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Cretaceous fossil vertebrates

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CRETACEOUS FOSSIL VERTEBRATES

EDITED BY

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with 68 text-figures, 14 plates and 5 tables

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PREFACE

ONE of the most dynamic phases of vertebrate evolutionary history, characterized by two contrasting patterns of events, took place in the Cretaceous (165–145 Ma). On the one hand, many 'classic' Mesozoic groups such as ornithischian and sauropod dinosaurs, pterosaurs, and marine reptiles, reached peak levels of taxonomic, morphological and ecological diversity, but subsequently declined and became extinct, either before the end of the Cretaceous, or in the event that punctuated the end of this period. On the other hand several modern groups of vertebrates, including the teleosts, turtles, squamates (lizards and snakes), birds and mammals, radiated during this interval and although some of these suffered a drop in diversity at the K-T boundary, none of them became extinct. Not all groups fit neatly within these patterns, however. The choristoderes, for example, a group of gavial-like aquatic reptiles, have a long Mesozoic record, survived the K-T event, and only finally became extinct in the Oligocene (Evans and Hecht 1993).

Patterns of vertebrate evolution in the Cretaceous have been derived from three main sources of evidence: first, and most importantly, the fossil record; second, phylogenetic analyses based on the anatomy of extinct and extant taxa; and third, molecular phylogenies, although so far, these have been almost completely restricted to modern taxa. Taking these three categories in reverse order, molecular phylogenies are playing an increasingly important rôle in the reconstruction of the early history of major living groups such as birds and mammals, but this work has often been highly controversial. As an example, molecular phylogenies proposed by Sibley and Ahlquist (1990) and, more recently, by Hedges *et al.* (1996) suggested that early representatives of most if not all orders of living birds had already appeared before the end of the Cretaceous, possibly much earlier. These claims have sparked considerable debate between molecular phylogeneticists and palaeontologists, although some rapprochement between the two groups now seems to be under way following recent revisions of estimates for the timing of cladogenetic events, and the discovery, in Late Cretaceous deposits, of fossil remains that seem to belong to several orders of neornithine birds (e.g. Hope 1997; Hutchison *et al.* 1997). Ultimately, however, the potential for molecular phylogenies to give insights into events that took place in the Cretaceous is likely to prove somewhat limited, since this methodology cannot inform us as to the existence or history of extinct lineages, the total number of which is likely to exceed considerably that of their living relatives.

Turning to phylogenetics, previously palaeontologists reconstructed evolutionary histories essentially by aligning fossil taxa from different stratigraphical horizons into ancestor–descendant sequences. The widespread adoption of phylogenetic systematics (cladistics) during the last 20 years has had a radical impact both on the reconstruction of patterns and the way in which they are interpreted. To give a simple, well known example, this method enables the correct elucidation of potentially misleading situations where taxa nearer the crown group occur in older strata than those further from the crown group, or vice versa. Perhaps more importantly, cladistic studies can be used to predict the existence of 'ghost lineages' as yet unknown from fossils. This can have a profound impact on our understanding of the history of major clades: for example, a recent study of the relationships of sauropod dinosaurs (Wilson and Sereno 1998) suggested that many important lineages, as yet unknown in the fossil record, existed in the Early and Mid Jurassic.

Whilst cladistics and molecular phylogenetics have much to offer, the fossil record remains the principal source of evidence regarding patterns of vertebrate evolution in the Cretaceous and, irrespective of their origin, the final arbiter of hypotheses regarding these patterns. Huge collections of fossil vertebrate material from Cretaceous deposits have been accumulated over the last two centuries, partly as a result of commercial activity, and partly through organized collecting by palaeontologists. The 1990s have witnessed a series of dramatic discoveries, sometimes from new

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localities such as the Early Cretaceous lake deposits of Liaoning, China, the source of numerous primitive birds and some non-avian feathered dinosaurs (Ji *et al.* 1998), or from long-known locations, for example the Late Cretaceous aeolian deposits of the southern Gobi desert, Mongolia, which recently yielded the remains of a theropod dinosaur, *Oviraptor*, preserved intact and lying upon a nest containing what are now presumed to be its eggs (Norrell *et al.* 1995).

Despite these discoveries, the fossil record of Cretaceous vertebrates remains highly biased in at least two important ways. First, although the Late Cretaceous is relatively well represented, much of the rest of the record is rather poor. The Early Cretaceous is patchy, and the late Early to early Late Cretaceous interval is notoriously incomplete, especially for terrestrial vertebrates (e.g. Benton 1987). Second, the vast majority of discoveries, so far, has been made in the northern hemisphere. Thus, whilst North America and, to some extent, Eurasia are relatively well represented, the record for South America is very patchy and, with one or two notable exceptions, very little is yet known from Africa or Australia.

The nine contributions that form this volume add to our knowledge of Cretaceous fossil vertebrates, but the important feature of these papers is that they report on taxa that have been recovered from stratigraphical intervals or palaeogeographical regions that have a relatively poor fossil record. Selachians (Underwood and Mitchell), a lizard (Evans and Barbadillo), a snake (Gardner and Cifelli), a choristodere (Evans and Manabe), goniopholidid crocodiles (Salisbury *et al.*) and ankylosaurian dinosaurs (Pereda Suberbiola and Barrett) reported in this volume were recovered from the Lower, or the lower Upper Cretaceous, and in most cases the genera described represent the first record for a particular stage. The snake described by Gardner and Cifelli is of particular interest as it also represents the oldest record for North American ophidians. In complementary fashion, the African teleost *Enchodus* (Cavin), the Japanese choristodere (Evans and Manabe), and the Madagascan crocodile (Buckley and Brochu) are all welcome additions to our knowledge of vertebrate faunas from regions that are as yet poorly represented. The new crocodile is a particularly timely discovery, since the origin and palaeobiogeographical history of Madagascan vertebrates has long been, and remains, a focus of interest and controversy. The crocodile, which forms part of an important new collection from the Upper Cretaceous of the Mahajanga Basin, adds further weight to the idea that faunal exchange across Gondwana continued until late in the Mesozoic, primarily via Antarctica, rather than directly between Africa and South America.

The final contribution, an analysis of stance and gait in ornithopods based on fossil tracks from the Purbeck of England (Wright), is an excellent example of how another type of gap in our palaeobiological knowledge, direct evidence of the locomotory ability of fossil vertebrates, might be filled. Vertebrate palaeoichnology is currently undergoing a long-awaited renaissance and Wright's study of the Purbeck tracks, which reveals the correct orientation and positioning of iguanodontid forelimbs as they walked, is typical of the work that is showing how important palaeobiological information can be wrested from this type of fossil material.

Acknowledgements. My thanks to all colleagues who contributed and refereed the papers published here. Special thanks go to David Loydell for his advice, help and support throughout the editorial process.

REFERENCES

BENTON, M. J. 1987. Mass extinctions among families of non-marine tetrapods: the data. *Mémoires de la Société Géologique de France*, **150**, 21–32.

EVANS, S. E. and HECHT, M. K. 1993. A history of an extinct reptilian clade, the Choristodera: longevity, Lazarus-taxa, and the fossil record. *Evolutionary Biology*, **27**, 323–338.

HEDGES, S. B., PARKER, P. H., SIBLEY, C. G. and KUMAR, S. 1996. Continental breakup and the ordinal diversification of birds and mammals. *Nature*, **381**, 226–229.

HOPE, S. 1997. Birds of the Lance Formation: a window on Late Cretaceous avifaunas. *Journal of Vertebrate Paleontology*, **17** (supplement to No. 3), 53A.

HUTCHISON, J. R., STIDHAM, T. A. and SNIVELY, E. 1997. New birds and other Late Cretaceous theropods from Montana in the University of California Museum of Paleontology. *Journal of Vertebrate Paleontology* **17** (supplement to No. 3), 55A.

JI, Q., CURRIE, P. J., NORELL, M. A. and JI, S. 1998. Two feathered dinosaurs from northeastern China. *Nature*, **393**, 753–761.

NORELL, M. A., CLARK, J. M., CHIAPPE, L. M. and DASHZEVEG, D. 1995. A nesting dinosaur. *Nature*, **378**, 774–776.

SIBLEY, C. and AHLQUIST, J. 1990. *Phylogeny and classification of birds*. Yale University Press, New Haven.

WILSON, J. A. and SERENO, P. C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Memoir of the Society of Vertebrate Paleontology*, **5**, 1–68.

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ALBIAN AND CENOMANIAN SELACHIAN ASSEMBLAGES FROM NORTH-EAST ENGLAND

by CHARLIE J. UNDERWOOD *and* SIMON F. MITCHELL

ABSTRACT. Bulk sampling of the marls and marly limestones of the Hunstanton Formation (Red Chalk) and associated deposits at two sites in north-east England has yielded rich and diverse assemblages of small selachians, largely represented by dissociated teeth. This fauna contains over 35 taxa and is dominated by small to very small nectobenthic forms. A large proportion of these are new, and five new species are described here: *Protosqualus pachyrhiza* sp. nov., *Pseudospinax heterodon* sp. nov., *Cretorectolobus gracilis* sp. nov., *Parasymbolus reticularis* sp. nov. and *Pteroscyllium ornatum* sp. nov. *Cretascyliorhinus* gen. nov. is erected for *Scyliorhinus destombesi* Cappetta and related forms. The earliest records of *Squalus* and the Etmopterinae are noted. The fauna is considered a specialist low-nutrient selachian fauna probably confined to the North Sea Basin.

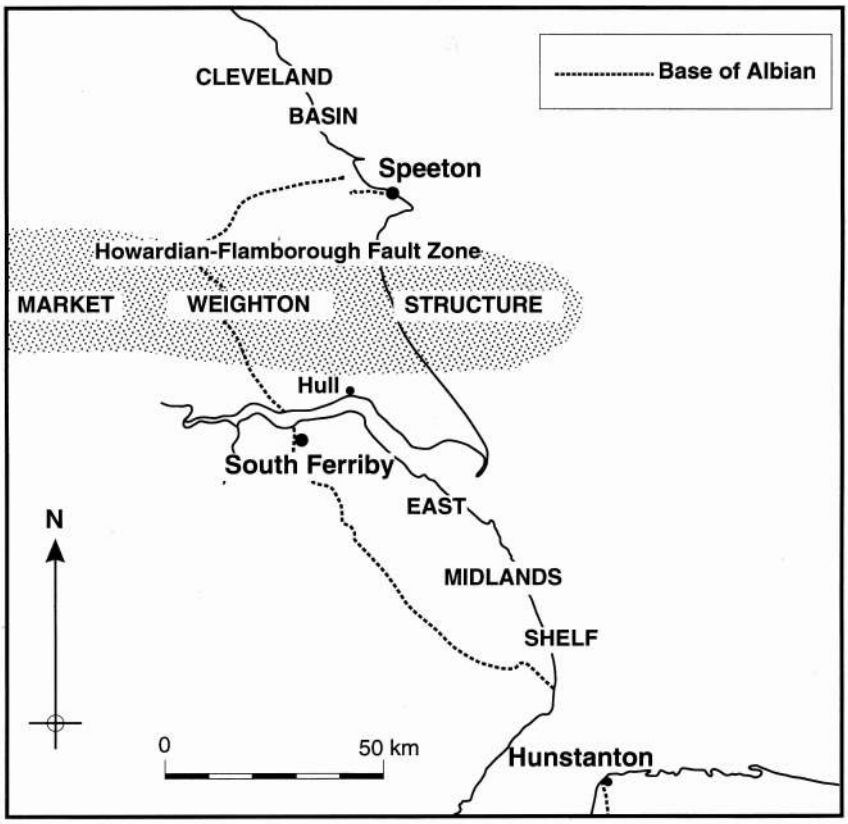
THE fossil remains of selachians (sharks and rays) are present, often abundantly, within many rocks of Late Palaeozoic to Recent age. Despite this widespread occurrence, published records of selachian fossils have often been biased towards certain stratigraphical intervals. Although selachians from the Upper Cretaceous of northern Europe have been well documented (e.g. Woodward 1912; Dalinkevicius 1935; Herman 1977; Cappetta 1980*a*), those of the marine Lower Cretaceous have received less attention. Despite this, studies have revealed diverse Barremian (Biddle and Landemaine 1988), Aptian (Cappetta 1975; Batchelor and Ward 1990) and Albian (Biddle 1993) assemblages. The bulk of published research on the Albian selachian assemblage has been carried out on material from the Gault Clay facies (Cappetta 1977*b*; Biddle 1993; Smart 1995). Other than a few records from the Greensand facies of Britain (e.g. Woodward 1889) and a clastic marginal complex of Texas (Thurmond 1971), assemblages from other environments are almost unknown. Studies of European Cretaceous selachians have generally been restricted to the Anglo-Paris Basin, with very few studies of pre-Campanian selachians from the North Sea Basin (e.g. Dalinkevicius 1935; Müller and Diedrich 1991).

Sampling of the marls within the Hunstanton Formation (Red Chalk) and associated deposits of northern England has yielded a high diversity selachian assemblage, containing over 35 species, although some of these are represented by specifically indeterminate material. The samples are dominated by small nectobenthic taxa, and represent an assemblage that is strikingly different from those described from the Gault Clay (Albian) and Lower Chalk (Cenomanian) of the Anglo-Paris Basin.

GEOLOGICAL SETTING

The Hunstanton Formation or Red Chalk was deposited on the East Midlands Shelf and in the Cleveland Basin (north-east England) during the interval between the Mid Albian and the early Early Cenomanian (Mitchell 1995, 1996*a*; Mitchell and Langner 1995). Similar deposits of red marls and chalks were also deposited widely throughout the North Sea region (Lott *et al.* 1985; Hancock 1986). We studied selachian assemblages from the Hunstanton Formation at two localities: Speeton (North Yorkshire) in the Cleveland Basin; and South Ferriby (Lincolnshire) on the East Midlands Shelf. We have also studied a small amount of material from Rifle Butts (North Yorkshire) (see Text-fig. 1).

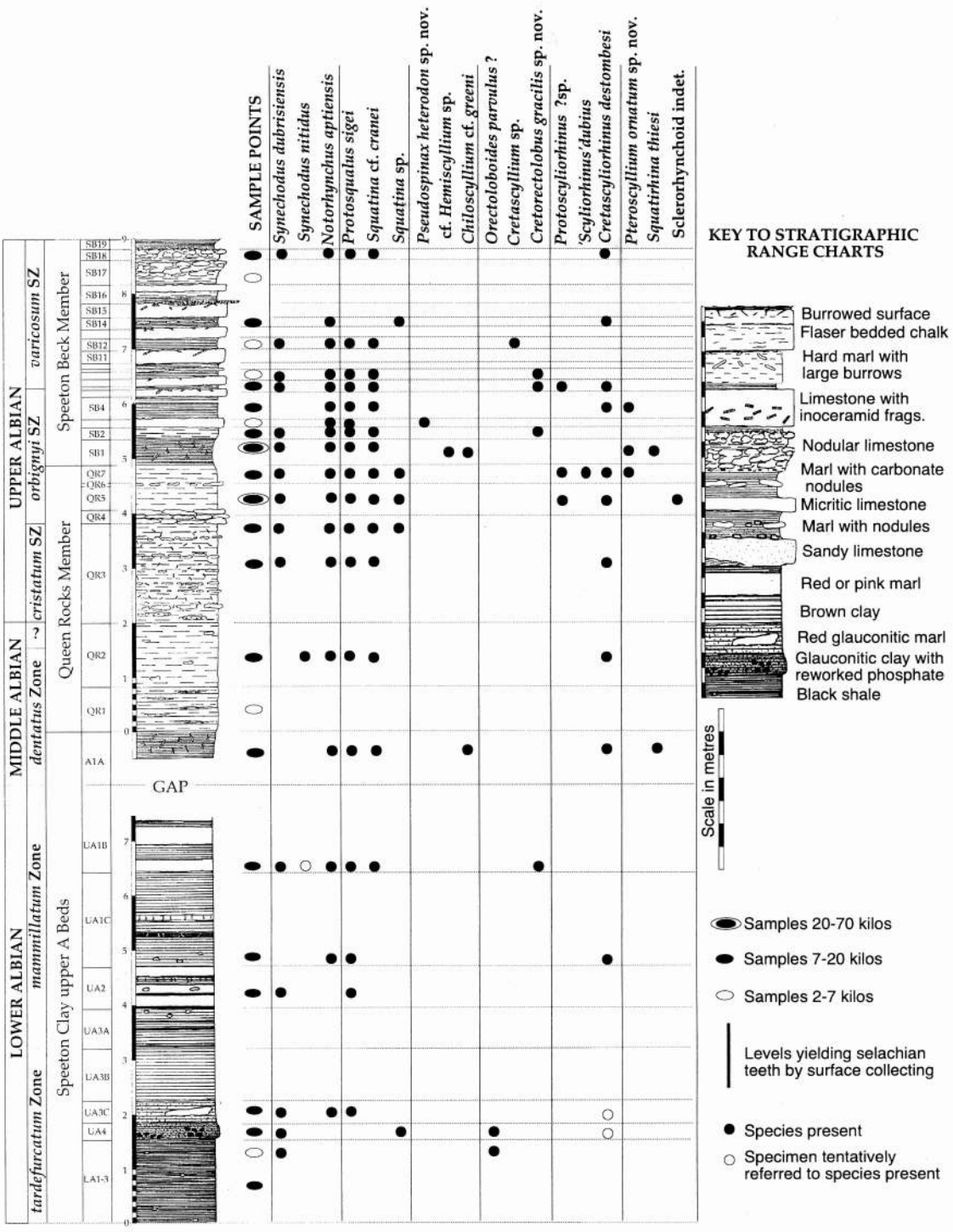
[Special Papers in Palaeontology No. 60, 1999, pp. 9–56, 9 pls]



TEXT-FIG. 1. Locality map of Speeton and South Ferriby and their palaeogeographical relationships (from Mitchell 1996*a*).

The Cretaceous succession at Speeton is particularly complete with a relatively continuous record from the Berriasian (Ryazanian) to the Turonian. The Albian to Cenomanian interval is represented by the upper part of the Speeton Clay, the Hunstanton Formation and the Ferriby Formation. The Albian portion of the Speeton Clay has previously been described by Ennis (1932) and Wright and Wright (*in* Swinnerton 1955). We have logged much of the upper A Beds (Text-fig. 2), *c.* 8 m thick, but not fully exposed, which consist of bioturbated grey clays with interbedded reddish marls and a prominent bed of unconsolidated greensand (bed UA4, the Greensand Streak) near the base. Full details will be given elsewhere. The upper A Beds range from Lower Albian (*Leymeriella tardefurcatum* Zone) to lower Middle Albian (*Hoplites dentatus* Zone). The Hunstanton Formation at Speeton, considered by Mitchell and Langner (1995) to have been deposited in deep water close to, or below, storm wave base, is represented by a 24 m thick unit of alternating reddish marl and nodular reddish or grey micrites (Mitchell 1995). Internal variations have allowed the establishment of five members within the formation (Mitchell 1995; Text-figs 2–3) which ranges from the lower Middle Albian (*Hoplites dentatus* Zone) to the lower Lower Cenomanian (basal *Mantelliceras mantelli* Zone). The Ferriby Formation at Speeton has been discussed by Jeans (1980) and Mitchell

TEXT-FIG. 2. Lower part of the sampled succession at Speeton (Albian part of the Speeton Clay Formation and the Queen Rocks and Speeton Beck members of the Hunstanton Formation) showing the horizons sampled and occurrences of selachian teeth, with key for all three range diagrams. Scale in metres.



TEXT-FIG. 2. For caption see opposite.

(1996*b*). We consider only the lower part of the Ferriby Formation (the Crowe's Shoot Member, 1·7 m of hard nodular white and pink chalk with some marl partings; Mitchell 1995), and a single comparative sample from the lower Middle Cenomanian (bed SLC11C of Mitchell 1996*b*). Additionally, we have sampled various levels in the Speeton Clay for comparative material from the Hauterivian to Aptian.

The mid Cretaceous succession at South Ferriby has been discussed by Mitchell and Langner (1995) (Text-fig. 4). The Lower Albian and lower part of the Middle Albian are represented by the Carstone Formation, 0·6 m of ferruginous sand which lies unconformably on the Jurassic basement; it is largely devoid of macrofossils. The Hunstanton Formation consists of 3·2 m of nodular pink and, rarely, greenish limestones and marls, that are sandy towards the base and more massive towards the top. Near the top of the formation there is a distinctive omission surface beneath which there is an idiomorphic *Thalassinoides* burrow network (Mitchell and Langner 1995). There is extensive evidence of wave reworking throughout the Hunstanton Formation and Mitchell and Langner (1995) suggested that it was deposited in a shallow water environment, of perhaps only a few metres to a few tens of metres water depth.

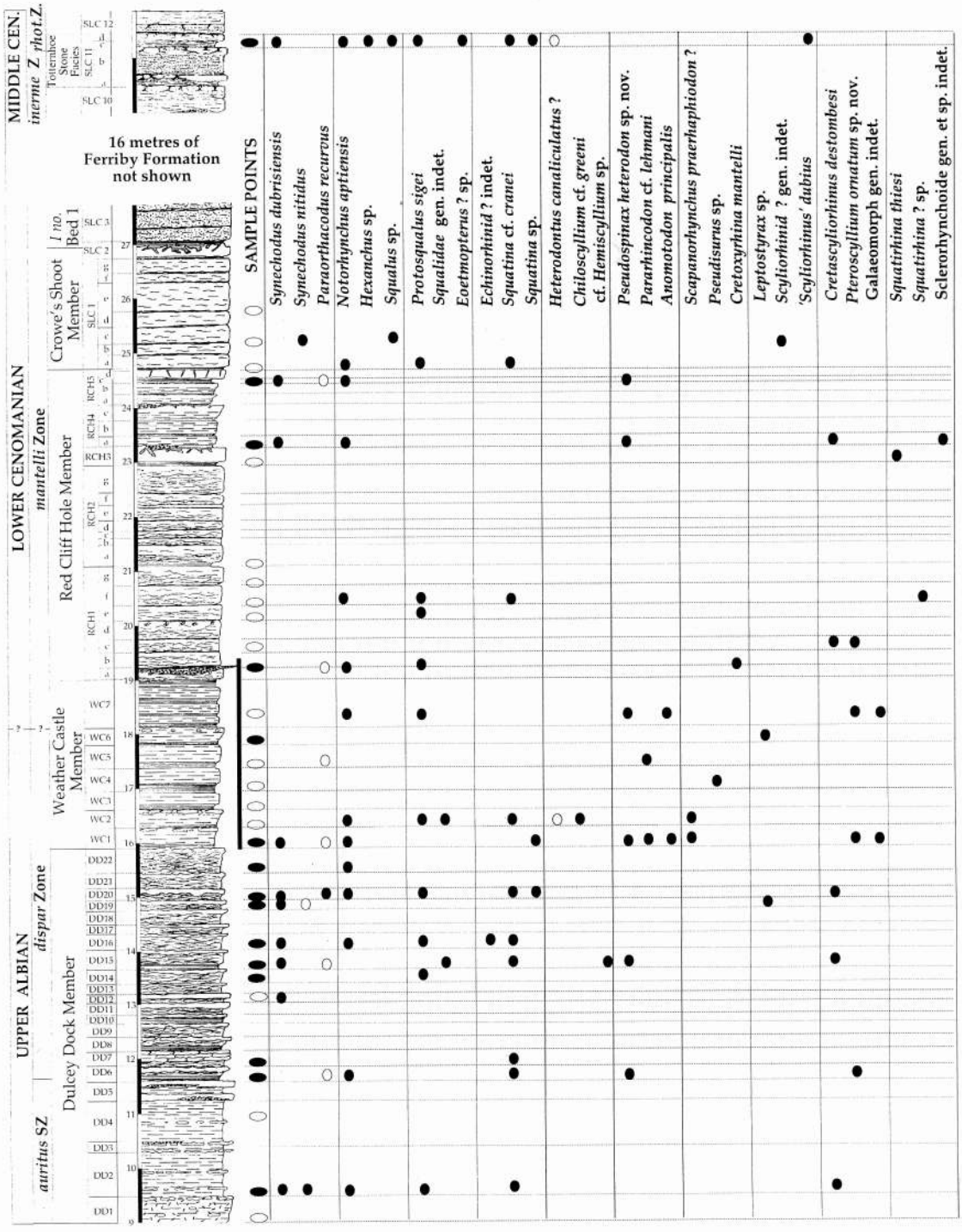
The Hunstanton Formation at Rifle Butts is very thin (0·6 m) and only the upper part of the Upper Albian is represented (Mitchell 1996*a*). It consists of stromatolitic and sponge-rich micritic limestones that were deposited in a subtidal to intertidal environment (Mitchell and Langner 1995).

MATERIAL AND METHODS

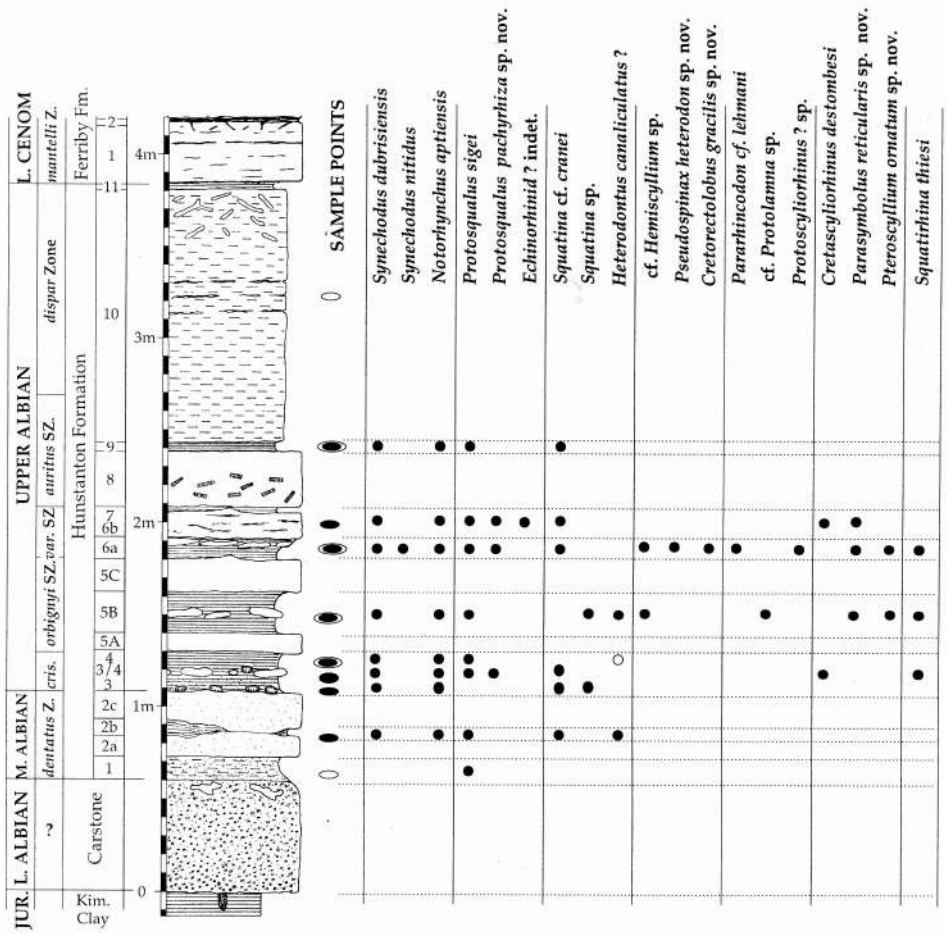
We collected bulk samples from all exposed levels in the Hunstanton Formation at South Ferriby and Speeton that could be sampled for selachian remains (i.e. marls and marly limestones). At South Ferriby all the marls within the Hunstanton Formation were sampled, individual samples ranging up to 70 kg. At Speeton, samples from 2 kg to 30 kg were taken from levels ranging from the Speeton Clay Upper B Beds (Lower Albian) to the Crowe's Shoot Member of the Ferriby Formation (Cenomanian); this included samples from several horizons in all five members of the Hunstanton Formation at Speeton (Text-figs 2–3). The lower part of the Hunstanton Formation (lower Queen Rocks Member) was very poorly exposed, and consequently little Middle Albian material could be collected; the thin, discontinuous nature of the marls in the Cenomanian (Red Cliff Hole and Crowe's Shoot members) prevented large scale sampling. In total, about 260 kg of material from South Ferriby and 350 kg from Speeton was collected. This produced about 1500 selachian teeth and tooth fragments.

The South Ferriby section is well exposed and easily accessible, but the marls are thin, nodular and commonly sandy. Although much of the material breaks down easily, several wet/dry cycles are often needed to break down the bulk of the material. The section at Speeton requires transport of material some distance along the beach, and, in many cases, considerable processing. The Speeton Clay and marls of the lower part of the Hunstanton Formation generally break down after one or two wet/dry cycles, but material from the upper part of the section required several freeze/thaw cycles in the laboratory, frequently with the addition of a saturated solution of sodium sulphate before vigorous manual sieving. Most material was sieved at 125 μm, and the fish material picked from the 355 μm or 250 μm residues. The bulk of the selachian material was recovered from these sub-1 mm fractions. Concentration with acid was rarely used, as both the calcitic and vertebrate fauna was required for study.

The preservation of the selachian material is on the whole rather poor. There is a very strong incidence of bioerosion by the hyphate boring *Mycelites*, which preferentially attacks the tooth root (Underwood *et al.* in press). This results in the almost complete destruction of roots in a large proportion (85–95 per cent.) of specimens, and the destruction of root surface detail in most of those that remain. Many of the larger teeth, especially those of lamniforms, are also split longitudinally, and at some horizons are present as little more than elongate shards. Much of this breakage and removal of roots occurred prior to burial, as adherent foraminifera are occasionally present



TEXT-FIG. 3. Upper part of the sampled succession at Speeton (Dulcey Dock to Red Cliff Hole members of the Hunstanton Formation and parts of the Ferriby Formation) showing the horizons sampled and occurrences of selachian teeth. Scale in metres.



TEXT-FIG. 4. Stratigraphical succession at South Ferriby showing the horizons sampled and occurrences of selachian teeth within the Hunstanton Formation. Scale in metres.

attached to the broken edges. This has also been recognized within the Gault Clay facies (Biddle 1993). At some levels, there is some degree of exfoliation of the enameloid, especially in small teeth with a relatively thick enameloid layer. Mechanical abrasion of the teeth is generally insignificant, but occurs within the sandy beds 2 and 3 of the Hunstanton Formation at South Ferriby.

SYSTEMATIC PALAEONTOLOGY

The taxonomic scheme and dental terminology that are used here are based largely on Cappetta (1987). Full synonymies and descriptions are provided only where considered necessary for taxonomic review. Some specifically indeterminate material has been included to give a more complete record of taxonomic diversity. Figured specimens are deposited in Liverpool City Museum (National Museums and Galleries on Merseyside; prefix LIVCM).

Subclass ELASMOBRANCHII Bonaparte, 1838
Superorder SQUALOMORPHI Compagno, 1973
Order SYNECHODONTIFORMES Duffin and Ward, 1993
Family PALAEOSPINACIDAE Regan, 1906

Genus SYNECHODUS Woodward, 1888*a*

Synechodus dubrisiensis (Mackie, 1863)

Plate 1, figures 1–5

Materials. Twelve near complete teeth along with about 150 fragmented crowns; LIVCM 1998. 20. A–C.

Horizon and localities. Present in many samples (Text-figs 2–4). Speeton: Speeton Clay (bed A5A: lower Lower Albian) to Ferriby Formation (bed SLC11C: lower Middle Cenomanian). South Ferriby: Hunstanton Formation (bed 2b: Middle Albian to bed 9: middle Upper Albian). Also present in the Hauterivian and Aptian Speeton Clay.

Description. Teeth strongly heterodont with a gradation from a piercing to crushing morphology in anterior to lateral files. Cusps are well defined in anterior teeth, but in posterolateral teeth may be almost absent and evident only as low domes with a radiating ornament. The main cusp is roughly circular in cross section and somewhat lingually curved in anterior teeth. There are at least two pairs of lateral cusplets, although on no specimens were these strongly defined. Both lingual and labial faces of main cusps and lateral cusplets are ornamented by strong folds, at least some of which extend to the apex or, in the lateral cusplets, the well-developed cutting edge. Towards the base these folds typically bifurcate or become anastomosing to form a polygonal ornament. The crown is wide, extending some distance down the labial face to form a prominent overhang. The pseudopolyaulacorhize root is expanded lingually and has large folds which project labially. A small, well preserved tooth referred to this taxon (Pl. 1, figs 3–5; LIVCM 1998. 20. C) has a more flared basal face to the root and lacks the pseudopolyaulacorhize folds typical of the genus. This may represent a parasymphyseal tooth; teeth from the symphyseal region having been noted as having a modified root morphology (Biddle 1993, pl. 5, fig. 1).

Synechodus nitidus Woodward, 1912

Plate 1, figure 6

Material. Two near complete teeth and nine or more incomplete to fragmented crowns; LIVCM 1998. 20. D.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR 2 (Middle Albian) to Crowe's Shoot Member (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian) (Text-figs 2–4). Also present in the Aptian Speeton Clay.

Description. The lateral teeth are considerably wider than high. The wide crown carries a rather conical main cusp with three or four mesial and one or two distal cusplets. The principal cusp and lateral cusplets project labially to give a flat occlusal surface in one of the teeth, but are somewhat more erect in the others. The crown strongly overhangs the root labially. Ornament is weak, consisting of a few faint ridges on the labial surface of anterior teeth, which become less evident in more posterior teeth. The cutting edge is weak, and absent in the most posterior tooth seen. The pseudopolyaulacorhize root is flat-based with very strong labial folds and numerous foramina on the lingual face.

Remarks. Although generally poorly preserved, this material compares well with teeth of *S. nitidus* from the Albian (Dalinkevicius 1935) and Cenomanian (Woodward 1912).

Genus PARAORTHACODUS Glückman, 1957

Paraorthacodus recurvus (Trautschold, 1877)

Plate 1, figure 7

Material. One anterolateral tooth lacking lateral cusplets, and several isolated cusps probably referable to this taxon; LIVCM 1998. 20. E.

Horizon and localities. Speeton: Hunstanton Formation, Dulcey Dock Member, bed DD 20; (Text-fig. 3), (broken cusps from bed DD 6) (upper Upper Albian) to Red Cliff Hole Member, bed RCH 5c (lower Lower Cenomanian).

Description. This is one of the largest teeth from the Hunstanton Formation at Speeton, with a height of 5 mm. The relatively high, biconvex main cusp is ornamented with a series of fine, non-bifurcating folds on the lower half of both the labial and lingual faces. This ornament continues on to the lateral cusplets, two of which were originally present on the distal side of the main cusp. The cusps are connected by a very narrow crown, which does not form a labial overhang of the root. The root is broad and flat based with well-developed labial folds.

Order HEXANCHIFORMES Compagno, 1973
Family HEXANCHIDAE Gray, 1851

Remarks. Although isolated cusps of hexanchid teeth are present in almost all of the Hunstanton Formation samples from South Ferriby and Speeton, complete teeth are uncommon. Whilst most of this fragmentary material appears to belong to the described species of *Notorhynchus*, occasional very robust cusps from the Speeton Beck and Dulcey Dock members at Speeton suggest that a second species of Albian hexanchiform may also be present.

Genus NOTORHYNCHUS Ayres, 1855

Notorhynchus aptiensis (Pictet, 1865)

Plate 1, figures 8–12

Material. Seventeen nearly complete or complete teeth and fragmentary remains of more than 58 others; LIVCM 1998. 20. F–J, LIVCM 1997. 51. H.

Horizon and localities. Speeton: Speeton Clay, bed A4 (lower Lower Albian) to Ferriby Formation (bed SLC11C: lower Middle Cenomanian). South Ferriby: Hunstanton Formation (bed 2b: Middle Albian to bed 9: middle Upper Albian) (Text-figs 2–4). Also present in the Hauterivian, Barremian and Aptian of the Speeton Clay.

Description. Teeth have been found from both lower and upper jaws, including lower symphyseal and upper parasymphyseal teeth. The anterolateral teeth present are 1·2–11·1 mm in crown width, suggesting that teeth

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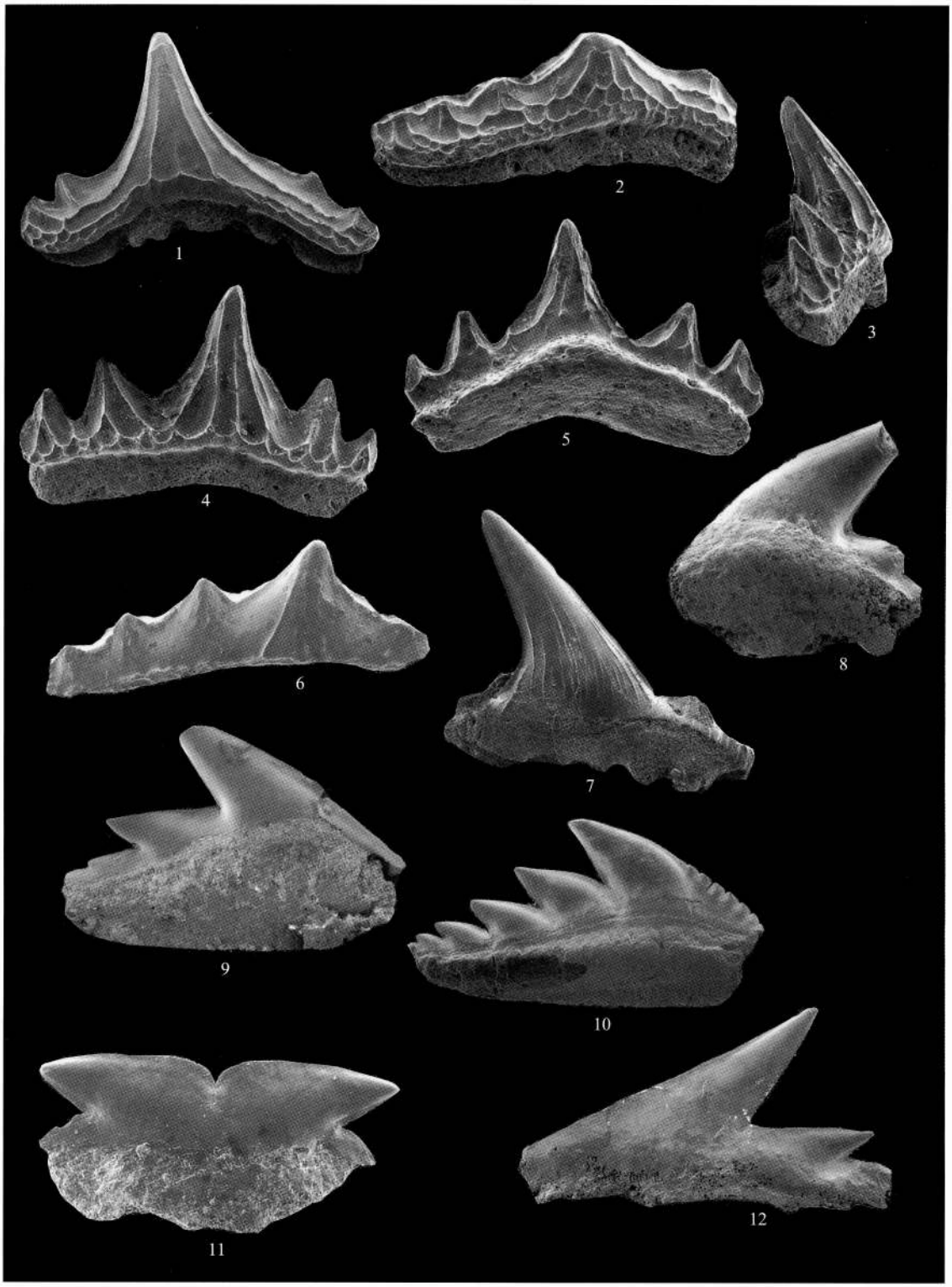
EXPLANATION OF PLATE 1

Figs 1–5. *Synechodus dubrisiensis* (Mackie, 1863); Hunstanton Formation. 1, LIVCM 1998. 20. A; South Ferriby, bed 5b; anterolateral tooth, labial view, width 1·5 mm. 2, LIVCM 1998. 20. B; Speeton, bed QR7; posterolateral tooth, labial view, preserved width 1·8 mm. 3–5, LIVCM 1998. 20. C; Speeton, bed RCH4a; parasymphyseal tooth, width 1·2 mm. 3, lateral view. 4, labial view. 5, lingual view.

Fig. 6. *Synechodus nitidus* Woodward, 1912; LIVCM 1998. 20 D; Hunstanton Formation; South Ferriby, bed 6a; lateral tooth, labial view, width 3·5 mm.

Fig. 7. *Paraorthacodus recurvus* (Trautschold, 1877); LIVCM 1998. 20. E; Hunstanton Formation; Speeton, bed DD20; anterolateral tooth, oblique labial view, height 5 mm.

Figs 8–12. *Notorhynchus aptiensis* (Pictet, 1865); Hunstanton Formation. 8, LIVCM 1998. 20. F; South Ferriby, bed 6a; immature upper anterolateral tooth (?UA-L 2 to 3), lingual view, width 2·3 mm. 9, LIVCM 1998. 20. G; South Ferriby, bed 4; immature upper anterolateral tooth (?UA-L 4 to 6), lingual view, width 3·3 mm. 10, LIVCM 1998. 20. H; Speeton, bed DD6; adult lower anterolateral tooth (LA–L 2 to 5), lingual view, width 11·1 mm. 11, LIVCM 1998. 20. J; Speeton, bed QR3; lower symphyseal tooth, labial view, width 1·5 mm. 12. LIVCM 1997. 51. H; Speeton, bed WC1; anterolateral tooth (?lower) of small juvenile, labial view, width 1·2 mm.



UNDERWOOD and MITCHELL, sharks' teeth

from both juvenile and adult individuals are represented. This taxon, as in all hexanchiforms, shows a strong degree of monognathic and diagnathic heterodonty (Ward and Thies 1987; Siverson 1997). This is particularly evident as a greater number of cusps on lower teeth than upper teeth. Anterolateral teeth have a principal cusp which is triangular and inclined distally. This is followed by between one and five distal cusps, depending on the position of the tooth in the mouth. These decrease regularly in size from the mesial to most distal cusplet. A very small ?anterolateral tooth, probably from a small individual (Pl. 1, fig. 12; LIVCM 1997. 51. H) shows only a single distal cusplet, suggesting an increase in cusplet number with ontogeny as in other hexanchiformes (Ward and Thies 1987). In adult lower teeth, these retain a constant angle to the root, whereas in upper and juvenile teeth, successive cusplets may be at a progressively lower angle. The lower half of the mesial edge of the principal cusp commonly has several serrations or cusplets. These are very variable in form, and may be absent altogether in juvenile teeth and immature upper teeth. In larger lower teeth, these serrations are regular in spacing, but vary in their degree of separation from the mesial edge of the tooth. In smaller lower teeth, the cusplet spacing is less regular, and may fuse to form an irregularly serrated blade. The anaulacorhize root is deep and rather massive, with a faint ridge along the lingual face. There are several foramina of various sizes concentrated along this ridge. Two poorly preserved lower symphyseal teeth are generally similar (Pl. 1, fig. 11; LIVCM 1998. 20. J), with two cusps pointed in opposite directions and a distal pair of cusplets forming curved heels, giving a 'squaliform' appearance. These differ from the rather large symphyseal tooth figured by Siverson (1997) in lacking a high central cusp. It is therefore likely that the central cusp of the symphyseal teeth is gained during ontogeny. Upper parasymphyseal teeth are rather different, consisting of a single conical cusp, often showing some degree of torsion, and a globular root.

Remarks. Many Cretaceous hexanchiforms have generally been referred to *Hexanchus microdon* (Agassiz, 1843). It is likely that a number of these records refer to *Notorhynchus aptiensis* (Siverson 1997), which appears to be widely distributed across Europe at levels from the Hauterivian to Cenomanian.

Genus HEXANCHUS Rafinesque, 1810

Hexanchus sp. indet.

Plate 2, figure 1

?1991 *Hexanchus* aff. *microdon* (Agassiz, 1843); Müller and Diedrich, pl. 1, fig. 5.

Material. Two partial crowns; LIVCM 1998. 20. K.

Horizon and localities. Speeton: Ferriby Formation (bed SLC11C: lower Middle Cenomanian) (Text-fig. 3).

