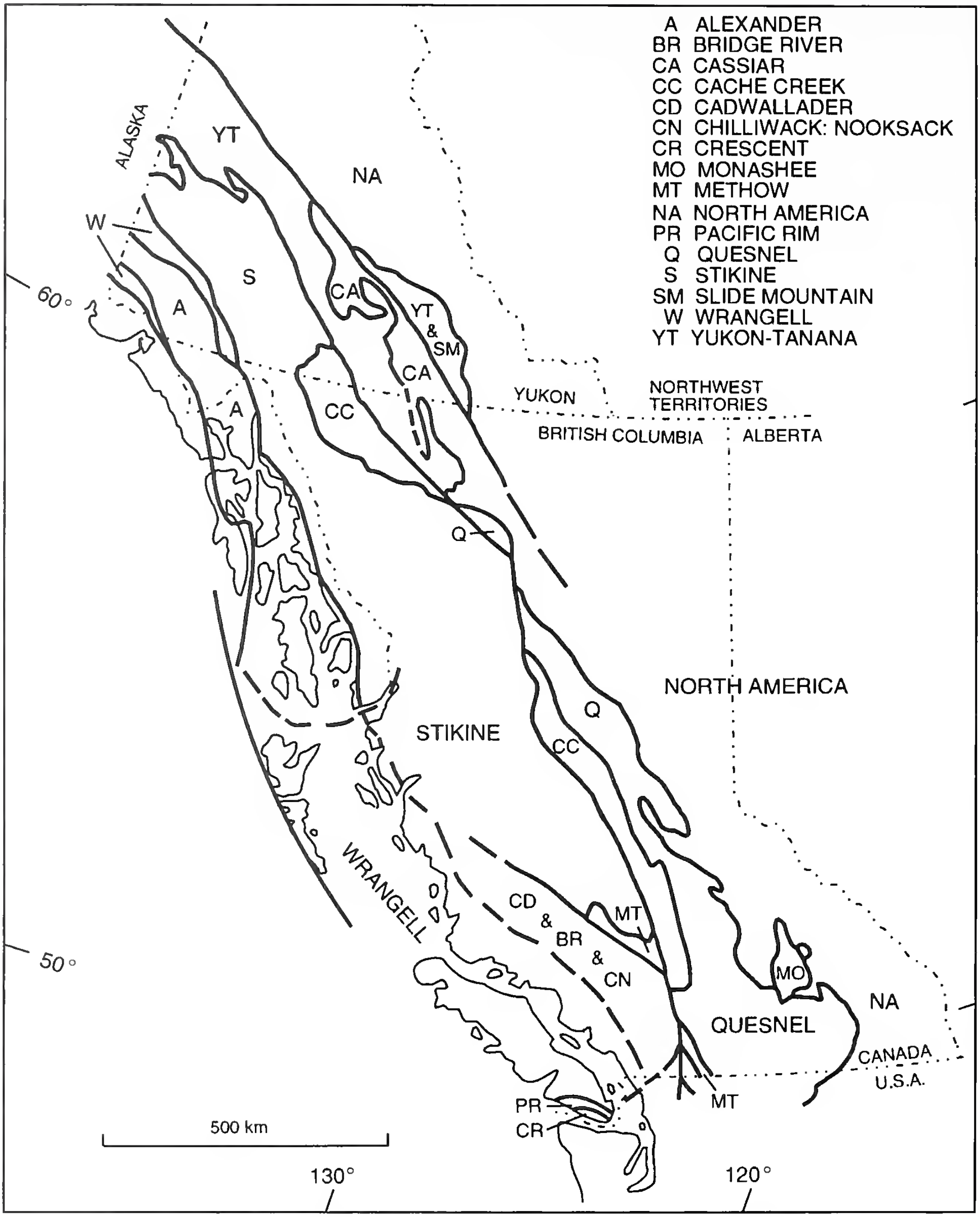
by GISELLE K. JAKOBS *and* PAUL L. SMITH

Abstract. Latest Toarcian (Early Jurassic) strata crop out in southern Alaska, southern Yukon, British Columbia, south-western Alberta, and eastern Oregon. Work in the Queen Charlotte Islands, British Columbia has proved a relatively complete Toarcian sequence which has provided the basis for a North American Toarcian ammonite zonation. The Upper Toarcian Yakounensis Zone is characterized by a diverse ammonite fauna, previously assigned to the Middle Toarcian. Species of *Hammatoceras*, *Dumortieria*, *Sphaerocoeloceras*, *Pleydellia*, *Holcophylloceras*, and *Pseudolioceras* allow correlation with the younger part of the Levesquei Zone of north-west Europe. The new genus *Yakounia* and seven new species (*Yakounia yakounensis*, *Y. pacifica*, *Y. freboldi*, *Y. silvae*, *Pleydellia maudensis*, *P. crassiornata* and *Dumortieria*? *phantasma*) are introduced, all of which are endemic to western North America. A global regression during the Late Toarcian may have restricted migration between the eastern Pacific and western Tethys resulting in the development of endemic taxa.

Western North America is a tectonically complex area made up of numerous accreted terranes (Text-fig. 1). These are commonly fault-bounded regions and each appears to have a separate and distinct geological history. Palaeomagnetic and palaeontological evidence suggests that some terranes may have undergone significant latitudinal displacement since the Jurassic (Irving *et al.* 1980; Taylor *et al.* 1984; Smith and Tipper 1986; Irving and Yole 1987; Irving and Wynne 1991). Understanding this complex history requires correlation within and between terranes, and between the terranes and the craton. To date, Toarcian strata in western North America have been recognized from Alaska to Oregon, both on the craton (southern Canadian Rocky Mountains) and in the following terranes: Peninsular, Stikine (Stikinia), Quesnel (Quesnellia), Wrangell (Wrangellia), Izee (in Oregon), as well as in several small slivers in south-western British Columbia (Text-figs 1–2).

Previous ammonite workers (Frebold 1957, 1964*a*, 1964*b*, 1969, 1976; Frebold *et al.* 1967, 1969; Imlay 1968, 1981; Frebold and Tipper 1970) had difficulty interpreting the Toarcian succession of western North America because of the complex geology of the Cordillera and the lack of stratigraphical sections. They relied on the north-west European zonation and compared the North American fauna with common north-west European taxa. However, work on the Early Jurassic of the Americas has shown consistently that eastern Pacific faunas have closer affinities with Tethyan faunas, contain endemic Pacific species, lack certain European elements, and may have different age ranges for common taxa. For example, a re-assessment of some older collections previously assigned to the Middle Toarcian based on the supposed presence of *Haugia* (Frebold 1976; Imlay 1981), indicates that they are in fact of latest Toarcian age, as had been suggested tentatively by Hall (1987). This latest Toarcian fauna includes *Hammatoceras*, *Sphaerocoeloceras*, *Dumortieria*, *Pleydellia*, and a new genus of the Phymatoceratinae; the genus *Haugia* does not occur along the Pacific rim. Such observations clearly point to the need for a regional zonation. A significant step in this direction has been the discovery of a relatively complete Toarcian succession in the Queen Charlotte Islands, British Columbia (Text-fig. 2; Jakobs 1992; Jakobs *et al.* 1994, 1995). The purpose of this paper is to review the distribution of Late Toarcian rocks in North America, and to describe the latest Toarcian ammonites from successions that form the basis of a North American ammonite zonation.

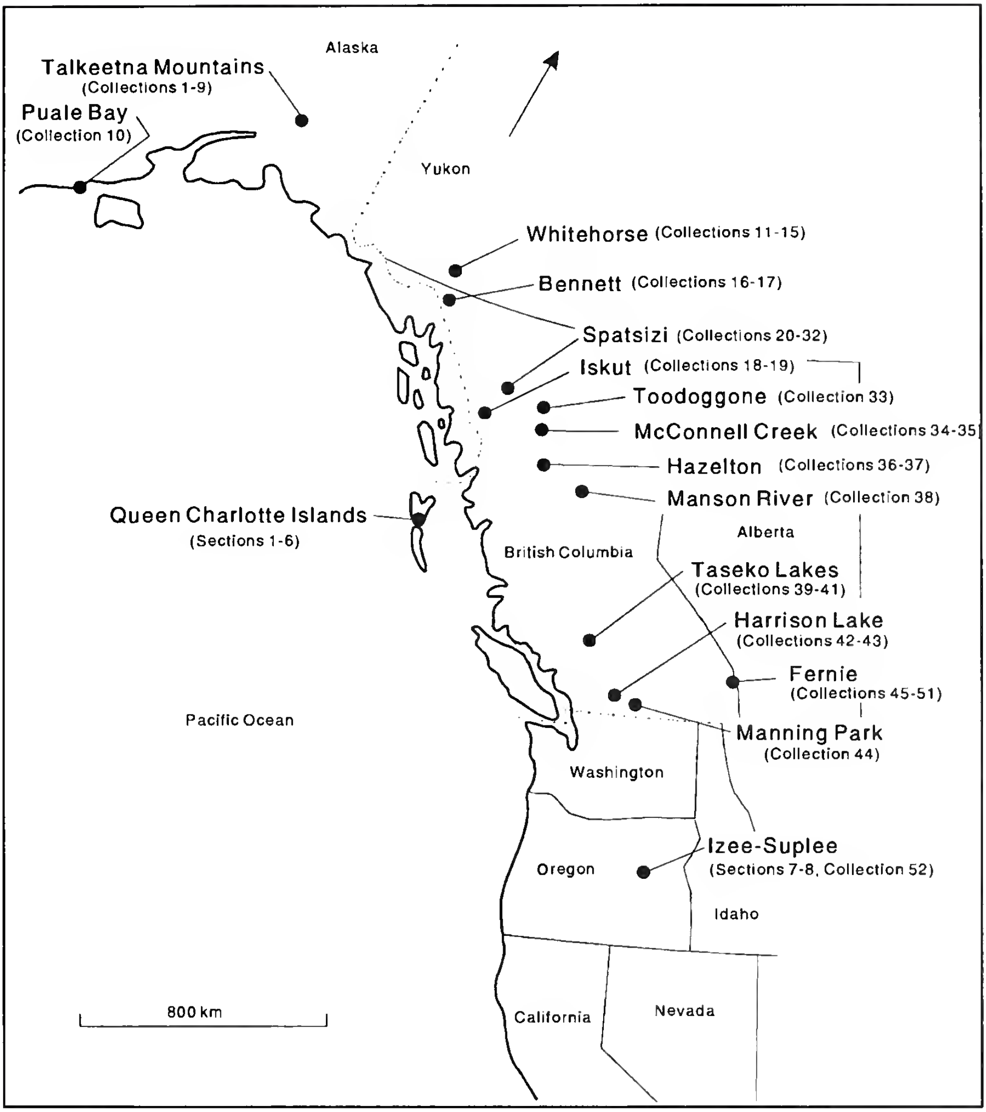
[Palaeontology, Vol. 39, Part 1, 1996, pp. 97–147, 7 pls]



TEXT-FIG. 1. Generalized terrane map of the Canadian Cordillera.

UPPER TOARCIAN ZONES OF NORTH AMERICA

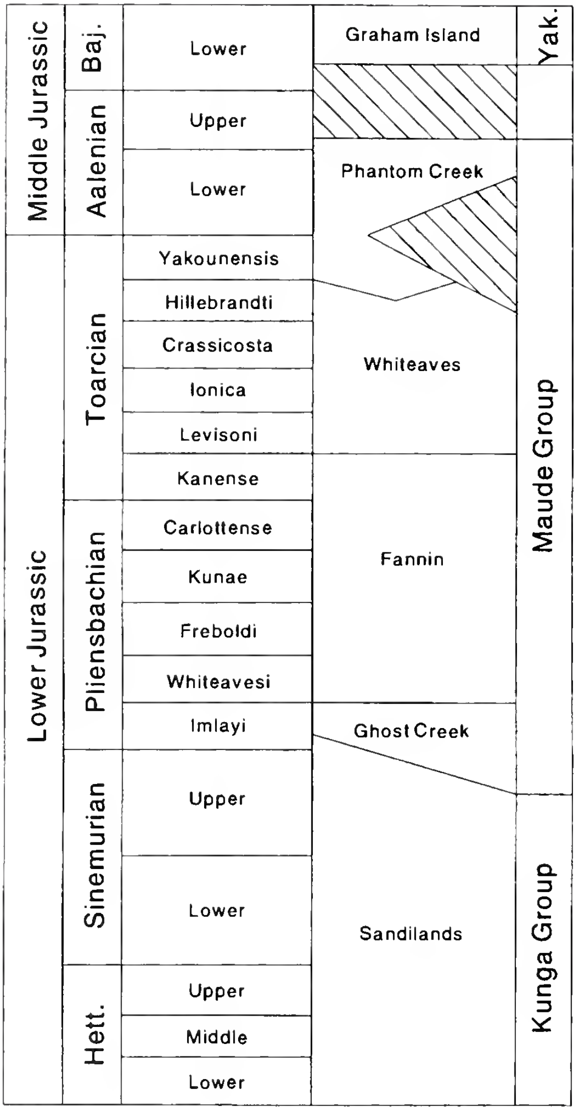
The two Upper Toarcian ammonite zones detailed below were outlined by Jakobs *et al.* (1995), and have been formally described by Jakobs *et al.* (1994).



TEXT-FIG. 2. Map showing Upper Toarcian localities in western North America. The biostratigraphy of sections 1–8 is shown in Text-figures 7–14. Locality data and faunal listings for Collections 1–52 are available from the British Library as Supplementary Publication No. SUP 14044.

Hillebrandti Zone

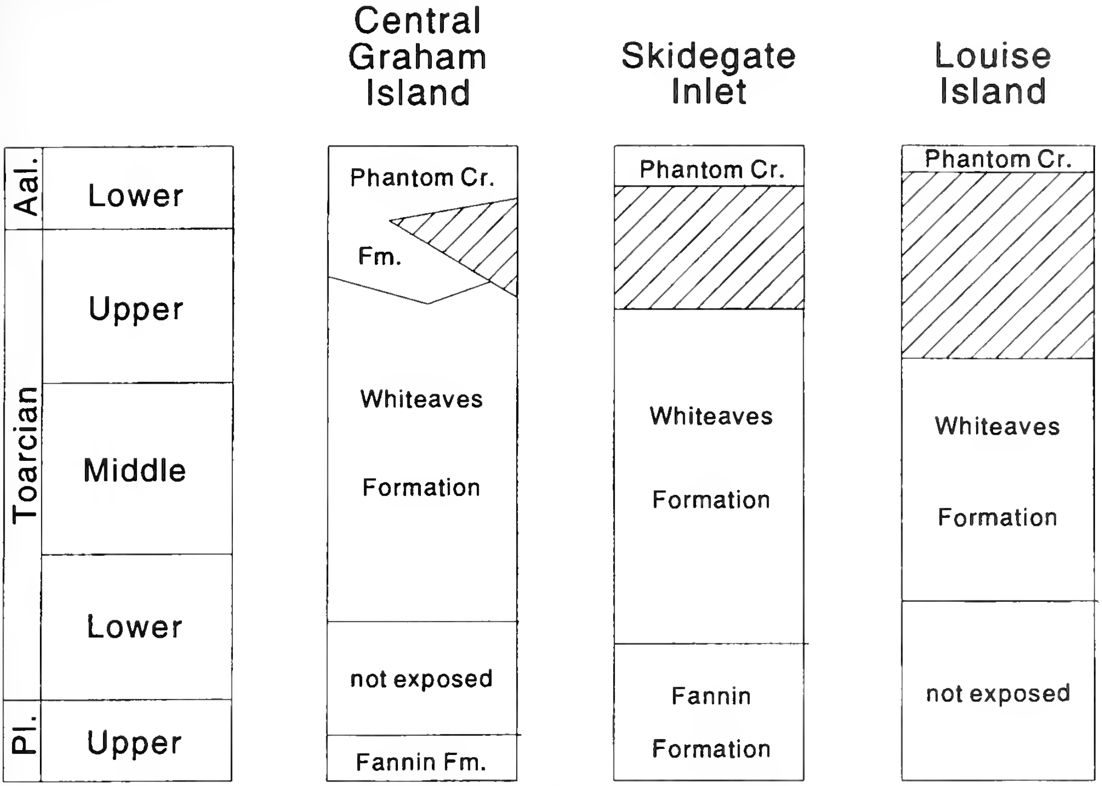
This zone (Zone 5 of Jakobs *et al.* 1995) contains a prolific, albeit low diversity fauna that includes *Phymatoceras hillebrandti* Jakobs, 1994, *Podagrosites latescens* (Simpson, 1834), and *Grammoceras thouarsense* (d'Orbigny, 1843). The Hillebrandti Zone correlates roughly with the Thouarsense Zone of north-west Europe, based on the occurrence of *Grammoceras thouarsense* and *Podagrosites latescens*, and correlates with the Copiapense Zone of South America based on the similarity between *Phymatoceras copiapense* (Moericke, 1894) and *P. hillebrandti*.



TEXT-FIG. 3. Lower Jurassic stratigraphy of the Queen Charlotte Islands. Hett., Hettangian; Baj., Bajocian; Yak., Yakoun Group.

Yakounensis Zone

This zone (Zones 5a and 6 of Jakobs *et al.* 1995) is widespread in western North America, being recognized in southern Alaska, Stikinia, Wrangellia, Quesnellia, south-western British Columbia, Oregon, and on the craton. The interval is thin and stratigraphical relationships between the different species are sometimes difficult to establish. The diverse fauna includes *Pleydellia maudensis* sp. nov., *Pl. crassiornata* sp. nov., *Pl. aalensis* (Zieten, 1832), *Yakounia yakounensis* gen. et sp. nov., *Y. freboldi* sp. nov., *Y. pacifica* sp. nov., *Y. silvae* sp. nov., *Sphaerocoeloceras brochiiforme* Jaworski, 1926, *Hammatoceras speciosum* Janensch, 1902, *Dumortieria insignisimilis* (Brauns, 1865), *D. raricostata* Géczy, 1967, *D. exacta* Buckman, 1905, *D.* cf. *dumortieri* Thiollière *in* Dumortier, 1874, *D.*? cf. *pusilla* Jaworski, 1926, *D.*? *phantasma* sp. nov., *Pseudolioceras compactile* (Simpson, 1855)



TEXT-FIG. 4. Extent of the Toarcian/Aalenian hiatus in the Queen Charlotte Islands. Pl. Pliensbachian; Aal., Aalenian.

and *Holcophylloceras calypso* (d'Orbigny, 1841). It contains several taxa endemic to North America and the eastern Pacific.

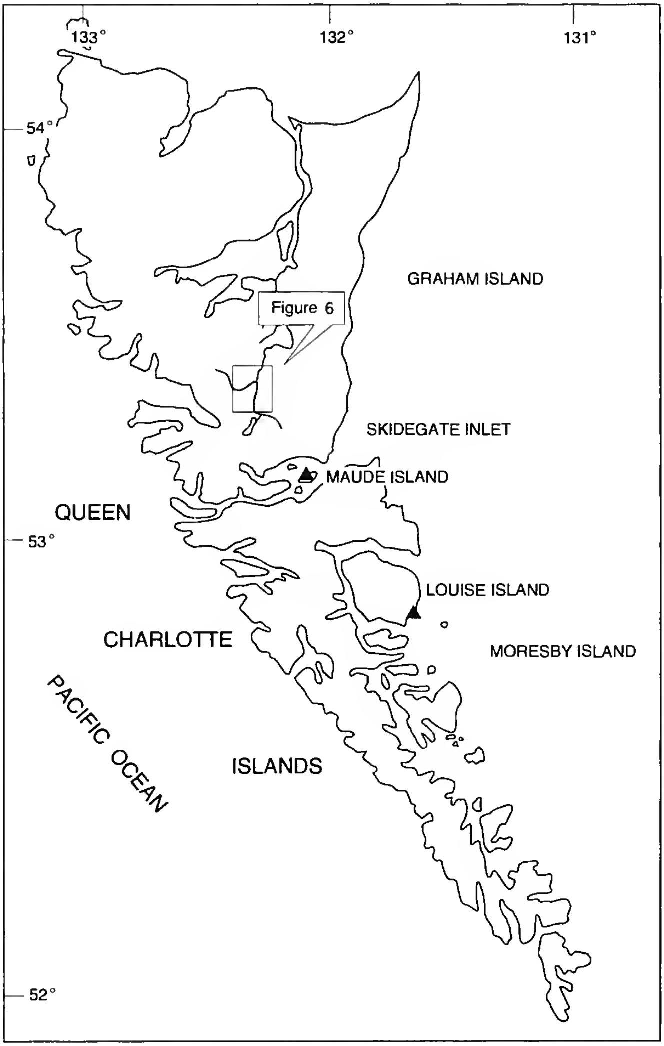
Both Frebold (1976) and Imlay (1981) assigned this interval to the Middle Toarcian based on the erroneous recognition of *Haugia* (in fact, specimens of *Pleydellia* and *Yakounia*, a new genus endemic to western North America). A rough correlation can be made with the '*Pleydellia fluitans*' and '*Pleydellia lotharingica*' zones of South America, based on the co-occurrence of *Sphaerocoeloceras brochiiforme*, *Dumortieria* cf. *pusilla*, and species of *Pleydellia*. Both *Pleydellia lotharingica* (Branco, 1879) and *Phlyseogrammoceras*? *tenuicostatum* (Jaworski, 1926) are similar to *Pleydellia maudensis* which spans the Yakouensis Zone. According to Poulton and Tipper (1991), the base of the Aalenian Stage in North America is defined by the first appearance of *Tmetoceras scissum* (Benecke, 1865). Although *T. scissum* is abundant above the Yakounensis Zone fauna in east-central Oregon, only a single specimen of *Tmetoceras* has been collected from central Graham Island in the Queen Charlotte Islands, the Aalenian there being more commonly characterized by species of *Planammatoceras*, *Bredyia*, and *Erycitoides*.

OCCURRENCES OF LATE TOARCIAN STRATA IN NORTH AMERICA

Queen Charlotte Islands, British Columbia

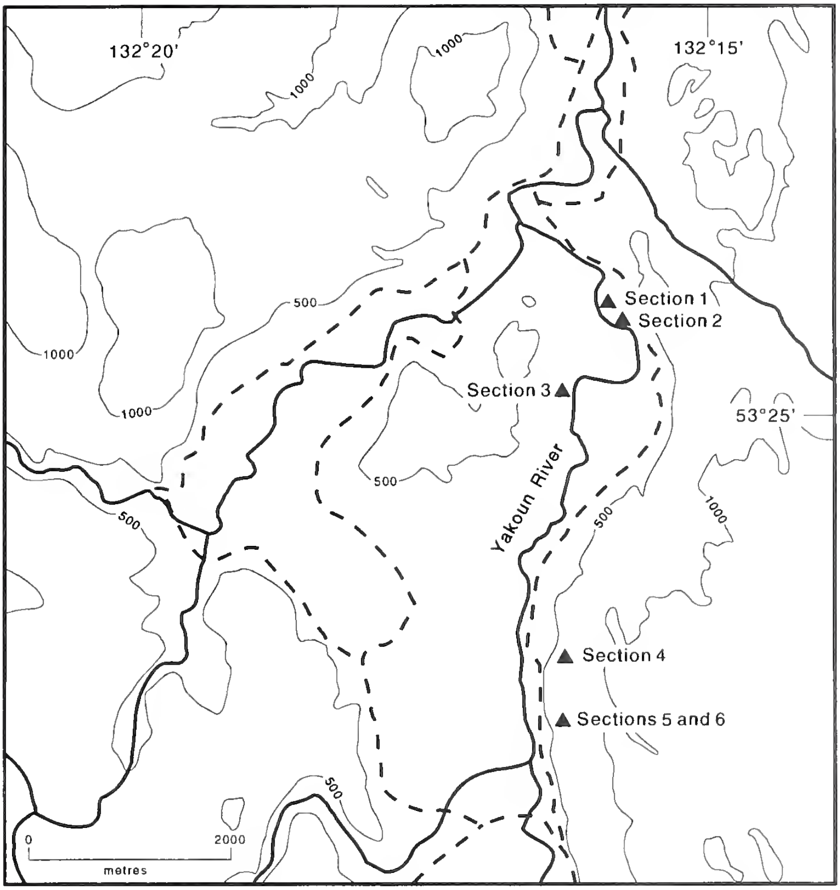
Mesozoic strata in the Queen Charlotte Islands include the most complete marine Lower Jurassic depositional sequence in North America (Sutherland Brown 1968; Cameron and Tipper 1985; Jakobs 1990; Tipper *et al.* 1991) (Text-fig. 3). Toarcian strata of the Maude Group are represented by the Fannin, Whiteaves and Phantom Creek formations.

The Whiteaves Formation is a grey-green siltstone, weathering brown-grey, which is recessive and commonly poorly exposed in road and stream cuts in central Graham Island, the Skidegate Inlet area and on Louise Island (Text-fig. 5). Neither bedding nor lamination were observed in the siltstones but sandy layers occur at intervals. The siltstones are rich in pyrite and glauconite; ash layers and buff-weathering, calcareous concretions are common. The contact with the overlying Phantom Creek Formation is conformable on much of Graham Island, whereas a hiatus is probably present on Maude island (Skidegate Inlet) and Louise Island (Text-fig. 4).



TEXT-FIG. 5. Toarcian localities in the Queen Charlotte Islands.

The Phantom Creek Formation is a resistant sandstone unit exposed in stream and road cuts. It is best exposed in central Graham Island where it is 25 m thick. Thin (< 2 m) sequences crop out on Maude Island and Louise Island. The formation can be subdivided into two units, a lower

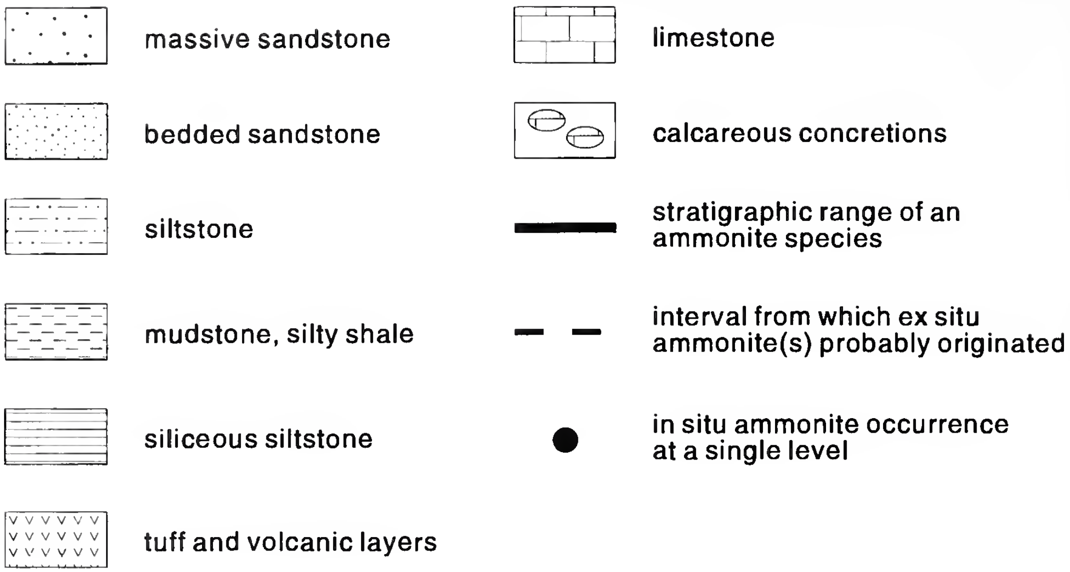


TEXT-FIG. 6. Location of Upper Toarcian sections in central Graham Island, Queen Charlotte Islands.

Coquinoid Sandstone Member and an upper Belemnite Sandstone Member (Cameron and Tipper 1985); these are separated by an erosional hiatus that increases in magnitude toward the south (Text-fig. 4). In central Graham Island, the two members are conformable at Sections 1–3 (Text-figs 5–6), with a cumulative thickness of over 25 m, but at Sections 5 and 6, the Coquinoid Sandstone Member is absent. At Maude Island, Skidegate Inlet, the Coquinoid Sandstone Member is also absent, and a thin (2–3 m) layer of the Belemnite Sandstone Member separates the Whiteaves Formation from the overlying Yakoun Group. The contact between the Phantom Creek Formation and the overlying Yakoun Group is an angular unconformity, best exposed in central Graham Island.

Southern Alaska

In the Talkeetna Mountains (Text-fig. 2), Early Jurassic strata are represented by the Upper Sinemurian to Upper Toarcian Talkeetna Formation, a thick (4600–5800 m) unit of volcanic and volcaniclastic rocks deposited in a marine to non-marine environment (Imlay 1981). Imlay (1981) identified a Middle Toarcian fauna from the Talkeetna Mountains which he assigned to the



Key for Text-figures 7–14.

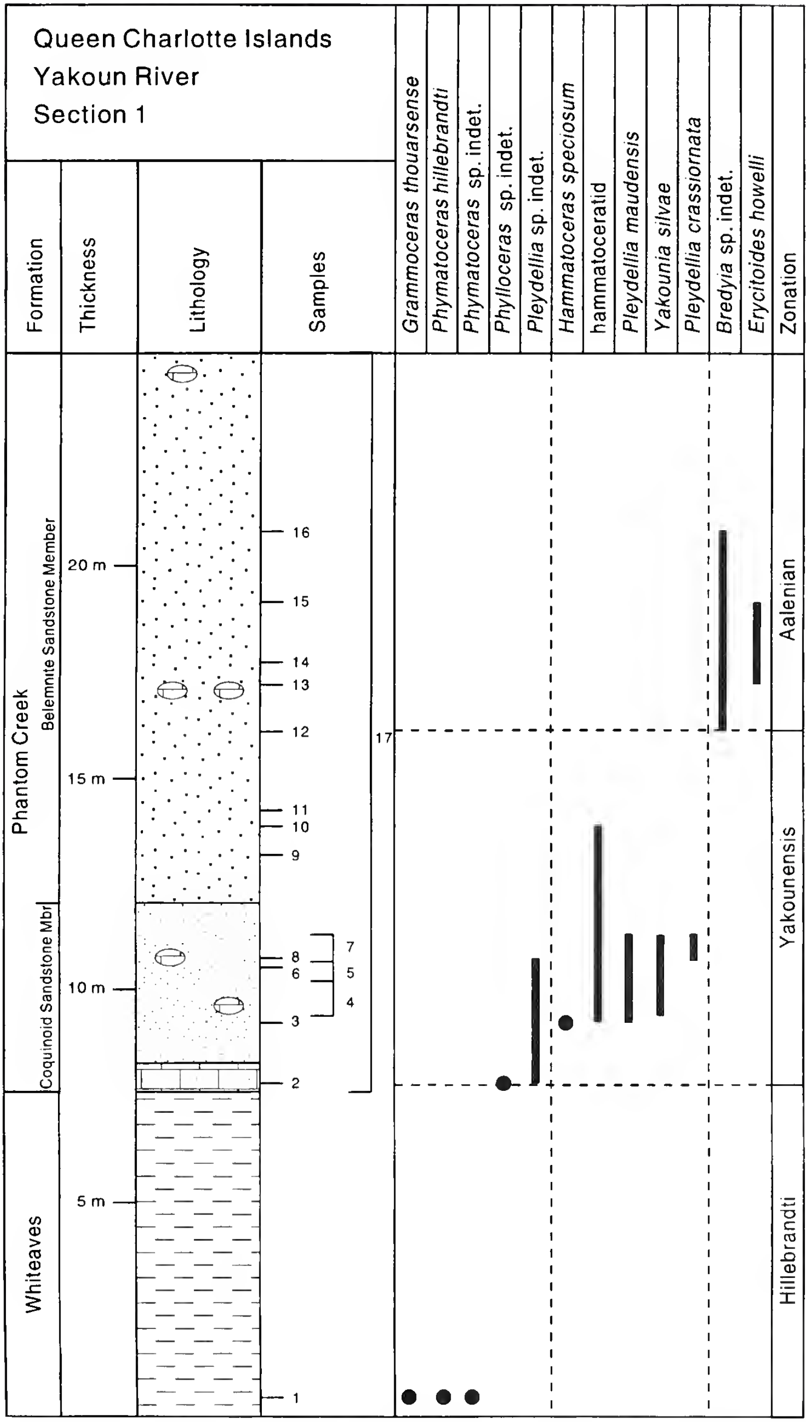
north-west European Variabilis Zone. Recent work in the Queen Charlotte Islands has shown that the Alaskan fauna is identical to the Late Toarcian Yakounensis Zone assemblage from the Queen Charlotte Islands and contains *Hammatoceras* sp. indet. (= *Phymatoceras*? sp. of Imlay (1981)), *Yakounia yakounensis* (= *Haugia* cf. *variabilis* (d'Orbigny, 1842) of Imlay (1981)), *Pleydellia maudensis* (= *Haugia* cf. *grandis* Buckman, 1898 and *Haugia* cf. *compressa* Buckman, 1898 of Imlay (1981)), *Pleydellia* sp. indet. (= *Brodieia* cf. *tenuicostatum* var. *nodosa* and probably *Haugia* sp. of Imlay (1981)), and *Pseudolioceras* sp. indet. (Collections 1–9).

A small section of Jurassic strata exposed at Puale Bay (Text-fig. 2) includes the Upper Toarcian to Lower Bajocian Kialagvik Formation, a dark grey to black, sandy siltstone containing some hard, buff sandstone (Imlay 1981). Imlay (1981) assigned a single collection to the Middle Toarcian, Variabilis Zone. The fauna is identical to that from the Talkeetna Mountains and Queen Charlotte Islands and contains *Pleydellia maudensis* (= *Haugia* cf. *compressa* of Imlay (1981)), *Pl.* sp. indet. (= *Haugia* cf. *grandis* of Imlay (1981)), and *Pseudolioceras* sp. indet. (Collection 10).

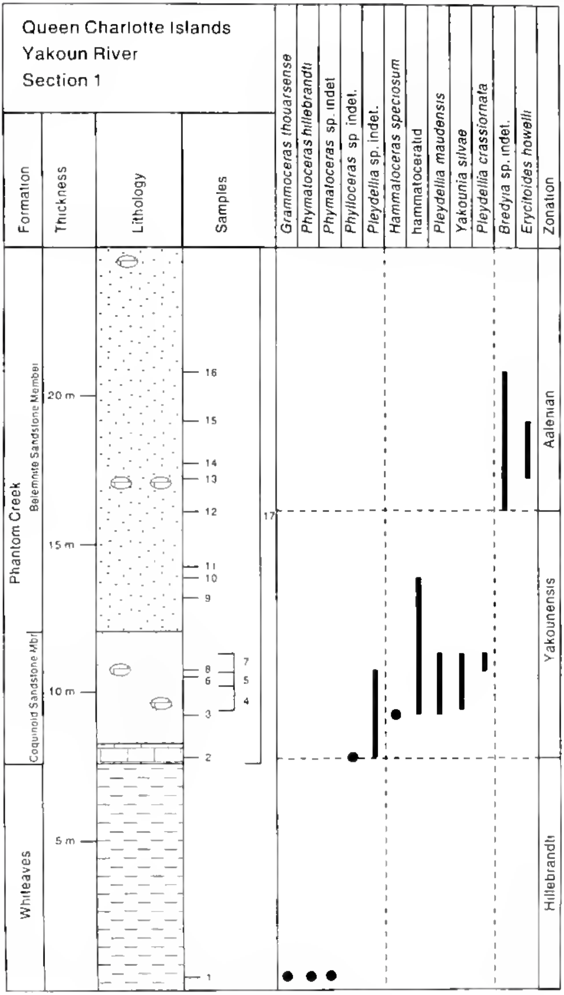
Northern Stikine Terrane

In the northern part of the Stikine Terrane, sediments of the Lower to Middle Jurassic Laberge Group have yielded Late Toarcian ammonites. Two facies were recognized by Souther (1971): the coarse-grained, near-shore Takwahoni Formation in the south-west; and the argillaceous, basinal Inklin Formation in the north-east. Toarcian fossils occur in the former and possibly in the latter (H. W. Tipper, pers. comm. 1992).

Late Toarcian ammonites identified by Frebold (1964*a*) from the Whitehorse area, southern Yukon (Text-fig. 2; Collections 12–15) include *Catulloceras*? (probably a *Dumortieria*), *Dumortieria*?, and *Harpoceras*? (probably a *Pseudolioceras*). A poorly preserved specimen of *Yakouonia*? sp. indet. has also been identified (Collection 11). The reported *Grammoceras* aff. *G. fallaciosum* (Bayle, 1878) and *Grammoceras*? *boreale* (Whiteaves, 1889) (Frebold 1964*a*, p. 17, pl. 7, figs 1–4) are actually Middle Jurassic forms (Poulton and Tipper 1991; D. G. Taylor, pers. comm. 1991). Frebold (1964*a*, p. 4) mentioned the presence of *Catulloceras*? sp. indet. (= *Dumortieria* cf. *dumortieri*) from the Bennett area (Text-fig. 2; Collections 16–17).



TEXT-FIG. 7. Biostratigraphy of Section 1 (Latitude 53° 25′ 20″ N, Longitude 132° 15′ 45″ W) along the Yakoun River, Queen Charlotte Islands.



TEXT-FIG. 7. Biostratigraphy of Section 1 (Latitude 53° 25' 20" N, Longitude 132° 15' 45" W) along the Yakoun River, Queen Charlotte Islands.

Central Stikine Terrane

Along the west-central margin of the Stikine Terrane, interbedded sediments and volcanics of the Triassic to Middle Jurassic Hazelton Group have yielded Late Toarcian ammonites. In the Iskut area, the Hazelton Group has been divided into four formations: the volcanogenic Unuk River, Betty Creek, and Mount Dilworth formations, overlain by sediments of the Salmon River Formation (Anderson and Thorkelson 1990). The Salmon River Formation in the Iskut area (Text-fig. 2) has yielded several collections of *Pleydellia* cf. maudensis from the Yakounensis Zone (Collections 18–19).

In the Spatsizi area, along the northern margin of the Bowser Basin, sedimentary rocks of the Lower to Middle Jurassic Spatsizi Group have been divided into five formations of which the Melisson Formation is probably Late Toarcian in age (Thomson *et al.* 1986). Isolated localities in the Spatsizi area (Text-fig. 2) have yielded *Pleydellia maudensis*, *Yakounia yakounensis*, *Y.* sp. indet., *Dumortieria*? cf. *pusilla*, *Dumortieria* sp. indet., and *Hammatoceras* sp. indet. (Collections 20–32).

A collection of Toarcian ammonites in volcaniclastic sediments from the Toodoggone area (Text-fig. 2) has yielded *Pleydellia* sp. indet. and *Podagrosites*? sp. indet. (Collection 33).

In the McConnell Creek area (Text-fig. 2), along the eastern margin of the Bowser Basin, Lower to Middle Jurassic sediments of the Hazelton Group have yielded isolated collections of Late Toarcian ammonites (Tipper and Richards 1976) from the Smithers Formation, a unit of interbedded, shallow marine volcaniclastic sediments. Poorly preserved specimens of *Dumortieria* sp. indet. and *Yakounia yakounensis* have been collected from the Yakounensis Zone (Collections 34–35).

Toarcian ammonites occur at isolated localities in the Hazelton area (Text-fig. 2). Two collections in the Hazelton Group yielded *Pleydellia* cf. *maudensis* and *Dumortieria* sp. indet. (Collections 36–37) from the Yakounensis Zone.

Quesnel Terrane

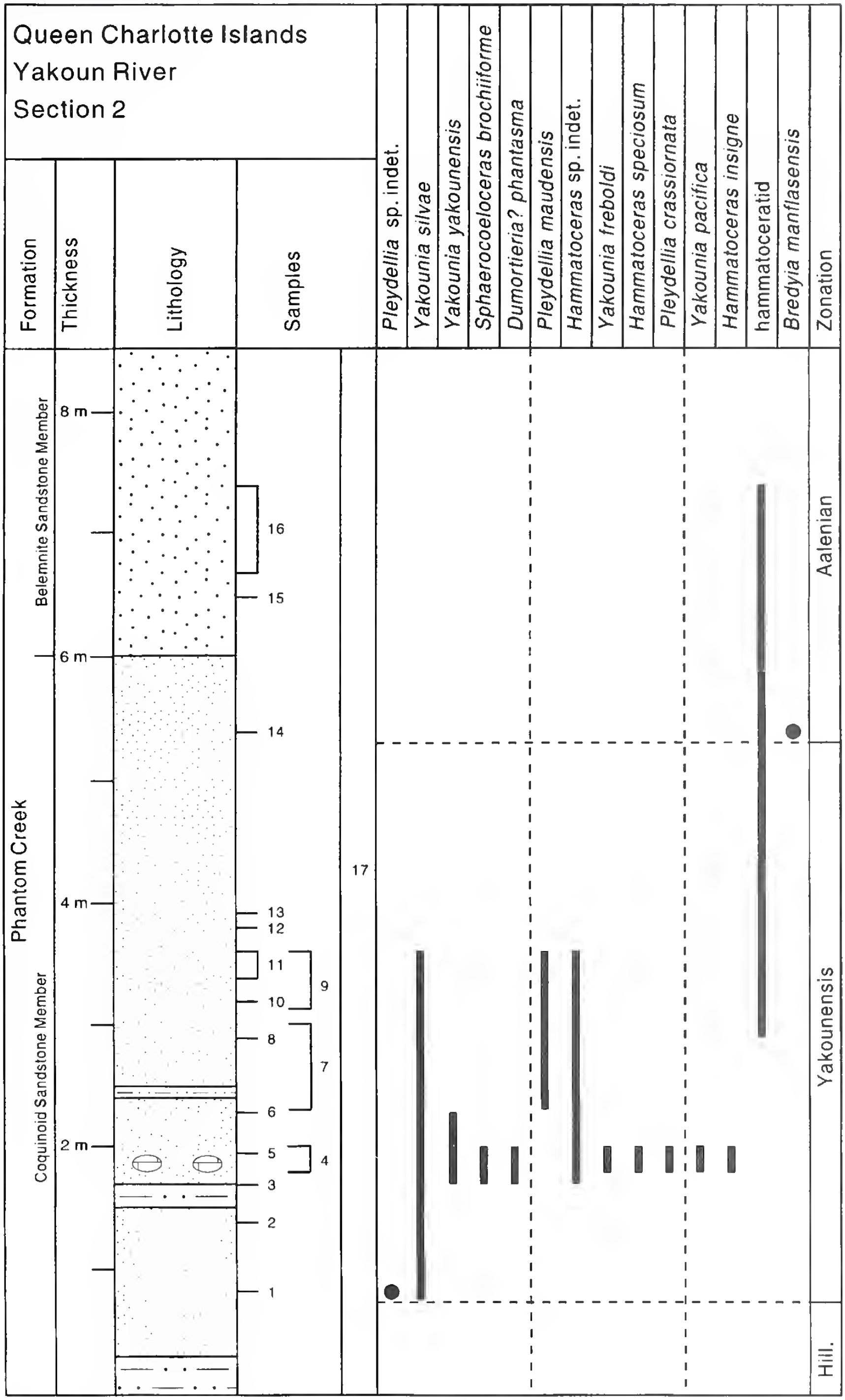
Late Toarcian ammonites including *Pleydellia maudensis*, *Yakounia silvae*, *Polyplectus*, and *Dumortieria*? *phantasma* (Collection 38) have been found in the Manson River area on the Quesnel Terrane (Text-fig. 2).

South-western British Columbia

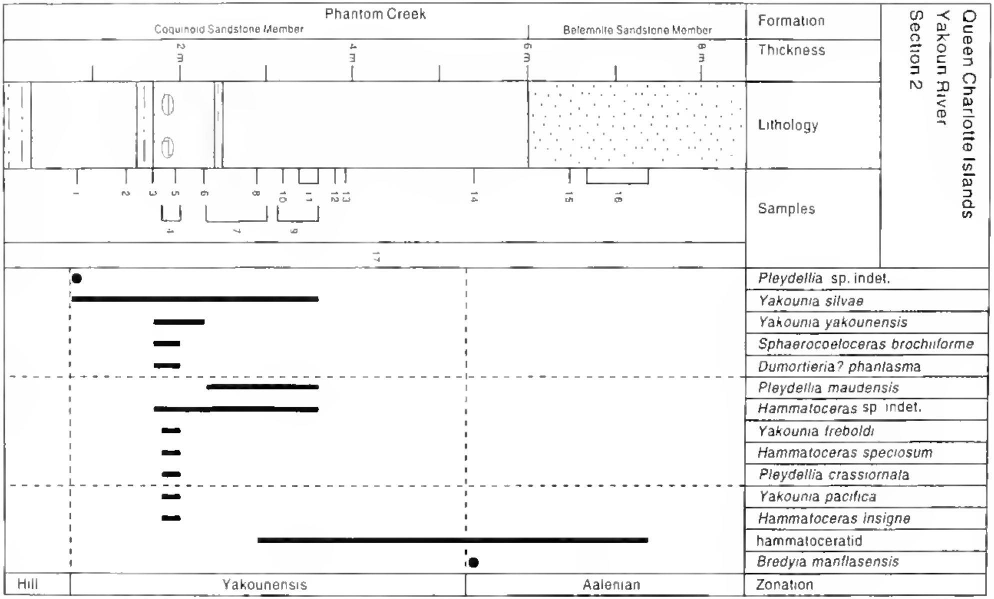
In the Taseko Lakes area (Text-fig. 2), the Lower to Middle Jurassic (Upper Hettangian to Lower Bajocian) Last Creek Formation rests unconformably on the Tyaughton Group (Umhoefer 1989). The upper part of the poorly exposed Last Creek Formation (Upper Sinemurian to Lower Bajocian) is composed of black, calcareous shales, minor sandstones, and thin ash beds. Toarcian shales of the Taseko Lakes area contain *Dumortieria*? sp. and *Hammatoceras* sp. of the Yakounensis Zone (Collections 39–41).

On the west side of Harrison Lake in south-western British Columbia (Text-fig. 2), the Jurassic Harrison Lake Formation rests unconformably on Triassic rocks (Arthur *et al.* 1993). The lowest two of four members (the Celia Cove and Francis Lake members) have yielded rare ammonites of probable Toarcian age with the highest assemblage containing species of *Dumortieria* indicating the Yakounensis Zone (Collections 42–43).

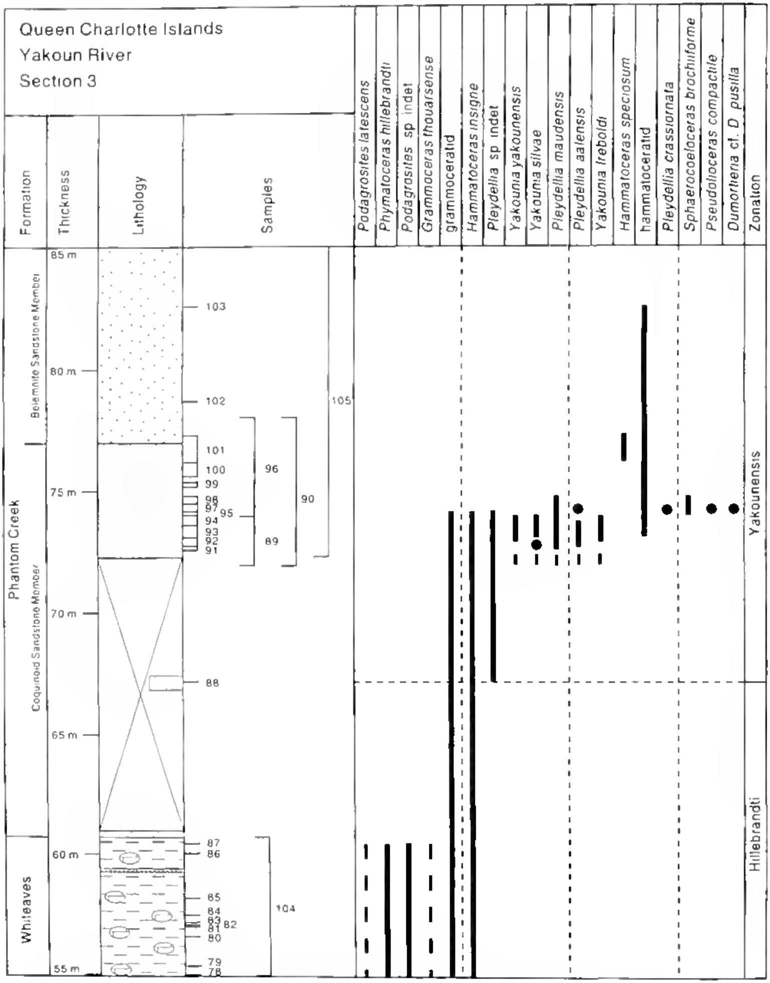
O'Brien (1987) subdivided the Ladner Group in the Boston Bar area into the Lower Jurassic Boston Bar Formation, a sequence of argillite, siltstone, greywacke and conglomerate, and the Middle Jurassic Dewdney Creek Formation, a sequence of volcanic breccia, lava and argillaceous sediments. This sequence is similar to that found to the south in Manning Park (Text-fig. 2). Toarcian ammonites collected from the Ladner Group of Manning Park were assigned to *Phlyseogrammoceras* aff. *P. dispansiforme* (Wunstorf, 1907) by Frebold (Frebold *et al.* 1969) but are comparable with *Yakounia silvae* from the Yakounensis Zone (Collection 44).



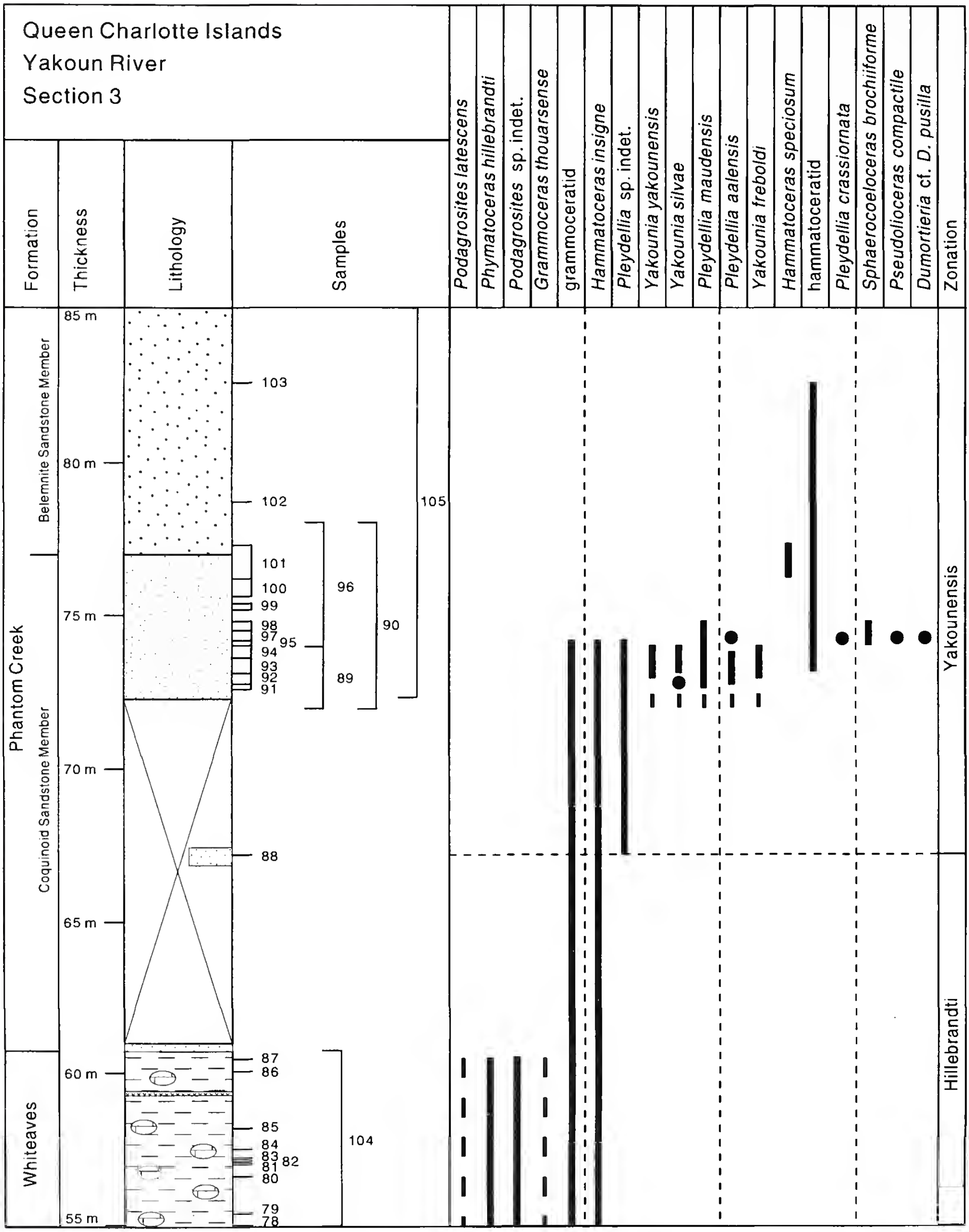
TEXT-FIG. 8. Biostratigraphy of Section 2 (Latitude 53° 25′ 05″ N, Longitude 132° 15′ 30″ W) along the Yakoun River, Queen Charlotte Islands.



TEXT-FIG. 8. Biostratigraphy of Section 2 (Latitude 53° 25′ 05″ N, Longitude 132° 15′ 30″ W) along the Yakoun River, Queen Charlotte Islands.



TEXT-FIG. 9. Biostratigraphy of Section 3 (Latitude 53° 25′ 00″ N, Longitude 132° 16′ 05″ W) along the Yakoun River, Queen Charlotte Islands.



TEXT-FIG. 9. Biostratigraphy of Section 3 (Latitude 53° 25′ 00″ N, Longitude 132° 16′ 05″ W) along the Yakoun River, Queen Charlotte Islands.

Southern Canadian Rocky Mountains

The Jurassic Fernie Formation, deposited on the North American craton, crops out from south-western Alberta to the Peace River area of north-eastern British Columbia. It includes the Toarcian Poker Chip Shale, a laterally extensive black shale, 10–38 m thick, that appears to be overlain conformably by sandstones and siltstones of the Lower Bajocian Rock Creek Member; no Aalenian ammonites have been found (Hall 1984, 1987).

In the southern outcrop area (Text-fig. 2; Collection 45), a Late Toarcian fauna of *Pleydellia mandensis* (= ?Grammoceratinae gen. et sp. indet. of Hall (1987)), *Yakounia silvae* (= ?Grammoceratinae gen. et sp. indet. of Hall (1987)), *Y. yakounensis* (= ?Grammoceratinae gen. et sp. indet. of Hall (1987)), *Sphaerocoeloceras* sp. indet. (= ?Hammatoceratidae gen. et sp. indet. of Hall (1987)), and *Dumortieria*? *phantasma* (= ?Hildoceratinae gen. et sp. indet. of Hall (1987)) has been collected. Frebold (1976) identified several forms as Middle Toarcian but these are actually Late Toarcian in age and include *Pleydellia mandensis* (= *Haugia* sp. indet. and *Haugia* aff. *H. illustris* (Denckmann, 1887) of Frebold (1976)) and *Yakounia freboldi* (= *Haugia* aff. *H. navis* (Dumortier, 1874) of Frebold (1976)) (Collections 46–51).

BIOSTRATIGRAPHY OF THE MEASURED SECTIONS

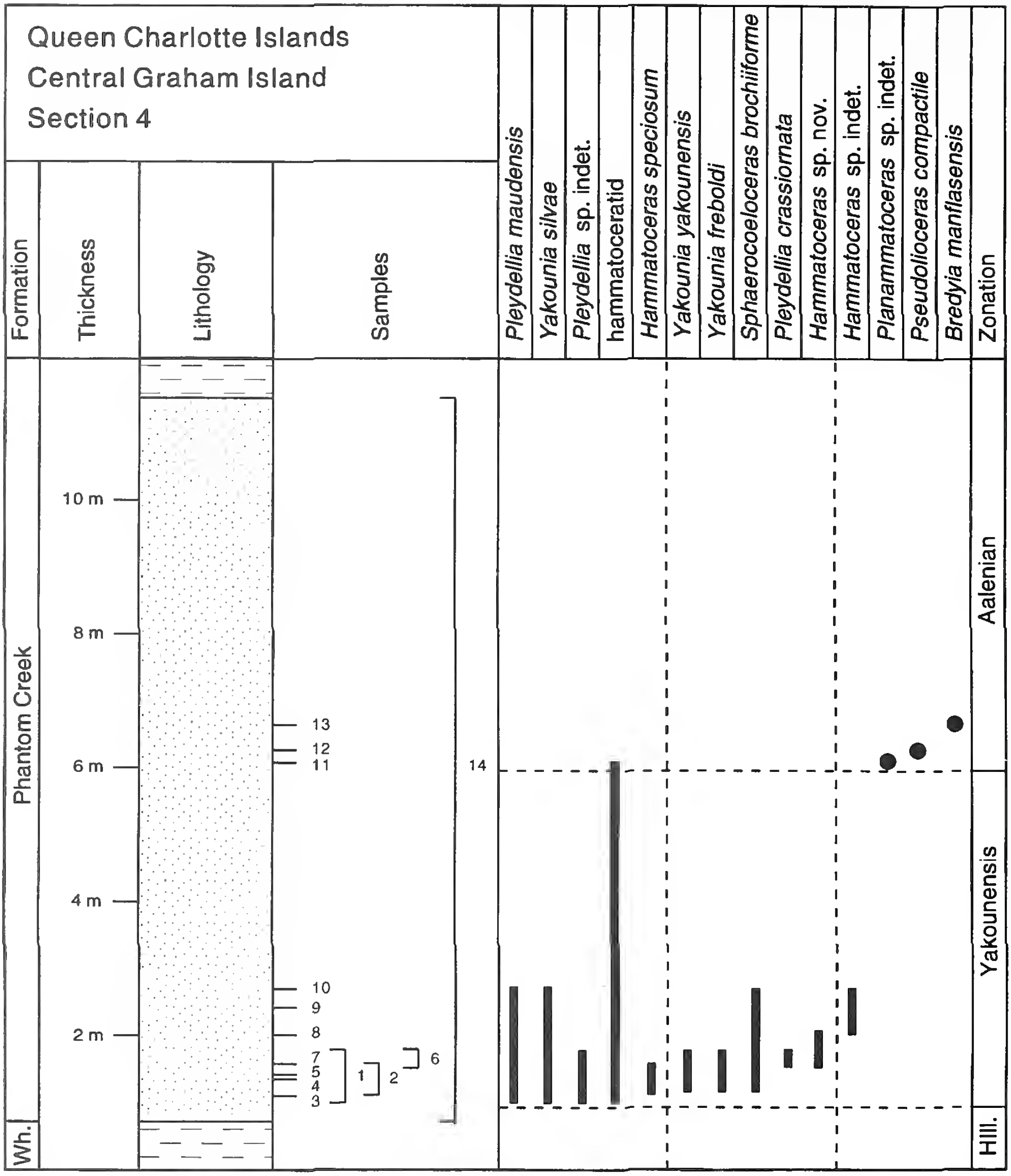
Section 1: Yakoun River. This section (Text-figs 5–7) was measured and figured originally by Cameron and Tipper (1985, Section 12) who inadvertently inverted the stratigraphy as a result of misinterpreting a poorly exposed and faulted succession. The section was re-measured during the summers of 1987–90 when lower water levels had increased exposure significantly. Siltstones of the Whiteaves Formation lie conformably beneath sandstones of the Phantom Creek Formation. The boundary between the Hillebrandti and Yakounensis zones is not well documented because of poor exposure. The boundary between the Yakounensis Zone and the Aalenian Stage is similarly not well constrained, although it appears to occur above the contact between the Coquinoid Sandstone and Belemnite Sandstone members (Jakobs 1990). The presence of *Bredyia* and *Erycitoides howelli* (White, 1889) at 17 m indicates that such taxa as *Tmetoceras* and *Troitsia* could be expected below. Radiolaria identified by E. S. Carter from concretions at 11·4 m indicate a Late Toarcian age; those at 17 m are Aalenian (Carter and Jakobs 1990).

Section 2: Yakoun River. A sequence similar to Section 1 occurs a few metres upstream (Text-figs 6, 8). The Whiteaves Formation is not exposed, but the Phantom Creek Formation is better exposed. The scarcity of ammonites makes the boundary between the Yakounensis Zone and the Aalenian Stage difficult to determine, but it appears to occur below the contact between the Coquinoid Sandstone and Belemnite Sandstone members of the Phantom Creek Formation.

Section 3: Yakoun River. This section (Text-figs 6, 9), originally measured and figured by Cameron and Tipper (1985, Section 11), was re-measured during the summers of 1987–90. The Whiteaves Formation is overlain by a sandstone unit, and a 10 m thick covered interval separates this sandstone unit from the remainder of the Phantom Creek Formation; a fault is possibly present. The top of the section is faulted.

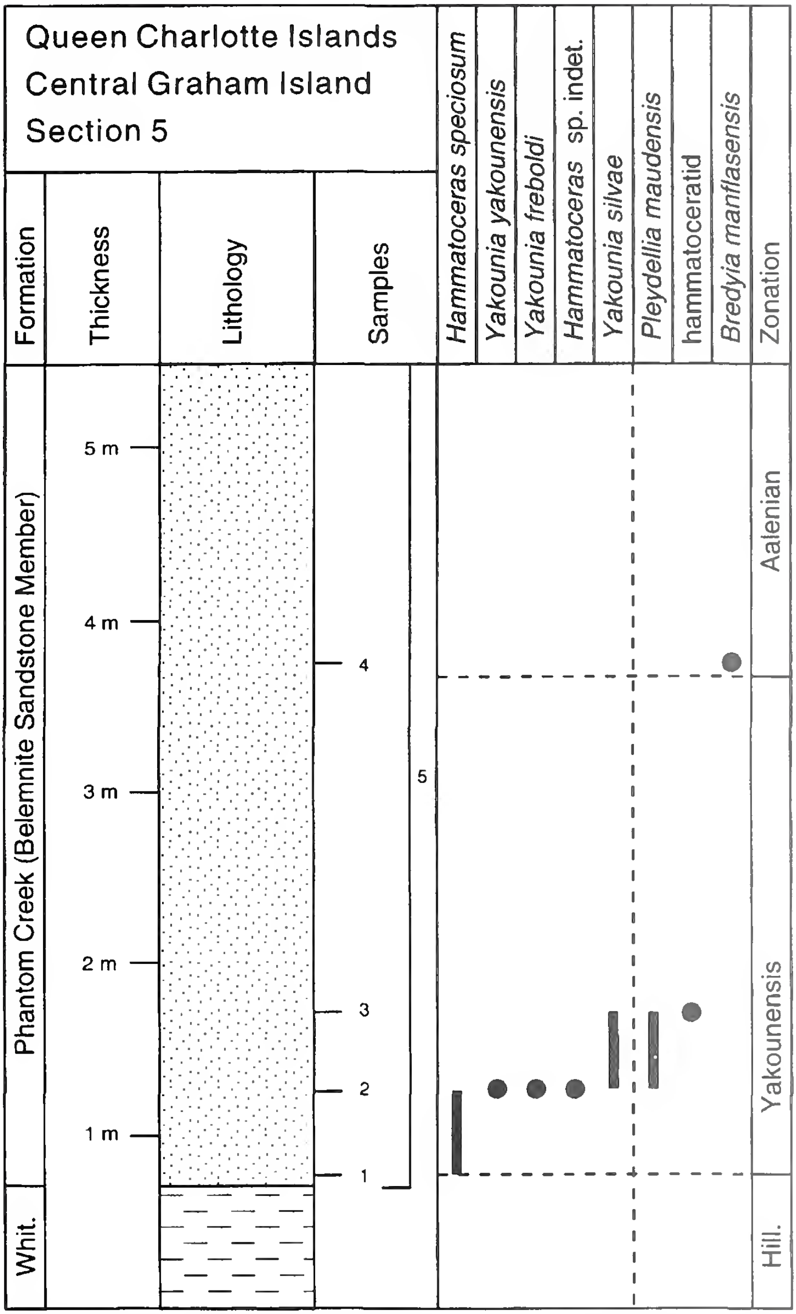
Section 4: Central Graham Island. This section (Text-figs 6, 10), measured and figured originally by Cameron and Tipper (1985, Section 14), was re-measured during the summers of 1987–90. The Whiteaves Formation appears to be overlain conformably by the Phantom Creek Formation. No fossils were collected from the Whiteaves Formation in this section, but another section nearby yielded *Phymatoceras hillebrandti* just below the contact. The boundary between the Yakounensis Zone and the Aalenian Stage is not well constrained because of poor recovery of fossils.

Sections 5–6: Central Graham Island. These two sections (Text-figs 6, 11–12) were measured at Road 59 in Central Graham Island. Section 5 had been measured and figured previously by



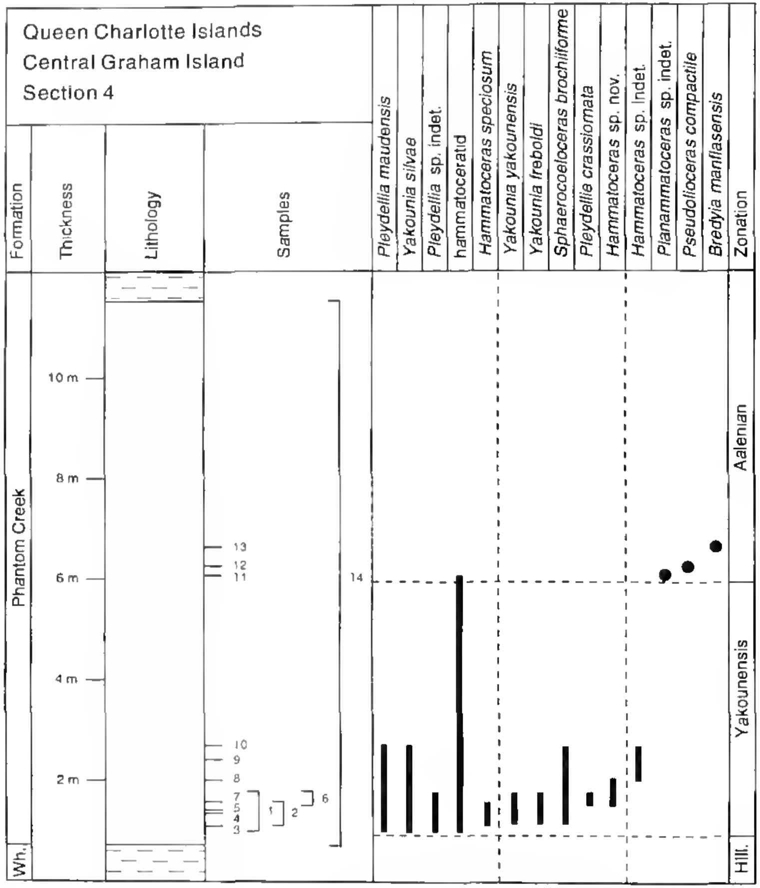
TEXT-FIG. 10. Biostratigraphy of Section 4 (Latitude 53° 23′ 35″ N, Longitude 132° 15′ 30″ W) in central Graham Island, Queen Charlotte Islands. Wh., Whiteaves; Hill., Hillebrandti.

Cameron and Tipper (1985, Section 13). The base of both sections is covered. The top of Section 5 is truncated by a fault whereas Section 6 is overlain unconformably by the Yakoun Group. The erosional hiatus between the two members of the Phantom Creek Formation has cut out the Coquinoid Sandstone Member in both sections. A single *Tmetoceras scissum* was collected from a faulted section of the Belemnite Sandstone Member.



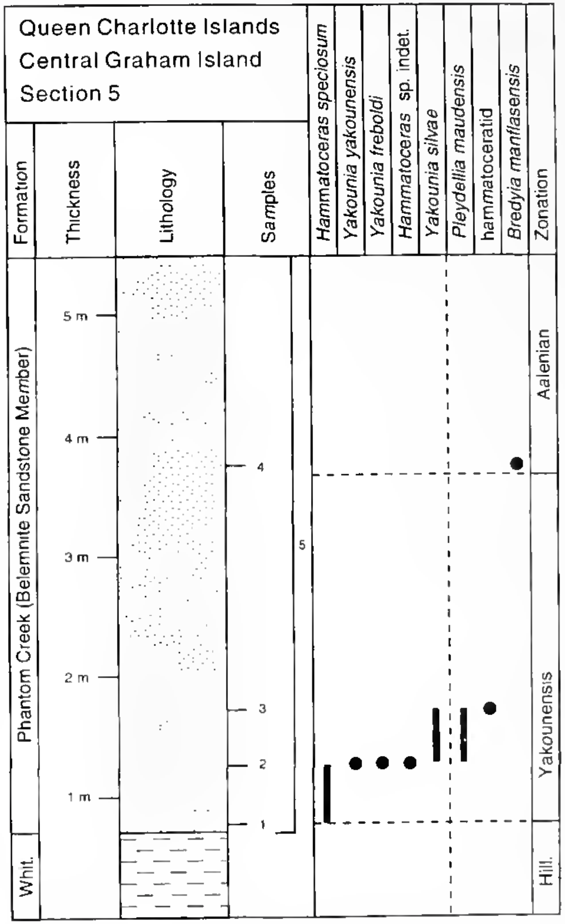
TEXT-FIG. 11. Biostratigraphy of Section 5 (Latitude 53° 23′ 00″ N, Longitude 132° 15′ 30″ W) in central Graham Island, Queen Charlotte Islands. Whit., Whiteaves; Hill., Hillebrandti.

Sections 7–8: Izee Area, Oregon. South-west of the abandoned town of Izee in east-central Oregon (Text-fig. 2), the basal Warm Springs Member of the Snowshoe Formation has yielded Late Toarcian ammonites (Dickinson and Vigrass 1964; Imlay 1968; Smith 1980). Representatives of this poorly preserved fauna were first described by Imlay (1968) but the stratigraphy at that time



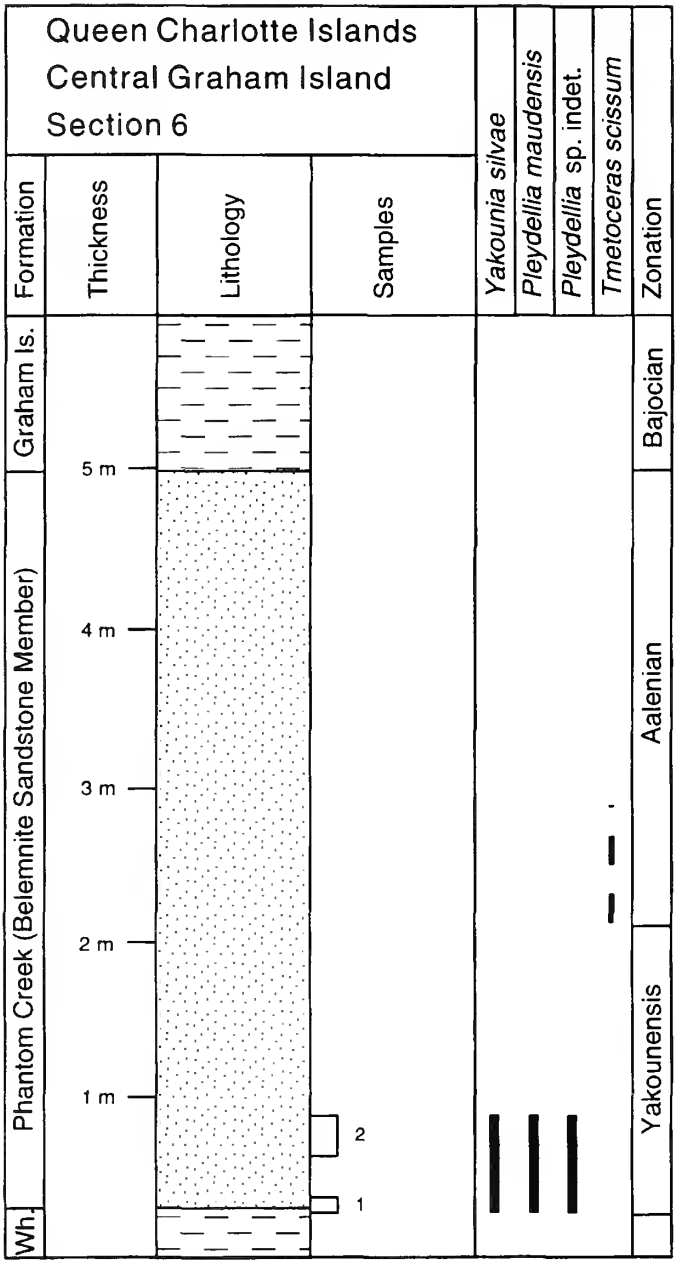
TEXT-FIG. 10. Biostratigraphy of Section 4 (Latitude 53° 23′ 35″ N, Longitude 132° 15′ 30″ W) in central Graham Island, Queen Charlotte Islands. Wh., Whiteaves; Hill., Hillebrandti.

Cameron and Tipper (1985, Section 13). The base of both sections is covered. The top of Section 5 is truncated by a fault whereas Section 6 is overlain unconformably by the Yakoun Group. The erosional hiatus between the two members of the Phantom Creek Formation has cut out the Coquinoid Sandstone Member in both sections. A single *Tmetoceras scissum* was collected from a faulted section of the Belemnite Sandstone Member.



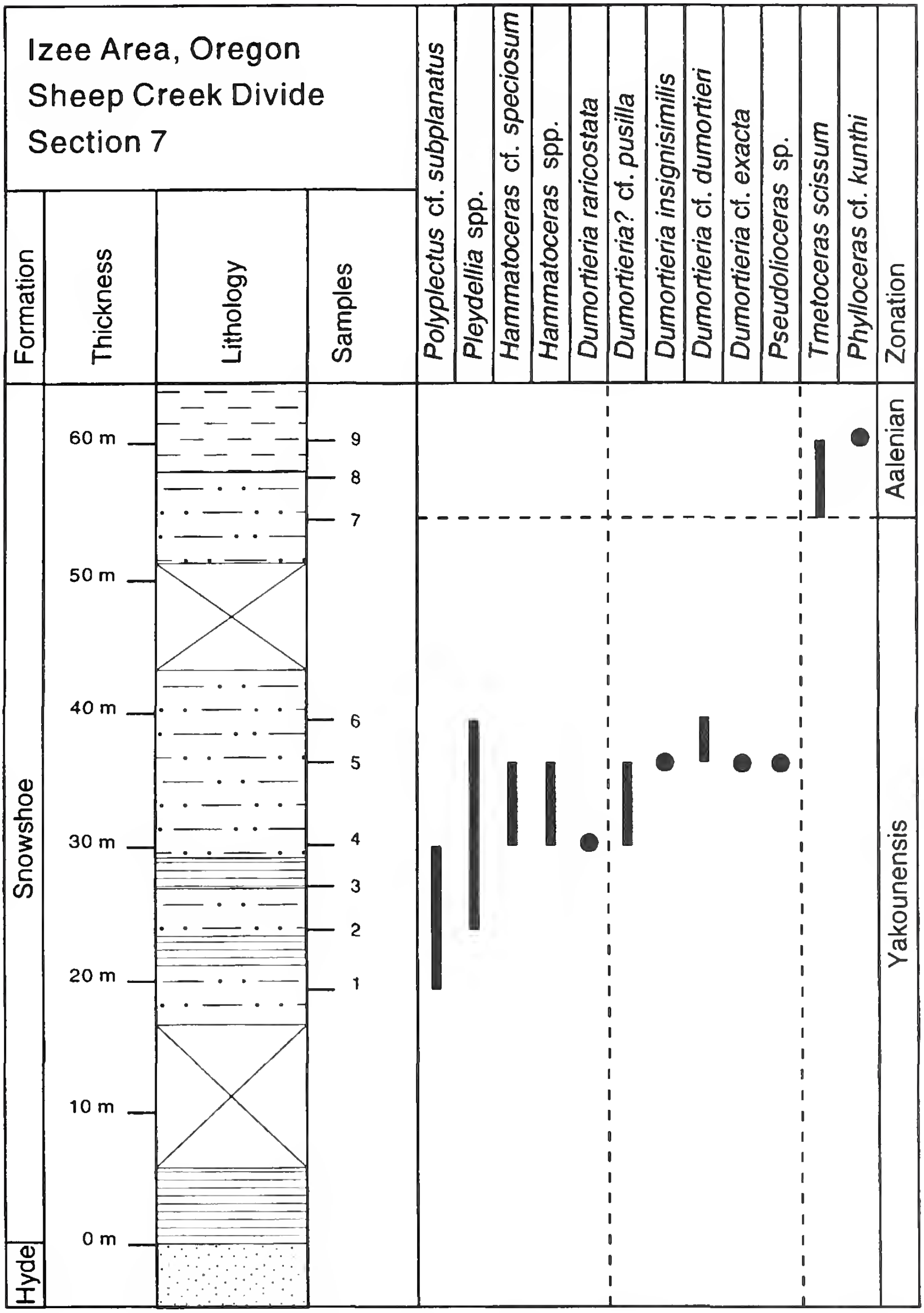
TEXT-FIG. 11. Biostratigraphy of Section 5 (Latitude 53° 23′ 00″ N, Longitude 132° 15′ 30″ W) in central Graham Island, Queen Charlotte Islands. Whit., Whiteaves; Hill., Hillebrandti.

Sections 7–8. Izee Area, Oregon. South-west of the abandoned town of Izee in east-central Oregon (Text-fig. 2), the basal Warm Springs Member of the Snowshoe Formation has yielded Late Toarcian ammonites (Dickinson and Vigrass 1964; Imlay 1968; Smith 1980). Representatives of this poorly preserved fauna were first described by Imlay (1968) but the stratigraphy at that time



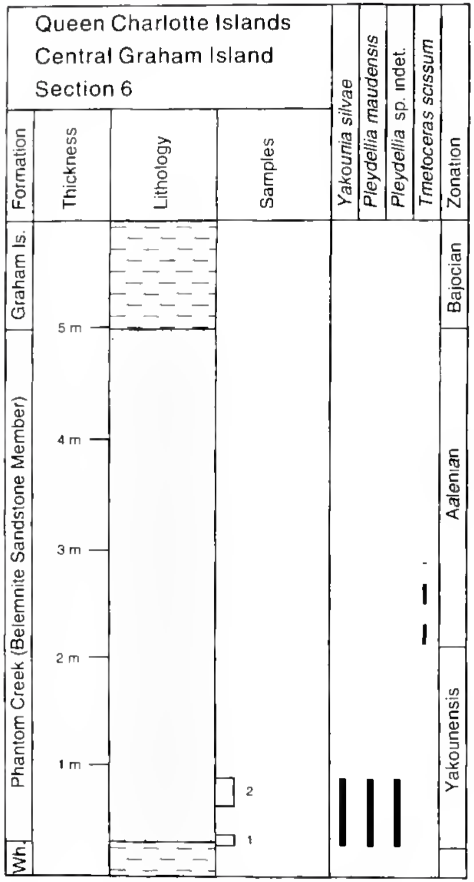
TEXT-FIG. 12. Biostratigraphy of Section 6 (Latitude 53° 23′ 00″ N, Longitude 132° 15′ 30″ W) in central Graham Island, Queen Charlotte Islands.

was poorly understood. Stratigraphical sections have now been measured at Sheep Creek Divide (Section 7; Text-fig. 13) and Flat Creek (Section 8; Text-fig. 14) where the recessive siltstones and mudstones of the Warm Springs Member rest with a gradational contact on the resistant, volcaniclastic sandstones of the Hyde Formation. Some of the original identifications of the basal Snowshoe Formation ammonites (Imlay 1968) must now be revised in the light of richer collections



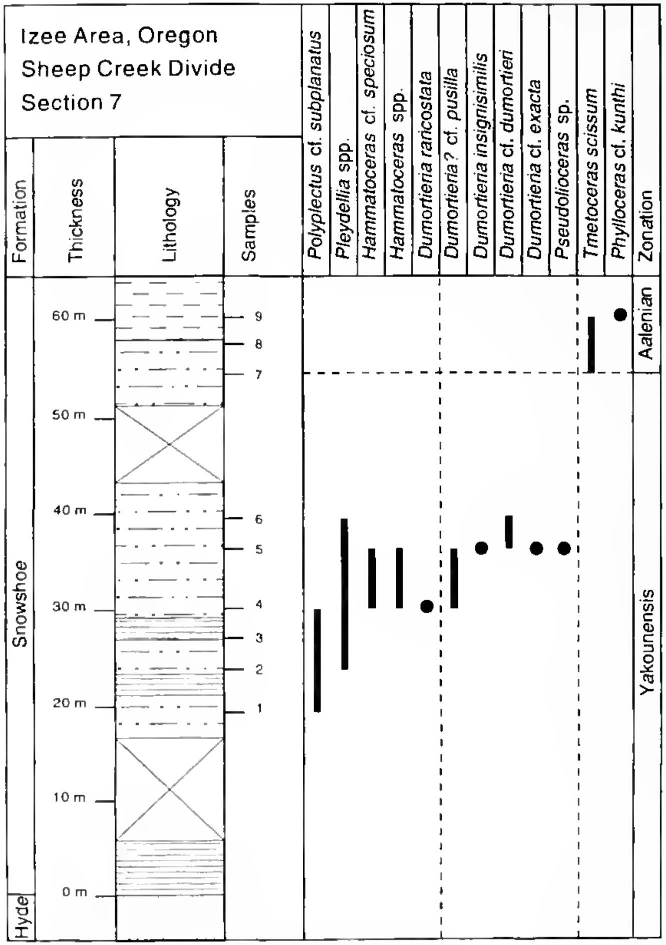
TEXT-FIG. 13. Biostratigraphy of Section 7 (Latitude 44° 03′ 17″ N, Longitude 119° 25′ 54″ W) at Sheep Creek Divide, Izee area, Oregon.

and a better understanding of the biostratigraphy. Several species of *Dumortieria* occur together with *Hammatoceras speciosum*, *Hammatoceras* spp. (= *Hangia* spp. of Imlay (1968)), *Pleydellia* spp. (= *Grammoceras* spp. of Imlay (1968)), and *Polyplectus* sp. This association is stratigraphically



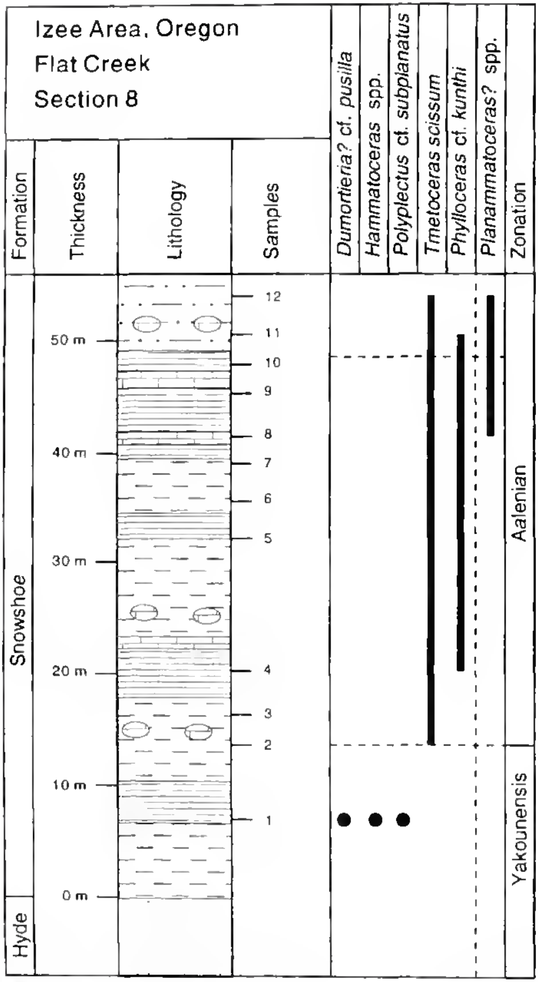
TEXT-FIG. 12. Biostratigraphy of Section 6 (Latitude 53° 23′ 00″ N, Longitude 132° 15′ 30″ W) in central Graham Island, Queen Charlotte Islands.

was poorly understood. Stratigraphical sections have now been measured at Sheep Creek Divide (Section 7; Text-fig. 13) and Flat Creek (Section 8; Text-fig. 14) where the recessive siltstones and mudstones of the Warm Springs Member rest with a gradational contact on the resistant, volcaniclastic sandstones of the Hyde Formation. Some of the original identifications of the basal Snowshoe Formation ammonites (Imlay 1968) must now be revised in the light of richer collections

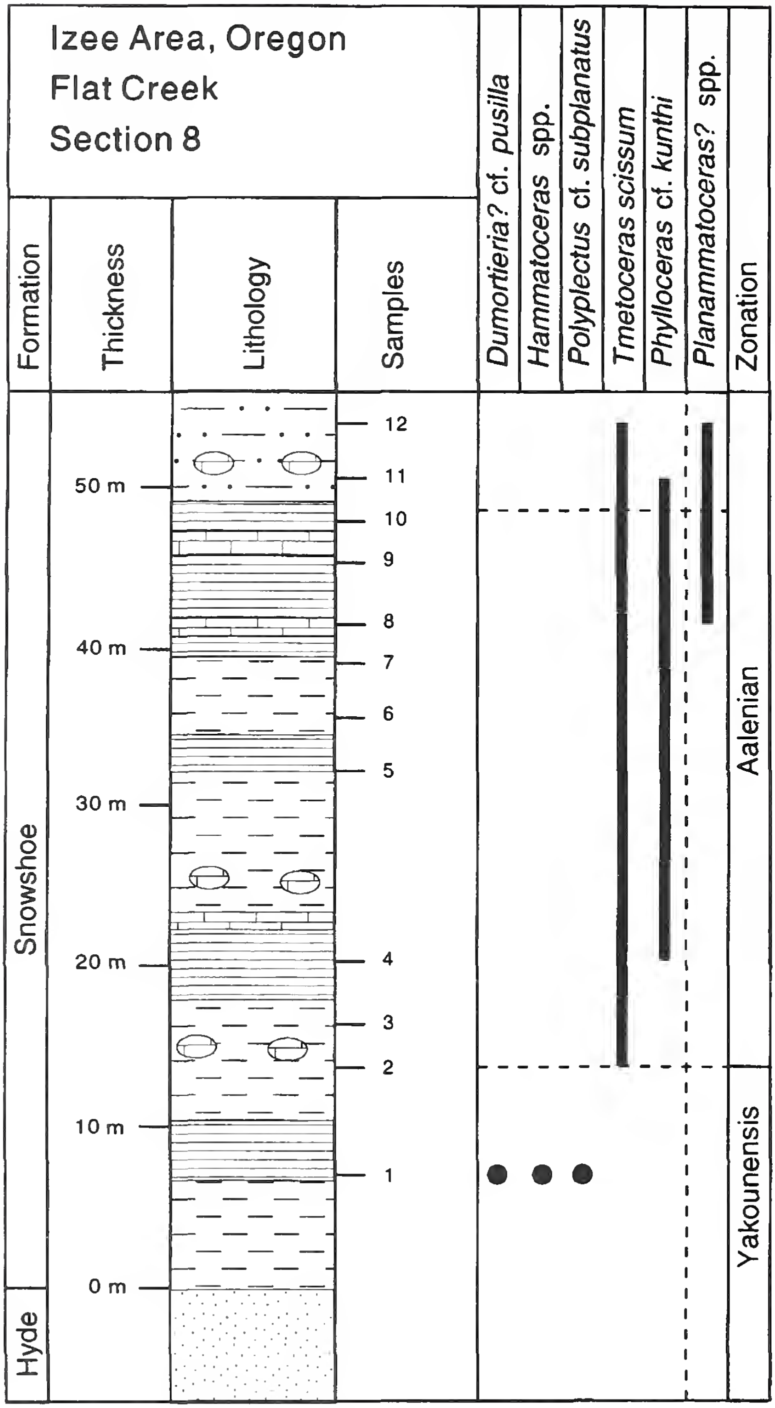


TEXT-FIG. 13. Biostratigraphy of Section 7 (Latitude 44° 03′ 17″ N, Longitude 119° 25′ 54″ W) at Sheep Creek Divide, Izee area, Oregon.

and a better understanding of the biostratigraphy. Several species of *Dumortieria* occur together with *Hammatoceras speciosum*, *Hammatoceras* spp. (= *Haugia* spp. of Imlay (1968)), *Pleydellia* spp. (= *Grammoceras* spp. of Imlay (1968)), and *Polyplectus* sp. This association is stratigraphically



TEXT-FIG. 14. Biostratigraphy of Section 8 (Latitude 44° 00′ 58″ N, Longitude 119° 28′ 23″ W) at Flat Creek, Izee area, Oregon.



TEXT-FIG. 14. Biostratigraphy of Section 8 (Latitude 44° 00′ 58″ N, Longitude 119° 28′ 23″ W) at Flat Creek, Izee area, Oregon.

beneath the first occurrence of the Aalenian ammonite *Tmetoceras scissum* (see Imlay 1973) and is assigned to the Yakounensis Zone. Although the Yakounensis Zone correlates in part with the Levesquei Zone of north-west Europe, the ammonite assemblage, and particularly the common occurrence of *Polyplectus* sp., is more typical of Mediterranean successions (Donovan 1958; Géczy 1967; Goy and Martinez 1990).

Detailed locality data for Sections 1 to 8 and Collections 1 to 52 have been deposited with the British Library, Boston Spa, Yorkshire, U.K., as Supplementary Publication No. SUP 14044. The information includes geographical and stratigraphical position, locality numbers, the lithostratigraphical unit sampled, and the fauna present.

SYSTEMATIC PALAEONTOLOGY

Specimens described and illustrated in this paper are housed at the Geological Survey of Canada in Ottawa (GSC) and the University of British Columbia in Vancouver, Canada (UBC).

Abbreviations are as follows (after Smith 1986): CHW, constrictions per half whorl, counted on adoral half whorl; D, shell diameter at which measurements were made; PRHW, primary ribs per half whorl, counted on the adoral half whorl; U = (UD/D) × 100; UD, umbilical diameter; WH, whorl height; WW, whorl width; WWWH = (WW/WH) × 100. Measurements are in millimetres.

Order AMMONOIDEA von Zittel, 1884
Suborder PHYLLOCERATINA Arkell, 1950
Superfamily PHYLLOCERATACEAE von Zittel, 1884
Family PHYLLOCERATIDAE von Zittel, 1884
Subfamily CALLIPHYLLOCERTINAE Spath, 1927

Genus HOLCOPHYLLOCERAS Spath, 1927
[= *Salfeldiella* Spath, 1927; *Telegdiceras* Kovács, 1939]

Type species. *Phylloceras mediterraneum* Neumayr, 1871.

Diagnosis. Involute shell with high oval whorl section and plain venter; periodic, acutely sigmoidal or angular constrictions present at all stages of ontogeny; outer half of whorl appears to be ribbed; septal sutures with diphyllic saddles except for first lateral saddle which becomes triphyllic in later forms.

Distribution. *Holcophylloceras* is found world-wide from the Lower Jurassic (Toarcian) to the Cretaceous.

Holcophylloceras calypso (d'Orbigny, 1841)

Plate 5, figures 7–8

*1841 *Ammonites calypso* d'Orbigny, pl. 110, figs 1–3.
1976 *Holcophylloceras calypso* (d'Orbigny); Schlegelmilch, p. 26, pl. 1, fig. 6.

Material. Three specimens collected from calcareous concretions within sandstones of the Phantom Creek Formation, Queen Charlotte Islands (Section 2, loc. 17, talus).

Measurements.	D	UD	U	WH	WW	WWWH	CHW
GSC 107260	27·3	2·8	10·3	14·8	10·5	0·71	4
GSC 107260	—	—	—	8·9	6·4	0·72	—
GSC 107304	—	—	—	6·9	5·7	0·83	—
GSC 107305	17·1	2·3	13·5	8·1	6·9	0·85	3

Description. Involute shell with a high oval whorl section and gently sloping umbilical wall. Ornament consists of about eight sinuous constrictions per whorl. Sutures are diphyllic.

Distribution. Holcophylloceras calpyso is found world-wide in the Toarcian.

Suborder AMMONITINA Hyatt, 1889
Superfamily HILDOCERATACEAE Hyatt, 1867
Family HILDOCERATIDAE Hyatt, 1867
Subfamily GRAMMOCERATINAE Buckman, 1904

Genus PLEYDELLIA Buckman, 1899

[= *Cotteswoldia* Buckman, 1902 (= *Gotteswaldia* Théobald, 1950); *Canavaria* Buckman, 1902
(*non* Gemmellaro, 1886) (= *Canavarina Buckman*, 1904); *Walkeria* Buckman, 1902
(= *Walkericeras* Buckman, 1913)]

Type species. Pleydellia comata Buckman, 1899.

Diagnosis. Involute to evolute shell with tall, compressed whorls; whorl section lanceolate to triangular; umbilical shoulder abrupt to moderately rounded; venter carinate with weak ventro-lateral shoulders; ribbing sinuous, prorsiradiate on upper flank, and terminating at ventro-lateral shoulder. Ribs may bifurcate at or near umbilical shoulder, and may fade on inner or outer half of flanks.

Distribution. Pleydellia is common in the uppermost Toarcian of Europe, South America and North America.

Pleydellia maudensis sp. nov.

Plate 1, figures 1–2; Plate 2, figures 1–2, 11–12; Text-figure 15A

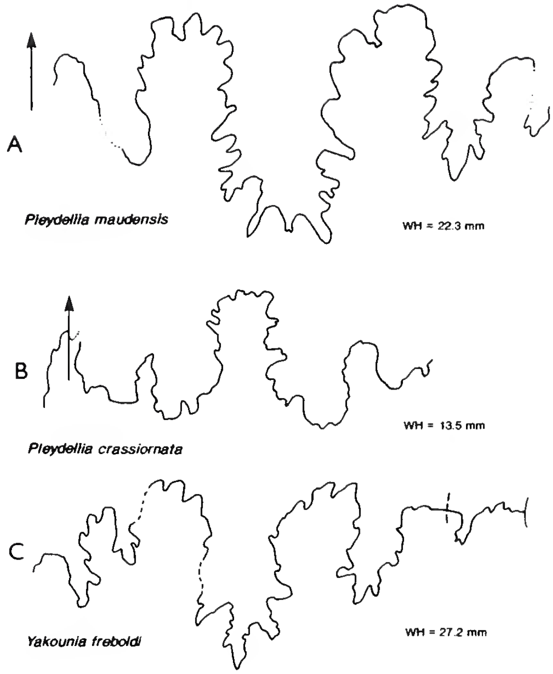
1981 *Haugia* cf. *compressa* Buckman; Imlay, p. 43, pl. 12, figs 3, 7, 9.
1981 *Haugia* cf. *grandis* Buckman; Imlay, p. 42, pl. 12, figs 4, 10, 15.
1981 *Brodieia* cf. *B. tenuicostata* var. *nodosa* Jaworski; Imlay, p. 42, pl. 12, fig. 8.
v 1987 ?Grammoceratinae gen. et sp. indet., Hall, p. 1702, pl. 5, figs A–J, P, W.
1991 *Phlyseogrammoceras* (?) sp., Tipper *et al.*, pl. 7, fig. 3.
1992 *Haugia* cf. *compressa* Buckman; Hillebrandt and Smith, pl. 4, fig. 7.
1992 ?*Haugia* sp. indet., Hillebrandt and Smith, pl. 7, fig. 5.

Derivation of name. After Maude Island in Skidegate Inlet, site of some of the first discoveries of Jurassic fossils in the Queen Charlotte Islands.

Material. About 150 specimens in sandstones and calcareous concretions of the Phantom Creek Formation, Queen Charlotte Islands (Section 1, locs 3, 5, 17; Section 2, locs 3, 7, 9, 12, 17; Section 3, locs 89–92, 94–95, 97–98; Section 4, locs 1–3, 5–6, 8–10, 14; Section 5, locs 2–3, 5; Section 6, locs 1–2). Other specimens from the Upper Toarcian of the Talkeetna Mountains (Text-fig. 2, Collection 2), Puale Bay (Collection 10), the Iskut area (Collections 18–19), the Spatsizi area (Collections 21–22), the Hazelton area (Collection 36), the Manson River area (Collection 38), and the southern Canadian Rocky Mountains (Collections 45–46, 48).

Holotype. GSC 99523 (Pl. 2, figs 11–12) from the lower part of the Phantom Creek Formation (Yakounensis Zone), Yakoun River, Queen Charlotte Islands.

Paratypes. GSC 99519 (Pl. 2, figs 1–2), GSC 99524 (Pl. 1, figs 1–2), GSC 99509, GSC 107267–107277.



TEXT-FIG. 15. Septal suture lines of *Pleydellia maudensis*, *Pleydellia crassiornata* and *Yakounia freboldi* from the Queen Charlotte Islands. A, GSC 99519; Section 4, loc. 14; B, GSC 107347; Section 3, loc. 95; C GSC 107286, Section 4, loc. 4. WH, whorl height.

Measurements.	D	UD	U	WH	WW	WWHH	PRHW
GSC 99523	112·2	40·0	35·7	42·1	23·0	0·55	14
GSC 99523	93·7	31·0	33·1	35·0	24·9	0·71	—
GSC 99523	81·8	24·7	30·2	32·0	19·1	0·60	*c.* 16
GSC 99519	98·5	28·9	29·3	40·0	21·4	0·54	*c.* 15
GSC 99519	79·4	22·0	27·7	34·1	19·7	0·58	14
GSC 99519	75·0	20·1	26·8	31·8	—	—	13
GSC 99524	153·0	57·9	37·8	—	—	—	—
GSC 99524	124·0	38·0	30·6	—	—	—	—
GSC 107267	—	—	—	8·3	6·2	0·75	—
GSC 107268	58·5	22·1	37·8	21·6	14·8	0·69	16
GSC 107268	46·1	17·0	36·9	17·0	10·9	0·64	11
GSC 107269	42·9	11·1	25·9	18·4	—	—	—
GSC 107269	37·5	10·0	26·7	—	—	—	—
GSC 107269	34·0	9·0	26·5	15·0	—	—	12
GSC 107270	98·9	32·7	33·1	—	—	—	17
GSC 107271	71·8	22·0	30·6	29·8	18·1	0·61	11
GSC 107271	56·5	17·1	30·3	24·0	14·5	0·60	12
GSC 107272	47·5	12·5	26·3	20·7	10·7	0·52	13
GSC 107273	79·3	25·4	32·0	32·1	—	—	15
GSC 107273	63·7	21·1	33·1	25·1	—	—	15
GSC 107273	58·5	20·0	34·2	22·6	—	—	*c.* 13
GSC 107274	87·4	29·0	33·2	36·0	—	—	15
GSC 107275	64·7	20·3	31·4	25·2	19·0	0·75	11
GSC 107275	55·2	16·4	29·7	—	—	—	10
GSC 107276	91·1	28·1	30·8	36·2	21·0	0·58	13
GSC 107276	67·3	19·0	28·2	28·4	15·8	0·56	12
GSC 107277	82·6	21·7	26·3	36·1	—	—	13

Diagnosis. Moderately evolute shell; ogival whorl section and flat flanks; umbilical wall gently sloping, becoming undercut on outer whorls; umbilical shoulder gently rounded becoming sharp on outer whorls; venter carinate-sulcate; lateral sulci fade during ontogeny; ribbing sinuous. On inner whorls, primary ribs bifurcate at about one-third flank height. On outer whorls, ribs arise singly and in pairs from small tubercles at umbilical shoulder. Ribs weaken on upper flank. Some ribs bifurcate on upper flank or intercalatory ribs may appear. Ribs terminate at ventro-lateral shoulder.

Description. The holotype, GSC 99523, is a moderately well preserved specimen, septate up to 77·4 mm shell diameter with approximately 190° of body chamber, ending in an incomplete aperture at 111·4 mm shell diameter. One side is slightly distorted. The shell is moderately evolute with an ogival whorl section, flat flanks, and a carinate-sulcate venter. The umbilical wall is gently sloping on the inner whorls becoming steeper with age until, at approximately 82 mm shell diameter, it becomes slightly undercut. The umbilical shoulder is gently rounded on the inner whorls, becoming angular as the umbilical wall steepens. The venter possesses shallow lateral sulci which fade on the outer whorls. On the inner whorls, the primary ribs are slightly prorsiradiate. On the outer whorls, the primary ribs arise from small tubercles at the umbilical shoulder and have a more pronounced prorsiradiate trend. The primary ribs are stronger than the secondary ribs which appear at approximately mid-flank. The paratype, GSC 99519, is a moderately well preserved specimen, septate to 77·1 mm shell diameter with approximately 130° of body chamber, ending in an incomplete aperture at 100·4 mm shell diameter. The phragmocone is damaged on one side and is partially obscured by encrusting bivalves. The body chamber is partially crushed. This specimen illustrates the ribbing on the outer whorls of the phragmocone. From the umbilical tubercles, a primary rib proceeds across the flank and bifurcates at approximately one-quarter to one-third the flank height. At approximately two-thirds to three-quarters the flank height, the ribs may bifurcate again or weak intercalatory ribs may arise. The ribbing fades on the body chamber. The paratype, GSC 99524, is a larger specimen, albeit less well preserved. It is septate to 121·7 mm shell diameter with approximately 190° of body chamber ending in an incomplete aperture at 165 mm shell diameter. One side is poorly preserved and partially obscured by encrusting bivalves. The body chamber is fragmented and parts of the venter have been eroded or broken away. The phragmocone lacks fine detail because of the medium-grained sandstone that forms the matrix. This specimen, whilst having faint ribbing on the outer whorls, maintains the tubercles at the umbilical shoulder and these do not fade but remain prominent. Of the other paratypes, one specimen (GSC 107268) differs slightly in that it is slightly more evolute and has more pronounced umbilical tubercles from which three ribs commonly arise. Two other specimens (GSC 99509 and GSC 107267) are fragments of inner whorls. Both show strong primary ribs which bifurcate at mid-flank. The venter is more strongly carinate-sulcate than on the larger specimens.

Remarks. This form is similar to several Late Toarcian genera including *Pseudolillia*, *Gruneria*, *Phlyseogrammoceras*, as well as *Pleydellia*. The whorl shape and rib pattern on the outer whorls are similar to species of *Pseudolillia* figured by Elmi and Rulleau (1987) but the inner whorls are different. Ribbing on the inner whorls of *Pseudolillia* is much denser and finer, and the ribs tend to bundle or remain single rather than bifurcating as markedly as in *Pleydellia maudensis*. In addition, *Pseudolillia* lacks the small umbilical swellings characteristic of the North American species. *Gruneria* has a similar ribbing pattern in which the primary ribs on the inner whorls bifurcate on the lower to mid-flank; however, the whorl shape is more rounded and ellipsoidal, the ribs are finer and denser, and the outer whorls lack the small umbilical swellings that characterize *Pl. maudensis*. *Phlyseogrammoceras* has a similar ribbing pattern, and a steep to undercut umbilical wall on the outer whorls, but the whorl section is more compressed and the venter is sharper, lacking the ventral sulci of *Pl. maudensis*. Hillebrandt (1987) figured several specimens which he assigned to *Phlyseogrammoceras* (?) *tenuicostatum*, a form similar to the North American species but with a more involute shell. Hall (1987) described specimens from the Fernie Formation (?Grammoceratinae gen. et sp. indet.) which he compared with species of *Pleydellia* such as *Pl. fluitans* (Dumortier, 1874)

EXPLANATION OF PLATE 1

Figs 1–2. *Pleydellia maudensis* sp. nov.; GSC 99524, paratype; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-87111, Section 3, loc. 89; × 1.

PLATE 1

JAKOBS and SMITH, *Pleydellia maudensis* and *Pl. lotharingica*. *Pl. fluitans* has coarse, distant, rectiradiate ribs and a bisulcate venter, whereas *Pl. lotharingica* has a narrow venter and an ogival whorl section (Knitter and Ohmert 1983, pl. 3, figs 12–14). Hillebrandt (1987, pl. 13, fig. 7, pl. 14, fig. 8) figured several specimens of *Pl.* cf. *lotharingica* which have a bisulcate venter on the inner whorls and a similar ribbing pattern, but lack the undercut umbilical shoulder and umbilical swellings on the outer whorls that characterize *Pl. mandensis*. The North American form has a strong carinate-sulcate inner whorl and subdued umbilical swellings that are significantly different from other *Pleydellia*, and a new species designation is warranted.

Pleydellia crassiornata sp. nov.

Plate 3, figures 1–8; Text-figure 15B

Derivation of name. The name refers to the thick ornamentation (Latin *crassus*, thick; *ornatus*, ornament).

Material. About 24 well preserved specimens in sandstones and calcareous concretions of the Phantom Creek Formation (Section 1, locs 5, 17; Section 2, locs 4, 17; Section 3, locs 90, 95; Section 4, locs 6, 14), Queen Charlotte Islands.

Holotype. GSC 99513 (Pl. 3, figs 7–8) from the lower part of the Phantom Creek Formation (middle Yakounensis Zone), Yakoun River, Queen Charlotte Islands.

Paratypes. GSC 99510 (Pl. 3, figs 1–2), GSC 99511 (Pl. 3, figs 3–4), GSC 99512 (Pl. 3, figs 5–6), GSC 107278–107279

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 99513	48·7	19·4	39·8	—	—	—	—
GSC 99513	38·7	14·5	37·5	—	—	—	9
GSC 99513	—	10·8	—	9·6	7·4	0·77	9
GSC 99511	46·3	15·6	33·7	17·1	9·0	0·53	—
GSC 99511	40·0	12·4	31·0	16·1	9·5	0·59	—
GSC 99511	35·9	11·1	30·9	15·0	8·9	0·59	—
GSC 107278	—	20·3	—	18·1	12·7	0·70	13
GSC 107278	34·5	10·8	31·3	14·0	10·0	0·71	10
GSC 107278	28·3	10·0	35·3	11·5	8·8	0·77	—
GSC 107279	58·3	26·2	44·9	16·5	13·6	0·82	12
GSC 107279	53·1	21·3	40·1	17·2	11·6	0·67	11
GSC 107279	48·3	18·5	38·3	14·1	10·9	0·77	11

EXPLANATION OF PLATE 2

Figs 1–2, 11–12. *Pleydellia mandensis* sp. nov.; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 1–2, GSC 99519, paratype; GSC Loc. No. C-176555, Section 4, loc. 14. 11–12, GSC 99523, holotype; GSC Loc. no. C-87118, Section 3, loc. 95.

Figs 3–7. *Dumortieria? phantasma* sp. nov.; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 3–4, GSC 99520, holotype; GSC Loc. No. C-87220, Section 2, loc. 4. 5–6, GSC 99521, paratype; GSC Loc. No. C-93576, Section 2, loc. 4. 7, GSC 99522, paratype; GSC Loc. No. C-87220, Section 2, loc. 4.

Figs 8, 15–16. *Dumortieria?* cf. *pusilla* Jaworski; Yakounensis Zone, Warm Springs Member of the Snowshoe Formation; Izee area, eastern Oregon. 8, UBC 014; UBC Loc. No. F4-4-E, Section 7, loc. 5. 15, UBC 015; UBC Loc. No. F4-4-E, Section 7, loc. 5. 16, UBC 016; UBC Loc. No. F5-1-4, Collection 52.

Figs 9–10, 13–14. *Dumortieria pusilla* Jaworski; Arroyo Negro Argentina, Locality 22, Section 9, Horizon 6 of Jaworski (1926). 9–10, plaster cast of the paratype. 13–14, plaster cast of the holotype.

Arrows mark start of body chamber. All are × 1.

PLATE 2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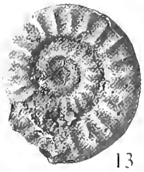
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JAKOBS and SMITH, *Pleydellia* and *Dumortieria*

Diagnosis. Moderately evolute shell; ogival whorl section; umbilical wall gently sloping, becoming steeper during ontogeny; umbilical shoulder gently rounded, becoming more angular during ontogeny; flanks slightly convex; venter carinate with weak lateral sulci on inner whorls; ribbing sinuous; thick, prominent primary ribs split into two or three weaker, secondary ribs at approximately one-third to one-half flank height; secondary ribs terminate at ventro-lateral shoulder; some variation in length of primary ribs.

Description. The holotype, GSC 99513, is a moderately well preserved specimen septate to 13·1 mm umbilical diameter with approximately 180° of body chamber ending in an incomplete aperture at 49·0 mm shell diameter. The body chamber is broken and slightly crushed. The shell is moderately evolute with an ogival whorl section. The umbilical wall is gently sloping and the umbilical shoulder is rounded. The flanks are gently convex and merge into the venter with only weak ventro-lateral shoulders. The venter is carinate, bounded by narrow, smooth strips. The ornament consists of sinuous ribs. The coarse primary ribs arise high on the umbilical wall. On the inner whorls, they are short and appear bullate. The primary ribs split into two or three weaker secondary ribs at approximately one-third to one-half the flank height. The secondary ribs terminate at the ventro-lateral shoulder. The paratype, GSC 99511, is a well preserved specimen septate to 43·1 mm shell diameter with approximately 70° of body chamber ending in an incomplete aperture at 47·5 mm shell diameter. The body chamber is slightly crushed. The shell is moderately evolute with an ogival whorl section and possesses similar shell characteristics to the holotype. The ornament differs slightly by being slightly more subdued, and the primary ribs are longer on the inner whorls and not as bullate. The paratype, GSC 99512, is a moderately well preserved shell, septate to 16·6 mm umbilical diameter with approximately 110° of body chamber ending in an incomplete aperture. Most of the venter on the outer whorl of the phragmocone has been eroded away. This specimen is similar to the previous two but has slightly longer primary ribs on the inner whorls than the holotype. The paratype, GSC 99510, is a moderately well preserved shell with approximately 180° of body chamber. The shell is fragmented and distorted with portions of the phragmocone broken away. This specimen is one of the largest, with a maximum shell diameter of approximately 66 mm. It possesses a similar ribbing pattern to the two previous paratypes. The ornament does not fade on the body chamber. The paratype, GSC 107279, is a well preserved specimen septate to 25·0 mm umbilical diameter and with approximately 190° of body chamber ending in an incomplete aperture. The primary ribs on the inner whorls, while not as bullate as the holotype, are shorter than in the other paratypes. The paratype, GSC 107278, is a moderately well preserved specimen with approximately 180° of body chamber ending in an incomplete aperture. Part of the venter on the body chamber is broken away. It is a smaller specimen than the others, and the whorl section is slightly more depressed. The ornament is similar to the other paratypes.

EXPLANATION OF PLATE 3

Figs 1–8. *Pleydellia crassiornata* sp. nov.; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 1–2, GSC 99510, paratype; GSC Loc. No. C-87118, Section 3, loc. 95. 3–4, GSC 99511, paratype; GSC Loc. No. C-87221, Section 2, loc. 17. 5–6, GSC 99512, paratype; GSC Loc. No. C-176555, Section 4, loc. 14. 7–8, GSC 99513, holotype; GSC Loc. No. C-87118, Section 3, loc. 95.

Figs 9–14. *Pleydellia aalensis* (Zieten); Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 9–10, GSC 99514; GSC Loc. No. C-87107, Section 3, loc. 95. 11–12, GSC 99515; GSC Loc. No. C-87233, Section 1, loc. 17. 13–14, GSC 99516; GSC Loc. No. C-87233, Section 1, loc. 17.

Fig. 15. *Dumortieria* cf. *exacta* Buckman; UBC 010; Yakounensis Zone, Warm Springs Member of the Snowshoe Formation; Izee area, eastern Oregon, UBC Loc. No. F4-4-E, Section 7, loc. 5.

Fig. 16. *Dumortieria* cf. *dumortieri* (Thiollière); UBC 011; Yakounensis Zone, Warm Springs Member of the Snowshoe Formation; Izee area, eastern Oregon, UBC Loc. No. F4-4-F, Section 7, loc. 6.

Fig. 17. *Dumortieria insignisimilis* (Brauns); UBC 012; Yakounensis Zone, Warm Springs Member of the Snowshoe Formation; Izee area, eastern Oregon, UBC Loc. No. F4-4-E, Section 7, loc. 5.

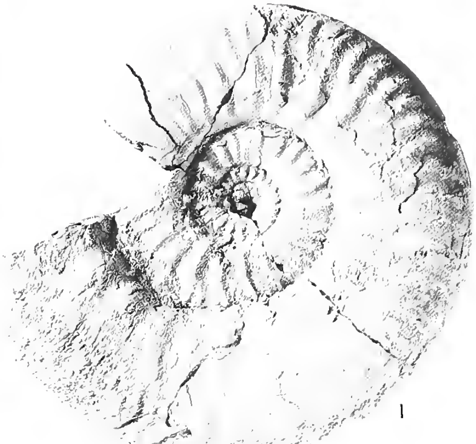
Fig. 18. *Dumortieria*? cf. *pusilla* Jaworski; GSC 99517; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-157740, Section 3, loc. 97.

Fig. 19. *Dumortieria insignisimilis* (Brauns); GSC 99518; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-81736, Section 5, loc. 5.

Fig. 20. *Dumortieria raricostata* Géczy; UBC 013; Yakounensis Zone, Warm Springs Member of the Snowshoe Formation; Izee area, eastern Oregon, UBC Loc. No. F4-3-D, Section 7, loc. 4.

Arrows mark start of body chamber. All are × 1.

PLATE 3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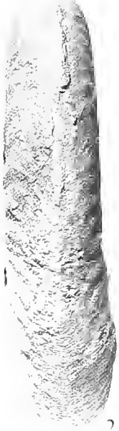
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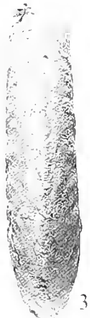
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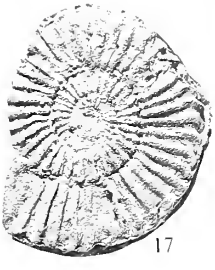
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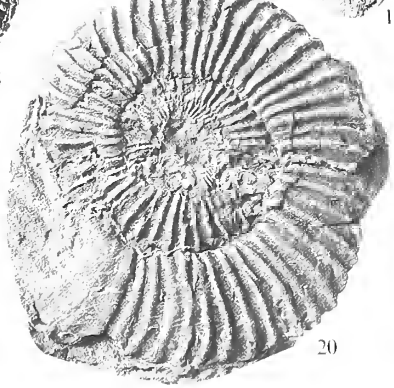
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JAKOBS and SMITH, *Pleydellia* and *Dumortieria*

Remarks. The shell shape and whorl section are similar to those of *Pleydellia aalensis* as figured by Schlegelmilch (1976, pl. 51, figs 8–9). *Pl. aalensis* encompasses a broad variety of forms and shows wide morphological variability. In general, the style of joined ribs distinguishes *Pl. aalensis* from other species of *Pleydellia* (Buckman 1890, p. 193), some of which have joined ribs but these tend to be fine and bundled, e.g. *Pl. subcompta* (Branco, 1879). The specimens of *Pl. aalensis* illustrated by Buckman (1890, pl. 32, figs 4–10) differ from *Pl. crassiornata* by lacking swollen primaries, by being slightly more involute, and by having a steeper umbilical wall. Géczy (1967) figured several forms of *Pl. aalensis*, creating several new subspecies that are similar to *Pl. crassiornata* but which lack the prominent and pervasive bifurcation and swollen primaries that characterize the North American species. *Pleydellia* from North America that have bifurcate and widely spaced ribbing show some differences in the coarseness of the primary ribs, but this may be intra-specific variation and is probably not sufficient to justify the recognition of two separate species.

Pleydellia crassiornata also shows similarity to the Leioceratinae which, according to Donovan *et al.* (1981, p. 115), evolved from *Pleydellia* during the early Aalenian. Schlegelmilch (1985) figured some species of *Leioceras* and *Staufenia* (pls 9–11) which are similar to *Pl. crassiornata. Leioceras* and *Staufenia* have acute venters and simple septal sutures.

Pleydellia aalensis (Zieten, 1832)

Plate 3, figures 9–14

*1832	*Ammonites aalensis* Zieten, pl. 28, fig. 3.
1890	*Grammoceras aalense* (Zieten); Buckman, p. 192, pl. 32, figs 7–8.
1976	*Pleydellia aalensis* (Zieten); Schlegelmilch, p. 94, pl. 51, figs 8–9.
1983	*Pleydellia aalensis* (Zieten); Knitter and Ohmert, pl. 3, figs 2–3.
1990	*Pleydellia aalensis* (Zieten); Goy and Martínez, pl. 4, fig. 10.

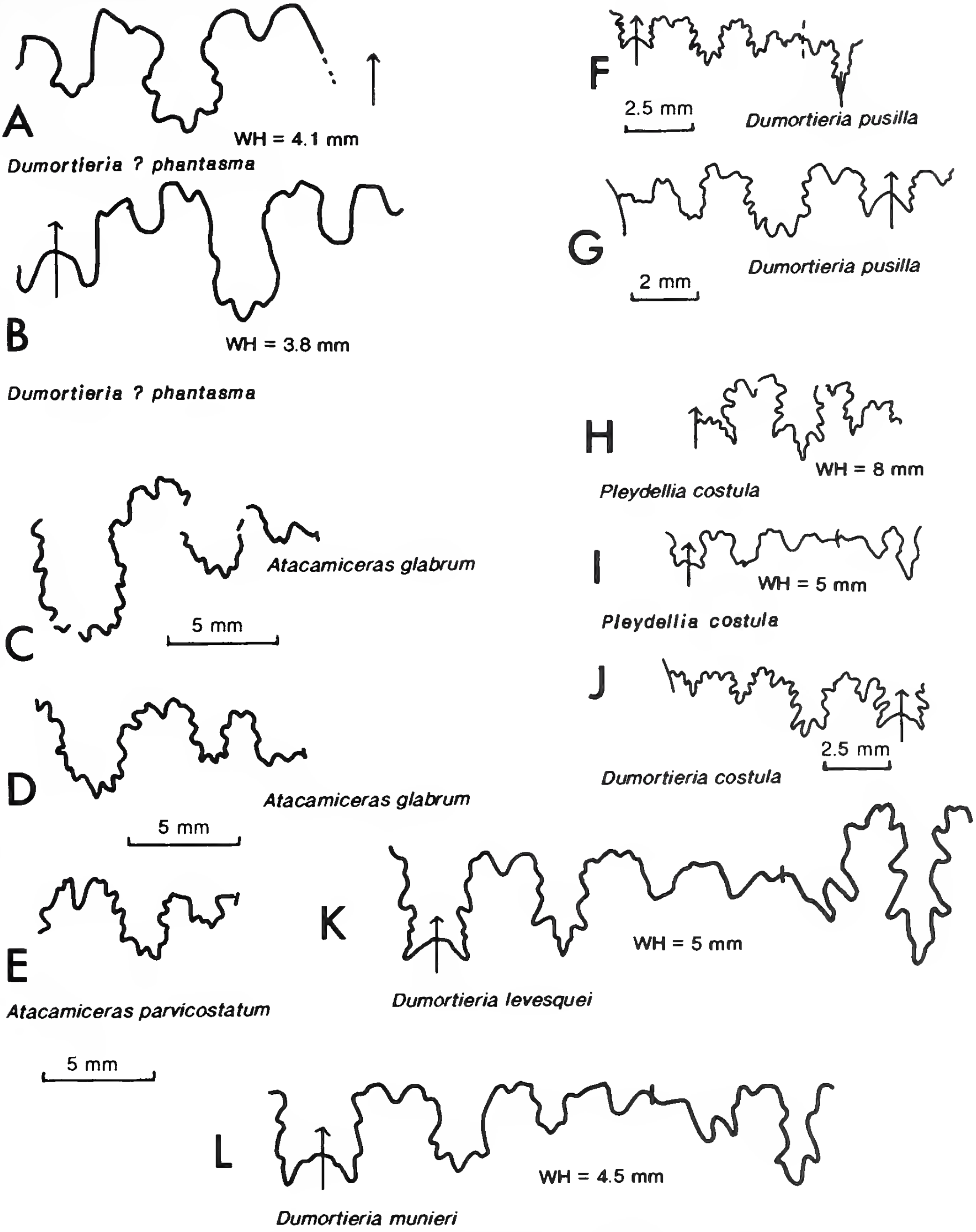
Material. 20 specimens in the sandstones and calcareous concretions of the Phantom Creek Formation, Queen Charlotte Islands (Section 1, loc. 17; Section 2, loc. 17; Section 3, locs 89, 95).

Measurements.	D	UD	U	WH	WW	WWHH	PRHW
GSC 99514	30·5	10·6	34·8	11·5	7·6	0·66	10
GSC 99515	24·7	7·5	30·4	10·4	6·7	0·64	8
GSC 99516	38·8	13·5	34·8	14·2	—	—	—
GSC 107280	19·0	6·7	35·3	7·3	5·0	0·68	7

Description. The moderately evolute shell has a high oval whorl section and shallow umbilicus. The umbilical wall and shoulder are gently sloping. Flanks are gently convex and merge into the venter with weak ventro-lateral shoulders. The venter is carinate. Ribbing density and strength vary. Primary ribs are slightly prorsiradiate to approximately one-third the flank height where, generally, they bifurcate. Secondary ribs are rectiradiate to the ventro-lateral shoulders, then become prorsiradiate and approach, but do not reach, the venter. Intercalatory ribs are common.

Remarks. Théobald and Moine (1959) studied *Pl. aalensis* in an attempt to define this variable species more clearly. They concluded that *Pl. aalensis* could be defined as possessing simple ribs that commonly bifurcate near the umbilical shoulder. The ribs are falciform, rounded and fade toward the venter. The whorl section is oval and the flanks are slightly flattened. The U value averages 31·5 but can range from 27 to 36, and WWWH averages 0·58, but can range from 0·50 to 0·66. Two varieties can be distinguished by ribbing density, a coarsely ribbed *aalensis* type and a densely ribbed *tenuicostata* type.

The North American specimens fall within the range of variability of *Pl. aalensis*, although the ribs tend to bifurcate higher on the flanks than in the holotype. However, the specimen figured by Schlegelmilch (1976, pl. 51, fig. 9) has ribs that bifurcate near mid-flank. *Pl. fluens* (Buckman, 1890) has much finer and dense ribbing. *Pl. subcompta* has fine, dense ribbing which bundles in threes or fives at the umbilical shoulder. *Pl. crassiornata* has a coarser ornament and swollen primary ribs.



TEXT-FIG. 16. Septal suture lines of *Dumortiera*, *Dumortieria*?, *Pleydellia* and *Atacamiceras*. A, GSC 107345; Section 2, loc. 4, Queen Charlotte Islands; B, GSC 107346; Section 2, loc. 4, Queen Charlotte Islands; C, Hillebrandt (1987, pl. 8, fig. 2; text-fig. 2*a*); D, Hillebrandt (1987, pl. 8, fig. 16; text-fig. 2*b*); E, Hillebrandt (1987, pl. 8, fig. 17; text-fig. 2*c*); F, Jaworski (1926, pl. 4, fig. 17); G, Jaworski (1926, pl. 4, fig. 22); H, Schlegelmilch (1976, p. 94); I, Schlegelmilch (1976, p. 94); J, Jaworski (1926, pl. 4, fig. 19); K, Schindewolf (1964, p. 293, text-fig. 178); L, Schindewolf (1964, p. 295, text-fig. 179). WH, whorl height.

Distribution. *Pleydellia aalensis* is common in the Upper Toarcian Aalensis Zone of Europe (Fischer 1966; Géczy 1967; Goy and Martínez 1990).

Genus DUMORTIERIA Haug, 1885
[= *Catulloceras* Buckman, 1925; *Dactyliogammites* Buckman, 1925; *Phenakoceras* Maubeuge, 1949 (*non* Frech, 1902); *Phenakocerites* Maubeuge, 1950]

Type species. *Ammonites levesquei* d'Orbigny, 1844 (subsequent designation by Buckman 1890).

Diagnosis. Moderately evolute planulates with ogival whorl sections; umbilical shoulder abrupt to moderately rounded; venter carinate; ribbing almost rectiradiate, becoming slightly prorsiradiate on upper flanks, terminating at venter; ribbing sparse or dense.

Distribution. *Dumortieria* is found almost world-wide in the Late Toarcian correlatives of the Levesquei Zone (Donovan *et al*. 1981).

Dumortieria insignisimilis (Brauns, 1865)

Plate 3, figures 17, 19

1865	*Ammonites insigni similis* Brauns, p. 106, pl. 5, figs 5–7.
1923	*Dumortieria insignisimilis* (Brauns); Ernst, p. 56, pl. 9, figs 1–3.
1967	*Dumortieria insignisimilis* (Brauns); Géczy, p. 144, pl. 31, fig. 6.
1993	*Dumortieria* cf. *insignisimilis* (Brauns); Arthur *et al*., p. 32, pl. 1, figs 11–15.

Material. Five specimens from eastern Oregon (Section 7, loc. 5) where the species is best represented. Poorly preserved specimens from the Queen Charlotte Islands (Section 5, loc. 5) and from Harrison Lake (Arthur *et al*. 1993; Text-fig. 2; Collections 42–43).

Description. The evolute shell bears a low rounded keel. The ribs are wiry and widely spaced, reaching a density of up to 20 per half whorl at umbilical diameters greater than 10 mm. The ribs are rectiradiate across the flank and project onto the venter where they abut directly against the keel.

Remarks. This species is more evolute and less densely ribbed than *D. exacta* Buckman, 1905. *D*. cf. *dumortieri* Thiollière *in* Dumortier, 1874 is more evolute and slowly expanding, and its ribs are more densely spaced and projecting. *D. raricostata* Géczy, 1967 has less rectiradiate, more projecting ribbing.

Distribution. In Europe, *Dumortieria insignisimilis* is known from the Upper Toarcian of Germany (Ernst 1923), Austria (Fisher 1966), Hungary (Géczy 1967) and possibly Spain (de Villalta and Rosell 1966).

Dumortieria cf. *dumortieri* (Thiollière *in* Dumortier, 1874)

Plate 3, figure 16

cf. 1874	*Ammonites dumortieri* Thiollière *in* Dumortier; figured by Roman 1938, p. 105, pl. 9, fig. 96; and Arkell *et al*. 1957, p. 262, fig. 296.
cf. 1892	*Catulloceras dumortieri* (Thiollière); Buckman, p. 277, pl. 39, figs 6–9.
cf. 1964*a*	*Catulloceras*? sp. indet.; Frebold, p. 16, pl. 7, figs 5–9.
cf. 1967	*Dumortieria dumortieri* (Thiollière *in* Dumortier); Géczy, p. 137, pl. 30, fig. 8.
1968	*Catulloceras* cf. *C. dumortieri* (Thiollière); Imlay, p. 46, pl. 9, figs 2–4 only.
cf. 1968	*Dumortieria dumortieri* (Thiollière *in* Dumortier); Setti, p. 329, pl. 30, fig. 3; pl. 31, fig. 1.
cf. 1975	*Catulloceras dumortieri* (Thiollière); Guex, p. 115, pl. 7, fig. 1.

Material. Three small and poorly preserved specimens from east-central Oregon (Section 7, locs 5–6). According to Imlay (1968), it is also present in the Bennett area, northern British Columbia (Text-fig. 2; Collections 16–17).

Description. The evolute shell expands slowly and has convex flanks. The ribbing is sharp, dense, rectiradiate, and only weakly projecting onto the venter.

Remarks. These specimens cannot be identified with confidence because of their small size and poor preservation. They are evolute and finely ribbed but not as markedly as, for example, *D. evolutissima* (Prinz, 1904), and we prefer to compare them with *D. dumortieri* which Imlay (1968) has already reported from Oregon on the basis of larger specimens.

Distribution. Dumortieria dumortieri is widely distributed in the Upper Toarcian of Europe: in Italy from the Meneghinii Zone (Donovan 1958), in Austria from the Aalensis Subzone of the Levesquei Zone (Fischer 1966), and in France from the Levesquei Subzone of the Pseudoradiosa Zone (Guex 1975; Elmi and Rulleau 1991).

Dumortieria cf. *exacta* Buckman, 1905

Plate 3, figure 15

cf. 1892	*Dumortieria subundulata* Buckman, pl. 45, figs 6–7 only.
cf. 1905	*Dumortieria exacta* Buckman, supplement, p. 187.

Material. A single specimen preserved in a siltstone of the Snowshoe Formation, east-central Oregon (Section 7, loc. 5).

Description. A small, moderately evolute specimen (U = 40) bearing a low keel. The ribs are sharp and slightly flexuous on early whorls. Ribbing density increases from 21 ribs per half whorl at an umbilical diameter of 6 mm to 29 at 11 mm.

Remarks. As far as the preservation permits comparison, this specimen is similar to a variant of *Dumortieria subundulata* (Buckman, 1892, pl. 45, figs 6–7) that Buckman (1905) elevated to the rank of species and named *D. exacta.* It differs from all other species of *Dumortieria* described from North America by its densely spaced, fine ribbing which is characteristic of the *pseudoradiosa* group of species, as described by Ernst (1923).

Dumorteria raricostata Géczy, 1967

Plate 3, figures 20–21

1967	*Dumortieria stefaninii ? raricostata* n. subsp. Géczy, p. 142, pl. 31, fig. 8.
1968	*Dumortieria raricostata* Geczy; Setti, p. 332, pl. 32, fig. 3.
?1968	*Catulloceras* cf. *C. dumortieri* (Thiollière); Imlay, p. 46, pl. 9, fig. 5 only.

Material. Three specimens, two of them fragments, preserved in a siltstone of the Snowshoe Formation, east-central Oregon (Section 7, loc. 4).

Description. The shell is evolute, secondarily compressed and bears a low rounded keel. The coarse ribs project onto the venter from the uppermost part of the flank; there are 26 ribs on the outer half whorl. Weak constrictions are evident and the figured specimen bears an 8 mm wide collar that shows faint growth lines and a constricted peristome.

Remarks. The figured specimen represents a mature individual, presumably a macroconch although its microconch is unknown. One specimen of *D. raricostata* is known from the Upper Toarcian of Hungary (Géczy 1967) and two from Italy (Setti 1968), but none show evidence of maturity in spite of reaching larger shell diameters than the Oregon specimen.

Dumortieria? *phantasma* sp. nov.

Plate 2, figures 3–7; Text-figure 16A–B

Derivation of name. After Phantom Creek in central Graham Island, Queen Charlotte Islands.

Material. 50 small casts in calcareous concretions and several flattened specimens in shales and siltstones of the Phantom Creek Formation, Queen Charlotte Islands (Section 2, locs 3–5). Also specimens from the Manson River area (Text-fig. 2; Collection 38) and the southern Canadian Rocky Mountains (Collection 45).

Holotype. GSC 99520 (Pl. 2, figs 3–4) from the lower part of the Phantom Creek Formation (Yakounensis Zone), Yakoun River, Queen Charlotte Islands.

Paratypes. GSC 99521 (Pl. 2, figs 5–6), GSC 99522 (Pl. 2, fig. 7)

Measurements.	D	UD	U	WH	WW	WWWH
GSC 99520	23·3	8·4	36·1	8·7	6·1	0·70
GSC 99521	18·6	7·5	40·3	6·5	4·6	0·71
GSC 99522	16·9	8·0	47·3	5·2	3·8	0·73

Diagnosis. Compressed, moderately evolute shell; elliptical whorl section; umbilical wall gently sloping; umbilical shoulder gently rounded; flanks gently convex, converging toward sharp venter; ornament generally weak or absent. On outer whorls of some specimens, there are simple, distant, rectiradiate ribs which fade on outer part of flank.

Description. The holotype, GSC 99520, is a moderately well preserved specimen, septate to 23·1 mm shell diameter with approximately 130° of body chamber ending in an incomplete aperture. The body chamber is slightly crushed. The shell is moderately evolute with a compressed, elliptical whorl section. The flanks are gently convex and converge toward the venter. The venter is sharp but plain. Faint, sparse, rectiradiate ribs are present on the last whorl and fade on the upper part of the flank. The holotype is one of the largest specimens collected, and the sutures on the last part of the phragmocone are approximated. The paratype, GSC 99521, is a moderately well preserved specimen, septate to approximately 5 mm umbilical diameter with approximately 180° of body chamber ending in an incomplete aperture. The body chamber is slightly crushed. The shell has similar features to the holotype. Faint, sparse, rectiradiate ribs are present on the body chamber. The paratype, GSC 99522, is a moderately well preserved specimen, septate to 19·2 mm shell diameter with approximately 100° of body chamber ending in an incomplete aperture. The body chamber is partially crushed.

Remarks. This form shows similarities to *Atacamiceras* and *Dumortieria*. Its ornament and septal suture are similar to the South American genus *Atacamiceras* described by Hillebrandt (1987). *Atacamiceras glabrum* Hillebrandt, 1987 is smooth except for rare mid-flank ribs. *A. parvicostatum* Hillebrandt, 1987 has smooth inner whorls and is ribbed on the last part of the phragmocone and on the body chamber. Both *Atacamiceras* and the North American form have simple septal sutures

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EXPLANATION OF PLATE 4

Figs 1–6, 9–10. *Yakounia silvae* gen. et sp. nov.; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 1–2, GSC 99525, holotype; GSC Loc. No. C-149652, Section 2, loc. 4. 3–4, GSC 99526, paratype; GSC Loc. No. C-149652, Section 2, loc. 4. 5–6, GSC 99527, paratype; GSC Loc. No. C-149652, Section 2, loc. 4. 9–10, GSC 99528, paratype; GSC Loc. No. C-149652, Section 2, loc. 4.

Figs 7–8, 11–14. *Yakounia yakounensis* gen. et sp. nov.; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 7–8, GSC 99529, paratype; GSC Loc. No. C-149652, Section 2, loc. 4. 11–12, GSC 99530, paratype; GSC Loc. No. C-149652, Section 2, loc. 4. 13–14, GSC 99531, holotype; GSC Loc. No. C-149652, Section 2, loc. 4.

Arrows mark start of body chamber. All are × 1.

PLATE 4


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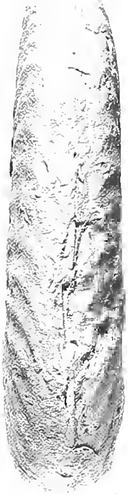
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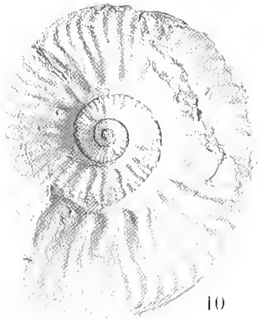
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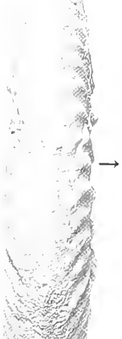
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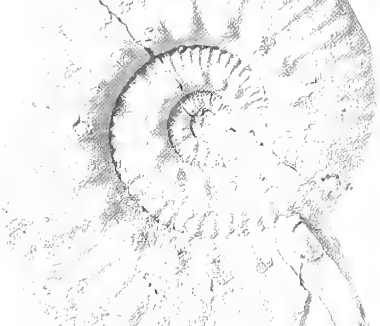
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JAKOBS and SMITH, *Yakounia*

(Text-fig. 16). *Dumortieria*? *phantasma* has a more compressed shell whereas *Atacamiceras* has convex flanks. In addition, *Atacamiceras* occurs in the Middle Toarcian of South America whereas the North American form occurs in the latest Toarcian. *Dumortieria*? *phantasma* is also similar to *D. pusilla* which has smooth internal whorls with distant, simple, rectiradiate ribs on the outer whorls (see below). *D. pusilla*, however, has prominent ribbing and achieves it at an earlier stage of development. *D.*? phantasma could be an offshoot of *D. pusilla* via neoteny. The paratype, GSC 99521, displays prominent simple ribs toward the end of the shell, and is similar to the early stages of *D. pusilla*. In addition, the simple septal sutures of *D.*? *phantasma* could represent the early sutures of *D. pusilla*.

Dumortieria? cf. *pusilla* Jaworski, 1926

Plate 2, figures 8, 15–16; Plate 3, figure 18

Material. 75 specimens from limestones, mudstones and siltstones of the Snowshoe Formation, east-central Oregon (Section 7, locs 4–5; Section 8, loc. 1), where the species is best represented. Rare and poorly preserved specimens from the Queen Charlotte Islands (Text-fig. 2; Section 3, loc. 97) and the Spatsizi area (Collection 28).

Description. The shell is moderately evolute bearing a weak keel. The ribbing is distant and simple. The ribs are rectiradiate on the flanks and project onto the venter where they fade. The inner whorls are smooth.

Discussion. *Dumortieria pusilla* was originally described from Argentina by Jaworski (1926) where it occurs in the South American '*Pleydellia fluitans*' Zone, a correlative of the upper Aalensis Subzone of the European Levesquei Zone, according to Hillebrandt (1987). Plaster copies of Jaworski's (1926) type material are figured in Plate 2, figures 9–10 and 13–14. The species is characterized by its smooth inner whorls, a feature that distinguishes it from other species of *Dumortieria* which, at most, have only a small smooth nucleus.

The generic assignment of *Dumortieria pusilla* is based on the simple, distant ribs which characterize many other *Dumortieria* species, such as *D. levesquei* (d'Orbigny, 1844), *D. insignisimilis* and *D. striatulocostata* (Quenstedt, 1885). No other *Dumortieria*, however, possesses smooth internal whorls to such large shell diameters.

Family PHYMATOCERATIDAE Hyatt, 1867
Subfamily PHYMATOCERATINAE Hyatt, 1900

Genus YAKOUNIA gen. nov.

Derivation of name. After the Yakoun River, central Graham Island, Queen Charlotte Islands where Toarcian outcrops are most abundant.

Type species. *Yakounia yakounensis* sp. nov.

EXPLANATION OF PLATE 5

Figs 1–2. *Yakounia freboldi* gen. et sp. nov.; GSC 99532, holotype; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-156390, Section 1, loc. 17.

Figs 3–6. *Yakounia yakounensis* gen. et sp. nov.; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 3–4, GSC 107258, paratype; GSC Loc. No. C-149652, Section 2, loc. 4. 5–6, GSC 107259, paratype; GSC Loc. No. C-149652, Section 2, loc. 4.

Figs 7–8. *Holcophylloceras calypso* (d'Orbigny); GSC 107260; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-87221, Section 2, loc. 17.

All are × 1.

PLATE 5


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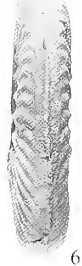
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JAKOBS and SMITH, *Yakounia* and *Holcophylloceras*

Diagnosis. Moderately evolute shell; ogival whorl section; umbilical wall gently sloping; umbilical shoulder rounded; flanks moderately flat, converging toward a carinate venter with weak ventrolateral shoulders. Venter on inner whorls may be weakly carinate-sulcate. Ornament distinctive, consisting of gently sinuous to approximately rectiradiate ribs that arise in twos or threes from strong umbilical tubercles or prorsiradiate bullae.

Remarks. This form can be compared with several genera of the Phymatoceratinae. According to Donovan (1958), *Brodieia* has sigmoidal ribs joined in groups of two or more to umbilical tubercles. *Brodieia* can be differentiated from *Phymatoceras* and *Haugia* by its non-septate keel. *Yakounia* possesses a septate keel, is more evolute, and the umbilical tubercles are more regular and prominent than in *Brodieia*. *Haugia* has a tall keel, and the ribs and tubercles tend to fade on the outer whorls. In addition, the ribs tend to be more rectiradiate. *Yakounia*'s keel is more subdued, the ornament is prominent on the outer whorls, and the ribs are generally more sinuous and project along the venter. *Phymatoceras* is similar, especially such species as *P. copiapense* and *P. hillebrandti*. In general, however, *Yakounia* has stronger tuberculation, shallower sulci, and a more gently rounded umbilical shoulder. *Yakounia*, especially *Y. pacifica* which has a pronounced angular bend of the ribs low on the flanks, may have evolved into *Ludwigia* or some of the Graphoceratidae.

Distribution. The genus is Late Toarcian in age, occurring with *Hammatoceras*, *Dumortieria*, *Sphaerocoeloceras* and *Pleydellia*. It has been collected from the Queen Charlotte Islands, the Fernie area, southern Alaska, and possibly the Spatsizi area.

Yakounia yakounensis sp. nov.

Plate 4, figures 7–8, 11–14; Plate 5, figures 3–6

1976 *Haugia* aff. *H. navis* (Dumortier); Frebold, p. 14, pl. 7, fig. 3.
1981 *Haugia* cf. *variabilis* (d'Orbigny); Imlay, p. 43, pl. 12, figs 1–2, 5.
v 1987 ?Grammoceratinae gen. et sp. indet., Hall, p. 1702, pl. 5, figs N–O.

Derivation of name. After the Yakoun River, central Graham Island, Queen Charlotte Islands where Toarcian outcrops are most abundant.

Material. 60 specimens from calcareous concretions and sandstones of the Phantom Creek Formation, Queen Charlotte Islands where the species is best represented (Section 1, loc. 17; Section 2, locs 3–6, 17; Section 3, locs 89, 105; Section 4, locs 2, 4, 6, 14; Section 5, locs 2, 5). Also specimens from the Talkeetna Mountains (Text-fig. 2; Collections 5, 9), the Spatsizi area (Collections 21, 26), and the southern Canadian Rocky Mountains (Collection 45).

Holotype. GSC 99531 (Pl. 4, figs 13–14) from the lower part of the Phantom Creek Formation (middle Yakounensis Zone), Yakoun River, Queen Charlotte Islands.

Paratypes. GSC 99529 (Pl. 4, figs 7–8), GSC 99530 (Pl. 4, figs 11–12), GSC 107258 (Pl. 5, figs 3–4), GSC 107259 (Pl. 5, figs 5–6), GSC 107281–107283

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 99531	64·0	28·0	43·8	19·6	12·3	0·63	10
GSC 99531	50·4	20·0	39·7	17·7	10·7	0·60	9
GSC 99529	65·8	32·4	49·2	17·7	13·0	0·73	11
GSC 99529	54·0	24·7	45·7	17·0	10·5	0·62	10
GSC 107259	40·5	15·8	39·0	15·0	8·5	0·57	10
GSC 107259	33·8	12·0	35·5	13·0	*c*. 6·6	*c*. 0·51	10
GSC 107281	54·0	22·4	41·5	17·3	11·6	0·67	10
GSC 107282	68·3	34·0	49·8	20·2	14·7	0·73	12
GSC 107282	53·6	25·0	46·6	16·0	11·2	0·70	10
GSC 107283	110·1	47·5	43·1	36·4	20·7	0·57	13

Diagnosis. Moderately evolute shell; ogival whorl section; umbilical wall gently sloping; umbilical shoulder rounded; flanks flat to gently convex; venter carinate-sulcate on inner whorls becoming carinate on outer whorls; ornament distinctive, consisting of sharp umbilical tubercles from which two to three secondary ribs proceed up the flanks with a gently sinuous trend.

Description. The holotype, GSC 99531, is a well preserved specimen, septate to 55·8 mm shell diameter with approximately 90° of body chamber ending in an incomplete aperture at 64·0 mm shell diameter. The specimen is cracked and a small part of the venter is absent. The shell is moderately evolute with a compressed ogival whorl section. The umbilical wall is gently dipping and the umbilical shoulder is rounded. The flanks are flat to slightly convex and converge toward the carinate venter. The ornament consists of sharp, prominent tubercles at the umbilical shoulder from which two to three secondary ribs proceed up the flank with a gently sinuous trend and terminate at the ventro-lateral shoulder. The tubercles are slightly prorsiradiate and are more prominent on the outer whorls. The paratype, GSC 99530, is a moderately well preserved specimen, septate to 24·6 mm umbilical diameter, with approximately 180° of body chamber ending in an incomplete aperture at approximately 52 mm shell diameter. The specimen is broken on one side. The shell is moderately evolute with a compressed, ogival whorl section. The umbilical wall is gently dipping and the umbilical shoulder is rounded. The flanks are flat to gently rounded. The venter is carinate-sulcate on the inner whorls becoming carinate on the outer whorls. The tubercles at the umbilical shoulder are slightly prorsiradiate and give rise to two or three gently sinuous ribs. The paratypes, GSC 99529 and GSC 107259, are moderately well preserved with parts of their body chambers but incomplete apertures. The body chamber of the latter is slightly crushed. The paratype, GSC 107258, is a moderately well preserved specimen with approximately 230° of body chamber ending in an incomplete aperture. The shell is cracked, slightly crushed and part of the nucleus and venter are absent. The shell is moderately evolute with an ogival whorl section. The whorl section is less compressed than in the previous forms and GSC 107282 has a similar shape. The tubercles at the umbilical shoulder are prominent, sharp and slightly prorsiradiate.

Remarks. This species is distinctive and easily recognized because of its prominent, pointed umbilical tubercles and the gently sinuous ribs. Imlay (1981) compared the southern Alaskan specimens to *Haugia variabilis*, but he noted that they were more evolute and more sparsely ribbed on the outer whorls. He also noted that the holotype of *H. japonica* (Neumayr, 1875) as figured by Kobayashi (1935, pl. 12, figs 3–4) had a much weaker ornament. He compared the southern Alaskan speciments to *Haugia* aff. *japonica* figured by Matsumoto and Ono (1947, pl. 2, fig. 5) but that specimen has much weaker tuberculation, that fades on the outer whorl, and sigmoidal ribbing; it is possibly *Phymatoceras hillebrandti*.

Yakounia yakounensis is distinguished from other species by its prominent umbilical tubercles. *Y. freboldi* sp. nov. has thick, distant ribs with prorsiradiate bullae. *Y. pacifica* sp. nov. has a prominent angular flexure of the ribs, and the ribs and tubercles are subdued. *Y. silvae* sp. nov. is an intermediate form which has characteristics of all three. It possesses tubercles similar to *Y. freeboldi*, but the ribbing density is similar to that of *Y. yakounensis*.

Yakounia freboldi sp. nov.

Plate 5, figures 1–2; Text-figure 15c

Derivation of name. After Dr H. Frebold who, for many years, was the Jurassic palaeontologist of the Geological Survey of Canada.

Material. Nine specimens in calcareous concretions and sandstones of the Phantom Creek Formation, Queen Charlotte Islands (Section 1, loc. 17; Section 2, loc. 4; Section 3, loc. 89; Section 4, locs 2, 4, 6; Section 5, locs 2, 5). Also from the southern Canadian Rocky Mountains (Text-fig. 2; Collection 47).

Holotype. GSC 99532 (Pl. 5, figs 1–2) from the lower part of the Phantom Creek Formation (Yakounensis Zone), Yakoun River, Queen Charlotte Islands.

Paratypes. GSC 107284–107287

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 99532	129·4	57·4	44·4	42·4	30·0	0·71	13
GSC 99532	109·0	48·6	44·6	35·8	25·0	0·70	14
GSC 99532	100·3	44·0	43·9	29·9	20·5	0·69	14
GSC 99532	—	31·3	—	25·5	16·2	0·64	11
GSC 107284	86·0	35·6	41·4	28·3	19·2	0·68	10
GSC 107284	65·8	27·0	41·0	23·1	14·5	0·63	10
GSC 107285	98·0	43·3	44·2	31·1	*c.* 19·1	*c.* 0·61	11
GSC 107285	88·4	37·0	41·9	30·7	*c.* 15	*c.* 0·49	11
GSC 107285	78·4	32·7	41·7	19·6	11·7	0·60	8
GSC 107286	81·6	30·5	37·4	28·5	19·5	0·68	11
GSC 107287	49·2	16·7	33·9	19·6	11·7	0·60	8
GSC 107287	43·1	14·4	33·4	17·6	11·2	0·64	8

Diagnosis. Moderately evolute shell; ellipsoidal to rectangular whorl section; venter carinate-sulcate on inner whorls becoming carinate on outer whorls; ornament coarse, consisting of prorsiradiate bullae on lower flank from which two to three secondary ribs arise.

Description. The holotype, GSC 99532, is a well preserved specimen with more than 360° of body chamber ending in an incomplete aperture at 129·4 mm shell diameter. Part of the venter is broken away on a small segment of the body chamber. The shell is moderately evolute with a rectangular to ellipsoidal whorl section. The umbilical wall is gently sloping, and the umbilical shoulder is rounded. The flanks are flattish to gently convex. The venter is carinate with weak ventro-lateral shoulders. The ornament is coarse. On the inner whorls, umbilical tubercles give rise to two or three gently sinuous ribs. During ontogeny, the tubercles lengthen into prorsiradiate bullae which give rise to two or three sinuous ribs. The ribs are strongly projecting along the ventro-lateral shoulder and occasionally may reach the venter where subdued swellings are sometimes seen on well preserved parts of the body chamber. The paratype, GSC 107286, is a moderately well preserved specimen wholly septate to a shell diameter of 87·0 mm. The shell is cracked and parts of the phragmocone have broken off. The inner whorls are not exposed. The shell is moderately evolute with a rectangular to ellipsoidal whorl section. The umbilical wall is gently sloping and the umbilical shoulder is rounded. The flanks are flattish, and the venter is carinate with rounded ventro-lateral shoulders. The ornament is coarse with prorsiradiate umbilical bullae, commonly giving rise to two sinuous ribs at approximately one-quarter the flank height. The ribs are strongly projecting along the ventro-lateral shoulder and, where the specimen is well preserved, may reach the venter, where subdued swellings are seen. The other paratypes are not as well preserved but all have similar features to the other types.

Remarks. This species has a coarser ornament than *Yakounia yakounensis*, and the bullae are not as sharp. The inner whorls are similar to *Phymatoceras copiapense* and *Ph. hillebrandti*, which may have been ancestors. *Y. freboldi* may, in turn, be ancestral to *Ludwigia*. The inner whorls have almost straight ribs and sharp tubercles. On the outer whorls, the ribs become more sigmoidal and the tubercles more elongated. The ornament on the outer whorls is similar to that on the inner whorls of species of *Ludwigia* but, in general, that genus has coarser, more sigmoidal ribbing, elongated bullae or primary ribs, and a less sulcate venter.

Yakounia pacifica sp. nov.

Plate 6, figures 1–2

Derivation of name. After the Pacific Ocean, along the north-eastern shore of which the genus is found.

Material. Three specimens in calcareous concretions and sandstones of the Phantom Creek Formation, Queen Charlotte Islands (Section 2, loc. 4).

Holotype. GSC 107261 (Pl. 6, figs 1–2) from the lower part of the Phantom Creek Formation (Yakounensis Zone), Yakoun River, Queen Charlotte Islands.

Paratype. GSC 107288

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 107261	113·4	44·7	39·4	37·5	24·6	0·66	12
GSC 107261	102·7	39·9	38·9	36·0	22·0	0·61	12
GSC 107261	89·5	32·7	36·5	33·6	20·0	0·60	13
GSC 107288	78·4	29·5	37·6	28·3	*c.* 15·1	*c.* 0·53	12
GSC 107288	65·8	21·6	32·8	24·4	—	—	11

Diagnosis. Moderately evolute shell; compressed, ogival whorl section; venter carinate-sulcate; ornament prominent, consisting of thick, prorsiradiate primary ribs that split into two or three sinuous secondary ribs low on flanks.

Description. The holotype, GSC 107261, is a moderately well preserved specimen septate to approximately 88 mm shell diameter with approximately 180° of body chamber ending in an incomplete aperture at 113·4 mm shell diameter. The specimen is slightly worn in places. The shell is moderately evolute with an ogival whorl section. The umbilical wall is gently sloping, and the umbilical shoulder is rounded. Flanks are flat, ventrolateral shoulders weak, and the venter carinate. The ornament consists of prorsiradiate primary ribs on the inner whorls that begin high on the umbilical wall. Some ribs may remain single but most bifurcate at approximately one-third the flank height. On the outer whorls, the primary ribs swell into bullae. The paratype, GSC 107288, is a moderately well preserved specimen ending in an incomplete aperture at 78·7 mm shell diameter. The specimen is slightly worn and one side is not exposed. Its morphology is similar to that of the holotype. Septal sutures are present.

Remarks. This species shows some similarity to certain Graphoceratidae such as *Ludwigia* (*Pseudographoceras*) (see Schlegelmilch 1976, pl. 12, figs 5, 7) in terms of whorl shape and ribbing style. However, the Graphoceratidae tend to have a sharp angular flexure of the ribs on the lower flank; this feature is less prominent in similar forms, such as *Phymatoceras hillebrandti*, *Yakounia freboldi*, and *Y. yakounensis*. The Graphoceratidae also tend to be more involute than the Phymatoceratidae although it is possible that they did evolve from them.

Yakounia silvae sp. nov.

Plate 4, figures 1–6, 9–10; Plate 6, figures 3–4

1969 *Phlyseogrammoceras* aff. *P. dispansum* (Wunstorf); Frebold *et al.*, p. 20, pl. 1, figs 10–15.
1987 ?Grammoceratinae gen. et sp. indet., Hall, p. 1702, pl. 5, figs K–L, Q.

Derivation of name. After the thick, old-growth forests that cover(ed) the Queen Charlotte Islands (Latin *silva*, wood, forest).

Material. Over 100 specimens in calcareous concretions and sandstones of the Phantom Creek Formation, Queen Charlotte Islands (Section 1, locs 4–5, 7–8, 17; Section 2, locs 1–6, 8, 10–11, 17; Section 3, locs 89–92, 105; Section 4, locs 1–2, 4, 6–8, 10, 14; Section 5, locs 2–3, 5; Section 6, locs 1–2). Also specimens from the Manson River area (Text-fig. 2; Collection 38), in the Manning Park area (Text-fig. 2; Collection 44), and in the southern Canadian Rocky Mountains (Collection 45).

Holotype. GSC 99525 (Pl. 4, figs 1–2) from the lower part of the Phantom Creek Formation (Yakounensis Zone), Yakoun River, Queen Charlotte Islands.

Paratypes. GSC 99526 (Pl. 4, figs 3–4), GSC 99527 (Pl. 4, figs 5–6), GSC 99528 (Pl. 4, figs 9–10), GSC 107262 (Pl. 6, figs 3–4), GSC 107289–107291

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 99525	82·0	31·0	37·8	29·2	*c.* 18	*c.* 0·62	11
GSC 99525	66·9	23·7	35·4	23·7	14·9	0·63	11
GSC 107289	79·0	32·8	41·5	27·0	16·0	0·59	10
GSC 107289	86·1	38·1	44·3	27·2	16·7	0·61	11
GSC 107290	102·9	39·0	37·9	37·0	22·0	0·59	11
GSC 107291	60·6	25·0	41·3	19·5	12·8	0·66	12
GSC 107291	53·0	21·3	40·2	18·6	11·4	0·61	12

Diagnosis. Moderately evolute planulate; ogival whorl section; venter carinate-sulcate; ornament prominent, consisting of umbilical tubercles or prorsiradiate bullae from which two or three secondary ribs proceed up the flanks with a gently sinuous to rectiradiate trend.

Description. The holotype, GSC 99525, is a moderately well preserved specimen wholly septate to a shell diameter of 83·0 mm. Part of one side of the outer whorl is crushed. The shell is moderately evolute with a compressed ogival whorl section. The umbilical wall is gently sloping and the umbilical shoulder is rounded. The flanks are moderately flat to gently convex. The venter is carinate with weak ventro-lateral shoulders. On the inner whorls, prorsiradiate primaries begin high on the umbilical wall and split into two or three primaries at approximately one-third the flank height. On the outer whorls, prorsiradiate umbilical tubercles develop and on the outer whorl are bullate. The tubercles/bullae give rise to two or three gently sinuous secondary ribs. The paratype, GSC 107262, is a moderately well preserved specimen with more than 180° of body chamber ending in an incomplete aperture at 96·9 mm shell diameter. The specimen, especially the body chamber, is partially crushed. The shell is moderately evolute. The umbilical wall is gently sloping with a rounded umbilical shoulder. The flanks are flattish and the venter is carinate. On the inner whorls, umbilical tubercles give rise to two or three secondary ribs. The tubercles become slightly prorsiradiate on the outer whorl. The secondary ribs are almost rectiradiate to gently sinuous. The paratype, GSC 99528, is a moderately well preserved specimen septate to 13·3 mm umbilical diameter with approximately 200° of body chamber ending in an incomplete aperture at 42·8 mm shell diameter. The body chamber is partially crushed. The shell form is similar to those described above. On the inner whorls, gently prorsiradiate primary ribs give rise to two or three secondary ribs at approximately one-third the flank height. Umbilical tubercles develop on the last part of the phragmocone and on the body chamber. The secondary ribs are rectiradiate to gently sinuous. The paratype, GSC 99527, is a moderately well preserved specimen with part of the body chamber ending in an incomplete aperture at 35·3 mm shell diameter. Part of the phragmocone venter is absent, and the body chamber near the aperture is partially crushed. The tubercles begin on the last whorl, and the secondary ribs are almost rectiradiate. The paratype, GSC 99526, is a moderately well preserved specimen, septate to 33·3 mm shell diameter with approximately 160° of body chamber ending in an incomplete aperture at 43·5 mm shell diameter. The body chamber is partially crushed. Tubercles begin on the last whorl, and give rise to two or three gently sinuous secondary ribs.

EXPLANATION OF PLATE 6

Figs 1–2. *Yakounia pacifica* gen. et sp. nov; GSC 107261, holotype; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-149652, Section 2, loc. 4.

Figs 3–4. *Yakounia silvae* gen. et sp. nov; GSC 107262, paratype; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-149652, Section 2, loc. 4.

Figs 5–6. *Pseudolioceras compactile* (Simpson); GSC 107263; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-157742, Section 2, loc. 95.

Figs 7–10. *Sphaerocoeloceras brochiiforme* Jaworski; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 7–8, GSC 95584; GSC Loc. No. C-87118, Section 3, loc. 95. 9–10, GSC 99485; GSC Loc. No. C-149652, Section 2, loc. 4.

Arrow marks start of body chamber. All are × 1.

PLATE 6


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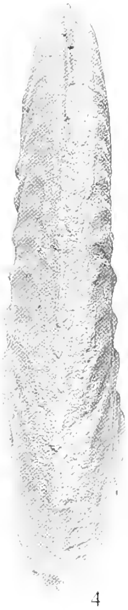
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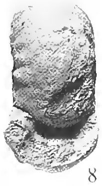
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JAKOBS and SMITH, *Yakounia*, *Pseudolioceras* and *Sphaerocoeloceras*

Remarks. This species has a weaker ornament than *Y. freboldi*, although the prorsiradiate bullae are similar. It lacks the sharp, round tubercles of *Y. yakounensis* and has more prominent tubercles than *Y. pacifica*. In general, the specimens belonging to *Y. silvae* are alike except that certain features may arise or fade at different points during ontogeny, and ribs and bullae may trend in slightly different directions.

Subfamily HARPOCERATINAE Neumayr, 1875

Genus PSEUDOLIOCERAS Buckman, 1889

[= *Praehaploceras* Monestier, 1931; *Pseudowalkericeras* Maubeuge, 1949; *Tugurites* Kalacheva and Sey, 1970; ?*Buckmanites* Guex, 1973]

Type species. Ammonites compactilis Simpson, 1855 (subsequent designation by Buckman 1889)

Diagnosis. Moderately involute shell with discoidal and compressed triangular whorl section; carinate venter with sharp, hollow keel bordered by narrow, smooth areas; umbilical wall vertical; umbilicus small and deep; ribs sub-falciform, only clearly visible on outer part of whorl where they are broad and rounded; on inner part of whorl, ribs either faint or absent.

Distribution. Pseudolioceras appears to have Boreal affinities, being common in Arctic Canada, Siberia, Japan and Great Britain.

Pseudolioceras compactile (Simpson, 1855)

Plate 6, figures 5–6

*1855	*Ammonites compactilis* Simpson, p. 75.
1911	*Pseudolioceras compactile* (Simpson); Buckman, pp. 41b, 41c, pl. 41A, figs 1–2.
1972	*Pseudolioceras compactile* (Simpson); Guex, pl. 5, fig. 13.
1974	*Pseudolioceras compactile* (Simpson); Dagys, pl. 18, fig. 1.
1976	*Pseudolioceras compactile* (Simpson); Schlegelmilch, p. 89, pl. 47, fig. 4.

Material. 11 small specimens in sandstones and calcareous concretions of the Phantom Creek Formation, Queen Charlotte Islands (Section 3, loc. 95; Section 4, loc. 12).

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 107263	22·8	3·7	16·2	13·2	6·9	0·52	—
GSC 107292	18·9	3·1	16·4	10·5	—	—	—

Description. The involute shell has a triangular whorl section. The umblical shoulder is rounded, and the umbilical wall steep. The flanks are gently convex. The venter is almost knife-sharp; the flanks converge toward the venter with weak ventro-lateral shoulders. The ribs are gently falcate, projecting along the venter. On the lower flanks, they are faint, becoming more prominent on the upper flank. They are much fainter on the early whorls, appearing almost like growth lines.

Remarks. The degree of involution, the discoidal nature of the shell, and the knife-edge venter of the Queen Charlotte Islands specimens are typical of *P. compactile*. *P. lythense* (Young and Bird, 1828) has coarser ribbing that is more prominent on the lower flanks. Some specimens are similar to *Leioceras opalinum* (Reinecke, 1818) with fine ribbing, and a similar whorl shape and volution. These could be juvenile features of *Pseudolioceras*, as they appear on specimens of small size.

Distribution. Pseudolioceras compactile has been collected from the Upper Toarcian of north-west Europe, and is common in the Arctic regions of North America and Siberia.

Subfamily HAMMATOCERATINAE Buckman, 1887

Genus HAMMATOCERAS Hyatt, 1867
[= *Ammatoceras* Hyatt, 1867; *Pachammatoceras* Buckman, 1921]

Type species. Ammonites insignis Zieten, 1831 (subsequent designation by Buckman 1887)

Diagnosis. Moderately evolute shell with sub-triangular to ogival whorl section; umbilical wall becomes vertical and commonly undercut on outer whorls; primary ribs short, with long secondary ribs arising near umbilical shoulder, commonly at tubercles; venter carinate; prorsiradiate ribs approach it at slight angle; ribs fade on outer whorls.

Distribution. With the exception of the Arctic regions, *Hammatoceras* is a cosmopolitan genus found in the Upper Toarcian and Lower Aalenian.

Hammatoceras insigne (Zieten, 1831)

Plate 7, figure 5

1831 *Ammonites insignis* Zieten, pl. 15, fig. 2.
1874 *Ammonites insignis* (Schubler); Dumortier, pl. 17, figs 1–3 (*non* 4–5).

Material. Only three specimens known, collected from calcareous concretions and sandstones of the Phantom Creek Formation, Queen Charlotte Islands (Section 2, loc. 4, Section 3, locs 71, 95).

Description. The shell is involute with a triangular whorl section. Flanks are convex to the carinate venter. On the outer whorls, the keel is bordered by smooth bands. The ornament is prominent with sharp umbilical tubercles from which two or three rectiradiate secondary ribs arise which approach the venter at an angle of approximately 90°.

Remarks. This species can be distinguished from *H. speciosum* by the latter's more compressed whorl section, and ribs that approach the venter with a slightly prorsiradiate trend.

Distribution. Hammatoceras insigne is well known from the Upper Toarcian of Europe (Guex 1975; Schlegelmilch 1976; Elmi and Rulleau 1991).

Hammatoceras speciosum (Janensch, 1902)

Plate 7, figures 1–4, 6

1874 *Ammonites insignis* (Schubler); Dumortier, pl. 18.
1885 *Ammonites insignis variabilis* Quenstedt, pl. 50, fig. 1.
*1902 *Ammonites speciosum* Janensch, pl. 10, fig. 1.
1974 *Hammatoceras speciosum* (Janensch); Elmi *et al.*, pl. 5, fig. 1.
1975 *Hammatoceras speciosum* (Janensch); Guex, p. 111, pl. 9, fig. 8; pl. 10, figs 1, 3.
1976 *Hammatoceras speciosum* (Janensch); Schlegelmilch, p. 91, pl. 49, fig. 2.
1991 *Hammatoceras speciosum* (Janensch); Tipper *et al.*, pl. 7, fig. 1.
1992 *Hammatoceras speciosum* (Janensch); Hillebrandt and Smith, pl. 4, fig. 1.

Material. 20 specimens from calcareous concretions and sandstone of the Phantom Creek Formation, Queen Charlotte Islands (Section 1, loc. 3; Section 2, loc. 4; Section 3, locs 90, 99–100, 105; Section 4, loc. 2; Section 5, locs 1–2, 5). Two poorly preserved specimens from the Snowshoe Formation, east-central Oregon (Text-fig. 2; Section 7, locs 4–5).

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 95583	130·8	55·0	42·0	43·3	34·8	0·80	18
GSC 95583	119·2	50·6	42·4	39·5	32·0	0·81	17
GSC 107264	29·3	9·6	32·8	12·4	11·4	0·92	9
GSC 107264	23·6	7·0	29·7	10·0	9·8	0·98	8
GSC 107293	—	—	—	23·0	17·0	0·74	—
GSC 107294	133·1	—	—	45·1	38·5	0·85	—
GSC 107295	*c.* 135	55·0	40·7	45·5	—	—	—
GSC 107295	92·4	33·9	36·7	33·3	—	—	12

Description. The shell is moderately evolute with an ogival to triangular whorl section. The umbilical wall is steep, becoming vertical and undercut on the outer whorls. The umbilical shoulder is rounded but abrupt. The flanks are gently convex, converging toward the carinate venter. The ornament is coarse, consisting of strong umbilical tubercles from which two or three secondary ribs arise. The primary ribs are rursiradiate on the umbilical wall. The secondary ribs are gently curved and approach, but do not reach, the venter at an angle of approximately 70°.

Remarks. The whorls are much taller and narrower than those of *Hammatoceras insigne*, and the ribbing is finer and denser. In addition, the ribs of *H. insigne* approach the venter at an angle of almost 90°. *H. bonarelli* Parisch and Viale, 1906 is more evolute, and the whorls are not as high as those of *H. speciosum.*

Distribution. Hammatoceras speciosum is common in Europe and the Mediterranean region: in Algeria from the Insigne Zone (Elmi *et al.* 1974), in southern Germany from the Levesquei Zone (Schlegelmilch 1976), and in France from the Insigne Zone (Guex 1975; Elmi and Rulleau 1991).

Hammatoceras sp. nov.

Plate 7, figures 7–8

Material. Three incomplete specimens in sandstones and calcareous concretions of the Phantom Creek Formation, Queen Charlotte Islands (Section 4, loc. 6; Section 5, loc. 2)

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 107296	—	—	—	12·7	13·3	1·05	—
GSC 107297	—	—	—	9·5	14·0	1·47	—

Description. The shell is moderately evolute with a depressed, almost wide oval whorl section. The flanks are flat, becoming convex on the outer whorls. The venter is carinate with a subdued keel. The ornament is coarse and sparse. Umbilical tubercles give rise to two or three secondary ribs which are rectiradiate on the flank, but become prorsiradiate and approach the venter at an angle of approximately 70°.

EXPLANATION OF PLATE 7

Figs 1–4. *Hammatoceras speciosum* Janensch; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands. 1, 4, GSC 95583; GSC Loc. No. C-87215, Section 2, loc. 4. 2–3, GSC 107264, GSC Loc. No. C-87216, Section 2, loc. 4.

Fig. 5. *Hammatoceras insigne* (Zieten); GSC 107265; Hillebrandti Zone, upper part of the Whiteaves Formation; Queen Charlotte Islands, GSC Loc. No. C-159396, Section 3, loc. 71.

Fig. 6. *Hammatoceras speciosum* Janensch; UBC 017; Yakounensis Zone, Warm Springs Member of the Snowshoe Formation; Izee area, eastern Oregon, UBC Loc. No. F4-4-E, Section 7, loc. 5.

Figs 7–8. *Hammatoceras* sp. nov.; GSC 107266; Yakounensis Zone, lower part of the Phantom Creek Formation; Queen Charlotte Islands, GSC Loc. No. C-158077, Section 5, loc. 2.

All are × 1.

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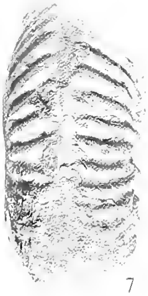

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JAKOBS and SMITH, *Hammatoceras*

Remarks. This species is similar to *H. insigne* but differs in possessing much coarser and more distant ribbing, and in that the ribs approach the venter at a more acute angle.

Genus SPHAEROCOELOCERAS Jaworski, 1926

Type species. Sphaerocoeloceras brochiiforme Jaworski, 1926

Diagnosis. Small involute shell with wide ellipsoidal to rounded whorl section; venter plain, but sometimes weakly carinate; ribbing blunt, sparse, bifurcating low on flank; no tubercles present.

Remarks. This genus has been known previously only from South America. It was placed initially within the Dactylioceratidae by Jaworski (1926) because of the similarity of its suture line to that of *Coeloceras crassum* Young and Bird, 1828. Arkell *et al.* (1957) retained this classification. Donovan *et al.* (1981) placed it within the Hammatoeratinae. It is similar to small specimens of *Hammatoceras* in appearance except for the missing keel. The genus is of Late Toarcian age in South and North America.