Description. The more complete of these fragmentary teeth shows only three complete and one partial cusp, although the nature of the breakage suggests that this crown is not complete. The mesial cusp is unserrated

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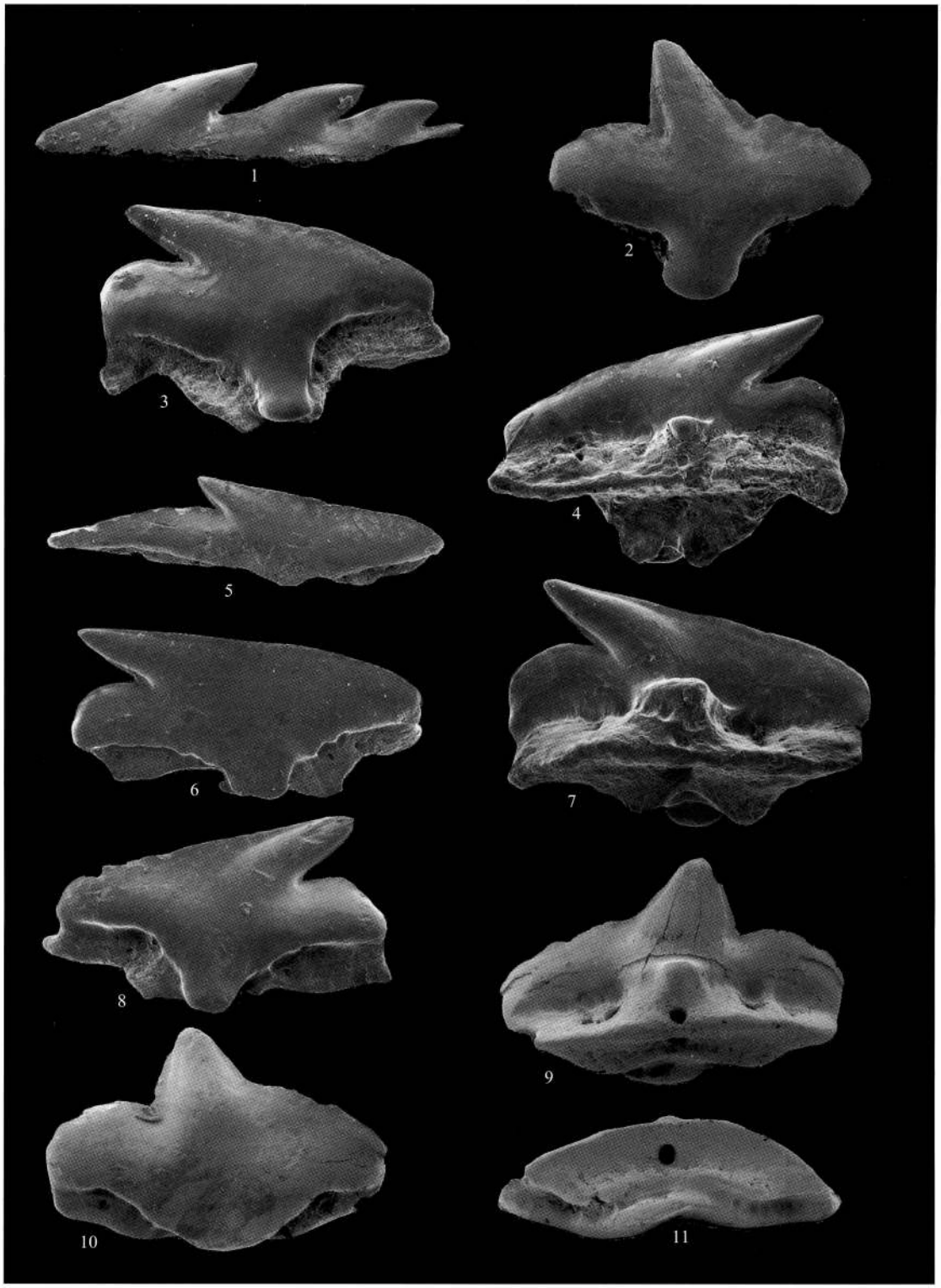
EXPLANATION OF PLATE 2

Fig. 1. *Hexanchus* sp. indet.; LIVCM 1998. 20. K; Ferriby Formation; Speeton, bed SLC11C; partial lower anterolateral tooth, preserved width 2 mm.

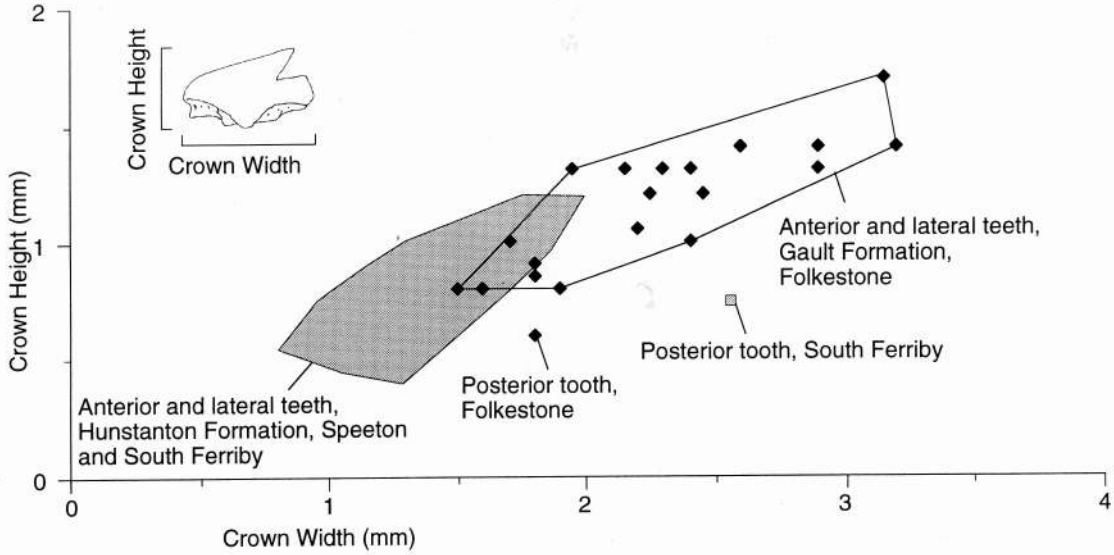
Figs 2–4. *Squalus* sp.; Ferriby Formation. 2. LIVCM 1998. 20. L; Speeton, Crowe's Shoot Member; incomplete tooth, labial view, preserved width 0·8 mm. 3–4. LIVCM 1998. 20. M; Speeton, bed SLC11C; width 0·83 mm. 3, labial view. 4, lingual view.

Figs 5–8. *Protosqualus sigei* Cappetta, 1977*b*; Hunstanton Formation. 5, LIVCM 1998. 20. N; South Ferriby, bed 6a; large posterior tooth, labial view, width 2·8 mm. 6, LIVCM 1998. 20. P; Speeton, bed SB12; lateral tooth, labial view, width 1·3 mm. 7, LIVCM 1998. 20. Q; South Ferriby, bed 6a; anterior tooth, lingual view, width 1 mm. 8, LIVCM 1998. 20. R; South Ferriby, bed 5b; anterolateral tooth, labial view, width 0·9 mm.

Figs 9–11. *Protosqualus pachyrhiza* sp. nov.; LIVCM 1998. 20. S, holotype, Hunstanton Formation; South Ferriby, bed 6a; anterior tooth, width 1·4 mm. 9, lingual view. 10, labial view. 11, basal view.



UNDERWOOD and MITCHELL, sharks' teeth



TEXT-FIG. 5. Graph showing the relative sizes of specimens of *Protosqualus sigei* Cappetta, 1977*b*, from the Hunstanton Formation (East Midlands Shelf and North Sea Basin) and Gault Clay Formation (Anglo-Paris Basin).

and rather low, being sharply inclined posteriorly. The successive cusps are similar in form and decrease in height only gradually; the third cusp still being 60 per cent. of the height of the mesial.

Remarks. Although specifically indeterminate, these teeth can readily be assigned to *Hexanchus* on the basis of gross crown morphology. Although hexanchiforms have previously been recorded from levels throughout the Jurassic and Cretaceous, *Hexanchus* has not been recognized below the Cenomanian; figured pre-Cenomanian specimens belong to species from a range of Mesozoic genera (Ward and Thies 1987; Cappetta 1990). The many records of *Hexanchus* from the Cenomanian (e.g. Woodward 1912; Müller and Diedrich 1991) generally refer to specimens of *Notorhynchus aptiensis* (Siverson 1997), with a single specimen from the German Cenomanian (Müller and Diedrich 1991) possibly being conspecific with the teeth recorded here. This is therefore one of the earliest records of *Hexanchus sensu stricto*.

Order SQUALIFORMES Goodrich, 1909
Family SQUALIDAE Bonaparte, 1834

Genus SQUALUS Linnaeus, 1758

Squalus sp.

Plate 2, figures 2–4

Material. Two teeth, one well preserved; LIVCM 1998. 20. L–M.

Horizon and localities. Speeton: Ferriby Formation, Crowe's Shoot Member, 0·43–0·55 m above base (lower Lower Cenomanian); and bed SLC 11C (lower Middle Cenomanian) (Text-fig. 3).

Description. The better preserved tooth (Pl. 2, figs 3–4; LIVCM 1998. 20. M) is strongly linguo-labially compressed, especially the crown which is rather blade-like. The cusp is relatively narrow and directed posteriorly over a semicircular distal heel. The crown overhangs the root labially, but is rather excavated along its contact with the root lingually. The labial apron is relatively small, and is parallel-sided for much of its

length. The lingual boss is small but projects strongly lingually. The root has a generally flat basal face with a distinct ridge along its lingual margin broken by an infundibulum. There is a wide and deep expansion of the basal face, with prominent lobes on either side of the labial apron. There are numerous small foramina on both lingual and labial faces of the root. In the incomplete tooth (Pl. 2, fig. 2; LIVCM 1998. 20. L), the crown is rather high and short and quite bilaterally symmetrical. The mesial edge is irregular, being convex and faintly denticulate anteriorly with a pronounced notch before the straight leading edge of the relatively erect cusp. The distal heel is large and robust. The labial apron is well developed and parallel sided with a bulbous tip. The root is unknown.

Remarks. Although rather different, there is no evidence to suggest that these two teeth do not belong to the same species, as they show no more variation in morphology than is seen within the heterodonty of the type species of *Squalus*, *S. acathius* Linnaeus, 1758. *Squalus* is abundant and diverse in the Campanian (e.g. Müller and Schöllmann 1989) and Maastrichtian (e.g. Siverson 1993), but has not previously been recorded in pre-Campanian rocks, Cenomanian and Turonian squalids (Dalinkevicius 1935) being referable to *Protosqualus* (Cappetta 1987). Although this therefore represents a considerable range extension for *Squalus*, it is not unexpected, as other dentally advanced squalids (*Protosqualus*) are known from as low as the Barremian (Thies 1981).

Genus PROTOSQUALUS Cappetta, 1977*b*

Protosqualus sigei Cappetta, 1977*b*

Plate 2, figures 5–8

Material. Approximately 460 teeth from all parts on the jaw, ranging from pristine to partial or poorly preserved crowns, LIVCM 1998. 20. N–R.

Horizon and localities. Present in most horizons sampled (Text-figs 2–4). Speeton: Speeton Clay, bed A3C (upper Lower Albian) to Ferriby Formation, bed SLC11C (lower Middle Cenomanian). South Ferriby: Hunstanton Formation, bed 1 (lower Middle Albian) to bed 9 (middle Upper Albian).

Description. The majority of the teeth correspond well with previous descriptions (Cappetta 1977*b*; Müller and Diedrich 1991; Biddle 1993). The main cusp is relatively narrow and strongly inclined posteriorly with an unserrated mesial edge which is straight or slightly convex for most of its length. Occasional specimens have a notch along the mesial edge of the cusp, but in other respects do not differ from normal anterior teeth. The distal heel is roughly semicircular and extends slightly posterior to the point of the main cusp. The labial apron is well developed and broad, extending below the basal face of the root, but may be narrower and almost parallel-sided in some very small teeth. There is a well-developed lingual bulge which is narrow and often rather pointed. The root is low and flat-based and rather expanded lingually with well-developed foramina on the labial face. Most specimens show separate basal and lingual axial foramina; only rarely is an infundibulum developed. The basal face of the root is rather variable, often having a wide mesial expansion, and more rarely, a narrow mesial and distal expansion which may extend below the base of the apron. Posterior teeth show extreme antero-distal elongation. The principal cusp length is over twice the maximum height, whilst this length is nearly matched by the distal heel, now a narrow, horizontal blade.

Remarks. Although *Protosqualus sigei* is well known from the Albian (Cappetta 1977*b*; Biddle 1993; D. Ward, pers. comm.) and Cenomanian (Müller and Diedrich 1991), the species from the Hunstanton Formation assemblage appears to be rather more morphologically variable than those previously described. The variations in root morphology probably relate to subtle dignathic, sexual and ontogenetic heterodonty, as recognized in Maastrichtian *Squalus* species (Siverson 1993).

Specimens of *P. sigei* from the Hunstanton Formation appear to be consistently small, not exceeding 2 mm long. This compares with the type assemblage in which specimens reach 2·4 mm (Cappetta 1977*b*) and comparative specimens from the Lower Gault at Folkestone that reach 3·2 mm (Text-fig. 5). This does not appear to be of taxonomic significance; modern squalids may show regional size differences (Siverson 1993), and similar differences have been noted in other Cretaceous selachian taxa such as *Squalicorax* (Siverson 1992).

Protosqualus pachyrhiza sp. nov.

Plate 2, figures 9–11; Plate 3, figures 1–2

Derivation of name. From the generally bulky root.

Holotype. LIVCM 1998. 20. S (Pl. 2, figs 9–11); South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Referred material. One well preserved tooth (LIVCM 199. 20. T) and fragmentary remains of at least ten others.

Horizon and localities. South Ferriby: Hunstanton Formation, beds 3/4, 6a and 6b/7 (lower Upper Albian).

Diagnosis. Squaliform tooth of generally bulky aspect. Cusp short and robust with straight or sigmoidal anterior edge. Distal heel well developed and rounded in profile. Labial apron with gently sloping anterior and posterior edges and rounded tip projecting below root. Lingual bulge poorly defined. Separate lingual axial and basal foramen. Basal face of root flat with rounded lingual edge. Weak basal expansions of root anterior and posterior of labial apron.

Description. On the type specimen, the mesial edge is faintly convex proximally, with a distinct concavity at the base of the erect cusp. In the other specimens, the cusp is less erect, and the mesial edge is either straight or shows only a faint sigmoidal outline. The cusp is short and thick and only weakly distally inclined. The distal heel is large and semicircular. The labial apron is very wide, over half the width of the tooth, and shallow, with a gently rounded outline. The labial face of the apron is flat or slightly concave and the apron is composed of rather thick enameloid. The crown strongly overhangs the root labially. The labial bulge is poorly defined, and occurs largely as a swelling of the area of the root/crown junction above the axial foramen. This swollen area is as wide as the base of the cusp and has a rounded tip that does not project lingually far beyond the edge of the root. The root is rather bilaterally symmetrical. The basal face is flat, with poorly developed mesial and distal expansions not reaching the base of the apron. The lingual edge of the basal face is either smoothly convex or with a slight depression anterior to the axial foramen. The lingual axial and basal foramina are relatively small, and an infundibulum has not been observed. Other foramina are also small and few in number, being restricted to the upper lingual and labial faces of the root.

Remarks. Protosqualus pachyrhiza sp. nov. is rather similar to *Protosqualus sigei*, but is readily recognized by its generally robust stature with the crown being only weakly compressed, the rounded form of the labial apron and the poorly defined lingual bulge. It is only recorded from the lower Upper Albian at South Ferriby, where it co-occurs with relatively uncommon *P. sigei*. It is, however, absent in rocks of the same age at Speeton where *P. sigei* is extremely abundant. It is therefore possible that *P. pachyrhiza* sp. nov. represents a shallower water ecological analogue to *P. sigei* that was restricted to more nutrient-rich shelf settings.

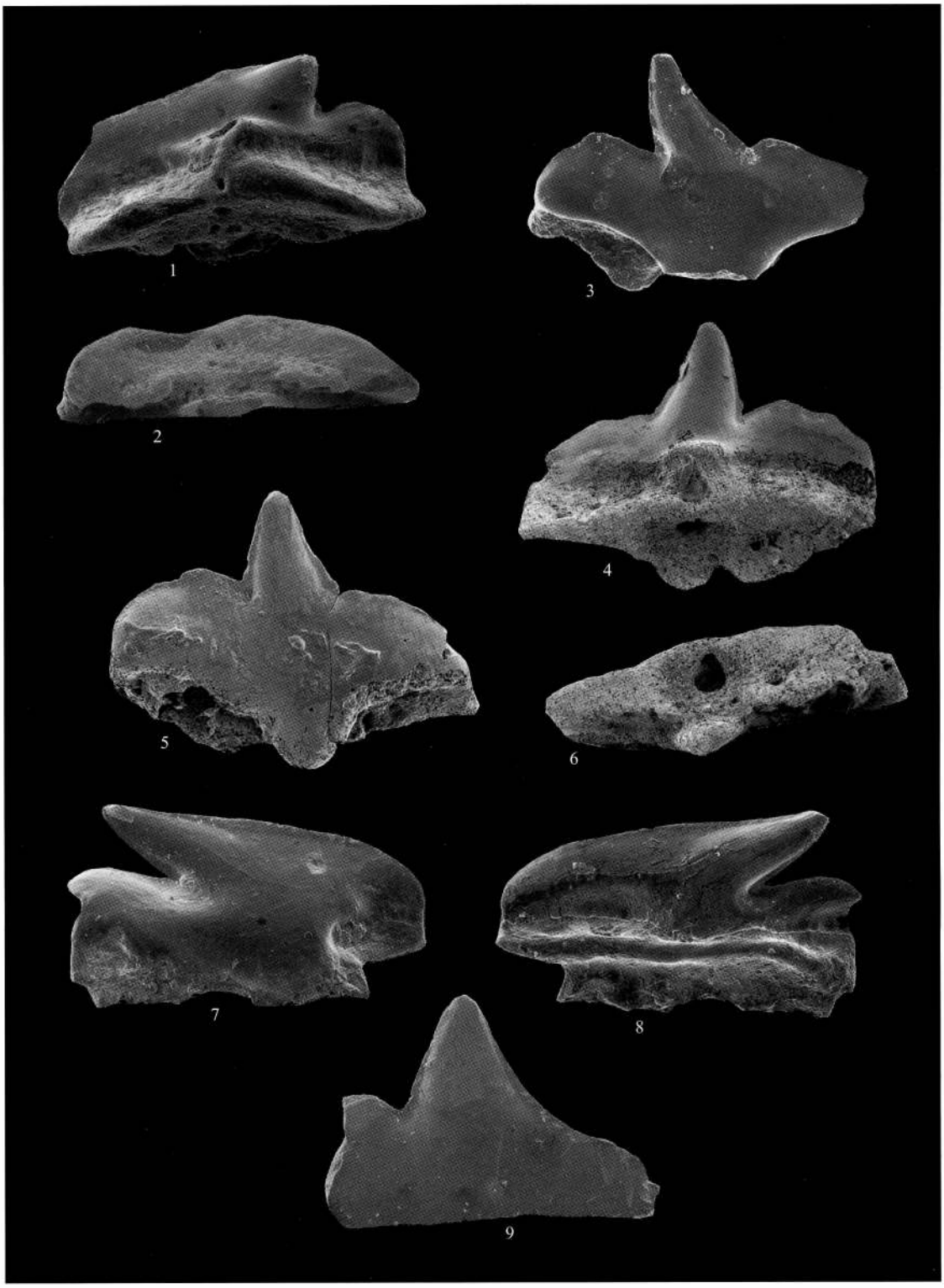
EXPLANATION OF PLATE 3

Fig. 1–2. *Protosqualus pachyrhiza* sp. nov.; LIVCM 1998. 20. T; Hunstanton Formation; South Ferriby, bed 6a; lateral tooth, width 1·9 mm. 1, lingual view. 2, basal view.

Figs 3–6. Squalidae gen. indet.; Hunstanton Formation. 3, LIVCM 1998. 20. U; Speeton, bed DD15; incomplete tooth, labial view, width 0·7 mm. 4–6, LIVCM 1998. 20. V; Speeton, bed WC2; width 1·2 mm. 4, lingual view. 5, labial view (specimen broken). 6, basal view.

Figs 7–8. *Eoetmopterus*? sp.; LIVCM 1998. 20. W; Ferriby Formation; Speeton, bed SLC11C; Ferriby Formation; lower tooth, width 1·45 mm. 7, labial view. 8, lingual view.

Fig. 9. Echinorhinid? indet.; LIVCM 1998. 20. X; Hunstanton Formation; Speeton, bed DD16; labial view, preserved width 1·1 mm.



UNDERWOOD and MITCHELL, sharks' teeth

Squalidae gen. indet.

Plate 3, figures 3–6

Material. Two teeth, neither perfectly preserved; LIVCM 1998. 20. U–V.

Horizon and localities. Speeton: Hunstanton Formation, Dulcey Dock Member, bed DD 15 and Weather Castle Member, bed WC 2 (upper Upper Albian).

Description. These small teeth, up to 1·2 mm wide, have a mesial edge that is strongly divided into two parts: a relatively straight proximal section at a low angle to the root, followed by a pronounced notch, and a slightly concave leading edge to the erect cusp. The cusp is narrow and oriented with the distal edge vertical relative to the basal face of the root. The distal heel is large and narrow with a rather triangular profile. The labial apron is large and triangular, extending below the root, and tapers to a rounded point from a base rather wider than that of the cusp. A small lingual boss is present below the cusp at the crown-root junction. The basal face of the root is flat with a compressed distal expansion which does not reach the base of the labial apron. The two axial foramina are well developed, and the basal-most is particularly large.

Remarks. This taxon is unlike any previously described squalid tooth, and is very characteristic due to the proximal notch and erect cusp. The quantity and quality of material, however, prevents a specific diagnosis. Teeth referable to *P. sigei* occasionally have a mesial notch, but this species is significantly different in both crown and root morphology. It is possible that the crown morphology demonstrates a transitional stage between homodont squalid teeth and the trifid cusp on the upper teeth of etmopterids.

Genus EOETMOPTERUS Müller and Schöllmann, 1989?

Eoetmopterus? sp.

Plate 3, figures 7–8

Material. One fairly well preserved lower tooth; LIVCM 1998. 20. W.

Horizon and locality. Speeton: Ferriby Formation, bed SLC 11C (lower Middle Cenomanian).

Description. This tooth, 1·45 mm wide, and strongly labio-lingually compressed, is readily distinguished from the other squalids collected. The occlusal edge of the crown is rather *Squalus*-like, with the root being distinctly etmopterid. The cusp is at a low angle to the root and extends almost to the distal edge of the tooth. Initially, the leading edge is strongly convex, but is then straight for much of its length. The cusp is narrow with well-

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EXPLANATION OF PLATE 4

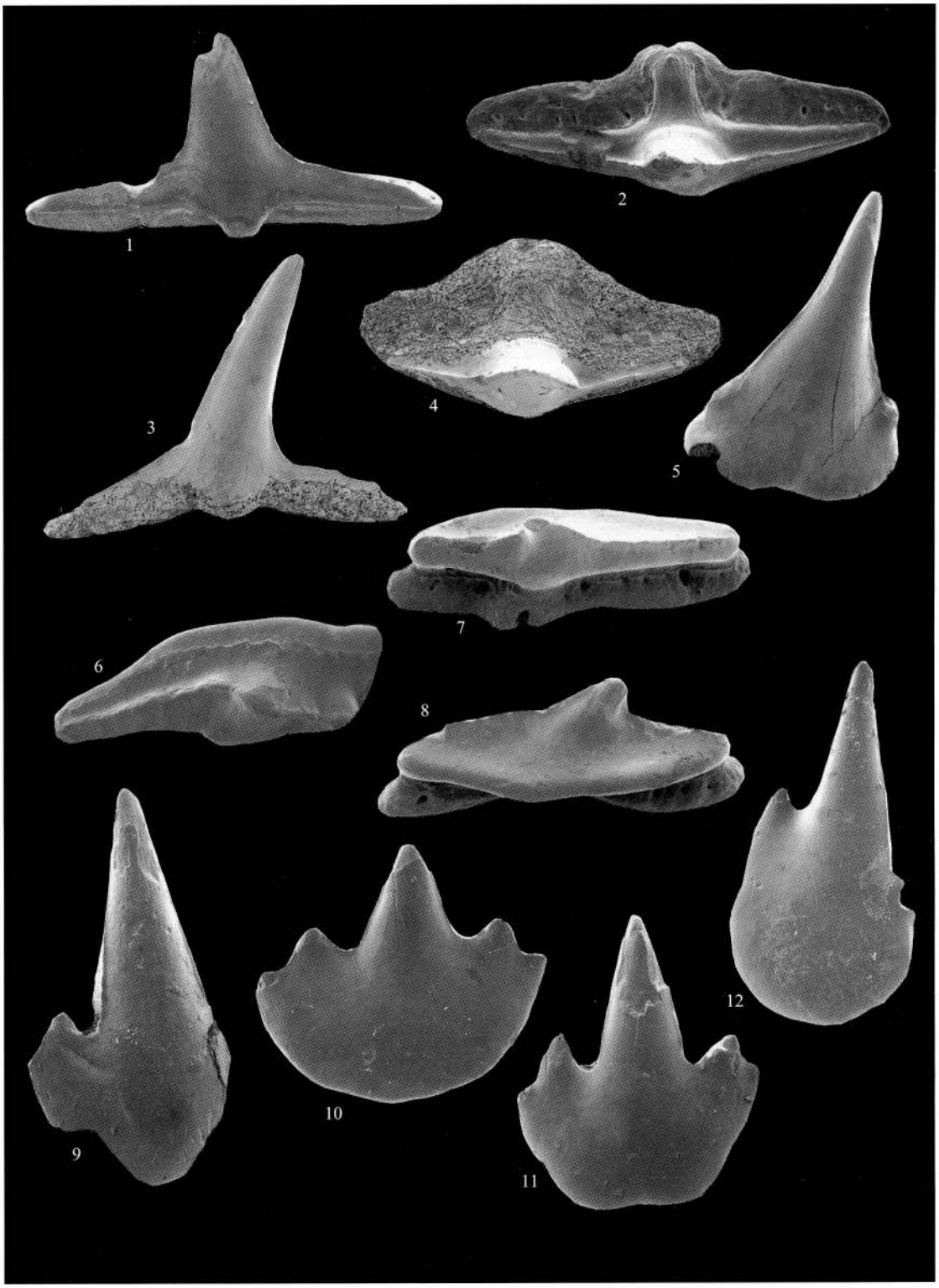
Figs 1–2. *Squatina* cf. *cranei* Woodward, 1888*b*; LIVCM 1998. 20. Y; Ferriby Formation; Speeton, bed SLC11C; lateral tooth, width 4·9 mm. 1, labial view. 2, occlusal view.

Figs 3–4. *Squatina* sp.; LIVCM 1998. 20. Z; Hunstanton Formation; Speeton, bed WC1; lateral tooth, width 1·2 mm. 3, labial view. 4, occlusal view.

Figs 5–8. *Heterodontus canaliculatus* (Egerton, *in* Dixon, 1850)?; Hunstanton Formation. 5, LIVCM 1998. 20. AA; South Ferriby, bed 5b; anterior tooth, labial view, height 2·15 mm. 6, LIVCM 1998. 20. AB; South Ferriby, bed 2; worn lateral tooth, occlusal view, preserved width 3·9 mm. 7–8, LIVCM 1998. 20. AC; South Ferriby, bed 5b; juvenile anterolateral tooth, width 2·1 mm. 7, lingual view. 8, labial view.

Fig. 9. *Chiloscyllium* cf. *greeni* (Cappetta, 1973); LIVCM 1998. 20. AD; Hunstanton Formation; Speeton, bed WC2; incomplete ?anterior tooth, labial view, height 1·3 mm.

Figs 10–12. cf. *Hemiscyllium* sp.; Hunstanton Formation. 10, LIVCM 1998. 20., AE; Speeton, bed DD15; lateral tooth, labial view, height 0·8 mm. 11, LIVCM 1998. 20. AF; South Ferriby, bed 5b; ?anterolateral tooth, labial view, height 1 mm. 12, LIVCM 1998. 20. AG; South Ferriby, bed 6a; ?parasymphyseal tooth, labial view, height 1 mm.



UNDERWOOD and MITCHELL, sharks' teeth

developed cutting edges, and overhangs a small and low distal heel. The distal edge of the heel is strongly concave in profile. Labially, the basal edge of the crown does not overhang the root, but merges into it with the loss of enameloid. Anteriorly, the base of the crown is rather excavated, and curves strongly toward the base at the position of a major foramen. There is a well-developed labial apron. This is short and rounded, the base of the crown being straight distally with at least three foramina at the boundary. The crown-root junction is straight and strongly excavated lingually, immediately overlying a very strong longitudinal ridge. This is shallow and basally forms the basal face of the root. There is a number of well developed foramina on both its upper and lower surfaces. The labial face of the root has a deep basal expansion with a distinct anterior notch. This is shallower than in most etmopterids, with no sign of a groove on the lingual face.

Remarks. This taxon seems to represent the earliest specimen of an etmopterid, extending the first occurrence of this group from the Campanian to the Cenomanian. The Speeton specimen strongly resembles a Campanian tooth referred to *Eoetmopterus supracretaceus* (Müller and Schöllman 1989, pl. 4, fig. 3), but does not appear to belong to the same species as the type specimen (pl. 4, fig. 4) of *E. supracretaceus* which is based on a heterogeneous assemblage of several taxa (Siverson 1993). It is therefore likely that this tooth represents the second record of an unnamed genus that ranges from the Cenomanian to the Campanian, but more material is needed to verify this.

Family ECHINORHINIDAE Gill, 1862?

echinorhinid? gen. et sp. indet.

Plate 3, figure 9

Material. Two poorly preserved partial teeth; LIVCM 1998. 20. X.

Horizon and localities. Speeton: Hunstanton Formation, Dulcey Dock Member, bed 16 (upper Upper Albian). South Ferriby: Hunstanton Formation, bed 6b/7 (lower Upper Albian).

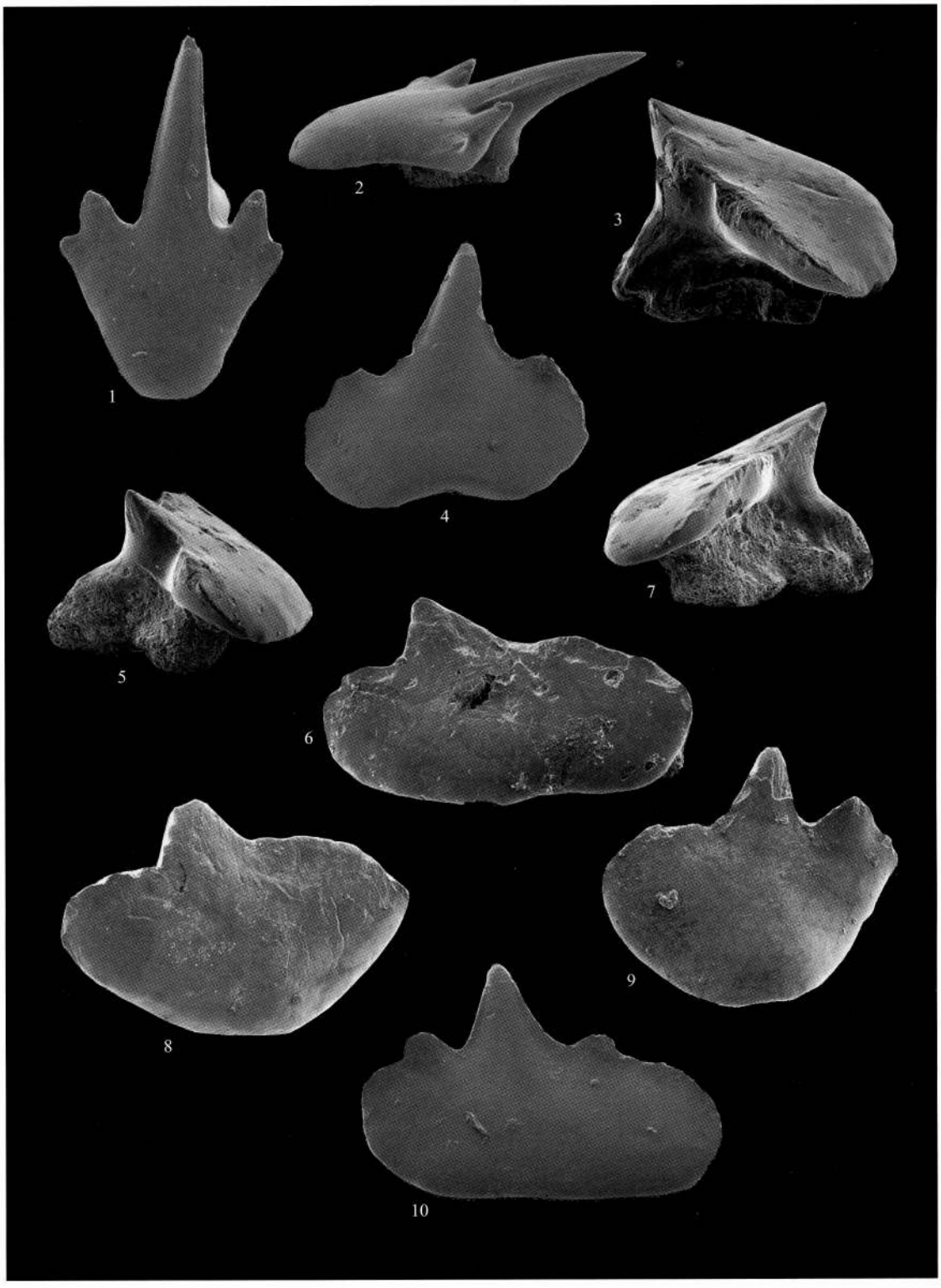
Description. The crown is compressed and rather blade-like. The mesial edge is strongly concave leading to a vertical cusp, short on one specimen, rather high on the other, the distal edge of which is weakly convex. The distal heel is wide on the specimen where it is preserved. The labial face is almost flat, and the bioeroded basal edge shows no sign of the former presence of an apron.

Remarks. Despite their very poor preservation, these specimens are sufficient to indicate the presence of another squalid taxon. The affinities are uncertain, but the straight crown base suggests that they may represent a member of the Echinorhinidae (e.g. Cappetta 1987).

EXPLANATION OF PLATE 5

Figs 1–2. cf. *Hemiscyllium* sp.; LIVCM 1998. 20. AH; Hunstanton Formation; South Ferriby, bed 6a; anterior tooth height 1 mm. 1, labial view. 2, lateral view.

Figs 3–10. *Pseudospinax heterodon* sp. nov.; Hunstanton Formation. 3, LIVCM 1998. 20. AJ, Speeton, bed DD6; 'small cusped' anterior tooth, oblique view, width 0·65 mm. 4, LIVCM 1998. 20. AK; Speeton, bed RCH5c, 'large cusped' anterior tooth, labial view, width 0·6 mm. 5–7, LIVCM 1998. 20. AL, holotype; Speeton, bed DD7; 'small cusped' lateral tooth, width 0·76 mm. 5, posterior lateral view; 6, labial view; 7, anterior lateral view. 8. LIVCM 1998. 20. AM; Speeton, bed WC1; 'small cusped' anterior tooth, labial view, width 0·71 mm. 9, LIVCM 1998. 20. AN; Speeton, bed WC7; 'large cusped' anterior tooth, labial view, width 0·41 mm. 10, LIVCM 1998. 20. AP; Speeton, bed RCH5c; 'large cusped' lateral tooth, labial view, width 0·65 mm.



UNDERWOOD and MITCHELL, cf. *Hemiscyllium*, *Pseudospinax*

Superorder SQUATINOMORPHII Compagno, 1973
Family SQUATINIDAE Bonaparte, 1838

Genus SQUATINA Duméril, 1806

Remarks. The tooth morphology of the genus *Squatina* is both simple and conservative, and it is therefore unlikely that teeth alone will always prove to be a reliable guide to taxonomic identity (Herman 1977; Batchelor and Ward 1990). As a result, many Cretaceous specimens have been referred either to *S. cranei* Woodward, 1888*b* (which is known from a partial skeleton), or *S. decipiens* Dalinkevicius, 1935, depending on whether the teeth are robust or gracile respectively. This situation has been further complicated by the assignment of robust teeth to *S. decipiens* and gracile teeth to *S. cranei* by Cappetta (1975), Batchelor and Ward (1990) and Biddle (1993). This taxonomic lumping of morphotypes probably conceals the true specific composition of the genus, which would probably only be revealed by detailed study of large populations of teeth, preferably with associated dentitions or skeletons. It is also likely that a large number of Cretaceous teeth figured as *Squatina* are from orectolobiformes such as *Cederstroemia* (Siverson 1995) or related taxa.

Squatina cf. *cranei* Woodward, 1888*b*

Plate 4, figures 1–2

1977 *Squatina cranei* Woodward; Herman, p. 123, pl. 5, fig. 2.

Material. Approximately 165 fragmentary teeth and isolated cusps from many of the horizons sampled, as well as a single, well preserved tooth from the Middle Cenomanian; LIVCM 1998. 20. Y.

Horizon and localities. Speeton: Speeton Clay, bed A1B (upper Lower Albian) to Ferriby Chalk Formation, bed SLC 11C (lower Middle Cenomanian). South Ferriby: Hunstanton Formation, bed 2b (Middle Albian) to bed 9 (middle Upper Albian).

Description. The general tooth morphology is relatively heterodont and strongly reminiscent of the extant *Squatina squatina* (Linnaeus, 1758). The teeth have a single cusp which is relatively elongate, but still robust and may be either straight or slightly lingually curved. The lateral blades are narrow and taper in some teeth, with a cutting edge running the width of the crown. The labial bulge is triangular or rounded and, at its origin, usually as wide as the base of the cusp. It extends below the base of the root, but does not project labially; the profile of the labial face being straight or slightly convex. The root is relatively narrow and low, being at least twice as wide as the height of the cusp. Lingually, the root is narrow with a well-developed enameloid-covered lingual boss. There is a number of small foramina along the upper lingual surface of the root, with a large foramen at the termination of the lingual projection. The basal face is flat with a large basal foramen.

Squatina sp.

Plate 4, figures 3–4

1975 *Squatina cranei* Woodward; Cappetta, fig. 8.
1993 *Squatina cranei* Woodward; Biddle, p. 199, pl. 1, fig. 2.

Material. At least 15 poorly to well preserved teeth; LIVCM 1998. 20. Z.

Horizon and localities. Speeton: Speeton Clay, bed A4 (lower Lower Albian) to Ferriby Formation, bed SLC 11C (lower Middle Cenomanian). South Ferriby: Hunstanton Formation, beds 3, 5b and 6a (lower Upper Albian).

Description. The teeth are small (rarely more than 1 mm high) and gracile in respect to both the crown and root. The cusp is slender and biconvex with a well-developed cutting edge that grades into the narrow lateral blades with a smooth, but tight curve. There is a slight lingual, and occasional distal curvature. The labial bulge is variable in form, but may project both labially and below the base of the root. The root is roughly diamond-shaped in basal view, being relatively expanded lingually for its width. It is low and may be slightly excavated basally. The lingual boss is wide, but relatively low. Foramina are well marked on the upper lingual surface and at the end of the lingual boss.

Remarks. Teeth of this morphology have been figured by Cappetta (1975) and Biddle (1993) as *S. cranei*, probably due to Woodward's (1912) comments on the gracile nature of some *S. cranei* teeth. In general form, however, the Red Chalk teeth resemble far more closely those of *S. decipiens* Dalinkevicius, 1935, although both this species and the (?conspecific) *Squatina* species B of Batchelor and Ward (1990), differ in having a robust labial bulge and overall are larger in size. It is therefore uncertain whether this taxon represents a small form of *S. decipiens* or a separate species.

Superorder GALEOMORPHII Compagno, 1973
Order HETERODONTIFORMES, Berg, 1940
Family HETERODONTIDAE Gray, 1851

Genus HETERODONTUS de Blainville, 1816

Heterodontus canaliculatus (Egerton, *in* Dixon, 1850)?

Plate 4, figures 5–8

Material. One near complete, but abraded, lateral tooth; one well preserved small anterolateral tooth; and one anterior crown; eight partial lateral crowns are also tentatively assigned to this taxon; LIVCM 1998. 20. AA–AC.

Horizon and localities. South Ferriby: Hunstanton Formation, beds 2 and 5b (Middle and lower Upper Albian) (fragmentary material from South Ferriby: Hunstanton Formation beds 4 to 9 and Speeton: Hunstanton Formation, Weather Castle Member, bed WC 2 (upper Upper Albian) and Ferriby Chalk Formation, bed SLC11C (lower Middle Cenomanian)).

Description. On the lateral tooth (LIVCM 1998. 20. AB), the occlusal face of the crown is somewhat sigmoidal in outline, tapering to a rounded end. There is a very strong occlusal ridge, rising to an elevated central cusp and smaller lateral cusp. The ornament is somewhat abraded, but with weak transverse ridges visible, whilst strong, rather irregular ridges are seen on the referred partial lateral teeth. The root is massive and overhung by the crown, and has a well-developed central foramen. The anterolateral tooth (LIVCM 1998. 20. AC) is similar, but smaller, and not sigmoidal. It lacks occlusal or labial ornament and has a small, erect cusp with a well-developed cutting edge. The single anterior tooth (LIVCM 1998. 20. AA) is triangular in outline and unornamented, with a concave edge to the labial apron and a pair of lateral cusplets reduced to shoulders.

Remarks. The relatively high crown, sigmoidal outline and dominant transverse ornament on the lateral teeth corresponds well with the specimens of *H. canaliculatus* figured in Woodward (1912) and of *H.* cf. *canaliculatus* in Cappetta (1975), whilst the anterior tooth resembles that referred to the third file of *H. canaliculatus* by Herman (1977). *Heterodontus upnikensis* Dalinkevicius, 1935, was erected on anterior teeth lacking lateral cusps, similar to the anterior tooth described here. This name was also used for unornamented small anterolateral teeth by Biddle (1993). Although it is possible that *H. upnikensis* represents a separate taxon, it is more likely that it refers to unornamented (Dalinkevicius 1935) and juvenile (Biddle 1993) teeth of *H. canaliculatus*.

Order ORECTOLOBIFORMES Applegate, 1972
Family HEMISCYLLIIDAE Gill, 1862

Genus CHILOSCYLLIUM Müller and Henle, 1838–1841

Chiloscyllium cf. *greeni* (Cappetta, 1973)

Plate 4, figure 9

1990 *Chiloscyllium* sp. Batchelor and Ward, pl. 3, fig. 1a–c.

Material. Five imperfect teeth; LIVCM 1998. 20. AD.

Horizon and localities. Speeton: Speeton Clay Formation, bed A1A (lower Middle Albian) and Hunstanton Formation, Weather Castle Member, bed WC 2 (upper Upper Albian). Also recorded in the Lower Aptian of the Speeton Clay.

Description. The teeth are bilaterally symmetrical. The principal cusp is rather elongate and triangular in shape with a well developed cutting edge. The lateral cusplets are poorly developed and present a laterally expanded heel, labial to which is a concavity on the apron profile. The crown is unornamented and only slightly convex. An incomplete root is preserved in one specimen. The root is gracile and narrow, with a relatively low profile. The basal face is strongly V-shaped with a well-developed central foramen.

Genus cf. HEMISCYLLIUM Smith, 1837

cf. *Hemiscyllium* sp.

Plate 4, figures 10–12; Plate 5, figures 1–2

Material. Seven incomplete teeth; LIVCM 1998. 20. AE–AH.

Horizon and localities. Speeton: Hunstanton Formation, Speeton Beck Member, bed SB 1 (lower Upper Albian). South Ferriby: Hunstanton Formation, beds 5b and 6a (lower Upper Albian).

Description. The teeth represent anterior (including possibly symphyseal) and lateral positions within a relatively heterodont jaw. The crown is only faintly convex and has a large, unornamented labial apron, semicircular in the lateral tooth (Pl. 4, fig. 10; LIVCM 1998. 20. AE), but rather more labially expanded anteriorly. On one specimen (Pl. 4, fig. 11; LIVCM 1998. 20. AF) it has a slightly concave labial edge. The lingual edge has a triangular principal cusp, rather elongate in the anterior teeth, with one or generally two pairs of lateral cusplets. Where two pairs are present, the inner pair is well developed, but far shorter than the principal cusp, the outer pair forming little more than lateral heels. There is a narrow cutting edge along the lingual edge of the crown and a poorly developed lingual boss below the principal cusp. Fragmentary material suggests that the root is hemiaulacorhize with a rather high, rounded lingual edge. One anterior tooth is symmetrical, whilst there is some degree of asymmetry within the other teeth. One of the teeth (Pl. 4, fig. 12; LIVCM 1998. 20. AG) has only a single pair of lateral cusps and a greater degree of asymmetry than the others. It is unclear, due to the small quantity of material available, whether this morphology lies within the normal range of heterodonty or represents a separate taxon.

Remarks. The overall morphology of the teeth of this species is similar to that of *Hemiscyllium* Smith, 1837, but differs from modern forms by the presence of well-developed lateral cusplets and a well-developed cutting edge. These teeth may therefore represent an as yet unnamed genus of orectolobid closely related to *Hemiscyllium*. Several teeth of very similar morphology have been noted from the Lower Cretaceous (Aptian), and have been referred to the genera *Mesiteia* (Cappetta 1975) and *Heterodontus* (Thies 1979). These are probably congeneric with the taxon described here, and may represent examples of the same species, although the small quantity of material prevents a clear demonstration of synonymy.

Genus PSEUDOSPINAX Müller and Diedrich, 1991

Type species. Pseudospinax pusillus Müller and Diedrich, 1991.

Amended diagnosis. Heterodonty gradient monognathic and, in some species, dignathic or sexual. Labial face flat to slightly convex and oval in outline, being somewhat extended antero-distally. Small principal cusp triangular or reduced and rounded in some lateral teeth. This takes up less than half the width of the occlusal edge, which bears a distinct cutting margin. Lateral cusplets small and triangular, as poorly defined serrations, or absent and do not extend to the lateral edges of the crown. Lingual bulge well developed, especially in lateral files, and enameloid covered almost to base of the root. The hemiaulacorhize root is low and narrower than the crown.

Remarks. The tooth morphology of *Pseudospinax* is superficially rather similar to that of the anterior teeth of some species of *Protospinax* such as *P. annectans* Woodward, 1918 and *P. lochensteinensis* Thies, 1983, but may be distinguished by the lack of a concave labial surface, a lower root with more prominent lingual bulge and a less well defined uvula. The general tooth morphology appears simpler than that of other genera of hemiscylliids, but more closely resembles members of this family than that of other extant groups. It is possible, however, that Mesozoic orectolobids represent a suite of families whose dentition is only superficially similar to modern forms (Cappetta 1987).