Sphaerocoeloceras brochiiforme Jaworski, 1926

Plate 6, figures 7–10

*1926 *Sphaerocoeloceras brochiiforme* Jaworski, p. 259, pl. 1, fig. 10; pl. 3, fig. 10; pl. 4, fig. 23.
v 1987 *Sphaerocoeloceras brochiiforme* Jaworski; Hillebrandt, pl. 13, fig. 9a–c; pl. 14, fig. 10a–b.
v 1987 ?Hammatoceratidae gen. et sp. indet. Hall, p. 1702, pl. 5, figs R–V.
v 1991 *Sphaerocoeloceras brochiiforme* Jaworski; Tipper *et al.*, pl. 7, fig. 2.
v 1992 *Sphaerocoeloceras brochiiforme* Jaworski; Hillebrandt and Smith, pl. 4, fig. 2.
v 1994 *Sphaerocoeloceras brochiiforme* Jaworski; Jakobs *et al.*, pl. 5, figs 7–8.

Material. 40 specimens in calcareous concretions and sandstones of the Phantom Creek Formation, Queen Charlotte Islands (Section 1, loc. 17; Section 2, locs 3–4, 17; Section 3, locs 95, 97–98; Section 4, locs 2, 6, 10; Section 5, loc. 5). Poorly preserved specimens from the southern Canadian Rocky Mountains (Text-fig. 2; Collection 45).

Measurements.	D	UD	U	WH	WW	WWWH	PRHW
GSC 107298	20·4	7·9	38·7	5·0	9·5	1·90	14
GSC 107299	17·8	6·7	37·6	4·6	8·6	1·87	15
GSC 107300	16·2	5·0	30·9	5·5	9·0	1·64	14
GSC 107301	24·7	9·7	39·3	7·4	9·9	1·34	16
GSC 107302	17·0	6·2	36·5	5·7	10·7	1·88	13
GSC 107303	19·0	7·0	36·8	5·0	8·2	1·64	15

Description. The shell is moderately evolute with a depressed, rounded whorl section. The umbilical wall is gently sloping and the umbilical shoulder is weak. The flanks are gently convex, converging towards the plain venter. No keel is evident but a faint ridge may sometimes be present. The ornament is generally faint. Ribs are blunt and begin near the umbilical shoulder, prorsiradiate to the upper flank, then rursiradiate to the venter. The ribs approach the venter with an angle of slightly less than 180°, and their ventral ends may be separated by a smooth area. They commonly bifurcate at the top of the flank, and single intercalatory ribs may also appear. The venter is similar to that of *Hammatoceras* except for the absence of a keel. Ribbing strength and density vary slightly between the specimens.

Remarks. Slight variations in ribbing density and strength are not considered sufficiently important to warrant splitting the group into several species.

Distribution. Sphaerocoeloceras brochiiforme has been collected in South America, from the *Phlyseogrammoceras* (?) *tenuicostatum*, '*Pleydellia lotharingica*' and '*Pleydellia fluitans*' zones of Hillebrandt (1987).

CONCLUSIONS

The latest Toarcian ammonite fauna of North America contains endemic Athabascan (*sensu* Taylor *et al.* 1984) and eastern Pacific taxa, as well as pandemic taxa. Eastern Pacific taxa such as *Sphaerocoeloceras brochiiforme* and *Dumortieria pusilla* provide correlative ties with South American faunas described by Hillebrandt (1981, 1987). Pandemic taxa, such as *Pleydellia aalensis*, *Hammatoceras speciosum*, *Dumortieria levesquei*, and *D. insignisimilis*, allow correlation with European successions. Athabascan forms are the most widespread and prolific taxa in western North America; these include *Yakounia yakounensis*, *Y. freboldi*, *Y. silvae*, and *Pleydellia maudensis*. A global sea-level fall during the Late Toarcian (Hallam 1988; Haq *et al.* 1988) may have encouraged endemism by restricting migration between the eastern Pacific and western Tethys.

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AN OCCURRENCE OF THE AUGURITID AMMONOID *CELAECERAS* IN THE LOWER DEVONIAN OF NORTHERN SPAIN

by J. R. MONTESINOS *and* J. L. GARCÍA-ALCALDE

ABSTRACT. The rare Bohemian genus *Celaeceras*, a primitive auguritid ammonoid with a rather bizarre suture, has been found in late Emsian strata (Upper Zlíchovian) in the Palentine Domain of northern Spain. This occurrence provides the first precise age for the genus, and considerably extends its palaeogeographical range in the Devonian of northern Gondwanaland.

THE affinity of the Palentian Devonian succession of northern Spain (Text-fig. 1A) with that of Bohemia and the Harz Mountains, the Hercynian/Bohemian Magnafacies of Erben (1962, 1964*a*), has been recognized by many workers (Brouwer 1964; Jahnke *et al.* 1983; García-Alcalde *et al.* 1988, 1990). Lower Devonian ammonoids are relatively common in the area. Particularly interesting is a primitive fauna, comprising representatives of the simple-sutured genera *Mimagoniatites*, *Erbenoceras* and *Mimosphinctes* (Kullmann 1960; Montesinos and Truyols-Massoni 1987; Montesinos 1991), which has been known for many years from beds of the Abadia Formation, above the Requejada Member (Text-fig. 1B–C). During recent research, the bizarre genus *Celaeceras* Hyatt, 1884 has also been identified.

Celaeceras, the type species of which, *C. praematurum* (Barrande, 1867, p. 110; 1877, pl. 522, figs 1–4), was originally described from Bohemia (Chlupáč and Turek 1983). It has a more complex suture than any other Lower Devonian or lower Middle Devonian goniatite, and its affinities are problematical. Bogoslovskiy (1961) described a very similar form from the Ural Mountains. He named it *Augurites* and assigned it to a new family, the Auguritidae, and a new Suborder, the Auguritida. The genera *Celaeceras* and *Augurites* have been regarded as synonyms by most authors (House 1964; Erben 1966; Solle 1972; Chlupáč and Turek 1983). The type material of both genera is of late Emsian age. This is also the age of the last known auguritid genus, *Gaurites* Bogoslovskiy, 1984 from the Zeravshan Range in the Tien-Shan. The new Spanish material has been found in beds correlating with the dacryoconarid *elegans* Zone (Lütke 1979, p. 284; Alberti 1993), and this is a more precise age constraint (M. Truyols-Massoni, pers. comm. 1993).

The widespread palaeogeographical distribution of the Auguritidae (Text-fig. 2) is similar to that of other primitive ammonoid faunas. It suggests a greater capacity for pelagic spreading than other contemporary marine organisms. *Celaeceras sensu stricto* seems to have spread throughout northern Gondwanaland, on the northern tropical side of the Rheic Ocean. On the other hand, *Augurites* and *Gaurites* colonized respectively, the northern, Laurussian part of Baltica, and south Kazakhstan in the southern tropical boreal zone. According to recent palaeogeographical reconstructions (Bergström 1990; Scotese and McKerrow 1990), this distribution encompasses a linear separation between extreme auguritid occurrences of more than 6000 km. Specifying the point of origin of auguritids would be pivotal to an understanding of their evolution, but the sparse distribution of the group makes this difficult. Considering general morphology and the more simple ventral suture, *Gaurites* is a good candidate for the ancestral stock; this agrees with the views of Bogoslovskiy (1984). Models of ocean pattern circulation, such as that of Bergström (1990) for the Silurian, would partially support this hypothesis. Bergström's model is characterized by a great

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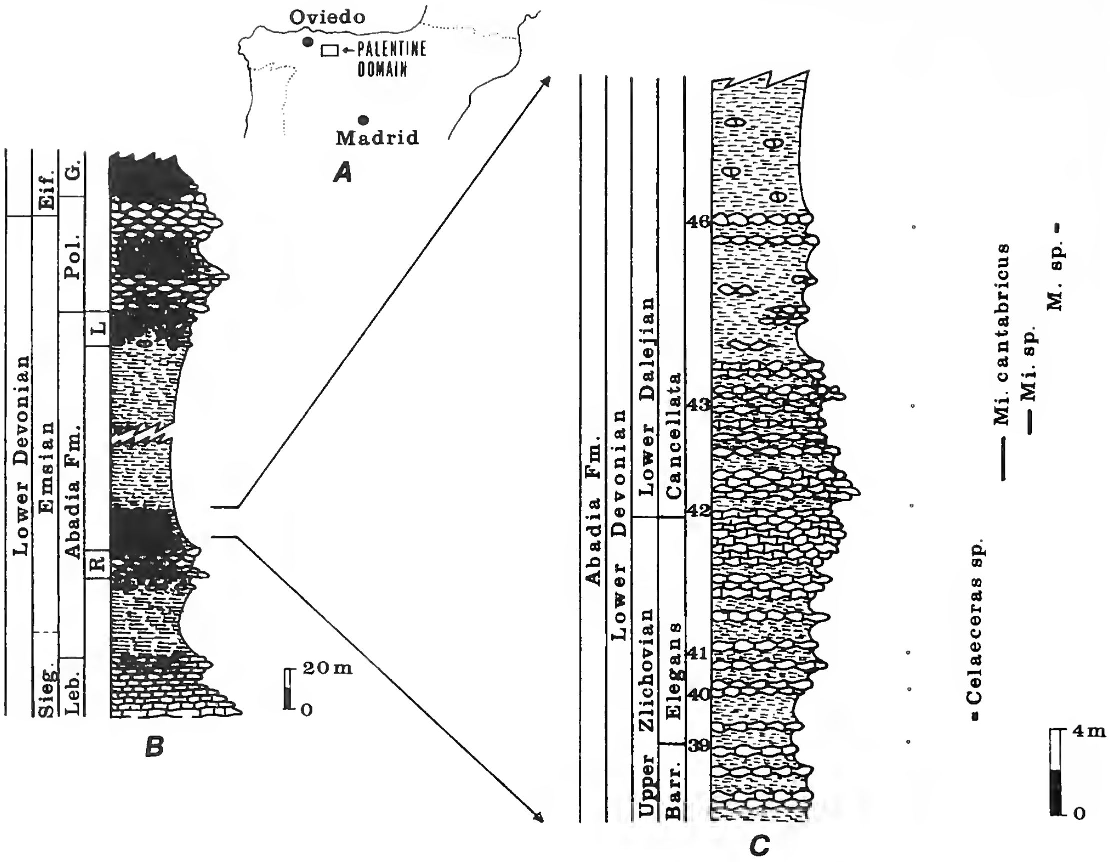


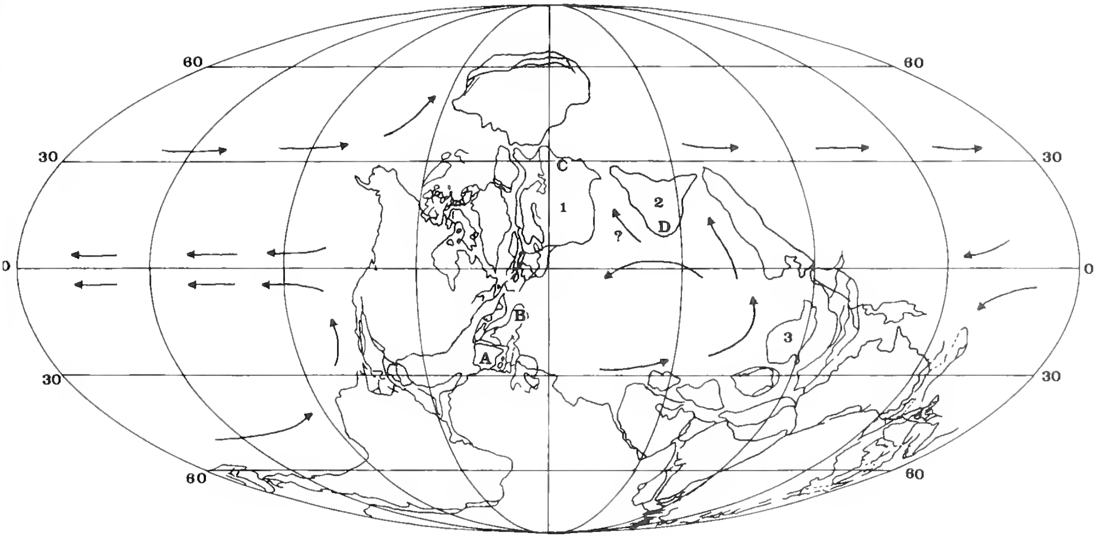
TEXT-FIG. 1. Map and sections illustrating the Lower Devonian localities in northern Spain. A, locality map showing the Palentine Domain. B, generalized Lower Devonian section in the Palentine Domain. C, detailed sequence in the Arauz stream section showing substage and dacryoconarid zone boundaries, numbered collecting horizons and the distribution of Lower Devonian goniatites. Abbreviations: R, Requejada Member; L, Lezna Member; Leb., Lebanza Formation; Pol., Polentinos Formation; G., Gustalapiedra Formation; Sieg., Siegenian; Eif., Eifelian. M., *Mimagoniatites*; Mi., *Mimosphinctes*; Barr., *barrandei* Zone.

counter-clockwise gyre in the Paratethys area, with diverging currents towards the Northern Hemisphere between the South China, Kazakhstan and Baltica plates.

SYSTEMATIC PALAEONTOLOGY

Order ANARCESTIDA Miller and Furnish, 1954
Suborder AGONIATITINA Ruzhencev, 1957
Superfamily AUGURITACEAE Bogoslovskiy, 1961
Family AUGURITIDAE Bogoslovskiy, 1961

Remarks. Two or three genera are currently referred to the Auguritidae. As already stated, *Augurites* may be a junior synonym of *Celaeceras*; in addition, there is *Gaurites*. House (1964), who



TEXT-FIG. 2. Distribution of auguritid ammonoids shown on an Emsian palaeogeographical map (modified from Scotese (1986) with ocean circulation pattern based on Bergström (1990)). Abbreviations: A, Spain; B, Bohemia; C, Ural Mountains; D, Tien-Shan; 1, Baltica Plate; 2, Kazakhstan Plate; 3, South China Plate.

had examined the holotypes of *Celaeceras* and *Augurites*, recommended that these two genera be treated as synonyms. Bogoslovskiy (1984) rejected this and emphasized differences in involution, umbilical covering and whorl cross-section. Chlupáč and Turek (1983) took the view that the differences between the holotypes were unclear (compare Text-fig. 4C–E with Bogoslovskiy 1961, pl. 7, figs 4–5 and text-fig. 4a–b). However, despite the clear similarities between the two genera, we think it advisable, for the time being at least, to keep them separate in view of the often sparse and fragmentary material available and the wide geographical distance between them.

The general view (Bogoslovskiy 1961, 1969, 1984; Erben, 1964*b*; Chlupáč and Turek 1983), though far from clear, is that the auguritids arose from anetoceratid stock (strongly-ribbed, VO-sutured, evolute shells with poor hydrodynamic characters) probably via mimagoniatitids (weakly sculptured, VO:D-sutured, more or less involute, hydrodynamically advanced shells).

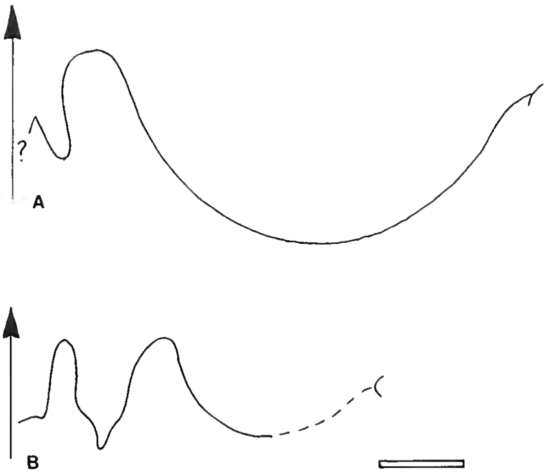
Genus CELAECERAS Hyatt, 1884

Type species. Goniatites praematurus Barrande, 1887, p. 110, pl. 522, figs 1–4.

Diagnosis Involute, lenticular, and laterally-flattened shell; perforate and rather broad umbilicus; sutural formula, $V_{1-1}V_{1-2}V_2O{:}D$. The V_{1-2} lobe is within a funnel-shaped ventral lobe; rounded, broad, nearly omnilateral lateral lobe (Text-figs 3B, 4C–D).

Remarks. Sufficient comment has already been made on the great similarity between *Celaeceras* and *Augurites*. *Gaurites* differs from *Celaeceras* in lacking the V_{1-2} lobe and in the occurrence of a small umbilical lobe.

Despite the distinctive shell features of *Celaeceras* compared with near-contemporary ammonoids such as *Mimagoniatites*, *Mimosphinctes*, *Anetoceras* and *Erbenoceras*, the genus had rather meagre evolutionary success. On present data, there are only one or two species of *Celaeceras*, which are of Late Zlíchovian age (and doubtfully Dalejan). Only four specimens are known.



TEXT-FIG. 3. Suture diagrams of *Celaeceras*. A, *Celaeceras* sp., from the Palentine Domain, northern Spain; based on DPO 113.901; drawn at whorl height 35 mm. B, *Celaeceras praematurum* (Barrande); based on the holotype from the uppermost part of the Zlíchov Limestone, Praha-Zlíchov, Svagerka (see Chlupáč and Turek 1983). Scale bar represents 10 mm.

Celaeceras sp.

Text-figures 3A, 4A–B

Material. A fragment of an internal calcareous mould, rather well preserved. Palaeontological Collections, University of Oviedo, DPO 113.901. The specimen comes from the 1·3 m-thick un-named bed overlying M-39 in the nodular marly limestone-marlstone-shale alternations above the Requejada Member of the Abadia Formation in the Arauz section (Palentine Domain, northern Palencia). It occurs some metres below beds with *Mimosphinctes cantabricus* Kullmann, *M.* cf. *tripartitus* Eichenberg and *Mimagoniatites erbeni* Kullmann (see Montesinos 1991). The level is referred to the dacryoconarid *elegans* Zone of the Upper Zlíchovian (Text-fig. 1C).

Description. A lenticular whorl fragment (height, 37 mm; width, 10·5 mm) showing the last four septa of the phragmocone, and the beginning of the body-chamber. The suture is badly preserved in the ventral area (Text-figs 3A, 4A). There is a narrow, deep and rounded V_2, but the rounding could be due to abrasion. A broad, rather than deep, O lobe extends over most of the whorl side. Judging from the partially preserved umbilical border, the umbilicus was rather wide.

Remarks. The lenticular profile and lateral suture of the specimen allows assignment to *Celaeceras*. The fragmentary nature of the specimen prevents detailed comparison with *C. praematurum*, the type species.

Acknowledgements. The authors thank Prof. M. R. House, University of Southampton, for the critical reading of a draft of this note and both him and Prof. I. Chlupáč, Charles University, Prague, for supplying photographs and diagrams of the holotype of *Celaeceras praematurum* used for comparison and in the text-figures.

TEXT-FIG. 4. Illustrations of *Celaeceras* from Spain and the Czech Republic. A–B, *Celaeceras* sp.; internal calcareous mould from the Abadia Formation, Arauz Section (Lower Devonian, Palentine Domain, northern Palencia, Spain); A, lateral view, B, ventral view. From 1·3 m above the M-39 level (see Text-fig. 1), DPO 113.901; × 1·5. C–E, *Celaeceras praematurum* (Barrande), holotype, from Svagerka. C, lateral view of fragment of a whorl in restored position to the corresponding external mould, coated with ammonium chloride sublimate; × 1. E, lateral view of the uncoated fragment; × 1 (photos for C and E kindly supplied by I. Chlupáč). D, apertural view of the fragment, coated with ammonium chloride; × 1 (photo for D kindly supplied by M. R. House).

TEXT-FIG. 4. For caption see opposite.

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ADAPTATIONS OF VERMETID AND SILIQUARIID GASTROPODS

by ENRICO SAVAZZI

ABSTRACT. Most vermetids are cemented to hard substrates, and can extend the shell aperture high above the substrate. The shell can be bent sharply around obstacles, and internal septa allow it to become much longer than the soft parts. Several vermetids use these adaptations to live as facultative soft-bottom dwellers, but no species appears to be permanently adapted to this environment. In contrast, siliquariids are not cemented. *Siliquaria* lives embedded within sponges as a commensal or parasite, letting its exhalant current flow out of the shell and into the host sponge through a very long slit. *Siliquaria* is unique among gastropods in that it periodically increases the width of the shell slit and/or the cross sectional area of the whorl by cracking the whorl periphery into wedges, pushing them outward, and subsequently reattaching them together.

MOLLUSC shells that deviate from a regular, closely coiled helicospiral have often been described as bizarre, aberrant, peculiar and anomalous. The etymology of the term heteromorph, originally coined for non-spiral or loosely coiled ammonoids, bears a connotation of difference and deviation. The commonness of heteromorphs in the Upper Cretaceous has previously been interpreted incorrectly as an expression of decadence, heralding the impending extinction of the group.

To the functional morphologist, these and other 'peculiar' shapes constitute a promising subject for study, since a morphology that has been freed from geometric constraints (in this case, isometric growth) is likely to have specialized for a specific function, or set of functions, to a higher degree than a constrained morphology.

Heteromorphy, described as the deviation from a closely coiled, logarithmic spiral pattern, occurs also in gastropods, bivalves and serpulid polychaetes. Heteromorphic shells are actually an artificial aggregate of two radically different morphologies. In the first category, deviation from a logarithmic spiral is the result of an allometric growth programme, and shell morphology follows at all times a rigid morphogenetic programme. Heteromorphic ammonoids and strombid gastropods exemplify this group (e.g. Savazzi 1991; Seilacher and Gunji 1993). In the second category, shell morphology is largely under environmental control. This group contains serpulid polychaetes, vermetid and siliquariid gastropods, and a few unrelated gastropod genera (see concluding section). The shells of these organisms are usually cemented to, or embedded in a substrate, and conform to its topography. As a result, their shell geometry displays a large amount of individual variation.

Seilacher (*in* Seilacher and Gunji 1993, p. 243) mentioned briefly some of the adaptive values of shell morphology in openly coiled turritellids, vermetids and siliquariids with reference to the morphogenetic significance of allometric growth. Earlier studies on these families (Keen 1961; Morton 1965, and references therein) concentrated on Recent forms and on the morphology of the soft parts. In the present paper, special attention is paid to the adaptive and constructional aspects of shell morphology within these two families.

Not much is known of the life history and habits of these gastropods, and especially of the Siliquariidae (see below). Representatives of this family are usually scarce, and their secretive life habits make them difficult to study. Therefore, the approach normally followed for studies of functional morphology of Recent organisms, consisting of direct observations on the habits of living specimens, cannot be used on this occasion. On the other hand, plentiful Recent and fossil shell material was available for this study. In these circumstances, it is legitimate to treat Recent material

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as fossils, and to apply to this material the inferential techniques developed for palaeobiological analysis.

MATERIAL AND METHODS

The following vermetids mentioned in this paper were collected by the author: *Dendropoma* (*s.s.*) *annulata* (Daudin), Recent, on intertidal sandstone and shells in Harrington Sound, Bermuda; *Dendropoma* sp., Recent, from shells of intertidal epibyssate bivalves on Bantayan Island, the Philippines; *Serpulorbis* (*s.s.*) *arenarius* (Linnaeus), Middle and Upper Pliocene, from several localities in the provinces of Piacenza and Asti, Italy; *Serpulorbis* (*Cladopoda*) *colubrinus* (Sowerby), Recent, on shallow subtidal coral reefs of Mactan Island, the Philippines; *Serpulorbis* (*s.s.*) *roussaei* (Vincent) on corals reefs in 3–4 m water depth near Tayud, Ceby Island, the Philippines; *Petaloconchus* (*Macrophragma*) *cereus* (Carpenter), Recent, on shells from subtidal sand flats around Bantayan Island, the Philippines; *Petaloconchus* (*M.*) *intortus* (Linnaeus), Middle Pliocene, from several localities in the province of Piacenza, Italy.

The siliquariids collected by the author are: *Siliquaria anguina* (Linnaeus), Recent, from unidentified sponges in 2–3 m water off Tayud, Cebu Island, the Philippines; and a Middle Pliocene *Siliquaria* from Castell'Arquato, Italy. This latter material is usually referred to in the literature as *S. anguina* (Linnaeus) (e.g. Rossi Ronchetti 1952). However, Linnaeus' species is a large Recent form from the tropical Indo-Pacific, while the Italian Pliocene species is obviously distinct, and more closely related to *S. ponderosa* and *S. cumingi* (see below). It is possible that the valid name of the Italian species is *Siliquaria ammonoides* (Brocchi). Since this nomenclatural problem lies outside the scope of this paper, the question is left open, and the Italian species is referred to herein as *S.* sp.

Unless otherwise indicated in the figure captions, illustrated specimens are in the author's collection, Institute of Earth Sciences, Uppsala University. Other repositories are the Department of Invertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden, (abbreviated SM in the figure captions), the Department of Historical Geology and Palaeontology, Uppsala University, Sweden (As, It, UU) and the Muséum National d'Histoire Naturelle, Paris, France (MN).

Sections of specimens were prepared by embedding in epoxy resin for materialographic samples, cutting, grinding on diamond laps to avoid contamination by grit particles, polishing with cerium oxide bound on acetate laps, briefly etching with 1·5 per cent. hydrochloric acid, and gold-sputtering for SEM observation.

VERMETIDAE

The origin and early evolutionary history of this family are not known. As noted by Keen (1961), the earliest forms likely to belong to this family are from the Upper Cretaceous. All records from the Triassic and Jurassic (together with several records from later periods) probably refer to serpulid polychaetes.

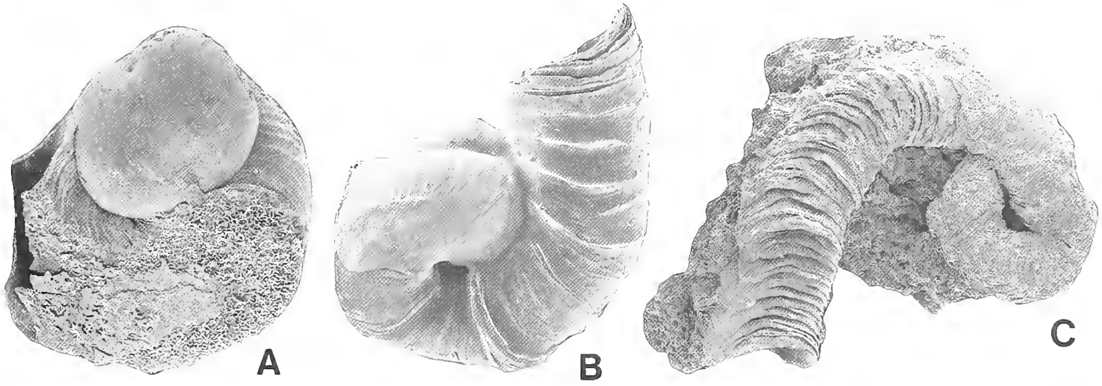
The morphological convergence between serpulids and vermetids has prompted the search for criteria to distinguish between the shells of the two groups. Shell microstructure is the safest criterion (e.g. Wrigley 1950; Schmidt 1951). Unfortunately, this character may not be preserved in fossils (especially from the Mesozoic). Vermetids differ further from serpulids in the presence of a protoconch and, usually, of internal septa or internal longitudinal ridges. Other criteria (e.g. external sculpture, colour and hardness; e.g. Mörch 1861) are unreliable or cannot be applied to fossils.

Most vermetids are loosely and irregularly coiled (always in a dextral fashion) or uncoiled, but rarely form zigzag meanders in alternating directions. This may be a result of the asymmetrical placement of the columellar muscle, inherited from regularly coiled, mobile Cerithiacea (see also discussion and references in Seilacher and Gunji 1993).

The foot of the Vermetidae is highly reduced and modified (e.g. Morton 1965). This precluded the evolutionary return to a mobile life habit.

Cementation. Vermetids are typically cemented to a solid substrate. The following discussion of growth and morphogenesis is based principally on the Recent *Dendropoma annulata*, with exceptions noted below.

Like most vermetids (Keen 1961), *D. annulata* lacks a veliger stage, and newly hatched larvae are mobile creepers. During this free-living stage, the shell reaches approximately 1·5 whorls (up to three to four whorls in other genera: Keen 1961; Morton 1965). Axial ribs appear toward the end of this phase. Subsequently, the shell becomes cemented to the substrate by the outer lip (Text-fig. 1A).



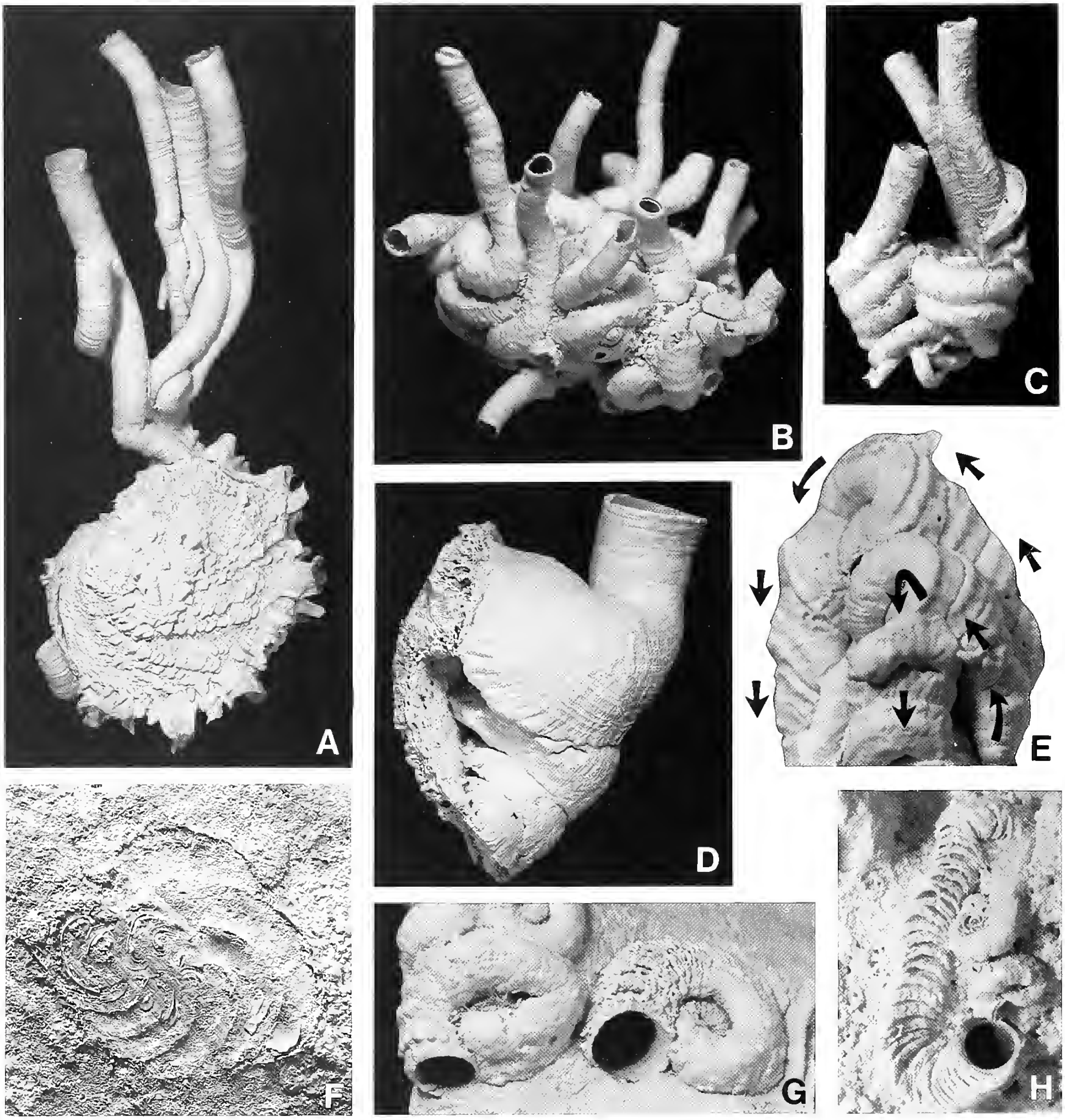
TEXT-FIG. 1. Juvenile stages of *Dendropoma annulata*, Recent, Bermuda. A, As18, larval shell with attachment scar, × 80. B, As19, specimen showing change in coiling direction; the attachment scar is to the left, × 55; C, As20, specimen showing subsequent irregular growth, × 18.

Afterwards, helical growth causes the shell aperture to lift from the substrate and to continue to grow in a regular fashion for another quarter whorl. The coiling axis then tilts approximately 90° and becomes roughly perpendicular to the surface of the substrate (Text-fig. 1B). This change in the mode of coiling is a constant character, and does not appear to be influenced by the orientation of the shell relative to the substrate or by the local topography of the substrate. The shell becomes again attached to the substrate, and begins to grow irregularly (Text-fig. 1C). Rough collabral frills (or different sculptures in other species) appear at this stage or shortly thereafter.

The mode of coiling of the adult shell differs in the various genera and subgenera. Typically, *Vermetus* (*s.s.*) is irregularly and loosely coiled, and adheres continuously to the substrate. Adult *V.* (*Thylaeodus*), *Trypsicha* and *Petaloconchus* (*s.s.*) are cemented to the substrate as juveniles, but afterwards pile successive whorls on top of each other to form irregular, cone-shaped shells (Text-fig. 2C; see also Seilacher and Gunji 1993). The occurrence of sudden changes in the direction of coiling, apparently caused by disturbances of the life position (Text-fig. 2E), suggests that this morphogenetic process is controlled by negative geotaxis.

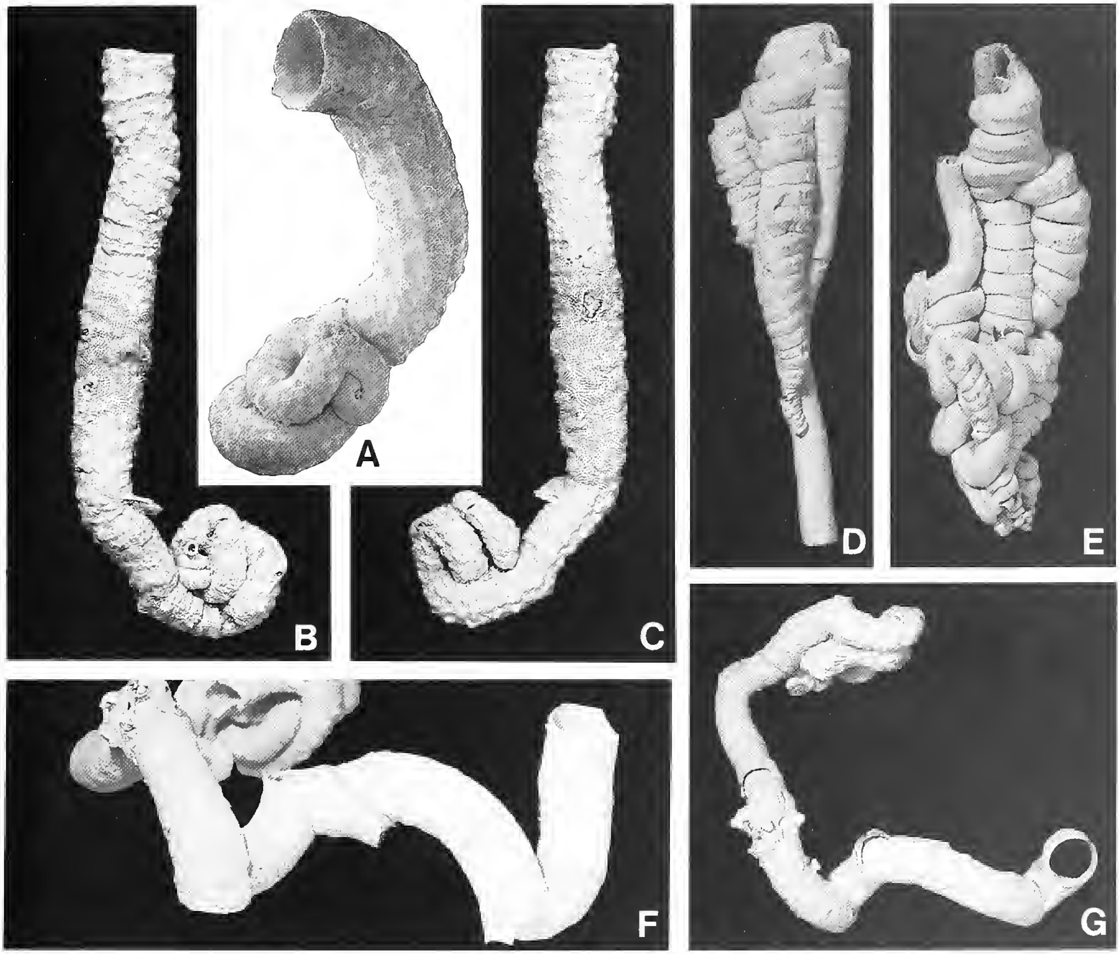
Petaloconchus (*Macrophragma*) is coiled in a manner similar to *Petaloconchus* (*s.s.*), but its spire is compressed sideways, and typically adheres to the substrate along one side, rather than by its apical whorls only. Juvenile *Serpulorbis* (*s.s.*) tend to coil planispirally and to remain adherent to the substrate, while coiling relaxes and becomes more irregular in adults (Text-fig. 2A–B, D). *S.* (*Cladopoda*) usually remains planispiral throughout life (Keen 1961).

At the end of growth, or at irregular intervals during growth, most vermetids build a straight, uncoiled portion of shell directed away from the substrate, called the feeding tube (Text-figs 2B–D, 3E–F). This structure carries the shell aperture high above the substrate, and therefore facilitates feeding (especially by the mucous-trap mechanism). However, feeding tubes are not cemented to the



TEXT-FIG. 2. A, *Serpulorbis roussaei* on *Chama brassica*, As21, Recent, Cebu Island, the Philippines, ×0·8. B, *Serpulorbis riisei*, Recent, Bermuda, ×1·5 (SM). C, *Petaloconchus* (*s.s.*) sp., Recent, Bay of Bengal (SM), ×1·5. D, *Serpulorbis colubrinus*, As22, Recent, Mactan Island near Cebu Island, the Philippines, ×0·7. E, *Petaloconchus* (*Macrophragma*) *intortus*, It10, Pliocene, Cyprus, ×2 (UU). The arrows indicate the general direction of growth of two individuals. F, etching of the substrate (*Pinna* sp.) by *Petaloconchus* (*M.*) *cereus*, As23, Recent, Bantayan Island, the Philippines, ×2. G, *Dendropoma* sp. semi-endolithic on *Malleus malleus*, As24, Recent, Bantayan Island, the Philippines, ×2·5. H, *Dendropoma annulata* semi-endolithic on sandstone, Recent, Harrington Sound, Bermuda, ×4.

substrate, and must be abandoned periodically and rebuilt. Earlier feeding tubes are apparently bored-through near their bases by the mollusc, and usually break away, leaving scars on the shell surface (Text-fig. 3F–G).



TEXT-FIG. 3. A, free-living specimen of *Serpulorbis riisei*, Recent, St Bartholomew, × 9 (SM). B–C, two views of a specimen of *Serpulorbis* sp. cemented only in its juvenile stage, Recent, Guaiaquil, Ecuador, × 1 (SM). D–E, *Petaloconchus* (*Macrophragma*) *intortus*, It11–12, Pliocene, Cyprus, × 1·5 and × 1·2, respectively (UU). The specimens in D are attached to a tube of the polychaete *Protula isseli*, and grew in the same general direction as the host. The specimens in E show a 'relay-race' growth pattern (see text for details). F–G, *Serpulorbis* sp., Recent, unknown locality, × 0·8 and × 0·5, respectively (SM); see text for details.

Boring. Vermetids are often capable of removing small amounts of material from calcareous substrates (e.g. Text-fig. 2F). The actual mechanism is unknown, but the weak radula and thin, chitinous operculum tend to exclude mechanical abrasion as the principal boring action. It is possible that this capability has evolved from a character common among closely coiled gastropods, in which a thin layer of shell material is etched from the surface of the preceding whorl, prior to cementation of this to the inner margin of the shell aperture. This may remove epibionts and outer shell layers weakened by micro-borings, thereby increasing the adhesion between adjacent whorls and enhancing the mechanical stiffness of the shell. It is likely that substrate-etching in vermetids enhances the adhesion of the shell to the substrate.

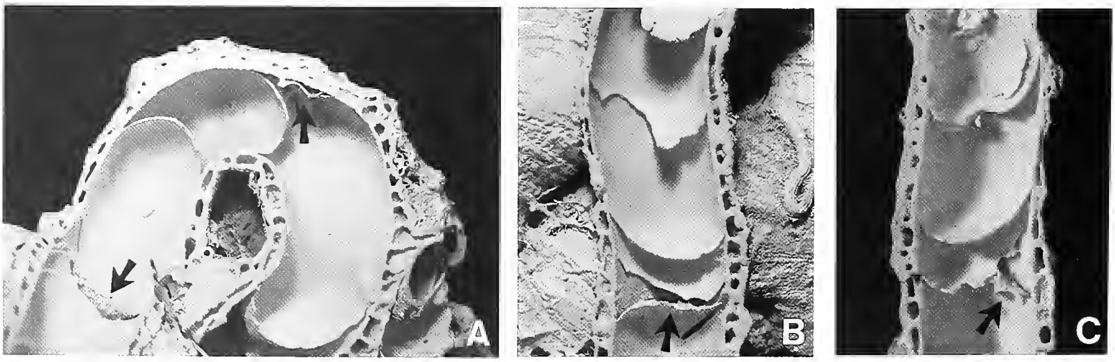
Some species etch the substrate to a larger extent, and their whorls are partly or totally embedded in it (Text-fig. 2G–H). In these cases, substrate-etching may provide the gastropod with a way to economize on the amount of shell material secreted: in fact, the shell wall lining the etched region is extremely thin. Another possible function for substrate-etching is in providing a source of calcium carbonate that may allow an increased growth rate of the shell.

Dendropoma annulata, after reaching 5–10 mm in shell length, becomes embedded in the substrate, and its exposed region is flush with or slightly elevated from the surrounding surface of the substrate (Text-fig. 2H). This semi-endolithic habit requires the substrate to be gradually removed in order to provide growing space. In most of the observed specimens, the aperture is bent at an angle of about 90° to the direction of growth, and its whole perimeter is surrounded by shell material. In this case, periodic removal of shell material, in addition to substrate, must take place in the direction of growth. As noted by Gray (1833, p. 801), *Dendropoma*, when coiled, is often semi-endolithic in its own earlier whorls.

D. meroclista (see Hadfield *et al.* 1972) possesses a characteristic constriction of the shell aperture. Since the inner shell diameter increases posterior to the constriction, the constriction itself must be secreted continuously at its anterior margin and resorbed simultaneously at its posterior margin during growth, thus effectively 'moving' forward.

The Palaeogene *Elliptovermetus* was deeply semi-endolithic in calcareous substrates. For this reason, it was regarded as a subgenus of *Dendropoma* by Keen (1961). However, *Elliptovermetus* is unique in the elliptical cross-section of its whorls. It is possible that this taxon was simply convergent with, rather than related to *Dendropoma*.

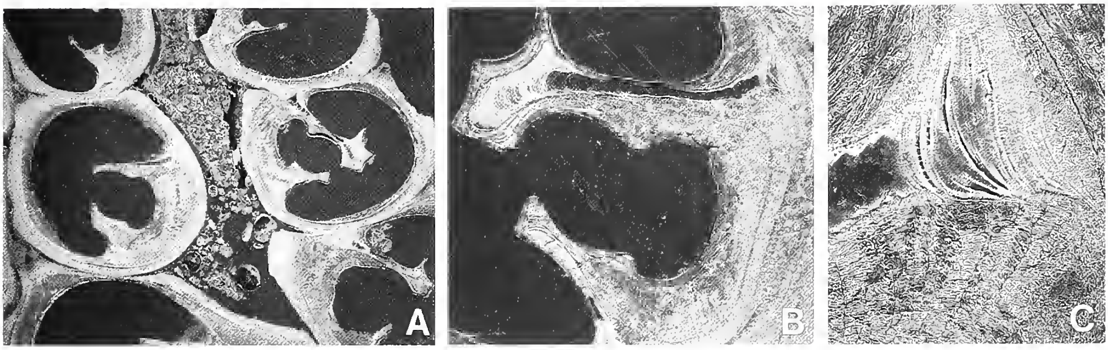
Adaptations to sessile life. Sessile cemented organisms face two problems: overgrowth or fouling by epibionts, and erosion of the substrate. In *Vermetus* and *Spirorbis*, earlier shell portions are closed-off by a series of anteriorly concave septa deposited on the inner shell wall (Text-fig. 4). In extreme cases, the total length of the shell can be several times the length of the shell cavity. Septa are built at rather irregular intervals (Text-fig. 4), but their invariable occurrence and the approximately constant length of the body cavity in synpatric individuals suggests that construction of the septa is pre-programmed, and not triggered by external events such as shell breakage or boring.



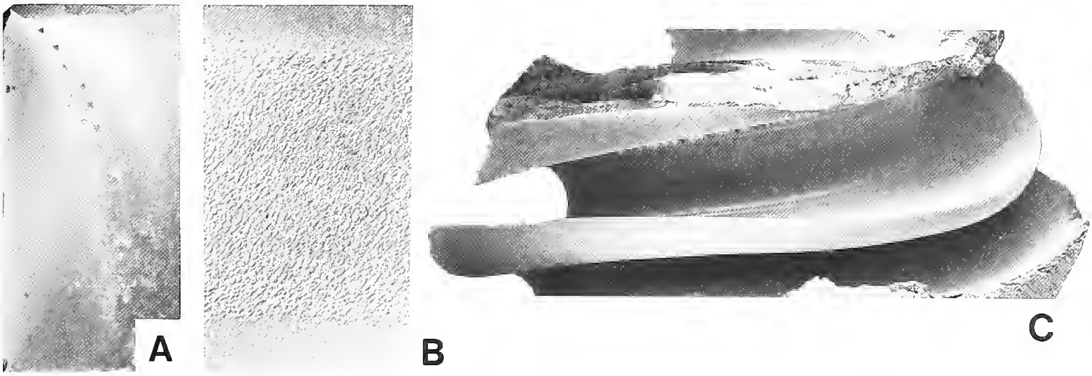
TEXT-FIG. 4. A–C, longitudinal sections of *Serpulorbis* sp. (same species as in Text-fig. 3F–G), Recent, unknown locality, × 1·5 (SM). Several anteriorly concave calcareous septa are visible. Arrows indicate the remains of a few organic, anteriorly convex septa.

One of the adaptive values of septa is obvious: the shell can be quickly extended to avoid overgrowth, without waiting for the soft parts to keep up with growth. Septation and fast shell growth are also indirect defences against endolithic organisms, which settle preferentially on old and worn portions of the shell. In addition, these adaptations may counteract erosion of the substrate by continuously attaching the most recent portion of the shell to a new region of substrate.

Septa are rare in *Petaloconchus*, and appear to be secreted only as a response to shell breakage or boring. Instead, this genus builds two internal ridges adherent to the columellar region of the



TEXT-FIG. 5. A–C, transversal sections of *Petaloconchus intortus*, It13, Pliocene, Cyprus, × 18, × 30 and × 180, respectively (UU). The apex is at top.



TEXT-FIG. 6. A–C, columellar region of *Petaloconchus intortus*, It14, Pliocene, Cyprus (UU). A, spinose processes, *c*. one whorl inside the aperture, × 8. B, myostracum, about three whorls inside the aperture, × 50. C, adapical ridge (lowermost) and incipient abapical ridge (uppermost), about five whorls inside the aperture, × 8.

inner shell wall (Text-figs 5, 6C). The two ridges display a structurally distinct, probably organic-rich core (Text-fig. 5B–C). A few smaller, secondary ridges are often located on the two main ones (Text-fig. 5B).

The extent of the two ridges is not constant throughout the shell. The following description is based on adult specimens of *P. intortus*, and therefore does not necessarily reflect a developmental sequence (which might be masked by secondary secretion and resorption). Both ridges are totally absent in the earliest whorls. The adapical ridge appears first, followed by the abapical one. After two to three whorls of approximately constant appearance, the abapical ridge gradually disappears, followed by the adapical one (Text-fig. 6C). The ridges are again absent in the last three–four whorls.

The soft parts of *Petaloconchus* reflect the presence of the ridges. Unlike in other vermetids, the posteriormost region of the viscera consists of a long and narrow appendix, which apparently contains only gonad tissues (Morton 1965). The appearance of the ridges may, therefore, be associated with the onset of sexual maturity. The appendix is housed between the two ridges, and is apparently responsible for their secondary thickening, which takes place almost exclusively on their facing sides (Text-fig. 5B). The ridges appear to sustain the appendage, and may also provide a resting surface for the 'bottom' of the visceral sac near the insertion of the appendix. In the absence of septa, the ridges may therefore function in reducing the size of the soft parts with respect to the shell cavity, and in allowing the mollusc to abandon quickly earlier portions of the shell.

The inner shell wall in the columellar region bears, in the last one or two whorls, several roughly aligned, irregularly spaced spinose processes (Text-fig. 6A). The significance of these structures is unknown. The preceding one to two whorls bear an elongated myostracum with a rough surface (Text-fig. 6B).

Secondary soft-bottom forms. Sessile life on the soft bottoms requires adaptations to counteract sinking into the substrate, burial by sedimentation and accidental overturning. Like many other sessile organisms, vermetids can colonize soft bottoms by attaching to objects lying on the sediment.

A Pliocene species of *Petaloconchus* (*Macrophragma*) is often attached to the tubes of the soft-bottom serpulid *Protula*. These polychaetes build a straight upward tube that may reach a few hundreds of mm in length and is anchored at its bottom by cementation to a solid substrate and/or burial in the sediment. *Petaloconchus* built a spiral shell adhering to the upward portion of the polychaete and following its upward direction of growth (Text-fig. 3D).

The vermetid in Text-figure 3B–C was attached to a small substrate in the juvenile stage. It later uncoiled and started to grow away from the substrate (as indicated by bryozoans encrusting the whole perimeter of the shell in its central portion) and probably straight upwards. At this stage, the shell was probably stabilized by burial of its early, coiled portion. The capability of attaching to solid substrates was not lost, as shown by a small shell fragment attached to the vermetid shell a short distance from its coiled portion.

Several vermetids are cemented in the juvenile stages, but become uncoiled and unattached during growth, and lie freely on or within the sediment. The cluster of two specimens in Text-figure 3F–G was cemented to a substrate (probably a piece of wood) that decayed during the juvenile stage, as shown by the fact that the attachment scar visible on the early whorls is missing in the adjacent regions of later whorls. One of the two specimens died and partly broke off, while the second was evidently collected alive. The approximately flat outline of this cluster causes it to have two stable orientations on a horizontal surface. The zigzag geometry of the last portion of shell and the numerous scars of feeding tubes directed in opposite directions (Text-fig. 3F) show that the organism was frequently flipped over, and that each time it reacted by building a feeding tube in the upward direction.

Certain soft-bottom vermetids are less dependent on the presence of a suitable substrate. A few species are commonly non-cemented, or possibly attach to substrates not larger than their protoconchs (Text-fig. 3A). These forms lie freely on or within soft sediments, and are small and irregularly shaped. As in other secondary soft-bottom dwellers, miniaturization, probably coupled with a short life span and early sexual maturity, may represent a stepping-stone into the new environment. The onset of reproduction at an early stage would decrease the risk of premature death from the hazards of sessile life on unstable sediments. All these species, however, are also known to cement facultatively to large substrates in the manner typical of vermetids.

Septation is an excellent preadaptation to sessile life on soft sediments. In addition to preventing smothering by sedimentation or overturning, this character allows the shell to achieve a large size, and therefore a large surface area, without increasing shell weight excessively. This reduces the chances of sinking into the sediment and of accidental disturbance. At the same time, shell growth can take place without the need for the soft parts to increase correspondingly in length. Not surprisingly, the shell portion closed off by septa is especially long in soft-bottom species.

A cluster of several individuals of the same species as the one shown in Text-figure 3F–G, probably collected from soft sediments, was sectioned. In addition to numerous anteriorly concave calcified septa, traces were found of a few organic septa, anteriorly convex, immediately preceding a calcareous septum, and apparently extending backwards into a lining of the inner shell walls (Text-fig. 4). These organic septa are apparently a membrane secreted before the shell chamber was sealed off. This membrane may retard or prevent the closed-off chamber from being filled with sediment pouring in through small borings (in fact, early whorls are heavily bored by clionid sponges, with openings on the outer and, sometimes, inner shell surfaces). The anteriorly convex geometry of the organic septa may be a result of shrinking, either during the life of the mollusc, or as a result of desiccation after collecting. A tantalizing, but still unproven, possibility is that the organic septa may have contained bubbles of gas, decreasing the specific gravity of the shell and preventing it from sinking into a soft sediment. Field observations on the contents of the closed-off chambers in this and similar species will be necessary to test this hypothesis.

Several vermetids form monospecific clusters of tubes, occasionally of considerable overall size. Sometimes, these aggregates are not cemented to solid substrates but lie on soft sediments (e.g. see Mörch 1861). A large size is a common adaptational strategy in secondary soft-bottom dwellers (e.g. oyster-like bivalves; Seilacher 1984). Large organisms are stable because their bulk makes them difficult to dislodge. The same goal is achieved by a cluster or colony of small individuals attached to each other. This is the case in soft-bottom colonial corals and nodular calcareous algae.

Aggregates of vermetid tubes may also be regarded as mud-floats or snow-shoes, since their low specific gravity (compared with most oysters, corals and calcareous algae) makes sinking unlikely. As in solitary soft-bottom vermetids, shell septation becomes highly adaptive in this context by reducing shell weight and preventing sediment from filling empty shells. Thus, empty vermetid tubes retain their mud-floating function, and provide a stable substrate for subsequent generations.

In a few cases (especially in the genus *Petaloconchus*), juveniles settle on the uppermost portions of an older individual, and continue its upward growth (Text-fig. 3E). This 'relay-race' mode of growth may be an effective way to counteract rapid sedimentation, and has also been observed in soft-bottom oysters (e.g. Chinzei *et al.* 1982, fig. 4).

SILIQUARIIDAE

Unlike vermetids, most siliquariids are not cemented to a substrate but live (or, presumably, lived) embedded within sponges. Aside from this, very little is known of the life habits of this family. The earliest siliquariids are from the Middle Triassic.

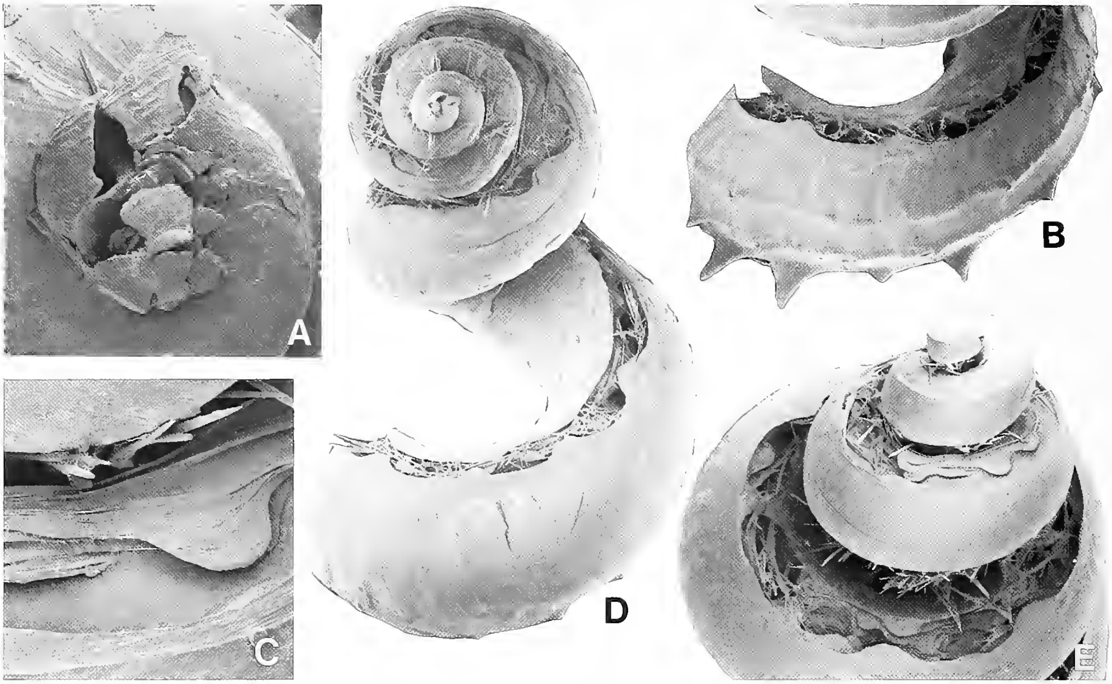
Most siliquariids possess an elongated apertural slit along the right side of the spire. This slit may remain open for several whorls, and sometimes spans the entire length of the shell cavity.

Growth. Several specimens of *Siliquaria anguina* were available embedded in their host sponges. It proved exceedingly difficult to clean these specimens without breaking the larval shell. The only intact protoconch collapsed when coated for SEM observation (Text-fig. 7A). Observations with a light microscope prior to coating showed a very thin, translucent shell composed of two to three whorls, significantly smaller than the larval shell of most vermetids and bearing a weak pustulose sculpture changing into an axial sculpture on the last whorl. At this stage, probably representing a free-living habit, the shell has no slit. Subsequent growth takes place without the change in orientation of the coiling axis observed in all vermetids.

Juvenile *Siliquaria* probably settle on a suitable sponge and become embedded passively by growth of the host. At this point, the shell starts to assume its adult shape and sculpture, and the slit originates as a broad sinus (Text-fig. 7A, D–E). The slit on the first 1–3 post-larval whorls is closed by a secondary deposit of shell material level with the surrounding regions of the shell (Text-fig. 7A, E). In later whorls, the edges of the slit are thickened by several subsequent layers, and the slit is closed by a final 'ceiling' deeply sunk within the slit (Text-fig. 7C, E).

The first few whorls are rather closely coiled, and adjacent whorls sometimes touch each other. Even in these cases, there is no cementation between successive whorls. Later whorls are coiled loosely but always visibly. Unlike vermetids, which are capable of bending their shell sharply, *Siliquaria* appears unable to 'manoeuvre' in close quarters. Instead, its whorls are wound laxly around obstacles, and the shells of intertwined individuals can usually be moved with respect to each other. The aperture projects slightly from the substrate, as shown by common encrustations by epizoans in the apertural region of live-collected specimens.

The earliest post-larval whorls are thickened secondarily and the apical region is closed by a septum. Occasionally, several septa are present. They are highly concave in the anterior direction, rather than approximately hemispherical like in the Vermetidae, and may occupy a quarter whorl or more.



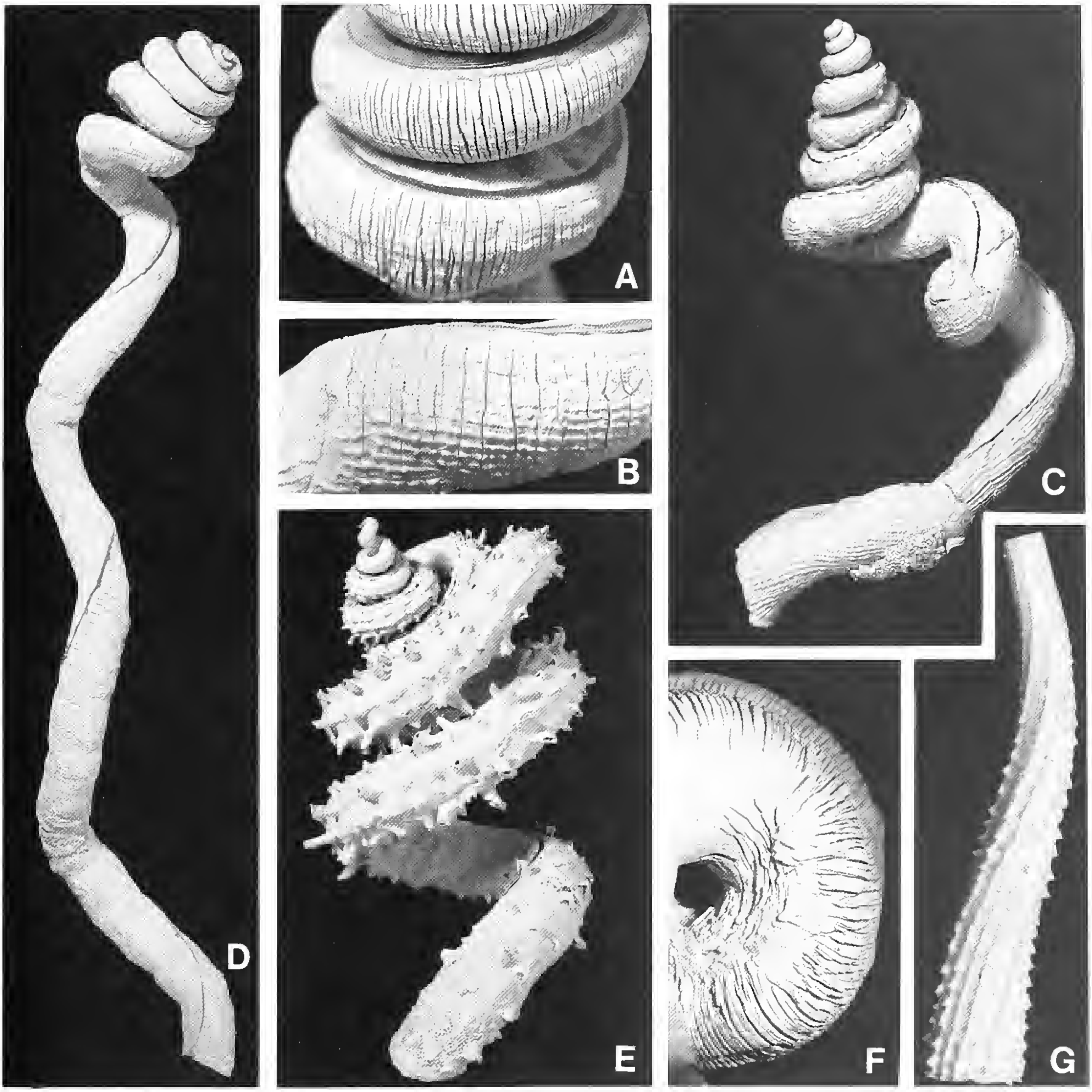
TEXT-FIG. 7. A–E, early whorls of *Siliquaria anguina*, Recent, Cebu Island, the Philippines. A, As26, collapsed protoconch, × 100. B, As27, onset of spiny sculpture, × 8. C, As28, secondarily closed shell slit, × 75. D, As26, juvenile shell, showing slit filled with sponge spicules (same specimen as in Text-fig. 7A), × 16. E, As28, early whorls of juvenile specimen, showing the changes in morphology of the shell slit, × 16.

Adaptations to embedding. Siliquaria can apparently adapt to the growth rate of its host sponge by varying the degree of translation of the shell aperture about the coiling axis and by changing the direction of growth (Text-fig. 8C–E). This is responsible for the rather irregular aspect of siliquariid shells.

In *Siliquaria*, the shell slit remains open for the whole length of the shell cavity, which in adult *S. ponderosa* (Text-fig. 8D) spans over 90 per cent. of the total shell length. In *Pyxipoma*, on the other hand, the slit is open for no more than half of the shell length (and often considerably less). A corresponding slit in the mantle faces the shell slit (Morton 1951). The mantle slit of the Siliquariidae is not homologous to the superficially similar mantle slit of vermetids, which is present only in females, functional in brooding, located in a different position and not matched by a shell slit. The gill of *Pyxipoma* is as long as the shell and mantle slits (Morton 1951). The same probably applies also to the much longer slits in *Siliquaria.*

It is very likely that the shell and mantle slits and the extremely elongated gill of the Siliquariidae are coadaptations to life within sponges. Morton (1951) proposed a function for these structures in eliminating waste products of the gastropod. However, my observations on *S. anguina* show that the slit is partly filled with sponge tissues and spicules (Text-fig. 7B, D). Any particulate material ejected by the mollusc through the slit should clog it in a short time. In addition, the mouth and anus of *Pyxipoma* (and, presumably, *Siliquaria*) are located close to the shell aperture, and faeces and other waste products are therefore discharged conveniently there.

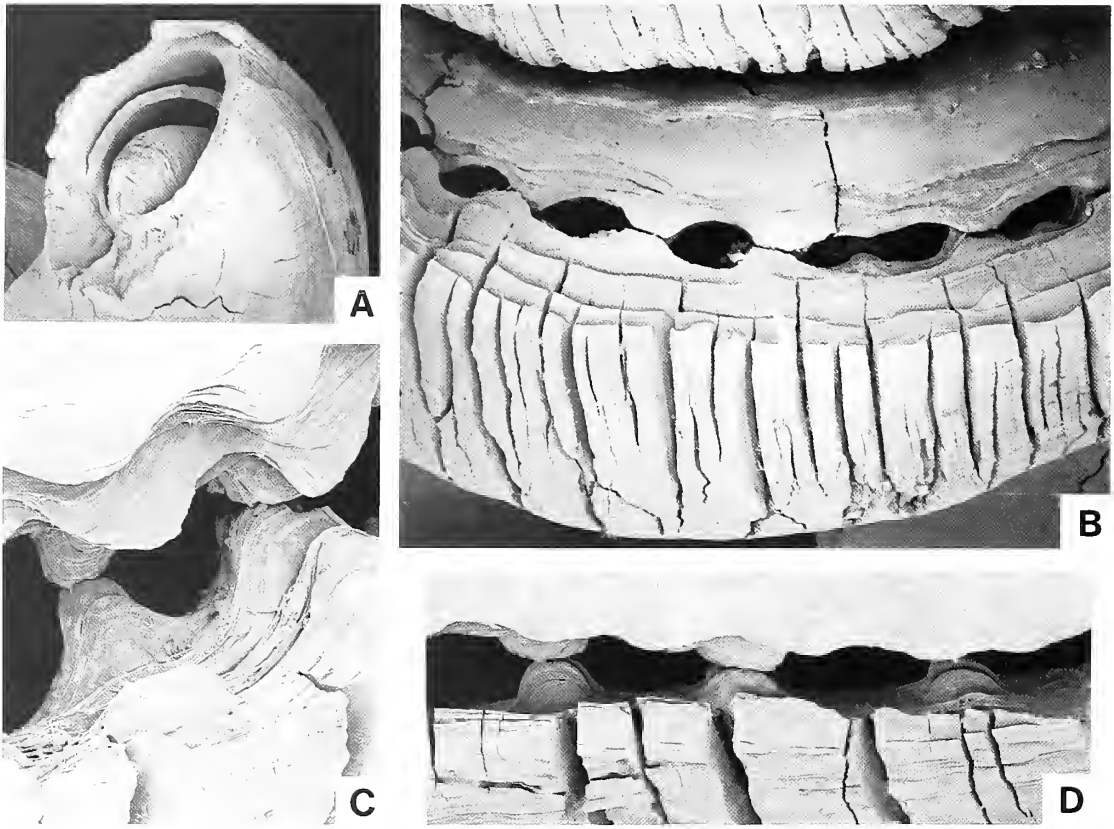
A passage of solid matter (e.g. fragments of sponge tissues) from the host into the mantle cavity of the gastropod appears unlikely. Although this might conceivably provide a source of food for the gastropod, it is unlikely that the mantle tissues and/or ctenidia are sufficiently strong to extend into the slit and tear apart pieces of sponge facing the shell slit. In addition, the region of the mantle



TEXT-FIG. 8. A–B, *Siliquaria ponderosa*, Recent, unknown locality, × 3 (SM); details of outer surfaces of the whorls in coiled (A) and uncoiled (B) regions. C, *Siliquaria cumingi*, Recent, Awaji-shima, Japan, × 1·5 (SM). D, *S. ponderosa* (same specimen as in Text-fig. 7A–B), × 0·7. E, *S. anguina*, As25, Recent, Cebu Island, the Philippines, × 1·3. F, *S. ponderosa* (same specimen as in Text-fig. 6A–B, D), umbilical view, with transversal and longitudinal crack patterns, × 3·5. G, *Pyxipoma brevifissurata*, Middle Eocene, Paris Basin, France, × 3·5.

cavity facing the slit houses the exhalant current. Any materials entering the slit would therefore be carried to and ejected from the shell aperture without passing through the ctenidia. The same consideration tends to exclude a water current passing from the sponge to the mollusc. Moreover, such a current would be of little use to the mollusc, since it would consist of water that has already been strained of food particles by the sponge.

The remaining alternative is a water flow from the mantle cavity of the gastropod into the canal system of the sponge. In contrast with the other alternatives, this would provide obvious advantages for the gastropod. Two interpretations are possible. If the slit is connected to the exhalant canals



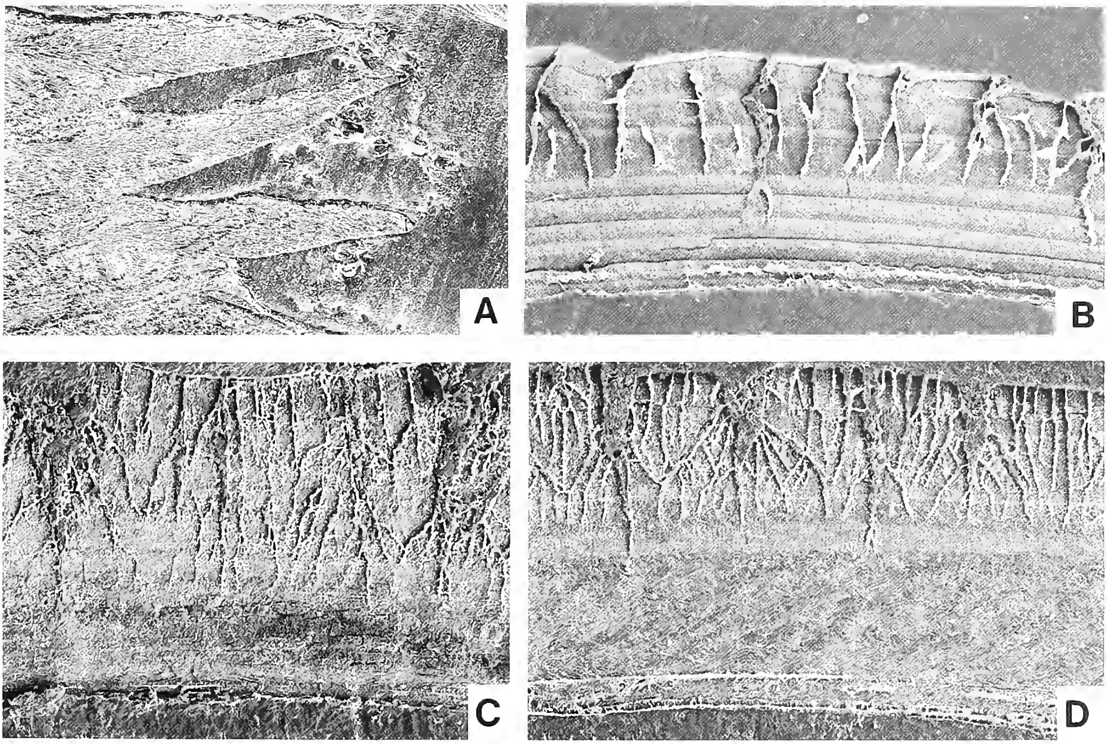
TEXT-FIG. 9. A–B, *Siliquaria* sp., Pliocene, Diolo, Italy. A, It15, septa in apical region, × 8. B, It16, secondarily enlarged slit and whorl, × 16. C–D, *Siliquaria cumingi*, Recent, Awaji-shima, Japan (SM). C, detail of denticles along facing margins of the shell slit, × 60. D, detail of shell slit, × 40.

of the sponge, the exhalant current of the gastropod would mix with the exhalant stream of its host. In this case, the adaptive value of the slit would be of reducing or avoiding the need for the mollusc to maintain an exhalant current following the extremely long and narrow path back to the shell aperture along the mollusc mantle.

A completely different effect would be achieved if the sponge tissues facing the shell slit of *Siliquaria* contain ostia or inhalant canals. In this case, the pumping action of the sponge would suck water from the mantle cavity of the gastropod. The resulting draft would continuously force new water into the shell aperture and through the ctenidia. In this case, *Siliquaria* might take advantage of the feeding activity of the host sponge and partly impair it (by feeding the host with strained water), with no corresponding advantage for the host. This habit could therefore be characterized as parasitism. Also this arrangement would reduce or avoid the need for the exhalant current to reach the shell aperture.

The topological relationships of *Siliquaria* and the tissues of its host have never been studied. In the available material of *S. anguina*, openings in the shell slit often seem to correspond to 'holes', or channels, in the sponge tissues (Text-fig. 7B, D). However, it is not possible to decide whether these holes are inhalant or exhalant canals.

The above interpretations could be verified in living material by observing whether the exhalant current of *Siliquaria* leaving the shell aperture is weaker than the corresponding inhalant current. A connection between the water systems of the mollusc and its host could be detected by injecting

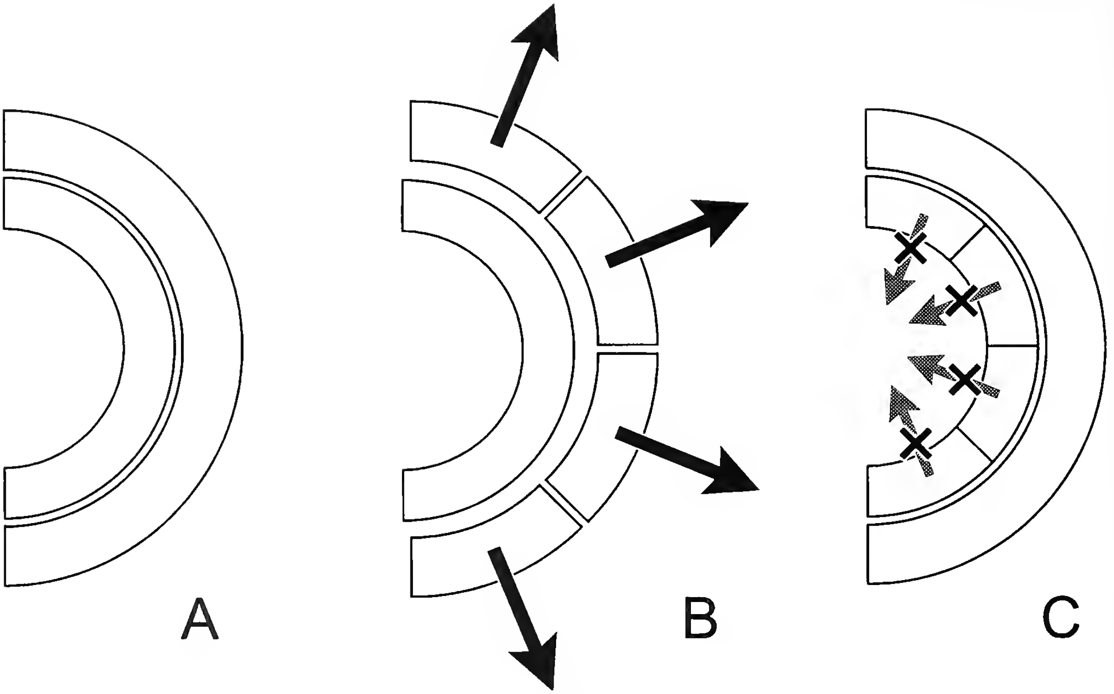


TEXT-FIG. 10. A, *Siliquaria anguina*, As29, transversal section of inner margin of the shell slit, Recent, Cebu Island, the Philippines, × 160. The small bodies located between the frills of the slit edge are transversally sectioned sponge spicules. B–D, *Siliquaria* sp., It17–19, longitudinal sections of the outer periphery of the shell whorl, Pliocene, Diolo, Italy, × 100, × 150 and × 150, respectively. The cracks are filled with embedding resin, and stand up in relief after chemical etching.

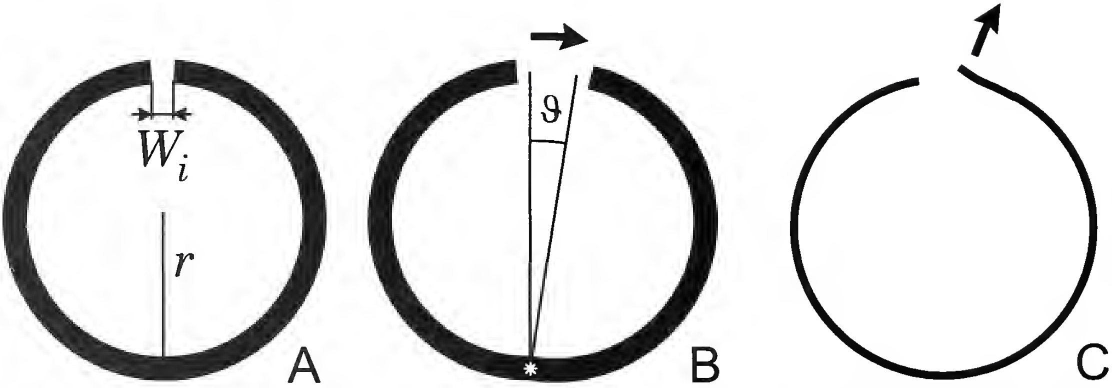
a soluble tracer in the inhalant stream of *Siliquaria*, and looking for the tracer in the exhalant stream or in the tissues of the sponge. Only a cytological examination, however, will show whether *Siliquaria* is commensal or parasitic on its host sponge.

Two types of shell sculpture are represented in *Siliquaria*. Most species, including *S. ponderosa* (Text-fig. 8D), *S. cumingi* (Text-fig. 8C) and *S.* sp. (Text-fig. 9), appear smooth or lightly sculptured at a superficial examination. On the other hand, a small group of species, including *S. anguina*, possesses long and fragile fluted spines (Text-figs 7E, 8B). This last type of sculpture is extremely effective in anchoring the shell within its host sponge (as easily experienced by trying to extract representatives of these species from their substrate). The spines may also have a simultaneous function as shock absorbers, by breaking under the impact of objects tossed by waves, and thereby protecting the shell in a manner analogous to the function proposed for echinoid spines (Strathmann 1981). Obviously, this function applies only to spines located close to or above the surface of the host sponge. The spiny *Siliquaria* are invariably thinner-shelled and more fragile than the smooth ones. Typically, spines are absent in the earliest whorls (Text-fig. 7D–E).

A close examination of the 'smooth' species of *Siliquaria* reveals a unique relief pattern consisting of deep, narrow cracks starting at the right rim of the slit and running up to 180° around the whorl in a roughly axial orientation (Text-figs 8A–B, F, 9B, D). These cracks cross the growth lines, and must therefore be a secondary feature. Since the cracks are wider near the surface, they must have appeared at the outer shell surface and extended progressively to deeper, secondary shell layers while the shell was gradually thickened. In *S. ponderosa* (but not in the other species observed for



TEXT-FIG. 11. Secondary enlargement of the slit in *Siliquaria* can take place by cracking into wedges and expansion of the outer half of the whorl (B versus A), but not of the inner half (C).



TEXT-FIG. 12. A, schematic cross-section of shell whorl in *Siliquaria*. B, the same after cracking and expansion. C, a thin shell wall can flex in the neighbourhood of the slit. See text for details.

this paper) a second pattern of cracks, perpendicular to the first one, occurs in the region of the whorl diametrically opposite to the slit (Text-fig. 8F).

Sections of the cracks in a plane parallel to the shell slit reveal that each of the major cracks visible at the shell surface branches toward the interior of the shell (Text-fig. 10B–D). The samples in the figures were embedded in epoxy resin, and the resin filling the cracks stands out in relief after etching. Major cracks are often intercalated by a hierarchical system of progressively shallower and narrower cracks (Text-fig. 10C–D). The smallest of these cracks do not branch, or show only an incipient branching. There is no visible difference in shell structure between the cracked and non-cracked regions. This, together with the fact that the spacing and orientation of cracks is slightly irregular, suggests that the location of each individual crack is not predetermined. Rather, the cracks probably become distributed in a self-organizing fractal pattern controlled by the local relief of strain in the immediate neighbourhood of each crack.

In a few cases (Text-fig. 10C), the outer shell surface between two major cracks is convex (in a manner reminiscent of mud cracks), possibly as a result of accumulating stresses within the shell material, rather than being the result of actual shrinkage of the outer layer. The increase in the radius of curvature of the whorl periphery, resulting from expansion of the shell slit (see also below), could be the source of these stresses. Accumulating stresses may also be adaptive in facilitating cracking and thereby in reducing the amount of pressure the mollusc must apply to the shell walls. In fossils, the presence of stresses in the shell material results in occasional post-mortem cracks of the inner margin of the shell slit (Text-fig. 9A–B). Cracks in this region are absent in live-collected Recent specimens.

Restricting the cracks to half of the shell wall prevents the shell stiffness from being compromised. The exclusive occurrence of the cracks on the right side of the shell slit is the result of an obvious geometric constraint. In a dextrally coiled shell (Text-fig. 11A), cracking the right margin of the slit allows the wedge-shaped fragments of the shell to separate as they move away from the slit (Text-fig. 11B). This is the cause of the progressive widening of the cracks during ontogeny. If cracks were located on the inner margin of the slit, instead, the shell wedges would be compressed together when pushed laterally away from the slit (Text-fig. 11C), which would prevent their movement.

As an analogue, architectural arches composed of wedge-shape bricks or stones bear their own weight, as well as the weight of overlying masonry, thanks to the fact that the shape of the arch transforms weight into a lateral force pressing adjacent wedges together. Applying an upward force to the arch, instead, would cause its wedges to separate and the arch to collapse.

That the spacing of cracks in *Siliquaria* is related to the amount of shell coiling is shown by the fact that cracks are less dense in shell portions displaying a large amount of uncoiling (Text-fig. 8B *versus* A). In these portions, widening of the slit results in a lesser amount of reciprocal distancing of the shell wedges. At a limit, transversal cracking would not be necessary at all to widen the slit in a straight portion of shell.

Secondary widening of the slit takes place in two stages. First, the shell is cracked, perhaps by hydrostatic pressure within the mantle tissues, and the wedges are pushed outward. Subsequently, a secondary layer of shell material is secreted on the inner side of the expanded shell, cementing the fragments together. The process is repeated periodically, and at each stage the cracks propagate to the latest shell layer. Obviously, this process would be impossible in a free-living mollusc, because the shell would literally fall to pieces. However, the sponge tissues surrounding the shell form a resilient container that holds the pieces in place until cemented together.

The pressure necessary to break the shell into wedges does not increase appreciably with shell thickness, since the cracks need only to propagate through the last layer of deposited material. It cannot be excluded that expansion of the slit is preceded by partial resorption of part of the inner shell layer. However, the very presence of cracks indicates that resorption of the inner shell layer is not total.

The outward displacement of the right side of the whorl broadens the slit and increases the cross sectional area of the whorl. A quantitative evaluation of these effects can be attempted by means of a simple geometric analysis (Text-fig. 12). I assume that half of the circumference of the whorl is pushed outward (arrow in Text-fig. 12B), pivoting at a point located 180° away from the slit (asterisk in Text-fig. 12B), i.e., where the second pattern of cracks, parallel to the slit, is located in *S. ponderosa*. For small angles of rotation, the cross-sectional area of the whorl and its volume increase by:

$$I \cong \frac{(2r)^2/2 \sin \vartheta}{r^2 \pi} 100,$$

where I is the percentage increase in area or volume, r the whorl radius, and ϑ the angle of rotation. On the other hand, the width of the slit (and hence its open area) increases by:

$$W \cong \frac{2r \sin \vartheta}{W_i} 100,$$

where W is the percentage increase in width and W_i the initial width.

As an example, from measurements of a specimen of *S. ponderosa* we can take an initial inner whorl diameter of 7·8 mm and a slit width of 0·8 mm. Based on the above formulas, rotation of the outer half of the whorl by 5·7° would cause a 10 per cent. increase in the width of the slit and a mere 1·6 per cent. increase in the cross sectional area and volume of the whorl. Actually, a considerable secondary thickening of the shell takes place, as necessary to cement the shell wedges together after each expansion. Therefore, a small displacement of the shell wedges causes the cross sectional area of the whorl to remain constant or actually decrease during growth. This is the situation observed in *S. ponderosa* and *S. cumingi*. In these species, the only significant effect of shell cracking is to widen secondarily the shell slit.

In the Pliocene *S.* sp., the shell slit was sometimes widened to a greater extent. In these cases, shell material was added along the inner and/or outer margins of the shell slit, apparently to counteract an excessive increase in width of the slit (Text-fig. 9B). In these cases, a significant secondary increase of the cross sectional area of the whorl, computed at 10–15 per cent. (or occasionally more) took place. This secondary increase in the volume of the shell cavity might have provided room for larger gills and/or gonads, or may have facilitated the respiratory currents. Therefore, shell cracking and expansion may have a different adaptive value in different species.

S. sp. and *S. cumingi* do not possess the longitudinal pattern of cracks observed in the larger and thicker *S. ponderosa*. In the first two species, the shell is thinner, and shell wedges apparently flex along their entire length, instead of breaking at their base as in *S. ponderosa*. Consequently, a mechanism is needed to prevent these resilient wedges from returning to their original position and close the shell slit once the mollusc stops applying a pressure from within the shell. This function is provided by rounded denticles projecting in facing positions from each side of the slit and touching each other in its middle (Text-fig. 9B–D). Once the facing denticles are separated by pressure within the shell and new shell material is added at their tips, the shell slit is forced to remain open. Significantly, denticles are absent in *S. ponderosa*.

The shell slit of siliquariids has been described in the literature as either being continuous (like in *S. ponderosa*) or consisting of a series of aligned holes (as in *S. cumingi* and *S.* sp.). This description is misleading, since the tips of facing denticles touch each other, but (unlike in the gastropod *Haliotis*), are not cemented together. This allows the denticles to separate at a subsequent growth stage, in order to allow further widening of the slit (Text-fig. 9C). It may be noted that the tips of facing denticles must be slightly separated during their construction, in order to allow mantle lobes to adhere to these regions. Once the mantle retracts from these regions, release of the internal pressure within the shell causes the resilient shell wedges to close the small gaps between the tips of the denticles. This causes an inevitable small 'loss' in the achieved increase of the width of the shell slit and/or whorl.

Transversal cracks, albeit much shorter, narrower and more broadly spaced, are also present in the spiny species *S. anguina* (faintly visible in Text-fig. 7B, D). This species is characterized by a thin shell. The higher flexibility of the shell wall may allow the wedges to flex outwards in proximity of the slit edge (Text-fig. 12C), allowing the cracks in this species to be shorter and less frequent. It is also possible that the minimal amount of secondary enlargement of the slit in *S. anguina* has no adaptive significance, and that the cracks in this species are a vestigial character, left over from earlier evolutionary stages. This is suggested also by the fact that the denticles along the sides of the slit are shaped and spaced irregularly, and sometimes do not occur in facing pairs.

It may be objected that shell resorption would be a more effective way to broaden the slit. However, resorption would necessitate mantle tissues to adhere periodically to the edges of the slit, possibly narrowing or closing it. If *Siliquaria* is dependent on the shell slit for expulsion of the exhalant current, as suggested above, this could impair the flow of water through the ctenidia for an unacceptable length of time. Adhesion of the mantle to the sides of the slit may also be prevented by invasion of this area by sponge tissues (e.g. Text-figs 7B, D–E, 10A).

A further explanation of the peculiar mechanism of secondary cracking could be that shell resorption may not be available (and, in fact, is not observed) in the siliquariid Bauplan. Lastly, no amount of secondary resorption could allow the increase in cross-sectional area of the whorl provided by shell cracking in Pliocene *S.* sp. (see above).

Other siliquariids. *Pyxipoma* differs from *Siliquaria* in its much shorter shell slit. The association of *P. weldii* with sponges is comparable to that of *Siliquaria* (Morton 1951). *Pyxipoma* never reaches large sizes, a factor that may be connected to its relatively shorter gill and slit.

Specimens of *P. brevifissurata* (Deshayes) from the Eocene of the Paris Basin are extremely uncoiled (Text-fig. 8G). Some fragments are practically straight, but remnants of the original dextral coiling are still detectable as a twisting of the sculpture around the shell surface. The morphogenetic significance of this character was discussed by Savazzi (1990*a*). The spiny sculpture and lack of cementation scars suggests life within sponges, but the very short and narrow slit might indicate the lack of a parasitic association like the one proposed for *Siliquaria*, or a lesser reliance on the feeding current of the host.

The Eocene genus *Agathirses* possessed a series of perforations instead of a slit. Each perforation originated as a shallow sinus at the shell margin. Only one or a few perforations were open simultaneously. The rest were closed secondarily by a calcareous plug. The gradually uncoiling shell, spiny sculpture and apparent lack of cementation scars suggests a life habit embedded in a sponge or a comparable organism.

Stephopoma differs from other siliquariids in living attached to rock surfaces (Morton 1951). This form is not truly cemented, but rather lives loosely embedded in the layers of encrusting epibionts that cover the substrate. This genus lacks a shell slit, and feeds by ciliary currents as well as ctenidial sweeping (Morton 1951). Unlike the Vermetidae, the shell of *Stephopoma* is not septate, and consequently the length of the soft parts imposes a limit on the maximum shell length. Also unlike the Vermetidae, dextral coiling in *Stephopoma* is always evident, even in the openly coiled portions.

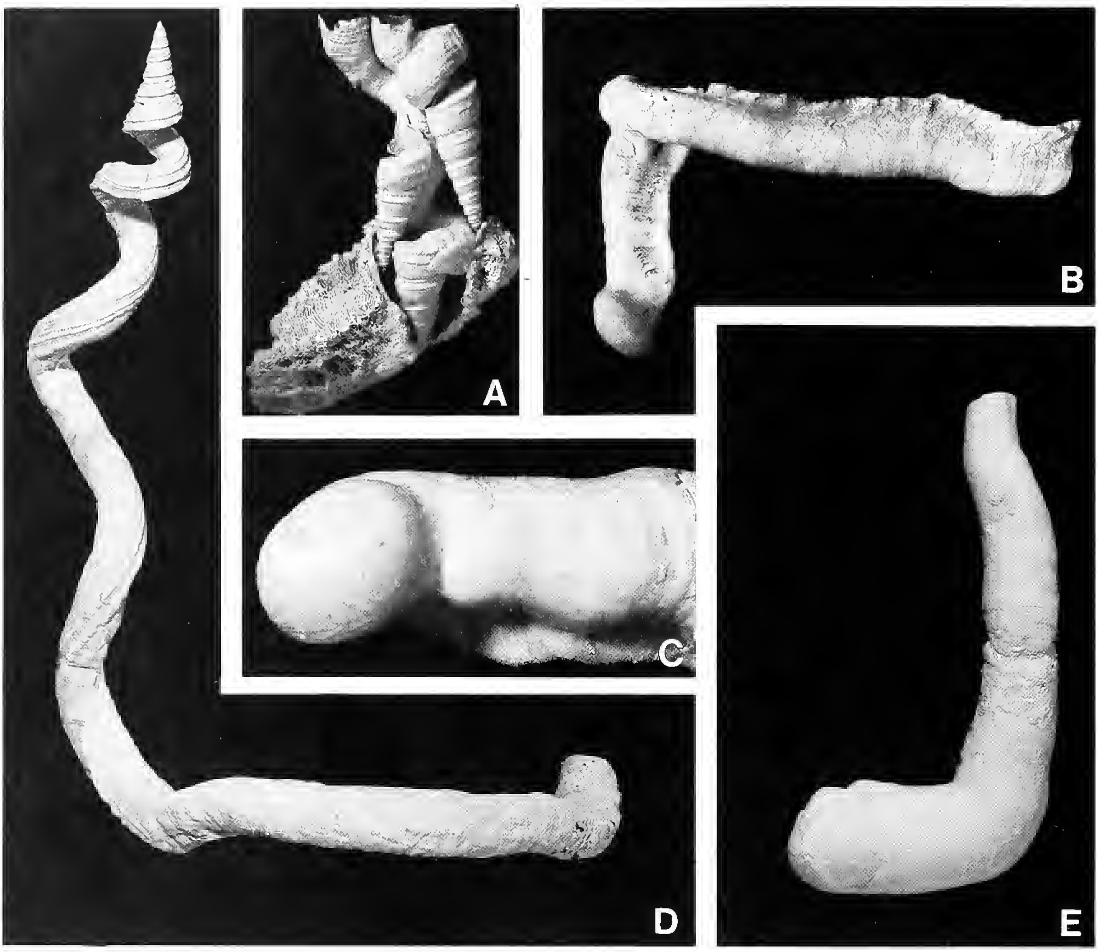
Judging from the illustration by Cossmann (1912, pl. 10, fig. 29), the Miocene '*Vermetus*' *circumlobatus* appears to possess many regularly spaced, slightly flaring traces of sinuses in a position corresponding to the siliquariid slit. These traces are too small and numerous to be the scars of broken feeding tubes. It is possible that this species is actually a siliquariid related to *Agathirses*.

None of the above forms displays the secondary shell-cracking pattern described in *Siliquaria*.

OTHER ATTACHED GASTROPODS

The turritellid *Vermicularia* is convergent with the Vermetidae in the habit of cementing to a solid substrate (Morton 1953; Gould 1968, 1969). Unlike the Vermetidae, however, *Vermicularia* has a relatively large free-living, regularly coiled stage (Text-fig. 13A, D). In addition, this genus can remain facultatively at the free-living stage by retaining its juvenile life habit (Gould 1968). *Vermicularia* builds internal septa only in the first shell whorls, usually as a response to boring by clionid sponges. In these cases, the septa usually continue forward into a thick lining of the inner shell wall that may extend for several whorls and reduces considerably their inner cross sectional area (pers. obs.). Usually, these septa do not reduce substantially the length of the shell chamber with respect to the total shell length.

A few Eocene species referred by Cossmann (1912) to *Vermicularia* (*Anguillospira*) are septate and completely uncoiled. They might be vermetids, rather than turritellids. Since they appear to lack attachment scars, they probably were obligatory soft-bottom dwellers. A few other forms, also referred to *Vermicularia* by Cossmann (1912), resemble this genus but show only an incipient



TEXT-FIG. 13. Other Recent attached gastropods. A, *Vermicularia spirata* attached to coral, Harrington Sound, Bermuda, × 1·5. B–C, *Magilus antiquus*, Mauritius, × 0·5 and × 1·2, respectively (MN). D, *Vermicularia lumbricalis*, Senegal, × 0·7 (SM). E, the tube-dwelling bivalve *Teredina personata*, Middle Eocene, Grignon, France, × 1·2. This specimen shows a conspicuous secondary elongation of the crypt at its siphonal extremity.

uncoiling, or (in the subgenus *Casimiria*) possess closely coiled whorls with a broad umbilicus. Since these forms display neither attachment scars nor the irregular development that should be expected from completely sessile forms, they may represent different life habits. It is possible that the resemblance of these forms to *Vermicularia* and to each other is due to convergence, and that they represent a polyphyletic evolutionary trend within the Turritellidae.

The coralliophilid *Magilus* cements its shell to colonial corals and becomes embedded by growth of the host. Its shell uncoils irregularly, much like a vermetid but without cementation scars (Text-fig. 13B–C), and becomes filled secondarily with a solid, very heavy deposit, leaving a short conical cavity for the soft parts. The regularly coiled apical whorls of *Magilus* are much larger than in *Vermicularia* (Text-fig. 13C). However, it is likely that *Magilus*, like most coralliophilids, is also essentially sedentary during the regularly coiled stage.

The coralliophilid *Rapa* becomes embedded in soft coral. The shell of *Rapa*, however, is regular or only slightly irregular. The only shell character that may be related to its life habit is the very elongated, ventrally closed siphonal canal present in a few species. Other coralliophilids attach to soft corals by folding the margins of the aperture around thin coral branches (e.g. see Kosuge and Suzuki 1985).

The Hipponicidae are permanently attached to a substrate (typically a mollusc shell) by a calcareous plate, probably not homologous to an operculum, secreted by the foot. The Miocene *Rothpletzia rudista* is an extremely specialized hipponicid attached to nodules of calcareous red algae lying on soft sediments (Rothpletz and Simonelli 1890). The foot plate is deeply cup-shaped and much larger than the shell proper, which is flattened into a broad cone (in fact, the original description regarded the foot secretion as an apically cemented shell, and the true shell as an operculum; Rothpletz and Simonelli 1890). The soft parts and the shell margins were continuously elevated above the surface of the substrate by growth of the foot secretion and by septation of its internal cavity. *Rothpletzia* may be regarded as morphologically convergent with rudist bivalves.

The shell of the Silurian tubinid *Semitubina sakoi* was embedded in a symbiotic colonial coral. In the adult shell of *S. sakoi*, the last whorl was openly coiled and extremely thin-walled (Kase 1986). Other tubinids possess long and slender spines, comparable to the sculpture of *Siliquaria anguina* (see Knight *et al.* 1960). It is likely that these gastropods were embedded within sponges, hydroids or other organisms. The regular (albeit uncoiled) shell geometry of these forms suggests that they were mobile epifaunal forms carrying a relatively small encrusting host, rather than sessile forms like the Siliquariidae.

The Carboniferous pseudozygopleurid *Helminthozyga* possessed a regularly coiled shell in the juvenile stage, but later in ontogeny became irregularly uncoiled in a manner reminiscent of *Vermicularia* and *Siliquaria*. *Helminthozyga* does not appear to have been cemented to a substrate. It is possible that, like *Siliquaria*, it was sessile and embedded within a larger organism.

CONCLUDING REMARKS

The adaptations that enable cemented vermetids to survive fouling, overgrowth and shell breakage appear to be reasonably good preadaptations to the evolution of free-living forms. In fact, several vermetids can live facultatively in soft-bottom environments, but no Recent or fossil species can be characterized as an obligatory soft-bottom form.

Vermetids can be compared with tube-dwelling bivalves (Savazzi 1982). Several genera of Gastrochaenidae, Teredinidae, Pholadidae and Clavagellidae have evolved into secondary soft-bottom dwellers, either as a facultative or obligatory life habit. These bivalves build calcareous envelopes, or crypts, that completely encase the soft parts and isolate them from the surrounding sediment except for siphonal and, sometimes, accessory openings. The shell may be free within the crypt, or one or both valves may be attached to it. The siphonal extremity of the crypt can be secondarily extended in length (Text-fig. 13E). This allows the organism to avoid smothering by sedimentation and to react to disturbances of life position by changing the direction of growth, and therefore has essentially the same adaptive significance as growth of the vermetid shell at its aperture.

Tube-dwelling bivalves have no analogue of the septation observed in vermetids. Instead, these bivalves react to burial or encroaching epibionts by extending their siphons. This is enabled by the higher efficiency of the gills in most boring and tube-dwelling bivalves, compared with gastropods. The Lithophaginae are the only boring bivalves that react to overgrowth of the substrate (typically, a living coral) by moving in the posterior direction and filling the anterior region of the borehole with meniscus-shaped layers of secondary lining (e.g. see Krumm and Jones 1993). This filling material could be regarded as a potential preadaptation to life on soft bottoms, like septation in the Vermetidae. However, the Lithophaginae did not evolve into soft-bottom forms, probably because the lesser efficiency of their gills did not allow the development of long siphons (cf. Savazzi 1982).

The Siliquariidae possess morphological adaptations partly resembling those of the Vermetidae. However, the obligatory association with sponges of most siliquariids may have constituted an evolutionary closed-alley that prevented the radiation of these gastropods into the soft bottoms. Association of the Coralliophilidae with coelenterates, together with the heavy nature of the secondary filling in *Magilus*, may have had a similar constraining effect on the evolution of this family.

The secondary enlargement of the shell slit and/or cross sectional area of the whorl in *Siliquaria* has no parallel among gastropods. However, a few bivalves are known to modify their shell geometry secondarily by cracking selected portions of their shells and moving them relative to each other (Chinzei *et al.* 1982; Savazzi 1990*b*). Secondary cracking also takes place in the pseudoligamental region of rostroconchs. In all these cases, only one crack (or bundle of cracks) is present in each valve or shell. In contrast, the shell of *Siliquaria* typically cracks into several hundred wedges during growth.

Siliquariid gastropods have been largely neglected by both taxonomists and functional morphologists. As shown by this paper, these gastropods display several extremely peculiar characters, some of which need to be confirmed by studies on living specimens. So far, only one siliquariid species has been observed alive (Morton 1951), and its morphology and life habits are atypical of the family.

The general failure of attached gastropods to mimic the evolutionary pathways of bivalves (e.g. see Seilacher 1984) and become secondary soft-bottom dwellers may be explained, at least in part, by the constraints imposed by earlier evolutionary 'choices' (see above). An additional reason may be that gastropods have evolved into hard-bottom sessile organisms later than bivalves (mostly in the late Mesozoic and/or early Cenozoic for gastropods, *versus* the late Palaeozoic and Mesozoic for most bivalve lineages). Therefore, the time available for the evolution of secondary changes of life habits in these gastropods has been considerably shorter than in bivalves, and competition for the soft-bottom niches may have been correspondingly harder.

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REDESCRIPTION AND INTERPRETATION OF THE ASTEROID SPECIES *TROPIDASTER PECTINATUS* FROM THE JURASSIC OF ENGLAND

by DANIEL B. BLAKE

ABSTRACT. *Tropidaster pectinatus* is redescribed based on the original collection from Lower Jurassic (Pliensbachian) strata of England. It is the only recognized member of the Tropidasteridae, which is assigned to the Order Velatida in an intermediate phylogenetic position between the extant families Solasteridae, the earliest known representative of which is from Middle Jurassic (Bathonian) strata and considered primitive in the order, and the Korethrasteridae, known only from Holocene species. Surviving asteroids have been separated into three superorders; all are recognized from strata of Early Jurassic age, and *Tropidaster* provides additional evidence for the early diversification of extant asteroids. Based on arm curling and robust disc construction, *Tropidaster* might have been a selective predator.

TROPIDASTER PECTINATUS Forbes, 1850 is the only known member of the Tropidasteridae. It is significant because it represents an important surviving echinoderm order only rarely encountered in the fossil record. Unlike many fossil asteroids, *Tropidaster* is represented by a large suite (42) of well-preserved, more or less complete specimens (Pl. 1, fig. 1) and therefore relatively detailed treatment is possible.

The stratigraphical occurrence of *Tropidaster pectinatus* was indicated by Simms (1986, 1989) in his studies of Lower Jurassic crinoids. The type suite was collected from the Lower Lias at Mickleton Tunnel (town of Mickleton, SP 1.45 W, 52.06 N), near Chipping Campden (SP 1.45 W, 52.06 N), Gloucestershire. Strata are Pliensbachian (Carixian) in age, from the *Aegoceras capricornis* Subzone of the *Prodactylioceras davoei* Zone. The locality unfortunately no longer is exposed (D. Lewis, pers. comm.).

Included among the echinoderms from this locality are the asteroids '*Asterias*' *gaveyi*, an undescribed member of the Astropectinidae, the ophiuroid *Palaescoma milleri*, the crinoid *Chladocrinus robustus* and the echinoid *Procidaris edwardsi*. Echinoderms were found at many horizons at interfaces between different lithologies; Simms (1986) interpreted these occurrences as obrution deposits, and he suggested periodic smothering resulting from the influx of sand and finer sediments.

The fossil record of asteroid echinoderms is unfortunately sketchy, and timing of events must be pieced together from incomplete evidence. The Velatida represents one of three post-Palaeozoic asteroid superorders (*sensu* D. B. Blake 1987); representatives of the other two have been recognized from the Hettangian (D. B. Blake 1984, 1990), and therefore diversification of all major groups of modern asteroids was under way during the Early Jurassic. The Superorder Spinulosacea includes the Spinulosida as well as the Velatida. The superorder is based largely on developmental characters, whereas the two orders are separated on a number of characters of the adult skeleton. In D. B. Blake (1987), the Solasteridae was considered to be the primitive velatidan family, and the oldest known velatidans are the Pliensbachian *Tropidaster* and *Solaster murchisoni* (Wright 1863; J. F. Blake 1887; D. B. Blake 1993). In addition to the Solasteridae and Tropidasteridae, several families are known only from living representatives. The Tropidasteridae shares a number of features with both the Solasteridae and the Korethrasteridae (Pl. 1, fig. 3; Pl. 2, fig. 1) and it is here

[Palaeontology, Vol. 39, Part 1, 1996, pp. 179–188, 2 pls]

assigned an intermediate position between the two (Text-fig. 1). Fossils therefore are known only from relatively primitive families; differentiation of the Velatidae was under way by the Pliensbachian, but it cannot be demonstrated to have proceeded to more advanced families at that time.

Tropidaster morphology and preservational nature suggest aspects of life mode. In 18 (mostly smaller) of the 42 available specimens, arms are more or less strongly arched downward, enveloping a space below the mouth (Pl. 1, fig. 1). Ambulacrals are strongly imbricated (Pl. 2, fig. 8), demonstrating a capacity for considerable arm motion in the vertical plane, although exaggerated flexure might have been a near-death protective response. The rounded petaloid outline of the arm suggests limited lateral motion or twisting about the longitudinal axis of the arm (a fragmentary larger specimen noted in the description section might have had different proportions and different abilities). Podial basins are large, suggesting well developed tube feet. Although arms might have been lifted for suspension-feeding, both preservation and ambulacral overlap suggest downward motion was more natural.

Disc construction of *Tropidaster* is robust. The mouth frame is particularly sturdy and provided strong support to the disc. Modern Asteriidae and the Ordovician *Promopalaeaster* share a so-called 'adoral carina' formed by adambulacral ossicles abutted across the interbrachial area immediately distal to the oral frame; the arrangement provides disc support during feeding. In a similar if less strongly differentiated manner, the abradial ends of the adambulacrals abut across the actinal interbrachial areas in *Tropidaster* (Pl. 2, figs 3–4) suggesting a comparable bracing function. Naturally truncated dorsal paxillae (Pl. 1, figs 5–6) apparently abutted across the interbrachial plane, further bracing *Tropidaster* in certain orientations.

Stegnaster inflatus, a flattened member of the Asterinidae, uses its flexible body to trap small amphipods beneath its disc (Grace 1974). *Tropidaster* also would seem to have been capable of enclosing small food particles, and the sturdy mouth frame and large tube feet (suggested by large podial basins) might have helped subdue even active prey. Although no shells have been recognized within discs of available specimens, small arthropods, annelids and other soft organisms might have provided appropriate food.

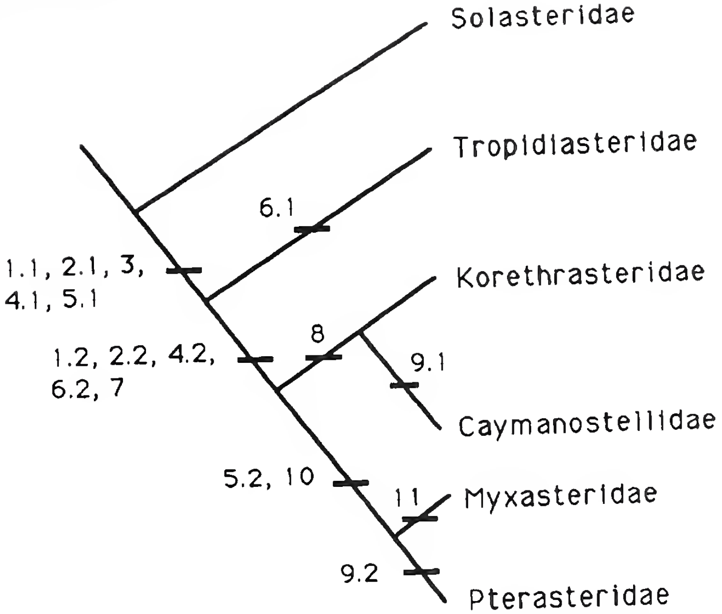
Phylogenetically, *Tropidaster* is derived relative to the Solasteridae, members of which are aggressive predators. It is primitive to the Pterasteridae, which have been observed feeding on smaller invertebrates (Mauzey *et al.* 1968), and which have been collected with echinoderms, molluscs and crustaceans in the gut (Carey 1972). Clark and Downey (1992) reported that nothing is known about feeding in the rare Korethrasteridae except that at least one species has an eversible stomach.

SYSTEMATIC PALAEONTOLOGY

Class ASTEROIDEA de Blainville, 1830
Order VELATIDA Perrier, 1891
Family TROPIDASTERIDAE Wright, 1880

Diagnosis. A velatidan family in which the ossicles are stout in comparison with most members of the order. A distinct groove on the dorsal interbrachial axis is plated, lined by partially differentiated paxillae. The ossicles about the anus are enlarged and block-like. On the ambulacral ossicles, the adradial ambulacral body is prolonged and strongly overlapping and a ventral medial articular flange linking subsequent ambulacrals is developed. Adambulacral ossicles are large, occupying the entire ventral surface of the arms beyond the ambulacra; they are like those of the Solasteridae except that the ambulacral articular structures are restricted to the adradial end of the adambulacral; actinal ossicles are lacking, and the adambulacrals abut across the ventral interbrachial surface.

Remarks. D. B. Blake (1987) assigned the Tropidasteridae to a derived position relative to the Korethrasteridae; the opportunity for more extended study suggests an intermediate position between the Solasteridae and Korethrasteridae (Text-fig. 1). D. B. Blake (1987) did not recognize



TEXT-FIG. 1. Revised phylogeny of the basal families of the Velatida modified from Blake (1987); the diagram clarifies the position of the Tropidasteridae but does not treat comprehensively the Myxasteridae and Pterasteridae, which are unchanged from D. B. Blake (1993). Key: 1p, ambulacrals robust with ambulacral bodies overlapping but not prolonged; ambulacral–adambulacral articular structures are sturdy and a ventral medial articular flange is lacking. $1d_1$, as 1p except that the ambulacral body is prolonged and strongly overlapping and a ventral medial articular flange is developed. $1d_2$, like $1d_1$ except that the ossicles, including the ambulacral–adambulacral articular structures, are delicate in comparison with equivalent structures in $1d_1$. 2p, adambulacrals robust, transversely elongate; ambulacral articular structures extend across the dorsal surface of the ossicle. $2d_1$, like 2p except that ambulacral articular structures are restricted to the adradial end of the ossicle. $2d_2$, adambulacrals reduced to an elongate, transverse bar with the ambulacral articular structures restricted to the adradial end of the ossicle. 3p, in some species, the dorsal interbrachial axis appears as a leathery line of tissue. 3d, the dorsal interbrachial line is a distinct plated groove lined by partially differentiated paxillae. 4p, actinals present. $4d_1$, actinals absent; adambulacrals abut across the interbrachial surface. $4d_2$, actinals absent; actinal interbrachial surface covered only by soft tissue. 5p, marginals paxilliform, inferomarginals large; in addition, superomarginals are reduced in size in most taxa. $5d_1$, marginals paxilliform, only one series differentiated, and that only marginally, so that recognition requires careful inspection. $5d_2$, differentiated marginals not developed. 6p, ossicles around anus not differentiated. $6d_1$, ossicles around anus enlarged, block-like. $6d_2$, ossicles around anus paxilliform but enlarged in comparison with closest neighbours. 7p, mouth angle ossicles keel-like, relatively large, prominent. 7d, mouth angle ossicles not significantly enlarged nor prominent. 8p, terminal of typical asteroid U-shaped. 8d, terminal either circular or nearly circular but not fully closed, rather than U-shaped. 9p, abactinals paxilliform, pedicels not highly elongate. $9d_1$, abactinals flattened, tessellated. $9d_2$, abactinals paxilliform, pedicels highly elongate. 10p, osculum absent. 10d, an enlarged, webbed osculum surrounds the anal area. 11p, spines are not webbed with flesh. 11d, various spines are webbed with flesh.

differentiated marginals in *Tropidaster*; these ossicles are weakly enlarged in at least one member of the Korethrasteridae (*Remaster palmatus*) as well as in *Tropidaster*.

Plumaster ophiuroides Wright was tentatively included in the family by Spencer and Wright (1966). Available material is poorly preserved. The broad adambulacrals and prominent spines in *Plumaster* are suggestive of those of *Tropidaster*. However, the large, triangular ambulacrals are unlike those of the Velatida, but are like those of the Astropectinidae; adambulacrals and spines are unusual but not sufficiently so as to preclude reassignment. Although poorly known, *Plumaster* is reassigned tentatively here to the Astropectinidae.

Genus TROPIDASTER Forbes, 1850

Type species. Tropidaster pectinatus Forbes, 1850.

Diagnosis. As for the family

Tropidaster pectinatus Forbes

Plate 1, figures 1–2, 4–7; Plate 2, figures 2–8

1850	*Tropidaster pectinatus* Forbes, p. 1.
1853	*Tropidaster pectinatus* Forbes; Gavey, p. 33.
1863	*Tropidaster pectinatus* Forbes; Wright, p. 102.
1966	*Tropidaster pectinatus* Forbes; Spencer and Wright, p. U67.
1993	*Tropidaster pectinatus* Forbes; Lewis, p. 66.
1993	*Tropidaster tropidatus* Forbes; Lewis, p. 67.

Material. The type suite consists of approximately 42 specimens, including some that are incomplete, partially enclosed in sediment, or fragmentary. Although preservation on portions of specimens is strikingly good, details differ among specimens and careful comparisons are needed (e.g. see comments on the squamose plates of Forbes under Remarks). There was some disruption; most spines are lost and a few isolated ossicles are present. In spite of the size of the sample, certain features, such as the proximal side of the ambulacrals and the nature of the odontophore, are unavailable. Specimens available to the writer included Department of Palaeontology, Natural History Museum (NHM) syntypes, 75690, 75691, E2693 and E3760; E1871; E2693; E3335; E3336; and E52345.

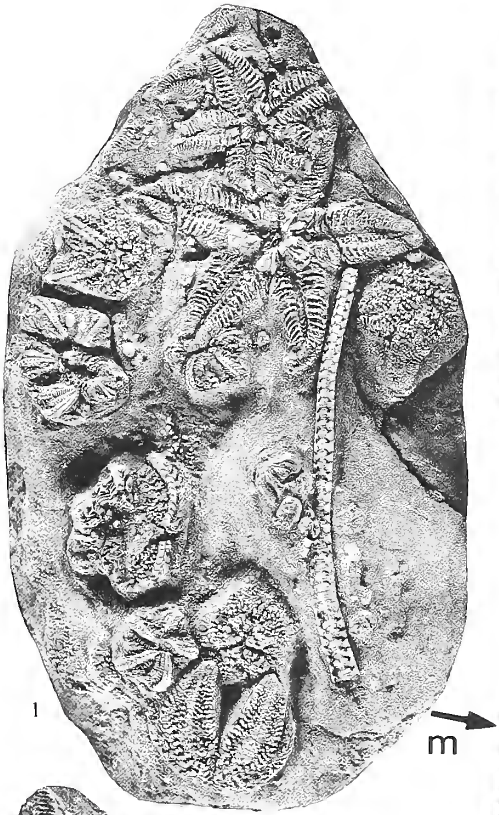
Diagnosis. As for the family.

Description. Five-armed species; disc large, arms sub-petaloid, the ratio of arm length to interbrachial radius is approximately 2:1 in the relatively small specimens dominating the type suite. The primary radius of most specimens is 33 mm or less but the species apparently reached a significantly larger size because a single fragmented and crushed, but partially reconstructed (by Forbes?), individual consists of a proximal fragment (including part of the disc) 30 mm long aligned with an arm fragment 20 mm long; the 50 mm interval does not represent a complete arm. Arm cross-sections have been somewhat distorted by compaction but in life the ventral surfaces probably were arched, following the curvature of the adambulacrals; dorsally, the steep orientation of the ambulacrals suggests the mid-arm was relatively high and perhaps angular, if the dorsal surface closely followed the arch.

EXPLANATION OF PLATE 1

Figs 1–2, 4–7. *Tropidaster pectinatus* Forbes; dorsal aspects; Mickleton Tunnel, near Chipping Campden, Gloucestershire; Lower Lias, Pliensbachian. 1, NHM E3335; overall view of a single block with numerous specimens in various orientations; note curling of arms in a ball-like pattern; a large ophiuroid arm fragment is to the right; × 1. 2, NHM E3335 (specimen is at the middle right of fig. 1); hemispherical madreporite (arrow) and adjacent paxillae (compare with figure 3); × 10. 4, NHM E1871; disc and portions of arms showing interbrachial groove (i), marginal rows (m) and form of the paxillae; paxillae from the midarm position have been truncated taphonomically; × 10. 5–6, syntype, NHM 75691; 5, overall dorsal aspect showing form, paxillary arrangement, central area collapsed into disc; double row of ambulacrals breaches dorsal surface of midarm; × 3; 6, detail of abutted paxillae (arrows) at mid-interbracial position; × 10. 7, NHM E52345; detail showing central ring of stout plates to left, and paxillary form; × 6.

Fig. 3. *Remaster palmaster* (Perrier), NHM E20985; Florida Straits between 304 and 320 m; Recent; dorsal aspect, madreporite (m), paxillae, paxillary spines and mid-interbrachial furrow (arrows) are similar to corresponding features in *Tropidaster*; × 6.



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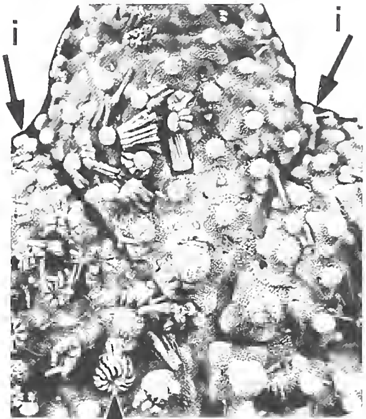

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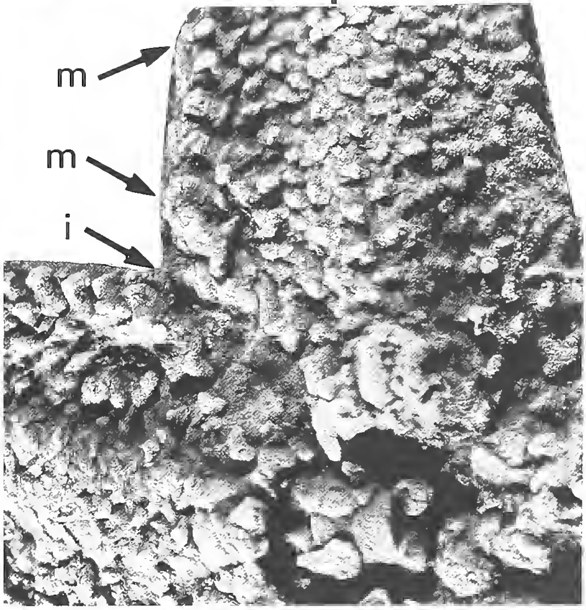

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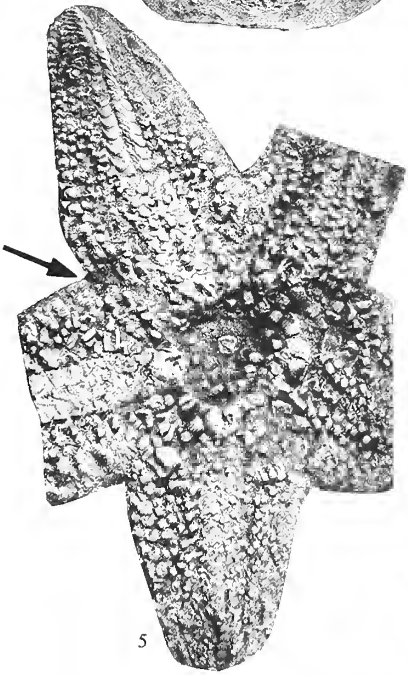

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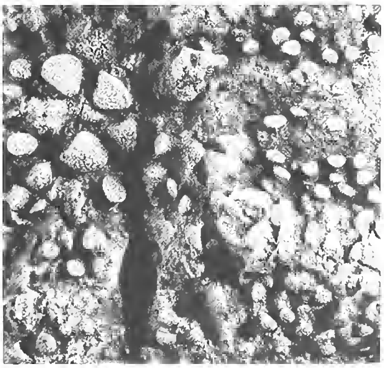

7

BLAKE, *Tropidaster*, *Remaster*

Ossicular series beyond the ambulacral column are paxilliform. Dorsal ossicles are arranged in well defined transverse and longitudinal rows on the disc and arms, and they gradually diminish in size distally (Pl. 1, fig. 5). Marginal differentiation is limited (Pl. 1, fig. 4), and there are no actinal ossicles (Pl. 2, figs 2–4). Paxillary row numbers on the arms are uncertain but numerous, with six longitudinal rows exposed on one side of the arm of one small (R approximately 12 mm) individual. Paxillae are stout with a weakly enlarged, domal crown tapering into a short pedicel; bases apparently are scalar with digitate margins; ossicular bases on the disc and laterally on arms appear weakly scalar, perhaps digitate. The apparently reduced pedicel of certain specimens (Pl. 1, fig. 4) is a taphonomic feature. Crown diameter is 0·5 mm to 1 mm on the disc in a specimen of R about 12 mm. A closely plated skeletal groove lies between the columns of the interbrachial paxillae (Pl. 1, fig. 4); some paxillae are abutted, truncated and apparently slightly enlarged along this plane (Pl. 1, figs 4, 6). Paxillary crowns are covered by many closely arranged glassy (?) or openly spicular spinelets of a length apparently somewhat greater than crown diameter. Close spacing of paxillae suggests any papulae were single, small and located between overlapping basal facets.

The central portion of the disc is not well preserved on available specimens. A ring of five stout triangular ossicles which probably enclosed the periproct is present in the central area (Pl. 1, fig. 7); the ossicles are about 1 mm in breadth in a recurved specimen of diameter in life probably of 20–25 mm; the dorsal surfaces of the ossicles are weakly arched and bear small spinelet bases. The madreporite is small, polygonal and somewhat domed (Pl. 1, fig. 2). It abuts the juncture of two of the ring ossicles; gyri apparently do not form continuous grooves.

A single row of marginals is present (Pl. 1, fig. 4); morphology is similar to that of the paxillae. Interbrachial marginals are clearly enlarged and differentiated relative to adjacent paxillae; crowns are elongated transversely and bases stout, probably scalar. Marginals rapidly become more equidimensional away from the interbrachial angle; the fourth marginal is rounded in outline rather than elongate transversely, and distal marginals are enlarged and differentiated rather weakly. Actinal ossicles are lacking; proximal adambulacral ossicles curve across the actinal interbrachial areas with the adradial extremities from neighbouring arms closely adjacent (Pl. 2, fig. 4).

Ossicles of the ambulacral column are robust (Pl. 2, figs 2–8; Text-fig. 2A) with approximately seven in 7 mm on the arm of syntype, 75690. In dorsal view, ambulacrals are dominated by a prolonged, strongly overlapping, flange-like ambulacral body (Pl. 2, figs 7–8). On the dorsal (or distal) side of the flange, the adradial part of the ossicle is broad and smooth, apparently a sliding surface for arm flexure; the surface extends ventrally and abradially to a depressed apparent tissue basin; a narrow articular groove is along the proximal edge. A deep, subcircular groove is present on the distal side of the ossicle for the podium (Pl. 2, fig. 7). Although exposed incompletely in available specimens, the podial pore seems less well defined on the proximal side of

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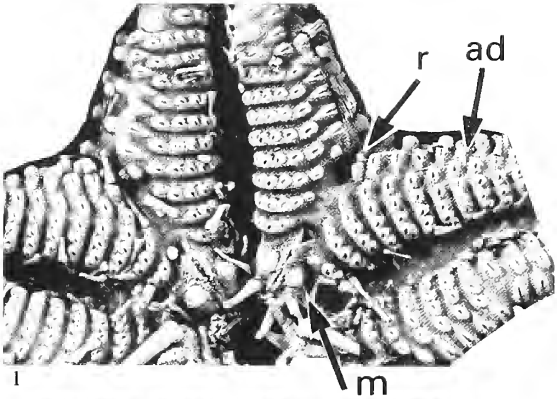
EXPLANATION OF PLATE 2

Fig 1. *Remaster palmatus* (Perrier), NHM E20985; Florida Straits between 304 and 320 m; Recent; ventral aspect; adambulacrals occupy entire vental surface beyond furrow; flange (right arrow) is a part of the adambulacral; ventral interbrachial area lacks actinal ossicles, although the adambulacrals do not abut across surface, as in *Tropidaster*; re-entrant (left arrow) at interbrachial edge of disc is suggested in some specimens of *Tropidaster*; mouth angle ossicles (m) are less prominent than in *Tropidaster*; × 6.

Figs 2–8. *Tropidaster pectinatus* Forbes; ambulacra and ventral aspects of morphology; Mickleton Tunnel, near Chipping Campden, Gloucestershire; Lower Lias, Pliensbachian. 2, NHM E3335 (specimen is at the top of Pl. 1, fig. 1); overall ventral aspect showing form, prominent adambulacral and mouth angle ossicles; interbrachial re-entrants (r) are similar to those in *Remaster*; × 3. 3, syntype, NHM 75690; subpetaloid arm showing ambulacrals with mid-ossicular articular facets (f), broad adambulacrals; × 6. 4, syntype, NHM E2693; adambulacrals abut across interbrachial areas; prominent muscle scars for first adambulacral (arrow); × 6. 5, NHM E3336; arm tip with terminal (arrow), arrangement of distal paxillae and dorsal aspect of strongly imbricate ambulacrals; × 10. 6, NHM E2693; mouth angle ossicles and first ambulacral are somewhat flattened but near to life orientation; the area is illustrated in Text-fig. 2C; × 10. 7, syntype, NHM E3760; ambulacral row in distal-dorsal aspect with podial pore (p) and articular groove (g) along proximal edge of adradial body; adambulacral (ad) row with spine bases strengthened by radial ridges; paxillae are above adambulacrals; × 10. 8, NHM E3335 (specimen is the disrupted, isolated individual at the middle left of Pl. 1, fig. 1); inclined view of ambulacral-adambulacral series; the area is illustrated in Text-fig. 2A; × 10.

PLATE 2



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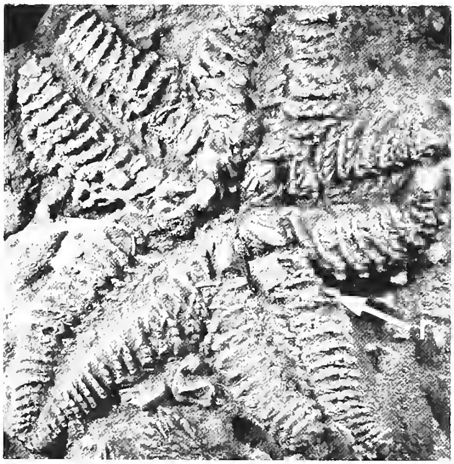

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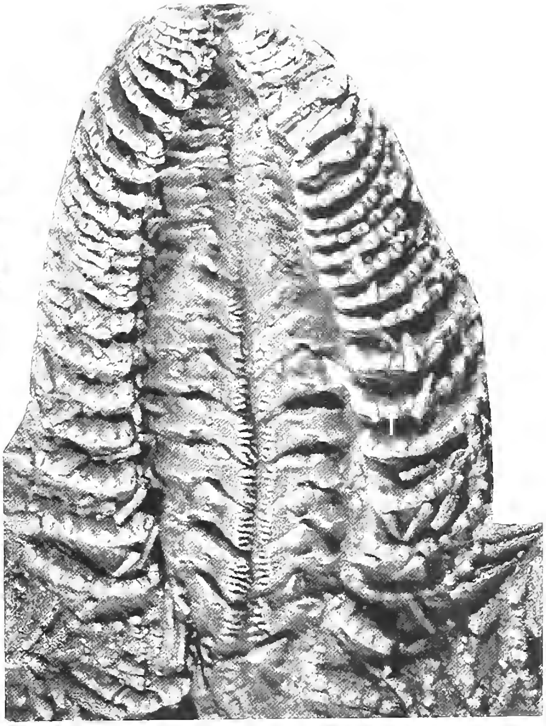

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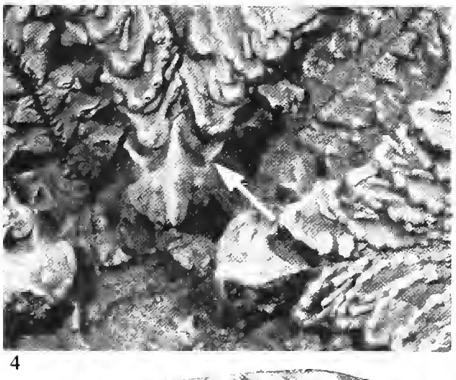

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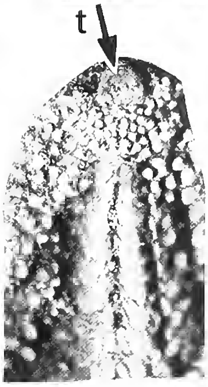

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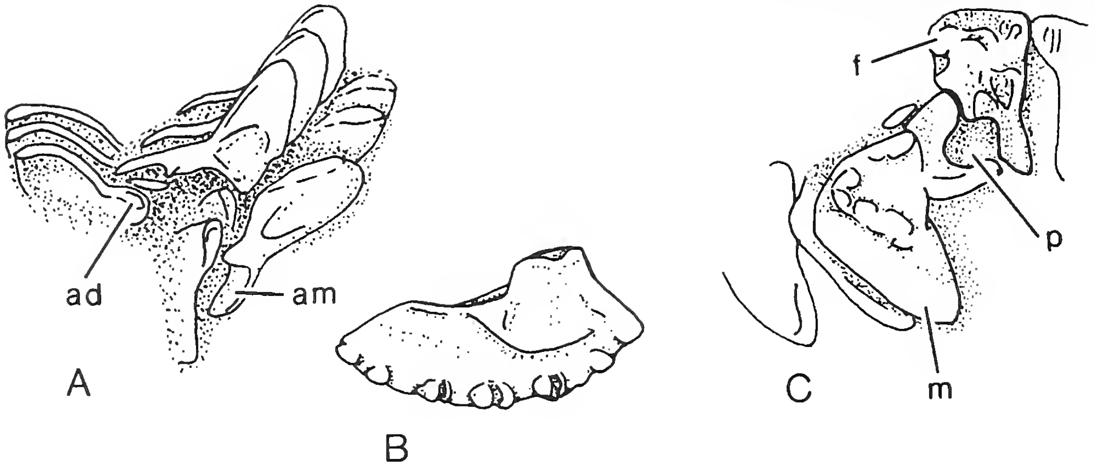
BLAKE, *Remaster*, *Tropidaster*



TEXT-FIG. 2. Ossicular arrangement and detail of *Tropidaster pectinatus*. A, ambulacral (am) and adambulacral (ad) rows from Pl. 2, fig. 8; lines point to articular surfaces. B, distal adambulacral, furrow to right; ambulacral contact is the process at the right side of the ossicle. C, oral frame ossicles from Pl. 2, fig. 6; mouth angle ossicle (m), first ambulacral (f) and podial pore (p).

the ossicle. The podial pore lies immediately adradial to the flattened dorsal surface of the adambulacral articular flanges. There is no well-defined dorsal ossicular ridge, although the medial dorsal part of the ossicle is angular.

In ventral view (Pl. 2, fig. 3), the ambulacrals are somewhat sinuous in appearance with approximately half of the adradial part of the ossicle deflected toward the disc. The cross-furrow articular facets-and-grooves are well defined and oriented largely in the vertical plane. Inferior transverse muscle scars are not clearly defined, although they might have extended from the medial articular surface on the proximal side of the ambulacral. A prominent inter-ambulacral articular flange-and-facet structure is developed medially; as preserved in different specimens, either the proximal or distal side of the flange can project more prominently producing very different appearances. Adradial to the medial flange, the distal ossicular edge is somewhat raised; the corresponding proximal edge of the next distal ossicle is bevelled, the two together forming a subtle articular contact. Abradially, the ventral ossicular surface in the furrow is quite broad, and is deflected ventrally to the ambulacral-adambulacral articular area. The terminal (Pl. 2, fig. 5) is small, approximately trapezoidal in dorsal outline, 0·55 mm wide and 0·5 mm long in a specimen of R between 15 and 20 mm; the dorsal ossicular surface is flat.

Adambulacral width in the syntype, 75690, reaches about 3·0 mm at the widest portion of the arm; adambulacrals are proportionately large and apparently formed all of the ventral portion of the arm beyond the furrows. The adambulacrals are prolonged laterally beyond the abradial edge of the ambulacrals (i.e. ambulacrals articulate at the adradial ends of the adambulacrals; Pl. 2, fig. 8; Text-fig. 2A–B), and they are strongly overlapping with large inter-ossicular furrows; outer faces are short and crescentic with the convex edge of the crescent directed proximally; the adradial end is angled distally to form a subtle adradial furrow prominence. Dorsally, the ossicle is prolonged into a broad, semicircular flange with proximal ossicles apparently larger (taller) than those from more distal arms positions. About seven prominent spine bases are spaced evenly across the outer face; adambulacral spines are conical, the most complete spine remaining on the syntype, 75690, is about 2 mm in length.

The oral frame is robust (Pl. 2, fig. 6; Text-fig. 2C). The mouth angle ossicular pair is keel-like and about 3 mm long in the syntype, 75690; ossicular faces directed toward the furrow are convex so that the ossicular pair is broadly rounded. The first ambulacral articular flange is near the oral end of the ossicle; it is large and flares over the furrow. This area is raised above the surface of the remainder of the ossicle, forming the proximal side of a large, first podial pore. Three or four spine bases are aligned along the ventral and proximal edges of the articular flange but away from the ventral edge of the ossicle; spines are about 0·75 mm in length in a specimen with a radius of approximately 12 mm; there are no spine bases on the remainder of the outer face. Most of the distal portions of the mouth angle ossicles abut the first adambulacral. The articular surface is large and deep. An odontophore is not exposed in available material.

The ambulacral body of the first ambulacral is robust and square in outline (Pl. 2, fig. 6; Text-fig. 2c). The proximal articular flange is relatively small, and the distal articular flange is similar to the abradial part of the ambulacrals. The ventral cross furrow muscle depression is clearly defined; its position and shape suggest that the proximal interambulacral articular flange of the ambulacrals also served as a transverse muscle support.

Remarks. Forbes (1850, p. 1) suggested the presence of a 'kind of keel' along the centre of each arm (Pl. 1, fig. 5; Pl. 2, fig. 5); the keel as interpreted by Forbes is formed by a double row of squamose ossicles. Certain eroded paxillae have low pedicels and broad, overlapping bases and therefore a squamose appearance, but the keel-like appearance noted by Forbes was probably produced by the underlying ambulacral ossicles. In certain specimens, these ossicles breached the dorsal surface producing a double row.

Asteroids are complex organisms; nevertheless some belonging to separate orders are remarkably similar. *Tropidaster* is an exception; a number of complex features (Text-fig. 1) establish its position relative to closely related families. It is assigned to the Velatida based in part on overall appearance (a relatively large disc and thickened, rounded arms), its exclusively paxilliform ossicles beyond the ambulacra with only weakly differentiated marginals and its prominent, keel-like mouth angle ossicles.

Adambulacrals are similar to those of the Solasteridae but are relatively broad, with small ambulacral articular surfaces; ambulacrals are also similar to those of the solasterids in overall form whereas both adambulacrals and ambulacrals of korethrasterids and pterasterids are more delicate and almost rod-like. The inter-ambulacral articular flanges of *Tropidaster* are similar to those found in korethrasterids and pterasterids. *Tropidaster* is like members of the Korethrasteridae and Pterasteridae in overall body shape, the shape of the mouth angle ossicles and the presence of strongly interlocking ambulacrals. It is also like members of the Korethrasteridae in the presence of relatively short paxillae. The interbrachial row of abutted paxillae is a feature shared with the Korethrasteridae and suggested in certain Solasteridae (e.g. *Lophaster gaini* (Koehler)) by the presence of a leathery membrane along the interbrachial axis. (The development sequence of marginal and paxillary ossicles is unclear from adult morphology; it is possible that the abutted ossicles (Pl. 1, fig. 6) are marginal in origin.) Inferomarginals are rather weakly differentiated in *Tropidaster*, yet very similar to those in certain korethrasterids, e.g. *Remaster palmatus*.

Tropidaster differs from *Peribolaster* in the presence of only two rows of tube feet (*Peribolaster* has four) and it differs from *Korethraster* in the presence of paxilliform abactinal ossicles rather than rounded, somewhat flattened, imbricate ossicles. The stout, articulated ambulacrals and very broad adambulacrals serve to separate *Tropidaster* from all three korethrasterids, whereas in korethrasterids and pterasterids, the adambulacral is a reduced ossicle in which the abradial end forms a distinct process. The Pterasteridae is distinct in the presence of highly elongate paxilliform abactinals which serve to support the unique supradorsal membrane.

Adambulacral form is distinct in *Tropidaster* and the robust form of the ambulacrals, with medial-lateral articular flanges, is also distinctive. The stout periproctal ossicles of *Tropidaster* are unique, although somewhat enlarged ossicles about the periproct occur in korethrasterids, e.g. in *Remaster palmatus*. Given the unifying characteristics of velatidan families, these differences warrant continued recognition of the Tropidasteridae.

Tropidaster tropidatus is a slip of the pen (D. N. Lewis, pers. comm.).

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PAST GLOBAL FLORISTIC CHANGES: THE PERMIAN GREAT EURASIAN FLORAL INTERCHANGE

by WANG ZI-QIANG

ABSTRACT. It is widely held that during the Permian, especially the Late Permian, the Subangara flora spread southwards into China, where it mingled with the 'Cathaysian flora'. However, the reputedly Angaran or Subangaran elements found in North China, which are common in, or even characteristic of the *Psygmophyllum* Zone of that region, include gymnosperms such as callipterids, peltasperms and psygmophylloids, which are in fact Euramerican in origin. The evidence rather suggests that many Eurasian gymnosperms moved into Angara in the Late Permian, and were part of a large scale biotic exchange that may be termed the Great Eurasian Floral Interchange. It can be recognized as having occurred from two directions: from western Europe, via the Russian Platform into Angaran Pechora; and from the northern border of South China, via North China into Angaran Mongolia and eventually to the Kuznetsk. There was also some migration of Angaran elements into the neighbouring areas, but to a much lesser extent, and the floral interchange was thus clearly asymmetrical. The functional mechanisms driving the interchange were palaeomonsoons in the northern Palaeotethys, and the expansion of the Eurasian Arid Province.

MAJOR palaeobiotic invasion and interchange were first recognized over a century ago, but it has only been over the last two decades that the processes involved have been properly understood, following their incorporation into the continental drift model. The collision of plates, previously occupying different latitudes, provided routes for the migration and interchange of faunas and floras that had long-separated evolutionary histories. The subject is currently an important part of the Past Global Changes project (Ricklefs *et al.* 1990). Well documented examples include the Great American Biotic Interchange that occurred in the Late Pliocene, after the development of the Panama Isthmus between North and South America (Marshall 1981; Webb 1991), and the Trans-Arctic molluscan interchange in the Early Pliocene, after the opening of the Bering Strait between the North Pacific and the Arctic Atlantic (Vermeij 1991).

During the Permian, one of the major significant palaeogeographical changes was the collision between the Siberian and Laurasian plates (Sengör *et al.* 1993). This provided the opportunity for the migration of land vegetation that had previously developed along quite independent evolutionary paths. Important for understanding this problem is the relationship between the plant fossils from Angara, and those of the so-called 'Northern Cathaysian Subprovince' (Li and Yao 1979). Since Norin (1924) referred to the Permian of central Shanxi as the 'Angara Series', the relationship between its fossils and those of Siberia has been a topic of considerable debate. Of central importance to this debate was the report of Angaran-like plant fossils from the C-Bed in Bexell's Nanshan Section in western China by Halle (1937). The potential significance of this discovery was immediately realized (Jongmans and Gothan 1937), and it has now become generally accepted that there are Angaran plant fossils in the Permian of North China (Sze 1953, 1954; Lee 1963; Chaloner and Meyen 1973; Chaloner and Creber 1988; Lemoigne 1988; Scotese and McKerrow 1990; Cleal and Thomas 1991; Durante 1992). Meyen (1981, 1982, 1987) incorporated the area within what he called the Subangara Palaeoarea – a transitional zone (ecotone) surrounding the Angara Palaeokingdom proper, extending from the Russian Platform, through Ural-Kazakhstan, Junggar and south Mongolia. According to Meyen, the northernmost part of

China was on the southern extension of this Subangara Palaeoarea, linking the Ural-Kazakhstan deposits to the west with those of the Far East.

Although on the face of it this model appears very reasonable, there have been widely diverging views as to the floristic composition and thereby the affinities of the Nanshan plant fossil assemblage, expressed variously by Russian and Chinese palaeobotanists. The present author has published a number of studies on the Permian and Triassic palaeophytogeography of North China, including extensive comparisons with the Russian literature (Wang 1985, 1989, 1991; Wang and Wang 1986). The present paper is an attempt to provide a comprehensive analysis of the problem, with special reference to certain key groups of gymnosperm foliage which are thought to have particular palaeophytogeographical significance. Chaloner and Creber (1988) have pointed out the problems of trying to establish the relationships between floristic provinces based on isolated plant leaves usually lacking reproductive features. However, the original recognition of the four main Late Palaeozoic phytochoria (Gondwana, Euramerica, Angara, Cathaysia) was based on the distribution of isolated leaves, and so it does not seem unreasonable to try to extend the database of such fossils. Furthermore, recent discoveries of reproductive structures attached or associated with some of the gymnosperm foliage have helped clarify their taxonomy and thus their palaeophytogeographical standing.

THE 'ANGARAN PLANTS' FROM NANSHAN

Halle's (1937) announcement of the presence of 'Angaran plants' at Nanshan appears to have been accepted by most palaeobotanists, despite the fact that he did not illustrate any of the material. The first illustrations of specimens from Nanshan were not until Chao (1963) and Gu and Zhi (1974) published examples of *Zamiopteris glossopteroides* Schmalhausen and *Iniopteris siberica* Zalessky, which had been returned to China from Sweden.

More detailed studies began in the late 1970s, by both Russian and Chinese palaeobotanists. Durante (1980, 1992) re-examined the Bexell collection of Nanshan specimens, stored at the Swedish Natural History Museum, and which included material identified by Halle. Her paper includes illustrations of about 30 species, albeit in many cases based on indeterminate specimens. Durante (1992, p. 36) argued that the assemblage was directly comparable with the Late Permian (Tatarian) assemblages of Subangara, and that characteristically Cathaysian elements are very rare ('with a small admixture of Cathaysian plants').

At about the same time, a Chinese professional working-group re-investigated Bexell's Nanshan section and collected a number of plant fossils. A series of stratigraphical and palaeontological reports were produced (Liang *et al.* 1979; Liu *et al.* 1981; Shi and Liu 1981; Zhang and Shen 1987*a*, 1987*b*). These Chinese palaeobotanists argued that one-third of the species are commonly found in the lower Upper Permian 'Upper Shihhotze Formation' in North China, and that neither Angaran nor Cathaysian taxa are typical in the mixed assemblage. According to Zhang and Shen (1987*a*, 1987*b*), *Paracalamites tenuicostata* Neuburg, *Zamiopteris*, *Comia* and *Pursongia* are the only Angaran immigrants at Nanshan.

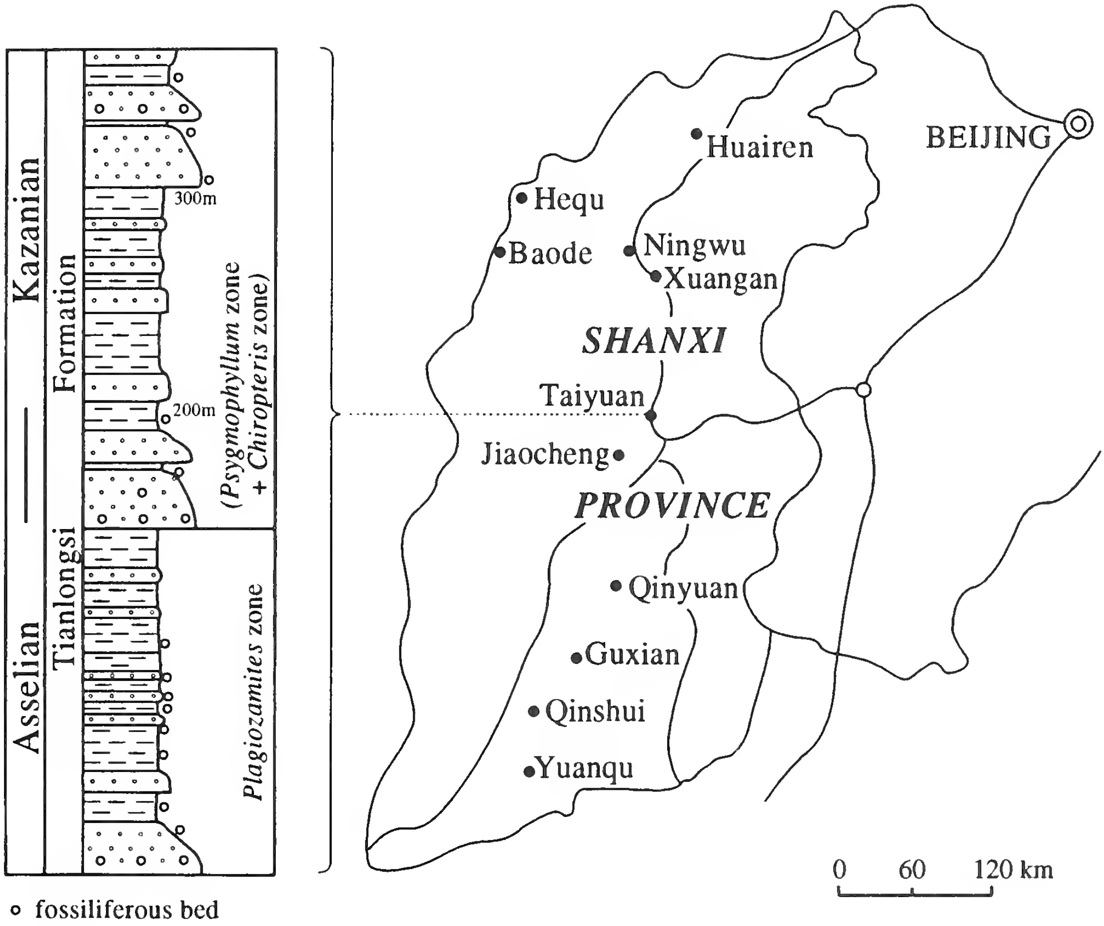
Wang *et al.* (1984) illustrated plant fossils from areas adjacent to Nanshan and their taxonomic list included genera of apparently Angaran affinities. Judging from the photographs, however, many of their identifications are doubtful.

The species lists provided by these two schools of workers have upwards of two-thirds of the genera in common, e.g. *Psygmophyllum*, *Peltaspermum*, *Callipteris* and *Protoblechnum-Compsopteris*. From a palaeophytogeographical point of view, the most significant difference is the presence in Durante's list of rare Tatarian taxa (e.g. *Pursongia*, cf. *Sashinia* and questionable *Phylladoderma* and *Comia*). It is important to point out, however, that the Nanshan specimens do not yield cuticles, and epidermal structure is needed to identify these taxa reliably. On the other hand, judging from the illustrations, there are no obvious mistakes in the identifications by either Durante or the Chinese palaeobotanists; it would be expected, after all, that Russian palaeobotanists should be able to recognize typically Angaran taxa, while Chinese palaeobotanists should be able to identify Cathaysian forms. The differences between the lists may thus reflect hitherto unrecognized relationships between the Late Permian floras of North China and Siberia. To try to understand this better, it is therefore necessary to re-examine the relevant Chinese plant fossils, i.e. those from the 'Upper Shihhotze Formation'.

A NEW ASSEMBLAGE OF PERMIAN PLANT FOSSILS

In Halle's (1927) memoir, most of the documented Permian plant fossils originated from the 'Upper Shihhotze Formation' in central Shanxi. However, they were mainly from the lower part of that formation; plant fossils from the middle and upper parts of the formation are rare and so the biostratigraphical position of these higher strata was problematical.

For the past five years, the geology of the classic Upper Paleozoic sections at West Hill of Taiyuang, Shanxi (Text-fig. 1), has been extensively re-investigated. As a result, the 'Upper



TEXT-FIG. 1. Generalized stratigraphical log of the Tianlongsi Formation in Shanxi. Also locality map showing sites mentioned in text.

Shihhotze Formation' has been renamed the Tianlongsi Formation, to avoid a duplication of names with the Shihhotze Group (Chen and Niu 1993). At the same time, the present author has undertaken a comprehensive revision of the plant biostratigraphy, palaeoecology and systematics of the red beds of the Tianlongsi Formation, and has recognized two more-or-less stable biozones (Wang 1993*a*, fig. 1).

1. *Plagiozamites* Zone (early Early Permian). The base of this zone is placed at the first occurrence of *Gigantonoclea*, and coincides with the first occurrence of red beds in the Shihhotze Group.
2. *Psygmophyllum* Zone (late Early Permian). This occurs in the middle and upper parts of the Tianlongsi Formation, and is identified by the first occurrence of *Psygmophyllum*.

The present paper concentrates on the plant fossils from the *Psygmophyllum* Zone, most of which have hitherto not been studied in detail.

So far, 45 species belonging to 35 genera have been identified from this new zone. They include a number of relic Carboniferous genera, such as *Lepidodendron*, *Sphenophyllum*, *Annularia*, *Cordaites*, *Pecopteris* and *Sphenopteris*. Also present are abundant Mesophytic gymnosperms, these being the oldest assemblages with such gymnosperms known from North China; psygmophylloids are unique to this zone. Also important are peltasperms, including callipterid fronds, *Autunia* and *Peltaspermum* fructifications, and other allied genera (*Supaia*, *Protoblechnum-Compsopteris*, *Neuropteridium*, *Comia*, etc.). Cycad leaves and megasporophylls, although known from the basal Permian of China (Gao and Thomas 1989), increase significantly in diversity in the *Psygmophyllum* Zone. They include a series of *Taeniopteris* leaves varying from small, narrow, linear forms, to large, broad or elliptical ones. Cycad ovuliferous scales range from the fan-like *Norinia* to the pinnate *Tianbaolinia* Gao and Thomas, 1989 (similar to *Chulakia* Salmenova, 1984). Ancestors of ginkgos (*Sphenobaiera*, *Ginkgophyton*? *spirata* Sze, *Ginkgophytopsis*) and conifers (*Walchia*, *Majonica*) also appear here and sometimes are dominant.

The rest of this paper will concentrate on the psygmophylloids and peltasperms, these being the taxa regarded by Meyen (1988, pp. 344–357) as endemic to the Subangara Palaeoarea. The main difficulty is trying to compare species described by Russian palaeobotanists from Angaran floras with species described by Chinese palaeobotanists from North China. To avoid exaggerating the palaeobiogeographical differences that such subjective difference could introduce at the rank of form-species, the discussion and comparison will be kept at the rank of genus, following the practice of earlier studies (e.g. Chaloner and Creber 1988; Cleal and Thomas 1991). The descriptive style of the form-genera follows that of Zodrow and Cleal (1993).

SYSTEMATIC PALAEONTOLOGY

The synonymy lists of each taxon are not complete, those entries prefixed by an asterisk include cuticular evidence. All figured specimens are stored in the Tianjin Institute of Geology and Palaeontology (TIGP).

EXPLANATION OF PLATE 1

Figs 1–2, 6 *Supaia* sp. A. Forked fronds; Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1. 1, TIGP 9306-1. 2, TIGP 9306-2. 6, TIGP 9306-4.

Fig. 3. *Psygmophyllum multipartitum* Halle. K-1-6; narrow segment similar to *Zamiopteris*-type leaf; Kuantou village, Taiyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.

Fig. 4. Cf. *Zamiopteris*-type leaf. TIGP Th7126-061; Hoshan village, Jiaocheng district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.

Fig. 5. *Autunia*-type fructification. TIGP 930-33; numerous megasporophylls attached to rachis, with seeds on inner side; Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 2.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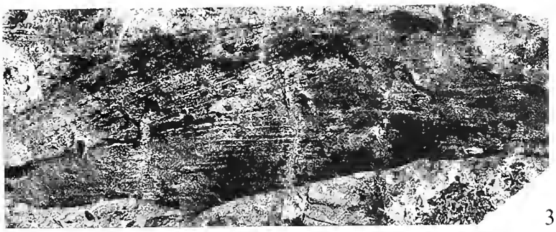
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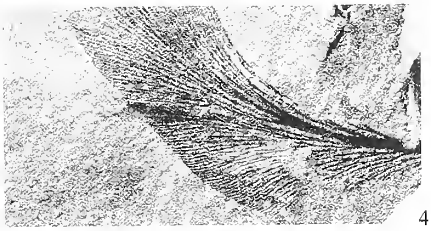
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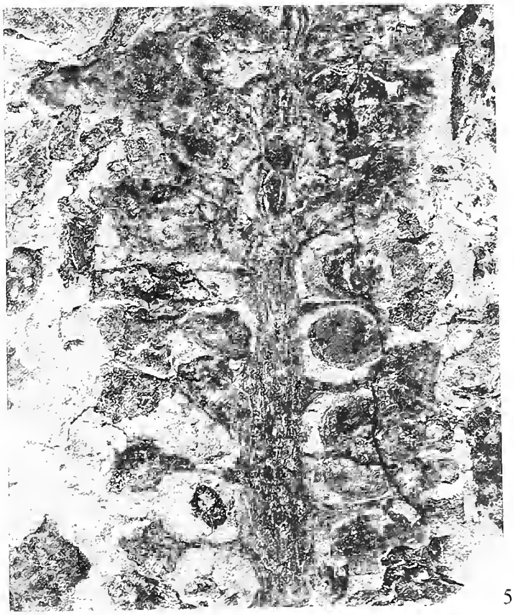
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WANG, Permian plant fossils

PSYGMOPHYLLOIDS

Yao (1989) used this name for certain Permian palmate leaves, including *Psygmophyllum* Schimper *sensu stricto* and several allied genera such as *Ginkgophytopsis* Høeg and *Ginkgophyllum* Saporta. In this paper, other palmate gymnosperm leaves, including *Chiropteris*, *Rhipidopsis* and *Saportana* are also included within this group.

Form-genus PSYGMOPHYLLUM Schimper, 1870 emend. Saporta, 1878

*1870	*Psygmophyllum* Schimper, p. 192.
1878	*Psygmophyllum* Schimper; Saporta, p. 869.
1927	*Psygmophyllum* Schimper; Halle, p. 214.
1982	*Psygmophyllum* Schimper; Burago, p. 133.
1989	*Psygmophyllum* Schimper; Yao, p. 171.

Type species. Psygmophyllum expansum (Brongniart) Schimper, 1870.

Psygmophyllum multipartitum Halle

Plate 1, figure 3; Plate 4, figures 1–2; Plate 5, figures 1–3;
Plate 6, figures 5–8

*1927	*Psygmophyllum multipartitum* Halle, p. 214, pls 57–58.
1989	*Psygmophyllum multipartitum* Halle; Yao, p. 174, pl. 1, figs 1–7; pl. 2, figs 1–11; text-fig. 1.

Remarks. From their mode of preservation, foliage physiognomy, cuticles, and petiole anatomy, this species is interpreted as an aquatic or seasonally emergent plant with a rosette-like habit (Wang 1993*b*). The long, thick petioles extend from their base and then dissolve into a large, dissected lamina.

Halle (1927, p. 221) compared the general mode of division in these Chinese leaves with that of two Permian species from the Urals (*Psygmophyllum cuneifolius* (Kutorga) Schimper and *P. expansum* Brongniart). However, he suggested that they may be more closely related to *Odontopteris siberica* Zalessky from Kutznetsk, a species subsequently transferred first to *Iniopteris* (Zalessky 1934) and eventually to *Psygmophyllum* (Burago 1982). Burago's study was important because she demonstrated the great diversity of *Psygmophyllum* leaves from Angara and Subangara, and reclassified numerous genera from those floras as later synonyms of *Psygmophyllum* (*Syniopteris*, *Idelopteris*, *Iniopteris*, *Comipteridium*, *Biarmella*, *Uralopteris* and *Zalesskyella*). The Chinese specimens from the *Psygmophyllum* Zone illustrated in the present paper, which originate from various locations in Shanxi, show a similar diversity in gross morphology and are consistent with the generic diagnosis re-written by Meyen (1987, p. 221).

EXPLANATION OF PLATE 2

Fig. 1. *Callipteris changii* Sze. TIGP 8837-1; apical part of frond showing overtopped branching; Gaomao village, Hequ district, Shanxi; middle Tianlongsi Formation, Upper Permian; × 1.

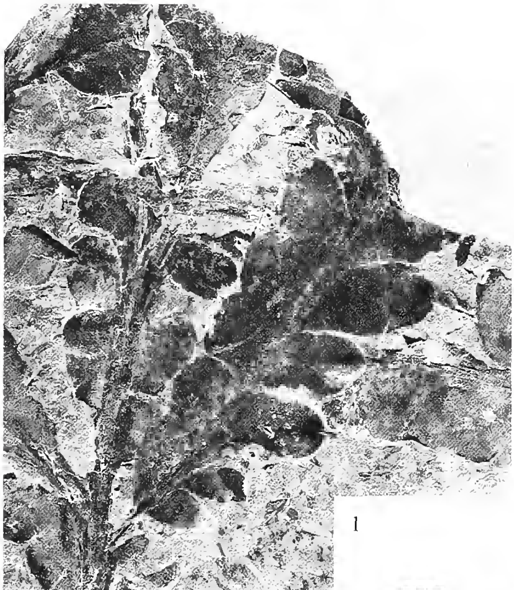
Fig. 2. *Chiropteris reniformis* Kawasaki. TIGP 8851-1; small leaf; Wangtao village, Qingyuan district, Shanxi; middle Tianlongsi Formation, Upper Permian; × 1.

Figs 3, 5. *Supaia* sp. A. Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian. 3, TIGP 9306-28; single pinnule; × 2. 5, TIGP 9306-5; basal part of a large, forked frond; × 1.

Fig. 4. *Autunia*-type fructification. TIGP 9306-36; many megasporophylls attached to rachis, but from which seeds have become detached; Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 2.

Fig. 6. *Supaia* sp. B. TIGP 8915-1; part of forked frond, with pinnules constricted at base; Hekou village, Xuangan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.

PLATE 2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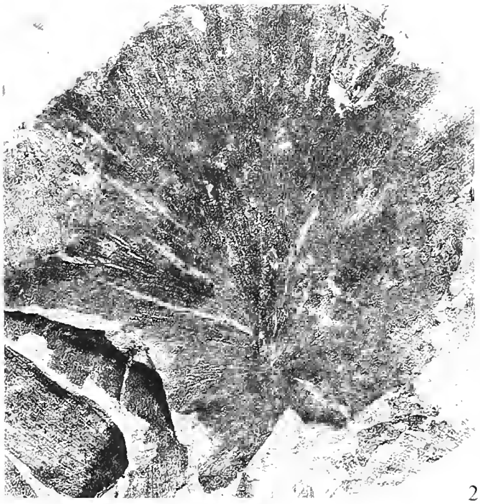
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WANG, Permian plant fossils

There is relatively little known of the cuticles of the Subangara *Psygmophyllum* species. However, Meyen (1982, p. 60) claimed that they had petalocyclic stomata randomly arranged over the lamina. This is very similar to the stomata described from Chinese material by Yao (1989, p. 186). In fact, the specimens figured in the present paper (Pl. 6, figs 5–8) show that *P. multipartitum* exhibits considerable variability in its cuticular features.

Distinguishing *P. multipartitum* from the Angaran and Subangaran species is clearly difficult, although the former appears to have larger leaves which have a thicker limb, more rugose surface, less dissected lobes, and occasional vein anastomoses. There is also the possible phytogeographical difference, with *P. multipartitum* being considered as a Cathaysian endemic (Yao 1989), while the Uralian species were regarded by Meyen (1982) as endemic to Subangara. Durante's (1992, p. 29) proposal to establish *Psygmophyllopsis* for the Chinese specimens is unconvincing.

The floristic significance of *Psygmophyllum* has tended to be ignored by most palaeobotanists, due to its reputedly wide distribution in Angara, Cathaysia and Euramerica. In fact, the genus may be regarded as a distinctive group of Middle–Late Permian foliage from eastern Laurasia.

Form-genus NYSTROEMIA Halle, 1927

Type species. Nystroemia pectiniformis Halle.

Nystroemia pectiniformis Halle

Plate 3, figure 5

*1927 *Nystroemia pectiniformis* Halle, p. 221, pl. 59.

Remarks. This type of inflorescence, bearing numerous possible ovules or seeds, is associated in Shanxi with *Psygmophyllum* foliage. Although not found in attachment, the constant association

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EXPLANATION OF PLATE 3

Figs 1–2. Aff. *Comia* sp. Large pinnae showing lateral veins clustered in fascicle. 1, TIGP 87Y5-28; Yaotou village, Yuanqu district, Shanxi; upper Tianlongsi Formation, Upper Permian; ×2. 2, TIGP 8833-6; Maliankou village, Hequ district, Shanxi; lower Tianlongsi Formation, Lower Permian; ×1.

Fig. 3. *Cordaites* sp. (right) and *Taeniopteris* aff. *tingii* Halle (left). TIGP 8833-5; reduced cordaitean leaf with denser venation in central part, more or less similar to *Zamiopteris*; Maliankou village, Hequ district, Shanxi; lower Tianlongsi Formation, Lower Permian; ×1.

Fig. 4. *Peltaspermum* sp. TIGP 9494-p; isolated peltate disc; Hekou village, Xuangan district, Shanxi; upper Tianlongsi Formation, Upper Permian; ×2.

Fig. 5. *Nystroemia pectiniformis* Halle. TIGP 8851-8; fructification with many possible seeds, with two filiform hairs extending from the micropylar end of each seed; Wangtao village, Qingyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; ×2.

Fig. 6. *Lesleya* sp. TIGP 8908-O; cuticles of apical part of leaf, showing rare anastomosing veins; Nanhegou village, Baode district, Shanxi; upper Tianlongsi Formation, Upper Permian; ×2.

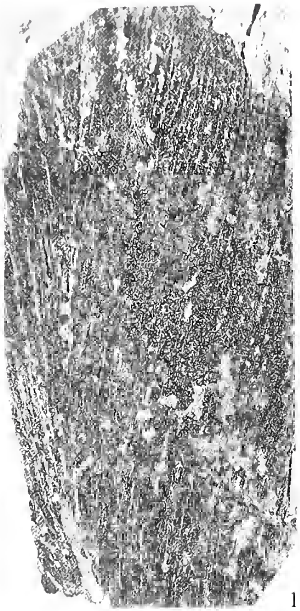
Figs 7–8. *Cordaites* sp. Upper Tianlongsi Formation, Upper Permian; ×1. 7, TIGP TH1210-32; short leaf similar to *Petscheria*-type scales; Tianlongsi temple, Taiyuan district, Shanxi. 8, TIGP 9106-1; small leaf similar in outline to *Zamiopteris*; Nanhegou village, Baode district, Shanxi.

Fig. 9. *Supaia* sp. A. TIGP 87Y5-19; partial frond showing its decurrent base; Yaotou village, Yuanqu district, Shanxi; upper Tianlongsi Formation, Upper Permian; ×1.

Fig. 10. *Wattia* sp. TIGP K-1-18; aphlebia-type scale; Kuantou village, Taiyuan district, Shanxi; upper Tianlongsi Formation, Upper Permian; ×1.

Fig. 11. *Supaia* sp. B. TIGP TH7126-21; isolated pinna, showing constricted base and fine, fascicular veins; Hoshan village, Jiaocheng district, Shanxi; upper Tianlongsi Formation, Upper Permian; ×1.

PLATE 3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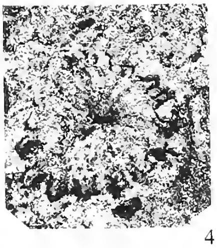
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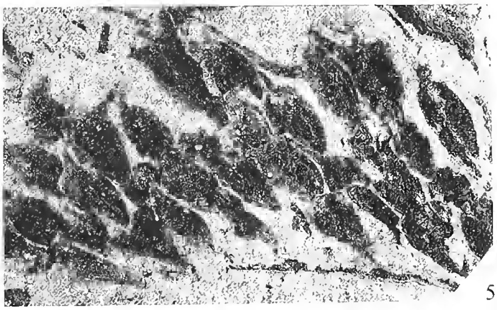
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WANG, Permian plant fossils

suggests that they may have belonged to the same plant. Two apical hairs extend from the top of each of the ovules, possibly indicating wind dispersal (Wang 1994). Although this type of inflorescence is so far unknown from Angara, Neuburg (1948) has reported *Samaropsis*-type seeds from Kuznetsk, with two apical, spine-like projections similar to those of *Nystroemia*.

Form-genus CHIROPTERIS Kurr *in* Bronn, 1858

Type species. Chiropteris digitata Kurr *in* Bronn, 1858, p. 143.

Chiropteris reniformis Kawasaki

Plate 2, figure 2

*1925 *Chiropteris reniformis* Kawasaki, p. 27, pl. 17, fig. 56; pl. 18, figs 57–58.
1927 *Chiropteris reniformis* Kawasaki; Halle, p. 175, pl. 55, figs 5–8.

Remarks. This genus is another distinctive type of foliage found in the mid–upper parts of the Tianlongsi Formation, although it ranges down a little lower than *Psygmophyllum*. The genus shows great diversity in gross morphology. It is generally smaller than *Psygmophyllum*, with a more or less dissected limb, and the veins are anastomosing. *C. reniformis* has no midvein, but the other species, *C. kawasakii* Kon'no, sometimes shows a weakly developed midvein. The distinction of the latter from *Psygmophyllum multipartitum* can sometimes be very difficult.

Until now, there has been only one record of the genus from Angara or Subangara: *Chiropteris palmilobata* Zalessky from the Upper Permian of Kuznetsk (Neuburg 1948, text-figs 25–26). This Angaran species has a more or less dissected lamina, rarely anastomosing veins and no midvein, and is thus very similar to *C. reniformis* from China.

PELTASPERMS

In this paper, the peltasperms are taken to include the callipterids and their associated fructifications, from the Permian, and the lepidopterids and their fructifications, from the Permo-Triassic. Kerp and Haubold (1988) revised much of the European material, and assigned it to a natural genus *Autunia*, and five foliage form-genera: *Dichyphyllum*, *Rhachiphyllum*, *Lodevia*, *Gracilopteris* and *Arnhardtia*. At the same time Meyen (1982, 1988) reviewed the Angaran and Subangaran peltasperms, assigning them to the foliage form-genera *Callipteris* (*Foenia*), *Comia* and *Compsopteris*, and various genera of reproductive organs, including *Permotheca* and *Peltaspermum*. In North China, the callipterids are the main component of the *Psygmophyllum* assemblage, including the foliage *Callipteris*, *Supaia*, *Protoblechnum-Compsopteris* and *Comia*, as well as probably *Neuropteridium* and *Autunia*-like fructifications.

EXPLANATION OF PLATE 4

Figs 1–2. *Psygmophyllum multipartitum* Halle. Upper Tianlongsi Formation, Upper Permian; × 1. 1, TIGP TH1209-9; linear segment; Tianlongsi temple, Taiyuan district, Shanxi. 2, TIGP 87Y5-24; small leaf similar to that seen in Angaran species; Taotou village, Yuanqu district, Shanxi.

Fig. 3. *Cordaites* sp. TIGP 9010-1; leaf similar to the Angaran *Crassinervia*; Jiuxian village, Guxian district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.

Figs 4–6. Aff. *Comia* sp. 4, TIGP 9406-c4; partial pinna; Hekou village, Xuangan district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1. 5, TIGP 8837-6; forked frond with fascicular veins; Gaomao village, Hequ district, Shanxi; middle Tianlongsi Formation, Upper Permian; × 1. 6, TIGP 87y5-29; large pinna showing venation; Yaotou village, Yuanqu district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1.


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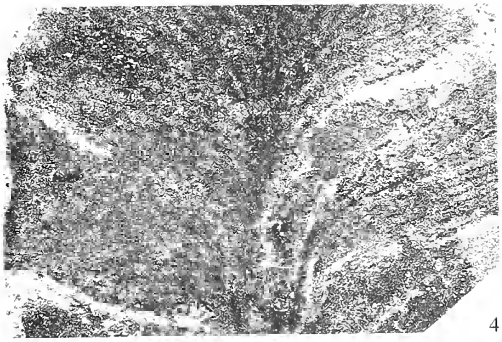
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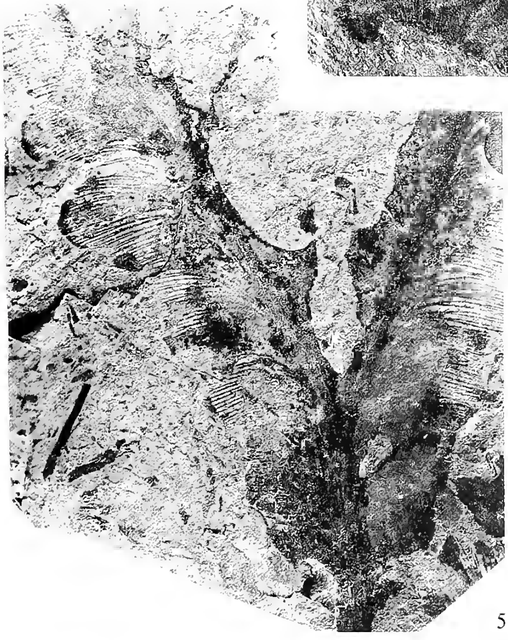
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WANG, Permian plant fossils

Form-genus CALLIPTERIS Brongniart, 1849 (*non* Bory, 1804)

*1849 *Callipteris* Brongniart, pp. 66, 73.
1970 *Callipteris* Brongniart; Meyen, p. 525.
1980 *Callipteris* Brongniart; Barthel and Haubold, p. 49.
1981 *Callipteris* Brongniart (*non* Bory, 1804); Kerp, p. 660.

Type species. Callipteris conferta (Sternberg) Brongniart, 1849, p. 73.

Callipteris changii Sze

Plate 2, figure 1; Plate 6, figures 1–4

*1954 *Callipteris changii* Sze, p. 83, pl. 1, fig. 1; pl. 3, fig. 2.
1989 *Callipteris changii* Sze; Si, p. 47, pl. 57, figs 1–3.

Remarks. Sze (1954) compared the leaf-size and venation of this species to those of the Angaran *C. zeilleri* Zalessky. However, its basic frond architecture, including features such as the presence of a pseudo-dichotomy in the distal part of the primary rachis (Barthel and Haubold 1980; Kerp 1988), appears to be identical to that of the European callipterids. The same architecture has also been demonstrated in a specimen of the Angaran *C. adzvensis* Zalessky from the Upper Permian of Pechora (Meyen 1983, pl. 10, fig. 1). The cuticles of *C. changii* (Pl. 6, figs 1–4) have clear papillae similar to the Angaran material (Meyen 1970). Meyen proposed that the Angaran callipterids with papillate, amphistomatic cuticles should be assigned to a separate sub-genus, *Foenia*, but the European callipterids were subsequently shown to have the same cuticular characteristics (Barthel and Haubold 1980) and so the distinction breaks down.

Callipteris? *laceratifolia* Halle

*1927 *Odontopteris*? (*Callipteris*?) *laceratifolia* Halle, p. 118, pl. 32, figs 1–2 (*non* pl. 20, figs 15–17).
1974 *Callipteris*? *laceratifolia* Halle; Gu et Zhi, p. 123, pl. 93, figs 1–2.

Remarks. This type of callipterid is characterized by large fronds with more or less dissected pinnules, and its generic position is still in question. The species is restricted to the mid–upper part of the Tianlongsi Formation, where it forms a distinctive member of the assemblage. Interestingly, Neuburg (1948, p. 182) compared the Shanxi fronds to the Angara plant *Comia*(?) *primitiva* Neuburg from the Permian of Kuznetsk.

Form-genus SUPAIA White, 1929

Type species. Supaia thinnfeldioides White, 1929, p. 54.

Supaia spp.

Plate 1, figures 1–2, 6; Plate 2, figures 3, 5–6; Plate 3, figures 9, 11

Remarks. Two forms of *Supaia* have been recognized in North China. They will be formally described elsewhere, and will be referred to here simply as *Supaia* sp. A and sp. B. The genus is characterized by a dichotomous primary rachis producing two monopinnate branches. The individual pinnules of sp. A are broadly attached to the rachis and decurrent at the base, whilst in sp. B they are constricted at the base.

For a long time, the genus was regarded as characteristic of the Upper Permian of the western United States (Read and Mamay 1964; Chaloner and Meyen 1973). However, the fronds also occur widely in coeval strata in North China, forming one of the main components of the *Psygmophyllum* Zone. In earlier Chinese studies, such bipartite fronds with monopinnate branches were mistaken for *Protoblechnum wongii*; examples include the specimen figured by Si (1989, pl. 65, fig. 2) from the Permian Shihhotze Group, and that designated *Compsopteris wongii* (Halle) Gu and Zhi (1974, pl. 130, fig. 6).

Rare evidence of *Supaia* has also been seen in the Upper Permian of Subangara and Angara. For instance, *S. tomiensis* Tschirkova from the Late Permian of Kuznetsk (Neuburg 1948, p. 131) and the specimens figured as *Callipteris bella* and *Comia biarmica* by Vladminovich (1986, pl. 140, fig. 6; pl. 149, fig. 4), from the Kungarian–Ufimian of the Urals, clearly have bipartite fronds. In addition, *Supaia tieliensis* Huang (1977), from the Upper Permian Hongshan Formation of north-east China, is from an Angaran terrane.

Form-genus PROTOBLECHNUM Lesquereux, 1880

Type species. Protoblechnum holdeni (Andrews) Lesquereux, 1880, p. 188.

Protoblechnum wongii Halle

*1927 *Protoblechnum wongii* Halle, p. 135, pls 35–36; pl. 64, fig. 12.
1989 *Protoblechnum wongii* Halle; Liu, p. 447, pls 1–5 (*non* pl. 4, fig. 1).

Remarks. The superficial similarity between this species and the Angaran *Compsopteris adzvensis* Zalessky has been noted by many authors (e.g. Halle 1927; Sze 1954; Lee 1963; Meyen 1970) and Gu and Zhi (1974) went as far as to transfer Halle's species to *Compsopteris*. However, *P. wongii* has been revised recently by Liu (1989), based on numerous good specimens from the lower part of the Shihhotze Group, and it has been shown that the fronds were bipartite, with bipinnatifid branches. They thus clearly differ from the unforked, monopinnate fronds of *Compsopteris*. *P. wongii* is most abundant at levels below where *Supaia* occurs in North China, although its occurrence at higher levels cannot be ruled out. Using Asama's (1960) 'growth retardation' hypothesis, it is possible to interpret *Supaia* as a retarded form of a *Protoblechnum* frond, reflecting an increase in climatic aridity.

Form-genus COMIA Zalessky, 1934

*1934 *Comia* Zalessky, p. 268.
1973 *Comia* Zalessky; Fefilova, p. 118.

Type species. Comia pereborensis Zalessky.

Aff. *Comia* spp.

Plate 3, figures 1–2; Plate 4, figures 4–6

Remarks. Comia is a monopinnate form-genus characterized by fasciled veins, found in Subangaran and Angaran assemblages. There has been a number of earlier records of similar specimens from the Permian of North China. For instance, the types of *Fascipteris hallei* Gu and Zhi (1974) have a very similar venation, and Zhang *in* Zhang and Mo (1979) erected a new genus, *Fascipteridium*, for specimens from the 'Upper Shihhotze Formation' of Henan with fasciled veins. Xiao (1985, pl. 187, figs 2–3) described specimens as *Comia* sp. from the lower Upper Permian of Shanxi, while very similar specimens from higher stratigraphical levels were described as *Scytophyllum sunjiagouense* Wang and Wang (1986, pl. 16, figs 4–8). Illustrated here are isolated pinnae from the Tianlongsi Formation of North China, again with fasciled veins very similar to those of *Comia*.

Meyen (1970) argued that the specimen illustrated by Read and Mamay (1964, pl. 19, fig. 5) as *Callipteris* cf. *adzvensis* Zalessky from the Permian of North America, which also has fasciled veins, probably belongs to *Comia*.

Genus AUTUNIA Krasser, 1919

*1919	*Autunia* Krasser, p. 20.
1982	*Autunia* Krasser; Kerp, p. 423.

Type species. Autunia milleryensis (Renault) Krasser, 1919, p. 20.

Autunia-type fructification

Plate 1, figure 5; Plate 2, figure 4

Remarks. The ovule-bearing reproductive structures figured in the present paper consist of small, spirally arranged, peltate megasporophylls, which are bilaterally symmetrical, and are very similar to *Autunia* as re-defined by Kerp (1982). They are closely associated with the foliage *Supaia* sp. A in one biostrome. They are quite different from the seed-bearing pteridosperm frond described by Mamay and Watt (1971), which resembles both *Callipteris* and *Supaia* of the Hermit Shale. On the other hand, they compare well with the specimens illustrated by Meyen (1982, text-fig. 18) as *Peltaspermum*? sp. A from the Upper Permian of Pechora, which were associated with *Compsopteris adzvensis* Zalessky foliage. There is clearly a possibility of a close relationship between *Supaia* and *Protoblechnum*/*Compsopteris* in Asia.

Genus PELTASPERMUM Harris, 1937

Type species. Peltaspermum rotula Harris, 1937, p. 34.

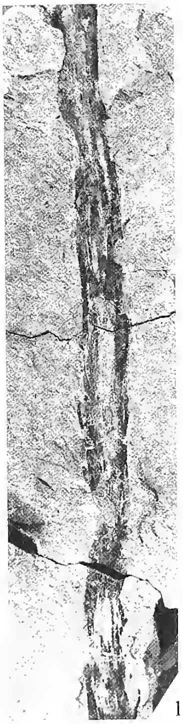
Peltaspermum sp.

Plate 3, figure 4

Remarks. A peltate disc, showing clear 'rib-lobelets', is indeed similar to *P. multicostatum* Zhang and Shen (1987*a*) from the C-bed of the Nanshan section.

EXPLANATION OF PLATE 5

Figs 1–3. *Psygmophyllum multipartitum* Halle. Xinyu village, Qingshui district, Shanxi; upper Tianlongsi Formation, Upper Permian; × 1. 1, TIGP 8802-14; long petiole. 2, TIGP 8802-15; basal part of leaf with thick petiole. 3, TIGP 8802-11; average-sized leaf.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WANG, *Psygmophyllum*

CORDAITEAN FOLIAGE

Besides the above mentioned pteridosperms, there are other plant fossils which give an Angaran feel to the assemblages, in particular the cordaite-like leaves. These leaves in the Permian of North China are mainly of the short, scale-like forms, probably reflecting the relatively arid climate. Some can be compared quite closely with Angaran cordaitean scales. For instance, one figured on Plate 3, figure 7 is very similar to the Upper Permian *Petscheria tomiensis* Zalessky of Kuznetsk (Neuburg 1948, p. 198, pl. 45, fig. 8) and another, on Plate 4, figure 3, hardly differs from a coeval specimen assigned by Durante (1976, pl. 70, fig. 5) to *Crassinervia* sp. nov. 1 from Mongolia. The specimen illustrated as Plate 3, figure 3 can be compared with *Zamiopteris*, as it has a denser venation in the central part of the leaf than near the margins (e.g. Meyen 1970, p. 530, pl. 77, fig. 1). The aphlebia-like scale shown in Plate 3, figure 10 appears identical to *Wattia*, a Permian genus of uncertain affinities, originally described from North America, but which was also recorded from the Kazanian of Subangara by Meyen (1982, pl. 16, fig. 128).

It should finally be pointed out that all specimens from Nanshan previously recorded as *Zamiopteris*, by both Russian and Chinese palaeobotanists, are almost certainly misidentified. They all show a rather pronounced midvein, and some of them compare more closely with the Euramerican leaves *Lesleya* and *Taeniopteris*.

PALAEOPHYTOGEOGRAPHY

During the Permian, the pteridosperms described above had an extensive distribution throughout the Northern Hemisphere, including Euramerica (western Europe, south-west USA), Angara, Subangara, Cathaysia and North China. I cannot therefore agree with Meyen (1982, 1987, 1988) that these plants were endemic to Subangara.

Western Europe

The callipterids have been traditionally used as an important index for the Lower Permian Rotliegend, in which they are very diverse, with one natural genus and five foliage form-genera (Kerp 1988). Broutin (1986) has also reported psygmophylloid foliage from the Lower Permian of Spain. In the Upper Permian Zechstein flora, lepidopterids are common (Schweitzer 1986; Poort and Kerp 1990).

South-west USA

This area has yielded well documented pteridospermous assemblages. The Lower Permian Hermit Shales assemblages are dominated by *Callipteris*, *Supaia*, '*Brongniartites*', *Protoblechnum* and what Meyen (1970, p. 530) referred to as *Comia*. In addition, White (1929) described a questionable

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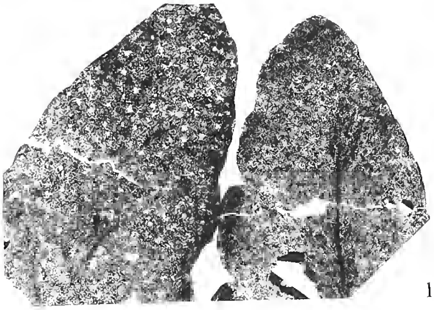
EXPLANATION OF PLATE 6

Figs 1–4. *Callipteris changii* Sze. TIGP 8908-0; Nanhegou village, Baode district, Shanxi; upper Tianlongsi Formation, Upper Permian. 1, lower and upper cuticles; ×4, 2, fragment of lower cuticle; ×100. 3, lower cuticle from pinnule apex; ×60. 4, upper cuticle from pinnule apex; ×60.

Fig. 5. *Psygmophyllum multipartitum* Halle. TIGP 9016-2; thin cuticle; Jiuxian village, Guxian, Shanxi; upper Tianlongsi Formation, Upper Permian; ×60.

Figs 6–8. *Psygmophyllum multipartitum* Halle. Thick cuticles showing stomata varying from randomly distributed (6) to arranged in regular files (7–8); upper Tianlongsi Formation, Upper Permian; ×60. 6, TIGP 9016-2; Jiuxian village, Guxian, Shanxi. 7, TIGP 8912-1; Hekou village, Xuangan district, North Shanxi. 8, TIGP 8822-25; Shandaogou village, Pingliang district, East Gansu.

PLATE 6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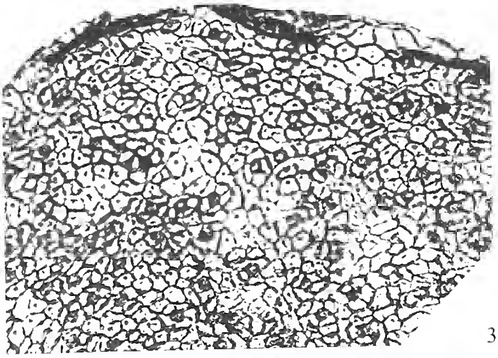
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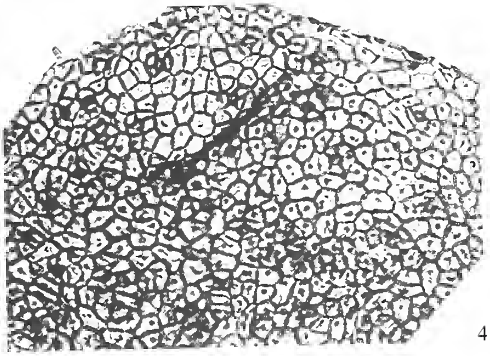
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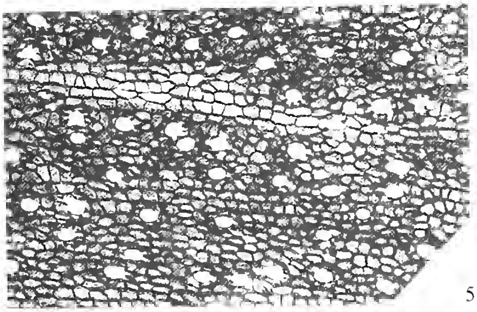
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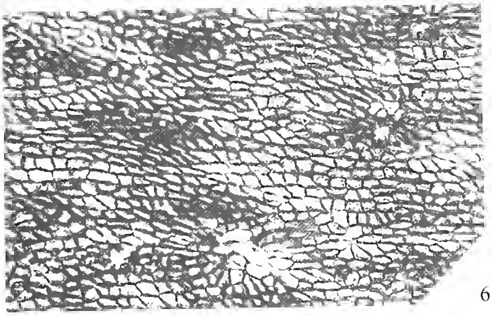
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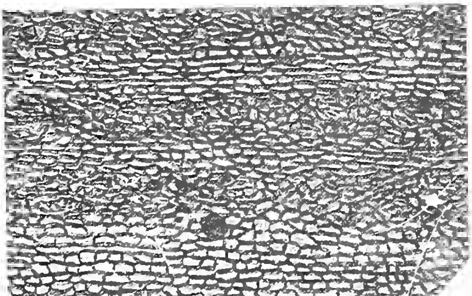
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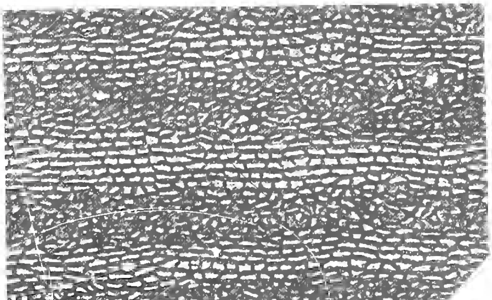

8

WANG, *Callipteris*, *Psygmophyllum*

Psygomophyllum from these strata. The Upper Permian (Leonardian) is, in contrast, characterized by unusual gigantopterids and taeniopterids (e.g. Mamay *et al.* 1984).

Subangara

Meyen (1981) proposed the name Subangara for the western periphery of Angara proper during the Permian, including most of what was previously called West Angaraland (Meyen 1978*a*), i.e. the Russian Platform, the Urals, west and south Kazakhstan, etc. In the Late Permian, 'the Subangara flora spread out to the south and east from areas proximal to the Urals' (Meyen 1987, p. 309). He regarded it as an intermediate zone (ecotone) between the Angara and adjacent areas; it yielded typical Angaran elements (*Rufloria*, *Protosphagnum*, *Paracalamites*) associated with elements characteristic of the other areas: the Euramerican *Quadrocladus*, *Pseudovoltzia* and *Callipteris*; the North American *Wattia* and *Pseudovoltzia*-like conifers; the Cathaysian *Lobatannularia* and *Taeniopteris*, amongst others (Meyen 1982, p. 73; 1987, p. 308). Significantly, most of the elements regarded by Meyen as endemic to the Subangara belt are peltasperms (*Callipteris*, *Compsopteris*, *Peltaspermum*, etc.) and psygmophylloids (*Syniopteris*, *Psygmophyllum*), which are found in strata of Artinskian to Tatarian age.

Vladiminovich (1986) illustrated most of the *c.* 160 species that have been described by Russian palaeobotanists from the Asselian to Tatarian floras of the Urals and Russian Platform. In the Artinskian to Ufimian interval, 15 per cent. of the reported genera are peltasperms (*Callipteris*, *Comia*, *Permotheca*, '*Odontopteris*') and psygmophylloids (*Syniopteris*/*Psygmophyllum*). The total assemblage comprises 69 species belonging to 38 genera, and includes some Angaran elements (*Rufloria*, *Viatscheslavia*, *Zamiopteris*, *Paracalamites*) together with some common Euramerican form-taxa (*Pecopteris*, *Sphenopteris*, *Walchia*, *Calamites*, *Cordaites*, etc.). The Kazanian to Tatarian has yielded 21 plant form-genera. Many of the Lower Permian callipterids were replaced by *Phylladoderma*, *Tatarina* and *Peltaspermum*, amongst others, although rare *Comia*, *Brongniartites*, '*Odontopteris*' and *Syniopteris* persisted; together, the callipterids make up 40 per cent. of the genera. Only a few Angaran elements, such as *Paracalamites*, persisted into these later assemblages. It is noteworthy that, in the Asselian to Sakmarian, assemblages listed by Vladiminovich with only Euramerican elements are rare. On the other hand, Angaran taxa are not dominant in any part of the Permian of western Subangara, and only in the Kungurian do they achieve any sort of diversity, reaching a maximum of 17 per cent. of the assemblage (e.g. *Rufloria*, *Paracalamites*, *Crassinervia*, *Zamiopteris*, *Nephropsis*).

In south-western Kazakhstan, Salmenova (1979) recognized four successive plant assemblages in the Upper Carboniferous and Permian. All four included characteristic Euramerican form-taxa (*Calamites*, *Walchia*, *Lebachia*, *Dicranophyllum*, etc.). Only in the uppermost assemblage do rare and questionable Subangaran elements occur (*Paracalamites*, *Noeggerathiopsis*?, *Koretrophyllites*?), associated with Euramerican elements (e.g. *Dzungariella*, *Chulakia*, *Peltaspermum*, *Ulhmannia*, *Voltzia*). *Chulakia* may be a type of cycad cone scale similar to *Tianbaolinia* from the Permian of Shanxi (Gao and Thomas 1989), while *Peltaspermum dzungariense* Salymenova has been transferred to *Autuniopsis* by Poort and Kerp (1990). The palaeophytogeographical position of this area has been discussed by several authors (Meyen 1982; Chaloner and Creber 1988; Cleal and Thomas 1991). Superficially, the assemblage appears to be most similar to the Zechstein flora of western Europe. However, Cleal and Thomas (1991, p. 164) have argued that it in fact represents an ecotonal assemblage between Angara and Cathaysia, and that its apparent Euramerican aspect is the result of errors of biostratigraphical and taxonomic interpretation.

Southern periphery of Angara

This belt, which Meyen claimed to be the extension of Subangara to the south and east in the Late Permian, is situated to the south of the suture between the Siberian Platform and the Sino-Korean Block, and extends from the Junggar (Dzungar) Basin of North Xinjiang (China) in the west, via southern Mongolia and the northern Da Khinggan Range of north-east China, to the South Primorye.

In the Junggar Basin, the Upper Permian *Callipteris-Comia* assemblage consists of 19 genera, including *Callipteris*, *Comia*, *Compsopteris*, *Supaia*? and *Iniopteris* (= *Psygmophyllum*) (Dou and Sun 1985*a*, 1985*b*). The assemblage overlies the *Angaropteridium-Zamiopteris* assemblage, and includes a mixture of Angaran (*Zamiopteris*, '*Noeggarathiopsis*', *Crassinervia*), Euramerican (*Walchia*, *Ullmannia*, *Taeniopteris*, *Schizoneura*) and rare Mesophytic (*Pterophyllum*, *Sphenobaiera*) elements.

Durante (1976, tables 1–2, p. 80) described five plant assemblages in the Carboniferous and Lower Permian of Mongolia, and two assemblages from the Upper Permian. In south Mongolia, the Upper Carboniferous to Lower Permian assemblages are typically Angaran, with *Angaropteridium*, *Angaridium*, *Zamiopteris*, *Gaussia*, *Vojnovskya*, *Rufloria*, *Crassinervia*, *Nephropsis*, *Cardioneura*, *Tomiodendron* and *Angarophloios*. The Upper Permian assemblages, as well as including *Callipteris*, *Comia*, *Iniopteris* and *Compsopteris*, together with Angaran elements such as *Zamiopteris*, *Rufloria*, *Lepeophyllum*, *Crassinervia* and *Paralacamites*, contain elements also found in the Permian of North China (*Taeniopteris*, *Cladophlebis*, *Sphenopteris*, *Pecopteris*, *Rhipidopsis*, etc.). The psygmophylloids and peltasperms comprise about 16 per cent. of the 25 genera in both assemblages.

A synthesis of the Carboniferous and Permian plant fossils from the northern Da Khinggan Range has been presented by Huang (1993). The assemblages from the Carboniferous (referred to as the Baolige flora) are typically Angaran and include '*Noeggerathiopsis*', *Lepeophyllum* and *Nephropsis*. The Upper Permian contains some of these Angaran elements, together with *Callipteris*, *Comia*, *Supaia*, *Compsopteris*, *Rhipidopsis*, *Crassinervia* and *Paracalamites* amongst others, but also includes taxa characteristic of the Permian of North China, such as *Schizoneura*, *Pecopteris*, *Taeniopteris*, *Nilssonia* and *Pterophyllum*. Huang thus suggested that this reflected a northwards migration of the North China vegetation during the Late Permian.

In the South Primorye, Zimina (1977) has described the plant fossils from three Permian Formations as being typically Angaran, with *Zamiopteris*, *Vojnovskya*, *Rufloria*, *Gaussia*, *Angaropteridium*, *Paracalamites*, *Crassinervia* and *Annulina*, amongst others. The Upper Permian also included the callipterids *Callipteris*, *Compsopteris* and *Comia*. She also described leaves with a midvein and anastomosing lateral veins as *Glossopteris*, although they are more likely to be fragments of *Psygmophyllum* leaves.

More recently, Burago (1986, 1989) reported a 'Cathaysian flora' from the Kazanian–Tatarian of the South Primorye, consisting of some 200 species. They included species of *Bicoemplectopteridium* (= *Gigantonoclea*), *Annularia*, *Protoblechnum*, *Lobatannularia*, *Pecopteris*, *Callipteris*, *Comia*, *Neuropteridium*, *Syniopteris* and *Taeniopteris*, which are all undoubtedly common plants of what is referred to in the present paper as the *Psygmophyllum* assemblage of North China. They were associated with a number of typically Angaran elements (e.g. *Zamiopteris* and *Rufloria*-like leaves). Among the approximately 50 genera in this Sizinskaya flora, 14 per cent. were either peltasperms (*Callipteris*, *Comia*, *Protoblechnum*, *Peltaspermum*), *Phylladoderma* or psygmophylloids (*Psygmophyllum*, *Ginkgophytopsis*).

From the above, it is clear that the fossil record reflects significantly different vegetational histories between Subangara and its extension. In the west, psygmophylloids and peltasperms occurred throughout the Permian, sometimes in association with Angaran plants; in the south and east, these pteridosperms did not appear until the Late Permian, the Early Permian vegetation being typically Angaran in character.

Angara proper

The most typical Angaran assemblages are found in the Kuznetsk Basin, where the Lower and Upper Permian are known respectively as the Upper Balakhonskaya and Kolchuginskaya 'subseries'. Meyen (1982) assigned the former to the *Rufloria* Cordaitean 2 Assemblage, dominated by the typical Angaran taxa *Rufloria*, *Vojnovskya*, *Gaussia*, *Zamiopteris*, *Crassinervia*, *Nephropsis* and *Lepeophyllum*. In contrast, the Kolchuginskaya 'Subseries' was placed in his *Rufloria*-cordaitean 3(–4) Assemblage, containing *Callipteris*, *Comia*, *Compsopteris*, *Supaia* and psygmophylloids (*Iniopteris*). The photographic illustrations of the Kuznetsk Upper Permian plant fossils by Neuburg (1948) show that, in addition to the callipterids listed above, there are also present in the Kuznetsk taxa very similar to those found in similar aged strata in North China, e.g. *Pecopteris anthriscifolia* (Göppert) Zalessky (as pointed out by Halle 1927) and *Taeniopteris norinii* Halle. *Annularia lanceolata* var. *tenuinervis* Radchenko (Neuburg 1948, pl. 3, fig. 2) has bi-lobed leaf whorls similar to *Lobatannularia*. Also, *Zamiopteris glossopteroides* Schmalhausen (Neuburg 1948, pl. 45, figs 1–2) is very similar to *Lesleya* in North China. These taxa form only a small portion of the overall flora, but may be of considerable palaeophytogeographical significance.

The palaeobotany of the famous Pechora area of north-west Angara has been reviewed by Meyen (1982). A few plant fossils occur in the Artinskian, but are too poorly preserved to identify. The higher horizons were divided into the Vorkutskaya (Kungurian–Ufimian) and Pechorskaya (Kazanian–Tatarian) 'series'. The Vorkutskaya plant assemblages are dominated by *Rufloria*-cordaitean elements (*Rufloria*, *Vojnovskaya*, *Zamiopteris*, *Crassinervia*, *Nephropsis*), associated with mosses (*Protosphagnum*, *Intia*), articulates (*Sphenophyllum*, *Annularia*, *Annulina*, *Phyllotheca*), ferns (*Sphenopteris*, *Pecopteris*, *Danaeites*), conifers (*Walchia*) and *Psygmophyllum expansum*. In the uppermost part of the 'Series', rare callipterids (*Callipteris*, *Compsopteris*) appear, and become increasingly diverse at higher levels. In the upper Pechorskaya, these groups, including *Callipteris*, *Peltaspermum*, *Comia*, *Compsopteris*, *Permotheca* and *Psygmophyllum*, form about one-sixth of the 43 genera found. Meyen (1982, p. 71) reported that the Pechora Palaeoarea grades into the Subangara Palaeoarea to the south, indicating a close relationship between the two regions in the Late Permian.

In the north-eastern part of Kazakhstan (e.g. Balkhash) which belongs to Angara proper, Salmenova and Koshkin (1990, pp. 40–51) recognized three plant-bearing horizons in the Permian. Mostly, they are dominated by typically Angaran elements (*Rufloria*, *Zamiopteris*, *Paracalamites*, *Angaropteridium*). However, the highest one also contains a few peltasperms (*Peltaspermum*?) and psygmophylloids (*Rhipidopsis* and *Psygmophyllum*, assigned by Meyen).

To summarize, the peltasperms and psygmophylloids did not appear in Angara proper until the Late Permian, which is significantly later than in Subangara. They are also much less diverse than in Subangara.

THE GREAT EURASIAN FLORAL INTERCHANGE

The collision of the Siberian plate with Laurasia was the most important tectonic event in the Northern Hemisphere during the Permian. Initially, the European (Baltic) Platform collided with Siberia in the Early Permian, while the Sino-Korean Block did not fuse with the rest until the Late Permian (Nie *et al.* 1990, p. 406; Scotese and McKerrow 1990, p. 17). This difference in timing is in full agreement with variations in the vegetational histories in the western and southern parts of Subangara, as discussed above. It would appear to be contradicted by the palaeomagnetic data (Opdyke *et al.* 1986; Zhao and Coe 1987) which suggests that there was a considerable latitudinal difference between Siberia and the Sino-Korean Block at the end of the Permian, hindering floral interchange between the blocks. However, Scotese and McKerrow (1990, p. 17) have proposed that the western part of the Sino-Korean Block (Tarim) collided with Siberia in the Early Permian, while the north-eastern part of China (Manchuria) did not fuse with Siberia until the Late Permian. This would explain the apparent latitudinal separation between the two blocks, while still allowing floral interchange.

The relative positions of the North and South China blocks in the Permian is also not certain, due to the superimposition of post-Palaeozoic tectonic movement (Sengör 1985).

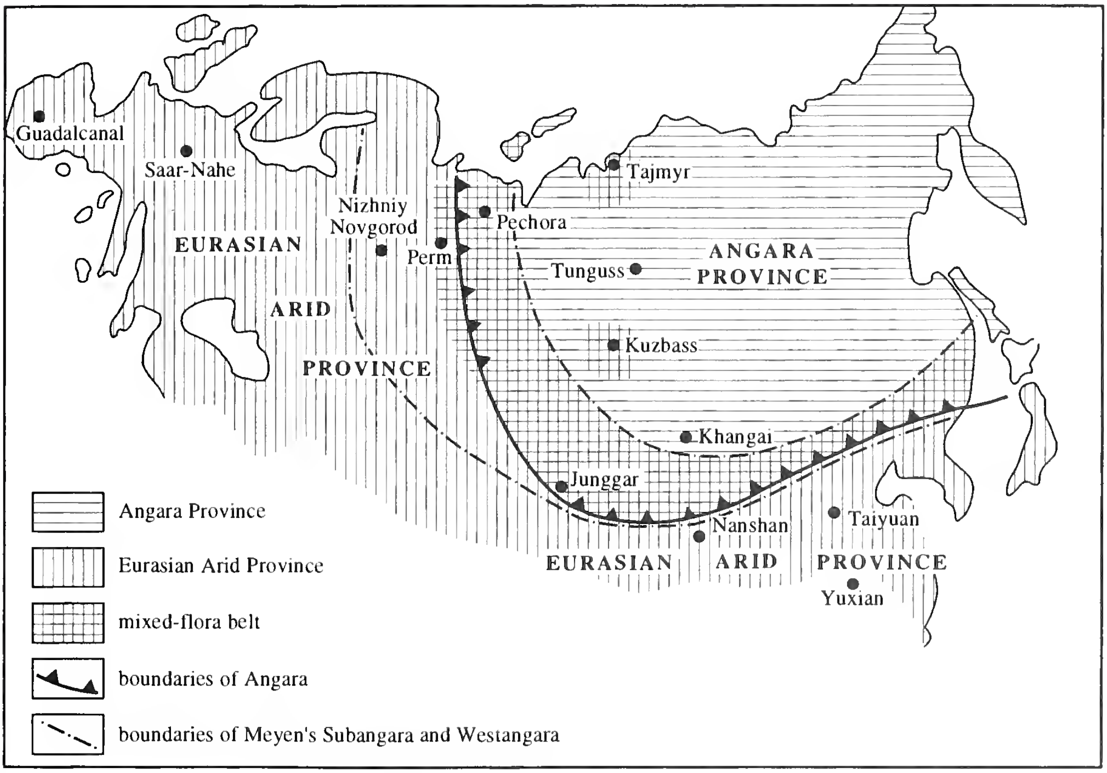
Based on palaeobotanical evidence, Wang (1985, p. 39) proposed that, during the Permian and Triassic, the North China Block was much closer to western Europe than at present, adjacent to the

Urals. This has been further supported by a map showing the expansion of the Isoetaceae during the Triassic (Wang 1991, text-fig. 11).

Floral migrations

Biotic migration or invasion is a topic of current interest in both palaeontology (e.g. Chaloner and Lacey 1973; Vermeij 1991; Webb 1991) and biology (e.g. Sauer 1988; Hengeveld 1989). However, establishing the details of such large-scale biotic movements in such distant times as the Permian is difficult, due to lack of reliable data and a feasible mechanism.

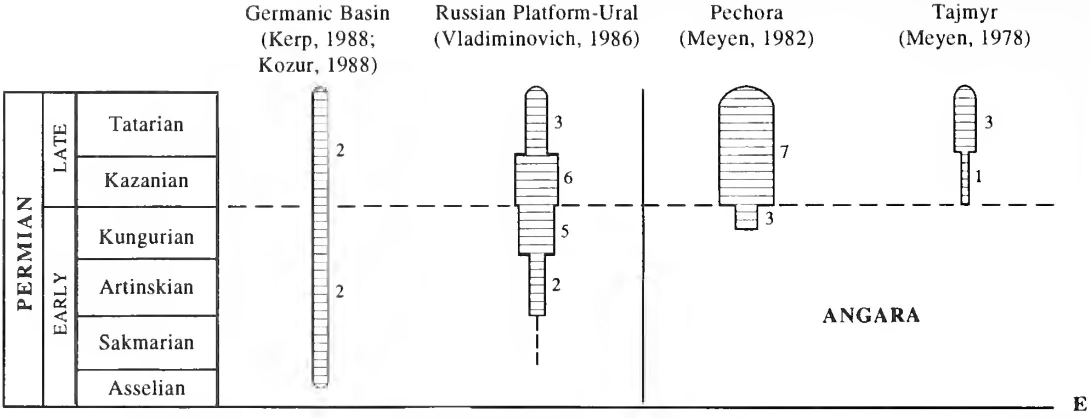
I recently proposed that there had been a northwards migration of the Permian vegetation in North China (Wang 1994). This was based on an ascending trend of the first occurrences of *Psygmophyllum* in a series of ten sections of the Tianlongsi Formation from the south to the north of Shanxi. A similar method can also be used to estimate larger-scale vegetational migrations, such as that being considered in this paper. Using this approach, the data suggests that there had been two discrete routes by which low-latitude vegetation migrated into the Angara region (Text-fig. 2):



TEXT-FIG. 2. Upper Permian palaeophytogeography of Eurasia.

a western route, from western Europe, via the Russian Platform, into Pechora and Tajmyr; and a southern route from North China, via south Mongolia to the Kuznetsk.

Western route (Text-fig. 3). Vegetational migration along this route is indicated by the first occurrences of the callipterids. In western Europe, they first appear in the Lower Permian



TEXT-FIG. 3. Ranges and diversity of peltasperm and psygmophylloid genera (combined) in the Permian, from west Europe to Siberia.

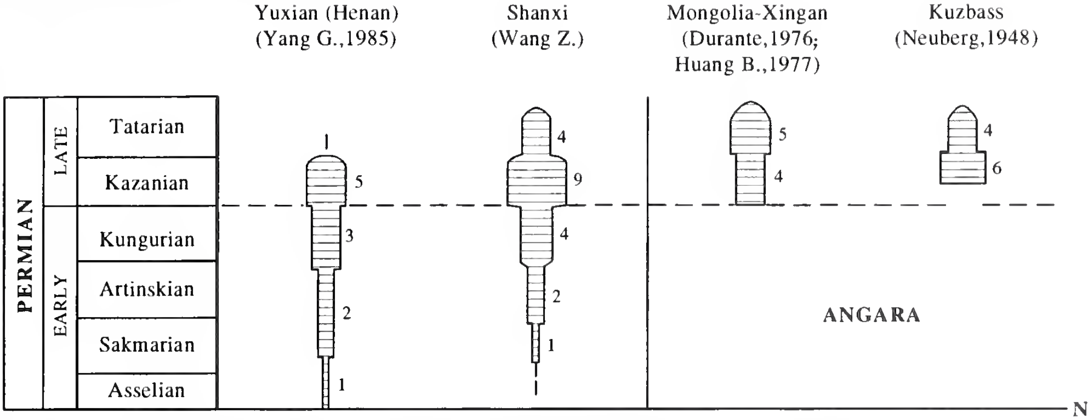
Rotliegend with *Autunia*, and are replaced by lepidopterids with ovuliferous *Peltaspermum* in the Upper Permian Zechsteins.

In the Urals and the Russian Platform (Subangara), the callipterids first appear in the Artinskian. In these assemblages, the Euramerican gymnosperms tend to be dominant, and the Angaran *Rufloria*-like cordaite leaves with narrow dorsal furrows, and articulates with narrow stems (*Paracalamites*, *Phyllotheca*) are rare. Farther east in Pechora, the Permian assemblages are dominated by Angaran taxa, and the callipterids (and psygmophylloids) do not appear until the Lower Kungurian, although they then persist right up to the topmost Permian (Meyen 1982). Further east again, in Tajmyr (Meyen 1982, p. 70), the callipterids do not appear until the Upper Permian (Kazanian). The evidence thus clearly indicates an eastwards migration of these pteridosperms from western Europe to Angara during the Permian.

Southern route (Text-fig. 4). Vegetational migration along this route is even more clearly demonstrated by the ascending trend of first occurrences of psygmophylloids, from northern South China, via North China (Henan, Shanxi) and the southern part of Meyen's Subangara, to Angara proper. In Jiangsu and Fujian of South China, *Psygmophyllum* and *Compsopteris* (= *Protoblechnum*) occur in the Longtanian (Lower–Upper Permian), in association with typical Cathaysian elements (Yao 1989). In Central Henan, *Psygmophyllum* first occurs in the middle part of the 'Upper Shihhotze' Formation, becoming progressively more diverse until it reaches a maximum in the upper part (Yang 1985). In North Shanxi, the first occurrence of the psygmophylloids is rather higher, in the upper Tianlongsi Formation (Wang 1992).

Farther north, in the northern Khinggan Range and in south Mongolia, the Kazanian peltasperm-bearing strata immediately overlie upper Carboniferous–Lower Permian deposits with typical Angaran assemblages including *Angaropteridium*, *Zamiopteris* and *Rufloria*, corresponding to the Balakhongskaya assemblages of the Kuznetsk (Huang 1993; Durante 1976). Finally, a few callipterids and peltasperms appear in Angara proper in the upper Kazanian, where they persist through to the end of the Permian in association with the declining Angaran taxa. In comparison with the western migration route, the southern migration was on a much larger scale, and was also more complex, involving both Permian components from North China and Cathaysian elements from South China (Wang 1989).

It is noticeable that there was little reverse migration of plants from Angara into the adjacent areas. Some of the few exceptions include the rare presence of the Angaran taxa *Rufloria* and *Paracalamites* in the Kungurian of western Subangara, associated with the previously mentioned



TEXT-FIG. 4. Ranges and diversity of peltasperm and psygmophylloid genera (combined) in the Permian, from North China to Siberia.

pteridosperms (Meyen 1982, p. 74). However, it never occurred to the same extent as the migration in the other direction.

In summary, after the collision of the Laurasia and Siberia plates in the Permian, there was a marked floral interchange, predominantly of Euramerican and Chinese elements into Angara, although also to a lesser extent in the opposite direction. The former was by far the more marked, representing the movement of plants over hundreds or thousands of kilometres, from either Euramerica or South China into Siberia. The reverse migration, in contrast, merely represents the outwards diffusion of a few Angaran taxa into the areas marginal to Siberia, such as the Urals and the Russian Platform.

Meyen's (1982, p. 77) comments on the position of the Subangaran assemblages are confusing. On the one hand he stated that 'since the Early Permian, the Angara Kingdom was divided into the Angara and Subangara areas', which implies that the Angara Kingdom contracted due to floral invasion from adjacent areas. On the other hand, he clearly suggested that the Subangara flora with its endemic pteridosperms was expanding from areas proximal to the Urals, eventually arriving in Nanshan in North China. This can make it difficult to distinguish between what are Subangaran and what are Angaran taxa, and may give the misleading impression of an expanding Angara.

An asymmetrical interchange

Marked asymmetry in the pattern of migration is a characteristic of almost all well known biotic interchanges, usually reflecting an imbalance in the ecosystems. Such an asymmetry is clearly observable in the Permian floral interchange between Angara and Laurasia. Among the taxa discussed in this paper, most are Eurasian genera that migrated towards Angara: pteridosperms *Callipteris*, *Comia*, *Compsopteris*, *Rhaphidopteris*, *Supaia*, *Peltaspermum*, *Phylladoderma*, *Tatarina*, *Psygmophyllum*, *Rhipidopsis*, *Chiropteris*, *Neuropteridium*, *Gigantonoclea*; conifers *Walchia*, *Ullmannia*; cyads *Nilssonia*, *Taeniopteris*, *Pterophyllum*; ginkgos *Sphenobaiera*, *Dicranophyllum*; and articulates *Calamites*, *Schizoneura*, *Lobatannularia* and *Annularia*. In contrast, only five Angara genera migrated into the adjacent areas (*Rufloria*, *Zamiopteris*, *Crassinervia*, *Nephropsis* and *Paracalamites*). Although the data presented in this paper are still far from complete, it is already evident that the appearance of exotics in Angara, either via the western or southern route, is roughly coincident with when those taxa achieved their greatest diversity.

The invasion of exotics can result in the extinction of endemic taxa. An outstanding example is the Great American Biotic Interchange (Marshall 1981), which resulted in a mass extinction of the endemic vertebrates in both North and South America during the Cenozoic. The floral interchange that is the subject of this paper has been interpreted as one of the three major palaeobotanical events during the Permian of North China (Wang 1989), and may have resulted in increased extinction rates. This in turn may have resulted in an acceleration of the transition from Palaeophytic to Mesophytic vegetation towards the end of the Permian. When interpreting the Palaeophytic–Mesophytic transition in North China, I previously suggested (Wang 1992) that the unidirectional migration of the *Psygmophyllum* assemblage might be linked with the end-Permian mass extinction, that caused the disappearance of many Palaeozoic dominants, such as cordaitaeans, lepidodendroids, calamites and sphenophylls. Meyen (1982, p. 79) also pointed out that the invasion of Mesophytic elements from Subangara may have reduced the areal extent of Angara and eventually caused its end.

Mechanism

Seed dispersal is obviously one of the main means of seed-plant migration and can be strongly influenced by environmental selection (Sauer 1988); high-speed winds can provide an effective means of dispersing seeds over large distances (Hengeveld 1989). Many of the Permian gymnosperms of North China were particularly well adapted to wind dispersal, such as the platyspermic *Samaropsis*-like seeds of callipterids, the winged *Pityospermum* and the plumed *Nystroemia* (Wang 1994).

In general, plant migration is the result of two types of dispersal: short- and long-distance. According to Hengeveld (1989), short-distance dispersal was the result of neighbourhood diffusion between adjacent areas, while long-distance reflects discontinuous jumps between non-adjacent areas and consequently progressed patchily.

A vast semi-arid area, known as the Eurasian Arid Province (Wang 1985) had developed and expanded after the collision between the Siberian Platform and Laurasia. In western Europe, aeolian sandstones and evaporites began to be deposited in the Early Permian (Glennie 1972; Turner 1980). Such deposits extended into North China in the Late Permian (Norin 1924; Wang 1993*a*), where there is evidence of alternating arid and wet climates with seasonal rainfall. This resulted in the vegetation being restricted and subdivided into small niches, where it would have been subjected to strong selective pressure, and where long-distance, 'jump' dispersal would have had to play a significant role.

As stated above, the migration of gymnosperms into Angara may have been by long-distance, 'jump' dispersal. In contrast, the much weaker migration of Angaran plants into Subangara may reflect short-distance dispersal by neighbourhood diffusion. The mechanism behind these migrations was probably influenced most strongly by palaeowind activity and moisture-limitation.

Monsoon activity. I have argued earlier (Wang 1993*a*) that the northwards migration of the *Psygmophyllum* assemblage was linked with the palaeomonsoon prevailing in North China in the Permian. The existence of the Palaeomonsoon is indicated by several phenomena, such as the deposition of biotic silica indicating coastal upwelling, and the taphonomy of *Psygmophyllum* indicating deposition in ephemeral channel deposits resulting from rainstorms in an alternating wet–arid climatic setting. In the Permian palaeogeography of Nie *et al.* (1990), North China is located on the north-eastern margins of Palaeotethys, at latitudes of 20°–30° and thus within the range of the monsoonal circulation. The existence of a strong monsoonal system having developed in West Pangaea during the Sakmarian (Early Permian) is supported by Patzkhowsky *et al.* (1991) using the Fujita–Ziegler palaeoclimatic model. The patchy dispersal of the vegetation in North China in the Middle–Late Permian (Wang 1992) also supports its movement by long-distance wind dispersal.

Moisture-limitation. Such stress can be a major factor promoting plant migration, especially in vast arid and semi-arid areas. For example, the steppe of the Sahel zone, along the southern margins of the Sahara desert, moved up to over 100 km per annum between 1984–1985 (estimated from satellite observation; Tucker *et al.* 1991). In the Great American Interchange, increasing aridity of the subtropical regions also resulted in an asymmetrical interchange, i.e. the southwards movement of the Savanna-adapted biota through the American tropical zone during the Cenozoic (Webb 1991).

After the collision between Siberia and Laurasia, an imbalance of ecological pressure occurred on the two sides of the plate suture. On the Laurasian side, there was the Eurasian Arid Province, where moisture-limitation must have imposed a major stress on the vegetation. On the other side of the suture, such stress was far less marked and an archaic flora with low levels of innovation had developed there (Meyen 1982, p. 78). This strong asymmetry would clearly favour the migration of the newly evolved and more innovative plants from Eurasia, where they would have a competitive advantage over the more primitive Angaran vegetation.

Much of the above evidence for the Great Eurasian Floral Interchange in the Permian is based on the relationship between Angara and North China. However, it almost certainly involved other regions, such as South China and Euramerica. There is clearly much potential for future work in establishing the detailed patterns of vegetational migration during this key time in the evolution of terrestrial vegetation.

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IMPLICATIONS OF NORMAL AND ABNORMAL GROWTH STRUCTURES IN A SCOTTISH SILURIAN DENDROID GRAPTOLITE

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Abstract. Normal growth patterns and structure of one species of dendroid, *Dictyonema pentlandica*, from the North Esk Inlier, Pentland Hills, Lothian, UK, are described and considered to be the result of the secretory zooids adhering to a strict and characteristic growth pattern. Aberrant and abnormal structures include: stipe truncation and compensatory growth by neighbouring stipes; changes in growth pattern; abnormal bursts of growth; tearing or splitting; and abnormal thecal growth. The possible causes of these abnormalities are considered to be the result of mutation, injury or trauma, disease and/or parasites, environmental change, and preservation. Dendroids could repair their rhabdosomes after damage, the nature of the repair being dependent on where the injury had taken place. It is suggested that more palaeoenvironmental and palaeoecological data could be obtained by the recognition of aberrant features in other animal groups.

Dendroids were marine invertebrate fossil organisms, that ranged from the Cambrian to the Carboniferous. They are thought to be ancestors of the widely studied, biostratigraphically important, graptoloids. Pterobranchs are considered to be their closest living relatives (Rigby and Dilly 1994).

They were colonial animals, with a complex skeleton (or rhabdosome). This consisted of stipes of overlapping thecae, made of collagen. Each theca was occupied by a zooid, that secreted the precisely determined shape of theca in which it lived. These thecae developed in a remarkably constant and regular pattern, with thecal size, shape, ornament, and orientation very accurately repeated and constant for each species. The zooids in each stipe, it is thought, were all linked in some way by living tissue. Each dendroid had an internal stolon system of connecting canals which at regular nodal points, divided into three (the triad bud); this produced two thecae (the bitheca and autotheca) which opened into the ocean, and a third stolotheca that continued the stipe. Each theca overlapped its neighbour by a predetermined amount, combining to form long chain- or rope-like stipes, which in turn split, bifurcated or terminated according to seemingly predetermined patterns. This built, throughout the dendroid's life, three dimensional structures that included fan, shrub, disc or conical forms, specific to the pattern (blueprint), of growth characteristic of each species. Each colony was highly integrated, the size and shape of each theca being independent of its position in the colony. Unlike the graptoloids, there is no proximal to distal thecal size gradient (Urbanek 1973). More details of dendroid growth patterns, including the form of holdfasts, extrathecal tissue, and sexual interaction can be found in Palmer and Rickards (1991).

Dendroid species are identified from the details of standard rhabdosome structure. Taxonomically important features include: thecal morphology and distribution; stipe width, separation and branching patterns (including the number of primary branches or stipes); presence, dimensions, and arrangement of dissepiments; gross rhabdosomal morphology and dimensions; and proximal growth (siculate or with a stem, root or holdfast structure). Measurement and description of these features can enable production of statistically reproducible data. During this study, a detailed examination of normal thecal and rhabdosome structure has been made. The blueprint of thecal

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structure and rhabdosome shape of one species, *Dictyonema pentlandica* Bull, 1987, is described and illustrated, as are abnormal structures.

Studies of living colonial animals such as bryozoans have concentrated on two-dimensional encrusting colonies (Taylor 1988), where not only standard patterns of bryozoan colony growth have been identified, but also more complex histories of zooid mortality, colony fission, regrowth, repair, and fusion. For the dendroid discussed herein, a comparison with regenerative and reparative patterns described for bryozoams and other taxa is included below.

Recent work on the pterobranch *Rhabdopleura* (Rigby 1994), has shown that zooids are 'aware' of their spatial position in the tube that they are secreting. Even when successive generations of zooids are involved in the secretion of one tube, tube growth is a highly ordered process. The overall shape of the final tube is less ordered than that of dendroids, because of the encrusting nature of *Rhabdopleura*. The comparison of dendroids with these, their closest living relative, has not yet been attempted. Relationships between patterns of colony construction and ultrastructure of graptolites and pterobranchs were discussed by Rigby (1994) and Rigby and Dilly (1994).

Astogeny is not easy to study in three dimensional, complex, erect colonies such as dendroids. Controls on colony growth are dependent on both internal forces (such as the genetic design of colony with which each species is programmed, i.e. the normal structure), and external forces, such as competition for space with neighbouring dendroids or other taxa, and environmental parameters (temperature, food supply, predation, and mechanical damage).

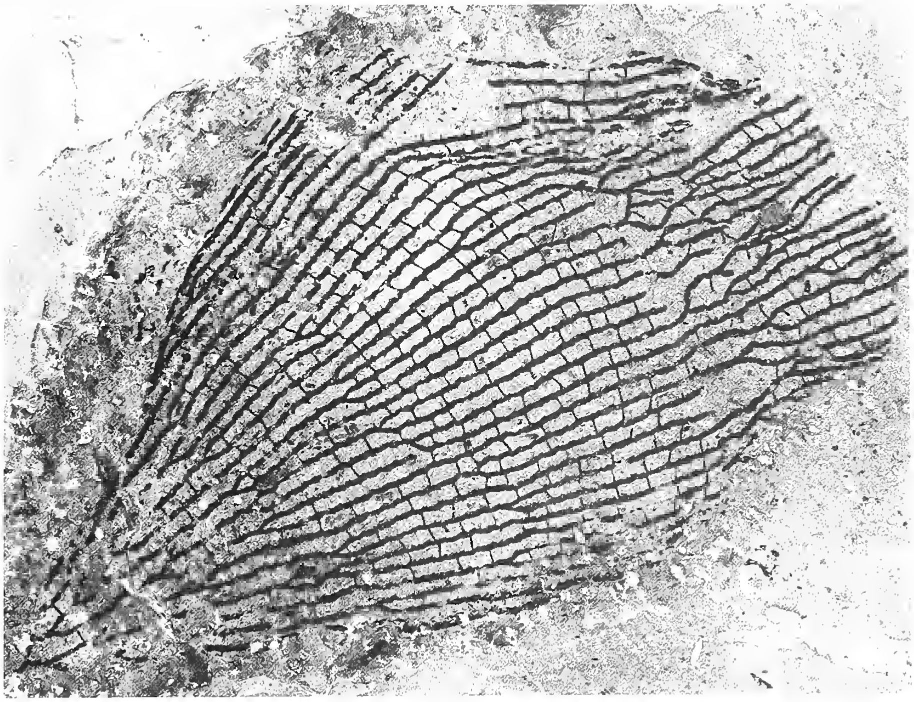
Study of this species has revealed that a number of aberrant structures are present in the growth patterns of dendroids, similar to those described in bryozoans. Whilst it is difficult in fossil material to distinguish pre-mortem from post-mortem damage, certain forms of damage, and changes occurring during the life of the colony can be identified by their effect on surrounding stipes. The probable causes of these aberrant structures, including trauma, predation, mutation, and change in external conditions, are discussed below. While this study concentrates on the regrowth of the dendroid mesh, it also focuses attention on our understanding of the growth patterns of the whole rhabdosome.

Bulman (1950) described a single well-preserved specimen of *Dictyonema flabelliforme* cf. var. *anglica* (Text-fig. 1) from the Shineton Shales (Tremadoc) of Shropshire, which displayed an unusual discontinuity at the periphery of the rhabdosome. In Bulman's opinion, this showed the species to be capable either of regeneration after damage, or rejuvenated growth after a pause. He favoured the latter explanation. This specimen is doubly important as it was not only the first described indication of such renewed growth, but it is also used as the illustration of the zones of bifurcation characteristic of the species '*Dictyonema*' *flabelliforme* in the *Treatise* (Bulman 1970, p. 3); only part of the specimen is illustrated.

Whilst Bulman (1950) recognized the implications of the specimen he was describing, a number of other workers have figured, without comment, species with aberrant structures, such as *Reticulograptus snajdri* (Kraft 1982); *Dictonema delicatulum* (Kraft 1984); *D. desmoides* (Bassler 1909), and various species figured by Ruedemann (1947). However, only one other author (Bouček 1957, p. 22) mentioned the phenomenon directly. His statement on regeneration is as follows: 'It happens sometimes that one or several of the lateral branches finishes its growth prematurely. So a certain gap in the uniform network of the rhabdosome should arise. But such gaps did not form completely. The adjacent branchlets reacted namely very quickly to the space in the neighbourhood and began at once to furcate laterally into the gap, soon healing it'.

Bulman (1950) discussed the variation in dendroid thecal structure with time. He noted that increased thecal isolation is the only trend that has been proved, but the increase in the production of thecal spines also seems to indicate another line of development. The information obtained from the specimens described in this paper is therefore a quite important addition to the scant knowledge of any evolutionary patterns for Lower Palaeozoic dendroids.

Dictyonema is now considered to include only sessile dendroids, and *Rhabdinopora* has replaced *Dictyonema* as the generic name for the planktonic forms, although the phylogenetic differences between the two have not yet been clearly established. The response of *Rhabdinopora flabelliforme*



TEXT-FIG. 1. *Rhabdinopora flabelliformis anglica* (Bulman, 1950); Sedgwick Museum, Cambridge A23397; Shineton Shales, Tremadoc (Ordovician); Shropshire, UK; the original of Bulman (1950, pl. 17); also figured in Bulman (1970, fig. 26, this figure copied by Urbanek (1973, fig. 24)); in these last two figures the magnification is wrongly given as × 1; see also Palmer and Rickards (1991, fig. 126); eight zones of branching are apparent, five before the specimen reaches the normal adult proportions for this subspecies, and three in the zone of rejuvenation; × 2.

to environmental pressure was discussed by Erdtmann (1982); he suggested that some species were capable of 'gerontic astogeny' by thickening of stipes and addition of extra dissepiments, in response to exposure to high energy environments. This may be a record of ecophenotypic variation in dendroid species.

Both planktonic and benthonic dendroids are found only sporadically in the fossil record. It is thought however, that they were once widely distributed in shallow marine environments or perhaps throughout the oceans and the relative rarity of dendroids, particularly as completely articulated fossils, is a result of the low preservation potential of such fragile three dimensional colonies. As discussed below, it is possible that the benthonic forms were able to withstand quite rough conditions in life, but fairly exceptional conditions are required to preserve the biota from such environments.

The dendroid specimens described in this study were deposited in an active tectonic regime (Stone *et al.* 1987), in an environment possibly subject to frequent changes in conditions. The dendroids seem to have been able to cope with these changes, whereas those in other areas may not have been able to. This suggests that the amount of disruption that a species could withstand may have important implications for our understanding of the environment of deposition. Similarly, we may eventually be able to identify dendroid species that have evolved to inhabit different niches or colonize distinct environments.

Aberrant structures in dendroids are not of universal occurrence, and this survey is not exhaustive. In the material from the Pentland Hills here studied, there is usually at least one 'imperfection' per colony, which is a higher incidence compared with specimens from other areas; it is possible that it reflects high energy conditions at the time of deposition.

MATERIAL, LOCATION AND STRATIGRAPHY

Most of the dendroids studied for this paper are excellently preserved, some in partial relief, although no isolated material is yet available. *D. pentlandica* is known from more than 50 specimens. It is the most common species of a varied dendroid fauna from the *Oktavites spiralis* Biozone, late Llandovery (Telychian), of the North Esk Inlier, Pentland Hills, near Edinburgh, Scotland, (locality details are outlined in Bull 1987, and the stratigraphy in Bull and Loydell 1995). All of the specimens of *D. pentlandica* are from the Reservoir Formation, and most specimens were preserved within 15 m thick series of calcareous siltstones found at one locality, the site of the well known 'Gutterford Burn Limestone Beds' (Robertson 1990) and 'Gutterford Burn Eurypterid Bed' (Waterston 1979). The presence of these dendroids fills a gap in the fossil record of dendroids, and particularly of *Dictyonema* in Britain. *D. pentlandica* has not yet been identified from any other locality.

The North Esk Group (Robertson 1989) represents a continuous sequence of marine sediments recording a regression from outer shelf environments (BA 3–4), through lagoonal conditions, to terrestrial sediments. The tectonic history is complex. The depositional basin was restricted, separated from the remnant Iapetus Ocean by the emergent mass of the Southern Uplands. The sediments are now considered to have been deposited at the margins of the eastern end of a rapidly subsiding, elongate (Midland Valley), interarc basin, deepening to the west (Cope *et al.* 1992, fig. S7). The dendroid specimens are found mostly in the Reservoir Formation, the deepest water sediments preserved, which were previously thought to have been deep marine turbidites (Robertson 1989). My subsequent analysis and reinterpretation in the light of current models for the tectonic history of the south of Scotland has suggested that, although distal turbidites cannot be ruled out, there is some evidence for storm-generated deposits. Furthermore, faunal evidence (articulated dendroids, starfish and crinoids deposited *in situ*, along with articulated shallow water eurypterid specimens) is not consistent with a deep marine environment of deposition, and an outer shelf depositional environment is considered more likely.

High faunal diversity in the Pentlands Hills extends to other fossil groups (Robertson 1989). Some have been well documented, such as the crinoids (Brower 1975), trilobites (Clarkson and Howells 1981), eurypterids (Waterston 1979), echinoids (Kier 1973), and starfish (Spencer 1914–1940), whilst others require further revision, such as the brachiopods (Davidson 1868) and bivalves (Lamont 1954).

All specimens described, except for that figured in Text-figure 1 are housed in the collections of Royal Museum of Scotland (RMS), Chambers Street, Edinburgh, Scotland, or in the Grant Institute of Geology (EDCM), Edinburgh University, Scotland.

NORMAL STRUCTURE OF *DICTYONEMA PENTLANDICA*

In the course of this study of *D. pentlandica*, details of the gross morphology have been elucidated by the use of a Scanning Electron Microscope; in particular, the autothecae have now been observed in detail, and the bithecae are also described. This section is a description of the normal growth pattern, or the 'blueprint' for growth, which was adhered to as closely as possible by the zooids when constructing the thecae, and hence the rhabdosome. This normal growth pattern is remarkably regular, and is probably the result of genetically controlled processes, characteristic of each species. It is vital to the understanding of dendroids to ascertain a clear picture of normal growth patterns. Any abnormalities can then be considered independently in terms of variations in external, internal and environmental factors, as discussed below.

Whole rhabdosome. The rhabdosome forms a broad cone with opposing sides diverging at an angle of 30–50°. Most specimens are preserved with some relief. There may be some increase in the angle of divergence because of compression. The walls of the cone fall into gentle folds (Bull 1987, fig. 6). At the base of the cone is a short stem, up to 10 mm long, which was attached generally to a solid object such as a pebble or shell (Pl. 2, fig. 3) or has root fibres attached to secure the specimen to the substrate. The base of the cone is sometimes secondarily thickened (Bull 1987, text-fig. 7A), and usually consists of four primary branches.

The specimens include sections of rhabdosome up to 0·6 m long which represent portions of even larger specimens. Most species of *Dictyonema* previously described are 30–50 mm long, only exceptionally reaching 100 mm. The preservation of this species is remarkable since its constituent stipes are some of the most slender (0·22 mm wide and spaced 0·29 mm apart, or 17–22 in 10 mm). This is, to some extent, consistent with the graptoloid material from the Pentland Hills (Bull and Loydell 1995). Some of the more robust species, characteristic of the *Oktavites spiralis* Biozone, are rare or absent, but more slender forms are present (e.g. *Oktavites excentricus*, *Monoclimacis geinizti*).

The vast majority of the stipes of *D. pentlandica* attain remarkably even distribution, with constant positioning of thecae and dissepiments at standard spacing (Pl. 1, fig. 1) with zones of bifurcation evenly arranged, occurring every 20 mm (Pl. 2, fig. 3). Bulman (1950, p. 351), noted ‘well-marked zones of branching’, suggesting that these might become features of systematic importance. These zones are apparently present in other genera, and although clear enough in the published plates, they rarely feature in the descriptions. This was discussed by Urbanek (1973, p. 475) who noted how the branching pattern can determine the shape of the whole colony. He also suggested that changes in branching frequency could indicate that dendroids had a ‘latent gradient of morphogenetic ability’, or that the branching pattern was part of the essential predetermined normal structure or blueprint of dendroid construction. The main obstacle to the systematic use of such zones in classification (Bulman 1950) is the need for well-preserved rhabdosomes. Such specimens are uncommon. As noted below, when some species grow beyond a certain size the growth pattern can appear to revert irregularly to the juvenile pattern; the whole structure of the rhabdosome can then become contorted. Some *Dictyonema* species are characterized by stipes that bifurcate irregularly and sporadically (Bouček 1957); others do not have zones of stipe bifurcation recognizable as regularly spaced branching zones.

Autothecae. The autothecae of this species were previously thought to be the bithecae (Bull 1987). Further study has revealed more detail, and an idealized reconstruction is given in Text-figure 3. From their base, the thecae expand rapidly to form a tube with a diameter occupying most of the stipe (0·2 mm). Towards the end of the theca the tube again swells rapidly to form the large (up to 0·3 mm diameter), bulbous, spherical termination, which narrows again to form a narrow aperture. This aperture is a simple opening in the middle of the ventral wall of the autotheca, *c.* 0·06 mm in diameter, considerably narrower than the main body of the theca. The thecal aperture is adjacent to the thecal wall of the succeeding theca. The autothecae are not isolated, but their terminal swellings are displaced alternately to either side of the main stipe so that the apertures are angled at 60–70° to either side of the ventral line of the stipe. The upper surface of the autotheca curves inwards, and in some cases back on itself, forming a distinct notch in the wall of the main stipe above the flat upper surface of the autotheca. This notch is occupied by the bitheca curving over the top of the autotheca (Text-fig. 2). It is the distal swellings of the autothecae, regularly spaced along the stipe at intervals of 0·6 mm (28–30 in 10 mm), that gives the rhabdosome the very distinctive knobbly appearance (Pl. 1; Text-fig. 2). There is as yet no clear explanation for the terminal swelling of the autothecae, although it is probably related in some way to zooecial behaviour.

Lateral views of the autothecae show that each theca has a slight geniculum, and the supra-genicular wall is strongly convex; each autotheca has a large ventral sub-apertural spine. This spine is angled towards the open end of the dendroid rhabdosome cone at about 70° to the stipe. The spines are about 0·07 mm wide for most of their length, tapering very slightly distally. Spines can reach up to 0·1 mm long but the average length observed in 0·3 mm. These dimensions are almost identical to those of the dissepiments; in normal preservation, therefore, the thecal spines and dissepiments are indistinguishable and can only clearly be differentiated in profile view (Pl. 1, fig. 3; Text-figs 3–4, 7).

Ruedemann (1947, p. 27) discussed spinosity in dendroids and suggested that species armoured in this way were the weaker taxa. Since then, very few spinose specimens have been described. The bulbous, spinose nature of the autothecae of *D. pentlandica* may have evolved to protect the zooids, particularly from predation. This species had relatively slender stipes, possibly as an aid to directing the currents through the mesh with maximum efficiency and least drag; the spines may also have directed water currents within the cone.

Spines may have been developed by this species to form platforms enhancing zooidal feeding efficiency. By providing support for the zooids to extend themselves considerable distances from the aperture of the theca, this may have resulted in a greatly improved water sampling capacity for the colony. Living *Cephalodiscus* zooids (Rigby 1994) have been observed using spines for feeding in this way. The distinctive swellings of the ends of the autothecae may suggest that the autothecal zooids could have been larger than average. This is unlikely, however, as it has been shown that graptoloid (Sudbury 1991) and pterobranch (Rigby and Dilly 1994) zooids are generally small relative to their thecae.

The dorsal faces of the autothecae of this species are often subject to slightly more weathering than neighbouring parts of the stipe. It is relatively common in even fairly well preserved specimens for a number of thecae to be abraded, leaving the matrix infilling the thecal cavity exposed (Pl. 1; Pl. 2, fig. 2). These openings appear superficially to be the autothecal apertures, although none have the distinct edges expected for apertural margins. This pattern has been studied using the Scanning Electron Microscope; they are clearly artefacts caused by weathering. The true position of the thecal apertures is described above. The autothecae originally may have had thinner walls at the point of curvature; they certainly protrude a little from the plane of the rock because of the partial three-dimensional preservation, being therefore more prone to abrasion and weathering. Alternatively, this feature could be a result of compression and stretching at the time of deposition.

Dissepiments. A dissepiment is associated with every other autotheca. In the area of normal rhabdosome growth they are very thin (0·06 mm diameter; Text-fig. 5), and arranged in a regular pattern with 11–13 in 10 mm (0·8 mm apart) and perpendicular to the main stipe. The fenestellae

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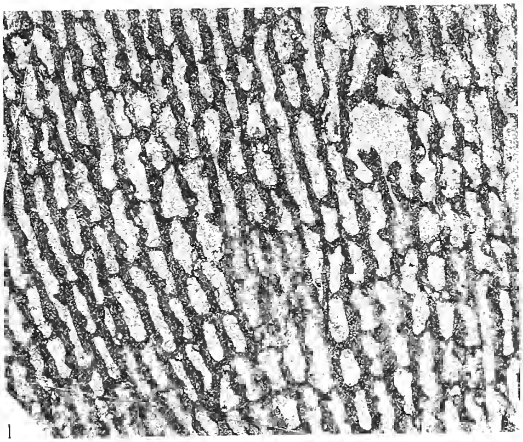
EXPLANATION OF PLATE 1

Figs 1–3. *Dictyonema pentlandica* Bull, 1987; Gutterford Burn; Reservoir Formation, *Oktavites spiralis* graptolite Biozone, Upper Llandovery. Examples of holes in the rhabdosome. 1, RMS.GY.1985.29.5. An area of normal growth with regular spacing of stipes and dissepiments, suddenly interrupted as two stipes terminate, presumably when they constituted the outer growth margin, as a result of either growth pattern defect or predation. Neighbouring blocks of stipes have moved relative to one another due to weakening in one area, and surrounding stipes bifurcate after the termination of the two stipes to regain normal stipe spacing. Some of the autothecae have been slightly weathered where they protrude from the specimen, giving the false impression of being matrix-filled thecal apertures; × 7. 2, RSM.GY.1985.29.2. Extra growth of one stipe has caused it to bulge (middle arrow); and withered stipes (lower arrow). Stipe termination is followed by bifurcation of other stipes to fill the gap (top arrow); × 10. 3, RSM.GY.1985.29.2. Edge of flattened cone of the rhabdosome. The upper portion (top arrow) shows the stipes rotated into profile view, showing the apertural spines. The middle arrow indicates the result of a hole formed in a strong section of the rhabdosome; the surrounding stipes crumpled with the extra load that they were forced to bear and became secondarily thickened to strengthen the remaining stipes. The ends of the stipes left trailing backwards appear to have withered slightly. The lowest arrow indicates a sudden growth within the rhabdosome, which probably formed a bulge in the side of the cone, which is seen here compressed; × 10.

PLATE 1



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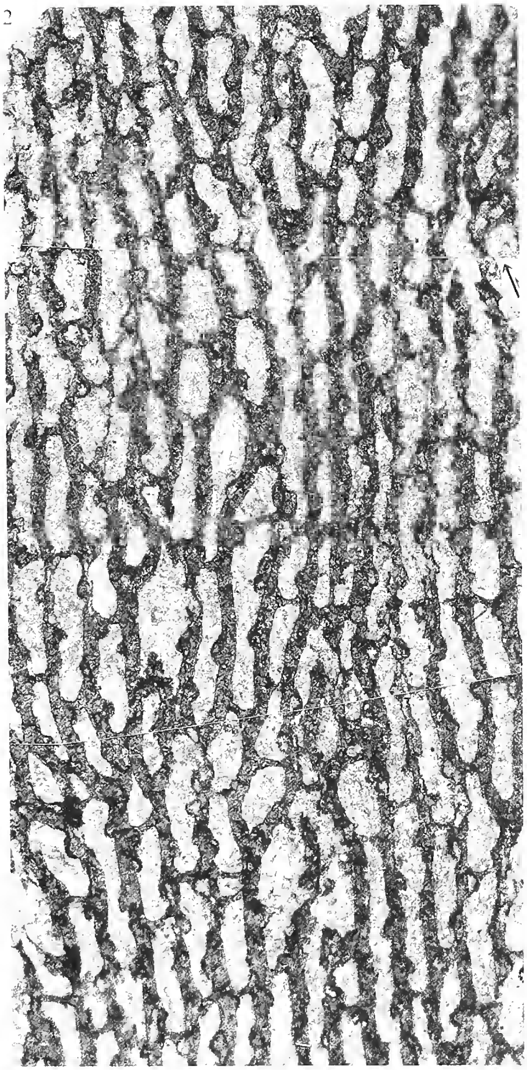

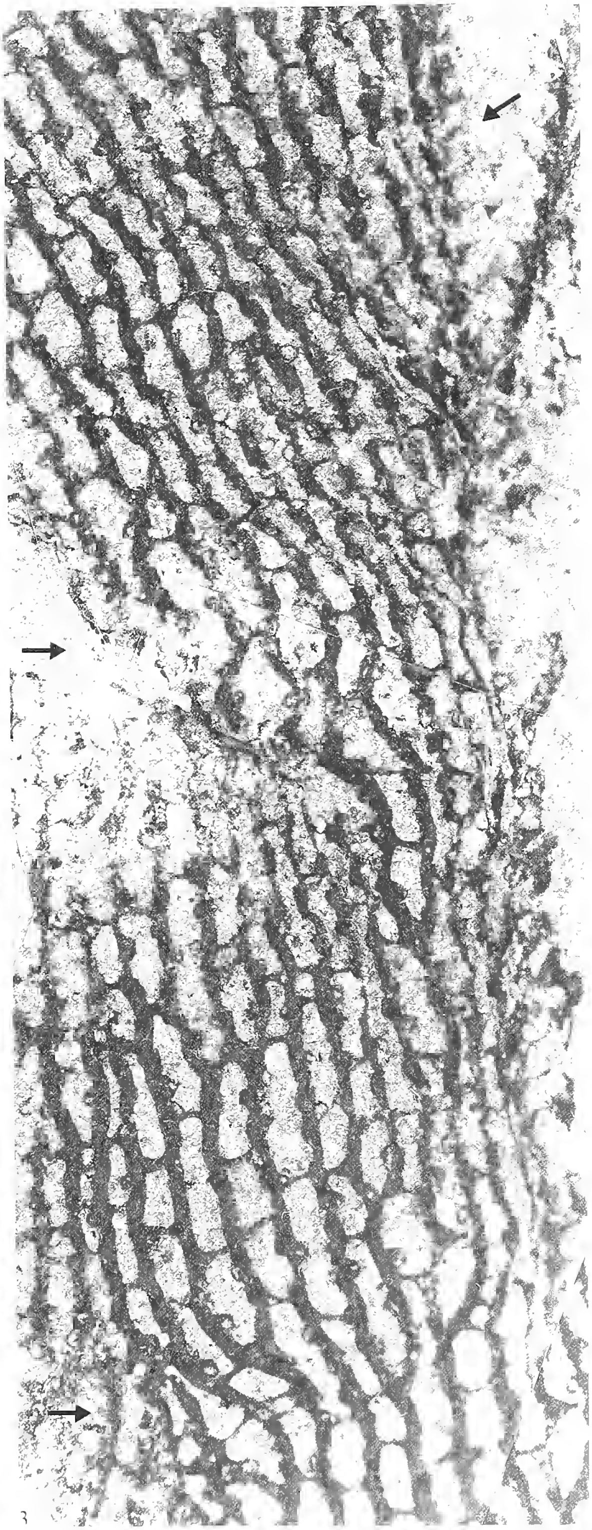

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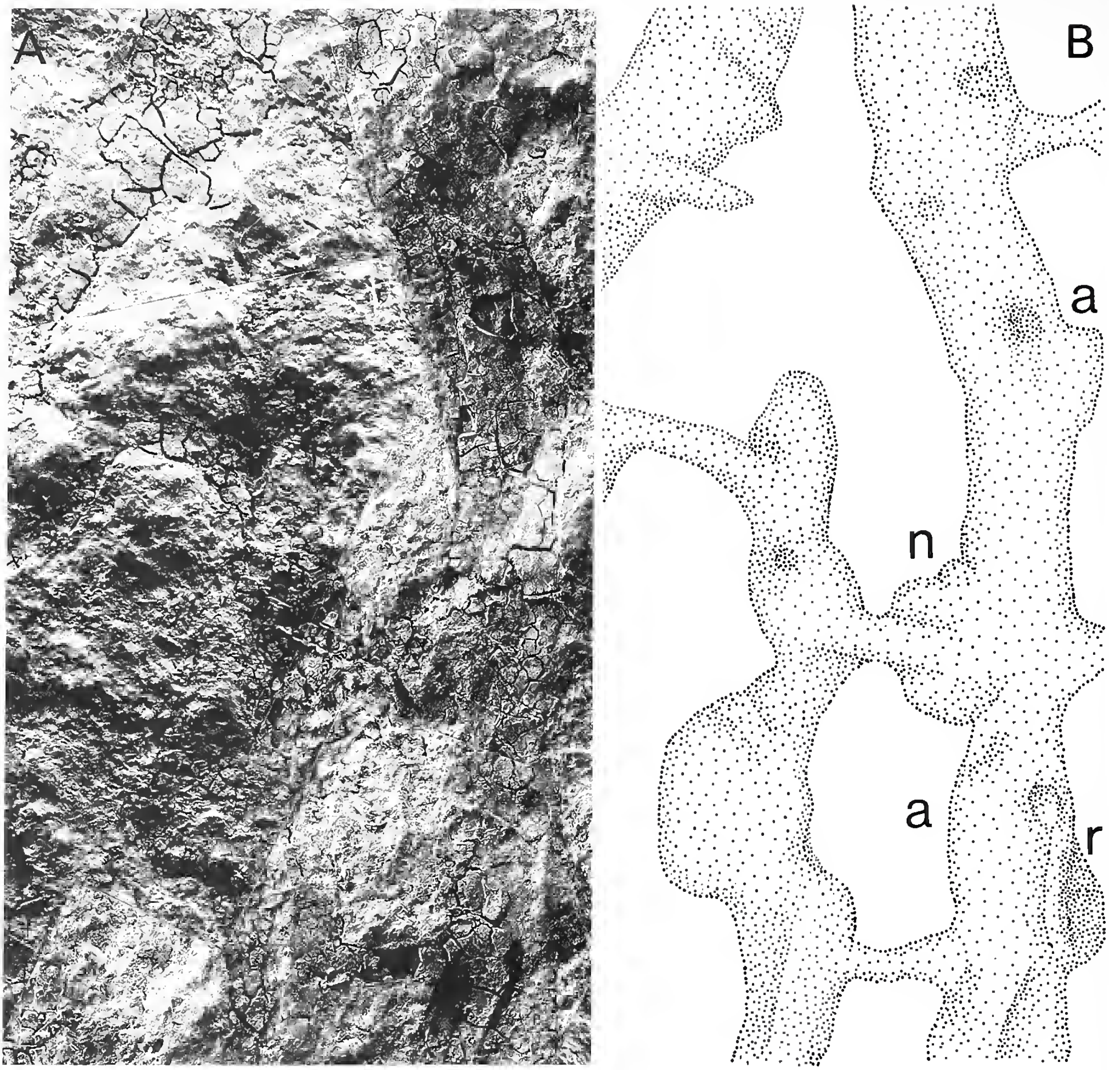
BULL, *Dictyonema pentlandica*



TEXT-FIG. 2. *Dictyonema pentlandica* Bull, 1987; NMS.G.1955.95.1; *O. spiralis* Biozone, Reservoir Formation; North Esk Inlier, Pentland Hills, Lothian, UK. A, montage of scanning electron micrographs; × 70. B, drawing to illustrate important features. The autothecae (a) form large bulges on alternate sides of the stipe. The upper surface curves inwards and in some cases back on itself forming a distinct notch (n) in the wall of the main stipe above the flat upper surface of the autotheca. This notch is observed in some cases to be occupied by a bitheca curving over the top of the autotheca. Bithecae occupy the ridge seen crossing the autotheca at (r), and structures seen at (a) are thought to be bithecal apertures.

so formed are of fairly constant size, one-fifth longer than wide. Continuous lines of dissepiments often form at the site of bifurcation (Bull 1987, text-fig. 8).

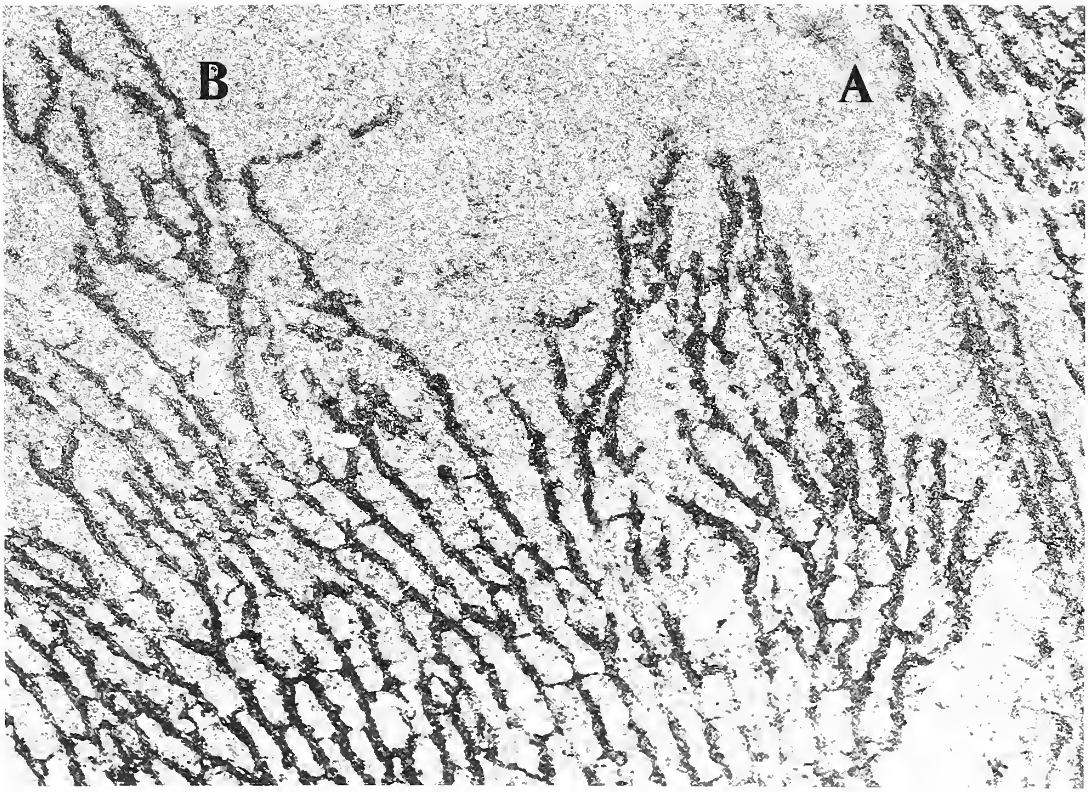
Dissepiments probably originated from the bithecae as described by Bulman (1927) and therefore consist of bithecal tissue, formed by continued growth of alternate bithecae. They arise from the stipe close to, opposite, or passing over, the distinctive bulge of the autothecae (Text-figs 2, 5A).

TEXT-FIG. 3. *Dictyonema pentlandica* Bull, 1987. Reconstruction of the idealized thecal structure, showing the relative positions of the autothecae and bithecae in profile view, and the apertural spines and bulbous nature of the genicular margin.

Strengthening, seen in scanning electron micrographs as concentric rings, appears to follow the margin of the fenestrule symmetrically rather than supporting a dissepiment in its direction of growth. The stipe from which the dissepiments originate is, therefore, not apparent; rather the dissepiments and stipes define the margin of the fenestrule, maintaining the rectangular shape at a regular size (0·4 × 0·6 mm). This latter feature may reflect the importance of controlling the water currents passing through the mesh to the zooids within, as the size of any aperture and the thickness of the walls will dictate the flow rate and turbulence of currents passing through that aperture (Stratton and Horowitz 1974).

Bithecae. The bithecae of this species are narrow, with a constant width of 0·03 mm, and are inconspicuous. They do not protrude from the stipe in normal circumstances, but are thought to form a slight ridge crossing above the upper margin of the terminal swelling of the autothecae. Each autotheca is associated with a bitheca, which loops across the side and curves around the bulbous part above the aperture of the adjacent autotheca before the swelling of the next autotheca commences. This can give the impression of an apparent geniculum when viewed in profile. The bithecae have simple, unornamented apertures, opening in the side of the stipe (Text-figs 2–3).

Discussion. The taxonomically significant features of this species have been described and discussed above and in the original systematic description (Bull 1987, 1995), in which comparisons with other species are made. The presence of a holdfast structure confirms the attribution to *Dictyonema*. Combinations of the following features allow its distinction from other described species: the presence of simple (unforked) autothecal apertural spines; the identification of the swelling of the stipe giving its distinctive knobbly appearance being caused by swelling of the autothecae and not by bithecae passing round the outside of the stipe; the very slender dimensions of the stipes and high stipe density; and the regular, close arrangement of the dissepiments. *D. pentlandica* is subject to growth of aberrant structures on both microscopic and macroscopic scales, including tubular outgrowths of the bithecae and large scale regrowth or mending of the rhabdosome, following changes in growth patterns or predatorial attacks, or as a result of other environmental factors. The details of these aberrant structures are described below.



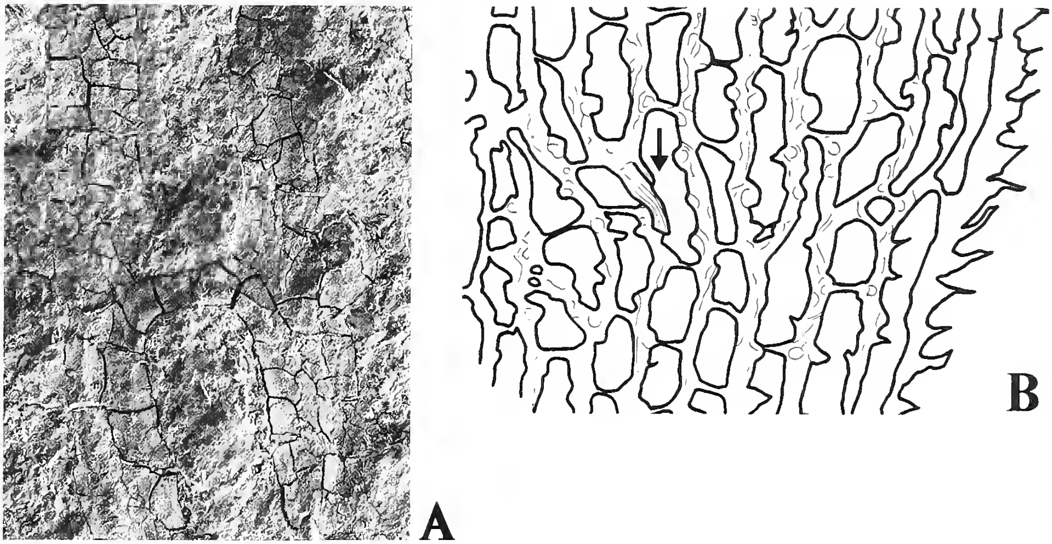
TEXT-FIG. 4. *Dictyonema pentlandica* Bull, 1987; RSM.GY.1985.29.5; from the same horizon and locality as the specimen in Text-figure 2. The slab shows two specimens (A and B), preserved with the openings of the cones facing one another. A, an area of rhabdosome with an inverted view of the stipes, with the thecae rotated giving a profile view and showing the apertural spines of the autothecae. B, an uneven regeneration zone at the growing margin of the rhabdosome; the specimen started to grow again in one region, but was not able to reinstate the normal pattern of growth, being unable to produce dissepiments; × 7.

DESCRIPTION OF TYPES OF ABERRANT AND ABNORMAL STRUCTURES

Abnormal structures are not usually discussed in taxonomic work as they distract attention from the features considered typical of (or normal for) the species. Yet almost every specimen of *D. pentlandica* has some feature which does not conform to the standard taxonomic description. Despite the abnormalities, however, much of the rhabdosome of each specimen is of the normal size and shape, with a normal stipe and dissepiment distribution pattern. Examples of the different types of aberrant structure observed are illustrated and explained in Plates 1–2 and Text-figures 4–7. They fall into five main categories.

Stipe truncation and compensatory growth by neighbouring stipes

1. One or more stipes may be truncated within a section of otherwise unaffected rhabdosome. The surrounding stipes filled the gap so formed either by bifurcation, or by curving across the gap (Pl. 1, figs 1–2; Text-fig. 4). The normal pattern of rhabdosome growth was continued afterwards.



TEXT-FIG. 5. *Dictyonema pentlandica* Bull, 1987; from the same horizon and locality as the specimen in Text-figure 3. A, NMS.G.1995.95.1; scanning electron micrograph of a dissepiment not preferentially attached to either stipe; strengthening appears to follow the margin of the fenestrule rather than showing a dissepiment growing from one stipe to another; × 50. B, RSM.GY.1985.29.2; showing growth (arrowed) of a single stipe towards the sicula. The right hand margin shows thecae twisted partially to show a profile view; × 20.

2. A hole was formed in the centre of an otherwise strong section of rhabdosome; the surrounding stipes may have crumpled with the extra load they were forced to bear and became secondarily thickened to support the remaining stipes (Pl. 1, fig. 3). The ends of the truncated stipes, which were left trailing backwards, may appear to have withered slightly.

Change in rhabdosome growth pattern

An increase or decrease in the rate of growth could have affected large areas of a rhabdosome at the same time. Not every stipe was necessarily involved. Some stipes may be terminated (Pl. 2, fig. 4; Text-figs 1, 7); some continue unaffected through the area of disruption, while neighbouring stipes seem to have been unable to regenerate, forcing those stipes that were able to grow to bifurcate immediately and regularly thereafter, presumably in order to reunite the mesh. In some areas of the rhabdosome, all of the stipes bifurcated at the same time, causing the rhabdosome to grow in another plane, giving the appearance of a frill forming at the margin (Pl. 2, fig. 3). In other areas the stipes started to regrow but did not attain the normal pattern (Text-fig. 4). This is the type of rejuvenation described by Bulman (1950; Text-fig. 1). The growth pattern that emerged following renewed activity can represent either a return to the juvenile pattern (Bulman 1950), a continuation of the adult pattern, or growth in an apparently random fashion.

One section of the main body of the rhabdosome may be enlarged, forming a bulge in the normal surface of the cone. An increase in the density of stipes commenced with a number of stipes bifurcating at the same time. The resultant bulge may have been resorbed into the main body of the rhabdosome by one or more stipes terminating. More usually, however, the normal bifurcation pattern of the main rhabdosome continued in the surrounding stipes and, eventually, regular stipe spacing was achieved. The extra sections of the stipes were compressed on top of one another on burial (Pl. 2, figs 1–4; Text-fig. 7).

Abnormal bursts of growth by one or more stipes

Individual stipes may have accelerated that growth; the result is a distortion of the regularity of the meshwork. Normal patterns usually resumed after the formation of the next dissepiment, although one or two dissepiments may be omitted. The section of stipe in question became either slightly longer than expected (Pl. 2, fig. 2) or began to grow in a completely different fashion, e.g. growing towards the sicula (Text-fig. 5B). In the former case the stipe was deflected because it had to curve relative to the stipes around it to accommodate the extra length. In the latter case the growth was superimposed on the pre-existing stipe.

Tearing or splitting of the rhabdosome

A split may have formed in the rhabdosome and the whole mesh pulled apart. The proximal end of the split may have become secondarily thickened and the remainder of the stipes on either side of the split continued growing unaffected, with normal stipe spacing (Text-fig. 7). The stipe on one side of the split has not been observed to have attempted to form dissepiments to join up with the stipe on the other side, or to have grown new stipes in the gap formed.

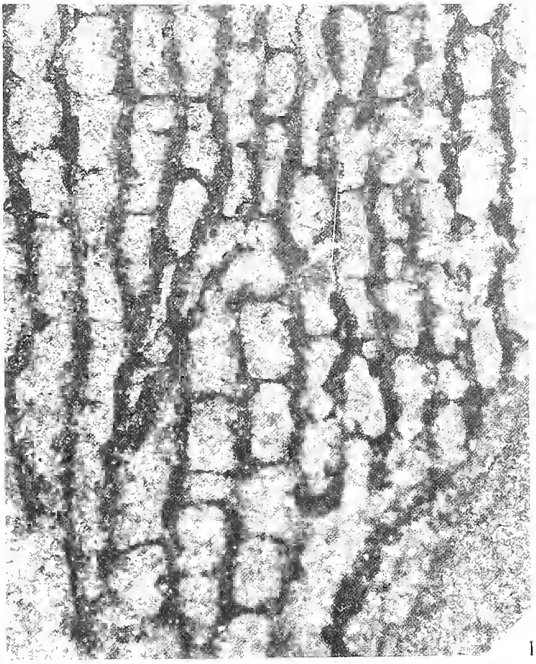
Abnormal thecal growth

Although the bithecae of *D. pentlandica* are usually narrow (0·03 mm) and inconspicuous, rarely they are enlarged and distorted, and have developed tubular outgrowths, which form no regular pattern. Such growth structures are usually difficult to distinguish from broken or incomplete dissepiments, and only in exceptionally well-preserved material can they be identified clearly. Bithecal outgrowths are normally either narrower than dissepiments (0·03 mm compared with 0·06 mm dissepiment diameter), or, where they grew around the dissepiment, this appears thickened for at least part of its length. Initially apparent as disruption of the regular dissepiment arrangement (Text-fig. 6), they are easily confused with autothecal apertural processes (spines). These are usually of constant diameter, are straight, and arise from the centre of the bulbous part of the autotheca on the ventral surface of the rhabdosome. Thus, if spines are seen in the normal, dorsal view of the rhabdosome, they will be displaced to one side of the centre of the autotheca and will not be in any other position; abnormal outgrowths occur at irregular intervals and positions, and usually are not straight.

EXPLANATION OF PLATE 2

Figs 1–4. *Dictyonema pentlandica* Bull, 1987; Gutterford Burn; Reservoir Formation, *Oktavites spiralis* graptolite Biozone, Upper Llandovery. Examples of bursts of growth of the rhabdosome. 1, RSM.GY.1985.29.1. Sudden surge in growth indicated in the centre of the rhabdosome. Increase in stipe density in one area only, forming a bulge in the side of the cone as a response to increased activity and growth of a few stipes, which have been superimposed on one another on deposition; × 10. 2, RSM.GY.1985.29.1. One stipe has grown longer than normal, relative to the stipes around it. The stipe that has experienced extra growth had to curve to accommodate the extra length on deposition. Normal growth resumed after the formation of the next dissepiment; × 10. 3, RSM.GY.1985.30.1. All of the stipes are involved in this case; some terminate, the rhabdosome expands and the new growth area forms a frill at its outermost margin (the dendroid is attached to the brachiopod *Leptaena*); × 3. 4, RSM.GY.1985.29.5. Some stipes terminate (arrowed); neighbouring stipes bifurcated and curved to fill the gap, resulting in stipes obliquely approaching one another. Some stipes then terminate on reaching normal stipe separation distance from the adjacent part of the cone. Pattern continues until normal stipe separation is achieved distally; × 3.

PLATE 2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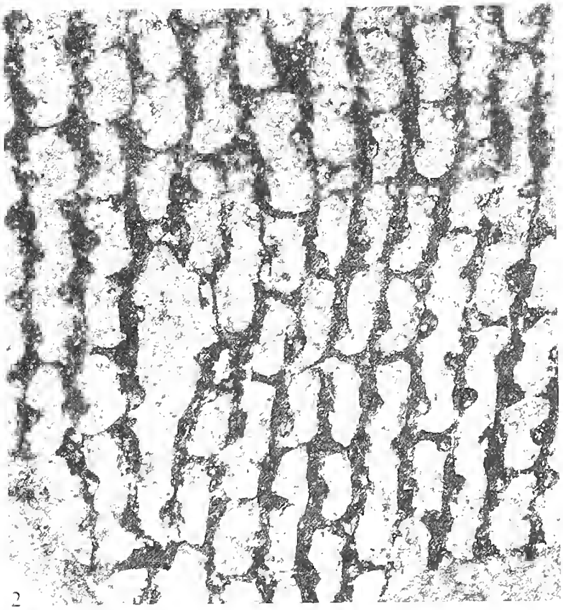
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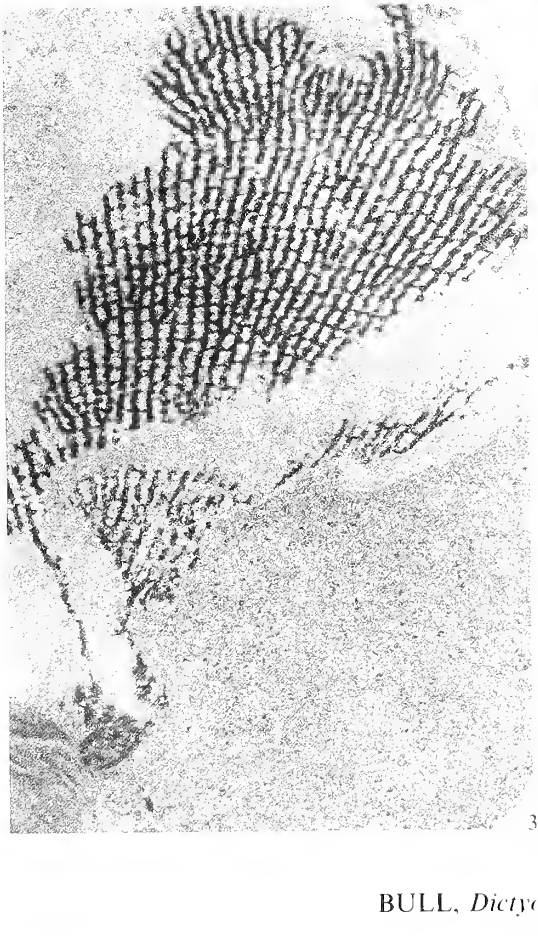
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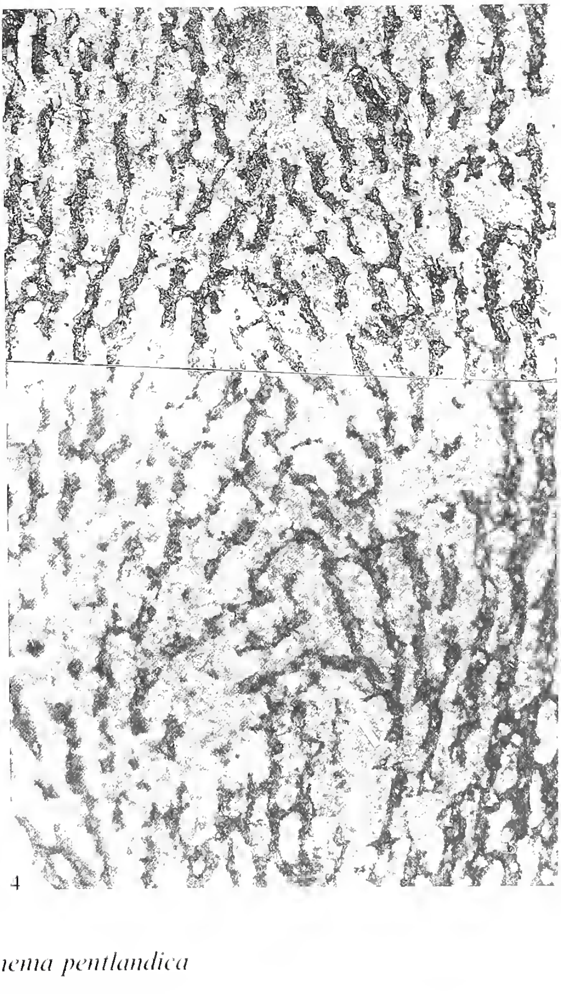
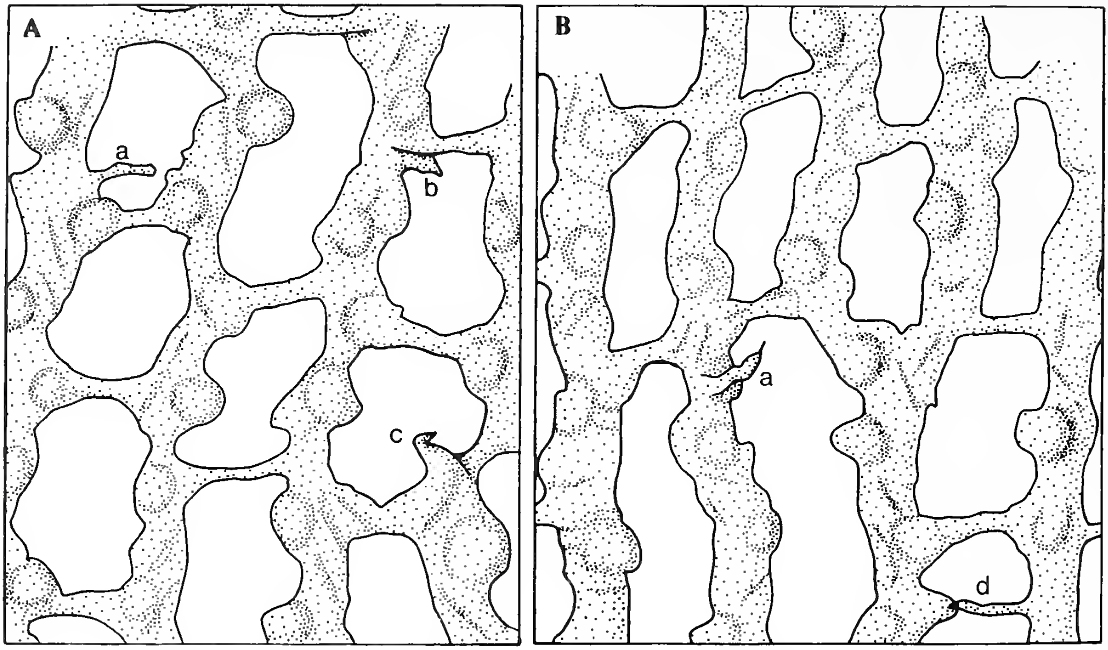

4

BULL, *Dictyonema pentlandica*



TEXT-FIG. 6. *Dictyonema pentlandica* Bull, 1987; RSM.GY.1985.30.1; from the same horizon and locality as the specimen in Text-figure 2. A and B, camera-lucida drawings of specimens oriented with proximal portions towards base of drawing. Types of aberrant growth of bithecae. a, tubular outgrowth; b, growth along a dissepiment; c, outward growth from the stipe, recurving back later; d, outgrowth crossing to adjacent stipe; *c.* × 12.

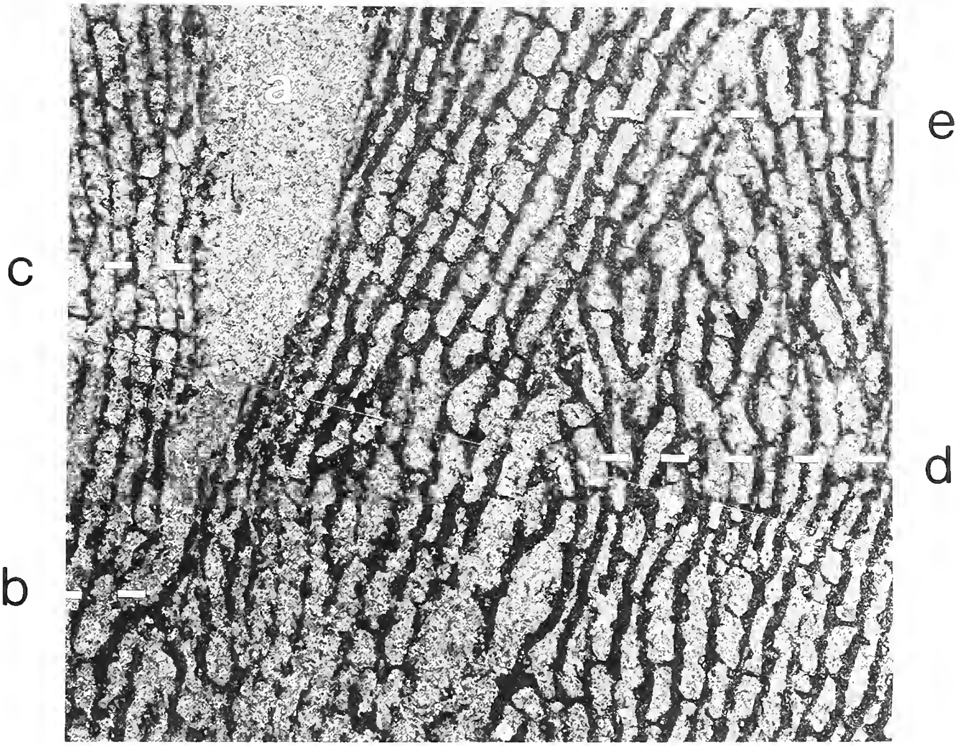
Bithecal outgrowths (Text-fig. 6) are short, narrow (0·02 mm diameter), tubular structures, most commonly extending the bithecae across the fenestrule instead of following the normal path and wrapping around the top of the autotheca. This is usually followed by the next autotheca at a reduced spacing, and the stipe may be thinner at that point. Alternatively the outgrowth may eventually curve back towards the original stipe, or approach another stipe, or may have grown around or along a dissepiment, giving the impression of thus being further strengthened. In other examples, the outgrowths are indistinguishable from broken parts of the stipe wall.

As yet, no distinctive abnormal structures of the autothecae have been observed, although apertural spines may be broken. Abnormal growth of the dissepiments and bithecae were noted by Bulman (1927, 1933); two types of abnormal growth were illustrated. Similarly Chapman *et al.* (1993) illustrated abnormal dendroid growth, in the form of sac-like outgrowths, which may be composed of autothecal tissue.

POSSIBLE CAUSES OF AND RESPONSES TO DENDROID ABNORMALITIES

The standard patterns of normal dendroid growth were probably controlled by a simple epigenetic phenomenon which dictated the species' 'blueprint', or normal structure common to each species.

It is possible to identify five processes which might have caused the identification of disruptions in normal growth patterns. These are: (1), mutation; (2), injury or trauma; (3), disease and/or parasites; (4), change in environmental conditions; and (5), preservation. Additionally, the timing of such changes cannot be identified, as a cessation of growth for a period will appear identical to a sudden change in growth, unless obvious 'wear and tear' of the margin during a halt in rhabdosome secretion can be seen.



TEXT-FIG. 7. *Dictyonema pentlandica* Bull, 1987; RSM.GY.1985.29.5; from the same horizon and locality as the specimen in Text-figure 2. Major split formed in the rhabdosome (a). The stipes on either side of the split have not formed dissepiments to join the stipes on either side of the split. The base of the split is secondarily thickened (b). Some of the autothecae are seen in profile as the stipes to the left of the split have been rotated on deposition, and autothecal spines are visible (c). An area (d) to the right of the split shows some stipes terminating, while those that continue to grow, curve in both directions until aligned with an adjacent stipe at the appropriate spacing. Certain areas of the rhabdosome are involved in stipe termination, whilst other areas (e) continued more or less unaffected growth; × 8.

Although it is possible that each rhabdosome was subject to more trauma than that for which there is morphological evidence, it is unlikely that the colonies were able to effect repairs to their framework that have no preserved trace (effectively 'invisible repairs'). We may, however, now be seeing the results of repairs which were incomplete at the time of death. Alternatively it is possible that *D. pentlandica* was not able to effect 'invisible repairs', leaving clear scars to be fossilized, or that it had an increased susceptibility to damage if it lived in a high energy environment.

Every specimen of *D. pentlandica* has at least one departure from a normal growth pattern. This suggests that these colonies suffered more trauma than species from other areas, and that the effects of trauma are possibly more common elsewhere than has been previously recorded.

This species attained larger than average sizes, with some specimens reaching at least 0·6 m long. It is uncertain if the attainment of this size was the result of an extended growth period, or of more rapid growth. Estimates of graptolite growth rates have been attempted by comparison with living pterobranchs (Rigby and Dilly 1994), and study of the response of pterobranchs to trauma, predation, and change in conditions, might lead to more information about dendroid growth patterns. Estimates of the degree of regeneration that the animal was able to effect for itself may then become possible.

Mutation in the genetically controlled growth pattern. If mutations were generally the cause of abnormalities, the growth pattern would be irrevocably changed. In most cases the original growth pattern is resumed after a change.

Bulman (1970, fig. 13) noted that for some species the distance between the regions of bifurcation increases gradually distally. If a regrowth had been spurred by mutation, a return to the juvenile pattern as described by Bulman (1950), would be unlikely (Text-fig. 1). In *D. pentlandica* the zones of bifurcation are approximately evenly spaced (Pl. 2, fig. 3) and this remains unchanged after any regrowth, as does the size and shape of fenestellae, and general rhabdosome morphology. Occasionally, the growth pattern of a section of rhabdosome appears completely changed, which could be the result of an individual zooid mutation; it is more likely, however, to be local manifestation of disease. Growth in a distorted fashion does not seem to continue for long before the complete cessation of growth (Text-fig. 4).

Teratology is the study of genetically or externally controlled malfunctions at an embryological stage. This is considered quite an important and relatively common factor in the abnormalities of some arthropods, including trilobites (Owen 1985) and conulariids (Babcock *et al.* 1987). In the former, abnormalities usually involve substantial deviation from normal morphology; in the latter, examples are exceedingly rare, in the reference quoted above only one indisputable teratological specimen was identified in a sample of 5000.

When considering teratology of dendroids, there is the added difficulty of studying a colonial organism, with poorly known embryology and juvenile stages. It is unlikely that dendroids with teratological abnormalities would have survived into adult form in a recognizable shape and they may account for some of the species described from a single specimen but with affinities with another species. It is thought that teratological dendroid specimens, like conulariids, are rare.

Injury or trauma. Large splits occurring in the mesh are almost certainly the result of damage (Text-fig. 7). After tearing, the broken remnants of the dissepiments might have dangled loosely at the edge of the mesh. Such irregular margins have not been observed however, suggesting that they have probably been resorbed, possibly to avoid impairing the action of the remaining zooids. The normal pattern of growth for this species is to fill all of the available space, and the obvious growth direction to the side of the torn stipe is not exploited. No further growth seems to occur in the gaps formed by splits, and it does not seem possible to trigger regrowth in an already mature area. Such growth would rapidly result in the two sides of the mesh becoming superimposed or interfering with one another. In Bull (1987, p. 124) it was noted that 'Bifurcation is concentrated on certain stipes, while others are continuous, straight and unbroken.' This phenomenon also seems to have been a control on the ability of the rhabdosome to spread out and fill any gaps caused by injury to its structure. The areas at the bases of splits are secondarily thickened, acting as strengthening for a weakened area.

Different responses to injury might be expected depending on whether it was the outermost growing edge of the cone or the already formed central part of the mesh that was attacked. As small holes in the structure are fairly common, in most cases the reaction of the dendroid has resulted in a mesh stretched around the hole (Pl. 1, fig. 1). The dendroid seems to have been capable, almost always, of repairing its mesh at whatever point it had been attacked, although details of early stages of astogeny of this species are unknown. The zooids are thought to have been able to plaster cortical bandages on the surface of the mesh (Crowther and Richards 1977), and this method could have been used to mend damage to the rhabdosome, particularly in cases where the stipes are now seen to be slightly thickened at the site of damage (Pl. 1, fig. 3; Text-fig. 7).

The sites of individual predatorial attacks may be determined by looking at patterns of regrowth. Thus, where the associated, succeeding and surrounding stipes were activated to either bifurcate, or curve and stretch across to heal the gap (Pl. 1, figs 1–2; Text-fig. 2) it is probable that the attacks took place at the outermost growing edge. It is only here that new growth in an outward direction would be expected to have occurred and new phases of bifurcation and thecal production stimulated. In order to rejoin with pre-existing stipes on the other side of an area of damage, it is unlikely that the stipes would have been able to grow back towards the sicula for any distance (Text-fig. 5B), as this would have involved either producing thecal apertures that faced the 'wrong way' (into the current passing through the cone), or secreting the distal end of the theca first.

A traumatized area, particularly in the main body of the rhabdosome, where a hole had been made through the side of the pre-existing mesh, could have been mended by the application of cortical bandages to the damaged area by the zooids from neighbouring thecae (Pl. 1, fig. 3; Text-fig. 7). Any obvious holes remaining in the fossilized rhabdosome are usually fairly large (Pl. 1, fig. 1), involving two or more stipes, where the injury incurred was too much for the dendroid to mend without disrupting the normal growth pattern. The impetus was only for onward growth, and dendroids appear to have had little capacity for reinstatement of growth in an area already abandoned (Pl. 1, fig. 3; Text-fig. 7). This does seem to have occurred rarely, however, although it was not always completely successful (Pl. 1, fig. 2).

Parasites and disease. Conway Morris (1981, p. 497), suggested that tubular outgrowths on graptolites consist of thickened cortical tissue plastered on by the zooids in an attempt to contain intruding parasites. It is thought possible that the tubular outgrowths of the bithecae described above, could be the result of parasitic invasion (Text-fig. 8.). The sac-like outgrowths, possibly of autothecal tissue, described by Chapman *et al.* (1993, p. 307) are suggested to have been possibly also caused by parasites.

It is difficult to attribute observed features to disease, but it is possible that it may have caused the apparent abrupt loss of the ability to grow in a normal pattern (Text-fig. 4). That this can occur to just a few stipes of one colony, suggests that only zooids in that area of the colony were affected. Where only part of a single stipe seems to have withered away (Pl. 1, fig. 2) it is possible that only part became infected.

Change in environmental conditions. If prevailing conditions changed, it is highly likely that growth patterns would have been affected. There is no certainty as to which conditions dendroids were sensitive, but various can be suggested (see Berry and Boucot 1972). Although graptolites were possibly generally widely dispersed throughout the oceans, some planktonic forms were affected by depth of water, as could benthonic *Dictyonema* species also have been. Changes in both salinity and water temperature are not known to have affected graptoloids, but it is possible that we are observing their effects here. It is possible that a change in temperature, or shortage in food, would cause a dendroid temporarily to cease growth, and to regrow on reinstatement of the original conditions. In a high energy environment, inevitable damage would be followed by a temporary halt in growth; this would not be seen in calm conditions. Short-term changes, such as caused by storms, could contribute to irregular growth patterns, as could the presence of some impediment to growth, such as another dendroid growing close by. Temporarily turbid water conditions, such as caused by the fall of volcanic ash, would leave the water column unsuitable for filter feeding by the zooids for some time; many graptolite bearing beds are associated with bentonite horizons (Batchelor and Weir 1988). If changes in environmental conditions are considered to be causes of cessation of growth, they would have to be major and universal to affect so many of the dendroid colonies.

Regular bifurcation is one of the few ways in which an expanding cone consisting of longitudinal rods of constant diameter and constant spacing can grow. Zones of bifurcation may be triggered by seasonal fluctuations in external conditions, such as a new spurt of growth in the spring after a relatively dormant winter period. Rough calculations of the life span of fossilized colonies can be based on estimates of the growth rates of pterobranchs (Rigby and Dilly 1994), and result in estimates of age in years approximately consistent with the number of zones of bifurcation present. But such growth rate calculations applied to dendroids rely on making many assumptions; more research on pterobranchs and dendroids is necessary before these calculations can be confirmed.

Preservation. Growth abnormalities can usually be distinguished from preservational breakage. Post-mortem damage and displacement of the rhabdosome on deposition were mentioned by

Bulman (1950) as a possible cause of the distorted structures observed at the margins of dendroid rhabdosomes. This is commonly observed, and where damage has occurred during the depositional process, it usually forms a recognizable pattern. Whole sections of stipe are displaced, so that all of the affected stipes take up the same angle of curvature, or the mesh is visibly stretched, and the stipes are either superimposed on other stipes, or the distance between stipes is reduced or increased (Pl. 2, fig. 2). This is shown well in a specimen of *Palaeodictyota* from the Pentland Hills (Bull 1987, pl. 20, fig. 2). Stipes are unlikely to have remained in positions producing a great deal of torsion in life; the elastieity of the rhabdosome would have returned the stipes to their stable position.

COMPARISONS WITH OTHER GROUPS

Other authors have discussed the biological implications of abnormalities in other fossil groups. Such abnormalities are considered as possible indicators of pathways to evolutionary change (Gould 1980).

It has been established (Owen 1985) that trilobite abnormalities provide important data on the biology of an extinct group and should therefore not be considered as mere morphological curiosities. The abundance of abnormalities has been used in the study of trilobite palaeoecology, and has provided indicators of selection pressures, and direct evidence of aspects of trophic structure. Unlike dendroids however, trilobite growth involved regular ecdysis. High mortality rates were associated with the moulting process, as trilobites had a very vulnerable period prior to the mineralization of the new exoskeleton; thus, many injuries were inflicted in this period, and include damage caused not only by predation, but also by the moulting process itself. But, most trilobites were capable of enrollment, which might have been to protect themselves, and additionally were able to escape by moving away. These factors make application of conclusions drawn from trilobite abnormality patterns difficult to compare directly with dendroid rhabdosomes.

Following injury to trilobites, it is thought that their survival was promoted by some degree of healing, expressed by exoskeleton thickening and callus formation (Owen 1983, 1985). Other groups of invertebrates developed their own response to injury. Particularly well known is the ability of crinoids to regenerate, following the loss of brachia or even part of the calyx. Also, bivalve molluscs and brachiopods are known which have disruption to their normal shell ridge patterns. However, none of these groups have colonial representatives, and whilst the biological implications of their abnormal features are important, they are not immediately comparable with colonial animals such as dendroids.

From Conway Morris (1981) it is clear that the fossilized remains of animals with relatively robust and solid skeletons or exoskeletons are more likely to preserve the remains of parasites and their related borings, galls, or tumours. The effects of parasitism at ultrastructural level on graptolites were discussed, but a great deal more evidence is required before parasitic relationships can be identified and fitted into evolutionary models.

The effects of disease upon fossil animals has been studied, particularly with respect to human remains. Palaeopathology remains of interest to those studying the evolution of current diseases; Moodie (1923) noted that 'disease is apparently one of the manifestations of life'. He also noted that not many diseases will leave traces in 'bones', that diseases affect individuals and not whole races, and that diseases become extinct as do animal species. He also suggested that early faunas were disease-free, and that parasitism did not appear until the Devonian. However, Conway Morris (1981) gave evidence of parasites from the Cambrian, but commented that the low level of disease and parasite interaction recorded in these early metazoan faunas seems to be a feature of the relatively simple ecosystems of the Precambrian and early Palaeozoic.

It is difficult in fossil material to differentiate between the effects of changes in environmental conditions and the effects of disease. If every fossil specimen above or below a certain horizon is affected, then a change in external conditions should be suspected. Moodie (1923) suggested that an increase of salinity would result in shell thickening, and diminution could be caused by crowding, or by a change in chemistry, such as a decrease in the oxygen content of the water. This does not account for long-lived individuals having to cope with rapid fluctuations in conditions. In this study, although more than 50 specimens have been considered, from a number of horizons, no overall trend has been recognized. Each specimen has a different range of 'aberrant' features. Therefore, it is difficult to imagine that any one disease or change in environmental conditions was responsible for all of these aberrant features.

Urbanek (1973) described regrowth of monograptids after fracture. He noted that the resultant pattern depended upon whether the sicula remained. If the sicula was present in the regrown fragment, then the growth pattern returned to the juvenile form; if the sicula was not present the regrowth was in the adult form. This is consistent with the pattern observed for dendroids; with the sicula present return is to the juvenile pattern (Text-fig. 1). Urbanek (1990) discussed the viability of the 'regenerative morphoses'; although he was describing planktonic forms, his comments are relevant to the regeneration of dendroids, as he suggested that although the regenerated forms were viable, in the normal environment they were inferior compared with their parent colonies. Their survival would be constrained by imperfect hydrodynamic stability, feeding depression as a result of the presence of fewer zooids, and as a direct result of the injury.

The study and comparison of dendroids with their nearest living relatives, the pterobranchs, is as yet in its infancy. Living pterobranchs, although secreting their skeleton from the same material and in a homologous manner to graptolites and dendroids (Rigby 1994), have not yet been described as having a strongly ordered growth pattern. The zooids of *Cephalodiscus* can recolonize old tubes, and mend them to some extent. They can either work on (or feed from) many different tubes at one time or all work from one tube at the same time. They seem to co-operate to expand the colony into the available space, growing tubes with seemingly no preferred polarity (Rigby and Dilly 1994). The zooids of *Rhabdopleura* generate the material of their own aperture, and if damaged can repair what is within their reach, either from inside or outside of the tube (Dilly 1986). Successive generations of zooids secrete each tube to a precise pattern, and each tube is completed to (and possibly maintained to) a precisely predetermined overall size and shape (Rigby 1994).

Therefore, by comparison, it is reasonable to suggest that dendroid zooids were to some extent able to mend their rhabdosome, and this could have been done without formation of calluses for small areas of damage. Some areas of damage may have been out of the range of the zooids. It seems that, unlike pterobranchs, however, dendroids were not able easily to reverse the polarity of their growth, and do not seem to have been readily able to regenerate stipe growth in a proximal direction. This may have some bearing on our understanding of whether zooids were concentrated at the outer margin of the cone or whether most of the rhabdosome's thecae were occupied at any one time. More information on this will require more research on the relationship between dendroids and pterobranchs.

One group of colonial animals with known modern and fossil representatives is the bryozoans. The effects of damage on and the regrowth capabilities of this group, may give clues to the response of colonial animals in general to damage, and potentially lead to the development of models of the environmental pressures acting on colonial animals. A few of the observations made about bryozoans are relevant to dendroid abnormalities even though, during growth, bryozoan colonies have a more complex and more commonly changing colony morphology than dendroids.

If living bryozoans are intentionally broken they are able to continue growing, and partially to repair the damage (Lutaud 1983). The resultant structures depend upon the original degree of damage, but the overall tendency is to cover up any weaknesses and resume normal growth as soon as possible; it is more usual to leave a much enlarged fenestrule than to effect a perfect repair. Maintenance of physiological continuity by providing intramural links between living zooids, despite the mortality of intervening zooids, seems to be a most important factor to the bryozoans (Taylor 1988). The same factors probably controlled dendroid regrowth in similar conditions. Like modern pterobranchs, bryozoan zooids can extend the colony with either polarity. Similarly, bryozoan reparative buds clearly can occupy the same sites as the damaged zooids and completely overgrow the original structure (Taylor 1988); dendroid growth patterns seem to have been less flexible, with large holes in the rhabdosome being sealed less efficiently.

Clearly, as more information from all fossil groups becomes available, fossil abnormalities and their causes and implications have the potential to yield more valuable evolutionary, palaeobiological, palaeoecological, and palaeoenvironmental information. Study of abnormalities has implications for workers in other fossil groups, particularly if members of these groups were to be discovered in the same sedimentary horizons. Where similar abnormalities occur in other fossil groups, conclusions drawn for one fossil group should be considered for their implications to others.

CONCLUSIONS

Dictyonema pentlandica, figured here, and the other dendroids described from the Pentland Hills (Bull 1987), are generally slender forms. They had well developed holdfasts and were able to withstand the effects of some currents, and probably required the presence of constant current action to bring regular food supplies. The 11 species of dendroid and six graptoloids (Bull and Loydell 1995) preserved, probably co-existed in the same environment, which appears to have suited the dendroids particularly well (Bull 1991). These dendroid specimens have not been transported far, or damaged badly on deposition, which is why so many of the growth features of the species can be described.

The mode of preservation and amount of detail remaining can give information about the environment of deposition. The conditions at the time of deposition of the late Llandovery sediments in the North Esk Inlier must have been subject to frequent changes; it was possibly a relatively shallow environment with strong sediment-laden currents and frequent storms. Spinosity, large overall size with slender stipes and the ability to withstand injury may be adaptations that allowed *D. pentlandica* to survive with an attached mode of life in a harsh environment.

The bulbous, spinose nature of the autothecae of *D. pentlandica* may have been a form of protection for the zooids. Slender stipes possibly facilitated efficient current deflection through the mesh. Spines may have enhanced zooid feeding strategies, protected zooids from predation, or further directed water currents through the cone.

Each dendroid rhabdosome housed zooids for some time, which secreted the meshwork in a very regular pattern according to a genetic code. Each was subject both to mutations, and to ever-changing and probably often quite harsh external conditions. Consequently, fossilized rhabdosomes are rarely perfect. For convenience and for clarity of identification, particularly for descriptions of new species, only the most characteristic areas are usually mentioned in systematic descriptions. Descriptions of abnormalities can be used in analysis of palaeoenvironment, palaeobiology and palaeoecology.

Dendroids could rejuvenate after a cessation of growth, probably caused by change in external conditions. They could also regenerate after trauma, such as injury caused by predation, natural abrasion or disease.

Dendroids could repair damage to the rhabdosome, the nature of the repair being dependent on where the injury had taken place. Following injury at the periphery of the rhabdosome the characteristic pattern of growth for each species was returned to as soon as possible, although some stipes may have been too greatly affected to return to the 'standard' pattern. Dendroids appear to have been able, to a limited extent, to patch up holes made in the side of the rhabdosome. They do not seem to have been able to repair growth in a mature area opened up by damage, such as a major split in the mesh in the side of the rhabdosome.

Aberrant growth structures were also observed on a microscopic scale; tubular outgrowths, probably from the bithecae, could be the result of parasitic invasion.

Further comparison of dendroids with modern pterobranchs and other colonial animals, studying the latter's mode of generation and secretion of normal rhabdosome and their response to environmental change, trauma, mechanical damage, predation, disease and other changes, may lead to a more complete understanding of the generation of the normal and abnormal features observed in dendroids. Each of the variations from the norm that is observed can tell us something of the life history of each individual specimen and by implication the environment in which the animal lived.

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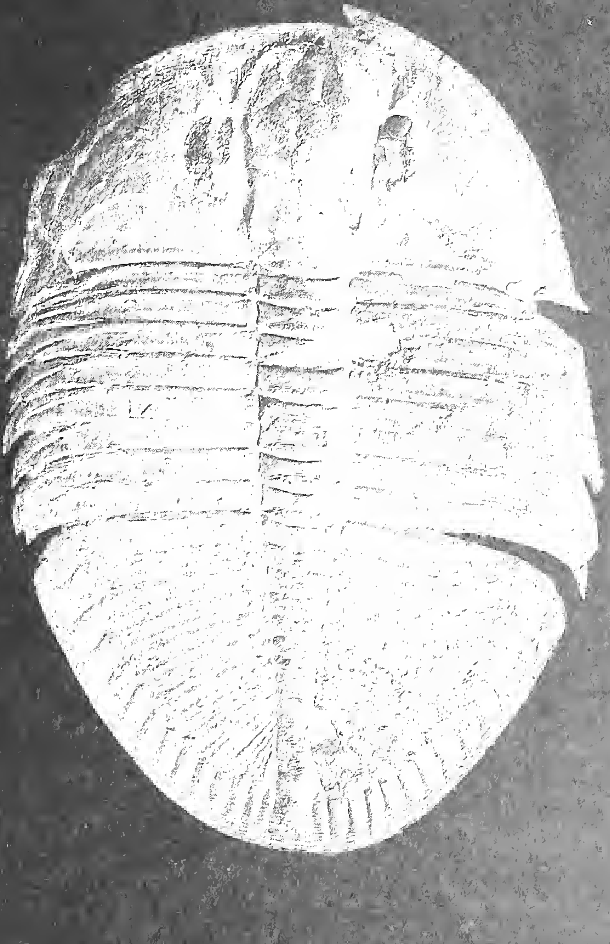

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Cover: The Middle Ordovician trilobite *Ogygiocarella* from Builth was one of the first fossils described from Britain, being figured by Edward Lhwyd in 1698.

EARLY DEVONIAN ACANTHODIANS FROM NORTHERN CANADA

by PIERRE-YVES GAGNIER *and* MARK V. H. WILSON

ABSTRACT. Two unusual new genera and species of acanthodian fishes are described from the Lower Devonian of the Mackenzie Mountains, Northwest Territories, Canada. *Kathemacanthus rosulentus* gen. et sp. nov. is a deep-bodied species that lacks a dermal shoulder girdle, but has a pectoral 'collar' or 'necklace' of large spines and enlarged scales, positioned in series with a large pectoral fin and spine inserted high on the animal's flank. *K. rosulentus* is assigned to the new monotypic family Kathemacanthidae. This family and the Brochoadmonidae constitute the new suborder Brochoadmonoidei, characterized by the high pectoral spine and numerous short intermediate spines. *Cassidiceps vermiculatus* gen. et sp. nov. is also relatively deep-bodied, and it has a heavily armoured, small head. *Brochoadmones*, *Kathemacanthus* and *Cassidiceps* all lack dermal shoulder girdle elements. Together they support the hypothesis that a dermal shoulder girdle is not primitive either for Acanthodii or for Climatiiformes.

In the Brochoadmonoidei a complete series of ventral intermediate spines precedes the well-developed pelvic fin and spine. In *Brochoadmones* the pectoral spine is greatly reduced, inserted high on the flank, and lacks a fin. In *Kathemacanthus* an oblique row of lateral intermediate spines precedes the well-developed pectoral fin and spine, whilst an apparently separate series of ventral intermediate spines precedes the pelvic fin and spine. These data support Miles' earlier view that the prepectoral spines of other acanthodians belong to the same series as pectoral spines.

ARTICULATED acanthodians are rare, and the articulated acanthodian assemblage from the Delorme Group, Mackenzie Mountains, Northwest Territories, represents only the fourth one known for the Early Devonian. The first acanthodian taxa from what is now referred to as the 'MOTH' fossil assemblage north-west of Avalanche Lake (Wilson and Caldwell 1993; Adrain and Wilson 1994) were described by Bernacsek and Dineley (1977), who recognized four species in four genera and four families, as well as fragments of several unnamed additional species. Based on collections made by University of Alberta parties in recent years, Gagnier and Wilson (in press) have been able to redescribe and reinterpret *Brochoadmones milesi*, which is one of the species named by Bernacsek and Dineley and is an extremely unusual acanthodian because of its pectoral anatomy, skull shape, and dentition. In the present paper we describe two additional and also unusual species. One of these has a pectoral anatomy which is, if anything, more unusual and more significant than that of *Brochoadmones milesi*. The other is most noteworthy for its heavily armoured head.

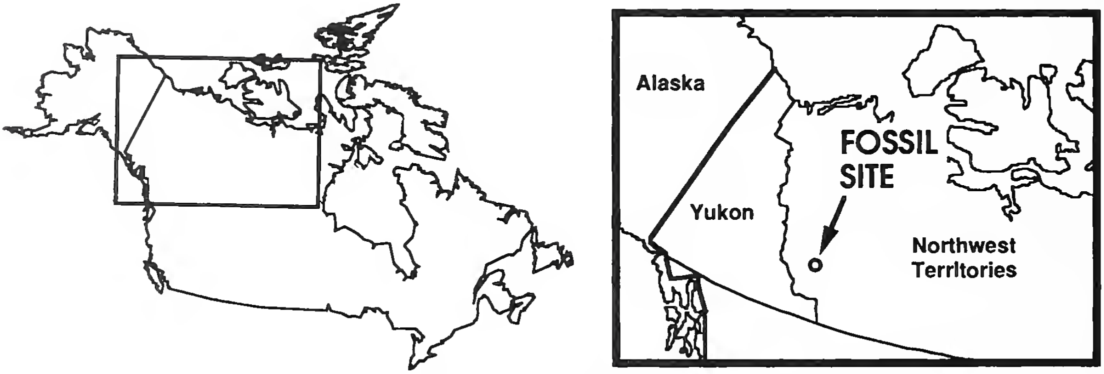
Dineley and Loeffler (1976) described and illustrated many agnathans from 'MOTH' in their monograph on Delorme ostracoderms. Like the acanthodians, the agnathan specimens from the locality are remarkable for their excellent, articulated preservation, for their abundance, and often for the presence of gut endocasts. Wilson and Caldwell (1993) recently announced the discovery of 'fork-tailed thelodonts' that are well represented in the 'MOTH' assemblage, and Adrain and Wilson (1994) have elaborated on the osteostracan species in the assemblage. A list of taxa known from the 'MOTH' locality appears in the latter paper.

The two new acanthodian species described here, together with *Brochoadmones milesi*, are evidently survivors of a primitive acanthodian radiation. They are treated here as members of the Climatiiformes, although that group may with further study prove to be unnatural. However, both *B. milesi* and one of the new species have their greatest significance in their pectoral anatomy. This feature justifies uniting them in a new subordinal taxon and shows that there is more than one distinct series of paired spines in primitive acanthodians.

[Palaeontology, Vol. 39, Part 2, 1996, pp. 241–258, 2 pls]

OCCURRENCE

The specimens described in this paper come from a site that was discovered by the Geological Survey of Canada, called locality 69014 in section 43 of Gabrielse *et al.* (1973), and located in the central Mackenzie Mountains, N.W.T., Canada (Text-fig. 1). Newly discovered specimens, not available to Dineley and Loeffler (1976) or to Bernacsek and Dineley (1977), were collected in 1983 by Dr B. D. E. Chatterton, Geology Department, University of Alberta, and in 1990 by M. V. H. Wilson, with the help of Chatterton and others. Contrary to statements by Dineley and Loeffler (1976) and Bernacsek and Dineley (1977), the acanthodians occur at the locality not only with heterostracans but also with cephalaspids and thelodonts, often in apparent mass mortalities on the same bedding planes and sometimes overlapping with specimens of those groups.



TEXT-FIG. 1. Map indicating the location of the fossil site in the central Mackenzie Mountains, Northwest Territories, Canada.

The geology of the deposit has been described by Gabrielse *et al.* (1973), Dineley and Loeffler (1976), Adrain and Wilson (1994) and Gagnier and Wilson (in press). Field parties from the University of Alberta refer to the measured section that includes GSC locality 69014 as the 'MOTH' section. The fish-bearing interval occurs at MOTH 180 m, in strata considered to correlate with parts of the Road River Formation and Delorme Group in that area. Faunal correlations, based primarily on pteraspidiforms, thelodonts, cephalaspids, and a placoderm in the assemblage, were summarized by Adrain and Wilson (1994). They point to an Early Devonian (Lochkovian) age.

METHODS

The acanthodian material from MOTH 180 m is preserved in argillaceous limestone. Most specimens were prepared by technician L. A. Lindoe of the University of Alberta. Acetic acid preparation (Rixon 1976) has been successful because of the calcareous matrix and the resistant nature of the bone. Between and following baths in acetic acid, fine clastic residues were carefully removed from specimens with a soft brush and exposed fossils were protected with an acetone-soluble glue. Most specimens were originally preserved intact and articulated, complete with fins and scales. However, weathering and rock breakage that occurred prior to collection resulted in partial specimens being included in the study. As well, there are naturally occurring fragmentary specimens, such as isolated fin spines, jaw bones, teeth and scales, in the assemblage.

Drawings were made with a camera lucida attachment on a Wild M8 stereo dissecting microscope. Photographs were taken with an Olympus OM2S 35 mm camera equipped with automatic exposure system, macro lens, bellows, and extension tubes. Ammonium-chloride sublimate was used to whiten some specimens before they were photographed.

Institutional abbreviations are: GSC – Geological Survey of Canada; NMC – Canadian Museum of Nature, Ottawa, Ontario, Canada; UALVP – Laboratory for Vertebrate Paleontology, Departments of Earth and Atmospheric Sciences and Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

SYSTEMATIC PALAEONTOLOGY

Order CLIMATIIFORMES Berg, 1940

Diagnosis. Acanthodian fishes having scales with, or derived from, *Nostolepis*-type of microstructure; relatively large bony plates ('scales') on the head; two dorsal fins.

Remarks. The presence of numerous intermediate paired spines is omitted because of Long's (1983) inclusion of *Culmacanthus*, a diplacanthoid without any intermediate spines, and their presence in Ischnacanthiformes (two pairs in *Uraniacanthus*). Presence of dermal ventral plates associated with the shoulder girdle, and the broad coracoid structure of Miles' (1966) definition are omitted because they are absent in Brochoadmonoidei. Miles' (1966) shoulder girdle characters undoubtedly represent synapomorphies within the Climatiiformes.

Suborder BROCHOADMONOIDEI subord. nov.

Diagnosis. Climatiiform acanthodians without dermal shoulder girdle but with numerous short intermediate spines; body scales overlapping, with low crown and neck and poorly differentiated base; pectoral spine and/or fin high on flank posterior to gill slits.

Remarks. This new suborder is created for climatiiforms lacking a dermal shoulder girdle. Body scale morphology is also peculiar. Because it lacks the latter characteristic, we tentatively do not include *Cassidiceps vermiculatus* gen. et sp. nov. in the suborder. Although presence or absence of the ventral dermal plates of the shoulder girdle is not clearly established in *Cassidiceps*, it has normal climatiiform scales and lacks the elevated pectoral spine.

Family KATHEMACANTHIDAE fam. nov.

Type genus. *Kathemacanthus* gen. nov.

Included genus. *Brochoadmones* Bernacsek and Dineley, 1977.

Diagnosis. As for the type and only species of the type genus.

Genus KATHEMACANTHUS gen. nov.

Derivation of name. A combination of the Greek word '*Kathema*', for necklace, referring to the collar of spines and modified scales, and the Latin word '*acanthus*', for spine, gender masculine.

Type species. *Kathemacanthus rosulentus* sp. nov.

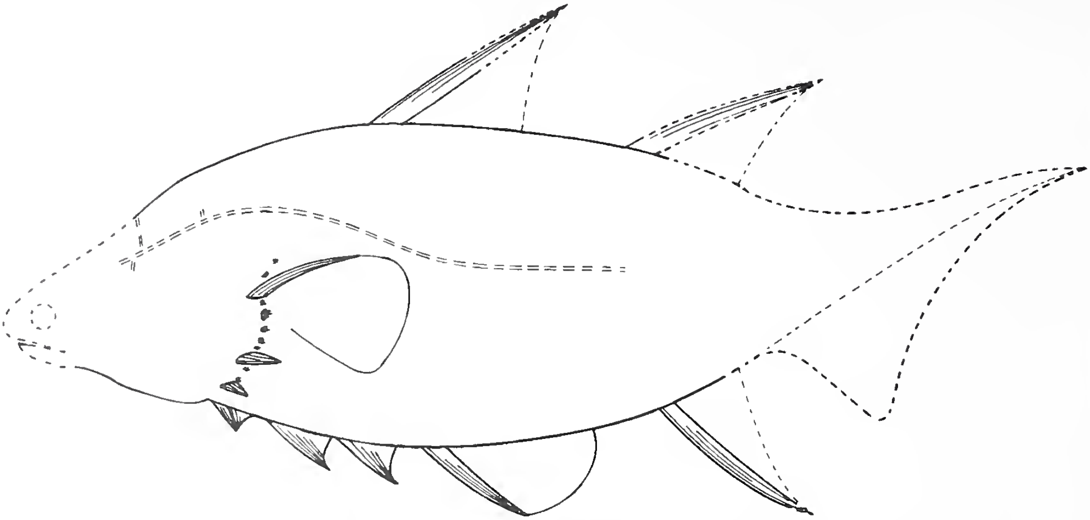
Diagnosis. As for the type and only species.

Age. Early Devonian (Lochkovian).

Kathemacanthus rosulentus gen. et sp. nov.

Plate 1; Text-figures 2–4

Derivation of name. The specific epithet *rosulentus* is a Latin adjective meaning 'full of roses', in reference to the rose-shaped tectal scales.



TEXT-FIG. 2. Reconstruction in left lateral view of *Kathemacanthus rosulentus*; dotted lines indicate parts unknown from the type specimen; approximately ×0·85.

Holotype. UALVP 32402, a specimen preserved in lateral view, with the anterior half of the head and posterior part of the body missing.

Material. In addition to the holotype, Bernacsek and Dineley (1977, p. 19, fig. 16B; pl. 10-1–2) illustrated and discussed an enigmatic spine and scales, NMC 22706C, that we refer here to this new genus and species.

Locality and age. UALVP Locality 129 in the MOTH section (Adrain and Wilson 1994), equivalent to GSC Locality 69014 in section 43 of Gabrielse *et al.* (1973), Mackenzie Mountains, N.W.T., Canada, in transitional beds between the Road River Formation and Delorme Group, Lower Devonian (Lochkovian).

Diagnosis. Brochoadmonoidei with an oblique row, 'collar', or 'necklace' of spines interspersed with enlarged and modified scales anteroventral to the pectoral spine and immediately posteroventral to the gill slits; pectoral fin large, extending beyond the tip of its spine; no dermal pectoral girdle elements; three pairs of ventral intermediate spines.

Description

Body shape. *Kathemacanthus rosulentus* is a relatively large acanthodian (Text-fig. 2), known from a single articulated specimen missing the anterior part of the head and the posterior part of the body behind the second dorsal and anal fins. The specimen is preserved flattened laterally. It shows numerous features seldom seen or rarely preserved in acanthodians. First, the type specimen exhibits one of the deepest bodies and shortest trunks known in acanthodians, with its pelvic fin origin anterior to the half-way point between the two dorsal spines and its body depth at the pelvic origin greater than the interdorsal length. Secondly, it possesses a pectoral spine

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EXPLANATION OF PLATE 1

Figs 1–2. *Kathemacanthus rosulentus*, holotype, UALVP 32402, shown dusted with ammonium chloride. 1, pectoral spine and fin, showing the central lobe-shaped region covered with larger scales surrounded by radiating rows of smaller scales; anterior to left; ×4·4. 2, 'necklace' of prepectoral and pectoral spines and 'artichoke' scales; anterior to bottom of page, ×7.

1

2

GAGNIER AND WILSON, *Kathemacanthus*

and fin in a high lateral (flank) position, along with three pairs of spines in apparent admedian or prepectoral position (Text-fig. 3).

The relative body depth is difficult to estimate because of the incompleteness of the specimen. However, it could perhaps be comparable to that of *Culmacanthus*, which has a body depth to total length ratio of 0·33, and seems likely to be greater than the value of 0·22 seen in most other articulated acanthodian specimens. The reconstruction (Text-fig. 2) is based on a ratio of 0·28.

Head and visceral skeleton. The branchial region appears to be completely covered with scales. There is no trace of either branchiostegal rays or subsidiary gill cover. The branchial chamber seems to extend just a little higher than the pectoral fin.

The lateral line (Text-fig. 3) runs between 2 rows of normal scales at mid depth on the body. Because of the state of preservation of the specimen we cannot follow the line to the head. Nevertheless, part of the otic portion of the infraorbital line is present (and seems to diverge into an occipital or otic commissure).

Axial skeleton. Approximately half of the first dorsal spine and part of the inserted portion of the second dorsal spine are present. From what is preserved of the second dorsal spine, it seems larger than the first one.

The first dorsal spine is deeply inserted in the body and forms a low angle of insertion with the dorsal body margin. The spine has three sharply rounded ridges separated by large grooves (Text-fig. 4E). The preserved part of the spine's posterior edge is hollow. The section of the spine shows that the inner cavity is constricted distally, the spine's lateral walls becoming thicker, enclosing a single central cavity, and forming a posterior keel. A fin web is present and covered with fine scales.

The inserted part of the second dorsal spine is of the same shape as the first one. In section, it forms a U-shape with a thick anterior wall.

The anal spine is smaller than the first dorsal spine but shows the same morphological features. The spine is inserted posterior to a point vertically below the second dorsal spine. The angle of insertion is high and the spine erect. The section at the distal end shows a greatly restricted central cavity divided into three separate canals. A posterior keel is present on more than half of the spine and probably extends to the tip.

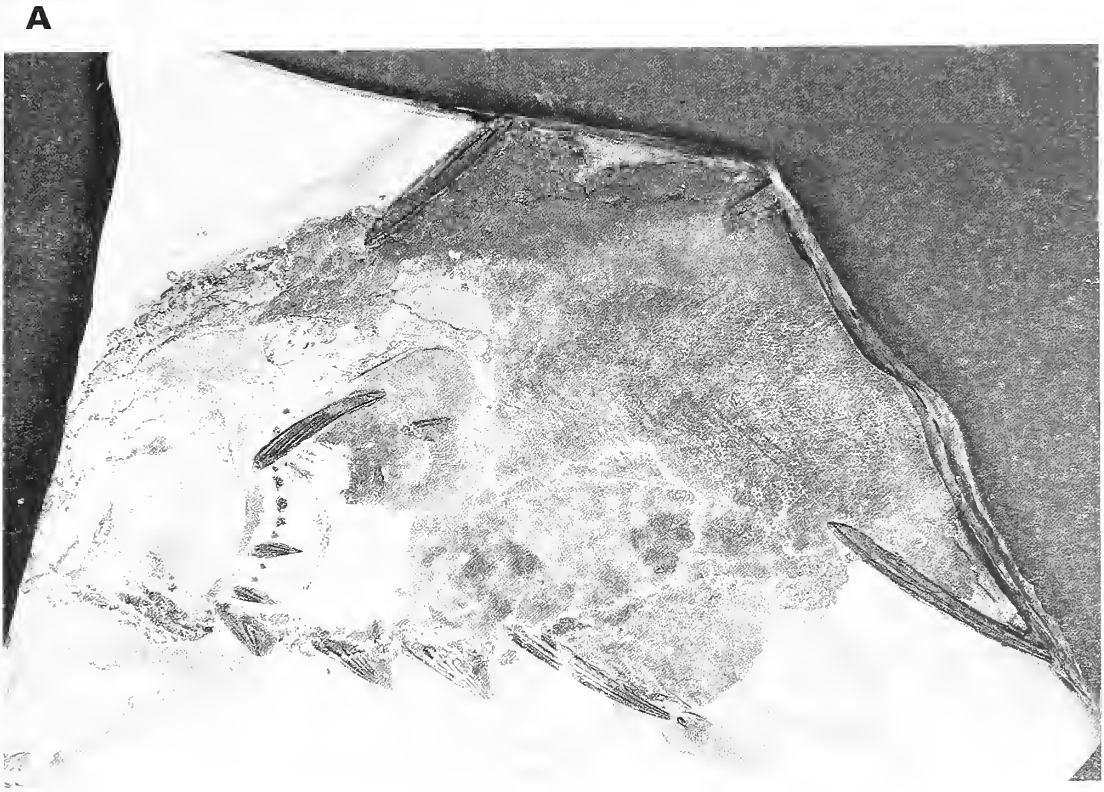
A series of 16–20 neural arches, 14 pairs of abdominal ribs and 6–7 haemal arches is preserved posterior to the pectoral fin (Text-fig. 3). This is the first account, to our knowledge, of abdominal ribs in acanthodians. They are thin, separate, elongate elements. Neural arches reach 4·4 mm in length, ribs 9·7 mm, and are separated by about 1·5 mm. The haemal arches are united ventrally. As in other acanthodians, the notochord, represented by the gap between neural arches and ribs or haemal arches, is persistent and unconstricted.

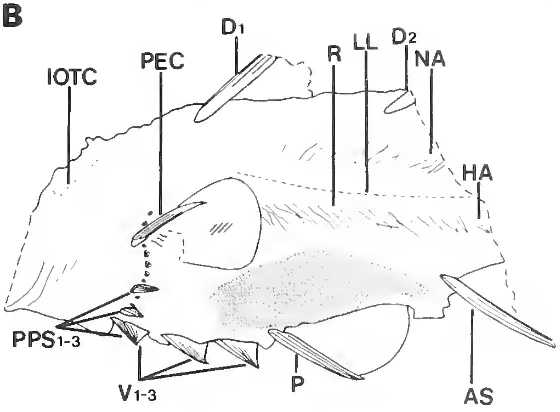
Appendicular skeleton. The pelvic spine is smaller than the anal spine and is shallowly inserted in the body. The vascularized bone of the inserted region extends posteriorly as far as the spine makes contact with the body margin. The spine bears a large anteromedian rib, somewhat rectangular in shape, followed posteriorly by three large grooves delimiting two sharply crested ridges and a large posterior ridge. This design of ribs and grooves is similar to that of the first dorsal and anal spines.

The pelvic spine bears a large fin web covered with scales. The fin web reaches the tip of the spine and is deployed in a fan-like shape posteriorly. The distal margin of the fin is convex and its medial side is attached to the body. Small scales form the distal part of the fin web, but obviously larger scales cover a large area near the base of the fin.

In the present paper, all paired ventral spines that are not pectoral or pelvic spines are designated as 'intermediate spines' without any necessary implications regarding their homology. Along the ventral margin of the body there are three large ventral intermediate spines (numbered from front to back, complex 3-1 [interpreted as a compound spine], 2 and 3); these are assumed to represent left members of spine pairs. These spines increase in size from front to back (Text-figs 3, 4D). The ratio of base length to maximum spine length of intermediate spine 3 is about 0·87. All have a very long base that is attached only superficially to the body wall, not deeply inserted. The two posterior intermediate spines (2 and 3) have seven smooth, unornamented ribs that narrow posteriorly. The posterior part of each spine bears no ribs and forms a wide flat fringe. There is not much difference in the base length to maximum spine length ratios (0·84 *vs* 0·87) or in the overall shape of the last two intermediate spines.

The ventral intermediate spine complex (3-1) differs in having five ribs and its distal part curved anteriorly (Text-fig. 4D). Moreover, this spine is peculiar in having a large groove in the middle of its side separating the two sets of crests. An X-radiograph clearly shows a lack of ossification in the groove where we suggest a fusion has occurred, leading us to term this a complex rather than simple spine. Small tubercles occur on the ribs of the anterior part of the spine but not on the posterior part.

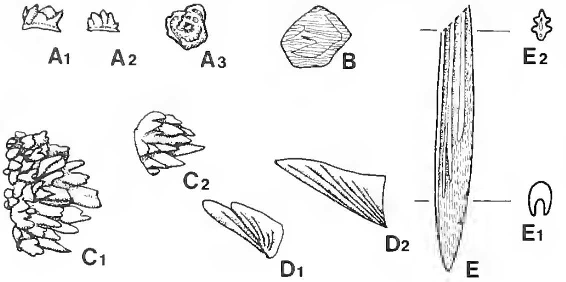




TEXT-FIG. 3. *Kathemacanthus rosulentus*, holotype, UALVP 32402, in left lateral view. A, photograph of specimen ×1·3. B, explanatory drawing. Abbreviations: AS = anal fin spine; D1 = anterior dorsal fin spine; D2 = posterior dorsal fin spine; HA = haemal arch; IOTC = otic part of infra-orbital sensory line; LL = lateral line; NA = neural arch; P = pelvic spine; PEC = left pectoral fin spine; PPS 1–3 = prepectoral spines; R = abdominal rib; V1–3 = intermediate spines. The shaded area represents gut infilling; the small hatched area on the pectoral fin represents a raised area on the specimen believed to contain the posterior tip of the right pectoral fin spine.

The X-radiograph also shows another spine in anteromedial position below the scales. It is possible that it belongs either to another pair not visible, hidden by the pectoral fin, or it could be the symmetrical spine (on the right side) of one already described from the left side.

The pectoral spine and fin are located at the middle of the height of the animal, immediately posterior to the branchial region (Text-fig. 3). The spine is slightly curved and bears five ribs separated by deep, but narrow, grooves. The insertion point forms a low angle, as in most of the other spines. A large pectoral fin web is seen posterior to the spine and is covered with scales (Pl. 1, fig. 1). The anterior border of the fin extends farther posteriorly than the spine. The fin web appears not to be attached to the spine, although there is no record in



TEXT-FIG. 4. Drawings of selected elements of the holotype of *Kathemacanthus rosulentus*, UALVP 32402. A, tectal tesserae; A1 and A2, lateral views; A3, dorsal view; × 7·5. B, large body scale from anterior to first dorsal spine; × 7.5. C, postbranchial modified 'artichoke' scales; C1, mid-way between pectoral spine and first prepectoral spine; C2, immediately dorsal to first prepectoral spine; × 7·5. D, intermediate spines; D1, prepectoral–intermediate spine complex '3-1'; D2, third ventral intermediate spine; × 1·5. E, first dorsal spine with transverse sections; E1 through base; E2 through median portion; × 1·5.

other acanthodians of spines independent of the fin. The fin has a rounded distal margin and the distribution of larger and smaller scales suggests a central lobe from which scale rows radiate.

Ventral to the pectoral spine is a series of two or three presumably paired spines, termed here 'lateral intermediate spines', interspersed with at least nine smaller structures that we treat as complexly modified scales; together these spines and scales form the necklace-like structure from which the generic name was derived. The lateral intermediate spines 1 and 2, those closest to the pectoral spine, differ from ventral intermediate spines in having only four ribs and no posterior flat fringe; the bases of the ribs bear a few small tubercles. The lateral intermediate spine closest to the pectoral (number 1) is slightly longer than number 2. The possible third one would be lateral intermediate 3 of the complex spine 3-1.

The modified scales of the 'necklace' vary in diameter from 0·89 to 1·63 mm (Pl. 1, fig. 2; Text-fig. 4C). The largest is located between the pectoral spine and the first lateral intermediate spine. These modified scales decrease both dorsal and ventral to that one. There are two located dorsal to the pectoral spine, five between the pectoral and the first lateral intermediate, and two between the first and second lateral intermediate spines. The two that are dorsal to the pectoral spine are located on a line extending posterodorsal to the pectoral, not in line with the others, while those ventral to the pectoral form an arc with the pectoral and the lateral intermediate spines.

Squamation. The modified scales are of a form unusual in acanthodians, with a bush of bluntly pointed tubercles resembling an artichoke, something like certain chondrichthyan scales. The number of tubercles is greater in the larger scales. In the largest one we counted 17 tubercles; in the smallest there are eight.

The body scales of *K. rosulentus* are large, thin, circular, and overlap one another extensively. Over most of the body they show a low crown with rounded sides and usually one, but as many as three points on the posterior edge. The ornamentation is variable but usually consists of 10–15 irregular, subparallel, smooth ribs. As well, most of them, though not all, show two or three concentrated ribs superimposed on the parallel ribs, and some exhibit large, pointed anterior ribs. The lateral edges of the crown seem to be bent upward, forming the most external of these concentric ribs. The scales are larger anterior to the first dorsal (Text-fig. 4B) and smaller on the anteroventral part of the animal. Much smaller scales are present on the extremities of the fins.

Modified scales occur on the head (Text-fig. 4A). On the upper part of the cheek region scales are small, bear five to eight subparallel ridges, and have a raised edge anteriorly. On the lower part of the cheek region the scales are larger, the concentric ribs are more marked, and some of the subparallel ridges bear tubercles. On the tectal region the necks of the scales are almost absent and the bases are very thin and concave. The crown of these scales is thicker, forming concentric rows of pointed tubercles with a central stellate tubercle (the rose-like appearance denoted by the specific epithet).

Digestive tract. Between the anal spine and the pelvic fin web is a bulge indicating the location of an endocast in the posterior end of the gut (Text-fig. 3). It meets the body margin where the anal opening must have been, surrounded by small, flexible scales. Beginning anteriorly dorsal to the first ventral intermediate spine, a longitudinal bulge beneath the scales reveals an endocast of a more anterior part of the digestive tract. It is large and apparently distended anteriorly (although there is no direct evidence, it can be interpreted as possibly a spiral-valve-containing part of the intestine as in sharks and the coelacanth *Latimeria chalumnae*), becoming more constricted posteriorly above the middle of the pelvic spine, and then turning ventrally toward the presumed anus. As in the description of *Homalacanthus* (Gagnier in press) or *Brochoadmones* (Gagnier and Wilson in press), there is no sign of an 'S' curve in the digestive tract; however, the gastric and anterior intestinal portions of the gut, where an 'S' curve would be expected, may not be visible. Indeed, if the intestinal endocast represents a spiral-valve-containing part of the intestine, an 'S' curve is virtually required to connect a stomach to it.

Referred material. Bernacsek and Dineley (1977, pl. 10-3, text-fig. 16A) noticed similarities between the ribbing of a large intermediate spine (discussed below) and of a differently shaped spine associated with it in the same block, NMC 22706B. The latter spine bears a large anterior rib followed by three smaller ribs. All ribs are smooth and unornamented and the last rib extends only along the distal half of the spine. This spine thus resembles the anal spine of UALVP 32402.

Bernacsek and Dineley (1977, pl. 10-1, text-fig. 16B) also figured a large example of an intermediate spine resembling those of *K. rosulentus*. The one figured by Bernacsek and Dineley reaches 16·4 mm in length rather than the 11·7 mm of the longest in the holotype. The ratio of base length to maximum spine length of the figured spine (NMC 22706C) is approximately 0·75, less than that of the largest intermediate spine in the holotype.

Remarks. Kathemacanthus has a deep body, and a pectoral spine inserted high on the flank like the presumed pectoral spine of *Brochoadmones*. However, with its necklace of spines, the gross morphology of *Kathemacanthus* is unlike that of any previously described articulated acanthodian. The major question raised by its morphology is that of the homology and appropriate terminology of the various paired spines.

The first issue to be settled is whether there is a single row of intermediate spines or two rows, with one spine row associated with the pectoral fin and the other associated with the pelvic fin. We conclude that the 'lateral intermediate' spines located anteroventral to the pectorals represent a series distinct from the 'ventral intermediates' both because their morphologies are different and because they are located in two distinct linear series.

As to the appropriate homologies, we are comfortable, for now, with the idea that the 'ventral intermediates' are equivalent to the typical intermediate spines of other climatiiform acanthodians. The count of three pairs of ventral intermediate spines is not unreasonable; it is close to the count in *Parexus recurvus* and *Ptomacanthus anglicus*, which both have two prepectoral and four intermediate spines. The two posterior ventral intermediates in UALVP 32402 and the isolated example NMC 22706C are large, like those found in numerous climatiiforms, such as *Vernicomacanthus waynensis*, but the size and shape of their ridges recall *Neosinacanthus planispinatus* from China (P'an *et al.* 1975) and *Sinacanthus*? sp. from Bolivia (Gagnier *et al.* 1988).

Obviously, the 'lateral intermediates' represent more of a problem, but also are more significant. As discussed in more detail below, we tentatively conclude that the lateral intermediates are homologues of the prepectoral spines of other acanthodians.

The unpaired spines of *Kathemacanthus* are not so problematical. Their morphology, especially of the inserted part (moderate length; hollow; making a low angle with the body margin), is like that of *Brochoadmones milesi*. They differ from diplacanthid spines, in which the inserted part is very long and usually forms nearly a right angle with the body margin. However, this feature is poorly documented for other climatiiforms. Transverse sections of the unpaired spines of *K. rosulentus* show few large ribs, separated by well marked grooves, and a prominent posterior keel. This is comparable to the situation in the Mid Devonian Baltic species *Archaeacanthus quadrisulcatus* which differs in having a smaller anterior ridge.

The scales of *K. rosulentus* are thin and circular. The only other acanthodian with similar scales is *Brochoadmones milesi*. In both species the scales are not so well preserved and thin sections have not given results suitable for comparison. The concentrically ornamented tectal scales or rosebud-like head tesserae are unique. Their ornamentation of stellate tubercles recalls scales of *Climatius reticulatus* and, to a lesser degree, *Vernicomacanthus uncinatus* and *Brochoadmones milesi*. Stellate tubercles on tectal tesserae could well be a common feature among climatiiforms. Elevated tectal ornament occurs in *Climatius reticulatus* and *Nostolepis wangi*, but those of *K. rosulentus* resemble more those of *Ptomacanthus anglicus* (see Miles 1973, fig. 1E). The modified artichoke-like scales that alternate with pectoral and 'lateral intermediate' spines recall the scales of chondrichthyans such as the Early Devonian *Ohiolepis*. All these modified scales could easily be derived from the morphology of the body scales which, in *Kathemacanthus*, show a tendency to produce pointed ridges or tubercles.

Suborder INCERTAE SEDIS
Family INCERTAE SEDIS

Genus CASSIDICEPS gen. nov.

Derivation of name. From the Latin words *cassidis*, 'helmet', and *ceps*, 'head', in reference to the heavy covering of dermal bones on the head, gender masculine.

Type species. *Cassidiceps vermiculatus* gen. et sp. nov.

Diagnosis. As for the type and only known species.

Age. Early Devonian (Lochkovian).

Cassidiceps vermiculatus gen. et sp. nov.

Plate 2; Text-figures 5–7

Derivation of name. The specific epithet is the masculine form of the Latin adjective *vermiculatus*, meaning 'worm eaten' or 'wormy', in reference to the sinuous ornament on the dermal skull bones.

Holotype. UALVP 32454, head and anterior part of the body, preserved in lateral view.

Locality and age. UALVP Locality 129 at 180 m in the MOTH section, equivalent to GSC Locality 69014 in section 43 of Gabrielse *et al*. (1973), Mackenzie Mountains, N.W.T., Canada. Transitional beds between Road River Formation and Delorme Group, Lower Devonian (Lochkovian).

Diagnosis. Deep bodied climatiiform with heavy cephalic armour; slender fin spines shallowly inserted in the body musculature; at least two pairs of intermediate spines; small, thick, rhombic, unornamented body scales.

Description

Body shape. *Cassidiceps vermiculatus* is also a relatively deep-bodied acanthodian (Text-fig. 5), with body depth probably close to that of *Kathemacanthus* and *Culmacanthus*, judging by the distance between the dorsal spines versus body length. The fish bears two small dorsal spines, a long pectoral spine and, in addition to the pelvic and anal spines, two or possibly three pairs of intermediate spines between the pectoral and pelvic fins (Pl. 2, fig. 1; Text-fig. 6A).

Head and visceral skeleton. The anterior part of the head is covered with large, thick tesserae with reticulate or vermiculate ornament (Pl. 2, fig. 2). The orbit is relatively small for an acanthodian. There is a circumorbital series of at least two long bones forming the anterior rim of the orbit; preservation is not good enough to discern the bones forming the posterior rim of the orbit.

The snout anterior to the orbit is formed by a large, dorsally arched nasal bone that borders with dorsorostral elements articulating with the circumorbital bones and with tectal tesserae. Ventrolateral to the nasal two pairs of bones enclose the nasal capsule (Pl. 2, fig. 2; Text-fig. 6B). The nares are not well delimited, but the general figure-of-eight shape of the external bony opening suggest the presence of separate nares. If so,

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EXPLANATION OF PLATE 2

Figs 1–2. *Cassidiceps vermiculatus*, holotype, UALVP 32454, in left lateral view. 1, entire specimen as preserved; ×2. 2, anterior part of head, shown dusted with ammonium chloride; ×11.

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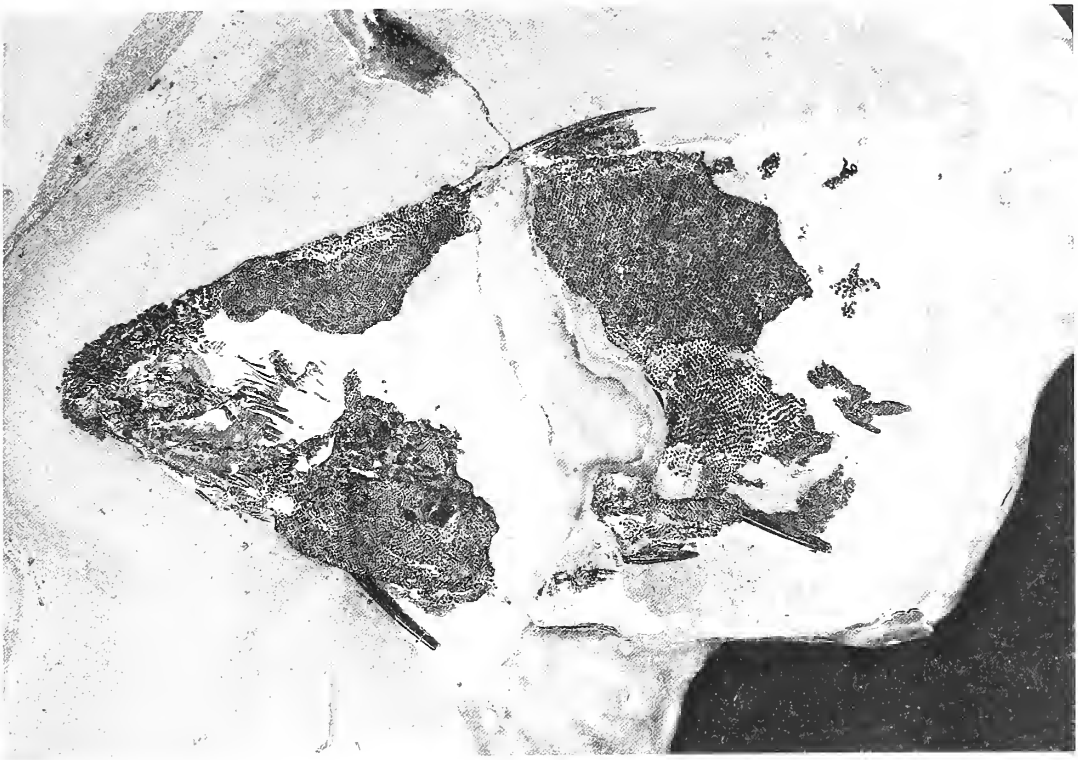

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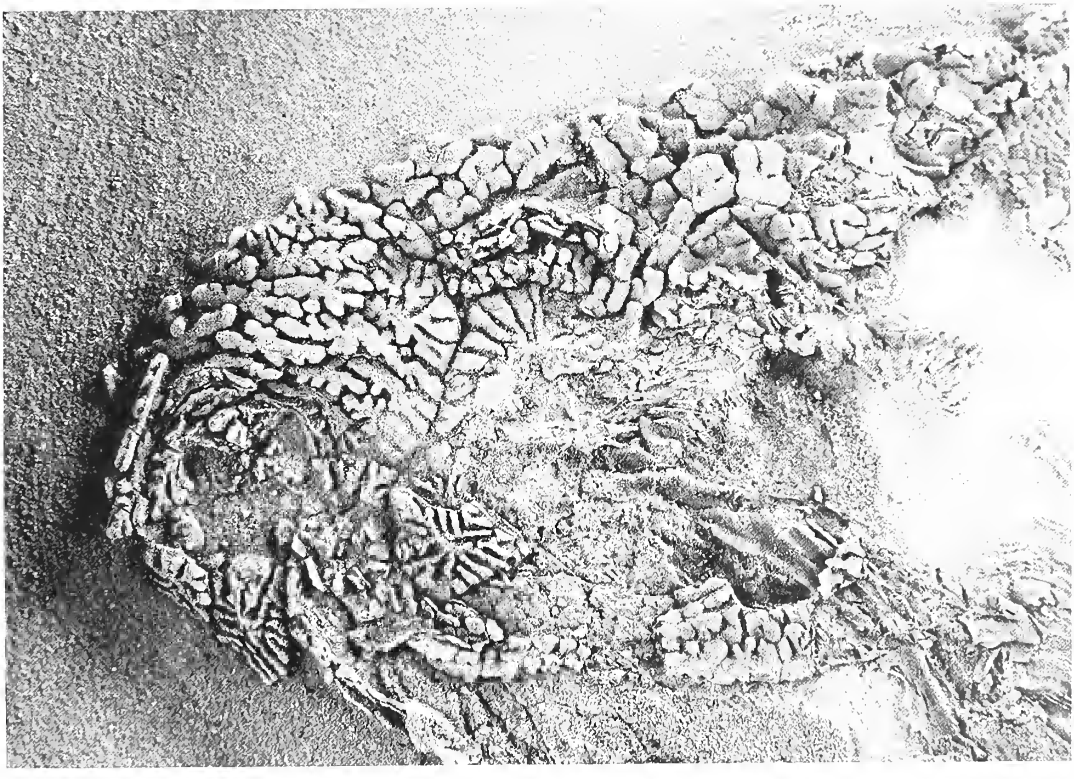
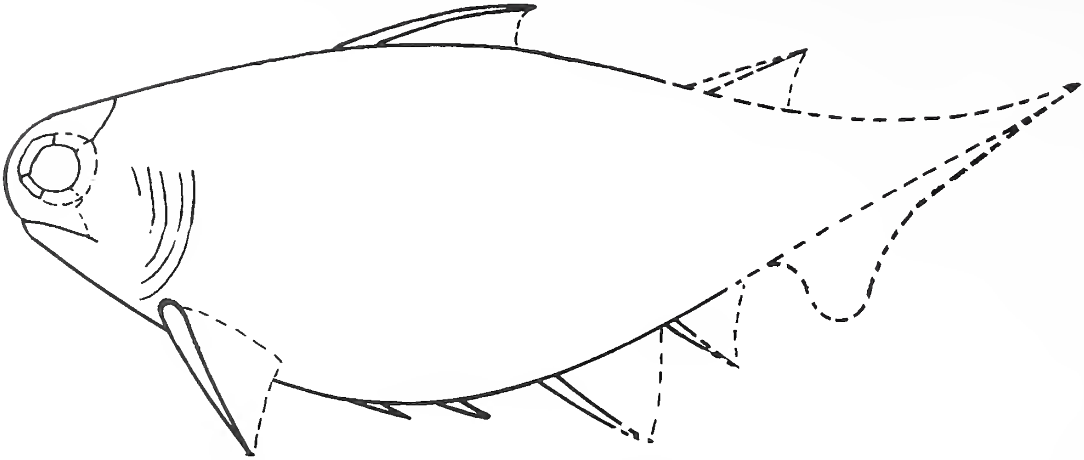
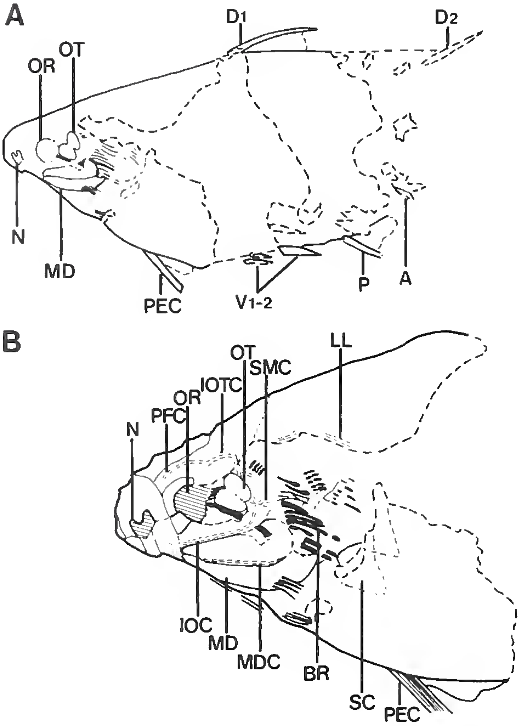


GAGNIER AND WILSON, *Cassidiceps*



TEXT-FIG. 5. Reconstruction in left lateral view of *Cassidiceps vermiculatus*; dotted lines indicate parts unknown from the type and only specimen; approximately × 2.