It is likely that *Pseudospinax* contains a number of species referred to the genera *Hemiscyllium* or *Protospinax*. Species probably referable to this genus include: *Protospinax*? *muftius* Thies, 1983 from Callovian clays of Southern England, *Hemiscyllium hermani* Müller, 1989 from Campanian chalks of Germany and *Hemiscyllium* sp. of Herman 1982 from German Maastrichtian chalks. The referral of these additional taxa to *Pseudospinax* gives the genus a greatly increased range, from Callovian to Maastrichtian.

Pseudospinax heterodon sp. nov.

Plate 5, figures 3–10

Derivation of name. Refers to the wide range of tooth morphologies compared with other members of the genus.

Holotype. LIVCM 1998. 20. AL (Pl. 5, figs 5–7); Speeton: Hunstanton Formation, Dulcey Dock Member, bed DD 6 (upper Upper Albian).

Referred material. Two complete teeth; LIVCM 1998. 20. AJ–AK; and nine incomplete teeth and crowns; LIVCM 1998. 20. AM–AP.

Horizon and localities. Speeton: Hunstanton Formation, Speeton Beck Member, bed SB3 (lower Upper Albian) to Red Cliff Hole Member, bed RCH 5e (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Diagnosis. Very small teeth with labial face almost flat. Form of cusps and outline of crown variable due to monognathic and diagnathic/sexual heterodonty. Principal cusp is small and narrow, not exceeding length of labial face of crown and almost absent in some lateral files. Lateral cusplets small, not exceeding one-quarter of the length of the main cusp and often present as little more than serrations. Uvula wide, but poorly defined over a root far narrower than the crown.

Description. These small (less than 1 mm wide) teeth show a variation in crown shape that suggests both a graded monognathic heterodonty and a dignathic or possibly sexual heterodonty. The labial face of the crown varies from almost circular to strongly laterally expanded with the width being more than twice the height. The surface is flat, with no ornament and only a very slight convexity at the margins. The teeth can be divided into strongly and weakly cuspate forms, both of which show the same range of labial face morphologies. The weakly cuspate teeth have a single triangular cusp directed slightly distally. This cusp is as wide at the base as it is long, and forms up to one-third of the height of the crown. The remaining occlusal edge of the crown has a cutting edge and is smoothly convex in profile. In the more strongly cuspate teeth, the principal cusp is longer than wide, with a well-developed cutting edge. It is flanked by a pair of small lateral cusps that are usually rounded in profile. The lingual face of the crown is short and angled acutely to the occlusal edge. The root is hemiaulacorhize, rather low, and displaced strongly lingually. The lingual boss is prominent and has a thin enameloid covering. The lateral and basal foramina are large, but poorly visible in the specimens.

Remarks. The presence of strongly and weakly cuspate specimens with the same range of crown shapes suggests that the presence of elongate cusps is either a dignathic or possibly sexual feature, with both morphologies present in anterior and lateral files. This has not been recognized in other members of this genus, or in other Mesozoic orectolobids.

Family INCERTAE SEDIS

Genus ORECTOLOBOIDES Cappetta, 1977*b*

Orectoloboides parvulus (Dalinkevicius, 1935)?

Plate 6, figure 1

Material. One lateral and two anterior teeth, all broken; LIVCM 1998. 20. AQ.

Horizon and localities. Speeton: Speeton Clay, beds A4 and A5a (lower Lower Albian).

Description. All teeth are poorly preserved. As in material previously described from the Gault Clay (Albian) (Cappetta 1977*a*; Biddle 1993), the teeth have a slender principal cusp with up to two lateral cusplets on anterior teeth. The labial face of the crown has a small number of irregular longitudinal ridges which may connect with the occlusal edge in lateral teeth.

Genus CRETASCYLLIUM Müller and Diedrich, 1991

Cretascyllium sp.

Plate 6, figures 2–4

Material. One imperfect tooth; LIVCM 1998. 20. AR.

Horizon and localities. Speeton: Hunstanton Formation, Speeton Beck Member, bed SB12 (lower Upper Albian).

Description. The single tooth, 4·2 mm high, has a strongly triangular outline. The cusp is biconvex and relatively compressed linguo-labially and inclined lingually. It is fairly elongate, almost twice as high as wide, and only slightly concave edged. The curve of the edges of the cusp is continued along narrow and poorly developed lateral blades which project weakly labially and basally. The labial bulge is not well developed, being both narrow and compressed, and does not reach the base of the root. The hemiaulacorhize root is rather high and is not expanded lingually. There is no clearly differentiated lingual boss above a raised area toward the lingual apex of the root. The basal face of the root is very strongly excavated, with a large foramen on the basal face and lingual apex. There are numerous small foramina around the edge of the basal face.

Remarks. This tooth shows greatest similarity to teeth of *Cretascyllium expansum* Müller and Diedrich, 1991 from chalks of the German Cenomanian, but differs in having greatly reduced lateral blades, a straighter crown edge and a more gracile root.

Genus CRETORECTOLOBUS Case, 1978

Cretorectolobus gracilis sp. nov.

Plate 6, figures 5–9

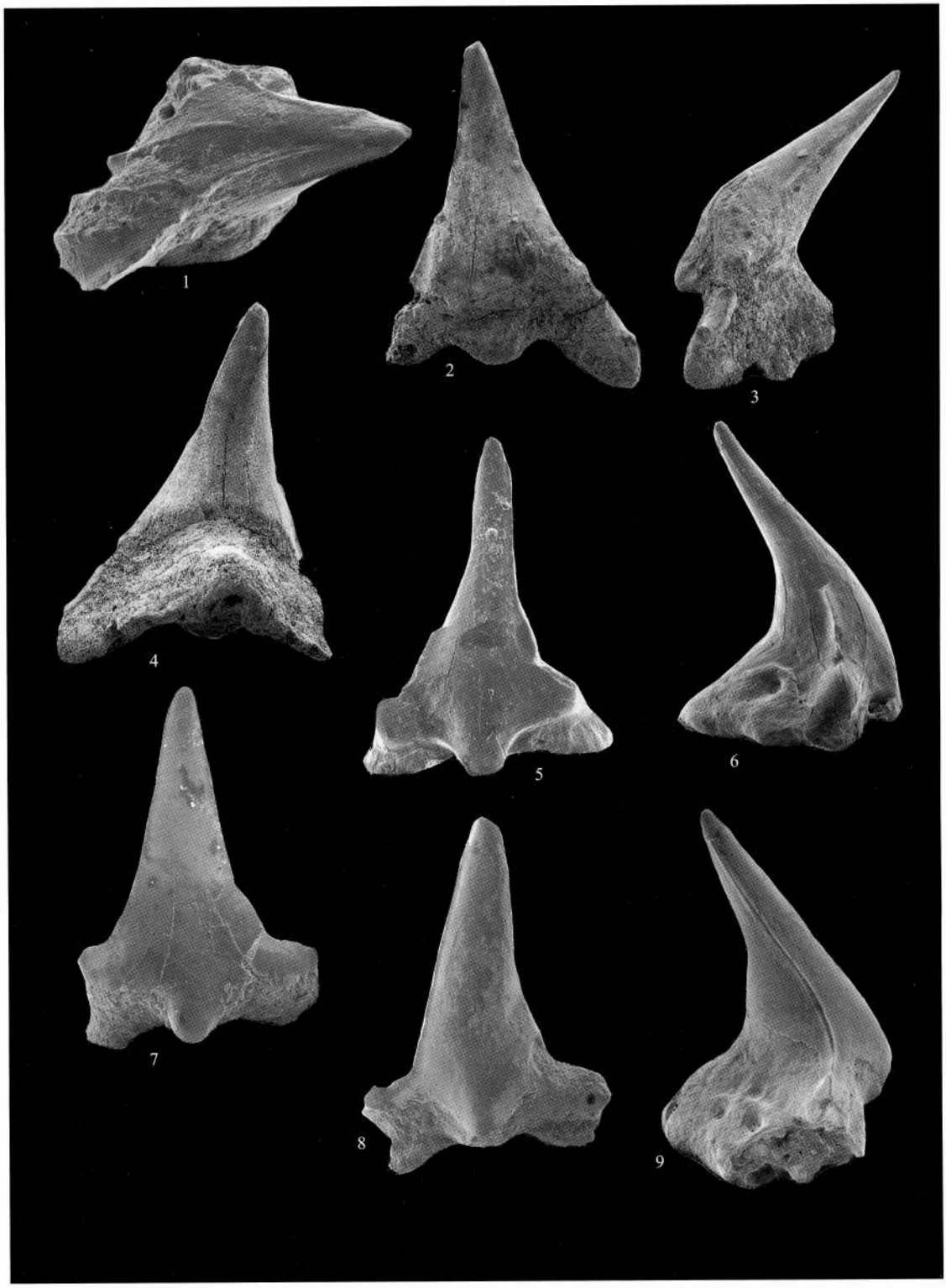
Derivation of name. Refers to the gracile and narrow form of the tooth.

EXPLANATION OF PLATE 6

Fig. 1. *Orectoloboides parvulus* (Dalinkevicius, 1935)?; LIVCM 1998. 20. AQ; Speeton Clay Formation; Speeton, bed A5A; lateral tooth, oblique lateral view, preserved height 0·8 mm.

Figs 2–4. *Cretascyllium* sp.; LIVCM 1998. 20. AR; Hunstanton Formation; Speeton, bed SB12; ?anterior tooth, height 2·3 mm. 2, labial view. 3, lateral view. 4, lingual view.

Figs 5–9. *Cretorectolobus gracilis* sp. nov.; Hunstanton Formation. 5–6, LIVCM 1998. 20. AS, holotype; South Ferriby, bed 6a; height 0·7 mm. 5, labial view; 6, lateral view. 7, LIVCM 1998. 20. AT; Speeton, bed SB4; labial view, height 1·5 mm. 8–9, LIVCM 1998. 20. AU; South Ferriby, bed 6a; height 1·5 mm. 8, labial view. 9, lateral view.



UNDERWOOD and MITCHELL, sharks' teeth

Holotype. LIVCM 1998. 20. AS (Pl. 6, figs 5–6); South Ferriby, Hunstanton Formation, Bed 6a (lower Upper Albian).

Referred material. Three moderately well preserved teeth and at least three partial teeth; LIVCM 1998. 20. AT–AU.

Horizon and localities. Speeton: Speeton Clay, bed A1B (upper Lower Albian) to Hunstanton Formation, Speeton Beck Member, bed SB 6 (lower Upper Albian).

Diagnosis. Small teeth with a single elongate cusp. Cusp narrow and only slightly compressed, with lingual curvature basally. Weak cutting edges continue over the tooth to the ends of the lateral blades. Lateral blades short, reaching lateral edges of root with incipient cusplets at extremities. Labial bulge small and rounded, reaching to base of root. Crown overhangs root labially. No well-developed lingual protuberance, enameloid does not reach lingual edge of root. Root low and hemiaulacorhize, and triangular basally. Basal face deeply excavated, and basal and lingual foramina large. Linguo-dorsal foramina well developed.

Description. The teeth are generally small (up to 3·2 mm high) and show a moderate heterodonty, with narrower anterior and wider lateral teeth. The cusps are bent lingually, but not distally to any degree. The unornamented cusp is triangular in labial view, only slightly compressed and with a small but continuously developed cutting edge. The labial boss is moderately developed, being rounded and inclined basally, giving the profile of the labial edge a rather pronounced curvature. The lateral blades are short and continue almost to the edge of the root. The ends of the lateral blades are bulbous in some specimens, giving the appearance of an incipient lateral cusplet. There is no true lingual protuberance. The root is thick, triangular in basal view and rather low lingually. The basal face is strongly excavated and a pair of large foramina is present on the basal face and at the lingual apex. There is a number of margino-lingual foramina and several on the basal face.

Remarks. In a review of Cretaceous 'squatiniform' orectolobids, Siverson (1995) recognized *Cretorectolobus olsoni* Case, 1978 as the only species of *Cretorectolobus*, other similar taxa being referable to *Cederstroemia* Siverson, 1995. *Cretorectolobus gracilis* sp. nov. is very similar in general morphology to *C. olsoni*, but differs in being generally narrower with less well developed lateral blades, resulting in a more piercing morphotype than the cutting/piercing form of the type species (Siverson 1995). The presence of *Cretorectolobus* in Albian sediments represents a far earlier occurrence than the Campanian age of the type species. It is possible that some lower Lower Cretaceous (e.g. Thies 1979) and Upper Jurassic (e.g. Thies 1983) teeth assigned to *Squatina* may be referable to *Cretorectolobus*, greatly extending the stratigraphical range of the genus.

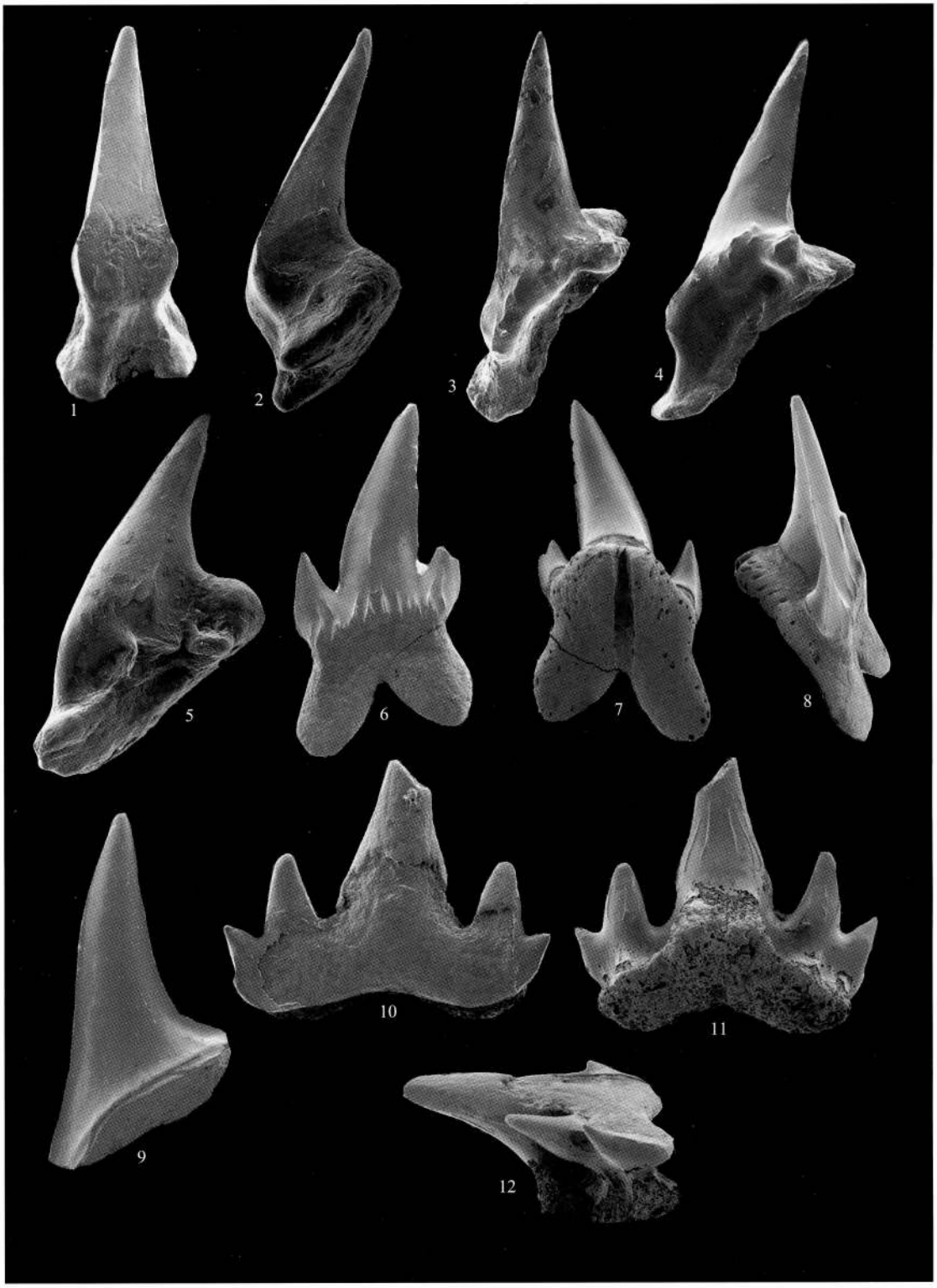
EXPLANATION OF PLATE 7

Figs 1–5. *Pararhincodon* cf. *lehmani* Cappetta, 1980*a*; Hunstanton Formation. 1–2, LIVCM 1998. 20. AV; Speeton, bed WC5; anterior tooth, height 0·7 mm. 1, labial view; 2, posterolateral view. 3–4, LIVCM 1998. 20. AW; South Ferriby, bed 6a; anterolateral tooth, height 1·2 mm. 3, labial view. 4, posterolateral view. 5, LIVCM 1998. 20. AX; South Ferriby, bed 6a; lateral tooth, posterolateral view, height 1·4 mm.

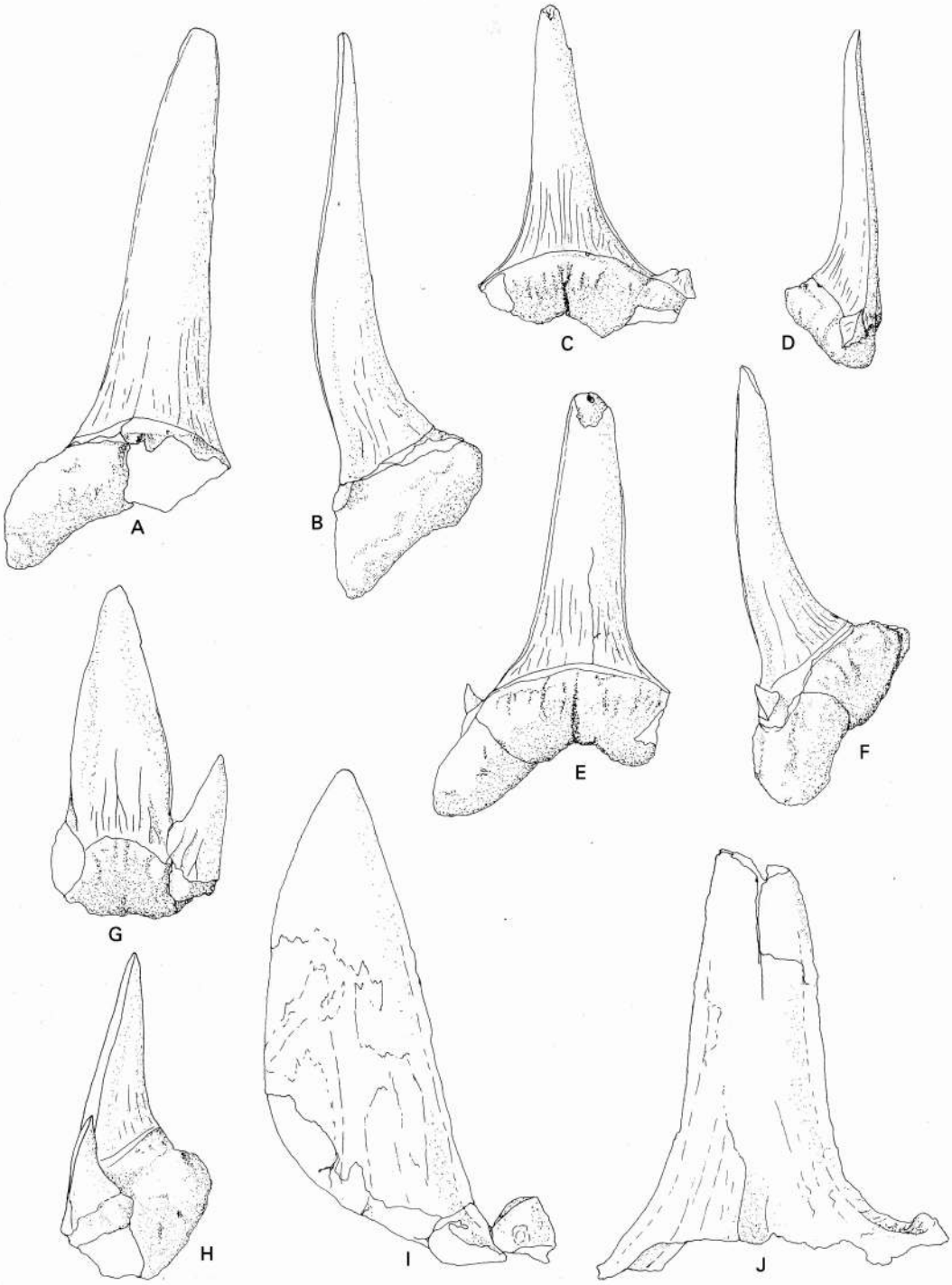
Figs 6–8. *Protolamna* sp.; LIVCM 1998. 20. AY; Hunstanton Formation; South Ferriby, bed 5b; anterolateral tooth, height 2·7 mm. 6, labial view. 7, lingual view. 8, lateral view.

Fig. 9. indet. lamniform.; LIVCM 1998. 20. AZ; Hunstanton Formation; South Ferriby, bed 4; typical specimen, lateral tooth, labial view, preserved height 4·4 mm.

Figs 10–12. Scyliorhinidae? gen. indet.; LIVCM 1998. 20. BA; Ferriby Formation; Speeton, Crowe's Shoot Member; ?anterior tooth, width 1 mm. 10, labial view. 11, lingual view. 12, lateral view.



UNDERWOOD and MITCHELL, sharks' teeth



TEXT-FIG. 6. A–B, *Anomotodon principalis* Biddle, 1993, *non* Cappetta, 1975; LIVCM 1998. 20. BS; Hunstanton Formation; Speeton, bed WC6; anterior tooth, height 12 mm; A, lingual view; B, lateral view. C–F, *Scapanorhynchus praerhaphiodon* Sokolov, 1978?; Hunstanton Formation. C–D, LIVCM 1998. 20. BT;

Family PARASCYLLIIDAE Gill, 1862

Genus PARARHINCODON Herman, *in* Cappetta, 1976

Pararhincodon cf. *lehmani* Cappetta, 1980*a*

Plate 7, figures 1–5

Material. Four moderately to well preserved teeth; LIVCM 1998. 20. AV–AX.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, beds WC 1 and WC 5 (upper Upper Albian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Description. The anterior tooth is very small and antero-distally compressed. The single cusp is bent lingually, its labial face being almost flat and separated from the strongly convex lingual face by a cutting edge which dies out near the tip of the cusp. The low root is hemiaulacorhize with poorly developed lobes. There is a pair of very prominent lateral foramina. The lateral teeth are rather more massive, the cusp being biconvex and rather wide at the base. The cusp is twisted distally and has a small shoulder at its base on the proximal side. The base of the crown is rather bulbous, with an ornament of fine to very fine irregular ridges. This overhangs a constriction at the contact with the low root. The root is bifid, but with a reduced anterior lobe. The lateral foramina are very prominent.

Remarks. The gracile nature of these teeth and the strong overhang of the crown suggest a closer affinity to *Pararhincodon lehmani* Cappeta, 1980*a*, from the Cenomanian of Lebanon than to *P. crouchardi* Herman, 1977, from the uppermost Cenomanian and Turonian of Belgium. The degree of heterodonty in *P. lehmani*, however, appears to be rather less than in this material, and so it is possible that a new species is represented. These specimens represent the oldest known occurrence of *Pararhincodon*. There is some doubt as to whether the Cretaceous and Tertiary species referred to *Pararhincodon* belong within the same genus (D. Ward, pers. comm.), and it is therefore possible that the Cretaceous species may represent a new genus.

Order LAMNIFORMES Berg, 1958

Remarks. Although often very common, lamniform teeth tend to be poorly preserved compared with other taxa. They generally lack a root and are commonly split longitudinally. It is therefore likely that although lamniforms were as diverse a part of the assemblage as in the Cretaceous elsewhere (e.g. Biddle 1993), the diversity recorded from the Hunstanton Formation is restricted by the number of identifiable specimens. Most of these better specimens were recovered by surface collection from the upper parts of the Speeton section, and, consequently, any species present prior to the terminal Albian are unlikely to be represented. Although several taxa could be identified from this material, the state of preservation makes it unlikely that any new information will be gained regarding the species concerned.

Family MITSUKURINIDAE Jordan, 1898

Remarks. Due to the homeomorphic nature of lamniform teeth, it is possible that a large proportion of the Cretaceous tooth taxa conventially placed within the Mitsukurinidae belongs to members of the Odontaspididae or Carcharinidae.

Speeton, bed WC2; lateral tooth, preserved height 7·2 mm; C, lingual view; D, lateral view. E–F, LIVCM 1998. 20. BU; Speeton, bed WC3, anterior tooth, height 10·5 mm; E, lingual view; F, lateral view. G–H, *Leptostyrax* sp.; LIVCM 1998. 20. BV; Hunstanton Formation; Speeton, bed DD19; anterior tooth, preserved height 5·5 mm; G, labial view; H, lateral view. I, *Pseudisurus* sp.; LIVCM 1998. 20 BW; Hunstanton Formation; Speeton, bed WC4; lingual view, preserved height 21 mm. J, *Cretoxyrhina mantelli* (Agassiz, 1843)?; LIVCM 1998. 20. BX; Hunstanton Formation; Speeton, bed RCH1a/b; lingual view, preserved height 10 mm.

Genus ANOMOTODON Arambourg, 1952

Anomotodon principalis Biddle, 1993, *non* Cappetta, 1975

Text-figure 6A–B

1993 *Anomotodon principalis* Cappetta 1975; Biddle, p. 204, pl. 3, figs 5–8.

Material. One broken anterior tooth and two crowns; LIVCM 1998. 20. BS.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, beds WC 1 and WC 6 (upper Upper Albian).

Description. The crown is high and narrow, being rather linguo-labially compressed distally, and shows a slight sigmoidal curvature. Ornament is very poorly developed, with approximately three pairs of faint, somewhat flexuous folds near the edges of the lingual face. There are no lateral cusplets and no significant crown tongue of enameloid extending along the top of the root. The preserved root branch is rather short and bulbous, with a well-developed lingual protuberance.

Remarks. Although the tooth is rather similar to specimens from the Gault Clay (Lower to Middle Albian) referred to *Anomotodon principalis* Cappetta, 1975, by Biddle (1993), both this specimen and the material figured by Biddle differ from the type material of *A. principalis* by the lack of a well-developed, and regular, lingual ornament and by the presence of more gracile root branches.

Genus SCAPANORHYNCHUS Woodward, 1889

Scapanorhynchus praeraphiodon Sokolov, 1978? *sensu* Biddle 1993

Text-figure 6C–F

Material. Two identifiable specimens; LIVCM 1998. 20. BT–BS; isolated cusps probably assignable to this taxon are common.

Horizon and localities. Speeton; Hunstanton Formation, Weather Castle Member, beds WC 2 and WC 3 (upper Upper Albian). Isolated cusps assignable to this species are present throughout the Hunstanton Formation at South Ferriby and more rarely within the Dulcey Dock and Weather Castle members at Speeton.

Description. The main cusp is high and slender, with a narrow, but well-developed, cutting edge. The labial face is almost flat, the convexity of the lingual face being greater in the anterior teeth than in the laterals. Ornament is restricted to a series of slight folds in the lower third of the lingual face. These are more strongly developed and straighter in the lateral teeth. A pair of small lateral cusplets is present on a poorly developed crown tongue. The root branches are strongly divergent, and a strong lingual protuberance is present in the anterior teeth. The nutritive groove is strongly developed.

Remarks. The specimens figured here correspond very closely to the teeth figured as ?*Scapanorhynchus praeraphiodon* by Biddle (1993), although it is unclear whether this is synonymous with *Scapanorhynchus praeraphiodon sensu* Sokolov 1978, as the taxonomy of this taxon is confused by poorly preserved type material and incorrect referral of subsequent specimens (Siverson 1992; Biddle 1993). This is further complicated by the possible synonymy with *Carcharias tenuis* (Davis, 1890), which was discussed in detail by Siverson (1992). As we have not studied the type material involved, further comment cannot be made here.

Family CRETOXYRHINIDAE Glückman, 1958

Genus PSEUDISURUS Glückman, 1957 *sensu* Siverson 1996

Pseudisurus sp.

Text-figure 6L

Material. One poorly preserved specimen; LIVCM 1998. 20. BW.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, bed WC 4 (upper Upper Albian).

Description. The single specimen has a straight, robust principal cusp with somewhat convex cutting edges and a short and robust triangular lateral cusplet. This is the largest tooth found in the Hunstanton Formation, with a crown length of 21 mm.

Genus CRETOXYRHINA Glückman, 1958

Cretoxyrhina mantelli (Agassiz, 1843)?

Text-figure 6J

Material. Two crowns; LIVCM 1998. 20. BX.

Horizon and localities. Speeton: Hunstanton Formation, Red Cliff Hole Member, bed RCH la/b (lower Lower Cenomanian).

Description. The unornamented cusp is elongate and straight-sided, flaring at the base to form short lateral blades. The cusp is biconvex, but rather compressed, with no ornament other than a slight groove near the base of the lingual face. The preserved lateral flare of the crown has a compressed, incipient cusplet at its termination.

Remarks. Although present only as isolated cusps, the shape of the cusp and blade-like form of the lateral cusplets allow tentative referral to this species.

Genus LEPTOSTYRAX Williston, 1900 *sensu* Cappetta 1987

Leptostyrax sp.

Text-figure 6G–H

Material. Two rather poorly preserved teeth and numerous isolated cusps of similar morphology; LIVCM 1998. 20. BV.

Horizon and localities. Speeton: Hunstanton Formation, Dulcey Dock Member, bed DD 19 and Weather Castle Member, bed WC 6 (upper Upper Albian).

Description. Each tooth consists of a short main cusp with (probably) a single pair of robust lateral cusplets over a bulbous root. The main cusp is straight and weakly convex labially, but more strongly so lingually. The cutting edge is well developed on both this and the single preserved lateral cusplet. The lateral cusplet is of a similar shape to the main cusp, and over half its length, but is inclined in a slightly more labial plane. The basal third of the cusps is ornamented on the labial side by small folds. These are sharp-edged, irregular and occasionally bifurcate. Ornament on the lingual face is restricted to a few very fine, parallel ridges. The root is not well preserved on any specimen, but is obviously robust and swollen lingually. There is no sign of a nutritive groove.

Remarks. Although *Leptostyrax* has often been recorded from the Albian of Europe (e.g. Biddle 1993), these specimens differ from the type material, and probably represent a species of *Protolamna* (Cappetta 1987). The Hunstanton Formation specimens more closely resemble the type material of *Leptostyrax* in both crown and root morphology, and as such represent the earliest European occurrence of *Leptostyrax sensu* Cappetta (1987).

Genus. cf. PROTOLAMNA Cappetta, 1980*b*

cf. *Protolamna* sp.

Plate 7, figures 6–8

Material. One well preserved tooth; LIVCM 1998. 20. AY.

Horizon and localities. South Ferriby: Hunstanton Formation, bed 5b (lower Upper Albian).

Description. The main cusp is relatively short, but sharp, with well-developed cutting edges and is inclined slightly to the rear. The labial face is slightly convex, becoming flat at the base; the lingual face remaining convex throughout, especially towards the base. The single pair of lateral cusplets are relatively well developed and lie in the same plane as the main cusp. Ornament is developed as a series of short and widely spaced sharp-edged folds, some bifurcate, on the basal part of the labial face of all cusps. The lingual face is unornamented. The root is large and strongly bilobate. The basal face is slightly concave and has a very prominent nutritive growth groove with a foramen at the lingual end. The margins of the basal face, especially lingually, are strongly marked by small foramina. The root lobes are long and rounded terminally, but are strongly flattened.

Remarks. This species has a similar overall morphology to *Protolamna sokolovi* Capetta, 1980*b*, but differs from it in several aspects of crown and root morphology, having a stronger crown ornament, flatter lingual face to the root and a wider nutritive groove. It shows stronger overall similarities to *Pseudodontaspis herbsti* Case, 1987, from the American Campanian, from which it differs in the possession of uncontorted lateral cusps and an unornamented nutritive groove. Additional material is required before this species can be fully described and its affinities resolved.

Family indet.

Plate 7, figure 9

Materials. Several hundred isolated and broken cusps; LIVCM 1998. 20. AZ.

Horizon and localities. Many levels at Speeton and especially common at all sampled horizons at South Ferriby.

Description. Although many of the isolated lamniform cusps fall within the range of morphology of the taxa described above, most exhibit morphologies suggesting the presence of other taxa. These are generically indeterminate and could represent species of genera such as *Eostratolamia*, *Paranomotodon*, *Carcharias* and *Archaeolamna*. Although variable in morphology, many of these isolated cusps (1–5 mm high) show a gracile cutting/piercing morphology and are either unornamented or possess a faint series of ridges on the labial face.

Order CARCHARHINIFORMES Compagno, 1973

Remarks. The teeth of scyliorhinids and similar forms are generally uncommon, but the material present suggests a low abundance, high diversity fauna. As well as the species described below, there are several poorly preserved crowns that do not appear to belong to any of these taxa. It is probable therefore that true 'scyliorhinid' diversity was even higher.

Family SCYLIORHINIDAE Gill, 1862?

Scyliorhinidae? gen. indet.

Plate 7, figures 10–12

Material. One ?anterior tooth, complete except for some exfoliation of the labial face; LIVCM 1998. 20. BA.

Horizon and localities. Speeton; Ferriby Formation, Crowe's Shoot Member, about 0·5 m above base (lower Lower Cenomanian).

Description. A very small tooth, 1 mm wide. The labial face of the crown is flat with a concave basal edge which overhangs the root, and appears to be unornamented. There is a robust principal cusp which is round in section and ornamented with five fine ridges on the lingual side. This is flanked by two pairs of well-developed lateral cusplets. The inner pair are rather elongate and bear the same ornament as the principal cusp. The outer pair are more triangular in profile and have a weak cutting edge. They are unornamented and slightly curved labially. The shallow root is hemiaulacorhize, with the nutritive groove closed over lingually, but open labially. The strongly divergent root branches are poorly developed and flat-based.

Remarks. This tooth is closest in respect of its morphology to teeth of members of the Scyliorhinidae, but bears little resemblance to any known scyliorhinid genus. The labial crown overhang may suggest orectolobid affinities, and it is possible that this represents a morphology intermediate between the Hemiscyllidae and Parascylliidae, but these affinities will probably not be clarified until more material is obtained.

Genus PROTOSCYLIORHINUS Herman, 1977?

Protoscyliorhinus? sp.

Plate 8, figures 1–3

Material. Eight incomplete teeth; LIVCM 1998. 20. BB–BC.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR7 and Speeton Beck Member, bed SB 6 (lower Upper Albian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Description. The teeth are all very small, up to 0·9 mm in crown height. The crown consists of a single cusp above the narrow crown tongues. The triangular cusp is slender, elongate and flattened at the tip, but with a deep lingual face basally. In the more anterior teeth, the crown widens steadily from the cusp along the crown tongues with no lateral cusplets or shoulders. In more lateral teeth, poorly developed shoulders may be present, especially on the distal side. A cutting edge is present almost to the base of the crown tongues. The crown is unornamented, other than occasional incipient ridges on the basal part of the labial face. The root is poorly preserved in all specimens, but appears hemiaulacorhize.

Remarks. These teeth are referred to *Protoscyliorhinus* because of their overall similarity to laterally compressed teeth of *P. lamaudi* Biddle and Landemaine, 1988. It is possible, however, that these teeth represent a genus of parascylliid, but the available material is not sufficiently well preserved to resolve clearly the affinities of this species.

Family SCYLIORHINIDAE Gill, 1862

Remarks. The generic affiliation of most Mesozoic scyliorhinids is very poorly known, and the majority has been placed within the extant genus *Scyliorhinus* de Blainville, 1816. So far, reassignment to other genera has been hampered by the lack of information on the dentitions of modern scyliorhinids (Halter 1994).

Genus SCYLIORHINUS de Blainville, 1816 *sensu lato*

'*Scyliorhinus*' *dubius* (Woodward, 1889)

Plate 8, figure 4

Material. Two anterior tooth crowns; LIVCM 1998. 20. BD.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR7 (lower Upper Albian) and Ferriby Formation, bed SLC11C (lower Middle Cenomanian).

Description. The principal cusp is elongate and accompanied by at least one elongate, but gracile, lateral cusp. Poorly developed cutting edges are present on both cusps. There is almost no ornament.

Remarks. Despite the poor preservation, these specimens compare favourably with the anterior tooth of the holotype specimen (Cappeta 1977*a*, fig. 5).

Genus CRETASCYLIORHINUS gen. nov.

Derivation of name. From the common and widespread occurrence of this genus in Cretaceous rocks.

Type species. *Scyliorhinus destombesi* Cappetta, 1977*b*.

Diagnosis. Scyliorhinid teeth of generally robust form. Crown of main cusp and a single pair of well-developed lateral cusplets that are relatively symmetrical in both anterior and lateral teeth. Main cusp short and robust, only slightly oval in cross section with poorly developed cutting edges. Lateral cusps similar and very weakly divergent. Labial ornament usually present as straight, regularly spaced folds which occasionally bifurcate towards base of crown and reach almost to the cusp apex. Lingual ornament absent or as fine ridges. Crown strongly overhangs root labially. Root compact and flat-based with flared lateral lobes to give basal face a 'heart-shaped' profile. Vascularization hemiaulacorhize with nutritive groove covered, except for distinct notch at labial end.

Remarks. *Cretascyliorhinus* is distinctly different from *Scyliorhinus*, from which it may readily be distinguished by the presence of well-developed lateral cusplets on lateral teeth and the absence of a massive lingual root protuberance (Halter 1994). It cannot be readily accommodated within any of the extant scyliorhinid subfamilies, and thus probably represents an extinct group. At present, *Scyliorhinus destombesi* Cappetta, 1977*b*, *S.* cf. *destombesi* of Müller and Diedrich (1991) and *S.* aff. *destombesi* of Müller (1989) are referred to *Cretascyliorhinus*; thus this genus ranges from Lower Albian to Campanian.

Cretascyliorhinus destombesi (Cappetta, 1977*b*)

Plate 8, figures 5–7

Material. Thirty-six teeth, ranging from well to poorly preserved; LIVCM 1998. 20. BE–BF.

Horizon and localities. Speeton: Speeton Clay, basal bed A1 (Lower Albian) to Hunstanton Formation, Red Cliff Hole Member, bed RCH 4a (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, beds 3/4 to 6b (lower Upper Albian).

Description. Teeth with a rather robust principal cusp and a single pair of well-developed lateral cusplets. The ornament is variable, but generally consists of prominent widely spaced longitudinal ridges on both faces, especially the labial face, of all cusps. These ridges rarely bifurcate, except at the extreme base of the crown. In some smaller teeth, these may be largely absent on the main cusp. The root is rather massive and hemiaulacorhize. The basal face is flat and flared, especially so on the short root branches.

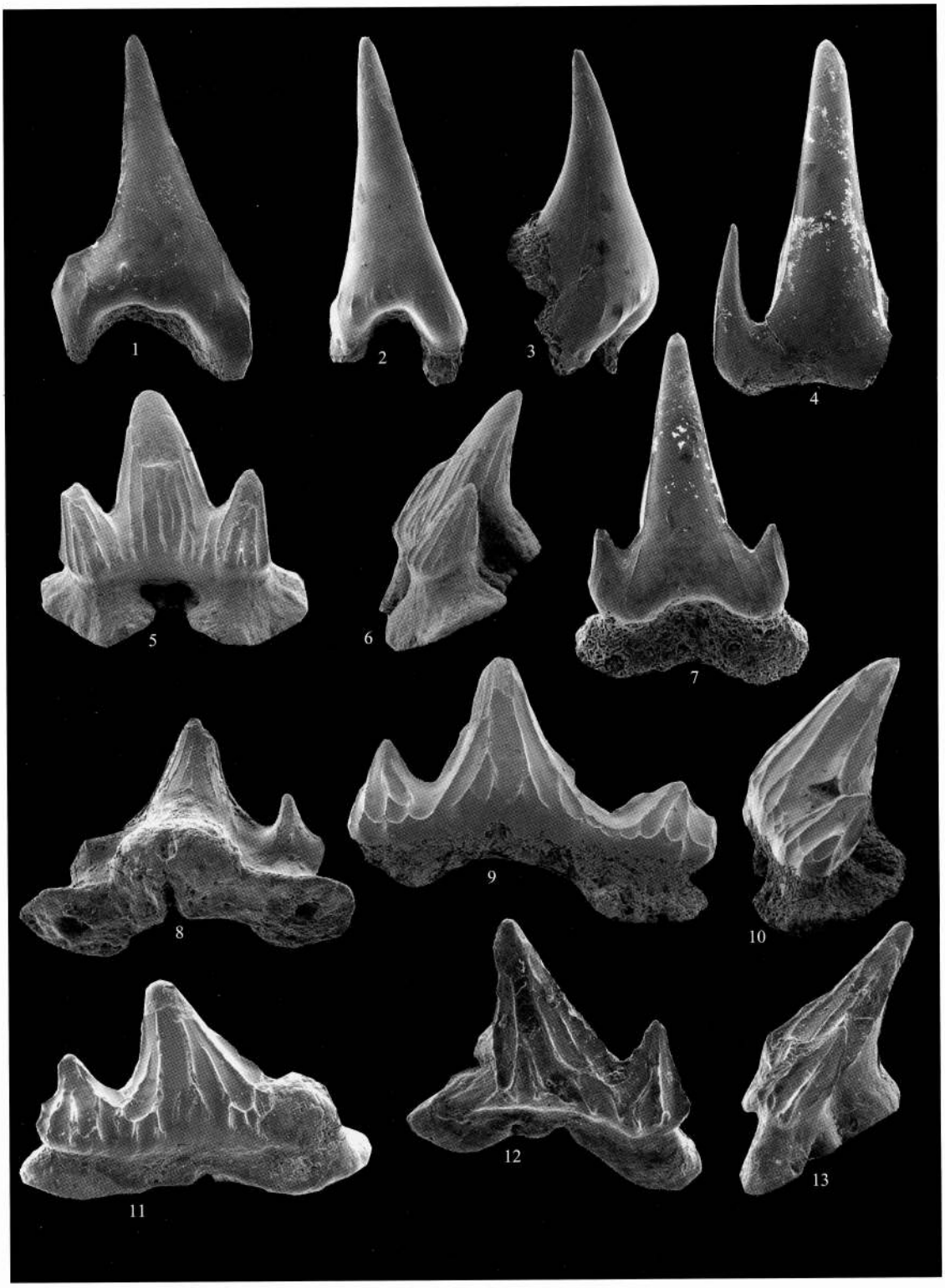
EXPLANATION OF PLATE 8

Figs 1–3. *Protoscyliorhinus*? sp.; Hunstanton Formation. 1, LIVCM 1998. 20. BB; Speeton, bed QR7; lateral tooth, labial view, preserved height 0·8 mm. 2–3, LIVCM 1998. 20. BC; South Ferriby, bed 6a; anterior tooth, preserved height 1 mm. 2, labial view. 3, lateral view.

Fig. 4. '*Scyliorhinus*' *dubius* (Woodward, 1889); LIVCM 1998. 20. BD; Hunstanton Formation; Speeton, bed QR7; partial anterior tooth, labial view, preserved height 0·9 mm.

Figs 5–7. *Cretascyliorhinus destombesi* (Cappetta, 1977*b*); Hunstanton Formation. 5–6, LIVCM 1998. 20. BE; Speeton, bed RCH1c; lateral tooth, height 1·3 mm. 5, labial view. 6, lateral view. 7, LIVCM 1998. 20. BF; Speeton, bed SB6; anterior tooth, labial view, height 0·7 mm.

Figs 8–13. *Parasymbolus reticularis* sp. nov.; Hunstanton Formation. 8, LIVCM 1998. 20. BG; South Ferriby, bed 6a; lateral tooth, lingual view, width 0·84 mm. 9–10, LIVCM 1998. 20. BH; South Ferriby, bed 5b; lateral tooth, width 1·1 mm. 9, labial view. 10, lateral view. 11, LIVCM 1998. 20. BJ, holotype; South Ferriby, bed 6a; lateral tooth, labial view, width 0·78 mm. 12–13, LIVCM 1998. 20. BK; South Ferriby, bed 6b/7; juvenile anterolateral tooth, width 0·5 mm. 12, labial view. 13, lateral view.



UNDERWOOD and MITCHELL, sharks' teeth

Genus PARASYMBOLUS Candoni, 1993

Parasymbolus reticularis sp. nov.

Plate 8, figures 8–13

Derivation of name. From the reticulate ornament on the labial face of the crown.

Holotype. LIVCM 1988. 20. BJ (Pl. 8, fig. 11); South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Referred material. Five teeth, four fairly well preserved; LIVCM 1998. 20. BG–BH, LIVCM 1998. 20. BK.

Horizon and localities. South Ferriby: Hunstanton Formation, beds 5b, 6a and 6b/7 (lower Upper Albian).

Diagnosis. Crown with main cusp and single pair of lateral cusplets. Shoulders suggestive of an incipient second pair of lateral cusplets may be present. All cusps are robust and biconvex with a well-developed cutting edge. Labial ornament is strong, with four to six main folds on the main cusp, and two or three on the laterals which reach almost to the apex. Basally, the folds bifurcate and form reticulate patterns across the width of the tooth. The lingual ornament consists of three to six fine ridges on the main cusp, and up to three on the lateral cusplets, which rarely bifurcate. The base of the crown is broad and overhangs the root labially. The root is low and flat-based, with a well-developed lingual bulge. The root lobes are strongly divergent and flared, with a flared base at the labial end bearing large basal foramina. The nutritive groove is open labially, but covered lingually in adults, and is probably open in juveniles.