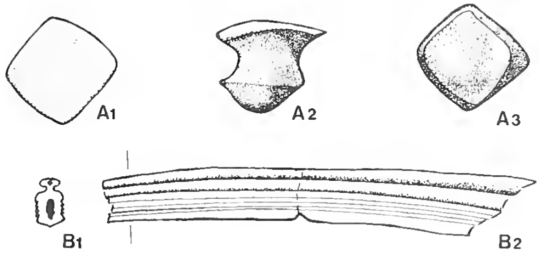
TEXT-FIG. 6. *Cassidiceps vermiculatus*, holotype, UALVP 32454, in left lateral view. A, explanatory drawing of the entire specimen; × 1. B, schematic enlargement of the head; × 2. Abbreviations: A = anal fin spine; BR = branchiostegal rays; D1 = anterior dorsal fin spine; D2 = posterior dorsal fin spine; IOTC = otic part of infraorbital sensory line; IOC = infraorbital sensory line; LL = lateral line; MD = mandible; MDC = mandibular sensory line; N = nostril; OR = orbit; OT = otic capsule; P = pelvic spine; PEC = pectoral spine; PFC = profundus sensory line; SC = scapula; SMC = supramaxillary sensory line; V1–2 = ventral intermediate spines.

the incurrent nares should be just below the excurrent nares, as in *Culmacanthus* (Long 1983), *Triazeugacanthus* (Gagnier in press), and *Brochoadmones* (Gagnier and Wilson in press).

On the tectal region, tesserae continue up to the otic region, where they grade rapidly into normal body scales (Pl. 2, fig. 2).

The Meckelian cartilage is made of a single, long, broad calcification. The mandible (Pl. 2, fig. 2; Text-fig. 6) reaches a point beneath the anterior part of the orbit.

The hyoid arch bears six to eight branchiostegal rays. They are long and cover two-thirds of the gill chamber. The hyoid bar forms an angle of about 30° with the vertical. Over the hyoidean rays, four other groups of



TEXT-FIG. 7. Drawings of selected elements of the holotype of *Cassidiceps vermiculatus*, UALVP 32454. A, body scales; A1, dorsal view, A2, lateral view, A3, ventral view; × 45. B, pectoral spine; B1, cross section near middle of spine at position indicated by vertical line; B2, lateral view of preserved portion of spine; × 6.

branchiostegal rays are visible, indicating the possible presence of a subsidiary gill cover (Text-fig. 6B). More than six long, slender branchiostegal rays are present on each side below the mandible.

Posterior to the orbit, a double oval cavity is filled with grey sandy matter, recalling the otic region of *Triazeugacanthus* (Gagnier in press) and *Brochoadmones* (Gagnier and Wilson in press). Some of the cephalic sensory lines are visible. In the suprabranchial region the lateral line runs between two rows of enlarged modified scales and is continuous anteriorly with the otic part of the infraorbital line. This line runs between tesserae to the orbit. One branch over the otic capsules leads to the preopercular line. Another branch leads to the postorbital and suborbital sections of the infraorbital line; there is a suggestion of an ethmoid commissure ventral to the narial region.

The supramaxillary canal extends posterior to the postorbital portion of the infraorbital line. A mandibular canal extends to the anterior region of the mandible (Text-fig. 6B).

Postcranial axial skeleton. The first dorsal spine is shallowly inserted in the body and its middle portion is slightly curved. The anterior rib is very large and flat and set off by a deep groove. Posterior to that groove are three to four fine ridges tapered anteriorly but truncated posteriorly. There is a fin web covered with scales. The fins do not appear to reach the tip of the spine. The spine makes a low angle with the body margin but the fin position suggests the spine was more erect in life.

Only an impression of the second dorsal spine is preserved (Pl. 2, fig. 1; Text-fig. 6A). The spine seems equal in length or perhaps shorter than the first dorsal, with a small inserted portion. A small part of the anal spine is preserved below the second dorsal.

Appendicular skeleton. The pelvic spine is partially preserved and shows the same characteristic morphology as the first dorsal. The spine bears a scale-covered fin web that must have almost reached the anal spine.

Between the pelvic and pectoral spines there are two pairs of intermediate spines (Pl. 2, fig. 1; Text-fig. 6A). They are broader than the pectoral and pelvic spines but otherwise are similar. They make a very low angle with the body margin. The more posterior pair is the longer. Their posterior position relative to the pectoral and pelvic fins suggests that one or more other pairs of intermediate spines might have been present.

The pectoral spine (Pl. 2, fig. 1; Text-figs 6, 7B), like the intermediate spines, has a second anterior rib (the first pair) which is larger than on the first dorsal, anal, or pelvic spines. The pectoral spine is slightly curved just beyond its middle. A fin is present, covered with minute scales.

Ossified scapulae are present but badly damaged. The scapular blade is short and has a flat internal face containing a foramen. There is a large anterior posterobranchial lamella. The lateral lamella does not seem to be well developed.

Part of the interpectoral region is visible on the holotype and is covered with scales. Scales anteroventral to the scapula are missing, but there is no sign of a dermal shoulder girdle.

Squamation. The scales are rhomboidal (Text-fig. 7A), relatively small and extensively overlapping. The crown is flat and unornamented. The neck is very high and constricted anteroposteriorly. The base forms a rounded point and has a prominent flange at the transition with the neck. The neck and base are anteriorly placed relative to the crown, which extends far posteriorly.

Digestive tract. Posterior to the pectoral girdle the digestive tract contains a small cephalaspid (or at least scales of a cephalaspid).

Remarks. The systematic position of *Cassidiceps vermiculatus* is uncertain. Like most climatiiforms it possesses two dorsal fins, relatively large dermal bones on the head, well-developed branchiostegal rays, and two or more pairs of intermediate spines. Like *Kathemacanthus* and *Brochoadmones* it differs from Climatioidei in having overlapping scales and lacking a dermal shoulder girdle; however, it lacks the main special feature of the Brochoadmonoidei, the high lateral position of the pectoral spines. Similarly it lacks the most important features of the Diplacanthoidei such as: dermal shoulder girdle made of a single pair of pinnal plates and paired or unpaired median anterior bone; large cheek plate bearing sensory lines; and high scapula. We therefore classify it as *incertae sedis* within the Climatiiformes, recognizing that the order as presently construed may well be paraphyletic.

DISCUSSION

The remarkable pectoral structures of *Kathemacanthus rosulentus* gen. et sp. nov. together with those described recently for *Brochoadmones milesi* raise important questions about the serial homology and terminology of intermediate spines, and about pectoral and pelvic spines and fins in acanthodians generally. Accordingly we begin this discussion by reviewing issues of acanthodian spine homology and terminology.

Paired spine homology and terminology

The descriptive terminology of anatomical structures in acanthodian fishes has been repeatedly modified by workers carrying out revisions and by those describing new material. Changes in our understanding of acanthodian skeletal homology and terminology have touched various parts of the body (Table 1). For instance, Gagnier (in press) points out the difference between circumorbital plates and the sclerotic ring. Denison (1979, p. 4) noted that so-called circumorbital bones are found in all families of Acanthodii except Gyracanthidae. However, in the Acanthodiformes in general, these bones are always associated with the sclerotic membrane and must thus correspond to sclerotic ossifications, whereas in Climatiiformes the circumorbital plates are part of the dermal head armour and, thus, different in origin.

In the case of the paired spines, various acanthodians show, in addition to pectoral and pelvic spines with attached fins, a paired series of spines, classically termed 'intermediate' spines, between the pectoral and pelvic spines. Many also show so-called 'prepectoral' spines (anterior to the pectoral spines), and finally some have so-called 'admedian' spines medial to the pectoral spines. These structures have also been the subject of changing nomenclature (Table 1).

So-called prepectoral and admedian spines have posed particular problems to previous workers. Writing of *Erriwacanthus falcatus*, Ørvig (1967, p. 133) stated '... all these small spines, the three anterior ones and the single postero-lateral one, are of the same nature as the intermediate spines which in the Climatiidae and various other acanthodians occur between the pectoral and the pelvic fins, and as these occupy a position in the paired fin-fold [Jarvik 1965]...'. On the question of the prepectoral spines Ørvig (1967) argued, from misinterpreted material of *Climatius reticulatus*, that these spines might have a development different from that of other intermediate spines, because those of *Erriwacanthus falcatus* were included in a dermal plate and those of *C. reticulatus* (he thought) were not. Miles (1973, p. 165) recognized that the spines of *C. reticulatus* were indeed on a dermal plate, and replied, 'Thus I cannot agree with Ørvig [1967, p. 137] that this spine differs from the prepectoral spines in its development.'

Ørvig (1967, p. 133) recognized the homology of the admedian pectoral spine (between the pectoral spines) in diverse acanthodians. For Miles (1973) the homology of the intermediate spines in prepectoral position (anterior to the pectorals) was revealed by their association with or position relative to the dermal elements of the shoulder girdle. Miles gave the designation 'true first intermediate spine' to the spine located in admedian position, emphasizing the difference between that and the intermediate spines in prepectoral position. The use of that distinction was justified by Miles' (1973) hypothesis that pectoral fin spines and prepectoral spines and plates were serial homologues and that, from a primitive condition with a well-developed dermal shoulder girdle, the general trend in the evolution of acanthodians was toward reduction of the dermal shoulder girdle.

TABLE 1. Changes in terminology of anatomical elements of the shoulder girdle in acanthodians.

	Woodward 1891	Watson 1937	Ørvig 1967	Miles 1966	Miles 1973
Endoskeletal shoulder girdle	Clavicle in *Diplacanthus*	Scapula	—	—	Scapula
	Infraclavicle in *Diplacanthus*	Coracoid in *Diplacanthus*	—	Coracoid	Procoracoid with fused dermal ventral plate in *Diplacanthus*
Dermal elements of the shoulder girdle	—	Median dermal bone	Median ventral plate	—	Anterior lorical plate
	—	—	—	—	Posterior lorical plate
	—	Cylindrical dermal bone	Paired median prepectoral fin-fold spine	—	Anterior pinnal plate
	—	Anterior lateral plate	First ventrolateral plate	—	Middle pinnal plate
	Clavicle in *Parexus*	Anterolateral bone in *Parexus*	Ventrolateral plate in *Parexus*	—	Anterior + middle pinnal plates fused in *Parexus*
	Basal cartilage in *Diplacanthus*	Dermal plate in *Diplacanthus*	Second ventrolateral plate	Dermal plate in *Diplacanthus*	Posterior pinnal plate
	—	—	Ventrolateral plate in *Erriwacanthus*	—	Copinnal plate in *Erriwacanthus*
Intermediate spines	—	—	Unpaired median prepectoral fin-fold spine	—	Median prepectoral spine (could be fused to anterior lorical plate)
	—	—	Paired prepectoral fin-fold spine	—	Paired prepectoral spines 1, 2, 3 (could be fused to anterior, median, and anterior part of posterior pinnal plate)
	Median spine in *Diplacanthus*	Ridged dermal bone, admedian spine in *Diplacanthus*	Posterolateral fin-fold spine of the ventrolateral plate	Ventral spine from shoulder girdle	First intermediate spine of ventral series (could be fused on middle or mesial part of posterior pinnal plate)

TABLE 1 Changes in terminology of anatomical elements of the shoulder girdle in acanthodians

	Woodward 1891	Watson 1937	Ørvig 1967	Miles 1966	Miles 1973
Endoskeletal shoulder girdle	Clavicle in *Diplacanthus*	Scapula			Scapula
	Infraclavicle in *Diplacanthus*	Coracoid in *Diplacanthus*		Coracoid	Procoracoid with fused dermal ventral plate in *Diplacanthus*
Dermal elements of the shoulder girdle		Median dermal bone	Median ventral plate	–	Anterior lorical plate
				–	Posterior lorical plate
		Cylindrical dermal bone	Paired median prepectoral fin-fold spine		Anterior pinnal plate
		Anterior lateral plate	First ventrolateral plate		Middle pinnal plate
	Clavicle in *Parexus*	Anterolateral bone in *Parexus*	Ventrolateral plate in *Parexus*		Anterior + middle pinnal plates fused in *Parexus*
	Basal cartilage in *Diplacanthus*	Dermal plate in *Diplacanthus*	Second ventrolateral plate	Dermal plate in *Diplacanthus*	Posterior pinnal plate
			Ventrolateral plate in *Erriwacanthus*	–	Copinnal plate in *Erriwacanthus*
Intermediate spines			Unpaired median prepectoral fin-fold spine	–	Median prepectoral spine (could be fused to anterior lorical plate)
			Paired prepectoral fin-fold spine	–	Paired prepectoral spines 1, 2, 3 (could be fused to anterior, median, and anterior part of posterior pinnal plate)
	Median spine in *Diplacanthus*	Ridged dermal bone, admedian spine in *Diplacanthus*	Posterolateral fin-fold spine of the ventrolateral plate	Ventral spine from shoulder girdle	First intermediate spine of ventral series (could be fused on middle or mesial part of posterior pinnal plate)

Miles did not elaborate on the homology of what he called the intermediate spines between the pelvic and pectoral fins, other than to state that the subject was beyond the scope of his paper. Indeed the number of such spines varies in the different genera and only the admedian one, the 'true first intermediate spine', could be consistently recognized.

Because all the intermediate spines, as well as the pectoral and pelvic fins, have been thought to be remnants of a once continuous fin-fold (Gregory 1951, p. 114), the terminology of Ørvig (1967) assumed fin-fold origins for some spines (based primarily on the condition in *Climatius reticulatus*; see Table 1). Miles (1973) used a modification of this terminology to describe the degree of fusion or division of the dermal shoulder girdle in various genera of climatiiforms. Characters from the prepectoral spines were also used in the classification of Climatiiformes (Miles 1973; Long 1986).

It seems to us that the anatomy of *Brochoadmones milesi* and especially that of *Kathemacanthus rosulentus* provides evidence that helps to settle the issue of the homology of prepectoral spines. In a previous paper on *B. milesi* (Gagnier and Wilson in press) we faced a problem concerning the homology of the pectoral spines and the intermediate series of spines, because that species appears to lack a pectoral fin, thus making it difficult to identify a pectoral spine. However, in *Brochoadmones milesi* not only is there no pectoral fin, neither is there an obvious pectoral spine nor an ossified shoulder girdle. What is present is just a pair of tiny, flattened spines, shaped like the valves of a brachiopod or a bivalve, on the flank of the animal immediately posterior to the gill slits. Homology of this tiny fin-less spine with the pectoral was proposed by us because no acanthodian known until then had a spine dorsal or lateral to the pectoral, whereas the reverse condition of intermediate spines ventral or medial to the pectoral is relatively common in Climatiiformes.

In addition to the flank 'bivalve' spine, *B. milesi* has a series of six pairs of intermediate spines in the usual ventral position, arranged from the pelvic spine to a point below the branchial region, i.e. reaching actually anterior to a vertical line through the tiny 'pectoral' spine on the flank. In other acanthodians, the pectoral fin and spine would be located at or near the anterior end of this 'intermediate' series, but this is apparently not so in *Brochoadmones*. The most anterior intermediates of *Brochoadmones* might normally be considered to be prepectorals; however, their homogenous morphology and their alignment with the posterior intermediate and pelvic spines suggests that they are all ventral intermediate spines.

The 'necklace' of spines leading to a high pectoral spine and fin in *Kathemacanthus* seems to link the tiny flank pectoral spine of *Brochoadmones* with the ventromedial prepectoral spines and ventral pectoral fin and spine of various climatiiforms. The spines in the 'necklace' of *Kathemacanthus* could represent: (1) dorsolaterally displaced homologues of some of the typical intermediate spines of other climatiiforms; (2) homologues of prepectoral spines located anteroventral to pectoral spines in other climatiiforms and usually attached to plates of dermal bone; (3) homologues of the spines located medial to the pectoral spines in other climatiiforms, also usually attached to plates of dermal bone, the so-called 'admedians'; or (4) a previously unknown kind of spine not homologous with any other.

We reject the first alternative for reasons stated earlier: the differences in morphology and serial position between these spines and the undoubted 'ventral intermediates'. The third alternative might possibly apply for one of the spines of *Kathemacanthus*: the most anteroventral spine that seems to represent a compound, fused structure, but is not a reasonable explanation for the others. The fourth alternative must remain a possibility that we cannot reject, though we think it unnecessary to postulate a new spine type when there is a simpler hypothesis.

The hypothesis, which seems to us to be the most reasonable of the four, is the second alternative: we suggest that the 'lateral intermediates' of *Kathemacanthus* are homologous to the 'prepectoral' paired spines of other climatiiform acanthodians. Even though the lateral intermediates of *Kathemacanthus* are not in the position of standard prepectoral spines ventral to the branchial arches and anteromedial to the pectoral fin spines, they are, nevertheless, immediately posterior to the branchial arches.

If the 'lateral intermediates' of *Kathemacanthus* are equivalent to the prepectoral spines of other acanthodians, then the new evidence strongly supports Miles' (1973) hypothesis that prepectoral spines are serial homologues of pectoral spines, or at least the idea that they belong to a pectoral spine series distinct from a pelvic series that includes ventral intermediate spines. Miles' hypothesis is also consistent with the condition seen in *Brochoadmones*, although in that taxon all the spines in the pectoral series, except for the greatly reduced, presumed pectoral spine, have been lost. The question of admedian spines is not addressed particularly by the new evidence; however, it is at least possible that admedians could represent anterior elements of the ventral intermediate (pelvic) series that have become associated with the pectoral girdle.

The dermal bones of the shoulder girdle

Miles (1973) also thought that presence of the dermal component of the shoulder girdle was a primitive condition for the Acanthodii. Denison (1979) used this character, along with the presence of tectal tesserae and body proportions, as diagnostic of the Climatiiformes. It was Long (1986), however, who suggested that presence of the dermal component of the shoulder girdle could be a synapomorphy of the Climatiiformes, in part because of his interpretation of pectoral anatomy in another genus, *Lupopsyrus* Bernacsek and Dineley (1977), from the same fossil assemblage as the taxa described in the present paper. *Lupopsyrus* has multiple intermediate spines but a free pectoral spine (not fused to a dermal shoulder girdle), as in acanthodiforms and ischnacanthiforms, together with a dermal shoulder girdle that is only 'weakly developed'. Long (1986, p. 335) 'proposed an alternative explanation that does not rely on out-group comparisons or assume knowledge of the hypothetical primitive condition. It is based on one assumption only: that the shoulder girdle armour was primitively absent in acanthodians (Denison 1979, p. 20) and that it developed only once within acanthodians, in climatiiforms.'

Brochoadmones milesi Bernacsek and Dineley, 1977, treated by us (Gagnier and Wilson in press) as a climatiiform lacking dermal shoulder girdle elements, represents another reason why the dermal component of the shoulder girdle in climatiiforms should not be considered to be a synapomorphy of the order. The present paper presents an additional reason: the existence of one, and possibly two, new genera of presumed Climatiiformes which also lack a dermal shoulder girdle. It now seems more likely than before that the dermal elements of the shoulder girdle are derived characters for both acanthodian fishes in general and for climatiiforms in particular, since both brochoadmonoids and *Cassidiceps* lack a dermal shoulder girdle, yet have other primitive acanthodian features such as multiple ventral intermediate spines and two dorsal fins. Brochoadmonoids also have presumably primitive, shark-like gill slits unencumbered by branchiostegals or other gill-cover elements.

Plate persistence following spine loss

Miles' (1973, p. 197) statement, 'I have concluded that a plate may persist following the loss of its spine (e.g. the anterior pinnal in *Brachyacanthus*, *Parexus*, and *Vernicomacanthus*), but I have found no evidence of a prepectoral spine surviving after the loss of its pinnal plate', must now be qualified. If, as now seems likely, prepectoral spines without associated dermal plates are more primitive than prepectoral spines with plates, the first part of Miles' statement has not been contradicted by the new evidence presented here. However, the condition of prepectoral spines persisting after loss of their plates, mentioned in the second part of the statement, would be difficult to distinguish from what we thank may be the real primitive condition: prepectoral spines existing prior to their supporting dermal plates, the condition exemplified by *Kathemacanthus*.

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THE DAWN OF THE VERTEBRATES: CHARACTERS VERSUS COMMON ASCENT IN THE RISE OF CURRENT VERTEBRATE PHYLOGENIES

by PHILIPPE JANVIER

ABSTRACT. Armoured fossil jawless fishes, or 'ostracoderms', have long been regarded as being ancestral to Recent hagfishes and lampreys. The latter were supposed to have lost the mineralized exoskeleton and undergone a 'degeneracy' linked with their burrowing or ectoparasitic modes of life. However, recent cladistic analyses suggest that most, if not all 'ostracoderms' are more closely related to jawed vertebrates than to either lampreys or hagfishes, although they are clearly jawless. These views are very similar to those expressed by the early British palaeontologists who made the first attempts at placing these extinct taxa in the classification of the vertebrates. The chaotic history of the phylogenetic position of the 'ostracoderms' seems to be due to varying approaches to the use of either characters or common ascent in phylogeny reconstruction.

ALTHOUGH not very attractive as fossils, the Palaeozoic jawless vertebrates, or agnathans, have always raised interest among both professional palaeontologists and the public. This may be because they often are bizarrely shaped animals, but it is certainly because they are supposed to tell us something about the origin of the vertebrates in general. Therefore, textbooks on vertebrate evolution may sometimes overlook some major fossil taxa, but Palaeozoic jawless vertebrates are always included. During the last 150 years the principal advances in this field of vertebrate palaeontology were triggered essentially by new material and methods which gave access to more characters, in particular those based on internal anatomy and histological structure. The discovery of such new major clades as the galeaspids, arandaspids and pituriaspids has also enriched our perception of the diversity of vertebrate taxa and revealed new character combinations. As well as this progress, the expected result of more thorough investigation of material, the rise of cladistic methodology has given a new analytical dimension to the debates on the interrelationships of these early vertebrates. There is still a wide diversity of opinions on 'basal' vertebrate phylogeny, but most current theories suggest that jawed vertebrates are more closely related to one particular agnathan taxon than to others, i.e. that jawless vertebrates are not a clade.

The purpose of this address is firstly, to highlight the role played by early British vertebrate palaeontologists in the rise of interest in these 'basal' vertebrates, and then to show how circumstances led to the development of a number of long-lived scenarios about their evolution, all these scenarios dependent on the way in which taxa are defined. Finally, I shall deal with propects; suggestions of investigations in this particular field, i.e. how to get more taxa and more characters.

RECENT AND FOSSIL VERTEBRATES: THE CLADES

Recent vertebrates (or craniates, depending on which theory of their interrelationships and nomenclature is accepted) comprise three major clades: the jawed vertebrates, or Gnathostomata, and two clades of jawless vertebrates, the Hyperotreti (hagfishes) and the Hyperoartia (Lampreys). As discussed below, the latter two clades have long been united in the taxon Cyclostomi Duméril,

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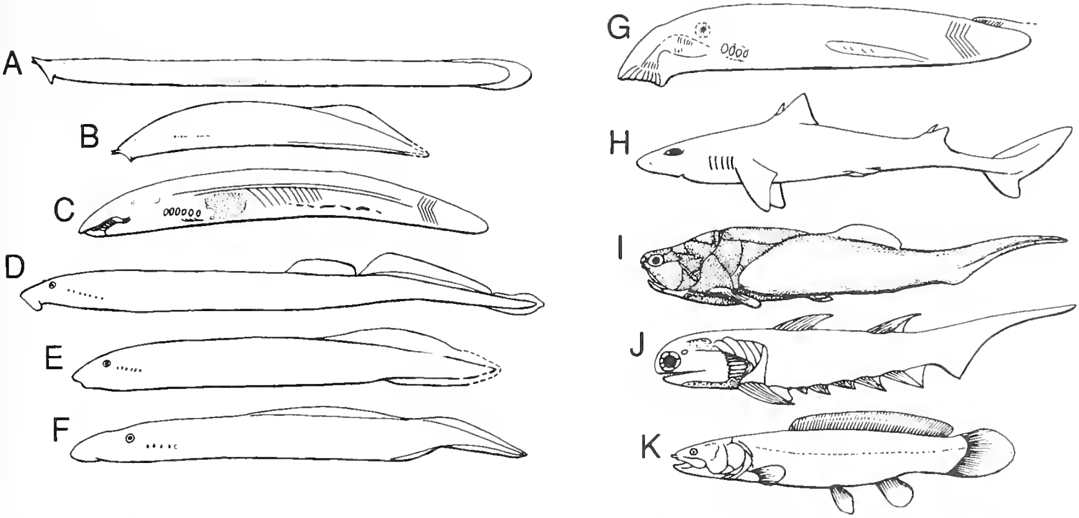
1806, which was subsequently treated as a clade by most authors (e.g. Jarvik 1981), until the late 1970s, by which time the numerous unique characters shared by lampreys and the gnathostomes were regarded as evidence for cyclostome paraphyly.

Lampreys and hagfishes are known as fossils from as early as the Carboniferous. All other jawless vertebrate taxa (except the conodonts if these are regarded as craniates) are pre-Carboniferous in age and, in contrast to lampreys and hagfishes, often possess a strongly calcified exoskeleton. They are, therefore, traditionally referred to as 'ostracoderms', a name erected initially by Aristotle for molluscs, but revived by Cope (1889) who used it to include the armoured jawless vertebrates known at that time. 'Ostracoderms' cannot be shown to be a clade but, for historical reasons, this name is still widely used in Britain and North America. After having fought for years against the use of this term, which is no better than 'pachyderms', I think it is time to surrender and make this concession to the Anglo–American tradition. 'Ostracoderms' range from the Early Ordovician to the Late Devonian (Late Frasnian). They were not recognized as jawless vertebrates until the end of the nineteenth century. Then, in the light of the rising Darwinian theory of evolution, their early age and potentially primitive (jawless) condition raised considerable interest among palaeontologists. This concept, that the presence of jaws was derived relative to their absence, was foreshadowed in early classifications or evolutionary trees based on Recent taxa only (Milne-Edwards 1844; Haeckel 1866). The fact that the earliest known fishes were apparently devoid of jaws gave palaeontological support for this theory. Only two major 'ostracoderm' taxa, the Osteostraci (cephalaspids) and Heterostraci (pteraspids) were defined initially by Lankester (1868), on the basis of the material from Britain referred to earlier as *Cephalaspis* by Agassiz (1835) and as *Pteraspis* by Kner (1847). The latter author, however, regarded the shields of *Pteraspis* as cephalopod shells, and it was Huxley (1858) and Lankester (1864) who showed that they were actually vertebrates, despite the acellular microstructure of the armour. Later, Traquair (1899, 1900) added the unarmoured Anaspida and Thelodonti (or 'coelolepids', which he thought were possibly related to sharks) and, in the second half of the twentieth century, several new major clades were discovered, such as the Silurian and Devonian Galeaspida (Liu 1965), the Ordovician Arandaspida (Ritchie and Gilbert-Tomlinson 1977) and the Devonian Pituriaspida (Young 1991). Many of the controversies about the relationships of the major 'ostracoderm' clades stem from the fact that some taxa (thelodonts, anaspids and heterostracans in their original sense, i.e. including the poorly known Ordovician forms) could not be defined by unique characters, and, consequently, were not taxa in the sense that cladists recognize. I shall thus briefly define and comment upon the terminal taxa that we can now recognize in a consideration of vertebrate or craniate phylogeny. All these taxa are craniates, since they share a head, comprising the skull, brain and sensory capsules, and a unique embryonic cell source, the neural crest, which gives rise to the formation of cells and tissues such as the pigment cells, dermal skeleton, gill arches and dorsal nerve ganglia. To date, the presence of the neural crest in hagfishes is only inferred from the presence of the tissues which, in other craniates, are known to be neural crest derivatives. Moreover, the presence of a neural crest in 'ostracoderms' is inferred from the presence of dermal skeleton (Smith and Hall 1991). In some non-mineralized fossils preserved as impressions, the presence of a skull is inferred from that of well-developed eyes (e.g. *Jamoytius*, *Euphanerops*, Conodonta).

1. *Hyperotreti* (*Pennsylvanian to Recent*; Text-fig. 1A–C)

Hagfishes are exclusively marine, slender-bodied fishes, characterized by a large, ventrolateral slime gland, four pairs of tentacles surrounding the mouth and nasal opening, and a duct leading from the oesophagus to the exterior on the left side only (the oesophago-cutaneous duct). In Recent hagfishes, the gill pouches are posteriorly placed and lie well behind the head. There are other characters which are unique to hagfishes, but many of them can be interpreted as general for craniates (e.g. aneural heart, single semicircular canal in the ear, fibrous braincase). Hagfishes display various conditions as to the number of gill openings. The Myxinidae possess a single pair of common gill openings whereas other hagfishes have up to 15 pairs of separate gill openings. The ontogeny of the Myxinidae suggests that separate gill openings is the general condition for the group. The only undoubted fossil (Pennsylvanian) hagfish known to date, *Myxinikela* (Bardack 1991; Text-fig. 1B), differs from extant forms in having a stouter body, a more extensive dorsal fin and a lancet-shaped caudal fin. This condition can be regarded as general for hagfishes on the basis of the palaeontological argument (i.e. the assumption that a character state found only in the geologically older members of a taxon is primitive, relative to the state found in the geologically younger or the Recent members of the same taxon). *Myxinikela* occurs in the same locality (Mazon Creek, Illinois) as another fossil, *Gilpichthys* (Bardack and Richardson 1977; Text-fig. 1C), which seems to display comb-shaped horny teeth and has been regarded by Janvier (1981*a*) as a possible fossil hagfish as well.

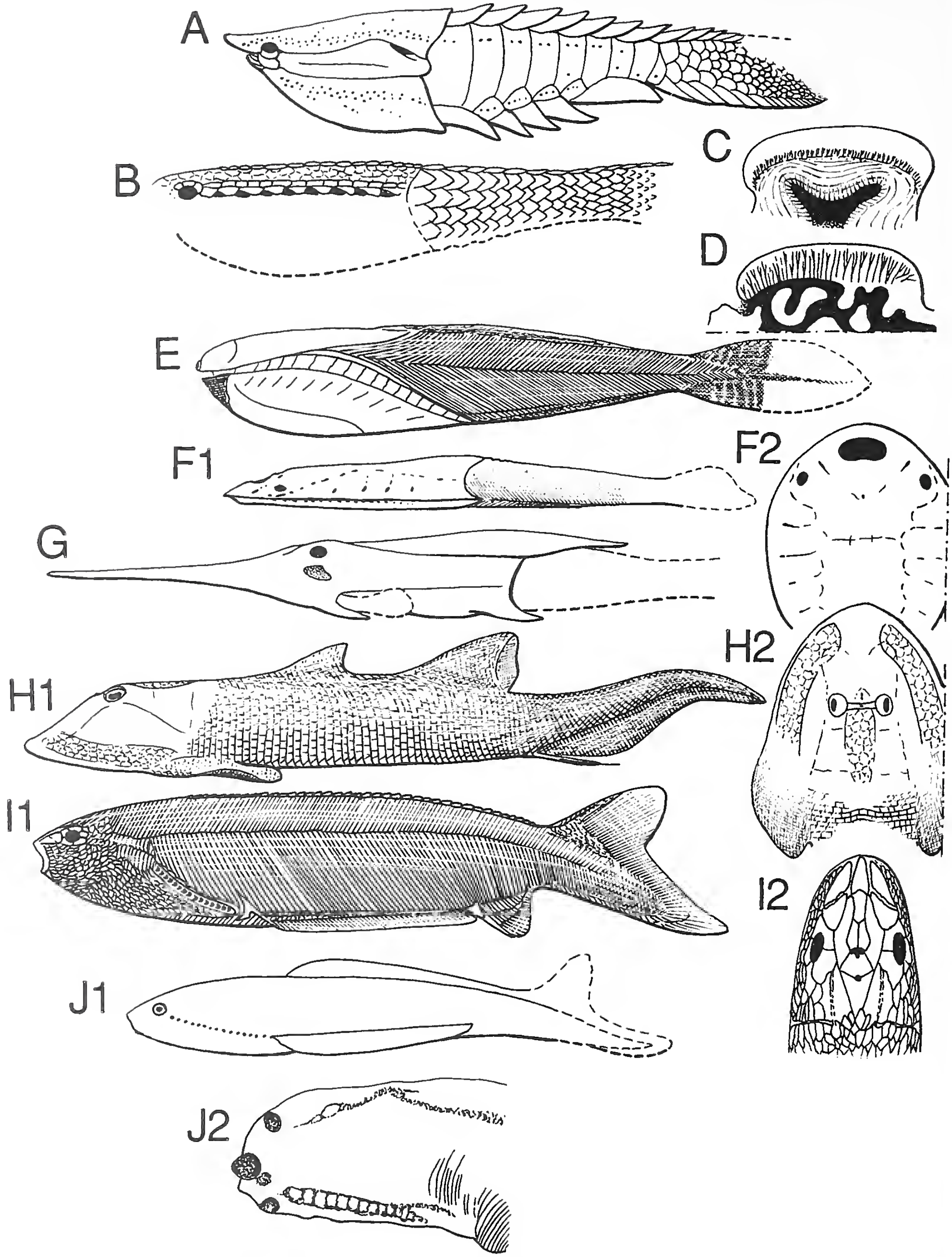


TEXT-FIG. 1. Representatives of the major fossil and Recent craniate taxa, in lateral view, not to scale. A–C, Hagfishes (Hyperotreti) or presumed hagfishes; A, the Recent hagfish *Eptatretus*; B, *Myxinikela*, Pennsylvanian of Illinois (from Bardack 1991); C, *Gilpichthys*, Pennsylvanian of Illinois (from Bardack and Richardson 1977). D–G, Lampreys (Hyperoartia) or presumed lampreys; D, the Recent lamprey *Petromyzon*; E, *Mayomyzon*, Pennsylvanian of Illinois (from Bardack and Zangerl 1971); F, *Hardistiella*, Late Mississippian of Montana (from Janvier and Lund 1983); G, *Pipiscius*, Pennsylvanian of Illinois (from Bardack and Richardson 1977). H–K, the four major gnathostome taxa. H, the Recent chondrichthyan *Squalus*; I, the placoderm (extinct) *Coccosteus* (based on Moy-Thomas and Miles 1971); J, the acanthodian (extinct) *Climatius* (based on Moy-Thomas and Miles 1971); K, the Recent osteichthyan *Amia*.

Since the discovery of the 'conodont animal' (Briggs *et al.* 1983), some authors have tried to revive the old idea that conodont jaw elements are comparable to the horny 'teeth' of hagfishes and that the two groups may be closely related (Krejsa *et al.* 1990). This interpretation had already been argued in the nineteenth century by H. C. Pander, the discoverer of conodonts. Notwithstanding a striking resemblance between the slender body shape of the 'conodont animal' *Clydagnathus* (Text-fig. 3D) and that of extant hagfishes, there is still no conclusive argument to support this relationship, either in the histological structure of the conodonts, or in the anatomy of the soft tissue preserved in the body imprint. The question of conodont relationships will be discussed below.

2. *Hyperoartia* (*Late Mississippian to Recent*; Text-fig. 1D–G)

Lampreys are either freshwater or anadromous eel-shaped fishes, characterized by a sucker surrounding the mouth and a complex rasping and sucking device, usually referred to as a 'tongue'. The latter differs from the 'tongue' of hagfishes in the presence of a piston cartilage which permits



TEXT-FIG. 2. Representatives of the major fossil craniate taxa, not to scale. A, the Early Devonian heterostracan *Anglaspis* (based on Blieck and Heintz 1983); B, the Late Ordovician astraspid *Astraspis* (based on Elliott 1987); C, a vertical section through a tubercle of the presumed astraspid *Pycnaspis* (based on Ørvig 1989);

anteroposterior movement of the entire apparatus. Other characters, which are unique among extant craniates, are the dorsal position of the nasohypophysial opening and the cartilaginous spine-shaped processes on the branchial arches. The dorsally placed nasohypophysial opening can be regarded as a more general condition when fossils are considered. In their life history, lampreys have a larval stage and undergo a metamorphosis. All extant lampreys have seven separate branchial openings.

The three fossil lampreys known to date are *Hardistiella* (Late Mississippian; Text-fig. 1F), *Mayomyzon*, and probably *Pipiscius* (both Middle Pennsylvanian; Text-fig. 1E, G). They are small forms (*c*. 50–100 mm in length) and are found in shallow water marine sediments. Only *Pipiscius* displays a typical sucker armed with horny plates, and only *Mayomyzon* displays a piston cartilage (Bardack and Zangerl 1971; Bardack and Richardson 1977). *Hardistiella* is poorly preserved but appears to retain an anal fin (Janvier and Lund 1983), whereas all other fossil and extant lampreys have no anal fin. The anal fin may reappear in some abnormal individuals of *Petromyzon marinus* (Vladykov 1973). These fossil lampreys differ from extant ones essentially in that their branchial apparatus is situated closer to the skull and may have contained only six gill pouches.

3. *Gnathostomata* (*Llandovery to Recent*; Text-fig. 1H–K)

The jawed vertebrates, or gnathostomes, have a large number of unique characters, such as jaws, medially placed and jointed gill arches, horizontal semicircular canal, united spinal nerve roots, myelinated nerve fibres, etc. There is no reason to interpret these unique characters as general for craniates (and subsequently modified in lampreys and hagfishes) and the Gnathostomata can reliably be regarded as a clade, despite its great diversity. Among extant craniates, only the gnathostomes possess a calcified skeleton. There is, however, a considerable debate as to which Recent or fossil gnathostome displays the most generalized condition for this clade. Using gnathostomes as a single terminal taxon in any cladistic analysis means that many characters, such as scales, unpaired fin structure, or organization of the exoskeletal skull, would be scored as polymorphic. Chondrichthyans (Text-fig. 1H) are often used to reconstruct the morphotype of the gnathostomes, essentially because of the supposedly generalized microsquamose condition of their exoskeleton (i.e. simple, non-growing placoid scales derived from a single odontode). There is, however, no guarantee that this condition is general for either the chondrichthyans or the gnathostomes. The extinct placoderms (Text-fig. 1I), for example, may be the sister-group of all other gnathostomes (Young 1986) and the exoskeleton is always macromeric or macrosquamose (i.e. composed of large dermal plates and compound, growing scales) as in the fossil acanthodians and the osteichthyans (Text-fig. 1J–K). In this review, however, I have scored each state for scale morphology (microsquamose and macrosquamose) as present in the gnathostomes.

4. *Heterostraci* (*Late Llandovery to Frasnian*; Text-fig. 2A)

Heterostracans are exclusively fossil jawless craniates, which possessed a calcified exoskeleton and are characterized by a single, common external branchial opening on either side. This character is admittedly not unique among craniates, and occurs in the hagfish family Myxinidae and in all major

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D, vertical section through a tubercle of *Eriptychius*, Late Ordovician (based on Ørvig 1989); E, the Ordovician arandaspid *Sacabambaspis* (after Gagnier 1993*a*); F, the Early Devonian galeaspid *Polybranchiaspis* in lateral view (F1) and dorsal view of head (F2, based on Liu 1965); G, the Early-middle Devonian pituriaspid *Pituriaspis* (based on Young 1991); H, the Silurian osteostracan *Ateleaspis* in lateral view (H1) and dorsal view of head (H2, based on Ritchie 1967); I, the Silurian anaspid *Pharyngolepis* in lateral view (I1; from Ritchie 1964) and dorsal view of head (I2); J, the Early Silurian *Jamoytius* reconstructed in lateral view (J1, from Ritchie 1968) and sketch of a head in a specimen showing the 'branchial basket' (J2, from Ritchie 1984).

gnathostome taxa, the placoderms, holocephalan chondrichthyans, some acanthodians and all osteichthyans. However, considering heterostracans as most closely related to any one of these taxa (as did Stensiö, 1927, with hagfishes) would be unparsimonious with respect to many other characters and would imply too many homoplasies (i.e. it would imply that either hagfishes or the gnathostomes are not clades, or that heterostracans underwent many reversals on other characters).

5. *Astraspida* (*Caradoc to ?Early Llandovery*; Text-fig. 2B–C)

Astraspids, in which I include only *Astraspis* (Text-fig. 2B) and possibly *Pycnaspis* (Text-fig. 2C; if different from the former), are characterized by a dermal ornamentation of large, costulated tubercles made of a thick, glassy enameloid cap. This cap rests directly on the underlying acellular bone, or aspidine, although *Pycnaspis* may show a thin, intervening layer of dentine or mesodentine (Ørvig 1989). Other characters met with in *Astraspis* (polygonal dermal units, longitudinal ridges on the dorsal shield, separate gill openings, large body scales) have a higher degree of generality. Astraspids have long been regarded as heterostracans on the basis of the acellular structure of their exoskeleton, but it is now clear that they differ from the latter in retaining separate external gill openings (Elliott 1987) and that the acellular exoskeleton is more general, as it occurs also in anaspids, galeaspids, and thelodonts.

6. Eriptychius (*Caradoc*; Text-fig. 2D)

This genus has sometimes been associated with astraspids, essentially because they occur together in some North American Ordovician localities and share a dermal armour composed of polygonal platelets. However, *Eriptychius* clearly differs from astraspids in its histological structure, its tubercles being made up of a peculiar type of dentine with large tubules (Ørvig 1989). Whether or not this is mesodentine is uncertain, but it clearly differs from the thin-tubuled orthodentine of heterostracans. *Eriptychius* possesses a partly calcified endoskeleton made up of globular calcified cartilage and pervaded by a network of vascular canals, the walls of which are possibly lined with perichondral bone (Denison 1967).

7. *Arandaspida* (*?Arenig to Ashgill*; Text-fig. 2E)

Arandaspids are characterized by the extreme anterior position of the eyes, which are housed in an elliptical notch of the dorsal dermal shield. All the other characters that they show (oak leaf-shaped tubercles, elongated body scales, large ventral and dorsal exoskeletal 'discs', numerous branchial plates and gill openings, paired pineal opening (if correctly interpreted), tesserae in exoskeleton, cancellar (honeycomb-like) layer of exoskeleton also occur in other taxa. Arandaspids occur essentially in the Llandeilo and Caradoc of Australia, Bolivia, and Argentina, with the genera *Arandaspis*, *Porophoraspis*, *Sacabambaspis*, and perhaps *Andinaspis*, but fragments of arandaspid-like dermal armour occur in Australia from the Arenig to the Ashgill (Young *in* Shergold 1991). They are thus the earliest known undisputed vertebrates.

8. *Galeaspida* (*Llandovery to Famennian*; Text-fig. 2F)

Galeaspids are characterized by large sensory-line canals arranged in a scalloped pattern in the dorsal exoskeleton of the head. These canals lie partly below the level of the exoskeleton and open only at their distal ends and through a few slits (there are no series of sensory-line pores). Another galeaspid character is the dorsal position of the median opening for the prenasal sinus, into which open the olfactory organs, and which communicates ventrally with the oralobranchial cavity (Text-fig. 2F2). However, and notwithstanding the differences in the organization of the nasohypophysial complex, a comparable condition occurs also in lampreys and osteostracans (Text-fig. 2H2), although here the prenasal sinus is continued backwards by a blind hypophysial tube and does not communicate with the underlying oralobranchial cavity. The galeaspid condition may be general relative to that of either osteostracans or lampreys. Galeaspids are known exclusively from China (including Tarim) and Vietnam and seem thus to be endemic to the North and South China continental blocks.

9. *Pituriaspida* (*Emsian to Eifelian*; Text-fig. 2G)

Pituriaspids are known only by a few poorly preserved head-shields from a single locality in Queensland, Australia (Young 1991). Two genera have been recognized, *Pituriaspis* and *Neeyambaspis*, but only *Pituriaspis* shows interpretable morphology. It resembles osteostracans in the overall shape of the head-shield, but is devoid of cephalic fields and a dorsal nasohypophysial opening. The position of the nasal openings is still unknown, but is assumed by Young (1991) to have been situated on the ventral side of the shield, anterior to the mouth. As well as the elongated rostral process, which is known to occur also in some osteostracans (e.g. Boreaspididae) and galeaspids (e.g. Hunnanaspidiformes), the only unique character of the Pituriaspidida is a peculiar pit lying ventrally to each orbit, but these do not communicate with the underlying oralobranchial cavity.

10. *Osteostraci* (*Wenlock to Frasnian*; Text-fig. 2H)

Osteostracans are characterized by paired and median depressions in the dorsal surface of the head endoskeleton, which are linked to the labyrinth cavity by means of large, branching canals. These structures have been variously interpreted as dynamo-sensory or electric organs, but neither of these interpretations is fully satisfactory. Another osteostracan character is the ventral, leaf-shaped horizontal lobe which underlies the caudal fin web, and may possibly be a modified anal fin. However, this horizontal lobe is lacking (supposedly lost) in some osteostracans (Tremataspididae). Other characters met with in osteostracans (dorsal nasohypophysial opening, blind hypophysial tube, paired pectoral fins, epicercal caudal fin, tessellate exoskeleton) may have a higher degree of generality.

11. *Anaspida* (*Llandovery to Přídolí*, Text-fig. 2I)

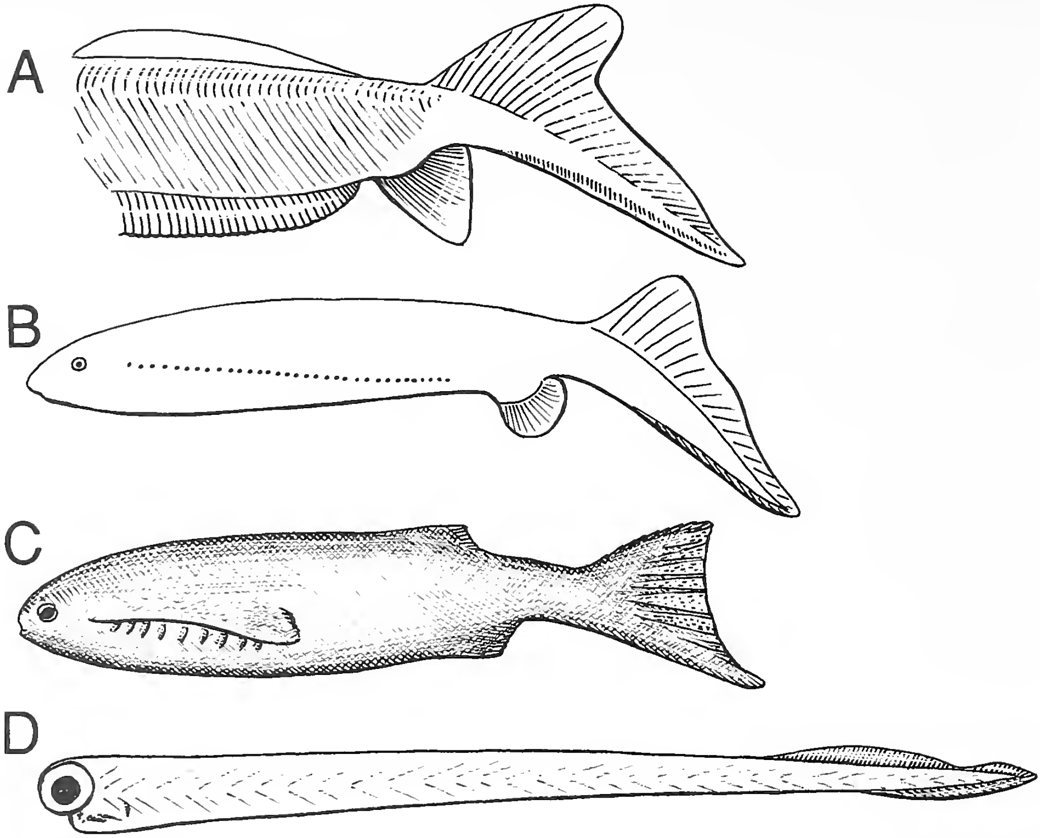
Anaspids are characterized by large triradiate scales or spines, situated behind the series of external branchial openings. Other characters currently used to define anaspids (e.g. strongly hypocercal tail, elongated body scales, presumed dorsal nasohypophysial opening, paired fins, acellular dermal skeleton) have a higher degree of generality. It has been suggested that the lack of a dorsal fin and the presence of a series of enlarged median dorsal scutes are unique to anaspids, but these characters also occur in heterostracans, advanced osteostracans, and some advanced galeaspids.

12. Jamoytius (*Llandovery to ?Early Devonian*; Text-fig. 2J)

Jamoytius has variously been interpreted as the most generalized craniate, a naked anaspid, or a lamprey. It is non-mineralized, preserved in the form of organic films, and shows no unique characters. It is only defined by an association of characters which are unique for this period: nakedness and lamprey-like body with paired fins. If restricted to the material of *J. kerwoodi* from Scotland, it is probably a clade. It is uncertain whether the Early Devonian material from New York referred to by Janvier and Busch (1984) as a '*Jamoytius*'-like craniate belongs here.

13. Endeiolepis (*Frasnian*; Text-fig. 3A)

Endeiolepis is characterized by a peculiar, undulating, ventrolateral series of weakly mineralized 'scales'. It shares with anaspids a strongly hypocercal caudal fin. Although often regarded as an anaspid, it shows no evidence of triradiate postbranchial spines.



TEXT-FIG. 3. Reconstructions of the representatives of the major fossil craniate taxa, not to scale. A, the Late Devonian *Endeiolepis* (head virtually unknown; from Arsenault and Janvier 1991); B, the Late Devonian *Euphanerops* (based on Arsenault and Janvier 1991); C, the Silurian thelodont *Loganellia* (modified from Turner 1991); D, the Carboniferous conodont *Clydagnathus* (based on Aldridge *et al.* 1993).

14. Euphanerops (Frasnian; Text-fig. 3B)

Euphanerops is also an 'anaspid-like' craniate, with a strongly hypocercal tail and a probably non-mineralized or weakly mineralized exoskeleton. It possesses an astonishingly long 'branchial basket' with more than 30 gill units. *Legendrelepis* (Arsenault and Janvier 1991) occurs at the same locality as *Euphanerops* (Miguasha, Quebec), and closely resembles the latter (they may well be synonyms). Despite the fact that numerous gills occur in another unrelated genus (*Jamoytius*), one may provisionally consider that *Euphanerops* and *Legendrelepis* form a clade.

15. *Thelodonti* (*Latest Ordovician to Frasnian*; Text-fig. 3C)

Thelodonts are represented by an ensemble of forms whose exoskeleton consists of minute scales, sometimes fused side-by-side near the gill openings and around the orbits. Each of these scales is supposed to correspond to a single papillary unit, or odontode. Although thelodont scales occur in abundance in marine sediments, the overall shape of the entire animal is known only from a few specimens from Scotland, Estonia and Canada, and provides evidence for a rather wide range of form, some animals being flat-bodied and others deep-bodied (Turner 1991; Wilson and Caldwell 1993). Turner (1991) considered the thelodonts to be monophyletic on the basis of the anchoring devices (processes) around the roots of the scales. This character, however, is not general to all thelodont scales. Other authors (Karatayute-Talimaa 1978; Janvier 1981*a*) considered that thelodonts do not represent a clade but include microsquamose members of other taxa (possibly stem-heterostracans, stem-galeaspids, stem-anaspids, and even stem-gnathostomes). Some thelodonts are unique among jawless craniates in having internal denticles lining the pharynx, like the gnathostomes (Van der Brugghen and Janvier 1993). Most thelodonts have a hypocercal tail (Text-fig. 3C) but some forms have an apparently diphycercal tail (Wilson and Caldwell's 'fork-tailed thelodonts') which is similar to that of heterostracans and may support the idea that some thelodonts are stem-heterostracans. One must, however, keep in mind that this type of diphycercy is only superficial, since the notochord was probably prolonged into the ventral lobe, as in hypocercal thelodonts.

16. *Conodonta* (*Late Cambrian to Triassic*; Text-fig. 3D)

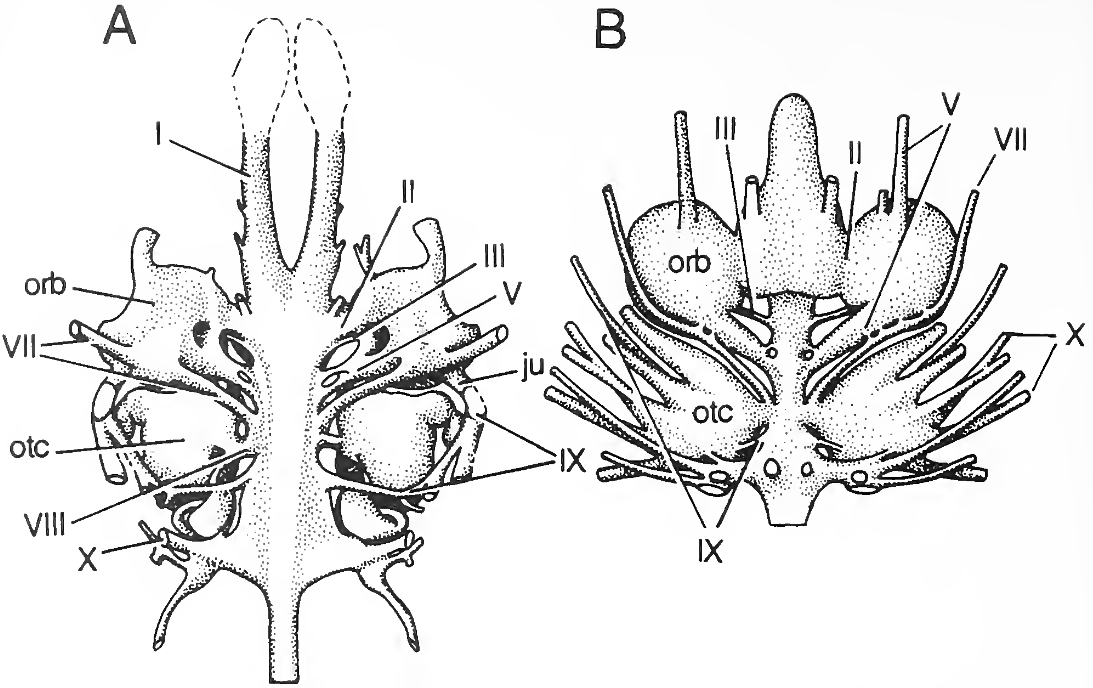
The controversy about the vertebrate affinities of the conodonts continues, following the discovery of the first articulated 'conodont animal' (Briggs *et al.* 1983). Although I have long been among the sceptics, I admit that there is now impressive evidence for the vertebrate affinities of this group, in particular the chevron-shaped myomeres, median fin with radials, and the large eyeballs. The histological structure and the organization of the conodont elements remains ambiguous, although they are likely to have contained osteocytes or odontocytes. In other respects, the conodont elements seem to represent a highly specialized feeding device, with no clear homologue in other craniates. At any rate, the vertebrate or craniate affinity of the conodonts can be accepted only for the para- and euconodonts, the protoconodonts being almost certainly of a different nature (Aldridge *et al.* 1993).

VERTEBRATE CLASSIFICATION AND INTERRELATIONSHIPS: HISTORICAL ACCOUNT

There are various ways of considering the history of theories about fossil and Recent vertebrate interrelationships, but here I shall divide it into four periods: from Agassiz (1835) to Cope (1889), Cope to Stensiö (1927), Stensiö to Lovtrup (1977), and Lovtrup to the present.

During the first of these four periods, Recent jawless vertebrates (or cyclostomes), first regarded as either 'degenerate' fishes or intermediate in some way between some invertebrates (e.g. worms) and fishes, became progressively considered as an early offshoot from the vertebrate tree. Their jawlessness was acknowledged as primitive, but their single nostril and pouch-shaped gills were viewed as specializations. The only fossil forms known during this period were osteostracans and heterostracans, almost unanimously regarded as peculiar bony fishes, possibly related to sturgeons and catfishes. Only a few authors, such as Schmidt (1866) alluded to the possible presence of a single, median olfactory organ in osteostracans, and compared it with the condition in lampreys, with no further bearing on their systematic position. The advent of Darwinian evolutionary theory, which had a significant influence on the interpretation of other fossil taxa (e.g. sarcopterygians), had no major impact on the interpretation of these early forms. The only consequence was that they supported T. H. Huxley's opinion that bony fishes were very ancient (Huxley 1861).

The second period began with a note on vertebrate classification by Cope (1889), where all the fossil vertebrates in which no evidence of jaws had been found (i.e. osteostracans, heterostracans, and also antiarchs, a group of placoderms which later turned out to have jaws) were placed in a taxon 'Agnatha', along with hagfishes and lampreys. Contrary to Agassiz, Huxley, and Lankester, who referred osteostracans and heterostracans to osteichthyans on the basis of characters (large bony scales and dermal bones, fin rays), Cope defined his 'Agnatha' on the basis of the absence of



TEXT-FIG. 4. Ventral aspect of the internal cast of the cavities and canals of the braincase of the placoderm *Macropetalichthys* (A, from Stensiö 1969) and the osteostracan *Nectaspis* (B, from Janvier 1981*b*), to show the basically similar relationships between the main cranial nerves and the sensory capsules. I–X, cranial nerves; ju, dorsal jugular vein; orb, orbital cavity; otc, otic capsule.

gnathostome characters. By erecting such a 'non-group', Cope hindered our understanding of vertebrate interrelationships.

The following period was a period of controversies. Firstly, Traquair (1899, 1900) described two new 'ostracoderm' taxa, the Thelodonti and Anaspida. He regarded the minute, placoid-like scales of thelodonts as evidence for a relationship between 'ostracoderms' and sharks. Goodrich (1909) remained convinced that osteostracans were bony fishes, but he was inclined to accept Traquair's views that 'pteraspidomorphs' (i.e. heterostracans and thelodonts) were related to sharks. A third ensemble was that of Cope, including Dean (1895) and later Woodward (1898), who considered that all 'ostracoderms' were definitely jawless. This period shows little consideration for characters, but instead a great desire for scenarios of anatomical transformation and adaptation, owing to the burgeoning enthusiasm for evolutionary theories (the two review articles by Kemna (1903, 1904) reflect precisely the kind of debates taking place and questions being asked during this period). This period ended with a major discovery by Kiaer (1924), who showed that anaspids possess a median opening on the dorsal surface of the head (Text-fig. 2I2), anterior to the pineal opening, which he regarded as a nasohypophysial opening, similar to that of lampreys. He also extended this interpretation to osteostracans, though with some reservation. In contrast, Kiaer considered that heterostracans possessed two separate olfactory organs, as in the gnathostomes. He thus classified vertebrates into two taxa, the Monorhina (anaspids, osteostracans, lampreys, and hagfishes) and the Diplorhina (heterostracans, thelodonts, and gnathostomes), thereby implying that jawlessness is not a character and cannot define a taxon.

A few years later, Stensiö (1927) opened the third period with a major work on the Devonian osteostracans from Spitsbergen. By using Sollas' grinding section method, Stensiö unravelled the internal anatomy of the endoskeletal cephalic head shield of osteostracans, and thereby confirmed the striking resemblance of the cavities in their ethmoid region with the nasohypophysial complex of lampreys. Although he had described a few years earlier (Stensiö 1925) the internal anatomy of the skull of an early gnathostome, the placoderm *Macropetalichthys*, he does not seem to have been impressed by the striking resemblance (which he may have considered as a general craniate condition) between the organization of the cranial nerves of this placoderm and that of osteostracans (Text-fig. 4). On the contrary, he focused on a point-by-point comparison with the anatomy of lampreys and pointed out some resemblances between the these two taxa, some of which are merely general vertebrate characters. The massive, perichondrally ossified head-shield of osteostracans was regarded by Stensiö as a general vertebrate character, remaining in lampreys in the form of the muco-cartilage of the ammocoete larva. The radically different skull of adult lampreys, made up of cartilaginous bars and plates, was thus viewed by him as the result of a 'degeneracy' or 'regression'. The same skeletal regression had been invoked by him (Stensiö 1925) to justify the evolution of sharks from placoderms. Today, Stensiö would probably have invoked heterochrony or paedomorphosis to justify such a difference between fossil and modern forms. Clearly, all of Stensiö's reasoning was strongly influenced by one character, the dorsal nasohypophysial opening. He then adapted other, less convincing, characters (e.g. the asymmetry of the dorsal aortic groove or of the habenula) to his initial theory. I shall leave aside the heated debates engendered by Stensiö's interpretation of the cranial nerves in osteostracans, linked with the premandibular arch theory. Since osteostracans displayed the earliest known vertebrate internal anatomy, they had to be primitive and thus meet the expectations of such embryology-based theories on head segmentation. Later studies on osteostracans have shown that there is no reason to believe that they possessed a visceral arch anterior to the mandibular arch. Their branchial organization was probably quite similar to that of larval lampreys (Whiting 1977; Janvier 1985). Having grouped osteostracans and anaspids with lampreys in the taxon Cephalaspidomorphi, on the basis of the dorsal position of the naso-hypophysial opening, Stensiö was left with hagfishes, whose nasohypophysial region is quite different from that of lampreys. In particular, the nasohypophysial duct communicates posteriorly with the pharynx (nasopharyngeal duct) and the median 'nostril' (nasohypophysial opening) has a terminal position. He thus suggested that hagfishes were related to heterostracans (including the thelodonts) and *Palaeospondylus* (an enigmatic fossil now regarded as a larval sarcopterygian) in the taxon Pteraspidomorphi, initially with some reservation and on very tenuous grounds (the pair of common external branchial openings of *Myxine*, and the vague resemblance between the embryos of *Eptatretus* and the shield of pteraspids). In subsequent works, Stensiö (1932, 1964, 1968) added more conviction to this suggestion and the poorly known internal anatomy of heterostracans was interpreted to match that of hagfishes. The Recent cyclostomes were thus diphyletic when considered together with the fossil jawless vertebrates, i.e. their nakedness, 'rasping tongue', and elongated body shape were viewed as homoplastic. For Stensiö, however it was absolutely clear that all known fossil and Recent agnathans formed a clade (Stensiö 1927, fig. 103), and thus that none of them could be regarded as more closely related to the gnathostomes than to other agnathans. This was the generally accepted view at that time, and was validated by the structure of the branchial apparatus in agnathans, where the endoderm-derived gills were situated medially to the gill arches. This condition was regarded as irreconcilable with that in the gnathostomes, where the gills are derived from the ectoderm and are lateral to the gill arches. Whether one or the other of these two conditions could be general for all craniates was, however, never questioned, and Jarvik (1980, 1981) still considered agnathans and gnathostomes to be two sister-clades that arose from a hypothetical gill-less ancestor. Although many palaeontologists rejected Stensiö's theory that hagfishes are relatives or descendants of heterostracans, there was a consensus that agnathans were a 'natural group'. Some evolutionary 'spindle' diagrams, however, often showed heterostracans as arising slightly closer to the gnathostomes (e.g. Romer 1945), essentially because of their restored paired olfactory organs, but also mainly because of their lack of cephalaspidomorph characters. It is unclear how important the weight of Cope's taxon 'Agnatha' may have been to this way of considering 'ostracoderms' in craniate phylogeny, but the history of palaeontology shows many similar instances (e.g.

Crossopterygii, Dinosauria, Condylarthra, etc.), where groups based on overall, presumed primitive, resemblance may sit like monoliths and hinder further research for years.

Until the late 1970s, very little changed in the phylogenetic position of the various 'ostracoderm' groups, apart from debates about the affinities of heterostracans which, while retaining their 'agnathan' status, were preferably put closer to the gnathostomes by Russian and some Anglo–American authors (e.g. Halstead 1973, 1982; Novitskaya 1983; see also review in Janvier and Blieck 1993). Those who did not accept the heterostracan-hagfish relationship generally regarded cyclostomes as either a clade characterized by a 'rasping tongue' and pouch-shaped gills, but nevertheless derived from some ostracoderms, or closely allied to anaspids and osteostracans only. The discovery of the galeaspids in China raised some interest but this new group was soon 'shoe-horned' either into the Cephalaspidomorphi (Janvier 1975) or the Heterostraci (Moy-Thomas and Miles 1971). Halstead (as Tarlo 1967) was the first to recognize them as clade, yet within the Cephalaspidomorphi. In the same way, the first arandaspids described by Ritchie and Gilbert-Tomlinson (1977) were regarded as just a new order (Arandaspidiformes) of the Heterostraci. In sum, by the mid-1970s, the widely used taxon Agnatha was still defined by its common ascent from some supposedly agnathous ancestral vertebrate, and not by characters.

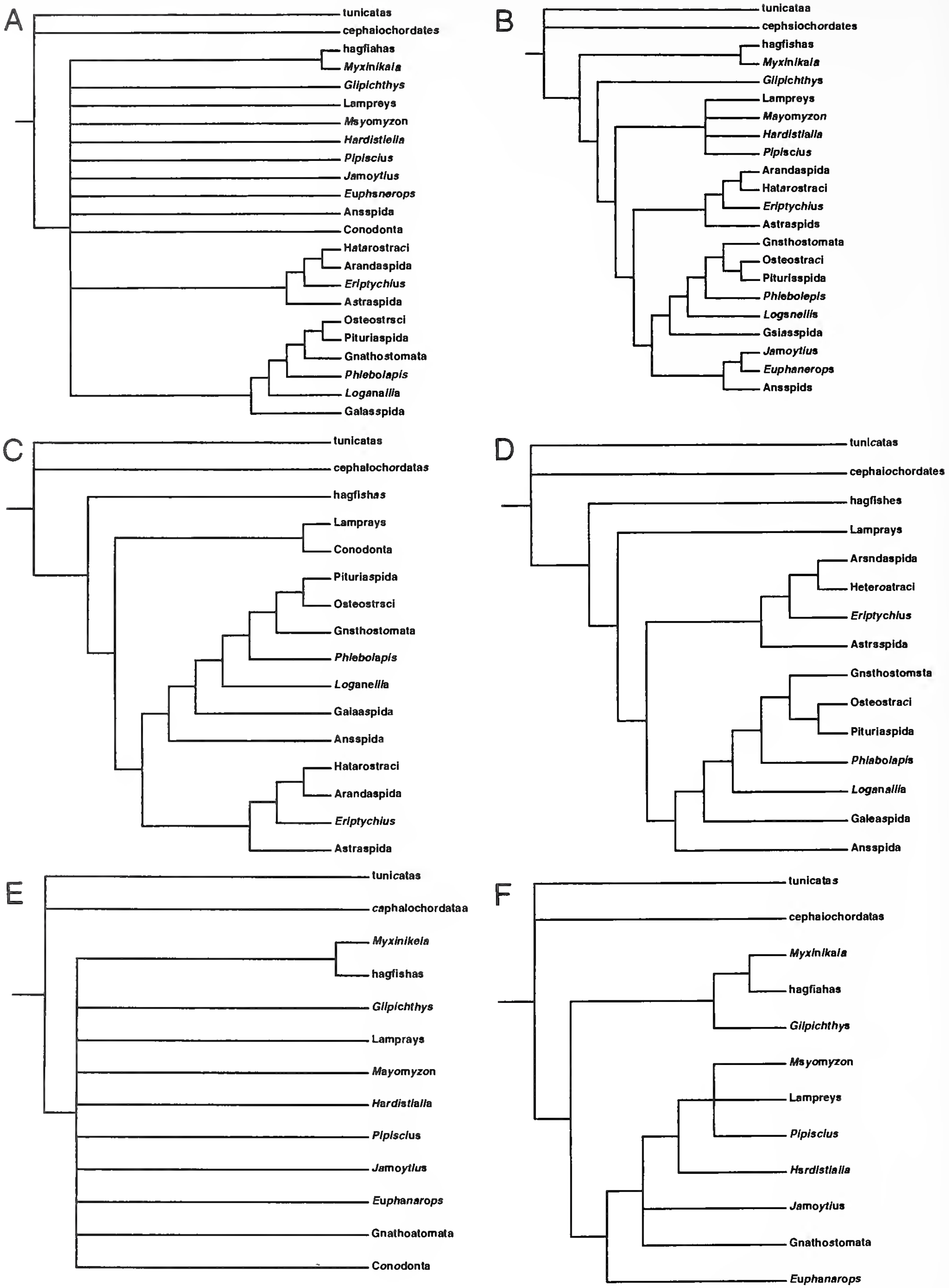
At the end of this third period, some biologists working on Recent lampreys and hagfishes began to consider hagfishes as the 'most primitive vertebrates' (see e.g. Brodal and Fänge 1963), essentially because of their numerous physiological and biochemical peculiarities. This was also the era when phylogenetic systematics, now know as cladistics, began to develop, in particular among lower vertebrate specialists. Løvtrup (1977) opened the fourth period by publishing a cladogram in which lampreys were shown to be more closely related to the gnathostomes than to hagfishes. This was the first clear attempt at breaking through the 'agnathan barrier'. He was immediately followed by a number of biologists and also some palaeontologists. Janvier (1981) suggested that the name Vertebrata should be used only for the taxon including some fossil taxa, lampreys and the gnathostomes, all of which possess vertebral elements (arcualia), and the taxon Craniata would include hagfishes and the Vertebrata, all of which possess a skull. Although many biologists and palaeontologists considered that this solution solved some problems (i.e. it avoids assumptions about the 'degeneracy' of hagfishes') they were reluctant to accept the conclusions of character distribution and break through other barriers, such as that of the Cephalaspidomorphi. It took nearly six years for me (Janvier 1978, 1981, 1984; see also Forey and Janvier 1993) to accept that the characters shared only by osteostracans and the gnathostomes (cellular bone, epicercal tail, pectoral fins, etc.) had not been lost by lampreys and, consequently, that cephalaspidomorphs are either paraphyletic or diphyletic. In these first cladograms published in the mid-1980s, lampreys are still assumed to have lost their paired fins and exoskeleton, being the sister-group of anaspids or osteostracans. However, the suggestion that the naked Silurian form *Jamoytius* may be either the closest relative of lampreys (Forey and Gardiner 1981) or 'intermediate' between anaspids and lampreys (Ritchie 1968, 1984) implied that the loss of exoskeleton, if any, must have occurred very early. The addition of yet another new taxon, the pituriaspids (Young 1991), and better knowledge of the arandaspids (Gagnier 1993*a*), galeaspids (Wang 1991), and thelodonts (Turner 1991; Van der Brugghen and Janvier 1993) allowed researchers to make larger and more complete data matrices and produce cladograms and trees that implied that it was less and less likely that lampreys had undergone some skeletal regression. One may see this fourth period as ending with the publication of a cladogram by Gagnier (1993*b*), where all 'ostracoderms' are placed more crownward than lampreys, implying thus that lampreys never possessed paired fins nor exoskeleton. This solution has recently been accepted by Forey and Janvier (1994) and Forey (1995). In other words, 'ostracoderms' would be stem-group gnathostomes.

This brief review of the research on vertebrate or craniate phylogeny shows, as usual, that theories about relationships are supported and defended for a time, by means of *ad hoc* explanations involving preservation, evolutionary scenarios (assumptions about common ancestry, paths of character evolution and/or character reversions), and they collapse suddenly when they go too far beyond the bounds of parsimony. Their fall is often caused by the discovery of new taxa and new assemblages of characters, and also by a cold look at characters, as free as possible from assumptions about transformation processes.

'OSTRACODERMS' AND CRANIATE PHYLOGENY: CURRENT PROBLEMS

Future tasks in research on vertebrate or craniate phylogeny are obviously to test this latest phylogeny by using other characters, or by finding new associations of characters in new or still poorly known taxa, such as galeaspids, pituriaspids and thelodonts. To begin with, however, the first task is to settle more clearly the question of the interrelationships of extant taxa, i.e. hagfishes, lampreys and the gnathostomes. Lovtrup's 'vertebrate theory' (the Vertebrata being composed of the lampreys and gnathostomes alone) is fairly well supported by anatomical and physiological characters (Hardisty 1982), but molecular sequence data still provide ambiguous results (Stock and Whitt 1992; Lecointre 1994), which depend on the out-group used in the analysis (those generally used are the cephalochordates or tunicates). There are admittedly some characters shared by hagfishes and lampreys which cannot clearly be proved to be general craniate characters. The most impressive of these is the complex musculature and skeleton of the 'lingual' apparatus, which acts to move the horny teeth back and forth. The resemblance in structure between the 'tongue' of hagfishes and lampreys suggests homology (Yalden 1985), although that of hagfishes is certainly more simple than that of lampreys. The mechanism of the hagfish 'tongue' may represent a general craniate condition, further modified in lampreys, and lost in the gnathostomes. However similar this organ may look in hagfishes and lampreys, this potential homology is outnumbered by many other characters shared by lampreys and the gnathostomes, and which cannot be rejected by means of an appeal to either convergences (in lampreys and gnathostomes), or reversions due to 'degeneracy' (in hagfishes). Whatever the status of the cyclostome versus vertebrate problem, this does not influence the relationships between 'ostracoderms' and the gnathostomes if these are regarded as a clade, characterized by, for example, the ability to produce a dermal skeleton.

The major problem in this phylogeny reconstruction is the heterogeneity of the available characters. The characters used in elucidating the interrelationships of extant craniates concern essentially the soft tissue anatomy and physiology, whereas histological and morphological characters of hard tissues are widely used when fossils are considered. Moreover, 'ostracoderms' display very few informative characters: that is, those that are not either unique characters of the terminal taxa, or general craniate or vertebrate characters. As an example of this problem, the conodonts display some general characters of the myomerozoans (i.e. craniates + cephalochordates), craniates or vertebrates, such as the chevron-shaped myomeres, the notochord, and the large eyes, respectively, along with unique characters, such as the morphology and histology of the conodont elements. Only the presence of a phosphatic dermal skeleton with possible dentine or bone cells (osteocytes or odontocytes) is shared only by the conodonts, osteostracans, and the gnathostomes. Also, some anatomical characters are known to some extent in some taxa, as a result of good conditions of fossilization or to extensive endoskeletal ossification, whereas their homologue in other taxa is known only from impressions or indirect evidence. The olfactory organs and associated hypophysial region, for example, are important character-bearing structures and are reasonably well known in osteostracans and galeaspids but not known, or poorly so, in anaspids, arandaspids, astraspids, heterostracans and thelodonts. This imbalance in the quality of the characters is perhaps worse than mere question marks (missing data) in a data matrix, since each palaeontologist has his own propensity to follow one or another interpretation, inferred from such tenuous evidence as impressions of the internal surface of the exoskeleton or poorly defined tarry imprints. This is a general problem with fossils, but here it becomes crucial, due to the paucity of the available characters. Such questions as whether arandaspids have two separate external nostrils, whether anaspids have a dorsal nasohypophysial opening, or whether thelodonts and heterostracans have a nasopharyngeal duct are subjects of controversies but have decisive bearings on the resulting phylogeny. A solution would be to use exclusively histological characters of the dermal skeleton, which are a widespread source of data in 'ostracoderms', but this requires assumptions about the


A
tunicates
cephalochordates
hagfishes
Myxinikela
Gilpichthys
Lampreys
Mayomyzon
Hardistiella
Pipiscius
Jamoytius
Euphanerops
Anaspida
Conodonta
Heterostraci
Arandaspida
Eriptychius
Astraspida
Osteostraci
Pituriaspida
Gnathostomata
Phlebolepis
Loganellia
Galeaspida
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Myxinikela
hagfishes
Gilpichthys
Mayomyzon
Lampreys
Pipiscius
Hardistiella
Jamoytius
Gnathostomata
Euphanerops

degree of generality of some of them, which are often difficult to make because of the lack of dermal skeleton in hagfishes, lampreys, and cephalochordates/tunicates, the possible outgroups.

We are now in a situation where no clade, apart from the terminal taxa mentioned above (except thelodonts, which may not be a clade), can be regarded as satisfactorily robust. None of those which includes fossils is supported by more than five characters actually observable in all terminal taxa. The most robust clade is perhaps that including osteostracans (+pituriaspids) and the gnathostomes. Even the Pteraspidomorphi (*sensu* Gagnier 1993*b*, i.e. including the Arandaspida, Astraspida, Heterostraci, and *Eriptychius*) is a poorly supported clade (Text-fig. 5A–C), which rests on the assumption that the large median ventral and dorsal shields of their head armour are homologous, although quite different in structure. The peculiar 'naked anaspids' *Euphanerops* and *Endeiolepis* are classically regarded as highly derived anaspids, because of their typical strongly hypocercal tail and geological age (Late Devonian). However, their numerous gill units (up to 30), also found in the Silurian *Jamoytius*, are suggestive of the condition in cephalochordates (Wickstead 1969) and may thus represent a general craniate condition. The data matrix in Table 2 is slightly different from that used by Gagnier (1993*b*) and Forey (1995), since I have tried to include all the terminal taxa mentioned above, including those for which we have very little data, such as *Eriptychius*, pituriaspids, thelodonts and conodonts. The thelodonts are represented by two genera (*Loganellia* and *Phlebolepis*) which differ in some histological and anatomical characters. Only *Endeiolepis* is not included in this matrix because we know nothing of its head, and it would appear as redundant as *Euphanerops* with respect to all other characters. I have also reduced the number of soft anatomy and physiological characters for extant taxa, and some anatomical characters of fossils are inferred (from neighbouring structures linked in some way to these characters, e.g. scales and myomeres) but not directly observed. Table 1 (see Appendix) provides an annotated list of the characters used in the matrix. Characters are classified according to their availability in Recent taxa only, in all taxa, in mineralized taxa only, and in non-mineralized taxa only. The reader may run this data matrix with any program, any option, and any weight or ordering given to the character states. The strict consensus tree (of 79 shortest trees) in Text-figure 5A is produced by using the program HENNIG86 (Farris 1988), options mhennig, branch-breaking*, with character 35 as non-additive (unordered), and tunicates as an outgroup. In order to avoid imbalance in the nature of the characters and fossil taxa, I have run five other data matrices, where some taxa or characters are deleted. In the first modified matrix, only conodonts are deleted, and the strict consensus tree (of 5 shortest trees) is much better resolved (Text-fig. 5B). In the second modified matrix, only extant taxa and fossil mineralized taxa are considered. The only shortest tree obtained (Text-fig. 5C) shows no difference as to the relationships of the mineralized taxa, except for conodonts which appear as the sister-group of lampreys. The third modified matrix is the same as the preceding one, but conodonts are deleted. The only shortest tree (Text-fig. 5D) shows no difference as to other relationships. In the fourth modified matrix, only the extant taxa, the non-mineralized taxa, and the conodonts are considered. The strict consensus tree (Text-fig. 5E) is largely unresolved and remains the same, whether or not characters 42–81 (irrelevant to non-mineralized fossils, but relevant to extant taxa) are deleted. Finally, the fifth modified matrix is the same as the preceding one, but conodonts are deleted. The resulting strict consensus tree (of six shortest trees) differs in some respects from the relationships of the corresponding taxa in the tree derived from the first modified matrix, whether or not characters 42–81 are deleted (Text-fig. 5F). This seems to show that

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TEXT-FIG. 5. Strict consensus trees of the equally most parsimonious trees of the Craniata, obtained from the data matrix in Table 2 with the program HENNIG86 (Farris 1988). See text for options. A, all fossil and Recent terminal taxa cited in the text, except *Endeiolepis*; thelodonts are represented by the two genera *Loganellia* and *Phlebolepis* (tree length 150, consistency index 60, retention index 72); B, as for A, but conodonts deleted (t.l. = 148, ci.i. = 61, r.i. = 73); C, only Recent craniates and mineralized fossil taxa (t.l. = 145, ci.i. = 62, r.i. = 70); D, as for C, but conodonts deleted (t.l. = 143, ci.i. = 63, r.i. = 70); E, only Recent taxa, non-mineralized fossils, and conodonts (t.l. = 103, ci.i. = 81, r.i. = 77); F, as for E, but conodonts deleted (t.l. = 101, c.i. = 83, r.i. = 79).

conodonts generate a great uncertainty, probably because of their large number of unknown characters.

It is probable that different specialists of 'ostracoderms' would propose somewhat different matrices, but most of the characters used here would appear with much the same codings, and I doubt that the position of osteostracans, for example, would change, unless a high weight is given to the dorsal nasohypophysial opening, for example. One could also add more anatomical or biochemical characters relevant to extant taxa but, again, they would just reinforce the node (lampreys ('ostracoderms' + gnathostomes)). Certainly, controversies about character interpretation or weighting will continue for a long time, and other theories will be proposed. When considering the imbalance in the quality of the available data, the uncertainties about some histological characters (dentine or mesodentine in Ordovician forms and conodonts, enameloid in galeaspids, etc.) and about the morphotype (most generalized condition) of the gnathostomes, a 'stabilization' of craniate phylogeny cannot be expected in the near future.

THE 'OSTRACODERMS' AS STEM-GROUP GNATHOSTOMES: THE IMPLICATIONS

The well-resolved strict consensus tree in Text-figure 5B reflects the most parsimonious distribution of characters, but it has many implications for their history. The tree is roughly consistent with the distribution of the mineralized exoskeleton or body sensory-lines which appear as unique to 'ostracoderms' and the gnathostomes, yet it implies a loss of the exoskeleton in *Jamoytius*, *Endeiolepis* and *Euphanerops*. It suggests homoplasies for other characters, previously regarded as having a high weight as synapomorphies of some clades. The most surprising of these homoplasies is the dorsal position of the nasohypophysial opening in lampreys and osteostracans (the condition in anaspids remains uncertain, as there is no endoskeleton to tell whether the hypophysial tube was posteriorly closed, as in lampreys and osteostracans, or open toward the pharynx, as in hagfishes and galeaspids). The dorsal position and posteriorly closed nasohypophysial tube of osteostracans may be regarded as a convergence with lampreys, resulting from the loss of the inhalent function of the hypophysial tube and a subsequent close association of the two nasal sacs. One may assume that the common ancestor to osteostracans and the gnathostomes had a large, inhalent terminal duct (the prenasal sinus), like those of hagfishes, galeaspids, and probably also heterostracans and some thelodonts. The two separate nasal sacs opened into the duct, more or less as in galeaspids. Whether the external opening of this duct was slightly dorsal (as in galeaspids) or terminal (as in hagfishes) cannot be decided on the basis of direct evidence, but the history of this character (character 24) in the equally most parsimonious trees suggests that a terminal position could be primitive for the clade including the gnathostomes and osteostracans. Conversely, a primitively dorsal position may find support in the fact that the Rathke's pouch of embryonic gnathostomes (from which the prenasal sinus and hypophysial duct of lampreys is derived and, presumably, also in all 'ostracoderms') has a dorsal position in early osteichthyan embryos (Bemis and Grande 1992). It is thus the loss of the inhalent function of this duct in the osteostracans and gnathostomes that triggered the development of the nasal sacs in two different ways: reduction and close association in osteostracans, separation and direct opening to the exterior in the gnathostomes. The hypothetical common ancestor of osteostracans + pituriaspids and the gnathostomes probably looked more like a flat-bodied 'thelodont' with a microsquamose exoskeleton and true paired fins, than either an osteostracan or a shark.

Another question raised by this tree is that of the appearance of the paired fins. Janvier (1978) regarded true paired fins (with musculature and possibly radials) as a character unique to osteostracans, anaspids, lampreys and the gnathostomes, and supposedly lost in lampreys. If we consider the tree proposed by Forey and Janvier (1994) or Forey (1995), in which anaspids are the sister-group of all other 'ostracoderms' and the gnathostomes, we are faced with the problem of having paired fins either arising twice (in anaspids and in the common ancestor to osteostracans, pituriaspids and gnathostomes), or having been lost in heterostracans and galeaspids (without any evidence). In the tree in Text-figure 5B, the same discrepancy remains, since galeaspids have no paired fins and it is uncertain whether the lateral flaps of thelodonts are really paired fins. The implication of the analysis is that anaspids never possessed true paired fins but merely ventrolateral fin-folds devoid of musculature. What is unique to osteostracans, pituriaspids and the gnathostomes is the presence of muscularized and 'concentrated' pectoral fins in the postbranchial region, which are inserted on an endoskeletal shoulder girdle.

The supposed closest relatives of the gnathostomes, the osteostracans and pituriaspids, possess a massive, shield-shaped head endoskeleton that contrasts with the lightly built skull of chondrichthyans and actinopterygians. This difference fades away when one considers the broadly expanded braincase of most placoderms. This condition is generally regarded as unique to this group but, when considering the fact that placoderms lack a number of unique characters shared only by chondrichthyans and osteichthyans (e.g. their myodome for the superior oblique muscle is posterodorsal, as in osteostracans and lampreys, and not anterodorsal, as in other gnathostomes) and may thus be the sister-group of all other gnathostomes, it is possible that this vague resemblance to osteostracans, pituriaspids and galeaspids in the extension of the braincase over the branchial apparatus is not a convergence but a general gnathostome character.

Although some 'ostracoderms' provide information about the rise of the calcified skeleton, cellular bone, paired and unpaired fins, they tell us nothing about the origin of jaws and medially placed branchial arches of the gnathostomes. The osteostracan braincase may resemble that of a placoderm more than that of a lamprey, but it shows no evidence of any device that might foreshadow jaws. Only the presence of two large pits for the insertion of muscles that may be interpreted as adductor muscles of the lower lip suggests that the mouth of osteostracans opened and closed vertically, like that of the gnathostomes. Jaws probably developed first in microsquamose, thelodont-like forms, and the early stages of their development can be expected to be observed only in exceptionally well preserved fossils of this kind.

Evolutionary patterns

The distribution of the 'ostracoderms' in time is peculiar, since most of them are from the Silurian and Devonian, with a few taxa in the Ordovician, and the in-group relationships of the Siluro–Devonian taxa (in particular osteostracans, anaspids and galeaspids) strongly suggest that their diversification occurred long before their earliest fossil occurrence (Blieck and Janvier 1991). It seems that, being bound to particular, marginal or deltaic environments, their occurrence as fossils largely depends on low-energy conditions of deposition. Nevertheless, there has been some speculation about how they evolved and disappeared. The sudden appearance of most 'ostracoderm' taxa, along with the earliest known gnathostomes, in the Early Silurian shows the kind of pattern that would be called a 'radiation' by most evolutionary palaeontologists. Whether this is a 'recovery' of the vertebrates after the Late Ordovician extinction event, or a consequence of the expansion of marginal marine environments is difficult to tell, and is perhaps not that important. The recent field-work undertaken in Central Asia and Siberia by Karatayute-Talimaa and Predtechenskyj (1995), in continuous sequences which straddle the Ordovician-Silurian boundary, tends to show that such classically Ordovician taxa as astraspids survived into the Silurian, whereas reputedly Siluro–Devonian ones (e.g. thelodonts) were already present in the Late Ordovician. One must keep in mind that a similar 'radiation' was envisaged two decades ago for the gnathostomes in the earliest Devonian, until chondrichthyans, acanthodians, placoderms (including highly derived taxa like antiarchs), and osteichthyans (actinopterygians and lungfishes) were recorded from the Late Silurian, and even the Early Silurian (Llandovery).

There is a widespread belief that 'ostracoderms' were 'outcompeted' by the gnathostomes. However, this ignores the fact that they coexisted with the gnathostomes for 70 million years, and they appear to have been most diverse in the localities where they occur with many gnathostomes (Spitsbergen, Arctic Canada). What may have caused the 'fall' of 'ostracoderms' is perhaps more likely to have been the reduction of their preferred type of environment, that is, vast tidal flats and lagoons, as a consequence of the mid-Devonian transgression. They subsequently survived in disjunct areas until the end of the Frasnian. Whether the end-Frasnian event, which is supposed to have impoverished all invertebrate faunas, played a role in their ultimate extinction is unknown. The fact that the youngest known 'ostracoderms' (*Endeiolepis*, *Euphanerops*, and representatives of osteostracans, heterostracans, galeaspids and thelodonts) are all Frasnian (possibly early Famennian for galeaspids) may well be due to chance, and it would not be surprising to find them in younger levels, when suitable facies are explored. Conversely, and as predicted by the tree in Text-figure 5B, lampreys and hagfishes may be found much earlier than the Carboniferous, at any rate as early as the earliest 'ostracoderms' or perhaps conodonts. As claimed by Forey and Gardiner (1981), the Early Silurian 'naked anaspid' *Jamoytius* is perhaps a lamprey, although in one of the trees shown here (Text-fig. 5B), it comes together with anaspids, *Euphanerops*, and *Endeiolepis*, as classically assumed by previous authors (Ritchie 1968).

In conclusion, the distribution of these early vertebrates in the fossil record tells us little about the timing of the appearance of their characters, except at the scale of minor terminal taxa. It is clear that the Ordovician vertebrate record is abnormally poor and that field palaeontologists have to look carefully for Ordovician vertebrates.

Craniate-related fossils

Paradoxically, the earliest known vertebrates tell us less about the 'dawn' of the vertebrates than do extant hagfishes and lampreys. In fact, as we have seen above, they may tell us more about the dawn of the gnathostomes, although they have no jaws. There have been desperate attempts to plug the systematic gap between the 'protochordates' (tunicates and cephalochordates) and the craniates with fossils. Generally, these attempts have been faithful to the belief that the ancestral craniate was a naked, gracile, fish-like animal, in many ways similar to the extant cephalochordates. The recent assessment of the Conodonta as craniates also follows this trend. A radically different theory is that of Jefferies (see Jefferies 1986 for details) proposing that all recent chordates are rooted in an ensemble of heavily calcified, echinoderm-like fossil creatures, commonly referred to as the 'calcichordates'. Other fossils have been referred to as craniate relatives, or just chordates, such as the Cambrian *Pikaia* or the Silurian *Ainiktozoon* (Ritchie 1985; see Blieck 1992 for a review). The major problem in this field rests on the fact that the characters used to assess the position of these forms are often of a different nature from those commonly used for reconstructing craniate phylogeny. In the case of the conodonts, the characters which are compared with those of craniates are preserved as imprints (fin rays, muscle blocks, eyeballs) and can be interpreted in different ways. In the case of the calcichordates, the characters of the internal anatomy are preserved inside or on the surface of a calcitic endoskeleton which has no homologue in craniates, and the resemblances are remote. Nevertheless, I feel more comfortable with calcichordate anatomy than with conodont anatomy, because, here, there is little ambiguity as to the shape of the structures, whatever their interpretation may be. In many ways, the quality of Jefferies' characters is similar to that which we have for osteostracans or galeaspids. I shall not comment upon the 'calcichordate theory' in the present connection and it is clear that the test, and possible failure of the test, lies in the discovery of characters (other than the calcitic endoskeleton) which would unambiguously prove them to be a sub-group of the echinoderms (see Peterson 1995 for a recent criticism of this theory). Nevertheless, the discovery of a single, unambiguous craniate character (e.g. a labyrinth with at least one semicircular canal) in a mitrate would be more than welcome.

As for conodonts, the series of discoveries on their morphology made during the last twelve years has led many palaeontologists to accept that they are craniates (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1993). My initial enthusiasm for conodonts as craniates (Janvier 1983) had ups and downs (Tillier and Janvier 1986). I now favour this theory, although conodonts still show some ambigous characters. Craniates are defined as having a skull (not necessarily a neurocranium), and otic, optic and olfactory capsules. An important additional character is the neural crest, which is unavailable in fossils, unless interpreted to have been present as a result of its expression in the form of dermal calcified tissues or a cartilaginous branchial apparatus. Conodonts almost certainly had optic capsules, and the recent description of the latter in an Ordovician conodont from South Africa (Aldridge and Theron 1993) provides evidence that these were highly developed, possibly with a lens and extrinsic eye muscles (Gabbott *et al.* 1995). Whether the conodont apparatus can be regarded as evidence for a craniate exoskeleton (and thus a neural crest) is still undecided, despite the description of a somewhat craniate-like histology (Sansom *et al.* 1992, 1994). My impression is that the structure of conodont elements is much derived, relative to that of the classical dentinous tissues of the vertebrates. One must also keep in mind that 'ostracoderms' display a large variety of dermal hard tissues, and that fragments of galeaspid exoskeleton, for example, would never have been referred to the vertebrates if not found on complete skulls (they would probably have been referred to an arthropod). To date, no gill apparatus, either in the form of gill-pouch or gill-arch imprints, has been observed in conodonts, but negative evidence is not evidence. On several occasions, I have played the role of devil's advocate as to the relationships of the conodonts. This time, I shall try to support what is now the current theory, yet with somewhat different viewpoints. Aldridge *et al.* (1993) placed conodonts as the sister-group of the Vertebrata (craniates minus hagfishes) in the cladogram of the craniates of Janvier and Blieck (1979), which assumed that lampreys have lost the mineralized exoskeleton. Conodonts were thus regarded as sharing with lampreys, gnathostomes and all 'ostracoderms' the ability to produce a mineralized exoskeleton and, perhaps, well-developed eyeballs. Now, when considering the extensive consensus tree proposed here (Text-fig. 5A), conodonts appear in a polytomy with lampreys, anaspids and other non-mineralized taxa. When non-mineralized fossil taxa are deleted, conodonts appear as the sister-group of lampreys (Text-fig. 5C). One can, indeed, reconcile the reconstruction of the conodont feeding apparatus as proposed by Purnell (1994) with what may have been the pharyngeal anatomy of the common ancestor to the Vertebrata (lampreys, 'ostracoderms', and the gnathostomes) simply by considering that the ramiform 'M' and 'S' elements were situated near the mouth opening (more or less like the oral plates of many 'ostracoderms', yet internal), and the pectiniform 'Pa' and 'Pb' elements as being attached to a transversely moving structure derived from a velum of larval lamprey type. This suggests that the transformation of the velum into a biting apparatus may have occurred quite early. Yet another possibility is that the conodont apparatus, in particular the S and M elements, is in fact associated with gill arches lying beneath the braincase (or at any rate the eyes). The presence of mineralized dermal denticles in the branchial apparatus would thus make them closer to the gnathostomes than previously believed (Janvier 1995), although such a position does not appear from the present analysis. Finally, the conodont apparatus may turn out to be associated with a 'tongue'-like device homologous to that of lampreys and hagfishes, but this would not necessarily mean that conodonts are particularly close relatives of any of these taxa (contrary to Text-fig. 5C), since such a device is probably general for craniates. The present enthusiasm for research on conodont structure and affinity will certainly provide many new data to argue for and against their position in craniate or chordate phylogeny, but, at the moment, it seems to be firmly established that conodonts possessed a notochord (a chordate character), chevron-shaped muscle blocks (a myomerozoan character), radials and eyes (craniate characters), large eyeballs, possibly with extrinsic eye muscles (vertebrate characters), and a mineralized skeleton (gnathostome, including 'ostracoderms', character). Putting conodonts with the cephalochordates (Nowlan and Carlisle 1987) would imply either that craniates are diphyletic (as suggested by Bjerring 1984), or that cephalochordates have lost the eyes and radials.

A short remark must be made about yet another taxon of supposedly craniate affinities, *Anatolepis*. First recorded from the Ordovician of Spitsbergen (Bockelie and Fortey 1976), then from North America (Repetski 1979), this form is known only from fragments of phosphatic carapace ornamented with small, elongated tubercles and displaying a three-layered structure, with a cancellar middle layer. The tubercles show some ascending tubules which recall the structure of the vertebrate dentine (for a recent reconsideration of *Anatolepis* see Smith and Sansom 1995). These fragments were originally referred to an armoured vertebrate (Bockelie and Fortey 1976; Repetski 1978) and then became the subject of a controversy as to their possible arthropod derivation (Peel and Higgins 1977; Briggs and Fortey 1982). If the structure of *Anatolepis* is somewhat suggestive of that of the heterostracan exoskeleton (Janvier 1981*a*; Ørvig 1989), some of the spine-shaped elements described from the Ordovician of Greenland are difficult to reconcile with what we know in some of the 'ostracoderms' that bear spine-shaped scales or plates. They look too thin-walled and hollow. Putting *Anatolepis* in the vertebrates, and even among 'ostracoderms' should await the discovery of more characteristic elements (e.g. fragments with sensory-line canals or grooves).

Prospects: more characters or more 'ostracoderms'?

The recent history of research on 'ostracoderms' shows that the discovery of new major taxa, such as the galeaspids, pituriaspids and arandaspids, brought forth new viewpoints and new associations of characters. Galeaspids provided the first evidence for an inhalent prenasal sinus associated with separate nasal cavities, and the first evidence of perichondral bone associated with an acellular exoskeleton. Pituriaspids probably provide the first evidence of true paired fins associated with a terminal (at any rate non-dorsal) nasal opening in 'ostracoderms'. Arandaspids are more puzzling in probably having sclerotic rings, a character regarded by Janvier (1984) as unique to osteostracans and gnathostomes, and perhaps two separate nostrils, like the gnathostomes (Gagnier 1993*a*), although some other characters rather support affinities with heterostracans (Text-fig. 5A–B). One of the problems met with in reconstructing the phylogeny of extant and fossil higher vertebrate taxa is the distribution of known characters as opposed to the many question marks. Moreover, as we have seen above, many of the characters observed in 'ostracoderms' are either unique to the respective terminal taxa or general for the vertebrates or craniates. Some more anatomical characters can certainly be obtained from the available 'ostracoderm' material, in particular galeaspids, and one may expect the discovery of exceptionally well preserved material that yields new characters in the body and fin squamation. Histological characters and ornamentation characters are sometimes difficult to assess and polarize, but they are diverse enough to be informative in a data matrix. it is probable that much useful information will be provided by articulated 'thelodonts', and possibly by the examination of large numbers of specimens of non-mineralized forms, such as *Jamoytius* and *Euphanerops*. These provide information on the cartilaginous endoskeleton and soft tissues which can be compared with the skeletons of lampreys or hagfishes.

The ideal future for 'ostracoderm' research would thus be to acquire more characters of equivalent 'quality' (Nelson 1994), but the nature of currently available material has its limits.

CONCLUSIONS

The history of research on early vertebrates since the mid-nineteenth century shows once more that many controversies and perhaps misleading statements have been due to the propensity of palaeontologists to define taxa by their common ascent rather than by the characters that they possess (Nelson and Patterson 1993). Clearly, Huxley and Lankester considered characters (the large scales and bony plates) to put 'ostracoderms' with osteichthyans. Traquair used common ascent (of heterostracans from thelodonts, and of thelodonts from sharks) to suggest chondrichthyan affinities for heterostracans. He accepted the primitiveness of the microsquamose exoskeleton of thelodonts, but used this general gnathostome or vertebrate character to draw relationships with sharks. Cope used absence of jaws (thus ascent from a theoretical jawless craniate ancestor) to put 'ostracoderms' with lampreys and hagfishes, and so did Stensiö when he put the cyclostomes among 'ostracoderms', although he later proposed reasons other than jawlessness to consider agnathans as a clade. Although the early cladograms of the craniates put emphasis on the characters, the common ascent of lampreys, anaspids and osteostracans, for example, was invoked to justify many assumed reversions in lampreys. Common ascent is also underlying many of the assumptions about evolutionary patterns (radiations, extinctions), since they deal with successions of grades. There may be a radiation of heterostracans, but there is no radiation of the 'ostracoderms' or 'agnathans' in general. Similarly, the gnathostomes did not outcompete agnathans but, in the best case, jawed gnathostomes outcompeted several groups of jawless gnathostomes.

This may seem a pointless discussion, largely concerning semantics, but words and names of taxa do have considerable weight when characters are scarce and when the subject concerns the 'origins' of taxa.

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APPENDIX

TABLE 1. Characters and codings.

Characters that can be observed in extant craniates only

0. Eye lens absent = 0; present = 1. (For a recent consideration of this character in hagfishes, see Wicht and Northcutt 1995.)
1. Ribbon-shaped synaptic organelles in retina absent = 0; present = 1.
2. Tubular muscle in 'tongue' musculature absent = 0; present = 1.
3. Lateral-line neuromasts absent = 0; present = 1. (Some fossils are assumed here to have possessed neuromasts when they possess sensory-line canals, since no extant vertebrate is known to have canals but no neuromast. (For a recent consideration of this character in hagfishes, see Wicht and Northcutt 1995.)
4. Nervous control of heart absent = 0; present = 1.
5. Heart response to catecholamine absent = 0; present = 1.
6. Blood system open = 0; closed = 1.
7. Spleen absent = 0; present = 1.
8. Concentrated exocrine pancreas absent = 0; present = 1.
9. Typhlosole in intestine absent = 0; present = 1.
10. Larval stage present = 0; absent = 1.
11. Compartmentalized adenohypophysis absent = 0; present = 1.
12. Pituitary control of melanophores absent = 0; present = 1. (This character may be correlated with the presence/absence of a pineal foramen in fossils. Absence of a pineal foramen and thus of a photosensory pineal organ would preclude pituitary control of melanophores.)
13. Kidney tubules with glomerulae absent = 0; present = 1.
14. Osmoregulation absent = 0; present = 1.
15. Granulocytes and neutrophils absent = 0; present = 1.
16. Two types of giant Mauthner cells in the central nervous system absent = 0; present = 1.
17. Electroreceptive cells absent = 0; present = 1.
18. Sperm not shed through coelomic cavity = 0; shed through coelomic cavity = 1.

Characters that can potentially be observed or inferred in all extant and fossil craniates

19. Skull absent = 0; present = 1. (This refers to any cranial component, i.e. splanchno- or neurocranial.)
20. Cartilaginous or calcified braincase (neurocranium) absent = 0; present = 1.
21. Dorsally closed cartilaginous or calcified braincase (neurocranium) absent = 0; present = 1.
22. Olfactory organ absent = 0; present = 1.
23. Terminal nasohypophysial opening (inhalent or not) absent = 0; present = 1. (The nasohypophysial opening is assumed to be terminal when there is no evidence that it is dorsal. This is the situation in e.g. astraspids or heterostracans.)
24. Dorsal nasohypophysial opening (inhalent or not) absent = 0; present = 1. (It is assumed to be dorsal in *Mayomyzon*, on account of the position of the imprint of the olfactory capsule.)
25. Optic capsules (exclusive of the lens) absent = 0; present = 1.
26. Transversely biting teeth absent = 0; present = 1. (This generally refers to horny teeth of lampreys and hagfishes, but can potentially be extended to the mineralized teeth of conodonts.)
27. Heart absent = 0; present = 1.
28. Closed pericardium absent = 0; present = 1. (The pericardium of *Mayomyzon* is assumed to have been similar to that of modern lampreys, i.e. closed, because of the shape of its imprint.)
29. Trunk and tail musculature with chevron-shaped muscle blocks absent = 0; present = 1. (In mineralized fossils, the arrangement of the musculature may be inferred from that of the scales, as in anaspids, arandaspids, etc.)
30. Radials in fins absent = 0; present = 1. (In many mineralized fossils, the presence of radials is inferred from the alignment of the overlying scales or fin rays.)
31. Numerous and closely set radials in unpaired fins absent = 0; present = 1. (In many fossils, this character is inferred from the arrangement of the scale rows corresponding to the position of the underlying radials.)

TABLE 1 (*cont.*)

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32. Radial muscles in fins absent = 0; present = 1. (The presence of radial musculature is mainly inferred from the muscle insertions on the surface of the endoskeleton, e.g. in osteostracans and possibly pituriaspids, but imprints of muscles can potentially be preserved in non-mineralized fossils, such as *Jamoytius*.)
33. Separate dorsal fin absent = 0; present = 1. (This refers to a separate fin anterior to epichordal lobe in the case of forms having a hypocercal tail.)
34. Anal fin absent = 0; present = 1.
35. Tail isocercal = 0; hypocercal = 1; epicercal = 2. (Although apparently pad-shaped, isocercal or diphycercal, the tail of heterostracans is coded here as hypocercal, because it is assumed to be derived from the hypocercal tail of generalized thelodont type by enlargement of the epichordal radials, as suggested by the 'fork-tailed' thelodonts which display the same tail morphology as heterostracans. The actual path of the notochord has, however, never been observed in heterostracans.)
36. Paired fin folds or fins absent = 0; present = 1. (This refers to any lateral skin fold, be it with radials and radial musculature or not. The small lateral skin fold of the extant hagfish *Neomyxine* is not considered here as a fin fold.)
37. Paired fin folds or fins concentrated in the pectoral or epibranchial regions absent = 0; present = 1.
38. Muscles in paired fins absent = 0; present = 1. (In fossils, this can mainly be inferred from the muscle insertions on the endoskeletal girdle.)
39. Arcualia absent = 0; present = 1. (Arcualia are assumed to be present in heterostracans on the basis of the series of median impressions observed in some species, e.g. *Seretaspis*.)
40. Gill openings arranged in a posteriorly slanting line absent = 0; present = 1. (In some non-mineralized fossils, e.g. *Euphanerops*, the position of the gill openings are inferred from that of the series of rounded imprints regarded here as trematic rings.)
41. More than ten gill units = 0; less than ten = 1.

Characters that can be observed in extant craniates and mineralized fossil craniates only

42. Olfactory tract absent = 0; present = 1. (An olfactory tract is assumed to be present in heterostracans on account of the two divergent ridges that link the impressions of the olfactory organs to the pineal, or diencephalic region. Moreover, the distance between these two impressions is such that it implies the presence of a long tract, as in galeaspids and gnathostomes.)
43. Olfactory organ unpaired or with closely set and confluent nasal sacs, absent = 0; present = 1.
44. Olfactory organ paired with entirely separated nasal sacs, absent = 0; present = 1.
45. Nasohypophysial duct serving branchial respiration, absent = 0; present = 1. (This character is assumed to be present in *Loganellia*, because of the similarity between its denticle-covered median duct and that of galeaspids.)
46. Nasohypophysial duct posteriorly closed and serving only as a common 'nostril', absent = 0; present = 1.
47. Extrinsic eye muscles absent = 0; present = 1. (This character is coded as present in conodonts, but the evidence for muscle fibres associated with the optic capsules remains very slight. It is assumed to be present in osteostracans and galeaspids on the basis of the presence of myodomes.)
48. Photosensory pineal organ (or pineal foramen) absent = 0; present = 1. (In fossils, the pineal organ is assumed to be photosensory when there is a distinct pineal foramen.)
49. Semicircular canals absent = 0; present = 1.
50. Single semicircular canal absent = 0; present = 1. (This character is present only in hagfishes, but there is debate as to whether this is a general craniate condition or a uniquely derived condition.)
51. Two vertical semicircular canals absent = 0; present = 1.
52. Two vertical semicircular canals forming distinct loops, absent = 0; present = 1. (This refers to the distinct canals of e.g. osteostracans, galeaspids or gnathostomes, in contrast to those of lampreys, which lie against the vestibular division of the labyrinth.)
53. Lateral lines enclosed in canals, absent = 0; present = 1.

TABLE 1 (*cont.*)

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54. Lateral-line grooves or canals, absent = 0; present on head = 1; present on head and body = 2. (The presence of sensory-line grooves on the body is not clearly shown in anaspids, but nevertheless is coded here as present based on the description made by Smith 1957. In galeaspids, it is not observed, but inferred from the orientation of the main lateral-line canal in the posterior part of the head shield, which suggests that it continued on the body. In hagfishes, the peculiar grooves on the head are now regarded by Wicht and Northcutt 1995, as true lateral-line grooves, associated with the lateralis nerve fibres, although they show no evidence of neuromasts.)
55. Cerebellum absent = 0; present = 1.
56. Large and paired cerebellum absent = 0; present = 1. (This is based on the assumption that the large, dorsal, paired swellings in the brain cavity of osteostracans and galeaspids, and the similarly placed paired impression in heterostracans actually corresponds to the position of the metencephalon, as proposed by Stensiö in 1927. This character is coded as present in pituriaspids, based on the reconstruction proposed by Young 1991.)
57. Vagus and glossopharyngeus nerves included in occipital region, absent = 0; present = 1.
58. Closely set atrium and ventricle, absent = 0; present = 1. (In fossils, this character is known only in osteostracans, where the heart was enclosed in an ossified pericardium.)
59. Large dorsal jugular vein absent = 0; present = 1.
60. Subaponeurotic vascular system absent = 0; present = 1. (This refers to the vascular network which lies at the limit between the exo- and endoskeleton. It is assumed here to be present in heterostracans on the basis of the vascular impressions in the cyathaspidiform *Torpedaspis*.)
61. Calcified cartilage absent = 0; present = 1. (Calcifications of the cartilage are now known to occur in adult lampreys.)
62. Perichondral bone absent = 0; present = 1. (Perichondral bone may be present in *Eriptychius* on account of the vascular canals of the subaponeurotic network on the surface of the calcified cartilage, which seem to be lined with perichondral bone. This, however, remains to be checked and this character is coded here as '?'. It is also assumed to be present in pituriaspids on account of the mode of preservation of the internal structures, which is comparable to the condition in osteostracans and galeaspids.)
63. Head endoskeleton expanded into a massive shield covering the gills, absent = 0; present = 1. (This refers to the massive endoskeletal shield that covers that branchial region in osteostracans and galeaspids. The large endoskeletal expansions of the braincase over the branchial region in some placoderms are provisionally regarded here as being not general for the gnathostomes.)
64. Endoskeletal scleral ossification or calcification absent = 0; present = 1. (The remnants of the eye cup described by Gagnier 1993*a* in *Sacabambaspis* are almost certainly evidence for a calcified sclera, but it is uncertain whether it is perichondral bone or calcified cartilage.)
65. Orthodentine or metadentine absent = 0; present = 1. (Conodonts are coded here as '0' for both types of dentinous tissue, since the structure of the conodont organs remains ambiguous in this respect.)
66. Mesodentine absent = 0; present = 1.
67. Enameloid or enamel (hypermineralized superficial layer) absent = 0; present = 1. (In osteostracans, enameloid is known with certainty in thyestiids, but it is probably present also in many other forms with a shiny superficial layer of the exoskeleton. Conodonts possess a fibrous external layer that may be considered here as enamel or enameloid.)
68. Acellular dermal bone absent = 0; present = 1. (Gagnier 1993*a* suggested that the exoskeleton of arandaspids might have been cellular on account of peculiar cavities observed in the dermal bone of *Sacabambaspis*. This, however, remains unconvincing and arandaspids are coded here as having acellular bone.)
69. Cellular dermal bone absent = 0; present = 1. (Conodonts are coded here as having bone cells, although this is still a matter of considerable debate.)
70. Honeycomb-like middle layer of exoskeleton absent = 0; present = 1.
71. Oakleaf-shaped tubercles or odontodes in ornamentation, absent = 0; present = 1. (The scalloped scale crowns of *Phlebolepis* and *Loganellia* might be coded here as being homologues of the oak leaf-shaped tubercles of arandaspids, *Eriptychius* and early heterostracans. However, since scale crowns are not tubercles, this character is coded here as absent.)

TABLE 1 (*cont.*)

72. Large median dorsal and ventral dermal shields in head, absent = 0; present = 1. (Although made up of polygonal units, the dorsal and ventral shields of arandaspids and astraspids are coded here as being homologous to the ventral and dorsal shields of heterostracans. The large median ventral plate of galeaspids is not considered as being a ventral shield.)
73. External opening of endolymphatic duct absent = 0; present = 1. (The opening of the endolymphatic duct is known only in one galeaspid, *Xiushuiaspis*, but since this genus is regarded as quite generalized for the group the character is assumed to have been lost in more advanced galeaspids.)
74. Opercular flaps on external branchial openings absent = 0; present = 1. (This refers to the small scale-covered flaps that extend in front of each gill opening in osteostracans and thelodonts, in contrast to the puncture-shaped gill openings in most other taxa, including arandaspids. The small 'plica trematica' of lampreys is not regarded here as an opercular flap, as it is inside the gill opening.)
75. Preanal skin fold or scale ridge present = 0; absent = 1.
76. Sclerotic ring absent = 0; present = 1. (The ornamented platelets surrounding the eyes in arandaspids are regarded here as true sclerotic rings, as they seem to be independent of the shield and, thus, are probably not circumorbital plates.)
77. Scales made up by a single odontode (microsquamose), absent = 0; present = 1.
78. Scales made up by several odontodes (macrosquamose) and diamond-shaped, absent = 0; present = 1. (The scales of some heterostracans and osteostracans can be rather elongated in shape, but the most generalized members of these taxa have diamond-shaped scales.)
79. Scales made up by several odontodes (macrosquamose) and rod-shaped, absent = 0; present = 1.
80. Pharyngeal dermal denticles absent = 0; present = 1. (Conodonts are coded here as having pharyngeal denticles, as the rearmost conodont organs are likely to have lain relatively far back in the pharynx.)
81. Scale-covered zones on tail absent = 0; present = 1. (This refers to the large, finger-like zonations of small scales in the tail of heterostracans and many thelodonts. The thin and closely set rows of lepidotrich-like scales in osteostracans are not included in this character.)

Characters that can be observed only in extant craniates and potentially in soft-bodied fossil craniates preserved as imprints as well as in mineralized craniates fossilized in anoxic facies (thus preserving imprints of cartilages and keratinized tissues)

82. Horny teeth absent = 0; present = 1.
83. Piston cartilage absent = 0; present = 1. (The peculiar, calcified dumb-bell-shaped element described by Gagnier 1993*b* in *Sacabambaspis* might correspond to a piston cartilage, but it is coded here as '?', because this interpretation is too poorly supported.)
84. Dentigerous cartilage absent = 0; present = 1.
85. Tentacles strengthened by cartilage, absent = 0; present = 1. (Cartilage-supported tentacles are coded as absent in many of the mineralized forms, because the structure of the oral region shows no evidence for the passage of such organs.)
86. Sucking disc with an annular cartilage around mouth, absent = 0; present = 1. (A sucking disc is coded as absent in most of the mineralized forms, such as osteostracans, heterostracans, and galeaspids, because the organization of the dermal oral plates lining their mouth is incompatible with the presence of a sucker. An annular cartilage is clearly present in *Mayomyzon*, and the large rounded snout of *Hardistiella* suggests the presence of some sucker. The presence of an annular cartilage in *Jamoytius* and *Euphanerops* remains controversial and this character is coded here as '?' for these two taxa.)
87. Pouch-shaped gills absent = 0; present = 1. (This refers to pouches that enclose anterior and posterior hemibranchs, as in hagfishes and adult lampreys. Although often depicted as having 'gill pouches', osteostracans, galeaspids and heterostracans show no direct evidence of such pouches. Gill pouches are assumed here to be present in *Mayomyzon*, on account of the aspect of the gill imprints.)
88. Trematic rings absent = 0; present = 1. (The endoskeletal imprints of *Jamoytius* and *Euphanerops* show lateral series of rings, fused side-by-side, that are interpreted here as being trematic rings, rather than branchial arches proper.)

TABLE 2. Data matrix.

		1		2		3		4		5		6		7		8		
	012345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	678
Tunicata	000000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	000
Cephalochordata	000000	00000	00000	00000	00000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	000
Hyperotreti (hagfishes)	001000	00001	00000	00110	01101	11011	00000	00000	00101	00011	00010	00000	00000	00000	00000	00000	01011	011
Myxinikela	??????	?????	?????	???1?	?1101	1??1?	??000	0?0??	??101	0????	?????	?????	00000	00000	00???	00000	01011	0??
Gilpichthys	??????	?????	?????	???1?	????1	1??1?	??000	0?000	1????	?????	?????	?????	00000	00000	00???	00000	010?0	0??
Hyperoartia (lampreys)	111111	11111	11111	11111	01011	11111	11101	00011	10100	11110	10001	00111	10000	00000	00001	00000	01110	111
Mayomyzon	??????	?????	?????	???11	?1011	11111	1?00?	0?0??	1?100	1????	?????	?????	00000	00000	00???	00000	0?110	11?
Hardistiella	??????	?????	?????	???11	?1??1	????1	1?111	??0??	?????	?????	?????	?????	00000	00000	00???	00000	0???0	1??
Pipiscius	??????	?????	?????	???1?	????1	???11	1??0?	?????	1????	?????	?????	?????	00000	00000	00???	00000	01??0	1??
Jamoytius	??????	?????	?????	???1?	????1	???11	1??11	1?0??	0????	?????	?????	?????	00000	00000	00???	00000	00??0	??1
Euphanerops	??????	?????	?????	???1?	????1	?1?11	0?011	??0?1	0????	?????	?????	?????	00000	00000	00???	00000	00??0	??1
Anaspida	??????	?????	?????	???1?	?1011	???11	0?011	1?0?1	0????	??1??	??02?	?????	?0000	00100	00?01	00010	1???0	0??
Astraspida	??????	?????	?????	???1?	???01	?????	??00?	000?0	1????	??0??	??0??	?????	????0	01100	01000	?010?	?????	???
Eriptychius	??????	?????	?????	???1?	?????	?????	?????	?????	?????	?????	??0??	????1	1???0	10100	1????	?010?	?????	???
Arandaspida	??????	?????	?????	???1?	?1?01	???1?	??00?	000?1	0????	??1??	??02?	?????	???10	00101	11000	10010	????0	0??
Heterostraci	???1??	?????	?????	???1?	?1?01	???11	0?001	00010	1101?	?0110	11121	1???1	00?01	00101	11000	00100	1???0	0??
Phlebolepis	???1??	?????	?????	???1?	???01	????1	0?111	11??0	1????	?????	??12?	?????	00000	10100	00???	0100?	1???0	???
Loganellia	???1??	?????	?????	???1?	?1101	????1	0?111	11??0	1?011	0????	??12?	?????	00001	00100	00?1?	01001	1???0	???
Galeaspida	???1??	?????	?????	???11	11011	???11	000??	000?0	11011	01110	11121	11?11	?1100	01100	00101	0100?	1???0	0??
Pituriaspida	??????	?????	?????	???11	11??1	?????	?1???	111?0	?????	?????	????1	1????	?11??	?????	00??1	?????	????0	0??
Osteostraci	???1??	?????	?????	???11	11011	?1111	11102	11110	1?100	11110	11121	11111	11110	11010	00111	10100	0???0	0??
Gnathostomata	110111	11110	11111	11011	11001	01111	11112	11110	11010	11110	11121	11111	11011	11010	00111	11101	00000	000
Conodonta	??????	?????	?????	?????	????1	1??11	1?001	000??	?????	?1???	?????	?????	?0000	01000	00???	00001	00??0	0??

TABLE 2 Data matrix

		1		2		3		4		5		6		7		8		
	012345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	678
Tunicata	000000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	000
Cephalochordata	000000	00000	00000	00000	00000	00010	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	000
Hyperotreti (hagfishes)	001000	00001	00000	00110	01101	11011	00000	00000	00101	00011	00010	00000	00000	00000	00000	00000	01011	011
Myxinikela	??????	?????	?????	???1?	?1101	1??1?	??000	0?0??	??101	0????	?????	?????	00000	00000	00???	00000	01011	0??
Gilpichthys	??????	?????	?????	???1?	????1	1??1?	??000	0?000	1????	?????	?????	?????	00000	00000	00???	00000	010?0	0??
Hyperoartia (lampreys)	111111	11111	11111	11111	01011	11111	11101	00011	10100	11110	10001	00111	10000	00000	00001	00000	01110	111
Mayomyzon	??????	?????	?????	???11	?1011	11111	1?00?	0?0??	1?100	1????	?????	?????	00000	00000	00???	00000	0?110	11?
Hardistiella	??????	?????	?????	???11	?1??1	????1	1?111	??0??	?????	?????	?????	?????	00000	00000	00???	00000	0???0	1??
Pipiscius	??????	?????	?????	???1?	????1	???11	1??0?	?????	1????	?????	?????	?????	00000	00000	00???	00000	01??0	1??
Jamoytius	??????	?????	?????	???1?	????1	???11	1??11	1?0??	0????	?????	?????	?????	00000	00000	00???	00000	00??0	??1
Euphanerops	??????	?????	?????	???1?	????1	?1?11	0?011	??0?1	0????	?????	?????	?????	00000	00000	00???	00000	00??0	??1
Anaspida	??????	?????	?????	???1?	?1011	???11	0?011	1?0?1	0????	??1??	??02?	?????	?0000	00100	00?01	00010	1???0	0??
Astraspida	??????	?????	?????	???1?	???01	?????	??00?	000?0	1????	??0??	??0??	?????	????0	01100	01000	?010?	?????	???
Eriptychius	??????	?????	?????	???1?	?????	?????	?????	?????	?????	?????	??0??	????1	1???0	10100	1????	?010?	?????	???
Arandaspida	??????	?????	?????	???1?	?1?01	???1?	??00?	000?1	0????	??1??	??02?	?????	???10	00101	11000	10010	????0	0??
Heterostraci	???1??	?????	?????	???1?	?1?01	???11	0?001	00010	1101?	?0110	11121	1???1	00?01	00101	11000	00100	1???0	0??
Phlebolepis	???1??	?????	?????	???1?	???01	????1	0?111	11??0	1????	?????	??12?	?????	00000	10100	00???	0100?	1???0	???
Loganellia	???1??	?????	?????	???1?	?1101	????1	0?111	11??0	1?011	0????	??12?	?????	00001	00100	00?1?	01001	1???0	???
Galeaspida	???1??	?????	?????	???11	11011	???11	000??	000?0	11011	01110	11121	11?11	?1100	01100	00101	0100?	1???0	0??
Pituriaspida	??????	?????	?????	???11	11??1	?????	?1???	111?0	?????	?????	????1	1????	?11??	?????	00??1	?????	????0	0??
Osteostraci	???1??	?????	?????	???11	11011	?1111	11102	11110	1?100	11110	11121	11111	11110	11010	00111	10100	0???0	0??
Gnathostomata	110111	11110	11111	11011	11001	01111	11112	11110	11010	11110	11121	11111	11011	11010	00111	11101	00000	000
Conodonta	??????	?????	?????	?????	????1	1??11	1?001	000??	?????	?1???	?????	?????	?0000	01000	00???	00001	00??0	0??

NEW MATERIAL OF *YOUNGINA*: EVIDENCE OF JUVENILE AGGREGATION IN PERMIAN DIAPSID REPTILES

by ROGER M. H. SMITH *and* SUSAN E. EVANS

ABSTRACT. An unusual specimen of *Youngina* is described from a new locality in the Karoo Basin of South Africa. The locality is in the *Tropidostoma* Assemblage Zone (equivalent to the former Lower *Cistecephalus* Zone), making the specimen the oldest recorded example of this genus. It comprises an association of five immature skeletons which are fully articulated and thus provide the first clear indication of body proportions in *Youngina*. In addition, the material yields new information on the pectoral girdle, pelvis and foot. It is clear that *Youngina*, unlike many of its known relatives, was an agile, fully terrestrial animal. This conclusion is reinforced by the preservation of the young skeletons in positions which suggest group denning behaviour in response to adverse climatic conditions.

YOUNGINIFORMS are a small but well-defined clade of Permo-Triassic diapsid reptiles known from the upper Permian of South Africa (*Youngina*), Tanzania (*Tangasaurus*) and Madagascar (*Hovasaurus*, *Thadeosaurus* and *Acerosodontosaurus*) (Gow 1975; Currie 1980, 1981*a*, 1982; Carroll 1981; Currie and Carroll 1984), and from the lower Triassic of Kenya (*Kenyasaurus*; Harris and Carroll 1977). Once thought to be related to lepidosaurs (lizards, snakes and their relatives) (e.g. Evans 1988), younginiforms are now placed closer to the base of the diapsid tree (Laurin 1991).

The genus *Youngina* was erected by Broom (1914) on the basis of a single skull, now in New York (AMNH 5561). Further specimens followed (e.g. Broom 1922), but many of these were assigned to new genera and species (*Youngopsis kitchingi* Broom, 1937; *Youngoides romeri* Olson and Broom, 1937; *Youngopsis rubidgei* Broom and Robinson, 1948 and *Youngoides minor* Broom and Robinson, 1948). Gow (1975) published the first comprehensive review of the known cranial and postcranial material, and concluded that all specimens could be referred to a single genus and species, *Youngina capensis*.

Youngina has often been considered to be an archetypal Permian diapsid, but its morphology remains incompletely known. As with all small diapsid reptiles, the fossil record of younginids in the Karoo Basin of southern Africa is comparatively sparse. There are 13 known skulls, only one of which (BPI 3859) has an associated postcranial skeleton. This skeleton is incomplete (missing parts of the fore- and hindlimbs and pectoral girdle) and was disarticulated to permit detailed description of individual bones (Gow 1975). Furthermore, all the *Youngina* specimens collected so far are from Beaufort Group strata assigned to the *Dicynodon* Assemblage Zone (Kitching in press). Previously termed the *Daptocephalus* Zone (Kitching 1977), these strata are considered to be of uppermost Permian age (Anderson and Cruickshank 1978).

Recently, one of us (RMHS) recovered an unusual specimen of *Youngina* from 700 m lower in the Beaufort succession than previous finds. The new locality is in the *Tropidostoma* Assemblage Zone (Smith and Keyser in press) which is equivalent to the former lower *Cistecephalus* Zone of Kitching (1977) (Smith and Keyser in press). The specimen, designated SAM K7710, in the collections of the South African Museum, Cape Town, is thus some 2·3 My older than other known specimens. It contains five fully articulated immature *Youngina* skeletons (plus a hindlimb of one other) preserved in attitudes and orientations that strongly resemble those of modern lizards when displaying group denning behaviour.

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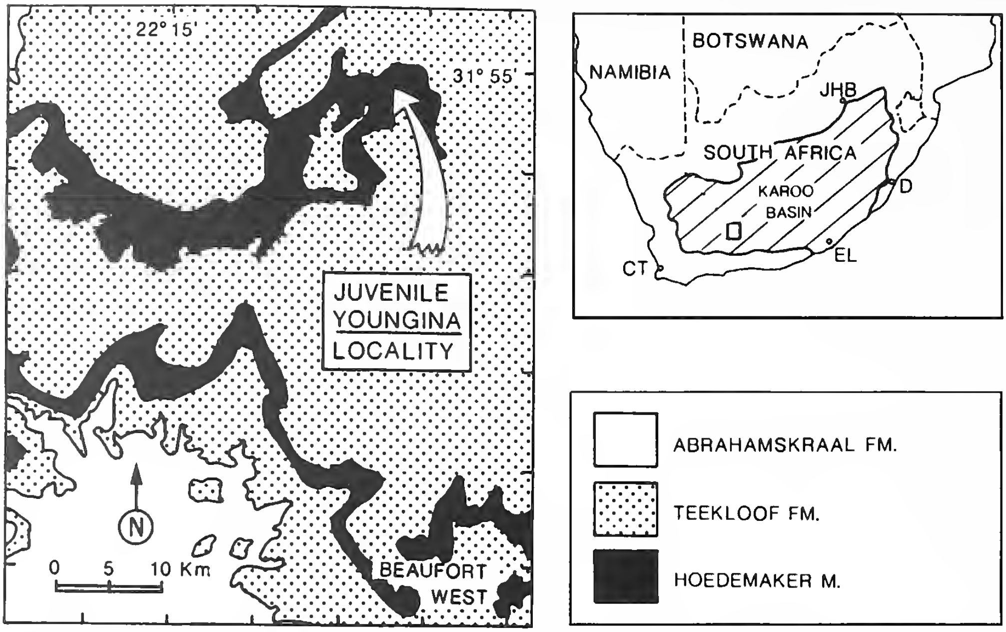
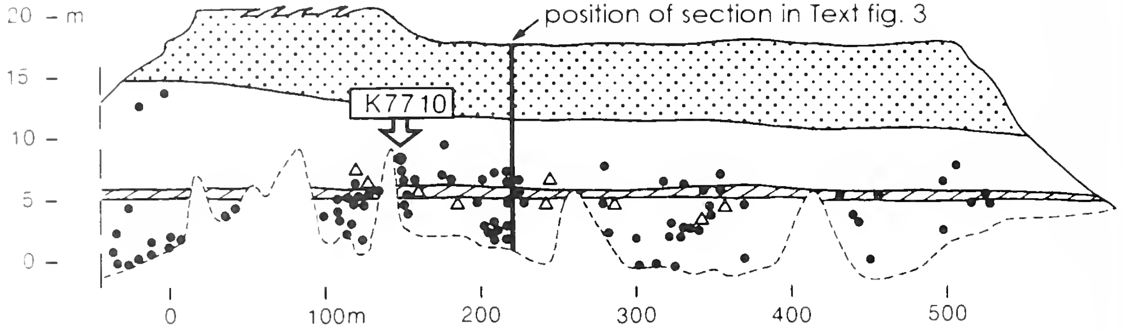
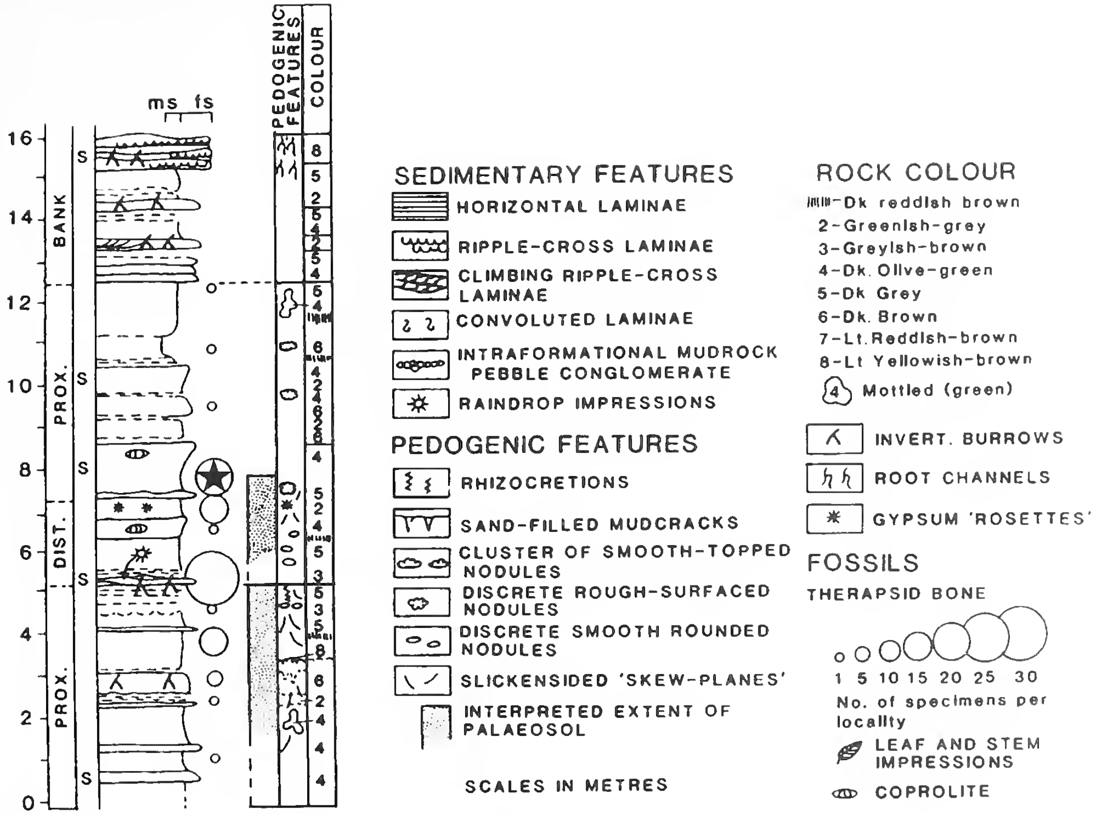


TEXT-FIG. 1. Lithostratigraphy of the area surrounding the new younginid fossil locality (SAM K 7710) in the south-western Karoo Basin.



TEXT-FIG. 2. Panel section of cliff exposure containing the new younginid locality showing interpreted sedimentary environments and distribution of all embedded therapsid fossils including other juveniles.

The aims of this study are to describe the significant morphological features and juvenile characteristics of these skeletons, and to investigate their taphonomic history through sedimentological analysis of the host sequence.



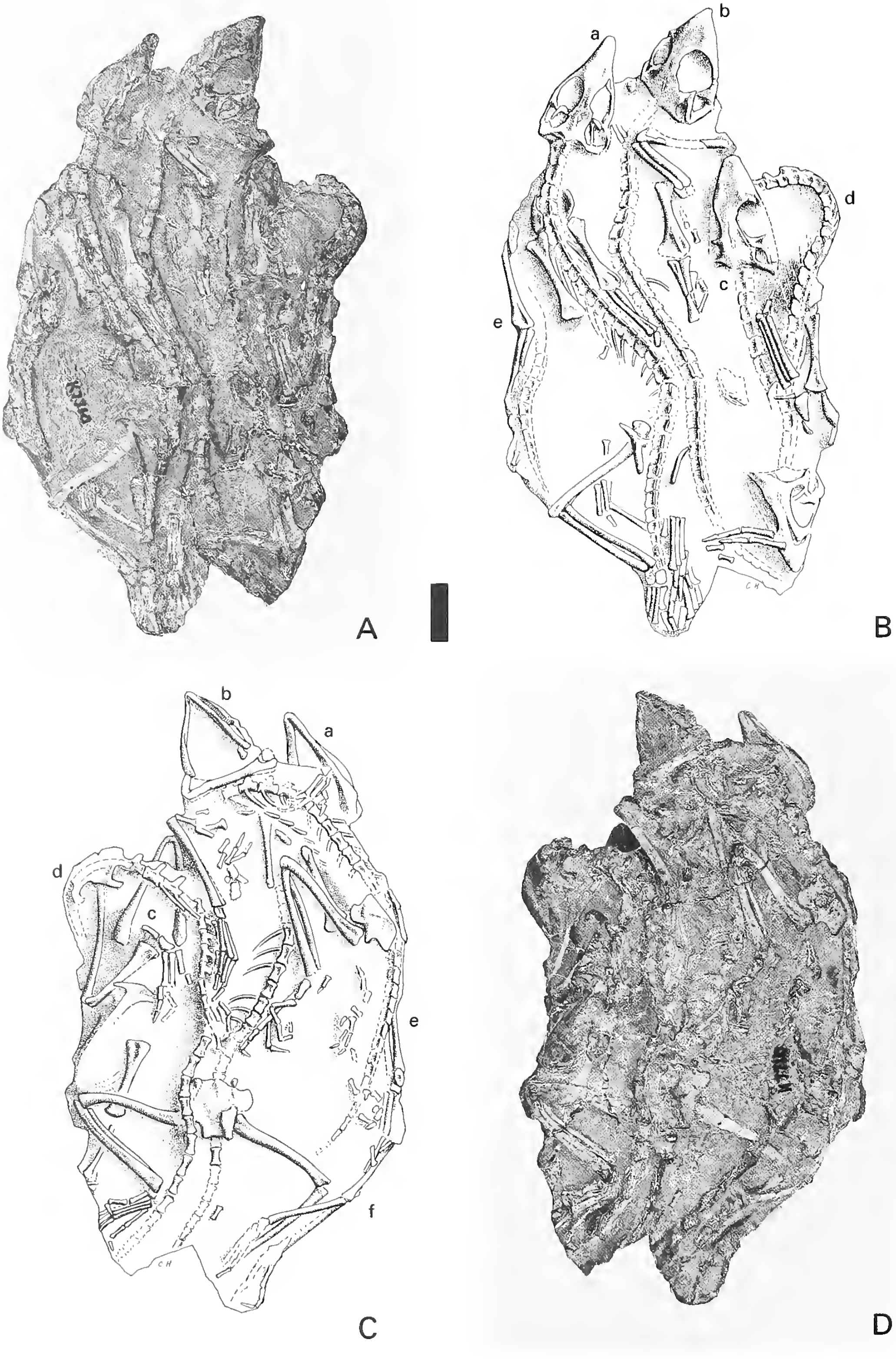
TEXT-FIG. 3. Columnar section at new younginid locality showing details of lithology, sedimentary structure, palaeosols and fossils.

Institutional abbreviations: AMNH – American Museum of Natural History, New York; BPI – Bernard Price Institute of Palaeontology, Johannesburg; KNM – Kenya National Museum, Nairobi; MNHN – Muséum National d'Histoire Naturelle, Paris; SAM – South African Museum, Cape Town; TM – Transvaal Museum, Pretoria.

THE SEDIMENTARY ENVIRONMENT OF THE *YOUNGINA* LOCALITY

The new *Youngina* locality is on the border between the Beaufort West and Loxton districts of the Cape Province of South Africa, within a regionally extensive mudrock sequence, the Hoedemaker Member, which makes up part of the Teekloof Formation of the Beaufort Group (Adelaide Subgroup) in this area (Text-fig. 1). The Hoedemaker mudrocks form the upper part of a large fining-upward megacycle. Several of these 150–450 m thick first order cycles were deposited in a foreland trough by northerly flowing drainage nets. They formed in response to increased subsidence in the foreland basin which was probably synchronous with renewed thrusting in the rising 'Gondwanide' orogenic belt. The basal, predominantly channelized, portion of the megacycle (the Poortjie Sandstone Member) consists of multistoried and multilateral medium to high sinuosity meander-belt sandstone bodies with interbedded overbank mudrocks in ratios of up to 1:2. The overlying Hoedemaker Member has channel to overbank ratios of 1:4–1:6 and has been described as a 'floodplain facies association' (Turner 1978) with sedimentation dominated by unconfined sheet flow, and suspension settling in ponds and lakes.

Previous research on the Hoedemaker mudrocks involving detailed mapping of sedimentary facies and palaeosols, and taphonomic analysis of embedded vertebrate fossils, has led to the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recognition of various sedimentologically defined floodplain environments (Smith 1993). The *Youngina* specimen was found during a systematic search for every embedded fossil that was visible in a 1300 m long by 15 m high cliff section exposure (Text-fig. 2). A total of 243 *in situ* fossils were located, mostly skulls and postcrania of small herbivorous dicynodonts such as *Diictodon*, *Pristerodon*, *Emydops* and *Oudenodon*. The younginid fossil was found in a sequence of drab grey, greenish grey and maroon mudrocks with interbedded light brown fine-grained sandstone sheets. It was embedded in a 2 m thick structureless greenish-grey siltstone which contained no evidence of pedogenic alteration (Text-fig. 3). The host sequence is interpreted as having accumulated on the proximal floodplain areas flanking a large Mississippi-sized meandering river (Smith 1987*a*). Sedimentary structures in the point bars making up the main channel sandstones in this sequence indicate that the river was perennial and prone to large discharge fluctuations resulting in flood dominated sedimentation (Stear 1985). The structureless siltstone in which the younginids were buried is interpreted as sheetflood alluvium, rapidly deposited by sediment-laden floodwaters which overtopped the channel banks and then flowed as an unconfined sheet down the meander-belt ridge and across the proximal floodplain (Smith 1980).

Calcic palaeosols in the associated sediments (see Text-fig. 3) confirm that floodplain sedimentation was highly episodic and semi-arid climatic conditions prevailed in this part of the basin. Comparison of the palaeosol profiles with those of modern soils allows estimates of mean annual temperatures, of between 16 °C and 20 °C, and highly seasonal rainfall, of 500–700 mm/y (McPhereson and Germs 1979; Smith 1990). The distribution of rooted horizons is evidence that vegetation flourished along riverbanks and abandoned channel furrows and consisted of *Glossopteris* trees, horsetails, ferns and clubmosses (Rayner 1992). This supported a stable terrestrial vertebrate fauna dominated by a variety of therapsids, the fossils of which are common enough to be used as biostratigraphical indicators throughout the Beaufort succession. When found, the new younginid specimen (SAM K7710) was completely encased in a thin layer (5 mm) of micrite-cemented siltstone. Such preferential peri-mineralization of fossil bone is common in the proximal floodplain facies of the Hoedemaker Member and is interpreted to be of early diagenetic, probably pedogenic origin.

DESCRIPTIVE PALAEONTOLOGY

The five younginid skeletons are preserved in a dorsalside-up attitude along the floor of a shallow depression. Their skeletons are superimposed (Text-figs 4–5), but show no evidence of disturbance other than that attributable to vertical compaction. The high degree of articulation of these delicate skeletons and the presence of free-floating sternal plates indicates that they were buried with their flesh intact. This, coupled with the spatial arrangement of limbs and the parallel orientation of the skeletons in a dish-shaped depression, is compelling evidence for them having been preserved in 'life position' as a behaviourally arranged aggregation of young animals within an underground burrow.

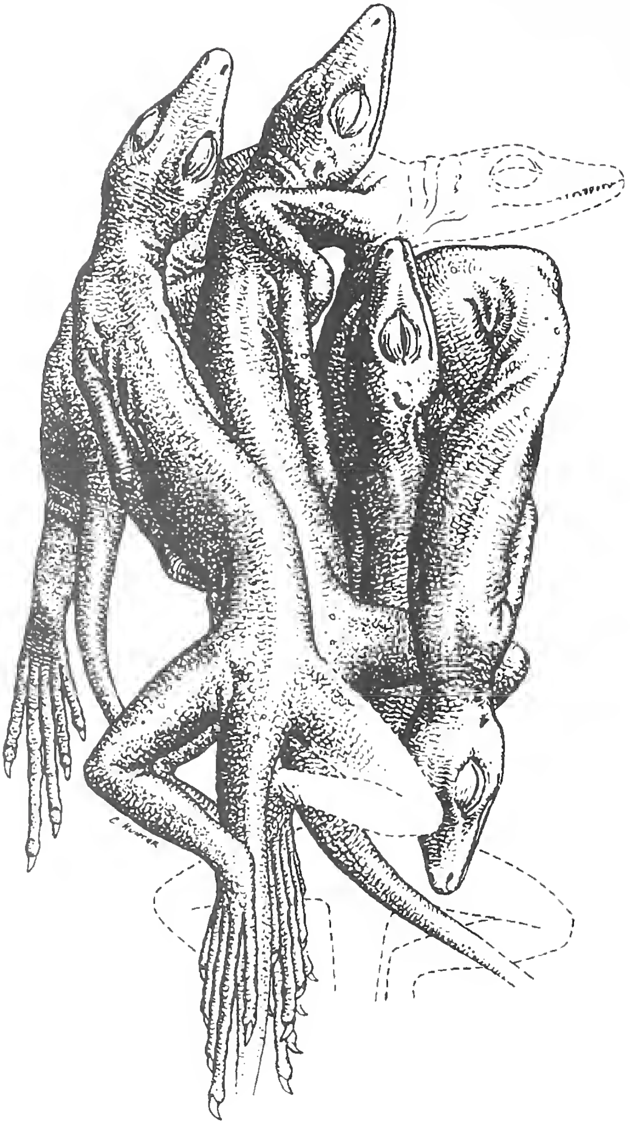
Both dorsal and ventral surfaces were prepared mechanically with dental drill and needle under magnification. Anatomical details were recorded on transparent film using radiographs to maintain positional accuracy. These drawings were then enlarged in a photocopier and reversed onto clear film making it possible to superimpose dorsal-on-ventral views (and vice versa) in order to reveal the intricacies of their taphonomy (Text-fig. 4A–D).

To aid identification in the descriptive section that follows, the articulated skeletons have been coded a–e (Text-fig. 4B–C); f is an isolated hindlimb from another individual.

Identification and ontogenetic age

The five articulated individuals are of closely similar size (snout-vent length 87–95 mm) and are of roughly the same level of skeletal development. In the skull, several features (the elongated posterior process of the post-orbital; the U-shaped configuration of the fronto-parietal suture; the rod-like

TEXT-FIG. 4. *Youngina capensis*; SAM K7710. A–B, the dorsal surface; C–D, the ventral surface. a–f mark individuals as described in the text. Scale bar represents 10 mm.



TEXT-FIG. 5. Fleshed-up reconstruction of the juvenile younginids shortly after their death some 255 Ma.

quadratojugal contacting the jugal below the lower temporal fenestra) identify these animals as younginiforms. This is further corroborated by the short neck (four or probably five cervicals), the form of the vertebrae (midline accessory processes), the structure of the pectoral girdle (long-stemmed interclavicle, sternal plates) and the shape of the distal head of the humerus (well-developed entepicondyle).

In the detailed pattern of preserved skull elements e.g. narrow premaxilla, parietal shape (posterior process angle and orientation; tabular and supratemporal facets), slender dentary; the dentition (tooth shape, maxillary and dentary tooth counts of 20–22 and 19–20 respectively); and in most features of postcranial anatomy (e.g. broad, nearly horizontal dorsal zygapophyses; low rectangular neural spines; the shape of the fifth metatarsal), these small skeletons show no marked morphological differences from previous descriptions of the genus *Youngina* (e.g. Goodrich 1942; Gow 1975). They are, however, only about half the size of other specimens, although many of these are immature (Currie 1981*a*).

The skeletons on SAM K7710 are too well ossified to represent hatchlings. The neurocentral sutures are closed; tarsal and carpal elements are at least partially ossified; the components of pectoral and pelvic girdles are in close proximity (i.e. there were no large areas of cartilage separating them); and the sacral and caudal ribs are fused to their respective vertebrae (although there remains a trace of a suture on one individual). However, there is also evidence that these small reptiles were immature. In the skull, the roofing bones are unsculptured; the paired frontals and parietals are joined by simple sutures and the bones have separated easily; the postorbital bar is slender; and the eyes and the parietal foramen are proportionally large. In the postcranium, the sternal plates are only weakly ossified and remain paired, although the coracoid foramen is already enclosed and the scapula and coracoid appear to have fused; the pubis and ischium are separated by a weakly ossified area and are commonly notched (giving the appearance of a small thyroid fenestra); the obturator foramen of the pubis is open posteriorly in some individuals; and the ends of the long bones lack well-formed joint surfaces. There is no trace of the dermal armour seen in the postcranial skeleton described by Gow (1975) (BPI 3859). The carpals and tarsals appear incompletely preserved and there is no trace of a notch on the calcaneum or astragalus for a perforating artery.

Developmental stages have been described for two other younginiforms, *Hovasaurus* (Currie 1981*a*) and *Thadeosaurus* (Currie and Carroll 1984). *Hovasaurus* was almost certainly aquatic whilst *Thadeosaurus* is thought to have been more terrestrial. Currie (1981*a*) divided his specimens of *Hovasaurus* into a series of age classes from A (hatchling) to H (fully mature adult) on the basis of growth increments, and the same system was used for *Thadeosaurus* (Currie and Carroll 1984). Allowing for the difficulties of comparing aquatic animals with terrestrial ones, and the absence of a full series for *Youngina*, the small younginid skeletons on SAM K7710 would seem to correspond with age class D/E in the Madagascan genera. The sequence of ossification, however, may have been slightly different. Currie (1981*a*), for example, reported that the obturator foramen of the pubis is fully enclosed by stage B in *Hovasaurus*, when the neurocentral sutures are still open. In the young skeletons on SAM K7710, the neurocentral sutures are closed but the obturator foramen is open in several individuals (K7710e for example).

Morphology

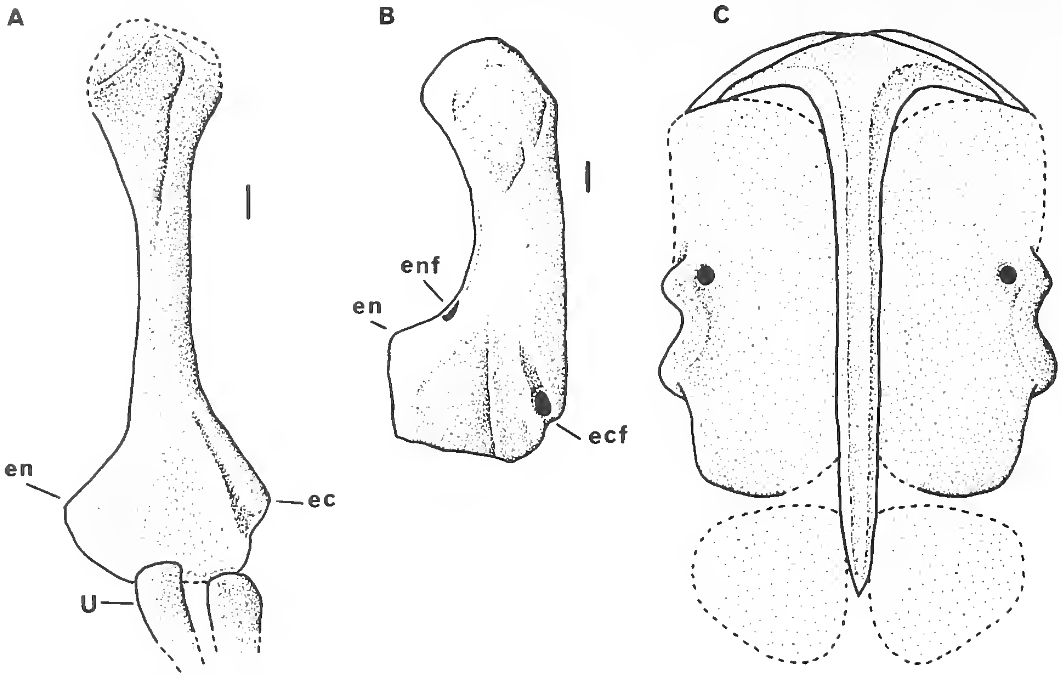
Skull and vertebrae. The skull of *Youngina* is well-known through the work of Gow (1975), and SAM K7710 serves only to confirm details of previous accounts. Gow (1975) described the only associated postcranial skeleton of *Youngina capensis* (BPI 3859) as 'jumbled together in a tight bundle behind the skull' with part of it already rotted away. He estimated that only the atlas, axis and sacral 1 had been lost, giving a presacral count of 23, of which four were cervical. SAM K7710a, however, suggests that there were at least 24 presacrals, probably with five in the neck.

The atlas/axis complex is partially exposed in SAM K7710a. The atlas is eroded but the axis spine is anteroposteriorly extended and there appears to be a small double-headed axial rib (as in *Hovasaurus* Currie, 1981*a*).

Details of vertebral structure are given by Gow (1975) and Currie (1981*b*) and need not be repeated here. As preserved, the vertebrae of SAM K7710 accord with previous descriptions. As in other younginiforms, the last five or six presacral ribs are very short. The sacrum is preserved in SAM K7710d; sacral 1 is robust with a rounded end, sacral 2 and caudal 1 match those figured by Gow (1975), although their tips are damaged. The tail is long with anterior caudals (about 12) bearing strong transverse processes for the caudifemoral muscles. Deep haemal spines begin on the second or third postsacral (a shorter pygal region than that suggested by Gow 1975).

Pectoral girdle and forelimb. Broom (1921) and Gow (1975) described briefly and figured parts of the pectoral girdle and forelimb (from TM 200 and BPI 3859 respectively). Broom's material suggested the presence of small paired sternal plates (as in other younginiforms) and this is confirmed in SAM K7710. By comparison with other genera, these plates presumably fused in the adult.

Several of the individuals on SAM K7710 preserve elements of the pectoral girdle and permit a rather more detailed description and reconstruction of this region (Text-fig. 6c). K7710a reveals only the dorsal parts of

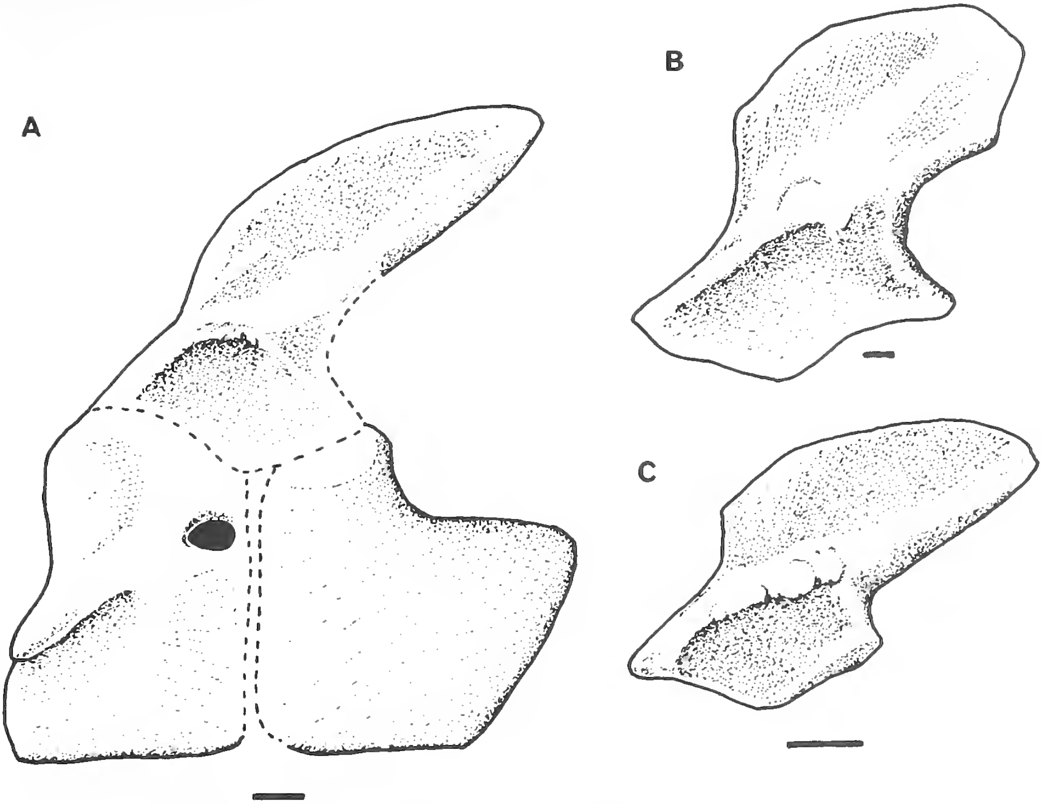


TEXT-FIG. 6. A, *Youngina capensis*, SAM K7710, reconstruction of the left humerus in dorsal view, based mainly on SAM K7710b and e; B, *Hovasaurus boulei*, reconstruction of humerus in dorsal view (redrawn and reversed from Currie 1981*a*, fig. 25); C, *Youngina capensis*, SAM K7710, reconstruction of the pectoral girdle in ventral view. Scale bars: A, C represent 1 mm; B represents 5 mm. Abbreviations: ec, ectepicondyle; ecf, ectepicondylar foramen; en, entepicondyle; enf, entepicondylar foramen; U, ulna.

the scapulae, supporting Gow's (1975) reconstruction of a tall blade, which contrasts with the shallower condition in related aquatic genera (e.g. Currie 1981*a*). The clavicle is preserved in several individuals, but is seen best in K7710a. It is a robust sickle-shaped element with no indication of facets or notches to suggest the presence of a cleithrum (*contra Acerosodontosaurus* Currie, 1980 and *Hovasaurus* Currie, 1981*a*), although the absence of a cleithrum cannot be taken as certain. Ventrally, the coracoid plate appears to be more extensive than shown in Gow's figure (1975, fig. 9c). The coracoid foramen is fully enclosed in K7710a and the glenoid is large. The head of the interclavicle is broadly T-shaped, as illustrated by Gow (1975), but the stem is long (extending the length of about six trunk vertebrae) and supports both the posterior extensions of the coracoids and the sternal plates (Text-fig. 6C). This resembles closely the condition in other younginiforms (Harris and Carroll 1977; Currie 1981*a*).

Most individuals on the SAM K7710 block have elements of the forelimbs preserved. The humerus is preserved on several individuals, and appears as a long, rather slender bone (Text-fig. 6A), ranging in length from 15–17 mm (5–5·7*x*, where *x* is the length of a dorsal centrum, a standard used by Currie 1981*a*). The humeral shaft is twisted so that proximal and distal ends lie at an angle to one another (though at rather less than 90°). The proximal end is narrower than the distal and its dorsal surface bears a distinct depression (corresponding to the insertion of the scapulohumeralis muscle in other taxa; Currie 1981*a*). The distal end is very similar to that of BPI 3859, as described by Gow (1975). It bears an expanded entepicondyle (although less developed than in related genera, e.g. *Hovasaurus*; Text-fig. 6B). This region is pierced by an entepicondylar foramen, but the foramen opens laterally and is not clearly visible in dorsal view. There is an ectepicondylar groove but, at least at this developmental stage (and that of BPI 3859), no ectepicondylar foramen.

The radius and ulna are preserved most clearly in K7710e; they are substantially shorter (70–73 per cent.) than the humerus. According to Gow (1975), the radius of BPI 3859 is somewhat longer than the ulna (18:16 mm), a condition seen in the adults of derived younginiforms, but not in *Acerosodontosaurus* (Currie 1980). However, in immature individuals, this difference can be negligible (e.g. *Thadeosaurus* Currie and Carroll, 1984). In SAM K7710, the radius and ulna are exposed together only in individuals d and e. The



TEXT-FIG. 7. A–B, *Youngina capensis*. A, SAM K7710; reconstruction of the pelvic girdle in left lateral aspect (based mainly on SAM K7710a+e). B, BPI 3859; lateral view of left ilium (drawn from original). C, *Acerosodontosaurus piveteaui*; MNHN 1908-32-57; lateral view of left ilium (redrawn from Currie 1980, fig. 7B). Scale bars: A–B represent 1 mm; C represents 5 mm.

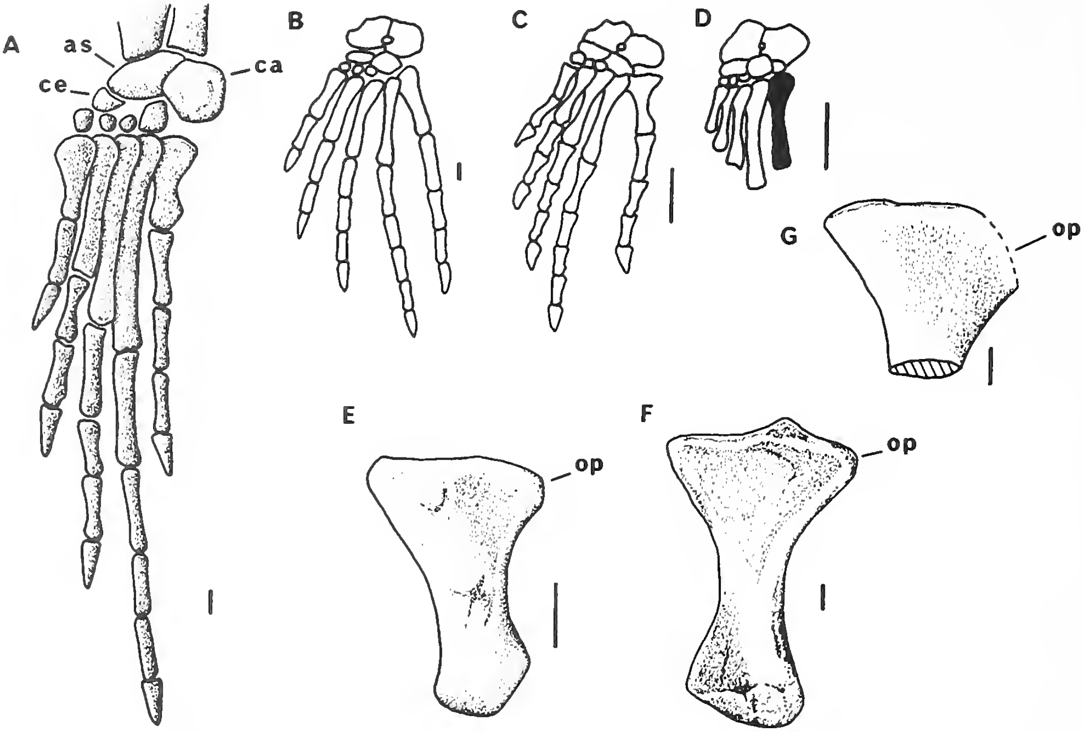
elements appear to be of roughly equal length (3·5*x*), but allowing for the age of the individuals, and the imperfect preservation of the proximal and distal ends, this is not significant. As in other younginiforms, however, the radius is slightly twisted.

None of the wrist and hand elements is clearly preserved. They serve only to support Gow's (1975) general reconstruction of a rather sturdy hand with digits substantially shorter than those of the foot. As in the foot, however, the first and fifth metacarpals appear to be shorter and more robust than those of the intervening digits (seen also in BPI 3859, although not obvious in Gow's fig. 9A). Each claw bears a strong flexor tubercle.

Pelvic girdle and hind limb. Gow (1975) figured a complete pelvis with a notch between the pubis and ischium, interpreting the notch as being due to incomplete ossification rather than an incipient thyroid fenestra. SAM K7710 supports this view. In K7710e, for example, the notch is larger than that shown in BPI 3859 and, anteriorly, incorporates the obturator foramen; in K7710b, ossification is a little more advanced and there is bone filling the puboischiadic notch. The pubis and ischium are short and robust (Text-fig. 7). The former bears a strong pectineal tuberosity and is somewhat inflated anteriorly, both conditions seen in other younginiforms. The ilia are best preserved in K7710a and K7710e. These individuals show the iliac blades to be more attentuated and horizontal than those in Gow's reconstruction (1975, fig. 9d). As preserved, there is certainly a difference in the shape of the blades in BPI 3859 (Text-fig. 7B) and SAM K7710a+e (Text-fig. 7A). However, allowance must be made for the difference in size of the animals, the uncertainty with respect to the shape of the posteroventral margin in SAM K7710, and the possibility that the blade of BPI 3859 is incomplete posterodorsally. Removing the posterior tip from the iliac blade of *Acerosodontosaurus* (Text-fig. 7C), for example, would leave an ilium of a shape similar to that of BPI 3859.

In BPI 3859 the hind limb elements are restricted to a femur, a partial tibia and a fourth metatarsal. By contrast, the hind limbs are well preserved in several individuals on SAM K7710. The femora are long (6·3–7x) and slender, without conspicuous muscle attachments (possibly age-related). The tibia and fibula are also long (6·3–6·7x), with the tibia slightly longer and broader than the fibula.

The ankle is missing in BPI 3859, but was described and figured by Broom (1921) and Goodrich (1942); according to Gow (1975), this material is now lost. In SAM K7710, parts of the ankle are preserved in several individuals (Text-fig. 8A). The proximal tarsal row consists of a large, subtriangular astragalus (intermedium of Broom) which carries facets for the tibia and much of the fibula; laterally it overlaps an almost square calcaneum (fibulare of Broom). Distal to the astragalus is a medial centrale (tibiale of Broom), but the precise size, shape and relations of this bone cannot be determined. The distal tarsal row bears at least four elements (the presence or absence of DT5 cannot be confirmed) of which DT4 is the largest.



TEXT-FIG. 8. A, *Youngina capensis*, SAM K7710, reconstruction of left foot in dorsal view (based mainly on SAM K7710a); B–D, for comparison, reconstructions of the same foot in B, *Hovasaurus boulei* (redrawn from Currie 1981*a*, and based on more than one specimen); C, *Kenyasaurus mariakaniensis* KNM Ma1 (redrawn from Harris and Carroll 1977); D, *Youngina capensis*, TM 200 (redrawn from Broom 1921). E, *Youngina capensis*, SAM K7710d, right fifth metatarsal in plantar view. F, *Kenyasaurus mariakanensis*, KNM Ma1, right fifth metatarsal in plantar view (redrawn from Harris and Carroll 1977). G, *Youngina capensis*, TM 200, the proximal head of the fifth metatarsal as drawn by Goodrich (1942; reversed to aid comparison). Scale bars: A, E–G represent 1 mm; B–D represent 10 mm. Abbreviations: as, astragalus; ca, calcaneum; ce, medial centrale; op, outer process.

The foot is asymmetrical with digit 4 longest (Metatarsal 4, 3–3·3x). The fifth metatarsal is essentially straight but has an expanded proximal head with a conspicuous outer process for the peroneus brevis muscle (Text-fig. 8E). In length, the fifth metatarsal is intermediate between the first and second (Table 1). This interpretation differs from that of Broom (1921, figs 19–20; Text-fig. 8D), who described, and reconstructed the element as being 'a long slender bone, nearly as long as the fourth metatarsal'. Goodrich's (1942, p. 311) account of the same element, based on the original specimen, differs markedly. The bone is described as being considerably shorter than the fourth metatarsal and as having a very broad proximal head (as shown in his accompanying figures and photograph; Text-fig. 8G). Clearly, the shaft of the fifth metatarsal was broken just distal to the proximal head; Broom's reconstruction relied on impressions which must have included the proximal phalanx. The known specimens of *Youngina* are thus closely comparable. All mature younginiforms show some widening of the proximal head of the fifth metatarsal, but, apart from *Youngina*, it is most marked in *Kenyasaurus* (Harris and Carroll 1977; Text-fig. 8F). The phalanges are generally short and robust, with strong unguals; the phalangeal formula is 2:3:4:5:4.

Body and limb proportions. The preservation of the skeletons with the limbs fully articulated permits better estimation of body proportions, even allowing for subsequent changes during growth. Table 1 gives details of the lengths of individual elements, while Table 2 provides a comparison between SAM K7710 and other younginiforms.

TABLE 1. Body proportions in SAM K7710, individuals a–f (all lengths in mm).

	a	b	c	d	e	f
Snout-vent length	89	95	—	87	—	—
Skull length	21	21	22	20	—	—
Humerus	16·5	17	16	14+	15	—
Radius	—	—	—	11	10·5	—
Ulna	—	—	—	11	10·5	—
Femur	18·5	21	—	19	19	13+
Tibia	18·5	20	—	18	19	11+
Fibula	17·5	20	—	—	18	—
MT5	4·5	4	—	—	—	—
MT4	10	—	—	9	—	—
MT3	8·5	7·5	—	7·5	—	—
MT2	6	6·5	—	5·5	—	—
MT1	—	3	—	3	3	—
Reconstructed foot	30	—	—	25+	30	—
Mid trunk centrum	—	3	—	—	3	—
Interclavicle length	—	—	16·5	—	—	—
Tail	—	—	—	90+	78+	—

The young skeletons on SAM K7710 are characterized by their long hind limbs (75 per cent. of snout-vent length), in which all elements, femur, tibia and foot, are elongated. The forelimb is much shorter (around 58 per cent. of the hind-limb length).

SAM K7710 is very similar to BPI 3859 in the relative lengths of the radius, the femur and the fourth metatarsal. The two main differences relate to the lengths of the humerus and the tibia, both of which appear shorter in BPI 3859. The tibia, however, is incomplete in BPI 3859 and was reconstructed by Gow (1975) on the basis of the fragmentary remains of TM 200. Allowing for some underestimate, and the ontogenetic age difference between the *Youngina* specimens, the differences are not significant. In general, the lengths of the radius and tibia are remarkably consistent in younginiforms (Table 2).

The differences in the humerus length, however, are rather greater. Laurin (1991) commented on the unusually short humerus in *Youngina*, but the humeri of SAM K7710 are comparable in length to those of other younginiforms. There are three possible explanations for the differences between BPI 3859 and SAM K7710: there is a genuine, taxonomically significant length disparity; the humerus of BPI 3859 is incomplete; or humeral growth lags behind that of other limb elements in *Youngina*. A combination of the last two alternatives seems most likely. In this case, the humerus of *Youngina* would show a growth pattern the reverse of that in *Hovasaurus* (Currie 1981*a*) and *Thadeosaurus* (Currie and Carroll 1984) where humeral growth is accelerated in relation to other limb elements, leaving the humerus of equal, or greater, length than the femur in the mature adult. Furthermore, the difference between BPI 3859 and SAM K7710 in their humerus/femur ratios (10–20 per cent.) is greater than that between their radius/humerus ratios (8 per cent.), suggesting that accelerated growth of the femur may also have played a part. Growth processes in *Youngina* would therefore have tended to increase the forelimb/hindlimb disparity (as might be expected in a terrestrial cursor) whilst in *Hovasaurus*, they tended to decrease it (as might be expected in a swimmer, although this does not explain the condition in the supposedly terrestrial *Thadeosaurus*).

TABLE 2. Body proportions of Younginiformes. x, length of dorsal vertebra; F, femur; H, humerus; Mt, metatarsal; R, radius; T, tibia. Data from Harris and Carroll 1977; Currie 1980, 1981*a*, 1982; Carroll 1981; Currie and Carroll 1984. * indicates proportions affected by estimate of tibial length.