Description. These small (up to 1·1 mm wide) teeth are very distinctive due to the strong ornament and flared root lobes. The triangular principal cusp is flanked by a single pair of prominent lateral cusps of similar shape, which, in some specimens, have a shoulder or incipient outer lateral cusp on either the mesial or posterior side. In some specimens one of the lateral cusps is poorly developed and rather rounded. There is a well-developed cutting edge along the occlusal edge of the tooth, reaching to the top of the root laterally. The ornament is strong on the labial face of the cusps, with spaced, sharp-edged folds reaching almost to the tip of both the main and lateral cusplets. Towards the base, this ornament bifurcates in an irregular manner, connecting the ridges to form a continuous band of reticulation across the base of the labial face of the crown. This reticulation is less evident in the juvenile tooth. Ornament on the lingual faces consists of regularly spaced fine ridges extending to the tips of the cusps, but rarely bifurcating. The root is low, but with a broad basal face that is flared below the lingual boss and below the extremities of the root branches. Although hemiaulacorhize, the nutritive groove is only closed over along its lingual half. An imperfectly preserved root of a juvenile tooth (0·5 mm wide) shows a completely open nutritive groove. Small foramina are abundant along the labial and lingual faces of the root.

Remarks. The genus *Parasymbolus* Candoni, 1993 was erected for *P. octevillensis* Candoni, 1993 from the French Upper Jurassic. *Parasymbolus reticularis* sp. nov. very closely resembles the type

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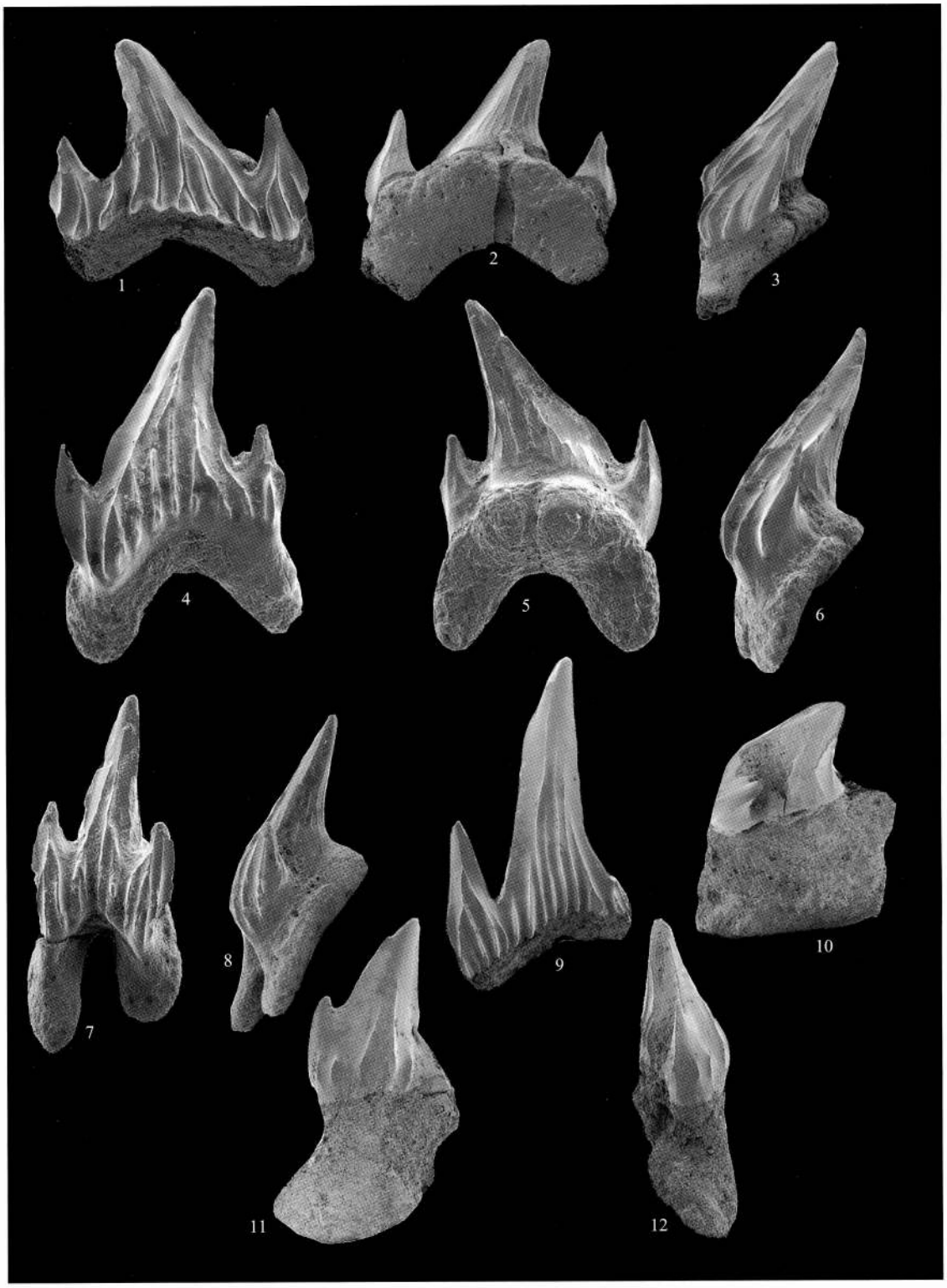
EXPLANATION OF PLATE 9

Figs 1–9. *Pteroscyllium ornatum* sp. nov.; Hunstanton Formation. 1–3, LIVCM 1998. 20. BL, holotype; Speeton, bed WC1; lateral tooth, height 2 mm. 1, labial view. 2, lingual view. 3, lateral view. 4–6, LIVCM 1998. 20. BM; Speeton, bed QR7; anterolateral tooth, height 1·3 mm. 4, labial view. 5, lingual view. 6, lateral view. 7–8, LIVCM 1998. 20. BN; Speeton, bed SB4; anterior (?parasymphyseal) tooth, height 2·1 mm. 7, labial view. 8, lateral view. 9. LIVCM 1998. 20. BP; South Ferriby, bed 5b; partial anterior tooth, labial view, preserved height 1·9 mm.

Figs 10–12. Galeomorph gen. et sp. indet.; Hunstanton Formation. 10. LIVCM 1998. 20. BQ; Speeton, bed WC5; ?lateral tooth, ?oblique lateral/lingual view, height 1·1 mm. 11–12, LIVCM 1998. 20. BR; Speeton, bed WC1; ?anterior tooth, height 1·6 mm. 11, ?labial view. 12, lateral view.



UNDERWOOD and MITCHELL, *Pteroscyllium*, indet. galeomorph

species in overall morphology of the crown and root, as well as in possessing a similar ornament of sharp-edged ridges on the labial face of the crown and fine ridges on the lingual face, but differs largely in possessing a generally lower and wider crown with a reticulate ornament at the base of its labial face. The root vascularization differs in that the nutritive groove is closed over in juveniles of *P. octevillensis*. The presence of *P. reticularis* sp. nov. in the Hunstanton Formation extends the range of this genus from the Kimmeridgian to the Albian. Scyliorhinids probably referable to *Parasymbolus* are also present in the British Oxfordian and Bathonian (CJU, pers. obs.), suggesting that it was a long-lived genus ranging throughout the Mid Jurassic to Early Cretaceous.

Genus PTEROSCYLLIUM Cappetta, 1980*a*

Pteroscyllium ornatum sp. nov.

Plate 9, figures 1–9

Derivation of name. From the ornate ornament on the teeth.

Holotype. LIVCM 1998. 20. BL (Pl. 9, figs 1–3); Speeton: Hunstanton Formation, Weather Castle Member, bed 1 (lower Lower Cenomanian).

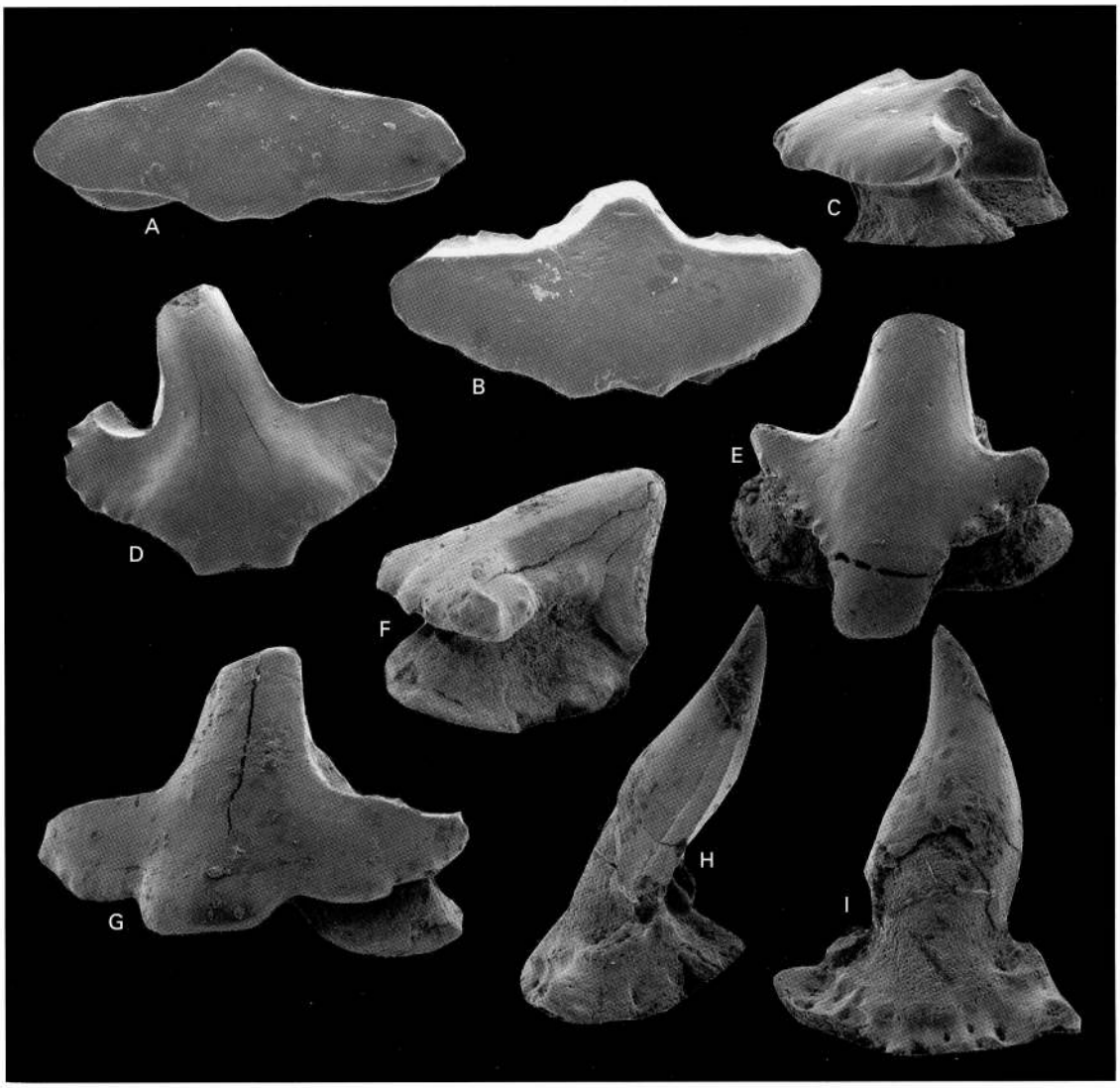
Referred material. Ten poorly to well preserved teeth; LIVCM 1998. 20. BM–BP.

Horizon and localities. Speeton: Hunstanton Formation, Speeton Beck Member, bed SB 1 (lower Upper Albian) to Red Cliff Hole Member, bed RCH 1c (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, beds 5b and 6a (lower Upper Albian).

Diagnosis. Relatively heterodont form with a single pair of prominent lateral cusplets. Cusps strongly biconvex with well-developed cutting edges. Strong labial ornament of spaced bifurcating folds reaching almost to the apex of the cutting edge. Finer lingual ornament of spaced and discontinuous longitudinal ridges, only rarely bifurcating. The root is large with a wide nutritive groove and somewhat concave basal face.

Description. This species includes the largest scyliorhinid teeth recovered during this study (up to more than 4·5 mm high). The tooth shape varies from as wide as high in lateral teeth to the height being 2·5 times the width in anterior teeth. The principal cusp is robust, but sharply pointed, and often curved posteriorly, with a single pair of large lateral cusplets, generally of equal size. There is a very strong cutting edge over all three cusps. The labial face of the crown is ornamented with prominent, somewhat sinuous, longitudinal folds which reach almost to the cusp tips and generally bifurcate towards the base. The lingual face is ornamented with weaker, more closely spaced ridges that are discontinuous and rarely bifurcate. The root is low with a rather concave basal face. The root branches are variable in length, but are rarely wider than the crown and are oval in cross section. Vascularization is holoaulacorhize, with a well-developed nutritive groove. Small foramina are abundant across the root.

Remarks. Pteroscyllium was initially defined on the basis of two species (*P. dubertreti* and *P. signeuxi*) represented by complete skeletal remains with well preserved dentitions from the Lebanese Santonian (Cappetta 1980*a*). The teeth of *P. ornatum* are similar in overall morphology to the teeth of the Lebanese specimens, which have well-developed lateral cusplets, strong and anastomosing labial crown ornament and a curved root basal face with very prominent nutritive groove. *P. ornatum* possesses a coarser and more widely spaced crown ornament than either of the Lebanese taxa, as well as having wider and flatter root branches than *P. dubertreti* Cappetta, 1980*a*, and a less prominent lingual root protuberance than *P. signeuxi* Cappetta, 1980*a*. *P. ornatum* resembles *P. nolfi* Müller and Diedrich, 1991, from German Cenomanian chalks, but differs from it in several ways. The labial ridges of *P. nolfi* are more gracile and closely spaced than in *P. ornatum*, rarely reaching nearer to the apex of the cusps and only occasionally bifurcating near the base of the



TEXT-FIG. 7. A–E, *Squatirhina thiesi* Biddle, 1993; Hunstanton Formation. A, LIVCM 1998. 20. BY; South Ferriby, bed 4; tooth of small juvenile, labial view, width 0·7 mm. B–C, LIVCM 1998. 20. BZ; South Ferriby, bed 6a; juvenile tooth, width 0·8 mm; B, labial view; C, lateral view. D, LIVCM 1998. 20. CA; South Ferriby, bed 5b; adult lateral tooth, width 1·3 mm. E, LIVCM 1997. 51. G; Speeton, bed RCH3; adult anterior tooth, width 1·1 mm. F–G, *Squatirhina*? sp.; LIVCM 1998. 20. CJ; Hunstanton Formation; Speeton, bed RCH1f; ?juvenile tooth, width 0·56 mm; F, labial view; G, lateral view. H–I, Sclerorhynchoide gen. et sp. indet.; LIVCM 1998. 20. CB; Hunstanton Formation; Speeton, bed RCH4a; rostral tooth, height 1·3 mm; H, lateral (?anterior) view; I, dorsal view.

crown. The lingual ornament of *P. nolfi* is stronger and the ridges more closely spaced and continuous, whereas the root branches of *P. nolfi* are generally less massive and with a narrower basal face than in *P. ornatum*. A poorly preserved specimen of *Pteroscyllium* from the Hythe Beds (Aptian) of southern England (Batchelor and Ward 1990) has very widely spaced labial ridges and may represent an undescribed species.

Galeomorphii *incertae sedis*

Plate 9, figures 10–12

Material. Two imperfect teeth; LIVCM 1998. 20. BQ–BR.

Horizon and localities. Speeton: Hunstanton Formation, Weather Castle Member, beds WC 1 and WC 7 (upper Upper Albian).

Description. These teeth bear little resemblance to known Cretaceous taxa, but are too poorly preserved to serve as a basis for a new taxon. The teeth are small (up to 1·7 mm high) and consist of a linguo-labially flattened crown above a rather featureless root of similar height. The crown consists of a principal cusp which seems to be curved labio-posteriorly, and a small, probably mesial, cusplet. In both specimens, the position of a potential second cusplet is broken. The root is massive and compressed and appears anaulacorhize. The supposed basal face is at a low angle to the crown, and the lingual face of the root in one specimen has a prominent foramen.

Remarks. The presence of more than one tooth of the same type in a relatively unfossiliferous unit suggests that this does not simply represent a malformed tooth. Among Cretaceous selachians with an anaulacorhize root, none is known to have a crown of this morphology. Among living sharks, this general tooth shape (small, conical crown and massive root) is possessed by filter feeding taxa in which the root is secondarily anaulacorhize. It is possible, therefore, that these teeth represent a filter feeding species of unknown affinities.

Superorder BATOMORPHII Cappetta, 1980*a*
Order RAJIFORMES Berg, 1940
Family RHINOBATIDAE Müller and Henle, 1839

Genus SQUATIRHINA Casier, 1947

Squatirhina thiesi Biddle, 1993

Text-figure 7A–E

Material. Ten complete and partial teeth including those of juveniles; LIVCM 1998. 20. BY–CA, LIVCM 1997. 51. G.

Horizon and localities. Speeton: Speeton Clay Formation, bed A1A (lower Middle Albian) and Hunstanton Formation, Red Cliff Hole Member, bed RCH 3 (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, beds 3/4, 5b and 6a (lower Upper Albian).

Description. In the teeth of adults the crown consists of an elongate cusp with a cutting edge only in lateral teeth. At the base the crown is flared laterally, and is distinctly pectinate along its labial edge with a sharply angled lingual edge. The labial apron is well developed and the root is high and strongly bifid with a large nutritive groove. The smallest teeth, presumably of juveniles, have a poorly developed cusp and labial apron, and a distinctly lozenge-shaped crown. In larger specimens the angled and pectinate lingual crown edge is reduced, while both the angled surface and pectination are absent in the smallest tooth. The roots of the juvenile teeth are low and have a flatter basal face and wider nutritive groove than in those of adults. As with the crown, in juveniles the root is compressed labio-lingually.

Remarks. The presence of teeth of a series of growth stages demonstrates how the unusual adult tooth morphology of *Squatirhina* develops from the smooth, broad teeth of juveniles. Thus the elongate cusp and pectinate lateral portions of the crown are seen to develop by elongation of the lingual edge of teeth with a more standard rhinobatid morphology.

Squatirhina? sp.

Text-figure 7F–G

Material. One incomplete tooth; LIVCM 1998. 20. CJ.

Horizon and localities. Speeton: Hunstanton Formation, Red Cliff Hole Member, bed RCH 1F (lower Lower Cenomanian).

Description. This tooth resembles the adult teeth of *Squatirhina thiesi* Biddle, 1993, but is considerably smaller (0·55 mm wide, as opposed to 1·0–1·5 mm wide in *S. thiesi*). The cusp is elongate and deep with a weak cutting edge. At its base, the crown has wide lateral expansions that are somewhat pectinate on both labial and lingual edges, almost developing into incipient lateral cusps. There is a strongly angled edge connecting the apex of this expansion and the cutting edge of the cusp. The labial apron is wide and shallow, and there is a narrow enameloid-covered lingual boss. The holoaulacorhize root is distinctly V-shaped and extends laterally as far as the edge of the crown. The basal face is flat and rather flared, with a large foramen in the centre of the preserved root lobe.

Remarks. In some respects this tooth resembles *Squatirhina thiesi*, but is sufficiently different to represent a separate, related species. The laterally expanded, denticulate crown is similar to that possessed by adult lateral teeth of *S. thiesi*, although somewhat more linguo-labially compressed. These features are not, however, differentiated in *S. thiesi* teeth of the size of the Speeton specimen. The flat basal face of the root is seen only in juveniles of *S. thiesi*, and thus it is possible that this is a juvenile of a species of *Squatirhina*, or similar genus, with very ornate teeth and for which adults are still unknown. The general morphology of the tooth, in particular the rather crusiform crown, also resembles teeth of some genera of sclerorhynchoids, such as *Ischyrhiza* and *Onchopristis*. Despite this, the pectinate crown ornament differs from that recorded on any sclerorhynchoid tooth, and thus a close affinity seems unlikely.

Family SCLERORHYNCHOIDAE Cappetta, 1980*a*

gen. et sp. indet.

Text-figure 7H–I

Material. Two exfoliated rostral teeth; LIVCM 1998. 20. CB.

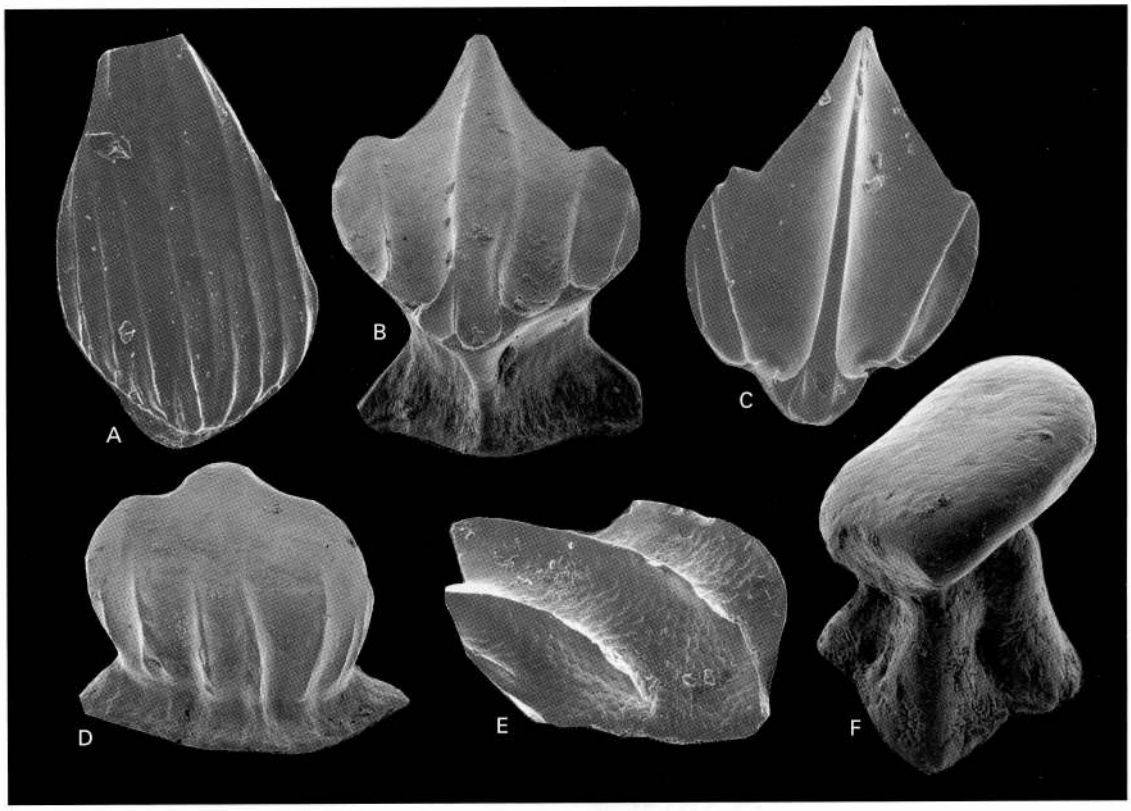
Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR5 (lower Upper Albian) and Red Cliff Hole Member, bed RCH 4a (lower Lower Cenomanian).

Description. A small rostral tooth, 1·3 mm high. The cusp is rather compressed with a weakly sigmoidal curvature. There is a weak cutting edge and a pair of parallel ridges on the ?distal margin. The base of the cusp has exfoliated, but it appears that enameloid originally extended to the top of the root. The basal face of the root is flared and flat, being oval in outline. The upper face of the root has many small foramina.

Remarks. The generic affinities of this rostral tooth are unclear. The small size and general shape of the crown bear resemblance to rostral teeth of several genera such as *Libanopristis* Cappetta, 1980*a* and *Micropristis* Cappetta, 1980*a*, and some smaller species of *Ischyrhiza*, such as *I. viaudi* Cappetta, 1981. The flared root, however, is unlike that of any described taxon, and it is thus likely that these rostral teeth belong to an as yet undescribed genus. Sclerorhynchoids are well known from the Albian (e.g. Thurmond 1971) and Cenomanian (e.g. Cappetta 1980*a*), but these early occurrences are restricted to areas of strong Tethyan influence, the earliest recorded sclerorhynchoid rostral teeth from boreal northern Europe being Santonian in age (Herman 1977). These remains from the Hunstanton Formation thus represent the oldest known occurrence of boreal sclerorhynchoids.

OTHER SELACHIAN MATERIAL: DENTICLES

Remarks. All of the denticles recovered exhibit a fairly simple 'placoid' morphology (Reif 1978). Other forms of dermal bone (such as dermal thorns or fin spines) or hybodont-type denticles were not found. Denticle terminology is based on Duffin and Ward (1993).



TEXT-FIG. 8. A, Denticle type 1; LIVCM 1998. 20. CC; Hunstanton Formation; Speeton, bed QR3; surface view, crown length 0·4 mm. B–C, Denticle type 2. B, LIVCM 1998. 20. CD; Speeton, bed RCH5c; anterior view, crown length 0·3 mm. C, LIVCM 1998. 20. CE; Speeton, bed DD6; surface view, crown length 0·5 mm. D, Denticle type 3; LIVCM 1998. 20. CF; Hunstanton Formation; Speeton, bed RCH5c; anterior view, width 0·5 mm. E, Denticle type 4; LIVCM 1998. 20. CG; Hunstanton Formation; Speeton, bed DD6; oblique view, crown length 0·4 mm. F, Denticle type 5; LIVCM 1998. 20. CH; Hunstanton Formation; South Ferriby, bed 6a; oblique view, crown length 0·5 mm.

Denticle type 1

Text-figure 8A

Material. One imperfect specimen; LIVCM 1998. 20. CC.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR 3 (lower Upper Albian).

Description. The crown is elongate, widening rapidly from the anterior edge and then smoothly tapers towards the apex, which is missing. There are nine straight, faint longitudinal ridges that fade out distally. The base is poorly preserved, but there is a slender vertical neck below the anterior part of the crown and a rather small ?tetraradiate base.

Denticle type 2

Text-figure 8B–C

Material. Twenty specimens; LIVCM 1998. 20. CD–CE.

Horizon and localities. Speeton: Speeton Clay Formation, bed A1A (lower Middle Albian) to Hunstanton Formation, Red Cliff Hole Member, bed RCH 5c (lower Lower Cenomanian). South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Description. The crown has a relatively pointed anterior end, in some cases with a pair of small indentations either side of the origin of the central keel. The distal apex is sharply pointed and often has a pair of small lateral points. The surface is ornamented by several strong longitudinal ridges, which run from the proximal to distal edges. The central ridge is either flat topped or with a central indentation, whilst the one, or less often two, pair of lateral ridges are sharp-edged. The neck is robust and leads to a wide tetraradiate base.

Denticle type 3

Text-figure 8D

Material. One specimen; LIVCM 1998. 20. CF.

Horizon and localities. Speeton: Hunstanton Formation, Red Cliff Hole Member, bed RCH 5c (lower Lower Cenomanian).

Description. This is the largest denticle recovered, being about 450 μm across. The crown is inclined to the basal plate at *c.* 60 degrees, and has a convex surface. The anterior (curved) portion is ornamented by five strong, parallel ridges, that fade out distally to give a flat posterior portion. The apex is blunt with some suggestion of lateral points or shoulders. There is no true neck, merely a constriction, and the base is wider than the crown.

Denticle type 4

Text-figure 8E

Material. Two specimens; LIVCM 1998. 20. CG.

Horizon and localities. Speeton: Hunstanton Formation, Queen Rocks Member, bed QR3 and Dulcey Dock Member, bed DD 6 (lower Upper Albian).

Description. The rather asymmetrical crown is strongly convex on its proximal edge, but less so distally. The apex is flanked by two lateral points, all three points occurring at the end of extremely strong, sharp-edged, ridges which run in parallel to each other for the length of the crown. Over much of the crown, especially proximally, there is a fine and very regular ornament of small polygonal pits, each about 10 μm across. The base is not preserved.

Denticle type 5

Text-figure 8F

Material. Two specimens; LIVCM 1998. 20. CH.

Horizon and localities. South Ferriby: Hunstanton Formation, bed 6a (lower Upper Albian).

Description. The crown is rounded, being angled anteriorly and rounded posteriorly. It is thick, unornamented and the posterior edge is angled upwards. The root is high and tetraradiate, flaring steadily from the base of the crown to a flat base.

Possible assignment of denticles

The assignment of denticles to particular taxa is fraught with difficulties due to their generally conservative morphology and the degree to which they vary over the body of an individual fish (e.g. Cappetta 1987). When compared with material from known Cretaceous taxa, denticle type 1 is similar to denticles from squalids (Cappetta 1980*a*, pl. 5, fig. 7), orectolobids (Cappetta 1980*a*, pl. 17, fig. 4) and scyliorhinids (Cappetta 1980*a*, pl. 20, fig. 4). Evidently, this is simply a generalized

denticle morphotype used in streamlining. Denticle type 2 is very similar to specimens figured for *Hexanchus* (Cappetta 1980*a*, pl. 1, fig. 3), *Synechodus dubrisiensis* (Duffin and Ward 1993, text-fig. 12h–i), and Jurassic material referred to *Synechodus* (Thies 1995), and probably represents a mixed suite of synechodontiform (*sensu* Duffin and Ward 1993) scales. Denticle type 3 is, in most respects, a more robust version of denticle type 2, and may simply be a scale from a more exposed part of the body of the same type of fish. This denticle type bears a strong resemblance to a denticle from the dorsal margin of the tail of a specimen of *Synechodus* from the Lower Jurassic (Duffin and Ward 1993, text-fig. 9k). The general morphology of type 4 is, again, rather cosmopolitan, but the distinctive ornament is very similar to that of denticles of *Pteroscyllium* (Cappetta 1980*a*, pl. 23, figs 9–10). Denticle type 5 has the most robust morphology, and was presumably positioned in an area of maximum skin abrasion.

ASSEMBLAGE VARIATIONS AND COMPARISONS WITH OTHER LOCALITIES

The Albian to Cenomanian Cretaceous selachian assemblages of Speeton and South Ferriby are generally similar, but differ in several ways. In part, this may be due to stratigraphical factors such as the greater completeness of the section at Speeton, although even in parts of the succession where sampled levels are equivalent (the Queen Rocks to Dulcey Dock members of the Speeton succession are equivalent to the sampled part of the succession at South Ferriby), the assemblages differ. The dominant faunal element at Speeton is *Protosqualus* (which comprises up to 70 per cent. of the assemblage at some horizons), a form relatively uncommon at South Ferriby. There is also a far greater abundance of *Notorhynchus* at Speeton, which remains common until at least the Middle Cenomanian. Scyliorhinids are also more abundant and diverse at Speeton. By contrast, the dominant elements in the South Ferriby assemblage are teeth of small lamniforms. These are relatively uncommon at Speeton, where larger lamniforms are restricted to occasional specimens in rocks immediately adjacent to the Albian–Cenomanian boundary. These occurrences coincide with a positive stable carbon isotope excursion (Mitchell 1995), which may be interpreted as a temporary increase in nutrient levels within the North Sea Basin watermass. The difference in assemblage composition between the two localities is probably related to a combination of water depth and water mass nutrient levels, and hence differing quantities and types of potential prey items.

There is no compelling evidence for a temporal change in the assemblages at South Ferriby, although at Speeton such a change is present. Most of the common species at Speeton persist from the Albian portion of the Speeton Clay (Upper A Beds) to the chalks of the basal Ferriby Formation, although the relative abundance of some taxa varies. There is very little difference in the assemblages from the Upper A Beds and the Queen Rocks and Speeton Beck members of the Hunstanton Formation. However, the assemblages of the Dulcey Dock to Crowe's Shoot members are noticeably dissimilar. The most marked difference is the change in the frequency of *Protosqualus sigei*. This is by far the commonest species in the lower part of the succession (usually 50–70 per cent. of the assemblage) and, although still common, it is far less abundant higher up (usually 20–40 per cent. of the assemblage). Larger lamniformes and *Pseudospinax* appear to be largely restricted to the upper part of the succession (Text-figs 3–4). This change in assemblage composition coincides with a facies change from more carbonate-poor to more carbonate-rich lithologies. It is possible therefore, that the change in selachian assemblages was either indirectly substrate controlled (via a change in available food), or controlled by the same factors that led to the increase in carbonate production (such as a change in water depth or primary nutrient levels).

Selachian assemblages from other Hunstanton Formation localities are very poorly known. Acid digestion of the shallow water limestones of Rifle Butts Quarry on the Market Weighton Structure has yielded fragmentary teeth probably referable to *Synechodus*, *Protosqualus* and *Squatina*. Fish remains are rare at Hunstanton (Le Strange 1974) at the southern limit of the Red Chalk facies, although *Hispidaspis* Sokolov, 1978? is present (SFM, pers. obs), whilst collections from this site in the Sedgwick Museum, Cambridge, contain teeth of lamniforms and chimaeroid remains (CJU, pers. obs.).

Assemblages from the Gault Clay facies of southern England and northern France differ markedly from those of the Hunstanton Formation. *Notorhynchus* is rare in the Gault Clay of the English East Midlands (Smart 1995) and Kent (D. Ward, pers. comm.) and was not recorded in northern France in a study by Biddle (1993). Gault Clay assemblages are dominated by medium to large lamniforms and contain groups such as hybodonts, *Ptychodus*, anacroacids, *Spathobatis* and chimaeroids none of which has been recorded from the Hunstanton Formation. Conversely, the Gault Clay facies contains few small benthic taxa, with squalids, scyliorhinids and hemiscylliids being uncommon and of low diversity. The Cambridge Greensand of the English East Midlands, a hiatal deposit at least partly of Albian age, contains a rich selachian assemblage. Collections in the Sedgwick Museum, Cambridge, and British Geological Survey Museum, Keyworth, contain numerous *Notorhynchus* and chimaeroids in an assemblage dominated by medium to large lamniforms (CJU, pers. obs.). Unfortunately, no studies of the smaller teeth have been published.

The Cenomanian of northern Germany contains an assemblage that is in many ways intermediate between the Hunstanton Formation and the Gault Clay assemblages. It contains abundant and diverse scyliorhinids, squalids and orectolobids associated with numerous small to large lamniformes (Müller and Diedrich 1991). Although further removed stratigraphically and geographically from the Hunstanton Formation than Gault Clay sections, northern Germany was within the same North Sea Basin as north east England during the Cretaceous (Mitchell 1996*b*).

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REFERENCES

AGASSIZ, J. L. R. 1833–44. *Recherches sur les poissons fossiles*. 3. Imprimerie de Petitpierre, Neuchâtel, 390+32 pp.

APPLEGATE, S. P. 1972. A revision of the higher taxa of orectolobids. *Publication of the Marine Biological Association of India*, **14**, 743–751.

ARAMBOURG, C. 1982. Les vértebrés fossiles des Gisements de Phosphates (Maroc-Algerie-Tunisie). *Notes et Mémoires, Service Géologique Maroc*, **92**, 1–372.

AYRES, W. O. 1855. A shark of a new generic type: *Notorhynchus maculatus*. *Proceedings of the Californian Academy of Natural Sciences*, **1**, 72–73.

BATCHELOR, T. J. and WARD, D. J. 1990. Fish remains from a temporary exposure of Hythe Beds (Aptian-Lower Cretaceous) near Godstone, Surrey. *Mesozoic Research*, **2**, 181–203.

BERG, L. S. 1940. Classification of Fishes, both recent and fossil. *Transactions of the Institute of Zoology, Academy of Sciences USSR*, **5**, 85–517. [In Russian].

—— 1958. *System der rezenten und fossilen Fischartigen und Fische*. Deutscher Verlag Wissenschaft, Berlin, 310 pp.

BIDDLE, J. P. 1993. Les Elasmobranches de l'Albien inférieur et moyen (Crétacé inférieur) de la Marne et de la Haute-Marne (France). *Professional Paper of the Belgian Geological Survey*, **264**, 191–240.

—— and LANDEMAINE, O. 1988. Contribution à l'etude des sélachiens du Crétacé du Bassin de Paris. Découverte de quelques nouvelles espèces associées à une faune de type wealdien dans le Barrémien supérieur (Crétacé inférieur) des environs de Troyes (Aube). *Musée de Saint-Dizier Publication*, **2**, 1–22.

BLAINVILE, H. M. D. de 1816. Prodrome d'une distribution systématique du regne animal. *Bulletin de la Société Philomatique de Paris*, **8**, 105–124.

BONAPARTE, C. L. J. L. 1834. Selachorum tabula analytica. *Nuovi Annali della Scienze Naturali, Bologna*, (1), **2**, 195–214.

CANDONI, L. 1993. Découverte de *Parasymbolus* gen. et sp. nov. (Scyliorhinidae-Elasmobranchii) dans le Kimméridgien de Normandie, France. *Professional Paper of the Belgian Geological Survey*, **264**, 147–156.

CAPPETTA, H. 1973. Selachians from the Carlile Shale (Turonian) of South Dakota. *Journal of Paleontology*, **47**, 504–514.

—— 1975. Sélachians et holocéphale du Gargasien de la région de Gargas (Vaucluse). *Géologie Méditerranéenne*, **2**, 115–134.

—— 1976. Sélachians nouveaux du London Clay de l'Essex (Yprésien du Bassin de Londres). *Géobios*, **9**, 551–574.

—— 1977*a*. Observations sur quelques sélaciens Crétacé Supérieur d'Angleterre avec la description d'un genre nouveau. *Géobios*, **10**, 479–485.

—— 1977*b*. Sélachians nouveaux de l'Albian supérieur de Wissant (Pas-de Calais). *Géobios*, **10**, 967–973.

—— 1980*a*. Les sélaciens du Crétacé supérieur du Liban. *Palaeontographica, Abteilung A*, **168**, 69–229.

—— 1980*b*. Modification du statut genérique de quelques espèces de sélachiens crétacés et tertiaires. *Palaeovertebrata*, **10**, 29–42.

—— 1981. Sur la découverte des genres *Ischyrhiza* et *Ptychotrygon* (Selachii, Batomorphii) dans le Crétacé Supérieur de Vendée (France). *Géobios*, **14**, 807–812.

—— 1987. Mesozoic and Cenozoic elasmobranchii. Chondrichthyes II. *In* SCHULTZE, H. P. (ed.). *Handbook of paleoichthyology*, 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.

—— 1990. Hexanchiforme nouveau (Neoselachii) du Crétacé Inférieur du sud de la France. *Palaeovertebrata*, **20**, 33–54.

CASE, G. R. 1978. A new selachian fauna from the Judith River Formation (Campanian) of Montana. *Palaeontographica, Abteilung A*, **160**, 176–205.

—— 1987. A new selachian fauna from the late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). *Palaeontographica, Abteilung A*, **197**, 1–37.

CASIER, E. 1947. Constitution et évolution de la racine dentaire des Euselachii. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique*, **23**, (13) 1–15, (14) 1–32, (15) 1–45.

COMPAGNO, L. J. V. 1973. Interrelationships of living elasmobranchs. 15–61. *In* GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds). Interrelationships of fishes. *Zoological Journal of the Linnean Society*, **53** (supplement).

DALINKEVICIUS, J. A. 1935. On the fossil fishes of the Lithuanian Chalk. I. Selachii. *Mémoires de la Faculté des Sciences de l'Université de Vytautas le Grand*, **9**, 274–305.

DAVIS, J. W. 1890. On the fossil fish of the Cretaceous Formations of Scandinavia. *Scientific Transactions of the Royal Dublin Society*, **4**, 363–434.

DIXON, F. 1850. *The geology and fossils of the Tertiary and Cretaceous formations of Sussex*. London, 408 pp.

DUFFIN, C. J. and WARD, D. J. 1993. The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. *Professional Paper of the Belgian Geological Survey*, **264**, 53–102.

DUMÉRIL, A. M. C. 1806. *Zoologie analytique ou methode naturelle de classification animaux*. Allais, Paris, 344 pp.

ENNIS, W. C. 1932. The upper beds of the Speeton Clay. *Transactions of the Hull Geological Society*, **1932**, 80–82.

GILL, T. 1862. Analytical analysis of the order of Squali and revision and nomenclature of genera. *Annals of the Society of Natural History of New York*, 367–408.

GLÜCKMAN, L. S. 1957. [Genetic relationships of the Lamnidae and Odontaspidae and new genera of lamnids from the Upper Cretaceous.] *Trudy Geologischeskogo Muzeia Akademia Nauk SSSR*, **1**, 110–117. [In Russian].

—— 1958. [Rates of evolution in lamnoid sharks.] *Akademia Nauk SSSR*, **123**, 568–571. [In Russian].

GOODRICH, E. S. 1909. Vertebrate Craniata (First fascicle: Cyclostomes and Fishes). *In* LANKESTER, E. R. (ed.). *A treatise on zoology*, part 10. Adam and Charles Black, London, 518 pp.

GRAY, J. E. 1851. *List of specimens of fish in the collection of the British Museum*, Part 1. British Museum (Natural History), London, 160 pp.

HALTER, M. C. 1994. Additions to the fish fauna of N.W. Europe. 3. Three new species of the genus *Scyliorhinus* from the late Cretaceous (Campanian and Maastrichtian) of the Limburg area (Belgium and the Netherlands) with the reassignment of four additional species to the genus *Scyliorhinus* sensu stricto. *Professional Paper of the Belgian Geological Survey*, **278**, 65–110.

HANCOCK, J. M. 1986. Cretaceous. *In* GLENNIE, K. W. (ed.). *Introduction to the petroleum geology of the North Sea*. Second edition. Blackwell, Oxford, 161 pp.

HERMAN, J. 1977. Les Sélachians des néocrétacés et paléocénes de Belgique et des contrées limitrophes Eléments d'une biostratigraphie intercontinentale. *Mémoires pour server a l'Explication des Cartes Géologiques et Minières de la Belgique*, **15**, 1–450.

—— 1982. Die Selachier-Zähne aus der Maastricht-Stufe von Hemmoor, Niederelbe (NW-Deutschland). *Geologisches Jahrbuch, Series A*, **61**, 129–159.

JEANS, C. J. 1980. Early submarine lithification in the Red Chalk and Lower Chalk of east England: a bacterial control model and its implications. *Proceedings of the Yorkshire Geological Society*, **43**, 81–157.

JORDAN, D. S. 1898. Description of a species of fish (*Mitsukurina owstoni*) from Japan, the type of a distinct family of lamnoid sharks. *Proceedings of the Californian Academy of Science*, **3**, 119–202.

LE STRANGE, H. 1974. Notes on Hunstanton Red Rock fossils. *Bulletin of the Geological Society of Norfolk*, **26**, 47–48.

LINNAEUS, C. 1758. *Systema naturae*. Vol. 1. 10th edition. Salvi, Stockholm, 824 pp.

LOTT, G. K., BALL, K. C. and WILKINSON, L. P. 1985. Mid Cretaceous stratigraphy of a cored borehole in the western part of the Central North Sea Basin. *Proceedings of the Yorkshire Geological Society*, **45**, 235–248.

MACKIE, S. J. 1863. On a new species from the Lower Chalk. *The Geologist*, **6**, 241–246.

MITCHELL, S. F. 1995. The Hunstanton Red Chalk Formation (Albian–Cenomanian, Cretaceous) at Speeton, Yorkshire. *Proceedings of the Yorkshire Geological Society*, **50**, 285–303.

—— 1996*a*. The Jurassic–Cretaceous succession at Rifle Butts Quarry (SSSI) and its implications for sedimentation on the Market Weighton Structure. *Proceedings of the Geologists' Association*, **107**, 161–166.

—— 1996*b*. Foraminiferal assemblages from the late Lower and Middle Cenomanian of Speeton, North Yorkshire: relationships with sea-level fluctuations and watermass movements. *Journal of Micropalaeontology*, **15**, 37–54.

—— and LANGNER, D. 1996. Palaeobiology of isocrinid crinoids from the Red Chalk of north-east England, 197–207. *In* EMSON, R., SMITH, A. and CAMPBELL, A. (eds). *Proceedings of the Fourth Echinoderms Colloquium, London/United Kingdom/10–13 April 1995. Echinoderm Research 1995*. Balkema, London.

MÜLLER, A. 1989. Selachier (Pisces, Chondrichthyes) aus dem höheren Campanium (Oberkreide) Westfalens (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **14**, 1–161.

—— and DIEDRICH, C. 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Ascheloh am Teutoberger Wald (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **20**, 1–105.

—— and SCHÖLLMANN, L. 1989. Neue Selachier (Neoselachii, Squalomorphii) aus dem Campanium Westfalens (NW-Deutschland). *Neues Jahrburch für Geologie und Paläontologie, Abhandlungen*, **178**, 1–35.

MÜLLER, J. and HENLE, J. 1838–41. *Systematische beschreibung der Plagiostomen*. Veit and Co., Berlin, 200 pp.

PICTET, F. J. 1865. Note sur une dent de l'étage aptien des environs d'Apt, appartenant à un *Notidanus* non décrit. *Annales de la Société Litéraire Scientifique et Artistique d'Apt*, **1**, 67–70.

RAFINESQUE, C. S. 1810. *Caratteri di alcuni nuovi generi e nuove specie di animale e piante della Sicilia*. San Filippo, Palermo, 105 pp.

REGAN, C. T. 1906. A classification of selachian fishes. *Proceedings of the Zoological Society of London*, **1906**, 722–758.

REIF, W.-E. 1978. Types of morphogenesis of the dermal skeleton of fossil sharks. *Paläontologische Zeitschrift*, **52**, 110–128.

SIVERSON, M. 1992. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. *Palaeontology*, **35**, 519–554.

—— 1993. Maastrichtian squaloid sharks from southern Sweden. *Palaeontology*, **36**, 1–20.

—— 1995. Revision of *Cretorectolobus* (Neoselachii) and description of *Cederstroemia* n. gen., a Cretaceous carpet shark (Orectolobiformes) with a cutting dentition. *Journal of Paleontology*, **69**, 974–979.

—— 1996. Lamniform sharks of the mid Cretaceous Alinga Formation and Beedagong Claystone, Western Australia. *Palaeontology*, **39**, 813–849.

—— 1997. Sharks from the mid-Cretaceous Gearle Siltstone, southern Carnarvon Basin. Western Australia. *Journal of Vertebrate Paleontology*, **17**, 453–465.

SMART, P. J. 1995. Hexanchid shark teeth (Chondrichthyes, Vertebrata) from the Lower Cretaceous Albian sediments of Leighton Buzzard, south-central England. *Proceedings of the Geologists' Association*, **106**, 241–246.

SMITH, A. 1837. On the necessity for a revision of the groups included in the Linnean genus *Squalus*. *Proceedings of the Zoological Society of London*, **5**, 85–86.

SOKOLOV, M. I. 1978. Requins comme fossiles-guides pour la zonation et la subdivision der couches Cretaces de Tourousk. *Niedra, Moscou*, **61**, 1–60.

SWINNERTON, H. H. 1955. A monograph of the British Lower Cretaceous belemnites. Part 5. *Monograph of the Palaeontographical Society*, **108** (469), 63–86, pls 16–18.

THIES, D. 1979. Selachierzähne aus der nordwestdeutschen. 211–222. *In Aspekte der Kreide Europas. IUGS Series A*, No. 6.

—— 1981. Vier neue Neoselachier-Haiarten aus der NW-deutschen Unterkreide. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1981**, 75–86.

—— 1983. Jurazeitliche Neoselachier aus Deutschland und S-England. *Courier Forschungsinstitut Senckenberg*, **58**, 1–117.

—— 1995. Placoid scales (Chondrichthyes: Elasmobranchii) from the Late Jurassic (Kimmeridgian) of Northern Germany. *Journal of Vertebrate Paleontology*, **15**, 463–481.

THURMOND, J. T. 1971. Cartilaginous fishes of the Trinity Group and related rocks (Lower Cretaceous) of North Central Texas. *Southeastern Geology*, **13**, 207–227.

TRAUTSCHOLD, H. 1877. Über Kreidefossilien Russlands. *Bulletin de la Société des Naturalistes de Moscou*, **11**, 332–349.

UNDERWOOD, C. J. , MITCHELL, S. F. and VELTKAMP, C. J. in press. Microborings in mid-Cretaceous fish teeth. *Proceedings of the Yorkshire Geological Society*.

WARD, D. J. and THIES, D. 1987. Hexanchid shark teeth (Neoselachii, Vertebrata) from the Lower Cretaceous of Germany and England. *Mesozoic Research*, **1**, 89–106.

WILLISTON, S. W. 1900. Cretaceous Fishes, Selachians and Pycnodonts. *Publications of the University Geological Survey Kansas*, **6**, 237–256.

WOODWARD, A. S. 1888*a*. On the Cretaceous selachian genus *Synechodus*. *Geological Magazine*, **3**, 496–499.

—— 1888*b*. On some remains of *Squatina cranei* sp. nov. and the mandible of a *Belonstomus cinctus*, from the Chalk of Sussex, preserved in the collection of H. Willett. *Quarterly Journal of the Geological Society, London*, **44**, 144–147.

—— 1889. *Catalogue of the fossil fishes in the British Museum*. Part 1. British Museum (Natural History), London, xlvii + 474 pp.

—— 1912. The fossil fishes of the English Chalk. Part 7. *Monograph of the Palaeontographical Society*, **65** (320) i–viii, 225–264, pls 47–54.

—— 1918. On two new elasmobranch fishes (*Crossorhinus jurassicus* sp. nov. and *Protospinax annectans* sp. nov.) from the Upper Jurassic lithographic stone of Bavaria. *Proceedings of the Zoological Society of London*, **1918**, 231–235.

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OCCURRENCE OF A JUVENILE TELEOST, *ENCHODUS* SP., IN A FISH GUT CONTENT FROM THE UPPER CRETACEOUS OF GOULMIMA, MOROCCO

by LIONEL CAVIN

ABSTRACT. A skull and some post-cranial elements of *Enchodus* sp. found in the gut contents of *Goulmimichthys arambourgi* from the Upper Cretaceous (Lower Turonian) of Goulmima, Morocco is described. It shares similarities with *E. venator* from the Lower Cenomanian of Jebel Tselfat, but is not complete enough for specific identification. The skull and several other enchodontid microremains from the matrix surrounding the specimen of *G. arambourgi* show juvenile characters: weak state of ossification of the palatine, of the lower jaw and of the vertebral centra. The presence of an unpaired premaxillary fenestra and of a small jugular canal in the trigemino-facialis chamber are also probably juvenile characters. The large number of microremains of juvenile enchodontids at this locality suggests that it was an *Enchodus* nursery.

THE Upper Cretaceous (Lower Turonian) locality of Goulmima, named after a nearby town on the southern slope of the Moroccan Atlas (Text-fig. 1A), yields a rich ichthyofauna (Cavin 1995, 1997*a*). The exact origin of the specimen described herein is unknown, but preliminary fieldwork located several localities of fossil fishes situated east of the villages of Tadirhoust and Asfla, 15 and 20 km to the north of Goulmima (Text-fig. 1A). The fishes are contained in ovoid, early diagenetic calcareous nodules that occur at the top of a Cenomanion–Turonian limestone sequence (unit 4 of Ferrandini *et al.* 1985). This unit is exposed at the base of a calcareous plateau, at an average height of *c.* 1500 m above sea level and overhanging the plain situated between Goulmima and Er Rachidia. A simplified stratigraphical log based on exposures in a cliff *c.* 2 km east of Tadirhoust exhibits the following units from the bottom to the top (Text-fig. 1B): a red sequence composed of continental cross-bedded sandstone; a 40 m thick unit of gypsiferous marl; and the Cenomanian–Turonian limestone (about 45 m thick). The last-named unit forms the top of the plateau. The Cenomanian–Turonian limestone is composed of interbedded limestones and marly limestones. The Cenomanian–Turonian boundary is situated somewhere near the base of this unit (Ferrandini *et al.* 1985) and the fossiliferous nodules occur *c.* 3 m below the last set of limestone beds, in layers corresponding to a high sea level (external platform environment). The ammonite *Mammites*, which is restricted to the Lower Turonian, is associated with the nodules. The concentration of nodules is high at some localities, but most are not fossiliferous.

The nodules observed *in situ* lay horizontally in the sediment, their long axes parallel to stratification. Most of the fish-bearing concretions are formed only around the body and skull of the fishes, and most appendages and the extremities are not preserved. Some concretions are formed around parts of the skeleton only, in particular skulls and tails. Occasionally, concretions enclose an entire specimen, its shape reflecting the shape of the fish that it contains, but concretions containing several complete fishes have not yet been found. No laminae have been observed in the matrix of the nodules. Sections through a concretion reveal voids in the body cavity and in the neurocranium of the enclosed fish.

The vertebrate fauna comprises several forms of marine reptiles and fishes, especially sclerorhynchids, pycnodontids, ichthyodectids, araripichthyids, osmeroidids, pachyrhizodontids

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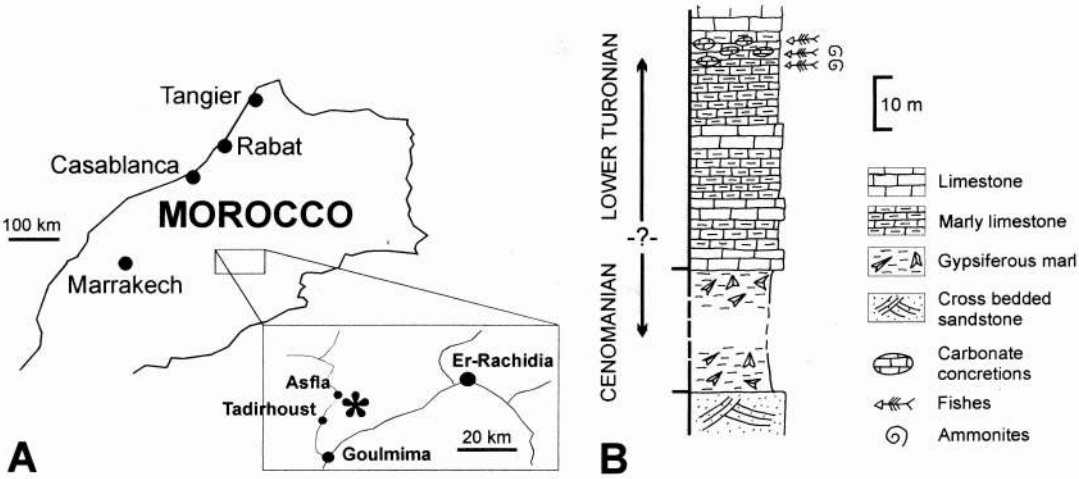


TEXT-FIG. 1. A, map of Morocco. The approximate site of the Goulmima locality is indicated by a star. B, simplified stratigraphical log based on exposures in a cliff *c.* 2 km east of Tadirhoust.

and enchodontids. Some of these families are represented by partially complete three-dimensional fishes, whilst others (sclerorhynchids and pycnodontids) are known, until now, only from microremains. Microremains are found in the matrix of the nodules and sometimes form concentrations in the body cavity of articulated fishes, or are associated with supposed fossilized soft tissues of the alimentary tract; in these cases they are considered as gut contents. Soft tissues of the alimentary tract are preserved as elongate structures lying below the vertebral column and parallel to the long axis of the body. In some specimens of the most common species, the pachyrhizodontid *Goulmimichthys arambourgi* Cavin, 1995, they form a compressed tube. The wall of the tube (*c.* 1 mm thick) is made of a porous, non-carbonate material, similar to the phosphatized stomach wall observed in a specimen of *Rhacolepis* from the Santana Formation (Martill 1988, pl. 3, fig. 2).

Microremains of enchodontids were found in the matrix of some nodules, or associated with the alimentary tract of *G. arambourgi*. A partially articulated skull, partly enclosed by supposed soft tissues of the alimentary tract, and some post-cranial elements of a very small enchodontid of uncertain taxonomic affinities have been found in the body cavity of a partially preserved specimen of *G. arambourgi* (BHN 2P3, Text-figs 2A, 3A). The state of preservation of these remains enables a precise description of some details of the neurocranium and the splanchnocranium. Some features of the specimen suggest that it was a juvenile and provide new evidence regarding the ontogeny of enchodontids.

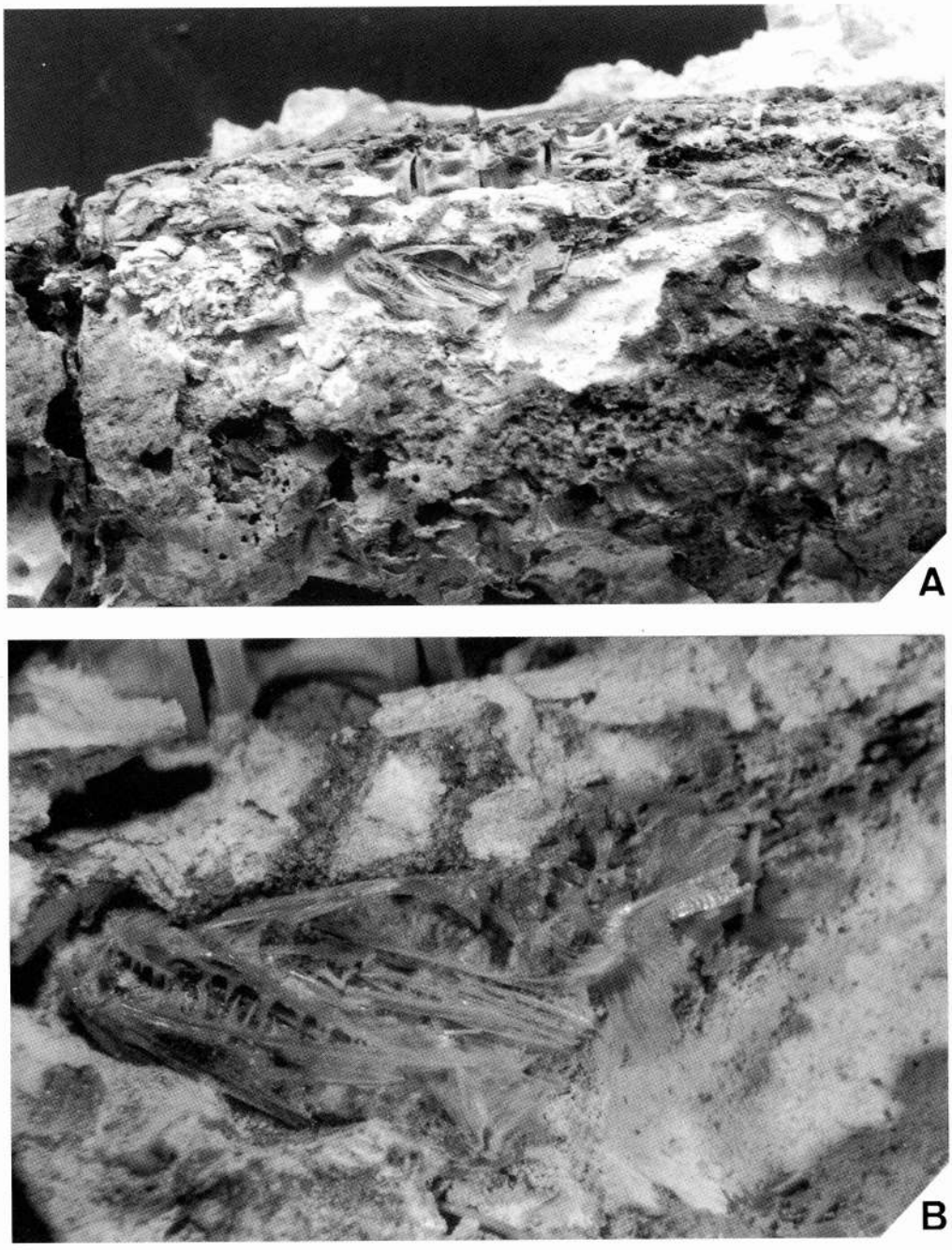
BHN 2P3 was prepared using 10 per cent. formic acid. The nodules from Goulmima referred to in this work are deposited in the Natural History Museum of Boulogne-sur-Mer (France).

SYSTEMATIC PALAEONTOLOGY

Order AULOPIFORMES Rosen, 1973
Suborder ENCHODONTOIDEI Berg, 1940
Family ENCHODONTIDAE Woodward, 1901

Genus ENCHODUS Agassiz, 1835

Type species. Esox lewesiensis Mantell, 1822.



TEXT-FIG. 2. A, *Goulmimichthys arambourgi* Cavin, 1995; BHN 2P3; Goulmima, Morocco; Lower Turonian; ventral view of the abdominal region with the skull of *Enchodus* sp.; ×2·8. B, *Enchodus* sp.; enlargement of A; ×6·5.

Enchodus sp.

Text-figures 2–7

DESCRIPTION

Skull (Text-figs 2B, 3B)

The specimen (BHN 2P3a) consists of a skull 12 mm long (without the opercular bones) represented by components of the neurocranium, the palate and the jaws. A few bones from the opercular series, pectoral girdle and vertebral column are also visible behind the skull. Some bones are *in situ* (skull roof, palate and jaws) whilst others are slightly displaced (otic and occipital portions of the endocranium, post-cranial bones). The skull is situated in the ventral part of the body cavity of an individual of *Goulmimichthys arambourgi* (BHN 2P3) between the pectoral and pelvic fins. The distance between these two structures is 90 mm.

Neurocranium. Only the left frontal (Fr) is preserved. It is a large bone with very thin and shallow tubercular protuberances. The lateral margin is excavated above the orbit and forms a fine spine near the suture with the autosphenotic. The orbit is large and the supraorbital sensory canal is proportionally very large, a feature that probably reflects the juvenile nature of this individual. The sensory canal opens antero-laterally at the level of a spine in the first quarter of the lateral margin of the frontal and an antero-median opening of this canal is apparently present in the mid-length of the frontal as in *Enchodus faujasi* (Goody 1968) and *E. lewesiensis* (Goody 1969). The posterior branch of the canal is not preserved. Four small pores open in a curve of the canal above the orbit and the exit opens at the level of the spine of the frontal.

The post-temporal fossa, unroofed in enchodontids (Goody 1969), is not preserved. The supraoccipital (Soc) bears a small postero-dorsally pointed crest. It is similar to those of *E. lewesiensis* (Goody 1969) and *E. petrosus* (Goody 1976), but is a little more developed dorsally.

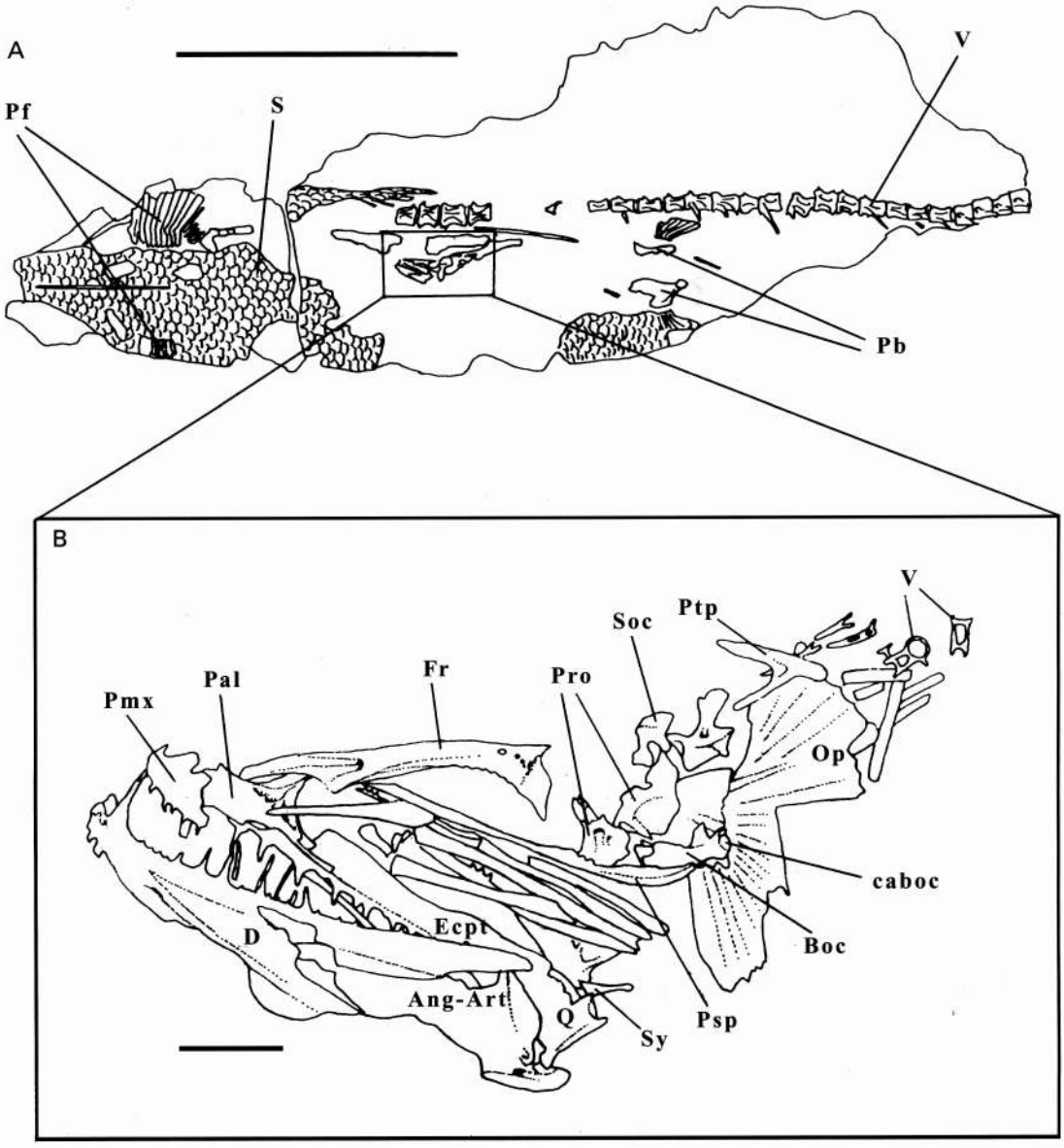
The lateral ethmoid, mesethmoid and vomer are missing.

The parasphenoid (Psp) is long and slender. The ascending process is well developed, but its very fine dorsal margin is missing. The foramen of the internal carotid artery is partially visible in the postero-ventral edge of the ascending process. Posteriorly, the parasphenoid takes the form of a median keel forming an angle of about 120° in lateral view and constitutes the floor of the posterior myodome. The latter opens on the posterior face of the skull between two lateral laminae of the parasphenoid below the occipital condyle, as in *E. faujasi* (Goody 1968).

The basioccipital (Boc) forms the lower third of the occipital condyle (caboc), whilst the lateral two-thirds are formed by the exoccipitals, as in other enchodontids (Goody 1969). Only the postero-ventral portion of the basioccipital is preserved. Its lateral walls are rounded and constitute the postero-ventral portions of the otolith chambers. The basioccipital has a reversed V-shaped median ridge, that decreases in height from front to back, separating the otolith chambers from the posterior myodome and roofing the latter.

The left prootic and a portion of the right prootic are visible (Text-fig. 4). The prootic is a complex bone, *c.* 1 mm long and 2 mm high. In dorsal view, a foramen for the abducens (VI) nerve pierces the prootic bridge (ppro) from the cranial cavity to the myodome. The structure of the trigemino-facialis chamber is as follows: the *pars ganglionaris* communicates with the *pars jugularis* by two large pores. The dorsal pore represents the trigeminal foramen (ft), whilst the ventral pore represents the facial foramen (ff). The orbital face of the prootic exhibits a large, laterally situated foramen, corresponding to the anterior opening of the *pars jugularis* (oacj), and two smaller foramina medially situated. The more medial of these two foramina accommodated the oculomotor nerve (III), whilst the more lateral was probably for the ophthalmic superficial branches of the trigeminal and facial nerves (V + VII oph). The *pars jugularis* ran across the lateral face of the prootic. A large opening is present anteriorly for the hyomandibular branch of the facial (VII hm) and perhaps for the orbital artery (Goody 1969). An antero-dorsally aligned groove (sao) is impressed below the opening for the orbital artery. This opening is separated from the posterior opening of the *pars jugularis* (opcj) by a very thin bridge of bone. The dorsal part of the orbital face of the prootic is formed by two vertical laminae defining a deep groove. Two foramina pierce the bottom of this groove: one opens into the anterior extremity of the *pars jugularis*, perhaps allowing the transmission of the otic branch of the facial nerve (VII ot), whilst the other communicates with the foramen for the ophthalmic nerves. The structure of the trigemino-facialis chamber will be discussed later. Other bones of the neurocranium are present, but their determinations are doubtful.

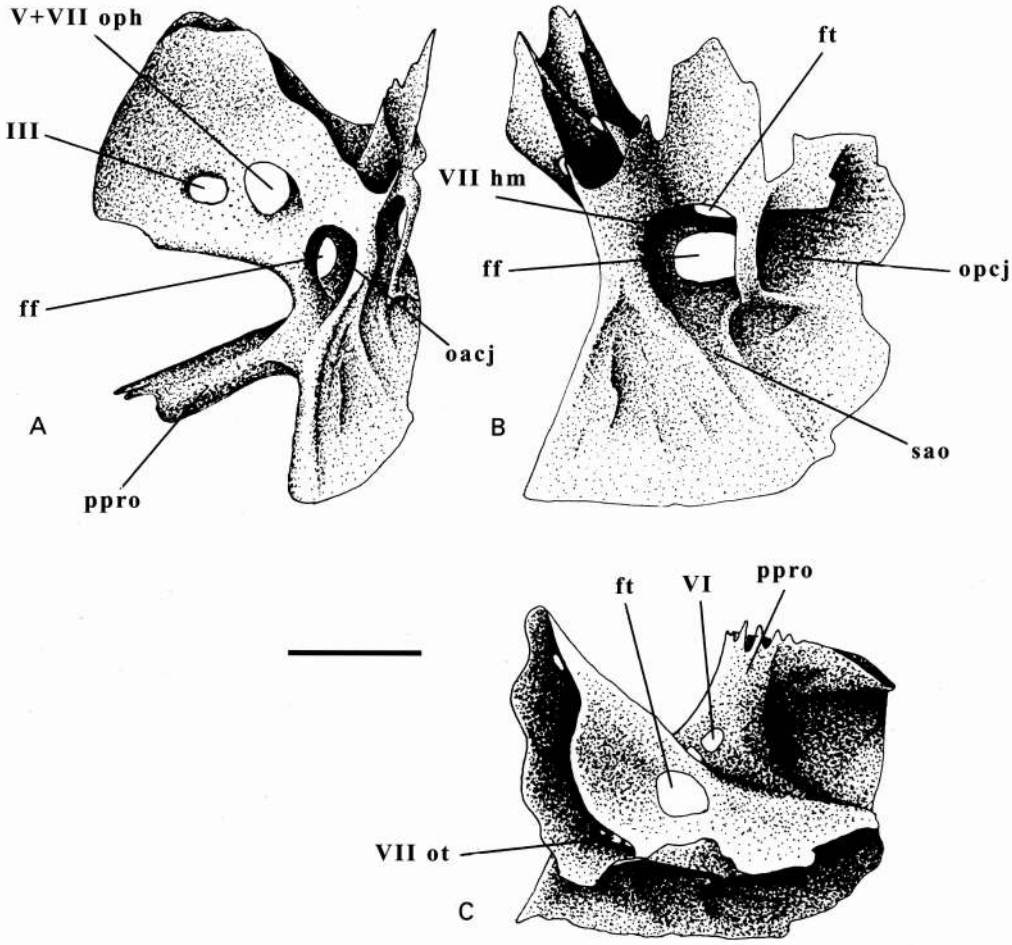
Hyopalatine bones (Text-fig. 5). The hyomandibular and metapterygoid are not present. The quadrate (Q) is stout and triangular. The articular condyle is transversally broad with a median constriction. A groove which housed the symplectic, a narrow rod of bone (less than 2 mm long) and located near the quadrate in this



TEXT-FIG. 3. A, *Goulmimichthys arambourgi* Cavin, 1995; BHN 2P3; Goulmima, Morocco; Lower Turonian; ventral view. Abbreviations: Pb, pelvic bone; Pf, pectoral fin; S, scale; V, vertebra. Scale bar represents 50 mm. B, *Enchodus* sp.; BHN 2P3a; Goulmima, Morocco; Lower Turonian. Enlargement of A. Abbreviations: Ang-Art, angulo-articular; Boc, basioccipital; caboc, occipital condyle; D, dentary; Ecpt, ectopterygoid; Fr, frontal; Op, operculum; Pal, palatine; Pmx, premaxilla; Pro, prootic; Psp, parasphenoid; Ptp, posttemporal; Q, quadrate; Soc, supraoccipital; Sy, symplectic; V, vertebra. Scale bar represents 2 mm.

specimen (Sy, Text-fig. 3B) is present on the posterior margin of the medial face of the quadrate. The posterior margin of the quadrate is thick and bears a groove that probably accommodated the anterior edge of the preoperculum, as in *E. faujasi* (Goody 1968) and *E. zinensis* (Chalifa 1996).

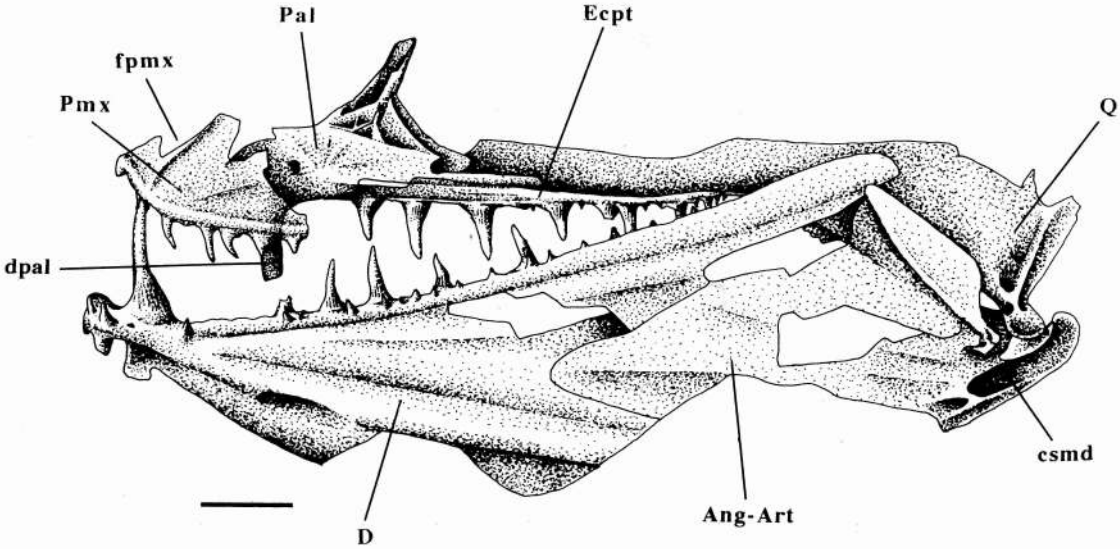
The body of the ectopterygoid (Ecpt) forms an angle of *c.* 30° to the posterior portion that overlaps the lateral face of the quadrate. This angle is roughly equal to that seen in *E. lewesiensis* (Goody 1969), but unlike



TEXT-FIG. 4. Left prootic of *Enchodus* sp.; BHN 2P3a; Goulmima, Morocco; Lower Turonian. A, anterior view; B, lateral view; C, dorsal view. Abbreviations: ff, facial foramen; ft, trigeminal foramen; oacj, anterior opening of the *pars jugularis*; opcj, posterior opening of the *pars jugularis*; ppro, prootic bridge; sao, groove for the orbital artery; III, foramen for oculomotor nerve; V + VII oph, foramen for the superficial ophthalmic of the trigeminal and facial nerves; VI, foramen for abducens nerve; VII hm, foramen for the hyomandibular branch of the facial nerve and possibly the orbital artery; VII ot, foramen for the otic branch of the facial nerve. Scale bar represents 0·5 mm.

E. faujasi in which it reaches *c.* 45° (Goody 1968). The ectopterygoid is a long rod of bone with a ventral edge that is concave in dorsal view. A thin lamina rises up along the medial margin of the concavity and is probably formed by the entopterygoid (the suture with the ectopterygoid is not visible). This lamina is slightly medially inclined and its height increases from back to front. The concavity forms a groove which houses the ventral edge of the palatine. Ventrally, the ectopterygoid bears a row of large teeth that decrease in size posteriorly. Seven functional teeth, *c.* 0·8 mm high, appear to be present. Their extremities are slightly posteriorly recurved and their bases are expanded and bear fine striations. A row of minute teeth, probably borne by the entopterygoid, is present medial to the row of large lateral teeth.

The palatine (Pal) has a typical shape, but is very light with large cavities, unlike the dense bone commonly described for this genus (Goody 1968, 1969). This difference is probably due to the early stage of development of this individual. The maximum depth of the palatine is approximately equal to half of its length. A well developed dorsal process is present in the mid-length of the dorsal margin of the bone. A single, enlarged



TEXT-FIG. 5. Left upper and lower jaws of *Enchodus* sp.; BHN 2P3a; Goulmima, Morocco; Lower Turonian. Abbreviations: see caption for Text-figure 3B; csmd, mandibular sensory canal; dpal, palatine tooth; fpmx, premaxillary fenestra. Scale bar represents 1 mm.

terminal tooth (dpal) is partially hidden by the premaxilla, its base located at 90° to the main body of the bone. The ventral face of the palatine is convex in its posterior half and rests in a groove on the ectopterygoid. On the lateral face of the palatine is a shallow depression that housed the anterior extremity of the maxilla.

Dermal upper jaw (Text-fig. 5). The premaxilla (Pmx) is large with an anterior premaxillary pedicel and a lateral region arranged at about 45° to this. The pedicel contains a large premaxillary fenestra (fpmx) which housed the largest anterior mandibular tooth. As in *E. faujasi* (Goody 1968) and *E. lewesiensis* (Goody 1969), the lateral region bears external grooves: one lies parallel to the angle formed by the lateral and anterior regions, whilst the other runs parallel to the oral margin. The anterior extremity of the palatine rested in a convexity situated between these two grooves. The posterior portion of the premaxilla is not preserved. The oral margin bears a few teeth, comparable in size to those borne by the posterior region of the ectopterygoid. Their extremities are slightly posteriorly recurved and their bases are expanded. The maxilla, usually very slender in enchodontids (Goody 1968, 1969), is not preserved.

Mandible (Text-fig. 5). As in other enchodontids, the mandible is very large. The entire oral margin and most of the ventral margin is formed by the dentary (D), which also bears longitudinal ridges. The symphysis is constricted and its ventral surface bears three finger-like processes increasing in size posteriorly. The dorso-lateral margin of the anterior extremity of the dentary bears two teeth comparable in size and shape to those of the premaxilla. Postero-medially there is a much larger tooth (1·5 mm high), thin, sinuous in shape and slightly laterally compressed. The remainder of the oral margin bears about seven functional teeth comparable in size and shape to those borne by the ectopterygoid, and slightly compressed; the plane of compression is orientated postero-medially. The teeth are located on the internal face of the dorsal margin of the jaw and the gaps between them increase posteriorly. Lateral to the large teeth, a row of about 14 minute teeth is present on the margin of the mandible. The posterior quarter of the oral margin is edentulous.

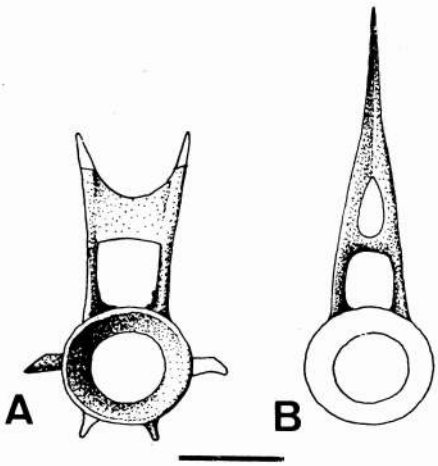
The angulo-articular (Ang-Art) (= 'articular' of Goody 1968, 1969) is laterally expanded into a V-shaped excavation for the dentary, at about half the length of the mandible. It bears ridges that radiate from the postero-ventral edge of the mandible. The posterior part of the articular facet is transversely oriented and medially it bears a ridge corresponding to the groove on the articular condyle of the quadrate. The anterior part of the articular region is formed by a small independent facet that continues as a dense sheet of bone to the coronoid process. This part of the bone is fused with the angular and probably corresponds to the enchondral articular. There is a small foramen below the articular facet, probably for the *rami mandibularis*

of the trigeminal and facial nerves. A large specimen of *E. petrosus* exhibits an apparently similar articular portion of the angulo-articular (Goody 1976, fig. 4). There is a small retroarticular process with a groove (csmd) that runs down the articular facet and leads to a foramen for the mandibular sensory canal.

Opercular bones. The only preserved bone of this series is the right operculum (Op, Text-fig. 3B). It is deeper than long and its lateral face is ornamented with fine radiating ridges. A large ridge similar to that seen in *E. marchesetti* (Goody 1969) runs horizontally from the articular facet along the internal face of the operculum and probably strengthened this bone.

Pectoral girdle. Only the right post-temporal is visible (Ptp, Text-fig. 3B). It is similar to that of *E. marchesetti* (Goody 1969): the upper limb articulating with the epiotic is oval and flattened, whilst the ventral limb articulating with the intercalar is a long, slender rod of bone.

Vertebral column. A few disarticulated vertebrae are present behind the skull (V, Text-fig. 3B). The lateral faces of the centra are not visible. Each centrum consists of a thin ring of bone without a constriction for the notochord. It bears paired ventro-lateral processes at its anterior extremity for the articulation of the ribs. The neural arches typically occupy the entire length of the dorsal region of the centra. In anterior view the neural canal is delimited dorsally by a horizontal bridge between the two neural spines. In some vertebrae these neural spines are low and divergent (Text-fig. 6A), whilst in some others the neural spines are higher and form an



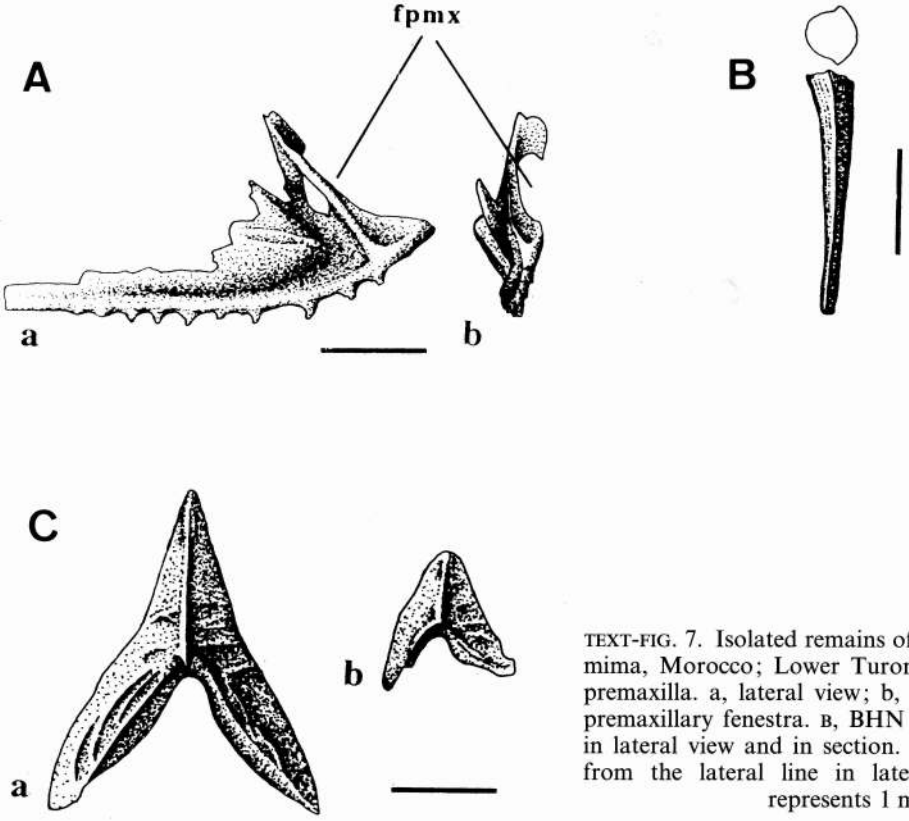
TEXT-FIG. 6. Vertebrae of *Enchodus* sp.; BHN 2P3a; anterior views; Goulmima, Morocco; Lower Turonian. A, posterior abdominal vertebra (?); B, anterior abdominal vertebra (?). Scale bar represents 1 mm.

unpaired spine creating a longitudinal canal above the neural arch (Text-fig. 6B). The latter type of vertebra probably occurred anterior to the former.

Microremains

The matrix of the nodule containing the fish described herein yielded numerous microremains during acid preparation and some are undoubtedly enchodontid. Some of these elements cannot belong to the skull described above because of their number or size: other bones may be from this individual but became detached during preparation. Bones from other nodules also help to supplement the description given above.

Premaxilla. (Text-fig. 7A). This bone (BHN 2P11a) comes from another nodule also containing a large, complete specimen of *G. arambourgi*. It is closely comparable in size and in shape to those of the semi-articulated *Enchodus*, but is more complete. The anterior premaxillary fenestra is large and not closed medially (fpmx). An unpaired median opening is present and contains two large anterior mandibular teeth. A second fenestra, apparently not present on the semi-articulated specimen, opens at the bottom of a vertical groove on the lateral face of the bone. The posterior portion of the premaxilla is preserved as a slender and thin lamina of bone. The bases of about nine middle-sized teeth are present.



TEXT-FIG. 7. Isolated remains of *Enchodus* sp.; Goulmima, Morocco; Lower Turonian. A, BHN 2P11a; premaxilla. a, lateral view; b, anterior view. fpmx: premaxillary fenestra. B, BHN 2P3d; palatine tooth in lateral view and in section. C, BHN 2P3e; scales from the lateral line in lateral view. Scale bar represents 1 mm.

Mandible. Several pieces of mandible (BHN 2P3b) are present in nodule BHN 2P3. Two anterior extremities of dentaries bearing a typically large tooth, are present. The posterior portion of a mandible (BHN 2P3b) from an individual one-and-a-half times to twice as large as BHN 2P3a and exhibiting a more advanced degree of ossification, is referred to cf. *Enchodus* sp. A thickening of the posterior edge of the coronoid process is present and the shape of the articular is no longer visible in lateral view. The groove for the sensory mandibular canal is shallower below the articular facet than in BHN 2P3a and does not penetrate the bone in the posterior portion of the jaw. No trace of a retroarticular is visible.

Teeth. Several laterally compressed and sinuous teeth (1·5–3 mm long) with fine striations, are probably mandibular or ectopterygoid teeth of enchodontids. Two sections of long, straight teeth are present (BHN 2P3d). As is typical for some enchodontid palatine teeth, their cutting edges delimit two faces: one slightly, the other very, convex (Text-fig. 7B).

Scales. Two triradiate scales (*c*. 3 mm and 1·5 mm long) were found in the '*Enchodus* skull' nodule (BHN 2P3e). The angle between the posterior arms of the larger is about 70° (Text-fig. 7Ca). It bears thickened ridges along the axes of the arms and a posteriorly pointed spine projects from the centre. The smaller scale (Text-fig. 7Cb) has the same general shape, but the posterior arms are asymmetrically oriented and the central spine is blunter. No foramen for the lateral line canal is visible.

Ontogenetic status of the Enchodus *remains*

Small size is not a juvenile character for fishes or indeed other vertebrates. Wenz and Poyato-Ariza (1994) compared adults and juvenile specimens from several species of actinopterygians from the Lower Cretaceous of Montsec and Las Hoyas in Spain in order to establish the validity of

characters as diagnostic at different levels of the systematic hierarchy. For these authors, morphometric patterns and degree of ossification were the best characters for recognizing juvenile forms. The degree of ossification of different bones is the only practical character for determining the ontogenetic status of the *Enchodus* material described herein.

The bones of the skull roof of BHN 2P3a, in particular the frontal, bear a very light ornamentation, unlike the juveniles of some species from the Spanish localities which do not bear any ornamentation. Goody (1968) showed that small species of *Enchodus* have tubercular protuberances which develop into prominent ridges in larger species, although this character seems to be linked to the absolute size of the fishes and not their ontogenetic stage. However, the very light structure of the palatine and the presence of an independent articular portion in the angulo-articular are surely linked to the juvenile state of the specimen.

In addition, the relatively small number of teeth borne by the ectopterygoid and the lower jaw may also reflect the juvenile state of BHN 2P3a (Goody 1976), and the absence of any constriction of the notochord in the vertebral centra is more certainly a juvenile character (Wenz and Poyato-Ariza 1994). In sum, these observations indicate that BHN 2P3a represents a juvenile individual.

Other enchodid remains may represent juveniles. The medially open fenestra of the premaxilla BHN 2P11a, forming with its fellow an unpaired opening, is probably a juvenile character linked to an early state of ossification. The second opening on the lateral face of the premaxilla is perhaps also due to the incomplete ossification of the bone.

The posterior part of a mandible (BHN 2P3b) larger than that of BHN 2P3a provides information concerning growth in *Enchodus*. The articular is still not independent in an individual with a neurocranium *c.* 20–25 mm long (and thus twice the size of BHN 2P3a) and the mandibular sensory canal remains as a groove on the lateral face of the jaw. In *E. faujasi* (Goody 1968) and *E. lewesiensis* (Goody 1969) the sensory canal also runs in a groove, but in *E. marchesettii* (Goody 1969) the canal is located in a tube beneath the articular facet, and continues in a groove within the dentary. In the latter species, Goody (1969) indicated the presence of a very small bone, named the 'angular', on the postero-ventral angle of the jaw. However, following current nomenclature (Nelson 1973), it is probably a retroarticular. Chalifa (1996) observed a retroarticular forming the posterior margin of the mandible ventral to the articular facet in *E. zinensis*. This remarkably thin bone was probably present in all enchodontids, but may be lost during acid preparation.

The size of some of the teeth found in the matrix of the nodule BHN 2P3 provides further evidence that individuals substantially larger than BHN 2P3a are present at the Goulmima locality.

TAXONOMIC RELATIONSHIPS

Enchodus occurs in the Upper Cretaceous of North and South America, India, Europe, Africa and the Middle East, and possible *Enchodus* remains have been reported from the English Gault (Estes 1969) and the Lower Cretaceous of Equatorial Guinea (Gayet 1989). Arambourg (1952) recorded remains of *E. elegans* from the Lower Paleocene ('Montian') phosphates of Morocco, but this report is doubtful because the faunal assemblage may be the result of mixing between Cretaceous and Tertiary sediments (Cappetta 1987). *E. ferox* is reported from the Eocene of New Jersey (Goody 1976). This single Tertiary record remains to be confirmed.

Chalifa (1996) listed 21 species of *Enchodus*, but noted that the definition of species on the basis of disarticulated skeletal elements is open to question.