	Hx	Fx	Rx	Tx	Mt4x	Mt5x	Footx
Acerosodontosaurus	—	6·1	3·8	—	—	—	—
Youngina SAM K7710	5–5·7	6·2–7	3·7	6·2–6·7	3–3·3	1·3–1·5	10
Youngina BPI 3859	4·6	6·8	3·6	5·6*	3·4	—	—
Kenyasaurus	5·3	5·8	—	5·1	2·8	1·9	9·2
Thadeosaurus (Stage B)	5·0	6·7	3·5	5·8	3·2	2·8	12·1
Thadeosaurus (Stage D)	5·1	6·2	3·7	5·4	3·1	2·6	—
Thadeosaurus (Stage G)	6·1	6·2	3·7	—	—	—	—
Tangasaurus	5·5	6·3	3·5	5·5	2·8	2·3	9·5
Hovasaurus (Stage B)	4·2	4·9	2·8	4·1	2	1·4	6·7
Hovasaurus (Stage G)	6·9	6·2	3·9	5·5	—	—	—

	Dig4x	Dig5x	R/H%	T/F%	H/F%	R/T%	Mt5/4%	Dig5/4%
Acerosodontosaurus	—	—	—	—	—	—	—	—
Youngina SAM K7710	8	4·5	70	95–100	79–89	61	45	57
Youngina BPI 3859	—	—	78	89*	68	59*	—	—
Kenyasaurus	7·7	6	—	87	91	—	68	78
Thadeosaurus (Stage B)	10·1	7·5	70	87	75	60	79	83
Thadeosaurus (Stage D)	—	—	65	87	83	62	83	—
Thadeosaurus (Stage G)	—	—	60	89	97	66	—	—
Tangasaurus	8	7·3	66	85	89	63	82	91
Hovasaurus (Stage B)	6·1	5·3	66	84	85	67	80	89
Hovasaurus (Stage G)	—	—	52	85	110	73	—	—

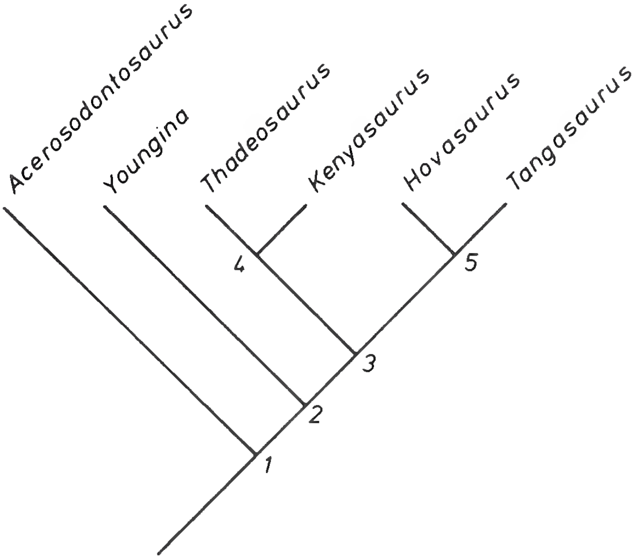
As reconstructed, the foot of *Youngina* also differs from that of other younginiforms in the proportions of the fourth and fifth digits. While the fourth metatarsal is of similar length in all taxa (with the possible exception of *Hovasaurus*), the fifth metatarsal is relatively shorter in *Youngina*, as is the complete fifth digit. The result is a more asymmetrical foot. In *Hovasaurus* and *Tangasaurus*, the fifth digit approaches the fourth in length (89 per cent. and 91 per cent. respectively), while the condition in the less specialized *Kenyasaurus* and *Thadeosaurus* is intermediate (78 per cent. and 83 per cent. respectively). Elongation of the fifth digit may have improved the effectiveness of the foot as a paddle, although without evidence of the foot structure in *Acerosodontosaurus*, the polarity of this character within younginiforms is difficult to assess. In general, however, a short fifth pedal digit appears to be primitive for diapsids; the fifth digit is 61 per cent. of the fourth in, for example, the late Carboniferous *Petrolacosaurus* (Reisz 1981).

DISCUSSION

This is the earliest recorded occurrence of *Youngina* in the Karoo Supergroup, with an estimated age of middle to upper Tatarian (250–255 Ma) based on correlation of the associated *Tropidostoma*/*Endothiodon* fauna with similar fossils in the Rio do Rasto Formation of Brazil (Keyser 1981). These specimens are the only completely articulated and undistorted skeletons of *Youngina* to have been discovered to date.

Relationships. SAM K7710 bears a strong resemblance to previously described material of *Youngina capensis*, differing only in the shape of the iliac blade and in the proportions of the humerus; both differences could be due to a combination of preservation and growth changes. Considering the geological age difference between the specimens, they may have been specifically distinct, but there are inadequate morphological grounds on which to base a new species and the individuals on SAM K7710 must be referred to *Youngina* cf. *capensis*.

These new specimens add to our knowledge of the morphology of the genus and aid comparison with other younginiforms. As concluded by Currie (1982) and Evans (1988), *Youngina* appears to have been distinct from the tangasaurs (*Hovasaurus*, *Tangasaurus*, *Kenyasaurus* and *Thadeosaurus*) which are linked by a number of derived features (Currie 1981*a*; Evans 1988; Text-fig. 9) including a more pronounced expansion of the entepicondylar region of the humerus and an apparent elongation of the fifth digit in relation to the fourth (Text-fig. 7B–C). In the absence of accessory processes on its vertebral neural spines, *Acerosodontosaurus* (Currie 1980) appears to lie at the base of the group, although its incomplete preservation limits its usefulness as an outgroup for *Youngina* and the tangasaurs.



TEXT-FIG. 9. Cladogram showing generally accepted relationships of the younginiform genera (based on Currie 1982 and Evans 1988). Nodes: (1) short neck with 4–5 cervicals; postorbital bone with posterior process reaching posterior margin of upper temporal fenestra; reduced, rod-like quadratojugal meeting jugal below lower temporal fenestra; enlarged humeral entepicondyle. (2) accessory articulation facets on neural spines; paired sternal plates which co-ossify in mature adult; radius longer than ulna in mature adult. (3) Tangasauridae: humerus = or > femur; radius 50–65 per cent. humerus length; medial centrale of wrist meets distal carpal 4; medial centrale of wrist = 2 × lateral centrale; first distal tarsal enlarged; fifth distal tarsal lost or fused; humeral entepicondyle greatly enlarged; scapula blade low; scapula subequal to coracoid. (4) 19–28 pairs of caudal ribs and transverse processes present. (5) high dorsal and caudal neural spines; 9–12 pairs of caudal ribs; anterior caudal ribs expanded distally; haemal spines enlarged and plate-like.

Lifestyle. The lightly built, long-limbed skeletons provide evidence that *Youngina*, unlike its Madagascan relatives, was a fully terrestrial animal occupying a niche similar to that of many modern lizards in semi-arid environments. This is in accord with the reconstructed palaeoenvironment (see above) and with aspects of the preservation which may provide evidence of behaviour.

The juveniles of some modern species of viviparous lizards, e.g. skinks, are known to huddle together with very similar intertwining and side-by-side disposition. These aggregations involve members of a single brood and are usually found in confined cavities beneath fallen logs or within underground burrows (Shine 1994). Under warm, semi-arid climatic conditions the advantages of such behaviour could be improved diurnal thermoregulation (Gregory 1982) and more efficient aestivation during drought (Seidel 1978).

Published reports of monospecific juvenile aggregation in other groups of fossil reptiles involve Cretaceous ornithopod dinosaurs, namely hypsilophodontids (Horner 1984), *Tenontosaurus* (Forster 1990) and hadrosaurs (Horner and Makela 1979), many of which have been found in association with nests and eggshells. To date, no eggs or nesting sites have been found in the

Beaufort Group although burrow casts containing curled-up skeletons of the small dicynodont *Diictodon* do occur in the vicinity of the younginid locality (Smith 1987*b*). Interestingly, an aggregation of ten juvenile skeletons of *Diictodon* (SAM K1650) was found within 100 m of the younginids and ten more isolated juvenile *Diictodon* skulls occurred along the 1300 m cliff section (Text-fig. 2). The relatively common preservation in the proximal floodplain facies of articulated juvenile skeletons belonging to more than one tetrapod group may indicate that this was a preferred 'nesting' area. However, the wide range of disarticulation classes amongst the rest of the fossil assemblage and the 'clustering' of fossils with comparatively unweathered bone surfaces suggests that the periodicity of flood events and the net floodplain accretion rate were the major factors determining the preservation of skeletons. Floodplain accretion rates of the strata that host the juvenile aggregations range from 14 mm/y in topographical lows to 9 mm/y on the flats (Smith 1993). These rates are high enough to suggest regular, possibly seasonal, flooding of the proximal floodplains and it is proposed that the greater frequency of overbank flows resulted in the increased preservation of juveniles in these sediments.

Acknowledgements. We thank Annelise Crean for painstaking preparation of these small skeletons, Clive Booth for photography and Cedric Hunter for his artistic flair on Text-figures 4–5.

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THE SKULL OF *DELTACEPHALUS WHITEI*, A LYDEKKERINID TEMNOSPONDYL AMPHIBIAN FROM THE LOWER TRIASSIC OF MADAGASCAR

by R. H. HEWISON

ABSTRACT. The holotype and only skull of *Deltacephalus whitei* from the Lower Triassic of Madagascar, is redescribed and reconstructed. *D. whitei* shares several morphological features with *Lydekkerina huxleyi* and *Limnoiketes paludinatans* and is argued to be a member of the family Lydekkerinidae. Derived characters distinguishing the Lydekkerinidae from other rhinesuchoid temnospondyls are given, and the genus *Deltacephalus* is diagnosed within the family. The Early Triassic littoral temnospondyl fauna from north-west Madagascar is reviewed and compared with contemporaneous temnospondyl faunas from the *Lystrosaurus* Zone of South Africa and the Sticky Keep Formation of Spitsbergen. The Rhytidosteidae and Capitosauridae are represented in all three faunas, whilst the Madagascan fauna is intermediate in sharing lydekkerinids with the South African fauna and trematosaurids with the Spitsbergen fauna.

DELTACEPHALUS *whitei* Swinton, 1956 is known only from the holotype, BMNH R6695, a small ironstone concretion enclosing natural moulds of a single skull. Swinton (1956) described it as a new genus of rhinesuchoid temnospondyl which he named *Deltacephalus whitei*. He believed *Deltacephalus* to be related to the poorly known lydekkerinid temnospondyl *Broomulus dutoiti* from the *Lystrosaurus* Zone of South Africa, and so assigned it to the Lydekkerinidae.

Deltacephalus is one of several temnospondyl genera described from the Lower Triassic Middle Sakamena Group of north-west Madagascar. Our knowledge of these temnospondyls derives mainly from the work of Lehman (1955, 1961, 1963, 1966, 1979) who described most forms and discussed their relationships. *Deltacephalus* was not, however, included in these studies and is considered by most recent authors to be unclassifiable below Stereospondyli *incertae sedis* (e.g. Cosgriff 1974, p. 43; Milner 1990, p. 348).

As part of a revision of the Lydekkerinidae, new casts were made at the Natural History Museum, London, and these, together with study of the original moulds and earlier plaster casts have permitted a more extensive description of the specimen, including many new details of the skull roof, palate and occiput.

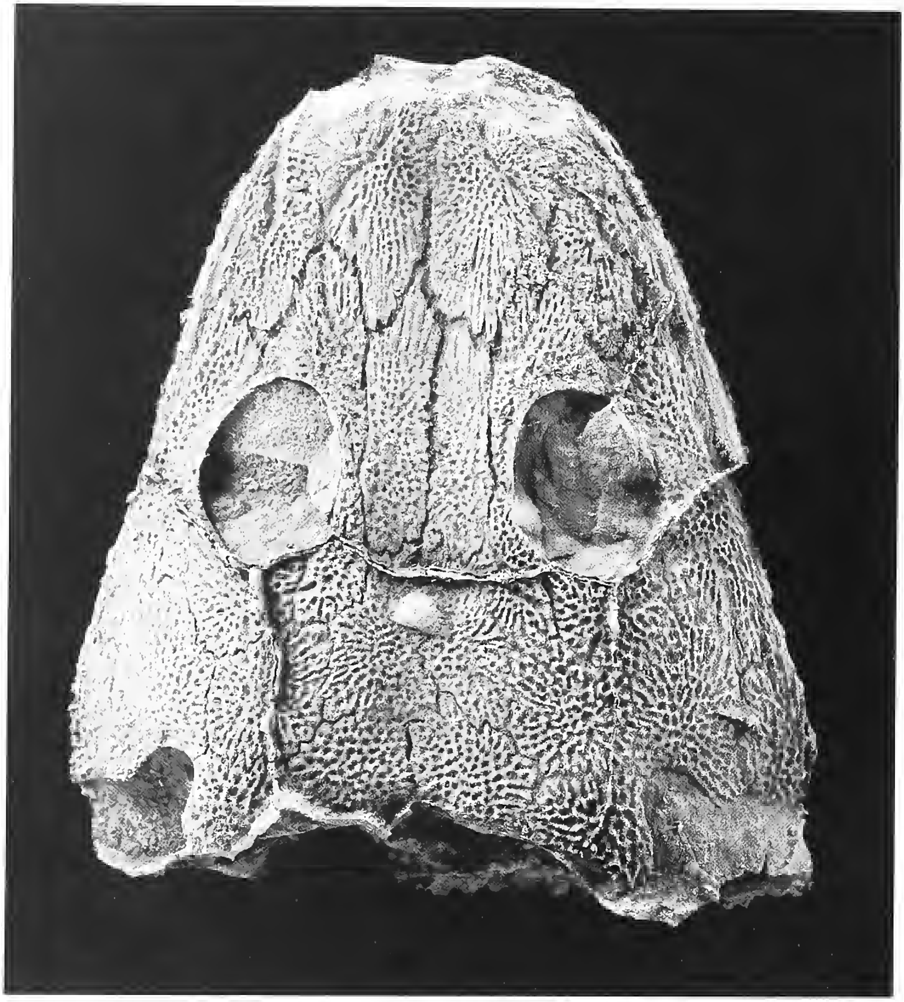
Institutional abbreviations used in this work are as follows: BMNH, The Natural History Museum, London, UK; BPI, Bernard Price Institute, Johannesburg, South Africa; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; UMZC, University Museum of Zoology, Cambridge University, UK.

MATERIAL AND METHODS

The concretion bearing the skull is broken into three closely fitting pieces, two larger fragments bearing impressions of the skull roof and palate respectively, while the smaller third piece bears an impression of the occipital surface. The impression of the dorsal surface of the skull is well preserved, those of the palate and the occiput less so. The skull lacks the extreme anterior region of the snout and a few small areas along its posterior edge, whilst much of the palate anterior to the interpterygoid vacuities is missing. The occipital surfaces of both cheek regions are obscure and the skull has suffered some compression over the snout region and also on its right side, particularly behind the orbit.

In 1993 new peels of the specimen were made at the Natural History Museum, London, using 'Wacker' cold cure silicone rubber, to complement older plaster and coloured 'Welvic' casts.

[Palaeontology, Vol. 39, Part 2, 1996, pp. 305–321]



TEXT-FIG. 1. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Silicone rubber peel of dorsal aspect of holotype skull BMNH R6695; ×2.

Photographs of these new peels, coated with graphite to highlight detail, illustrate this work (Text-figs 1, 4). Under the binocular microscope, detail was easier to see on the 'Welvic' casts and the following description and Text-figures 2–3 and 5–8 are based on study of these and the original specimen.

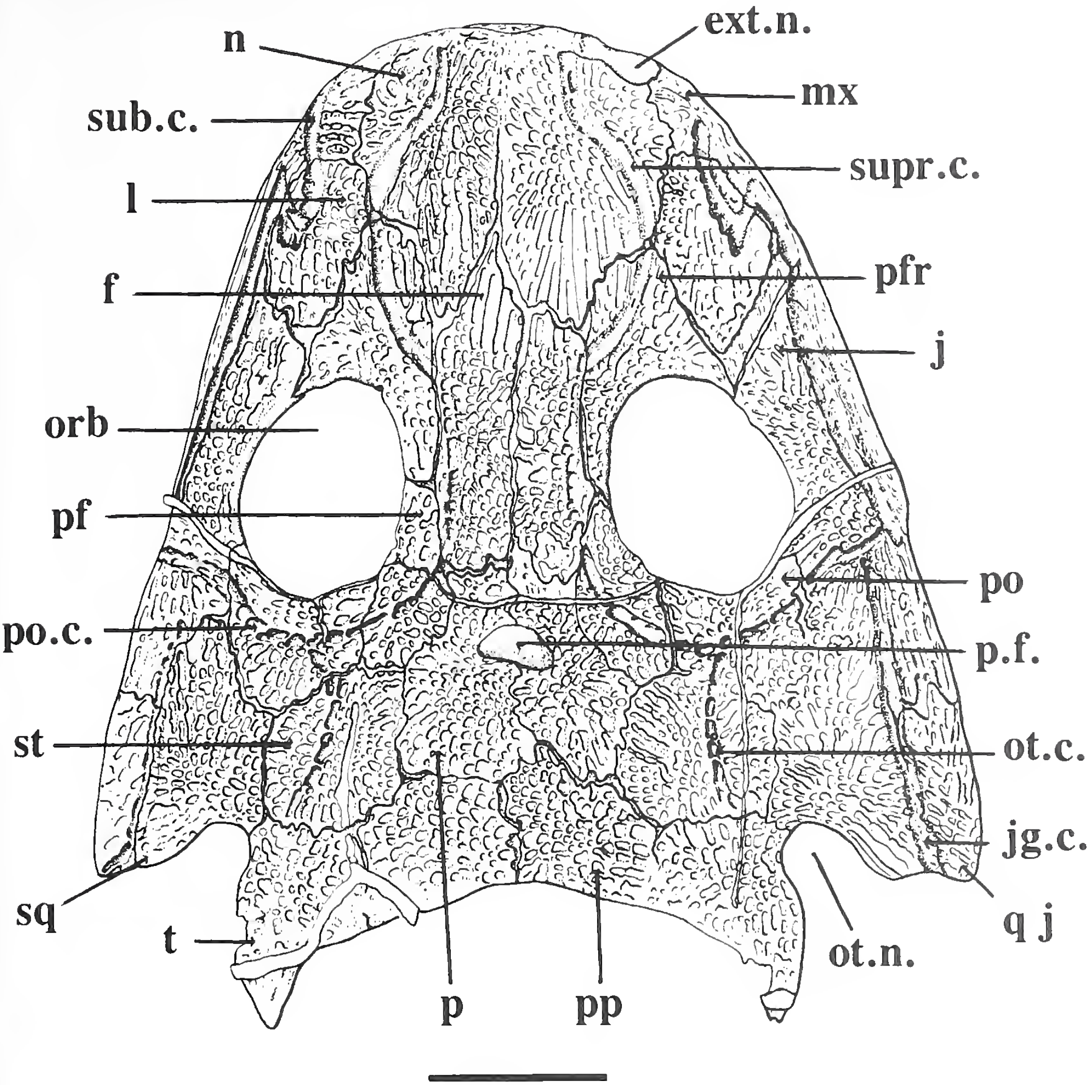
SYSTEMATIC PALAEONTOLOGY

Class AMPHIBIA Linnaeus, 1758
Order TEMNOSPONDYLI von Zittel, 1890
Family LYDEKKERINIDAE Watson, 1919

Genus DELTACEPHALUS Swinton, 1956

Type species. *Deltacephalus whitei* Swinton, 1956.

Diagnosis. As for the only species.



TEXT-FIG. 2. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Holotype skull BMNH R6695, dorsal surface, drawn from Welvic cast. For abbreviations see list on p. 321. Scale bar represents 10 mm.

Deltacephalus whitei Swinton, 1956

Text-figures 1–8

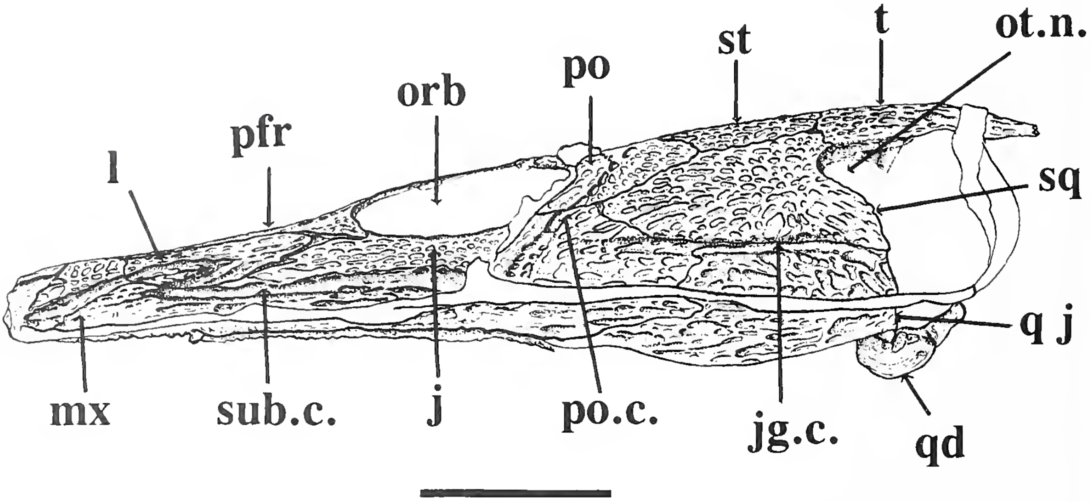
Holotype and only specimen. BMNH R6695, a small ironstone concretion enclosing a complete skull represented by natural moulds.

Locality and horizon. Ambarakaraka, 8 km north of Anaborano, north-west Madagascar; Middle Sakamena Formation, Induan, Lower Triassic.

Diagnosis. Distinguished from other lydekkerinids by the following combination of characters: skull parabolic with broadly rounded snout; lateral margins slightly sinuous; quadratojugal corners anterior to level of middle of posterior skull table margin; tabular horns long and curved; parietal foramen oval; prominent lateral-line system with deep lyrae; cultriform process striated ventrally with weak keel; parasphenoid corpus ridged, bearing poorly developed stapedial lappets; palatal ramus with slight pterygoid flange; interpterygoid vacuities and occipital openings relatively large; opisthotic not exposed in paroccipital bar.

Description

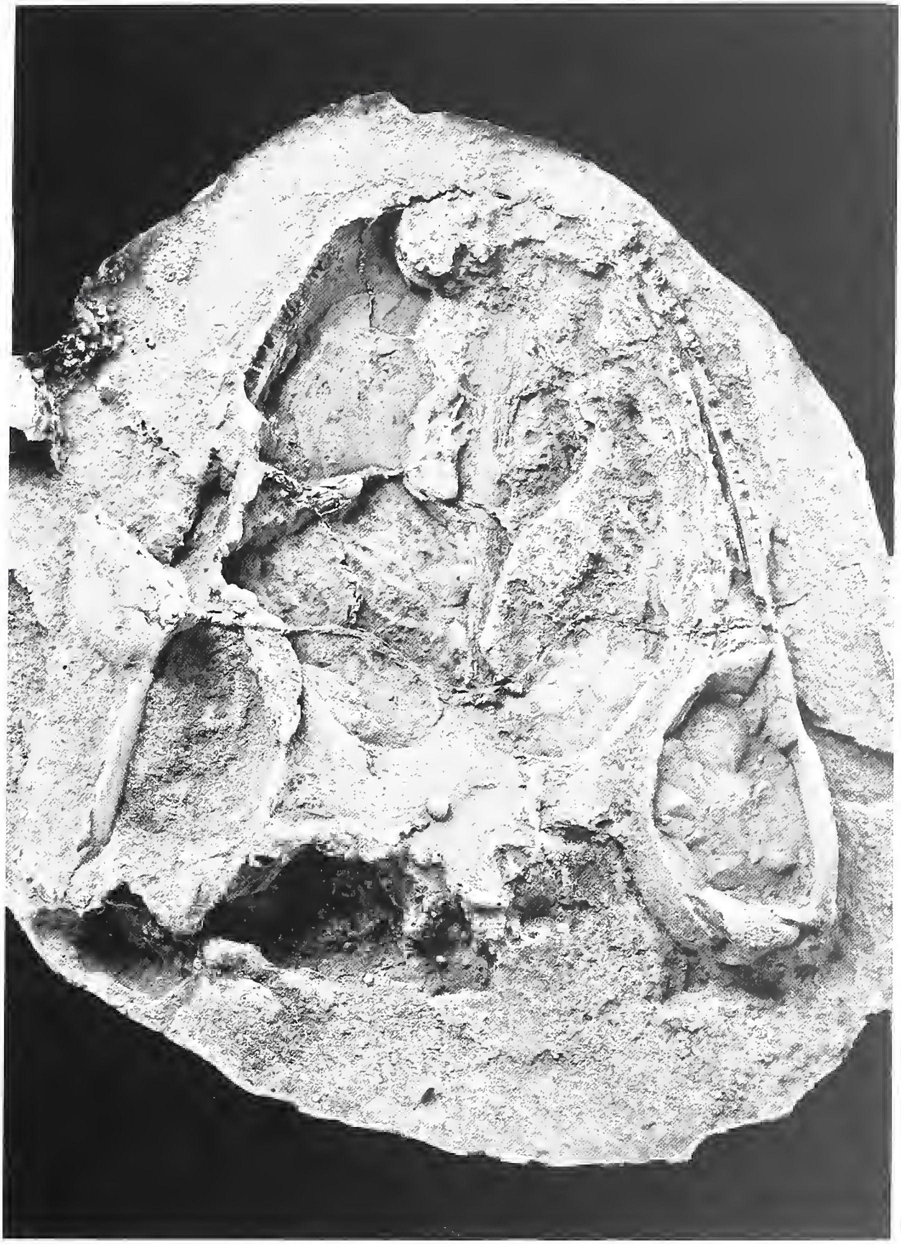
Skull roof (Text-figs 1–3, 7). This skull, like those of all lydekkerinids, is small, moderately flattened and as short as it is broad. As preserved, it has a median length of 48 mm and a maximum width of 49 mm (Text-fig. 2). It has a rounded snout and its slightly sinuous lateral borders give it a broadly parabolic outline. The posterolateral corners of the quadratojugals lie slightly ahead of the level of the midpoint of the posterior margin of the skull table. The tabular horns are relatively long and curved, and are more fully developed than Swinton's figure suggests. The large orbits have a central position on the skull roof, resulting in the short preorbital region that characterizes all lydekkerinids. In profile, the skull appears depressed, particularly in the facial region, exaggerated somewhat by the dorso-ventral compression of the snout (Text-fig. 3). The central hollowing seen on the roof of *Lydekkerina* is paralleled here, and the cheek regions similarly curve gently ventrolaterally from the skull table.



TEXT-FIG. 3. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Holotype skull BMNH R6695, left lateral view, drawn from Welvic cast. For abbreviations see list on p. 321. Scale bar represents 10 mm.

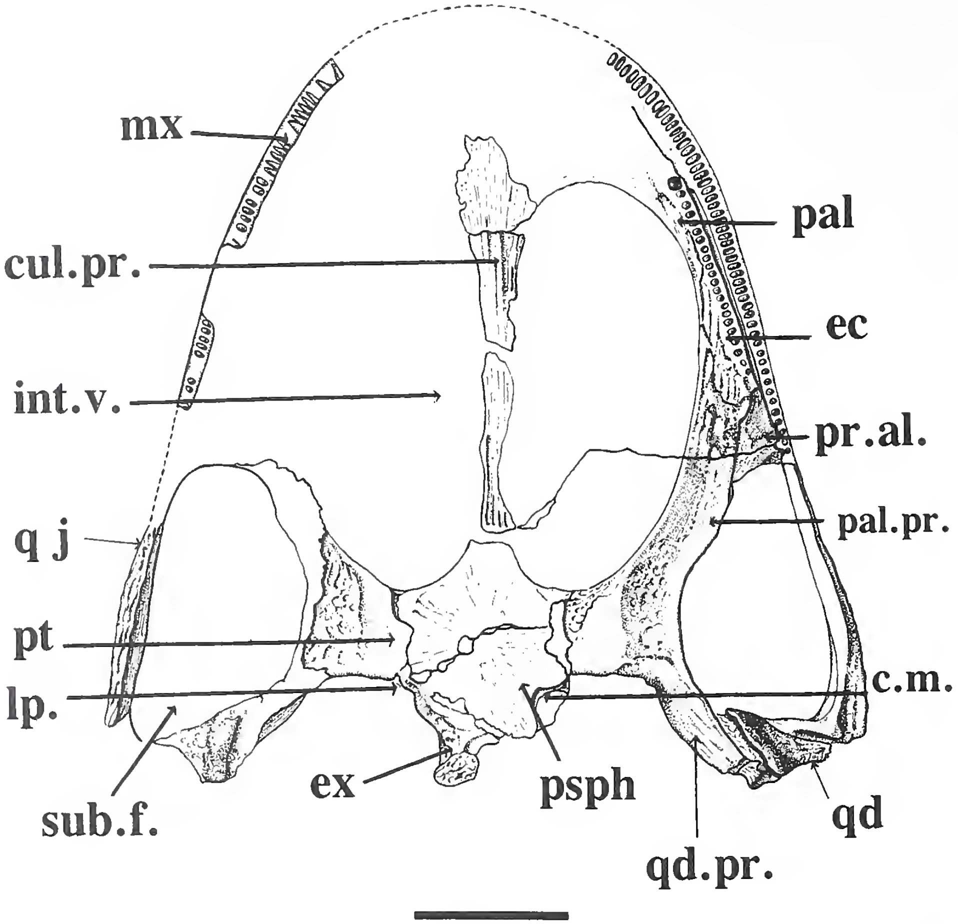
The impression of the dorsal surface of the skull is well preserved and most of the sutures are clearly visible. The sensory openings are relatively very large (Text-figs 1–3). Little can be seen of the external nares because of the loss of the anterior tip of the snout, but there appear to be traces of the posterior region of the right naris. There is no evidence to support Swinton's reconstruction of the nares as narrow and transversely situated. The large, oval orbits have less elevated margins than in *Lydekkerina* and the large parietal foramen, although distorted, appears to have been broader than long, and of an oval rather than circular shape. Its present kidney-shaped outline is probably an artefact of preservation. The well developed U-shaped otic embayments, which are incised quite deeply into the squamosals and open posteriorly, are similar to those of *Lydekkerina* and *Limnoiketes*.

As a result of local compression, the right roofing bones now appear as slightly larger than their left counterparts. Both premaxillaries are missing and septomaxillaries cannot be seen. Posterior to the exterior



TEXT-FIG. 4. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Silicone rubber peel of palatal aspect of holotype skull BMNH R6695; ×2.

naris, the nasal and maxillary meet to exclude the lacrimal from the narial border. The lacrimals, far from having the very unusual jagged outlines figured by Swinton, are relatively small elongated bones of orthodox shape. Swinton incorrectly identified part of the suborbital sulcus, with its characteristic lacrimal flexure, as the outer border of the lacrimal. As in *Lydekkerina* and *Limnoiketes*, the frontals are separated from the orbits by

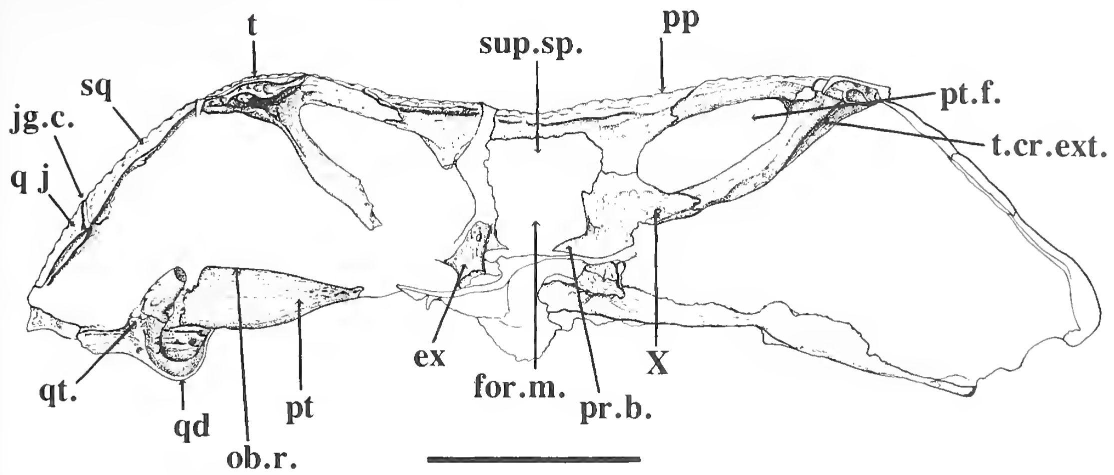


TEXT-FIG. 5. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Holotype skull BMNH R6695, palatal surface, drawn from Welvic cast. For abbreviations see list on p. 321. Scale bar represents 10 mm.

the prefrontal–postfrontal contact, and the supratemporals from the otic embayments by the squamosal–tabular contact.

As in other lydekkerinids, the dermal ornament of the roofing bones consists of a network of ridges which separate either rounded depressions or more elongated grooves. The ornament is best seen on the casts (Text-fig. 1), where, in the unworn areas, the ridges are smoothly rounded and form slight conules where they meet each other as in *Lydekkerina* and *Limnoiketes*. The depressions vary considerably in size and outline, and tend to cover the more central areas of the bones. Grooving is generally restricted to the peripheral areas, and ornamentation often appears to radiate away from the ossification centre of the bone. The presence of a preorbital zone of intensive growth is indicated by the pronounced grooving of the ornament over the posterior third of the nasals and the neighbouring portions of the frontals and prefrontals. Less pronounced postorbital grooving occurs over the posterior region of the jugal, and over the neighbouring margins of the squamosal and quadratojugal.

The lateral-line system is more extensive than Swinton indicated and, as is normal for lydekkerinids, the sulci appear partly as grooves and partly as rows of depressions (Text-figs 1–3). The grooves are deep and wide. Several sulci pass over, or close to, the ossification centres of bones. The supraorbital sulcus forms a typical lyra over the facial region where it is developed as a deep and wide groove, but its interorbital section consists of a series of separate shallow depressions. The suborbital sulcus, clearly visible on the left side of the skull, forms a deep and wide groove crossing the jugal and maxillary, and having the usual lacrimal flexure over the



TEXT-FIG. 6. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Holotype skull BMNH R6695, occipital surface, drawn from Welvic cast. For abbreviations see list on p. 321. Scale bar represents 10 mm.

maxillary and lacrimal. The jugal, postorbital and otic sulci were neither described nor figured by Swinton, but are visible on the new casts. The otic sulcus is an extensive series of depressions which leaves the postorbital sulcus and curves across the supratemporal.

Palate (Text-figs 4–5, 8A). The impression of the palatal surface is less well preserved than that of the cranial roof. Apart from the very poorly preserved region anterior to the interpterygoid vacuities, most of the structure of the palate can be described from one side or the other. The palate is slightly distorted, however, and the anterior region of the cultriform process has been crushed against the skull roof, while the left quadrate is partly detached from the quadrate ramus of the pterygoid.

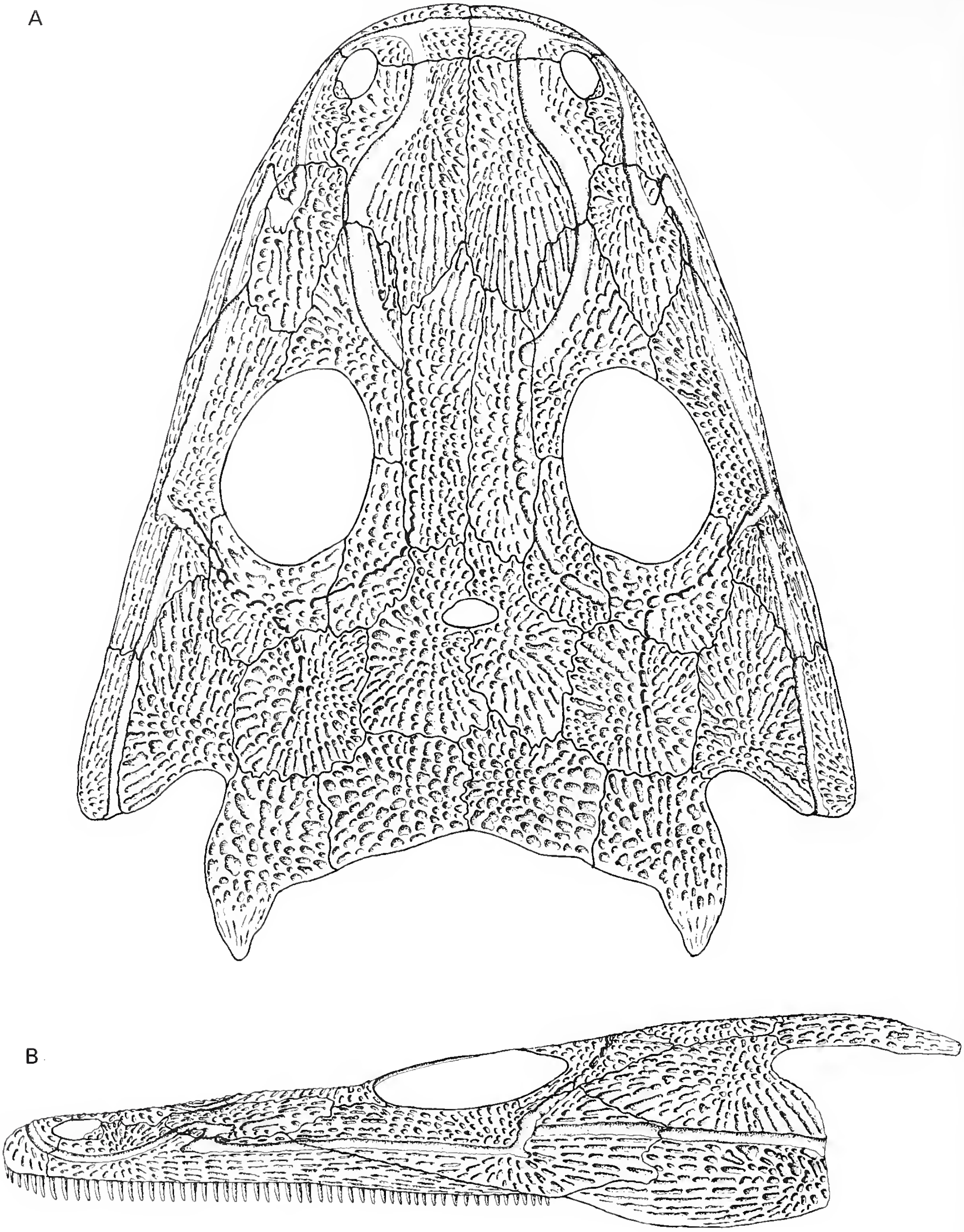
The palate is characterized by the very large interpterygoid vacuities and subtemporal fossae, separated and bordered by relatively slender struts of bone (Text-figs 4–5). The interpterygoid vacuities extend over half the length of the palate and are not so narrow and anteriorly pointed as depicted by Swinton. Nearly all of the outline of the left vacuity is visible and it is slightly broader anteriorly than posteriorly. The subtemporal fossae extend anteriorly well ahead of the posterior borders of the interpterygoid vacuities, and the well preserved left fossa has a length almost one-third of that of the skull. It lacks the simple hemispherical outline figured by Swinton, but is rather 'pear-shaped' being broadly rounded posteriorly, and narrower and more elongated anteriorly (Text-fig. 5).

The parasphenoid has a well-developed corpus with moderately long sutural contacts with the pterygoids, and with a series of fine ridges radiating away from the centre of the palatal surface. On its left side, towards its posterolateral corner, there appears to be a crescentic, ridge-like crista muscularis, which overhangs slightly a shallow depression which appears to represent a 'pocket' for the insertion of a rectus capitis muscle (Text-fig. 5). Both crista and pocket are less well developed than in *Lydekkerina* and *Limnoiketes*, but as in these forms, the crista faces posterolaterally and lies well ahead of the condylar region, towards the posterior end of the parasphenoid–pterygoid suture. The bone surface on the corresponding regions of the right side of the corpus has been abraded and shows no trace of either crista or pocket.

On both sides of the specimen, the posterior margin of the parasphenoid corpus gives the impression of having been produced backwards to form a stapedial lappet, but this is far less developed than in the other lydekkerinids. The sutures between the parasphenoid and the exoccipitals cannot be clearly seen.

The cultriform process, though broken, slightly displaced, and partly obscured by matrix, appears to have been a long and relatively broad blade. It terminates anterior to the interpterygoid vacuities as an expanded, broad, V-shaped wedge lying between the vomers. It bears a series of ventral ridges, generally parallel to its long axis, and there is a suggestion of a slight, narrow, median keel.

The left pterygoid is well exposed on the casts and closely resembles those of *Lydekkerina* and *Limnoiketes* in possessing ornament over the lateral portions of its corpus, the palatal ramus and the base of the quadrate ramus (Text-fig. 5). The proportions of the pterygoid differ considerably from those figured by Swinton. The



TEXT-FIG. 7. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Reconstruction of the skull in A, dorsal view; B, left lateral view.

corpus is broad and has a moderately long common suture with the parasphenoid, although details of this are not visible. Its ventral surface has a raised medial area almost devoid of ornament and a more depressed lateral ornamented area.

The long and moderately broad palatal ramus has a shallow pterygoid flange protruding into the subtemporal fossa and it tapers anteriorly to suture with a probable processus alaris of the jugal, and anterior to this, with an ectopterygoid. The ramus appears to extend slightly more than half-way around the border of the interpterygoid vacuity, but it is not clear where or not it sutured with the palatine. The ramus is hollowed out for most of its length, the hollow being bordered by a ridge mesially, and by a distinct upturned flange laterally which bounds the subtemporal fossa. The ornament on the anterior ramus is particularly striking, forming a series of elongate ridges and grooves.

The quadrate ramus is much shorter and more slender than the palatine ramus but is also ornamented proximally with depressions and ridges, although in a less pronounced manner. The quadrate, hitherto undescribed, is visible on the left side. It is a stout ossification, bearing a well-defined convex condylar keel medially but becoming lower and narrower laterally where it is firmly clasped anteriorly and posteriorly by mesially directed paraquadrate laminae from the quadratojugal (Text-figs 4–5). A ridged swelling at the base of the anterior lamina probably buttressed a smaller lateral condylar keel although this cannot be seen because the lateral end of the quadrate is missing.

A processus alaris from the jugal appears to have been exposed by disturbance immediately anterior to the left subtemporal fossa (Text-figs 4–5). It is a roughly triangular bone, lacking palatal teeth. Anterior to it lies a narrow ectopterygoid which bears the posterior portion of a palatal tooth row laterally, except at its posterior end. None of the ectopterygoid sutures are visible clearly and it is uncertain whether the ectopterygoid reached the margin of the interpterygoid vacuity or was excluded by a backward extension of the palatine. The palatine bears along its entire lateral border an anterior continuation of the tooth-row seen on the ectopterygoid. This row comprises 20 teeth and two pits, and terminates in a larger, more rounded, fang on a level just anterior to the front end of the interpterygoid vacuities. This fang is probably one of the pair of palatine fangs normally situated just posterior to the choana. The following palatal tooth-row is similar to that of other lydekkerinids in lacking ectopterygoid fangs.

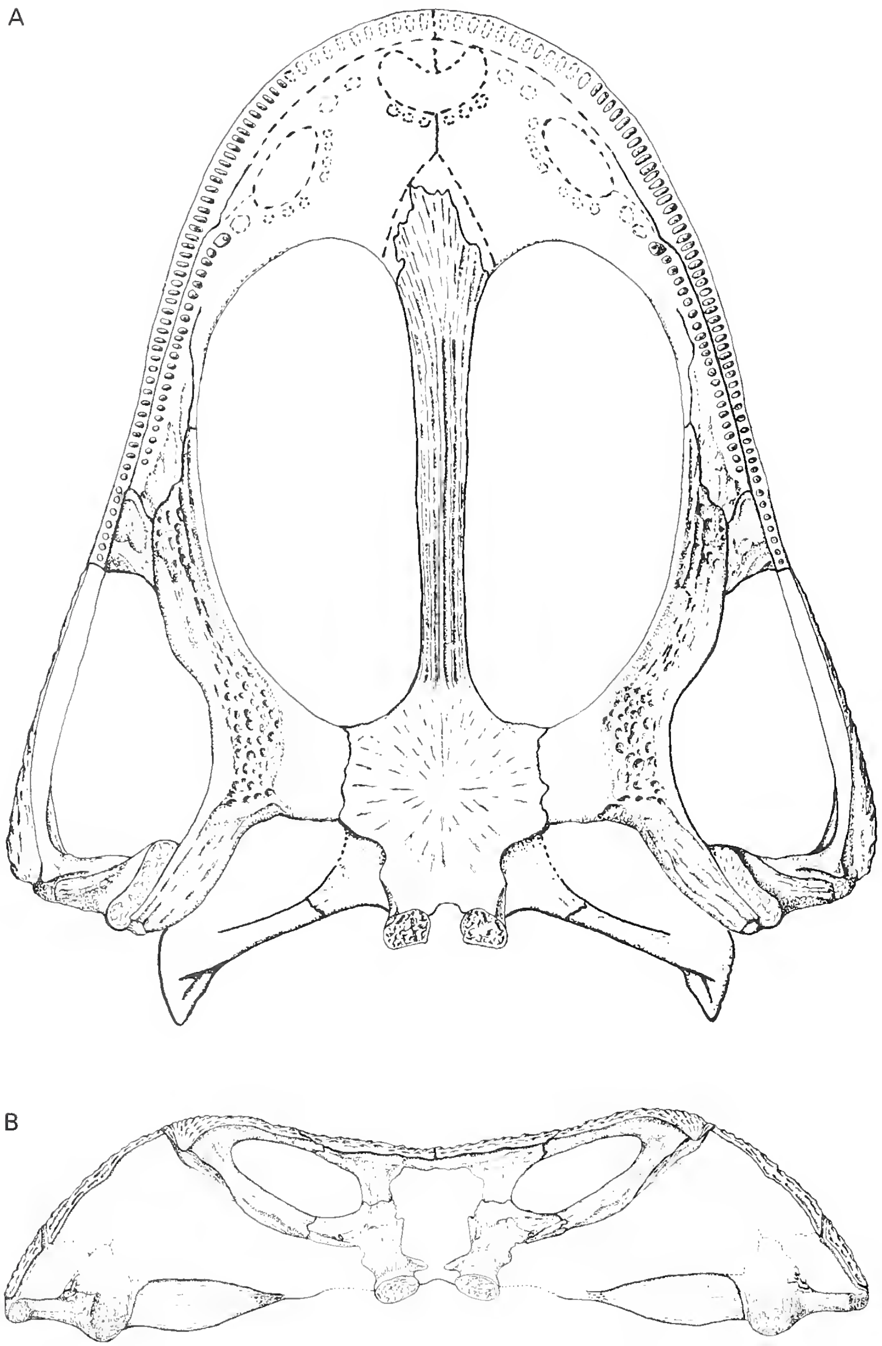
Some hitherto unreported details of the maxillary teeth can be made out. The palatal portion of the left maxillary forms a slender strip of bone extending from the anterior end of the subtemporal fossa along the whole of the preserved lateral border of the skull (Text-fig. 5). It bears a long, continuous row of closely set, small teeth which are relatively long and slender with slightly recurved tips. About 39 teeth and 11 pits have been preserved, suggesting space for 50 teeth in each maxillary. The teeth enlarge over the anterior half of the tooth row, reaching a maximum length of 2 mm. In the right maxillary, two toothed portions survive, the more anterior with 19 teeth and the posterior fragment with eight. The maxillary teeth are slightly larger than the palatal teeth.

Occiput (Text-figs 6, 8B). The impression of the occipital surface is only partly preserved, but is easier to interpret from the specimen than from the casts because of the contrast between its black colour and the paler surrounding matrix. Although the occiput has been crushed slightly on its right side, with parts having been displaced, certain aspects of its structure can be ascertained. Several new features can be added to Swinton's account, and the occipital surface is figured here for the first time.

The occipital surface, like the palate, is characterized by having large openings separated and bounded by relatively slender struts of bone (Text-figs 6, 8B). The posttemporal fossa is complete on the right side of the impression and is seen to be roughly egg-shaped with its narrower end directed dorsolaterally. The essentially triangular foramen magnum has a wide base that is floored partially by a pair of basal processes from the exoccipitals and it narrows dorsally before opening into a wide supraoccipital space. Also visible is the broken-off remnant of the right exoccipital process which once supported the cartilaginous supraoccipital.

On the right side, the occipital flanges of the postparietal and tabular are clearly visible, as are the rising flanges of the exoccipital which suture with them. The complete, right paroccipital bar shows that, as in *Limnoiketes*, the opisthotic is not incorporated, and that the tabular extends down to the exoccipital, forming the major part of the ventral border of the posttemporal fossa. The lateral limits of the exoccipital on the bar are indicated by a meandering suture on the impression, which crosses the bar a quarter of the way up its length from its base. The corresponding portion of the left paroccipital bar is missing.

The preserved right occipital process of the tabular is greatly expanded and thickened proximally to provide strong support for the tabular, whilst the tabular horn was also supported ventrally by a strongly developed crista tabularis externa which, as in *Lydekkerina* and *Limnoiketes*, runs along the posterolateral border of the process and onto the underside of the tabular horn.



TEXT-FIG. 8. *Deltacephalus whitei* Swinton; Lower Triassic; Madagascar. Reconstruction of the skull in A, palatal view; B, occipital view.

Each exoccipital consists of a relatively wide vertical column, bordering the foramen magnum, from which arise the usual four processes. Just below the origin of the processus basalis, each exoccipital gives rise to a condyle. The left condyle is exposed on the casts but is directed slightly ventrally, whilst the right condylar surface can also be seen in occipital aspect. The condyles are widely separated, as in all lydekkerinids. Each condyle terminates in an expanded, oval, unfinished articulatory surface, wider than deep and borne upon a short columnar stalk. The condyles probably projected slightly behind the plane of the occiput, with their articulatory surfaces facing posteromedially and slightly ventrally. Above the base of the left condyle is a small foramen, perhaps for a nutritive vessel, while a further foramen (X, Text-fig. 6), possibly for the vagal nerve, opens on the right parotic process just above a slight ridge running outwards along the process.

An oblique ridge appears to be present on the left quadrate ramus of the pterygoid, and a roughened, slightly nodular quadrate tubercle is visible just lateral to the upper end of the large inner condylar keel (Text-fig. 6). Both features are present in the other lydekkerinids.

Reconstruction (Text-figs 7–8). Much of the reconstruction of the skull roof and palate of *Deltacephalus* is based on the least distorted left side of the holotype skull, but for the occiput (Text-fig. 8B) the better preserved right side has been used. As reconstructed, the skull is narrower and deeper than it appears in the casts. The missing front end of the snout has been reconstructed on the basis of *Lydekkerina*, and a septomaxillary and an ethmoidal sulcus have been added. The ornamentation, although simplified, is based on the best preserved areas.

Systematic position

This redescription of the type skull of *Deltacephalus* supports Swinton's original conclusion that this genus belongs to the Lydekkerinidae. This family was established by Watson (1919) exclusively for *Lydekkerina* (*Bothriceps*) *huxleyi*, a relatively small, short-faced temnospondyl from the Lower Triassic *Lystrosaurus* Zone of South Africa. Subsequently, ten additional species have been referred to the family: *Lydekkerina putterilli* Broom, 1930; *Putterillia platyceps* Broom, 1930; *Broomulus dutoiti* (Broom) Romer, 1947; *Limnoiketes paludinatans* Parrington, 1948; *Lydekkerina kitchingi* Broom, 1950; *Deltacephalus whitei* Swinton, 1956; *Lydekkerina panchetensis* Tripathi, 1969; *Cryobatrachus kitchingi* Colbert and Cosgriff, 1974; *Chomatobatrachus halei* Cosgriff, 1974; and *Luzocephalus blomi* Shishkin, 1980.

A revision of the lydekkerinid genera *Lydekkerina* and *Limnoiketes* has recently been completed by the author, involving re-examination of much material of *Lydekkerina huxleyi* including the holotype (BMNH R507) and the skulls described by Broili and Schröder (1937; BSP 1934 VIII 44), by Parrington (1948; UMZC T206 and T238), and by Watson (1951; UMZC T110). Undescribed specimens studied included BMNH R504–R506, R508, R3909, R5482 and R6850 and the mandible BPI 1373. The holotype of *Limnoiketes paludinatans* (UMZC T214) was also studied. It is a conclusion of this reappraisal of the Lydekkerinidae that the content of the family should be restricted to the three determinate genera *Lydekkerina*, *Limnoiketes* and *Deltacephalus*, and so the following comparisons with *Deltacephalus* were made with the above listed material.

Deltacephalus is similar to *Lydekkerina* and *Limnoiketes* in many respects but can nevertheless be diagnosed as a separate genus. The following characters vary between the three genera.

1. Skull shape. All three forms have a skull which is parabolic in outline when seen from above. In *Lydekkerina* the lateral skull margins are gently convex, in *Deltacephalus* they are slightly sinuous, whilst in *Limnoiketes* the margins are more irregular, being convex near the snout and the temporal regions and concave in between. The skulls of both *Lydekkerina* and *Deltacephalus* are relatively depressed in comparison with that of *Limnoiketes* which is not only domed in the region of the parietal foramen but is also unusually deep in the orbital and postorbital regions. The orbits are more laterally directed in *Limnoiketes* than in *Lydekkerina* or *Deltacephalus*.
2. Lateral-line sulci. In *Deltacephalus* the well-developed lateral-line sulci take the form of deep grooves. The system is less prominent in *Lydekkerina* and the lyrae are not wide and deeply excavated but consist of a series of separate depressions. The system is only weakly developed in *Limnoiketes*.
3. Tabular horns. In *Deltacephalus* the tabular horns are stout, curved and backwardly directed. In

Lydekkerina and *Limnoiketes*, they are bluntly rounded and relatively laterally directed. The horns are prominent in *Lydekkerina* but are very reduced in *Limnoiketes*.

4. Quadratojugal extent. In *Deltacephalus* the posterior end of the quadratojugal lies ahead of the midpoint of the posterior edge of the skull table. In *Lydekkerina* and *Limnoiketes* the posterior end of the quadratojugal lies behind the midpoint of the posterior edge of the skull table.
5. Parietal foramen. In *Lydekkerina* and *Limnoiketes* the parietal foramen is circular; in *Deltacephalus* it is oval.
6. Palate shape. In *Deltacephalus* the interpterygoid vacuities and subtemporal fossae are relatively larger than in other lydekkerinids. The interpterygoid vacuities are of elongate oval shape whereas they are shorter and narrowly rounded posteriorly in *Lydekkerina* and shorter and broader posteriorly in *Limnoiketes*.
7. Parasphenoid. In *Deltacephalus* the parasphenoid has a narrow, striated and weakly keeled cultriform process. In *Limnoiketes* the cultriform is also narrow but is not striated or keeled. In *Lydekkerina* it is broader and is denticulate and grooved laterally over its posterior half. The corpus of the parasphenoid is ridged in *Deltacephalus* and bears poorly developed stapedial lappets. Well-developed stapedial lappets, protruding backwards, are present in *Limnoiketes* and pronounced in *Lydekkerina*.
8. Pterygoid. The palatine ramus of the pterygoid of *Deltacephalus* has a shallow pterygoid flange and is intermediate between that of *Limnoiketes* which has a pronounced pterygoid flange and that of *Lydekkerina* which lacks this feature entirely.
9. Occiput. In *Deltacephalus* and *Limnoiketes* the opisthotic is not exposed in the paroccipital bar. In *Lydekkerina* the opisthotic is fully ossified and occupies the central portion of the bar.

The above comparisons are summarized in the diagnosis of *Deltacephalus whitei*.

Deltacephalus *and the Lydekkerinidae*. Lydekkerinidae has always been a difficult family to define, principally because lydekkerinids are small forms with short, broad skulls which display so many 'juvenile' features that they are not easy to distinguish from the juvenile stages of larger temnospondyls. These features include the relatively large size of the sensory, palatal and occipital openings, the central position of the orbits on the skull roof, the proximity of the parietal foramen to the level of the posterior margin of the orbits, and the quadrates being on the same level as the exoccipital condyles.

Lydekkerinids have traditionally been associated with the temnospondyl families Rhinesuchidae and Uranocentrodontidae in the superfamily Rhinesuchoidea and are clearly closely related to them, although the Rhinesuchoidea may be a grade of organization rather than a clade (Milner 1990). Lydekkerinids can be distinguished from rhinesuchids and uranocentrodontids by the following derived characters: presence on the occiput of a distinct squamosal–quadratojugal trough; presence of pronounced dermal ornamentation on the main body and rami of the pterygoid instead of a denticulate surface; presence on the mandible of an extensive and complex postglenoid area in which a long surangular process is separated from a short retroarticular process by a prominent depressor groove; a large hamate process; a prearticular which does not extend past the splenial–postsplenial suture; and coronoid denticles confined to the posterior coronoid.

Some of these characters occur sporadically in other Triassic temnospondyl families such as the Rhytidosteidae, the *Derwentia*-group (Milner 1990), but particularly in the Capitosauridae which has long been recognized as being close systematically to the temnospondyls of the rhinesuchoid grade and which shares with them such features as a buttressed tabular horn, stapedial groove, oblique ridge and quadrate tubercle. In contrast with the Lydekkerinidae, in the Capitosauridae the cristae musculari have lost their crescentic form and are usually confluent, forming one continuous, shallow V-shaped ridge; stapedial lappets are almost always absent; and the frontals enter the orbit margins (Warren and Hutchinson 1988*a*). More significantly, the Capitosauridae never developed the complex postglenoid area of the lydekkerinids.

The small size of the lydekkerinids and the unusual abbreviation of their snout region may also be derived characters for the group. There is indirect evidence, based on the uniformity in size of specimens of *Lydekkerina*, growth studies of related temnospondyls, and the ontogeny of the temnospondyl skull, to suggest that lydekkerinids are small adult temnospondyls and not the growth stages of larger temnospondyls. The juvenile appearance would not seem to be due to neoteny, as is testified by the presence of a quadrate tubercle and by the high degree of ossification of the neurocranium in UMZC T110, and is more probably the result of progenetic dwarfing accompanied by reduced allometric growth of the snout, as suggested by Milner (1990, 1991).

Deltacephalus is not so completely preserved as either *Lydekkerina* or *Limnoiketes* and, lacking mandibles, does not display so many of the derived characters that serve to define the family. It can be confirmed as a lydekkerinid, however, by the well-developed dermal ornamentation on the pterygoid, and by the shortness of the snout region and the very low preorbital index to which this gives rise (for details see Colbert and Cosgriff 1974; Cosgriff 1974). In the reconstructed skull of *Deltacephalus* this index is 44, which is remarkably close to the index of 43 for the types of both *Lydekkerina huxleyi* and *Limnoiketes paludinatans*. It is well below the indices of similar sized skulls belonging to young growth stages of capitosaurids and benthosuchids, all of which exceed 53. The validity of this preorbital index as a criterion to distinguish lydekkerinids has been criticized (Warren and Black 1985) but has been confirmed to the present author's satisfaction by studies on the growth stages of temnospondyls. These indicate that the adult condition of the snout region (short or long) is already at least partly expressed in the skulls of immature post-metamorphic temnospondyls, just as other adult derived features are (Warren and Hutchinson 1988*b*). *Deltacephalus*, therefore, along with *Lydekkerina* and *Limnoiketes*, can be considered as a genuine small, short-snouted adult lydekkerinid and not merely the growth stage of a longer snouted form.

THE EARLY TRIASSIC TEMNOSPONDYL FAUNA OF MADAGASCAR

Lehman (1979) considered the Early Triassic temnospondyl fauna from the Sakamena Formation of Madagascar to be littoral, composed of marine trematosaurids and freshwater benthosuchids and a rhinesuchoid. The presence of associated ammonites confirmed the marine nature of the deposits and Lehman assumed that the freshwater forms were transported in via rivers, although they showed no traces of fluviatile erosion. The fauna, as identified by Lehman, comprised one rhinesuchoid (*Mahavisaurus dentatus*), two benthosuchids (*Benthosuchus madagascarensis*, *Wetlugasaurus milloti*) and five to seven trematosaurids (*Wantzosaurus elongatus*, *Lyrosaurus australis*, *Trematosaurus madagascarensis*, *Ifasaurus elongatus*, *Tertremoides ambilobensis*, together with *Aphaneramma* sp. and *Tertrema* sp.).

Lehman briefly compared this fauna with others from the Early Triassic and concluded that it most closely resembled that of the Sticky Keep Formation of Spitsbergen. This was also a littoral assemblage, containing both ammonites and a mixture of presumed marine and freshwater temnospondyls. The fauna as known then comprised one possible capitosaurid (*Sassenisaurus spitsbergensis*), one possible brachyopid (*Boreosaurus thorslundi*), two rhytidosteids (*Peltostega erici* and *P. wimani*) and four trematosaurids (*Aphaneramma rostratum*, *Lyrocephaliscus* (= *Lyrocephalus*) *euri*, *Platystega depressa* and *Tertrema acuta*). Lehman believed that the Madagascan trematosaurids *Wantzosaurus* and *Lyrosaurus* resembled the Spitsbergen trematosaurids *Aphaneramma* and *Lyrocephaliscus* respectively, but in other respects, the faunas seemed quite distinct.

Many of Lehman's taxonomic conclusions have, however, been superseded by later work. *Benthosuchus madagascarensis*, described by Lehman (1961, 1966), was reinterpreted by Shishkin and Lozovskiy (1979) and Warren and Hutchinson (1988*a*) as a capitosaurid. The latter authors redescribed the holotype as *Parotosuchus madagascarensis* and argued that all Madagascan material assigned by Lehman to *Benthosuchus* and *Wetlugasaurus* should be referred here, and that this was the only capitosaurid in the fauna. However, Welles and Cosgriff (1965) had suggested that the Madagascan *Wetlugasaurus* was more closely allied to the rhinesuchids than to the capitosaurids. *Mahavisaurus dentatus* and *Lyrosaurus australis* were described by Lehman as a rhinesuchoid and a trematosaurid respectively (Lehman 1966, 1979), but have been perceived subsequently by many authors to be immediately related members of the family Rhytidosteidae (Howie 1972; Cosgriff and

Zawiskie 1979; Shishkin 1980; Warren and Black 1985; Milner 1990, 1991). Cosgriff and Zawiskie (1979) concluded that they were two species of the genus *Mahavisaurus*, a view subsequently endorsed by Warren and Black (1985) and Milner (1990, 1991). Of the many trematosaurids described by Lehman, subsequent workers have accepted only *Wantzosaurus elongatus*, *Trematosaurus madagascarensis* and *Tertremoides ambilobensis* as valid taxa, while the other taxa are perceived as indeterminate (Cosgriff 1984; Welles 1993).

The taxonomy of the Spitsbergen temnospondyls has remained much more stable, the only revision being that of Shishkin and Vavilov (1985) who argued that the poor material of *Boreosaurus thorslundi* is probably rhytidosteid rather than brachyopid.

Thus, with the revision here of *Deltacephalus*, the Early Triassic temnospondyl fauna from Madagascar now comprises the following taxa:

Capitosauridae: *Parotosuchus madagascarensis*
Lydekkerinidae: *Deltacephalus whitei*
Rhytidosteidae: *Mahavisaurus dentatus*
Mahavisaurus australis
Trematosauridae: *Wantzosaurus elongatus*
Trematosaurus madagascarensis
Tertremoides ambilobensis

The Early Triassic fauna of Spitsbergen is:

Capitosauridae: *Sassenisaurus spitsbergensis*
Rhytidosteidae: *Peltostega erici*
Peltostega wimani
Boreosaurus thorslundi
Trematosauridae: *Aphaneramma rostratum*
Lyrocephaliscus euri
Platystega depressa
Tertrema acuta

These taxonomic revisions serve to enhance the limited resemblance that Lehman had noted between these faunas, with both possessing presumed marine trematosaurids and presumed freshwater rhytidosteids and capitosaurids.

The only other Early Triassic temnospondyl assemblage which contains undoubted lydekkerinids is that of the *Lystrosaurus* Zone of South Africa. Lehman (1961, 1979) found little in common between this fauna and that from the Sakamena Formation, but the taxonomic changes noted above suggest some similarity.

The *Lystrosaurus* Zone temnospondyl fauna is currently perceived as:

Rhinesuchidae: *Uranocentrodon senekalensis*
Capitosauridae: *Kestrosaurus dreyeri*
Lydekkerinidae: *Lydekkerina huxleyi*
Limnoiketes paludinatans
Rhytidosteidae: *Rhytidosteus capensis*
Pneumatostega potamia
Micropholidae: *Micropholis stowi*
Brachyopidae: unnamed fragments.

In both faunas, therefore, lydekkerinids, rhytidosteids and a capitosaurid are present. The South African fauna is not a littoral one, however, but a continental one in which the temnospondyls inhabited broad low-gradient flood-plains, transient shallow pools and lakes, and wide shallow impersistent rivers (Kitching 1978). The fauna is dominated by reptiles, and some of the amphibians, such as *Micropholis* (often associated with the procolophonid *Procolophon*) and *Limnoiketes* (a single exotic specimen), were probably largely terrestrial.

The *Lystrosaurus* Zone temnospondyls are more locally abundant than those in Madagascar, perhaps because the majority of them were preserved in the beds of the ponds and lakes in which they lived. Many are well preserved with articulated postcranial skeletons (e.g. *Lydekkerina*, *Micropholis*, *Uranocentrodon*). The presumed continental elements in the Madagascan fauna are less well preserved with postcranial material less in evidence. The presence of well preserved skulls, however, suggests that only restricted post-mortem transport occurred and hence that they may have lived in coastal lagoons or deltaic rivers or streams. In the Sticky Keep fauna, the presumed continental/freshwater forms are relatively scarce and more fragmentary than their Sakamena Formation counterparts which might indicate transport from a greater distance either from further inland or further out to sea.

Recent work on the $^{87}Sr/^{86}Sr$ ratio in the bones of Spitsbergen temnospondyls and in coprolites assigned to them indicates that they did not live exclusively in marine or freshwater conditions but possessed an intermediate ratio suggestive either of a littoral life-style or anadromy (Lindemann 1991). The presence of wrinkle-marks and channel-fillings in the temnospondyl-producing beds indicate shallow-water conditions, although sedimentological studies combined with the *in situ* embedding of the coprolites in the marine deposits suggest that part of the Sticky Keep Beds was laid down in open marine environments (Mork *et al.* 1982). It thus appears that at least some of the temnospondyls at Sticky Keep spent parts of their lives in the sea. It is possible to hypothesize that the more abundant and better preserved trematosaurids were truly marine forms as adults, though possibly anadromous, while the rhytidosteids and capitosaurids were littoral or continental and present only as exotic elements in the fauna.

The littoral fauna from the Sakamena Formation appears to occupy an intermediate position between the continental *Lystrosaurus* Zone fauna and the marine Sticky Keep fauna, sharing rhytidosteids and capitosaurids with both, a lydekkerinid only with the *Lystrosaurus* fauna and trematosaurids only with the Sticky Keep fauna.

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ABBREVIATIONS

c.m.	crista muscularis
cul.pr.	cultriform process
ec	ectopterygoid
ex	exoccipital
ext.n	external naris
f	frontal
for.m.	foramen magnum
int.v.	interpterygoid vacuity
j	jugal
jg.c.	jugal canal/sulcus
l	lacrimal
lp.	stapedial lappet
mx	maxilla
n	nasal
ob.r.	oblique ridge
orb	orbit
ot.c.	otic canal/sulcus
ot.n.	otic notch
p	parietal
pal	palatine
pal.pr.	palatine process
pf	postfrontal
p.f.	parietal foramen
pfr	prefrontal
po	postorbital
po.c.	postorbital canal/sulcus
pp	postparietal
pr.al	processus alaris
pr.b.	processus basalis
ps.ph	parasphenoid
pt	pterygoid
pt.f.	posttemporal fossa
qd	quadrate
qd.pr.	quadrate process
qj	quadratojugal
qt	quadrate tubercle
sq	squamosal
st	supratemporal
sub.c.	suborbital canal/sulcus
sub.f.	subtemporal fossa
supr.c.	supraorbital canal/sulcus
sup.sp.	supraoccipital space
t	tabular
t.cr.ext.	crista tabularis externa
X	foramen for vagal nerve

THE DIAPSID REPTILE, *PACHYSTROPHEUS RHAETICUS*, A PROBABLE CHORISTODERE FROM THE RHAETIAN OF EUROPE

by G. W. STORRS, D. J. GOWER *and* N. F. LARGE

ABSTRACT. The enigmatic Upper Triassic reptile, *Pachystropheus rhaeticus*, displays characters suggestive of choristoderan affinity and, as such, is potentially the oldest known choristoderan reptile. Examination of the known skeletal elements indicates that the choristoderan lineage remained morphologically conservative throughout its recorded history. The occurrence of *Pachystropheus* fossils in marginal marine bone beds, however, may reflect a previously unrecognized shift of habitat for the Choristodera, from the paralic environments occupied by early representatives, to the more typical freshwater, often fluvial, deposits containing later forms.

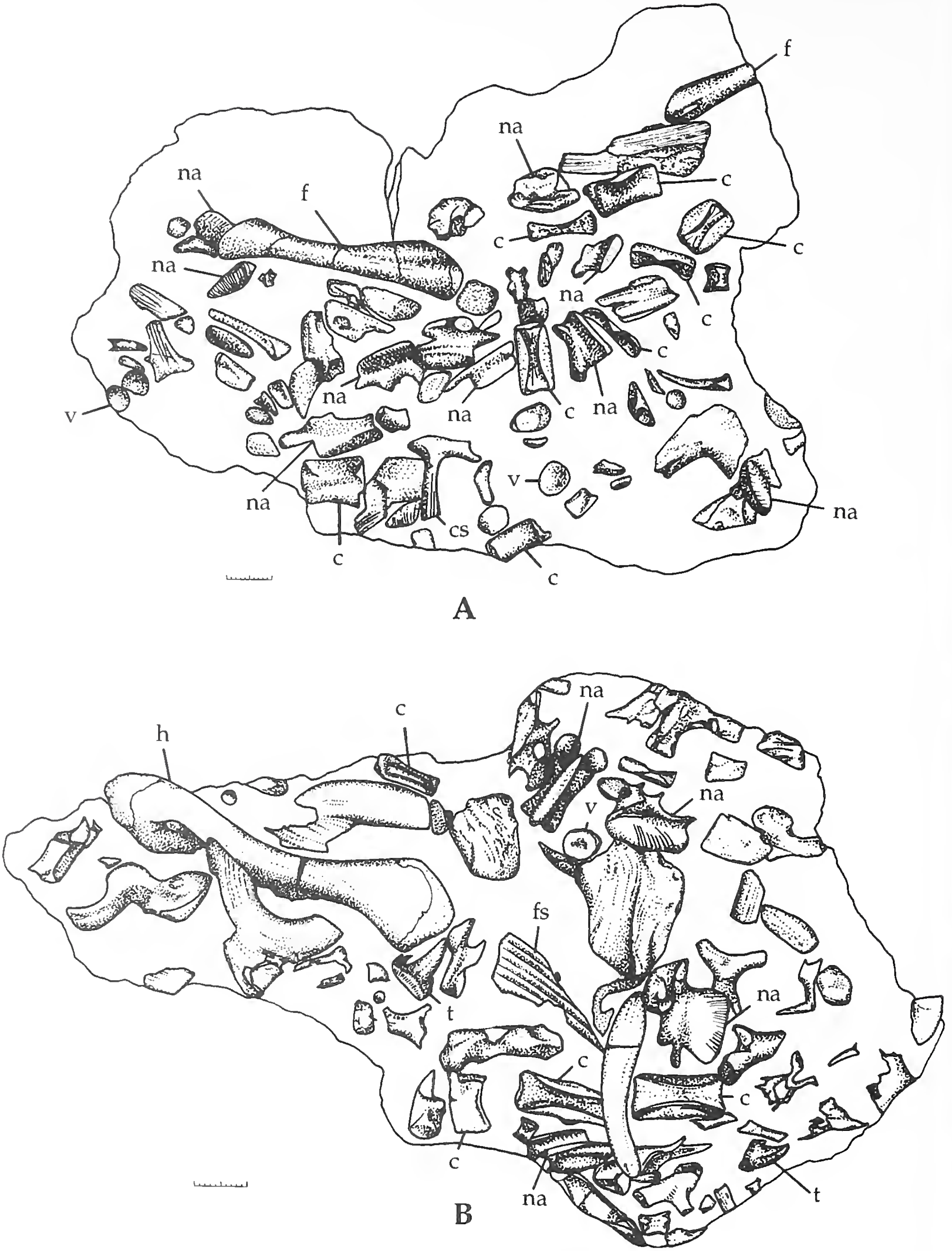
THE fossil reptile *Pachystropheus rhaeticus* was described by E. von Huene (1935) from generally isolated elements in the bone beds of the Rhaetian (uppermost Triassic) Westbury Formation, Penarth Group, of south-west England; in genetically and perhaps stratigraphically equivalent rocks of Baden-Württemberg (Gaisbrunnen near Bebenhausen and Olgahain), Germany; and in the famous Rhaetian fissure fill deposits of Holwell, Somerset, England (F. von Huene 1902; E. von Huene 1933, 1935).

Storrs and Gower (1993) have suggested that *Pachystropheus rhaeticus* may represent the earliest known member of the Choristodera. As such, it would predate the next occurrence of choristoderes in the Middle Jurassic (Bathonian) (Evans 1989, 1990, 1991; Metcalf *et al.* 1992) by approximately 45 million years. In fact, both E. von Huene (1935) and her father (F. von Huene 1956) had assigned *Pachystropheus* to the choristoderan Champsosauridae, at that time considered to be rhynchocephalians and known only from Cretaceous and Palaeogene representatives. This identification has been noted briefly in studies and listings of the Choristodera (e.g. Hoffstetter 1955; Kuhn 1961, 1969, 1971; Romer 1966; Appleby *et al.* 1967; Efimov 1975, 1988; Russell-Sigogneau and Russell 1978; Carroll 1988; Evans 1989, 1990; Benton 1993; Evans and Hecht 1993), but has not received general acceptance. Presumably, this was due in part to the brief description and relatively poor quality of the type material which contrast with those for late Mesozoic and early Palaeogene champsosaurs. It may also reflect an unwritten prejudice that such an early occurrence and resultant large gap in the fossil record precluded a true relationship with champsosaurs.

It is now known, however, that stratigraphical position is often a poor indicator of phylogenetic relationship and that substantial gaps occur in the records of many fossil vertebrates. This is in spite of recent studies showing that some clades actually exhibit a significant correlation between time of occurrence of member taxa and phylogenetic branching sequence (Norell and Novacek 1992*a*, 1992*b*; Benton and Storrs 1994, 1996). Furthermore, work subsequent to E. von Huene's (1935) description has documented the occurrence of choristoderes in deposits of Jurassic (Evans 1989, 1990, 1991; Metcalf *et al.* 1992) and Oligocene (Hecht 1992) age. In fact, the existence of Triassic, and indeed Permian, choristoderes has been predicted from cladistic analyses of relationships between early diapsid reptiles (Evans 1988, 1990; Gauthier *et al.* 1988; Storrs and Gower 1993).

Material of *Pachystropheus* is very common in the Westbury Formation but its morphology and relationships have remained obscure because of its general preservation as isolated or disassociated elements. The exposures from which came E. von Huene's (1935) fossils include two Somerset localities: Vallis Vale, near Frome [ST 755 490] and Blue Anchor Point [ST 034 435], and two well known Gloucestershire localities: Garden Cliff, Westbury-on-Severn [SO 717 130], and Sedbury ('Slime Road') Cliff [ST 555 930] (it should be noted that although E. von Huene (1933) listed Vallis

[Palaeontology, Vol. 39, Part 2, 1996, pp. 323–349, 2 pls]



TEXT-FIG. 1. For caption see opposite.

Vale as the site of origin of several of her specimens, the matrix on some of these matches that of undoubted Holwell [ST 727 452] material). Numerous *Pachystropheus* bones have come also from the classic Rhaetian exposure at Aust Cliff, Avon [ST 566 898] (Storrs 1994).

Most of the present material is from Aust and Garden cliffs, although useful examples have also been collected from 'bone beds' (once known collectively as the 'Rhaetic Bone Bed') at numerous localities in the south-west and midlands of England, and south Wales (Owen 1842; Browne 1894; F. von Huene 1902; E. von Huene 1933, 1935; Macfadyen 1970; Sykes *et al.* 1970; Duffin 1978, 1980; Antia 1979; Martill and Dawn 1986; Storrs 1994). A collection recently made by M. T. and S. A. Curtis from the Hampstead Farm (Curtis and Curtis 1987) and Southfields quarries, Chipping Sodbury, Avon [ST 726 839], has been particularly valuable, as have the 102 collecting visits made to Garden Cliff between 1987 and 1992 as part of this study (N.F.L.).

The few German specimens of this taxon are relatively poor (F. von Huene 1902; E. von Huene 1933, 1935), and E. von Huene's (1933) figured material from Gaisbrunnen (GPIT 19552) includes only half a sacral centrum, a small phalanx, a fragmentary 'metatarsal', and two elements from a selection of isolated neural spines. Six recently collected dorsal centra (SMNS 58791), one retaining most of the neural arch, from the 'Rhätbonebed' of Ochtersum, near Hildesheim, Lower Saxony, are identical to the English material in morphology and preservation. Numerous abraded dorsal centra (MNHN SNP101) are known from the Late Triassic sands of Saint-Nicolas-de-Port, near Nancy, north-eastern France. This occurrence is of interest because of its potential, although controversial, Norian age (Buffetaut and Wouters 1986; Cuny and Ramboer 1991; Duffin 1993). Another notable example (BRSMG Cd2678) was collected *in situ* from the lowermost Jurassic (Hettangian) Lower Lias, *Psiloceras planorbis* Zone, at Lilstock [ST 16 44], Somerset.

GEOLOGICAL SETTING

The Westbury Formation, the basal unit of the Penarth Group (Rhaetian) of south-west Britain (Warrington *et al.* 1980), is a widespread, 1–15 m thick unit of black, pyritic shale, thin siltstone bands and a few limestone beds and shelly horizons. It is particularly well known for its bone beds which, together with the base of the formation in general, represent the end of regional Triassic continental deposition and the onset of an extensive, disconformable, marine transgression. Westbury Formation rocks are cyclical in nature and suggestive of fluctuating depositional conditions and water depth in marginal marine environments (Ivimey-Cook 1974; Hamilton 1977; Storrs 1994). The water was never deep, but conditions within the sediment were often anoxic, as evidenced by abundant pyrite, especially at Garden Cliff. A plentiful supply of terrestrially derived iron (here the limiting factor for pyrite deposition) attests to nearshore conditions. Anoxia probably resulted from high organic input and possible salinity stratification (Storrs 1994).

Garden Cliff provides the most spectacular accumulations of *Pachystropheus* remains, including rare, potentially associated individuals (Text-fig. 1). Bones are most commonly, however, mixed with those of other vertebrate taxa. Most new specimens used in this study have come from Garden Cliff, an approximately 1 km long section beside the Severn Estuary, on the upstream side of the Arlingham meander loop. The exposed rocks range from the uppermost Triassic (Norian and Rhaetian) to the lowermost Jurassic (Hettangian). The section achieves its greatest height of 21 m near the downstream end, where the cliff face is entirely Triassic Mercia Mudstone. Upstream, the Westbury Formation appears in the cliff top; its entire thickness is present. Tidal erosion is active in the downstream half of the section, where Norian marls dominate; resistant rocks in the overlying Rhaetian become undercut, and cliff falls occur periodically. These falls provide the best

TEXT-FIG. 1. Garden Cliff bone bed specimens with associated remains of *Pachystropheus rhaeticus* E. von Huene, showing style of preservation and distribution of elements. A, STGCM 60.62/1, potentially a single individual; B, BRSMG Cb9065. Scale bars represent 10 mm. Abbreviations: c, centrum; cs, caudal spine; f, femur; fs, fin spine of *Hybodus* sp.; h, humerus; na, neural arch; t, tooth of *Hybodus minor*; v, neoselachian vertebra.

supply of fossils, and conspicuous amongst these are disarticulated but extremely well preserved bones of *Pachystropheus*.

The 'bone bed' occurs as a seam of pyritic siltstone, between 20 and 30 mm thick, between soft black shales. Vertebrate remains and pyrite crystals are locally common on the surface of 'bone bed' slabs. The 'bone bed' lies approximately 2 m above the base of the Westbury Formation, 430 mm above a 300 mm thick sandstone band locally known as the '*Pullastra* Bed', and 600 mm below a band of highly fissile black shale that develops a rust-coloured coating of limonite on weathering.

The abundance of *Pachystropheus* is a unique characteristic of Garden Cliff. Local conditions were extremely favourable for the preservation of *Pachystropheus*, in contrast with other known Rhaetian sites. The density of material is quite variable, however, and the presence in some places of faint oscillation ripples and small runnel features on the surface of the 'bone bed' suggests a sorting mechanism by which winnowed bones were concentrated (Storrs 1994). The 'bone bed' may preserve a shoal or strand line deposit. Certainly, a degree of sorting is evident in the distribution and preferred orientations of incorporated elements; most *Pachystropheus* bones (largely vertebrae and propodials) fall within the same relatively small size range. Bones from larger animals, or rare elements, are typically found at Aust and elsewhere.

Repository abbreviations. BATGM, Bath Royal Literary and Scientific Institution ('Bath Geological Museum'); BGS, British Geological Survey (including material from the former Geological Survey Museum), Keyworth; BMNH, The Natural History Museum, London; BRSMG, Bristol City Museum and Art Gallery; BRSUG, The University of Bristol Geology Museum; CMNHS, Geier Collections and Research Center, Museum of Natural History and Science, Cincinnati Museum Center, Cincinnati, Ohio; GPIT, Geologische und Paläontologische Institut, Tübingen; LEIUG, The University of Leicester Department of Geology; MM, Manchester Museum; MNHN, Muséum National d'Histoire Naturelle, Paris; PIN, Palaeontological Institute, Russian Academy of Science, Moscow; RSM, Royal Scottish Museum, National Museums of Scotland, Edinburgh; SMNS, Staatliches Museum für Naturkunde, Stuttgart; STGCM, Stroud Gloucestershire County Museum.

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA Osborn, 1903
ARCHOSAUROMORPHA F. von Huene, 1946
CHORISTODERA Cope, 1876
Family PACHYSTROPHEIDAE Kuhn, 1961

Genus PACHYSTROPHEUS E. von Huene, 1935

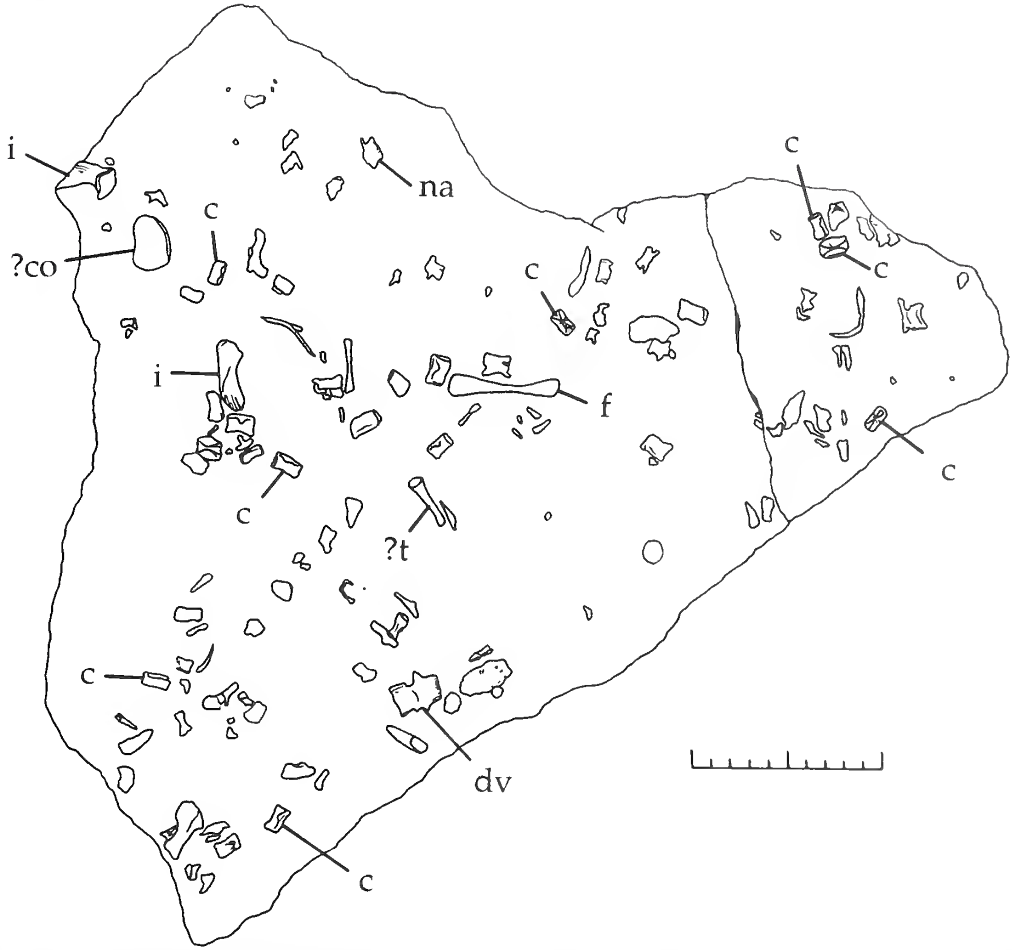
Type species. Pachystropheus rhaeticus E. von Huene, 1935.

Diagnosis. As for the type and only species.

Pachystropheus rhaeticus E. von Huene, 1935

Plates 1–2; Text-figures 1–13

?1842 *Rysosteus* Owen, p. 159.
?1854 *Rysosteus*; Morris, p. 353.
?1890 *Rysosteus oweni* Woodward and Sherborn, p. 282.
1935 *Pachystropheus rhaeticus* E. von Huene, pp. 441, 446–447.
1945 *Pachystropheus*; Romer, p. 595.
1946 *Rysosteus*; Reynolds, pp. 30, 35.
1955 *Pachystropheus*; Hoffstetter, p. 571.
1956 *Pachystropheus*; F. von Huene, pp. 637, 639, 683, 693.
1961 *Pachystropheus rhaeticus*; Kuhn, p. 38.
1964 *Pachystropheus*; Maleev, p. 455.
1966 *Pachystropheus*; Kuhn, p. 36.
1968 *Pachystropheus*; Müller, p. 225.



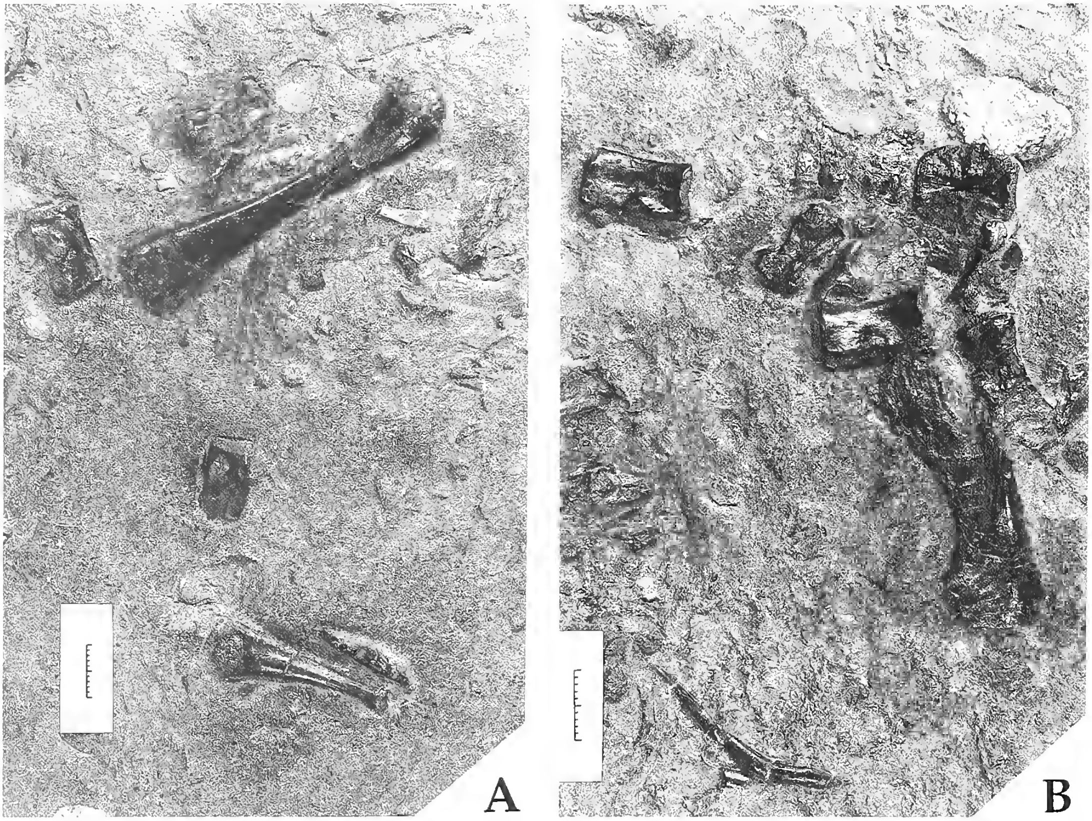
TEXT-FIG. 2. Holotype of *Pachystropheus rhaeticus* E. von Huene, BMNH R747; Blue Anchor Point, Somerset. Scale bar represents 100 mm. Abbreviations: c, centrum; ?co, ?coracoid; dv, dorsal vertebra; f, femur; i, ilium; na, neural arch; ?t, ?tibia.

1969 *Pachystropheus rhaeticus*; Kuhn, pp. 58, 64.
1970 *Rysosteus oweni*; MacFadyen, p. 202.
1970 *Rhysosteus oweni*; Sykes *et al.*, p. 260.
1971 *Pachystropheus rhaeticus*; Kuhn, pp. 6, 10, 55.
1975 *Pachystropheus rhaeticus*; Efimov, pp. 84, 93.
1978 *Rysosteus*; Duffin, p. 62.
1978 *Pachystropheus*; Russell-Sigogneau and Russell, p. 82.
1979 *Rysosteus*; Antia, p. 134.
1980 *Rysosteus oweni*; Duffin, pp. 258, 260.
1982 *Rysosteus oweni*; Duffin, p. 2.
1983 *Rysosteus*; Duffin *et al.*, p. 312.
1985 *Rysosteus*; Duffin, p. 143.
1986 *Rysosteus oweni*; Martill and Dawn, p. 130.
1987 *Rysosteus oweni*; Curtis and Curtis, p. 12.
1988 *Pachystropheus*; Carroll, p. 616.
1988 *Pachystropheus rhaeticus*; Efimov, p. 40.
1989 *Pachystropheus*; Evans, p. 586.

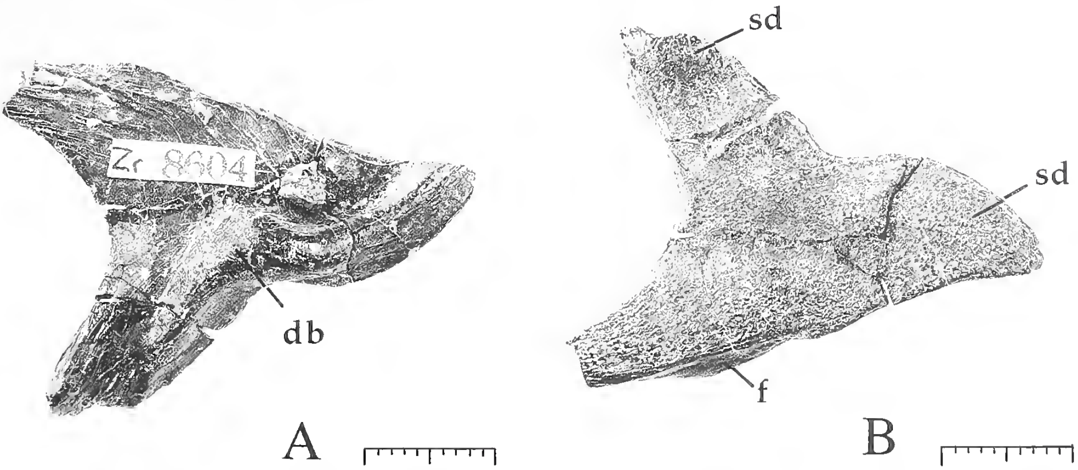
1990	*Pachystropheus*; Evans, p. 206.
1992	*Pachystropheus rhaeticus*; Storrs, p. 53A.
1993	*Pachystropheus rhaeticus*; Benton, p. 693.
1993	*Pachystropheus*; Evans and Hecht, p. 329.
1993	*Pachystropheus rhaeticus*; Storrs, p. 448.
1993	*Pachystropheus rhaeticus*; Storrs and Gower, p. 1103.
1994	*Pachystropheus rhaeticus*; Storrs, pp. 238, 241–242, 244, 251–253.

Remarks on synonymy. It is likely that *Pachystropheus rhaeticus* E. von Huene is synonymous with *Rysosteus oweni* Woodward and Sherborn (1890). *Rysosteus*, described on the basis of a single vertebra from the 'Rhaetic Bone Bed' exposures of Aust (Owen 1842), was supplemented with additional specimens from Aust and Westbury (Owen 1842; Browne 1894). Indeed, *Rysosteus* has been accepted as a senior synonym of *Pachystropheus* by Duffin (1978). However, *Rysosteus* cannot be diagnosed accurately from Owen's (1842) short description without illustration, and is thus a *nomen dubium*. This applies also to the specific name, *R. oweni* Woodward and Sherborn (1890), which was never diagnosed. The location of the holotype of *Rysosteus*, once in the private collection of a Mr James Johnson of Hotwells, Bristol, is unknown.

Holotype. Associated partial skeleton BMNH R747 (Text-figs 2–3).



TEXT-FIG. 3. Detail of *Pachystropheus rhaeticus* E. von Huene, holotype, BMNH R747; Blue Anchor Point, Somerset. A, vertebral centra, left femur and presumed epipodial (?tibia); B, centra, left ilium, gastralium and associated shark cephalic spine (left centre next to vertebrae). Scale bars represent 10 mm.



TEXT-FIG. 4. Ectopterygoid of *Pachystropheus rhaeticus* E. von Huene, BGS Zr 8604, in A, medial, and B, palatal aspects. Anterior to the right. Scale bars represent 10 mm. Abbreviations: db, dorsal boss; f, facet; sd, shagreen denticles.

Referred material. See appendix.

Type locality and horizon. Blue Anchor Point, Somerset, England (National Grid Reference ST 034 435; Westbury Formation, Penarth Group, latest Triassic (Rhaetian).

Diagnosis. Lacertiform reptile, approximately 1 to 2·5 m long, presumably a choristodere of relatively plesiomorphic proportions and morphology; triradiate ectopterygoid with vestigial tuberculate dentition; elongate amphi- to platycoelous vertebral centra; dorsal neural spines squarish in lateral aspect with transversely expanded, corrugated tips; tall, narrow, vertically oriented caudal neural spines; interclavicle with short posterior ramus; humerus with little relative torsion of articular ends; extremely sharp and prominent supinator ridge; pubic fenestration in at least juvenile condition; iliac blade narrow and heavily corrugated.

Description. The disarticulated fossils do not allow a full reconstruction, and examples of only one cranial element (the ectopterygoid) have been identified. However, many postcranial bones can be assigned to *Pachystropheus* on the basis of partial associations, the similarity of the bones to those of well known choristoderes, and the seeming lack of other semi-aquatic reptiles in the Westbury deposits. Each vertebral type (excepting atlas/axis), dorsal ribs, gastralia, several interclavicles, clavicles, humeri, pubes, ilia, femora, a probable tibia, and a few possible phalanges are known. The holotype contains at least 35 vertebrae (mostly mid-series dorsal centra, but also a probable anterior caudal centrum, possible cervical neural arches and the arches of two caudals), perhaps representing two or more individuals, two or more gastralia, a possible clavicle and coracoid, right and left ilia, a left femur, an epipodial (probably the tibia) and numerous unidentifiable fragments; a tooth of '*Hybodus*' *minor*, a selachian cephalic spine, and a few other shark remains are also present on the slab (Text-figs 2–3).

Whilst some enigmatic jaw fragments (e.g. Storrs 1992) are present in Westbury collections, these commonly belong to the giant palaeonisciform, *Severnichthys* Storrs, 1994. Other putative cranial elements are equivocal; the potential for some to belong to *Pachystropheus* remains to be investigated.

Skull

Ectopterygoid. This bone (Text-fig. 4) is known from several examples in a wide range of sizes; the largest (BRSUG 25332) is 51 mm long × 26 mm across; the smallest (CMNHS VP4128) is only 17 mm × 13 mm. It is generally shaped as in *Simoedosaurus* (Sigogneau-Russell 1981), but its anteromedial process is much longer, as in *Champsosaurus* (Erickson 1972). This process formed the posteromedial margin of the suborbital fossa; its medial edge is faceted for reception of the pterygoid. Conspicuous maxillary and jugal facets lie on the dorsolateral surfaces of the anterolateral and posterolateral processes, respectively. These latter two processes are subequal in length. The anterolateral process is broad and spatulate, with a rounded anterior edge, unlike the pointed process of *Simoedosaurus*; in *Pachystropheus* it is directed somewhat ventrally. The posterolateral process is pointed and slopes dorsally; its medial edge formed the anterolateral corner of the subtemporal fossa. The bone has a smooth dorsal surface, and ventrally (palatally), bears very fine, almost microscopic, shagreen tubercles on its gently concave central portion. This is an unusual, presumably primitive character. A large dorsal boss occurs above the middle of its lateral side, as in *Simoedosaurus* (Sigogneau-Russell 1981), for apparent contact with the 'postorbitofrontal'.

Axial skeleton

Vertebrae. The vertebrae are characteristic and readily identified (Pls 1–2, Text-figs 1, 3, 5–6), but disarticulation renders series counts impossible. Examples from all regions of the column are known; only the atlas and axis have yet to be identified. In general, these compare well with their counterparts in proven choristoderes. The centra are amphi- to platycoelous with subcircular articular faces, and are longer than tall. All presacral vertebrae retain an open neurocentral suture, even in the adult condition, often resulting in disarticulation of the neural arch and centrum, such that the broad neural arch facets and deeply incised neural canal floor are visible. Only five of the holotype vertebrae retain articulated neural arches. The holotype centra are 14–17 mm long.

The neural arch facets extend the entire length of the centrum and are lozenge-shaped in plan (Text-fig. 5H, J). The midpoint of the neural canal is conspicuously constricted. There is no median keel on the neural canal floor as in *Cteniogenys* (Evans 1991) and *Simoedosaurus* (Sigogneau-Russell 1981), save for slight indications of a remnant keel at the anterior and posterior ends, like the 'fine central ridge' of *Champsosaurus* (Parks 1956); the keel in *Simoedosaurus* may also be interrupted. The floor of the canal is deepest at its centre.

The centra of the cervical vertebrae are like those of *Cteniogenys* (Evans 1991) and *Lazarussuchus* (Hecht 1992) in being significantly longer than they are tall (at least 2·5 times so in most examples) (Text-fig. 5A). This central elongation is presumed to represent the plesiomorphic choristoderan condition (Evans 1991; Hecht 1992; Storrs and Gower 1993). Between the terminal articular surfaces, the centrum is strongly constricted and the ventral margin is arched. There is a marked, longitudinal ventral keel as in *Cteniogenys* (Evans 1991), *Champsosaurus* (Erickson 1972), *Ikechosaurus* (Brinkman and Dong 1993) and others (Sigogneau-Russell and Efimov 1984). In *Pachystropheus*, however, the keel does not protrude below the level of the articular face of the centrum as in other taxa.

The anterior edge of each anterior cervical bears a diapophysis just below the neurocentral suture; there is no sign of a parapophysis, a common condition amongst choristoderes (Brown 1905; Russell 1956; Erickson 1972; Evans 1991). The neural spine is very long and low, whereas advanced choristoderes (e.g. *Champsosaurus*, *Simoedosaurus*) have spines taller than long (Russell 1956; Erickson 1972; Sigogneau-Russell 1981). The *Pachystropheus* spine increases in transverse width distally; the flat, or slightly convex, tip is broader than the base. The lateral surfaces of the anterior cervical spines may be only slightly rugose, or else are smooth and featureless. The zygapophyses are broad, spatulate and nearly horizontally oriented. The posterior cervical vertebrae are generally similar, but have taller neural spines.

The anterior dorsal vertebrae are distinguished from the posterior cervicals by their bilobed rib facets, positioned at approximately one-third of the length of the centrum across the neurocentral suture (Plate 1, figs 1–6). A parapophysis lies anterior and ventral to the diapophysis, together forming an hourglass-shaped surface. The centra are again long (at least twice as long as high) and low, with a sharp longitudinal keel, but with a straight ventral margin. The neural spines remain low and essentially smooth.

A number of morphological changes occurs through the dorsal series (Pls 1–2; Text-fig. 5). For example, the centra become shorter relative to their height (approximately 1·5 times longer than tall), and the rib facets migrate to the middle of the centrum. The parapophysis becomes vertically aligned with the diapophysis and

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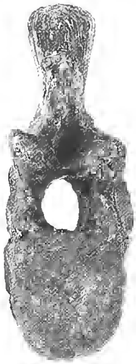
EXPLANATION OF PLATE 1

Figs 1–6. Anterior dorsal vertebra of *Pachystropheus rhaeticus* E. von Huene, BATGM C28, in 1, anterior, 2, posterior, 3, left lateral, 4, right lateral, 5, ventral (anterior to left) and 6, dorsal, views. Scale bar represents 10 mm.

Figs 7–10. Mid-series dorsal vertebra of *Pachystropheus rhaeticus* E. von Huene, BMNH R6851, in 7, anterior, 8, left lateral, 9, posterior and 10, right lateral views. Scale bar represents 10 mm.

PLATE 1


1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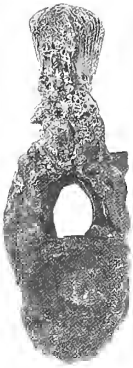
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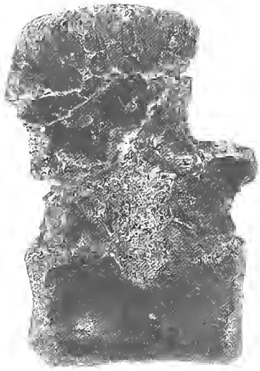
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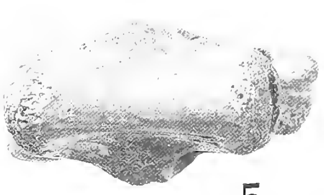
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STORRS *et al.*, *Pachystropheus*

gradually merges with it as an undifferentiated synapophysis. Most of the rib facet lies on the arch; a small portion arises from the dorsal edge of the centrum. The transverse process is extremely short; its dorsal edge may overhang its ventral edge. The neural spine becomes much larger and taller in the posterior dorsals. Its posterior margin lies above or behind the posterior edge of the postzygapophyses, whereas the anterior rises almost vertically from the posterior edge of the prezygapophyses. The distal tip is transversely expanded and rugose, as in *Khurendukhosaurus* (Sigogneau-Russell and Efimov 1984), and the dorsolateral surfaces strongly corrugated, much as are the dorsal to caudal spines of *Simoedosaurus* (Sigogneau-Russell 1981; Erickson 1987). Indeed, save for relative proportions and spine length, which may be partly dependent upon column position, *Pachystropheus* dorsal vertebrae are largely indistinguishable from examples of *Khurendukhosaurus*, as evidenced by BRSUG 25334 and others (e.g. PIN 3386/6-1-1). In lateral aspect, the posterior dorsal spine of *Pachystropheus* is more squarish than in the anterior dorsals. The longitudinal keel of the centrum is lost, although its lateral constriction may persist.

Many of the dorsal vertebrae possess a shallow, pit-like depression or foramen in the lateral surface of the centrum, representing the lateral fossa typical of many choristoderes (see e.g. Evans 1991). This usually lies immediately below the synapophysis, although there is some slight variation in its presence and position; it may itself lie in a broad depression. In BRSUG 25325, a thin horizontal flange of bone extends from the top of the diapophysis to ventral to the postzygapophysis, and shelters a deep cavity in the arch posterior to the transverse process. Similar struts and fossae are present both anterior and posterior to the transverse process in an example from SMNS 58791, although the posterior fossae are the deeper. There are no accessory articulations such as are found in *Simoedosaurus* (Sigogneau-Russell 1981).

In the sacral vertebrae there is, of course, stronger fusion between centrum and arch than in the presacrals. The sacral centra are never more than 1·5 times longer than tall, and approximate the posterior dorsals in shape. The synapophysis covers much of the lateral surface across the neurocentral suture (Text-fig. 6A, C–D). The neural spine is similar to that of a posterior dorsal vertebra, but is clearly taller than long.

As in other choristoderes (e.g. Erickson 1972), the anterior caudal vertebrae are similar to the sacrals. The centrum of a more typical caudal is subrectangular and it is at least twice as long as high (Text-fig. 6E–G). The articular ends are also subquadrate, and are tall and narrow. The ventral surface bears a deep longitudinal furrow bordered by a pair of carinae; this distinctive morphology is common to other choristoderes (e.g. *Champsosaurus*, Erickson 1972; *Simoedosaurus*, Erickson 1987; *Cteniogenys*, Evans 1991). The lateral surfaces of the centrum are weakly constricted. The neural arch is firmly sutured to the centrum. The neural spines of mid-series and distal caudals are anteroposteriorly narrow, vertically aligned, posteriorly positioned and very tall (Text-fig. 6E). Whereas in other parts of the column the articular faces of the zygapophyses are essentially horizontal, those of the caudal vertebrae are oriented more or less vertically. Nowhere has an articular surface for a caudal rib been identified, but they were probably confined to the anteriormost caudal vertebrae.

Ribs. No cervical ribs have been identified, but dorsal ribs (Text-fig. 5I) are known from several specimens. As in typical choristoderes, the tuberculum and capitulum form distinct areas of a single, confluent articulatory surface whose relative sizes vary. Following champsosaurs (*Champsosaurus*, Russell 1956; Erickson 1972; *Simoedosaurus*, Sigogneau-Russell 1981; Erickson 1987), it is probable that the capitulum was increasingly dominant caudally. The shaft is tapered, first curving ventrally at a sharp angle, then straightening to a blunt tip. Proximally, the anterior surface bears a shallow but distinct depression, also as in champsosaurs; the posterior surface has a wide and distinctive groove that fades distally. This posterior groove may be the 'deep sulcus' of *Lazarussuchus* (Hecht 1992), also seen in *Champsosaurus* (Parks 1927; Erickson 1972). The anterodorsal edge of the shaft bears a gentle crest that also recedes distally. In some *Pachystropheus* ribs, the

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EXPLANATION OF PLATE 2

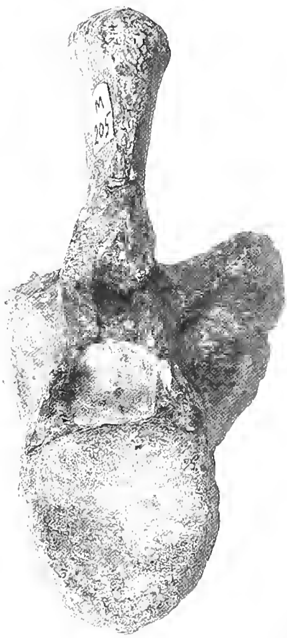
Figs 1–4. Dorsal vertebra of unusually large individual of *Pachystropheus rhaeticus* E. von Huene, BATGM M205, in 1, left lateral, 2, posterior, 3, ventral (anterior to the top) and 4, right lateral views. This specimen represents the largest known vertebra of this taxon.

Figs 5–6. Size variation in *Pachystropheus* humeri. 5, complete left humerus of young individual of *Pachystropheus rhaeticus* E. von Huene, BRSMG Cb4907. 6, proximal head of right humerus of *Pachystropheus rhaeticus* E. von Huene, BRSMG Cd2422. Fig. 6 represents the largest known individual of *Pachystropheus*.

Scale bar represents 10 mm.

PLATE 2

1



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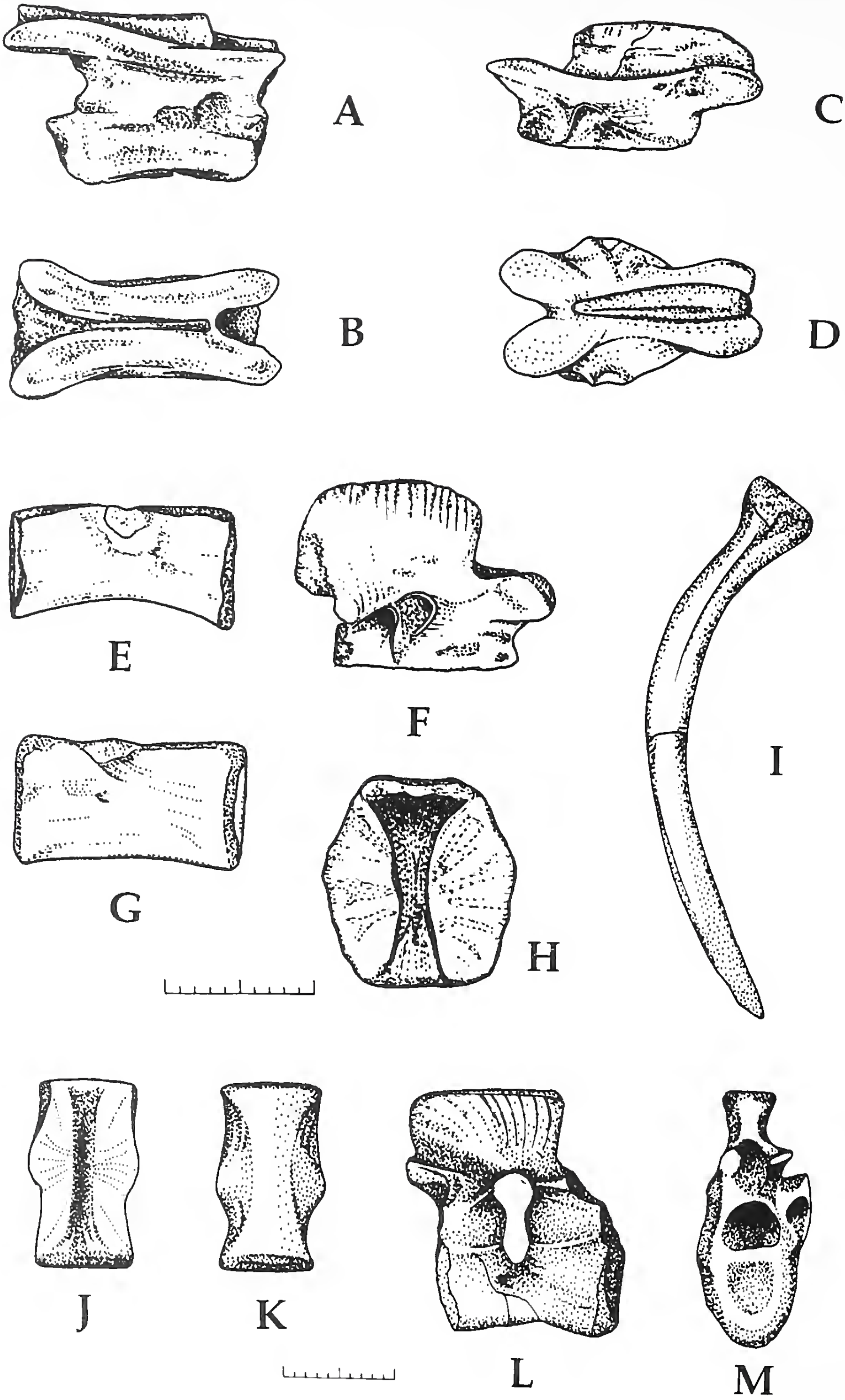


TEXT-FIG. 5. For caption see opposite.

ventral edge of the shaft forms a thin flange ventral to the posterior sulcus, again as in other taxa. There is as yet no evidence for true histological pachyostosis as may have existed in, for instance, *Champsosaurus* (Erickson 1972), but the ribs are generally dense and thickened as an apparent aquatic adaptation. There are no 'uncinate processes' as are found in *Champsosaurus* (Parks 1927; Erickson 1972).

The stout sacral ribs are fused to the transverse processes (Text-fig. 6A), are long (40 mm for a vertebra 32 mm high), and broadly downturned so that the distal end is directed at an angle of approximately 10° below horizontal. The proximal end is robust and circular in transverse section; distally the rib is dorsoventrally flattened with a broad extremity and lateroventrally directed iliac articulation.

The known caudal ribs are extremely flat and rather short (27 mm in BMNH R6245), and are broad anteroposteriorly as in *Champsosaurus* (Erickson 1972; Parks 1927). The flattened distal end is rounded and blunt and approximately twice as wide as the proximal end (Text-fig. 6B).

Gastralia. The best preserved gastral rib (BRSMG acc. no. 45/1991), a median element, is unexceptional (see Storrs and Gower 1993). It is 'V'-shaped at an angle of approximately 120°, is about 80 mm long, and tapers to blunt lateral ends. These are flattened dorsoventrally, while the mid-section is stout. Such heavy gastralia, like the dense ribs, potentially aided *Pachystropheus* in its buoyancy compensation efforts. Lateral elements are similarly dense, but are relatively straight. Judging from their size, each gastral segment probably consisted of only three elements.

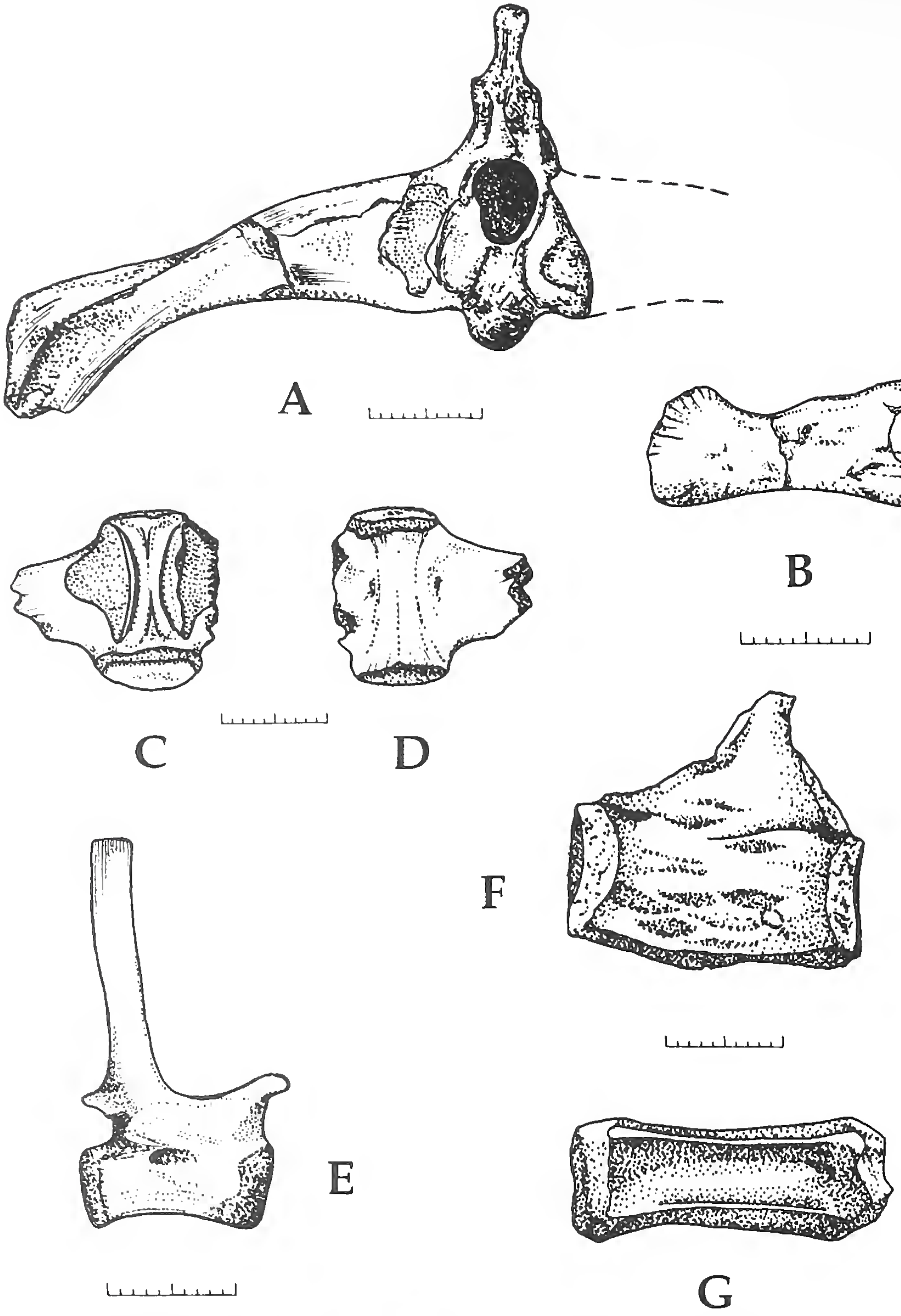
Appendicular skeleton

Pectoral girdle. As in many primitive diapsids, the interclavicle is a flat, triradiate to diamond-shaped bone; the best example, RSM 1911.5.5887 (Text-fig. 7A–B), is 35 mm across by 28 mm long. Both the dorsal and ventral surfaces of the bone are smooth and unsculptured. A significant posterior process is present, but this is no longer than the maximum width of the body of the interclavicle; it tapers smoothly to a narrow, blunt point. In this respect, it differs from those of later choristoderes, in which the posterior process is long and may be rather broad (Parks 1927; Russell 1956; Erickson 1972; Sigogneau-Russell 1981; Hecht 1992). The convex (in plan view) anterior margin bears prominent, trough-like, clavicular facets on its anteroventral edge. Laterally, these facets are deeply incised grooves, but they shallow anteromedially to form simple, non-confluent depressions.

BRSMG acc. no. 45/1991 contains a clavicle from an unusually large individual (Text-fig. 7D–E) which is very similar to the clavicles of *Champsosaurus* and *Simoedosaurus*. It is a robust, curved bone with well defined articular facets at each end; the tapered ends form an angle of about 125°. The bone is subcylindrical and is stout at its middle. As in *Champsosaurus* (Erickson 1972), the medial end of the clavicle is broadly expanded in dorsal aspect at the point where the interclavicular articulation is found. A possible clavicle is also represented in the holotype by a slender curved bone that is partially obscured by matrix. The ends of this element meet an angle of approximately 100°. A subovate, plate-like bone associated with the holotype could represent a coracoid, but this is uncertain. It is smooth and measures 34 mm by 22 mm. There is no obvious indication of any articular facets.

Forelimb. The rather unusual and characteristic humerus of *Pachystropheus* is well known from a range of specimens (Plate 2; Text-figs 1B, 8–10), yet in many respects, it is similar to the humeri of proven choristoderes. For example, it possesses moderately expanded ends separated by a slender shaft that is generally oval in cross section; the anterolateral edge of the shaft is essentially straight, whereas the posteromedial edge is broadly concave. The distal end is broader, although very much thinner, than the proximal, and their long axes lie in different planes, separated by approximately 55° of torsion. However, the greater amount of torsion (approximately 85–90°) found in most choristoderes is lacking in *Pachystropheus*.

TEXT-FIG. 5. Selected axial elements of *Pachystropheus rhaeticus* E. von Huene. A–B, anterior cervical vertebra, BRSMG Ce17166, in right lateral and dorsal views (anterior to right), respectively; C–D, mid-series cervical neural arch, BRSUG 17037, in left lateral and dorsal views (anterior to left), respectively; E, dorsal centrum, BMNH R747 (holotype), in right lateral aspect; F, dorsal neural arch, BRSMG Ce17146, in right lateral aspect; G, dorsal centrum, BRSMG Cb4887, in left lateral aspect; H, posterior dorsal or sacral centrum, BMNH R747 (holotype), in dorsal aspect (?anterior to top); I, dorsal rib, BMNH R3711; J–K, dorsal centrum, BRSMG Cb4887, in dorsal and ventral views (anterior at top), respectively; L–M, mid-series dorsal vertebra, BRSMG Ce17165, in right lateral and anterior views, respectively. Scale bars represent 10 mm.



TEXT-FIG. 6. Axial elements of *Pachystropheus rhaeticus* E. von Huene. A, young adult sacral vertebra and rib, BRSUG 25331, in ?posterior aspect; B, ?left caudal rib, BRSMG Ce17775, in dorsal aspect; C–D, anterior caudal or posterior sacral, BATGM C25a, in dorsal and ventral views (anterior at top), respectively; E, mid-series caudal, BMNH R12478, in right lateral aspect; F–G, mid-series caudal, BRSUG 25302.1, in left lateral and ventral views (anterior to left), respectively. Scale bars represent 10 mm.

The articulatory surfaces of the humerus were cartilage-capped. The distal end possesses a broadly expanded posterior corner with only a moderately sized entepicondyle; this covers a small area of the medial as well as the ventral edge of the bone. There is a somewhat more expanded, bulbous ectepicondyle extending well on to the ventral side of the humerus; the anterodistal corner is sharp. Also distally, an inconspicuous supinator process is present ventrolaterally. On the anterodorsal surface, a well defined ectepicondylar groove or sulcus lies between this and the ectepicondyle. There is, however, neither an ectepicondylar nor entepicondylar foramen. The anterolateral (radial) edge of the humerus is drawn into a characteristic, narrow, blade-like supinator ridge that extends from the supinator process to the base of the humeral head. This ridge, typical of choristoderes is, nevertheless, far sharper and more pronounced than in later examples, perhaps as a more fully aquatic adaptation. The posteromedial edge of the humerus is well rounded.

The proximal end of the humerus is weakly ossified and the humeral head indistinct. Posteroventrally, but separated from the head, is a short, well defined crest, generally referred to as the ectotuberosity (Parks 1927; Russell 1956; Sigogneau-Russell 1981; Evans 1991; Storrs and Gower 1993). This is homologous with the 'deltopectoral' crest of primitive tetrapods (Romer 1956). Another crest ('deltoid crest' of Storrs and Gower 1993) is also evident on the proximal anterodorsal face of the bone. The two crests are separated by the dorsal extension of the supinator ridge. A shallow fossa is present medially for the insertion of the *M. coracobrachialis*. A concavity proximal and dorsal to the supinator ridge was probably for the insertion of the *M. scapulohumeralis*; the distal portion of the ridge may have served as part of the *M. triceps* origin.

The largest complete *Pachystropheus* humerus known, BRSMG Cd2678, is some 90 mm in maximum length and differs from smaller examples in the exaggeration of its major features (Text-fig. 9). Most notably, this includes a more expanded distal end, a deeper ectepicondylar groove, a larger supinator process, a small radius of curvature to the concave posteromedial edge and a deltopectoral crest that lies more distally on the humeral shaft. Unlike smaller specimens, it is also characterized by the greater downward (subaxial) curvature of its distal end. Small examples, such as BRSMG Ce17778, typically lack condyles and crests; the reduced ectepicondyle noted by Storrs and Gower (1993) is now known to represent the immature condition.

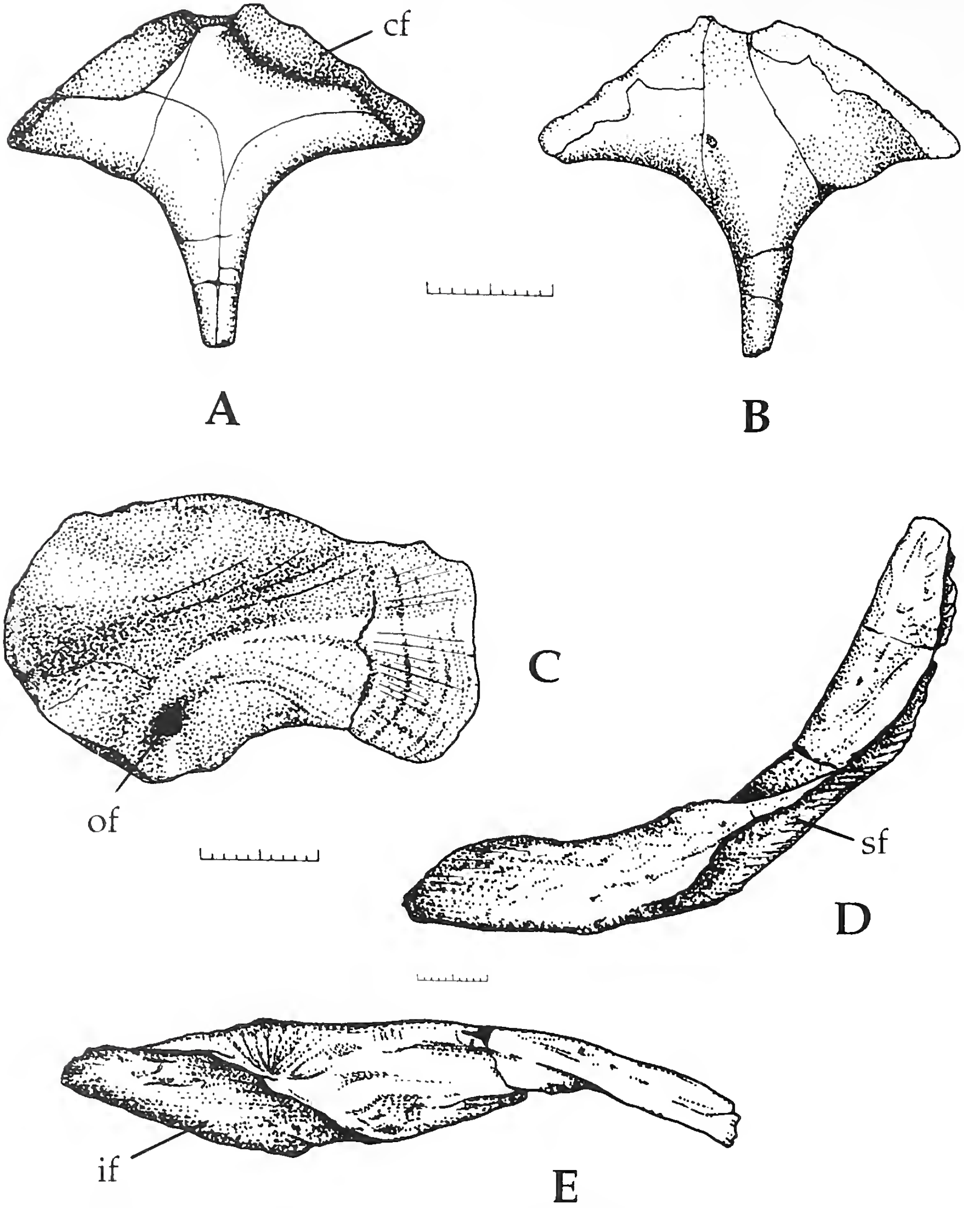
The most notable differences of *Pachystropheus* humeri from those of undoubted choristoderes, such as a lesser degree of torsion, flatter distal end and extremely sharp and prominent supinator ridge, may be related to a more aquatic existence for the Rhaetian form, in keeping with its marginal marine provenance. The sharp supinator ridge, in particular, is an apparent autapomorphy that distinguishes *Pachystropheus* within Choristodera.

Pelvic girdle. The pubis (Text-fig. 7c) is best known from a complete example exposed in dorsal view only. It is a broad, smooth, plate-like bone of subrectangular plan. The long (medio-lateral) axis of the bone (40 mm) is approximately twice the length of the longitudinal axis (21 mm maximum); the symphyseal edge is 15 mm long. A clear series of growth lines parallel the symphysis. The posterior edge of the pubis is concave, suggesting the presence of a small pelvic fenestra in this individual, perhaps the result of immaturity. The slightly worn anterior edge is similar to that of *Champsosaurus* (Erickson 1972) in being laterally convex but concave medially. The anterior edge in *Simoedosaurus* is much straighter and the medial symphysis longer (Sigogneau-Russell 1981). The anterolateral corner is thickened in *Pachystropheus* and bears a 'pectineal tuber' which, by inference (Erickson 1972), perhaps served as an attachment site for the *M. pubotibialis*.

The posterolateral corner of the pubis is the most robust portion of the bone and forms the anterior limit of the acetabulum. The acetabular surface forms an angle of approximately 140° with the posterior border. A low, curving ridge, for intracorporeal transmission of hindlimb-generated forces, extends from the posterolateral corner to the centre of the symphysis. The obturator foramen is completely enclosed and lies between the acetabulum and this transverse ridge.

Most of the acetabulum is formed by the ilium (45 mm in total length in the holotype) and is a shallow, subcircular depression, ventral to a pronounced supraacetabular crest (Text-fig. 11). The acetabular ramus is rhomboidal in lateral aspect with an angle between the pubic and ischial facets of approximately 100°; their crescentic articular surfaces are similar in area. The ilium is constricted at the supraacetabular crest before expanding into an iliac blade that projects almost entirely caudally, with little or no anterior ramus. At this constriction, there is a small but pronounced anterior prominence as in *Champsosaurus* and *Simoedosaurus* (Erickson 1972; Sigogneau-Russell 1981). The tip of the iliac blade is blunt and transversely thickened; the blade's ventral edge is oriented more or less horizontally.

There are no obvious facets for sacral rib articulation, but the middle of the blade's medial surface bears a thickened brow-like ridge potentially associated with the sacrum. The posterodorsal portion of the blade is strongly striated; the striae run more or less longitudinally and are heavier and longer medially than laterally. Except for the greater breadth of their dorsal blades, the ilia of *Simoedosaurus* (Sigogneau-Russell 1981;



TEXT-FIG. 7. Appendicular arch elements of *Pachystropheus rhaeticus* E. von Huene. A–B, interclavicle, RSM 1911.5.5887, in medial and ventral views, respectively; C, young adult left pubis, BRSUG 25330, in dorsal (internal) aspect; D–E, adult right clavicle, BRSMG lot acc. no. 45/1991, in dorsal and posterior views, respectively. Scale bars represent 10 mm. Abbreviations: cf, clavicular facet; if, interclavicular facet; of, obturator foramen; sf, scapular facet.

Erickson 1987), *Ikechosaurus* (Brinkman and Dong 1993) and *Champsosaurus* (Parks 1927; Erickson 1972) are comparable with similar striations.

BMNH R4837 (Text-fig. 11A) represents the largest known *Pachystropheus* ilium, although incomplete (the next largest, BMNH R12535, is complete and approximately 80 mm long), and has a broader blade and heavier ribbing than other examples, perhaps a consequence of its greater size. Sykes *et al.* (1970, pl. 17, fig. 13) reproduced a photograph of a smaller ribbed ilium ('?pelvic bone' of an 'indeterminate archosaur') with a far narrower dorsal blade. It is presumed that the blade grew in relative dorsoventral height with increased ontogenetic age and absolute size.

Hind limb. The femur is long (63 mm in the holotype) and slender with expanded ends (Text-figs 3A, 12–13), and is very similar to known choristoderan femora, although these conform to a rather primitive reptilian morphotype. The shaft is essentially straight with an inconspicuous adductor ridge on its postaxial surface. The distal end is broader than the proximal head, yet is thinner dorso-ventrally while slightly 'downturned' towards the postaxial surface. The distal condyles are very weakly defined with a shallow popliteal space between them, but no intercondylar fossa on the superaxial surface of the femur. The head occupies the whole of the proximal and proxomedial faces of the bone; its unfinished surface lies at nearly 90° to the longitudinal axis of the shaft. In anterodorsal and posteroventral views, the preaxial edge of the proximal part of the shaft is concave and the postaxial edge convex.

The posteroventral surface of the proximal edge of the femur bears a substantial internal trochanter which, in large specimens, is positioned a significant distance from the proximal end. The head and trochanter are therefore not confluent. In smaller, i.e. younger, individuals, the gap between the internal trochanter and the femoral head is less conspicuous, and occasionally is nonexistent. However, the intertrochanteric fossa, adjacent to the internal trochanter, is more clearly defined. Variation in these relationships has attracted attention in other studies of choristodere morphology (e.g. Erickson 1972, 1987; Brinkman and Dong 1993). On the posterodorsal edge of the femur's proximal end, near the end of the internal trochanter, is a low, rugose prominence or 'external trochanter'.

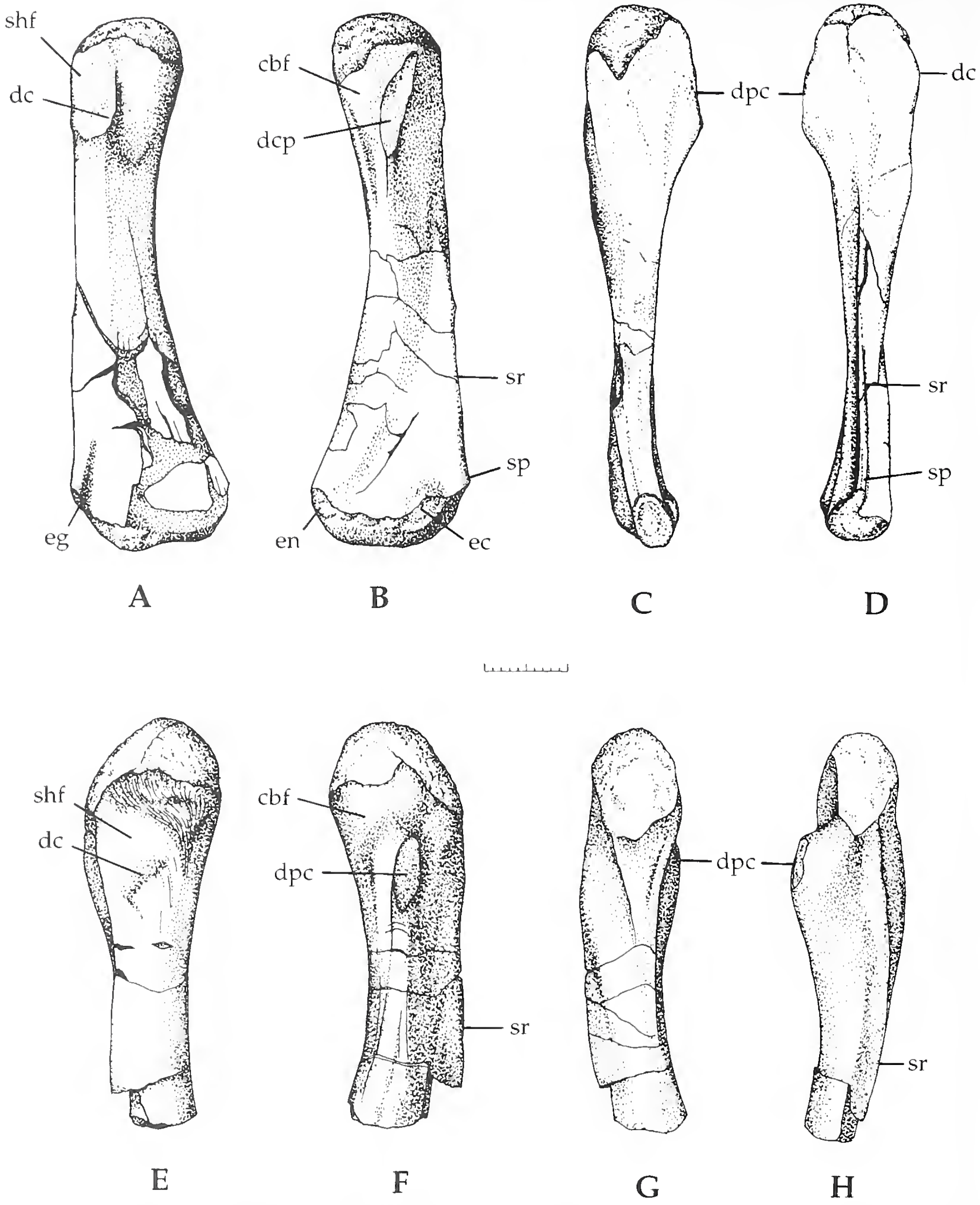
The best epipodial is part of the holotype and, from the associated remains, probably represents a tibia. In primitive reptilian fashion, it is short in comparison with the femur (34 mm versus 63 mm), and the subcircular (in transverse section) proximal end is markedly broader than the ovate distal end. The smooth, exposed (posterior?) edge is longitudinally concave. A similar bone (BRSMG acc. no. 45/1991) exhibits a relatively sharp and straight ?anterior edge. Except for its smaller size and lesser development of muscle attachment sites, the putative tibia of *Pachystropheus* resembles that of *Champsosaurus* (Erickson 1972).

A few phalanges from Rhaetian deposits may belong to *Pachystropheus*. E. von Huene (1933, fig. 28) illustrated a specimen from Gaisbrunnen (GPIT 19552) that she ascribed to this animal. It is 5 mm long with a constricted shaft and expanded articular ends, the proximal larger than the distal. The distal articulation is divided by a trochlear groove. At least two specimens in lot BRSMG acc. no. 45/1991 are similar. The 'distal end of a metatarsal' (E. von Huene 1933, fig. 29) is problematical.

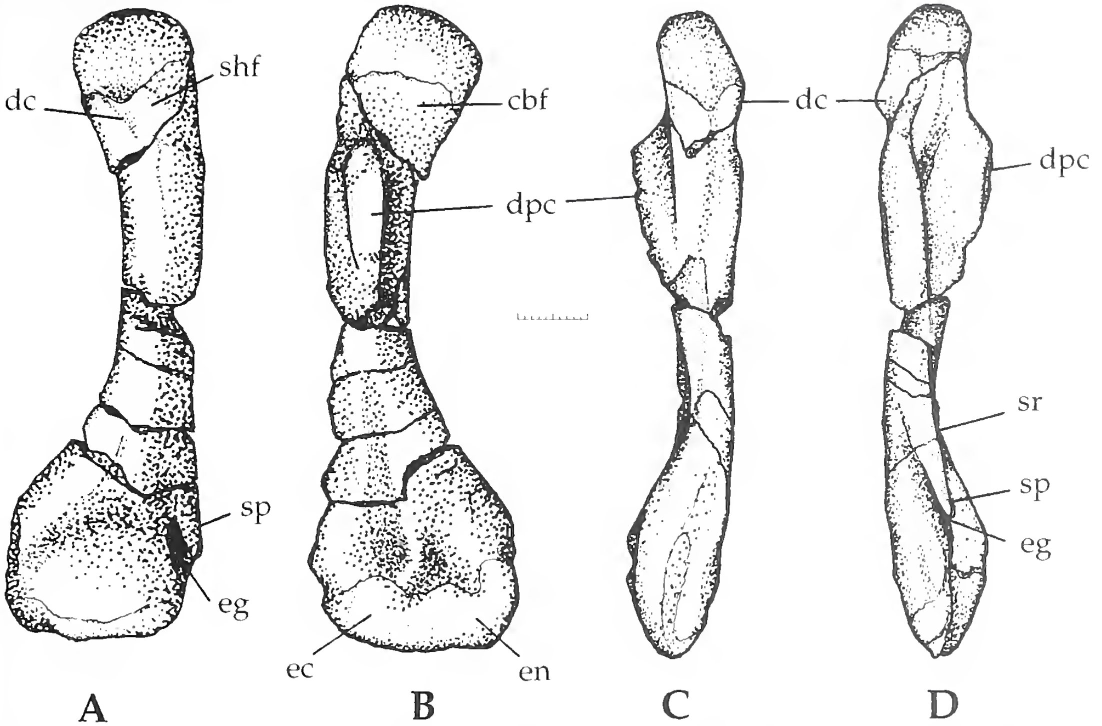
RELATIONSHIPS

The relatively common champsosaurs of the Cretaceous (Aptian–Albian, Santonian–Maastrichtian) and Palaeogene (Danian–Ypresian) of North America, Europe and central Asia are the best known choristoderes (Cope 1876; Gervais 1877; Brown 1905; Parks 1927; Russell 1956; Erickson 1972, 1987; Efimov 1975, 1983, 1988; Russell-Sigogneau and Russell 1978; Sigogneau-Russell 1981; Sigogneau-Russell and Efimov 1984). Until recently they formed an isolated group with problematical links with other taxa. Primitive Choristodera, however, are now known from the Jurassic (Bathonian, Oxfordian/Kimmeridgian) of America and Europe (Evans 1989, 1990, 1991; Metcalf *et al.* 1992), and the Oligocene (?Stampian) of France (Hecht 1992). *Pachystropheus* seemingly represents the Choristodera in the European Rhaetian (E. von Huene 1935; Hoffstetter 1955; F. von Huene 1956; Kuhn 1961; Storrs 1992, 1993, 1994; Storrs and Gower 1993).

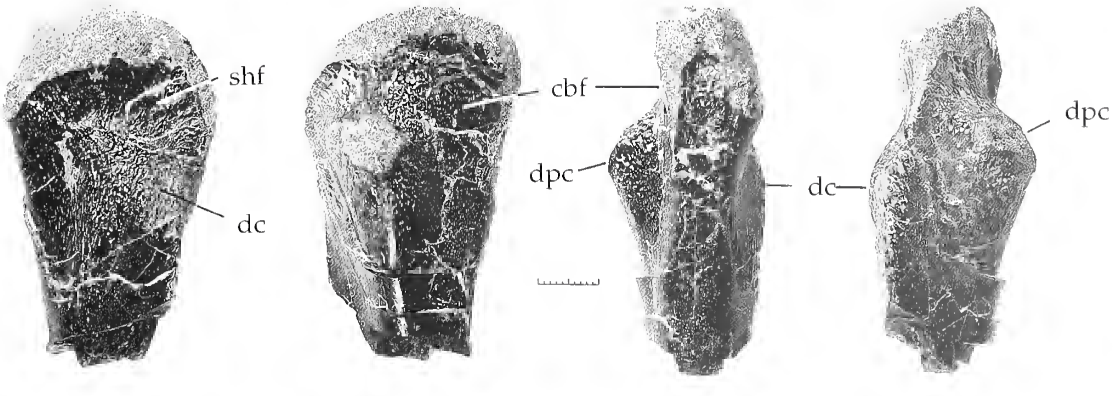
Pachystropheus (sometimes '*Rysosteus*') has been identified as an archosaur of unknown affinity (Halstead and Nicoll 1971; Duffin 1978, 1980; Antia 1979; Duffin *et al.* 1983), dinosaur (Reynolds 1946; Macfadyen 1970), crocodilian (E. von Huene 1933; Duffin 1982, 1985), or indeterminate reptile (Sykes *et al.* 1970; Martill and Dawn 1986) as well as a champsosaur/choristodere. The material



TEXT-FIG. 8. Humeri of *Pachystropheus rhaeticus* E. von Huene. A–D, left humerus of young individual, BRSMG Cb4907, in A, superaxial, B, subaxial, C, postaxial, and D, preaxial views; E–H, proximal end of left humerus of mature individual, RSM 1911.5.5918, in E, superaxial, F, subaxial, G, oblique postaxial, and H, preaxial views. Scale bar represents 10 mm. Abbreviations: cbf, coracobrachialis fossa; dc, deltoid crest; dcp, deltopectoral crest; ec, ectepicondyle; eg, ectepicondylar groove; en, entepicondyle; shf, scapulohumeralis fossa; sp, supinator process; sr, supinator ridge.

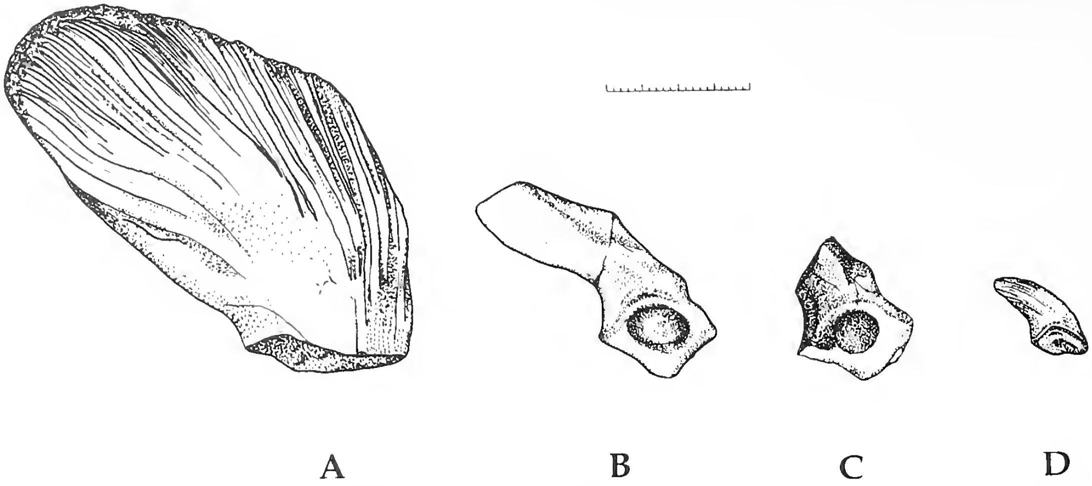


TEXT-FIG 9. Right humerus of large individual of *Pachystropheus rhaeticus* E. von Huene, BRSMG Cd2678, in A, superaxial, B, subaxial, C, postaxial, and D, preaxial views. Scale bar represents 10 mm. Abbreviations as in Text-figure 8.

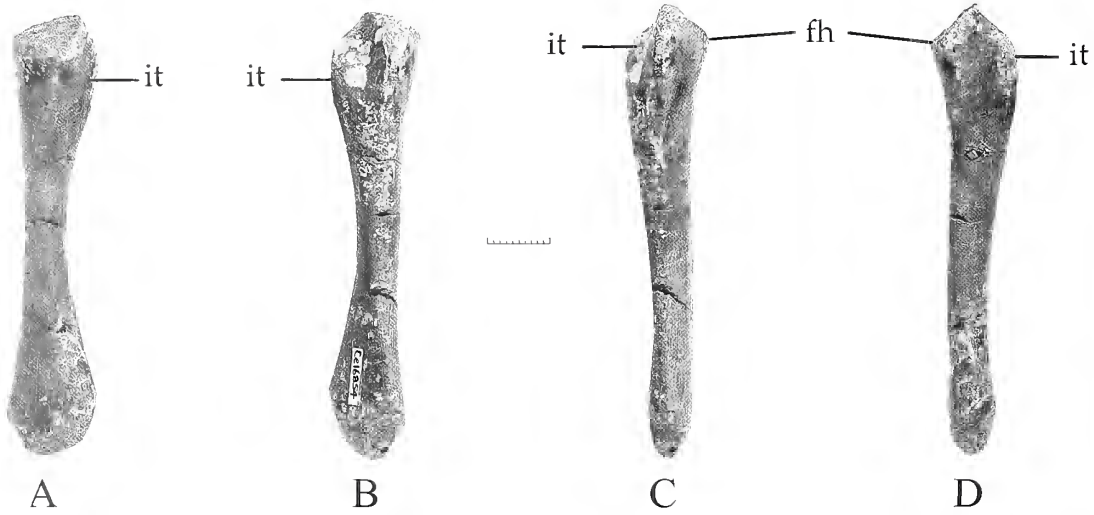


TEXT-FIG. 10. Proximal head of right humerus of extremely large individual of *Pachystropheus rhaeticus* E. von Huene, BRSMG Cd2422, in A, superaxial, B, subaxial, C, postaxial, and D, preaxial views. Scale bar represents 10 mm. This specimen represents the largest known humerus of this taxon. Abbreviations as in Text-figure 8.

described here confirms that *Pachystropheus rhaeticus* may be an early choristodere, or at least belongs to the lineage that gave rise to that group. It possesses several group synapomorphies and E. von Huene's (1935) original hypothesis of choristoderan ('rhynchocephalian') affinity (by comparison with champsosaurs) cannot be rejected.



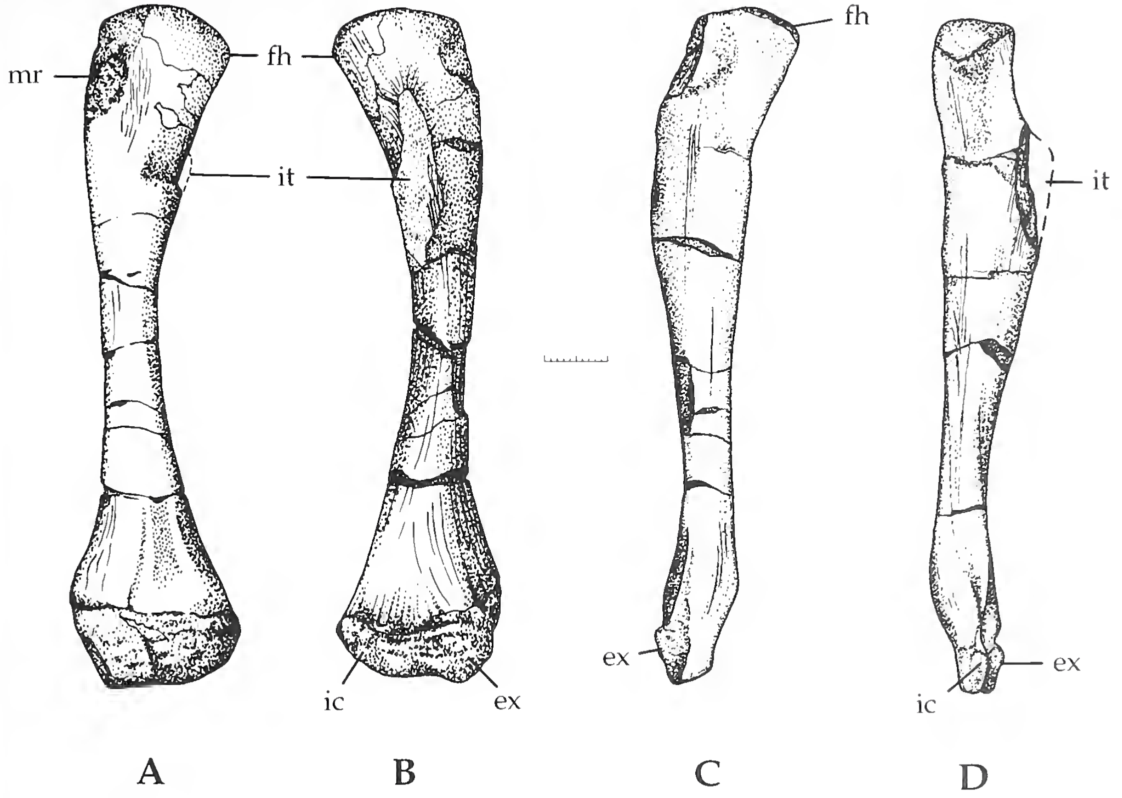
TEXT-FIG. 11. Ontogenetic series of *Pachystropheus rhaeticus* E. von Huene ilia. A, large adult left iliac blade, in medial aspect, BMNH R4837; B, typical left ilium in lateral aspect (image reversed), BRSUG 25329; C, acetabular region of right ilium of young adult individual, BMNH R2727, in lateral aspect; D, complete right ilium of juvenile, in lateral aspect, BRSMG lot acc. no. 45/1991. Scale bar represents 20 mm.



TEXT-FIG. 12. Right femur of immature individual of *Pachystropheus rhaeticus* E. von Huene, BRSMG Ce16854, in A, superaxial, B, oblique subaxial, C, postaxial, and D, preaxial views. Ends slightly abraded. Scale bar represents 10 mm. Abbreviations as in Text-figure 13.

Pachystropheus is linked with typical choristoderes by:

1. constricted, amphicoelous to nearly platycoelous, non-notochordal adult vertebrae (only rarely retaining a notochordal pit in juveniles);
2. unfused neurocentral sutures in the presacral portion of the column in all but the oldest individuals;
3. broad neural arch facets;
4. deeply incised, yet constricted neural canal;



TEXT-FIG. 13. Right femur of fully adult individual of *Pachystropheus rhaeticus* E. von Huene, BRSUG 7010.4, in A, superaxial, B, subaxial, C, postaxial, and D, preaxial views. Scale bar represents 10 mm. Abbreviations: ex, external condyle; fh, femoral head; ic, internal condyle; it, internal trochanter; mr, muscle rugosity.

5. small fossa in the lateral surface of the centrum;
6. strongly corrugated, subrectangular neural spines in the middle and posterior dorsal vertebrae;
7. caudal vertebrae with deep, midventral, longitudinal furrows and strong border keels;
8. vertical articular faces to the caudal zygapophyses;
9. dorsal ribs with flange-like ridge and posterior sulcus;
10. broad, flat sacral ribs;
11. elongate iliac blade, heavily ribbed with longitudinal striae; and
12. humerus bearing very sharp, long and prominent supinator ridge.

Plesiomorphic characters that are not definitive, but nevertheless suggestive, of choristoderan relationships are:

1. simple, thickened ribs and gastralia;
2. confluent capitulum and tuberculum;
3. cervical parapophyses absent;
4. dorsal transverse processes lying across the neurocentral suture;
5. triradiate interclavicle with strong posterior process;
6. robust, L-shaped clavicle;
7. simple humerus with broad, flat distal end;
8. deep ectepicondylar sulcus;

9. no entepicondylar foramen;
10. plate-like, subrectangular pubis with fully closed obturator foramen; and
11. largely straight femur with robust internal trochanter and poorly ossified articular ends.

The complete character suite strongly suggests that *Pachystropheus* either lies within, or very close to, Choristodera. No obvious characters are incongruent with this interpretation, and therefore, we believe *Pachystropheus rhaeticus* to be the earliest known representative of this enigmatic group of semi-aquatic reptiles. Currently, if somewhat tenuously, choristoderes are envisaged as primitive members of the Archosauromorpha (Evans 1988, 1990; Gauthier *et al.* 1988; Storrs and Gower 1993). Additional material of *Pachystropheus*, particularly cranial elements, could conceivably elucidate the relationship of the Choristodera with other diapsid reptiles.

DISCUSSION

The identification of *Pachystropheus* as a potential choristodere pushes back their known fossil history by nearly 45 million years (Storrs and Gower 1993). It seems, at least on the basis of postcranial morphology, and excepting the few autapomorphies of the *Pachystropheus* humerus, that choristoderes have been a remarkably conservative lineage since at least the latest Triassic (Rhaetian). A relative shortening of the vertebral centrum over time is one of the few obvious morphological trends within the clade, although *Lazarussuchus*, as the latest known representative, nevertheless retained the primitive condition (Hecht 1992).

The known *Pachystropheus* material comes from individuals of a wide size range. The majority of specimens are from animals of approximately 1 m or less in size, and seemingly immature. However, occasional examples indicate animals in the range of 2–2·5 m (Plate 2; Text-figs 10, 11A), as typically were *Champsosaurus* and *Simoedosaurus*, although champsosaurs also grew unexpectedly large (Langston 1958). To date, *Cteniogenys* and *Lazarussuchus* are known only from much smaller individuals (Gilmore 1928; Seiffert 1973; Evans 1989, 1990, 1991; Hecht 1992; Metcalf *et al.* 1992), while most Asian forms (*Tchoiria*, *Ikechosaurus*, *Khurendukhosaurus*) were apparently intermediate in size (Efimov 1975, 1988; Sigogneau-Russell and Efimov 1984; Brinkman and Dong 1993). There is thus no demonstrable size trend for choristoderes. The only obvious anatomical variation within Choristodera, other than size and centrum length, may be rostrum length/breadth ratio, a metric unknown for *Pachystropheus*.

A notable feature of *Pachystropheus* accumulations is their environment of deposition. All other accepted choristoderes are known from freshwater, usually fluvial, palaeoenvironments, although *Lazarussuchus* was preserved in a freshwater limestone, presumably a fossil pond or marsh (Hecht 1992). *Pachystropheus* is uniquely preserved in marginal marine sediments. While marine elements, such as selachians, plesiosaurs and ichthyosaurs, dominate the Westbury Formation fauna, occasional terrestrial components, such as dinosaurs (cf. *Camelotia*, *Megalosaurus*?) and lungfish (*Ceratodus*), are also found; their presence suggests a fluvial contribution to the deposit (Storrs 1993, 1994). Interestingly, the lungfish teeth and *Pachystropheus* bones are generally unabraded with little evidence of transportation; their source must have been close. Similarly mixed elements occur in the French and German 'Rhaetic' localities containing *Pachystropheus*, but the French fossils in particular, are abraded and clearly allochthonous.

Discovery of an articulated specimen of *Pachystropheus rhaeticus* from Rhaetian 'bone beds' is unlikely. However, intervening shales, although rarely suitable for bedding plane prospecting, may offer the hope of better material from which a clearer picture of *Pachystropheus* may emerge. Significantly, the occurrence of a single humerus (BRSMG Cd2678) in the lower Lias of Lilstock, Somerset, is the only example of *Pachystropheus* above the Rhaetian. Although lying only a few metres above the Westbury Formation, this range extension gives a tantalizing reminder that rare semi-terrestrial to terrestrial fossils can be found in Lias Group shales.

The age of the vertebrate-bearing sands of Saint-Nicolas-de-Port is a matter of some dispute. Although generally considered Rhaetian (Russell *et al.* 1976; Clemens *et al.* 1979; Clemens 1980), Buffetaut (1985), Buffetaut and Wouters (1986), and Cuny and Ramboer (1991) have suggested that this French locality is Norian, although equating the late Norian with the Rhaetian. Duffin (1993) tentatively supported a Norian age, but left open the possibility of a Rhaetian assignment. All of these chronostratigraphical determinations have been based solely on the vertebrate assemblage, and therefore are not wholly reliable. If, however, the Saint-Nicolas-de-Port material is older than that of the Westbury Formation, a further range extension is provided for *Pachystropheus* and, presumably, Choristodera. As Storrs and Gower (1993) have discussed, this is not an unexpected development.

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APPENDIX

List of referred material:

BATGM C18, C25, C25a (anterior caudal? vertebra; Text-fig. 6C–D; E. von Huene 1933, pl. 3), C28 (anterior dorsal vertebra; Plate 1, figs 1–6; E. von Huene 1933, pl. 3; Duffin 1978, pl. 2, fig. 6), M205 (large, matrix-free, dorsal vertebra, Plate 2, figs 1–4; F. von Huene 1956, fig. 649) and others, uncatalogued.

BGS GSM 610, GSM 53508 (large femur), GSM 53594–53598, GSM 112033, GSM 112036, GSM 112039, Zr 8601–8604 (isolated, matrix-free ectopterygoid; Text-fig. 4).

BMNH R395, R2728 (right iliac acetabulum; Text-fig. 11C; Storrs and Gower 1993, fig. 2), R3711 (dorsal rib; Text-fig. 5I; Storrs and Gower 1993, fig. 1), R4837 (large left iliac blade; Text-fig. 11A; Storrs and Gower 1993, fig. 2), R6242 (dorsal rib), R6243 (dorsal centrum), R6245 (caudal rib), R6259, R6851 (mid-series dorsal vertebra; Plate 1, figs 7–10), R12466–12478 (mid-series caudal vertebra; Text-fig. 6E); R12479–12488 (slab with large femur, 100 mm long), R12489–12494, R12496–12498, R12500, R12505, R12507–12508, R12510–12512, R12514, R12516–12517, R12520–12521, R12523–12525, R12527–12528 (slab bearing an ectopterygoid), R12529, R12531–12535 (includes a large partial pubis and ilium), R12536–12537 (indeterminate epipodial), R12539–12543, R12546–12548, R12550–12554 (miscellaneous postcranial remains on Garden Cliff slabs), 44835 (block containing anterior dorsal vertebra, dorsal rib).

BRSMG Cb4887 (isolated dorsal centrum; Text-fig. 5G; Storrs and Gower 1993, fig. 1), Cb4907 (matrix-free left humerus; Text-fig. 8A–D; Plate 2, fig. 5; Storrs and Gower 1993, fig. 2; Storrs, 1994, fig. 7), Cb9065 (slab of associated remains; Text-fig. 1B), Cd2422 (proximal end of large right humerus; Text-fig. 10; Plate 2, fig. 6), Cd2678 (large, matrix-free, right humerus; Text-fig. 9), Cd3174, Cd3365, Ce16854 (matrix-free, immature, right femur; Text-fig. 12), Ce17081 (interclavicle; Storrs and Gower 1993, fig. 2), Ce17082, Ce17093–17094, Ce17102, Ce17112, Ce17146 (dorsal neural arch; Text-fig. 5F), Ce17151, Ce17165 (mid-series dorsal vertebra; Text-fig. 5L–M; Storrs and Gower 1993, fig. 1), Ce17166 (anterior cervical vertebra; Text-fig. 5A–B), Ce17173, Ce17191–17192, Ce17200 (interclavicle; Storrs and Gower 1993, fig. 2), Ce17322–17323, Ce17330 (small femur), Ce17656 (distal caudal vertebra), Ce17770 (slab with associated postcrania; Storrs 1994, fig. 8), Ce17775 (?left caudal rib; Text-fig. 6B), Ce17777–17778 (juvenile humerus), Ce17801 and numerous specimens in lot acc. no. 45/1991 (including a large, matrix-free, right clavicle; Text-fig. 7D–E; a juvenile right ilium; Text-fig. 11D; a ?tibia and phalanges; also a matrix-free gastralium; Storrs and Gower 1993, fig. 1).

BRSUG 7010.4 (matrix-free, right femur, 100 mm long; Text-fig. 13; Storrs and Gower 1993, fig. 2), 17037 (mid-series cervical neural arch; Text-fig. 7), 19415.3, 19969 (interclavicle), 25301 (dorsal centrum), 25302.1 (mid-series caudal vertebra; Text-fig. 6F–G; Storrs and Gower 1993, fig. 1), 25302.2, 25304, 25305.1 (anterior caudal? vertebra), 25306, 25308–25314 (dorsal rib), 25315–25320 (dorsal vertebra), 25321–25323 (dorsal rib), 25324–25325 (anterior dorsal vertebra), 25326–25329 (left ilium; Text-fig. 11B), 25330 (isolated left pubis; Text-fig. 7C), 25331 (sacral vertebra and rib; Text-fig. 6A), 25332–25333 (ectopterygoids), 26161.

CMNHS VP4112 (humerus), VP4113, VP4114 (ectopterygoid), VP4115–4116, VP4117 (humerus), VP4118, VP4119–4120 (right humeri), VP4121–4124, VP4125 (partial pubis), VP4126–4127, VP4128 (small ectopterygoid), VP4129–4131, VP4132 (propodials), VP4133 (vertebrae), VP4134, VP4135 (dorsal vertebra), VP4136–4138, VP4139 (vertebrae and partial femur), VP4140, VP4642 (femur), VP4644.

GPIT 19552 (one half a sacral centrum, phalanx, isolated neural arches; E. von Huene 1935, pl. 3; Kuhn 1971, fig. 20).

LEIUG 88988 (proximal end of humerus, Martill and Dawn 1986, pl. 8, fig. B), 88989 (juvenile humerus, Martill and Dawn 1986, pl. 8, fig. C), 88990 (?sacral vertebral centrum, Martill and Dawn 1986, pl. 8, fig. G).

MM LL.8018 and others (associated postcrania from 'Slime Road' Cliff, E. von Huene, 1933, pl. 3 and various in E. von Huene 1935, currently unlocated).

MNHN SNP101 (abraded dorsal centra).

RSM 1888.87.1, 1911.5.5887 (matrix-free interclavicle; Text-fig. 7A–B), 1911.5.5918 (proximal end of matrix-free, left humerus; Text-fig. 8E–H), 1911.5.6023.

SMNS 58791 (six isolated dorsal centra).

STGCM 60.62/1 (slab of associated remains, including vertebrae and limbs, potentially a single individual; Text-fig. 1A), 1986.145/1-8 (W9).

A NEW ALLIGATOR FROM THE UPPER CRETACEOUS OF CANADA AND THE RELATIONSHIPS OF EARLY EUSUCHIANS

by XIAO-CHUN WU, DONALD B. BRINKMAN *and* ANTHONY P. RUSSELL

ABSTRACT. A new alligatorine eusuchian, *Stangerochampsa mccabei* gen. et sp. nov., is described on the basis of a partial skeleton from the Horseshoe Canyon Formation (Early Maastrichtian) of southern Alberta. It is unique in possessing an ectopterygoid/palatine contact, a ventrolateral process of the quadrate, a groove-like recess for nerves and blood vessels in the upper jaw, a rectangular palatine with a lateral process at its midpoint, and a basioccipital with a ventral exposure longer than that of the pterygoid. Several derived characters indicate a close relationship of *S. mccabei* with two Late Cretaceous alligatorines, *Brachychampsa montana* and *Albertochampsa langstoni*. A preliminary phylogenetic analysis, based on 46 characters of selected taxa, leads to the hypothesis that *Leidyosuchus*, rather than *Hylaeochampsa*, is the most primitive eusuchian, supports the monophyly of the Alligatorinae (with the exclusion of *Prodiplocynodon*), and suggests that the Alligatorinae may consist of at least two distinct assemblages.

Two genera of alligatorines have been reported from the Upper Cretaceous of North America, *Albertochampsa langstoni* from the middle Campanian Dinosaur Park Formation (Judith River Group) of southern Alberta (Erickson 1972), and *Brachychampsa montana* from the upper Maastrichtian Hell Creek Formation of Montana (Gilmore 1911; Norell *et al.* 1994). A well-preserved skeleton of an alligatorine recently unearthed from the lower Maastrichtian Horseshoe Canyon Formation, southern Alberta, Canada, here described as *Stangerochampsa mccabei* gen. et sp. nov., represents a third alligatorine genus in the Late Cretaceous and the first crocodylian from these beds to be represented by relatively complete material.

The detailed understanding of the skeleton of *Stangerochampsa mccabei* provides a basis for reconsidering the phylogenetic relationships of early members of the Eusuchia. Recent phylogenetic studies have established the successive sister groups of the Eusuchia (Clark *in* Benton and Clark 1988; Norell 1989; Buscalioni and Sanz 1990; Norell and Clark 1990; Clark and Norell 1992; Willis 1993; Clark 1994), but a number of Mesozoic (Cretaceous) eusuchians, represented by fairly well-preserved specimens, have not been subjected to phylogenetic study. These Mesozoic taxa include *Hylaeochampsa vectiana* (Owen, 1874), *Leidyosuchus* spp., *Brachychampsa montana*, *Prodiplocynodon langi* (Mook, 1941*a*) and *Albertochampsa langstoni*. These taxa are included in the present analysis. A number of Cenozoic alligatorines are also included in order to establish a suite of synapomorphies of the Alligatorinae. Norell *et al.* (1994) recently argued for a close relationship between *B. montana* and *A. langstoni*. The present study further suggests that these two taxa and *S. mccabei* form a monophyletic group of alligatorines from the Upper Cretaceous of western North America.

Institutional abbreviations used in this study are as follows: the American Museum of Natural History, New York (AMNH); the Field Museum of Natural History, Chicago (FMNH); the Royal Ontario Museum, Toronto (ROM); the Royal Tyrrell Museum of Palaeontology, Drumheller (RTMP); the Museum of Paleontology, University of California, Berkeley (UCMP); National Museum of Natural History, Smithsonian Institution, Washington D.C., (USNM); and the Peabody Museum of Yale University, New Haven, (YPM).

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SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Clark *in* Benton and Clark, 1988
EUSUCHIA Huxley, 1875
CROCODYLIA Gmelin, 1788
CROCODYLIDAE Cuvier, 1808
ALLIGATORINAE Kälin, 1955

Genus STANGEROCHAMPSA gen. nov.

Type species. Stangerochampsa mccabei.

Derivation of name. Refers to the Stanger family, owners of the ranch from which the type specimen was collected.

Diagnosis. As for type and only known species.

Stangerochampsa mccabei sp. nov.

(Plates 1–3; Text-figures 1–3)

Holotype. RTMP.86.61.1, a skeleton including an almost complete skull with mandibles lacking articulars and coronoids, partial postcranium, and many osteoderms.

Locality and Horizon. Quarry L1524 (NE1/4 LD11 S3 T30 R21W 04), about 8 km north-west of the Royal Tyrrell Museum of Palaeontology at Drumheller, southern Alberta, Canada; from the lower half of the Upper Cretaceous Horseshoe Canyon Formation (lower Maastrichtian), 7 m below coal seam number nine.

Derivation of name. A patronym erected in honour of Mr James Ross McCabe who found, collected, and prepared the specimen.

Diagnosis. A small to medium-sized alligatorine distinguished from all other alligatorines in having the following unique derived characters: an enlarged, groove-shaped recess for blood vessels and nerves in upper jaw; a distinctly laterally directed process of quadrate above condyle on ventral surface; palatine of rectangular outline and with a lateral process at its midlength; ectopterygoid contacting palatine along anterior border of suborbital fenestra; ventral exposure of basioccipital longer than that of pterygoid; and suborbital fenestra with a straight anterolateral border formed entirely by ectopterygoid.

This species shares with *Brachychampsa montana* a strongly curved quadratojugal/quadrate suture; with *Albertochampsa langstoni* a palatine with its anterior portion equal in length to its interfenestral portion; and with *B. montana* and *A. langstoni* a lacrimal having an elongate posteroventral process reaching the midpoint of the ventral border of orbit, a skull table strongly rounded anterolaterally, a large incisive foramen, and a maxilla with a broad lateral portion lateral to tooth row.