The semi-articulated skull

Apomorphies of Enchodontoidei (*sensu* Goody 1969, i.e. Enchodontidae + Eurypholidae) evident in BHN 2P3a include: the apparent absence of orbitosphenoid, basisphenoid, supraorbital and antorbital; palatine bone with a terminal tooth; and premaxillae with fenestrated pedicel (absent in *Saurorhamphus*).

Diagnostic features of Enchodontidae (Goody 1969; Raab and Chalifa 1987) that are also present in BHN 2P3a include: lower jaw long and deep behind the constricted symphysis; articular facet visible in lateral aspect; operculum convex posteriorly and deeper than broad.

Goody (1969) included two genera in the Enchodontidae: *Enchodus*, which has a large geographical range during the Cretaceous; and *Palaeolycus*, a monospecific genus known only from the Campanian of Sedenhorst in Germany. Specimens of the latter genus are rare, and the description of the only species, *P. dreginensis*, is deficient in many features (Goody 1969). Indeed, Goody (1976) noted that 'since the vast majority of *Enchodus* recoveries are skull fragments certain of them might well be *Palaeolycus* and not *Enchodus*'. Most importantly, the diagnosis of *Palaeolycus* is based on post-cranial features, thus preventing comparison with BHN 2P3a. To the Enchodontidae Raab and Chalifa (1987) assigned a new genus, *Parenchodus*, from the Upper Cenomanian of Israel. The Goulmima enchodontid (BHN 2P3a) lacks derived characters, such as an unfenestrated premaxilla, that are present in *Parenchodus*, and thus does not belong to this taxon.

No autapomorphies of the genus *Enchodus* (*sensu* Goody 1976) can be observed on BHN 2P3a, but because this specimen cannot be compared with *Palaeolycus* and because it is different from *Parenchodus*, the most parsimonious hypothesis is to assign BHN 2P3a to the genus *Enchodus*.

The skull of *Enchodus* is well known in five species: *E. faujasi*, from the Maastrichtian of Belgium (Dollo 1892), and perhaps from the Maastrichtian of southern France (Buffetaut and Cavin 1995), and *E. petrosus*, from the Upper Cretaceous of North America, both described in detail by Goody (1968, 1976); *E. lewesiensis*, from the Turonian and Senonian of England (Woodward 1901) and from the Senonian of northern France (Leriche 1902; Goody 1969); *E. zinensis*, represented by some skull bones from the Lower Maastrichtian of Northern Negev, Israel (Chalifa 1996); and *E. marchesetti*, from the Cenomanian of Hakel in Lebanon (Goody 1969), although the neurocranium is less precisely known in this form because it is represented only by flattened specimens.

Although the skull is generally similar in these five species and BHN 2P3a, there are distinct dissimilarities between the various taxa. There are notable differences in the structure of the trigemino-facialis chamber: in *E. lewesiensis*, *E. faujasi* and *E. zinensis* the trigeminal foramen opens into the posterior wall of the orbit, but in BHN 2P3a this foramen opens inside the *pars jugularis*. In *E. lewesiensis*, the superficial ophthalmic, otic and buccal branches of the trigeminal and facial nerves, and possibly the profundus nerve, crossed the prootic via the trigeminal foramen and the oculomotor nerve exited through a notch in the medial edge of the prootic (Goody 1969). The general structure of the trigemino-facialis chamber of *E. zinensis* is similar to that of *E. lewesiensis*, but the oculomotor nerve foramen was completely enclosed in bone and exited just in front of the trigeminal foramen (Chalifa 1996). In *E. faujasi* (Goody 1968) a single trigeminal foramen seems to pierce the internal face of the prootic, but within this bone the different nerve components split up and exited through several foramina on the orbital face of the prootic: one for the buccal branches of the trigeminal and facial nerves, one for the superficial nerve and one for the otic of the facial and the profundus nerves. The oculomotor exited by a separate medial foramen. The structure of the trigemino-facialis chamber of BHN 2P3a is similar to that of *E. faujasi*, but differs in some details: there is more than one opening for the trigeminal foramen on the internal face of the prootic, and the foramen for the buccal branches of the trigeminal and facial nerves opens inside the *pars jugularis*. Moreover, the otic branch of the facial (and perhaps the profundus) probably opened in the bottom of the groove formed by the two vertical laminae of the orbital face of the prootic. This groove has not been described in other species of *Enchodus*. In *E. faujasi* (Goody 1968, fig. 8A) the otic branch of the facial open into a dorsal depression. Chalifa (1996) described a short jugular canal in *E. zinensis* that is not enclosed in bone, but forms a groove through a robust crest (Chalifa 1996, figs 2b, 4e). Goody (1969, fig. 38B) observed on the lateral face of the prootic of a small *Enchodus* sp. (neurocranium < 40 mm long) a large opening situated anterior to the posterior opening of the *pars jugularis* that served for the transmission of the hyomandibular branch of the facial nerve and probably for the orbital artery. A narrow splint of bone forms the jugular canal in this specimen, as in BHN 2P3a, and confirms that important differences occur in the structure

of the trigemino-facialis chamber within a single genus. Both specimens exhibit the plesiomorphic condition (i.e. the presence of a jugular canal; Patterson 1964) but are also small in size and are perhaps juveniles; this suggests that the disappearance of the jugular canal may be an ontogenetic phenomenon in some species of *Enchodus*.

Enchodus faujasi and BHN 2P3a share a number of characters in common: the shape of the teeth (they are large, slightly compressed and their bases are expanded); the anterior mandibular tooth is almost twice as long as subsequent teeth; and an opening on the posterior face of the skull, below the occipital condyle, for the posterior myodome. Features shared in common by BHN 2P3a and *E. lewesiensis* are: a weakly developed supraoccipital crest; less than ten teeth on the mandible and seven on the ectopterygoid; an angle of about 30° formed posteriorly by the ectopterygoid; and the ornamentation of the mandible, by particulate ridges that radiate from the postero-ventral edge. *Enchodus zinensis* and BHN 2P3a share one feature: a palatine with a posterior margin that does not extend dorsally, although in BHN 2P3a the dorsal process is higher and more anteriorly situated than in *E. zinensis*. *Enchodus marchesetti* and BHN 2P3a share the following features: less than ten mandibular teeth, the presence of two small teeth situated anterior to the large mandibular teeth; and the size of the latter, almost twice as long as subsequent teeth. In addition, the vertebrae of *E. marchesetti* and BHN 2P3a have a neural arch that occupies the entire dorsal surface of the centrum, but the preservation of the Lebanese species does not show the structure of the neural arches and spines. Raab and Chalifa (1987) described paired neural spines in the abdominal vertebrae of *Parenchodus longipterygius* from the Upper Cenomanian of Israel, and Goody (1976) described anterior precaudal neural spines as separate lateral elements in *E. petrosus*, as in some vertebrae of BHN 2P3a. *Enchodus* sp. described by Goody (1969, pp. 83–85) also shows similarities to the species described herein: the lateral margin of the frontal is excavated above the orbit and there is a jugular canal in the trigemino-facialis chamber.

Arambourg (1954) described *E. venator* from the Lower Cenomanian of Jebel Tselfat, Morocco, a locality that is stratigraphically and geographically relatively close to the locality of Goulmima. The fishes from Jebel Tselfat are flattened and preserved on slabs of shale: a mode of preservation that makes it difficult to compare them with three-dimensional fishes. Specimens of *E. venator* are small (skull about 40 mm long), and this species also shares some characters with *Enchodus* from Goulmima: few teeth on the ectopterygoid (respectively five or six and seven); ornamentation of the mandible and of the operculum, and the presence of at least one tooth anterior to the large mandibular tooth. They differ from one another by the presence, in *E. venator*, of a premaxilla bearing numerous small teeth.

Microremains

The thin lamina of bone forming the posterior part of the premaxilla (BHN 2P11a) recalls the situation observed in *E. venator* (Arambourg 1954, fig. 60), and the palatine tooth (BHN 2P3d) appears similar to those of *E. venator* and several other species of *Enchodus* from Europe, Africa and North America (Arambourg 1954; Goody 1976).

The isolated scales (BHN 2P3c) compare well with the scales of other Cretaceous Enchodontoidei. Most of them have a reduced squamation, often restricted to enlarged specialized lateral-line scales (Rosen 1973). In *E. marchesettii* the scales marking the passage of the lateral line are rectangular with a deeply excavated posterior margin and a backwardly directed spine (Goody 1969). Arambourg (1954) described these scales in *E. venator* as '*écussons ornés*'. Goody (1976) observed only two large scutes that would have lain on either side of the caudal peduncle in *E. petrosus*. This type of scale is not known in other species of *Enchodus*. Other Enchodontoidei from the Upper Cretaceous, including eurypholids, dercetids and cimolichthyids, have these types of scales (Goody 1969). In some species, such as *Dercetis gracilis* from the Santonian of Sahel Alma, Lebanon (Goody 1969, fig. 82B), *Rhynchodercetis gortanii* from the Lower Cenomanian of Komen, Slovenia (Goody 1969, fig. 82C) and *Hastichthys gracilis* (= '*Rhynchodercetis*' *gracilis*) from the Lower

Cenomanian of Israel (Chalifa 1989, fig. 5), these scales are triradiate. The arms are thinner than those observed in the specimens from Goulmima and a posteriorly pointed central spine is also present. In conclusion, the triradiate scales from Morocco (BHN 2P3c) have the typical shape of Enchodontoidei scales and, lacking further information, they are assigned to *Enchodus* sp.

In addition to the taxa cited above, many other species of *Enchodus* have been erected on the basis of fragmentary material. In his review of North American enchodontid species, Goody (1976) pointed out some characters that are useful for specific designations. He followed in part Arambourg (1954) in creating two groups of *Enchodus* species based on palatine tooth morphology. Unfortunately, the palatine tooth of the specimen described herein is poorly known. However, if the palatine teeth found in the matrix of the nodule belong to the same species as BHN 2P3a, this form should be included in the group containing, amongst others, *E. venator*, *E. petrosus*, *E. marchesetti* and *E. lewesiensis*. The other group of species, characterized by a sigmoidal palatine tooth with one full-length cutting edge placed anteriorly, contains, amongst others, *E. libycus* from the Upper Cretaceous of North Africa (Arambourg 1952) and *E. gladiolus* from the Upper Cretaceous of North America (Goody 1976). Notably, *E. faujasi* exhibits characters of both groups in that the palatine tooth has two cutting edges and a sigmoidal curvature (Goody 1976).

Enchodus sp. from the Goulmima fauna can be characterized by the following features: the depth of the palatine bone above the maxillary groove is equal to approximately half the palatine length, the dorsal process of the palatine is well developed, the palatine tooth appears to have two laterally placed cutting edges, the mandible and ectopterygoid teeth have a slight sigmoidal curvature and are finely striated, the mandible has a marginal row of minute teeth, and the premaxilla has a few middle-sized teeth. This last feature seems to be unique among *Enchodus*, but, unfortunately, the characters listed are not sufficient to erect a new species, especially since some of them may be related to the juvenile state of BHN 2P3a. In any case, the Goulmima *Enchodus* is certainly very close to *E. venator*.

PALAEOECOLOGICAL IMPLICATIONS

Palaeoecology of the Goulmima assemblage

Many enchodontid microremains have been found in the matrix of the 40 nodules hitherto prepared from the localities in the vicinity of Goulmima. A complete analysis of these microremains has not yet been completed, but some preliminary results can be presented here. The enchodontid bones are generally from very small individuals. The largest remain found so far is a palatine tooth 9 mm long and with the same general shape as that of smaller specimens. Based on comparisons with the morphological proportions of *E. petrosus*, this tooth belonged to an individual with a skull *c.* 60 mm long (including the opercular bones). The closely related species *E. venator* is represented at the locality of Jebel Tselfat also by small specimens, but their head length (*c.* 40 mm) is longer than the estimated skull length of the majority of the individuals found at Goulmima. The presence of numerous juvenile *Enchodus* is unusual, especially since other species found in this fauna are rarely or never represented by juvenile specimens. It is unlikely that this unusual situation is a taphonomic artefact because taphonomic factors can produce size or shape biases, but not systematic biases. These observations suggest that the environment of deposition might have been used as a nursery ground for this species of *Enchodus*.

A previous study of the trophic structure of the assemblage from Goulmima (Cavin 1997*b*) showed that another specimen of *G. arambourgi*, the holotype (BHN 2P2), also exhibits direct evidence that this species preyed on *Enchodus* sp. because microremains form a concentration in the body cavity of the specimen and are associated with fossilized soft tissues of the alimentary tract. Microremains of *Enchodus* sp. are also found in the matrix of nodules containing sub-complete specimens of other species, for instance an individual of *Ichthyodectes bardacki* (BHN 2P28). This specimen also exhibited a small vomer of a pycnodont (*c.* 5 mm long) in its pelvic region, although it became detached during preparation. Other direct evidence of predation on small fishes is evident on a specimen of *Osmeroides rheris* (BHN 2P36) which exhibits in its pelvic region a coprolite

(*c*. 8 mm long) which bears five fish vertebrae in anatomical connection (Cavin 1997*b*, fig. 1). Piscivorous fishes are the most abundant, in terms of numbers of species and of individuals, in the fish assemblage of Goulmima and may have been attracted by the presence of numerous small *Enchodus*. Moreover, *Osmeroides rheris* could have been both piscivorous (as indicated by the presence of microremains in the body cavity) and durophagous (presence of crushing teeth). The only exception is *Araripichthys corythophorus*, known by a single specimen (BHN 2P35), which, because of its edentulous mouth and its general morphology indicating a slow-swimming fish, was probably microphagous.

Comparison with other localities

The occurrence of large numbers of juveniles of various species of actinopterygians has been reported for the Early Cretaceous continental deposits of Las Hoyas and Montsec in Spain (Wenz and Poyato-Ariza 1994). At these localities a few species are represented only by adult specimens, but these are rare and the absence of juveniles may be a bias related to our, as yet, incomplete knowledge of the Las Hoyas and Montsec assemblages. All other species are known from both juvenile and adult individuals. In addition, at both localities, rare forms that are represented almost exclusively by juveniles are either of doubtful determination or belong to species that need systematic revision and, consequently, are of little significance.

Reconstruction of trophic relationships has been established on the basis of stomach contents for the well-known ichthyofauna from the Santana Formation of Brazil (Maisey 1994). The upper part of this Formation (the Romualdo Member), commonly considered to be Albian in age, yields fossil fishes contained in calcareous concretions. In the trophic network based on these fishes, all but one species found in the alimentary canals of predators are known to be represented in other nodules by articulated specimens, and the majority of them are adult individuals (Maisey 1994).

The trophic structure seems to be different in the Spanish and Brazilian ichthyofaunas and those of Goulmima: in the former localities, the smaller individuals (and the smaller prey items) are also known from larger specimens, but in the latter, the smaller individuals do not seem to co-occur with larger specimens. Differences in the environmental conditions of these localities may be responsible for the differences in the structure of the fish faunas. The localities of Las Hoyas and Montsec are clearly located in continental deposits, whilst the palaeoecology of the Romualdo Member suggests a basin with a dominant freshwater phase at the base, followed by a lagoon with saline and hypersaline phases (Maisey 1994). A marine phase occurs some metres above the Romualdo Member but contains no fish remains (Martill 1993). By contrast, the deposits at Goulmima are marine, as indicated by the presence of ammonites and marine reptiles.

CONCLUSIONS

The presence at Goulmima of a species of *Enchodus* very similar to *E. venator* from the Lower Cenomanian of Jebel Tselfat in Morocco is the first occurrence of a closely related form common to both these localities. Other components of the Goulmima assemblage show affinities with the possibly older fish assemblage from the Lower Cretaceous of Araripe, Brazil. Taxa occurring in both these assemblages include *Araripichthys*, a genus restricted to these localities, and closely related pachyrhizondontids (*Rhacolepis* in Brazil and *Goulmimichthys* in Morocco), ichthyodectids (*Cladocyclus* in Brazil and *Ichthyodectes* in Morocco) and albuloids (*Brannerion* and *Paraelops* in Brazil and *Osmeroides* in Morocco). Differences between the palaeoenvironments are emphasized, but there may also have been some similarities in physico-chemical conditions and/or taphonomic conditions as suggested by the more-or-less similar mode of preservation in Goulmima and Araripe (Martill 1988), in particular, the similar morphology of the fish-bearing concretions, mineralogy of the cement (early diagenetic calcite), and presence of weakly deformed fish remains. The predominance of juvenile forms of one taxon at Goulmima indicates a type of palaeoenvironment or taphonomic history so far unique among Upper Cretaceous ichthyofaunas.

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REFERENCES

AGASSIZ, L. 1833–44. *Recherches sur les poissons fossiles*. 5 vols. Neuchâtel, 1420 pp., 396 pls.

ARAMBOURG, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc, Algérie, Tunisie). *Notes et Mémoires, Service Géologique du Maroc, Rabat*, **92**, 1–372.

—— 1954. Les poissons crétacés du Jebel Tselfat (Maroc). *Notes et Mémoires, Service Géologique du Maroc, Rabat*, **118**, 1–188.

BERG, L. S. 1940. Classification of fishes both recent and fossil. *Transactions of the Zoological Institute of Leningrad*, **5** (2), 1–519.

BUFFETAUT, E. and CAVIN, L. 1995. Nouveaux restes de vertébrés du Maastrichtien supérieur de la carrière du Jadet. *Bulletin trimestriel de la Société Géologique de Normandie et Amis du Muséum du Havre*, **82** (4), 31–34.

CAPPETTA, H. 1987. Extinctions et renouvellements fauniques chez les Sélaciens post-jurassiques. *Bulletin de la Société Géologique de France, Nouvelle Série*, **150**, 113–131.

CAVIN, L. 1995. *Goulmimichthys arambourgi* n.g., n. sp., un Pachyrhizodontidae (Actinopterygii, Teleostei) d'une nouvelle localité à nodules fossilifères du Turonien inférieur marocain. *Comptes Rendus de l'Académie des Sciences, Paris, Série IIa*, **321**, 1049–1054.

—— 1997*a*. Nouveaux Teleostei du gisement Turonien inférieur de Goulmima (Maroc). *Comptes Rendus de l'Académie des Sciences, Paris, Série IIa*, **325**, 719–724.

—— 1997*b*. Supposed and direct evidence of trophic relationships within the fish community of the Lower Turonian of Goulmima, Morocco. First European Workshop on Vertebrate Palaeontology, Copenhagen, 1996. *Geological Society of Denmark, On Line Series*, **1**, www.purl.dk/net/9710-0100.

CHALIFA, Y. 1989. Two new species of longirostrine fishes from the Early Cenomanian (Late Cretaceous) of Ein-Yabrud, Israel, with comments on the phylogeny of the Dercetidae. *Journal of Vertebrate Paleontology*, **9**, 314–328.

—— 1996. New species of *Enchodus* (Aulopiformes: Enchodontidae) from Northern Negev, Israel, with comments on evolutionary trends in the Enchodontoidei. 349–367. *In* ARRATIA, G. and VIOHL, G. (eds). *Mesozoic fishes – systematics and paleoecology*. Verlag Dr Friedrich Pfeil, Munich, 575 pp.

DOLLO, L. 1892. Première note sur les téléostéens du Crétacé supérieur de la Belgique. *Bulletin de la Société Belge de Géologie, Paléontologie et Hydrogéologie*, **6**, 180–189.

ESTES, R. 1969. Studies on fossil phyllodont fishes: *Casierius*, a new genus of albulid from the Cretaceous of Europe and North America. *Eclogae Geologicae Helveticae*, **62**, 751–755.

FERRANDINI, M., PHILIP, J., BABINOT, J.-F., FERRANDINI, J. and TRONCHETTI, G. 1985. La plate-forme carbonatée du Cénomano-Turonian de la région d'Erfoud-Errachidia (Sud-Est marocain): stratigraphie et paléo-environnements. *Bulletin de la Société Géologique de France*, **4**, 559–564.

GAYET, M. 1989. Note préliminaire sur le matériel paléoichthyologique éocrétacique du Rio Benito (sud de Bata, Guiné Equatoriale). *Bulletin du Muséum National d'Histoire Naturelle, Série 4, Section C*, **11** (1), 21–31.

GOODY, P. C. 1968. The skull of *Enchodus faujasi* from the Maastrichtian of southern Holland. *Proceedings of the Koninkliske Nederlandse Akademie van Wetenschappen, Amsterdam, Series B*, **71**, 209–231.

—— 1969. The relationships of certain Upper Cretaceous teleosts with special reference to the myctophoids. *Bulletin of the British Museum (Natural History), Geology Series*, Supplement **7**, 1–255.

—— 1976. *Enchodus* (Teleostei: Enchodontidae) from the Upper Cretaceous Pierre Shale of Wyoming and South Dakota with an evaluation of North America enchodontid species. *Palaeontographica, Abteilung A*, **152**, 91–112.

LERICHE, M. 1902. Révision de la Faune ichthyologique des Terrains crétacés du Nord de la France. *Annales de la Société Géologique du Nord*, **31**, 87–155.

MAISEY, J. G. 1994. Predator–prey relationships and trophic level reconstruction in a fossil fish community. *Environmental Biology of Fishes*, **40**, 1–22.

MANTELL, G. A. 1822. *The fossils of the South Downs; or illustrations of the geology of Sussex*. Lupton Relfe, London, 320 pp., 42 pls.

MARTILL, D. M. 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. *Palaeontology*, **31**, 1–18.

—— 1993. *Fossils of the Santana and Crato formations*. Field Guides to Fossils: Number 5. Palaeontological Association, London, 159 pp.

NELSON, G. J. 1973. Relationships of clupeomorphs, with remarks on the structure of the lower jaw in fishes. 333–349. *In* GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds). Interrelationships of fishes. *Zoological Journal of the Linnean Society*, **53**, Supplement 1, 1–536.

PATTERSON, C. 1964. A review of Mesozoic acanthopterygian fishes, with special reference to those of the English Chalk. *Philosophical Transactions of the Royal Society of London*, **247**, 213–482.

RAAB, M. and CHALIFA, Y. 1987. A new enchodontid fish genus from the Upper Cenomanian of Jerusalem, Israel. *Palaeontology*, **30**, 717–731.

ROSEN, D. R. 1973. Interrelationships of higher euteleostean fishes. 397–513. *In* GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds). Interrelationships of fishes. *Zoological Journal of the Linnean Society*, **53**, Supplement 1, 1–536.

WENZ, S. and POYATO-ARIZA, J. 1994. Les Actinoptérygiens juvéniles du Crétacé inférieur du Montsec et de Las Hoyas (Espagne). *Géobios, Mémoire Spéciale*, **16**, 203–212.

WOODWARD, A. S. 1901. *Catalogue of the fossil fishes in the British Museum (Natural History)*. Part 4. British Museum (Natural History), London, 636 pp.

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A SHORT-LIMBED LIZARD FROM THE LOWER CRETACEOUS OF SPAIN

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ABSTRACT. The Early Cretaceous (Barremian) locality of Las Hoyas (Cuenca Province, Castilla-La Mancha), Spain, has yielded a relatively diverse lizard assemblage dominated by the scincomorph genus *Meyasaurus*, but including at least two further taxa: one with long limbs and the other with relatively short limbs. The short-limbed lizard is described here. It resembles *Meyasaurus* in having a waisted frontal, but differs in many other features including the absence of sculpture on the skull bones, the presence of simple conical rather than bicuspid teeth, and the relative proportions of the limbs to the presacral body length. Comparison with other Jurassic and Early Cretaceous lizards supports the erection of a new taxon, here named *Hoyalacerta sanzi* gen. et sp. nov. Parsimony analysis suggests that *Hoyalacerta* is a primitive stem-group lizard, lying outside crown-group Squamata (Iguania + Scleroglossa).

LAS Hoyas is a lithographic limestone locality in eastern Spain (Cuenca Province, Castilla-La Mancha) representing a freshwater lacustrine environment of Barremian age (Fregenal-Martínez and Meléndez 1995). The site has yielded a rich assemblage of plants, invertebrates and vertebrates (Sanz *et al.* 1988), the last including birds (Sanz and Buscalioni 1992), an ornithomimosaurid dinosaur (Pérez-Moreno *et al.* 1994), salamanders (Evans and Milner 1996) and the first complete albanerpetontid amphibians (McGowan and Evans 1995). It is also one of several Spanish localities that have produced Early Cretaceous lizards (Evans and Barbadillo 1997), but is unique in yielding specimens which are complete and fully articulated. Las Hoyas produced the first complete specimens of the derived scincomorph *Meyasaurus*, establishing the synonomy of *Meyasaurus* Vidal, 1915 and *Ilerdaesaurus* Hoffstetter, 1966 (Evans and Barbadillo 1996, 1997), both originally described from the Catalan site of Montsec, but on the basis of a postcranial skeleton and an isolated skull respectively. Lizards have also been described from Uña (Cuenca Province, Castilla-La Mancha; Richter 1991, 1994*a*, 1994*b*), with four known taxa: *Meyasaurus* (*Ilerdaesaurus*); two paramacellodid scincomorphs – *Becklesius* and *Paramacellodus*; and the indeterminate *Cuencasaurus* Richter, 1994*b* represented by a fragmentary dental element. In addition, Richter (1994*b*) has reported both *Meyasaurus* and paramacellodids from Galve (Teruel Province, Castilla-La Mancha). Thus, on the basis of these four sites, Spanish Early Cretaceous lizard assemblages appear to be characterized by the presence of *Meyasaurus* and paramacellodids, but additional specimens from Las Hoyas show that lizard diversity was greater than expected. Furthermore, no trace of paramacellodids, characterized by a body armour of small rectangular osteoscutes, has been found at Las Hoyas. Of the eight lizard specimens currently known, six can be referred to *Meyasaurus* (Evans and Barbadillo 1996, 1997). The others, LH 11000 and LH 11001, are quite distinct and each represents a new genus. LH 11001 is a small specialized long-limbed lizard with broad ribs and exceptionally long penultimate phalanges (Evans and Barbadillo in press). In marked contrast, LH 11000 is relatively long-bodied and short-limbed. It forms the subject of this paper.

The Early Cretaceous was an important period in lizard evolution during which there was a gradual changeover from assemblages dominated by the archaic lineages of the Jurassic to the essentially modern assemblages which characterize the Upper Cretaceous. Early Cretaceous lizards are currently known from Japan (SEE, pers. obs.), Brazil (Evans and Yabumoto 1998), Morocco (Richter 1994*b*; Broschinski and Sigogneau-Russell 1996), North America (Nydam *et al.* 1997),

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Mexico (Reynoso 1996*a*, 1996*b*), Britain (Hoffstetter 1967), Italy (D'Erasmo 1915) and China (Endo and Shikama 1942; Keqin Gao, pers. comm. 1995). However, most of these localities yield only fragmentary specimens. Whilst these are of considerable value in discussions of palaeobiogeography and phyletic radiation, their contribution to morphological studies (character evolution, phylogeny reconstruction) is limited. Complete specimens, like those from Las Hoyas, China and Mexico, are rare and important.

Institutional abbreviations. LH, Museo de Cuenca, Cuenca, Castilla-La Mancha, Spain; UCL, University College London.

SYSTEMATIC PALAEONTOLOGY

LEPIDOSAURIA Haeckel 1866
SQUAMATA Oppel 1811
Family indet.

Genus HOYALACERTA gen. nov.

Derivation of name. From Las Hoyas, the type locality, and *lacerta*, Latin, lizard.

Type species. Hoyalacerta sanzi sp. nov.

Diagnosis. A lizard showing the following character combination: frontals paired, constricted between orbits; jugal a slender arc, extends to anterior margin of orbit; premaxilla paired with relatively large teeth; ectopterygoids with anteroposterior alignment between pterygoid flange, maxilla and jugal; quadrate with large lateral conch, but no medial wing; squamosal slender, with no posterodorsal expansion; dentary shallow and parallel-sided with 40 small, close-packed teeth in each ramus; 27 or 28 presacral vertebra, dorsal vertebrae somewhat elongated with extended neural arch pedical reducing size of intervertebral foramina; vertebral centra procoelous; fore and hind limbs less than one-third of snout–vent length.

Range. Lower Cretaceous, Barremian, Spain.

Hoyalacerta sanzi sp. nov.

Text-figures 1–5

Derivation of name. To honour Professor José-Luis Sanz, Universidad Autónoma Madrid, who has directed the Las Hoyas project since its inception.

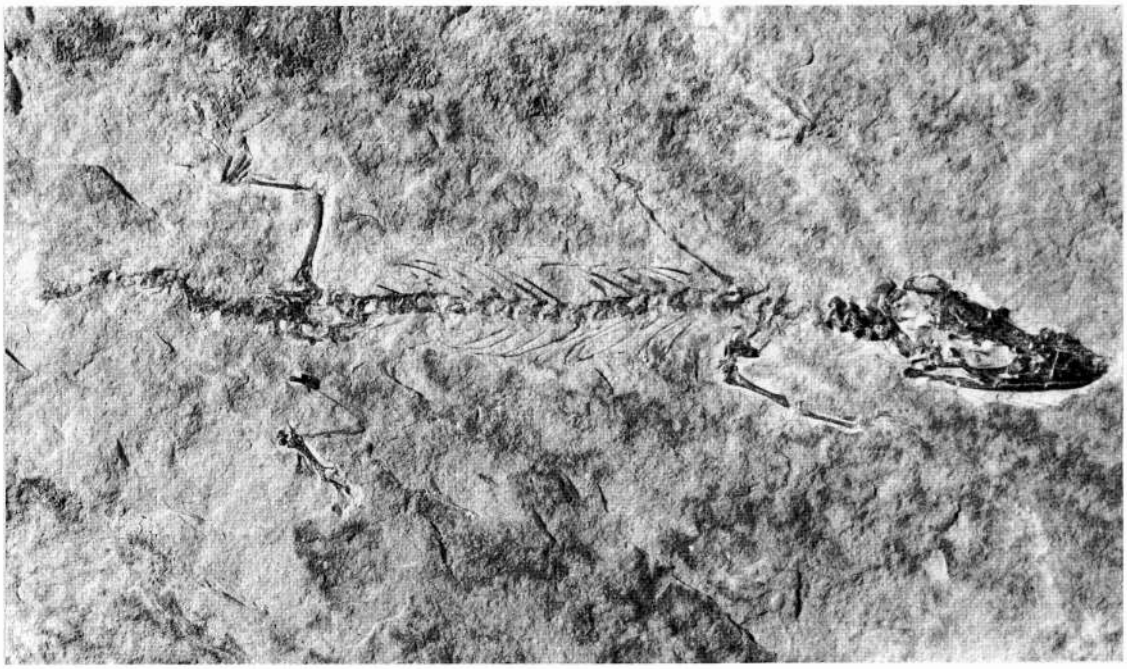
Material. Single holotype specimen: LH 11000, Museo de Cuenca, Cuenca, Spain.

Type locality. Las Hoyas, Cierva Township, Cuenca, Castilla-La Mancha, Spain.

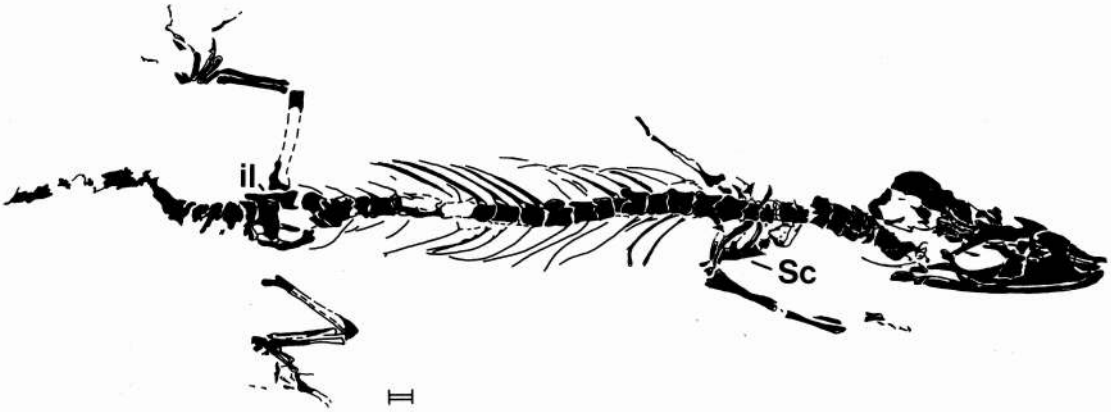
Type horizon. Calizas de la Huérguina Formation (Limestone Unit III), Lower Cretaceous (Barremian).

Diagnosis. As for genus.

Comparisons. Hoyalacerta differs from *Meyasaurus* in having a homodont dentition of simple conical teeth (*contra Meyasaurus* which has a heterodont dentition with bicuspid posterior teeth, even in very young animals); no posterior expansion of the squamosal (*contra Meyasaurus* which is characterized by a posteriorly expanded squamosal); trunk ribs of almost uniform length (elongated anterior dorsal ribs in *Meyasaurus*); 27 or 28 presacral vertebrae (25 in *Meyasaurus*); elongated neural arch pedicels that reduce the size of the intervertebral foramina (round open foramen in *Meyasaurus*); and relatively short limbs (longer in *Meyasaurus*). Tooth numbers alone are insufficient to distinguish *Hoyalacerta* from *Meyasaurus*, since *Meyasaurus unaensis* Richter, 1994*a*, from Uña, is diagnosed as having more than 40 small teeth, as compared with around 30 in other known species. However, the teeth in *M. unaensis* are still clearly bicuspid. Together with



TEXT-FIG. 1. *Hoyalacerta sanzi* gen. et sp. nov.; holotype, LH 11000; Las Hoyas; main block, LH 11000b, showing skeleton; × 3.



TEXT-FIG. 2. *Hoyalacerta sanzi* gen. et sp. nov.; holotype, LH 11000; Las Hoyas; outline drawing of main block to show main features and proportions of the specimen. Scale bar represents 1 mm.

differences in squamosal shape, vertebral shape and number, rib and limb proportions, the differences in the dentition distinguish *Hoyalacerta* from the other Las Hoyas lizard taxa.

Hoyalacerta differs from the third Las Hoyas lizard specimen, LH 11001, in having procoelous vertebrae (amphicoelous in LH 11001), thin ribs (proximally broad but tapering in LH 11001), presacral vertebral number (25 or 26 in LH 11001); and limb proportions. The latter represent the most striking difference between these animals. In *Hoyalacerta*, the forelimb is 23·5 per cent. of the snout–vent length (53 per cent. in LH 11001), whilst the hindlimb is 32·3 per cent. of the snout–vent length (57 per cent. in LH 11001). Furthermore, LH 11001 is characterized by exceptionally

elongate penultimate phalanges on both manus and pes, a feature lacking in all other described Jurassic and Cretaceous fossil lizards (Evans and Barbadillo in press), including *Hoyalacerta* and *Meyasaurus*.

Comparison with other early fossil lizards is complicated by the fact that many are represented by isolated jaws. There are no traces of osteoderms in association with the body of *Hoyalacerta* (*contra* paramacellodids) and the high tooth number precludes attribution to the indeterminate *Cuencasaurus* from Uña (Richter 1994*b*). The Purbeck (Berriasian) *Pseudosaurillus* (Hoffstetter 1967) also has delicate jaws with small teeth, but the frontals bear pustulate sculpture, lacking in *Hoyalacerta*. Of the anguimorphs, *Dorsetisaurus* has sculptured roofing bones and distinctive keeled teeth (Hoffstetter 1967), whilst *Parviraptor* (Evans 1994) has fewer, highly trenchant teeth. No known Jurassic or Early Cretaceous lizard shows the combination of skull, jaw and vertebral characters found in *Hoyalacerta*, and none shows its body proportions (Estes 1983; Evans 1993, 1994). Erection of a new genus for the short-limbed Las Hoyas lizard is therefore justified.

Description

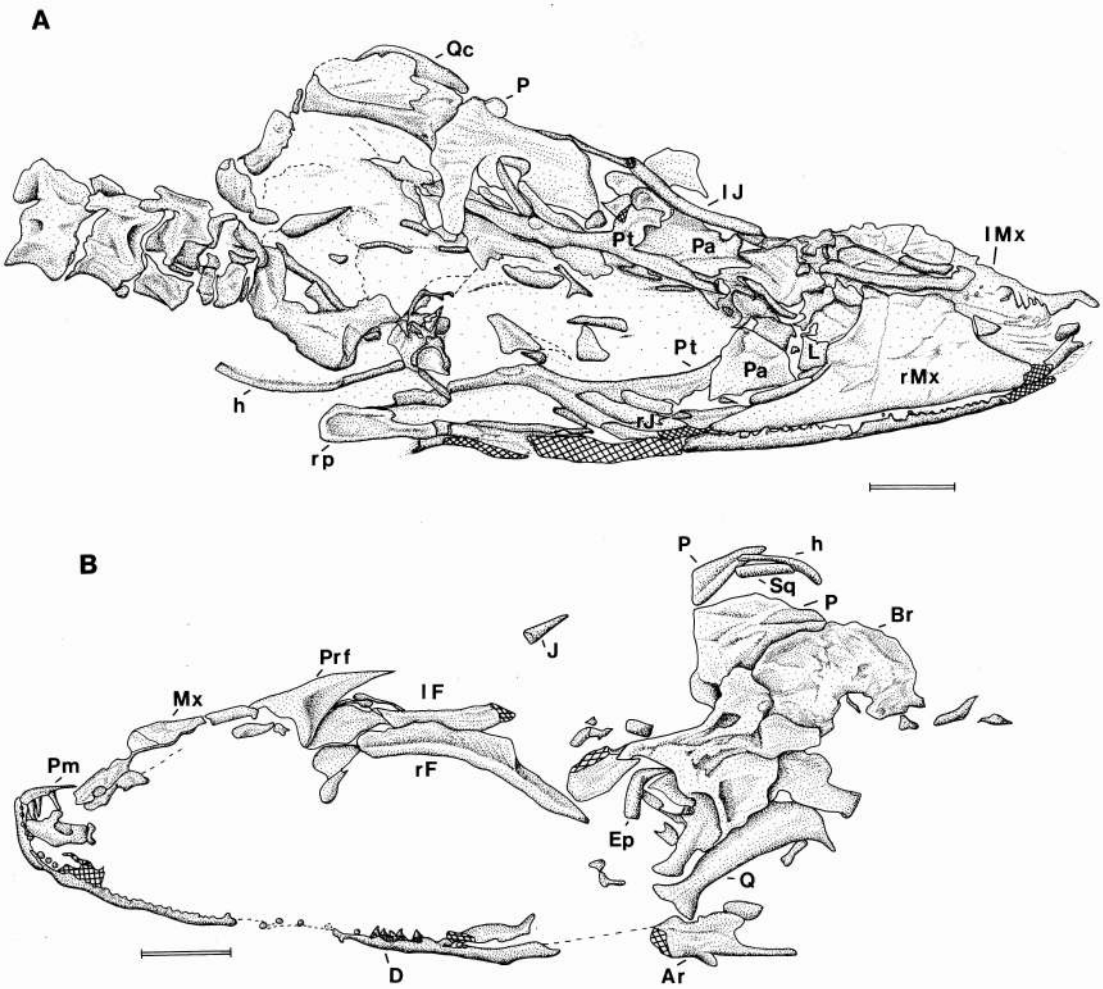
The single specimen of *Hoyalacerta sanzi* is a small skeleton preserved as part and counterpart. The skeleton is divided between the blocks such that most of the skull and part of the skeleton lies on the main block LH 11000b, whilst part of the skull (frontals, right prefrontal, right quadrate, jaw fragments, braincase, Text-fig. 3B) and the remainder of the skeleton lies on LH 11000a (Text-figs 1–3). On the main block, the skeleton is preserved in essentially dorsal aspect, although the anterior part of the skeleton is twisted to the left so that the skull is seen in a right dorsolateral view and has been compressed obliquely so that the left temporal region and left jaw lie below the skull roof and palate (Text-fig. 3A). The postcranial skeleton is largely complete, missing only parts of the left forelimb, of the femora and of the feet, although dorso-ventral compression makes the pectoral and pelvic girdles difficult to interpret.

The specimen is small and this raises the question of its ontogenetic status. The scapula and coracoid appear to be fused without an obvious suture, the neural arch pedicels are fully ossified and the skull bones have a finished appearance. However, the weak ossification of the limb bone epiphyses, and of the carpus and tarsus, suggests skeletal immaturity. There have been few published studies of post-hatching skeletogenesis in lizards, but comparison with stained and skeletal series of lizards in the collections of the Universidad Autónoma Madrid and at University College London (Fabiola Barahona, pers. comm. 1997), suggests that LH 11000 was subadult. Allowing for some variation between living taxa in the timing of fusion of the scapula and coracoid, the combination of features shown by LH 11000 is well matched by that of a cleared and stained subadult specimen of the lacertid lizard genus *Acanthodactylus erythrurus* (Spain, Africa), currently in the UCL collections. At 50 mm snout–vent length, the *Acanthodactylus* specimen is roughly 75 per cent. of the length of a large adult male of the same species. On this basis, a large adult of *Hoyalacerta* may have had a snout–vent length (roughly equivalent to snout to second caudal vertebra length on a skeleton) of about 45 mm (34 mm in LH 11000).

Skull. Even allowing for crushing, the skull appears to have been relatively shallow and lightly built. The right maxilla is clearly visible. It is unsculptured and bears around 40 small, closely packed, fully pleurodont teeth. The premaxillary process is slender and medially incurved, the facial process is broad and deep, and the posterior process is slender. The last is excluded from the orbital margin by the prefrontal, lacrimal and jugal. Of the paired premaxilla, only the left is visible (Text-fig. 3B). Its dorsal process rises at a low angle to the horizontal. There are four or five tooth positions, and the three teeth preserved *in situ* are at least twice the size of those on the dentary and maxilla.

The nasals are too fragmentary to yield useful information. The frontals are strongly built, but narrow between the orbits, although the effect is exaggerated because the right bone has rotated so that its orbital margin, rather than the dorsal surface, faces the viewer (Text-fig. 3B). The cristae cranii (subolfactory processes) are weakly developed and would have made little, if any, contribution to the orbitonasal flange. The midline suture appears simple (not interdigitated) and the frontals may have been co-ossified in fully adult individuals. Posteriorly, each orbital border is extended into a long narrow process which met the lateral margin of the parietal.

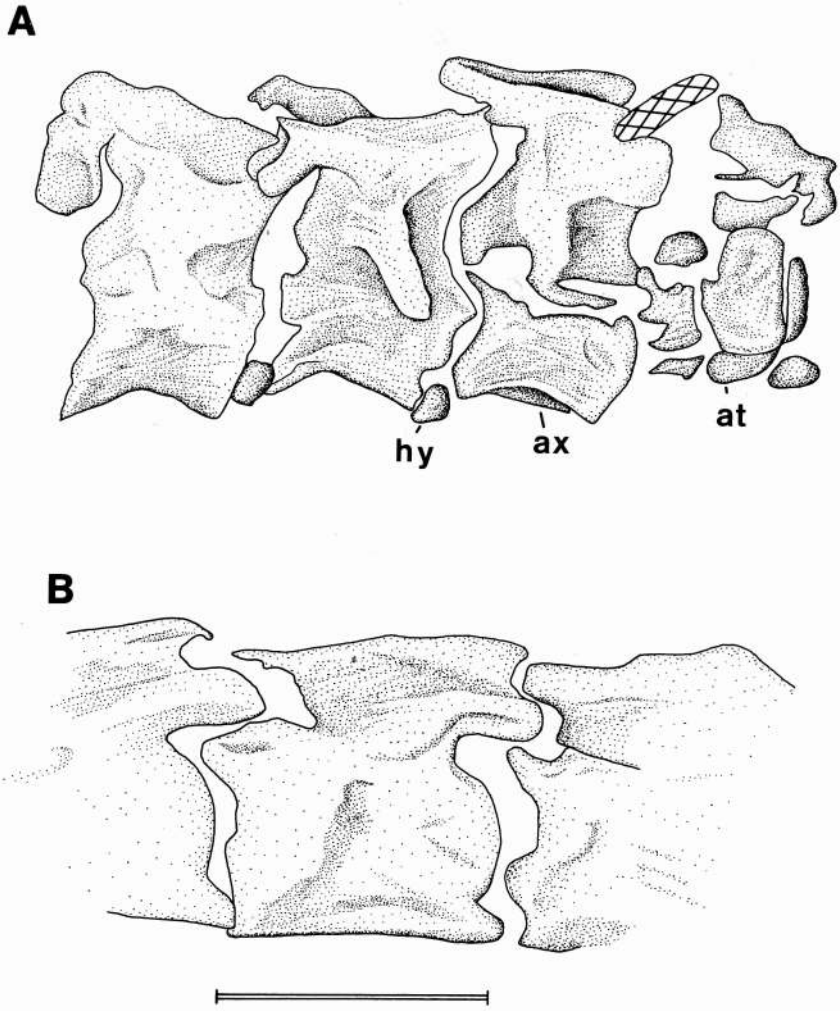
The parietal region is not well preserved and appears as flat plates crushed into the palate, so that it is not clear if the parietal was single or paired. The bone surface is unsculptured, but there are strong anterolateral



TEXT-FIG. 3. *Hoyalacerta sanzi* gen. et sp. nov.; holotype, LH 11000; Las Hoyas. A, LH 11000b; main part of skull, right dorso-lateral view. B, LH 11000a; remainder of skull, left ventrolateral view. Scale bars represent 1 mm.

facets, either for contact with the postfrontal/postorbitofrontal, or for the posterior process of the frontal. The lateral margin of the parietal is sufficiently deep to have accommodated the attachments of the jaw adductor muscles and the upper temporal fenestra was presumably fully open (the derived condition is a flat parietal plate into which the adductor muscles have a ventral insertion; the upper temporal fenestra is often closed or reduced in size). Posteriorly, each parietal was extended into a deep postparietal process with a strong lateral facet, presumably for the supratemporal. It is not possible to determine whether a parietal foramen was present.

The prefrontals have an inflated body and a relatively short, tapering posterior orbital process. A small lacrimal is interposed between the prefrontal and the anterior process of the jugal. The jugal forms a slender arc which extends to the anterior tip of the orbit and ascends posteriorly to the postorbital region. The midsection is missing on the right side, but the bone is seen in medial view in the left orbit and lacks any trace of a posterior quadratojugal spur. The temporal region is damaged on both sides, but LH 11000*a* bears the pointed posterior process of a postorbital/postorbitofrontal in contact with two slender elements, one of which is interpreted as the anterior part of a delicate squamosal, whilst the other seems to be part of the hyoid (Text-fig. 3B).



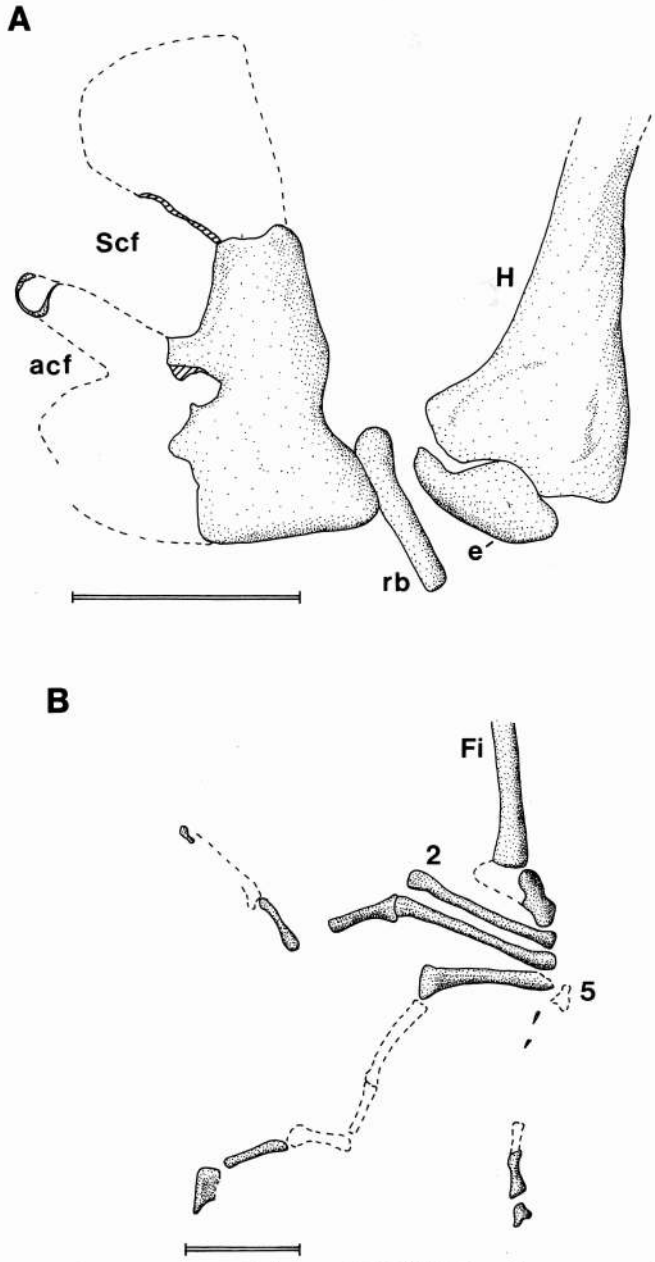
TEXT-FIG. 4. *Hoyalacerta sanzi* gen. et sp. nov.; holotype LH 11000; Las Hoyas; vertebral structure. A, cervical region, right lateral view. B, dorsal region, left lateral view, counterpart, LH 11000a. Scale bar represents 1 mm.

The quadrate is preserved on both sides, although that on the right (Text-fig. 3A) has been twisted through 180° by the movement of the skull roof relative to the braincase and palate. It is seen from above on the left side (Text-fig. 3B). Both bones provide evidence of a well-developed lateral conch, but little or no medial expansion. This accords with the slender structure of the pterygoid. Columnar epipterygoids are present.

Of the palate and braincase, relatively little can be seen clearly. The pterygoids are the most obvious elements: slender Y-shaped bones which meet plate-like palatines anteriorly, ectopterygoids antero-laterally, and quadrates posteriorly (Text-fig. 3A). Medially, they bordered a broad interpterygoid vacuity and the palatine processes appear to have been relatively elongate. Fossae for the epipterygoids are clearly visible, and the left epipterygoid is roughly in position. The pterygoid flange is rather weakly developed, probably because the slender ectopterygoid runs anteroposteriorly rather than mediolaterally. Despite this arrangement, however, the maxilla probably entered the margin of the suborbital fenestra.

Parts of the braincase overlie the parietal on the counterpart block, but little detail is preserved.

Hyoid Fragments of the hyoid apparatus are preserved on both blocks.



TEXT-FIG. 5. *Hoyalacerta sanzi* gen et sp. nov.; holotype LH 11000; Las Hoyas; appendicular skeleton. A, right pectoral girdle, lateral view, and disarticulated humerus, proximal part, dorsal view. B, left foot, dorsal surface. Scale bars represent 1 mm.

Lower jaw. The dentary is a long slender bone with roughly parallel borders. It bears *c*. 40 teeth, most of which are broken, but are of constant small diameter. The few complete posterior teeth show the crowns to be simple. No details are available of the medial surface of the dentary. The accessory bones form a postdentary region which is almost as long as the dentary, and equally slender. The region is incomplete, but the surangular tapers anteriorly and the adductor fossa appears to have been relatively small. The retroarticular process is wide and

parallel-sided, and without any obvious medial torsion so that it lies roughly in line with the postdentary bones.

Postcranial skeleton. A series of eight cervical and 19 or 20 dorsal vertebrae are preserved in articulation. The cervicals are short with long oblique synapophyses (Text-fig. 4A) whilst the dorsal vertebrae are elongated, with long neural arch pedicels and small, rounded condyles (Text-fig. 4B). The intervertebral spaces are restricted laterally by small bony flanges which form posterior extensions from the arch pedicels. The neural spines are very low in both the cervical region and trunk. Accessory articulations (zygosphenes) are not evident. In the neck, a hypapophysis is preserved in association with the atlas intercentrum, and there is a trace of a keel on the axis. There are fully intercentral hypapophyses between the third and fourth, and fourth and fifth centra, but these lack any development of a ventral keel. No hypapophyses are visible beyond this point. In some lizards (e.g. *Meyasaurus*), the sacral transverse processes fuse distally to enclose a foramen sacral; this does not appear to be the condition in *Hoyalacerta*. The first two or three caudals bear long slender rib processes; beyond this, the centra are autotomous.

Ribs are certainly present on the fifth cervical, and perhaps anterior to this. The fifth to seventh ribs are short but expanded, whilst the eighth resembles the sternal ribs that follow it in all but length. The thoracic ribs are slender and of constant width. They are present on all but the last two or three presacrals.

In general, the limbs, although unspecialized, are relatively short (forelimb = 23·5 per cent. of snout–vent length; hindlimb = 32·3 per cent. of snout–vent length), although this appearance is exaggerated by the elongation of the presacral column by two or three vertebrae.

The right scapulocoracoid is partially preserved and shows a narrow scapular blade with a strong scapulocoracoid fenestra, and a relatively small coracoid with a single (anterior) fenestra (Text-fig. 5A). The suture between the bones is closed. Neither the clavicular head nor the interclavicle is preserved. The forelimb is slender, without ossified epiphyses (apart from the proximal humeral head), and the radius/ulna are roughly 83 per cent. of the humeral length. The hands are poorly preserved, with a weakly ossified carpus and short metacarpals, but no visible phalanges.

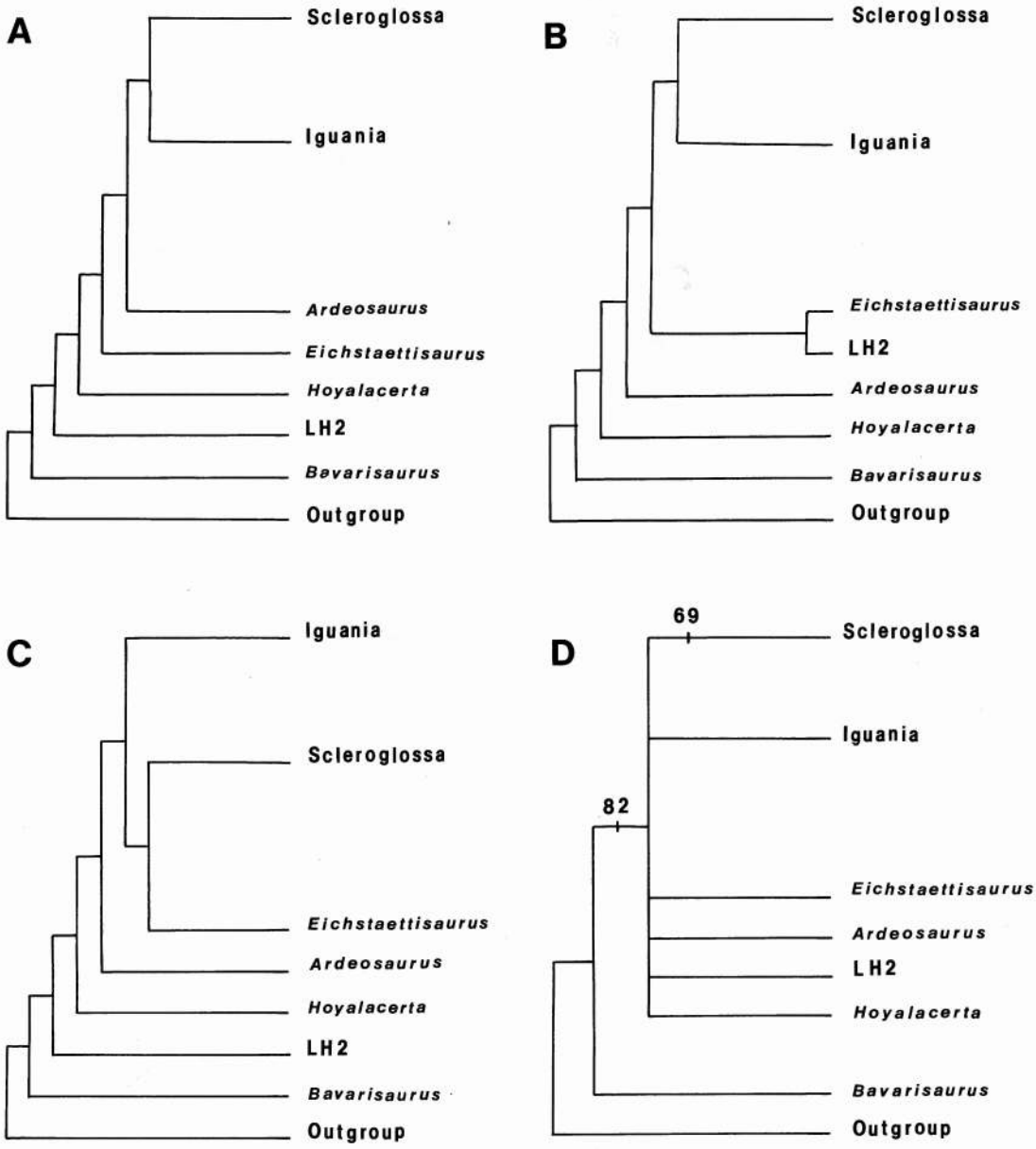
Little of the pelvis is visible except the dorsal parts of the slender tapering iliac blades. The femur is relatively robust by comparison with the gracile tibia and fibula. The latter reach around 75 per cent. of the femoral length and are without marked ridges or processes. The tarsus is obscured by the metatarsals, but appears to be only partially ossified with rounded proximal elements. The foot (Text-fig. 5B) is comparatively long, with slender metatarsals, of which the third is of roughly the same length as the fourth, and a long fourth digit. The phalangeal formula is 2:3:4:5:3/4, and the claws are delicately built with small tapering tips.

PHYLOGENETIC POSITION

Method

A parsimony analysis was performed using a matrix of 254 characters taken from lists originally formulated by Estes *et al.* (1988) and Gauthier *et al.* (1988), but with a number of two state characters combined into multistate characters; several characters extended to include character states possessed by both crown-group and outgroup taxa; and with autapomorphies removed (Evans and Barbadillo in press). The full character list includes soft part characters which cannot be coded for fossil taxa, but are important in the resolution of modern groups. Most of the data on living groups was taken from Estes *et al.* (1988) and Gauthier *et al.* (1988), whilst that on the fossil taxa is mostly from published and unpublished work by the senior author (Evans 1988, 1991, 1993, 1994; Evans and Barbadillo 1996, 1997, in press; Evans and Chure 1998*a*, 1998*b*; Waldman and Evans 1994). The initial runs included 27 living and fossil taxa (Evans and Barbadillo in press), and used the heuristic search option of PAUP 3.1.1 (Swofford 1993), with multistate characters treated as polymorphisms, and an outgroup composed of Rhynchocephalia, Kuehneosauridae, *Marmoretta*, *Saurosternon* and *Youngina*. Of the original 254 characters, PAUP deemed 76 redundant in this analysis (5, 27, 32, 43–44, 62, 67, 92, 105, 115, 126, 135–136, 139, 146, 150–151, 155–156, 165–192, 195–197, 201, 211, 215, 218, 221–223, 228, 230–234, 240–244, 246–252, 254), leaving 178 operational characters. The full character list and data matrix will be published elsewhere (Evans and Barbadillo in press); the data set for *Hoyalacerta* is given in Appendix 2.

Data runs using the full matrix produced six equally most parsimonious trees (length = 833 steps, CI (Consistency Index) = 0·73, RI (Retention Index) = 0·58, RC (Rescaled Consistency Index)



TEXT-FIG. 6. A–C, cladograms showing three equally parsimonious hypotheses of relationships for *Hoyalacerta sanzi*. Note that the taxon designated LH2 is the long-limbed lizard (LH 11001) from Las Hoyas (Evans and Barbadillo in press). D, bootstrap 50 per cent. Majority-Rule Consensus Tree for the same data, showing the two strongly supported nodes and their bootstrap values. See text for further details.

= 0·42), but the major differences between the trees related to the positions of outgroup taxa and of specialized in-group taxa, which are beyond the scope of the present discussion. Running a reduced matrix of 12 living (Iguania, Gekkota, Scincomorpha, Anguimorpha, Amphisbaenia, Dibamidae and Serpentes) and extinct (the Late Jurassic Solnhofen *Bavarisaurus*, *Ardeosaurus*,

Eichstaettisaurus, with *Hoyalacerta* and LH 11001) taxa, and with the outgroup combined into a single cluster, had no effect on the positions of the new Las Hoyas taxa.

Results

Text-figure 6A–C shows the three equally most parsimonious trees derived from a Branch-and-Bound search (stepwise addition, branch swapping algorithm–tree bisection reconnection, TBA) on the reduced matrix (length = 678 steps, CI = 0·91, RI = 0·54, RC = 0·49), with Gekkota, Scincomorpha, Anguimorpha, Dibamidae, Amphisbaenia and Serpentes represented simply as Scleroglossa (Estes *et al.* 1988). Also shown (Text-fig. 6D) is the bootstrap 50 per cent. majority-rule consensus tree (length = 697 steps, CI = 0·88, RI = 0·40, RC = 0·49; random addition, 100 Bootstrap replicates) for the same matrix.

Previous authors (e.g. Hoffstetter 1967; Estes 1983) classified the three Solnhofen lizard taxa (*Bavarisaurus*, *Ardeosaurus* and *Eichstaettisaurus*) as gekkotans, a position questioned by Evans (1993) and, more recently, Reynoso (1996*a*, 1996*b*) whose analyses suggested that the Solnhofen genera occupied a more basal position on the squamate stem (that is, they form successive sister taxa to crown-group Squamata). Reynoso's conclusion is supported by the analysis of *Hoyalacerta* and LH 11001 which emerge in a similar position, with *Hoyalacerta* usually lying crownward of LH 11001 and *Bavarisaurus*, but below *Ardeosaurus* and *Eichstaettisaurus*. However, the bootstrap consensus tree suggests that the precise relationships of all except *Bavarisaurus* are still somewhat equivocal. This is particularly true of *Eichstaettisaurus* and, to a lesser extent LH 11001, which moved in and out of the crown-group (Iguania + Scleroglossa). A Branch-and-Bound search of the matrix omitting *Eichstaettisaurus* gave a single tree (length = 666, CI = 0·92, RI = 0·53, RC = 0·49) with (outgroup (*Bavarisaurus* (LH 11001 (*Hoyalacerta* (*Ardeosaurus* (Iguania + Scleroglossa)))))). The main difficulty with resolving the phylogenetic relationships of the fossil taxa results from missing data. None of the five fossil taxa can be coded for more than 50 per cent. of the 178 operational characters (LH 11001, 40 per cent.; *Bavarisaurus*, 50 per cent.; *Eichstaettisaurus*, 44 per cent.; *Ardeosaurus*, 38 per cent.; *Bavarisaurus*, 50 per cent.; *Eichstaettisaurus*, 44 per cent.; *Ardeosaurus*, 38 per cent.; *Hoyalacerta*, 41 per cent.). The resolution would probably be improved with more complete data (for example, the two Las Hoyas taxa and *Eichstaettisaurus* are known from single individuals, and the skull of LH 11001 is poorly preserved).

If the relationships proposed above are correct, then LH 11001, *Hoyalacerta*, *Bavarisaurus* and *Ardeosaurus* (*Eichstaettisaurus* is more problematical) are not strictly squamates (the common ancestor of Iguania and Scleroglossa and all its descendants), but, with squamates, form a clade which is the sister group of Rhynchocephalia. This clade would be diagnosed by at least the following characters (subsequently reversed in some modern families): jugal forming most or all of the ventral orbital margin; loss of the dorsal process of the squamosal; reduced, deeply placed, supratemporal; reduction of the palatal process of the pterygoid; reduction of pterygoid/quadrate overlap; shortened angular; coronoid eminence formed by coronoid alone; anterior cervical ribs single-headed; loss of entepicondylar foramen in humerus; and loss of gastralia. At least three character states place *Hoyalacerta* above *Bavarisaurus* (loss of trunk intercentra; anterior coracoid fenestra, procoelous vertebral centra), and one places *Hoyalacerta* tentatively above LH 11001 (procoelous vertebral centra), although LH 11001 resembles *Eichstaettisaurus*, and crown-group scleroglossans, in having deep anterior descending processes of the frontals. *Ardeosaurus* and *Eichstaettisaurus* share at least two additional features with crown-group squamates: a medially forked postfrontal (lost or reduced in Iguania, and unknown in the Las Hoyas taxa) and a reduced lacrimal.

On present evidence, therefore, Jurassic and Early Cretaceous lizard assemblages contain both derived taxa which can be nested within the crown-group (for example, the third Las Hoyas lizard, *Meyasaurus*, consistently groups with teioid scincomorphs (Evans and Barbadillo 1997); whilst paramacellodids group with scincoids (Evans and Chure 1998*b*)), and primitive taxa which must be relicts from an earlier squamate radiation. The presence of undoubted rhynchocephalians in the

Middle Triassic provides strong evidence that their sister group must also have begun to diversify by this time. To date, however, the earliest certain squamate records are from microvertebrate horizons in the Middle Jurassic (Evans 1993). Whilst these provide evidence of early lizard diversity, they yield only limited morphological information. Until more complete early lizard material becomes available, Late Jurassic and Early Cretaceous stem taxa like *Bavarisaurus* and *Hoyalacerta* provide the only available evidence of primitive lizard morphology.

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REFERENCES

BROSCHINSKI, A. and SIGOGNEAU-RUSSELL, D. 1996. Remarkable lizard remains from the Lower Cretaceous of Anoual (Morocco). *Annales de Paléontologie*, **82**, 147–175.

ENDO, R. and SHIKAMA, T. 1942. Mesozoic reptilian fauna in the Jehol mountainland, Manchoukuo. *Bulletin of the Central National Museum of Manchoukuo*, **3**, 3–13.

ERASMO, G. d' 1915. La fauna e i'eta dei calcari ad illioloiti de Pietroroja, in provincia di Benevento. *Palaeontologia Italia*, **21**, 29–111.

ESTES, R. 1983. *Sauria terrestria, Amphisbaenia. In* WELLNHOFER, P. (ed.). *Handbuch der Paläoherpetologie* 10A. Gustav Fischer Verlag, Stuttgart, 249 pp.

—— GAUTHIER, J. and QUEIROZ, K. de 1988. Phylogenetic relationships within Squamata. 119–281. *In* ESTES, R. and PREGILL, G. (eds). *Phylogenetic relationships of the lizard families*. Stanford University Press, Stanford, 631 pp.

EVANS, S. E. 1988. The early history and relationships of the Diapsida. 221–260. *In* BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods, Volume 1: amphibians, reptiles, birds*. Systematics Association Special Volume 35A. Clarendon Press, Oxford, 377 pp.

—— 1991. A new lizard-like reptile (Diapsida, Lepidosauromorpha) from the Middle Jurassic of Oxfordshire. *Zoological Journal of the Linnean Society*, **103**, 391–412.

—— 1993. Jurassic lizard assemblages. *Second Georges Cuvier Symposium. Revue Paléobologie, Volume Speciale*, **7**, 55–65.

—— 1994. The Solnhofen (Jurassic: Tithonian) lizard genus *Bavarisaurus*: new skull material and a reinterpretation. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **192**, 37–52.

—— and BARBADILLO, J. 1996. The early Cretaceous lizards of Montsec (Catalonia: Spain). *Treballs del Museu de Geologia de Barcelona*, **5**, 5–13.

—— —— 1997. Early Cretaceous lizards from Las Hoyas, Spain. *Zoological Journal of the Linnean Society*, **119**, 23–49.

—— —— in press. An unusual lizard (Reptilia: Squamata) from the early Cretaceous of Las Hoyas, Spain. *Zoological Journal of the Linnean Society*, **124**.

—— and CHURE, D. C. 1998*a*. Morrison lizards: structure, relationships and biogeography. *Modern Geology*, **23**, 35–48.

—— —— 1998*b*. Paramacellodid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology* **18**, 99–114.

—— and MILNER, A. R. 1996. A metamorphosed salamander from the early Cretaceous of Las Hoyas, Spain. *Philosophical Transactions of the Royal Society of London, Series B*, **351**, 627–646.

—— and YABUMOTO, Y. 1998. A lizard from the early Cretaceous Crato Formation, Araripe Basin, Brazil. *Neues Jahrbuch für Geologie und Paláontologie, Monatshefte*, **1998** (6), 349–364.

FREGENAL-MARTÍNEZ, M. A. and MELÉNDEZ M. N. 1995. 1.1. Geological setting. 1–10. *In* MELÉNDEZ, N. N. (ed.). *Las Hoyas. A lacustrine konservatlagerstätte, Cuenca, Spain. 2nd International Symposium on Lithographic Limestones. Field trip guide book – July 16, 1995*. Ediciones de la Universidad Autónoma de Madrid, Madrid.

GAUTHIER, J., ESTES, R. and QUEIROZ, K. de 1988. A phylogenetic analysis of Lepidosauromorpha. 15–98. *In* ESTES, R. and PREGILL, G. (eds). *Phylogenetic relationships of the lizard families*. Stanford University Press, Stanford, 631 pp.

HAECKEL, E. 1866. *Generelle Morphologie der Organismen. Allgemeine Grundzuge der organischen Formen-Wissenshaft mechanisch begrundet durch die von Charles Darwin reformierte Deszendenz-Theorie. 2: Allgemeine Entwicklungsgeschichte der Organismen. Kritische Grundzuge der mechanischen Wissenshaft von den entstehenden Formen der Organismen, begrundet durch die Deszendenz-Theorie*. Berlin, clx + 462 pp.

HOFFSTETTER, R. 1966. Les Sauria (= Lacertilia) du Jurassique supérieur du Montsech (Espagne). *Bulletin de la Société Géologique de France*, **7**, 549–557.

—— 1967. Coup d'oeil sur les Sauriens (= lacertiliens) des couches de Purbeck (Jurassique supérieur d'Angleterre. Résumé d'un Mémoire). *Colloques Internationaux du Centre National de la Recherche Scientifique*, **163**, 349–371.

McGOWAN, G. and EVANS, S. E. 1995. Albanerpetontid amphibians from the Cretaceous of Spain. *Nature*, **373**, 143–145.

NYDAM, R. L., CIFELLI, R. L., BRINKMAN, D. L. and GARDNER J. D. 1997. Preliminary report on the vertebrate fauna of the Antlers Formation (Lower Cretaceous: Aptian–Albian) of Oklahoma. *Journal of Vertebrate Paleontology*, **17** (Supplement to No. 3), 67A.

OPPEL, M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien, als Prodrom einer Naturgeschichte derselben*. Joseph Lindauer, Munich, 87 pp.

PÉREZ-MORENO, B. P., SANZ, J. L., BUSCALIONI, A. D., MORATALLA, J. J., ORTEGA F. and RASSKIN-GUTMAN, D. 1994. A unique multitoothed ornithomimosaur dinosaur from the Lower Cretaceous of Spain. *Nature*, **370**, 363–367.

REYNOSO, V. H. 1996*a*. A primitive lizard from the early Cretaceous of Mexico and the phylogenetic position of early lizards. *Journal of Vertebrate Paleontology*, **16** (Supplement to No. 3), 60*A*.

—— 1996*b*. Early Cretaceous lepidosaurs (Reptilia: Diapsida) from Central Mexico and the phylogeny of lepidosauromorphs. Unpublished Ph.D. thesis, McGill University, Montreal, Canada.

RICHTER, A. 1991. A new species of *Ilerdaesaurus* and other lizards from Uña, Spain (Lower Cretaceous). 55–56. *In* KIELAN-JAWOROWSKA, Z., HEINZ, N. and NAKREM, H. A. (eds). Fifth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Extended Abstracts. *Contributions of the Palaeontological Museum, University of Oslo*, **364**, 1–72.

—— 1994*a*. Der problematische Lacertilier *Ilerdaesaurus* (Reptilia: Squamata) aus der Unter-Kreide von Uña und Galve. *Berliner geowissenschaftliche Abhandlungen*, **13**, 135–161.

—— 1994*b*. Lacertilia aus der Unteren Kreide von Uña und Galve (Spanien) und Anoual (Marokko). *Berliner geowissenschaftliche Abhandlungen*, **14**, 1–147.

SANZ, J. L. and BUSCALIONI, A. D. 1992. A new bird from the Early Cretaceous of Las Hoyas, Spain and the early radiation of birds. *Palaeontology*, **35**, 829–845.

—— WENZ, S., YEBENES, A., ESTES, R., MARTINEZ-DECLOS, X., JIMINEZ-FUENTES, E., DIGUEZ, C., BUSCALIONI, A., BARBADILLO, L. J. and VIA, L. 1988. An early Cretaceous faunal and floral assemblage: Las Hoyas fossil-site (Cuenca, Spain). *Geobios*, **21**, 611–638.

SWOFFORD, D. L. 1993. *PAUP: Phylogenetic Analysis Using Parsimony. Version 3.1*. Computer program, distributed by Illinois Natural History Survey.

VIDAL, L. M. 1915. Nota geológica y palaeontógica sobre el Jurásico superior de la provincia de Lérida. *Boletin del Instituto Geológico de España*, **36**, 17–55.

WALDMAN, M. and EVANS, S. E. 1994. Lepidosauromorph reptiles from the Middle Jurassic of Skye. *Zoological Journal of the Linnean Society*, **112**, 135–150.

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APPENDIX 1: ABBREVIATIONS USED IN THE TEXT-FIGURES

acf – anterior coracoid fenestra
Ar – articular
at – atlas
ax – axis
Br – braincase
D – dentary
e – epiphysis
Ep – epipterygoid
F – frontal
Fi – fibula
H – humerus
h – hyoid
hy – hypapophysis
il – ilium
J – jugal
L – lacrimal
l – left
Mx – maxilla
P – parietal
Pa – palatine
Pm – premaxilla
Pof – postorbitofrontal
Prf – prefrontal
Pt – pterygoid
Q – quadrate
Qc – quadrate conch
r – right
rb – rib fragment
rp – retroarticular process
Sc – scapulocoracoid
Scf – scapulocoracoid fenestra
Sq – squamosal

APPENDIX 2

Data set for *Hoyalacerta sanzi* gen. et. sp. nov. The full character set and data matrix are given in Evans and Barbadillo (in press).

1
000?0 01?00 10??0 0?0?0 ?00?1 00100 ????0 ????0 1???? ?????
5
1
?0??0 ????? ???10 00000 0221/2? 00??? 02000 10030 ??110 ?????
1
0
1
??3?0 0000? ????? ????? ????? ????1 01110 ?00?? ??1?? ???1?
1
5
1
11??? ???2? ???1? ????? ????? ????? ????? ????? ?10?? 1?201
2
0
1
0111? ??1?1 0?0?? 11?00 0???? ????0 00??? 2???? ???1? ?????
2
5
1
??2?

A PRIMITIVE SNAKE FROM THE CRETACEOUS OF UTAH

by JAMES D. GARDNER *and* RICHARD L. CIFELLI

ABSTRACT. Recently discovered vertebrae of the anilioid-grade snake *Coniophis* from the Cretaceous (uppermost Albian/lowermost Cenomanian) upper Cedar Mountain Formation of Utah, USA, are among the oldest known snake fossils and extend the record of snakes in the New World back by at least 10 My. The vertebrae from Utah and other occurrences of Albian to Cenomanian snake fossils support suggestions that Alethinophidia and its inferred sister-taxon, Scolecophidia, originated before the Late Cretaceous, and indicate that 'anilioids' were widely distributed (Laurasia, Gondwana) by the early Late Cretaceous. If 'anilioids' emigrated from South to North America, as is widely believed, the fossils from Utah demonstrate that this must have occurred before the latest Cretaceous emigration event previously hypothesized. The broad distribution of 'anilioids' in the Late Cretaceous, coupled with the possibility that snakes may have first appeared in the Jurassic, suggests that snakes may have been present in North America prior to its separation from Gondwana.

THE fossil record of the earliest snakes is frustratingly sparse in terms of the temporal and geographical distribution of fossils, number and quality of specimens, and taxonomic representation, and this situation hinders our understanding of the origin and early diversification of snakes. The geologically oldest snakes hitherto reported date from the Barremian–Cenomanian of western Europe and northern Africa (Text-fig. 1), and most of these records consist of only a few, imperfect vertebrae. By the Cenomanian at least six taxa of snakes were present (see caption for Text-fig. 1), ranging from primitive forms with hindlimbs (Caldwell and Lee 1997; Lee and Caldwell in press) to members of highly derived lineages, such as colubroids (Werner and Rage 1994). This diversity suggests that the late Early to early Late Cretaceous was an important, albeit poorly understood interval in the early evolution of snakes.

Given the limited record of late Early to early Late Cretaceous snakes, it is evident that discoveries of additional fossils from this interval are critical for advancing our understanding of the early evolution of snakes. In 1995, two isolated vertebrae of the primitive, anilioid-grade snake *Coniophis* Marsh, 1892, were collected from the Cretaceous (uppermost Albian/lowermost Cenomanian) upper Cedar Mountain Formation in Utah, USA. These vertebrae are noteworthy because they: (1) are among the geologically oldest known snake fossils from anywhere in the world; (2) extend the documented temporal range of snakes in the New World back at least 10 million years (My) from the Coniacian; and (3) represent one of the two earliest known occurrences of anilioid-grade snakes. Herein we describe these vertebrae, discuss their affinities, and examine their contribution to our understanding of the early history of snakes.

As polarities of vertebral features remain largely undetermined for snakes (e.g. Estes 1985; Szyndlar and Böhme 1996), here we continue the historical practice of using unique combinations of vertebral features, rather than characters that are demonstrably apomorphic, to differentiate taxa of snakes. As the higher level systematics of snakes remain contentious, no classification of snakes is universally accepted. In general, we follow the classification proposed by Rage (1984, 1987), largely because it includes fossil taxa and utilizes vertebral features. Rage's classification recognizes two lineages of snakes, Scolecophidia and Alethinophidia, with the latter group including five superfamilies. In order of most primitive to most derived, these are: Simoliophioidea, Anilioidea, Booidea, Acrochordoidea, and Colubroidea. The monophyletic status and composition of the

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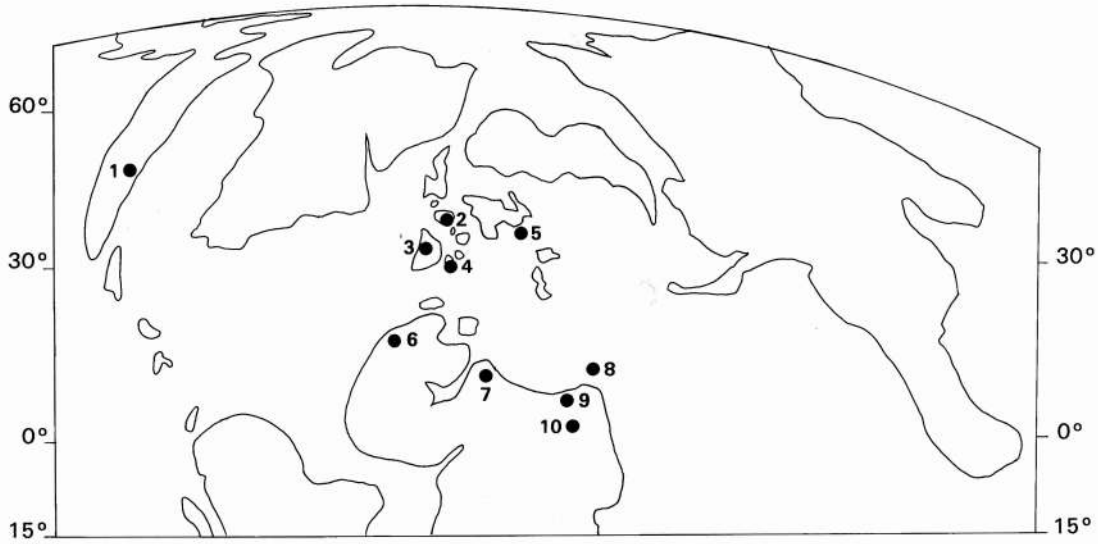


TEXT-FIG. 1. Palaeogeographical reconstruction of continents during the Cenomanian Stage (95 Ma), showing distribution of Barremian–Cenomanian snakes and snake-like squamates. Occurrences are: 1, *Coniophis* sp. (Aniliidae *sensu lato*), uppermost Albian/lowermost Cenomanian, Utah, USA (present study); 2, *Pouitella pervetus* (Lapparentopheidae?), lower or middle Cenomanian (Rage 1988*b*) and *Simoliophis rochebrunei* (Simoliophiidae), lower–middle and ?upper Cenomanian, France (Sauvage 1880; Rage 1984, 1987; Cuny *et al.* 1990); 3, *S. rochebrunei* (Simoliophiidae), middle Cenomanian, Portugal (Sauvage 1896; Cuny *et al.* 1990); 4, Serpentes *incertae sedis*, Barremian, Spain (Rage and Richter 1994); 5, *Mesophis nopcsa* and *Pachyophis woodwardi*, (Squamata *incertae sedis*), middle or upper Cenomanian (Slišković 1970), Bosnia-Herzegovina (Nopcsa 1923*b*; Bolkay 1925); 6, Palaeopheidae? sp., Cenomanian, Morocco (Sereno *et al.* 1996); 7, Lapparentopheidae? sp. and Serpentes *incertae sedis*, upper Albian (Cuny *et al.* 1990) and *Lapparentophis defrennei* (Lapparentopheidae), upper Albian or Cenomanian, Algeria (Hoffstetter 1959; Cuny *et al.* 1990); 8, *Pachyrhachis problematicus* (Haas 1979, 1980*a*, 1980*b*; Caldwell and Lee 1997; Lee and Caldwell in press) and unnamed *Pachyrhachis*-like taxon (Tchernov *et al.* 1996), lower Cenomanian, Israel; 9, *Simoliophis* sp. (Simoliophiidae), lower Cenomanian (Said 1962), Egypt (Nopcsa 1925; Stromer 1936); and 10, Aniliidae *sensu lato* sp., Colubroidea spp., Lapparentopheidae? sp., Madtsoiidae sp., Nigeropheidae? sp., and Serpentes *incertae sedis*, Cenomanian, Sudan (Werner and Rage 1994). Reconstruction of continents is from Smith *et al.* (1994, map 15).

Alethinophidia and many of its superfamilies are contentious (Rage 1997), and although a variety of primitive fossil taxa, such as *Dinilysia*, Madstoiidae, and Palaeopheidae, are generally considered to be alethinophidians (however, see McDowell 1987), support for these assignments is limited and often rests largely on vertebral features of uncertain polarities. We follow Caldwell and Lee (1997) and Lee and Caldwell (in press) in recognizing *Pachyrhachis* as a stem snake and the putative sister taxon to all other snakes. Measurements and osteological terminology in our paper follow Auffenberg (1963) and LaDuke (1991).

Institutional abbreviations. AMNH, American Museum of Natural History, New York; MNA, Museum of Northern Arizona, Flagstaff; OMNH, Oklahoma Museum of Natural History, Norman; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton; and USNM, United States National Museum, Washington.

SYSTEMATIC PALAEONTOLOGY

Suborder SERPENTES Linnaeus, 1758
Infraorder ALETHINOPHIDIA Nopcsa, 1923*a*
Superfamily ANILIOIDEA Fitzinger, 1826
Family ANILIIDAE *sensu lato* Stejneger, 1907

Remarks. Anilioidea includes about 12 extant genera of medium-sized, fossorial to semifossorial, tropical snakes (McDowell 1987) and four named fossil genera (Rage 1984; Bailon 1988) distributed among two or four families (cf. Rage 1984; McDowell 1987). Although it is universally accepted that the Anilioidea include the most primitive of living alethinophidians (e.g. Underwood 1967; Bellairs 1972; McDowell 1975, 1987; Rieppel 1979*a*, 1979*b*, 1988; Rage 1984, 1987; Kluge 1991; Cundall *et al.* 1993), the status, internal relationships, and content of this group are contentious. Monophyly of the extant Anilioidea, regardless of which taxa are included, is not well supported (Rieppel 1979*a*, 1988; Kluge 1991; Cundall *et al.* 1993), and we concur with Cundall *et al.* (1993) and Rage (1997) that the Anilioidea are best recognized as a paraphyletic assemblage of primitive alethinophidians. As is the case with most groups of snakes, relationships among fossil and extant anilioids remain unresolved.

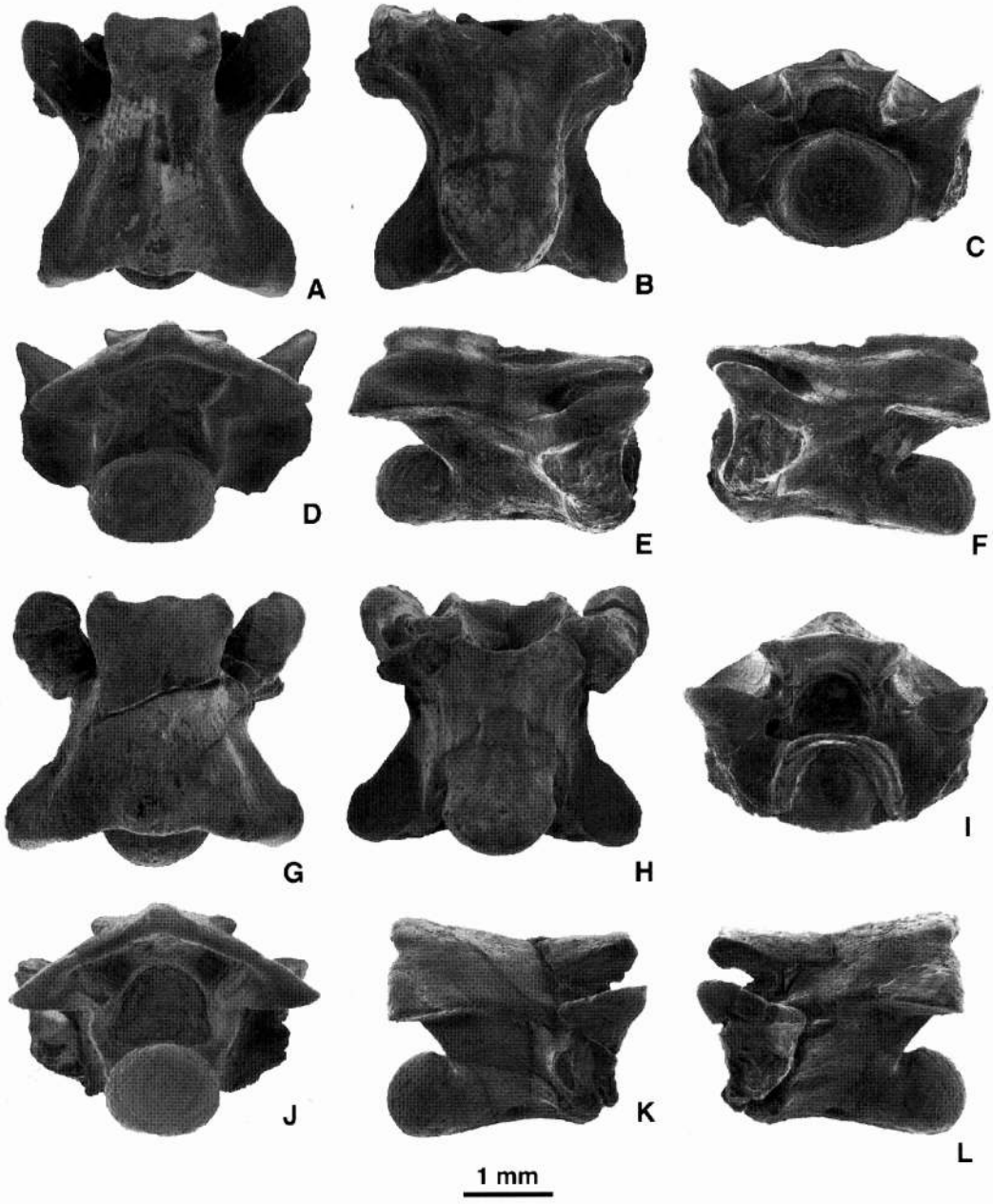
The Aniliidae *sensu lato* includes one or three extant genera and one to four fossil genera (Rage 1984, 1987; McDowell 1987; Bailon 1988). Even when extant members alone are considered, the Aniliidae is not demonstrably monophyletic (Cundall *et al.* 1993), and for this reason we use the name Aniliidae in a loose sense to denote all non-uropeltid anilioids. Aniliids *sensu lato* have a moderately extensive fossil record, and have previously been reported from the Campanian–Eocene of North America (Marsh 1892; Hecht 1959; Estes 1964, 1976; Estes *et al.* 1969; Fox 1975; Armstrong-Ziegler 1978, 1980; Holman 1979*a*; Breithaupt 1985), the Cenomanian of Africa (Werner and Rage 1994), the Paleocene and Miocene of South America (Hoffstetter and Rage 1977; Rage 1981, 1987, 1991; de Muizon *et al.* 1983; Albino 1990, 1996; Gayet *et al.* 1991; Hecht and LaDuke 1997), and the Eocene and Pliocene of Europe (Rage 1974, 1988*a*; Milner *et al.* 1982; Bailon 1988; Rage and Auge 1993; Szyndlar 1994). Supposed aniliid vertebrae from the French Maastrichtian (Astibia *et al.* 1990) have recently been re-identified by Rage (1996) on the basis of additional specimens as belonging to a new genus of madtsoiid (J.-C. Rage, pers. comm. 1996). Some or perhaps all of the aniliid vertebrae reported by Chkhikvadze (1984) and Zerova and Chkhikvadze (1984) from the lower Eocene of Middle Asia may instead be referable to an undescribed species of erycine booid (A. Averianov, pers. comm. 1996; Danilov 1997).

Genus CONIOPHIS Marsh, 1892

Type species. Coniophis precedens Marsh, 1892.

Content and known distribution. Four nominal species: *Coniophis carinatus* Hecht, 1959, middle Eocene, Bridger Formation, Wyoming, and Huerfano Basin, Colorado (Hecht 1959); *C. cosgriffi* Armstrong-Ziegler, 1978, upper Campanian, Fruitland Formation, New Mexico (Armstrong-Ziegler 1978, 1980); *C. platycarinatus* Hecht, 1959, middle Eocene, Bridger Formation, Wyoming (Hecht 1959); and *C. precedens* Marsh, 1892, upper Maastrichtian, Lance Formation, Wyoming (Marsh 1892; Gilmore 1938; Hecht 1959; Estes 1964), and Hell Creek Formation, Montana (Estes *et al.* 1969). *Coniophis* sp., cf. *C. precedens*: lower Campanian, Alberta (Fox 1975) and middle Paleocene, Brazil (Albino 1990); the latter record includes vertebrae identified by Rage (1987, 1991) and Albino (1996) as *Coniophis* sp. (J.-C. Rage, pers. comm. 1996). *Coniophis* sp.: uppermost Albian/lowermost Cenomanian, Utah (this paper); middle Campanian, Wyoming (Breithaupt 1985); lower Paleocene, Peru (Rage 1981, 1991; Albino 1996); middle Paleocene, Montana (Estes 1976); and upper Eocene, Wyoming (Holman 1979*a*) and France (Rage 1988*a*). Lower Paleocene vertebrae from Bolivia identified by de Muizon *et al.* (1983) as *Coniophis* sp. appear to represent an undescribed genus of aniliid *sensu lato* (Rage 1991; Albino 1996).