Additionally, two characters may be unique to *Stangerochampsa mccabei*, but their respective character-states are undetermined in other alligatorines: palatal process of maxilla forming a step-like structure posteromedial to tooth row; and a shallow but distinct groove present on the lateral surface of the anteromedial portion of the laterosphenoid.

DESCRIPTION

Skull

The skull, largely uncrushed and missing only the articular condyle of the left quadrate (Text-fig. 1), has strongly developed sinusoidal curves along the ventral, lateral and dorsal sides of the dental margin. The snout is short, triangular, and wider than long and is slightly longer than the postorbital region of the skull (measured from the anterior borders of the orbits to the posterior margin of the skull table). The large, undivided naris is longer than wide and wider anteriorly than posteriorly. The orbit and supratemporal fenestra are similar in shape, although the latter is about three-fifths of the former in both length and width. The supratemporal passage penetrates only the anterolateral portion of the supratemporal fossa. The relatively small skull table is shorter in length than the orbit, and its anterolateral border is strongly rounded. The infratemporal fenestra is triangular, with the three sides of subequal length, and is larger than the supratemporal fenestra. No distinct marginal ridge is formed around the naris, orbit, or temporal fenestrae. In occipital view, the posttemporal fenestra is closed and the foramen magnum is wider than high.

In ventral view, the skull is unique in that foramina for blood vessels and nerves anterior and posterior to the maxilla/jugal suture are greatly enlarged and connected with one another to form a deep, elongate, groove-shaped recess posterolateral to the tooth row (Text-fig. 1B–C). This recess resembles a common alveolar groove for the posteriormost maxillary teeth. The incisive foramen is large and oval in shape with a slightly smaller posterior end enclosed by the maxillae. The suborbital fenestra is of moderate size and is diagonally oriented with a straight anterolateral border formed entirely by the ectopterygoid. Lines drawn through the long axes of the two suborbital fenestrae cross at the median exit of the eustachian tube. The length of the long axis is about equal to the distance from the posteromedial edge of the suborbital fenestra to the posterolateral corner of the transverse flange of the pterygoid, as well as to the distance from the posteromedial edge of the suborbital fenestra to the centre of the median exit of the eustachian tube. The choana is wider than long, divided by a very thin lamina, and much smaller in size than the incisive foramen. The choana is positioned along the posterior half of the pterygoid and is surrounded posteroventrally by a strongly developed, V-shaped crest, as in many later alligatorines. Two pairs of large fossae for the large caniniform dentary teeth (fourth, and thirteenth or fourteenth) are present, one at the premaxilla/maxilla sutures and one at a position medial to the eighth (right side) or seventh (left side) maxillary tooth, respectively.

The outer surface of the skull is strongly sculpted. The sculpting is characterized by short grooves and ridges in the anterior half of the skull and pits in the posterior half, a pattern common in alligatorines.

Dorsal skull roof. The premaxilla (Text-fig. 1A–C) is elevated around the periphery of the external naris. Anterior to the naris, the premaxilla is very narrow and does not form a roof-like structure overhanging the nasal capsule. The posterodorsal process is sharply pointed, extending posteriorly beyond the level of the fourth maxillary teeth, and reaching the middle of the snout. In ventral view, the premaxillae are widely separated from one another and end at the level of the posterior margin of the large incisive foramen.

The nasal (Text-fig. 1A) is relatively broad. The sutures with the premaxilla, maxilla and prefrontal do not form a straight line. The nasal/premaxillary suture is almost as long as the nasal/maxillary suture. The anterior end of the nasal is much narrower than the posterior end. The two nasals form a W-shaped posterior margin.

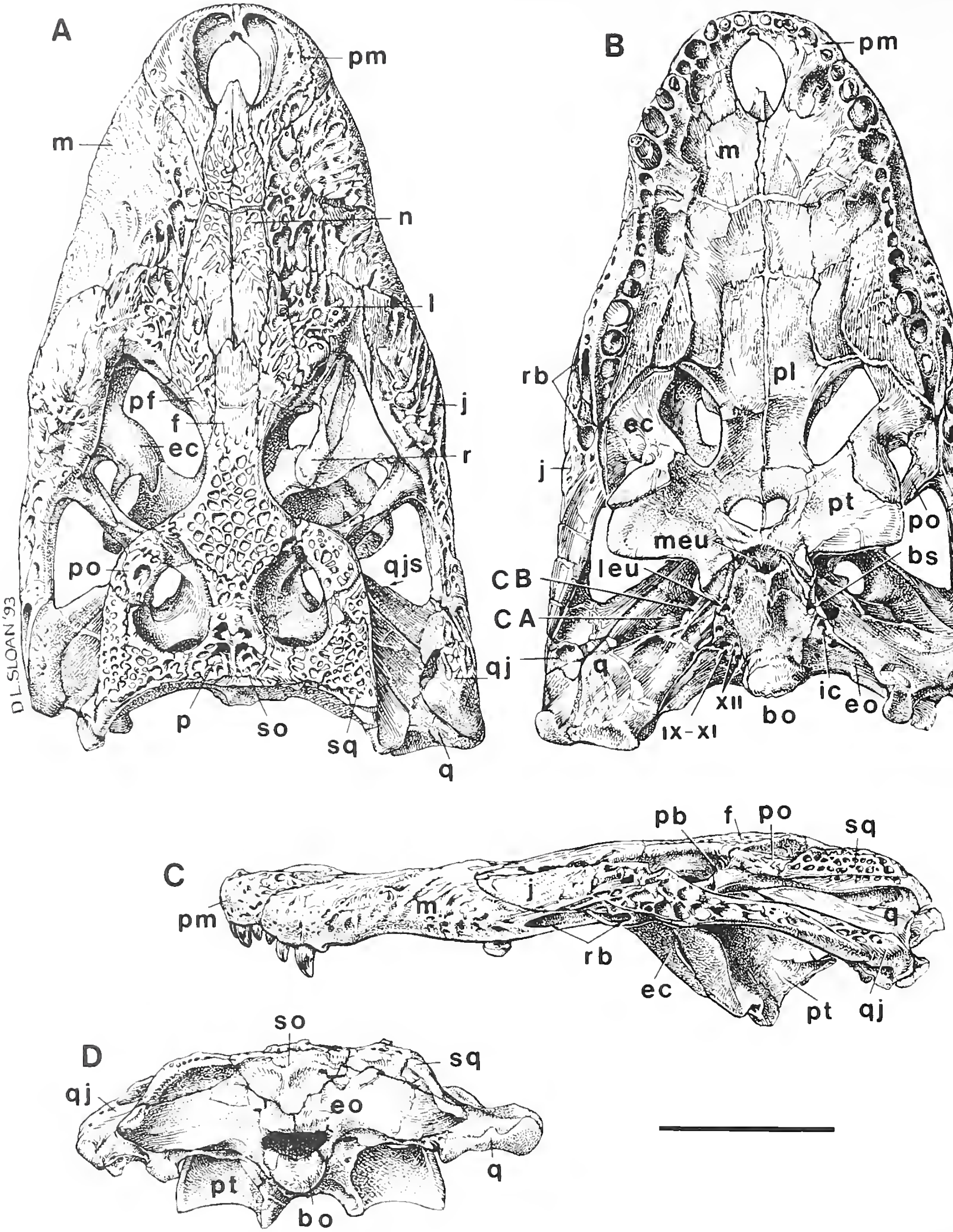
The maxilla (Text-fig. 1A–C) contacts the premaxilla, nasal, lacrimal, jugal and prefrontal. In dorsal view each maxilla is much broader than the maximum width of the nasals. In ventral view the maxilla has a broad portion lateral to the tooth row. The ventral surface of the broad palatal process forms a distinct, step-like structure medial to the last four massive crushing teeth. The elevated lateral portion of the step-like structure is heavily ornamented by fine striae.

The frontal (Text-fig. 1A) is relatively long, exceeding one-third of the skull length. The strongly convex posterior margin of the frontal contacts the postfrontal and parietal and forms a small part of the border of the supratemporal fossa. Its narrow anterior portion has a nearly straight suture with the prefrontal. The forked anterior end of the frontal extends slightly beyond the orbits. The narrow interorbital region of the frontal is about half the maximum width of the bone. The ventral surface of the frontal is not exposed, but its orbital portion, which forms the dorsomedial wall of the orbit, is less strongly concave than that of the extant species of *Alligator*.

The unpaired parietal is wider posteriorly than anteriorly (Text-fig. 1A). Both anterior and posterior margins of the parietal curve inwards. The parietal meets the postorbital posterolateral to the frontal, as in most eusuchians. Its sculpted interfenestral region is intermediate in width between that of *Albertochampsa langstoni* and *Brachychampsa montana* (Table 1).

The prefrontal is elongate and triangular in dorsal view (Text-fig. 1A). Its long, slightly convex medial side contacts the nasal and frontal. Its almost straight lateral border sutures mainly with the lacrimal and its anterior end abuts the maxilla. The prefrontal pillar is well-developed. The pillar contacts the palatine and pterygoid ventrally and meets its fellow of the opposite side, behind the space for the olfactory bulbs, by way of a median process.

The lacrimal is a more or less rectangular bone in dorsal view, with a convex anterior margin and a sharply



TEXT-FIG. 1. Skull of *Stangerochampsa mccabei* gen. et sp. nov. in dorsal (A), ventral (B), lateral (C), and occipital (D) views; RTMP.86.61.1, holotype. Abbreviations: bo, basioccipital; bs, basisphenoid; CA, Crest A; CB, Crest B; ec, ectopterygoid; eo, exoccipital; f, frontal; ic, foramen for internal carotid artery; j, jugal; l, lacrimal; leu, foramen for lateral branch of eustachian tube; m, maxilla; meu, foramen for medial branch of eustachian tube; n, nasal; p, parietal; pf, prefrontal; pb, bump just above postorbital/jugal suture; pl, palatine, pm,

TABLE 1. Measurements (in mm) of the skull of *Stangerochampsa mccabei* gen. et sp. nov.

feature	measurement	feature	measurement
Length of skull, from tip of snout to posterior edge of cranial table	195	Length of anterior border of left infratemporal fenestra	26·5
Length of skull, from tip of snout to posterior end of occipital condyle	200·3	Length of posterior border of left infratemporal fenestra	27
Maximal width of skull, across quadratojugals	130	Length of incisive foramen	23
		Width of incisive foramen	16·5
Length of snout	100	Length of long axis of left suborbital fenestra	35
Length of post-snout region of skull, from anterior border of orbit to posterior edge of cranial table	95	Length of short axis of left suborbital fenestra	15·5
		Maximal width of choanae	21·2
Maximal width of snout	114	Maximal length of choanae	14·5
Maximal length of naris	28	Interfenestral width of palatines	25
Maximal width of naris	25	Width across pterygoid flanges	84·2
Maximal length of right orbit	50	Length of mandible, from anterior tip of dentary to posterior tip of angular	232
Maximal width of right orbit	40·5		
Interorbital width	17		
Length of cranial table, through centre of supratemporal fenestrae	45	Length of mandible, from anterior tip of dentary to posterior edge of articular fossa	212
Width of cranial table, across centres of supratemporal fenestrae	75		
		Maximal depth of mandible	41
		Length of symphysis	36·5
Maximal length of supratemporal fenestra	30·2	Depth of symphysis	12
		Length of splenial in symphysis	3·3
Maximal width of supratemporal fenestra	20·5	Length of long axis of external mandibular fenestra	28·3
Interfenestral width	11	Length of short axis of external mandibular fenestra	13
Length of ventral border of left infratemporal fenestra	30		

incurved posterior orbital edge (Text-fig. 1A). It is excluded from the nasal by the maxilla/prefrontal contact. Its elongate posteroventral process reaches the midpoint of the ventral border of the orbit. The lacrimal foramen is situated close to the suture of the lacrimal with the prefrontal.

The jugal (Text-fig. 1A–C) has a relatively broad anterior process and a posterior process that is as long as the anterior one. The jugal/lacrimal suture is almost equal in length to the ventral border of the orbit. The ascending process of the jugal tapers dorsally, and interlocks with the descending process of the postorbital.

The postorbital has a remarkably rounded anterolateral border (Text-fig. 1A). An additional posterodorsal process (posterior descending process; Iordansky 1973) is retained, as is the contact of this process with the anterodorsal process of the quadratojugal along the posterodorsal border of the infratemporal fenestra. A weak, but distinct bump is present just dorsal to the suture of the descending process of the postorbital with the ascending process of the jugal. The descending process extends ventrally to meet the ectopterygoid at the ventral base of the postorbital bar, as in other eusuchians. A foramen for a blood vessel is located at the lateral side of the base of the descending process.

The squamosal has a relatively large posterolateral process (Text-fig. 1A). Medially, the squamosal forms almost the entire posterior border of the temporo-orbital foramen. A longitudinal groove for the attachment

premaxilla; po, postorbital; q, quadrate; qj, quadratojugal; qjs, quadratojugal spine; r, rib; rb, recess for blood vessels and nerves; so, supraoccipital; sq, squamosal; IX–XI, XII, foramina for cranial nerves IX–XI, XII. Scale bar represents 50 mm.

of the ear flap is clearly marked along its thickened lateral margin. In occipital view, the bone forms the dorsolateral portion of the occiput.

The quadratojugal (Text-fig. 1A–C) has a strongly curved suture with the quadrate. The quadratojugal is relatively large posterior to the infratemporal fenestra and is exposed as broadly as the quadrate and more broadly than the infratemporal bar in dorsal view. A weak, but distinct process, probably a remnant of the infratemporal spine, is present on the quadratojugal, running along the posterior margin of the infratemporal fenestra. The anterior process of the quadratojugal is elongate in ventral view, with a sharply pointed end wedging into the jugal and extending anteriorly beyond the midpoint of the ventral border of the infratemporal fenestra.

Palate. The quadrate is characterized by a distinct process arising from the lateral edge above the articular condyle on the ventral surface (Text-fig. 1B). Crest B (Iordansky 1973) is extraordinarily strongly developled. Crest A (Iordansky 1973) is weakly developed. It meets Crest B posteriorly and, together, they form a fairly strong ventral stem of a Y-shaped crest system. A depression is present on the ventral surface of the quadrate anterior and posterior to the ventral stem of the crest system. The quadrate body is broadly overlapped by the quadratojugal in dorsal view. Its dorsal process, for secondary contact with the squamosal and paroccipital process, is prominent and elongate. A ridge for the attachment of the tympanum, seen in extant alligators, is not clearly marked, but the dorsal (lateral to the external otic recess) and ventral (below the dorsal process) exits of the siphonal duct are present. On the lateral wall of the braincase the quadrate/laterosphenoid suture is strongly raised just above the trigeminal foramen. Ventral to the trigeminal foramen these two bones also meet one another, separating the pterygoid from the trigeminal foramen.

The palatine is elongate and rectangular in ventral view, with a lateral process projecting from its mid-region (Text-fig. 1B). The interfenestral portion of the palatine is as broad and long as its anterior portion (anterior to the lateral process). The lateral process of the palatine is much more strongly developed than it is in other alligatorines. The palatine/pterygoid suture is located entirely posterior to the suborbital fenestra.

The pterygoid is relatively strongly vertically oriented (Text-fig. 1B–C). Anteriorly it forms half the posterolateral border of the suborbital fenestra. The prechoanal portion of the pterygoid is much longer than the postchoanal portion. The pterygoid/ectopterygoid suture is curved, concave towards the pterygoid. No bulla is formed on the dorsal surface of the pterygoid. Dorsally, the bone is excluded from the ventral border of the lateral aperture of the trigeminal foramen by the quadrate/laterosphenoid contact. In addition, the pterygoid flange is positioned more anteriorly than that of any known alligatorine. This is indicated by the relatively great distance between the posterior edge of the transverse flange and the occipital condyle.

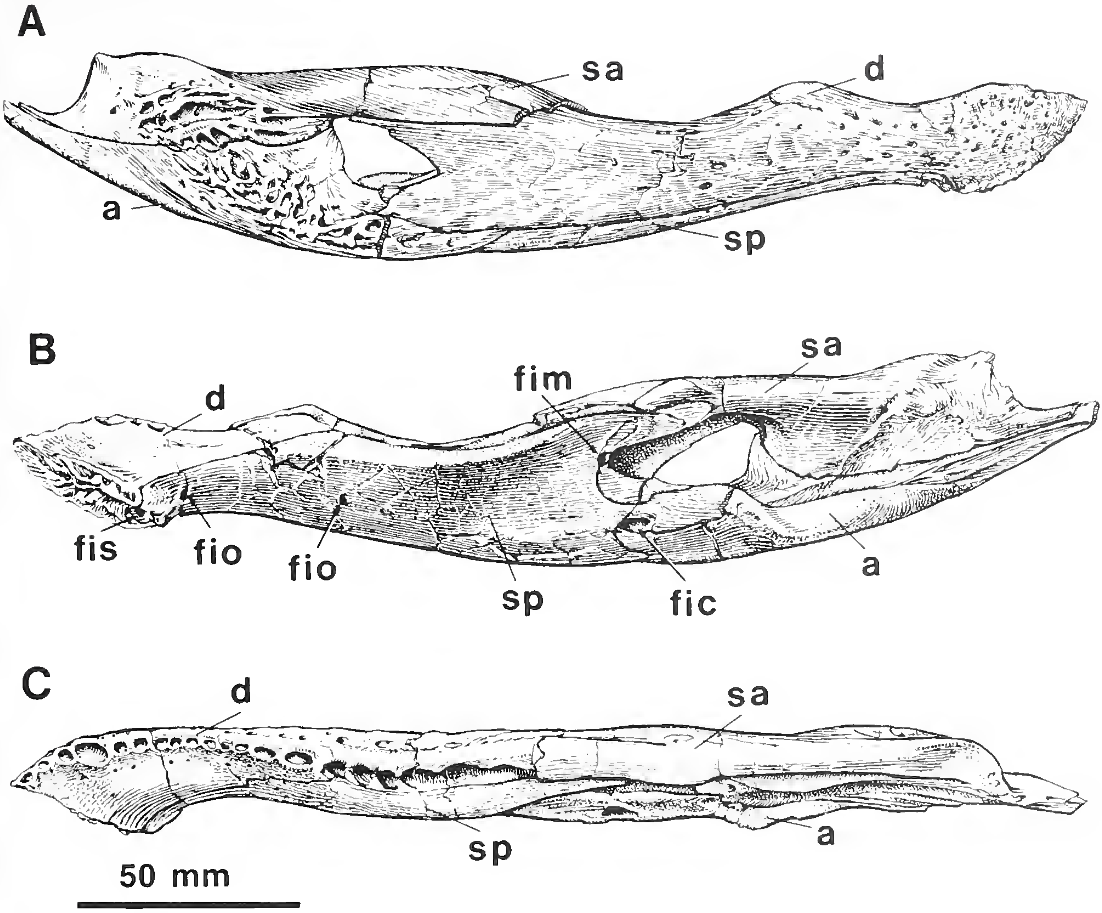
The ectopterygoid is unique in that its anterolateral process extends anteromedially along the anterior border of the suborbital fenestra and meets the lateral process of the palatine, separating the maxilla from the suborbital fenestra (Text-fig. 1B). The posterolateral process of the ectopterygoid turns medially and slightly dorsally. Its distal portion is overlapped by the descending process of the postorbital on the ventral surface of the postorbital bar. The ectopterygoid lacks a posterior jugal process, as defined by Norell (1989). Laterally, this bone does not contribute to the borders of the alveolar groove or the enlarged recess for the blood vessels and nerves. The medial process of the ectopterygoid is short but massive. It overlaps the anterodorsal half of the lateral margin of the pterygoid flange.

Braincase. The basioccipital is characterized by its extensive exposure on the ventral surface of the braincase, which results from the more horizontal orientation of the fan-shaped ventral plate (Text-fig. 1B, D). The ventral exposure of the bone is even longer than the central region of the pterygoid. The W-shaped ridge along the margin and midline of the fan-shaped ventral plate is well-developed. The occipital condyle is formed almost exclusively by the basioccipital. Two lateral and one median exits of the eustachian tube are clearly marked at the suture of this bone with the basisphenoid.

The exoccipital has a large upper portion that forms the major part of the occiput (Text-fig. 1B, D) and a lower portion that is relatively small and faces mainly ventrally. Thus, the four foramina for cranial nerves and the internal carotid artery are not visible in occipital view. The ridge between the upper and lower portions of the exoccipital becomes very strongly expressed laterally, just dorsal to the occipital extension of the cranio-quadrate canal. The median process, formed by the two exoccipitals dorsal to the foramen magnum, is strongly pronounced.

The supraoccipital is exposed on the skull roof (Text-fig. 1A, D). It is triangular in occipital view. A median ridge is weakly developed and does not run along the entire depth of the bone.

The laterosphenoid is well-exposed on both sides of the braincase. It possesses a shallow but distinct groove on the lateral surface of its anteromedial portion. This groove is anterodorsally-posteroventrally oriented,



TEXT-FIG. 2. Right mandible of *Stangerochampsa mccabei* gen. et sp. nov. in lateral (A), medial (B), and dorsal (C) views; RTMP.86.61.1, holotype. Abbreviations: a, angular; d, dentary; fic, foramen intermandibularis caudalis; fim, foramen intermandibularis medius; fio, foramen intermandibularis oralis; fis, foramen for ramus intermandibularis oralis of trigeminal nerve within symphysis; sa, surangular; sp, splenial.

extending from the dorsal condylar process to the trigeminal foramen. Such a groove in the laterosphenoid has not been reported in any other crocodyliforms. In other features, the bone shows no important differences from that of other eusuchians.

The prootic is only visible through the lateral aperture of the trigeminal foramen.

Mandible. The mandible (Text-fig. 2) is relatively straight, lacking a distinct ventral curve of its ventral margin. The anterior portion of the mandible is quite deep. The symphysis is relatively long, reaching posteriorly to the level of dentary tooth 9. The external mandibular fenestra is small, triangular in outline, and is enclosed only by the dentary and angular.

The dentary is, at most, 68 per cent. of the length of the mandible and has a strongly festooned dorsal margin (Text-fig. 2). Laterally, the anterior portion bears small, but deep, sculpted pits, in contrast to the very shallow grooves on the posterior portion. The dentaries form the major portion of the symphysis. The dorsal process of the forked posterior end of the dentary is longer than the ventral process. It meets the angular at the posterodorsal corner of the external mandibular fenestra, as indicated by the sutural mark on the medial surface of the surangular. The ventral process overlaps the angular extensively.

The splenial is half the length of the mandible (Text-fig. 2B). Its narrow anterior portion turns inward and contributes a small part to the symphysis. Two foramina for the ramus intermandibularis oralis of the trigeminal nerve are present on the lingual surface of the splenial. One is located in the middle region and the other is situated anteriorly, close to the symphysis. Within the symphysis, an additional foramen for the branch of the trigeminal nerve is present between the splenial and dentary. Dorsally, the splenial forms the medial wall of the alveolar groove and the individual sockets posterior to the fourteenth tooth on the right side and the thirteenth tooth on the left side. In the region of the massive crushing teeth (the last four), the dorsal surface of the splenial is extremely broadened, being as broad as that of the dentary. Thus, this region greatly overhangs the ventral portion of the bone, as it does in most alligatorines. Anterior to this region, the lingual surface of the bone is convex. Ventrally, the splenial forms the entire ventral border of the mandible anterior to the foramen intermandibularis caudalis.

The surangular lacks both extremities, but would have been about as long as the splenial (Text-fig. 2). It has a distinct convex-concave dorsal margin. A knob-like process along the dorsomedial margin opposes the pterygoid flange when the jaws are closed. Anteriorly, the surangular overlaps the dentary and ends just posterior to the tooth row. The thin posterodorsal portion lateral to the articular fossa of the articular rises upwards. The long, sharp posterior process ends near the posterior tip of the retroarticular process. The lateral suture of the bone curves anterodorsally. Posterior to the external mandibular fenestra, the bone is overlapped extensively by the angular.

The angular is slightly longer than the surangular, attaining 54 per cent. of the mandibular length (Text-fig. 2A). When in articulation, a pronounced dorsal process is present just posterior to the external mandibular fenestra in both lateral and medial views. This process forms the entire posterior border of the external mandibular fenestra. The dorsal contact of the process with the dentary separates the surangular from the border of the external mandibular fenestra. Anteriorly the angular is extensively wedged between the dentary and splenial. Anteromedially it, together with the splenial, encloses the foramen for the ramus intermandibularis caudalis of the trigeminal nerve. Posterior to the foramen, the buttress-like process for the pterygoid flange is strongly developed. The elongate posterior process is stronger than that of the surangular, and together with the latter, covers the lateral surface of the retroarticular process of the articular.

The coronoid is most probably a semicircular ring-like bone, as indicated by the articular facet on the lingual surface of the splenial, angular, and surangular (Text-fig. 2B). A foramen for the ramus intermandibularis medius of the trigeminal nerve is present between the coronoid and splenial.

The articular, as indicated by the pattern of articular faces on the medial surfaces of the surangular and angular (Text-fig. 2B), probably differs little from that of other alligatorines.

Dentition. Teeth of the upper and lower jaws are heterodont, with conical teeth anteriorly and four massive crushing teeth posteriorly. The teeth of the middle region of the upper jaw are similar to the unworn posterior teeth in having a strongly necked crown and a more or less round upper portion. All teeth have fine, radiating striae on their crowns.

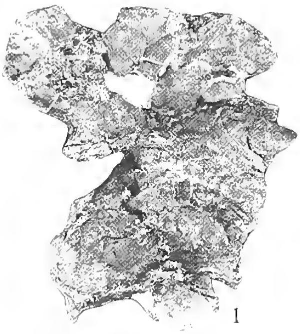
The left premaxillary dentition is complete, consisting of five teeth (Text-fig. 1B). The fourth premaxillary tooth is the largest; the others are all about the same size.

The maxillary dentition has 14 teeth (counting nine unoccupied tooth sockets) on the left side, but 15 teeth on the right (including six unoccupied tooth sockets). The fourth maxillary tooth is the largest and the third is slightly smaller (Text-fig. 1B). There are seven (right) or six (left) small teeth between the fourth tooth and the first crushing tooth. These teeth become larger posteriorly. The four crushing teeth are implanted in a common alveolar groove. One (right) or two (left) more anterior teeth are incorporated in the common groove. From the right side, it appears that only two of the four crushing teeth were functional in life, as suggested by their broad, worn surface. The entire upper dentition has 20 (right) or 19 (left) teeth, with the last one-and-a-half teeth located posterior to the anterior border of the suborbital fenestra.

EXPLANATION OF PLATE 1

Figs 1–9. Vertebrae of *Stangerochampsa mccabei* gen. et sp. nov.; RTMP.86.61.1, holotype. 1, axis in right lateral view; 2–3, cervical 3 in right lateral and ventral views, respectively; 4, cervical 4 in right lateral view; 5, an anterior dorsal in right lateral view; 6, a posterior dorsal in right lateral view; 7, a posterior dorsal in dorsal view; 8–9, sacral 1 in dorsal and ventral views. All × 0·95.

PLATE 1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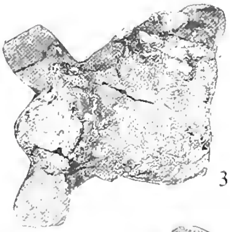
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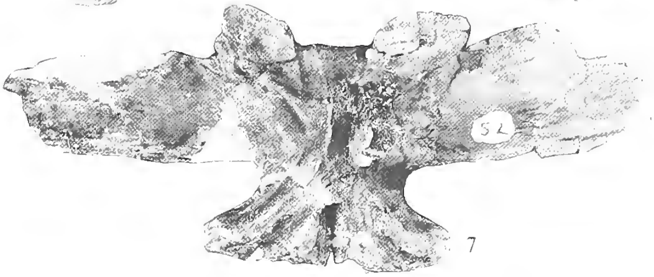

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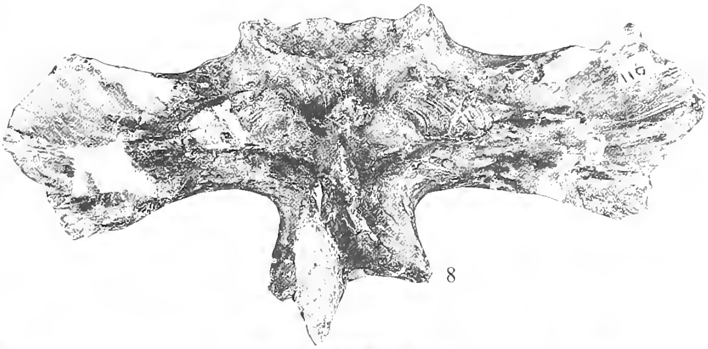

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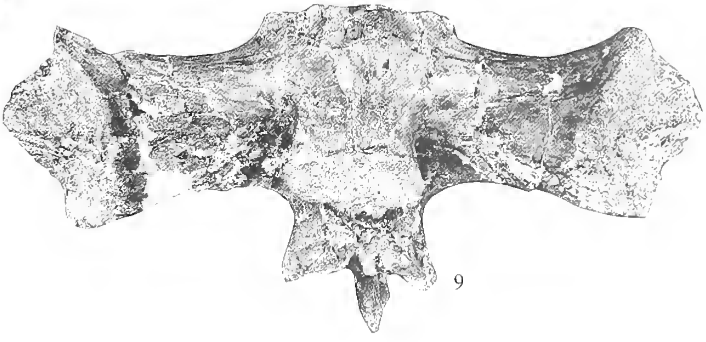
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TABLE 2. Measurements (in mm) of girdle and limb elements of *Stangerochampsa mccabei* gen. et sp. nov.

feature	measurement	feature	measurement
Maximal length of preserved portion of right scapula	74	Length of left ulna	83
		Length of right radius	70
Maximal width of preserved portion of right scapula	40·5	Length of left radius	70
		Length of metacarpal IV	26·9
Maximal length of preserved portion of left scapula	74·5	Maximal depth of left ilium	46·6
		Maximal length of right pubis	70
Maximal width of preserved portion of left scapula	35·5	Maximal width of ventral expansion of right pubis	41
Length of preserved portion of interclavicle	91·6	Length of left femur	142
		Length of right metatarsal II	59·5
Estimated length of interclavicle	97	Length of right metatarsal III	69
Length of right humerus	107	Length of right metatarsal IV	59
Length of right ulna	80		

No dentary teeth are preserved (Text-fig. 2C). The dentary dentition consisted probably, as suggested by tooth sockets, of 20 teeth on the right side and 19 on the left. Tooth sockets indicate that dentary teeth 4, and 13 (left) or 14 (right) were much larger than the others. Eight (left) or nine (right) small tooth sockets are present between dentary teeth 4, and 13 or 14, respectively. The last tooth of the small set is distinctly larger than the others. Teeth between dentary tooth 13 or 14 and the first crushing tooth become gradually larger and, together with the crushing teeth, are implanted in a common alveolar groove on both sides.

Postcranial Skeleton

The postcranial skeleton was largely disarticulated. Seventeen vertebrae are almost complete. Ten ribs and 12 gastralia are well-preserved. The one chevron preserved lacks its ventral portion. The pectoral girdles are respresented by a pair of scapulae and the interclavicle. The elements of the forelimbs include the right humerus, two radii, two ulnae, one metacarpal and one phalanx. The pelvic girdle lacks both ischia. The hindlimb is represented by the left femur, left calcaneum, three right metatarsals, and one phalanx. More than 100 dorsal osteoderms and ten ventral osteoderms are preserved. Measurements of postcranial elements are listed in Table 2.

Vertebral column. The vertebral column is represented by five cervicals, six dorsals, one sacral, and five caudals. The five cervicals include the axis, cervicals 3–5, and cervical 9, recognizable by the configuration of their spines and the position of their parapophyses (Pl. 1, figs 1–4). In contrast to that of any known alligatorines, the axis has a strongly developed hypapophysis, while cervical 3 entirely lacks a hypapophysis. In cervical 3, the parapophyses are situated far ventrally, and the ventral surface of the centrum is smoothly concave rather than convex, ridged or keeled as it is in other alligatorines. The hypapophyses on cervicals 4, 5 and 9 are very strong.

The presence of a strong hypapophysis indicates that one of the six dorsals is from the anterior section (Pl. 1, fig. 5). The remaining dorsals are from the posterior section as suggested by the morphology and position of the articular facets for ribs (Pl. 1, figs 6–7). These posterior dorsals are more massive than the anterior dorsal and cervicals, and their centra have a smooth ventral surface. The sacral vertebra is determined to be the first,

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EXPLANATION OF PLATE 2

Figs 1–9. Elements of pectoral girdle and forelimb of *Stangerochampsa mccabei* gen. et sp. nov.; RTMP.86.61.1, holotype. 1–2, right scapula in medial and lateral views; 3, interclavicle in lateral view; 4–7, right humerus in anterolateral, posterolateral, anteromedial, and posteromedial views; 8, right radius in lateral view; 9, right ulna in lateral view. All × 1.

PLATE 2

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on the basis of its articulation with the sacral rib (Pl. 1, figs 8–9). It is amphicoelous, and its centrum has a flat ventral surface. Its neural spine is broad and low and is taller posteriorly than anteriorly.

The five caudals all have well-developed transverse processes. One, probably from the anterior region of the tail, is relatively massive and short and has a weak, but distinct, median ridge along its ventral midline. The remaining four caudals, probably from the middle section, have a longitudinal groove on the ventral surface. This groove is deeper posteriorly than anteriorly in each caudal, and is relatively deeper in the most posterior caudals.

Ribs and chevron. Of the preserved ribs, seven are from the cervical region. These include the first pair, four from pairs 3–5, and one from pair 9. The first cervical rib is similar to that of extant alligatorines, differing only in that the lateral surface is more convex anteriorly and more concave posteriorly. This rib extends posteroventrally and ends at the middle of the fourth cervical vertebra. Cervical rib 9 resembles the anterior dorsal ribs, differing only in that its shaft is shorter and its dorsal ridge is much stronger. The five dorsal ribs come probably from the first five dorsal vertebrae, judging from differences in the position of the parapophyses and configuration of the dorsal ridges. The first sacral rib is still articulated with the sacral vertebra (Pl. 1, figs 8–9), and is very similar to that of later alligatorines. The preserved chevron is represented by its dorsal portion. The foramen for the blood vessel is transversely narrow but dorsoventrally deep.

Gastralia. Among the preserved gastralia, the last pair are massive and have a characteristic spatula-shaped end. The remaining gastralia are very slender, but also have an expanded end.

Pectoral girdle and forelimbs. The scapula (Pl. 2, figs 1–2) is longer than the radius. The broadened dorsal border is about three times as wide as the narrowest region of the shaft of the bone. The acromial crest on the ventrolateral surface is very strong. The scapula expands anteriorly beyond the acromial crest. A pronounced knob-like process for the attachment of the *caput scapulae* of the *M. triceps brachii* is present. Ventral to the process and acromial crest, the lateral surface of the scapula is deeply concave. In addition, a bump situated at the midpoint of the posteromedial margin of the bone probably marks the insertion of the scapular branch of the *caput coracoideum* of the *M. triceps brachii.*

The interclavicle (Pl. 2, fig. 3) lacks only its anterior tip. Its anterior end and middle region are relatively broad so the anterior portion of the shaft is strongly necked.

The right humerus is complete (Pl. 2, figs 4–7). The bone is relatively short, being about 76 per cent. of the length of the femur. The ridge-like scar of the *M. teres major*, extending from the head onto the shaft along the anterolateral margin of the bone, is strongly developed.

The radius and ulna (Pl. 2, figs 8–9) show no obvious differences from those of fossil or extant alligatorines.

The foot is represented by a single metacarpal, probably the fourth, and a single, probably penultimate, phalanx.

Pelvic girdle and hindlimbs. The right ilium is almost complete (Pl. 3, figs 1–2). The posterior process of the ilium is relatively broad and the anterior process is pronounced. Dorsally, the iliac blade turns medially so that its medial surface is strongly concave.

The complete right pubis (Pl. 3, fig. 3) differs from that of later alligatorines in that its shaft is relatively much shorter, and its broad distal portion extends more proximally.

The femur (Pl. 3, figs 4–6) resembles that of later alligatorines but is proportionally longer, when compared with the radius, than in the extant species of *Alligator*. On the dorsolateral surface the scars of the *M. puboischiofemoralis internus*, *M. iliofemoralis*, and *M. ischiotrochantericus* are strongly developed.

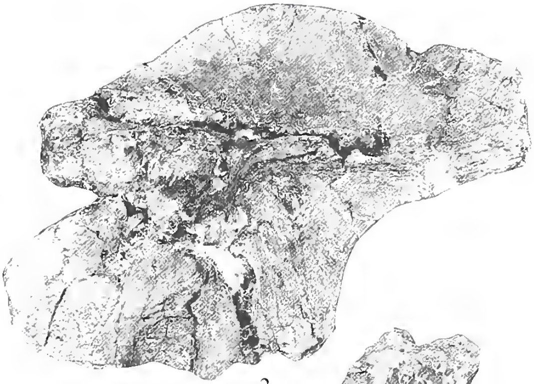
The left calcaneum (Pl. 3, figs 8–9) is almost identical to that of the extant species of *Alligator*. Two foramina (one small) are seen on the bottom of the socket for the astragalus, and three small foramina are present on the lateral surface.

EXPLANATION OF PLATE 3

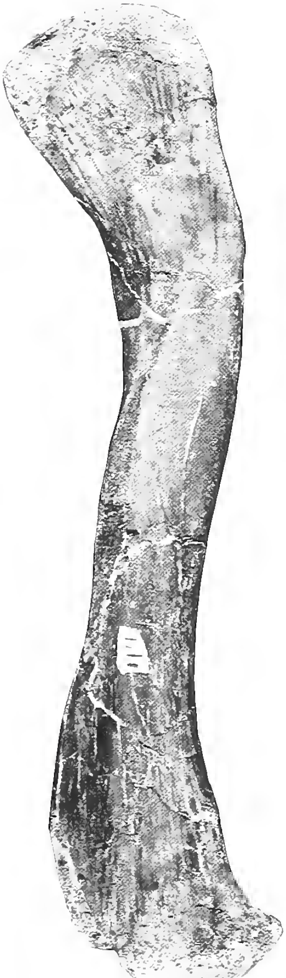
Figs 1–9. Elements of pelvic girdle and hindlimbs of *Stangerochampsa mccabei* gen. et sp. nov.; RTMP.86.61.1, holotype. 1–2, right ilium in lateral and medial views; 3, right pubis in lateral view; 4–6, left femur in lateral, medial and posterior views; 7, right metatarsal II in dorsal view; 8–9, left calcaneum in dorsal and ventral views. All × 1.

PLATE 3

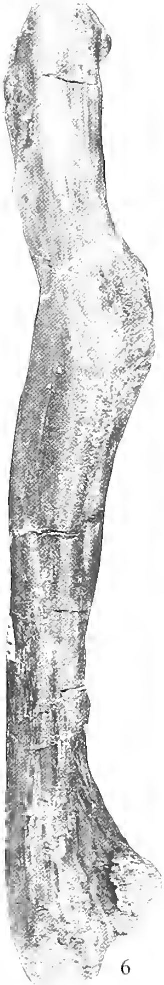

1


2


3


4


5


6


7


8


9

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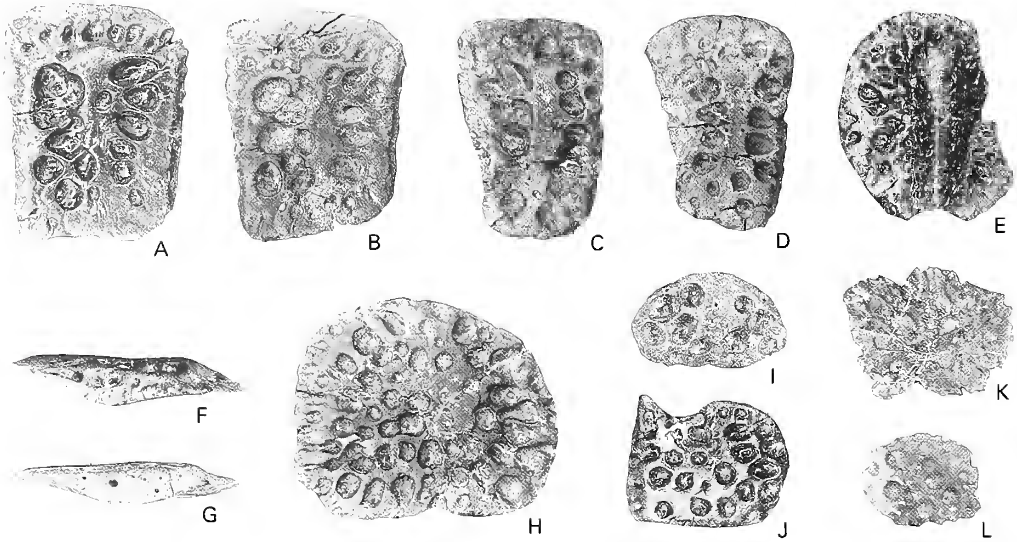
The three metatarsals (II–IV) are from the right foot, on the basis of the overlapping facet on the dorsomedial surface. Metatarsal II (Pl. 3, fig. 7) is the longest and most massive. The preserved phalanx is short but very massive when compared with these metatarsals. It is probably the first phalanx of the first digit.

Osteoderms. Of the preserved dorsal osteoderms, 98 are almost complete. Osteoderms from the medial rows of the trunk and anterior portion of the tail are rectangular in outline, with a slightly narrowed posterior border and a very weak dorsomedian ridge (Text-fig. 3A–B). A sutural facet is present on both lateral and medial sides and an overlapping facet is present along the anterodorsal margin. As in other early eusuchians, and unlike the situation in most non-eusuchian crocodyliforms, the overlapping facet of the dorsal osteoderms does not rise to form an elevated anterodorsal margin, but is very thin and grades smoothly into the sculpted posterior portion (Text-fig. 3F–G). Osteoderms from the more lateral rows of the trunk and anterior portion of the tail are much longer than wide and usually broader anteriorly than posteriorly (Text-fig. 3C–D). These osteoderms have a stronger median ridge, a sutural facet on both sides, and an overlapping facet anterodorsally. Osteoderms from the flank row of the trunk and tail are more or less triangular in outline or have a round lateral border. A sutural facet is present only on the medial side and most do not have an overlapping facet along the anterodorsal margin. An osteoderm, probably from the first transverse row of the trunk, is strongly keeled, but lacks a sutural facet on both sides and an overlapping facet anterodorsally (Text-fig. 3E).



TEXT-FIG. 3. Osteoderms of *Stangerochampsa mccabei* gen. et sp. nov.; RTMP.86.61.1, holotype. A–B, dorsal trunk osteoderms from medial rows in dorsal view; C–D, dorsal trunk osteoderms from lateral rows in dorsal view; E, a dorsal trunk osteoderm from the first transverse row in dorsal view; F–G, dorsal trunk osteoderms in side views (anterior to right); H, a large dorsal neck osteoderm from right side in dorsal view; I, small dorsal neck osteoderm in dorsal view; J, dorsal neck osteoderm from right side in dorsal view; K–L, two ventral osteoderms in lateral views. All × 1.

Eight osteoderms from the neck region are present. They are distinctive in being wider than long and in having no distinct dorsomedian ridge and no overlapping facet along the anterodorsal margin (Text-fig. 3H–J). They are either laterally, or both laterally and posteriorly, rounded. A sutural facet is present only on the medial side, which indicates that two longitudinal rows of osteoderms were present in the neck region, as in other alligatorines. Two of the eight cervical osteoderms are very small, elliptical in outline, and may be from

TABLE 3. List of taxa considered in the present analysis. * indicates that original specimens were studied directly.

Goniopholis: *G. lucasii*, *AMNH 5782, Upper Jurassic Morrison Formation, Colorado, North America (*Amphicotylus lucasii* Mook, 1942*a*).
Sunosuchus: *S.* sp., *IVPP 10606–611, Upper Jurassic Qigu Formation, Xinjiang, China (Wu *et al.* in press); *S. miaoi*, Middle Jurassic (previously Upper Jurassic, Sun *et al.* 1992) Xiangtung Formation, Gansu, China (Young 1948; Buffetaut 1986).
Shamosuchus: *S. djadochtaensis*, *AMNH 6412, Upper Cretaceous Djadochta Formation, Mongolia (Mook 1924); *Shamosuchus* spp. (Efimov, 1988).
Bernissartia: *B. fagesii*, Lower Cretaceous Bernissart Clay (Wealden Formation), Belgium (Norell and Clark 1990); Upper Cretaceous, Barremian, Galve, Spain (Buscalioni and Sanz 1990).
Leidyosuchus: *L. canadensis*, *ROM 1903 (Lambe 1908) and *L. gilmorei*, *AMNH 5352, Upper Cretaceous Judith River Group, Alberta, Canada (Mook 1942*b*); *Leidyosuchus* sp., *RTMP 86.221.1, Upper Cretaceous Judith River Group, Alberta, Canada; *L. formidabilis*, Paleocene Tongue River Formation, North Dakota, North America (Erickson 1976).
Crocodylinae: *Crocodilus americanus*, *AMNH 7121; *C. niloticus*, *AMNH 10081; *C. affinis*, *YPM 1345, Middle Eocene Bridger Beds, Wyoming (Marsh 1871); *Brachyuranochampsa eversolei*, *AMNH 4993, Eocene Middle Washakie, Wyoming (Zangerl 1944); (Iordansky 1973; Mook 1921*b*, 1921*c*).
Prodiplocynodon: *P. langi*, *AMNH 108 (cast), Upper Cretaceous Lance Formation, Wyoming, North America (Mook 1941*a*).
Brachychampsa: *B. montana*, *AMNH 5032 (Gilmore 1911); *UCMP V133901, Upper Cretaceous Hell Creek Formation, Montana, North America (Norell *et al.* 1994); Upper Cretaceous Hell Creek Formation, South Dakota, North America (Carpenter and Lindsey 1980).
Albertochampsa: *A. langstoni*, *RTMP 81.46.1 (cast), Upper Cretaceous Dinosaur Park Formation, Alberta, Canada (Erickson 1972).
Hylaeochampsa: *H. vectiana*, Lower Cretaceous Wealden Formation, Isle of Wight (Clark and Norell 1992).
Wannaganosuchus: *W. brachymanus*, Upper Paleocene Tongue River Formation, North Dakota, North America (Erickson 1982).
Allognathosuchus: *A. mooki*, *AMNH 6780, Eocene Puerco Formation, New Mexico, North America (Simpson 1930); *Allognathosuchus* sp. *YPM: PU 17111, 7472, 3964, 8383. *A. polyodon*, Eocene Wasatch Beds, North America (Mook 1921*a*).
Ceratosuchus: *C. burdoshi*, *FMNH 15576, Upper Paleocene Plateau Valley Beds, Colorado, North America (Schmidt 1938).
Alligator prenasalis: Lower Oligocene, South Dakota, North America (Mook 1932).
Procaimanoidea: *P. utahensis*, *USNM 15997, Upper Eocene Uinta Formation, Utah, North America (Gilmore 1946). *P. kayi*, Middle Eocene, Bridger Beds, Wyoming, North America (*Hassiacosuchus kayi* Mook 1941*b*).
Alligator mcgrewi: Lower Miocene Marseland Formation, Nebraska (Schmidt 1941); *AMNH 8700, Lower Miocene Marseland Formation, Nebraska, North America.
Alligator thomsoni: Middle Miocene Snake Formation, Nebraska, North America (Mook 1923).
Alligator mefferdi: Middle Pliocene Ash Hollow Formation, Nebraska, North America (Mook 1946).
Alligator mississippiensis: *RTMP 84.182.2, 84.183.18, 90.7.104.
Alligator spp: *A. luicus*, Middle Miocene Shanwang Formation, Shandong, China (Li and Wang 1987); *A. sinensis* (Cong *et al.* in press).

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the anterior portion of the neck (Text-fig. 3i–j). The remaining six, two of which are very large (Text-fig. 3h), are assumed to be from the four continuous transverse rows in the posterior region of the neck.

The ventral osteoderms are irregular in outline and variable in size (Text-fig. 3k–l). They are very thin and bear a sculpting of small and shallow pits. Their sculpted lateral surface is flat, but their medial surface is convex.

TABLE 4. Characters employed in the phylogenetic analysis. 0, primitive state; 1, derived state.

1. Premaxillae longitudinally narrow anterior to naris (0); wide, broadly overhanging nasal capsule (1).
2. Distinct lateral constriction between premaxilla and maxilla present (0); absent (1) (modified from Clark *in* Benton and Clark 1988).
3. Nares undivided or partially divided (0); fully divided (1) (modified from Clark *in* Benton and Clark 1988).
4. Nasal excluded from naris (0); entering into naris (1) (modified from Clark *in* Benton and Clark 1988).
5. Nasal ending posteriorly well before orbit (0); beyond, or at level of anterior borders of orbits (1).
6. Nasal/lacrimal contact present (0); absent (1) (Clark *in* Benton and Clark 1988).
7. Nasal/premaxillary suture shorter than nasal/maxillary suture (0); almost as long as the latter (1).
8. Two nasals narrower than each maxilla in dorsal view (0); broader than each maxilla (1).
9. Snout longer than wide (0); wider than long (1).
10. Snout longer than postorbital region (0), shorter than postorbital region (1).
11. Dorsal border of orbit flat (0); ridged (1) (modified from Buscalioni and Sanz 1990).
12. Lacrimal narrow and elongate (0); short and broad (1) (modified from Clark *in* Benton and Clark 1988).
13. Posteroventral process of lacrimal short (0); reaching midway along ventral border of orbit (1).
14. Lacrimal/jugal suture as long as or longer than ventral border of orbit (0); much shorter than ventral border of orbit (1).
15. Anterior and posterior processes of jugal different in length (0); similar (1).
16. Anterior process of quadratojugal absent or very short (0); long, reaching half-way along lower temporal bar (1) (modified from Norell 1989).
17. Quadratojugal spine pronounced (0); knob-like or absent (1) (modified from Norell, 1989).
18. Quadratojugal/quadrate suture slightly curved (0); strongly curved posteroventrally (1).
19. Posterodorsal process of postorbital present (0); absent (1) (Norell 1989).
20. Postorbital not forming supratemporal fossa (0); formaing supratemporal fossa (1).
21. Postorbital/parietal contact posterolateral to frontal absent (0); present (1) (Clark and Norell 1992).
22. Postorbital/ectopterygoid contact absent (0); present (1).
23. Skull table more or less square anterolaterally (0); strongly rounded (1).
24. Incisive foramen small (0); very large (1).
25. Incisive foramen enclosed by premaxillae and maxillae (0); entirely located within premaxillae (1).
26. Palatine/pterygoid suture situated before posterior edge of suborbital fenestra (0); entirely behind suborbital fenestra (1).
27. Portion of palatine anterior to lateral process short (0); as long as interfenestral portion (1).
28. Maxilla very narrow lateral to tooth row in ventral view (0); broad (1).
29. Choana located anteriorly, across level of posterior borders of suborbital fenestrae (0); positioned posteriorly, almost behind suborbital fenestrae (1) (modified from Clark *in* Benton and Clark 1988).
30. Choana situated between palatines and pterygoids (0); entirely within pterygoids (1) (Clark *in* Benton and Clark 1988).
31. Supraoccipital not exposed on skull roof (0); exposed (1).
32. Surangular forming border of external mandibular fenestra (0); excluded from external mandibular fenestra (1).
33. Splenial forming medial walls of a few posterior-most tooth sockets, less than 25 per cent. of length of tooth row (0); largely forming medial walls of posterior 7–9 tooth sockets or groove, more than 40 per cent. of length of tooth row (1).
34. Dorsal surface of splenial portion of medial walls of tooth sockets or groove narrow (0); very wide, as broad as that of lateral walls (1).
35. Three or more teeth present posterior to anterior border of suborbital fenestra (0); two or fewer teeth present posterior to anterior border of suborbital fenestra (1).
36. Posterior four or five massive crushing teeth absent (0); present (1) (modified from Clark *in* Benton and Clark 1988).
37. A few teeth present between dentary tooth 4 and tooth at the second peak of sinusoidal waves (0); eight or nine small teeth between dentary tooth 4 and dentary tooth 13 or 14 at the second peak of sinusoidal waves present (1).

TABLE 4. (*cont.*)

38. The fifth maxillary tooth as large as, or larger than the fourth (0); the fourth tooth largest, the fifth tooth much smaller than the fourth (1).
39. Hypapophysis of cervical vertebrae weak or absent (0); strong (1) (Clark *in* Benton and Clark 1988).
40. Posterior iliac process at same level as anterior iliac process (0); above level of anterior iliac process (1) (Buscalioni and Sanz 1990).
41. Anterior iliac process pronounced or small but distinct (0); knob-like or almost absent (1) (modified from Clark *in* Benton and Clark 1988).
42. Cervical rib 1 without a mid-posterior expansion (0); having a mid-posterior expansion (1).
43. Cervical rib 2 single-headed (0); double-headed (1).
44. Two longitudinal rows of dorsal osteoderms with anterolateral pegs (0); more than two longitudinal rows of osteoderms without anterolateral pegs (1) (modified from Clark *in* Benton and Clark 1988).
45. Dorsal osteoderms of trunk overlapped (0); not overlapped (1) (modified from Clark *in* Benton and Clark 1988).
46. Anterodorsal margin of dorsal trunk osteoderms for overlapping distinctly elevated (0); not elevated but smoothly continuing to sculpted posterior portion (1) (modified from Norell and Clark 1990).

PHYLOGENETIC RELATIONSHIPS

In order to interpret the phylogenetic position of *Stangerochampsa* within the Eusuchia, a phylogenetic analysis of *Stangerochampsa*, six Mesozoic and nine Cenozoic eusuchians has been undertaken (see Tables 3, 5). These taxa were selected because of the availability of original specimens or because good illustrations have been published (Table 3). As in Norell's study (1989), the Crocodylinae is treated as a single taxon. The outgroups used to polarize character-states are *Bernissartia*, *Shamosuchus*, *Goniopholis* and *Sunosuchus*. Most recent studies of *Bernissartia* (Buscalioni and Sanz 1990; Norell and Clark 1990), strongly support Clark's (*in* Benton and Clark 1988) hypothesis that this taxon is one of the closest sister groups of the Eusuchia among the neosuchians that are represented by relatively complete specimens. However, the phylogenetic relationships between *Bernissartia* and *Shamosuchus* are unresolved (Clark *in* Benton and Clark 1988), so both are included as outgroups. *Goniopholis* and *Sunosuchus*, both members of the Goniopholidae (Wu *et al.* in press), are used as more remote outgroups. These four genera are treated separately in scoring characters, in contrast with previous studies (Norell 1989; Willis 1993) in which the relevant taxa were combined to form two outgroups in scoring each character.

The data matrix is based on direct observation of 13 of the 20 included taxa. Published descriptions were relied on for the remaining seven taxa (see Table 3). Some anatomical features have been reinterpreted on the basis of restudy of original material. Gilmore (1911) reconstructed the premaxillae of *Brachychampsa montana* as meeting on the midline posterior to the incisive foramen, and Erickson (1972) followed this reconstruction in his interpretation of the palate of *Albertochampsa langstoni*. However, a new skull of *B. montana* (UCMP V133901) and re-examination of the original type specimen shows that the premaxilla is similar to that of *Stangerochampsa mccabei* in both configuration and relationship to the incisive foramen. We believe that the two premaxillae are most probably separated by the palatal processes of the maxillae posterior to the large incisive foramen in *A. langstoni* as well. Clark and Norell (1992) mentioned in the diagnosis of *Hylaeochampsa vectiana* that the ectopterygoid contacts the palatine anteriorly in that species. However, the relevant portion is incomplete in that taxon and no such contact is indicated in their figures and descriptions.

This analysis is based on 46 characters (Tables 4–5). Three-fifths of the characters are new, the remainder are derived or modified from those used in previous studies (Clark *in* Benton and Clark

TABLE 5. The distribution of 46 characters among the 20 taxa considered in this analysis. Characters are listed numerically to correspond with Table 3. '0', primitive; '1', derived; '?', missing or uncertain; 'N', not applicable. '%', indicates the completeness of the 20 taxa, measured as the percentage of the 45 characters scored for a taxon.

		1	1	2	2	3	3	4	4		
	12345	67890	12345	67890	12345	67890	12345	67890	12345	6	%
Outgroups											
Goniopholis	00000	00000	00000	000?0	00000	00000	00000	00000	0??00	0	93·5
Sunosuchus	00000	10000	00000	0?000	00000	00000	00000	00000	00000	0	97·8
Shamosuchus	00001	00000	00000	0?0?1	0?001	01010	0N000	0000?	?????	?	76·1
Bernissartia	00011	00000	11000	00000	01001	00010	0N000	1?000	0??10	0	91·3
Ingroups											
Hylaeochampsa	????1	1??0?	1110?	??011	110??	00011	1???1	?????	?????	?	43·4
Leidyosuchus	00000	00000	00000	00010	01001	00011	10000	00011	01110	1	100
Prodiplocynodon	00010	00000	00010	0?010	11001	00011	1???0	000??	?????	?	73·9
Albertochampsa	01011	01000	01100	0?0?1	11110	01111	1???1	1?1??	?????	?	69·7
Brachychampsa	01011	11010	01101	11101	11110	10111	10111	110??	?????	?	82·6
Stangerochampsa	01011	11010	01101	11101	11110	11111	11111	11111	01110	1	100
Wannaganosuchus	01011	10011	01010	??0?1	1?001	??011	??111	11111	01110	1	82·6
Allognathosuchus	01010	11011	01011	010?1	11001	00011	11111	111??	???10	1	87·0
Ceratosuchus	010??	?0010	0????	?????	??00?	??011	????1	??1??	?????	?	32·6
Procaimanoidea	01010	10101	01010	010?1	1?001	00011	001?0	111??	?????	?	76·1
Alligator mcgrewi	01010	10111	01010	010?1	11000	10011	01110	111??	?????	?	80·4
A. prenasalis	01011	10000	01010	0?0?1	11001	10011	101?0	11111	1????	?	82·6
A. thomsoni	11010	10000	11010	110?1	11001	?0011	001?0	111??	?????	?	76·1
A. mefferdi	11110	10000	11010	01001	11001	10011	00110	111??	???10	1	89·1
A. mississippiensis	11110	10000	11010	01001	11001	00011	00010	11111	11111	1	100
Crocodylinae	10010	00000	00000	00010	11001	00011	10000	00011	01111	1	100

1988; Norell 1989; Buscalioni and Sanz 1990; Norell and Clark 1990). Many characters in previous studies were modified by changing the character polarity. This is a result of restricting the outgroup comparisons to the four closest sister groups of the Eusuchia rather than using all crocodylomorphs. The genera that are multispecific, such as *Leidyosuchus*, *Allognathosuchus* and *Goniopholis*, are assumed to be monophyletic. Since there is no established phylogeny of the species in these genera, where both primitive and derived characters occur, the primitive character state is scored for the genus. The resulting data matrix was analysed by using PAUP (version 3.1.1; Swofford 1993). A list of characters applying to each node and the terminal taxa can be found in Text-figure 4. However, we emphasize that this is a very preliminary study because (1), it has not been demonstrated that multispecific taxa are monophyletic and (2), some Cenozoic taxa represented by well-preserved material, such as *Diplocynodon*, are not included.

Results and Discussion

The analysis of the present data matrix produces two equally parsimonious cladograms (tree length = 81, consistency index = 0·581, and retention index = 0·781). As shown in the strict consensus cladogram (Text-fig. 4), the two cladograms are congruent in the following points:

1. The monophyly of the Eusuchia is supported. It is defined here by five unequivocal characters; choana situated entirely within pterygoid (Character 30); supraoccipital exposed on skull

roof (character 31); presence of strong hypapophysis on cervical vertebrae (character 39); posterior iliac process above level of anterior iliac process (character 40); and anterodorsal margin of dorsal trunk osteoderms for overlapping not elevated, but smoothly continuing to sculpted posterior portion (character 46). These characters, except for character 31, were also considered to be synapomorphies of the Eusuchia in previous studies (Clark *in* Benton and Clark 1988; Buscalioni and Sanz 1990; Norell and Clark 1990; Wu and Brinkman 1993). Character 31 is included here because the presence of the primitive state in some ingroups is interpreted as a reversal and it is unequivocally primitive in all outgroups. Character 42 (cervical rib 1 with a mid-posterior expansion) and character 43 (cervical rib 2 double-headed) may also be synapomorphies of the Eusuchia, but the respective character-states are determined in only one of the outgroups and five ingroups.

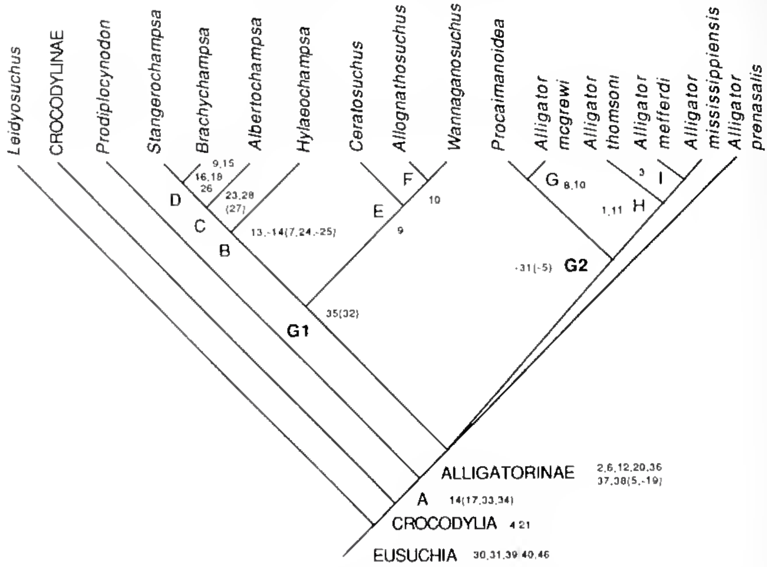
2. Although *Hylaeochampsa* is the oldest eusuchian yet known, it is not the most primitive representative of the Eusuchia. Rather, *Hylaeochampsa* is hypothesized to be a relatively derived alligatorine. This is based on the presence of three of seven newly recognized unequivocal synapomorphies of the Alligatorinae. These are character 6 (nasal/lacrimal contact absent), character 12 (lacrimal short and broad), and character 20 (postorbital forming supratemporal fossa). The states of the remaining four alligatorine synapomorphies are unknown in the genus.

3. In contrast to previous studies, *Leidyosuchus* is recognized to be the most primitive known eusuchian. It is primitive in that the nasals are excluded from the nares (character 4) and the postorbital fails to meet the parietal posterolateral to the frontal (character 21). The primitive state of character 4 is also seen in some members of the Crocodylinae. No other eusuchian exhibits the primitive state of character 21. Thus these characters define a group including all eusuchians except *Leidyosuchus* (Crocodylia; Text-fig. 4). *Leidyosuchus* is unequivocally more primitive than *Hylaeochampsa* in eight characters (characters 5, 6, 11, 12, 13, 20, 21 and 35). No character of *Leidyosuchus* is more derived than in *Hylaeochampsa*.

4. *Prodiplocynodon*, which was previously postulated to be an alligatorine (see Steel 1973; Carroll 1988), is unequivocally excluded from the Alligatorinae because it lacks all seven unequivocal synapomorphies of the latter (discussed below). A sister-group relationship between *Prodiplocynodon* and the Alligatorinae, rather than the Crocodylinae (Group A, Text-fig. 4), is suggested by character 14 (jugal/lacrimal suture much shorter than ventral border of orbit). However, this relationship is only weakly supported because the character is present as a derived feature within the Crocodylinae and is reversed in three ingroups of the Alligatorinae. The analysis recognized three additional characters supporting a close relationship of *Prodiplocynodon* and the Alligatorinae (characters 17, 33 and 34), but this evidence is equivocal because they are all uncertain in *Prodiplocynodon* and some alligatorines. Therefore, the phylogenetic relationship of *Prodiplocynodon* is relatively less strongly supported than are those of the other taxa included.

The species of *Diplocynodon* that are traditionally referred to the Alligatorinae (Steel 1973; Carroll 1988) are comparable morphologically with *Prodiplocynodon langi*. Like *Prodiplocynodon*, they are probably not alligatorines because, where known (characters 2, 20, 36, 37 and 38), none of the alligatorine synapomorphies are present. A similar phylogenetic position was concluded for *Diplocynodon* (represented by *D. hantoniensis*) in the study of Norell *et al.* (1994).

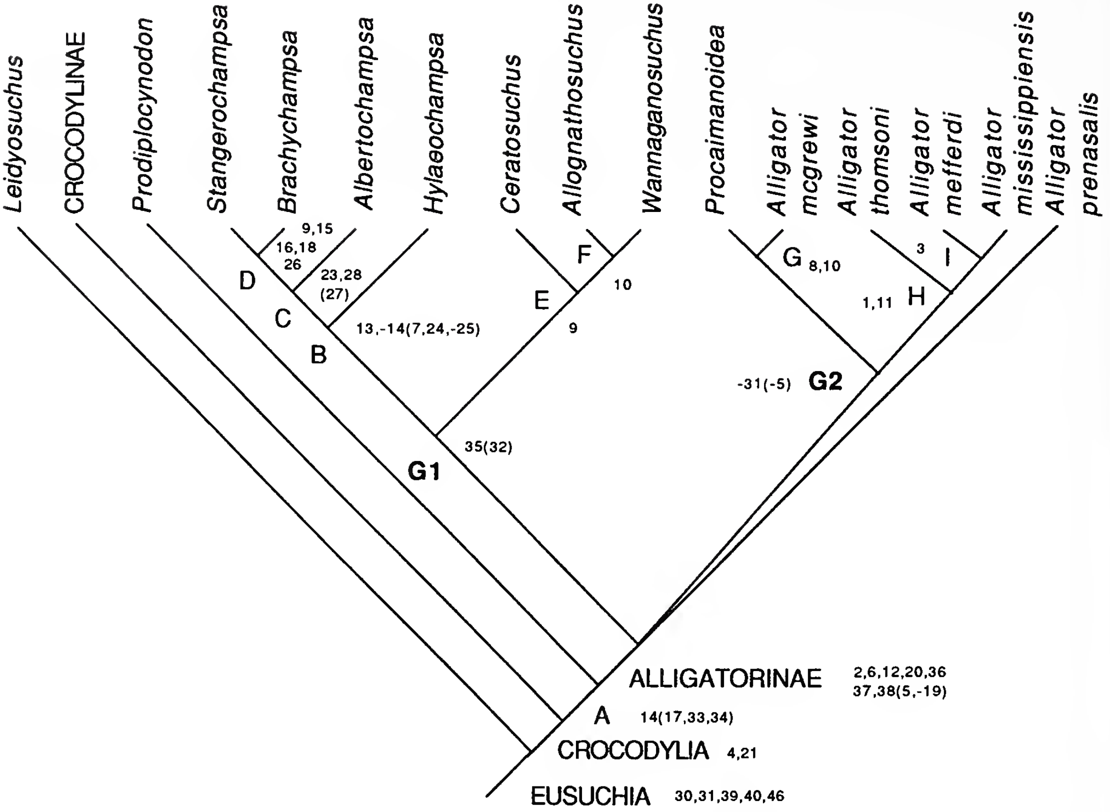
5. A monophyletic Alligatorinae, excluding *Prodiplocynodon*, is supported by seven unequivocal characters: character 2 (lack of a distinct lateral constriction between premaxilla and maxilla); character 6 (absence of a nasal/lacrimal contact); character 12 (lacrimal short and broad); character 20 (postorbital forming supratemporal fossa); character 36 (presence of four or five posterior massive crushing teeth); character 37 (dentary tooth 4 and dentary tooth 13 or 14 large, and presence of eight or nine small teeth between these large teeth); and character 38 (maxillary tooth 4 the largest and maxillary tooth 5 very small). Of these synapomorphies, characters 2, 37 and 38 are represented by their primitive states in all outgroups. The remaining four, characters 6, 12, 20 and 36 are represented by a derived character state in one of the four outgroups. The primitive states of character 6 (nasal/lacrimal contact present) and character 38 (maxillary tooth 5 largest) occur by reversal in *Albertochampsa* and *Brachychampsa*, respectively.



TEXT-FIG. 4. The consensus tree of two equally parsimonious cladograms generated by the present analysis, depicting relationships within the Eusuchia. In each node, unequivocal characters are followed by equivocal characters in brackets and '−' before a character indicates the reversal of the character. Characters of terminal taxa are as follows. *Hylaeochampsa*: 11, (19). *Albertochampsa*: −6; *Brachychampsa*: −38, (−27, −32); *Allognathosuchus*: 7, 15, (−5). *Procaimanoidea*: (−26). *Alligator mcgrewi*: 9, −25, 32; *Alligator thomsoni*: 16, *Alligator mississippiensis*: −33, 45, (−26). Crocodylinae: 1, 45.

6. Within the Alligatorinae two groups are recognized. *Hylaeochampsa*, *Albertochampsa*, *Brachychampsa*, *Stangerochampsa*, *Allognathosuchus*, *Wannaganosuchus* and *Ceratosuchus* (Group 1, Text-fig. 4) are linked by one unequivocal character (character 35, two or fewer teeth present posterior to anterior border of suborbital fenestra) and one equivocal character (character 32, surangular excluded from external mandibular fenestra). A second group, including *Procaimanoidea*, *Alligator mcgrewi*, *A. thomsoni*, *A. mefferdi* and *A. mississippiensis* (Group 2, Text-fig. 4), is supported by one unequivocal character, (character 31, no exposure of supraoccipital on skull roof [0 by reversal]) and one equivocal character (character 5, nasal ending posteriorly well before orbit [0 by reversal]).

7. Within Group 1, two monophyletic subgroups are present, Group B and Group E. Group B is supported by two characters (character 13, a long posteroventral process of the lacrimal reaching to the midpoint of the ventral border of the orbit, and character 14 [0 by reversal], the lacrimal/jugal suture being as long as the ventral border of the orbit). In addition, Group B is supported by three equivocal characters (character 7, nasal/premaxillary suture almost as long as nasal/maxillary suture; character 24, incisive foramen very large; and character 25 [0 by reversal], incisive foramen



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7. Within Group 1, two monophyletic subgroups are present, Group B and Group E. Group B is supported by two characters (character 13, a long posteroventral process of the lacrimal reaching to the midpoint of the ventral border of the orbit, and character 14 [0 by reversal], the lacrimal/jugal suture being as long as the ventral border of the orbit). In addition, Group B is supported by three equivocal characters (character 7, nasal/premaxillary suture almost as long as nasal/maxillary suture; character 24, incisive foramen very large; and character 25 [0 by reversal], incisive foramen

enclosed by premaxillae and maxillae). These three characters are equivocal because they are unknown in *Hylaeochampsa*, and two of them are shared by one (character 7) or more (character 25) taxa of other groups. Group E is defined only by one unequivocal character (character 9, snout wider than long), although the derived state of this character is also present in a subgroup of Group B and a taxon in Group 2.

8. Within Group B, *Stangerochampsa* and *Brachychampsa* are the most derived taxa. These genera (Group D, Text-fig. 4) share five unequivocal synapomorphies. They are character 9 (snout wider than long), character 15 (anterior and posterior processes of jugal similar in length), character 16 (anterior process of quadratojugal long, reaching half-way along ventral border of infratemporal fenestra), character 18 (quadrate/quadratojugal suture strongly curved) and character 26 (palatine/pterygoid suture lying entirely behind suborbital fenestra). Derived states of characters 15, 16 and 26 are also present in one or two taxa of Group 2.

9. *Stangerochampsa*, *Brachychampsa* and *Albertochampsa* are united in a monophyletic Group C by two characters, character 23 (skull table strongly rounded anterolaterally) and character 28 (maxilla broad lateral to tooth row on ventral surface [Text-fig. 1B]). Character 27 (anterior portion as long as interfenestral portion of palatine) might be an additional synapomorphy of Group C, but it is ambiguous because it is present in the primitive state in *Brachychampsa*, is unknown in two taxa of Group 1, and is also derived in one of the four outgroups.

10. Within Group E, *Allognathosuchus* and *Wannaganosuchus* are more closely related to one another than either of them is to *Ceratosuchus* (Group F, Text-fig. 4). This relationship is supported by one unequivocal character (character 10, snout shorter than postorbital region of skull). The derived state of this character is also present in Group G of Group 2.

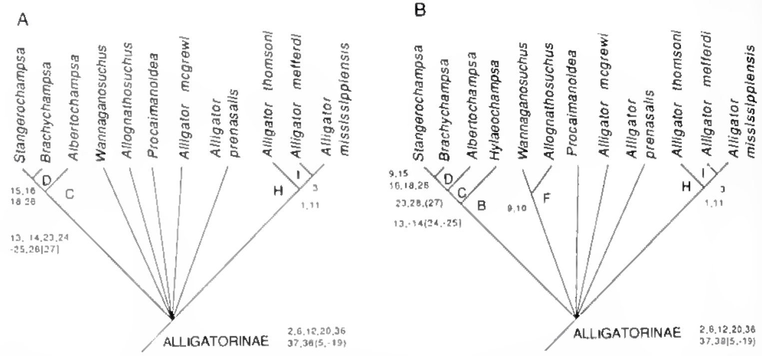
11. Within Group 2, two monophyletic subgroups are recognized. *Alligator mcgrewi* and *Procaimanoidea* form a monophyletic Group G, which is defined unequivocally by character 8 (two nasals broader than each maxilla in dorsal view) and character 10 (snout shorter than postorbital region of skull). Character 8 offers strong support for Group G because it is known in all taxa except *Hylaeochampsa* and is primitive in the taxa outside the group. The derived state of character 10 is also present in Group F of Group 1. *Alligator thomsoni*, *A. mefferdi* and *A. mississippiensis* are included in a monophyletic Group H, which is linked by two unequivocal synapomorphies: character 1 (premaxilla longitudinally wide anterior to naris and broadly overhanging nasal capsule) and character 11 (dorsal border of orbital ridged). Character 1 is unknown in *Hylaeochampsa* and is also derived in the Crocodylinae. Character 11 is also derived in *Hylaeochampsa*. Character 3 (nares fully divided) uniquely supports a close relationship between *A. mefferdi* and *A. mississippiensis* (Group 1, Text-fig. 4).

This analysis further supports a close relationship between *Bernissartia* + *Shamosuchus* and the Eusuchia. They share four unequivocal characters: character 22 (postorbital contacting ectopterygoid), character 25 (incisive foramen enclosed by premaxillae only), character 29 (choana almost entirely behind suborbital fenestra) and character 44 (more than two longitudinal rows of osteoderms without an anterolateral process). Characters 22 and 25 have not been recognized previously as synapomorphies of this clade.

The two most parsimonious cladograms produced by this analysis differ only in the position of *Alligator prenasalis* relative to Group 1 and Group 2. Character 5 (nasal ending posteriorly beyond or at level of anterior border of orbits) suggests unequivocally a close relationship between *A. prenasalis* and Group 1 (early alligatorines), while character 41 (anterior iliac process knob-like or absent) supports unequivocally a close relationship between *A. prenasalis* and Group 2 (late alligatorines). However, *A. prenasalis* is probably more closely related to Group 2 than it is to group 1, since the consistency index of character 41 is much higher than that of character 5.

The low percentage of the characters known for *Ceratosuchus* (32·6 per cent.) and *Hylaeochampsa* (43·4 per cent.) may have affected the phylogenetic relationships postulated. Therefore, further analyses, in which one or both of these genera were eliminated, have been carried out.

With both *Ceratosuchus* and *Hylaeochampsa* excluded, 14 equally parsimonious cladograms result. All of these cladograms support the phylogenetic relationships of the taxa outside the



TEXT-FIG. 5. A, part of the consensus tree of 14 equally parsimonious cladograms produced by eliminating *Hylaeochampsa* and *Ceratosuchus*; B, part of the consensus tree of three equally parsimonious cladograms produced by eliminating only *Ceratosuchus*. Explanations of characters and the letters on each node as in Text-figure 4.

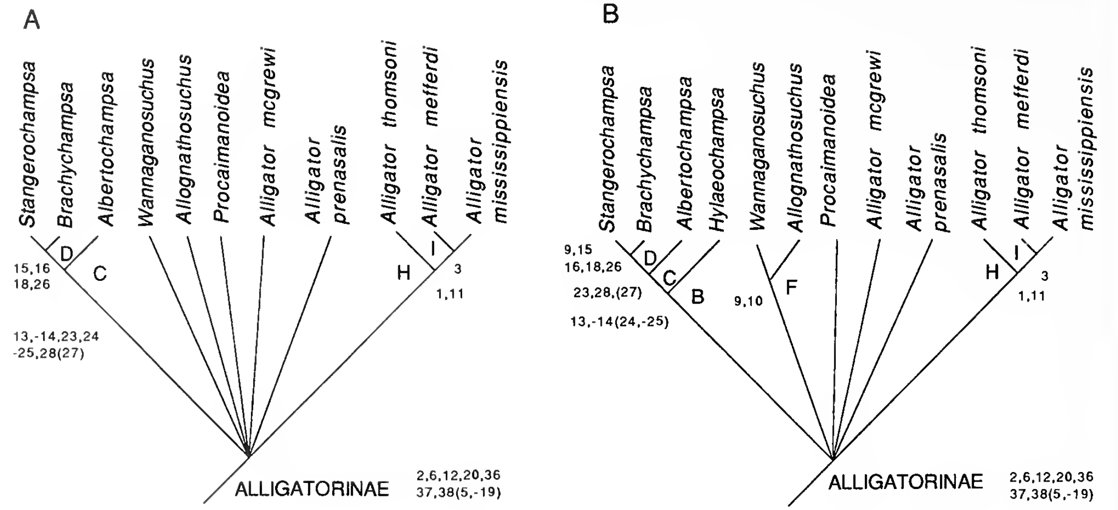
Alligatorinae and retain Group C (the monophyly of which is further supported by four additional synapomorphies) and Group H within the Alligatorinae (Text-fig. 5A). However, relationships among *Wannaganosuchus*, *Allognathosuchus*, *Procaimanoidea*, *Alligator mcgrewi*, *A. prenasalis*, Group C and Group H are unresolved.

If only *Ceratosuchus* is eliminated, the analysis produces three equally parsimonious cladograms. Relationships between the taxa are established slightly better in this analysis than in the previous one (Text-fig. 5B). This analysis supports a close relationship between *Wannaganosuchus* and *Allognathosuchus* and recognizes that *Hylaeochampsa* is the sister-taxon of Group C, as was the case in the first analysis. The relationships of *Procaimanoidea*, *Alligator mcgrewi*, and *A. prenasalis* remain unresolved, as they did in the second analysis.

These analyses demonstrate that the close phylogenetic relationship of the Mesozoic alligatorines is supported strongly and suggest that the genus *Alligator* is not a monophyletic group. These analyses also show that elimination of taxa with a relatively low percentage of known characters is not helpful in establishing a better resolved phylogeny of the taxa retained.

CONCLUSIONS

The primary results of this study are: (1), *Stangerochampsa mccabei* was a Late Cretaceous alligatorine with a durophagous feeding behaviour, indicated by the contact of the ectopterygoid with the palatine and crushing teeth at the back of the tooth row; (2), *Leidyosuchus*, rather than *Hylaeochampsa*, is the most primitive known eusuchian, and the latter is an alligatorine; (3), excluding *Prodiplocynodon* (and probably *Diplocynodon*), the monophyly of the Alligatorinae in a cladistic sense is well-established; (4), most of the Mesozoic and Early Cenozoic alligatorines form a monophyletic group while the Late Cenozoic alligatorines are members of a second monophyletic group, differences may reflect different feeding adaptations; (5), the Mesozoic alligatorines of western North America constitute a monophyletic group.



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SPHAEROIDAL ENROLMENT AND THORACIC CHARACTERS IN *BELTELLA DEPRESSA* AND OTHER OLENID TRILOBITES

by H. B. WHITTINGTON

Abstract. In sphaeroidal enrolment, the exoskeleton formed a closed capsule. Well known in post-Cambrian trilobites, many Cambrian species, in addition to Agnostina and eodiscoids, also enrolled in this manner. Characteristic features of such forms (other than Agnostina and eodiscoids) are: a fulcrate thorax; the fulcrum relatively close to the axis; the facets of the anterior segments large and backwardly directed; more posterior facets smaller, steeper, and less so directed. These features are described in detail in *Beltella depressa* and *Peltura scarabaeoides scarabaeoides*, and were shared by other olenids, including *Triarthrus*, in which sphaeroidally enrolled specimens are known. Other olenids, in which the fulcrum was distant from the axis, may have enrolled in the cylindrical manner, which left a lateral gap in the enrolled exoskeleton. The significance in classification of these and other characters of the thorax has yet to be evaluated in Olenidae and other groups.

Sphaeroidal enrolment, in which the exoskeleton forms a closed subspherical or ovoid form, is familiar in calymenids and *Phacops*. The tips of the thoracic pleurae and edge of the pygidium were tucked inside the cephalic doublure (calymenids), or in phacopids were accommodated in vincular notches and a groove in the cephalic doublure (e.g. Whittington 1992, pls 89, 115; Chatterton and Campbell 1993, figs 1a–f, 2a–c, e–g). In these and many other trilobites which enrolled in the same fashion, the thorax was fulcrate, the fulcrum situated in the adaxial half of the pleural width (tr.). The horizontal, inner portion of the pleura gave a precise, straight hinge, the anterior articulating flange fitting beneath the posterior flange of the preceding segment. The outer portion of the pleura was bent down and faceted, so that these portions overlapped one beneath the other in enrolment. The coaptative devices associated with the close fit between the tips of the pleurae and margin of the pygidium with the cephalon have been described in many species (e.g. Clarkson and Henry 1973; Henry and Clarkson 1975; Clarkson *et al.* 1977; Lespérance 1991; Chatterton and Campbell 1993). It is emphasized here that not only were such devices coaptative, but that the entire form of the exoskeleton was necessarily so – the convexity of its different portions, the width (tr.) and inclination of the outer portions of the pleurae, the size and inclination of the facets, and the shape of the cephalon *vis-à-vis* that of the thoracic segments and pygidium. Thus, for example, the anterior arch in the border of the cephalon, mentioned by Clarkson (1966, p. 82) as allowing the entry of respiratory and feeding currents when the animal was extended on the sea floor, must also have been shaped to accommodate the thoracic segments and pygidium in enrolment.

Sphaeroidal enrolment is known not only in the post-Cambrian trilobites referred to above, but also in the Lower Cambrian *Crassifimbra* (Palmer 1958), in Middle Cambrian ellipsocephalids (Westergaard 1936, pl. 11, fig. 9a–c; Geyer 1990) and in the Upper Cambrian examples described by Stitt (1983). The thorax was fulcrate, the outer portions of the pleurae faceted, and Palmer (1958, text-fig. 5) illustrated stops in the pleural doublures which limited overlap. Stitt emphasized the stronger backward deflection of the outer portions of the pleurae of the more anterior segments, the differing size and inclination of the facets, and that the flexure between the cephalon and anterior thoracic segments was strong. In Agnostina and eodiscoids (see Bergström 1973, p. 30) the

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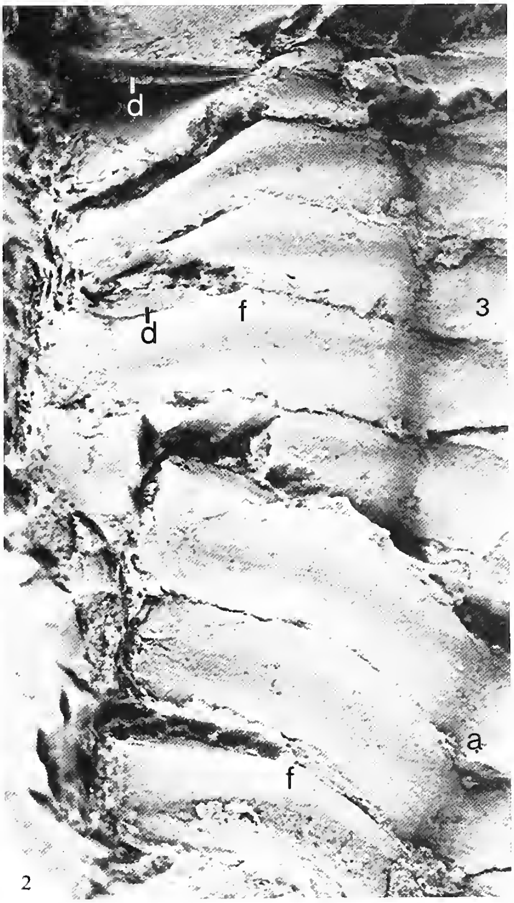
short thorax enabled the flat doublure of cephalon and pygidium to be brought into contact (Agnostina), or that of the pygidium to fit close inside the cephalic doublure (eodiscoids). Robison (1964, p. 515) described a vincular groove in the pygidial doublure of Agnostina, into which the inner edge of the cephalic doublure fitted on enrolment; Rushton (1966, p. 15) described vincular structures in eodiscoids. In both groups the thorax was fulcrate, but the outer portions of the pleurae did not overlap in enrolment, but fitted edge-to-edge against each other and the edges (or facet) of the cephalon and pygidium. To enable this fit the outer portions of the pleurae were narrow (tr.) and cut off by straight or curved edges anterolaterally and posterolaterally (Rushton 1966, text-figs 6, 8; Hunt 1967; Jell 1975; Whittington 1992, pls 55, 73). Robison (1964, p. 515) commented on the special shape of the segments in Agnostina and the lack of a doublure; the extremely narrow doublure in *Pagetia*, and the form of the segments were described by Jell (1975, p. 62).

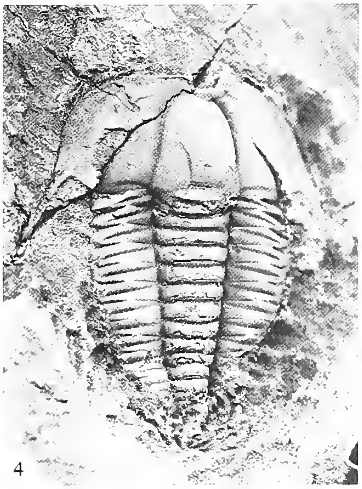
Sphaeroidal enrolment, then, is characteristic of many Cambrian trilobites. However, Fortey and Owens (1991*b*, p. 77) expressed the view that complete enrolment of the exoskeleton of *Beltella depressa* was not possible because flexure between posterior thoracic segments was limited and because these segments and the pygidium were not shaped to fit closely beneath the cephalon. Yet the fulcrate thoracic exoskeleton exhibits features noted above in trilobites that enrolled sphaeroidally, in particular the strong backward deflection of the large facets of anterior segments. Whether or not *B. depressa* could enroll sphaeroidally depended on the form of the entire exoskeleton. Here I contend (Text-fig. 2), on the evidence of the least flattened specimens, that the free cheeks were more steeply inclined than in Fortey and Owens' restoration (1991*b*, fig. 2), and that the outline of the thorax was slightly less convex abaxially. The convexity of the exoskeleton in Text-figure 2 is similar to that given to the closely related species *Leptoplastides salteri* by Fortey and Owens (1991*a*, fig. 9), and to that of *Peltura scarabaeoides scarabaeoides*. The illustrations of the latter species (Pl. 2) show the differences in appearance between an exoskeleton that has been relatively slightly flattened, and those of *B. depressa* (Pl. 1; Text-fig. 1E, H) which were originally of a similar convexity but have suffered much greater compaction. The differing size, shape and orientation of the facets on successive segments of these species appears to be coaptative, and to have enabled the greater flexure between anterior sclerites (and lesser between posterior sclerites) that facilitated the close-fitting enrolment.

Bergström (1973, p. 21) discussed enrolment in Olenidae, and concluded that many, possibly all, species were able to enroll. Clarkson's (1973, text-figs 2d–f, 5a–c, 6a–c, 7a–c, 8a–c) restorations revealed the strong convexity of the cephalon in certain species, and that of the entire exoskeleton was shown in Fortey's (1974) plates, and by those of the silicified material of Ludvigsen (1982). The latter author (p. 61) commented on the strong convexity of a species of *Parabolinella*, and the different appearance such material would have if it were flattened in shale. Among other details the doublure beneath the tips of the thoracic pleurae in *Parabolinella* (Ludvigsen 1982, pl. 49, figs *o*, *q*) are shown, and have a raised inner edge which may have provided a stop to enrolment at the posterior edge. In species of *Balnibarbi* (Fortey 1974, pl. 2, fig. 3; text-fig. 4), *Parabolinella*

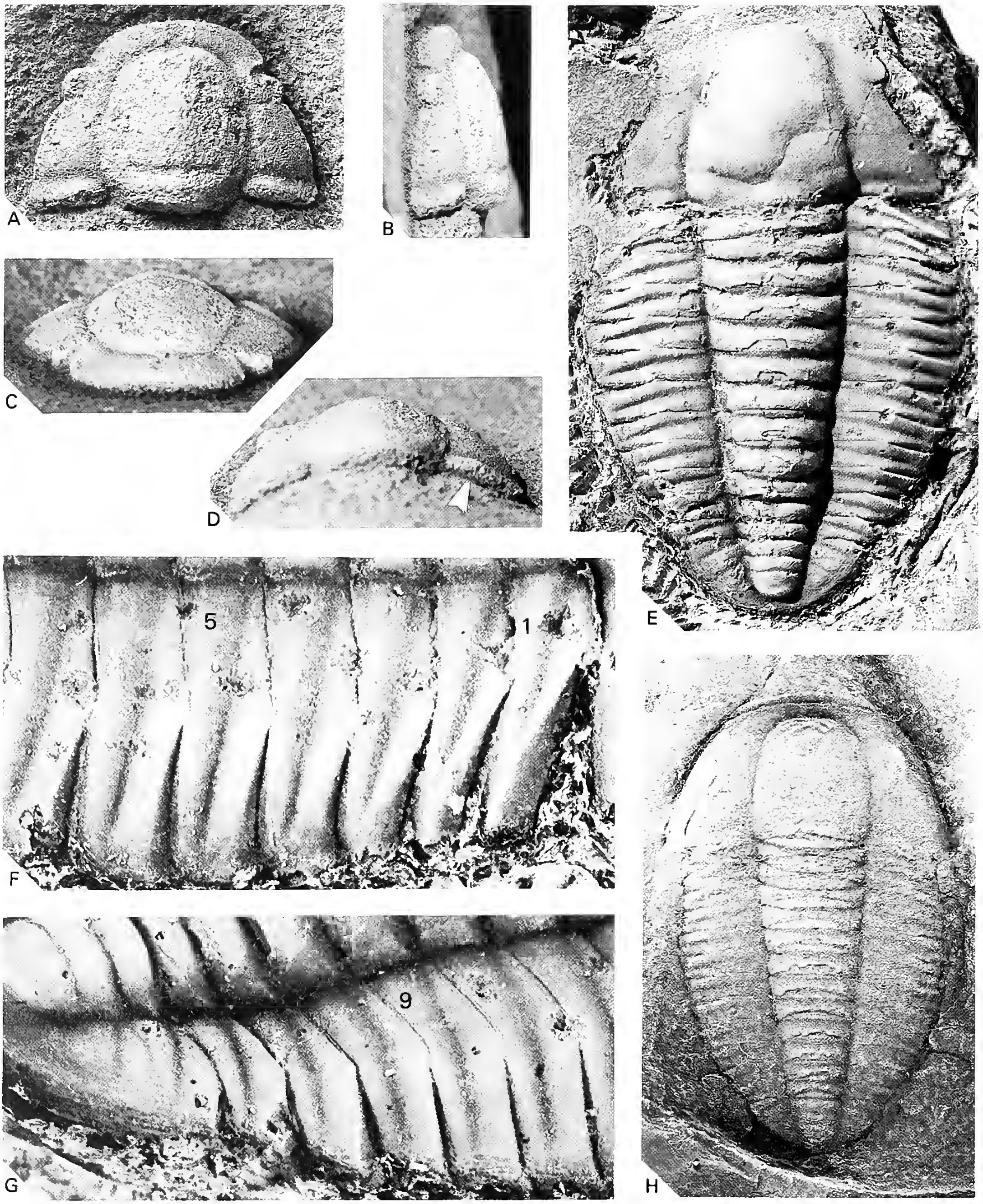
EXPLANATION OF PLATE 1

Figs 1–4. *Beltella depressa* (Salter *in* Murchison, 1859). 1–3, Lower Tremadoc, Clarenville Formation, south of mouth of Trilobite brook along south-west shore of Random Island, half-way between brook and Pelly's Mill, Newfoundland. 1–2, NHM It 20246; 1, internal mould of cranidium and partially disarticulated, incomplete thorax; dorsal view, articulating half ring of first segment has been exposed; × 3; 2, oblique view of left side, showing mould of doublure (d) of posterior border of cranidium and left pleurae of segments 1–8, axial (a) and fulcral (f) articulating processes, and further preparation of tip of pleura of segment three (numbered) to show part of doublure (d) lying on facet of pleura of segment 4; × 8. 3, NHM It 20229; posterior portion of external mould showing sculpture of last two thoracic segments and pygidium; × 5. 4, BRSMG Cd 550a; Breadstone Shales, Gloucestershire; original of Fortey and Owens 1991*b*, pl. 1, fig. A; flattened exoskeleton lacking pygidium; × 3.





WHITTINGTON, *Beltella*



TEXT-FIG. 1A–H, *Beltella depressa* (Salter *in* Murchison, 1859); Lower Tremadoc; Gloucestershire, England. A–D, BRSMG Cb 4400, original of Curtis 1968, pl. 9, fig. A; Micklewood Beds; cranidium, internal mould, dorsal, left lateral, anterior and posterior (arrow points to fulcrum) views, respectively; × 3. E–G, BRSMG Cc 860a, original of Fortey and Owens 1991*b*, pl. 1, fig. B; Breadstone Shales; E, dorsal view; × 3; F–G, oblique right lateral views of thoracic pleurae 1–7 (segments 1, 5 numbered), and pleurae 8–12 (segment 9 numbered) and pygidium, respectively; × 8. H, BRSMG Cc 2010, original of Fortey and Owens 1991*b*, pl. 1, fig. D; Breadstone Shales; dorsal view; × 2·6.

(Ludvigsen 1982, fig. 49*a–s*), *Anaximander* (Fortey 1974, pl. 21, fig. 3), *Bienvillia* (Fortey 1974, pl. 22, fig. 1) and *Triarthrus* (Ludvigsen and Tuffnell 1983, pls 2–3) the thorax was fulcrate, the fulcrum one-third or less of the width (tr.) of the pleura from the axial furrow. The facet on the anterior four thoracic segments was large and backwardly directed, facets on succeeding segments were less backwardly directed. I consider that in species of the genera mentioned above sphaeroidal enrolment was probable. The only examples known to me of such an enrolled holaspid form are those of *Triarthrus beckii* figured by Ross (1979, pl. 1, figs 1–12; for justification of this specific name see Ludvigsen and Tuffnell 1983, p. 571); Ludvigsen (1982, fig. 50C) showed an enrolled meraspid of *Parabolinella panosa*, and Ludvigsen and Tuffnell (1994, pl. 3*g*) figure a partially enrolled *Triarthrus*. Fortey (1974, p. 27, fig. 4) considered that *Balnibarbi pulvurea* could enroll, presumably completely.

As Bergström (1973, p. 21) recognized, some olenids had a thorax of a different form. *Westergaardites* (Henningsmoen 1957, fig. 18) had 19 thoracic segments, each with a wide (tr.), horizontal inner portion and a narrow, spinose outer portion. In *Leptoplastus norvegicus* (Henningsmoen 1957, pl. 15, fig. 7), the inner, horizontal portion of each pleura was wide (tr.), the outer narrow and faceted, as it was in *Ctenopyge modesta* (Henningsmoen 1957, pl. 19, figs 5, 9–10); in *C. pecten* (Westergaard 1947, pl. 3, fig. 12) there were long pleural spines on the thorax. Such species may not have formed a closed capsule on complete enrolment, rather there would have been a lateral opening partially covered by spines. Bergström (1973, p. 14, fig. 8b) referred to this type of enrolment as cylindrical, illustrating it by a drawing of *Fallotaspis* (Olenellina), and a model of *Ctenopyge* (1973, pl. 1, fig. 8). Figured examples of this type of enrolment are rare, but one is of *Remopleurides perspicax* (Nikolaisen 1983, pl. 5, figs 1–5).

How important thoracic characters may be in classification of Olenidae, including the controversial subfamilial divisions (Fortey and Owens 1991*b*, p. 74), is an open question. The above discussion suggests that the position of the fulcrum, close to, or far from, the axial region, may be a useful character. Fortey (1974, p. 13) recognized the pleural node, a triangular inflated area of the posterior pleural band adjacent to the axial furrow, as characteristic of Balnibarbiinae. Ludvigsen and Tuffnell (1994, p. 192, fig. 12) regarded a similar inflation as a cardinal character in Triarthrinae. They interpreted this inflation as bounded posteriorly by a posterior pleural furrow, but this furrow is the change in slope between the inflation and the short (exs.) posterior articulating flange; this change in slope dies out distal to the fulcrum and is not analogous with the true pleural furrow. The pleural node is not developed in *Beltella* or *Peltura*: in the former the posterior pleural band is but gently inflated; in *Peltura* (Pl. 2, fig. 3) more strongly, and separated by a distinct change in slope from the posterior flange.

SYSTEMATIC PALAEONTOLOGY

Family OLENIDAE Burmeister, 1844

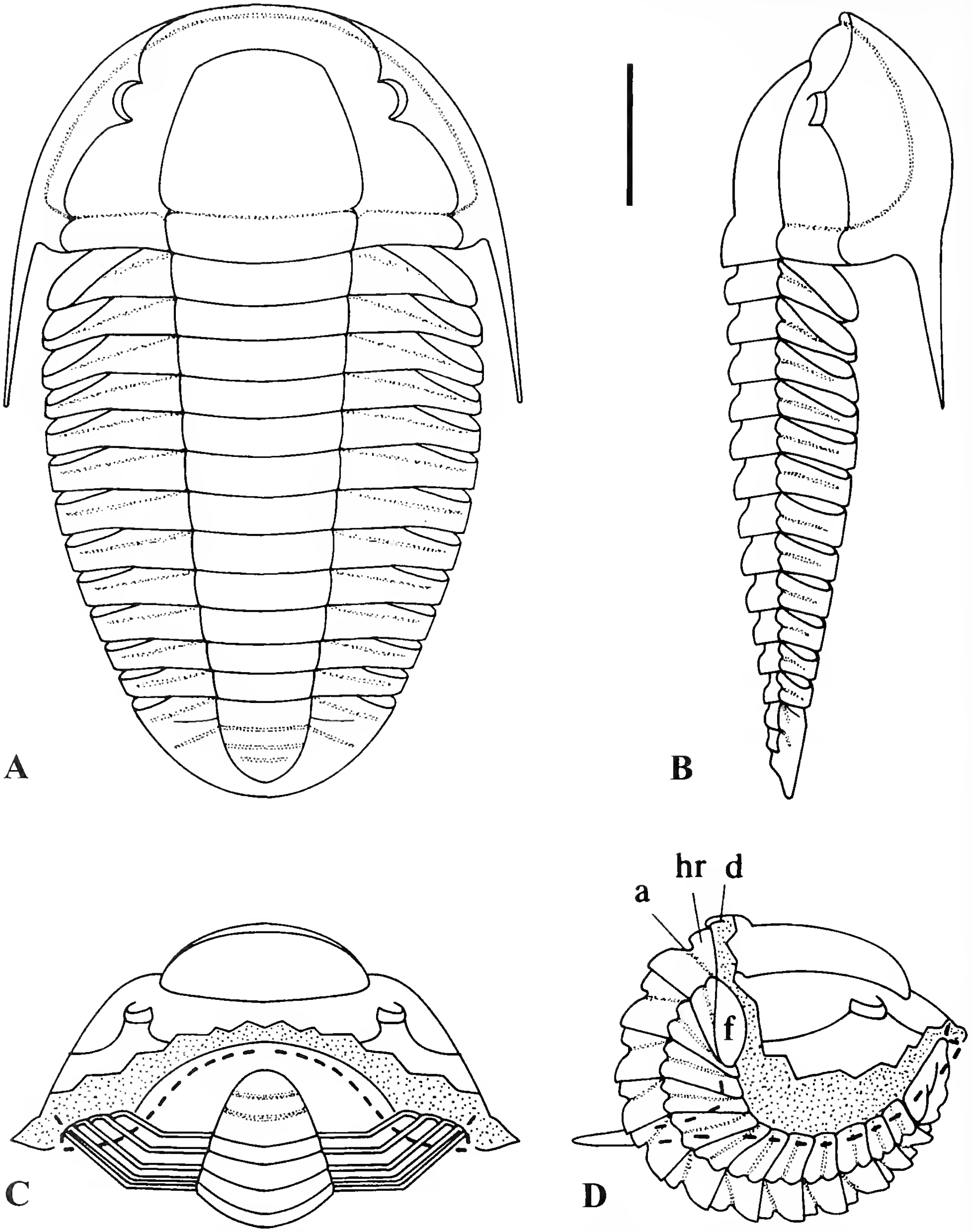
Genus BELTELLA Lake, 1919

Beltella depressa (Salter *in* Murchison, 1859)

Plate 1; Text-figures 1–2

Material. I accept the synonymy of this species as given by Fortey and Owens (1991*b*), and hence include material from the Breadstone Shales and Micklewood Beds of the Tortworth inlier, Gloucestershire, and from the Clarenville Formation, Random Island, Newfoundland, strata which are of Lower Tremadoc age.

Morphology. Fortey and Owens (1991*b*) described this species and referred to the effects of flattening on the original appearance of the exoskeleton; additional details are given herein and used in a new reconstruction (Text-fig. 2). The least flattened cranidium known (Text-fig. 1A–D) shows the minimum convexity of the cephalon, and that the posterior border had a horizontal inner portion, and was bent down at the fulcrum into a wider (tr.), downsloping outer portion. The free cheek conformed to this downslope and hence appears narrow (tr.) in dorsal view in one of the less flattened specimens from the Breadstone Shales (Text-fig. 1H); the trace of the genal spine continues the curve of the lateral border. In the original of Plate 1, figure 4, the free



TEXT-FIG. 2. *Beltella depressa*. A–B, restoration of extended exoskeleton in dorsal and right lateral views. C–D, restoration of enrolled exoskeleton in anterior and right lateral views. Heavy dashed line indicates margin of cephalon and doublure of cephalic border in section; parts of dorsal exoskeleton cut away to reveal tips of thoracic pleurae and edge of pygidium, and lateral view of first thoracic segment; interior of exoskeleton stippled. Abbreviations: a, articulating furrow; d, doublure of occipital ring; f, facet; hr, half ring. Scale bar represents 10 mm.

cheeks are spread out and pushed inwards, and the genal spine projects slightly outward, as it does in the originals of Stubblefield (*in* Smith 1933, p. 367, pl. 34, figs 10–11). This divergence from the lateral border may be the result of flattening. The mould of the doublure of the anterior border is preserved in the original of Text-figure 1H, as a narrow channel, and a similar narrow channel beneath the outer portion of the posterior border (Pl. 1, fig. 2) is the mould of the doublure. It is presumed that a narrow doublure, convex ventrally, also underlay the lateral border.

The thorax of 12 segments (Text-fig. 1E, H) was fulcrate, the inner portion of each pleura horizontal, the outer portion bent down at the fulcrum to slope in conformity with the posterior cephalic border. The long (sag.) articulating half ring of the first segment has been exposed in the partially disarticulated, flattened, incomplete Clarenville specimen (Pl. 1, fig. 1). In the succeeding four segments the axial rings are broken to expose a mould of the doublure of the ring, or of the half ring of the succeeding segment, or of a combination of both, as is the case in broken rings of other moulds (Text-fig. 1E, H). Each half ring was of similar length (sag.) to the axial ring in front of it, so that it reached the posterior slope of the articulating furrow. This furrow had a slight curvature, concave forward in dorsal view, a gentle posterior slope in profile, rising anteriorly vertically to the half ring. The anterior edge of the inner portion of each pleura bore an articulating flange (Pl. 1, fig. 2), which fitted beneath the posterior cephalic border or the posterior flange of the segment in front. The posterior flange is not visible in the internal mould (Pl. 1, fig. 2) because this edge is broken; on the external surface (Text-fig. 1F–G) the short (exs.) flange is defined faintly behind the gently convex posterior pleural band. An axial articulating process was situated where the axial furrow deepens at the posterior, adaxial end of the inner pleural portion (Pl. 1, fig. 2) and a fulcral process at the anterior abaxial end, with corresponding sockets at the extremities of the adjacent edges. The outer portion of each pleura had the posterior edge backwardly and outwardly directed, backwardly most strongly on the first segment, progressively less so on succeeding segments (Pl. 1, fig. 2; Text-fig. 1E–G). The anterior edge of the outer portion of the pleura was the steeply inclined facet, which appears to have had a concave surface. The size and shape of the facet changed along the thorax, those of the first three segments being largest, the posterior edge curved back so that the pleural furrow terminated against it. In more posterior segments the posterior edge of the facet was less strongly backwardly directed, and the pleural furrow extended behind the facet to die out close to the pleural tip. This change in form and direction of the facet meant that the shape of the outer portion of the pleura changed progressively backward (Text-fig. 1E–G), from short (exs.) and blade-like on the first segment to longer (exs.) and subparallel-sided posteriorly. The abaxial margin of the pleural tip of segments 4–12 was straight, the edge not sharp, but blunt as the dorsal exoskeleton curved under to meet the doublure. This blunt edge was terminated anteriorly by the facet, and, because the facet was concave, the anterior tip of the pleura curves forward at the posterolateral margin of the facet. Compaction caused the outer portions of some of the pleurae to be curved slightly, concave upwards, and flattened the tip. In such cases (e.g. segments 4–5, of Pl. 1, fig. 2; left side of Text-fig. 1E) this forward curvature at the anterior tip was exaggerated. I consider that this forward prolongation (Fortey and Owens, 1991*b*, p. 73) was too slight to have inhibited the pleurae in sliding one below the other in enrolment. The form of the pleural doublure could not be revealed completely in the moulds, but the fragment preserved (Pl. 1, fig. 2) suggests that it may have been short (exs.) proximally, but extended beneath the tip, the inner margin a U-shaped curve, as in *Peltura* (Pl. 2, fig. 5). The width (tr.) of the inner and outer portion of each pleura is approximately equal in segments 3–12; in the first segment the inner portion is markedly narrower than the outer, in the second segment less so. Hence, the outline of the tips of segments 1–6 was only slightly convex outward (Text-fig. 1H; Pl. 1, fig. 4), while segments 7–12 decreased progressively backwards in width. The outline of the thorax was like that in the original of Text-figure 1H, not more strongly bowed outward as in the flattened original of Text-figure 1E.

The axis of the pygidium is clearly defined in the English specimens, less so in those from Newfoundland. The fulcrum lies at more than half the width of the anterior margin of the pleural region, and a facet (Text-fig. 1G) truncates the anterolateral corner of the region, the external surface being concave. The edge of the pleural region, laterally and posteriorly, appears to curve down and become vertical distally, the margin continuing the line of the pleural tips. The doublure of the pygidium is not known; possibly it was narrow, curled beneath the margin. The external surface (Pl. 1, fig. 3; Text-fig. 1G) bears fine, anastomosing ridges, subparallel to the margin and arranged in a curve concave forward on the pleural region. Similar ridges, in a curve concave forward, are present on the axial rings of the thorax, and parallel to the margin of the pleural tips. These ridges are poorly preserved, but appear to be asymmetrical terrace ridges, the steep slope facing inwards (cf. Rushton 1982, p. 52).

Enrolment. The new reconstruction (Text-fig. 2) resembles the original of Text-figure 1H, rather than the more flattened and cracked specimens from Gloucestershire (Text-fig. 1E) and Random Island

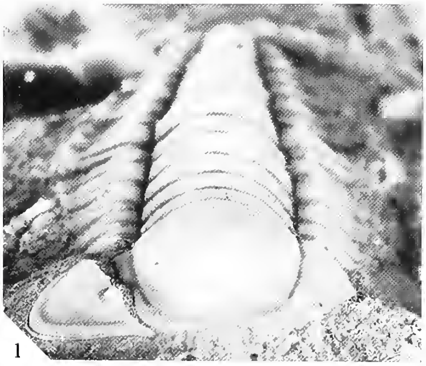
(Fortey and Owens 1991*b*, pl. 1, figs E–F), upon which Fortey and Owens' reconstruction appears to have been based. The convexity of the exoskeleton in Text-figure 2 is not unusual for some olenids, being similar to that of reconstructed olenid cephala (Clarkson 1973), to that shown by *Peltura* (Pl. 2, figs 1–2, 4), and to that given by *Leptoplastides* by Fortey and Owens (1991*a*, fig. 9). As a consequence of such convexity, the outline of the posterior thoracic segments and pygdium is similar to that of the inner edge of the cephalic doublure (Text-fig. 2), which approximated to that of the anterior and lateral border furrows. Thus I consider that the exoskeleton was able to enroll completely, the margins of the outer edges of the thoracic pleurae and pygidium having fitted against the inner surface of the cephalic doublure, the exoskeleton forming a closed capsule. In order to achieve this closure, some 220° of flexure had to take place between cephalon and pygidium, the first 90° between the cephalon and segment 4, the flexure between segments 4 to 12 and the pygidium being less. The strong backward inclination and large size of the facets of the anterior segments, and progressive reduction in the backward inclination in successive segments is coaptative, allowing these differing amounts of flexure between sclerites. The concavity of the facets facilitated their sliding beneath the convex doublure of the posterior cephalic margin and outer portions of the pleurae, and the tips of the pleurae fitted one behind another in the fully enrolled position. The steeply down-turned edge of the pygidium came to rest against the inner edge of the cephalic doublure. If this doublure bore terrace ridges, these ridges may have interlocked with those on the pleural tips and edge of the pygidium. An analogous change of form of the size and direction of the facets is seen in *Peltura* (Pl. 2, figs 3–4), and I think it probable that this species enrolled to form a closed capsule in much the same manner. In *Triarthrus beckii* (Ross 1979, pl. 1, figs 3, 6, 9, 12) there were 14 thoracic segments, so that some 250° of flexure between cephalon and pygidium was necessary for full enrolment. In lateral view the exoskeleton had a more nearly circular outline than that suggested here for *Beltella*, and the first 90° of flexure was achieved between cephalon and third segment.

Remarks. Fortey and Owens (1991*b*, p. 74) considered that the thoracic segments of *Beltella* were like those assigned to *Acerocare tullbergi* by Henningsmoen (1957, pl. 30, fig. 9). However, the inner, horizontal portion of these latter segments constitutes most of the width (tr.), only the outermost portion is bent down, the tip bearing two short spines one on the end of each pleural band. Each band had a ridge along the crest, and the anterior band bore a narrow (exs.) articulating flange. The thorax of *A. tullbergi* is thus different from that of *B. depressa.*

Fortey and Owens (1991*b*, p. 74) gave their reasons for rejecting the subjective synonymy of *Beltella* and *Leptoplastides*, which included the 'peculiar structure' of the thorax of *Beltella.* These authors' (1991*a*, p. 449, figs 8c–j, 9) illustrations of *Leptoplastides salteri*, the type species, show that in the relative width of inner and outer portions of the pleurae, and size and shape of the pleural facets, the two type species are similar. The distinctions between them lie in the median axial spines of the occipital ring and thoracic segments, and the blunt posterolateral pleural spines of *L. salteri.*

EXPLANATION OF PLATE 2

Figs 1–8. *Peltura scarabaeoides scarabaeoides* (Wahlenberg, 1818), PMO 139.137; Upper Cambrian, zone 2dγ–δ; Royken, Norway. 1–4, 6, 8, latex cast of external mould; 1–2, 4, anterior, right lateral, dorsal views; × 5; 3, oblique, left lateral view of thorax and pygidium, showing (arrowed) sharp flexure at fulcrum of right pleurae, and left pleurae; × 8; 6, oblique left posterolateral view of posterior six segments of thorax and pygidium with three spines at margin (arrowed); × 8; 8, oblique anterolateral view of right free cheek and right pleurae of anterior three thoracic segments; × 8. 5, incomplete, isolated left pleura of segment on same slab, excavated to reveal doublure beneath spinose pleural tip; inner margin of doublure arrowed; a = anterior articulating flange; p = posterior flange; × 8. 7, isolated free cheek on same slab, oblique anterolateral view; eye lobe broken; lateral border partially removed to show flat doublure, anterior arch of border arrowed; × 8.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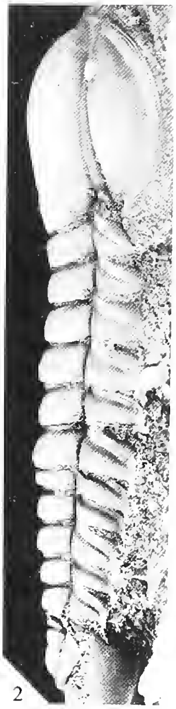
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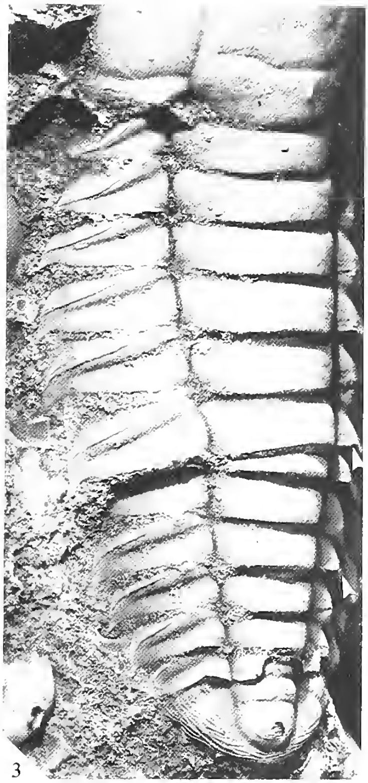
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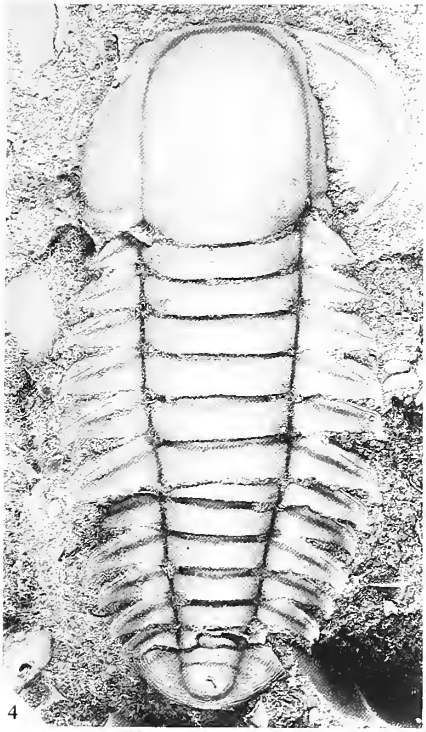
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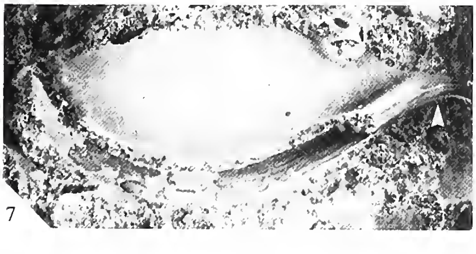
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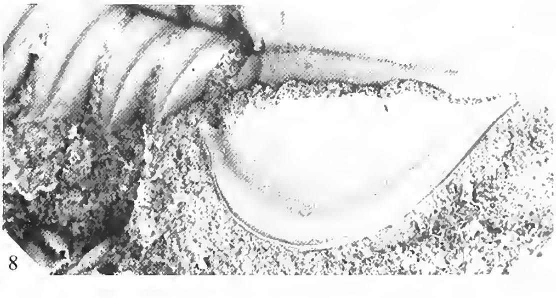
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WHITTINGTON, *Peltura*

Whether or not such distinctions are regarded as of generic significance is a matter of opinion; here I retain *Beltella*, albeit with doubt. Small pleural spines are present, for example, in the degree three meraspid stage of *Triarthrus beckii*, but are lost in later meraspid stages and the holaspid (Whittington 1992, pls 38*b*, 39*c*, 40).

Genus PELTURA Milne Edwards, 1840

Peltura scarabaeoides scarabaeoides (Wahlenberg, 1818)

Plate 2

Material. PMO 139.137, a small slab of dark grey calcareous mudstone showing the external mould of an almost complete exoskeleton, and abundant disarticulated sclerites of olenids. Most numerous are those of *P. s. scarabaeoides*, but cranidia, free cheeks and pygidia of *Sphaerophthalmus humilis*, and one thoracic segment of *Ctenopyge* type also occur. I conclude that this slab, from a loose boulder found opposite the entrance to the Slemmestad cement factory, Royken, Norway, came from rocks of the lower part of zone Vc(2dγ–δ) (Henningsmoen 1957, p. 299, pl. 5, Vc).

Description. The external mould of the complete exoskeleton closely resembles the original of Henningsmoen (1957, pl. 26, fig. 1), and is less disarticulated and more complete. In anterior view (Pl. 2, fig. 1) the steep downward curvature of the left fixed cheek is visible, the right free cheek having been displaced upwards and rotated during preservation. In its original position, the genal field of the free cheek would have sloped vertically adjacent to the lateral border, and the lateral and anterior borders would have been strongly arched in anterior view, as the detached free cheek shows (Pl. 2, fig. 7; cf. Clarkson 1973, text-fig. 4a). The doublure of the free cheek is flat peripherally, upturned at the inner margin beneath the border furrow. In his description of the eye of this species, Clarkson (1973, p. 746) noted that the external surface of the cornea was smooth, as it is in the complete specimen (Pl. 2, fig. 8) and in other, detached free cheeks.

The thorax was of 12 segments, and is disarticulated behind the sixth segment so that the seventh is partly concealed; only the left half of the twelfth segment is preserved. The inner portion of the pleura was narrow (tr.), horizontal, the outer portion sloping steeply, the anterior edge of the inner portion a flange which fitted beneath the posterior articulating flange of the segment in front. This short (exs.) posterior flange is defined by a change in slope from the inflated posterior pleural band (Pl. 2, fig. 3). A small, convex articulating process was situated at the anterior edge of the inner pleural portion, at the fulcrum, and fitted into a socket in the segment in front. The outer portion of the pleura bears a facet, the posterior edge of which, on the anterior segment, is directed strongly backward so that the pleural furrow ends against it distally. In the anterior four segments this backward inclination is progressively reduced so that the pleural furrow lies behind the facet in the fourth and succeeding segments (Pl. 2, fig. 3). Thus the facet was largest and most strongly backwardly directed on the anterior segments, proportionally smaller on more posterior segments. The tip of each segment was rounded anteriorly, drawn out into a short spine at the posterolateral angle. The doublure beneath the pleural tip has been exposed in an isolated segment (Pl. 2, fig. 5), the inner edge curved convexly outward, a narrow band extending inward beneath the facet and at the posterior edge, presumably narrowing to end before reaching the fulcrum. This specimen shows also the short (exs.) articulating flange on the anterior edge of the inner portion of the pleura, which fitted below the equally short posterior pleural flange.

The pygidium is like that of Henningsmoen's (1957, pl. 26, fig. 1) specimen, with a distinct first axial ring, the pleural region truncated anterolaterally by a facet and posterolaterally curving steeply downward. The pleural spines are partially preserved on the left side (Pl. 2, fig. 6), and were directed almost vertically downward. Anastomosing lirae run parallel to the posterolateral margin of the pygidium, and curve outward into the base of the pleural spines. Isolated pygidia in the slab also show these spines.

In the external surface of the axial exoskeleton the occipital furrow is shallow, the sigmoidal S1 faint, and S2 barely discernible. A low median tubercle is present on the occipital ring, and on each axial ring of the thorax, at the midlength in anterior segments, closer to the posterior edge in more posterior segments. The anterolateral portion of the occipital ring is gently inflated, as is the same portion of the anterior five or six thoracic axial rings. Terrace ridges, the steep slope outward-facing, are present on the outer edge and doublure of the convex cephalic border, strong and subparallel (Pl. 2, figs 7–8). A prominent terrace ridge, the steep slope backward-facing, bounds the posterior edge of the facet of each thoracic segment, with an additional one or two ridges distally curving back into the base of the spine. Lirae (symmetrical ridges) on the pleural region of the pygidium are referred to above, and are also present, curving concavely forward, on the axial ring and terminal portion of the axis. The lirae are strongest towards the margin of the pygidium, where they appear to become terrace ridges with the steep slope forward facing.

Remarks. Although this specimen retains much original convexity, the anterior view (Pl. 2, fig. 1) shows a slight upward and outward slope of the inner portions of the thoracic pleurae, and the outer portions have a slightly concave profile distally. I attribute this, and the detachment and upward rotation of the right free cheek, to compaction. The original form would have been similar to that shown in Text-figure 2, and I consider a similar sphaeroidal enrolment to have been possible. In the closed position, the terrace ridges on the down-turned pygidial border, and on the pleural tips, would have been approximately parallel to those of the cephalic doublure. Interlocking of these ridges and grooves may thus have occurred. Bergström (1973, pl. 3, figs 1–2) figured an asymmetrically flattened specimen, and used a paper model (1973, pl. 1, fig. 7) to show sphaeroidal enrolment in this species.

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VARIABILITY IN THE ORDOVICIAN ACRITARCH *DICRODIACRODIUM*

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ABSTRACT. Species of the Ordovician acritarch genus *Dicrodiacrodium*, with a single apical process, are evaluated critically, based on a review of published literature and new studies on material from Belgium, Bohemia, China, Germany, and Morocco. Investigations of large populations of such species show a wide variability between specimens. Biometric studies, including measurements on type area material, show that the subdivision into varieties and even into species is not justified. There is a complete gradation between all of the predescribed taxa, which are impossible to distinguish. Therefore, all specimens with a single apical process are classified as a single taxon: *Dicrodiacrodium ancoriforme* emend. nov. *D. ancoriforme* is very easy to recognize and of great biostratigraphical and palaeogeographical importance. Its First Appearance Datum (FAD) is in the Arenig *Undulograptus sinodentatus*/*Didymograptus nexus* graptolite Zone in South China (approximately equivalent to the British Arenig *Isograptus gibberulus* Biozone). Palaeobiogeographically, it is typical of the cold to temperate Gondwanan and peri-Gondwanan ('Mediterranean') Palaeoprovince.

A MAJOR problem of acritarch research is the abundant literature and the enormous number of published taxa; both very difficult to survey. In the Ordovician, taxonomic confusion is common: a great number of genera and species have been described without sufficient comparison with similar taxa, and the diagnoses commonly overlap from one taxon to another.

Acritarch taxa generally show a very wide variability. The study of larger populations indicates that the original descriptions are sometimes based on poorly preserved material and/or a small number of specimens. To establish the limits between taxa and to eliminate overlap, thorough reviews of existing species and genera are needed, rather than the publication of further 'new' taxa, which may only increase the existing taxonomic confusion.

The problem of variability is not unique to acritarchs. Hughes (1994), for example, published a review of the Late Cambrian trilobite *Dikelocephalus*, in which no fewer than 25 species were suppressed as junior synonyms of *D. minnesotensis*, following bivariate and multivariate analyses of variation. While such biometric investigations are today common in the study of most fossil groups, they are still neglected in acritarch research.

Burmann (1968) erected the genus *Dicrodiacrodium* for acritarchs with a heteropolar vesicle, one pole bearing a network of fine filaments, the other provided with one or several appendices which branch distally into simple pinnae. Burmann (1968) described the new genus, its five species, and nine varieties from (1) the 'upper Llanvirn' of the boreholes Rügen 3h and Arkona 101, both drilled on the Island of Rügen, Baltic Sea (north-east Germany), and (2) from exposures of the Griffelschiefer-section 'Bahnhang nördlich Unterhermsgrün', Vogtland (south-east Germany), which is assigned to the Arenig. The exact positions and the precise ages of the samples were not indicated and remain uncertain. The type material has not been accessible until now.

The present paper is an attempt to rationalize the taxonomy of *Dicrodiacrodium*. It is based on a review of published literature and on new investigations on material from different localities, including the type area. A biometric approach is used to study intraspecific variation in specimens with a single apical process. It is based on bivariate analyses of variation using parameters such as the process length and the central body length and width.

MATERIAL AND METHODS

The new material studied comes from Germany, Belgium, Morocco, Bohemia, and China. The German material is from the boreholes Binz 1 and Rügen 5 on the Island of Rügen (type area of

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the genus). The material from Binz 1 is of late Llanvirn *Didymograptus murchisoni* graptolite Zone age (Servais and Katzung 1993). Six samples from the following depths have been analysed: 5041·8 m (sample no. 4); 5102·4 m (22); 5117·1 m (27); 5139·1 m (28); 5163·0 m (34); 5217·6 m (37). The sample from Rügen 5 (sample no. 61, depth 3287·3 m) is of early Llanvirn *D. artus* graptolite Zone age (Jaeger, pers. comm.). The type material of all taxa with a single apical process (Burmann 1968) comes from levels attributed to the 'upper Llanvirn' (*D. murchisoni* graptolite Zone age) from the same area, but from other boreholes (Rügen 3 and Arkona 101). It has not been accessible for the present study.

The Belgian material was collected from exposures of the Huy Formation in the Bande de Sambre-et-Meuse, of early Llanvirn *D. artus* graptolite Zone age (Servais and Maletz 1992), and from levels in the Ordovician Rigenée Formation in the Brabant Massif, the precise age of which is unknown (Servais 1991).

The Moroccan material comes from the borehole Boujad-109, Tadla Basin. Two samples from depths 360 m and 511 m have been investigated. Previous acritarch studies on this material were published by Cramer *et al.* (1974*a*, 1974*b*) and Cramer and Díez (1976, 1977), indicating a late Arenig or a late Arenig to early Llanvirn age based on palynological evidence. Recent studies on Chitinozoa (Soufiane and Achab 1993) provide evidence for a late Arenig age for depths between 481 m and 512 m in borehole Boujad-109.

The Bohemian samples, of late Arenig age, were collected from the upper part of the Klabava Formation in the Mýto section, and in the lowermost layers of the Šárka Formation in the Drahouš section (cf. Kraft and Kraft 1993). The sample from the Mýto section is dated as belonging to the *D. bulla* chitinozoan Zone (Paris and Mergl 1984, sample 16). The samples from the Drahouš section (S-1 to S-15) were collected from the *Corymbograptus retroflexus* graptolite Zone (Fatka and Brocke in press, figs 1, 3).

The Chinese material occurs in the *Azygograptus suecicus* and *Undulograptus sinodentatus*/*Didymograptus nexus* graptolite zones in the Dawan Formation in the Wangjiazei and Datianba sections, Yangtze Platform, Hubei Province, south-east China (Fatka and Brocke in press; Brocke, unpublished data).

All samples were subjected to standard palynological preparation techniques and were sieved at 10 or 12 μm. The Belgian, German and Moroccan samples were oxidized using Schulze's solution.

SYSTEMATIC PALAEONTOLOGY

INCERTAE SEDIS

Group ACRITARCHA Evitt, 1963

Genus DICRODIACRODIUM Burmann, 1968

Type species. Dicrodiacrodium ancoriforme Burmann, 1968.

Original diagnosis. 'Heteropolar gebaute Formen mit starker morphologischer Betonung des länglich–ovalen oder zylindrischen Zentralkörpers. Der apikale Pol trägt ein, zwei oder mehrere Fortsätze, die sich terminal schwingenförmig oder ankerartig in einfache Fortsatzanhänge aufspalten. Das Längenverhältnis von apikalen Fortsätzen zum Zentralkörper schwankt (*c.* 0·2–1). Der Zentralkörper ist glatt oder von paralleler Längsrippung bedeckt, selten skulptiert. Der antapikale Pol trägt ein Netzwerk, das meist erst an der Polkappe ansetzt, aber auch auf den Zentralkörper übergreifen kann. Das Netzwerk besteht entweder nur aus dünnen Bögen und Streben, oder es wird von stärkeren Stützfortsätzen (zwei peripheren Hauptfortsätzen oder/und mehreren feineren Fortsätzen) getragen' (Burmann 1968).

Translation of original diagnosis (*new translation*). Heteropolar forms with a strong morphological accentuation of the cylindrical or oblong–oval central body. The apical pole bears one, two or several processes which split distally into simple anchor- or flail-shaped pinnae. The ratio of the length of the apical processes to that of the central body varies (approximately 0·2 to 1). The central body is smooth or covered by a system of longitudinally arranged parallel ribs; it is rarely sculptured. The antapical pole bears a network which generally originates at the polar cap but which may extend to the central body. The network consists of either thin arches and props only, or is borne by strongly developed supporting processes (two peripheral major processes and/or several thinner processes).

List of species and varieties of Dicrodiacrodium *described in the literature*

Dicrodiacrodium ancoriforme Burmann, 1968.
  var. *ancoriforme* (1968) Autonym.
  var. *minutum* Burmann, 1968.
Dicrodiacrodium bicrure Burmann, 1968.
Dicrodiacrodium fulcratum Burmann, 1968.
  var. *fulcratum* (1968) Autonym.
  var. *procerum* Burmann, 1968.
Dicrodiacrodium normale Burmann, 1968.
  var. *breviuscula* nomen nudum (cited in Burmann 1976)
  var. *cylindricum* Burmann, 1968.
  var. *doliiforme* Burmann, 1968.
  var. *longiusculum* Burmann, 1968.
  var. *normale* (1968) Autonym.
Dicrodiacrodium retiforme Burmann, 1968.

Remarks. All species and varieties attributed to the genus *Dicrodiacrodium* were described by Burmann (1968), based on material from eastern Germany. No further species, subspecies, or varieties have been described.

Only the two species with a single apical process, *D. ancoriforme* and *D. normale*, have been widely cited in later references. Their identification is very easy. The other species with two or more apical processes (*D. bicrure*: two processes; *D. retiforme*: more than two processes; *D. fulcratum*: *c.* four processes) have not been cited since Burmann's (1968) original description, except for one record of *D.* aff. *fulcratum* Burmann by Vavrdová (1990*b*, p. 241, specimen not figured).

Burmann (1968) described all species and varieties with a single apical process from the 'upper Llanvirn' of Rügen, while all species and varieties with two or more apical processes were recorded from the 'Arenig' Griffelschiefer of the Vogtland. Only *Dicrodiacrodium normale* var. *breviuscula* nomen nudum with a single apical process was indicated by Burmann (1976) to occur in the Griffelschiefer. This form, however, has never been described formally.

The specimens with more than one apical process, described from the 'Arenig' Griffelschiefer, appear to be very rare. In the present study, very few specimens were recorded (five specimens in the *A. suecicus* graptolite Zone in China and one in the Moroccan material). Future studies will possibly show that they should be related to another genus of the large 'diacrodian' group of acritarchs. This group includes a great number of genera with heteropolar vesicles, such as *Arbusculidium* Deunff, 1968, *Barakella* Cramer and Díez, 1977, *Buchinia* Volkova, 1990, *Calyxiella* Golub and Volkova *in* Volkova and Golub, 1985, *Dasydiacrodium* Timofeev, 1959, *ex* Deflandre and Deflandre-Rigaud, 1962, *Ladogella* Golub and Volkova *in* Volkova and Golub, 1985, *Nellia* Golub and Volkova *in* Volkova and Golub, 1985, *Schizodiacrodium* Burmann, 1968, and *Stephanodiacrodium* Vavrdová, 1986. The taxonomy of this group needs to be revised.

In the present paper, the genus *Dicrodiacrodium* is neither emended nor split, because information on the complete plexus of forms is still too poor. At present, no species are removed from the genus. The biometric investigations in the present study are limited to specimens with a single apical process. Further studies are needed to clarify the taxonomy of the complete genus and the relation to other genera of the 'diacrodian' plexus.

All specimens with a single apical process are here classified as *Dicrodiacrodium ancoriforme* emend., because the biometric studies clearly indicate that there are no arguments for splitting them into several species and varieties. The overloaded original diagnosis of *D. ancoriforme* in Burmann

(1968) is here emended and simplified to include all species and varieties of *Dicrodiacrodium* with a single apical process.

No excystment structure of *Dicrodiacrodium* has yet been observed.

Dicrodiacrodium ancoriforme Burmann, 1968 emend. nov.

Plate 1

ǂ = specimen(s) not illustrated
? = attribution to the species questionable
?? = attribution to the species very questionable
non = attribution to the species incorrect

Bold numbers after each synonym refer to Text-figures 4–5.

1968 *Dicrodiacrodium ancoriforme* Burmann, p. 643, pl. 3, fig. 1; pl. 7, fig. 2a–c. (**1**)
1968 *Dicrodiacrodium ancoriforme* var. *minutum* Burmann, p. 644, pl. 5, fig. 5. (**1**)
1968 *Dicrodiacrodium normale* Burmann, p. 644, pl. 3, fig. 2. (**1**)
1968 *Dicrodiacrodium normale* var. *doliiforme* Burmann, p. 645, pl. 3, figs 5–6. (**1**)
1968 *Dicrodiacrodium normale* var. *longiusculum* Burmann, p. 645, pl. 7, fig. 1a–c. (**1**)
1968 *Dicrodiacrodium normale* var. *cylindricum* Burmann, p. 645, pl. 3, figs 3–4; pl. 7, fig. 3. (**1**)
ǂ 1970 *Dicrodiacrodium normale* Burmann, 1968 (*cf.*) [*sic*]; Martin *et al.*, p. 344. (**2**)
ǂ 1970 *Dicrodiacrodium normale* Burmann; Martin *et al.*, p. 347. (**2**)
1973*a* *Dicrodiacrodium normale* Brm.; Burmann, p. 760, pl. 1, fig. 1a–b. (**3**)
?? 1973*a* *Dicrodiacrodium normale* Brm.; Burmann, pl. 2, fig. 2a–d. (**3**)
1973*b* *Dicrodiacrodium normale* Brm.; Burmann, p. 13, pl. 2, figs 1–2; pl. 3, fig. 2. (**4**)
non 1974*a* *Dicrodiacrodium ancoriforme* Burmann; Cramer *et al.*, p. 190, pl. 28, figs 13–14, 20. (**5**)
?? 1974*a* *Arbusculidium filamentosum* (Vavrdová 1965) [*sic*]; Cramer *et al.*, p. 190, pl. 28, figs 15–16, 18–19, 23. (**5**)
1974*b* *Dicrodiacrodium ancoriforme* Burmann; Cramer *et al.*, p. 64, pl. 26, fig. 18. (**6**)
ǂ 1974 *Dicrodiacrodium normale* Burmann; Jardiné *et al.*, p. 108, fig. 3:53. (**7**)
1974 *Dicrodiacrodium ancoriforme* Burm.; Lefort and Deunff, p. 77, pl. 1, figs 10, 14, 17. (**8**)
1974 *Dicrodiacrodium normale* Burm.; Rauscher, p. 106, pl. 7, fig. 1. (**9**)
?? 1975 *Dicrodiacrodium normale* Burm.; Deunff and Massa, p. 22, pl. 1, fig. 20. (**10**)
1976 *Dicrodiacrodium ancoriforme* n. sp. [*sic*]; Burmann, table 1:26. (**11**)
1976 *Dicrodiacrodium ancoriforme* var. *minuta* n. var. [*sic*]; Burmann, table 1:27. (**11**)
1976 *Dicrodiacrodium normale* n. sp. [*sic*]; Burmann, p. 51, table 1:22. (**11**)
1976 *Dicrodiacrodium normale* var. *breviuscula* Burmann, p. 51, table 1:21 (nomen nudum). (**11**)
1976 *Dicrodiacrodium normale* var. *longiuscula* n. var. [*sic*]; Burmann, table 1:23. (**11**)

EXPLANATION OF PLATE 1

Figs 1–9. *Dicrodiacrodium ancoriforme* Burmann, emend. nov. 1, Institut für Geologie und Paläontologie, Technische Universität Berlin, sample WJZDW-14, slide C2, England Finder graticule co-ordinates N 42/1; Dawan Formation, Wangjiazei section, south-east China; *Undulograptus sinodentatus*/*Didymograptus nexus* graptolite Zone; ×850. 2, Palaeontological Institute, Charles University, Prague, slide S-2. S-2/A, England Finder graticule co-ordinates S 55/4; Šárka Formation, Drahouš section, Bohemia; *Corymbograptus retroflexus* graptolite Zone; damaged specimens; ×850. 3–9, Services Associés de Paléontologie de l'Université de Liège. 3, 6, 9, Boujad-9 borehole, Tadla Basin, Morocco; *Desmochitina bulla* chitinozoa Zone; ×750. 3, slide 20542, England Finder graticule co-ordinates L42/3; depth 511 m. 6, slide 20539, England Finder graticule co-ordinates F 38/1; depth 360 m. 9, slide 20540, England Finder graticule co-ordinates S 38/3–4; depth 360 m. 4, 7, Rügen 5 borehole, north-east Germany, depth 3287·1 m; ?*Didymograptus artus* graptolite Zone; ×750. 4, slide 22821, England Finder graticule co-ordinates L 43. 7, slide 22804, England Finder graticule co-ordinates Y 47/4–Y 48/3. 5, slide 22835, England Finder graticule co-ordinates P 43/3; Binz 1 borehole, north-east Germany, depth 5117·1 m; *Didymograptus murchisoni* graptolite Zone; ×750. 8, slide 22250b, 22666, England Finder graticule co-ordinates G34/2; Sart-Bernard section, Belgium; Huy Formation, *Didymograptus artus* graptolite Zone; ×1000.


1


2


3


4


5


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7


8


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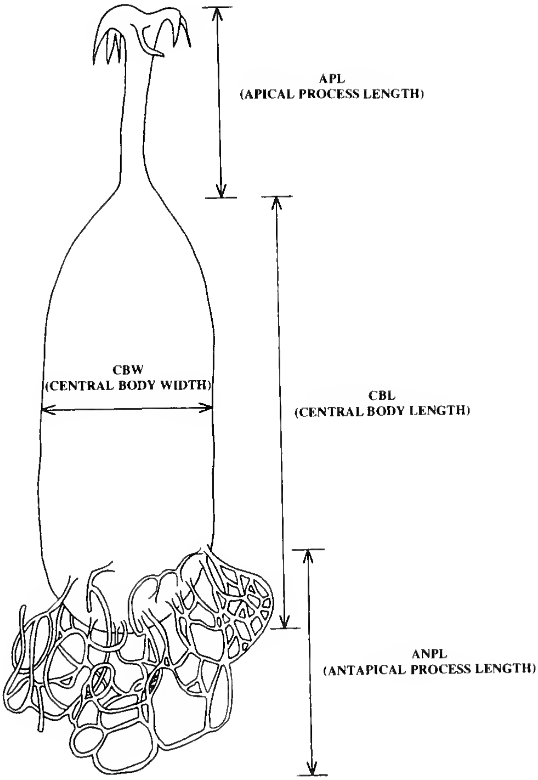
SERVAIS *et al.*, *Dicrodiacrodium*

1976 *Dicrodiacrodium normale* var. *cylindrica* n. var [*sic*]; Burmann, table 1:24. (**11**)
1976 *Dicrodiacrodium normale* var. *doliiformis* n. var. [*sic*]; Burmann, table 1:24. (**11**)
1976 *Dicrodiacrodium ancoriforme* Burmann 1968; Eisenack *et al*., p. 205. (**12**)
1976 *Dicrodiacrodium ancoriforme minutum* Burmann; Eisenack *et al*., p. 207. (**12**)
1976 *Dicrodiacrodium normale* Burmann; Eisenack *et al*., p. 215. (**12**)
1976 *Dicrodiacrodium normale cylindricum* Burmann; Eisenack *et al*., p. 217. (**12**)
1976 *Dicrodiacrodium normale doliiforme* Burmann; Eisenack *et al*., p. 219. (**12**)
1976 *Dicrodiacrodium normale longiusculum* Burmann; Eisenack *et al*., p. 221. (**12**)
ǂ 1976 *Dicrodiacrodium normale* Burmann, Vavrdová, p. 62. (**13**)
ǂ 1977 *Dicrodiacrodium ancoriforme* Burmann; Díez and Cramer, p. 3. (**14**)
ǂ 1977 *Dicrodiacrodium ancoriforme minutum* Burmann; Díez and Cramer, p. 3. (**14**)
ǂ 1977 *Dicrodiacrodium normale* Burmann; Díez and Cramer, p. 17. (**14**)
ǂ 1977 *Dicrodiacrodium normale cylindricum* Burmann; Díez and Cramer, p. 17. (**14**)
ǂ 1977 *Dicrodiacrodium normale doliiforme* Burmann; Díez and Cramer, p. 17. (**14**)
ǂ 1977 *Dicrodiacrodium normale longiusculum* Burmann; Díez and Cramer, p. 17. (**14**)
1977 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 110, pl. 2, fig. 3; text-fig. 3. (**15**)
1978 *Dicrodiacrodium normale* Burmann; Kalvacheva, p. 306, pl. 1, fig. 1. (**16**)
ǂ 1978 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 72. (**17**)
1979 *Dicrodiacrodium ancoriforme* Burmann; Cramer and Díez, p. 42, fig. 58. (**18**)
ǂ 1979 *Dicrodiacrodium normale*; Cramer and Díez, p. 127. (**18**)
ǂ 1979 *Dicrodiacrodium ancoriforme* Burmann; Martin and Rickards, p. 191. (**19**)
?? 1979 *Dicrodiacrodium* cf. *ancoriforme* Burmann; Martin and Rickards, p. 193, pl. 1, fig. 20. (**19**)
ǂ 1979 *Dicrodiacrodium normale* Burmann; Vanguestaine, p. 251. (**20**)
?? 1979 *Dicrodiacrodium* cf. *normale* Burmann; Vanguestaine, p. 249, pl. 5, fig. 11. (**20**)
1982 *Dicrodiacrodium normale* Burmann; Martin, p. 30, pl. 1, fig. 4. (**21**)
1982 *Dicrodiacrodium normale* Burmann; Turner, p. 122, pl. 17, fig. 5. (**22**)
ǂ 1982*a* *Dicrodiacrodium normale* Burmann; Vavrdová, p. 149. (**23**)
ǂ 1982*b* *Dicrodiacrodium normale*; Vavrdová, p. 338. (**24**)
1984 *Dicrodiacrodium ancoriferum* Burmann [*sic*]; Downie, p. 14, text-fig. 5: 59. (**25**)
1984 *Dicrodiacrodium normale* Burmann; Downie, p. 14, fig. 5:60. (**25**)
?? 1985 *Dicrodiacrodium normale* Burmann; Fournier-Vinas, p. 809, pl. 1, fig. 4. (**26**)
ǂ 1986 *Dicrodiacrodium normale* Burmann; Kalvacheva, p. 40. (**27**)
ǂ 1986 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 355. (**28**)
ǂ 1988 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 8. (**29**)
ǂ 1989 *Diacrodium* cf. *normale* Burmann [*sic*]; Steemans, p. 305. (**30**)
ǂ 1989 *Diacrodium normale* Burmann [*sic*]; Steemans, p. 331. (**30**)
? 1989 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 404, text-fig. 1:L5. (**31**)
ǂ 1990 *Dicrodiacrodium normale* Burmann; Fensome *et al*., p. 191. (**32**)
ǂ 1990 *Dicrodiacrodium ancoriforme* Burmann; Fensome *et al*., p. 191. (**32**)
ǂ 1990 *Dicrodiacrodium ancoriforme* var. *ancoriforme* Burmann; Fensome *et al*., p. 191. (**32**)
ǂ 1990 *Dicrodiacrodium ancoriforme* var. *minutum* Burmann; Fensome *et al*., p. 191. (**32**)
ǂ 1990 *Dicrodiacrodium normale* var. *cylindricum* Burmann; Fensome *et al*., p. 191. (**32**)
ǂ 1990 *Dicrodiacrodium normale* var. *doliiforme* Burmann; Fensome *et al*., p. 191. (**32**)
ǂ 1990 *Dicrodiacrodium normale* var. *longiusculum* Burmann; Fensome *et al*., p. 191. (**32**)
ǂ 1990 *Dicrodiacrodium normale* var. *normale* Burmann; Fensome *et al*., p. 191. (**32**)
ǂ 1990 *Dicrodiacrodium normale* Burmann [*sic*]; Ghavidel-Syooki, p. 217. (**33**)
ǂ 1990 *Dicrodiacrodium* spp.; Molyneux, p. 616. (**34**)
ǂ 1990*a* *Dicrodiacrodium normale* Burmann; Vavrdová, p. 238. (**35**)
ǂ 1991 *Dicrodiacrodium ancoriforme* Burmann; Fensome *et al*., p. 4. (**36**)
ǂ 1991 *Dicrodiacrodium normale* Burmann; Fensome *et al*., p. 66. (**36**)
1991 *Dicrodiacrodium* sp.; Servais, p. 240, pl. 1, fig. 10. (**37**)
1992 *Dicrodiacrodium ancoriforme minutum* Burmann; Millward and Molyneux, p. 81, fig. 3j. (**38**)
ǂ 1992 *Dicrodiacrodium normale* Burmann 1970 [*sic*]; Servais and Maletz, p. 272. (**39**)
ǂ 1993 *Dicrodiacrodium normale* Burmann; Vavrdová, p. 128. (**40**)
ǂ 1994 *Dicrodiacrodium* spp.; Servais, p. 574. (**41**)
ǂ 1994 *Dicrodiacrodium ancoriforme-normale* Burmann group; Servais *et al*., p. 37. (**42**)
ǂ 1994 *Dicrodiacrodium* spp.; Fatka *et al*., p. 35. (**43**)



TEXT-FIG. 1. Measurement parameters of *Dicrodiacrodium ancoriforme*.

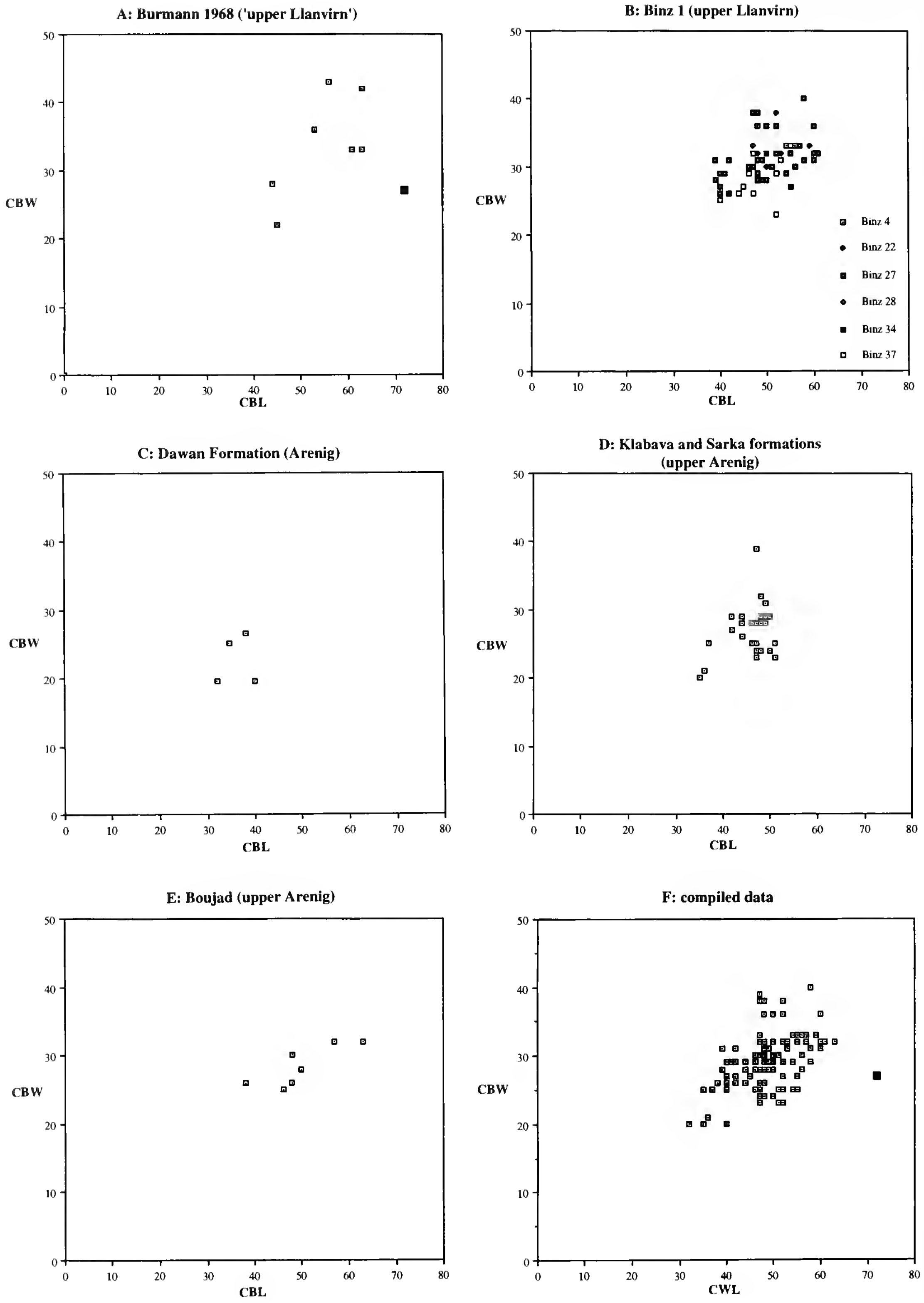
Holotype. Burmann (1968, pl. 3, fig. 1; pl. 7, fig. 2a–c). S 1880/65 (3,5/106,7).

Type locality. Borehole Rügen 3h, north-east Germany. Sample 117 ('upper Llanvirn'), exact depth and position of the sample unknown.

Original diagnosis. 'Heteropolar differenzierter Zentralkörper länglich-oval, am apikalen Pol in einen starken, sich nicht verjüngenden, jedoch relativ kurzen Einzelforsatz übergehend, der sich terminal ankerartig in mehrere (*c*. 6) stachelförmige Fortsatzanhänge aufspaltet. Das Längenverhältnis Fs (und Mh): Zk ist sehr gering. Eine Basisfassung des apikalen Fortsatzes ist nicht erkennbar, wohl aber stärkere Pigmentierung an der Ansatzstelle. Der gewölbte antapikale Pol trägt ein blasenartiges Maschenwerk unterschiedlicher Maschengrösse. Das Netzwerk besteht aus feinen ($d < 1$ μm), relativ kurzen Bögen und gleichartigen Stützstreben. Dadurch ist das Netz recht straff und gut erhalten. Stützfortsätze fehlen' (Burmann 1968).

Emended diagnosis. Heteropolar central body of variable oblong–oval to cylindrical shape, smooth or with longitudinal parallel ribs. The apical pole bears a single process of variable length, not tapering, with or without a basal plug, distally splitting from a single point into tapering, unbranched, barb-shaped pinnae, *c*. four to eight in number. The antapical pole bears a dense anastomosing network of fine threads with or without supporting rods.

Measurements (Text-fig. 1).
Central body length (CBL) 25–61 μm.
Central body width (CBW) 19–44 μm.
Apical process length (APL) 6–28 μm.


A: Burmann 1968 ('upper Llanvirn')
B: Binz 1 (upper Llanvirn)
C: Dawan Formation (Arenig)
D: Klabava and Sarka formations (upper Arenig)
E: Boujad (upper Arenig)
F: compiled data
CBW
CBL
CWL
0
10
20
30
40
50
60
70
80
Binz 4
Binz 22
Binz 27
Binz 28
Binz 34
Binz 37

Apical process width 2–4 μm.
Terminal pinnae up to 8 μm long.
Antapical process length (ANPL) up to 40 μm long.

Remarks. *D. ancoriforme* is very easy to recognize. Its characteristic shape, with one single apical process, is so typical that a scanning electron microscope is not needed for its determination.

Burmann (1968) erected two species (*D. ancoriforme* and *D. normale*) and four varieties, without autonyms, to describe her specimens. According to Burmann (1968), *D. ancoriforme* has a rather short apical process, whereas that of *D. normale* is longer. She subdivided *D. ancoriforme*, erecting var. *minutum* for specimens of smaller size. *D. normale* was divided into var. *cylindricum* for specimens with a cylindrical central body, var. *doliiforme* for those with a barrel-shaped central body, and var. *longiusculum*, for specimens with a very long apical process (Burmann 1968). This splitting into six different taxa appears exaggerated and may lead to the supposition that Burmann (1968) investigated very few specimens. Subsequent workers generally followed Burmann's (1968) classification scheme and determined their specimens at the species and even at the varietal level.

It is evident that the ratio between the central body length and the apical process length is the main diagnostic feature at the species level. However, Burmann's (1973*a*, 1973*b*) determinations of *D. normale* do not accord with the original diagnosis: the apical process length of the figured specimens is either too small or was not correctly measured (see below). Burmann (1973*a*, pl. 2, fig. 2a–d) even determined a specimen as *D. normale* with an apical process which is broken. Cramer *et al.* (1974*a*), Deunff and Massa (1975), Vanguestaine (1979), Martin *in* Martin and Rickards (1979) and Fournier-Vinas (1985) also determined specimens with broken processes at the species level.

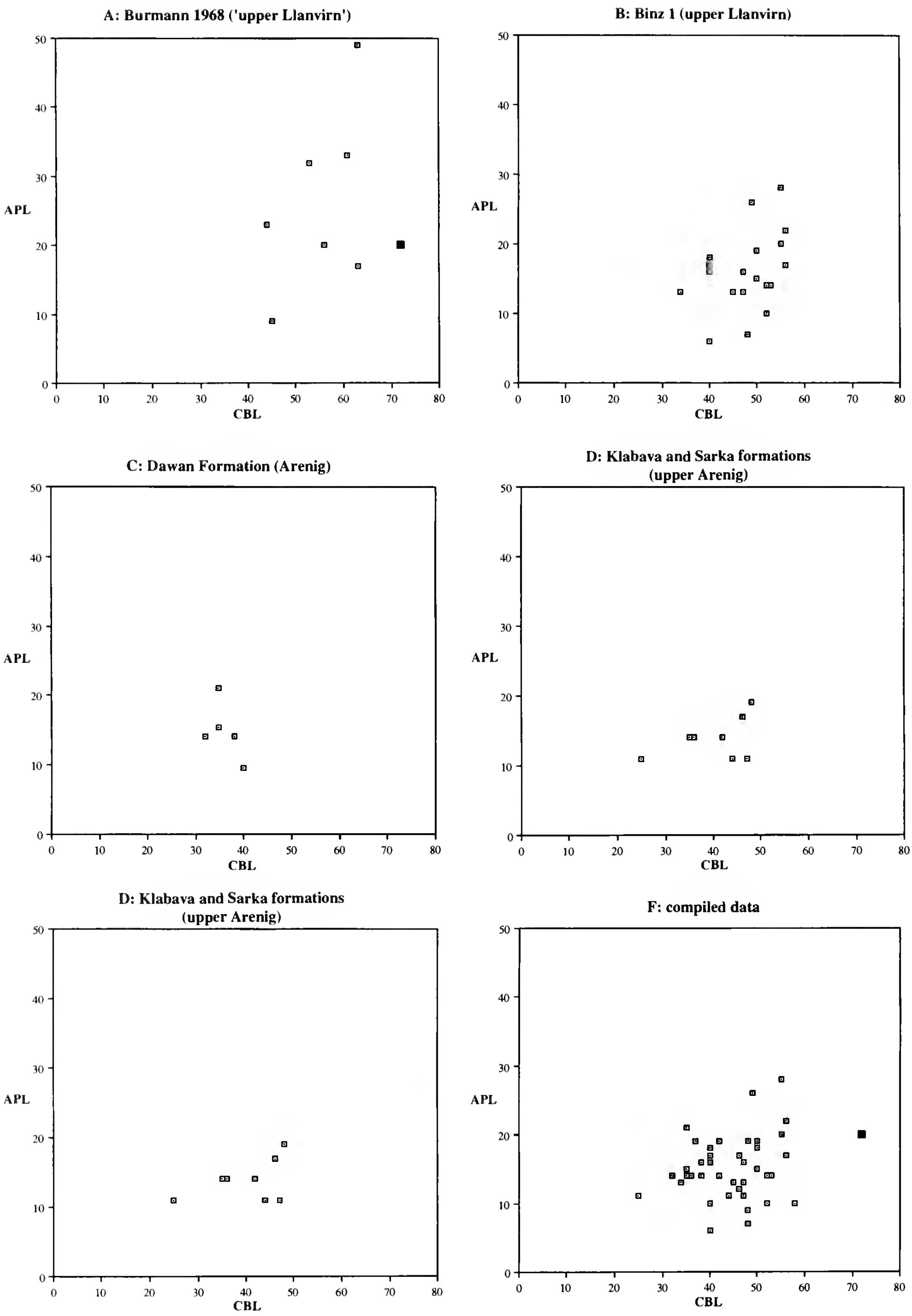
Biometric investigations. Cramer *et al.* (1974*a*, p. 188) noted that they found 'all kinds of transitional forms' in the Moroccan material and that a distinction between Burmann's taxa was difficult.

In the present work, large populations of *Dicrodiacrodium* specimens with a single apical process were measured to understand the relations between Burmann's taxa: 66 German, 33 Bohemian, 14 Belgian, 11 Chinese, and 9 Moroccan specimens were investigated. The following parameters were measured (Text-fig. 1): the central body length (CBL), the central body width (CBW), the apical process length (APL) and the antapical process length (ANPL). In addition, the width of the apical process, and the length of the terminal pinnae were also measured.

Text-figure 2A–F shows the scatter diagrams of CBL against CBW, Text-figure 3A–F the scatter diagrams of CBL against APL. The data plotted include Burmann's (1968) measurements, taken from the original descriptions (including that for the holotype), and new measurements of specimens from the upper Llanvirn of borehole Binz 1 (Germany), the Arenig Dawan Formation (South China), the upper Arenig of the Klabava and Šárka formations (Czech Republic) and the upper Arenig of borehole Boujad-9 (Morocco).

All scatter diagrams show that the data of each individual area (Text-figs 2B–E, 3B–E) are reasonably concentrated in clusters. Only minor differences between the data from different areas have been observed. The scatter diagrams of the compiled data (Text-figs 2F, 3F) indicate that all specimens are clearly concentrated in a single cluster. There are no arguments for splitting the specimens into several units, using either the ratio of CBL to CBW, or the ratio of CBL to APL. On the contrary, Text-figure 2F clearly shows that all intermediates between specimens with small and large central bodies exist. Text-figure 3F illustrates the presence of a continuous transition between specimens with short and long processes. Therefore, it appears evident that only one name should be used for all specimens: *C. ancoriforme*.

TEXT-FIG. 2. Scatter diagram of central body length (CBL) against central body width (CBW) for specimens of *Dicrodiacrodium ancoriforme* in Burmann (1968) (A); and samples from borehole Binz 1, Germany (B); the Dawan formation, China (C); the Klabava and Šárka Formations, Czech Republic (D); borehole Boujad-9, Morocco (E); and compiled data of all specimens investigated in the present study (F). The holotype of Burmann (1968) is represented by a larger black square in figures A and F.


A: Burmann 1968 ('upper Llanvirn')
B: Binz 1 (upper Llanvirn)
C: Dawan Formation (Arenig)
D: Klabava and Sarka formations (upper Arenig)
D: Klabava and Sarka formations (upper Arenig)
F: compiled data
APL
CBL
0
10
20
30
40
50
60
70
80

The only data which are not in accord with the clusters of Text-figures 2F and 3F are those from the original description of Burmann (Text-figs 2A, 3A). Neither do Burmann's (1968) measurements correspond with the data from Binz in the type area (Text-figs 2B, 3B).

There is, however, a very simple explanation for Burmann's exaggeration of some of her CBL, CBW, and APL values: Burmann (1968, 1973*a*, 1973*b*) worked with thin sections, not palynological slides. On specimens which were partly fragmented, she measured the total length (of CBL, CBW, and APL) by also including the interstices in her values. The APL of the holotype of *D. normale* var. *longiusculum*, for example, was measured as 49 μm, which is a value which has never been recorded in other populations; the longest apical process found in the present investigation is only 28 μm long (borehole Binz, sample 28). However, it is possible that long, slender apical processes were not observed after Burmann's (1968) description from thin sections, because poorly preserved material commonly breaks during palynological preparation treatment.

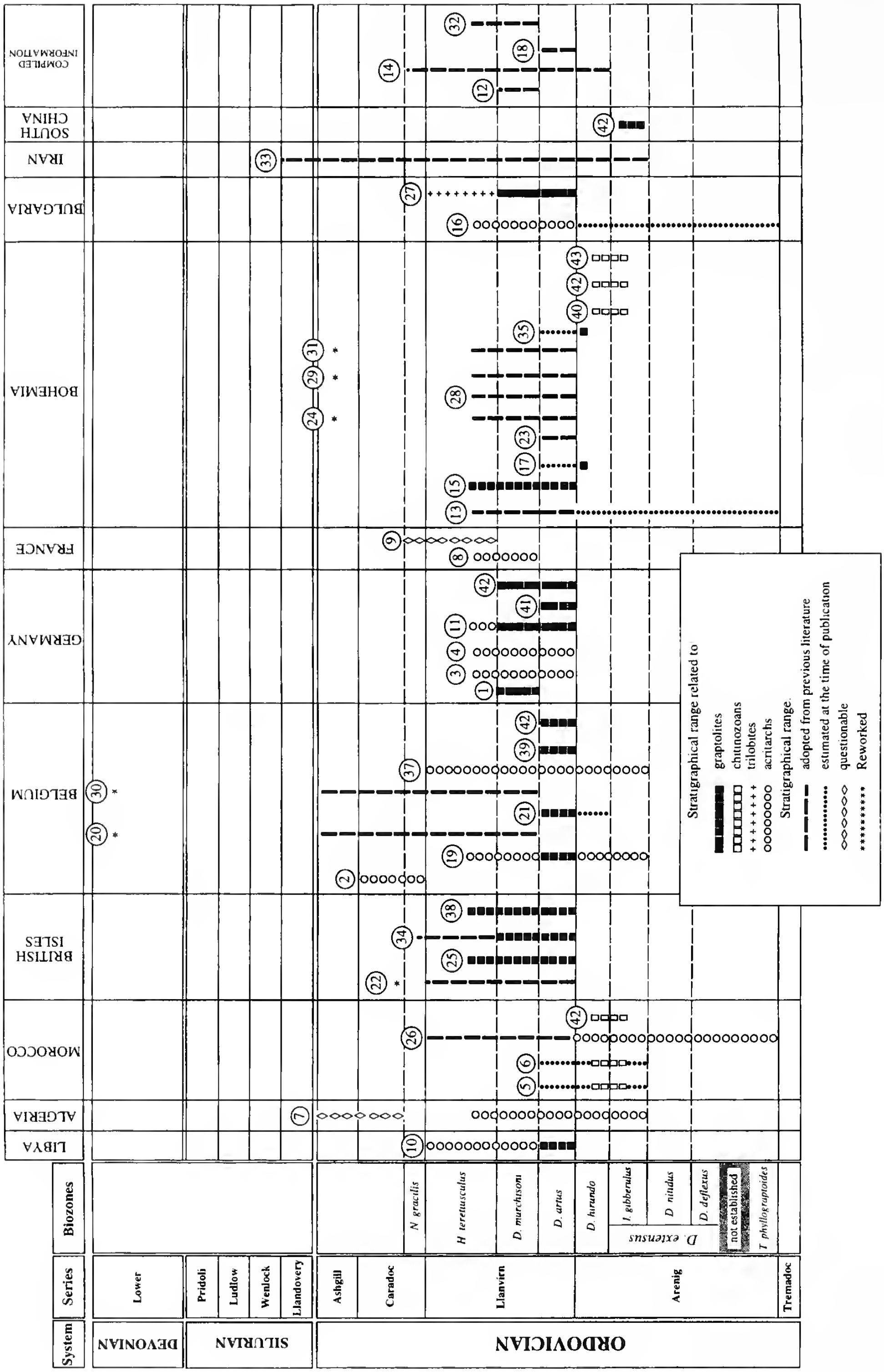
The holotype of *D. ancoriforme* emend. nov. is unfortunately also outside the clusters obtained in the present study (Burmann indicated a CBL of 72 μm, a CBW of 27 μm and a APL of 20 μm). The specimen of Burmann (1968) which corresponds more or less to the mean of the values (CBL about 45 μm; CBW about 30 μm, and APL about 15 μm) is the paratype of *D. normale* var. *cylindricum*. The problem of the holotype being outside of the measured range found in this study is not in contradiction with the attribution of all specimens to the taxon *D. ancoriforme*, because, according to Article 7.3 of the International Code of Botanical Nomenclature (Greuter *et al.* 1994), 'the nomenclatural type is not necessarily the most typical or representative element of a taxon'.

Stratigraphical range. Text-figure 4 shows the stratigraphical distribution of *D. ancoriforme*, based on a review of the literature. The stratigraphical ranges are those indicated by the original authors. They must be regarded critically, because some of them were not correct; others are no longer justified or still questionable. The ranges indicated by the authors were either based on other fossil groups, such as graptolites (e.g. Burmann 1968), chitinozoans (e.g. Fatka *et al.* 1994), and trilobites (e.g. Kalvacheva 1986), or were the result of acritarch evidence only (e.g. Lefort and Deunff 1974). In several works, the indicated stratigraphical range was adopted from previous publications (e.g. Downie 1984), or estimated by the author at the time of the publication, but not precisely documented (e.g. Vavrdová 1976). Some ranges indicated in the literature should be considered as questionable, because the levels bearing the species were insecurely dated (e.g. Rauscher 1974). In other papers, the occurrence of the species is the result of reworking into younger sediments (e.g. Steemans 1989). Finally, only few occurrences of the species are adequately dated and, therefore, only few of the indicated ranges can be justified.

Initially, *D. ancoriforme* was considered to be an indicator for rocks of late Llanvirn age (e.g. Burmann 1973*a*, 1973*b*; Lefort and Deunff 1974). Subsequently, the species was for a long time considered to be typical of Llanvirn or younger rocks, because the species had never been recorded in pre-Llanvirn rocks in the British Isles (Molyneux 1990), and because undisputed occurrences in the Arenig had not been published. However, such occurrences in the Arenig are now known. In Morocco, the samples of Cramer *et al.* (1974*a*, 1974*b*) from 'upper Arenigian to lower Llanvirnian' rocks have recently been redated by chitinozoans as being of late Arenig age (Soufiane and Achab 1993).

In Bohemia, precise biostratigraphical information on the Arenig–Llanvirn interval is missing from the numerous publications of Vavrdová (1976–1993). Recent studies on the Arenig–Llanvirn boundary indicate that the lowermost part of the Šárka Formation is of late Arenig age (Kraft and Kraft 1993, fig. 2). In the Bohemian sequence, *D. ancoriforme* first appears in the late Arenig

TEXT-FIG. 3. Scatter diagram of central body length (CBL) against apical process length (APL) for specimens of *Dicrodiacrodium ancoriforme* in Burmann (1968) (A); and samples from borehole Binz 1, Germany (B); the Dawan formation, China (C); the Klabava and Šárka Formations, Czech Republic (D); borehole Boujad-9, Morocco (E); and compiled data of all specimens investigated in the present study (F). The holotype of Burmann (1968) is represented by a larger black square in figures A and F.


System
Series
Biozones
DEVONIAN
SILURIAN
ORDOVICIAN
Lower
Pridoli
Ludlow
Wenlock
Llandovery
Ashgill
Caradoc
Llanvirn
Arenig
Tremadoc
N. gracilis
H. teretiusculus
D. murchisoni
D. artus
D. hirundo
I. gibberulus
D. nitidus
D. deflexus
D. extensus
not established
T. phyllograptoides
LIBYA
ALGERIA
MOROCCO
BRITISH ISLES
BELGIUM
GERMANY
FRANCE
BOHEMIA
BULGARIA
IRAN
SOUTH CHINA
COMPILED INFORMATION
Stratigraphical range related to
graptolites
chitinozoans
trilobites
acritarchs
Stratigraphical range.
adopted from previous literature
estimated at the time of publication
questionable
Reworked
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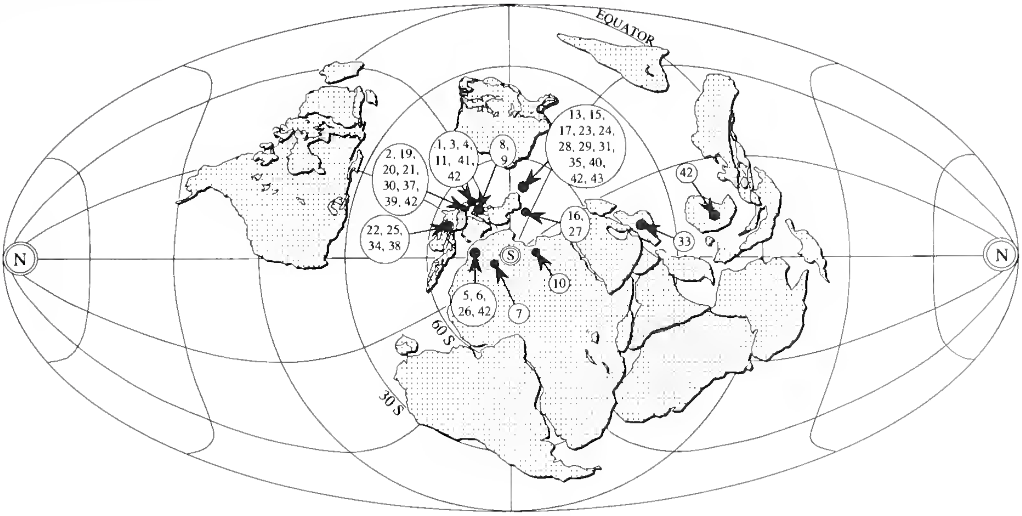

TEXT-FIG. 5. Palaeogeographical map for the Early Ordovician (Arenig), modified after Scotese and Denham (1988) and Torsvik and Trench (1991), showing the geographical distribution of *Dicrodiacrodium ancoriforme*. Numbers correspond with those listed in the synonymy.

D. bulla chitinozoan Zone in the Mýto section (Vavrdová 1993; Fatka *et al.* 1994) and is also present in the lowermost layers of the Šárka Formation in the Drahouš section.

The first appearance of *D. ancoriforme* in the Chinese Dawan Formation is in the *Undulograptus sinodentatus*/*Didymograptus nexus* graptolite Zone (Brocke, unpublished data), which can be correlated approximately with the British Arenig *Isograptus gibberulus* Biozone (Wang *et al.* 1992).

All other previously cited occurrences in the Arenig are not proven and are mainly dated on acritarch evidence only. Therefore, the First Appearance Datum of *D. ancoriforme* is in the *U. sinodentatus*/*D. nexus* graptolite Zone in South China.

The species is frequently recorded in rocks of Llanvirn age. Younger occurrences have not been clearly documented. The species is considered to be reworked in the Upper Ordovician (e.g. Turner 1982; Vavrdová 1982*b*) and Lower Devonian (Vanguestaine 1979; Steemans 1989), but the upper range of the species is as yet unknown.

Palaeogeographical distribution. Published information about the distribution of *D. ancoriforme* is plotted on a palaeogeographical map of the Early Ordovician (Text-fig. 5). The species has only been recorded in areas of cold to temperate water-masses in the southern hemisphere. It is widely distributed in sediments from Gondwana (Morocco, Algeria, Libya) and peri-Gondwana (British Isles, Belgium, Germany, France, Bohemia and Bulgaria). So far, the species has only been recorded from two areas which are supposed to be at a slightly lower latitude (Iran and South China), but it has never been cited from warmer water mass provinces, such as Baltica and Laurentia. *D. ancoriforme* can therefore be considered as typical of the cold to temperate Gondwanan and peri-Gondwanan ('Mediterranean') Palaeoprovince.

TEXT-FIG. 4. Stratigraphical distribution of *Dicrodiacrodium ancoriforme*, based on a literature review. Numbers correspond with those in the synonymy list. The stratigraphical ranges are those indicated by the authors. Some are questionable. For explanation, see text. Stratigraphical units and zones are modified from Rushton (1990), Fortey and Owens (1991), Wang *et al.* (1992), Cooper *et al.* (1995) and Fortey *et al.* (1995).

CONCLUSIONS

Biometric investigations (bivariate analyses) on *Dicrodiacrodium* specimens with a single apical process from Belgian, Chinese, Czech, German (type area), and Moroccan assemblages, show a wide variability and indicate clearly that splitting the specimens into two species and six varieties is not justified. A continuous transition exists between both small to long central bodies and short to long processes. Therefore, all specimens with a single apical process are classified as *D. ancoriforme*, of which the diagnosis is emended.

The species is very easy to recognize. It appears in the middle Arenig and is common in Llanvirn rocks. The top of its stratigraphical range is not certain, due to possible reworking. The palaeogeographical distribution of the species is limited to the cold to temperate peri-Gondwanan and Gondwanan Palaeoprovince.

The biometric investigation leads to the following conclusions.

1. Biometric investigations, generally neglected in acritarch taxonomy, are vital to the understanding of an acritarch taxon.
2. It appears evident that small populations cannot be used for the formal description of a new taxon. However, most described acritarch species are based on a very limited number of specimens. There should be a debate amongst a wider group of acritarch workers to consider a minimum number of specimens required for the description of a new taxon.
3. The description of (new) acritarch taxa necessitates absolutely a study of variability.
4. The study of assemblages from different areas and different stratigraphical horizons gives a more complete view of an acritarch taxon.
5. *Dicrodiacrodium ancoriforme*, with its easily measurable parameters, may serve as a typical example for future studies on acritarch biometrics with the aim of understanding acritarch variability and relationships between predefined taxa. The bivariate plots used for *Dicrodiacrodium* seem adequate for demonstrating the extent of intraspecific variation. In future studies the application of multivariate analyses should be tested also.

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TAXONOMY AND DISTRIBUTION OF THE UPPER CARBONIFEROUS NON-MARINE BIVALVE *CARBONICOLA ALDAMII*

by P. J. BRAND

ABSTRACT. Records of non-marine bivalves similar to *Carbonicola aldamii* (Brown) are listed and, where possible, specimens are figured. This species, originally described from Whitehaven, Cumbria has not so far been recorded again in collections from that district. Most known specimens referred to the species come from the Midlothian and Douglas coalfields of Scotland.

THE non-marine bivalve species described by Brown (1843) have been used over many years by workers on the Westphalian faunas of Britain, despite the fact that the type specimens must be presumed to be lost (Trueman and Weir 1947, p. 23). The interpretation of some of these described species, including *Carbonicola aldamii* (*aldamae*) (Trueman and Weir 1947; Weir 1968), was left in abeyance. Brown, in his original description, referred the species *aldamii* to the genus '*Pachyodon*', later transferring it to '*Unio*' (Brown 1849, p. 179). It was Trueman and Weir (1947, p. 56, pl. 9, figs 15–17) who placed the species in the genus *Carbonicola*. Despite the apparent loss of the type specimens it seems likely that Brown's figure (Pl. 1, fig. 2) is accurate, a conclusion reached by Eagar and Williamson (1970, p. 221) in their discussion on other material from Shedden, near Burnley, a locality from which Brown also described specimens in 1843. It has been suggested (J. D. D. Smith, pers. comm.) that the figure and description given by Brown is in itself sufficient to distinguish the species.

SYSTEMATIC PALAEONTOLOGY

Repositories. The specimens described and figured below are housed as follows: GSE, British Geological Survey, Edinburgh, E 7657, E 7664, E 7667, EU 8361, GSE 13706; GSM, British Geological Survey, Keyworth, FMT 550; HM, Hunterian Museum, Glasgow, S 6341, S 7103; NMW, National Museum and Gallery of Wales, 70. 17G. 29a.

Phylum MOLLUSCA
Class BIVALVIA Linné, 1758
Family ANTHRACOSIIDAE Amalitsky, 1892

Genus CARBONICOLA (*pars*) McCoy *in* Sedgwick and McCoy, 1855

Carbonicola aldamii (Brown) Trueman and Weir

Plate 1, figures 1–8

1843 *Pachyodon aldamii* Brown, p. 394, pl. 16*, fig. 3.
1849 *Unio aldamii* (Brown); Brown, p. 179, pl. 73, fig. 18.
1947 *Carbonicola aldamae* (Brown); Trueman and Weir, p. 56, pl. 9, fig. 17 [cop. Brown 1843, pl. 16*, fig. 3], *non* pl. 9, figs 15–16.

Holotype. Specimen figured by Brown (1843) and now believed lost.

Diagnosis. Subcompressed, flexuose and subtriangular; umbones subcentral, very obtuse, set 3 mm apart; hinge line slightly arcuated; anterior side descending abruptly from the umbones, beneath

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which it is slightly rounded with a flexure below, somewhat produced on the margin immediately under the umbones; posterior side gently sloping and rounded, with a shallow furrow emanating from below the umbones, and rapidly widening, terminates on the base; basal line flexuose. Length is 41 mm; breadth 54 mm; thickness 25 mm. The greatest thickness of the shell is at the middle of the discs, from where it rapidly thins to the margins (adapted from Brown 1843, p. 394).

Description. The shell outline is more an irregular trapezium than subtriangular and the shells are tumid but not strongly so. They become flattened towards the posterior margins. The umbones are subcentral or nearer the anterior third of the shell length. The shell material is thick in the umbonal region and thins towards the margins of the shell. The ventral margin shows a flexuosity towards the posterior which Trueman and Weir (1947, p. 57) suggested may be due to crushing. However, in all the specimens seen from Scottish locations this feature is present and is as marked as it is in Brown's original figure, serving to distinguish this form from other elements of the associated fauna. The shallow furrow emanating from below the umbones mentioned by Brown arises posterior to the umbones and widens towards the venter (Pl. 1, figs 1–2, 5, 7). It is, however, less obvious on internal moulds (Pl. 1, figs 4, 6, 8). Internal moulds of this species, as with some other species of *Carbonicola*, are unreliable guides to the external morphology, in part because of the varying thickness of the shell material, particularly in the umbonal region. Neither Brown nor Trueman and Weir were able to figure any examples of the interior or the hinge. That figured here (Pl. 1, fig. 3) shows that the hinge is typical of species of *Carbonicola* as illustrated by Maclennan (1944, pl. 1), and Eagar (1946, pl. 1). Thus there is a striated pit in the right valve anterior to a low striated tooth or ridge which is succeeded to the posterior by a shallow hollow. The narrow external ligament notch extends over this area on the upper surface of the commisure and leads into a broad area on the hinge face which continues and narrows to the posterior. So far, no left valve has been recovered in which the hinge structure is present, and even the right valve figured is incomplete to the posterior so that the posterior musculature is not seen. A deep pit at the extreme anterior marks the position of a major adductor scar whilst minor pedal scars lie posterior to it just below the hinge and anterior to the umbo.

Remarks. Brown (1843), in his original description, described the location for the type specimen of *Carbonicola aldamii* as 'from Coal Shale at Whitehaven'. This is insufficient to indicate what horizon is involved. Examination of the mining records for the Whitehaven area now held by the British Geological Survey at Edinburgh shows that the seam principally worked in the area was the Bannock Band. This seam lies near the base of the lower Similis-Pulchra Chronozone (Calver *in* Taylor 1961, p. 22). Wood (1988, p. 116) recorded that, at the time of Brown's paper, workings had begun in the Six Quarters Coal near the top of the Communis Chronozone (Calver *in* Taylor 1961, p. 20). Abandonment plans for various collieries suggest that this was the lowest seam commonly

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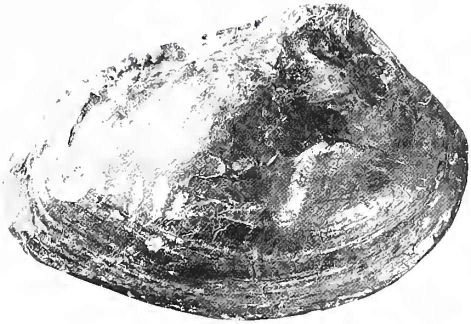
EXPLANATION OF PLATE 1

Figs 1–8. *Carbonicola aldamii* (Brown, 1843); Midlothian Fifteen Foot Coal; Langsettian. 1, GSE E7664; Newcraighall Colliery, Midlothian; right valve, composite mould. 2, reproduction of Brown (1843, pl 16*, fig. 3). 3, GSE EU 8361; Musselburgh Briarthorn Bore 5 at 405 m; interior of incomplete right valve showing part of hinge plate. 4, HM S7103; 274 m east-south-east of pit bottom, Newcraighall Colliery, Midlothian; internal mould of right valve. 5, GSE E7667; as fig. 1, composite mould of right valve. 6, HM S6341; as fig. 4, internal mould of right valve, figured Leitch (1936, pl. 1, fig. c). 7, GSE 13706; Pinkieburn Bore 74 at *c.* 24 m; incomplete composite mould of right valve. 8, GSE E7657; as fig. 1, composite mould of right valve.

Figs 9–11. *Carbonicola* sp. intermediate between *C. robusta* (J. de C. Sowerby, 1840) and *C. rhomboidalis* Hind, 1894. 9, GSM FMT 550; basal *Communis* Zone; stream on right bank of River Giedd, 613 m south-east of Pen-cae-moel, near Cwm Giedd, Breconshire; right valve, figured Trueman and Weir (1947, pl. 9, fig. 16) as *Carbonicola* cf. *aldamae*. 10, reproduction of Pastiels (1960, pl. 14, fig. 14). 11, NMW 70.17G.29a (formerly University College Swansea L 2093); *Lenisulcata* Zone; shales below Farewell Rock; Twrch Valley near Ystradgynlais, Breconshire; composite mould of crushed right valve, figured Trueman and Ware (1932, text-fig. 3c) as *Carbonicola* sp., and Trueman and Weir (1947, pl. 9, fig. 15) as *Carbonicola* cf. *aldamae*.

All × 1.

PLATE 1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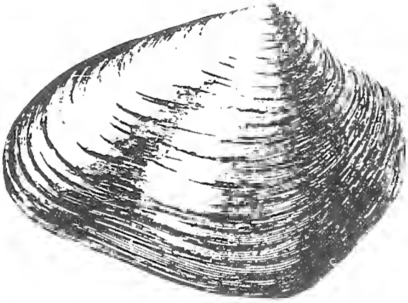
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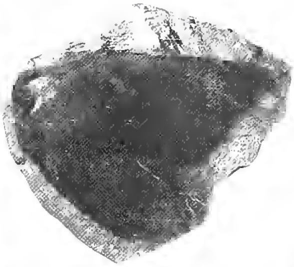
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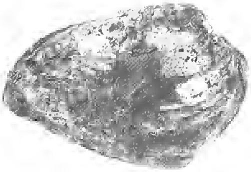
11

BRAND, *Carbonicola*

worked at that date in the area. Whilst it is eminently possible that the form described as *Pachyodon lateralis* (Brown 1843) from the same 'Coal Shale at Whitehaven' could have come from a horizon at about the Bannock Band it is unlikely that the form described as *P. aldamii* came from the same horizon, a conclusion also drawn by Weir (1968, p. 432). Calver (*in* Taylor 1961) examined the bulk of the material from the Cumberland Coalfield in the British Geological Survey collections and did not recognize the species. Further examination of these specimens and new material from the same area by the author has also failed to reveal any topotypic material. The Natural History Museum in London, the Hancock Museum in Newcastle and the Manchester Museum do not have any comparable shells in their collections. The museums at Carlisle, Kendal and Whitehaven are also devoid of these forms. Thus it seems possible that the original description concerning the location of the type specimen may be wrong. There are discrepancies in the listing of locations and specimen donors in the 1843 paper which Brown altered in the 1849 work, and it is possible that the type specimen did not originate from Whitehaven. Specimens similar to the original are to be found in collections from the Musselburgh Fifteen Foot Coal fauna from Dalkeith, and also at Newcraighall from a similar stratigraphical horizon. The location at Dalkeith was familiar to Brown who described *Pachyodon gerardi* from his own collection from there (1843, p. 390). The Musselburgh Fifteen Foot Coal lies near the base of the Communis Chronozone in the Midlothian Coalfield.

Leitch (1936) described the fauna of the Musselburgh Fifteen Foot Coal, with variation diagrams for the forms present. This material has been examined and in the opinion of the author the form labelled Norm β (C) in the diagram (Leitch 1936, pl. 1) represents *C. aldamii*. The specimen is figured here (Pl. 1, fig. 6), and is, in part, an internal mould with traces of external growth lines. It does, however, show the flexuosity of the margin which Trueman and Weir (1947, p. 57) noted as being rare in the genus *Carbonicola* and which appears to have been one of the features of the original specimen. As Leitch (1936, pl. 1) showed, the figured associated fauna consists of forms which may be termed *C.* aff. *browni* (Q–R); *C. polmontensis* (A, S); *C. rhindi* (B); with a few rare shells approaching *C. centralis* (M) together with others which exhibit features placing them between *C. robusta* and *C. rhomboidalis* (J–K). Other specimens shown in the variation diagram which approach *C. aldamii* are those lettered D–F. This paper by Leitch illustrates some of the principles which were used by Trueman and Weir (1946, p. xv) in their discussion of using morphological species of non-marine bivalves (see also Weir 1968, p. xxxviii).

Trueman and Weir (1947, p. 56, pl. 9, figs 15–16) figured shells from Wales which they referred with some doubt to *C. aldamae*. These have been examined and whilst they are similar to each other, neither specimen shows the ventral marginal features of *C. aldamii*. Both may be referred to a form intermediate between *C. robusta* and *C. rhomboidalis* similar to the forms found in the roof of the Fifteen Foot Coal. These are here re-figured (Pl. 1, figs 9, 11) in order to emphasize the differences in shell outline. Pastiels (1960, pl. 14, figs 12–14) also refers a specimen doubtfully to *C. aldamae*. It, too, may be referred to an intermediate form between *C. robusta* and *C. rhomboidalis*. A copy of Pastiels' original figure is added for comparison (Pl. 1, fig. 10). This form appears to have a wider distribution than *C. aldamii* both in geographical and stratigraphical terms and is known from horizons near the top of the Lenisculcata Chronozone to the middle part of the Communis Chronozone throughout the coalfields of Britain and also in Europe.

Occurrence. It appears that Brown's species *aldamii* may be recognized amongst Scottish material and so far has not been recorded again in collections from Cumbria. The species has an unusually restricted distribution in Scotland at the base of the Communis Chronozone, and has been only recorded from the Lothian Coalfield in the roof of the Musselburgh Fifteen Foot Coal and in the Douglas basin in the roof of the Castle Coal; both coalfields are on the southern margins of the Midland Valley of Scotland. Corresponding stratigraphical horizons in the remaining coalfields of Scotland appear devoid of the species.

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THE USE OF LATE JURASSIC CORAL GROWTH BANDS AS PALAEOENVIRONMENTAL INDICATORS

by ENZO INSALACO

ABSTRACT. A detailed Pan-European sclerochronological study was carried out on two Jurassic corals, *Thamnasteria concinna* (Goldfuss) and *Isastraea explanata* (Goldfuss), the aim of which was firstly, to identify the controls on the deposition of growth bands, on both a regional and local scale, and secondly, to assess the potential value of Mesozoic sclerochronology as a tool for palaeoenvironmental and palaeoclimatic interpretations.

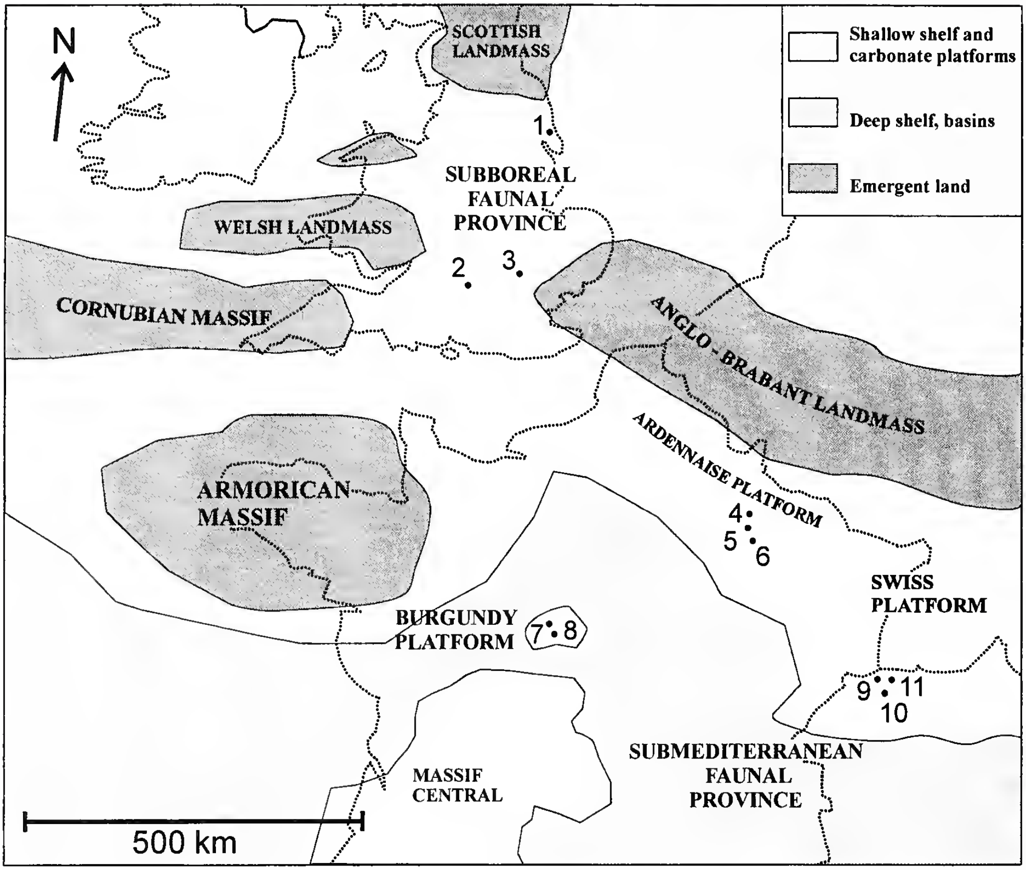
The results indicate that *Isastraea explanata* was the faster growing of the two species with growth rates reaching 4·0 mm/yr where conditions were optimal for coral growth (compared with 2·8 mm/yr for *Thamnasteria concinna* in the same environment). In deep-water environments, growth rates of both corals were considerably lower. This reduction in growth rate is accompanied by a change in growth form from dome-shaped colonies in shallow water to plate-shaped forms in deeper water. Both the reduction in growth rate and change in growth form are interpreted as a response to a reduction in light availability in the deep-water reefs. However, although *Thamnasteria concinna* had the lower growth rate of the two corals it showed a substantially greater variability in its growth rate between different reef environments (up to 50 per cent. of its optimal growth rate).

Data from similar reef types have been compared from different palaeolatitudes in an attempt to identify a palaeoclimatic gradient. No systematic palaeolatitudinal changes in the nature of the growth banding or the growth rate are seen. This is inferred to be a consequence of a Jurassic climate more equable than at present. Reefs from high palaeolatitudes have low growth rates and L/H (low/high) density band ratios. It is suggested that this is a response to low solar radiation. The study therefore shows that these corals can provide useful data for palaeoenvironmental and palaeoclimatic work and should be included, where possible, in such investigations.

GROWTH banding is a prominent feature of many modern corals and since the early 1970s there has been a vast amount of work carried out on their identification and interpretation. However, in their Mesozoic counterparts sclerochronology has received little attention, despite the fact that in many species growth banding is just as pronounced. This is surprising considering its potential value to the study of many aspects of palaeobiology, carbonate production and palaeoclimatology. The aim of this study is to compare the nature of the growth banding and the growth rates of two Late Jurassic corals, *Thamnasteria concinna* and *Isastraea explanata*, in two situations: (1) between *different geographical regions* though within the *same reef type*, thereby normalizing for local environmental effects, such as water depth and sedimentary influx, on growth rate; any difference in growth rates should therefore represent regional differences in factors controlling coral growth, such as temperature, seasonality and solar radiation; (2) between *different reef types* such as deep- and shallow-water reefs within the *same region*; differences in growth rates should be influenced only by differences in the local environment.

The material on which this study is based comes from the Oxfordian reefs of the following regions: Lorraine and Burgundy in France, Oxfordshire, Cambridgeshire and Yorkshire in England, and the Swiss Jura (Text-fig. 1). Within each region, both deep and shallow reef types were sampled. Detailed field work and subsequent laboratory work was carried out to establish the types of reefs and their environmental setting. The basis for such interpretations is based on litho- and

[Palaeontology, Vol. 39, Part 2, 1996, pp. 413–431, 3 pls]



TEXT-FIG. 1. Palaeogeographical map of northern Tethys during the Oxfordian (compiled from Enay and Mangold 1980, and Bradshaw *et al.* 1992). Dots indicate localities sampled. England: (1) Ayton Farm (Yorkshire) (YO); (2) Shellingford Cross-Roads Quarry (Oxfordshire) (OX), (3) Commissioner's Pit, Upware (Cambridgeshire) (UP). France, Lorraine: (4) Haudainville (HA); (5) St Mihiel (MI); (6) Foug (FO). Burgundy: (7) Saussois (SA); (8) Châtel-Censoir (CC). Swiss Jura: (9) Liesberg (LI); (10) Courtételle (CO); (11) St. Ursanne (UR).

biofacies analysis on both macro- and microfacies scales. The coral reefs chosen for this study can be placed into four broad categories that represent end-members in a complete spectrum of reef types in terms of their water depth and siliciclastic content. Differences in the environmental conditions between different reefs of the same reef type are negligible when compared with the environmental differences between reefs of different reef types. Brief descriptions of the reef types discussed in this study are given below; for more detailed descriptions and interpretation of reef localities, see Pumpin and Woltersdorf 1965 (UR and LI); Ali 1977, 1978, 1983 and Hitchings 1981 (YO, OX, UP); Geister and Lathuilière 1991 (MI, HA, F1 and F2); Menot 1991 (SA and CC). (See Text-fig. 1 for locality abbreviations.)

1. *Deep-water reefs: deep-water microsolenid biostromes*

Reefal unit dominated by an interlocking framework of platy corals in a bioclastic wackestone. Coral fauna dominated by microsolenids such as *Microsolena*, *Dimorpharaea* and *Comoseris*. Two reefal facies may be identified: (a) a siliciclastic-rich facies dominated by *Dimorpharaea* occurring within marly, clay-rich sediments (study examples F1, LI); (b) a siliciclastic-poor facies dominated by *Microsolena* occurring within pure limestones (study examples UP, F2, CC). Red algae are notably absent from both these reef sub-types. There is no evidence of current or wave action suggesting that reef development occurred well below normal wave base. Storm horizons are absent. These biostromes are the first coral-dominated reefal structures to develop in comparatively deep water aggradational sequences and often overlie more basinal sponge- and ammonite-bearing facies. The main environmental controls on the development of these reefs were the extremely low light levels associated with their relatively deep bathymetric position and, in some cases, muddy water (turbidity) from the high clay fraction of the siliciclastic influx (Geister and Lathulière 1991; Menot 1991; Leinfelder 1993, 1994; Leinfelder *et al.* 1994). Study examples from England and continental Europe do not show major structural or compositional differences.

2. *Shallow-water reefs*

Low siliciclastic influx (*study examples from continental Europe: MI, HA, SS, CO, UR*)*: clean, shallow-water patch-reefs*. High diversity coral patches have a rich association of corals (both in terms of taxa and growth forms). Dome-shaped and branching, ramose colonies dominate. No single coral taxon dominates the fauna. Red algae are present and can be locally common. Intra-reef sediments are clean, coarse-grained bioclastic packstones. These reefs have a high bioclastic component. Inter-reef sediments are also coarse grained bioclastic packstones with coated grains being common. Grain reworking and the development of coated grains suggest that current and wave action were present and water depths were very shallow. There is evidence that storm events were common. Light levels were not a limiting factor in the development of these reefs (Geister and Lathuilière 1991; Menot 1991). The study example from Yorkshire, England (YO) is different, although it is also developed in siliciclastic-free, very shallow water. The reefs occur as low diversity coral patches. Dome-shaped colonies of *Thamnasteria concinna* dominate. Intra-reef sediments are coarse grained oo-bioclastic packstones. Inter-reef sediments are oolitic grainstones. The sedimentological criteria again suggest that water depths were very shallow and above normal wave base. As with the continental examples, light levels were not a limiting factor in the development of these reefs (Hitchings 1981).

High siliciclastic influx (*study example OX*)*: low diversity coral thickets*. Typical coral genera are *Thamnasteria*, *Thecosmilia*, *Isastraea* and *Fungastraea*. Siliciclastic lenses and bands are well developed and common. Sedimentological criteria suggest deposition in very shallow water and above normal wave base. Storm horizons are frequent. The main controlling factor in the development of these reefs was the frequency and degree of siliciclastic influx (Ali 1977, 1978, 1983).

NATURE OF THE GROWTH BANDING, AND METHODS

Thamnasteria concinna and *Isastraea explanata* were chosen for this study because they are almost ubiquitous in Late Jurassic reefs but, more importantly, consistently show pronounced, well preserved growth banding; thus the large numbers of specimens needed for such a study were available. Furthermore, the quality of the growth banding was such that accurate measurements could be taken in the field by using silicon carbon grinding paper to grind down the surface to 800 grade. This method proved very successful on the soft limestones and increased the total size of the data set considerably. More detailed analysis of the banding regarding septal thickness and dissepiments distribution was carried out on selected polished slabs and thin sections with the use of optical microscopes. All growth rate measurements were measured in millimetres (mm) and were estimated to 1 decimal place.

Distinct growth banding is visible in longitudinal section in many of the specimens studied and is identical to the seasonal high- (H) and low (L) -density bands present in many modern corals and assumed to have developed in the same way (Knutson *et al.* 1972; Ali 1984; Geister 1989; Le Tissier and Scrutton 1993). The annual (seasonal) nature of these pairs of bands has been thoroughly confirmed by comparison with chronologies from radioactivity labelled environments (Knutson *et al.* 1972; Knutson and Buddemeier 1973; Buddemeier *et al.* 1974; Moore and Krishnaswami 1974; Noshkin *et al.* 1975), by the general agreement between radiographic growth rates and those from conventional radiometric dating (Dodge and Thomson 1974; Moore and Krishnaswami 1974), and by the general agreement with real-time measurements (Buddemeier and Kinzie 1976, table 2). The banding is depicted by alternating regions of thicker septa with more numerous dissepiments (high density band), and a band of thinner, less well developed septa with fewer dissepiments (low density band) (Pl. 1, figs 1–3; Pl. 2, figs 1–2; Pl. 3, figs 1–3).

On each colony the following measurements were recorded from five consecutive L/H density couplets: (1) spacing of the L/H density couplet (growth rate); and (2) the L/H thickness ratio. For each sample site, the arithmetical mean of the growth rate and L/H ratio for each species was calculated. The standard deviation for the growth rate was also calculated in order to indicate the degree of growth rate variability for a given species at each locality.

Two problems are encountered when measuring the growth rate on individual colonies. Firstly, there can be variations in growth rate along the section. Care is needed in assuring that the orientation of the section is truly vertical. Oblique sections give erroneously high measurements. This problem is compounded in some colonies by the fact that the corallites do not show straight vertical growth. This problem is especially pronounced in colonies that show mammilose growth surfaces. This results in sections that are in part vertical and in part oblique. This is illustrated in Plate 2, figure 2 where the bottom left of the figure shows an almost transverse section whereas the rest of the section is effectively vertical. Care needs to be taken to take measurements only from the fully vertical sections. The growth forms of the two species chosen for the study are tabular to domal with planar top surfaces, which suggests that divergent corallite growth was not marked. However, where this was marked, with a resultant axiallity in growth, the axial growth rate was taken. Marked axiallity was very rare and only encountered in three colonies (Pl. 1, fig. 3).

Another problem is one of the continuity in the definition of the low and high density bands. Even in colonies that are generally well preserved, there are often small areas of the colony that have undergone greater recrystallization than others, with a resultant loss in the sharpness of the bands. These areas were avoided when taking measurements. For example, in Plate 2, figure 2, the area which was measured is the far right and top of the specimen. The central area, which has experienced a greater amount of recrystallization, was not measured.

For each species, per sample locality, the distinctness of the L- and H- density was also recorded. This is an indication of the visual contrast in a L/H density couplet between the low density band and the high density band. Where the visual contrast between the two bands is high (high distinctness), the L/H couplets are easier to distinguish. The distinctness was recorded using an arbitrary scale of 1 to 5 (1 = low, 5 = high). This is based on a general assessment of all the colonies for each species per sample locality.

In none of the reefs studied were there any lateral or vertical changes in litho- or biofacies that

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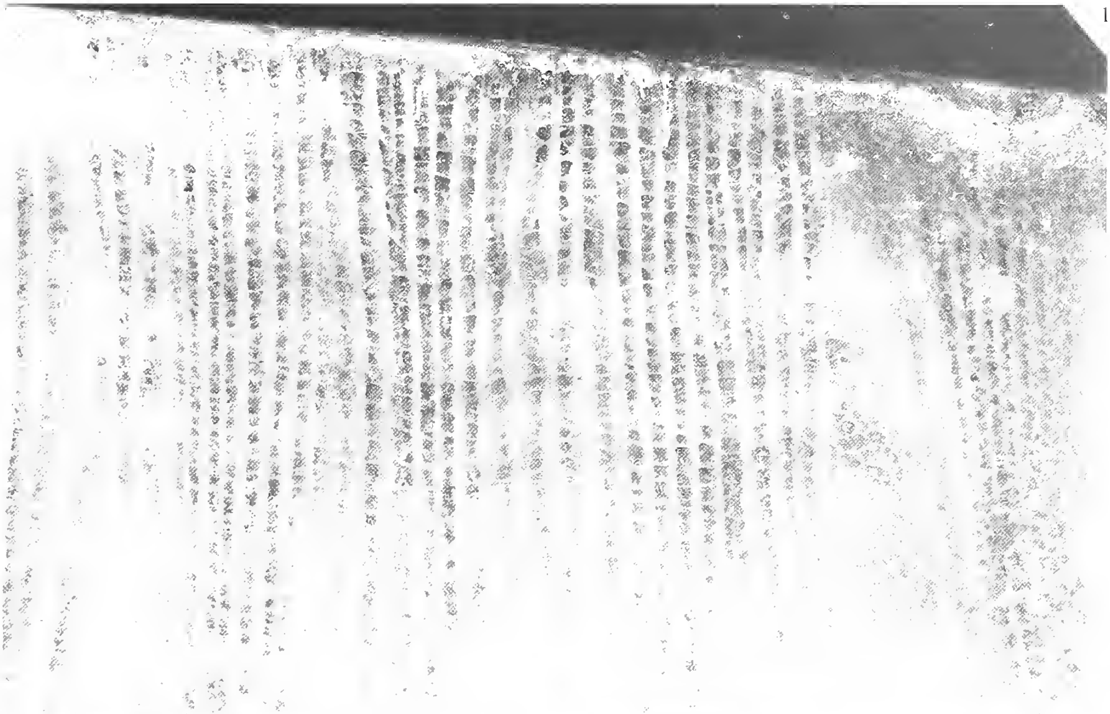
EXPLANATION OF PLATE 1

Figs 1–2. *Isastraea explanata* (Goldfuss); BU 100501; Liesberg Member (Oxfordian); Liesberg, Swiss Jura; polished slab from a deep-water microsolenid biostrome. 1, growth banding defined by high (light) and low (dark) density bands; growth rate *c.* 2·7 mm/yr; × 7. 2, details of the high and low density bands shown in Figure 1. In the high density band, most septa are thicker with more numerous and closely spaced dissepiments. In the low density band, the septa are less well developed with fewer dissepiments; × 9.

Fig. 3. *Thamnasteria concinna* (Goldfuss); BU 100101; Coral Rag (Oxfordian); Shellingford Cross Roads, Oxfordshire, England; polished slab from a shallow water reef; well developed, pronounced growth banding; axial growth rate *c.* 2 mm/yr. Note the marked distinctness of the high and low density bands, and the low/high density band ratio (approx. 0·5); × 6.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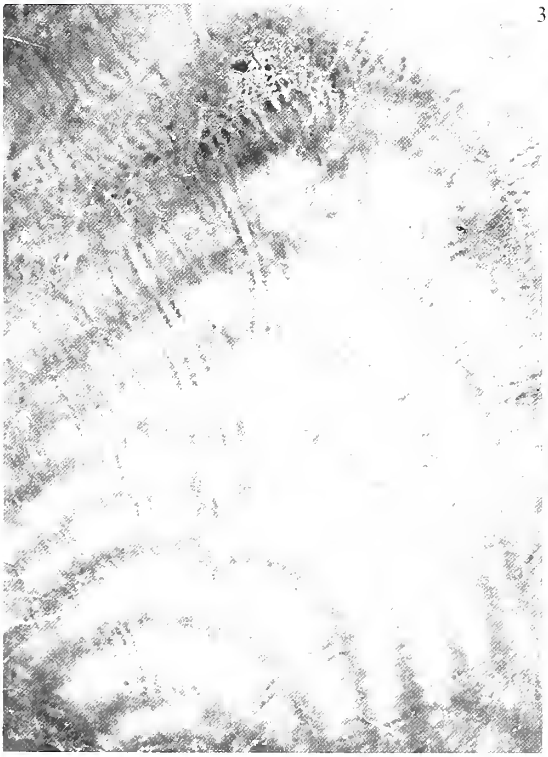
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INSALACO, *Isastraea*, *Thamnasteria*

could be attributed to changes in the environment. Therefore, since there is no evidence of ecological succession or zonation within these reefs, an indiscriminate sampling procedure over the total exposure of each reef complex was used to select colonies for measurement. Only well preserved colonies, where at least five consecutive L/H density couplets could be measured, were selected. The whole study is based on measurements of 875 L/H density couplets from 175 colonies. However, it should be noted that although, with one exception, both corals were present in all the reefs studied, they are not equally present in these different reefs. For example, the reef at Ayton Quarry, Yorkshire, is an almost monospecific patch of *Thamnasteria concinna* with only one colony of *Isastraea explanata* found (which has been excluded from the analysis because of the small sample size). Hence, at this locality, the analysis of *Thamnasteria concinna* is based on a large sample size (20 colonies). Conversely, in many of the reefs in France and Switzerland, these two corals are rare and generally less than eight well preserved colonies would be measured. In general, *Isastraea explanata* and, especially, *Thamnasteria concinna* became less dominant in the more southerly reefs (Bertling 1993).

Repositories. The author's collections are housed in the School of Earth Sciences, University of Birmingham (BU) and The Natural History Museum, London.

RESULTS

Growth rates

Table 1 and Text-figures 2–5 summarize the results of the study. Text-figure 2 shows the growth rate of the corals in the same reef type in different regions. In both plots, there is a weak trend, in both species, of decreasing growth rate with increasing palaeolatitude. The highest values were encountered in the Swiss Jura and the lowest in England. In both species, this trend is more marked in the shallower water facies where values range from 4 mm/yr (Swiss Jura) to 2·5 mm/yr (British Corallian) in *I. explanata*; and 2·8 mm/yr (Swiss Jura) to 0·8 mm/yr (British Corallian) in *T. concinna*. In the deeper water facies, this variation is less pronounced, with values ranging from 2·8 mm/yr (Swiss Jura) to 2·2 mm/yr (British Corallian) in *Isastraea explanata*, and 1·5 mm/yr (Swiss Jura) to 0·8 mm/yr (British Corallian) in *Thamnasteria concinna*. However, these decreases in growth rate are not significant at the 95 per cent. confidence level since the difference between adjacent points is less than 1·96 standard deviations. Also evident on the shallow-water plot (Text-fig. 2A) is a sharp decrease in the growth rate, again in both species, between the continental and the English localities. This shift from 3·6 to 2·5 mm/yr for *Isastraea explanata*, and 2·7 mm/yr to 1·3 mm/yr for *Thamnasteria concinna* between Haudainville (Lorraine, France) and Oxfordshire (England) is well above 1·96 standard deviations and therefore significant at the 95 per cent. confidence level. This feature is not visible in the deeper water facies. Text-figure 2B also shows that the difference in growth rate, for a given region, between *Thamnasteria* and *Isastraea* is greater in the deeper water facies.

Text-figures 3A and 3B illustrate the variation in the growth rates in the two corals between shallow- and deeper water facies. Comparing Text-figure 3A with 3B, it is immediately apparent that, in general, *Thamnasteria concinna* shows a greater variability in growth rate than *Isastraea explanata* between extreme reef types. It is also clear from Text-figure 3A, and to a lesser extent 3B, that the difference in growth rate between shallow and deeper water reefal units is much greater in

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EXPLANATION OF PLATE 2

Figs 1–2. *Thamnasteria concinna* (Goldfuss); Coral Rag (Oxfordian). 1, BU 100121; Ayton Farm, Yorkshire, England; photomicrograph of unstained thin section; ×7. 2, BU 100102; Shellingford Cross Roads, Oxfordshire, England; photomicrograph of stained thin section; ×5.

PLATE 2

1

2

INSALACO, *Thamnasteria*

TABLE 1. Summary of results. G.R., arithmetical mean growth rate (mm/yr); L/H, low/high density ratio; DIST, distinctness value; SD, standard deviation of the mean growth rate; NO, number of colonies measured. Approximate palaeolatitude of each location is indicated in parentheses.

Location	*Thamnasteria concinna*					*Isastraea explanata*				
	G.R.	L/H	DIST.	SD.	NO.	G.R.	L/H	DIST.	SD.	NO.
Yorkshire (YO; 39° N)	0.8	0.4	5	0.12	20	—	—	—	—	—
Oxfordshire (OX; 36.5° N)	1.3	0.6	5	0.11	11	2.5	0.5	5	0.28	8
Cambridgeshire (UP; 37° N)	0.8	0.5	5	0.11	8	2.2	0.5	5	0.35	4
Foug 1 (F1; 34° N)	1.1	0.4	5	0.15	13	2.6	0.6	5	0.29	7
Foug 2 (F2; 34° N)	1.3	0.5	5	0.11	10	3	0.7	4	0.31	5
Haudainville (HA; 34° N)	2.7	1.4	2	0.18	4	3.6	1.3	1	0.32	3
St. Mihiel (MI; 34° N)	2.4	1.2	2	0.17	5	3.4	1.3	3	0.27	3
Châtel-Censoir (CC; 33° N)	1.2	0.7	1	0.13	7	3.1	0.5	1	0.27	5
Saussois (SA; 33° N)	3	1.4	1	0.12	6	3.7	1.6	1	0.29	4
Liesberg (LI; 32° N)	1.5	0.5	5	0.14	17	2.8	0.5	5	0.26	14
Courtételle (CO; 32° N)	2.5	1.7	1	0.12	8	3.8	1.4	2	0.3	3
St. Ursanne (UR; 32° N)	2.8	1.3	2	0.12	6	4	1.5	2	0.31	4

Lorraine, Burgundy and the Swiss Jura, than in England, this being especially pronounced in *Thamnasteria concinna* (Text-fig. 3A).

Low/high (L/H) density band ratio

The L/H ratios of the corals studied are shown on Text-figure 4. L/H ratios range from 0·4 in Yorkshire to 1·7 in the Swiss Jura. L/H ratios of *Thamnasteria concinna* and *Isastraea explanata* do not seem to be significantly different, nor do they show any significant regional variations. The L/H ratio results can be grouped into three clusters.

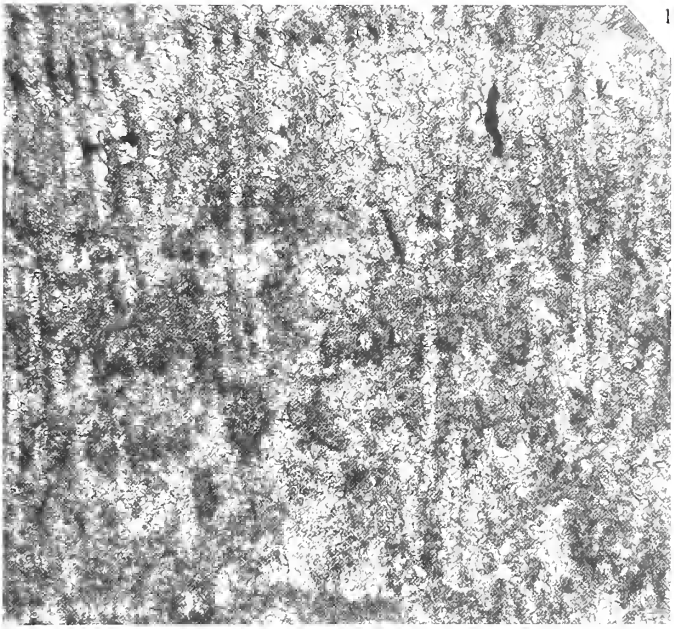
1. Colonies that show L/H ratios greater than 1·2 occurring in the shallow-water facies (Lorraine, Burgundy, Swiss Jura);
2. Colonies that show L/H ratios less than 0·7 occurring in the deep-water facies (Upware, Foug, Châtel-Censoir, and Liesberg);
3. Colonies occurring in shallow water though having an L/H ratio of less than 0·7 (Yorkshire and Oxfordshire).

EXPLANATION OF PLATE 3

Figs 1–3. *Thamnasteria concinna* (Goldfuss); BU 100401; Lower reef complex (Oxfordian); Châtel-Censoir, Burgundy, France; photomicrograph of unstained thin section from a deep-water microsolenid biostrome, showing thinning and thickening of skeletal relics and their neomorphic replacement by calcite (the light coloured coarsely crystalline material); low density bands (dark zones) show best preserved septa since they were originally thinner with fewer dissepiments resulting in less neomorphic replacement. Dark material between the septa is likely to represent early marine peloidal cements; Fig. 1, × 15; Fig. 2, × 40; Fig. 3, × 85.

Fig. 4. *Thamnasteria dendroidea* (Lamouroux); BU 100301; Upper reef complex (Oxfordian); Haudainville, Lorraine, France; polished slab; axial growth rate *c.* 13 mm/yr; × 1·5.

PLATE 3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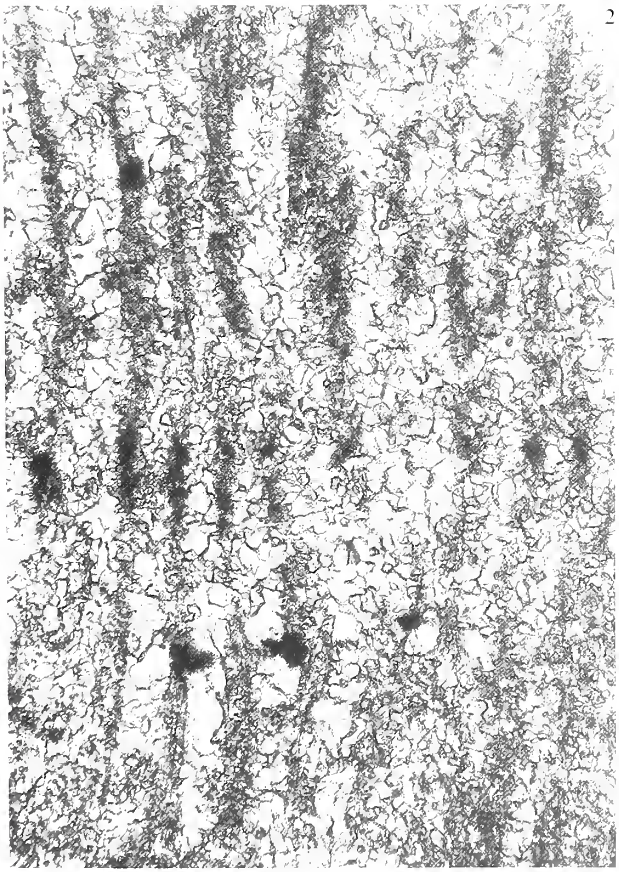
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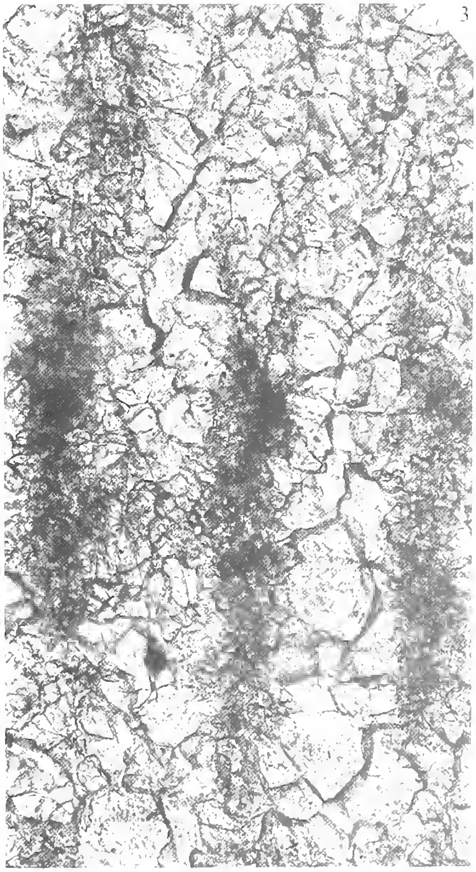
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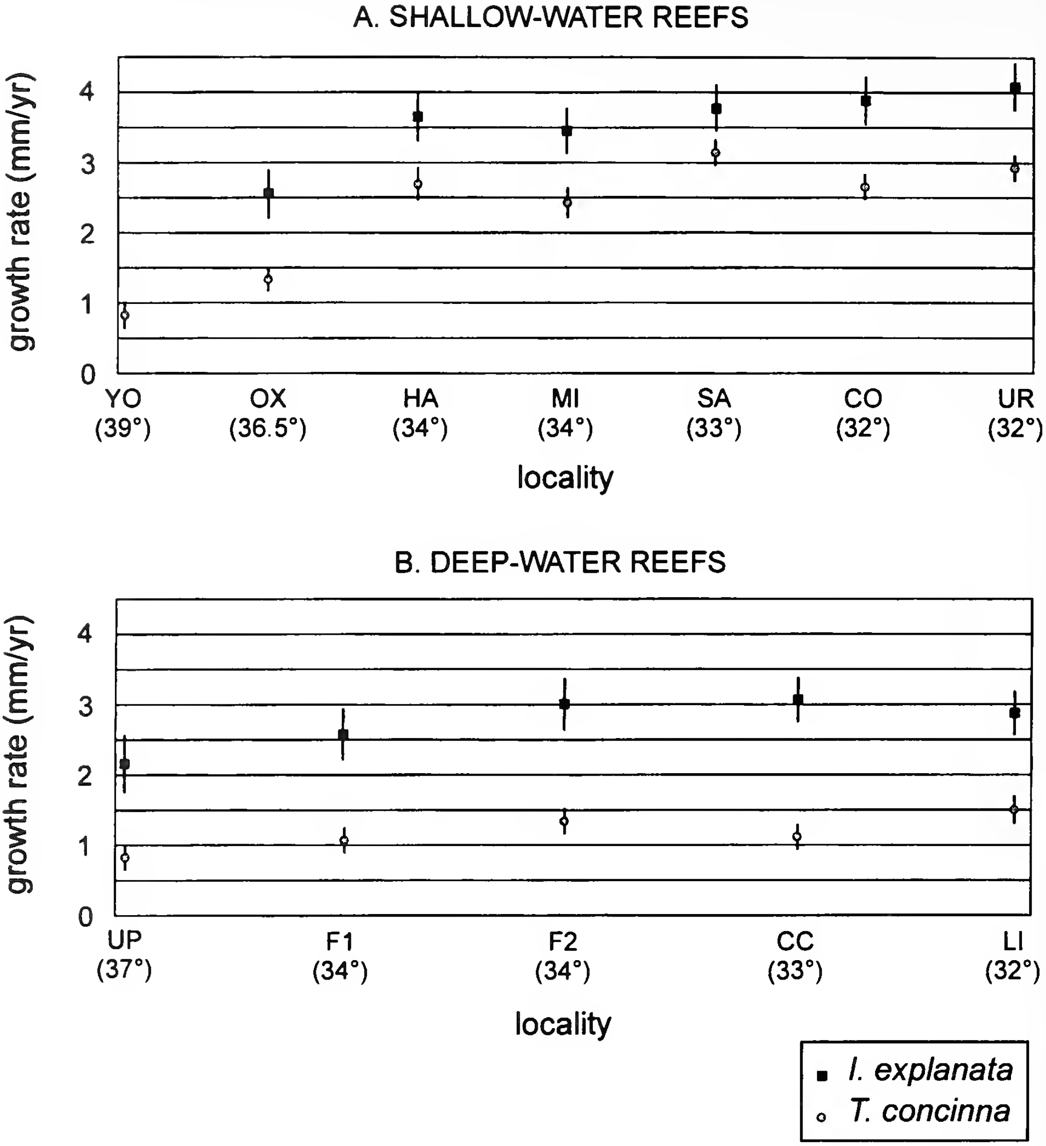
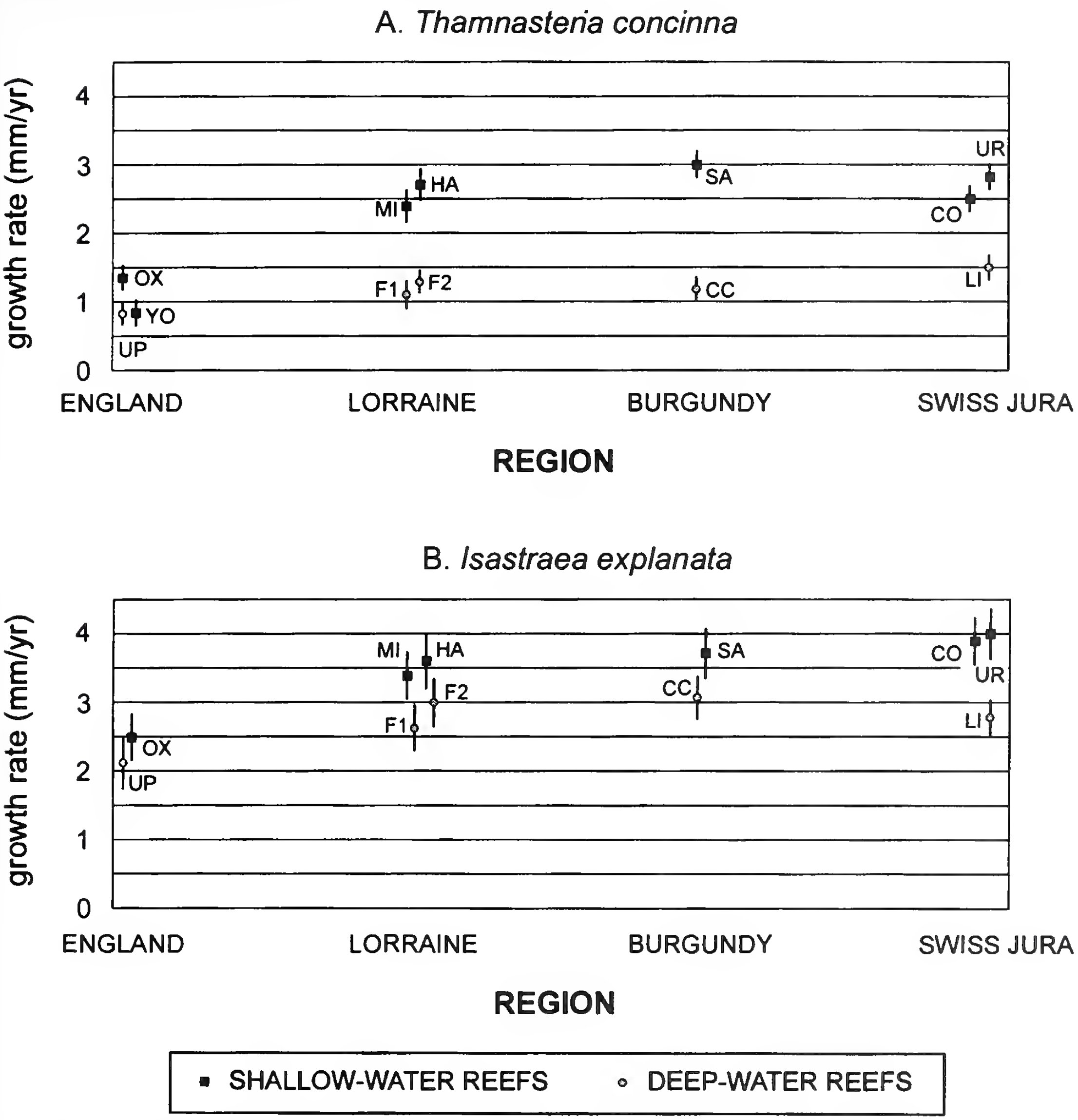
INSALACO, *Thamnasteria*



TEXT-FIG. 2. Variation in growth rate (mm/yr) between *Thamnasteria concinna* and *Isastraea explanata* in shallow (A) and deep water (B) reefs. The points plotted are the arithmetical means of all the measurements collected for each species per locality. Vertical line represents ±1 standard deviation. Also indicated in parentheses is the approximate palaeolatitude of each location in °N.

Distinctness (D)

D does not seem to vary systematically between the two species. Not all the colonies show distinct growth banding; however, this phenomenon is also encountered in modern corals (Weber and White 1974; Huston 1985). Diagenesis has probably altered the natural distinctness to an unknown extent but, since these reefs have undergone similar diagenetic histories, it seems probable that the relative distinctness has remained similar to the original values. D was extremely high (5, 4) in all



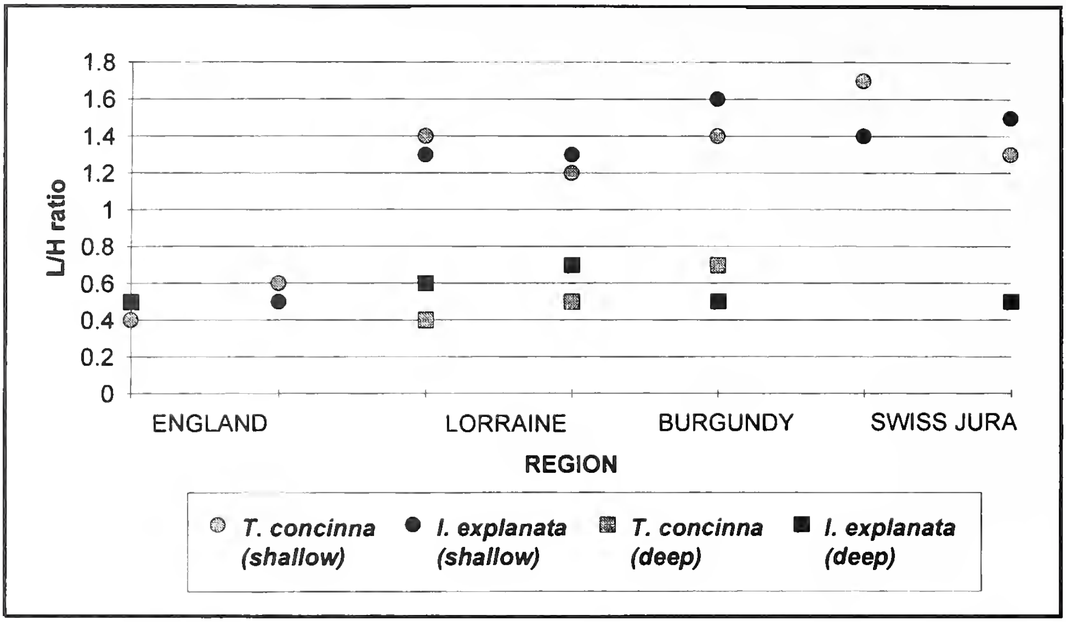
TEXT-FIG. 3. Variation in growth rate (mm/yr) between shallow and deep water reefs for *Thamnasteria concinna* (A) and *Isastraea explanata* (B). The points plotted are the arithmetical means of all the measurements collected for each species per locality. Vertical line represents ±1 standard deviation.

the English localities with outside England only Liesberg showing a similarly high value (Pl. 1, fig. 3). The European localities generally show low D values (2, 1) (Text-fig. 5).

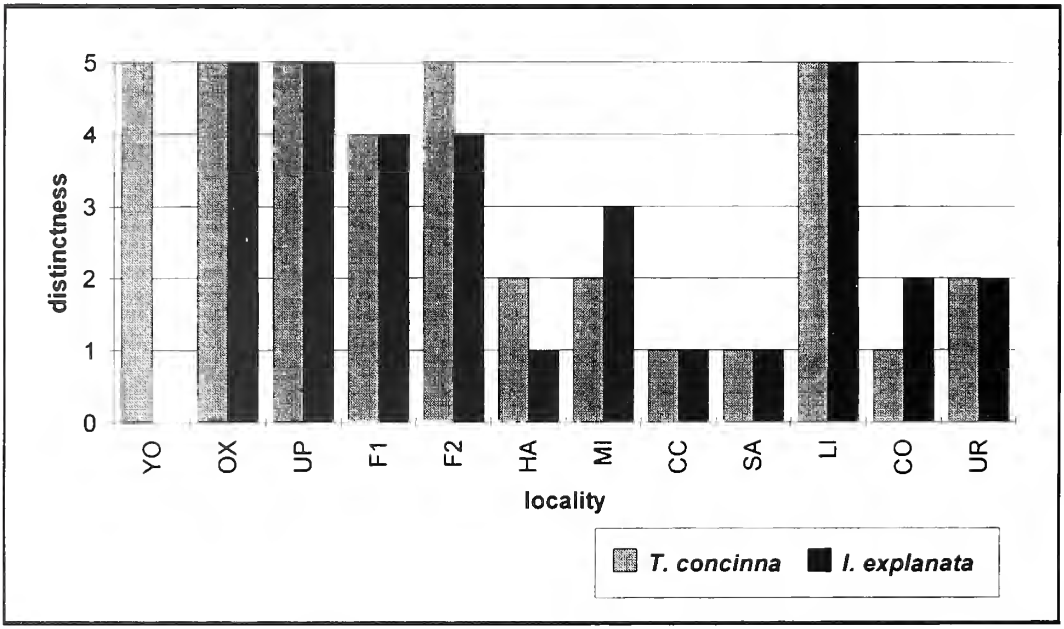
DISCUSSION

Growth rates

The weak general trends shown on Text-figures 2A and 2B are notable by their insignificance at the 95 per cent. confidence level. Since these plots are comparing corals from the same reef type across different regions (2A for shallow-water reefs and 2B for deep-water reefs), differences in growth rate



TEXT-FIG. 4. Low/high density ratios from both reef types and all localities for both species. The points plotted are the arithmetical means of all the measurements collected for each species per locality.



TEXT-FIG. 5. Distinctness values for the low- and high-density couplets.

should be independent of local environmental controls and should reflect more regional changes in climatic (temperature, solar radiation and seasonality) and/or oceanographic factors (Glynn 1977). One might therefore speculate that with an increase in palaeolatitude, there would be a decrease in regional average temperature and solar radiation, consequently resulting in a decrease in growth rate. This is not revealed in the data. However, it has been well established that the Jurassic climate was more equable than at present and therefore environmental gradients not as steep (Hallam 1975, 1984, 1993). This allowed a general spread of coral reefs as far north as Scotland which lay at approximately 43° N; this contrasts strongly with the present-day limits of reef growth which lie approximately 35° N and S of the equator (Rosen 1981). Hence, the lack of large variations in growth rates between the regions studied, all of which lie within a broad mid-latitude climatic belt, might be accounted for by the small difference in palaeolatitude between adjacent localities, and the equable palaeoclimatic regime. Growth-rate data are not yet available for reefs located farther south (such as the Portuguese and Slovenian reefs) or farther north (such as the Helmsdale corals in north Scotland). These areas would provide corals that grew outside this climatic regime and therefore differences in their growth rate might reflect climatic differences. What is now clear is that this climatic signal would be best searched for in corals such as *Thamnasteria concinna* and in shallow-water reefs with low siliciclastic influx, since these were evidently the most sensitive to environmental changes (see below).

The low growth rates recorded in the Yorkshire reefs (YO) are, however, significant. The difference in growth rate between Yorkshire and the continental European reefs, which developed in similar shallow-water siliciclastic free environments, is very marked (approximately 1·5 mm). As explained above, there is clear evidence to suggest that climatic gradients between these regions were not steep, and hence were unlikely to be responsible for the difference in growth rate. One possible explanation for the reduced growth rates of the corals from the Yorkshire reefs is the reduction in annual solar radiation as a consequence of their relatively high palaeolatitude. In this respect, it is interesting to note that it has been shown that most Mesozoic and Cenozoic shallow shelf carbonates occur within the sub-tropics, 5–35° N and S (Ziegler *et al.* 1984). Evidently, the carbonate belt did not shift northwards during warmer periods such as the Jurassic, suggesting that simple climatic considerations are not enough to explain coral distribution. However, year-round solar radiation falls markedly at about 35° from the equator, the present poleward limit of Bahamian-type environments. Ziegler *et al.* (1984) suggested that it is this latitudinally induced drop in light intensity which limits depositional systems that rely on algal-symbiotic fixation of calcium carbonate, either directly or indirectly, to within these latitudes. It is likely that this decrease in solar radiation adversely affected growth band development in the corals of Yorkshire, which lay approximately 39° N, resulting in low growth rates (Smith *et al.* 1980).

Another interesting feature of Text-figure 2A is the sharp decrease in the growth rate between Haudainville and Oxfordshire. This decrease is likely to be due to the increase of seasonal runoff and the adverse effects that this has on coral growth (increased sedimentation, increased turbidity and possibly the adverse effects of increased nutrient flux). This feature is absent in the deeper water reefs since all of these reefs shared similar ambient conditions. Text-figure 2B shows that growth rates in deeper water reefs show little variation between locations. This lack of regional variation may be explained by the fact that these deep-water biostromes developed in conditions of low light and high sedimentation with its associated high turbidity, hence any regional signal is probably masked by the strong local environmental overprint.

Text-figures 3A and 3B illustrate the variation in growth rates in the two corals between shallow and deeper water facies. Growth rates in the deep-water biostromes are likely to represent the slowest possible growth rates for these corals since these reefs developed in comparatively stressful environments. Any further deterioration in environment, such as would be caused by increases in sedimentary influx, turbidity and hence decreases in light, are likely to result in coral mortality rather than a further reduction in growth rate. On the other hand, growth rates in the shallow-water reefs, especially on the clean carbonate platforms of Burgundy and the Swiss Jura (Text-fig. 1) which provided near optimal conditions for coral growth, are likely to represent values close to the maximum linear extension possible for these corals. This contrast is reflected by a dramatic decrease in growth rate from shallow- to deep-water in all regions and in both species (Text-figs. 3A and 3B). The decrease in growth rate is accompanied by a change in growth form from dome-shaped colonies in shallow-water settings to flat platy forms in deep-water. These results are analogous to those of studies carried out at Discovery Bay, Jamaica (Huston 1985), in which four out of six coral species (*Porites astreoides*, *Montastrea annularis*, *Colpophyllia natans* and *Siderastrea siderea*) significantly decreased their growth rate over a 1–30 m depth interval. Also documented in these corals were changes in growth form from dome- to plate-shaped colonies along the same depth gradient. This was especially pronounced in *Montastrea annularis* as was the change in growth rate. Huston concluded that the major control over both these changes (form and growth rate) is decreasing light levels, which reduces calcification rates significantly. Other studies on the relationship between depth and growth rate on present-day reefs come to similar conclusions (Goreau 1959, 1963; Goreau and Goreau 1959; Goreau and Wells 1967; Baker and Weber 1975; Dustan 1975, 1979; Highsmith 1979). In the Jurassic deeper water, low light intensity reefs, further evidence of the suppression of the coral calcification process comes from: (1) a poorly developed wall structure in *Isastraea explanata*, resulting from a reduction in the number and density of dissepiments; (2) the dominance in these reefs of microsolenids which are well adapted to environments where calcification is hindered (Leinfelder 1993, 1994; Leinfelder *et al.* 1994).

Text-figures 3A and 3B also clearly show that the difference in growth rate, in both corals, between shallow- and deep-water facies is greater in continental European localities than in England. This simply reflects the fact that the environmental contrast between the shallow- and deep-water facies was much greater in the European areas. In Europe, the shallow-water reefs developed in near ideal conditions for intense reef growth, i.e. warm, well lit water on clean shallow-water carbonate platforms. The deep-water reefs, on the other hand, grew at the environmental limits of reef growth in conditions of extreme low light and in some cases high turbidity. The situation in England was clearly different, although the deep-water reefs developed in equally poor conditions resulting in equally low growth rates, the shallow-water reefs did not develop in the same ideal environments as their European counterparts due to sedimentary influx and, in the more northerly locations (such as Yorkshire), the possible effects of reduced solar radiation; as a result, their growth rates are not as high.

What is also clear from Text-figures 3A and 3B is that *Thamnasteria concinna* shows greater variability in its growth rate than *Isastraea explanata* (though *Isastraea explanata* shows more intra-colony variability, as reflected by its larger standard deviation), both between different reef types and also between different regions. This is consistent with the suggestion that *Thamnasteria concinna* possesses an extremely plastic ecomorphic behaviour (Geister and Lathuilière 1991; Bertling 1993). In deeper water environments, such as the deep-water microsolenid reef studied, this coral develops a marked platy growth form. In shallower water, it exhibits a much more massive appearance. Furthermore, if one accepts that *Thamnasteria dendroidea* (Lamouroux) is simply a branching morphotype of *Thamnasteria concinna*, as is now believed (Geister and Lathuilière 1991; B. Lathuilière, pers. comm. 1993), then it developed a branching habit in very shallow, quiet, water. What this study seems to show is that this plasticity in the growth form of *Thamnasteria concinna* is paralleled by a plasticity in its growth rate. *Thamnasteria concinna* seems to have varied its growth rate considerably in response to growing in a wide variety of different reef environments. This high degree of ecomorphic and ecophysiological plasticity suggests that *Thamnasteria concinna* was an *r*-strategist, hence its dominance in the unstable reef environments of the Sub-Boreal Province (Bertling 1993). In fact, there would appear to be an intimate relationship between plasticity in growth form and plasticity in growth rate, since differences in growth form are a function of contemporaneous intra-colonial variations in growth rate, though sites of budding are also important. Thus, platy forms developed when all the corallites on the surface of the coral grew at the same rate, whereas in dome-shaped forms, the corallites axial to the dome grew significantly faster than the peripheral corallites. In extreme cases, branching colonies developed where there was a number of very localized 'hot spots' in coral growth which subsequently exhibited extremely fast growth and formed branches. In the case of *Thamnasteria concinna* (type 'dendroidea'), branch growth rate could reach 13 mm/yr (approximately ten times the growth rate of their deeper water platy counterparts) (Pl. 3, fig. 4). A similar relationship seems to exist in present-day corals; for example, *Montastrea annularis* shows the highest variation in growth rate between deep- and shallow-water environments, but also shows the most marked variation in growth form between these extreme water depths (Huston 1985). It is interesting to note in this respect that although *Isastraea explanata* shows a higher growth rate of the two species studied, its inter-colony variation is relatively small, which is paralleled by its limited ecomorphic plasticity (*Isastraea* never develops a branching ramose form and only shows moderate morphological variation between thick plates and large heads). This suggests therefore that the ability for a coral to vary its growth rate substantially may be a prerequisite for the coral to attain a high degree of ecomorphic plasticity.

From 175 colonies studied (both *Isastraea* and *Thamnasteria*), no evidence of determinate growth, as hypothesized by Barnes (1973) for massive corals, was found. The present study is consistent with other studies (Buddemeier 1974; Dodge *et al.* 1974; Buddemeier and Kinzie 1976; Hudson *et al.* 1976; Highsmith 1979).

Low/high density ratio

The L/H ratios clearly fall into three groups. Ali's (1984) study of growth banding in the English Oxfordian showed that the corals from the reefs of the Sub-Boreal Province had relatively low L/H values (generally less than 1·0), compared with the values of present-day shallow-water corals in the Indo-Pacific and the Caribbean which are generally greater than 2·0 (Weber *et al.* 1975; Buddemeier and Kinzie 1976). The present study corroborates Ali's (1984) observation, with observed L/H ratios of 0·4–0·6. The argument put forward by Ali suggests that the reason for these low values is reduced light levels resulting from high local turbidity. This is probably a very significant factor; however, one must not discount increased cloud cover for a reduction in solar radiation, especially for a more northerly location such as Yorkshire. This has been shown to be of importance by a study on present-day growth rates in corals from the tropical Pacific (Buddemeier 1974). In Buddemeier's (1974) study, a positive correlation between the high density bands and lowered light levels (resulting from increased cloud cover) was identified. The latitude-related reduction in solar radiation as implied by Ziegler *et al.* (1984) is also likely to have affected growth band development in the corals of the Yorkshire reefs.

The present study also demonstrates that where strong siliciclastic influx is not present, such as in the shallow-water reefs of Lorraine, Burgundy and the Swiss Jura, L/H ratios increased (larger low density band) and approach the value of present-day corals, although they are still persistently and considerably lower. One explanation for this inconsistency between modern and Mesozoic values is again related to the relatively high palaeolatitudinal location of these reefs (lying approximately between 32° and 39° N). This would have had two adverse effects on coral growth: (1) although temperature gradients were not as steep as at present, temperatures in these high palaeolatitudes may still have been lower than those in present-day tropical reef-growing areas; (2) latitude-related reduction in solar radiation. These two factors would have inhibited extensive growth of the low density bands. More data from around the palaeoequator are needed to confirm this. From these low palaeolatitudes, it is predicted that L/H ratios will be significantly greater than found in the present study and would compare well with present-day values.

The third cluster of values is from the deep-water reefs, with values below 0·7. This again may be explained by applying a model which invokes a negative correlation between density and light levels. Although it is still unclear which factors control the density variations, there is strong evidence to suggest that the density bands correlate negatively with light level as well as temperature. Indeed, it has been demonstrated that L/H ratios decreased with depth in a study of the present-day corals of the Enewetak Atoll (Highsmith 1979). This suggests that light is the more important factor governing the deposition of these density bands, rather than temperature, which does not decrease as rapidly with depth.

Distinctness

It has been established that in modern corals the low density band is deposited during the summer when the linear extension is greater and consequently the skeletal structure more open, and the high density band is produced during the winter when the process is reversed (Buddemeier 1974). Although it is clear that the above process is the cause of the low and high density couplet, there is still debate as to which precise aspect of the seasonality is driving the process. It seems likely that it is a result of a complex interplay of factors, such as temperature, light and reproductive state, making accurate environmental deductions based solely on band distinctness more difficult (Tudhope 1994). Nevertheless, the model implies that where the difference between the summer and winter seasons is large (i.e. a highly seasonal climate), the gross difference between the density bands, and consequently their visual appearance, should also be correspondingly large, i.e. the greater the seasonality the greater the distinctness, all other factors being equal. If one accepts this model for the production of growth bands for Mesozoic corals, the data would suggest that at this time the study area was in a highly seasonal climatic belt, as reflected by pronounced growth bands. This would be consistent with both computer models and empirically based models for Late Jurassic climates that suggest that northern Tethys experienced a strongly seasonal climatic regime (Moore *et al.* 1992*a*, 1992*b*; Valdes and Sellwood 1992; Hallam 1993). This reasoning is similar to that used by Ma (1934, 1958) who used this technique with Palaeozoic corals to locate the position of the equator relative to drifting continents at various times during the Palaeozoic. A subsequent reinterpretation of Ma's (1934) data, in the light of continental drift theory, by Fischer (1964) shows that the method is reliable. In a similar study, though on Lower Jurassic to Lower Tertiary fossil tree trunks, Creber and Chaloner (1984) were able to recognize a broad equatorial zone ranging in latitude from approximately 30° N to 30° S, in which annual growth rings are either absent or very poorly developed. Either side of this zone, annual growth bands were more pronounced and well developed, and were interpreted as suggesting a strongly seasonal climate.

Text-figure 4 clearly shows that values of D varied not only between different areas but also between different reef types within the same region. This pattern cannot be explained by applying a simple seasonality model. Looking at the data in more detail one finds that the following localities have high D values: Ayton Farm, Shellingford Cross-Roads Quarry, Upware, Foug, and Liesberg, whereas for St Mihiel, Haudainville, Châtel-Censoir, Saussois, St Ursanne and Courtételle distinctness is low. Taking account of the lithofacies and palaeogeography, a very clear pattern emerges: the localities with high values of D are those that have a high siliciclastic component and/or are strongly influenced by nearby land masses; localities with low D values occur in very pure carbonate environments with very little influence from land masses. So, although seasonality does not seem to influence the degree of distinctness directly, its indirect influence is nevertheless considerable. Seasonal increases in precipitation and wind energy produced high runoff resulting in large influxes of sediments, and possibly nutrients, into the surrounding sea. Where this coincides with areas of reef development, the corals show greater contrast in their high and low density bands, resulting in higher D values. Further evidence for such a pronounced seasonal process is provided by thin veneers of sediment found at the top of the low density bands in a number of specimens from the English Oxfordian. A similar process was invoked for the corals of the Great Barrier Reef by Boto and Isdale (1985). They suggested that there was a strong correlation between the intensity of the fluorescence in the coral skeleton, and the seasonal pattern of rainfall and runoff from the adjacent Australian landmass. They suggested that the fluorescence in the coral skeleton is caused by organic acids of terrestrial origin that are washed in during periods of high runoff.

CONCLUSIONS

Palaeogeographical and palaeoenvironmental settings, in combination with the palaeoclimatic regime, have been found to exert a strong control on the nature of growth banding, and also the rates at which these bands were deposited. The combination of strong seasonal rainfall and proximity to land masses resulted in lowered growth rates and L/H ratios, though increased distinctness values. Where reef development was distal to sediment source areas, the effect of seasonality was much less marked; consequently, distinctness values decreased but L/H ratios and growth rates increased. All these changes were more pronounced in the shallow-water reefs, which seemed to have been more sensitive to environmental change. Growth rates also decreased markedly from shallow to deeper water, as they do in present-day coral reefs. This decrease in growth rate is in response to the decreased intensity and quality of light which adversely affects the calcification process in corals.

Due to the more equable Jurassic climate, no systematic regional changes in the nature of the growth banding or the growth rate were seen. Data from outside this broad mid-latitude climatic belt could provide suitable material to assess the effect of regional changes in temperature and seasonality on the production of these growth bands. Such areas would include reefs developed farther south, for example in Portugal and North Africa, and to the north, in the Sub-Boreal Province, such as the corals from the Helmsdale region of northern Scotland. The low growth rates and L/H ratios recorded from the corals in Yorkshire are likely to be a response to the low solar radiation received at high palaeolatitudes, and are consistent with the Ziegler *et al.* (1984) model for the distribution of Bahamian-type carbonates.

Marked differences between the two species studied can be inferred in their ecophysiological behaviour, as reflected by variations in growth rate. Although *Isastraea explanata* had a greater growth rate, it shows little variation between different reef environments. *Thamnasteria concinna*, on the other hand, had a lesser growth rate, though it shows a considerable variation between different reef types. It is suggested that this may be related to its strongly plastic ecomorphic behaviour.

This study has shown that it is possible to apply the methodology developed for present-day sclerochronology to Mesozoic Scleractinia. Moreover, the current concepts and ideas about the construction of present day corals seem also to apply to Mesozoic corals, which show similar growth behavioural patterns to modern forms. Thus Mesozoic sclerochronology is potentially an important tool for interpreting past environments and climates.

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PERISPHINCTID AMMONITES OF THE UPPER CALCAREOUS GRIT (UPPER OXFORDIAN) OF NORTH YORKSHIRE

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ABSTRACT. Twenty-three species of perisphinctid ammonite, belonging to the genera *Perisphinctes*, *Decipia* and *Microbiplices*, are described from the lowest Upper Oxfordian Upper Calcareous Grit Formation of North Yorkshire. A new species, *Decipia ravenswykensis*, is described, and *Pseudopomerania* is proposed as a new subgenus of *Perisphinctes*, to include some until now little understood perisphinctids previously assigned to *Decipia*. A comparison is made with successions of the same age elsewhere in Britain and in continental Europe. Revised correlations are proposed with the standard successions in the Wash area of England and in the French Jura.

DURING the 1960s and '70s, extensive quarrying of the Middle Oxfordian Malton Oolite and Coral Rag was carried out for lime and road building materials at a number of localities along the northern side of the Vale of Pickering (Text-fig. 1). These operations made available substantial exposures of the overlying Upper Calcareous Grit, the sandstones and siltstones of which were of no use to the quarrymen, and were dumped and could be picked over at leisure by collectors. As a result, the author, accompanied by Mr D. N. Wright, was able to collect some 370 Late Oxfordian ammonites from the Upper Calcareous Grit during the course of numerous visits extending over 20 years. Many of the quarries have now ceased production, or no longer work ammonite-yielding beds. The bulk of the ammonites are cardioceratids belonging to the genus *Amoeboceras*. This group has been dealt with by Sykes and Callomon (1979), and will not be considered further here. The present work is based on the author's collection of 152 perisphinctids.

Arkell (1935-48) described many species of Late Oxfordian perisphinctids from Dorset, the Midlands and North Yorkshire. However, much of the present Yorkshire material is of a slightly older date than the specimens described by Arkell and it includes a number of previously undescribed species; other specimens extend the range of variation in Arkell's species. Hancock (1954) recorded perisphinctids of a similar age from Cambridgeshire. The extensive literature of continental Europe which concerns Late Oxfordian perisphinctids will be referred to below under Systematic Palaeontology.

STRATIGRAPHY

Summary of the succession

The Upper Calcareous Grit Formation was divided by Wright (1972) into three members: the predominantly argillaceous Newbridge Beds, overlain successively by the Spaunton Sandstone and the Snape Sandstone. There is no single exposure which reveals the complete succession. However, a complete cored section through the formation was drilled at West Newton Grange [SE 628 802] by the Yorkshire River Authority in 1973, and the author's log of the borehole core is given below as a standard section of the Upper Calcareous Grit (total thickness 11·2 m).

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(AMPTHILL CLAY – dark grey clay with *Meleagrinella* sp. and *Serpula* sp. – seen to many metres)

SNAPE SANDSTONE

4. Grey, very tough, calcareous, laminated, bioturbated sandstone with white, infilled burrows, becoming argillaceous in top 0·5 m and passing up into Ampthill Clay. 3·95

SPAUNTON SANDSTONE

3. Massive, yellow, highly bioturbated, decalcified sandstone 2·1
2. Grey, partially bioturbated sandstone, becoming argillaceous towards base; bivalve fragments. 2·75

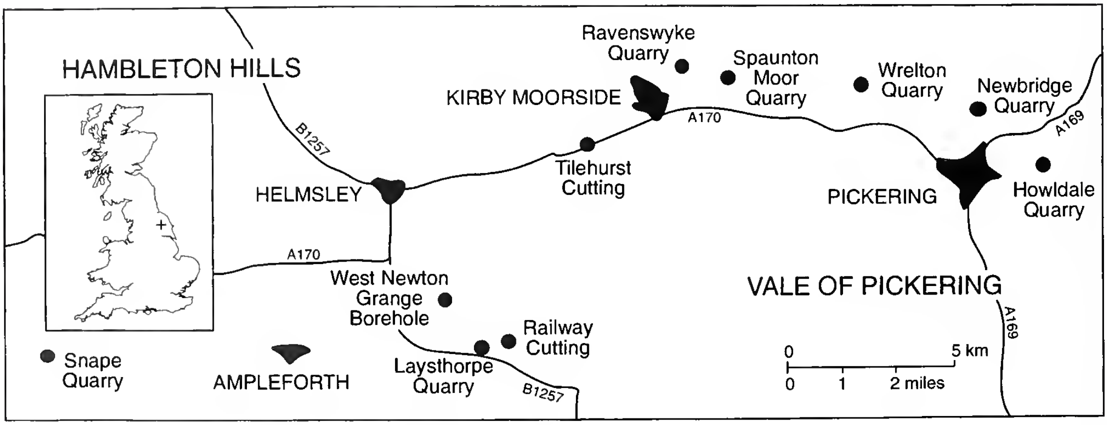
NEWBRIDGE BEDS

1. Grey, clayey silt passing up into laminated, clayey sandstone; bottom few tens of millimetres sandy and spicular. 2·4

– bored, erosive junction –

(CORAL RAG – creamy white, micritic limestone containing scattered coral colonies: 8·8 m).

This sequence of predominantly argillaceous beds, succeeded by a massive sandstone, and then a laminated, calcareous sandstone often with belemnites, is traceable across the western half of the Vale of Pickering, from Pickering westwards to Snape, and southwards to Laysthorpe (Text-fig. 1).



TEXT-FIG. 1. Map showing the localities mentioned in the text.

Details of exposures

The quarry sections are described from east to west, starting at Pickering.

Newbridge Quarry [*SE 800 860*]

SPAUNTON SANDSTONE MEMBER m

4. Rubbly, nodular, silicified, very fossiliferous sandstone containing *Amoeboceras nunningtonense* Wright, *A. glosense* (Bigot and Brasil), *A. ilovaiskii* (M. Sokolov), *A. transitorium* (Spath), *A. newbridgense* Sykes and Callomon, *Perisphinctes* (*Dichotomosphinctes*) spp., *Microbiplices* sp., *Myophorella clavellata* (Parkinson), *Pleuromya uniformis* (J. Sowerby), *Chlamys midas* (Damon), *C. fibrosus* (J. Sowerby), *Lucina lirata* Phillips, *Nanogyra nana* (J. Sowerby), *Camptonectes lens* (J. Sowerby), *Meleagrinella ovalis* (Phillips), *Goniomya literata* (J. Sowerby) and '*Pentacrinus*' sp. seen to 1·0
3. Moderately tough, flaggy sandstone, strongly bioturbated towards the top, containing *Amoeboceras* sp., *Perisphinctes* (*P.*) *cautisnigrae* Arkell, *P.* (*Pseudarisphinctes*) *pachachii* Arkell, *Decipia decipiens* (J. Sowerby), *D. lintonensis* Arkell and *Modiolus pulchrum* Phillips. 1·2

NEWBRIDGE BEDS

2. Flaggy, sandy siltstone with occasional *Decipia ravenswykensis* sp. nov. 3·0

1. Flaggy, sandy, sporadically oolitic limestone or marl, with numerous bored pebbles of the underlying Coral Rag limestone. Rare *Chlamys* sp. 0·6–0·9

(CORAL RAG – blue-grey, fine grained limestone with scattered *Rhabdophyllia phillipsii* Milne Edwards and Haime).

The Newbridge Beds weather readily, and form sloping ledges of soft material, making examination difficult. Numerous bored pebbles of Coral Rag, encrusted by *Nanogyra nana*, weather from this debris, and are scattered over the slopes. Most of the perisphinctids were collected from Bed 3. Bed 4 contains silicified masses of chert, the spicules of *Rhaxella* being readily visible in thin section. Ammonites and bivalves are extremely abundant in this bed, though the shells are commonly broken and distorted due to compaction.

Wrelton Quarry [SE 760 867]

SPAUNTON SANDSTONE m
2. Well bedded, poorly fossiliferous, fine grained sandstone. seen to 1·2
NEWBRIDGE BEDS
1. Flaggy, shaley sandstone with *Decipia ravenswykensis.* 2·0
(CORAL RAG – massive, smooth textured, fossiliferous limestone).

The Newbridge Beds rest on a well developed, bored erosion surface cut in Coral Rag. Ammonites are not common.

Spaunton Moor Quarry [SE 722 868]

(AMPTHILL CLAY – pale grey clay with perisphinctid fragments seen to 0·5 m) m
SNAPE SANDSTONE
5. Very flaggy, silty, very fine grained, decalcified sandstone with abundant poorly preserved bivalves, belemnites and ammonites: *Amoeboceras* aff. *serratum* (J. Sowerby), *Microbiplices* sp. and *Chlamys midas.* 1·5
SPAUNTON SANDSTONE
4. Oolitic sandy limestone with *Perisphinctes* (*Arisphinctes*) *osmingtonensis* Arkell, *P.* (*Pseudarisphinctes*) *pachachii*, *P.* (*P.*) *damoni* Arkell, *Decipia decipiens*, *D. lintonensis* and *Myophorella clavellata.* 0·25
3. Massive, heavily bioturbated, fine grained sandstone, blue-hearted and calcareous when fresh, containing *P.* (*Dichotomosphinctes*) spp., *P.* (*Pseudarisphinctes*) *damoni*, *P.* (*Pseudopomerania*) *dewari* (Arkell), *D. decipiens*, *D. lintonensis* and *Amoeboceras* sp. 5·0
NEWBRIDGE BEDS
2. Soft, flaggy, fine grained sandstone with sporadic *Decipia ravenswykensis.* 1·2
1. Soft, blue-grey marl containing *P.* (*Pseudopomerania*) *dewari.* 1·0
(CORAL RAG – tough, massive, blue-hearted limestone).

This description of the section is a revised version of that published previously by the author (Wright 1972). Most ammonites have been collected from the top of Bed 3 and from Bed 4. Bed 5 comprises only a remnant of the Snape Sandstone, presumably due to erosion beneath the Ampthill Clay. The upper half of the measured section was seen in an outlier on a hill between two valleys. The outlier has now been quarried away completely, and the quarry only rarely yields interesting ammonites.

Ravenswyke Quarry [SE 707 874]

NEWBRIDGE BEDS m
2. Flaggy, very fine grained, laminated sandstone with *Decipia ravenswykensis* and *Myophorella clavellata.* seen to 0·9
1. Dark grey, shaley siltstone. 1·2
(CORAL RAG – flaggy calcilutite).

This quarry has yielded the best specimens of *Decipia ravenswykensis*, first figured by Wright (1972) as *Decipia* sp.

Snape Quarry [*SE 507 786*]

		m
	SNAPE SANDSTONE	
7.	Massive, fine grained *Rhaxella* spiculite containing siliceous or calcified spicules in a calcareous matrix, and with characteristic argillaceous laminae and lustre mottling; *Belemnites* aff. *explanatus* Phillips very common.	seen to 4·5
	– fault – unknown gap –	
	SPAUNTON SANDSTONE	
6.	Tough, yellow-weathering, siliceous spiculite; occasional *Belemnites* sp. and shell fragments.	seen to 1·5
5.	Thin bedded to flaggy, shelly argillaceous spiculite with *Decipia* sp. and *Chlamys midas*.	1·3
4.	Rubbly weathering, massive spiculite.	1·0
	NORTH GRIMSTON CEMENTSTONE	
3.	Pale grey, fine grained ?peloidal limestone.	0·5
2.	Grey-brown, impure limestone with flaggy intercalations.	1·0
1.	Grey, brown weathering, silty, shaley flags with alternations of more and less calcareous, flaggy bands	seen to 9·0

The North Grimston Cementstone is an impure limestone facies present immediately above the Coral Rag throughout the Howardian Hills, and probably equivalent in age to the Newbridge Beds. Arkell (1947*b*) recorded *Perisphinctes* (*Ampthillia*) *ampthillensis* Arkell and *P.* (*Arisphinctes*) aff. *kirkdalensis* Arkell from this quarry. Sykes and Callomon (1979) recorded *Amoeboceras transitorium*, *A. newbridgense* and *A. glosense*. These probably came from Bed 4.

Laysthorpe Quarry [*SE 646 785*]

		m
	SPAUNTON SANDSTONE	
6.	Fine grained, spicular sandy limestone with septarian cracks; fauna including *Amoeboceras nunningtonense*, *A. glosense*, *A. ilovaiskii*, *A. transitorium* and *Perisphinctes* (*?Arisphinctes*) sp.	seen to 0·05
5.	Flaggy, spicular sandstone with occasional *Amoeboceras* sp. and *P.* (*Pseudarisphinctes*) *pachachii*.	approx. 2·0
4.	Massive, pale brown weathering, spicular sandstone full of infilled *Thalassinoides* burrows, and with *Amoeboceras glosense*, *A. ilovaiskii*, *A.* sp., *Perisphinctes* (*Dichotomosphinctes*) sp. and numerous bivalve fragments, including *Chlamys* sp.	1·0
	NEWBRIDGE BEDS	
3.	Massive, white, blocky, homogeneous spiculite containing *Amoeboceras glosense*, *A. transitorium*, *A. nunningtonense*, *A. ilovaiskii*, *A.* sp., *Perisphinctes* (*P.*) aff. *parandieri* de Loriol, *P.* (*P.*) *uptonensis* Arkell, *P.* (*Arisphinctes*) *kirkdalensis*, *P.* (*A.*) sp., *P.* (*Dichotomosphinctes*) aff. *elizabethae* de Riaz, *P.* (*D.*) spp. and *Nanogyra nana*.	0·6
2.	White, laminated sandstone with frequent flattened, distorted ammonites, including *Amoeboceras* aff. *transitorium*, *A. ilovaiskii*, *Perisphinctes* (*P.*) aff. *parandieri*, *P.* (*A.*) *kirkdalensis*, *P.* (*D.*) sp. and *Decipia ravenswykensis*.	0·3
1.	Soft, flaggy, decalcified laminated sandstone.	approx. 0·6
	(CORAL RAG – massive, coralliferous micrite).	

The Upper Calcareous Grit of this quarry has yielded one of the most interesting Late Oxfordian perisphinctid faunas found in England, coming between the two well known faunas described by Arkell (1935–48) from the Osmington Oolite and the *Trigonia clavellata* Beds [=Clavellata Beds] of Dorset. It thus fills a significant gap in British Oxfordian biostratigraphy. Unfortunately, the quarry is no longer being worked, access is difficult, and the quarry face dangerous. The nearby Nunnington Railway Cutting Quarry [SE 648 787] and Nunnington Railway Cutting [SE 649 788] both show similar sections, though both are becoming overgrown.

Conditions of deposition

The base of the Upper Calcareous Grit is marked by a widespread erosion surface. The indurated Coral Rag was raised in a basin-wide, block uplift. On a regional scale, the uplift was uniform, but on a localized scale it was irregular, with areas of substantial erosion of the Coral Rag. The most notable of these is at Howldale Quarry near Pickering, where the Coral Rag is reduced to a 0·23 m remnant resting on eroded Malton Oolite. Elsewhere, active erosion seems to have been in progress while the Newbridge Beds were accumulating, bored pebbles of Coral Rag being incorporated into the marls of that member at nearby Newbridge Quarry. The Coral Rag is thin again at Laysthorpe and, 5 km to the east at East Ness, mapping by the author shows it to be absent altogether.

The marine transgression which heralded the deposition of the Upper Calcareous Grit was sluggish, and the sea poorly circulated. The calcareous mudstones of the North Grimston Cementstones pass northwards into the variably argillaceous Newbridge Beds – soft, grey, pebbly marls at Pickering, and laminated, silty clays and siltstones further west. The marine incursion in the Vale of Pickering area was thus nowhere profound. Pebbles formed on beaches fringing islands of Coral Rag, and were swept into the surrounding poorly circulated muddy lagoonal areas. Only at the western end of the Vale of Pickering are ammonites common, and conditions assumed to have been more open marine. The change to fine grained, offshore sand deposition in the Spaunton Sandstone seems therefore to have been due to uplift and erosion of source areas rather than to any shallowing of an already shallow basin. The highest Spaunton Sandstone, very shelly and occasionally oolitic, indicates a well circulated shelf sea with sediments affected by wave action during storms. The Snape Sandstone is laminated and bioturbated, with randomly orientated belemnites, and indicates a return to deeper conditions.

Preservation

The Upper Calcareous Grit ammonite fauna is, unfortunately, rarely well preserved. Rapid compaction has often flattened all but the body chamber, and even this is commonly well compacted, with blunting of the ribs. Allowance has to be taken for this when studying the figured specimens.

SYSTEMATIC PALAEONTOLOGY

The perisphinctid genera and subgenera recognized in the North Yorkshire Late Oxfordian are listed below, with brief diagnoses. Fuller descriptions are given in the references cited. Specimens from the Newbridge Beds and the Spaunton Sandstone are then described separately, as almost all the species are exclusive to only one of these formations. All specimens whose numbers are prefixed by 'U.' or 'D.C.' are in the author's collection housed at Royal Holloway College. Arrangements have been made to donate this collection eventually to The Yorkshire Museum, York. All specimens whose numbers are prefixed by 'M' are in the geology collection at Woodend Natural History Museum, Scarborough. The usual convention for expressing shell dimensions is followed, i.e. after a given diameter, whorl height, whorl breadth, and then umbilical width are listed as decimal fractions of that diameter.

In the course of conventional, morphogenic/morphospecific studies, as undertaken by Arkell (1935–48), genera, subgenera and species are based purely on morphological similarities and differences. Generic ranges have no phylogenetic significance, and separate subgeneric and specific taxa are used in most cases for dimorphs. Such isochronous diversity may in fact be wholly artificial (see discussion on p. 460). However, the present feeling amongst workers on this ammonite group, summed up by Atrops and Melendez (1993), is that the typological taxonomy, as adopted by earlier workers, is a useful tool for recognizing and characterizing morphologies, and such an approach is used here.

Superfamily PERISPHINCTACEAE Steinmann, 1890
Family PERISPHINCTIDAE Steinmann, 1890

Genus PERISPHINCTES Waagen, 1869
Subgenus PERISPHINCTES Buckman, 1920

Type species. Ammonites biplex Sowerby, 1821, designated by Buckman 1920, p. 26.

Diagnosis. Macroconch perisphinctids with standard biplicate ribbing on inner whorls changing at beginning of body chamber to large, swollen, sometimes cuneiform ribs (Arkell 1936, pp. lii–liv).

Subgenus DICHOTOMOSPHINCTES Buckman, 1926

Type species. *Perisphinctes antecedens* Salfeld, 1914, designated by Buckman 1926, pl. 650.

Diagnosis. Medium sized, microconch perisphinctids with biplicate ribbing ending in lappets (Arkell 1936, pp. xlv–xlvi, 1937*a*, pp. xlvii–xlviii); microconchs of *Perisphinctes s.s.* included in this subgenus except those of *P. variocostatus* group, which are included in *Dichotomoceras*.

Subgenus ARISPHINCTES Buckman, 1924

Type species. *Arisphinctes ariprepes* Buckman, by original designation (Buckman 1924, p. 33 and pl. 511).

Diagnosis. Large macroconch perisphinctids with biplicate or triplicate ribbing. Secondary ribbing gradually lost. Large, swollen simple ribs on body chamber (Arkell 1939, pp. lvi–lvii). Microconchs of this subgenus included in *Dichotomosphinctes*.

Subgenus PSEUDARISPHINCTES Arkell, 1939

Type species. *Perisphinctes* (*Pseudarisphinctes*) *shortlakensis*, by original designation (Arkell 1939, pp. lxiii–lxiv).

Diagnosis. Large (macroconch) and medium–small (microconch) perisphinctids with coarse, biplicate or triplicate ribbing on inner whorls and, in macroconch, large, swollen ribs on body chamber. Suture very simple.

Subgenus PSEUDOPOMERANIA subgen. nov.

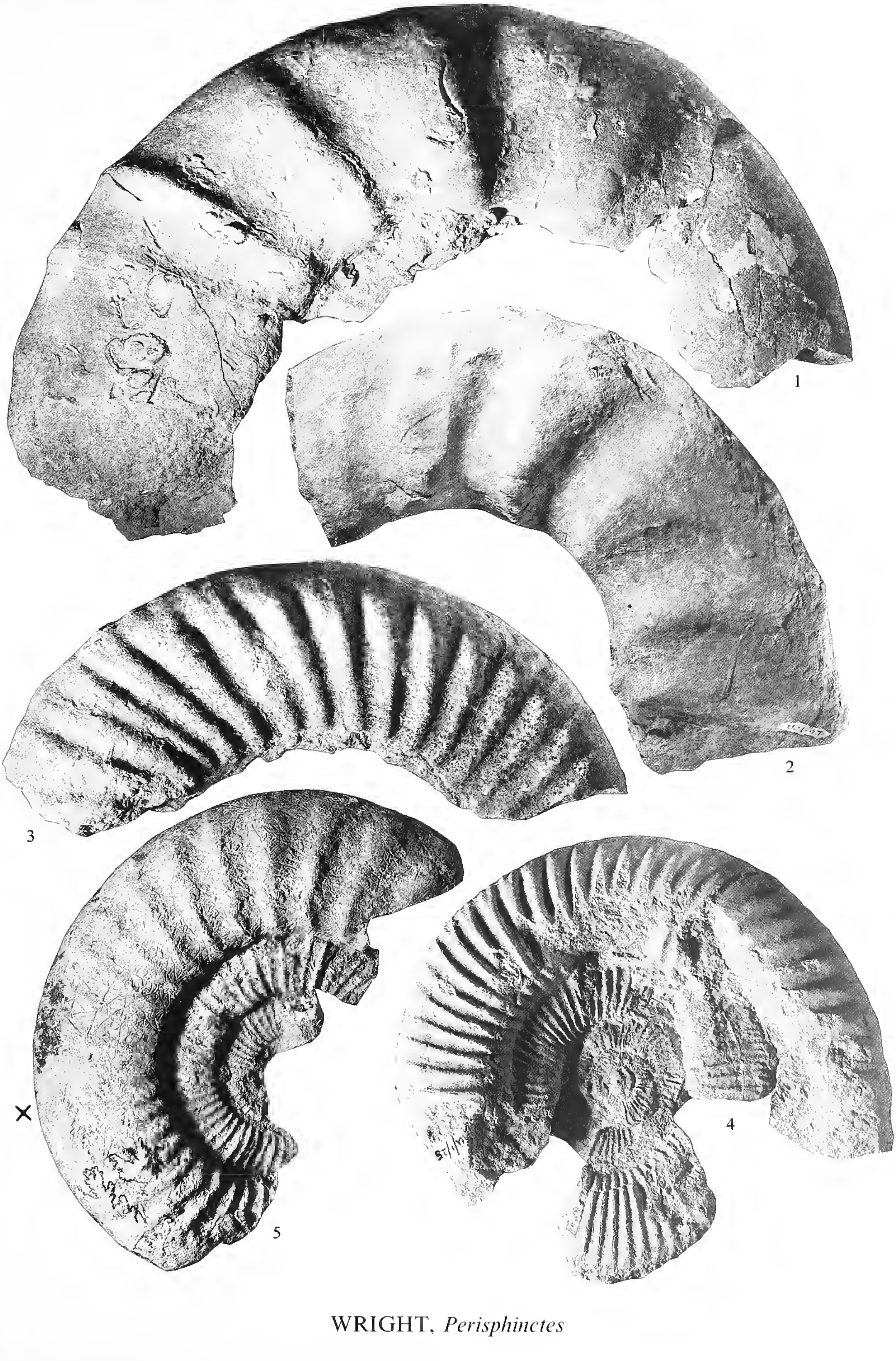
Type species. *Decipia* (*Pomerania*) *dewari* Arkell, 1947*b*, p. 375, pl. 77, fig. 1a–b).

Diagnosis. Medium-sized, macroconch perisphinctids with standard, biplicate ribbing on inner whorls, passing into smooth area near last septum. Coarse simple ribbing developed on body chamber. Sides and venter flat; whorl section quadrate. Microconch probably included in *Dichotomosphinctes*. Originally included by Arkell (1947*b*, pp. 374–377) in *Pomerania* as a subgenus of *Decipia*.

EXPLANATION OF PLATE 1

Fig. 1. *Perisphinctes* (*Perisphinctes*) *uptonensis* Arkell; M25; fragment of body chamber; ×0·4.
Fig. 2. *Perisphinctes* (*Perisphinctes*) aff. *parandieri* de Loriol; U.1.97; fragment of body chamber; ×0·4.
Figs 3–4. *Perisphinctes* (*Arisphinctes*) *kirkdalensis* Arkell. 3, U.1.107; fragment of body chamber. 4, U.1.25; probable immature specimen; suture visible on inner whorls but not on last half whorl; both ×0·5.
Fig. 5. *Perisphinctes* (*Arisphinctes*) sp. A; M23; ×0·5.
All specimens from the Newbridge Beds (Bed 3) of Laysthorpe Quarry, North Yorkshire.

Note: On this and following plates, the end of the phragmacone is marked by an ×. Specimens that are wholly septate and portions of non-septate body chambers are described as such in the plate descriptions; in all other cases, the presence and extent of suture lines cannot be determined.



WRIGHT, *Perisphinctes*

Subgenus DECIPIA Arkell, 1937*a*

Type species. Ammonites decipiens Sowerby, 1821, designated by Arkell (1937*a*, p. 68, 1938, p. 69).

Diagnosis. Medium-sized (macroconch) and small (microconch) perisphinctids with distinctive separation of groups of three or four secondary ribs, in bundles or sheaves, from widely spaced, swollen primary ribs. The macroconch adopts coarse simple ribs on the body chamber (Arkell, 1937*a*, pp. 44–45).

Genus MICROBIPLICES Arkell, 1936

Type species. Ammonites microbiplex Quenstedt, 1887–88, p. 876, pl. 94, fig. 36, designated by Arkell (1936, p. xli).

Diagnosis. Small (*c.* 100 mm) to very small (*c.* 40 mm) microconch perisphinctids with coarse biplicate ribbing and lappets.

Perisphinctids of the Newbridge Beds

Genus PERISPHINCTES Waagen, 1869
Subgenus PERISPHINCTES Buckman, 1920

Perisphinctes (*Perisphinctes*) *uptonensis* Arkell, 1935

Plate 1, figure 1

1935 *Perisphinctes* (*Perisphinctes*) *uptonensis* Arkell, p. 10, pl. 2, fig. 1a–b.
1936 *Perisphinctes* (*Perisphinctes*) *uptonensis*; Arkell, pl. 7, figs 2a–b, 3.
1963 *Perisphinctes* (*Perisphinctes*) *uptonensis* Arkell; Malinowska, p. 73, pl. 41.

Material. One body chamber fragment from Bed 3 at Laysthorpe Quarry (M25).

Description. The specimen consists of the final two-fifths of a whorl of an individual of 340 mm maximum diameter (Pl. 1, fig. 1). Although the aperture is broken away, the final 100 mm of whorl has two simple, fading ribs and numerous striations parallel to the aperture, showing that it was a mature adult. Three of the large, swollen cuneiform ribs, which are characteristic of this species, are preserved, matching closely those present in the holotype (Arkell 1935, pl. 2, fig. 1a). However, the holotype is larger, being an adult at 405 mm, as is the specimen figured by Malinowska (1963). Arkell (1936, pl. 7, figs 2a–b, 3) figured two specimens of a size comparable to the present specimen as a 'small variety' of *P. uptonensis*, considering that no new specific name was needed for these smaller forms.

Perisphinctes (*Perisphinctes*) aff. *parandieri* de Loriol, 1903

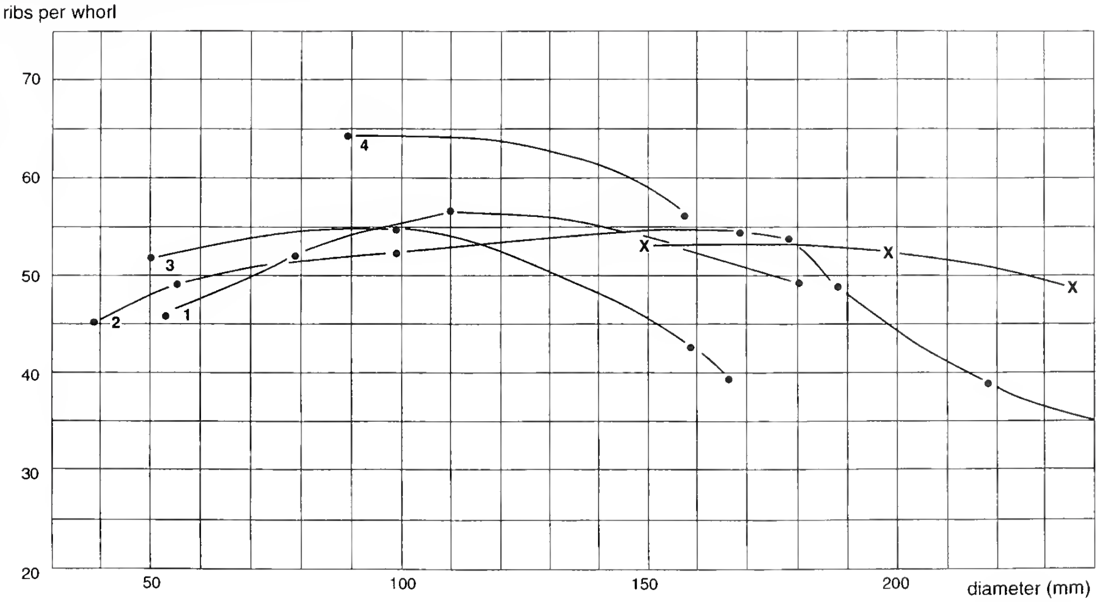
Plate 1, figure 2

1903 *Perisphinctes parandieri* de Loriol [*partim*], p. 90, pl. 7 only.
1939 *Perisphinctes* (*Perisphinctes*) *parandieri* de Loriol; Arkell, p. 105, figs 28–33 [includes detailed synonymy].
1966 *Perisphinctes* (*Perisphinctes*) *parandieri* de Loriol; Enay, p. 357, pl. 5, figs 1–3, pls 6–7.

Material. Two fragmentary specimens from Laysthorpe Quarry, U.1.97, a body chamber fragment from Bed 2, and U.1.111, the impression of part of the mid-whorl, from Bed 3.

Measurements. U.1.111.: ribs estimated at 68 per whorl at a diameter of 165 mm; U.1.97.: original whorl diameter *c.* 290 mm. Approximately eight ribs per half whorl at 290 mm diameter.

Description. The fragment of mid-whorl shows strong wiry primary ribs which bifurcate in most cases, but with occasional simple ribs and slight constrictions. The fragment of body chamber (Pl. 1, fig. 2) shows the characteristic ribbing with strong, swollen ridges developing at a diameter of approximately 240 mm. These are much more numerous than in *P. uptonensis*, and are not cuneiform in shape. They fade somewhat towards the



TEXT-FIG. 2. Rib curves of *Perisphinctes* (*Arisphinctes*) spp. from the Newbridge Beds; ×, *P.* (*A.*) *kirkdalensis* (holotype, after Arkell (1947*b*)); 1, *P.* (*A.*) *kirkdalensis* (U.1.106); 2, *P.* (*A.*) sp. B (M26); 3, *P.* (*A.*) sp. A (M23); 4, *P.* (*A.*) *kirkdalensis* (U.1.25).

aperture, which is partly present in this specimen. Most specimens of *P. parandieri* are adult at around 350 mm, but Arkell (1939, p. 107) refers to a smaller variety probably adult at less than 300 mm.

Subgenus ARISPHINCTES Buckman, 1924

Perisphinctes (*Arisphinctes*) *kirkdalensis* Arkell, 1947*b*

Plate 1, figures 3–4; Text-figure 2

1947*b* *Perisphinctes* (*Arisphinctes*) *kirkdalensis* Arkell, p. 367, text-fig. 130.

Material. Seven specimens from Bed 3 at Laysthorpe Quarry, U.1.25, U.1.107, U.1.89, U.1.92, U.1.93, U.1.105 and U.1.106.

Measurements. U.1.25: maximum diameter preserved 162 mm; at 155 mm, 0·30, –, 0·48; 56 ribs at 158 mm, 64 at 90 mm; U.1.106: specimen badly crushed, maximum diameter preserved *c.* 180 mm; 46 ribs at 53 mm, 52 at 80 mm, 56 at 111 mm, 49 at 180 mm.

Description. The coiling is moderately evolute, and the bifurcation points are high on the whorl side so that they are well hidden by the umbilical seam. At 50 mm, 45 ribs per whorl is the norm, though occasionally young individuals may have as many as 65 at this diameter. When the secondaries are first seen, at 70 mm, there is the standard bifid pattern. Occasional intercalated secondaries appear by 95 mm. By 130 mm, the secondary ribbing is beginning to fade. On U.1.25 (Pl. 1, fig. 4), faint bifid ribs run up on to the ventro-lateral edge at 150 mm, the venter being almost smooth. On other specimens, faint, trifid sheaves of secondaries are present at this stage, but fade rapidly. The change from bifid ribbing to strong, simple ribs is the feature which places these specimens in *Arisphinctes*. Bifid ribbing continues to the aperture in *Dichotomosphinctes*. U.1.25 is a substantially complete individual, and may be immature. Most specimens are still septate at this diameter (155 mm).

The rib curve (Text-fig. 2) thus shows the number of primary ribs rising gently to 55 to 65 ribs per whorl at 100 to 120 mm, and falling away to 50 ribs per whorl at 200 mm. This distinguishes this species from the slightly younger *A. ringsteadensis* Arkell, figured by Arkell (1935, pls 3–4, 1936, pls 7–8). *A. ringsteadensis* never has more than 45 ribs per whorl.

The holotype of *A. kirkdalensis* (Arkell 1947*b*, text-fig. 130) is not sufficiently well preserved in the inner whorls to make an accurate rib count, but where a count is possible it matches the Laysthorpe specimens well (Text-fig. 2). The very gradual adoption of simple ribbing is a common characteristic. The holotype has bifurcation only of the secondary ribs, whereas the Laysthorpe specimens show a complete range between bifurcation and trifurcation. This seems to be a variable feature in species of *Arisphinctes*; similar variation also occurs in the allied *A. ringsteadensis* (Arkell 1936, pl. 8). The exact horizon in the Kirkdale Cutting is not known, but the holotype probably came from the Spaunton Sandstone, as the Newbridge Beds are thin and shaly here.

Perisphinctes (*Arisphinctes*) sp. A

Plate 1, figure 5; Text-figure 2

Material. One specimen (U.1.80) from Bed 2 at Laysthorpe Quarry, and one specimen (M23) from Bed 3.

Measurements. M23: maximum diameter preserved 166 mm; at 165 mm, 0·29, 0·22, 0·50; *c*. 52 ribs at 50 mm, *c*. 55 at 100 mm, *c*. 40 at 166 mm.

Description. The specimen figured on Plate 1, figure 5 is distinguished by the presence of simple ribs with an almost smooth venter at a diameter of only 130 mm. At 165 mm, large, swollen ribs appear. The rib curve diverges markedly from that of *A. kirkdalensis* (Text-fig. 2). Specimen U.1.80, which is an entirely flattened body chamber not suitable for illustration, continues the rib pattern at the point where M23 is broken. The simple ribs present in the area of the last septum continue to at least 270 mm, becoming gradually more widely spaced so that there are only ten ribs on the last half whorl. The ribs are slightly raised and bulbous at the ventro-lateral edge. The venter is smooth. The maximum original diameter was probably 300 mm. There is insufficient material at present to decide whether these specimens represent a variant of *A. kirkdalensis*, or whether they belong to a new species.

Perisphinctes (*Arisphinctes*) sp. B

Plate 2, figure 1; Text-figure 2

Material. One large natural mould (M26) from Bed 3 at Laysthorpe Quarry, from which the figured Vinamould cast was made.

Measurements. Maximum diameter 330 mm complete with aperture; at 325 mm, 0·26, –, 0·51; 45 ribs at 38 mm, *c*. 49 at 55 mm, *c*. 52 at 100 mm, 54 at 170 mm, 53 at 180 mm, 49 at 190 mm, 38 at 220 mm, 28 at 320 mm.

Description. This specimen appears to be closely related to *A. kirkdalensis*, having the same very gradual appearance of simple ribbing. However, it adopts large swollen ribs at a diameter (230 mm) where *A. kirkdalensis* still has much less prominent ribs, and thus at this diameter M26 has 13 ribs per whorl fewer than the holotype of *A. kirkdalensis* (Text-fig. 2). Further material will be required before it will be possible to decide whether M26 is the adult body chamber of *A. kirkdalensis*, or whether U.1.80, described under *Arisphinctes* sp. A, represents the adult.

EXPLANATION OF PLATE 2

Fig. 1. *Perisphinctes* (*Arisphinctes*) sp. B; Vinamould cast of the original natural mould, M26; specimen complete, including part of aperture; ×0·36.

Figs 2–3. *Perisphinctes* (*Dichotomosphinctes*) aff. *elizabethae* de Riaz; 2, U.1.24; crushed inner whorls. 3, U.1.91; partial body chamber, with impression of inner whorl; both ×1.

Fig. 4. *Perisphinctes* (*Dichotomosphinctes*) sp. A; U.1.102; largely complete, markedly flattened specimen showing approximately three-quarters of body chamber; ×0·5.

All specimens from the Newbridge Beds (Bed 3) of Laysthorpe Quarry, North Yorkshire.

PLATE 2

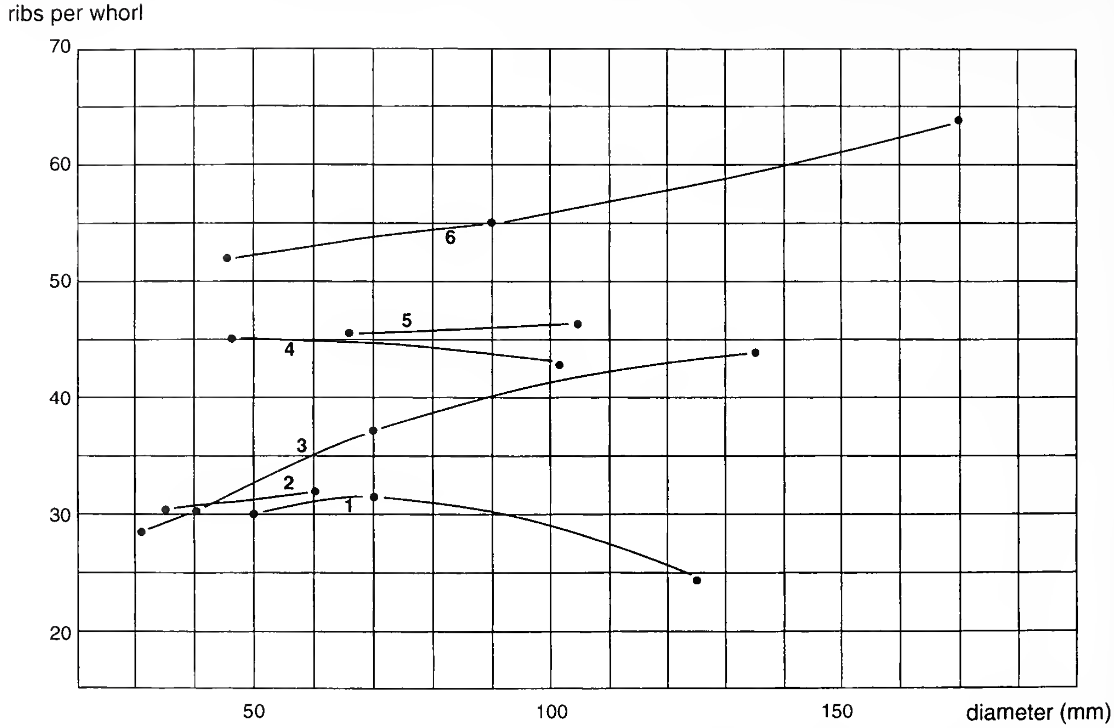

1


2


3


4

WRIGHT, *Perisphinctes*



TEXT-FIG. 3. Rib curves of *Decipia ravenswykensis* sp. nov. and *Perisphinctes* (*Dichotomosphinctes*) spp. from the Newbridge Beds: 1–2, *Decipia ravenswykensis* (U.5.7 and U.5.1 (holotype)); 3, *P.* (*Dichotomosphinctes*) sp. C (U.1.100); 4–5, *P.* (*D.*) sp. B (U.1.28, U.1.103); 6, *P.* (*D.*) sp. A (U.1.102).

Subgenus DICHOTOMOSPHINCTES Buckman, 1926

Perisphinctes (*Dichotomosphinctes*) aff. *elizabethae* de Riaz, 1898

Plate 2, figures 2–3; Plate 4, figure 3

1898	*Perisphinctes elizabethae* de Riaz, p. 22, pl. 12, figs 4 [lectotype], 5.
1966	*Perisphinctes* (*Dichotomosphinctes*) *elizabethae* de Riaz; Enay, p. 490, pl. 30, figs 4–5, pl. 31, figs 2–6 [includes detailed synonymy].
1977	*Perisphinctes* (*Dichotomosphinctes*) *elizabethae* de Riaz; Matyja, pl. 8, fig. 11.
1980*b*	*Perisphinctes* (*Dichotomosphinctes*) *elizabethae* de Riaz; Brochwicz-Lewinski, p. 210, pl. 1, fig. 1.
1989	*Perisphinctes* (*Dichotomosphinctes*) *elizabethae* de Riaz; Fisher and Gygi, p. 1588, fig. 5B.

Material. Three specimens, the compressed inner whorls (U.1.24) and a fragment of body chamber (U.1.91) from Bed 3 at Laysthorpe Quarry, and a body chamber fragment (U.1.88) found loose at Oswaldkirk.

Measurements. U.1.24: 56 ribs per whorl at 80 mm: U.1.88: preserved to *c*. 145 mm diameter, estimated as originally having 89 ribs per whorl at 145 mm.

Description. Both Laysthorpe specimens show fine, wiry, prorsiradiate ribbing bifurcating at about two-thirds of the whorl height, and with strong constrictions and simple ribs developing on the body chamber. This rib style and rib density match closely those of *P. elizabethae*, though the fragmentary nature of the material means that the identification must remain tentative. However, the high density of the ribbing of U.1.88, unique in the British Oxfordian, matches closely that of Enay's (1966) specimens, which have between 80 and 95 ribs per whorl at this diameter. The ribbing also matches closely that of the inner whorls of *P.* (*Perisphinctes*) *densecostatus* Enay, and this is almost certainly the microconch of that species. *Lithacoceras* (*Larcheria*) spp. are similarly densely ribbed, but the characteristic fading of the ribs about the mid-point of the whorl side is not present in these specimens.

Perisphinctes (*Dichotomosphinctes*) sp. A

Plate 2, figure 4; Text-figure 3

Material. One largely complete, crushed specimen which has most of the body chamber preserved, from Bed 2 at Laysthorpe (U.1.102), and one whorl fragment from Bed 3 (U.1.90).

Measurements. U.1.102: maximum diameter preserved 175 mm; 52 ribs at 45 mm, 55 at 90 mm, 64 at 170 mm.

Description. The coiling is quite evolute, with the umbilical seam only just covering the bifurcation points. The secondaries bifurcate normally, with occasional simple ribs. At 170 mm, bifurcation is strongly developed, with prominent wiry ribs, and the number of primary ribs is still increasing. Close to the aperture, which is partly visible on the reverse of the specimen, there is one more widely spaced simple rib.

Remarks. P. (*Dichotomosphinctes*) sp. A has broader, more rounded, less prorsiradiate ribbing than *P.* (*D.*) *elizabethae*, and has no marked constrictions, only occasional simple ribs. However, these are rather variable features in *Dichotomosphinctes*, and species of this subgenus are distinguished principally by means of rib curves. Enay (1966) figured rib curves for a number of species of *Dichotomosphinctes* from the Jura, including *D. elizabethae*, *D. luciaeformis* Enay, *D. wartae* Bukowski, *D. dobrogensis* Simionescu and *D. antecedens* Salfeld. The rib curve of *D.* sp. A (Text-fig. 3) comes close to few of these. The increase in number of ribs per whorl with increasing diameter is only moderate, so that the curve of *D.* sp. A does not match the steep increase in rib density of *D. dobrogensis* or *D. wartae*. *D.* sp. A has only 64 ribs on the last whorl as against an average of 80 in *D. wartae*. *D. elizabethae* has 85 to 95 ribs per whorl at this diameter. The closest fit is with *D. antecedens* var. C of the Middle Oxfordian, described by Enay (1966, p. 476) as having more densely ribbed inner whorls than is typical of this species. *D.* sp. A may well prove to be a new Late Oxfordian species closely related to *D. antecedens*. Enay (1966) did not specify the age of his var. C, although he recorded '*D. antecedens*' from the Parandieri Subzone.

Perisphinctes (*Dichotomosphinctes*) sp. B

Plate 3, figures 3–4; Text-figure 3

Material. One almost complete but poorly preserved specimen from Bed 2 at Laysthorpe Quarry (U.1.28), and one near complete specimen (U.1.103) and three whorl fragments (U.1.12, U.1.87, and U.1.112) from Bed 3.

Measurements. U.1.28: maximum diameter preserved 102 mm, with one third of a whorl of body chamber; at 95 mm, 0·37, –, 0·43; 43 ribs at 102 mm, *c.* 45 at 45 mm. U.1.103: maximum diameter preserved 118 mm, with half a whorl of body chamber; at 102 mm, 0·32, –, 0·45; 46 ribs at 105 mm, 45 at 65 mm.

Description. The strong, rectiradiate primary ribs may bifurcate at just below two-thirds of the whorl height or, commonly, they may carry on as simple ribs over the venter. Two or three bifurcating primary ribs are followed by a simple rib. One marked constriction is visible on U.1.103 (Pl. 3, fig. 4) and on U.1.12. The ribs run strongly over the venter. This bold, moderately spaced ribbing is very characteristic of the species. There are some 15 ribs per whorl fewer than on *P.* (*D.*) sp. A at the largest diameter seen. The probable maximum original diameter was *c.* 120 mm.

Remarks. None of the species of *Dichotomosphinctes* figured by Enay (1966) from the Jura, by Polish authors, or by Arkell (1935–48) from the English Corallian Beds, matches *P.* (*D.*) sp. B in its moderately dense and bold ribbing and flat rib curve (Text-fig. 3). This may well be a new species, although better material is required to differentiate it.

Perisphinctes (*Dichotomosphinctes*) sp. C

Plate 3, figure 2; Text-figure 3

Material. One almost complete specimen from Bed 3 at Laysthorpe Quarry.

Measurements. U.1.100: maximum size 135 mm; at 130 mm, 0·28, –, 0·46; 44 ribs at 135 mm, 37 at 70 mm, *c*. 30 at 40 mm, *c*. 28 at 30 mm.

Description. The specimen consists of a complete, microconch adult with the usual poor preservation of the inner whorls characteristic of the Newbridge Beds, though with a fairly well preserved body chamber. Although the inner whorls are poorly preserved, coarse, prorsiradiate primary ribs can be distinguished even at very small diameters. On the body chamber, the stout primary ribs generally bifurcate at two-thirds of the whorl height, with the secondaries running strongly over the venter. Every fourth or fifth primary rib continues as a simple rib, though marked constrictions are not evident. The ribbing coarsens slightly towards the aperture, where a flared final rib is visible, though any lappets, if originally present, appear to have been broken off.

Remarks. Dichotomosphinctes sp. C is unique amongst the Newbridge Beds material in its coarse ribbing (Text-fig. 3). It has 30 ribs per whorl at a diameter of 40 mm, whereas *P.* (*D.*) sp. B has 45 at this diameter. As with some of the other *Dichotomosphinctes* from these beds, comparison is more easily made with other Middle Oxfordian rather than Upper Oxfordian forms. Thus, the coarse early ribbing matches quite closely that of *P.* (*D.*) *rotoides* Ronchadzé *sensu* Arkell (1938, p. 90), though this species is mature at 100 mm with a more steeply rising rib curve than that of *P.* (*D.*) sp. C. *P.* (*D.*) *ouatius* (Buckman) is similarly coarsely ribbed, though mature at an even earlier diameter (Arkell 1936, p. xliv). Nothing similar appears to have been figured by French, German or Polish authors, and I am driven to the conclusion that this is a new species, although it would not be proper to define a new species on the basis of just this one specimen.

Subgenus PSEUDOPOMERANIA subgen. nov.

Perisphinctes (*Pseudopomerania*) *dewari* (Arkell, 1947)

Plate 3, figure 1a–b

1974*b* *Decipia* (*Pomerania*) *dewari*, Arkell, p. 375, pl. 77, figs 1, 5.

Material. One incomplete specimen consisting of the crushed inner whorls and an outer whorl fragment showing the first third of the body chamber, from Bed 1 at Spaunton Moor Quarry (U.3.19).

Measurements. U.3.15: maximum diameter preserved 215 mm; at 215 mm, 0·24, –, 0·56; 37 ribs at 40 mm, 44 at 55 mm.

EXPLANATION OF PLATE 3

Fig. 1a–b. *Perisphinctes* (*Pseudopomerania*) *dewari* (Arkell); U.3.19; Spaunton Moor Quarry, Bed 1; 1a, body chamber showing absence of ribs in area of last septum; × 0·5. 1b, inner whorls of same specimen, showing biplicate perisphinctid style ribbing; × 1.

Fig. 2. *Perisphinctes* (*Dichotomosphinctes*) sp. C; U.1.100; Laysthorpe Quarry, Bed 3; specimen complete, including aperture; inner whorls are crushed but body chamber still retains true cross section; × 0·8.

Figs 3–4. *Perisphinctes* (*Dichotomosphinctes*) sp. B; Laysthorpe Quarry, Bed 3; 3, U.1.112; fragment of body chamber; × 1. 4, U.1.103; specimen with crushed inner whorls and part of body chamber; × 0·7. Both body chambers substantially flattened.

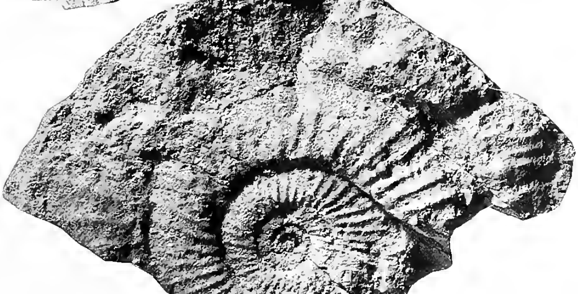
All specimens from the Newbridge Beds.

PLATE 3


1a


2


3


1b


4

WRIGHT, *Perisphinctes*

Description. Although the inner whorls of U.3.15 are badly crushed, sufficient is visible to determine most of the characters of the species (Plate 3, fig. 1b). The primary ribbing is quite fine and dense. No constrictions are visible. The junction between the primary and secondary ribs is crushed beneath the umbilical seam of the overlapping whorl, but the secondary ribs (two per primary) are visible on the venter at 60 mm. Regular bifurcation is not present as far as can be seen; some secondaries are not connected to the primaries but run between them. The body chamber (Pl. 3, fig. 1a) is almost smooth for the first quarter of a whorl, but then develops increasingly prominent prorsiradiate primary ribs which pass gently over the venter. Probably one third of a whorl is missing up to the aperture. The match with Arkell's (1947*b*) pl. 78, fig. 5 is very close.

Remarks. The specimens figured by Arkell (1947*b*, pl. 78) as *Decipia* (*Pomerania*) *dewari* came from the Ampthill Clay of Cambridgeshire, and are body chambers very similar to that of Plate 3, figure 1a, but not immediately associated with inner whorls. Arkell (1939, p. lxiv) reported that 'the ribbing of *Pomerania* is believed to be like that of *Decipia* on the inner whorls' but specimens have now been found in Yorkshire which show that the inner whorls have normal, biplicate, *Perisphinctes*-type ribbing (Pl. 3, fig. 1b). *Pomerania*, as defined by its type species, came from the Upper Jurassic of Pomerania thought by Arkell to be of Late Oxfordian age, presumably Pseudocordata Zone, but possibly Kimmeridgian. Thus its connection with Nunningtonense and Cautisnigrae Subzone forms from England is very tenuous. A new subgenus, *Pseudopomerania*, is established here as a subgenus of *Perisphinctes* to include the English forms which have a body chamber like *Pomerania*, but normal *Perisphinctes*-type inner whorls.

Genus DECIPIA Arkell, 1937

Decipia ravenswykensis sp. nov.

Plate 4, figures 1, 4–6; Plate 8, figure 5; Text-figure 3

1972 *Decipia* sp.; Wright, pl. 14, fig. 4.
1976 *Decipia* cf. *lintonensis* Arkell; Sykes and Surlyk, p. 431, fig. 5B.

Diagnosis. Decipia with very bold primary ribs, and secondaries which connect to primaries in bifid or trifid groups, with one intercalatory. Within bifid pair, one secondary usually more prominent, carrying on line of primary. Within trifid group, secondaries may join up in characteristic pitchfork prong arrangement. On macroconch, secondary ribs fade at about 100 mm, and secondaries reduced to simple nodes on umbilical edge by about 130 mm. Faint simple ribs develop close to aperture.

Material. The holotype (U.5.1, Pl. 4, fig. 1) plus seven other specimens (U.5.2–U.5.7, U.5.10) from Bed 2 at Ravenswyke Quarry. Three specimens (U.3.14, U.3.33 and U.3.44) from near the top of Bed 2 at Spaunton Moor Quarry; two specimens (U.6.1 and U.6.2) from Bed 1 at Wrelton Quarry; two specimens (M9 and U.1.94) from ?Bed 2 at Nunnington Railway Cutting Quarry, and two specimens (U.2.42–U.2.43) from Bed 2 at Newbridge Quarry.

EXPLANATION OF PLATE 4

Fig. 1. *Decipia ravenswykensis* sp. nov; U.5.1, holotype; Newbridge Beds; Ravenswyke Quarry, Bed 2; Plasticine squeeze of original natural mould; × 1.

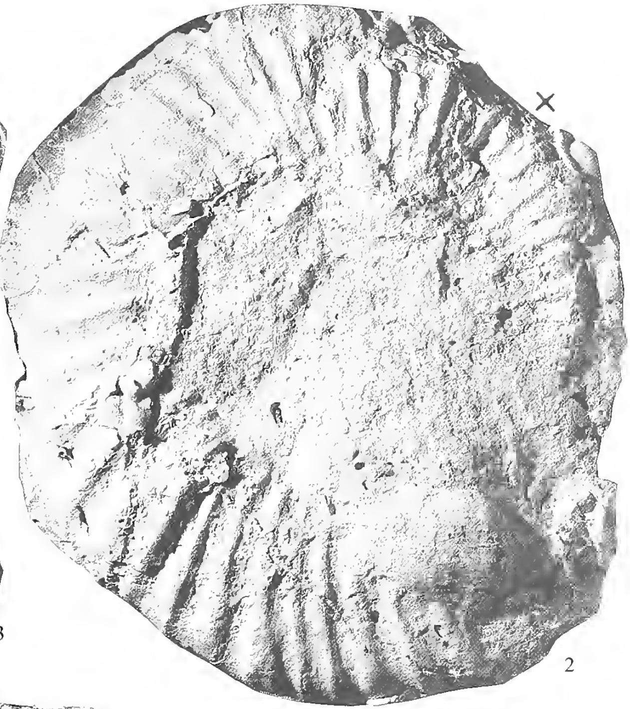
Fig. 2. *Perisphinctes* (*Arisphinctes*?) sp., U.1.110; Spaunton Sandstone; Laysthorpe Quarry, Bed 6; plaster of Paris cast of original natural mould; ×0·34.

Fig. 3. *Perisphinctes* (*Dichotomosphinctes*) aff. *elizabethae* de Riaz; U.1.88; ?Newbridge Beds; specimen found loose in a field at Oswaldkirk; ×0·52.

Figs 4–6. *Decipia ravenswykensis* sp. nov.; Newbridge Beds; 4, U.2.42; Newbridge Quarry, Bed 2; Plasticine squeeze of original natural mould; ×0·8. 5, U.5.4; Ravenswyke Quarry, Bed 2; × 1. 6, U.5.7; Plasticine squeeze of original natural mould of a macroconch, with initial part of body chamber preserved; inner whorls crushed; × 1.

PLATE 4


1



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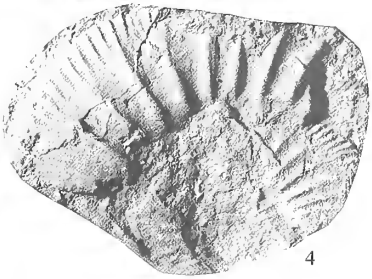
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6


5

WRIGHT, *Decipia*, *Perisphinctes*

Measurements. U.5.1 (holotype): maximum diameter preserved 63 mm; at 60 mm, 0·30, –, 0·47; 30 ribs at 35 mm, 32 at 60 mm. U.5.7: maximum diameter preserved *c.* 133 mm; at 133 mm, 0·29, –, 0·43; 24 ribs at 125 mm, *c.* 31 at 75 mm, 30 at 50 mm.

Description. The holotype consists of a well preserved natural mould (figured as a Plasticine squeeze in Pl. 4, fig. 1) and a counterpart showing poorly preserved inner whorls only. The coiling is moderately involute. The primary ribs are strong, wiry and widely spaced, 30 ribs per whorl being average for the species (Text-fig. 3). A spiral band of only slightly raised ribs follows the mid-point of the whorl side, and each succeeding whorl overlaps onto this band. There are 3·2 secondary ribs per primary on the last quarter whorl visible. Each primary rib will link up with a secondary if there is one suitably placed; otherwise, there may be an indistinct bifurcation at about the mid-point of the whorl side, or the secondaries may run down between the primaries and fade. The secondary ribs are strongly developed over the venter. Marked constrictions with a strong, simple rib occur two or three times per whorl. Sutures can be made out indistinctly in the counterpart, and the last quarter of a whorl is body chamber; the holotype is thus a microconch.

Specimen U.5.7 is a natural mould of a macroconch, and a plasticine squeeze is figured (Pl. 4, fig. 6). The inner whorls are nearly flattened, but the first third of the body chamber is present, enabling estimation of the maximum original size at probably 190 mm. The secondary ribs are just visible at the start of the body chamber, but rapidly fade away, leaving fairly widely spaced, rounded umbilical nodes as the only ornament. The coiling is slightly more involute than in the holotype. Specimen U.5.10 (Pl. 8, fig. 5) is heavily encrusted with oysters, but shows the body chamber close to the aperture at 230 mm. The umbilical nodes are more swollen than in U.5.7, and faint simple ribs are developed close to the aperture, which is not preserved.

One individual from Ravenswyke Quarry (Pl. 4, fig. 5) shows more delicate ribbing than is usual, and is thus transitional to *D. decipiens.* The bold primary ribs which link up with suitably placed secondary ribs are well seen in a fragment from Newbridge Quarry (Pl. 4, fig. 4). Specimens from Spaunton Quarry and Wrelton Quarry tend to be more coarsely ribbed, a specimen from the latter locality having only 2·3 secondaries per primary. A poorly preserved macroconch from Nunnington Railway Cutting Quarry shows the suture, with slender lobes lacking florid development and with wide saddles. The external, lateral and suspensive lobes are of equal length.

Remarks. Decipia ravenswykensis is distinguished from other species of *Decipia* by the sharp, rod-like primary ribs present on the inner whorls each linking up directly to one secondary, with other secondaries branching off in either a backwards or a forwards direction, or running down between the primaries. In *D. decipiens* and *D. lintonensis*, described below (pp. 456–460), the primary ribs broaden and flatten at the mid-point of the whorl side, and bundles of three or four secondaries arise in sheaves from each broadened primary. Specimen U.5.4 is intermediate in this respect, having the delicate ribbing of *D. decipiens*, but not having secondaries arising in sheaves. The macroconchs are easily distinguished, *D. ravenswykensis* having umbilical nodes on its body chamber, as distinct from the simple ribs of *D. decipiens* (compare Pl. 8, fig. 5 with Pl. 7, fig. 1).

Perisphinctids of the Spaunton Sandstone

Genus PERISPHINCTES Waagen, 1869
Subgenus PERISPHINCTES Waagen, 1869

Perisphinctes (*Perisphinctes*) *cautisnigrae* Arkell, 1935

1935 *Perisphinctes* (*Perisphinctes*) *cautisnigrae* Arkell, p. 14, pl. 1, figs 1a–b, 2; pl. 3, figs 1–2.

Material. One septate whorl fragment (U.2.117) from Bed 3 at Newbridge Quarry; the diameter of the complete whorl was approximately 160 mm. The fragment still shows strong, biplicate ribbing with about 70 primary ribs per whorl.

Remarks. Although the specimen is only a small fragment, the rib density, and the fact that there is no modification of the ribs at a diameter where it would be well marked in *Arisphinctes*, means that the specimen can be assigned quite confidently to *P. cautisnigrae.*

Subgenus ARISPHINCTES Buckman, 1924

Perisphinctes (*Arisphinctes*) *osmingtonensis* (Arkell, 1936)

1936 *Perisphinctes* (*Dichotomosphinctes*) *osmingtonensis* Arkell, p. 31, pl. 9, figs 1–4.
1947 *Perisphinctes* (*Arisphinctes*) *osmingtonensis*; Arkell, p. 369.

Material. One inner whorl fragment (U.3.3) from Bed 4 at Spaunton Moor Quarry.

Measurements. U.3.3: maximum diameter preserved 110 mm; at 110 mm, 0·31, –, 0·48; *c*. 54 ribs at 110 mm.

Description. This non-septate whorl fragment shows the characteristic high whorl side, strong, closely spaced primary ribs, and secondaries arising at rather indistinct furcation points at two-thirds of the whorl height. As in the specimens figured by Arkell (1936), the anterior secondary will commonly continue the line of the primary while the posterior of the pair will branch from it in a backwards direction. Trifurcation is also common, as are constrictions and a simple rib.

Perisphinctes (*Arisphinctes*?) sp.

Plate 4, figure 2

Material. One mould of a nearly complete body chamber (U.1.110) from a calcareous concretion from Bed 6 at Laysthorpe Quarry.

Measurements. U.1.110: maximum diameter preserved 275 mm; at 270 mm, 0·29, –, 0·48; estimated as having 52 ribs at 210 mm.

Description. The last quarter of a whorl of the septate part of the shell is visible but poorly preserved, with 13 strong, rounded primary ribs. These bifurcate or trifurcate, two or three secondaries per primary being seen indistinctly. At the position of the last septum, the primary ribs become slightly bolder and simple, swelling slightly at the ventro-lateral edge, and then largely fading on the venter. Thirty of these ribs are present in the two-thirds of a whorl of body chamber preserved. The whorl section is flat sided and flat ventered, although the width of the whorl is not known.

Remarks. Even placing this specimen into a subgenus is difficult, especially as the suture is very indistinct. Considering all the macroconch subgenera of *Perisphinctes*, the group of *P*. (*Arisphinctes*) *helenae* de Riaz and *P*. (*A*.) *vorda* Arkell fits best, having the same change from biplicate to simple ribs of exactly this number and style at the same diameter, and having a similar whorl section.

Subgenus DICHOTOMOSPHINCTES Buckman, 1926

Perisphinctes (*Dichotomosphinctes*) sp. D

Plate 5, figure 3; Text-figure 4

Material. Two poorly preserved but largely complete specimens, one from Bed 4 at Newbridge Quarry (U.2.119) and one from Bed 3 at Spaunton Moor Quarry (U.3.50).

Measurements. U.3.50: maximum diameter preserved 92 mm; at 90 mm, 0·28, –, 0·49; 51 ribs at 90 mm, 44 at 35 mm.

Description. The better specimen (Pl. 5, fig. 3) consists of a poorly preserved, almost complete, microconch adult *Dichotomosphinctes* of maximum original size of about 95 mm. The primary ribs are strong and wiry, and bifurcate quite regularly at about two-thirds of the whorl height. An unconnected secondary followed by a simple rib is present about every fifth primary. Marked constrictions are not evident. The secondaries run strongly over the venter.

Remarks. This species compares quite closely with *Dichotomosphinctes* sp. B from the Newbridge Beds, having a very similar rib style, but having slightly more ribs to the whorl (Text-fig. 4), and being adult at 95 mm rather than 135 mm as in *D*. sp. B.

Perisphinctes (*Dichotomosphinctes*) sp. E

Plate 5, figure 2; Text-figure 4

Material. Three specimens, one almost complete, from Bed 3 at Spaunton Moor Quarry (U.3.13, U.3.22, U.3.52), and one specimen (M18, a complete, internal mould) from Bed 4 at this locality; six specimens from Bed 4 at Newbridge Quarry (U.2.27, U.2.126, U.2.132, U.2.134, U.2.135 and U.2.137).

Measurements. M18: maximum size preserved 92 mm; at 89 mm, 0·24, –, 0·49; 34 ribs at 92 mm, 32 at 63 mm, 32 at 30 mm. U.3.13: 37 ribs at 95 mm, 33 at 50 mm. U.3.52: *c*. 39 ribs at 75 mm, *c*. 33 at 25 mm.

Description. This distinctive species is one of the most common perisphinctids in the Spaunton Sandstone. It has bold, widely spaced primary ribs and a very gently rising rib curve so that there are never more than 40 ribs per whorl (Text-fig. 4). The primary ribs bifurcate or trifurcate at about two-thirds of the whorl height with, on average, three bifurcations to two trifurcations. The secondary ribs are also bold, and run strongly over the venter. Simple ribs and constrictions are developed close to the aperture. The whorl section is slim, flat-sided, with a rounded venter. Specimen M18 (Pl. 5, fig. 2) is adult, showing uncoiling of the umbilical seam and a closing up of the primary ribs close to the aperture. It is thus adult at 90 mm, though these features are seen at 100 mm in specimen U.3.22.

Remarks. As in *P.* (*Dichotomosphinctes*) sp. C, the comparison is best made with previously described Middle Oxfordian, rather than Upper Oxfordian forms. *P.* (*D.*) *rotoides sensu* Arkell (1938) has a similar number of ribs per whorl at early diameters, but has a steeply rising rib curve (Arkell 1938, text-fig. 23), rather than the flat curve of *P.* (*D.*) sp. E. The latter species is distinguished from *P.* (*D.*) sp. C by its smaller size, being adult at 90–100 mm, rather than at 135 mm. The microconch of *Pseudarisphinctes damoni* (Pl. 6, figs 1, 5) is similarly coarsely ribbed, but *P. damoni* has a distinctive round whorl section, rather than the flat-sided whorl section of *P.* (*D.*) sp. E.

Subgenus PSEUDARISPHINCTES Arkell, 1935

Perisphinctes (*Pseudarisphinctes*) *pachachii* Arkell, 1935

Plate 5, figures 4–5; Plate 8, figure 2a–b; Text-figure 5

1935 *Perisphinctes* (*Biplices*?) *pachachii* Arkell, p. 26, pl. 2, fig. 2.

Material. Eight specimens, six (U.3.26, U.3.35, U.3.49, U.3.54, U.3.57 and U.3.63) from Bed 4 at Spaunton Moor Quarry, one specimen (U.2.122) from Bed 3 at Newbridge Quarry, and one from Bed 5 at Laysthorpe Quarry (U.1.104).

Measurements. U.3.57: maximum diameter preserved 108 mm; at 108 mm, 0·26, –, 0·49; 34 ribs at 109 mm. U.3.35: maximum diameter preserved 204 mm; 20 ribs at 200 mm, 30 at 115 mm. U.3.63: maximum diameter

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EXPLANATION OF PLATE 5

Fig. 1. *Perisphinctes* (*Pseudopomerania*) *dewari* (Arkell); U.3.65; Bed 3; Plasticine squeeze of original natural mould; ×0·48.

Fig. 2. *Perisphinctes* (*Dichotomosphinctes*) sp. E; M18; Bed 4; Vinamould cast of original natural mould; a substantially complete, microconch adult showing uncoiling of umbilical seam; ×1.

Fig. 3. *Perisphinctes* (*Dichotomosphinctes*) sp. D; U.3.50; Bed 3; ×0·52.

Fig. 4. *Perisphinctes* (*Pseudarisphinctes*) *pachachii* Arkell; U.3.57; Bed 4; Plasticine squeeze of original natural mould; ×0·57.

Fig. 5. *Perisphinctes* (*Pseudarisphinctes*) *pachachii* Arkell; U.3.63; Bed 4; substantially complete macroconch adult; inner whorls crushed, but body chamber largely uncrushed; aperture not preserved; ×0·33.

All specimens from the Spaunton Sandstone of Spaunton Moor Quarry, North Yorkshire.


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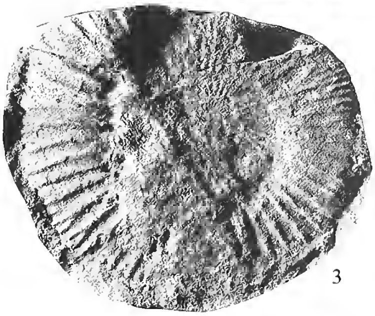
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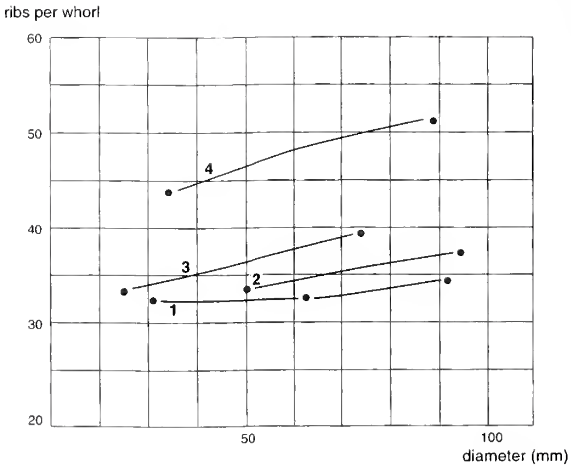
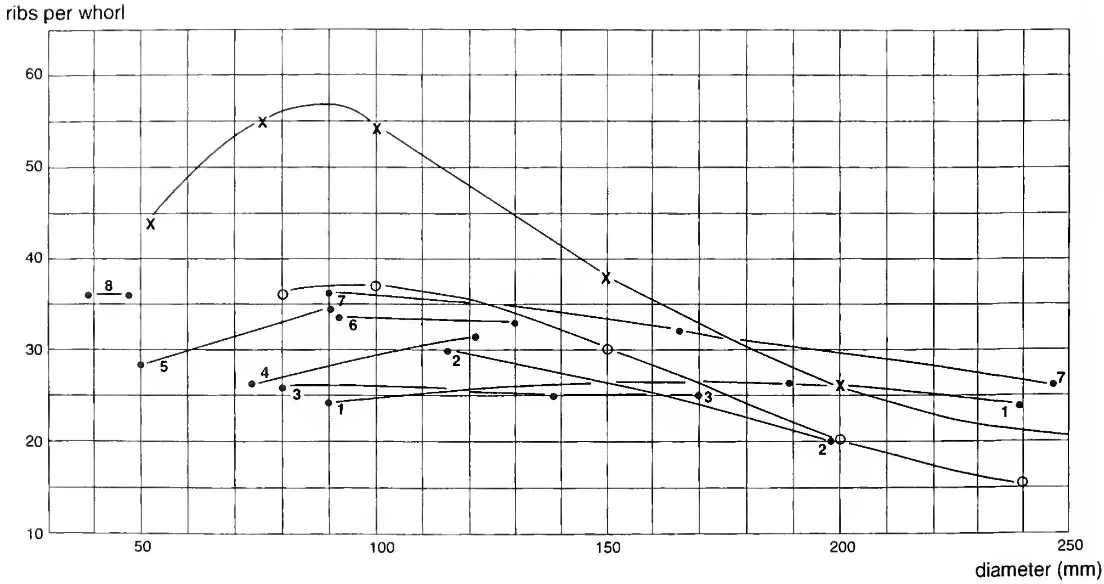
WRIGHT, *Perisphinctes*



TEXT-FIG. 4. Rib curves of *Perisphinctes* (*Dichotomosphinctes*) spp. from the Spaunton Sandstone: 1–3, *P.* (*D.*) sp. E; 4, *P.* (*D.*) sp. D.



TEXT-FIG. 5. Rib curves of *Perisphinctes* (*Pseudarisphinctes*) spp. and *Decipia* spp. from the Spaunton Sandstone and Clavellata Beds: ×, *P.* (*P.*) *durnovariae* (holotype, after Arkell 1935); ○, *P.* (*P.*) *shortlakensis* (holotype, after Arkell (1935)); 1–2, *P.* (*P.*) *pachachii* (U.3.63, U.3.35); 3, *D. decipiens* (U.3.64); 4. *P.* (*P.*) *damoni* (U.3.34); 5, *D. decipiens* (U.2.31); 6, *D. lintonensis* (U.2.34); 7–8, *D. decipiens* (U.3.17, U.3.1).

preserved 300 mm; at 300 mm, 0·28, –, 0·55; 22 ribs at 300 mm, 24 at 240 mm, *c.* 26 at 190 mm. *c.* 24 at 90 mm.

Description. The coiling is quite involute, with the umbilical seam running just above the mid-point of the previous whorl side. A fragment of inner whorl (Pl. 5, fig. 4) shows the typical ribbing, with strong, widely spaced primaries, and three secondaries per primary with true trichotomous separation of the secondaries. The whorl section is rounded. An immature adult (U.3.35) shows the style of ribbing up to 200 mm. At 130 mm, the secondaries have disappeared, and the primary ribs are stouter and more widely spaced. The fully grown adult (Pl. 5, fig. 5) has almost bullate primary ribs on the inner half of the whorl side, the ribs fading completely on the outer half of the whorl.

Remarks. The holotype from the Clavellata Beds of Dorset, the only specimen known previously, consists of septate inner whorls only. A macroconch adult is figured here for the first time (Pl. 5, fig. 5). The rib curve of *P. shortlakensis* Arkell comes quite close to that of *P. pachachii* (Text-fig. 5), but *P. shortlakensis* has a very distinctive quadrate whorl section on the body chamber, with stout ribs running up onto the ventro-lateral edge. *P. durnovariae* Arkell has a very similar style of ribbing on the body chamber, but has more than 20 extra primary ribs per whorl on the inner whorls (Text-fig. 5).

A specimen of *P. pachachii* from the Clavellata Beds is figured here (Pl. 8, fig. 2a–b) as it shows clearly the stage when the secondaries, four per primary, are fading. It shows too the stout, almost perfectly rounded whorl section with whorl breadth equal to whorl height. The specimen is completely septate.

Perisphinctes (*Pseudarisphinctes*) *damoni* Arkell, 1935

Plate 6, figures 1, 5; Text-figure 5

1935 *Perisphinctes* (*Biplices*?) *damoni* n.sp.; Arkell, p. 25, pl. 1, fig. 3; pl. 6, fig. 2.

Material. Three specimens from Spaunton Moor Quarry, one from Bed 3 (U.3.2) and two from Bed 4 (U.3.12 and U.3.34).

Measurements. U.3.2: maximum diameter preserved 92 mm; at 92 mm, 0·27, –, 0·50; *c.* 29 ribs at 92 mm. U.3.34: maximum diameter preserved 120 mm; at 120 mm, 0·27, –, 0·52; 31 ribs at 120 mm, 26 at 73 mm.

Description. P. damoni has the same style of coiling as *P. pachachii*, with an almost exactly circular whorl section, and the same stout, widely spaced primary ribs, with three secondaries per primary. Prominent constrictions and simple ribs appear on the body chamber, and the species is fully grown at about 120 mm. It is very clearly the microconch of *P. pachachii*. An excellent specimen from the Clavellata Beds (Pl. 6, fig. 1) shows the simple ribs and constrictions characteristic of the last half whorl. The whorl section is slightly narrower than high; the position of the aperture (broken away) is shown by the arrow. Several septae are visible where the test is broken on the reverse of the specimen. Although the last septum is not visible, the body chamber cannot be more than two-thirds of a whorl. The specimen from Bed 4 at Spaunton Moor Quarry (Pl. 6, fig. 5) lacks the marked constrictions and simple ribs of the Dorset specimen, as far as can be seen. The inner whorls, however, are crushed, and the body chamber is preserved only as an internal mould. This gives the ribbing a much less bold appearance.

Subgenus PSEUDOPOMERANIA subgen. nov.

Perisphinctes (*Pseudopomerania*) *dewari* Arkell, 1947*b*

Plate 5, figure 1

1947*b* *Decipia* (*Pomerania*) *dewari*, Arkell, p. 375, pl. 78, figs 1a–b, 5a–b.

Material. One specimen (U.3.65) from the top of Bed 3 at Spaunton Moor Quarry.

Measurements. U.3.65: maximum diameter preserved 225 mm; at 225 mm, 0·29, –, 0·51; at 170 mm, 0·26, 0·21, 0·45; *c.* 30 ribs at 140 mm, 10 on the last half whorl visible (225 mm).

Description. The specimen was badly damaged during quarrying, and exists only as fragments. However, it was possible to collect a near-complete natural mould, preserved in a calcareous concretion, and thus not crushed. A plasticine squeeze of this is figured as Plate 5, figure 1. When first seen, at a diameter of approximately 60 mm, the primary ribs are straight, slightly prorsiradiate, and moderately dense, of the order of 40 per whorl. At 90 mm, a portion of whorl with secondary ribs is seen. There are approximately two secondaries per primary. The secondaries do not bifurcate regularly from the primaries, and may run down between two primaries if there is not a primary conveniently placed to join.

At about 140 mm, the ribbing fades completely, and for a quarter of a whorl the shell is smooth. This feature marks the early part of the body chamber. The primary ribbing then becomes increasingly strong in the half whorl towards the aperture, where the primaries run right over the venter. The whorl section is rounded-quadrate. Although the aperture is not preserved in this specimen, the original adult size can be estimated at 230 mm.

Remarks. The specimen shows the key features of *Pseudopomerania*: smooth, unribbed shell at the start of the body chamber, and small adult size of the macroconch. Again, as in the specimen from the Newbridge Beds, the secondary ribbing of the early whorls is of the normal *Perisphinctes* type, and bears no relation to that of *Decipia*. There are 11 quite widely spaced ribs on the last half whorl seen. The holotype of *P. dewari* has 12 at a similar diameter. Faint ribbing over the venter, only loosely connected to the primary ribs, is seen as in the holotype, but is less prominent.

Genus DECIPIA Arkell, 1937*a*

Decipia decipiens (Sowerby, 1821)

Plate 6, figure 3; Plate 7, figures 1–4; Text-figure 5

1821 *Ammonites decipiens* Sowerby, p. 169, pl. 294
1937*a* *Decipia decipiens* (J. Sowerby); Arkell, p. 44, pl. F, figs 1–4
1947*b* *Decipia decipiens* (J. Sowerby); Arkell, p. 370, text-figs 132–133, pl. 78, fig. 7.

Material. Sixteen specimens, six from Bed 3 at Newbridge Quarry (U.2.1, U.2.31, U.2.46, U.2.48–U.2.49 and U.2.124), one from Bed 3 at Spaunton Moor Quarry (U.3.53), and nine from Bed 4 (U.3.1, U.3.15–U.3.17, U.3.25, U.3.27, U.3.55–U.3.56 and U.3.64).

Measurements. U.3.1: maximum diameter preserved 46 mm; at 41 mm, 0·37, –, 0·39; 36 ribs at 46 mm, 36 at 38 mm. U.3.16: maximum diameter preserved 67 mm, showing uncoiling of the umbilical seam, but the aperture broken away; at 63 mm, 0·38, –, 0·36; 26 ribs at 67 mm. U.2.31: maximum diameter 90 mm, showing the strong, simple ribs which develop close to the aperture; at 84 mm, 0·31, –, 0·44; approx. 34 ribs at 90 mm, 28 at 48 mm. U.3.17: maximum diameter *c*. 255 mm, with aperture visible; at 70 mm, 0·34, 0·20, 0·38; at 125 mm, 0·31, –, 0·47; at 255 mm, 0·24, –, 0·55; *c*. 26 ribs at 250 mm, *c*. 32 at 165 mm, *c*. 36 at 90 mm. U.3.64: maximum diameter preserved 170 mm; at 170 mm, 0·29, –, 0·50; 25 ribs at 170 mm, 25 at 138 mm, 26 at 93 mm; 26 at 80 mm.

Description. The coiling of the inner whorls (Pl. 7, fig. 4) is noticeably involute, with the umbilical seam lying at approximately two-thirds of the previous whorl height. The primary ribs are quite strong, but narrow and rod-like, with wide spaces in between them. They fade just above the mid-point of the whorl side. When the secondaries are first seen, at 24 mm, each primary passes rather indistinctly into two secondaries, with an intercalatory in between. Faint lateral constrictions, which become prominent on the venter, are common. By 43 mm, the primaries broaden and flatten at the mid-point of the whorl side, and the secondaries arise from them in groups or sheaves of three or four.

In the microconch (Pl. 6, fig. 3; Pl. 7, figs 2–3), this style of ribbing continues onto the body chamber, but becomes increasingly interrupted towards the aperture by constrictions and strong, simple ribs. Separating the

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EXPLANATION OF PLATE 6

Fig. 1. *Perisphinctes* (*Pseudarisphinctes*) *damoni* Arkell; D.C.45; Chief Shell Beds, Clavellata Beds; Black Head, Dorset; largely complete microconch adult with test preserved; position of flared aperture, visible on the reverse of specimen, is arrowed; × 1.

Fig. 2. *Decipia lintonensis* Arkell; U.2.32; Spaunton Sandstone; Newbridge Quarry, Bed 3; probable microconch adult with half a whorl of body chamber; × 0·5.

Fig. 3. *Decipia decipiens* (J. Sowerby); U.2.31; Spaunton Sandstone; Newbridge Quarry, Bed 3, probably microconch adult, inner whorls crushed, but body chamber preserved in three dimensions; × 0·52.

Fig. 4. *Decipia lintonensis* Arkell; U.3.24; Spaunton Sandstone; Spaunton Moor Quarry, Bed 4; Plasticine squeeze of original natural mould; × 0·7.

Fig. 5. *Perisphinctes* (*Pseudarisphinctes*) *damoni* Arkell; U.3.34; Spaunton Sandstone, Spaunton Moor Quarry, Bed 4; largely complete, microconch adult, inner whorls crushed, but body chamber preserved in three dimensions; × 0·82.

PLATE 6


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WRIGHT, *Perisphinctes*, *Decipia*

simple ribs, two or three primaries continue the pattern of becoming broad and low, and passing into sheaves of four secondaries. Typical rib curves are given in Text-figure 5. These are very flat, rarely rising above 35 ribs per whorl.

In the macroconch (Pl. 7, fig. 1), the same rib style, consisting of rod-like primary ribs, fading and passing indistinctly into groups of four secondary ribs, continues until septation ceases. The body chamber has widely spaced primary ribs which fade on the outer whorl side. The venter is smooth. Unusually for the Upper Calcareous Grit, the shell of this specimen became filled with calcareous matrix before compaction, showing that its compressed nature is an original feature. The holotype, a macroconch figured by Arkell (1937, pl. F), is much less compressed than the specimen figured in Plate 7, figure 1, and is more closely matched in this respect by Plate 7, figure 3. This specimen also shows the clear linking of primary and secondary ribs which is seen in the holotype, but hard to see in the other specimens figured.

Remarks. The name *Decipia decipiens* was used by Arkell (1947) for both microconchs and macroconchs, and this usage is continued here pending a resolution of the question of whether palaeontologists should continue to use different subgeneric names for the macroconch and microconch of the same species (see discussion on p. 437). Surlyk *et al.* (1973) pointed out that most of the Yorkshire specimens differ somewhat in rib style and whorl breadth from the holotype, which came from the drift of Highgate Hill, London. As the range of variation in the Yorkshire material includes the rib style and whorl breadth of the holotype, it is not considered necessary to employ a new specific name here.

Decipia lintonensis Arkell, 1937*a*

Plate 6, figures 2, 4; Plate 7, figure 5; Plate 8, figure 1; Text-figure 5

1937*a*	*Decipia lintonensis* Arkell, p. 45, pl. 12, figs 1–2
1947*b*	*Decipia lintonensis* Arkell; Arkell, p. 373, pl. 78, fig. 6
1973	*Decipia* sp. nov. aff. *decipiens* (J. Sowerby); Surlyk *et al.*, pl. 1, figs 1–2.

Material. Fourteen specimens, five from Bed 3 at Newbridge Quarry (U.2.32, U.2.37, U.2.44, U.2.47 and U.2.121), one from Bed 3 at Spaunton Moor Quarry (U.3.21), seven from Bed 4 at Spaunton Moor Quarry (U.3.4, U.3.24, U.3.28–U.3.29, U.3.47, U.3.51 and U.3.58), and one (U.8.1) from Tilehouse Cutting (SE 678 850) near Kirkby Moorside, from a level high in the Spaunton Sandstone.

Measurements. U.2.32: Maximum diameter preserved 92 mm, with two-thirds of a whorl of body chamber; at 92 mm, 0·27, –, 0·50; *c.* 34 ribs at 92 mm, *c.* 30 at 60 mm. U.3.24: maximum diameter preserved 128 mm; natural mould – no sutures visible; at 115 mm; 0·30, –, 0·48; 33 ribs at 128 mm, 34 at 87 mm.

Description. D. lintonensis has much bolder ribbing than *D. decipiens*, stout primaries each passing into three or four secondaries (Pl. 6, fig. 4). The primaries do not fade at the mid-point of the whorl side but swell, and the secondaries are grouped into sheaves or bundles of three or four. A fragment from the body chamber of a larger individual (Pl. 7, fig. 5) suggests that this rib style may continue almost up to the aperture of the macroconch. Only one microconch is known (Pl. 6, fig. 2). The body chamber has similar stout primary ribs as in the macroconch figured, but there are only three secondaries per primary. The ribbing becomes bolder, with constrictions, close to the aperture. The rib curve matches that of *D. decipiens* closely (Text-fig. 5).

The figured specimen (Pl. 8, fig. 1) from the Clavellata Beds is an immature macroconch. It shows, close to the aperture, a constriction followed by a ?damaged apertural margin (arrowed), and then, very thinly developed, the beginnings of new shell growth.

EXPLANATION OF PLATE 7

Figs 1–4. *Decipia decipiens* (J. Sowerby). 1, U.3.17; largely complete, macroconch adult, fully preserved in three dimensions, with aperture present; ×0·5. 2, U.3.16; microconch adult showing uncoiling of umbilical seam; inner whorls crushed; × 1. 3, U.3.15; non-septate whorl fragment; × 1. 4, U.3.1; inner whorls; × 1.

Fig. 5. *Decipia lintonensis* Arkell; U.3.4; body chamber fragment of a macroconch, showing distinctive ribbing; × 1.

All specimens from the Spaunton Sandstone (Bed 4) of Spaunton Moor Quarry, North Yorkshire.

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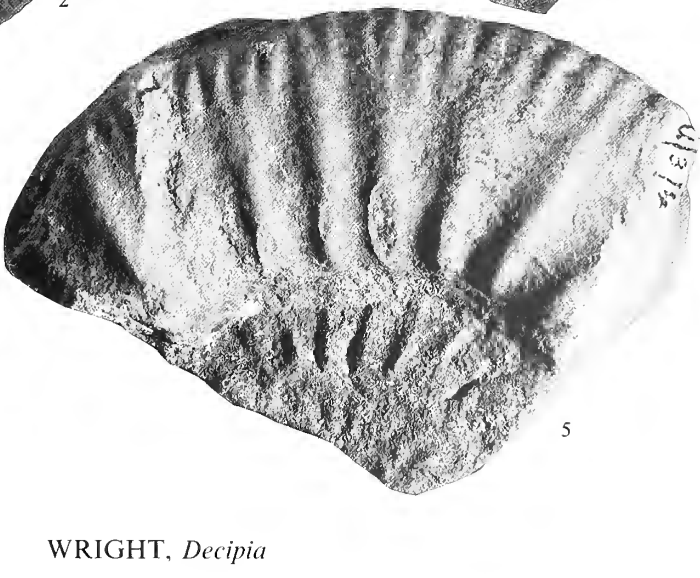

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WRIGHT, *Decipia*

Remarks. Although *Pseudarisphinctes pachachii*, *P. damoni*, *Decipia decipiens* and *D. lintonensis* have been treated here as separate taxa, it is apparent from the very close grouping of rib curves in Text-figure 5 that all are closely related. Intermediate forms linking these 'species' are common. It is quite impossible, for instance, to separate *D. decipiens* and *D. lintonensis* on a statistical analysis of the number of secondary ribs per primary. It seems likely that these taxa represent one continuously variable perisphinctid species.

Genus MICROBIPLICES Arkell, 1936

Microbiplices? sp.

Plate 8, figures 3–4

1974 *Microbiplices* sp.; Brochwicz-Lewinski and Rozak, pl. 1, fig. 1.
1991 *Microbiplices* sp.; Malinowska, pl. 1, fig. 26.

Material. Five fragments from Bed 4 at Newbridge Quarry (U.2.34, U.2.60, U.2.73–U.2.74 and U.2.133), and two crushed fragments from Bed 5 (Snape Sandstone) at Spaunton Moor Quarry (U.3.5 and U.3.7).

Measurements. U.3.5: maximum diameter preserved approx. 100 mm; 11 ribs on the third of a whorl present (equivalent to 35 per whorl at 100 mm).

Description. The specimens are fragments of microconch body chambers, adult at 100 mm. The primary ribs are strong and widely spaced, and bifurcate just above the mid-point of the whorl side, with occasional simple ribs and faint constrictions which become more prominent towards the aperture. The secondary ribs run strongly over the venter. The whorl section is somewhat quadrate.

Remarks. Fragmentary remains of this interesting microconch form are common in the highest part of the Cautisnigrae Subzone. Its assignment to *Microbiplices* must be tentative due to its large size. Typical *Microbiplices* from the Pseudocordata Zone are adult at 38–45 mm (Dorn 1930, pl. 6, fig. 4; pl. 12, fig. 1; pl. 13, fig. 5; Arkell 1947*b*, pl. 76, figs 6–7; Enay 1966, pl. 40, fig. 4; Wright 1986, fig. 6H). However, larger species of *Microbiplices*, up to 60 mm in diameter, have been recorded from older beds (i.e. the specimens cited in the synonomy). The Yorkshire specimens may thus mark the first appearance of *Microbiplices*, this larger form subsequently evolving into the diminutive forms of the Pseudocordata Zone.

ZONES AND SUBZONES OF THE UPPER OXFORDIAN IN THE BOREAL AND SUB-BOREAL PROVINCES

The position of the three members of the Upper Calcareous Grit Formation within the two alternative subzonal schemes used for Late Oxfordian strata in Britain is shown in Text-figure 6. Both schemes are relevant to North Yorkshire because the *Amoeboceras* faunas of the Boreal

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EXPLANATION OF PLATE 8

Fig. 1. *Decipia lintonensis* Arkell; D.C.48; Chief Shell Beds, Clavellata Beds; Black Head, Dorset; immature macroconch; note aperture (arrowed), followed by thinly developed growth of new shell material; ×0·75.

Figs 2a–b. *Perisphinctes* (*Pseudarisphinctes*) *pachachii* Arkell; D.C.46; Chief Shell Beds, Clavellata Beds, Black Head, Dorset; 2a, septate inner whorls of macroconch adult; ×0·48. 2b, reverse side of specimen showing simple suture, with short, stocky lobes; ×0·9. Specimen donated by Dr C. King.

Figs 3–4. *Microbiplices*? sp.; 3, U.3.5; Snape Sandstone; Spaunton Moor Quarry, Bed 5; fragment of body chamber, specimen markedly flattened; ×1. 4, U.2.133; Spaunton Sandstone, Newbridge Quarry, Bed 4; fragment of body chamber; ×1.

Fig. 5. *Decipia ravenswykensis* sp. nov.; U.5.10; Newbridge Beds, Ravenswyke Quarry, Bed 2; Plasticine squeeze of a natural mould of a heavily encrusted macroconch showing development of large, swollen ribs on later part of body chamber; ×0·31.

PLATE 8


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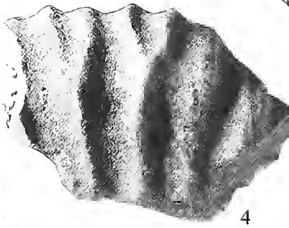
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2a


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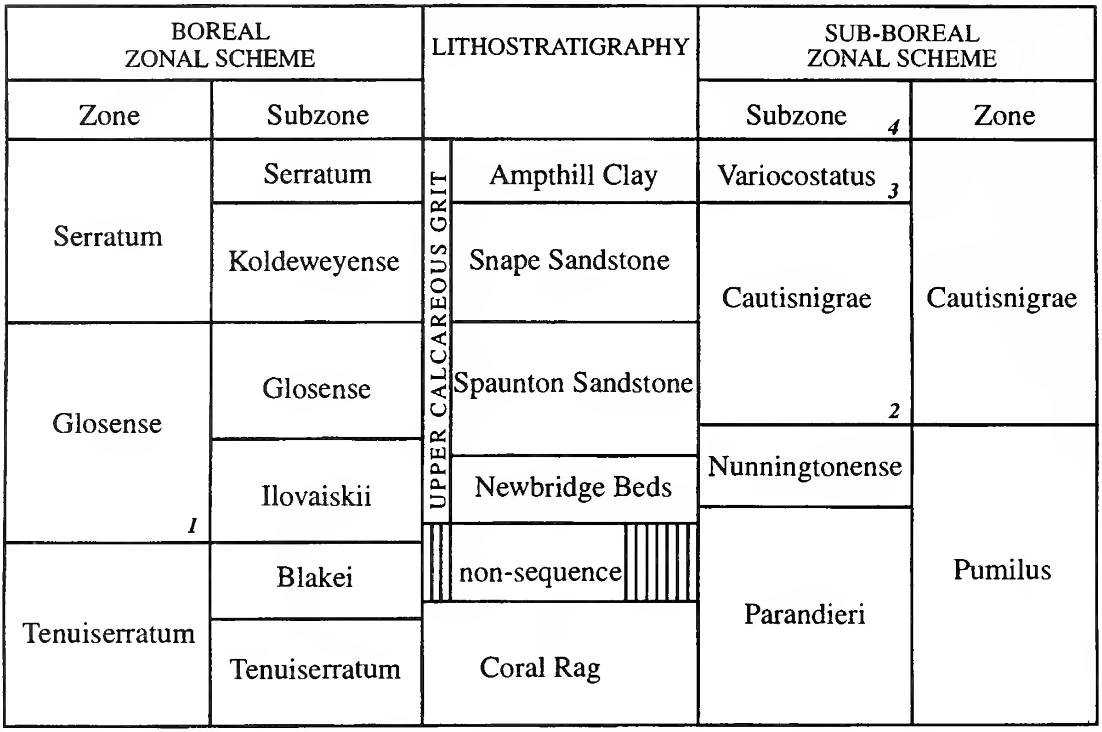
WRIGHT, *Decipia*, *Perisphinctes*, *Microbiplices*?



TEXT-FIG. 6. The position of the members of the Upper Calcareous Grit Formation of Yorkshire within the Boreal and Sub-Boreal zonal schemes. *1–4*: positions of the Middle–Upper Oxfordian boundary according to various authors; 1. Boreal Province (Sykes and Callomon 1979); 2. Malinowska 1991; 3. Sykes and Callomon (1979) – between the Sub-Mediterranean Transversarium and Bifurcatus zones, which correlates with this level in the Sub-Boreal zonal scheme; 4. Cariou *et al.* (1991), and most continental authors.

Province and the perisphinctid faunas of the Sub-Boreal Province overlap here in their occurrence; individual beds usually contain a predominance of one group or the other, but beds where a boreal fauna predominates may pass laterally into beds where a sub-boreal fauna predominates. Study of the North Yorkshire Late Oxfordian ammonite faunas is thus of considerable importance in the resolution of problems of correlation between the two zonal schemes.

Definitions of the Boreal zones and subzones were given by Sykes and Callomon (1979). In this scheme, the fauna of the Newbridge Beds is characteristic of the Ilovaiskii Subzone. The *Decipia ravenswykensis*, *Amoeboceras nunningtonense* and *A. transitorium* assemblage, so characteristic of the Newbridge Beds in Yorkshire, occurs in the highest part of that subzone in the type section at Staffin, Isle of Skye (author's collection). The Glosense Subzone is also defined at Staffin, and a good fauna of *Amoeboceras* characteristic of this subzone occurs in the highest Spaunton Sandstone at Newbridge Quarry. However, the intervening beds contain predominantly perisphinctids, and thus the precise position of the Glosense/Ilovaiskii subzonal boundary is not known in Yorkshire.

The Nunningtonense Subzone was originally proposed as a subzone of the Sub-Mediterranean Transversarium Zone by Wright (1972), but was transferred into a new Sub-Boreal Pumilus Zone by Sykes and Callomon (1979). It is characterized by the occurrence of *Amoeboceras nunningtonense* together with *Decipia ravenswykensis*, as typified by the fauna of the Newbridge Beds at Laysthorpe Quarry. The Cautisnigrae Subzone (originally the Variocostatus Zone of Arkell (1936, p. 62)) was regarded as the highest subzone of the Transversarium Zone by Wright (1972), but Sykes and Callomon (1979) transferred it into a new Sub-Boreal Cautisnigrae Zone. Its base is marked by the incoming of *Decipia decipiens* along with the other perisphinctids, particularly *D. lintonensis* and *Perisphinctes* (*Pseudarisphinctes*) spp., which typify the Clavellata Beds in Dorset. The *P.* (*Perisphinctes*) spp. and *P.* (*Arisphinctes*) spp. of the Clavellata Beds appear to range through both the Nunningtonense and Cautisnigrae subzones. In Yorkshire, the typical Cautisnigrae Subzone fauna occurs in the Spaunton Sandstone at both Spaunton and Newbridge quarries. The junction of the Nunningtonense and Cautisnigrae subzones must lie at or just above the base of the Spaunton Sandstone.

RELATIONSHIP WITH AMMONITE FAUNAS ELSEWHERE IN THE BOREAL AND SUB-BOREAL PROVINCES

Skye and the Boreal regions

Sykes and Callomon (1979) noted that the ammonite taxa recorded from the Newbridge Beds and Spaunton Sandstone occur in Bed 31 of the Flodigarry Shale at Staffin, Isle of Skye. Although the correlation is largely based on *Amoeboceras*, *Decipia ravenswykensis* occurs 2 m above the base of the Flodigarry Shale (author's collection), and Sykes and Callomon's record of *Perisphinctes* sp. suggests that a more precise correlation of the perisphinctid faunas may be possible. *D. ravenswykensis* has also been found in the Bernbjerg Formation of Cardiocerasdal, north-east Greenland, in beds underlying those with *A. glosense* (*Decipia* cf. *lintonensis* of Sykes and Surlyk, 1976). *Decipia lintonensis* occurs in the Harleelv Formation, Falsterselv, east Greenland (*Decipia* sp. nov. aff. *decipiens* of Surlyk *et al.* 1973).

'*The Ampthill Clay region*'

In Cambridgeshire, the Ampthill Clay is very poorly exposed, and the exact stratigraphical relationships between the various faunas which have been collected from clay pits and temporary exposures have presented problems to many workers. The problems were set out by Arkell (1937*b*, pp. 70–79, 1947*b*, pp. 354–356), and discussed by Torrens and Callomon (1968, pp. 293–296), Gallois and Cox (1977, pp. 278–279), Sykes and Callomon (1979, pp. 852–853) and Wright (1980, pp. 71–72). The key to an understanding of this area lies in determining the age of the Long Stanton fauna (Arkell 1937*b*, pl. 3). In Wright (1980), I placed this fauna with that of the Newbridge Beds at the base of the Ilovaiskii Subzone, following Sykes and Callomon (1979). However, the *Decipia* of the Long Stanton fauna (Arkell 1937*b*, pl. 3, fig. 2) is close to *D. decipiens*, and is not *D. ravenswykensis* which characterizes the Newbridge Beds. This suggests that the equivalent of the Long Stanton fauna should be sought in the Spaunton Sandstone where *D. decipiens* is abundant. In fact, the *Amoeboceras* fauna of Long Stanton, particularly *A. newbridgense*, occurs near the top of the Spaunton Sandstone at Newbridge Quarry, in the Glosense Subzone, and I would now place the Long Stanton fauna at that level. The *Amoeboceras* which occur in the Ilovaiskii Subzone in North Yorkshire (Laysthorpe Quarry beds 2 to 4) have a very distinctive rib style, with simple ribs alternating with bifurcating ribs, and in some cases several simple ribs together. Such a style of ribbing does not occur in *Amoeboceras* of the Glosense Subzone.

Ammonites occurring in slightly older beds in Fenland help to confirm this new age assignment for the Long Stanton fauna. Both Arkell (1947) and Gallois and Cox (1977) believed that beneath that fauna came an assemblage of *Decipia* and *Pseudarisphinctes* known as the Knapwell fauna (Hancock 1954). With its *P. pachachii*, *D. decipiens* and *D. lintonensis*, it is very similar to the fauna of the Spaunton Sandstone of Spaunton Moor Quarry (Beds 3 and 4) and Newbridge Quarry (Bed 3).

Since it is now clear that the Knapwell and Long Stanton faunas both belong to the Glosense Subzone, the junction between the Tenuiserratum and Glosense Zones (and thus the Middle/Upper Oxfordian junction) must be drawn much lower in figure 2 of Gallois and Cox (1977). Several metres of beds beneath those containing the Knapwell fauna are probably equivalent to the Nunningtonense Subzone with its *Decipia ravenswykensis*. The base of the Glosense Zone should therefore probably be drawn between Cox and Gallois' beds AC10 and AC11, or at the very highest between AC11 and AC12.

The Dorset coast

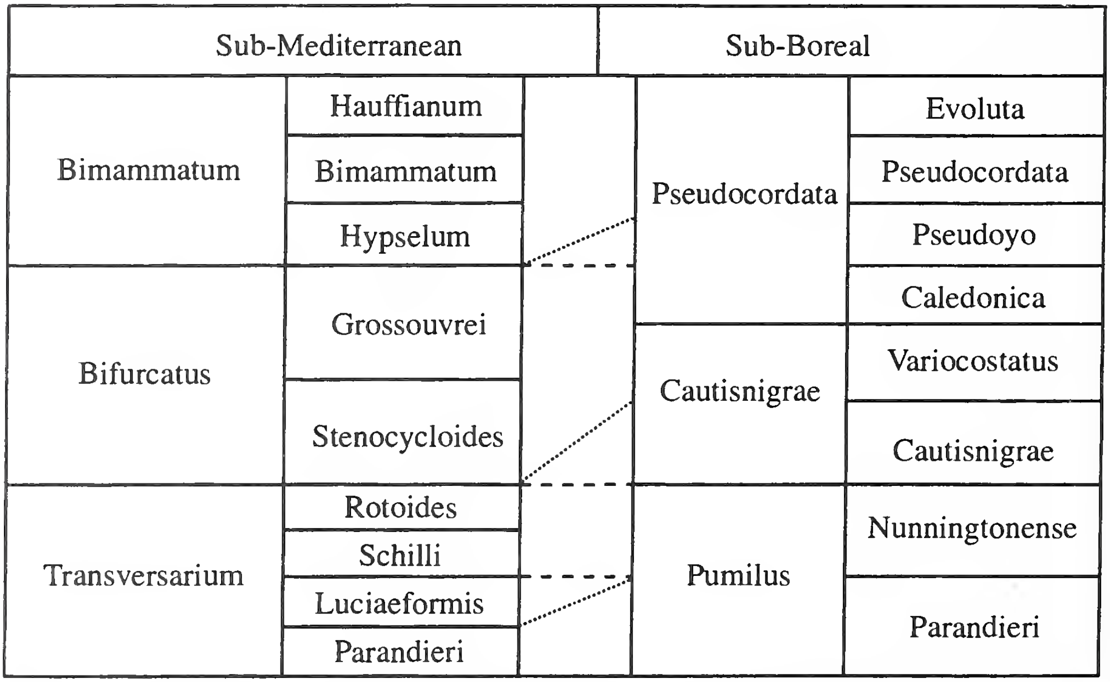
Wright (1986) has shown that the Nunningtonense Subzone is absent on the Dorset coast due to a non-sequence at the base of the Clavellata Beds. This formation yields the type Cautisnigrae Subzone fauna and, with its *Perisphinctes s.s.*, *Arisphinctes*, *Pseudarisphinctes* and *Decipia*, contains almost the exact equivalent of the fauna of the Spaunton Sandstone at Spaunton Moor Quarry.

Northern France

There is little to add to the summaries of Arkell (1937*a*, pp. 52–56 and 1956, pp. 42–43, 46), although Rioult *et al.* (1991) have refined the Oxfordian stratigraphy of the Normandy area. They noted that the highest Middle Oxfordian sediments, the Calcaire de Blangy, comprise whitish, calcareous, lagoonal muds belonging to the Blakei Subzone. There is then a hiatus, as in south Dorset, with the overlying Calcaire Gresieux de Henequeville resting on an important erosion surface. The lower Calcaire Gresieux may correlate with the Spaunton Sandstone and Clavellata Beds, but no ammonites have been recorded from it. The highest Calcaire Gresieux extends up into the Koldeweyense Subzone.

SUB-BOREAL AND SUB-MEDITERRANEAN ZONAL SCHEMES FOR THE OXFORDIAN

A considerable amount of research has been completed in recent years by workers in continental Europe on Mid and Late Oxfordian ammonites, and this has resulted in a radical re-appraisal of the sequences of faunas in the Sub-Mediterranean Province and their correlation with those of the British Late Oxfordian. The new, definitive, zonal scheme set out by Cariou *et al.* (1991) and Atrops *et al.* (1993) is shown in Text-figure 7. The Bifurcatus Zone has long been regarded as the equivalent



TEXT-FIG. 7. Comparison of the two alternative methods of correlation of the Sub-Boreal and Sub-Mediterranean Provinces currently proposed. Dashed line (Sykes and Callomon 1979; Malinowska 1990). Dotted line (Brochwicz-Lewinski 1980*a*, 1980*b*; Cariou *et al.* 1991; Atrops *et al.* 1993; and this work).

of the Sub-Boreal Cautisnigrae Subzone (Enay, 1966; Wright, 1972; Sykes and Callomon, 1979). However, Brochwicz-Lewinski (1980*a*, 1980*b*) pointed out that the rib curve of the innermost whorls of the microconch group of *P.* (*Dichotomoceras*) *bifurcatus* (Quenstedt) shows a characteristic 'U' shape, with dense initial ribbing followed by a trough at about 40 mm diameter, and then an increase in the number of ribs per whorl. Such a 'U' shape must inevitably be present in the rib curve of the equivalent *Perisphinctes s.s.* macroconch, and indeed it is present in *P.* (*P.*) *variocostatus* (Buckland) and its allies (Arkell 1947*b*, text-fig. 127). It is not present in the *P. cautisnigrae* group. Although few of the Cautisnigrae Subzone specimens figured by Arkell (1935, 1936, 1937*a*) can be traced to small enough diameters to demonstrate this, a number of specimens in the author's collection from both Yorkshire and Dorset demonstrate that this feature is not present in Nunningtonense and Cautisnigrae Subzone perisphinctids from Britain. This suggests that the Cautisnigrae Subzone correlates with the upper part of the Transversarium Zone, in which *Perisphinctes* without 'U'-shaped rib curves are common. Study of the rare *Amoeboceras* records from Switzerland (Atrops *et al.* 1993) suggests that, at the very latest, the Schilli Subzone correlates with the Cautisnigrae Subzone.

RELATIONSHIP WITH AMMONITE FAUNAS IN THE SUB-MEDITERRANEAN PROVINCE

The ammonite faunas of the Sub-Mediterranean Province were dominated in the early Late Oxfordian by such Tethyan genera as *Gregoryceras*, *Larcheria*, *Neomorphoceras* and *Epipeltoceras* which have never been found in Britain. *Perisphinctes* was common too, however, and occasional Tethyan *Perisphinctes* migrated northwards into the Sub-Boreal Province. In addition, *Amoeboceras* periodically migrated southwards as far as the Alpes Maritime. As a result, the two provinces now have a number of records in common, and these are reviewed below.

Southern side of the Paris Basin

On the southern side of the Paris Basin, extending south-west to the Aquitaine Basin, much work has been done on the sedimentology of the Oxfordian, and some new stratigraphical information has appeared. Cariou (1966*a*, 1966*b*, 1972) has published descriptions of many very fossiliferous Upper Oxfordian sections in the Poitiers region but, unfortunately, none of the material collected has been figured, and the work was undertaken on the erroneous assumption that the Bifurcatus Zone correlated with the Cautisnigrae Subzone. Cariou's records of *P. cautisnigrae* and its allies in the Bifurcatus Zone must be suspect. *Perisphinctes s.s.* does not occur in the beds underlying those containing the Bifurcatus Zone fauna, but the abundance of perisphinctid subgenera that do occur here may have some elements in common with those of the Clavellata Beds. One would require the fauna to be figured to establish this. Delance *et al.* (1982) described a section at Pont-St-Ours in which the beds equivalent to those in Yorkshire are thin (0·35 m), but do yield *P.* aff. *elizabethae* which occurs in the Nunningtonense Subzone.

The Jura

Several species of *Perisphinctes* found commonly in Yorkshire and Dorset have been recorded from the Jura by Enay (1966); these were collected from the Couches du Geissberg, beds which also contain *P.* (*Dichotomoceras*) *bifurcatus*, and are thus much too young for specific identity with the English forms to be likely. Of the specimens figured by Enay (1966), a partial body chamber (pl. 13, fig. 2) identified at *P. cautisnigrae* is not complete enough for specific identification, while the well preserved inner whorls (pl. 13, fig. 3) have 20 ribs per whorl less than Arkell's holotype. A complete specimen identified as *P. uptonensis* (pl. 15, fig. 2) has nearly twice as many ribs on the body chamber as Arkell's holotype. The inner whorls of a perisphinctid identified as *P. boweni* Arkell (pl. 15, fig. 4) have the coarse, bold rib style, with bifurcation points visible in the umbilical area, characteristic of *P.* (*Dichotomoceras*) *crassus* Enay; this feature has never been found in perisphinctids of the Cautisnigrae Subzone in England. The species which the areas do have in common is *P.* (*Dichotomosphinctes*) *elizabethae*, and needless to say, this occurs well below the Couches du Geissberg, in the Calcaires Hydraulique. The overlying Banc Limite already yields *P.* (*Dichotomoceras*) *bifurcatoides* Enay and *P. variocostatus*, indicators of a post-Cautisnigrae Subzone fauna.

Alpes Maritime

Dardeau and Marchand (1981) figured an *Amoeboceras*, identified as *A. newbridgense*, from beds yielding numerous *P. bifurcatus*. However, as was demonstrated above, the occurrence of such a typical Cautisnigrae Subzone ammonite in the Bifurcatus Zone is very unlikely. The specimen bears a close resemblance to forms of *Amoeboceras rosenkrantzi* Spath with rursiradiate secondary ribs (Sykes and Callomon 1979, pl. 119, fig. 10; pl. 120, fig. 5). Such a correlation of the latest Bifurcatus Zone with the early Rosenkrantzi Zone (early to mid Pseudocordata Zone) is just possible, though the major part of the Pseudocordata Zone correlates with the Bimammatum Zone (Text-fig. 7).

Southern Germany and northern Switzerland

The Oxfordian of this classic area, which includes the important Couches de Birmensdorf fauna, has been the subject of detailed study by R. A. Gygi and colleagues (Gygi 1966, 1977, 1990). A comprehensive ammonite list is given in Gygi (1977). Unfortunately, *Perisphinctes* occurs only rarely in the Transversarium Zone in which the equivalents of the Newbridge Beds and Spaunton Sandstone faunas are to be sought. *P.* (*Dichotomosphinctes*) *elizabethae* is recorded, but there are no records of *Perisphinctes s.s.* Exposures of these higher beds can be very disappointing for the ammonite collector, a 70 m section in Upper Oxfordian limestones and shales at Péry, northern Switzerland having yielded only three specimens (Gygi 1990). Atrops *et al.* (1993) recorded *Amoeboceras* aff. *glosense* from quarries at Hoelderbank and at Oberehrendigen, in both cases from beds with and just below occurrences of *Larcheria schilli* (Oppel).

The Spanish Cordillera

Melendez (1978*a*, 1978*b*), Goy *et al.* (1979) and Melendez and Fontana (1993) have described a number of fossiliferous sections of limestones and shales containing a succession of *Dichotomosphinctes* and *Larcheria* faunas. These have been used to establish four new subzones of the Transversarium Zone. Apart from the ubiquitous *P.* (*D.*) *elizabethae*, there is little to enable a close correlation with the English succession.

Poland

Many ammonites of Mid to Late Oxfordian age have been collected from the classic Oxfordian limestone outcrop in the area south-east of Czestochowa. In a meticulous study, Brochwicz-Lewinski (1976*a*, 1976*b*, 1980*a*, 1980*b*) and Rozak and Brochwicz-Lewinski (1978) have produced a revised correlation of these complex exposures, which yield a fauna of mixed Sub-Boreal and Sub-Mediterranean aspects, and thus are of great importance in the correlation of the two provinces. Significantly, careful collecting has shown that *P. cautisnigrae* and *P. martelli* (Oppel) (Cautisnigrae Subzone) occur below *P. variocostatus* and *P. panthei* Enay (Variocostatus Subzone).

Numerous *Ringsteadia* spp. have been collected from the Bimammatum Zone here, enabling a reasonable correlation of the Bimammatum and Pseudocordata zones. Occasional layers crowded with *Amoeboceras* suggest that a tentative correlation with the Boreal zonal scheme is possible, and this has been confirmed by Atrops *et al.* (1993). Numerous Rosenkranti Zone *Amoeboceras* have been recorded from the lowest Bimammatum Zone (Hypselum Subzone).

In the Holy Cross Mountains area near Kielce in south-west Poland, Matyja (1977) recorded numerous Oxfordian ammonites. He noted that the Morawice Limestone, with *P.* (*D.*) *elizabethae*, *P.* (*D.*) *wartae* Bukowski and *P.* (*P.*) *martelli* (Pumilus Zone), is succeeded by similar limestones with *P.* (*Dichotomoceras*) *bifurcatus* and *P.* (*P.*) *variocostatus* (Bifurcatus Zone). According to the original criteria of Arkell (1936, 1945), there is no definite Cautisnigrae Subzone fauna although Brochwicz-Lewinski (1980*a*, 1980*b*) would regard *P. wartae* and *P. martelli* as indicative of that Subzone.

Upper Oxfordian beds underlie large parts of central and northern Poland, and much information has been obtained from boreholes (Malinowska 1991). An abundant ammonite fauna of a substantially Boreal aspect, with some 30 species of *Amoeboceras*, has been recognized. However, the attribution of these species to those of the standard Boreal sequence described by Sykes and Callomon (1979) has proved difficult, many new species being present. Malinowska (1991) also recorded several specimens of *P. bifurcatus* from beds that are assigned to the Glosense Zone. The presence of *P. bifurcatus* at this level is surprising, and does not fit with the records of *P. bifurcatus* from other localities. However, the specimens in question have come from cores in which they were not in immediate association with known Glosense Zone *Amoeboceras* species. It should be possible to lower the upper boundary of the Glosense Zone in Malinowska's figure 3, thereby alleviating the problem. A good fauna of Ilovaiski Subzone *Amoeboceras* is recorded from these boreholes (Malinowska 1987).

DISCUSSION

This study has shown that most of the 22 species of perisphinctid from North Yorkshire described herein were endemic to the Sub-Boreal Province. None of the species of *Arisphinctes*, *Dichotomosphinctes*, *Pseudarisphinctes*, *Pseudopomerania* and *Microbiplices* has been recorded from outside the province. The closest connections were with the Boreal Province, *Decipia* being found quite commonly in Greenland (Surlyk *et al.* 1973; Sykes and Surlyk 1976). The perisphinctids seem to have been very 'reluctant' to migrate south; none of the common Yorkshire species has been recorded from the Sub-Mediterranean Province. Correlation with the south is only possible via rare records of Sub-Mediterranean species such as *P. elizabethae* and *P. parandieri* in Yorkshire, and the occasional records of Boreal *Amoeboceras* in the Sub-Mediterranean Province.

The recent division of the Sub-Mediterranean Transversarium Zone into four subzones, and some of these into faunal horizons (Cariou *et al.* 1991) has led to the previously accepted correlation of the Sub-Boreal and Sub-Mediterranean zonal schemes becoming untenable, with the Nunningtonense Subzone being equivalent to three Sub-Mediterranean subzones. The recognition of *Perisphinctes* (*Dichotomosphinctes*) *elizabethae*, a species which typifies the Luciaeformis Subzone, in the Newbridge Beds has enabled a more logical correlation of the two provinces (Text-fig. 7).

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ESTIMATION OF PARAMETERS OF FORAMINIFERAL TEST GEOMETRY BY IMAGE ANALYSIS

by LAURENCE P. WEBB *and* ANDREW R. H. SWAN

ABSTRACT. Outline analysis cannot be expected to yield good results when applied to foraminifera because of the uncertain relationship between outlines and three-dimensional morphology. Foram test morphology can often be described efficiently by means of a suite of geometrical parameters controlling chamber shape, size and accretion. These parameters can be obtained from images by an iterative optimization technique. The method has yielded good results when tested by application to simulated images.

PREVIOUS attempts at using image analysis to retrieve useful morphological information from foraminifera have focused on outline analysis. Outlines are easy to define by conventional image analysis (Hills 1988) and a range of techniques for processing outline information is available, including Fourier (Schwartz and Shane 1969) and eigenvector methods (Lohmann 1983; Lohmann and Schweitzer 1990). Although potentially useful for organisms such as ostracods (Kaesler and Waters 1972; Burke *et al.* 1987), this approach is unlikely to be successful in general application to foraminifera because their outlines are only an indirect consequence of the pattern of chamber accretion, the three-dimensional shape of the chambers, and the viewing direction. Consequently, it is difficult to argue that any derived numerical parameters have a meaningful relationship with biological information. Results based on outlines, such as those of Malmgren *et al.* (1984), do reflect genuine morphological information, but the relationship between the derived morphological characters and the true genotypic variation cannot be expected to be linear. The approach of Tabachnick and Bookstein (1990), using landmarks within and on foram outlines, involves similar problems.

The new approach proposed here is to break the information content of the foram into two constructional components: (1) the shape and texture of each chamber; and (2) the rules governing the spatial disposition of successive chambers. Such an approach must yield parameters that are more directly related to the processes by which the foram test is constructed and the genetically coded information required to control these processes. This study focuses on the second of these constructional components. Once these components are resolved, the 'within-chamber' morphology can be distinguished and resolved using other techniques, such as textural analysis (Swan and Garratt 1995). The objective, then, is to retrieve from foram images values of the geometrical parameters which describe the test shape. These can then be used in studies of taxonomy, ecology and functional morphology. The method will only be useful in application to forams with geometrically regular test morphology: this includes many species from the Globigerinacea and other rotaliinid superfamilies.

The method described here is tested using idealized simulated foram geometries: application to real foram images awaits further work.

FORAM GEOMETRY

In most forams, chambers are added to the test in a highly systematic way. The relative position and size of successive chambers is commonly consistent, resulting in a helicoid, logarithmic spiral

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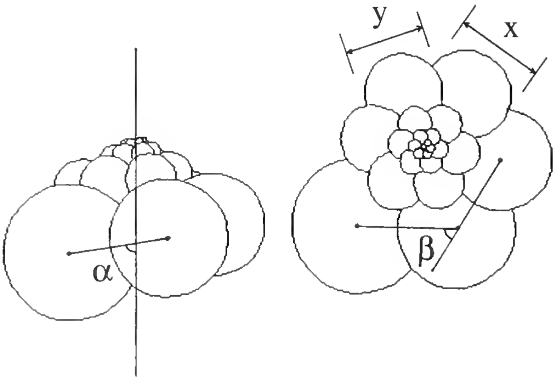
arrangement. In this mode, shape is maintained with growth. Such geometries can be defined by a number of parameters, of which the three most important are defined here as α, β and W (Text-fig. 1).



TEXT-FIG. 1. Definitions of three parameters of foram geometry: α, angle between coiling axis and line connecting centres of consecutive chambers; β, angle between lines connecting centres of two consecutive pairs of consecutive chambers, when viewed parallel to coiling axis; W, chamber expansion rate x/y.

The hypothetical range of morphologies possible in this geometrical scheme can be illustrated by constructing representative arrays of morphologies on two-dimensional slices through the three-dimensional α, β, W morphospace. In this study, we considered the axial view of the structure, in which direction the effect of the α parameter is not marked; we were therefore only considering the β, W morphospace. The β, W morphospace diagram (Text-fig. 2) shows axial views of each simulation in an array with various permutations of the two parameters. To simulate image analysis, the graphical representation was designed to try to emulate the three-dimensional appearance of real forams, as represented on digitized images (Macleod 1990). This was achieved by constructing each chamber from many disks or varying colour density, and this shows the geometry of chamber intersections with reasonable realism.

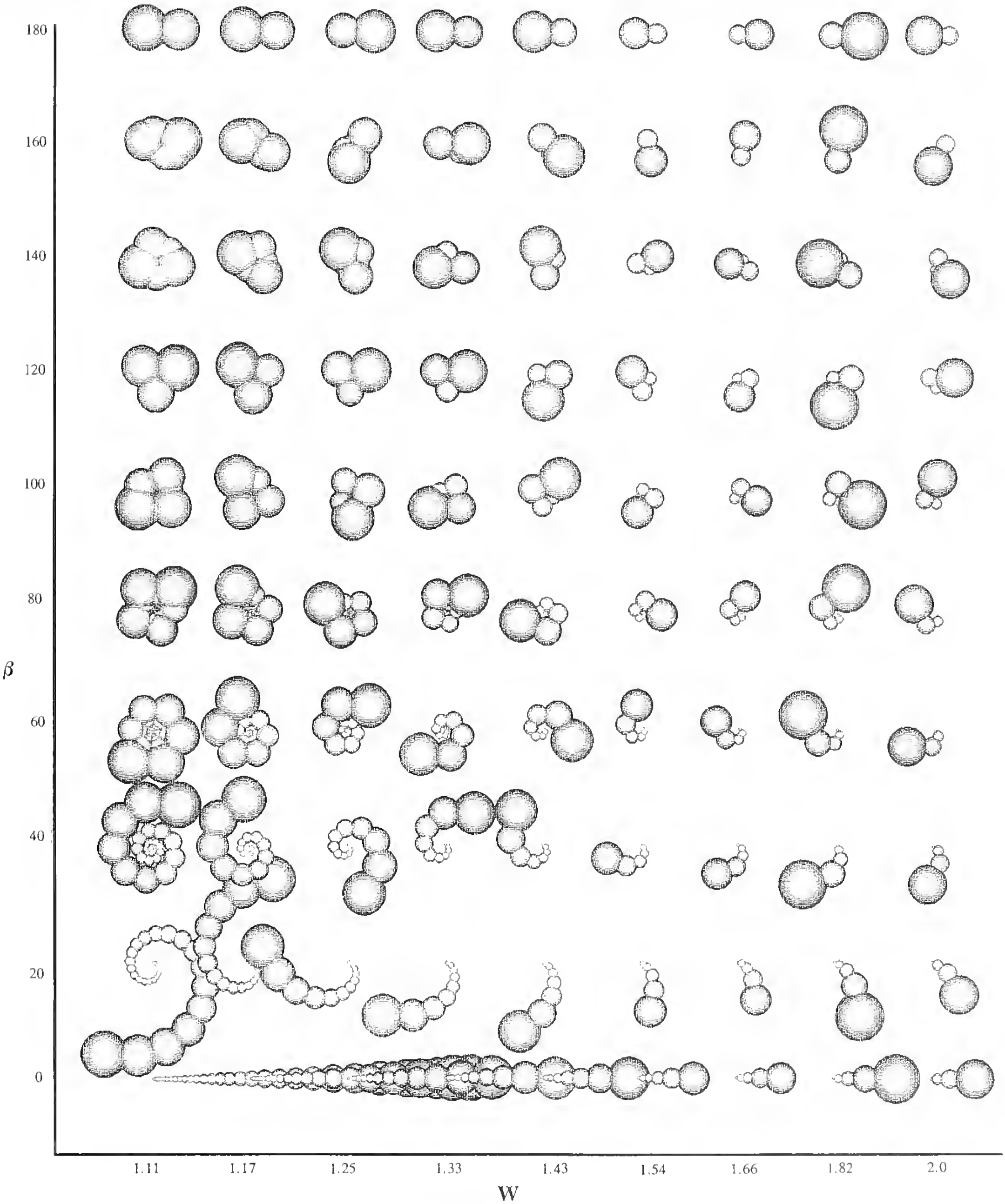
The β, W morphospace diagram demonstrates the morphological effects of changes in the geometrical parameters. It is clear that such morphological variations are of taxonomic importance (e.g. globigerinids tend to have high β) and functional significance (e.g. planktonic forms tend to have higher W). It is also apparent that this information is only indirectly reflected in the outlines.

The initial objective of the new method was to be able to find β and W from the pixel values on 'pseudo-images' such as those of Text-figure 2.

IMAGE ANALYSIS

A property of the present geometrical model, and of log spirals in general, is that the structures are self-similar on enlargement and rotation. In this case, the structures are self-similar on rotation by β and enlargement by W. Consequently, pairs of pixels related by that β, W transformation should have similar greylevel values. If, then, values of β and W could be found such that pairs of pixels on an image related by that transformation tend to have similar greylevel values, it could be inferred that those are the appropriate parameter values to describe the object under consideration. For a robust result, the correlation coefficient between greylevels of multiple pairs of pixels can be assessed (Text-fig. 3). In practice, 100 pixels within the object were selected at random and each paired with another found by the β, W transformation. This was then repeated for a range of combinations of β and W, the combination yielding the highest correlation giving the best estimate of these parameters.

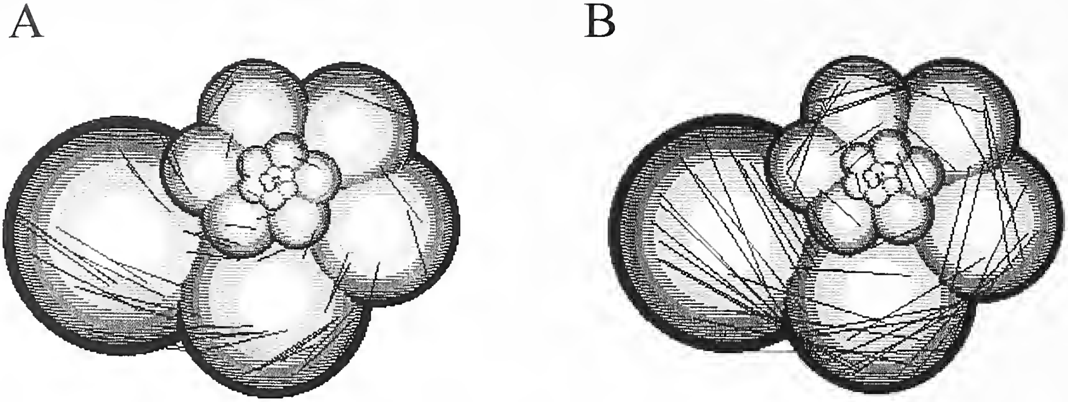
It is possible to plot the correlation coefficient for many combinations of β and W (e.g. Text-fig. 4). The palest parts of the graph show the highest correlation and indicate the β and W values for



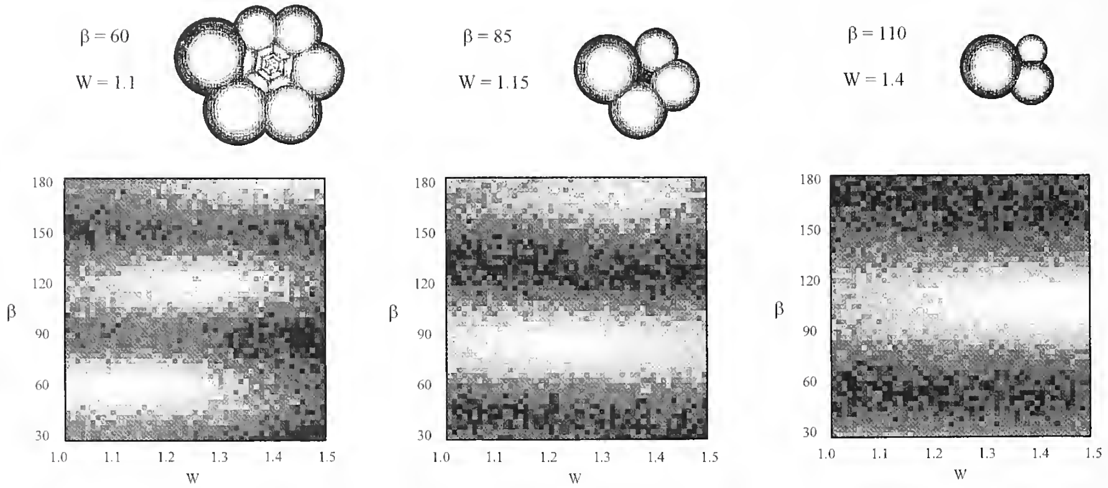
TEXT-FIG. 2. An array of simulated morphologies in β, W morphospace.

the structure. This procedure, using 100 pairs of pixels and 2601 combinations of β and W, requires excessive computer time and is not suitable for routine data retrieval.

The time taken to find the highest correlation coefficient amongst all possible β, W permutations can be reduced by an iterative search procedure. In this method, values of β and W are randomly 'mutated' to generate a set of 'descendant' combinations and the best of these becomes the



TEXT-FIG. 3. Lines connect pairs of pixels related by transformation by rotation β and enlargement W. A, little or no correlation between pixel greylevels. B, high correlation between pixel greylevels, the β and W values used matching the geometrical parameters of the foram structure.



TEXT-FIG. 4. Three simulated morphologies with specified β and W and the results of systematic searches of parameter space. The graphs show the correlation coefficient (paler = higher correlation) between pairs of pixels related by various combinations of β and W values. In all cases, the highest correlation occurs at the β, W values that correspond to the true values for the structure.

'ancestor' for the next iteration. This procedure finds an accurate estimate of the geometrical parameters in under 10 seconds on a PC 486 computer.

FUTURE DEVELOPMENTS

The 'pseudo-image' analysis procedure has achieved the objectives of a pilot study. However, the 'pseudo-images' are more geometrical and more ideally oriented and 'illuminated' than a real foram. The constraints under which the procedure will succeed on real forams need to be investigated. Modifications to allow for imperfections of orientation will be necessary but these should not present major difficulties. Developments in image analysis technology are such that it should be possible to resolve automatically any pattern of test morphology that can be perceived by the human observer.

Acknowledgements. Laurence Webb was killed in a tragic car accident in 1992 whilst in his first year of an NERC studentship at Kingston. The results shown here have been compiled using his computer programs and notes with the kind permission of Mr and Mrs Webb. Linda Parry assisted with some of the figures.

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THE SALAMANDER *BRACHYCORMUS NOACHICUS* FROM THE OLIGOCENE OF EUROPE, AND THE ROLE OF NEOTENY IN THE EVOLUTION OF SALAMANDERS

by ZBYNĚK ROČEK

ABSTRACT. All available material of the late Oligocene salamandrid amphibian *Brachycormus noachicus* is redescribed, with a reconstruction of its skeleton and an evaluation of its range of variation. This neotenous salamandrid is strikingly similar, in the shape of its visceral skeleton, to larvae of the contemporary *Triturus* in the final stages of metamorphosis, and to neotenous specimens of *Triturus alpestris*. However, in contrast to the latter facultative neotenous larvae, *Brachycormus*, though morphologically underdeveloped, was fully ossified. Occurrence of neoteny in the Tertiary tailed amphibians was associated with the global deterioration of climate during the Oligocene (a significant drop of mean annual temperatures and a broader range of annual temperatures). Prolongation of cold meant that larvae were not able to metamorphose in time and thus became permanent water dwellers. Subsequent improvement of climate in the Miocene permitted the amphibious life-cycle to resume; this was accompanied by completion of metamorphosis of the visceral skeleton but retarded osteogenesis in other respects (e.g. incomplete frontotemporal arch). Thus, *Brachycormus* may be taken as a phylogenetic link between the Oligocene Caudata related to *Chelotriton* and the contemporary genus *Triturus*.

THE first reported Tertiary tailed amphibians (apart from *Andrias scheuchzeri*, known since 1726, and initially variously misinterpreted as a diluvial human, catfish and reptile) were described by Goldfuss (1831) from the region of Siebengebirge near Bonn, Germany, namely from Orsberg near Erpel, Stösschen near Linz, and Rott near Hennef, where the famous 'Blatterkohle' underground mines operated until the 1870s. Biostratigraphy, based on the mammalian fauna found at Rott, suggests an uppermost Oligocene age for all these localities (von Koenigswald *et al.* 1992, p. 313) and the deposits represent a lacustrine biotope. Although the specimens are sometimes near complete articulated skeletons, the bones were dissolved and only natural moulds survive. In most specimens, dorso-ventral compression has resulted in the crushing of three-dimensional bones and structures such as vertebral centra and girdles, the twisting of ribs along their longitudinal axes, and of the tail through 90° relative to the trunk, because of its antero-posteriorly expanded haemal and neural vertebral processes, thus preserving its lateral aspect along the horizontal plane of the matrix. Only the long, thin bones of the limbs are preserved as relatively good imprints.

Goldfuss undoubtedly used for comparison the newts and salamanders that occur in the region today, namely *Triturus* and *Salamandra*. This may be concluded not only from the names he gave to his fossils (*Salamandra ogygia*, *Triton noachicus*) but also from his illustrations. The osteological details that he illustrated are not always observable on the specimens. The skeletons are incomplete in some cases (e.g. the left hind leg and the tail are missing in the holotype of *Brachycormus noachicus*; see Text-fig. 1), but Goldfuss illustrated them (1831, pl. 13, figs 5–6) as if they were complete. It can only be guessed as to whether the specimens were originally complete and damaged later, or if the illustrations are idealized reconstructions by Goldfuss (see also the note by von Meyer 1860, p. 64, who wrote as early as 30 years after Goldfuss's publication, that the holotype was 'in such bad shape that precise illustration of the complete animal is no longer possible').

In subsequent decades, further specimens were found at the same localities, and these were described by von Meyer (1852*a*, 1852*b*, 1858, 1860, 1863). Von Meyer (1860) based his redescription of *Brachycormus noachicus* on five specimens (including the original specimen of Goldfuss), and all

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but two are in the Paläontologisches Institut der Universität Bonn, and not lost as Estes (1981, p. 71) believed. The exceptions are one specimen that was preserved in lateral aspect (see von Meyer 1860, pl. 7, fig. 8) which does appear to be lost, and another which was sold to the British Museum (Natural History) where it is deposited as BMNH 30268. Von Meyer also recognized correctly the difference between these fossils and the genus *Triturus* and proposed (von Meyer 1860, p. 71) a new generic name *Brachycormus*.

After von Meyer's work, this material was not restudied until 1981 when Estes published his review of the fossil Caudata. He obviously did not investigate the original material from Rott thoroughly, but placed some of Herre's (1949) taxa, namely *Oligosemia gerhardti* and *Tylototriton kosswigi*, into the synonymy of *Brachycormus noachicus*.

Already Goldfuss (1831, p. 127) had pointed out that this amphibian differs from contemporary *Triturus* in its simplified skull structure. Von Meyer (1860, pl. 67) recognized some larval characters in its structure and Estes (1981, p. 71) stated that '... some of the individuals were gilled larvae, although their otherwise adult morphology indicates that they were near metamorphosis'. Neoteny and paedomorphosis are generally considered important phenomena in vertebrate evolution (Gould 1977) and, because the early phylogenetic origins of both Anura and Urodela are undoubtedly associated with developmental abbreviation (see temnospondyls described by Bolt 1969, 1977, 1979; Warren and Hutchinson 1988, 1990; Warren and Schroeder 1995), it became obvious that neoteny and paedomorphosis played an important role also in urodelan origin and evolution (Milner 1988, p. 94) and that their occurrence in fossil forms deserves some attention. Study of neoteny also has a practical impact on caudate systematics, because superficially different forms may actually be closely related if comparison is based on different developmental stages of the taxa under investigation. Therefore, the recognition of larval characters in the structure of fossil amphibians is important, as well as an understanding of those factors that influence (and modify) normal development. This, together with clarification of the phylogenetic position of the genus *Brachycormus*, is the aim of the present paper.

Institutional abbreviations are as follows: BMNH, The Natural History Museum, London; MB, Museum für Naturkunde, Berlin; NMP, National Museum, Prague; PIUB, Paläontologisches Institut der Universität, Bonn; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

SYSTEMATIC PALAEONTOLOGY

Order CAUDATA Scopoli, 1777
Family SALAMANDRIDAE Gray, 1825

Genus BRACHYCORMUS von Meyer, 1860

Diagnosis. As for *Brachycormus noachicus*, the type and only species.

Brachycormus noachicus (Goldfuss, 1831)

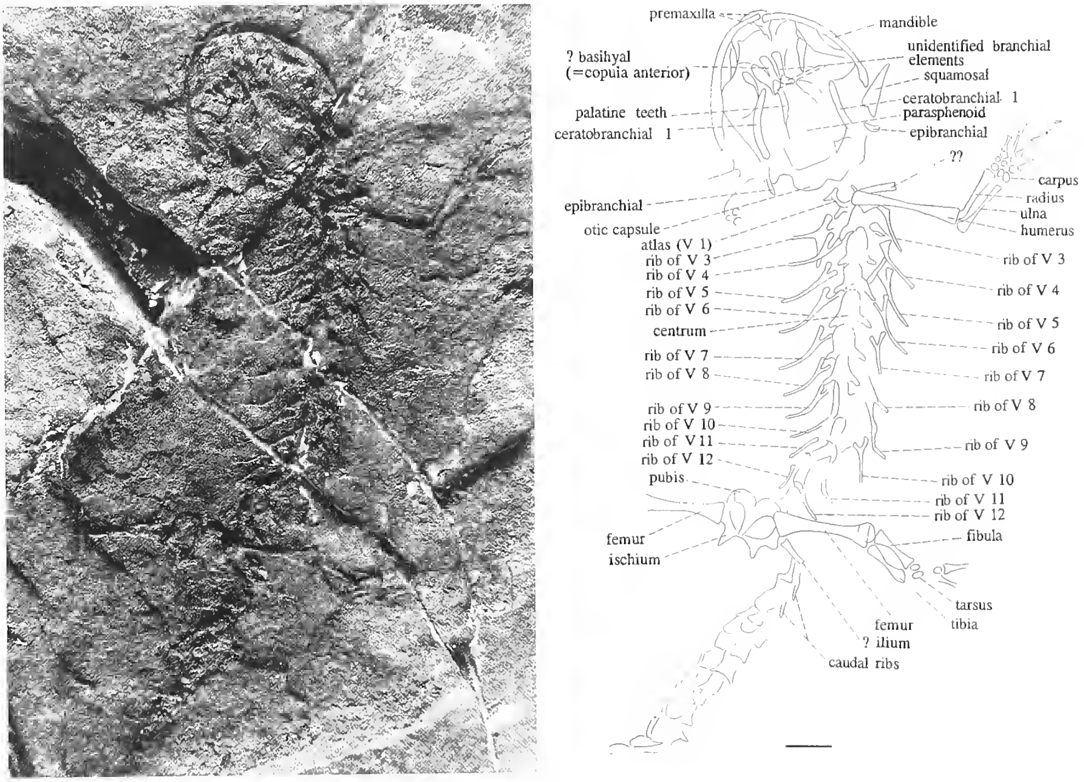
Text-figures 1–6, 8.

1831	*Triton noachicus* Goldfuss, p. 126, pl. 13, figs 6–7.
1831	*Triton Noachicus*; Goldfuss, p. 230.
1852	*Triton Noachicus*; Dechen, p. 502.
1860	*Brachycormus noachicus* (Goldfuss); von Meyer, p. 67.
1863	*Triton* (*Brachycormus*) *noachicus* Goldfuss; von Meyer, p. 297.
1890	*Molge noachica* (Goldfuss); Lydekker, p. 136.
1935	*Triturus noachicus* (Goldfuss); Herre, p. 54.

1949	*Oligosemia gerhardti* Herre, p. 229.
1949	*Oligosemia ankeli* Herre, p. 229.
1949	*Tylototriton kosswigi* Herre, p. 230.
1955	*Tylototiton kosswigi* (ex err.); Herre, p. 799.
1981	*Brachycormus noachius* (ex err.); Estes, p. 71.

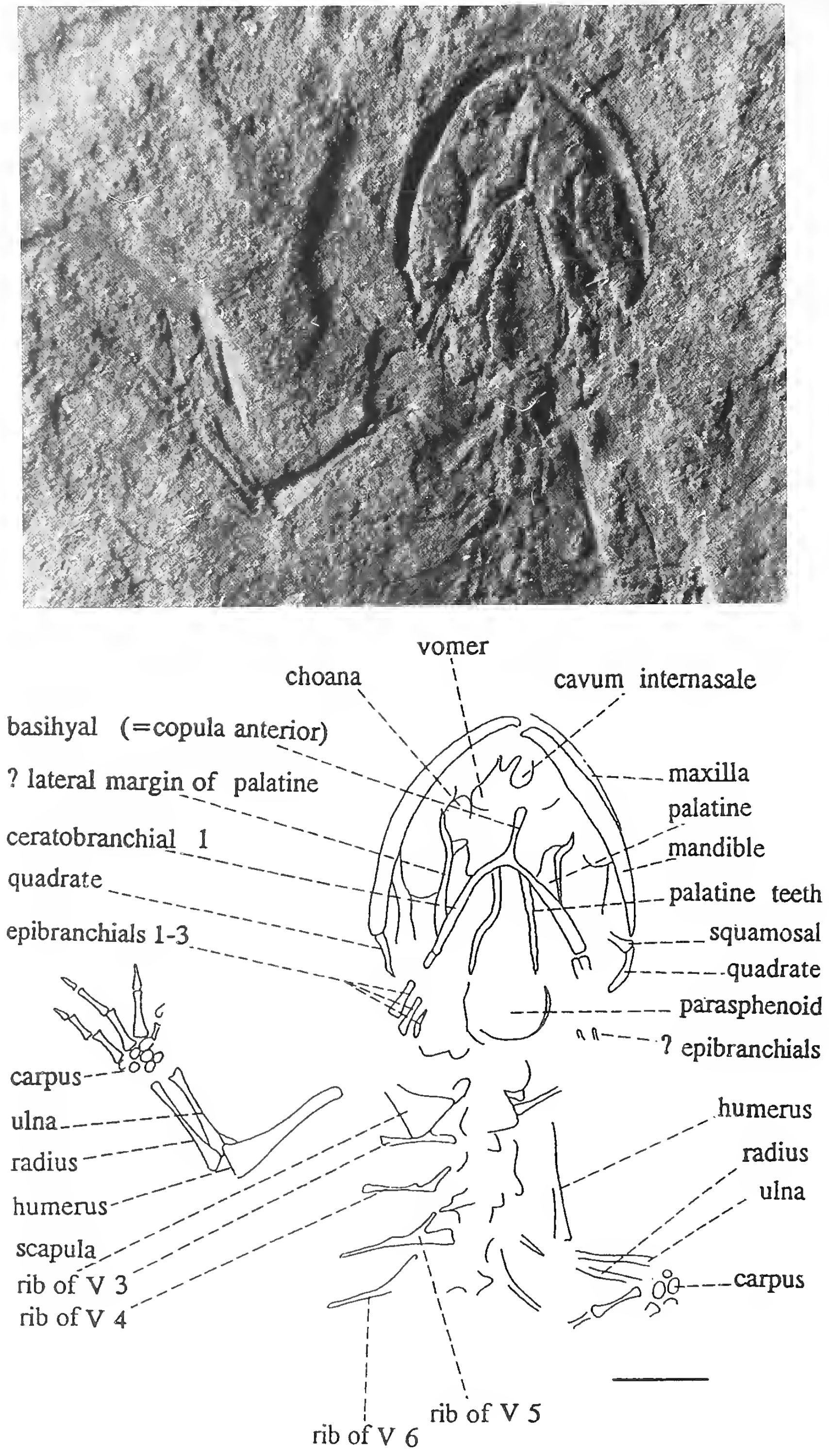
A complete synonymy up to 1990 is given in von Koenigswald *et al.* (1992, p. 319).

Holotype. PIUB Ro 4429 (previously 13207A), a mould of an almost complete skeleton in ventral aspect (Text-fig. 1).

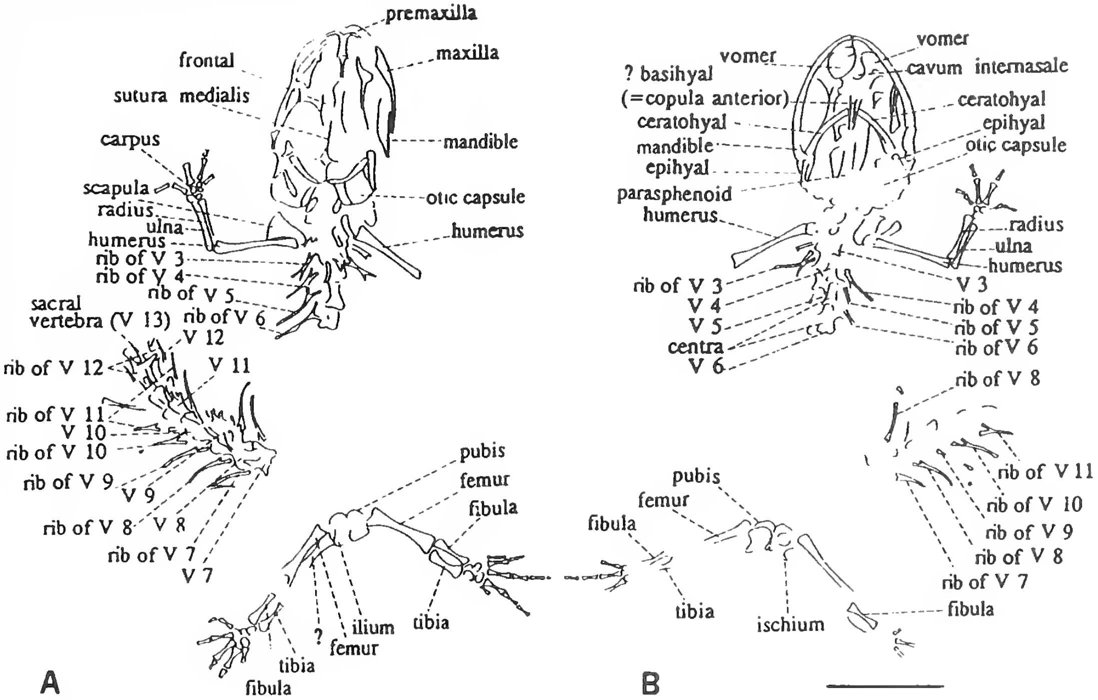


TEXT-FIG. 1. *Brachycormus noachicus* (Goldfuss, 1831). PIUB Ro 4429, holotype; (formerly Goldfuss 1307 A); Upper Oligocene; Orsberg. Scale bar represents 2 mm.

Comment. The original specimen figured by Goldfuss (1831, pl. 13, figs 6–7) was designated as the neotype by Estes (1981, p. 71). Curiously enough, Estes stated that the specimen was no longer in the collection of the Paläontologisches Institut der Universität Bonn and was probably lost. This statement was repeated by von Koenigswald *et al.* (1992, p. 320) who believed that the neotype was BMNH 30268 illustrated by Estes (1981, fig. 20*a*). However, the holotype was found, under the catalogue number 1307, in the collection of Goldfuss's types and Estes obviously saw it because there is a note written by his hand in the box with the specimen, namely '1307A = Typusexamplar (= Neotype by subsequent designation: Richard Estes 1979 ms, Handbuch der Paläoherpetologie)' and he even stated (loc. cit.) that it is well preserved. Now the specimen has a new collection number, PIUB Ro 4429, and it should be emphasized that it is not a neotype but the holotype by implication, and Estes's designation of the neotype is invalid. A second specimen PIUB Ro 4053*a*+*b*,



TEXT-FIG. 2. *Brachycormus noachicus* (Goldfuss, 1831). PIUB Ro 4244*b*; Upper Oligocene; Orsberg. Skull and anterior part of postcranial skeleton in ventral view. Scale bar represents 2 mm.



TEXT-FIG. 3. *Brachycormus noachicus* (Goldfuss, 1831). Upper Oligocene; Orsberg. PIUB Ro 4245*a–b*. A, skeleton in dorsal view and B, in ventral view. Scale bar represents 5 mm.

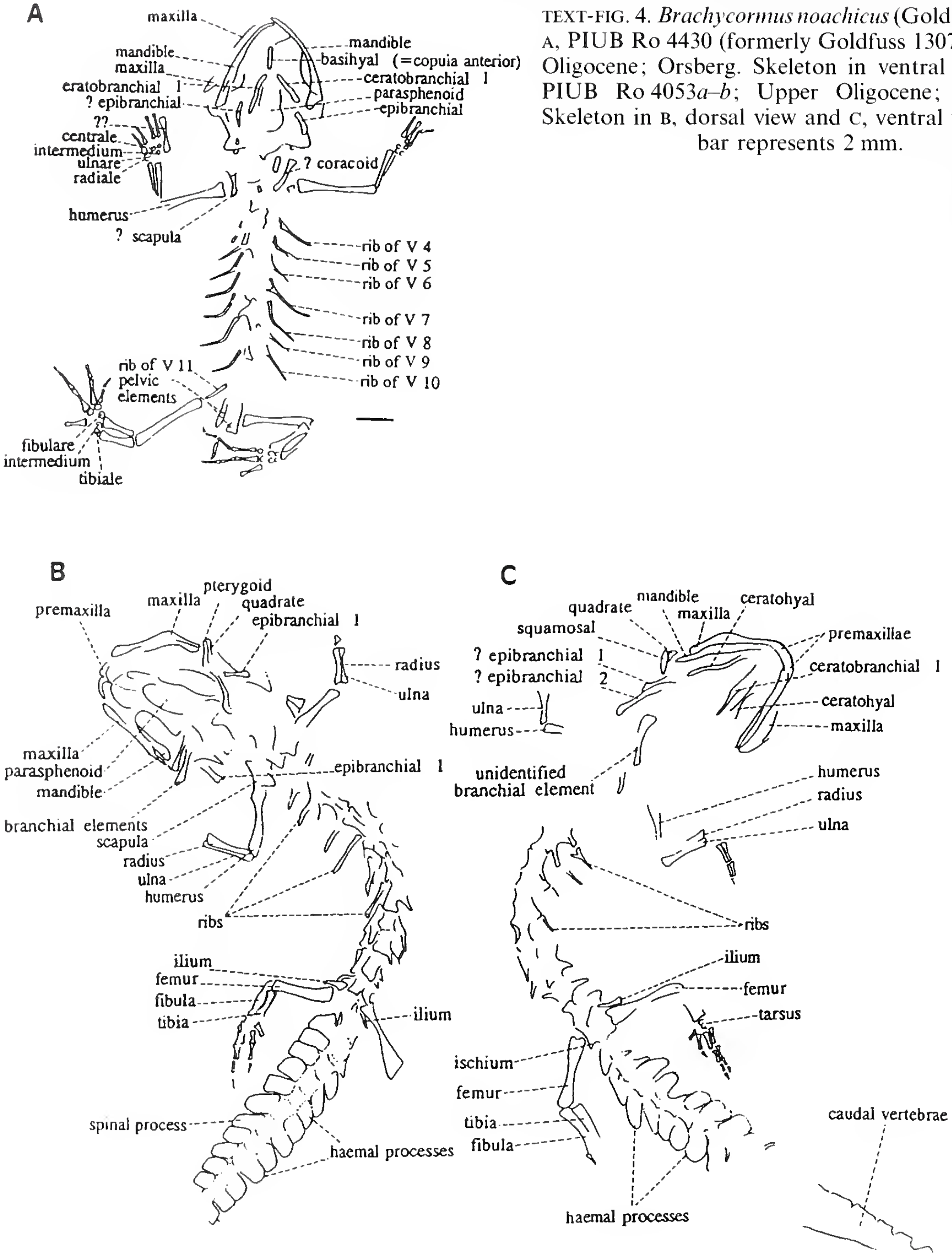
originally described by von Meyer (1860, pl. 8, fig. 7) was designated as the paratype (Koenigswald *et al.* 1992, p. 320) but this designation is also invalid, according to the International Code of Zoological Nomenclature.

Horizon and locality. Upper Oligocene; Orsberg near Erpel, Germany.

Referred material. All from the Upper Oligocene of the Siebengebirge Region near Bonn, Germany. From the type locality: PIUB Ro 4244*a*, *Ro* 4244*b* (Text-fig. 2), Ro 4245 (Text-fig. 3) and Ro 4430 (previously Goldfuss 1307B) (Text-fig. 4A). Attributed to Orsberg but locality uncertain: MB Am.928.1–2 (holotype of *Oligosemia gerhardti* Herre, 1949) (Text-fig. 6A), MB Am.930.1 (holotype of *Tylototriton kosswigi* Herre, 1949) (Text-fig. 6B). From Stösschen near Linz: PIUB Ro 4053 (Text-fig. 4B–C). From 'Rott' (exact locality uncertain): BMNH 30268 (Text-fig. 5).

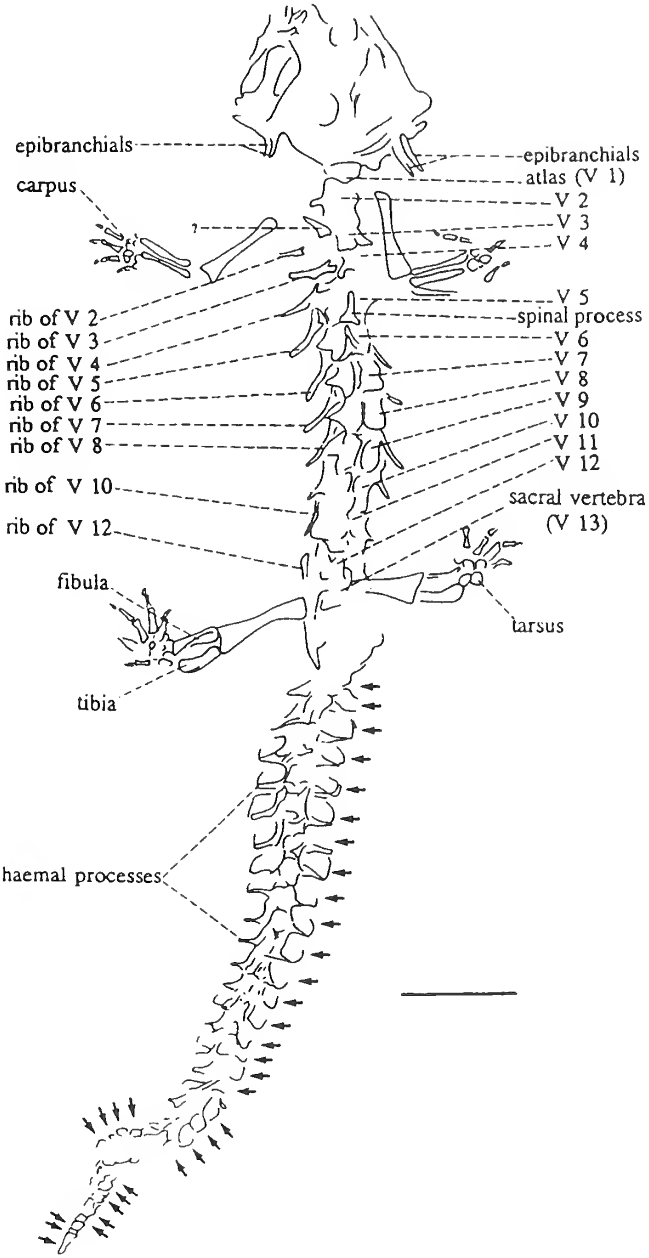
Diagnosis. *Brachycormus* is closely related to *Triturus* but differs from it in that (1) it is neotenous, with an ossified hyobranchial skeleton, specifically the copula anterior, ceratobranchial 1, ceratohyal and epibranchials, and with external gills apparently present, and (2) the skeleton shows incomplete ontogenetic development, with frontotemporal arch absent and vomers probably not fused with palatines, although it reached the final stage of ossification (including elements such as the carpals and tarsals).

Description. All specimens from Orsberg and Stösschen are preserved as natural moulds in matrix. It is obvious that in those specimens in which both counterparts are available, the whole skeleton was compressed dorsoventrally so that in the counterpart, which displays the dorsal aspect, ventral elements are also visible, though to a lesser degree. Nevertheless, the topographical relations between elements such as the maxilla and mandible may be deduced from these specimens (e.g. Text-figs 3A, 4B–C).



TEXT-FIG. 4. *Brachycormus noachicus* (Goldfuss, 1831). A, PIUB Ro 4430 (formerly Goldfuss 1307B); Upper Oligocene; Orsberg. Skeleton in ventral view. B–C, PIUB Ro 4053*a–b*; Upper Oligocene; Stösschen. Skeleton in B, dorsal view and C, ventral view. Scale bar represents 2 mm.

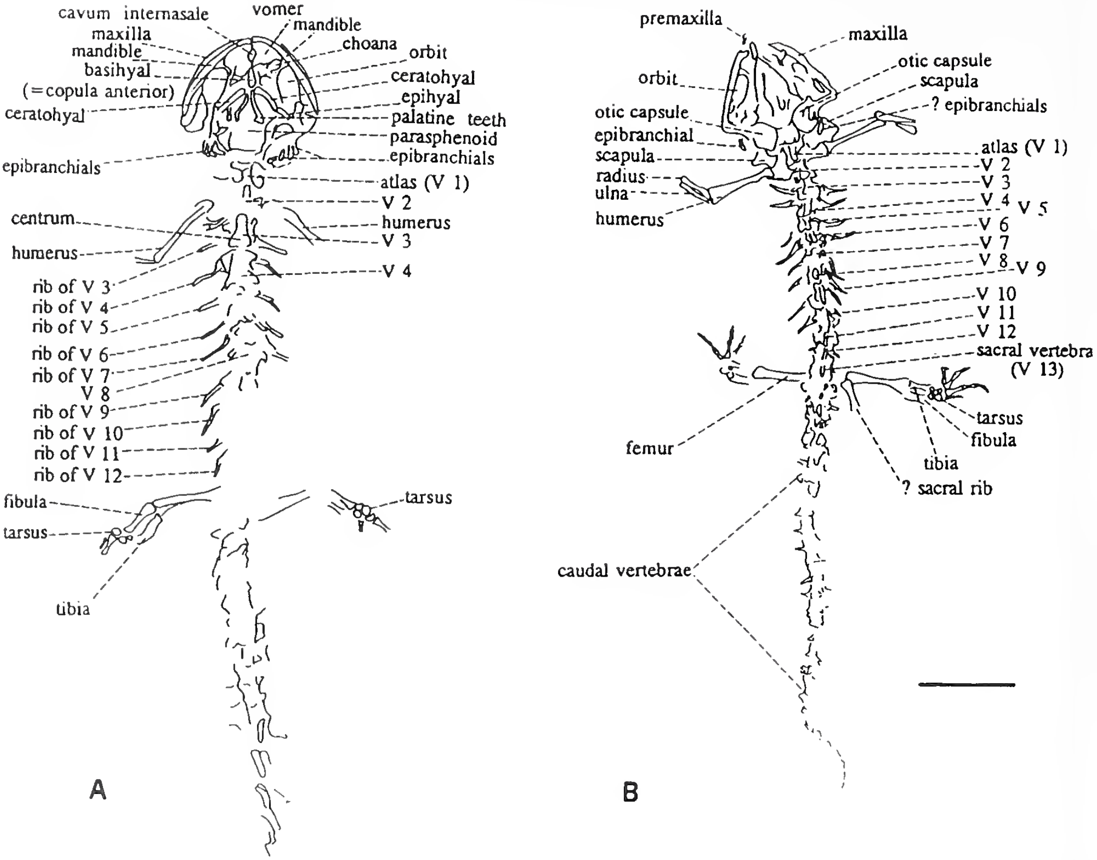
The snout–vent length is about 23 mm. The skull is longer than broad (LC:LtC 1·13–1·30) in the PIUB specimens; however, the two MB specimens collected by Bergemann (Text-fig. 6A–B) have skulls which are slightly broader than long (see Table 1). Although Herre (1949, p. 227) attributed these two specimens to the Orsberg locality, from which most of the others came, there are some doubts as to the accuracy of this attribution, because the locality is not given on the specimen labels and it is obvious that the specimens were



TEXT-FIG. 5. *Brachycormus noachicus* (Goldfuss, 1831). BMNH 30268. Skeleton in dorsal view. Arrows mark positions of caudal vertebrae. Scale bar represents 5 mm.

collected in the first decades of this century long after underground mining had ceased (*c.* 1860). Later collectors searched for fossils in spoil heaps on the surface and sometimes assigned these specimens to the locality of the original site where most specimens had previously been collected (likewise for BMNH 30268 for which the locality is recorded as 'Rott' although the nature of matrix indicates either Orsberg or Stösschen).

The premaxillae (and presumably also the other jaw elements) are dentate. As suggested by symmetrical position of premaxillae in PIUB Ro 4245*a* which represents the skeleton in dorsal view (Text-fig. 3A) and PIUB Ro 4053*b* (Text-fig. 4C), they were fused. The frontal processes of the premaxillae were long and slender, and



TEXT-FIG. 6. *Brachycormus noachicus* (Goldfuss, 1831), A, MB Am.928.1–2, holotype of *Oligosemia gerhardti* Herre, 1949; skeleton in ventral view. B, MB Am.930.1, holotype of *Tylototriton kosswigi* Herre, 1949; skeleton in dorsal view. Scale bar represents 5 mm.

probably fused to a variable extent. In palatal view, the lamina horizontalis of each premaxilla is in contact with the vomer and with the lamina horizontalis of the maxilla. The vomers are separated from one another by the median foramen into the cavum internasale, which is represented as a distinct rounded protrusion in some specimens (e.g. PIUB Ro 4244*b*, Ro 4245*b*, MB Am.928.1–2). The posterior margin of the vomer can be traced in PIUB Ro 4245*a* but it is not clear whether it was separated from the palatine or whether the border between them is an artefact. The vomers and the lamina horizontalis of the maxillae border the fenestra exochoanalis anteriorly and anterolaterally. Each palatine bears a row of teeth on its lateral margin which diverge slightly posteriorly. The parasphenoid is widely rounded posteriorly but narrow anteriorly; however, outlines of this anterior region are obscured by the palatines.

Other cranial elements can be seen in some specimens preserved in ventral aspect. One is a distinct triangular elongated element located within the quadrate region of the holotype (Text-fig. 1); as the skeleton was dorso-ventrally compressed it could be interpreted either as the squamosal or, if it was displaced laterally, the pterygoid. Distinct imprints bordering the medial margin of the orbit and bifurcating anteriorly (tentatively interpreted as the lateral margin of the palatine in Text-fig. 2) are difficult to interpret but occur also in other specimens (Text-fig. 3B, marked by a single line). It is probable that the bifurcation delimits the fenestra endochoanalis (marked as 'choana' in Text-fig. 6A).

In dorsal view the quality of preservation of the skull prevents much information being obtained. PIUB Ro 4245*a* (Text-fig. 3A) shows fused facial processes of the premaxillae and, immediately posterior to them, a pair of imprints that may represent parallel medial ridges of the nasals. Further posteriorly, the median suture may be traced, but the lateral margins of frontals and parietals are not distinct; however, in no specimen was the frontotemporal bridge found and apparently it was not developed. The maxilla does not reach posteriorly the level of the jaw articulation (Text-fig. 3A).

The hyobranchial apparatus consists of the copula anterior (= basihyal) which was articulated with the first ceratobranchials in some specimens (Text-figs 1, 4A), while in other specimens these structures seem to be confluent (Text-fig. 2). These differences may be explained in terms of variation in degree of ontogenetic development (only in fully developed individuals are both structures separated as in *Triturus*). In PIUB Ro 4245*b* (Text-fig. 3B) and probably (but not certainly) in MB Am.928.1–2 (Text-fig. 6A) similar elements are directed at their posterior ends towards the lower jaw, though anteriorly they are in contact with a median element that corresponds to the anterior copula. These elements thus can be interpreted, because of their different position, as the ceratohyals and not the first ceratobranchials. The absence of the ceratobranchials in PIUB Ro 4243 may be explained either by the loss of that part of the hyobranchial skeleton before fossilization or by insufficient ossification. The posterior tips of the ceratohyals were articulated with the epihyals (PIUB Ro 4245*b*; Text-fig. 3B). In other specimens, one (Text-figs 1, 4A) or several (Text-figs 2, 5–6) epibranchials may also be preserved. Although the articulated ossified branchial elements in most specimens recall the condition in normally developed *Triturus*, well-developed epibranchials are the principal evidence that *Brachycormus* was neotenous.

The vertebrae are opisthocoelous. The vertebral column consists of 12 (or 13) presacral vertebrae. Their spinal processes are dilated antero-posteriorly and their thickened (or even bifurcated, as suggested by BMNH 30268; Text-fig. 5) posterior part is somewhat protruding. Except for the atlas, the presacrals bear bicipital ribs. The rib associated with V3 bears a dorsal process, posteriorly situated in the flattened specimens, which is equal in length to the distance from its base to the tip of the rib (so the rib seems to be bifurcated distally as well; see Text-fig. 3). The rib of V4 has this dorsal spine shifted proximally. The remaining ribs do not have such processes. The caudal vertebrae are usually exposed laterally, because their tall neural spines and deep haemal processes (except for those on the first two caudals) resulted in the tail being twisted through 90° along the longitudinal axis and embedded in matrix in the horizontal position, as a result of post-mortem pressure. The posterior margin of both haemal and neural processes of the caudal vertebrae are thickened (Text-fig. 5) but this thickening cannot be recognized in some other specimens (Text-fig. 4B–C). The laminae on the haemal processes are not developed in the posterior caudal vertebrae (Text-fig. 5) whereas they are clearly visible on the neural processes. BMNH 30268 demonstrates the complete series of 34 caudal vertebrae.

From the elements of the shoulder girdle only the triangular scapula can be recognized (Text-fig. 3A). The ratio between the humerus and ulna (and also between the femur and tibia) deserves some attention (Table 1).

TABLE 1. Morphometric data of available material of *Brachycormus noachicus*. Abbreviations: LC, length of head; LtC, width of head; LH, length of humerus; LU, length of ulna; LF, length of femur; LT, length of tibia.

Specimen	Locality	LC:LtC	LH:LU	LF:LT
PIUB Ro 4429 (holotype)	Orsberg	1·13	1·78	2·1
PIUB Ro 4430	Orsberg	—	1·83	2·1
PIUB Ro 4053	Stösschen	—	1·56	—
PIUB Ro 4245	Orsberg	1·30	1·79	1·9
PIUB Ro 4244*b*	Orsberg	1·25	1·24	—
PIUB Ro 4244*a*	Orsberg	—	1·32	1·6
BMNH 30268	?Rott	—	1·61	2·06
MB MB.Am.928.1–2	?Orsberg	0·93	—	1·84
MB MB.Am.930.1	?Orsberg	0·95	1·87	—

LH:LU is 1·56–1·87 but in PIUB Ro 4244*a* and Ro 4244*b* (which represent two different individuals) the ratio is 1·24 and 1·32, respectively. These values suggest either rather wide intraspecific variation range or interspecific difference. The latter explanation seems to be supported by the fact that these differences are found in individuals of the same size (hence supposedly of similar individual age) and from the same locality (Orsberg). However, these morphometric data cannot be supported by morphological ones because of poor state of preservation.

In the pelvic girdle, the pubis and ischium are usually preserved as ventral imprints, with characteristic outlines (Text-figs 1, 3). The carpus and tarsus were ossified. The carpus consists of three proximal elements, namely the radiale, intermedium and ulnare (Text-figs 1, 4A), and two elements located more distally (Text-figs 1–2); the carpal element surrounded by other bones may be interpreted as the centrale, the marginal carpal as the prepollex. The most distal row associated topographically with the metacarpals is of the distal carpals. Similarly, the tarsus consists of three proximal elements (fibulare, intermedium, tibiale; Text-fig. 4A); however, other tarsal elements are displaced so that it is difficult to determine them. The phalangeal formula is 2-2-3-3 in the manus and 2-3-4-?4-?2 in the pes.

Developmental status. The ossification of the carpus and tarsus, the ossification of most of the hyobranchial skeleton, and the presence of epiphyses on the long bones, all suggest that these animals were fully mature adults (except for PIUB Ro 4244*b*). It is difficult to deduce how much of the hyobranchial skeleton was also present in cartilaginous form, but the shape of the ossified components (the copula, both first ceratobranchials and both ceratohyals) suggests that it was similar to the condition occurring in the final stages of metamorphosis in the normal development of *Triturus*. The imprints of the posterior elements of the branchial arches (epibrachials) suggest that external gills were present. This may be taken as evidence that *Brachycormus* was neotenous.

Variation. Apart from characters which may depend on the state of preservation (proportions of skull, precise shape of bones), there is one obvious variable feature which may cast doubt on the view that all specimens belong to a single taxon. This is the shape of the haemal and neural processes of the caudal vertebrae. Whereas in PIUB Ro 4053 they are developed as thin, flat laminae, in BMNH 30268 these processes are clearly thickened along the posterior margins and in some vertebrae only these parts are preserved but not the laminae themselves (Text-fig. 5). Von Meyer (1860, p. 65) gave the total number of caudals as 36 or possibly more. This count is in approximate agreement with the condition in BMNH 30268 (Text-fig. 5), in PIUB Ro 4053 (von Meyer 1860, pl. 7, fig. 7 probably illustrated the skeleton in the original state when there was still a complete tail; however, the position of the distal section of the right fore extremity, which is different from that in Text-fig. 4B–C, may suggest that von Meyer also idealized his illustrations somewhat), and in a lost specimen (von Meyer 1860, pl. 7, fig. 8) which is the only known specimen of *Brachycormus* to be preserved in lateral aspect. This latter specimen has only spines instead of laminae with thickened posterior margins, as is the case with the posterior caudals in BMNH 30268. Moreover, the shape of the caudal vertebrae in PIUB Ro 4053 (Text-fig. 4B–C) is similar to that in the holotype of *Archaeotriton basalticus* (von Meyer, 1859), figured by von Meyer (1860, pl. 7, figs 9–10), but differs from it in the shape of the presacral ribs and smaller size so that it is clear that both are different taxa (see below). The same holds for another, poorly preserved specimen of *Archaeotriton* [NMP ČM 1421 (Pb 23)] from the Upper Oligocene of Varnsdorf described by Laube (1901). This has clearly expanded spinal processes, but is much larger than *Brachycormus*. It may be concluded that although the neural and haemal spines are similar in shape in taxa distinguishable on the basis of other characters (e.g. *Archaeotriton*), significant variation may occur in this character, perhaps dependent on the degree of ossification, as in living *Triturus*. For this reason, all the studied specimens are referred to a single taxon, despite their variation.

On the other hand, as suggested by the condition in contemporary species of *Triturus*, the main differences between the species should be expected in the structure of the skull. The postcranial skeleton is relatively uniform. Since the important diagnostic characters of the skull (e.g. the dorsal circumorbital region) are not sufficiently preserved, it remains possible that the known specimens of *Brachycormus noachicus* represent more than one species.

Geographical and stratigraphical occurrence. Until now, *Brachycormus* has been reported only from Orsberg, Stösschen and Rott in Siebengebirge, Germany, all of which are believed to be of uppermost Oligocene age (von Koenigswald *et al*. 1992, p. 313). The holotype of *Triturus opalinus* von Meyer, 1852 from Lužice (Lower

Miocene) in the Czech Republic, which may be conspecific with *Brachycormus* (see below for comparison), is based on a fragment of the postcranial skeleton and, consequently, important diagnostic characters are missing. However, it is not impossible that the specimen from Lužice (Text-fig. 9; see discussion below) represents a record of *Brachycormus* in another Central European locality.

THE ROLE OF NEOTENY IN THE TERTIARY CAUDATA

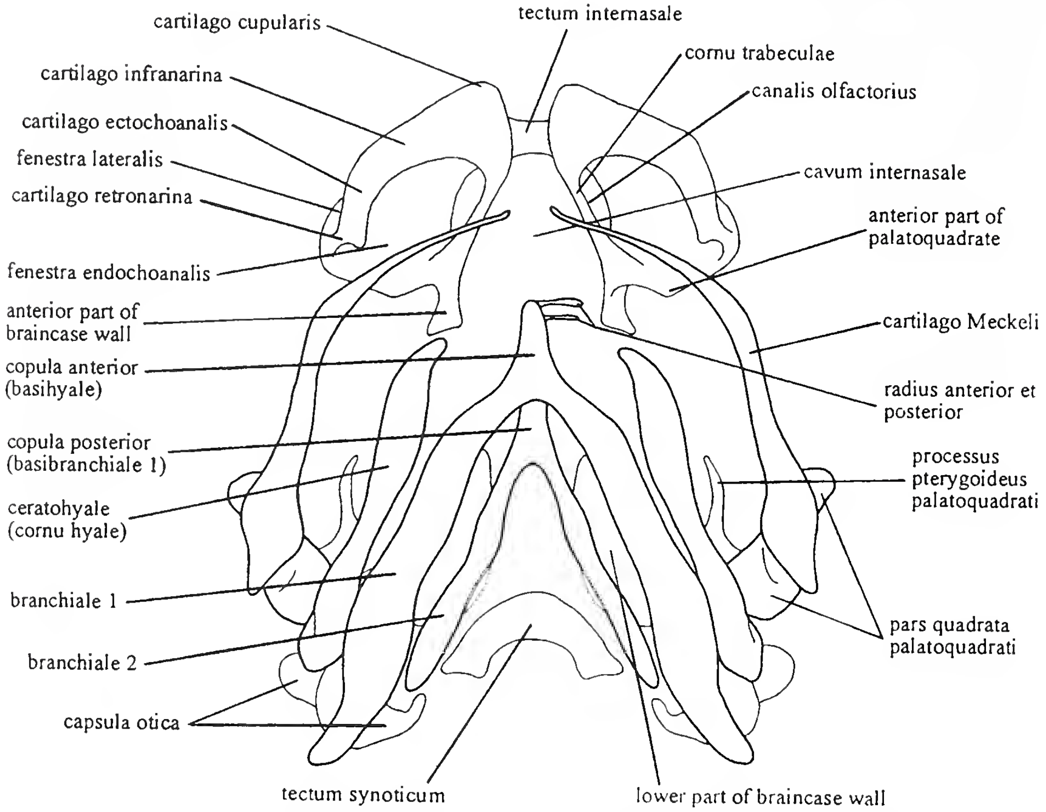
The presence of larval features in adult individuals with fully ossified skeletons is the simplest way to recognize neoteny in fossil urodeles. Neoteny (the shift of sexual maturity in premetamorphic stages) usually indicates deterioration of some aspect of the original normal environment. This may be either deterioration when aquatic habitats become surrounded by permanently harsh terrestrial conditions (Wilbur and Collins 1973), or deterioration when breeding seasons become shorter and periods of hibernation are prolonged due to increasing seasonality of climate. In the latter case, the animals are unable to complete their ontogenetic development over the normal time, i.e. the time which is usually available for complete development from egg to adult. However, the shift of appearance of some characters into earlier developmental stages is not necessarily accompanied by abbreviation of the chronological period in which morphogenesis of an individual is completed (i.e. is not accompanied by accelerated ontogenetic morphogenesis); quite the opposite – in amphibians it is usually associated with temporal prolongation of larval development. This clearly indicates that these animals are not able to complete their metamorphosis in time, due to unfavourable living conditions. In such cases, metamorphosis is postponed until conditions improve, provided that paedomorphosis is not genetically fixed.

The simplest example of a response to deterioration of climate manifested by prolongation of the cold seasons is an overwintering larva that hibernates and completes its metamorphosis in the following year. However, such developmental prolongation is associated with the retardation of sexual maturity, which is a disadvantageous phenomenon. Therefore, if long-term deterioration of climate causes such a situation to be repeated annually, then adaptations are developed that enable sexual maturity to be reached as in normal development. This seemingly results in a shift of sexual maturity into an earlier developmental stage (usually interpreted as acceleration of sexual development), but in fact it is the retardation of the somatic development; the sexual development is stable. When morphogenesis of the skeleton is retarded in this way, but the rate of ossification (which is dependent on time, not on morphogenetic degree attained) is normal, then the result is a neotenous individual, i.e. a permanent water dweller, with an ossified skeleton. This is no doubt the case with *Brachycormus*, as demonstrated by the hyobranchial skeleton and the expanded neural and haemal processes of the caudal vertebrae.

Timing of reproduction in paedomorphic and metamorphosed individuals of the same species is different, even under identical climatic conditions. For instance, paedomorphic adults of *Ambystoma talpoideum* lay eggs approximately six weeks earlier than terrestrial morphs, under the same living conditions. Early egg-laying and subsequent growth of hatchlings results in a significant size advantage for larvae from paedomorphic parents (Scott 1993). Also in *Triturus*, larval growth rate is higher and sexual maturity is attained sooner in paedomorphic forms (Kalezić *et al.* 1994). However, it should be noted that paedomorphosis may not only represent adaptation to deterioration of environmental conditions but may also occur for other reasons (see Whiteman 1994 and references therein for reviews).

When conditions become favourable in the long term, neotenous amphibians could be expected to invade dry land again and enter water only for breeding. It is obvious that such a shift in life strategy would be followed by the disappearance of gills and subsequent transformation of the hyobranchial apparatus into the hyoid. However, other features may remain unaffected and would retain their original paedomorphic state of somatic retardation. This might result in the retention of larval or juvenile characters which occurred in ancestral (neotenous) forms, even though living conditions correspond to those which existed before these ancestral forms were forced to adopt neoteny.

It is worth noting that neotenous features are usually associated with the viscerocranium because paedomorphs need to maintain branchial support of the gills. However, the branchial skeleton in *Brachycormus* is not preserved in the original larval form, but, judging from comparison with normal development in contemporary *Triturus alpestris* (Text-fig. 7), it corresponds to that of the final stages of metamorphosis. This means that restructuring developmental processes associated with metamorphosis (i.e. with the transition onto dry land) had already started but were blocked before their completion. As stated above, this can be caused either by prolongation of periods of inactivity (and corresponding shortening of breeding seasons) due to decrease of average temperature or, in contrast, by increase of average temperature and subsequent aridization making life on dry land difficult or impossible for insufficiently adapted forms. The former possibility may be illustrated by the irregular occurrence of overwintering larvae in central European populations of the Alpine newt [*Triturus alpestris* (Laurenti, 1768)] which is obviously correlated either with cold weather during the breeding season or the early onset of winter, or both. The second case may be exemplified by the occurrence of neotenous forms of *T. alpestris*, *T. vulgaris* and *T. carnifex* in the Balkan Peninsula (Roček 1974; Kalezić and Dzukić 1988; Kalezić *et al.* 1994). Aridization of climate in the Mediterranean area is a relatively recent phenomenon and this may explain why neoteny in these populations is only facultative and not genetically fixed. Both these contradictory reasons (decrease or increase of average temperatures) may have the same anatomical manifestations, namely retardation of developmental morphogenesis and shift of sexual maturity into earlier morphogenetic stages. This results in a larva capable of breeding.



TEXT-FIG. 7. *Triturus alpestris* (Laurenti, 1768); neotenous individual from Drakolimni Greece; chondrocranium in ventral view, reconstructed from serial sections.

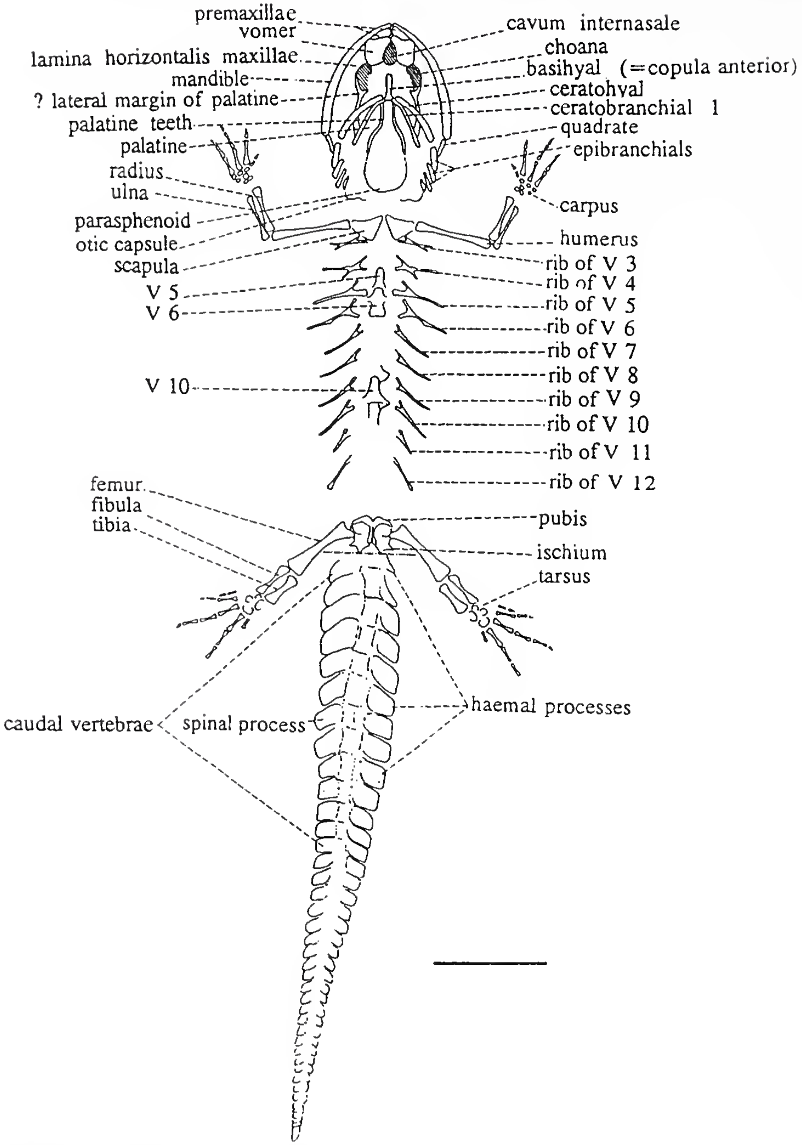
In the Tertiary urodeles, the evolutionary step characterized as retarded developmental morphogenesis accompanied by a shift of sexual maturity was only subsequently followed by full ossification of the skeleton, including its branchial parts. In populations with facultative paedomorphosis, the metamorphic phenotype predominates in temporary ponds that dry out in most years, and the paedomorphic phenotype predominates in nearly permanent ponds (Semlitsch and Gibbons 1985; Semlitsch *et al.* 1990). Thus it seems that absence of a metamorphosed counterpart to the neotenous *Brachycormus* suggests the latter case and thus that the reason for neoteny in *Brachycormus* was not aridization of climate. This seems to be supported by the fact that the appearance of *Brachycormus*, as well as the neotenous forms of *Chelotriton*, is chronologically correlated with the Oligocene cooling event.

In general, the Oligocene was a period of significant cooling (Crowley and North 1991, p. 192) that started with a sharp drop in mean annual temperature in the early Oligocene and has continued to the present day, disregarding some temporary insignificant warm intervals. The Oligocene decline in mean annual temperature is estimated to have reached over 10 °C (Wolfe 1978, p. 699) and it was accompanied by a similarly profound shift in temperature equability so that the mean annual range of temperature which was 3–5 °C in the mid Eocene increased to 21–25 °C in the Oligocene (Wolfe 1978, p. 700; the data concern the Pacific Northwest of North America). A global mid Oligocene cooling event caused by glacio-eustatic fall in sea level has been proposed as the cause of selective extinctions of some vertebrate taxa (Prothero 1985). Moreover, in Europe the Oligocene (and Late Oligocene in particular) was a period of major geodynamic events that were no doubt reflected in climatic changes. In the Rupelian to Eochattian there was still a subtropical climate with a mean annual temperature of about 13–18 °C and non-seasonal rainfall in the area (shown by the palaeoflora of Witznitz, south of Leipzig; see Walther 1990, p. 154). The Late Oligocene palaeofloras of the same region, e.g. Borna, Bockwitz and Thierbach (Walther 1990, p. 155), however, indicate clear distinctions from the older complexes (appearance of arcto-tertiary elements), and suggest a comparatively cooler climate (annual mean temperature 4–13 °C) with longer winter seasons, which indicate clear deterioration of climate. The latter palaeofloras are, according to Walther (1990), similar to those found in Mainz Basin in the Vilbeler Schichten, and in Orsberg, Rott and Stösschen. Palaeoclimatic data obtained from analysis of palaeofloral changes in the molasse of western Switzerland (Berger 1990, p. 193) suggest that the relatively warm and humid climate of the Oligocene was terminated by a temperature and humidity crisis at the end of Oligocene, marked by disappearance of taxads and palms; this was followed by rising temperature but low humidity in the early Miocene. Cícha and Kováč (1990, p. 71) summarized climatic development in central Paratethys during the Egerian and concluded that, whereas the subtropical macro- and microflora are characteristic for the early and mid Egerian, a drop of temperature in the late Egerian is evidenced by appearance of deciduous arcto-tertiary elements. Later in the Miocene the climate improved again as shown by the presence of evergreen tree species.

This deterioration of climate (decrease in mean annual temperature and increase in mean annual range of temperature, i.e. increase in seasonality) meant that amphibians had to adapt to these new conditions, or withdraw from the region (the latter is the case, for instance, with *Andrias* and *Chelotriton* (*Tylototriton*) at the Plio–Pleistocene boundary). *Brachycormus*-like amphibians could obviously adapt themselves to a form of water-dwelling neotenous larva in order to compensate for deterioration of living conditions. Once favourable climatic conditions were restored again to allow metamorphosis, the normal adult stage could retain features which at the ancestral level were larval or juvenile (e.g. the incomplete frontotemporal bridge). This may be the case with *Triturus* which is readily derivable from *Brachycormus*, provided that the hyobranchial apparatus is developed until its final stage.

PHYLOGENETIC RELATIONS AND SYSTEMATIC POSITION

Brachycormus noachicus is similar to the common Tertiary species *Chelotriton paradoxus* in all characteristic features of the postcranial skeleton, such as opisthocoelous vertebrae with antero-



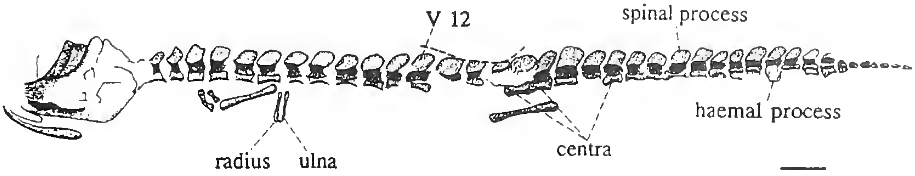
TEXT-FIG. 8. *Brachycormus noachicus* (Goldfuss, 1831). Reconstruction of skeleton in ventral view. The tail posterior to the transverse line is twisted through 90° along its longitudinal axis which corresponds to the preservational position. Scale bar represents 5 mm.

posteriorly expanded spinal processes, similarly enlarged haemal processes on caudals, bicipital ribs with dorsal spines, and the shape of the pelvis (Text-fig. 8). Also the basic structural scheme of the skull is similar (including the presence of an ossified hyobranchial skeleton). The principal difference is that *Chelotriton* is more heavily ossified. This is manifested both in the skull (all exocranial bones are large and covered with sculpture, often fused with each other, the frontotemporal arch is well-developed, the maxillary arch is complete, and at least some exocranial bones coalesced with endocranial ones) and in the postcranial skeleton (the spinal processes of most presacral vertebrae are terminated dorsally by a horizontal plate covered with sculpture which is similar to that on the dermal bones of the skull). The reduced degree of ossification in *Brachycormus* may be explained by retarded osteogenesis in the lineage which split from the *Chelotriton* stock in the late Oligocene. However, neoteny had already appeared in the *Chelotriton–Brachycormus* lineage as demonstrated by the presence of the ossified hyobranchial apparatus in *Chelotriton paradoxus* (the earliest records of which are also from the Oligocene), but in a specimen of *Chelotriton robustus* from the Middle Eocene (Westphal 1980), it is absent. The same may hold for *Chelotriton* recorded from the Upper Eocene of England (Milner *et al.* 1982) but represented only by isolated vertebrae and few skull fragments. It may be supposed that the shift to neoteny was the first response to the Oligocene cooling, and retarded osteogenesis followed later.

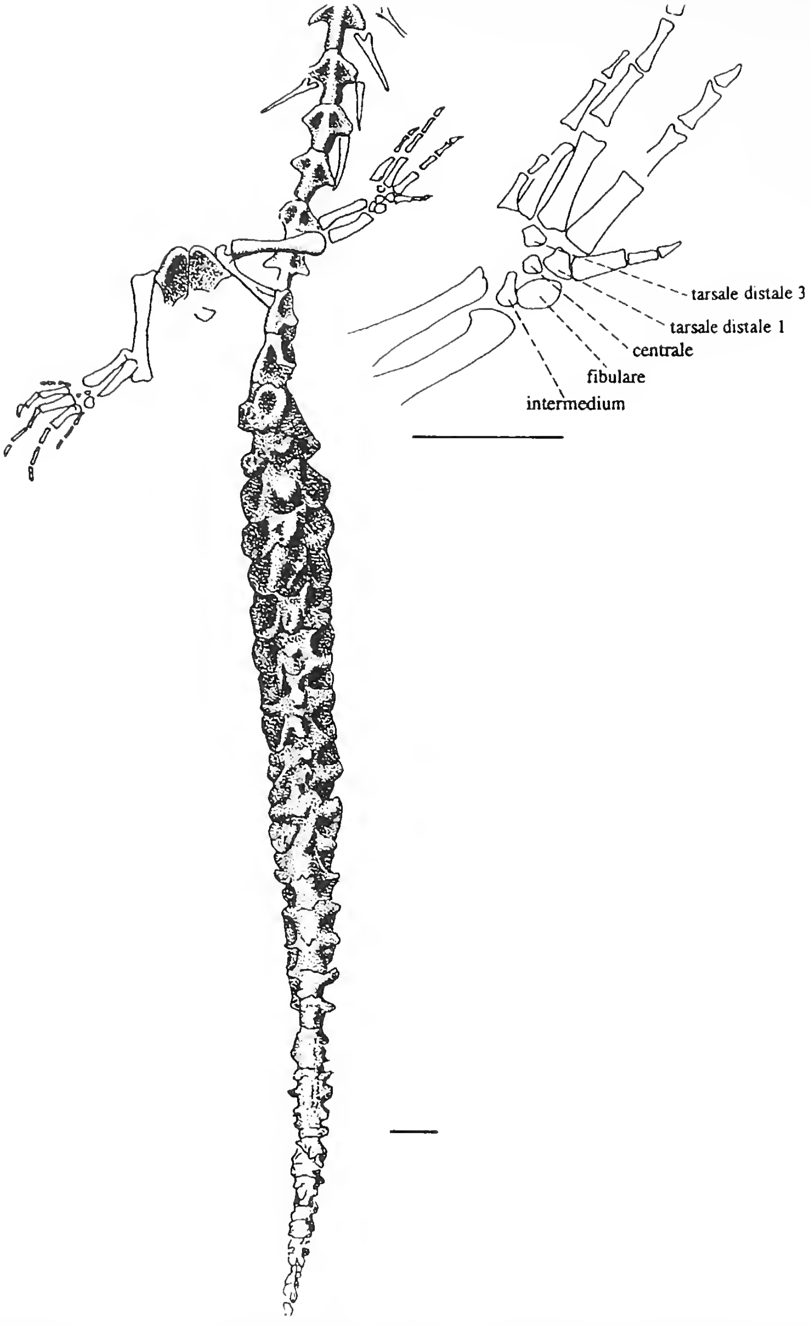
It is obvious from the list of diagnostic characters given above that the difference between *Brachycormus* and *Triturus* is based primarily on the neoteny of the former. Hence, the question arises whether *Brachycormus* can be distinguished from *Triturus* as a separate genus only on the basis of neotenous features, or if it was only a neotenous lineage from within the *Triturus* radiation. At the present state of knowledge, this question is rather difficult to answer. The differences between the two taxa are situated only in the ventral part of the skull but not in the postcranial skeleton, and only in some details of the dorsal part of skull (e.g. frontotemporal bridge that may be developed to a variable degree in *Triturus* and presence of sculpture in its larger and better ossified species). The problem arises from the fact that all the material described as *Triturus* consists either of isolated vertebrae or of articulated postcranial skeletons; if the skull is present, the distinguishing characters are not observable or preserved. Until now, no *Triturus* skeleton has been found that clearly displays the ventral part of the skull. For all these reasons, and also because the hyobranchial apparatus in *Brachycormus* was ossified, whereas in Recent populations of *Triturus* where facultative neoteny occurs (which is, e.g., the case with the Greek populations of *Triturus alpestris*; see Text-fig. 7) it remains cartilaginous, one should maintain *Brachycormus* and *Triturus* as separate genera. Then, it is a matter of discussion whether neoteny is sufficient to distinguish these two taxa at generic or only specific level.

Brachycormus may also be compared with some other similar forms, regardless of uncertainty concerning their taxonomic validity. It is similar in size to the holotype of *Triturus opalinus*, from the Miocene locality of Lužice near Bílina (Czech Republic), which was preserved only as a set of posterior limbs (von Meyer 1852*a*, table 10, fig. 9) with ossified tarsus and with poorly preserved caudals. However, late in the nineteenth century, this specimen, originally deposited in the Lobkowitz collections in Bílina, was moved to Budapest where it was destroyed in 1956, so that direct comparison with *Brachycormus* is no longer possible. Estes (1981, p. 88) located another, nearly complete skeleton from Lužice in the collections of the National Museum, Prague [ČM 1462 (Pb 26, 27)]. This specimen is poorly preserved (Text-fig. 9) and the principal diagnostic structures, such as the ribs and distal parts of the limbs, are lacking. However, the size of animal, the shape of the caudal opisthocoelous vertebrae, and the fact that all preserved skeletal parts are fully ossified, recall *Brachycormus*. On the other hand, absence of some important elements in an otherwise articulated skeleton might support Estes's view that the individual was not fully grown.

Brachycormus resembles *Archaeotriton basalticus* (von Meyer, 1859) from the Upper Oligocene locality of Varnsdorf near Rumburk in north Bohemia (Czech Republic), in the presence of



TEXT-FIG. 9. NMP ČM 1462 (Pb 26, 27). Miocene; Lužice near Bílina (north Bohemia, Czech Republic). Skeleton in lateral aspect, preserved in silicified diatomites. Scale bar represents 2 mm.



TEXT-FIG. 10. SMNS 58653. Part of postcranial skeleton of *Triturus*-like salamandrid from the Miocene of Randecker Maar (Germany). Presacral skeleton in ventral view, tail twisted through 90° along its longitudinal axis, preserving the lateral aspect along the horizontal plane of matrix. Scale bars each represent 2 mm.

opisthocoelous centra, the shape of the neural and haemal processes of the caudal vertebrae, the number of caudals (35), and in the ossified tarsal elements. However, according to von Meyer (1860, p. 72), who studied the holotype of *Archaeotriton*, the latter is twice as large as *Brachycormus* (its size is similar to that of *Triturus cristatus*) and even the posterior presacral ribs bore distinct dorsal process. On the other hand, it agrees with *Brachycormus* in stratigraphical occurrence because it comes from a locality which is of Upper Oligocene age (see Špinar 1972, p. 22).

Judging from the opisthocoelous vertebrae, the shape of the ribs and pelvic elements, and similarities between *Brachycormus* and metamorphosing *Triturus* in the shape of the branchial skeleton and, to a lesser extent, other cranial features, these genera are closely related. Furthermore, *Triturus* and *Brachycormus* are similar in that the premaxillae are fused, the row of palatine teeth is straight or only moderately arch-like (not S-shaped), the posterior part of the parasphenoid is broad and oval, the posterior tips of the maxillae reach almost to the level of the quadrate, and the nasal process of the premaxillae is long and slender. On the other hand, *Triturus* differs from *Brachycormus* in having more developed exocranial bones (the *Triturus* species have the frontotemporal arch developed to various degree, starting from only signs of it in *T. alpestris* to complete connection in *T. helveticus*) (see also Haller-Probst and Schleich 1994). Larger and better ossified forms of *Triturus* (*T. cristatus*, *T. marmoratus*) bear even sculpture on some roofing bones. If it is theorized that the hyobranchial apparatus of *Brachycormus* continued to develop until its definite shape, then the stage found in *Triturus* would be achieved.

Occurrence of the underdeveloped frontotemporal arch in *Triturus* and its presence in contemporary *Pleurodeles*, *Tylototriton*, *Echinotriton* and in Oligo-Miocene *Chelotriton* suggest that all these genera are related. This view is supported also by the dorsal spines on the ribs (although variably developed), and by the dilated processes on the caudal vertebrae. Since *Brachycormus* is closely related to *Triturus*, as shown above, this form should be included into this group of salamandrid amphibians too.

Brachycormus and/or *Triturus*-like forms were probably widespread from the Oligocene through Pliocene of Europe. This is supported by SMNS 58653, the nearly complete posterior part of a postcranial skeleton (Text-fig. 10) from the Miocene of Randecker Maar (south Germany), which can be recognized as a similar form by the shape of the caudal vertebrae (twisted through 90° along its longitudinal axis), the shape of pelvis in dorsal view, the proportions of the hind limb, and the ossified tarsus. In all these characters, SMNS 58653 agrees with *Brachycormus*, but as the principal diagnostic characters of that genus are in the anterior part of the skeleton, it cannot be determined whether SMNS 58653 belongs to *Brachycormus* or to *Triturus*.

This example of *Brachycormus*–*Triturus* relationships (similar to the relations between *Chelotriton*, *Tylototriton*, *Echinotriton* and *Pleurodeles*) illustrates that recognition of phylogenetic relations between taxa represented by normal adult forms and those that are represented by neotenous individuals, or which passed through a neotenous stage in their history, is rather complicated and depends on a correct understanding of past evolutionary processes. If these relations are deduced only from character comparisons, then it is necessary to follow two approaches: (1) comparisons should be based on only those characters in neotenous or post-neotenous forms that occur both in larva and adult (i.e. strictly larval characters should be excluded); (2) if neotenous or paedomorphic characters are used in such analyses, then they must be compared with those in corresponding developmental stage of normal development (i.e. adult characters must be excluded). This seemingly obvious rule is often overlooked and all available characters are compared without evaluation of their evolutionary history.

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KIMMERIDGIAN METRIORHYNCHID CROCODILES FROM ENGLAND

by DANIEL R. GRANGE *and* MICHAEL J. BENTON

ABSTRACT. Remains of metriorhynchid crocodilians are rare in the British Kimmeridgian. A new partial metriorhynchid skull, recently discovered at Westbury, Wiltshire is provisionally assigned to *Metriorhynchus superciliosus*, a common narrow-skulled species previously described from the Oxford Clay (Callovian) sequences of Peterborough. It is covered with encrustations on both dorsal and ventral surfaces, indicating a long period of exposure on the sea floor, in relatively oxic conditions, before burial. There is evidence for both predator damage and a phase of post-depositional deformation.

METRIORHYNCHID crocodilians are known from the Middle Jurassic (Bathonian) to the Lower Cretaceous (Hauterivian) of England, France, Germany and Switzerland (Steel 1973; Benton 1993). Primitive metriorhynchids include *Pelagosaurus* from England and France (Buffetaut 1980). The Bathonian record is *Teleidosaurus* from France (Benton 1993). Large quantities of metriorhynchid material were recovered from the lower Oxford Clay (Callovian) brick pit exposures of the Peterborough district, eastern England (Andrews 1913; Leeds 1956; Martill 1986). Callovian metriorhynchids are also abundant in northern France, Germany and South America (Steel 1973; de Gasparini and Diaz 1977). Material from these discoveries have been ascribed to 20 or more 'species' of *Metriorhynchus*. Oxfordian metriorhynchids are rare, with a record from France (Martill 1991). Kimmeridgian forms, including *Metriorhynchus* and *Dakosaurus*, have been reported from England and France (Benton 1993; Benton and Spencer 1995). Portlandian metriorhynchids include *Dakosaurus* and *Geosaurus* from Germany, and Lower Cretaceous (Neocomian) specimens are known from France, northern Germany and Italy (Steel 1973).

Metriorhynchids are distinguished from other Mesozoic crocodilians by their aquatic adaptations. They were the only archosaurs that became specially adapted to a marine habitat (Neill 1971). They possess reduced, web-like, fore- and hind-limb extremities, a streamlined skull and a laterally compressed tail that enabled efficient long-range swimming (Martill *et al.* 1994).

The Kimmeridge Clay of England crops out in a long narrow strip running from Dorset in the south-west to Yorkshire in the north-east (Text-fig. 1A), with fossil reptiles reported from more than 60 localities (Benton and Spencer 1995). The commonest discoveries include ichthyosaurs, such as *Grendelius*, *Macropterygius*, *Nannopterygius* and *Ophthalmosaurus*, and plesiosaurs, such as *Colymbosaurus*, *Kimmerosaurus* and *Pliosaurus* (Brown 1981; Taylor and Cruickshank 1993). Rare discoveries include turtles (*Pelobatochelys*), pterosaurs (*Germanodactylus*), dinosaurs ('*Megalosaurus*'), and crocodilians (*Metriorhynchus*). The purpose of the present paper is to describe a new metriorhynchid skull from the Kimmeridgian of Wiltshire, and to review other English Kimmeridgian metriorhynchid specimens. The new specimen is provisionally assigned to *Metriorhynchus superciliosus* (de Blainville, 1853) pending a revision of metriorhynchid taxonomy being undertaken by the senior author.

Repository abbreviations used: BMNH, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD; BRSMG, Bristol City Museum and Art Gallery, Queens Road, Bristol, BS8 1RL; CAMSM, Sedgwick Museum, Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ; OUM, Oxford University Museum, Parks Road, Oxford, OX1 3PW.

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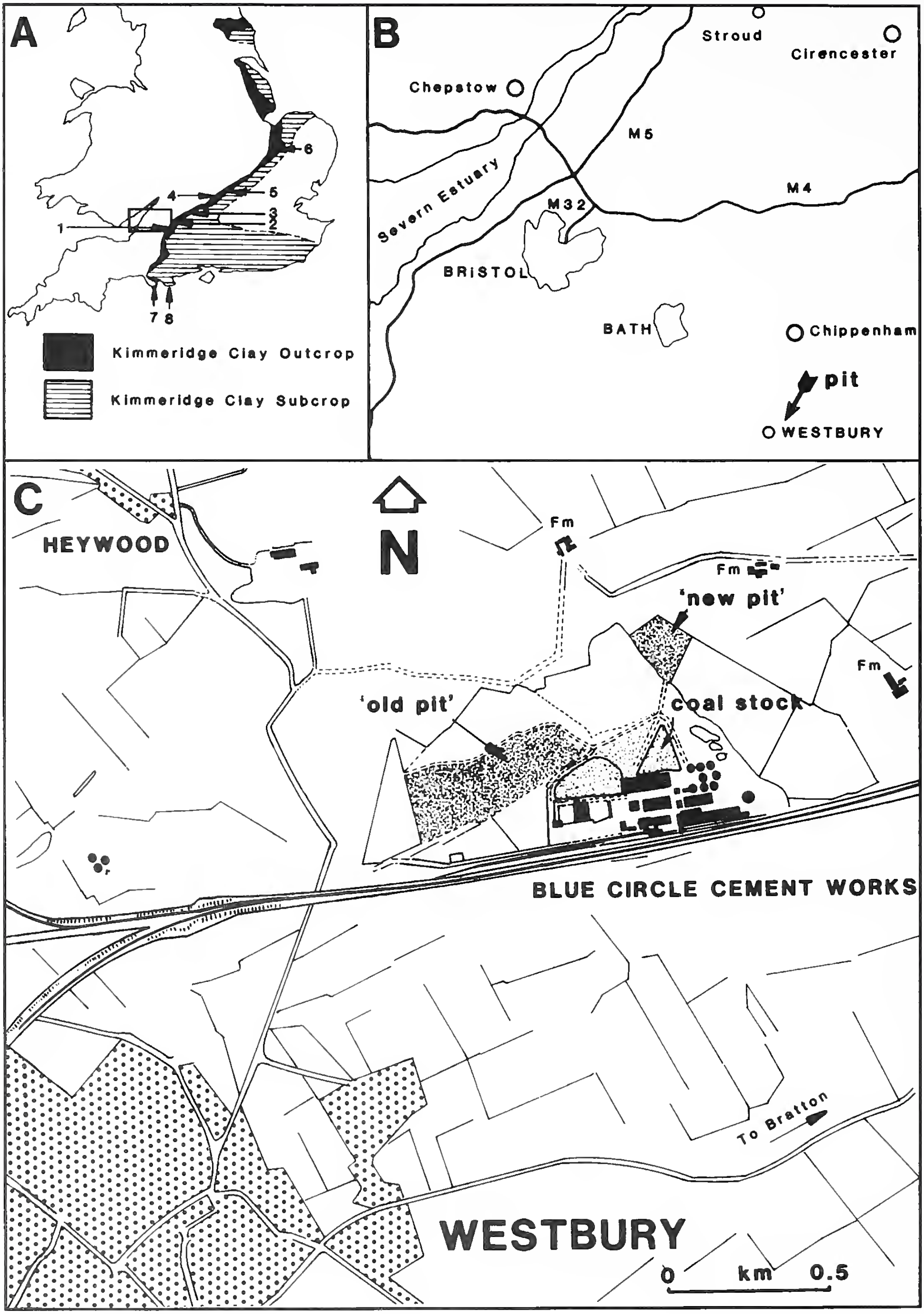
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M4
M32
Severn Estuary
BRISTOL
BATH
Chippenham
pit
WESTBURY
C
HEYWOOD
N
Fm
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'new pit'
Fm
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coal stock
BLUE CIRCLE CEMENT WORKS
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DESCRIPTION OF THE WESTBURY SKULL

Locality and stratigraphy

The *Metriorhynchus* skull from Westbury, Wiltshire (BRSMG Ce17365) was discovered on 30th December 1991, by Mr S. Carpenter in the 'old quarry' at the Blue Circle Industries plc Westbury Works, Wiltshire (NGR ST 8817 5267) (Text-fig. 1B–C). It lay *in situ* 1 m below the *Crussoliceras* limestone marker (*Aulacostephanus eudoxus* Zone (E6), Lower Kimmeridge Clay, of Birkelund *et al.* 1983) (Text-fig. 2).

The skull lay upside-down on a bedding plane surface, with the damaged posterior portions exposed in the section of the pit face. The remains had to be excavated rapidly, owing to the risk of further disturbance. The skull was contained in a large block of clay, which fragmented into three smaller pieces when an attempt was made to lift it. These pieces, and isolated bone fragments in the area, were collected (S. Carpenter, pers. comm. 1994).

Preparation and conservation

The blocks containing the *Metriorhynchus* skull were kept damp during transport to the conservation laboratory at Bristol City Museum and Art Gallery. The conservator was able to remove excess clay using a palette knife and scalpel. Distilled water and a brush were used to wash away the remaining dirt from the bone surfaces. Following this initial separation work, the skull elements were consolidated and reconstructed. A solution of Paraloid B72 dissolved in acetone was used for both surface consolidation (10 per cent Paraloid B72 in acetone) and as an adhesive (60 per cent Paraloid B72 in acetone) (D. B. Hill, pers. comm. 1994).

General description

The skull is fragmented, especially in the medial areas of the rostrum (Text-figs 3–5). There are numerous fractures over the surface of the skull some of which obscure surface features such as sutures. Several portions of the skull are missing, either as a result of erosion processes after the animal had died or by their being smashed at the site of discovery by quarry machinery and subsequently lost. Such missing areas include the nasal margins and portions of the snout. The majority of the braincase seems to have been lost prior to burial, as no attachment surfaces are present. The mandible is also missing. The skull is dorsoventrally flattened, and there has also been lateral compression.

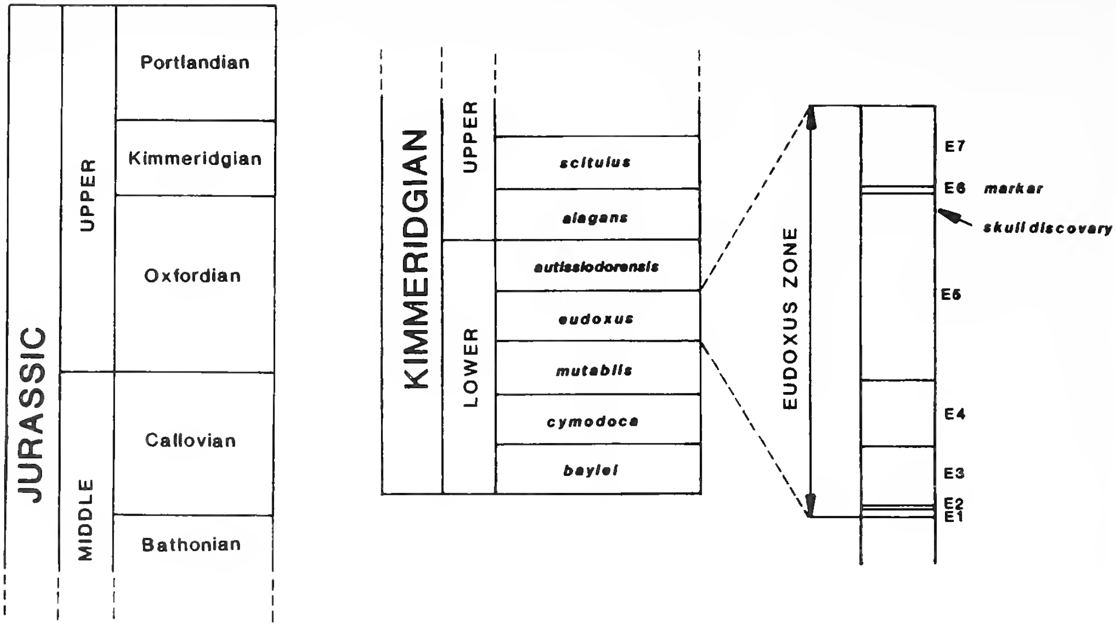
The general skull shape is typical of the Metriorhynchidae (Andrews 1913); elongate, with large temporal fenestrae, a well-developed nasal area, and little lateral expansion of the premaxillae. The major dorsal openings are nowhere fully delimited. The form of the heart-shaped narial aperture, although incomplete, can be discerned from the median posterior and anterior processes and lateral margin of the left premaxilla. Both orbital openings are defined anteriorly by the prefrontals and medially by the frontal, but the lateral boundaries are missing. The posterior margin of the right orbit borders the postfrontal bar, but this is absent on the left.

The temporal fenestrae are unusually large, far larger than those of Callovian metriorhynchids (Andrews 1913) and of the Kimmeridgian skull from Oxfordshire (OUM J.29823; Pl. 1). The right-hand fenestra is more defined than the left, as the postfrontal is complete on that side. Medially the fenestrae are bounded by the narrow frontal/parietal crest, but the posterolateral extensions of the parietal are missing.

Dermal elements of the skull roof

Premaxilla. The premaxilla on the left side is preserved, except at its anteroventral extremity where breakage has occurred. The right-hand element is largely absent (Text-figs 3–4). The border of the narial opening on the left-hand side is a shelf-like projection, which thickens anteriorly from a thin posterior concave embayment.

TEXT-FIG. 1. Kimmeridge Clay metriorhynchid crocodilian sites in England. A, map showing the Kimmeridge Clay outcrop and subcrop, with main metriorhynchid localities indicated. Numerical key: 1, Westbury (Wiltshire); 2, Devizes (Wiltshire); 3, Swindon (Wiltshire); 4, Wootton-Bassett (Wiltshire); 5, Shotover Hill, Heddington, Garsington (Oxfordshire); 6, Ely (Cambridgeshire); 7, Weymouth (Dorset); 8, Kimmeridge Bay (Dorset). B–C, maps showing the location of Blue Circle Industries plc, Westbury Works.

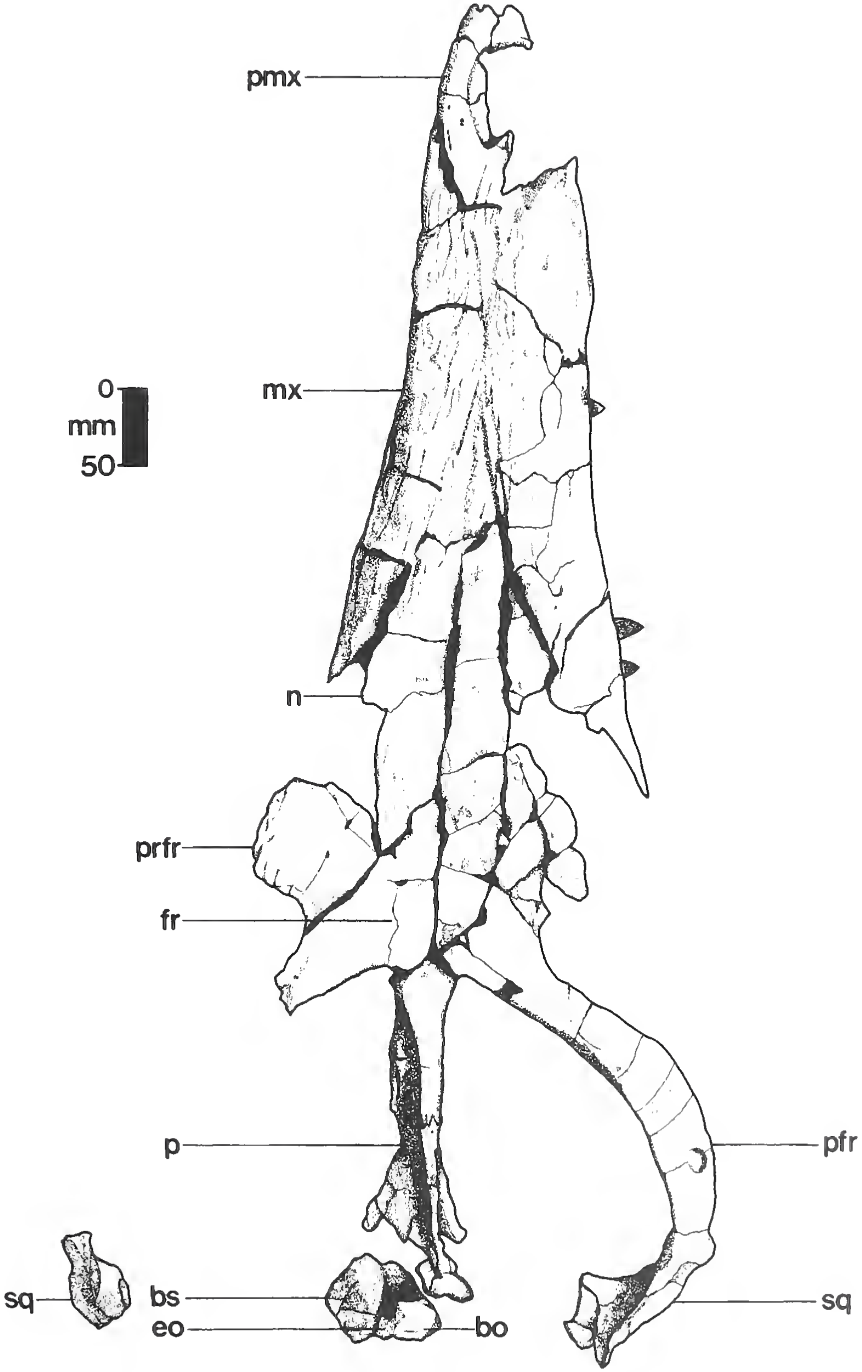


TEXT-FIG. 2. Biostratigraphical divisions of the Kimmeridgian and portion of the section at Westbury pit, showing the horizon of the metriorhynchid skull. Based on Birkelund *et al.* (1983) and Hallam (1992).

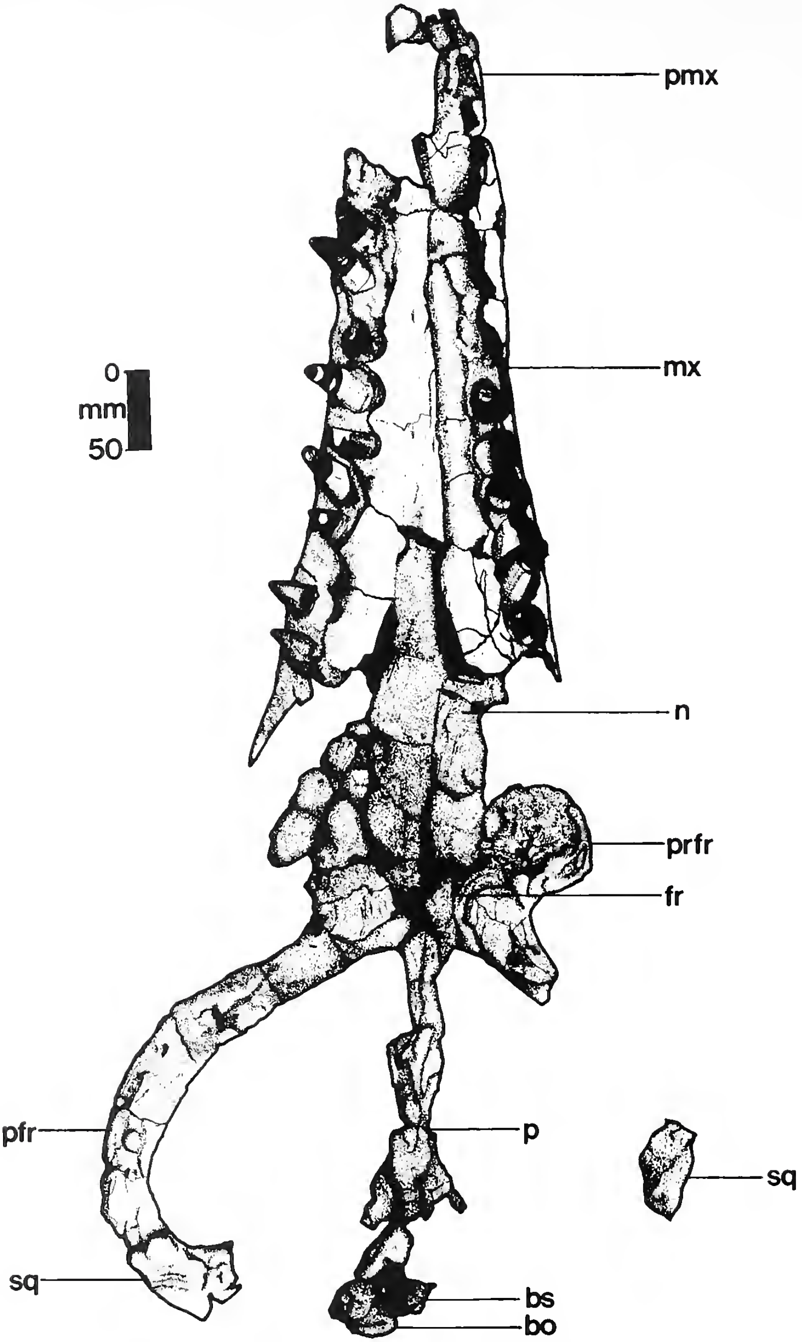
The anterior edge curves inwards to form the anterior margin of the narial opening. On the left side, the suture between premaxilla and maxilla is deep and ornate, and runs obliquely to join the deep furrow of the midline suture. The line of this suture on the right-hand side is barely discernible, and it appears to represent a line of weakness along which the skull has broken. The thick lateral surface of the left premaxilla is well preserved, and shows microfracturing and pitting, especially on the dorsal surface of the bone, but this diminishes laterally and posteriorly. The pits range from 0·5–5 mm in length, with a modal value of 1 mm. Most of the pits are ovate, the remainder subcircular. A preferred orientation is apparent, with the long axes trending approximately parallel to the midline of the skull.

Maxillae. Both left and right maxillae are present. Most of the left maxilla is complete, except for the posterior margin, where weathering has occurred along the suture line with the nasal. This is also the case with the right-hand side. The suture between the maxilla and nasal is smooth, and is marked by a deep groove which joins the medial suture in a sharp 'V'-shaped wedge (Text-figs 5A, 6A). Posteriorly, on either side, the suture is obscured because of breakage, and in these areas the contact with the frontal is absent. Both maxillae have been distorted. The lateral region of the right maxilla has been flattened dorsoventrally with respect to the left maxilla. The latter is thickened and overturned, verging towards the left side. In the area of convergence between the maxillae there has also been thickening on the right side, adjacent to the line of the midline suture. Both maxillae, and both nasals, have rolled inwards towards the midline, when seen in dorsal view (Text-fig. 6A), forming two convex surfaces which bound a 'V'-shaped depression, on what should really be a simple convex dorsal snout surface.

The maxillae show a great concentration of surface markings (Text-fig. 6A), a feature noted also in the Callovian specimens described by Mateer (1974). Grooves deviate from the midline suture on both sides and run obliquely, following the line of the maxilla/nasal suture. They are more pronounced on the left maxilla, but fade approximately half-way along the maxilla/nasal suture on either side. The grooves are discontinuous, ranging from 9–47 mm in length (modal value *c*. 25 mm), and less than 3 mm in width. Surface furrows are seen also at the anterior end of the left maxilla, running back from the premaxilla, but these are less clear on the right-hand side. Pitting on the right maxilla is more pronounced than on the left. On the latter, the pits are shallow and tend to merge with grooves, making distinction between the two extremely difficult. Anteriorly,

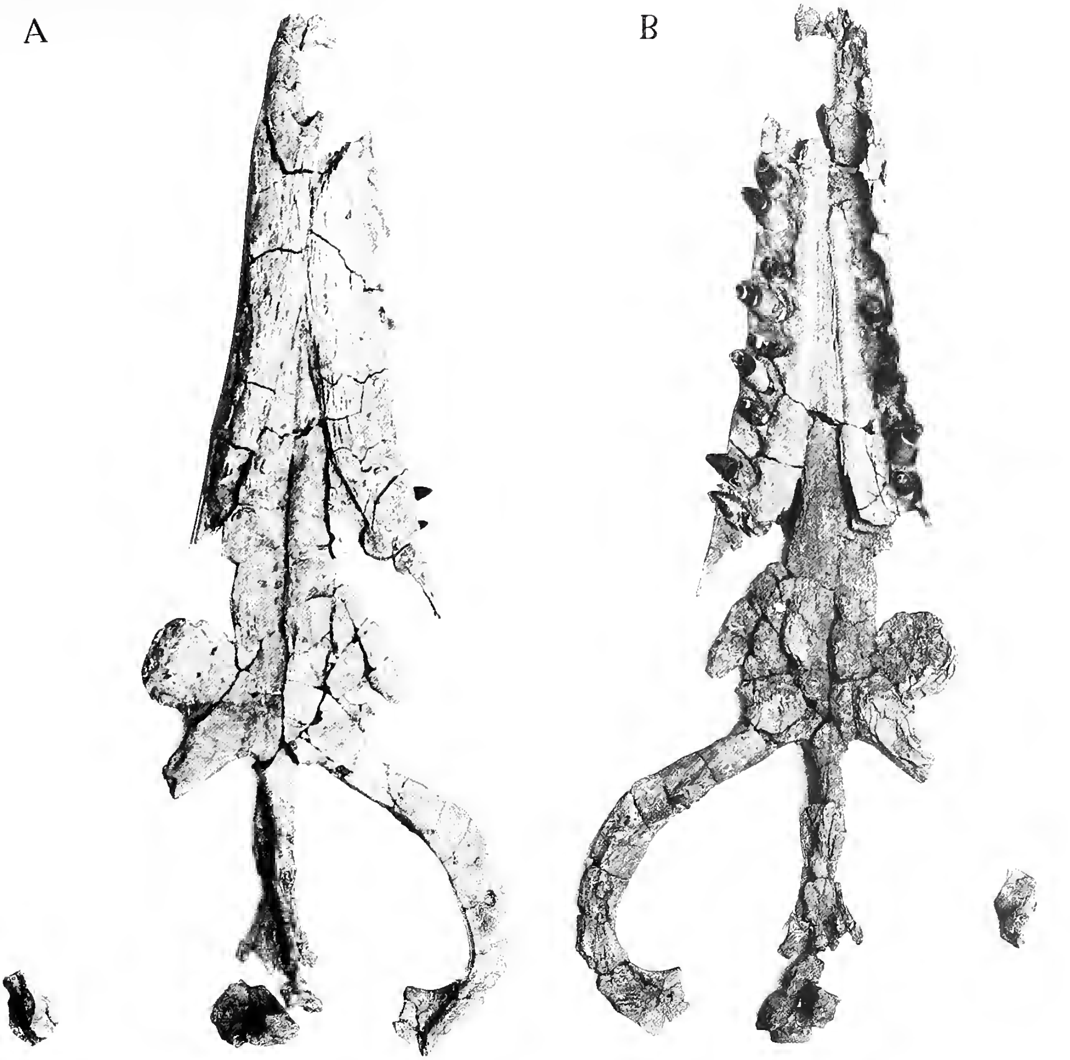


TEXT-FIG. 3. *Metriorhynchus superciliosus* de Blainville, 1853; skull (BRSMG Ce17365); dorsal view. Abbreviations: bo, basioccipital; bs, basisphenoid; eo, exoccipital; fr, frontal; mx, maxilla; n, nasal; p, parietal; pfr, postfrontal; pmx, premaxilla; prfr, prefrontal; sq, squamosal.



TEXT-FIG. 4. *Metriorhynchus superciliosus* de Blainville, 1853; skull (BRSMG Ce17365); ventral view. Abbreviations as in Text-figure 3.

the pits in the medial area have their long axes aligned parallel to the midline suture, and these diverge posteriorly, following the orientation of the maxilla/nasal suture. Pits near the lateral margin of the right maxilla are large and ovate, with long axes reaching 10 mm, and they become almost furrow-like posteriorly.



TEXT-FIG. 5. *Metriorhynchus superciliosus* de Blainville, 1853; skull (BRSMG Ce17365). A, dorsal view; B, ventral view; ×0·16.

The ventral surfaces of the maxillae are characterized by fine, longitudinal ridges trending parallel to a marked medial suture (Text-fig. 6B). Either side of the suture, convex surfaces are present adjacent to the dentition. Randomly distributed minute pitting is present on both sides, but fades adjacent to the teeth.

Nasals. Both nasals are present, but the posterolateral regions are missing. The suture between the nasal and the pre-frontal differs on the two sides on the right side, it is relatively straight to the contact between nasal and frontal, since the prefrontal has been compressed laterally, but on the right the suture would have been curved. The nasal/frontal suture is highly ornate and incised in front, and it curves back laterally towards the prefrontal. It is best preserved on the right-hand side. The nasal surfaces are relatively smooth, with occasional pitting anteriorly.

TEXT-FIG. 6. *Metriorhynchus superciliosus* de Blainville, 1853; BRSMG Ce17365. A, maxillary/nasal surface (note suturing and sculpturing). B, dentition. Scale bar represents 50 mm.

Prefrontals. Both prefrontals are present, but the anterior, lateral, and posterior margins are missing. The prefrontals form thick anterior borders to the orbits, a feature typical of the metriorhynchids (Mateer 1974). These elements show further evidence of the horizontal deformation event which affected the maxillae and nasals. The right prefrontal is narrow and elongate as a result of compression, whereas the left prefrontal is sub-circular. The left prefrontal is laterally thickened and convex, indicating that it has been compressed to a certain degree. The surfaces are pitted.

Frontal. The frontal is complete, but highly fragmented, especially to the right of the midline suture. The frontal/prefrontal suture, seen only on the right-hand side, is ornate on a fine scale, but retains an approximate straight line. The frontal crest rises slightly to meet the parietal ridge in a highly ornate and incised suture, which is complex, but not fused (Text-fig. 3). This suture may be traced laterally down the right-hand side of the ridge flank, where it ends abruptly at a break in the bone on the inner margin of the temporal fenestra. It is not so extensive on the left-hand side. The smooth frontal surface is interrupted by occasional pitting and fracturing. Fine striations radiate outwards from the midline towards the lateral margins.

Parietal. The parietal is broad anteriorly, and narrows posteriorly into a sharp ridge. The frontal/parietal suture is preserved on the ventral surface, but is weathered anteriorly and posteriorly. Fine longitudinal furrows and ridges extend both anteriorly and posteriorly from the suture, but eventually fade. The lateral compression of the skull has twisted the frontal/parietal crest towards the left in the medial and posterior region. The top of the crest is overturned towards the right, overhanging the temporal fenestra, and forming a broad concave left edge on the flank of the crest. Surface features are inconspicuous.

Postfrontal bar. The postfrontal bar is present only on the right-hand side (Text-figs 3–4). It is sutured with the frontal anteriorly, and with the squamosal posteriorly. The squamosal suture is ornate and deeply incised, but weathered. The postfrontal broadens along its outer curved edge and narrows towards the posterior suture. It is devoid of surface markings. Approximately half-way along the postfrontal, a large (16 mm) oval pit is present (Text-fig. 7A). Ventrally, the postfrontal surface is weathered in certain areas. The suture with the frontal can be seen anteriorly, although the preservation is poor, and the suture with the squamosal is difficult to follow.

Squamosal. The squamosal is incomplete on the right-hand side, and only a small piece exists on the left, which is weathered on its lateral edge. A sharp ridge runs down on the medial surface of the right squamosal, from the suture with the postfrontal to the end of the bone, showing the same sense of distortion as described for the parietal ridge. The squamosal surfaces on either side of the ridge are occasionally pitted and slope gently away towards the inner margin, and abruptly on the outer margin.

Dermal bones of the palate

All traces of the posterior palate elements are missing, as is the palatal portion of the premaxillae. The secondary palate formed by the junction of the maxillae in the midline is, however, nearly complete (Text-fig. 6B), and shows a long, straight, midline suture. As in other metriorhynchids, the posterior portion of the secondary palate was presumably formed by the palatines (Andrews 1913), which met in the midline behind the maxillae. The vomers were reduced and close to the midline above the secondary palate. There is no trace of these elements, nor of the pterygoids.

Endocranium

The basioccipital is the most prominent element of the braincase (Text-figs 3–4), showing the characteristic central depression and ventrally necked process. Below, the arched median eustachian opening is present, which defines laterally the innermost abraded margin of the exoccipital. Dorsally, the supraoccipital and parietal contacts are absent. The quadrate and epipterygoid are not preserved.

Anteriorly, the basisphenoid is only partly complete and is badly abraded, with the exception of a small section on either side of the midline. The bone is displaced to the left of the basioccipital, a further result of the compressional event that affected the skull.

Dentition

The dentition on both sides of the maxillae is robust (Text-fig. 6B). Nine teeth are present on the right maxillary margin, of which seven are complete. Two teeth in the process of eruption can be seen towards the rear of the tooth row as a result of breakage of the bone. Four teeth are present on the left maxillary margin, of which only one is complete. Four alveoli are preserved, with intervening convex ridges, and one bearing the remains of a tooth. The premaxillary margin has the remains of a tooth lying on its side over a depression, which possibly represented its socket.

The maxillary teeth conform to the typical metriorhynchid shape (Massare 1987), having laterally compressed pointed crowns, defined anteriorly and posteriorly by prominent carinae. The enamel displays fine longitudinal ridges that become coarser away from the smooth apex, until they end abruptly at the gum tissue boundary. The cross section of the teeth varies with size: large teeth are sub-circular, whereas smaller teeth are more ovate and laterally compressed.

Although only one wear facet is present, which probably resulted from abrasion on an opposing tooth, the apices of the teeth are highly polished, possibly indicating abrasion from hard prey (Massare 1987).

Nerve and vessel openings and other surface features

Many elements of the skull show openings, which have been described. They may be interpreted by reference to presumably homologous nerve and vessel positions in the skulls of modern reptiles, such as crocodilians (Iordansky 1973) and *Sphenodon punctatus* (O'Donoghue 1920).

The conspicuous foramina along the lateral margins of the maxillae are positioned adjacent to each tooth (or tooth socket) on both sides of the snout. These may be openings for accessory nerves to teeth and gum tissues from the *Ramus maxillaris* extension of the trigeminal nerve system. The *R. maxillaris* runs from the braincase laterally to musculature in the temporal fossae (M. pseudotemporalis) and dorsally to pterygoid musculature (M. pterygoideus anterior), and then into the upper jaw region (Romer 1956; Schumacher 1973).

The foramina on the premaxillary surfaces are likely to have accommodated the superior and inferior *Arteria nasalis*, the terminal branches of which supply the nasal tissues (O'Donoghue 1920). The *A. nasalis* is an anterior extension of the *A. orbitalis superior*, which accompanies the *R. opthalmicus* trigeminal nerve branch, from the main *A. stapedialis*. The *A. orbitalis superior*, and associated rami supplying orbital muscles (Romer 1956), may have caused the pitting on the pre-frontal surfaces which overhang the orbits and the minor pitting on the anterior and posterior areas of the nasal. However, the frontal pitting is more probably attributable to the *A. frontalis*, running upwards from the posterior region of the orbit to supply superficial tissues (O'Donoghue 1920).

Observations on modern adult crocodilians (Iordansky 1973) reveal a network of irregular ridges on the dorsal surfaces of the dermal skull elements, creating a 'sculpturing effect', caused by osteodermal accretion. This is possibly the reason for the linear sculpturing present along the length of the premaxilla and maxillae, where presumably there was little demarcation between the integument and skull surface (Steel 1989). Langston (1973) noted, however, that fossil taxa exhibiting the greatest degree of aquatic adaptation possess the least osteodermal accretion.

The large ovate cavity situated on the postfrontal bar (Text-fig. 7A) is problematical. It is almost certainly not a vessel opening, and may represent predator damage, inflicted before or after death. Predatory marks with a similar appearance, are present in Kimmeridgian marine reptile specimens from Kimmeridge Bay, Dorset (S. Etches Collection, pers. obs. DRG).

OTHER ENGLISH KIMMERIDGIAN MARINE CROCODILES

The Oxford skull

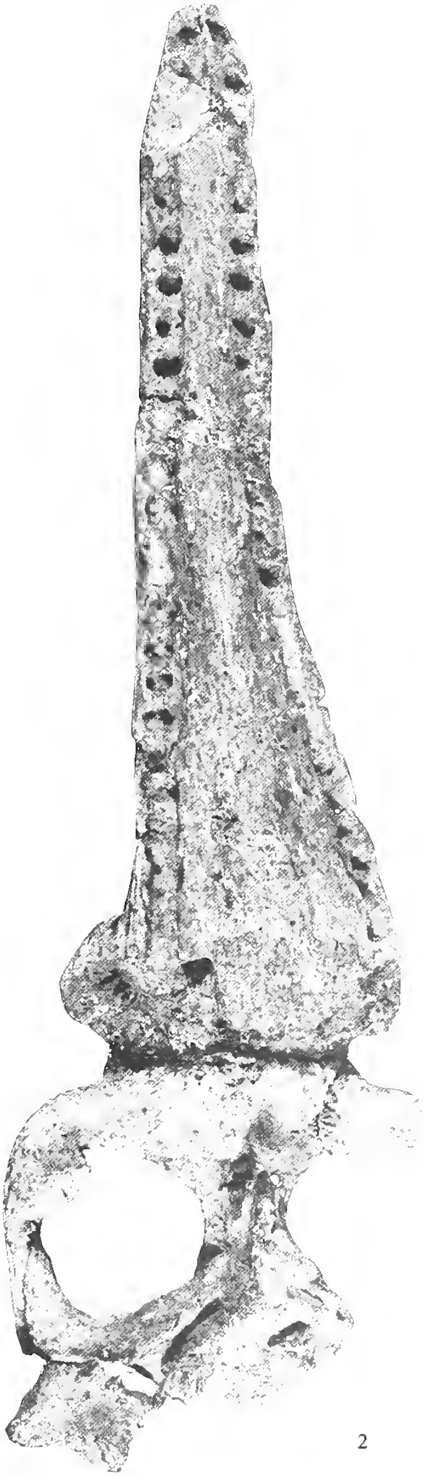
A partial skull and incomplete lower jaw from the Kimmeridge Clay pits of Shotover Hill, Oxfordshire (OUM J.29823) was mentioned by Owen (1884) and was made the type of *Steneosaurus palpebrosum* by Phillips (1871). It was re-identified as a metriorhynchid by Woodward (1885).

The temporal openings (Pl. 1) are small and circular, and are bordered anteriorly and laterally by wide, embayed shelves. The maxillary region shows distortion in a dorso-ventral plane. Suturing on the dorsal surface is marked in certain areas. A midline suture is apparent on the skull table and maxillary surfaces; it terminates in the medial portion of the frontal, but continues anteriorly across the nasal area, and along the majority of the anterior portion of the maxilla, but does not reach the posterior border of the premaxilla. A deeply incised groove defines an elevated and wide skull table, with a reduced nasal area. The unusually small nasal is approximately 100 mm in length, and is separated from the frontal by a sinuous suture, which transects the major division between the frontal and maxillae. The prefrontals are characteristically robust, and laterally, the lachrymals, and their corresponding foramen, are preserved. Other elements, such as the prefrontals and premaxillae, are bordered by faint sutures that are only apparent upon close inspection. The parietal crest is narrow and high. Dorsal surfaces have an unusual, roughened texture, which commonly obscures the suturing and sculpturing. There are no visible macro-epibionts.

EXPLANATION OF PLATE 1

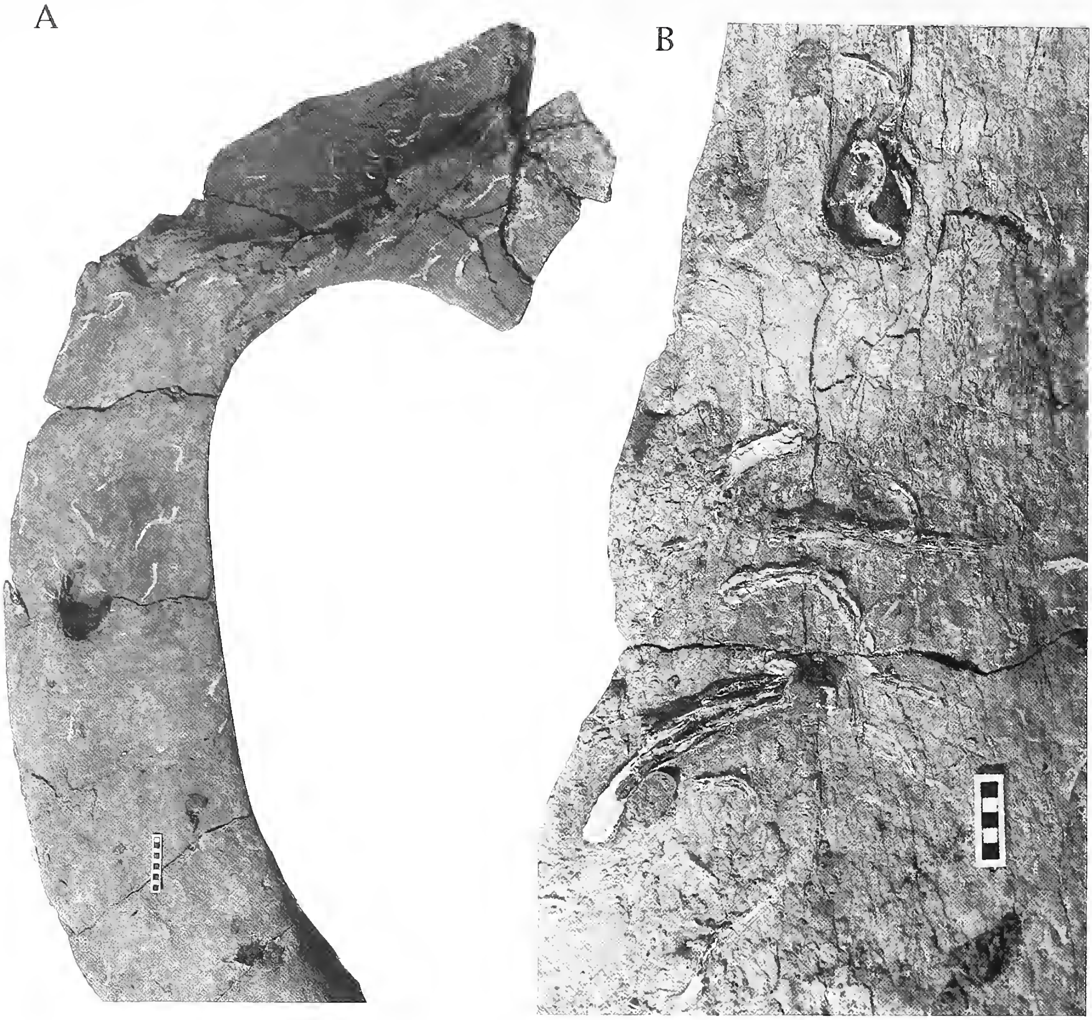
Figs 1–2. *Metriorhynchus palpebrosus* Woodward, 1885; OUM J.29823, Kimmeridge Clay, Shotover Hill, Oxfordshire. 1, dorsal view; 2, ventral view; ×0·4.

1



2

GRANGE and BENTON, *Metriorhynchus*

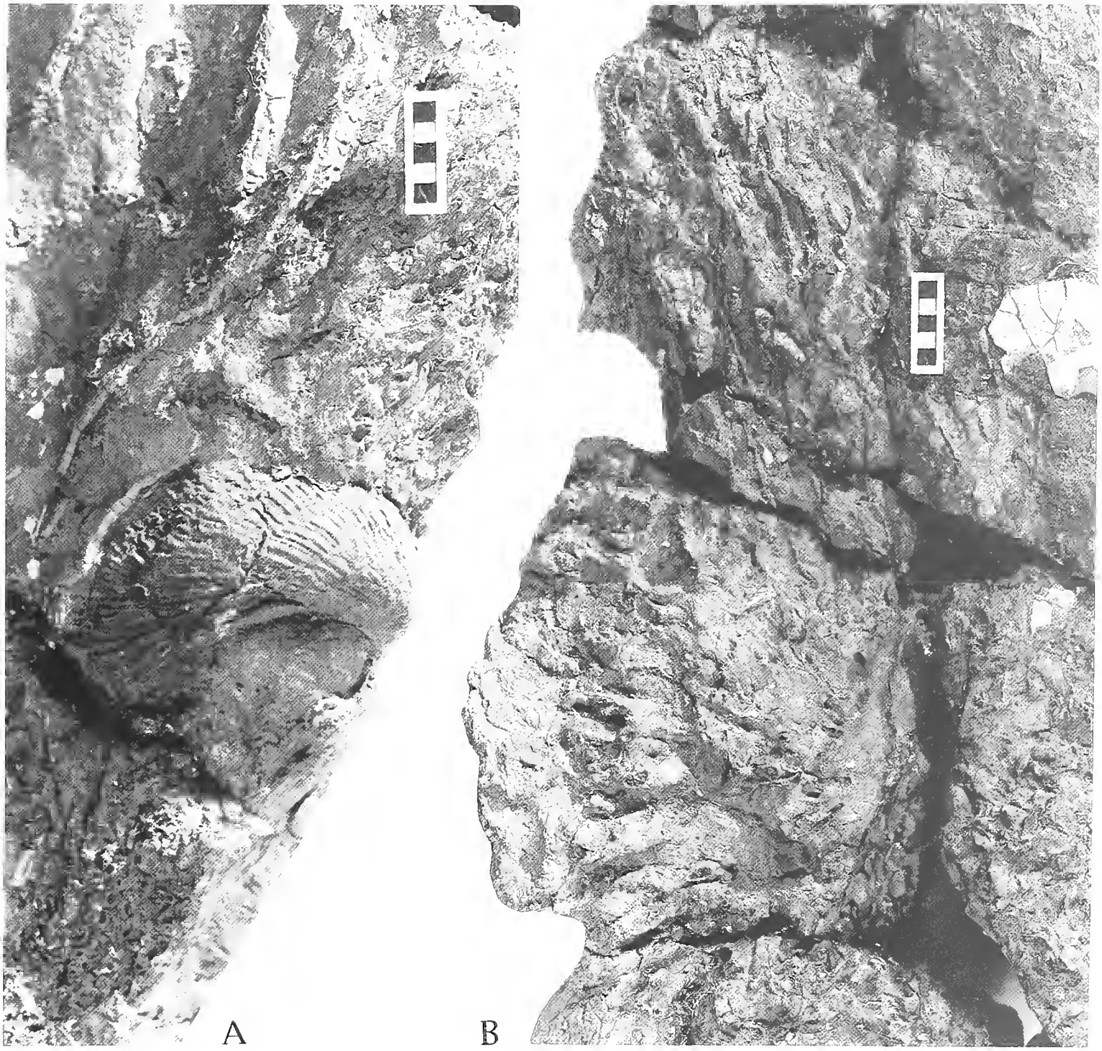


TEXT-FIG. 7. *Metriorhynchus superciliosus* de Blainville, 1853; BRSMG Ce17365. A, predator damage on right-hand postfrontal; scale bar represents 10 mm. B, medial portion of left-hand nasal (note oyster and serpulid encrustations); scale bar represents 5 mm.

On the ventral surface of the skull (Pl. 1, fig. 2), there are 23 alveoli on the right margin, and 25 on the left. No teeth are preserved. Although the posterior margin of the palate is weathered, two internal narial openings are well defined. The inner face of the jugal is partially preserved on the right-hand side, represented by an inwardly directed process attached to the ventral surface of the postfrontal. The pterygoid and parasphenoid are missing, but posteriorly the occipital area is preserved. On the right posterior margin of the skull, the mandibular condylar surface of the quadrate is present, and the contact with the squamosal is seen. The equivalent elements on the left-hand side are missing.

The Dorset skull

A lower jaw and various skeletal fragments from the Lower Kimmeridge Clay of Kimmeridge Bay, Dorset (BMNH 40103) were described and identified as *Dakosaurus maximus* (Hulke 1869). This material was



TEXT-FIG. 8. *Metriorhynchus superciliosus* de Blainville, 1853; BRSMG Ce17365. A, *Nanogyra*? sp., encrustation on ventral surface of right-hand postfrontal; scale bar represents 5 mm. B, *Stomatopora*? sp., encrustation on ventral surface of left-hand prefrontal; scale bar represents 5 mm.

subsequently re-identified as *Steneosaurus manseli*, following the recognition of a partial skull of the same individual at this locality (Hulke 1870). Owen (1884) referred this species to the new genus *Plesiosuchus*, but Woodward (1885) retained it in *Dakosaurus*, a metriorhynchid genus. Hulke (1870) assigned the material to *Steneosaurus* because of its apparent similarity to the Oxford skull, before the reidentification of the latter by Woodward (1885). Fraas (1902) further described the skull form of *D. manseli* from a specimen from this locality.

Lydekker (1889, 1890) noted teeth and scutes of *Metriorhynchus* from Smallmouth Sands, Weymouth. However, it is well known that metriorhynchids lacked dermal armour (Andrews 1913), and therefore this identification is erroneous. Other possible metriorhynchid material from the Kimmeridgian of the Dorset coast has been reported. Delair (1958) refers to 'teeth and some vertebral centra of several individuals from the Kimmeridgian of Weymouth' (BMNH 43032, 44179, 46805a, b, c, 49511). Isolated metriorhynchid limb, skull and vertebral column elements have been identified from Swindon, Devizes and Wootton-Bassett (Wiltshire), Ely (Cambridgeshire) and Shotover Hill, Headington and Garsington (Oxfordshire) (Text-fig. 1A) (OUM J.12367, J.12373, J.55470–J.55479; BMNH 24803, 24805, 31920, 46492; CAMSM J.67879–J.67899). These fragments are generically indeterminate (pers. obs., DRG), because they are unsuitable for identification purposes. It is quite possible that misidentification by previous workers has occurred.

Taylor and Benton (1986) noted two disarticulated crocodilian finds from the Upper Kimmeridge Clay of Egmont Bight on the Dorset coast, one of which at least (R. A. Langham Collection) is a metriorhynchid (see also Benton and Spencer 1995).

The Ely skull

A partial skull (CAMSM J.29419) from the Kimmeridge Clay of Ely, Cambridgeshire, was identified as *Dakosaurus lissocephalus* by Seeley (1869). Indeterminate material, including skull bones, jaw fragments, vertebrae, ribs, pectoral and pelvic girdle elements and limb bones, is possibly associated with the skull (Seeley 1869) (CAMSM J.29383–J.29418; J.29420–J.29446). The species *Metriorhynchus hastifer* Eudes-Deslongchamps, 1868, was identified by Watson (1911) on the basis of the anterior end of a snout.

TAPHONOMY OF THE WESTBURY SKULL

The Westbury skull is encrusted to varying degrees with diverse macro- and micro-epibionts. During pre-burial, and possibly after sediment covering, the skull surfaces provided a site for scavenging epibiont communities. Micro-epibionts are the most abundant encrusters on both dorsal and ventral surfaces, and in the surrounding sediments (Birkelund *et al.* 1983). There is evidence for surface scavenging in all epibionts, and scavenging between communities is also evident in certain areas.

Macro-epibionts. Serpulid polychaetes are present on the dorsal surfaces of all skull elements (Text-fig. 7B), particularly in the maxillary and nasal region, but they are rarer on the ventral face of the skull. Serpulids also encrust the argillaceous matrix within bone cavities where breakage had occurred, thus providing evidence of skull fragmentation before burial. They are preserved as white calcareous tubes exhibiting various degrees of curvature.

Both partial and complete 'oyster' shells (*Nanogyra*? sp.) are present on both dorsal and ventral surfaces (Text-fig. 8A), but mostly on the former. The majority are small, with shells no wider than 10 mm, and virtually all are disarticulated. They often have a close spatial association with the serpulid polychaetes. Many of the shells are abraded and it is often difficult to identify surface features such as growth lines. Shells in the vicinity of the midline suture have been overturned on to their edges as a result of the lateral distortion.

A large bryozoan colony (*Stomatopora*? sp.) encrusts the ventral surfaces of the postfrontal, prefrontals (Text-fig. 8B) and nasal. Most of the colony is abraded, but zooecial apertures are still well defined in certain areas.

Micro-epibionts. Cytheracean ostracods (order Podocopida) occur commonly in small clusters, and on the dorsal surfaces are often found in close association with oyster shells and serpulid polychaetes. The ovate dorsal convex margins are preserved, being highly impregnated with pore canals and creating a strong framework structure. The lateral selvage and dorsal hinge line can be seen where weathering of the carapace has not occurred, and the posterodorsal caudal process is also visible in certain instances. Inner surfaces of the valve are also discernible in certain examples, where a median sulcus and hinge line are preserved.

Rotaliine foraminifera are extremely abundant on the ventral surface of the maxillae and nasals, often occurring in clusters. Preservation varies considerably, from abraded and often indistinct tests, to an extremely well defined condition. In most cases, the planispiral perforated test form, with its prominent proloculus, is evident. A nodosariacean foraminiferan (*Lenticulina*? sp.) is the most abundant rotaliine on the skull surfaces. It possesses an involute planispiral form with lenticular growth, and the test surface is finely perforate with a reticulate sculpture. A lateral keel is also visible.

Textulariine foraminifera are also present. However, these are uncommon compared with the Rotaliina. They are multilocular, and therefore belong to the superfamily Lituolacea. The best preserved specimen (*Trochammina*? sp.) has globular ovate chambers, a deep umbilical region and shows trochospiral growth.

Interactions between epibionts. Evidence of fouling is apparent where serpulid polychaete tubes and 'oyster' shells have encrusted upon each other. Reciprocal overgrowth (Taylor 1990) is present where an 'oyster' shell clearly overlaps a serpulid polychaete tube in one area, but has one of its edges overlapped by the same polychaete tube in a different area. These two epibionts are also seen to have marginal contacts, where no overgrowth is observed at all (Text-fig. 7B). Ostracods, often in small clusters, foul the serpulid polychaete tubes, and are also found in close proximity to 'oyster' shells.

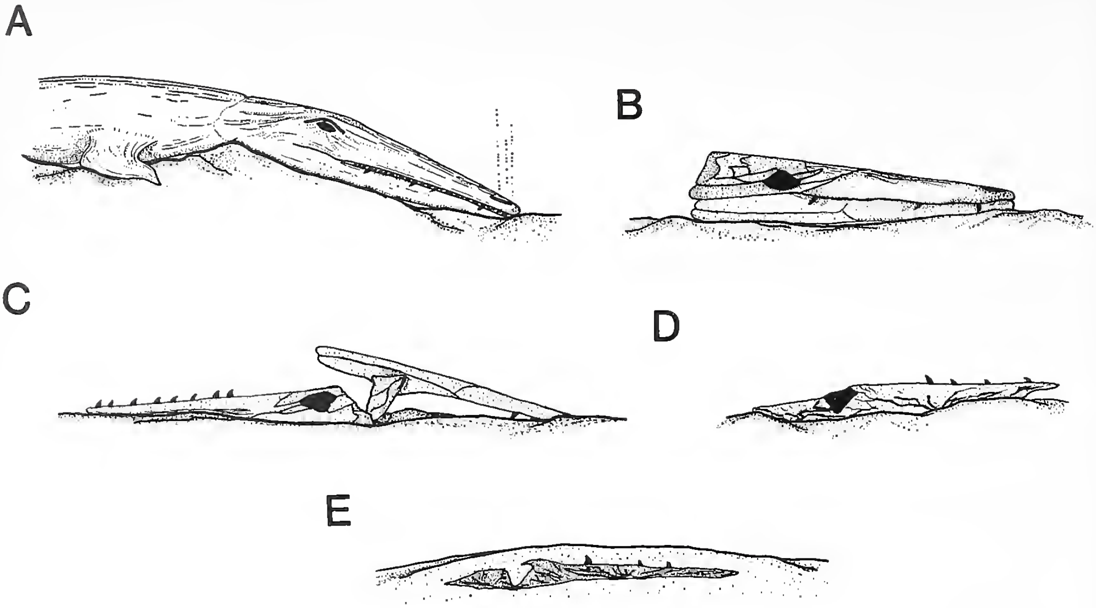
The close spatial relationship between these epibionts indicates competition for space on the skull substrate. Concentrated encrusted areas are situated on the lateral margins of the maxillae, the anterior regions of the nasal, and the left prefrontal. This clustering was possibly caused by local environmental forcing, associated with small-scale storm events (Wignall 1989) in the vicinity of the skull. The organisms were periodically driven on to relatively stable areas devoid of muddy sediment. Ostracods thrive in such environments (Brasier 1980), and this is substantiated by their numbers on both dorsal and ventral surfaces of the skull. The close association of ostracods with other epibionts suggests that they possessed a filter-feeding habit.

The above relationships suggest that there was no community hierarchy on dorsal or ventral substrates during colonization. Even if there was more substantial evidence of hierarchical encrustation, this would only present a snap-shot of a long-term colonization history, the outcome of which would be uncertain, because of complications such as rank reversals and colony recovery after overgrowth, as recorded in modern environments (Buss 1986).

Taphonomic history. After initial settling of the carcass (Text-fig. 9A), disarticulation of the skull probably occurred while the body floated, buoyed up by gases generated by degradation of supporting tissues (Schäfer 1972). However, the extent to which this can occur is dependent on the ambient hydrostatic pressure, which influences gas solubility and hence buoyancy of the carcass (Allison *et al.* 1991). The presence of various storm-induced sedimentary structures (Wignall 1989) and profuse benthic faunas (Birkelund *et al.* 1983) suggests that water depth was not excessive enough to generate extreme hydrostatic pressures, indicating that re-flotation of the carcass was feasible. Scotchman (1989) estimated that water depths over north-west Europe during the Kimmeridgian were in the range of 10–100 m. Assuming this to be correct, the maximum hydrostatic pressure possible would be approximately 10 atm., based on a surface pressure of 1 atm., and an increase of 1 atm. for every 10 m below the water surface. These pressure levels would not prevent re-flotation of a moderate-sized marine crocodilian carcass (based on experiments by Allison *et al.* 1991).

There may have been some scavenging of the carcass, either during post-mortem drifting in the water column, or after settling on the substrate. The cause of death cannot be ascertained.

The skull became separated from the rest of the carcass either in the water column or on the substrate, and settled with the dorsal surfaces facing upwards (Text-fig. 9B). The dorsal bone surfaces were partially exposed for a period of time to allow an initial epibiont encrustation event in certain areas. Following continued colonization, with low rates of contemporaneous background sedimentation, a sporadic storm event, for which there is abundant sedimentological evidence (Wignall 1989), probably flipped the skull over onto its dorsal surface (Text-fig. 9C). This presumably caused the conspicuous fragmentation and probably resulted in the loss of the posterior and mandibular elements. Another colonization event then commenced on the exposed ventral



TEXT-FIG. 9. Postulated taphonomic history of the skull of *Metriorhynchus superciliosus* de Blainville, 1853; BRSMG Ce17365. A, the carcass falls to the substrate; B, skull is detached from the body, soft tissues decay, and dorsal surface is encrusted; C, skull is flipped over on to its dorsal surface, mandible and posterior skull elements are lost, and ventral surface is encrusted; D, skull is further fragmented; E, sediment washes over, overburden pressure deforms the skull, and burial proceeds.

surfaces, in addition to further fragmentation (Text-fig. 9D). The encruster relationships do not indicate whether the substrate was continually oxic during these colonization events, or whether intermittent phases of anoxia occurred.

Abrasion on the ventral surface and on the epibionts suggests that a period of intense sediment-laden storm-current activity prevailed, before the skull was completely covered with sediment and subsequently deformed by overburden pressure (Text-fig. 9E) during burial.

A specimen of *Pliosaurus brachyspondylus* (BRSMG Cc332) collected at approximately the same stratigraphical level at Blue Circle Industries plc, Westbury Works in 1980 (Taylor and Cruickshank 1993), and a new skeleton of this genus discovered during the summer of 1994 from the same locality (Carpenter 1995), provide further evidence for horizontal deformation episodes that follow carcass burial. In these skulls, a similar distortion in the maxillary region can be seen. Deformed skull material is also common in Callovian marine crocodile material (pers. obs., DRG). Post-depositional processes, such as mass movement on an inclined substrate, or possibly the overburden pressure from wet sediment engulfing skull elements, are likely to have been responsible for deforming the bone in a plastic manner. Such processes seem to have occurred commonly in comparable marine mudstone facies (Martill 1986).

CONCLUSIONS

Metriorhynchid crocodilian remains are rare in the English Kimmeridgian, and only three reasonably well preserved skulls have been identified. Micro- and macro-epibiont communities on a new skull from the Lower Kimmeridgian of Westbury, Wiltshire testify to a complex taphonomic history, involving two phases of colonization. The absence of similar bone surface communities in other contemporary marine reptiles from the same locality (Taylor and Cruickshank 1993), indicates that encrusting episodes are localized, and influenced by sediment dispersal and rate of burial.

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