Remarks. The status, relationships, and composition of *Coniophis* are contentious (e.g. Hoffstetter



TEXT-FIG. 2. Trunk vertebrae of *Coniophis* sp.; Cretaceous (uppermost Albian/lowermost Cenomanian) upper unnamed member, Cedar Mountain Formation; Emery County, Utah, USA. A–F, OMNH 33250 from OMNH locality V695; dorsal, ventral, anterior, posterior, right lateral, and left lateral views. G–L, OMNH 33251 from OMNH locality V867; dorsal, ventral, anterior, posterior, right lateral, and left lateral views. All × 12.

1955; Hoffstetter and Rage 1977; Hecht 1982; Rage 1984, 1987; McDowell 1987; Albino 1990, 1996), and this genus warrants a thorough systematic revision. Although it is not our intention here to examine these matters rigorously, several comments are appropriate. As presently understood and in the sense used here, *Coniophis* is an extinct and primitive genus of anilioid snake whose members are differentiated from all other anilioids by the following combination of vertebral features: (1) neural arch moderately depressed; (2) accessory (= prezygapophysial) process greatly reduced or absent; (3) posterior margin of neural arch lacking a posteromedian notch; (4) neural spine forms a low ridge or is absent; and (5) haemal keel low and flattened or absent. Given that these features are probably primitive for snakes, *Coniophis* is not demonstrably monophyletic. We contend, however, that it is prudent to recognize *Coniophis* as a valid taxon until relationships and patterns of vertebral variation among fossil and extant anilioids are better understood.

We have examined the holotype vertebrae of *C. carinatus* (AMNH 3826), *C. cosgriffi* (MNA V9082; listed incorrectly as MNA Pl·1612 by Armstrong-Ziegler, 1978 (D. Hill, pers. comm. 1997)), *C. platycarinatus* (AMNH 3827), and *C. precedens* (USNM 2134), as well as vertebrae (UALVP 12001–12015) of *Coniophis* sp., cf. *C. precedens* from the lower Campanian of Alberta (Fox 1975) and uncatalogued UALVP vertebrae of *C. precedens* from the upper Maastrichtian of Wyoming and Montana. All of these vertebrae exhibit the diagnostic features of *Coniophis*, although we concur with Rage (1981, 1984, 1988*a*) that MNA V9082 probably is not distinctive at the specific level.

Coniophis sp.

Text-figure 2

Material. OMNH 33250 and 33251, nearly complete trunk vertebrae.

Localities and horizon. OMNH 33250 and 33251 were collected from OMNH localities V695 and V867, respectively, about 27 km south of Emery, Emery County, Utah, USA. Both sites occur in a restricted stratigraphical interval in the upper 15 m of the unnamed upper member (*sensu* Stokes 1952) of the Cedar Mountain Formation, and an ash layer overlying the sites is dated as latest Albian/earliest Cenomanian (Cifelli *et al.* 1997). These and other sites in the upper part of the formation in central Utah have produced a diverse non-marine vertebrate assemblage (Cifelli *et al.* in press).

Description. OMNH 33250 is missing a short section of the neural spine, the lateral edge of the right articular facet of the zygosphene, and the lateral edge of the left postzygapophysis (Text-fig. 2A–F). In OMNH 33251, the zygosphene roof is broken away and displaced slightly dorsal to the remainder of the neural arch; similarly, the distal parts of the prezygapophyses and the dorsal and lateral parts of the cotyle are displaced slightly to the left of and anterior to the remainder of the centrum (Text-fig. 2G–L). The anterodorsal rim of the right articular facet of the zygosphene and part of the base of the right prezygapophysis are missing from OMNH 32251. The articular facets of the paradiapophysis are eroded in both vertebrae.

Each vertebra is small in absolute size, robust, and moderately elongate, wide, and low. In absolute (Table 1) and relative terms, OMNH 32250 is longer, narrower and lower than OMNH 32251. Both vertebrae are constructed simply: the haemal keel is virtually absent, the neural spine is reduced, and many of the processes (accessory and parapophysial processes and epizygapophysial spine) and foramina (paracotylar, parazygosphenal, and parazygantral foramina), which in some combination are characteristic of vertebrae in most other groups of snakes, are absent.

The centrum is dorsoventrally depressed and, in ventral view, it widens slightly anteriorly. A low, indistinct haemal keel, anteroposteriorly oblong and moderately broad in ventral outline, extends along the median one-third of the centrum. To either side of the posterior end of the haemal keel lies a small, shallow depression that is anteroposteriorly elliptical in ventral outline. A subcentral foramen, small and oval in ventral outline, is located immediately lateral to the haemal keel and just anterior to the midpoint of the centrum. More dorsally and slightly anteriorly, a low ridge extends posteriorly from the base of the paradiapophysis to about the level of this foramen. In lateral view, a tiny lateral foramen penetrates the wall of the neural arch just ventral to the interzygapophysial ridge.

The paradiapophysis is placed moderately high on the centrum – i.e. in anterior view, a horizontal line extending from the dorsal margin of the diapophysis would intersect the cotyle at (OMNH 33250), or just

TABLE 1. Measurements (in mm) of trunk vertebrae of *Coniophis* sp.; Cretaceous (uppermost Albian/lowermost Cenomanian) upper unnamed member, Cedar Mountain Formation; Emery County, Utah, USA. Abbreviations 'L' and 'R' = left and right sides, respectively; 'neural arch length' = midline distance between anterior and posterior margins of neural arch in dorsal view; all other measurements follow Auffenberg (1963, figs 2–4) and LaDuke (1991, fig. 1).

Measurement	OMNH 33250	OMNH 33251
Centrum length	2·9	2·5
Cotyle height	~ 0·8	?
Cotyle width	~ 1·8	~ 1·4
Condyle height	0·9	1·1
Condyle width	1·5	1·4
Neural canal height (anterior view)	0·5	1·0
Neural canal width (anterior view)	~ 0·9	~ 1·1
Neural arch length	3·2	3·0
Neural arch width	2·1	2·2
Neural spine height	~ 0·3	~ 0·2
Neural spine length	2·4	~ 2·2
Zygosphene width	~ 1·5	~ 1·8
Width between outer edges of prezygapophysial articular facets	3·5	3·6
Width between outer edges of postzygapophysial articular facets	~ 3·3	3·7
Prezygapophysial articular facet length	L = 1·2; R = 1·3	L = 1·2; R = ?
Prezygapophysial articular facet width	L = 0·8; R = 0·9	L = 0·9; R = 0·8
Postzygapophysial articular facet length	L = ?; R = 1·4	L = 1·2; R = 1·1
Postzygapophysial articular facet width	L = ?; R = 0·9	L = 0·8; R = 0·8

ventral to (OMNH 33251) its dorsal rim. The parapophysial and diapophysial articular facets, best preserved on the right side in OMNH 33250, evidently faced lateroventrally and were somewhat constricted at their junction, with the diapophysial facet being the larger of the two.

The cotyle and condyle are dorsoventrally compressed. The cotyle is wider in OMNH 33250, and is slightly wider than the zygosphene in both specimens. In anterior outline, the cotyle on OMNH 33250 is elliptical; although broken, the cotyle on OMNH 33251 was evidently more nearly circular. In posterior view, the condyle on OMNH 33250 is elliptical in outline and slightly wider than on OMNH 33251. In the latter specimen, the condyle is more nearly circular. The neck of the condyle is unconstricted in both vertebrae.

The neural canal is moderately high and wide, and rhomboid in anterior outline, with a shallowly concave roof that is narrower than the floor. Although dorsal displacement of the zygosphene in OMNH 33251 has exaggerated the height of the neural canal in anterior view, it is nonetheless evident that the canal is broader and taller than in OMNH 33250. In anterior view, the height and width of the neural canal in OMNH 33251 are subequal to the equivalent dimensions of the cotyle, but in OMNH 33250 the neural canal is noticeably lower and narrower than the cotyle. In posterior view, the neural canal in OMNH 33251 is equivalent in height and width to the condyle, whereas in OMNH 33250 the neural canal is slightly lower and wider than the condyle. A shallow, median ridge is visible in posterodorsal view on the floor of the neural arch in OMNH 33251.

In dorsal outline, the neural arch is rectangular in OMNH 33250 and squarish in OMNH 33251. The lateral margins of the neural arch between the pre- and postzygapophyses are moderately constricted medially, with the point of maximum constriction located just anterior to the midpoint of the neural arch. The neural spine is a low ridge that is restricted to the posterior two-thirds of the neural arch. On OMNH 33250, the dorsal edge of the neural spine in lateral view is straight and inclined dorsally at about 12°. Displacement of the zygosphene dorsally has exaggerated the lateral profile of the neural spine on OMNH 33251, such that the posterior two-thirds of the spine appears to rise posterodorsally at a higher angle than it does more anteriorly. Along the anterior three-quarters of its length, the neural spine is narrow and has a keel-like (OMNH 33250) or blunt (OMNH 33251) dorsal edge. More posteriorly, the neural spine widens and terminates in a low, rounded

process. This process is smooth on OMNH 33251, but on OMNH 33250 its posterodorsal end bears a small, sub-circular facet that, in life, was evidently capped by cartilage. Lateral to the neural spine and posterior to the midpoint of the neural arch is a low, anteroposteriorly elongate mound, which is better developed on OMNH 33250. The posterior margin of the neural arch lacks a median notch in both specimens.

The zygosphene is well developed and wide on both vertebrae, being absolutely and relatively wider on OMNH 33251. In dorsal outline, the anterior edge of the zygosphene is slightly indented to either side of the midline. The dorsal surface of the zygosphene is flat. In anterior view, the roof of the zygosphene is thicker than the cotylar rim. The zygosphenal articular facets are elongate and oval in lateral outline, and face lateroventrally at about 30–40° in anterior view. The zygantrum is wide, with well-developed articular facets. Anterior and medial to each zygantral articular facet is a large zygantral foramen.

The interzygapophysial ridge is weakly developed. In dorsal view, the unbroken prezygapophyses on OMNH 33250 each extend anterolaterally at about 42°; the postzygapophyses extend posterolaterally at about 40° and 43° on OMNH 33250 and 33251, respectively. The pre- and postzygapophysial articular facets are of moderate size, elongate, and obovate in outline. The anterior rim of the prezygapophysial facet is acute (OMNH 33250), or obtuse (OMNH 33251) in dorsal outline. The zygapophyses are placed low on the lateral walls of the neural arch, such that in anterior view a horizontal line extending medially from the dorsal edge of the base of the prezygapophysis would pass ventral to the midpoint of the neural canal. In anterior view, the prezygapophysial articular facet on OMNH 33250 extends laterodorsally at about 30°, and its distal tip is level with the zygosphenal roof. In OMNH 33251, the prezygapophysial articular facet projects more laterally and its distal end lies well ventral to the level of zygosphenal roof; however, these conditions appear to have been exaggerated by breakage and displacement of the zygosphene and prezygapophyses in this specimen.

Remarks. We identify OMNH 33250 and 33251 as trunk vertebrae (*sensu* Hoffstetter and Gasc 1969) because both are generalized elements that lack: (1) the diagnostic morphologies of amniote atlantes and axes; and (2) the ventral processes characteristic of cloacal (fused lymphapophyses; haemapophyses variably present) and postcloacal (fused pleur- and haemapophyses present) vertebrae (Hoffstetter and Gasc 1969; LaDuke 1991). Both vertebrae appear to have originated from the middle or posterior part of the trunk series, as evidenced by their relatively robust build, moderately elongate centrum, and lack of a hypaphophysis (Auffenberg 1963; Hoffstetter and Gasc 1969; LaDuke 1991). Features suggesting that these vertebrae came from adults are: relatively robust construction; centrum moderately elongate; neural canal smaller than cotyle and condyle; and prezygapophysis well developed (e.g. Holman 1982; LaDuke 1991). Our identification of OMNH 33250 and 33251 as trunk vertebrae from adults is important because it is these vertebrae that historically have been considered most useful for identifying fossil taxa (e.g. Simpson 1933; Gilmore 1938; Auffenberg 1963; Holman 1979*b*, 1995; Rage 1984).

DISCUSSION

Relationships of Coniophis *sp. from Utah*

Hoffstetter and Gasc (1969) differentiated the vertebrae of snakes from those of lizards that have a procoelous centrum and zygosphene-zygantrum articulation (i.e. lacertids, teiids, gymnophthalmids, and some iguanids and cordylids; Estes *et al.* 1988) based on the following features: (1) zygosphene widens anteriorly in dorsal view, with each zygosphenal articular facet overhanging and forming an angle of less than 90° with the adjacent prezygapophysial facet; (2) zygosphenal and prezygapophysial articular facets separated from one another by a nonarticular area; and (3) anterior margin of zygosphene not deeply notched in dorsal view (see Hoffstetter and Gasc 1969, fig. 41). The presence of these features in OMNH 33250 and 33251 supports their identification as snake vertebrae.

As described by Lee and Caldwell (in press), trunk vertebrae of *Pachyrhachis* differ markedly from OMNH 33250 and 33251 in being pachyostotic and having a prominent, blade-like neural spine. Vertebral features that indicate OMNH 33250 and 33251 are referable to the Alethinophidia, rather than to the Scolecophidia, are: (1) neural arch moderately depressed dorsoventrally; (2) centrum widening anteriorly; (3) subcentral foramen consistently small; (4) cotylar lip not undercut; (5) parapophysial and diapophysial facets probably weakly divided; (6) neural spine present; (7) accessory process absent; and (8) long axes of pre- and postzygapophyses in dorsal view extend lateral to (rather than parallel to) long axis of centrum (Holman 1979*b*; Rage 1984; Rage and Prasad 1992).

Among vertebrae of alethinophidians, OMNH 33250 and 33251 evidently are more primitive than trunk vertebrae belonging to members of the Booidea, Acrochordoidea, and Colubroidea in the following features, the first four of which are widely considered to be primitive for snakes (Rage 1988*b*, 1996; Cuny *et al.* 1990; Rage and Prasad 1992; Rage and Richter 1994; Werner and Rage 1994; Prasad and Rage 1995): (1) accessory process absent; (2) posteromedian notch in neural arch absent; (3) zygapophysial articular facet inclined laterodorsally at a high angle in anterior view; (4) parapophysial and diapophysial facets probably weakly divided; (5) neural spine low; (6) haemal keel low; and (7) paracotylar, parazygosphenal and parazygantral foramina absent. Although vertebrae in some taxa of presumably more derived alethinophidians may superficially resemble anilioid vertebrae (for example, accessory processes are lacking and a low neural spine and haemal keel are present in the vertebrae of some small madtsoiids (see Scanlon 1993, fig. 1; Rage 1996, fig. 2) and some fossorial and secretive booids and colubroids (J.-C. Rage, pers. comm. 1996)), in combination the features listed above are distinctive for anilioid vertebrae. Trunk vertebrae in members of the Simoliophioidea, a late Albian–Cenomanian group known only by vertebrae and considered by Rage (1984, 1987) to be the most primitive alethinophidians, appear to be more primitive than OMNH 33250 and 33251 in retaining undivided par- and diapophysial articular facets and having zygapophysial articular facets that are inclined more dorsally in anterior view.

In exhibiting an intermediate, but evidently still relatively primitive level of vertebral organization, OMNH 33250 and 33251 compare most closely with vertebrae in anilioid snakes. The combination of vertebral features considered above to be diagnostic for *Coniophis* is the basis for our referral of OMNH 33250 and 33251 to this genus. These two vertebrae undoubtedly originated from separate individuals, because they were collected from different quarries that are located *c.* 2·6 km apart. We conservatively consider OMNH 33250 and 33251 to be from conspecific individuals because the differences between these two vertebrae, noted above, are within the range of intraspecific variation documented by LaDuke (1991) in extant species of more derived alethinophidians.

Coniophis and *Coniophis*-like vertebrae from the Paleocene of South America and vertebrae of *Coniophis* sp. from the Campanian to Eocene of North America are largely undescribed and, hence, cannot adequately be compared at present with OMNH 33250 and 33251. Similarly, the holotype vertebra of *C. cosgriffi* is an incomplete trunk vertebra that is too poorly prepared to be meaningfully compared with OMNH 33250 and 33251. The holotype trunk vertebrae of *C. carinatus* and *C. platycarinatus* (Hecht 1959, pl. 52, figs 1–5 and pl. 53, figs 1–2, respectively) differ from OMNH 33250 and 33251 in having short accessory processes. In lacking these processes (presumed to be the primitive condition), OMNH 33250 and 33251 resemble the holotype (Hecht 1959, pl. 53, figs 3–7) and unnumbered UALVP trunk vertebrae of *C. precedens*, as well as indeterminate *Coniophis* trunk vertebrae from the lower Campanian of Alberta (Fox 1975, figs 1A–C, 2A), the middle Paleocene of Brazil (Albino 1990, fig. 1A), and the Eocene of France (Rage 1988*a*, fig. 15). OMNH 33250 and 33251 are most similar to trunk vertebrae of *C. precedens* in having a low neural spine that may be unfinished distally, but they differ, particularly from the holotype of *C. precedens*, in having a moderately higher and longer neural spine, and an indistinct haemal keel that fails to reach the condylar lip. We suspect that OMNH 33250 and 33251 represent a distinct species of *Coniophis*; however, we defer formally naming and diagnosing this new species pending a better understanding of vertebral morphology and variation in *Coniophis*, and the possible recovery of additional fossils from the Cedar Mountain Formation or coeval rock units in western North America.

Significance of Coniophis *sp. from Utah*

The uppermost Albian/lowermost Cenomanian vertebrae described above from Utah are among the oldest known snake fossils, and are predated only by a few fragmentary vertebrae of lapparentopheids and an indeterminate taxon from the upper Albian of Algeria (Hoffstetter 1959; Cuny *et al.* 1990) and two crushed, indeterminate snake vertebrae from the Spanish Barremian (Rage and Richter 1994). Prior to our report, the geologically oldest New World snake was the

booid-like *Dinilysia* (e.g. Estes *et al.* 1970; Hecht 1982; Rage and Albino 1989). As fossils of *Dinilysia* come from Argentine deposits that are either Coniacian (Bonaparte 1991) or Campanian (Uliana and Dellapé 1981, cited in Rage and Albino 1989) in age, they are at least 10 My younger than the *Coniophis* vertebrae from Utah. The next oldest North American snake fossils are isolated vertebrae of *Coniophis* and an indeterminate aniliid *sensu lato* from the lower Campanian of Alberta (Fox 1975), specimens that are about 15 My younger than the fossils from Utah.

The lack of a well-corroborated phylogeny for primitive snakes precludes a detailed examination of the evolutionary history of anilioids, including *Coniophis* sp. from the Cedar Mountain Formation. Nevertheless, because OMNH 33250 and 33251 document one of the two oldest occurrences of anilioids and the oldest occurrence of snakes in the New World, they are potentially informative for examining the time of origin of alethinophidians, the centre of origin for anilioids, and the time and mode of arrival of anilioids in North America.

Besides *Coniophis* sp. from Utah, the only other anilioid that predates the Campanian is an indeterminate, as yet undescribed taxon represented by two *Coniophis*-like vertebrae from the Cenomanian of Sudan (Werner and Rage 1994). The latest Albian/earliest Cenomanian and Cenomanian ages of these oldest known anilioid fossils are consistent in terms of their stratigraphical distribution with phylogenetic interpretations that anilioids are primitive alethinophidians (e.g. Underwood 1967; Rage 1984, 1987; Kluge 1991; Cundall *et al.* 1993; Werner and Rage 1994). The disparate palaeogeographical distribution of these two roughly contemporaneous anilioids, along with the presence of more primitive alethinophidians in the upper Albian (Hoffstetter 1959; Cuny *et al.* 1990) and more derived alethinophidians in the Cenomanian (Werner and Rage 1994) indicate that anilioids, and by implication alethinophidians and their sister-taxon, the Scolecophidia, must have originated before the Cenomanian. Although *Pachyrhachis* is a stem snake and the putative sister-taxon to the Scolecophidia plus Alethinophidia (Caldwell and Lee 1997; Lee and Caldwell in press), this taxon is early Cenomanian in age and, therefore, is too young geologically to provide a minimum date for the origin of the Alethinophidia. Although considerably older, the two vertebrae from the Barremian of Spain are also uninformative as they are too poorly preserved to be identified beyond Serpentes indet. If correctly identified, however, the Spanish fossils are evidence that snakes of some sort were in existence by the mid Early Cretaceous.

Anilioids are thought to have originated in either Laurasia (Cracraft 1973; Hoffstetter and Rage 1977) or Gondwana (Rage 1981, 1987; Gayet *et al.* 1992). The fossil record of anilioids is of little assistance in resolving this debate, because the oldest known representatives are essentially contemporaneous in age and come from both Laurasia (uppermost Albian/lowermost Cenomanian, Utah) and Gondwana (Cenomanian, Sudan). Whatever the biogeographical origin of anilioids may have been, the presence of characteristic vertebrae of this group in Utah and Sudan demonstrates that these primitive snakes were already widely distributed by the Cenomanian.

Based on fossils known to them and the hypothesis that anilioids originated in Gondwana, most workers (e.g. Rage 1981, 1987, 1988*c*; Estes and Báez 1985; Gayet *et al.* 1992) have suggested that these snakes emigrated overland from South America to North America during the latest Cretaceous. OMNH 33250 and 33251 demonstrate, however, that anilioids were present in North America substantially earlier. If anilioids dispersed from South America to North America only once, they must have done so by at least the earliest Cenomanian. Given suspicions that snakes may have arisen in the Jurassic (Bellairs 1972; Carroll 1988) and the evidently broad geographical distribution of late Early to early Late Cretaceous anilioids, it is possible that anilioids may already have been present on the North American continent prior to its separation from Gondwana. Whether these snakes originated on the North American continent or immigrated from elsewhere remains unresolved.

CONCLUSIONS

As one of the most primitive and ancient groups of snakes, anilioids document an early stage in the evolution of snakes. The two uppermost Albian/lowermost Cenomanian vertebrae described above from the upper Cedar Mountain Formation are noteworthy because they: (1) are among the oldest

known snake fossils; (2) are the oldest known snake fossils in the New World; and (3) represent one of the two oldest known occurrences of anilioids. Our attempts to determine the taxonomic identity of these vertebrae and examine their evolutionary significance within a phylogenetic context have been hindered by a scarcity of information concerning the relative apomorphy and systematic reliability of vertebral features among snakes. These problems will continue to plague systematic studies of fossil snakes until patterns of vertebral variation among snakes are understood better.

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REFERENCES

ALBINO, A. M. 1990. Las serpientes de São Jose de Itaborai (Edad Itaboraiense, Paleoceno medio), Brasil. *Ameghiniana*, **27**, 337–342.

—— 1996. The South American fossil Squamata (Reptilia: Lepidosauria). *Münchner Geowissenschaftliche Abhandlungen A*, **30**, 185–202.

ARMSTRONG-ZIEGLER, J. G. 1978. An aniliid snake and associated vertebrates from the Campanian of New Mexico. *Journal of Paleontology*, **52**, 480–483.

—— 1980. Amphibia and Reptilia from the Campanian of New Mexico. *Fieldiana Geology, New Series*, **4**, 1–39.

ASTIBIA, H., BUFFETAUT, E., BUSCALIONI, A. D., CAPPETTA, H., CORRAL, C., ESTES, R., GARCIA-GARMILLA, F., JAEGER, J. J., JIMENEZ-FUENTES, E., LE LOEUFF, J., MAZIN, J. M., ORUE-ETXEBARRIA, X., PEREDA-SUBERBIOLA, J., POWELL, J. E., RAGE, J.-C., RODRIGUEZ-LAZARO, J., SANZ, J. L. and TONG, H. 1990. The fossil vertebrates from Laño (Basque Country, Spain); new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. *Terra Nova*, **2**, 460–466.

AUFFENBERG, W. 1963. The fossil snakes of Florida. *Tulane Studies in Zoology*, **10**, 131–216.

BAILON, S. 1988. Un Aniliidé (Reptilia, Serpentes) dans le Pliocène supérieur européen. *Comptes Rendus de l'Académie des Sciences, Série 2*, **306**, 1255–1258.

BELLAIRS, A. d'A. 1972. Comments on the evolution and affinities of snakes. 157–172. *In* JOYSEY, K. A. and KEMP, T. S. (eds). *Studies in vertebrate evolution.* Oliver and Boyd, Edinburgh, 284 pp.

BOLKAY, S. J. 1925. *Mesophis Nopcsai* n.g. n.sp. ein neues, schlangenähnliches Reptil aus der unteren Kreide (Neocom) von Bilek-Selišta (Ost-Hercegovina), *Glasnik Zemaljskog Muzeja u Bosni i Hercegovini*, **37**, 125–135.

BONAPARTE, J. F. 1991. Los vertebrados fósiles de la Formatión Río Colorado, de la ciudad de Neuquén y cercanías, Cretácico Superior, Argentina. *Revista del Museo Argentino de Ciencias Naturales, Paleontologia*, **4**, 17–123.

BREITHAUPT, B. H. 1985. Nonmammalian vertebrate faunas from the Late Cretaceous of Wyoming. *Wyoming Geological Association 36th Annual Field Conference Guidebook*, 159–175.

CALDWELL, M. W. and LEE, M. S. Y. 1997. A snake with legs from the marine Cretaceous of the Middle East. *Nature*, **386**, 705–709.

CARROLL, R. L. 1988. *Vertebrate paleontology and evolution.* W. H. Freeman and Co., New York, 698 pp.

CHKHIKVADZE, V. M. 1984. [New species of tortoise from the middle Eocene of Fergana.] *Paleontologicheskiy Sbornik*, **21**, 74–78. [In Russian].

CIFELLI, R. L., KIRKLAND, J. I., WEIL, A., DEINO, A. L. and KOWALLIS, B. J. 1997. High-precision $^{40}Ar/^{39}Ar$ geochronology and the advent of North America's Late Cretaceous terrestrial fauna. *Proceedings of the United States Academy of Sciences*, **94**, 11163–11167.

—— NYDAM, R. L., GARDNER, J. D., WEIL, A., KIRKLAND, J. I., EATON, J. E. and MADSEN, S. K. in press. Vertebrate

fauna of the upper Cedar Mountain Formation (Cretaceous; Albian/Cenomanian), Emery County: the Mussentuchit local fauna. *In* GILLETTE, D. D. (ed.). Fossil vertebrates of Utah. *Bulletin of the Utah Geological Survey*.

CRACRAFT, J. 1973. Vertebrate evolution and biogeography in the Old World tropics: implications of continental drift and palaeoclimatology. 373–393. *In* TARLING, D. H. and RUNCORN, S. K. (eds). *Implications of continental drift to the earth sciences*. Volume 1. Academic Press, London, 622 pp.

CUNDALL, D., WALLACH, V. and ROSSMAN, D. R. 1993. The systematic relationships of the snake genus *Anomochilus*. *Zoological Journal of the Linnean Society*, **109**, 275–299.

CUNY, G., JAEGER, J.-J., MAHBOUBI, M. and RAGE, J.-C. 1990. Les plus anciens Serpents (Reptilia, Squamata) connus. Mise au point sur l'âge géologique des Serpents de la partie moyenne du Crétacé. *Comptes Rendus de l'Académie des Sciences, Série 2*, **311**, 1267–1272.

DANILOV, I. 1997. Reptiles from the early Eocene of the Andarak 2 locality (southern Fergana, Kirghizia). 49. *In* ROČEK, Z. and HART, S. (eds). *Abstracts of the Third World Congress of Herpetology*, Prague, 2–10 August 1997.

ESTES, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. *University of California Publications in Geological Sciences*, **49**, 1–180.

—— 1976. Middle Paleocene lower vertebrates from the Tongue River Formation, southeastern Montana. *Journal of Paleontology*, **50**, 500–520.

—— 1985. Serpentes, by Jean-Claude Rage (book review). *Journal of Vertebrate Paleontology*, **5**, 375–376.

—— and BÁEZ, A. 1985. Herpetofaunas of North and South America during the Late Cretaceous and Cenozoic: evidence for interchange? 139–197. *In* STEHLI, F. G. and WEBB, S. D. (eds). *The great American biotic interchange*. Plenum Press, New York, 532 pp.

—— BERBERIAN, P. and MESZOELY, C. A. M. 1969. Lower vertebrates from the Late Cretaceous Hell Creek Formation, McCone County, Montana. *Breviora*, **337**, 1–33.

—— QUEIROZ, K. de and GAUTHIER, J. 1988. Phylogenetic relationships within Squamata. 119–281. *In* ESTES, R. and PREGILL, G. (eds). *Phylogenetic relationships of the lizard families: essays commemorating Charles L. Camp*. Stanford University Press, Stanford, 631 pp.

—— FRAZZETTA, T. H. and WILLIAMS, E. E. 1970. Studies on the fossil snake *Dinilysia patagonica* Woodward: Part I. Cranial morphology. *Bulletin of the Museum of Comparative Zoology*, **140**, 25–74.

FITZINGER, L. J. F. J. 1826. *Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des k. k. Zoologischen Museum zu Wien*. J. G. Hübner, Vienna, 66 pp.

FOX, R. C. 1975. Fossil snakes from the Upper Milk River Formation (Upper Cretaceous), Alberta. *Canadian Journal of Earth Sciences*, **12**, 1557–1563.

GAYET, M., MARSHALL, L. G. and SEMPERE, T. 1991. The Mesozoic and Paleocene vertebrates of Bolivia and their stratigraphic context: a review. *Revista Técnica de YPFB*, **12**, 393–433.

—— RAGE, J.-C., SEMPERE, T. and GAGNIER, P.-Y. 1992. Modalités des échanges de vertébrés continentaux entre l'Amérique du Nord et l'Amérique du Sud au Crétacé supérieur et au Paléocène. *Bulletin de la Société Géologique de France*, **163**, 781–791.

GILMORE, C. W. 1938. Fossil snakes of North America. *Special Papers of the Geological Society of America*, **9**, 1–96.

HAAS, G. 1979. On a new snakelike reptile from the lower Cenomanian of Ein Jabrud, near Jerusalem. *Bulletin du Muséum National d'Histoire Naturelle. Section C: Sciences de la Terre, Série 4*, **1**, 51–64.

—— 1980*a*. *Pachyrhachis problematicus* Haas, snakelike reptile from the lower Cenomanian: ventral view of the skull. *Bulletin du Muséum National d'Histoire Naturelle. Section C: Sciences de la Terre, Série 4*, **2**, 87–104.

—— 1980*b*. Remarks on a new ophiomorph reptile from the lower Cenomanian of Ein Jabrud, Israel. 177–192. *In* JACOBS, L. L. (ed.). *Aspects of vertebrate history: essays in honor of Edwin Harris Colbert*. Museum of Northern Arizona Press, Flagstaff, 393 pp.

HECHT, M. K. 1959. Amphibians and reptiles. 130–146. *In* McGREW, P. O., BERMAN, J. E., HECHT, M. K., HUMMEL, J. M., SIMPSON, G. G. and WOOD, A. E. The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. *Bulletin of the American Museum of Natural History*, **117**, 117–176, pls 50–57.

—— 1982. The vertebral morphology of the Cretaceous snake, *Dinilysia patagonica* Woodward. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1982**, 523–532.

—— and LADUKE, T. C. 1997. Limbless tetrapods. 95–99. *In* KAY, R. F., MADDEN, R. H., CIFELLI, R. L. and FLYNN, J. J. (eds). *The history of the neotropical fauna: vertebrate paleontology of the Miocene of tropical South America*. Smithsonian Institution Press, Washington, D. C., 592 pp.

HOFFSTETTER, R. 1955. Squamates de type moderne. 606–662. *In* PIVETEAU, J. (ed.). *Traité de Paléontologie*. Volume 5. Masson, Paris, 1113 pp.

—— 1959. Un Serpent terrestre dans le Crétacé inférieur du Sahara. *Bulletin de la Société Géologique de France, Série 7*, **1**, 897–902.

—— and GASC, J.-P. 1969. Vertebrae and ribs of modern reptiles. 201–310. *In* GANS, C., BELLAIRS, A. d'A. and PARSONS, T. S. (eds). *Biology of the Reptilia. Volume 1. Morphology A*. Academic Press, New York, 373 pp.

—— and RAGE, J.-C. 1977. Le gisement de Vertébrés Miocènes de La Venta (Columbie) et sa faune de serpents. *Annales de Paléontologie (Vertébrés)*, **63**, 161–190.

HOLMAN, J. A. 1979*a*. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 17. The late Eocene snakes. *Annals of Carnegie Museum*, **48**, 103–110.

—— 1979*b*. A review of North American Tertiary snakes. *Publications of the Museum, Michigan State University, Paleontological Series*, **1**, 200–260.

—— 1982. *Palaeophis casei*, new species, a tiny palaeophid snake from the early Eocene of Mississippi. *Journal of Vertebrate Paleontology*, **2**, 163–166.

—— 1995. *Pleistocene amphibians and reptiles in North America*. Oxford University Press, New York, 243 pp.

KLUGE, A. G. 1991. Boine snake phylogeny and research cycles. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **178**, 1–58.

LADUKE, T. C. 1991. The fossil snakes of Pit 91, Rancho La Brea, California. *Natural History Museum of Los Angeles County, Contributions in Science*, **424**, 1–28.

LEE, M. Y. S. and CALDWELL, M. W. in press. Anatomy and relationships of *Pachyrhachis problematicus* a primitive snake with hindlimbs. *Philosophical Transactions of the Royal Society*.

LINNAEUS, C. 1758. *Systema Naturae per Regna tria Naturae secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. 10th edition. Volume 1. Salvii, Stockholm, 824 pp.

MARSH, O. C. 1892. Notice of new reptiles from the Laramie Formation. *American Journal of Science, Series 3*, **43**, 449–453.

McDOWELL, S. B. 1975. A catalogue of the snakes of New Guinea and the Solomons, with special reference to those in the Bernice P. Bishop Museum. II. Anilioidea and Pythoninae. *Journal of Herpetology*, **9**, 1–80.

—— 1987. Systematics. 3–50. *In* SEIGEL, R. A., COLLINS, J. T. and NOVAK, S. S. (eds). *Snakes: ecology and evolutionary biology*. McGraw-Hill, New York, 529 pp.

MILNER, A. C., MILNER, A. R. and ESTES, R. 1982. Amphibians and squamates from the upper Eocene of Hordle Cliff, Hampshire – a preliminary report. *Tertiary Research*, **4**, 149–154.

MUIZON, C. de, GAYET, M., LAVENU, A., MARSHALL, L. G., SIGÉ, B. and VILLAROEL, C. 1983. Late Cretaceous vertebrates, including mammals, from Tiupampa, southcentral Bolivia. *Géobios*, **16**, 747–753.

NOPCSA, F. 1923*a*. Die Familien der Reptilien. *Fortschritte der Geologie und Paläontologie*, **2**, 1–210.

—— 1923*b*. *Eidolosaurus* und *Pachyophis*, Zwei neue Neocom-Reptilien. *Palaeontographica, Abteilung A*, **65**, 97–154, pls 7–8.

—— 1925. *Symoliophis* – Reste. *In* Ergebnisse der Forschungsreisen Prof. Stromers in den Wüsten Ägyptens. 2. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung*, **30**, 1–27.

PRASAD, G. V. R. and RAGE, J.-C. 1995. Amphibians and squamates from the Maastrichtian of Naskal, India. *Cretaceous Research*, **16**, 95–107.

RAGE, J.-C. 1974. Les serpents des Phosphorites du Quercy. *Palaeovertebrata*, **6**, 274–303.

—— 1981. Les continents péri-atlantiques au Crétacé supérieur: migrations des faunes continentales et problèmes paléogéographiques. *Cretaceous Research*, **2**, 65–84.

—— 1984. Serpentes. 1–80. *In* WELLNHOFER, P. (ed.). *Encyclopedia of paleoherpetology*. Part 11. Gustav Fischer Verlag, Stuttgart.

—— 1987. Fossil history. 51–76. *In* SEIGEL, R. A., COLLINS, J. T. and NOVAK, S. S. (eds). *Snakes: ecology and evolutionary biology*. McGraw-Hill, New York, 529 pp.

—— 1988*a*. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. I. Amphibiens et reptiles. *Palaeontographica, Abteilung A*, **205**, 3–27.

—— 1988*b*. Un serpent primitif (Reptilia, Squamata) dans le Cénomanien (base du Crétacé supérieur). *Comptes Rendus de l'Académie des Sciences, Série 2*, **307**, 1027–1032.

—— 1988*c*. Gondwana, Tethys, and terrestrial vertebrates during the Mesozoic and Cainozoic. 255–273. *In* AUDLEY-CHARLES, M. G. and HALLAM, A. (eds). *Gondwana and Tethys*. Oxford University Press, New York, 317 pp.

—— 1991. Squamate reptiles from the early Paleocene of the Tiupampa area (Santa Lucia Formation) Bolivia. *Revista Técnica de YPFB*, **12**, 503–508.

—— 1996. Les Madtsoiidae (Reptilia, Serpentes) du Crétacé supérieur d'Europe: témoins gondwaniens d'une dispersion transtéthysienne. *Comptes Rendus de l'Académie des Sciences, Série 2*, **322**, 603–608.

—— 1997. Phylogeny and the origin of snakes. 167. *In* ROČEK, Z. and HART, S. (eds). *Abstracts of the Third World Congress of Herpetology*, Prague, 2–10 August 1997.

—— and ALBINO, A. M. 1989. *Dinilysia patagonica* (Reptilia, Serpentes): matériel vertébral additionnel du Crétacé supérieur d'Argentine. Etude complémentaire des vertèbres, variations intraspécifiques et intracolumnaires. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1989**, 433–447.

—— and AUGE, M. 1993. Squamates from the Cainozoic of the western part of Europe. A review. *Revue de Paléobiologie*, **7**, 199–216.

—— and PRASAD, G. V. R. 1992. New snakes from the Late Cretaceous (Maastrichtian) of Naskal, India. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **187**, 83–97.

—— and RICHTER, A. 1994. A snake from the Lower Cretaceous (Barremian) of Spain: the oldest known snake. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1994**, 561–565.

RIEPPEL, O. 1979*a*. A cladistic classification of primitive snakes based on skull structure. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **17**, 140–150.

—— 1979*b*. The classification of primitive snakes and the testability of phylogenetic theories. *Biologisches Zentralblatt*, **98**, 537–552.

—— 1988. A review of the origin of snakes. 37–130. *In* HECHT, M. K., WALLACE, B. and PRANCE, G. T. (eds). *Evolutionary biology*. Volume 22. Plenum Press, New York, 291 pp.

SAID, R. 1962. *The geology of Egypt*. Elsevier, Amsterdam, 377 pp.

SAUVAGE, H.-E. 1880. Sur l'existence d'un Reptile du type Ophidien dans les couches à *Ostrea columba* des Charentes. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, **91**, 671–672.

—— 1896. Sur un Ophidien des terrains crétaciques du Portugal. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, **122**, 251–252.

SCANLON, J. D. 1993. Madtsoiid snakes from the Eocene Tingamarra fauna of eastern Queensland. *Kaupia: Darmstädter Beiträge zur Naturgeschichte*, **3**, 3–8.

SERENO, P. C., DUTHEIL, D. B., IAROCHENE, M., LARSSON, H. C. E., LYON, G. H., MAGWENE, P. M., SIDOR, C. A., VARRICCHIO, D. J. and WILSON, J. A. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science*, **272**, 986–991.

SIMPSON, G. G. 1933. A new fossil snake from the *Notostylops* beds of Patagonia. *Bulletin of the American Museum of Natural History*, **67**, 1–22.

SLIŠKOVIĆ, T. 1970. Die Stratigraphische Lage der Schichten mit Pachyophiidae aus Selište bei Bileća (Ostherzegowina). *Bulletin Scientifique Conseil des Academies des Sciences et des Arts de la RSF de Yougoslavie. Section A: Sciences Naturelles, Techniques et Médicales*, **15**, 389–390.

SMITH, A. G., SMITH, D. G. and FUNNELL, B. M. 1994. *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge University Press, New York, 99 pp.

STEJNEGER, L. 1907. Herpetology of Japan and adjacent territory. *Bulletin of the United States National Museum*, **58**, 1–577.

STOKES, W. L. 1952. Lower Cretaceous in Colorado Plateau. *Bulletin of the American Association of Petroleum Geologists*, **36**, 1766–1776.

STROMER, E. 1936. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. 7. Baharîje-Kessel und -Stufe mit deren Fauna und Flora Eine ergänzende Zusammenfassung. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung*, **33**, 1–102.

SZYNDLAR, Z. 1994. Oligocene snakes of southern Germany. *Journal of Vertebrate Paleontology*, **14**, 24–37.

—— and BÖHME, W. 1996. Redescription of *Tropidonotus atavus* von Meyer, 1855 from the upper Oligocene of Rott (Germany) and its allocation to *Rottophis* gen. nov. (Serpentes, Boidae). *Palaeontographica, Abteilung A*, **240**, 145–161, pl. 1.

TCHERNOV, E., POLCYN, M. J. and JACOBS, L. L. 1996. Snakes with legs: the Cenomanian fauna of 'Ein Yabrud, Israel. Abstracts of Papers of the 56th Annual Meeting of the Society of Vertebrate Paleontology. New York, Oct. 16–19, 1996. *Journal of Vertebrate Paleontology*, **16** (supplement), 68A.

ULIANA, M. A. and DELLAPÉ, D. A. 1981. Estratigrafía y evolución paleoambiantal de la sucesión maestrichtiana-eoterciaria del engolfamiento neuquino (Patagonia septentrional). *Actas del Congreso Geologico Argentino*, **8**, 673–711.

UNDERWOOD, G. 1967. A contribution to the classification of snakes. *Publication of the British Museum (Natural History)*, **653**, 1–179.

WERNER, C. and RAGE, J.-C. 1994. Mid-Cretaceous snakes from Sudan. A preliminary report on an unexpectedly diverse snake fauna. *Comptes Rendus de l'Académie des Sciences, Série 2*, **319**, 247–252.

ZEROVA, G. A. and CHKHIKVADZE, V. M. 1984. [Review of Cenozoic lizards and snakes of the USSR.] *Proceedings of the Academy of Sciences of the Georgian SSR, Biological Series*, **10**, 319–326. [In Russian].

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A CHORISTODERAN REPTILE FROM THE LOWER CRETACEOUS OF JAPAN

by SUSAN E. EVANS *and* MAKOTO MANABE

ABSTRACT. A new, small (*c.* 250 mm snout–vent length) choristoderan reptile, *Shokawa ikoi* gen. et sp. nov., is described from the early Cretaceous Okurodani Formation, Tetori Group, of Japan. It is distinguished from other known choristoderans in having a long neck with at least 16 cervical vertebrae. The skeleton is pachyostotic and the caudal neural spines are much taller than those of the Jurassic *Cteniogenys*, both features suggesting a more aquatic lifestyle. Phylogenetic analysis places the new Japanese form in a small clade with *Cteniogenys* and the Triassic *Pachystropheus*. This clade is the sister taxon of crown-group Neochoristodera.

FOR many years, the extinct reptilian group Choristodera encompassed only two medium-sized gavial-like aquatic diapsid reptiles: *Champsosaurus* and *Simoedosaurus* from the Upper Cretaceous and lower Tertiary of Europe and North America (e.g. Cope 1884; Erickson 1972, 1985, 1987; Russell-Sigogneau and Russell 1978). Romer (1956) classified choristoderes within his paraphyletic diapsid stem group Eosuchia, whereas most later authors have placed them either as basal archosauromorphs (e.g. Currie 1981; Erickson 1985, Evans 1990) or as the sister group of neodiapsids (e.g. Evans 1988; Evans and Hecht 1993). The temporal and geographical range of the group was extended by the recovery of *Tchoiria* (Efimov 1975, 1979) and *Ikechosaurus* (Sigogneau-Russell 1981; Brinkman and Dong 1993) from the Aptian/Albian of Mongolia and China, and the enigmatic Early Cretaceous *Khurendukhosaurus* (Sigogneau-Russell and Efimov 1984; Efimov 1996) from Russia, Mongolia and China. The last genus is very poorly known, but both *Tchoiria* and *Ikechosaurus* are similar in size and morphology to *Champsosaurus* and *Simoedosaurus*.

Over the last decade, several additional, but rather different, taxa have been recognized. Interpretation of the small Jurassic (North America, Europe) reptile *Cteniogenys* as a choristodere (Evans 1990, 1991), extended the temporal range of the group further, as did the re-examination of the Triassic genus *Pachystropheus* (Storrs and Gower 1993; Storrs *et al.* 1996). The latter was originally described as a choristodere by Erica von Huene (1935), but, with such a long apparent gap between typical choristoderes and *Pachystropheus*, her classification was not widely accepted. Finally, Hecht (1992) extended the stratigraphical range of the group in the opposite direction, by describing a new late Oligocene reptile from France, *Lazarussuchus*, as a primitive choristodere. Both *Lazarussuchus* and *Cteniogenys* are significantly smaller than the Cretaceous and early Tertiary taxa, and recent analyses (Evans and Hecht 1993; Gao and Fox in press) have placed them as successive sister-taxa to a clade, Neochoristodera (Evans and Hecht 1993), including *Champsosaurus*, *Tchoiria*, *Ikechosaurus* and *Simoeodosaurus*.

As a result of this new work on choristoderes, our perception of the group has changed substantially (Evans and Hecht 1993), from that of a rather small group of very similar aquatic reptiles with a short temporal range, to that of a long lived, geographically widespread group, showing considerable size variation but, apparently, only limited morphological diversity. This idea of morphological conservatism is challenged by material described here from the Lower Cretaceous of Japan which represents a new, long-necked genus.

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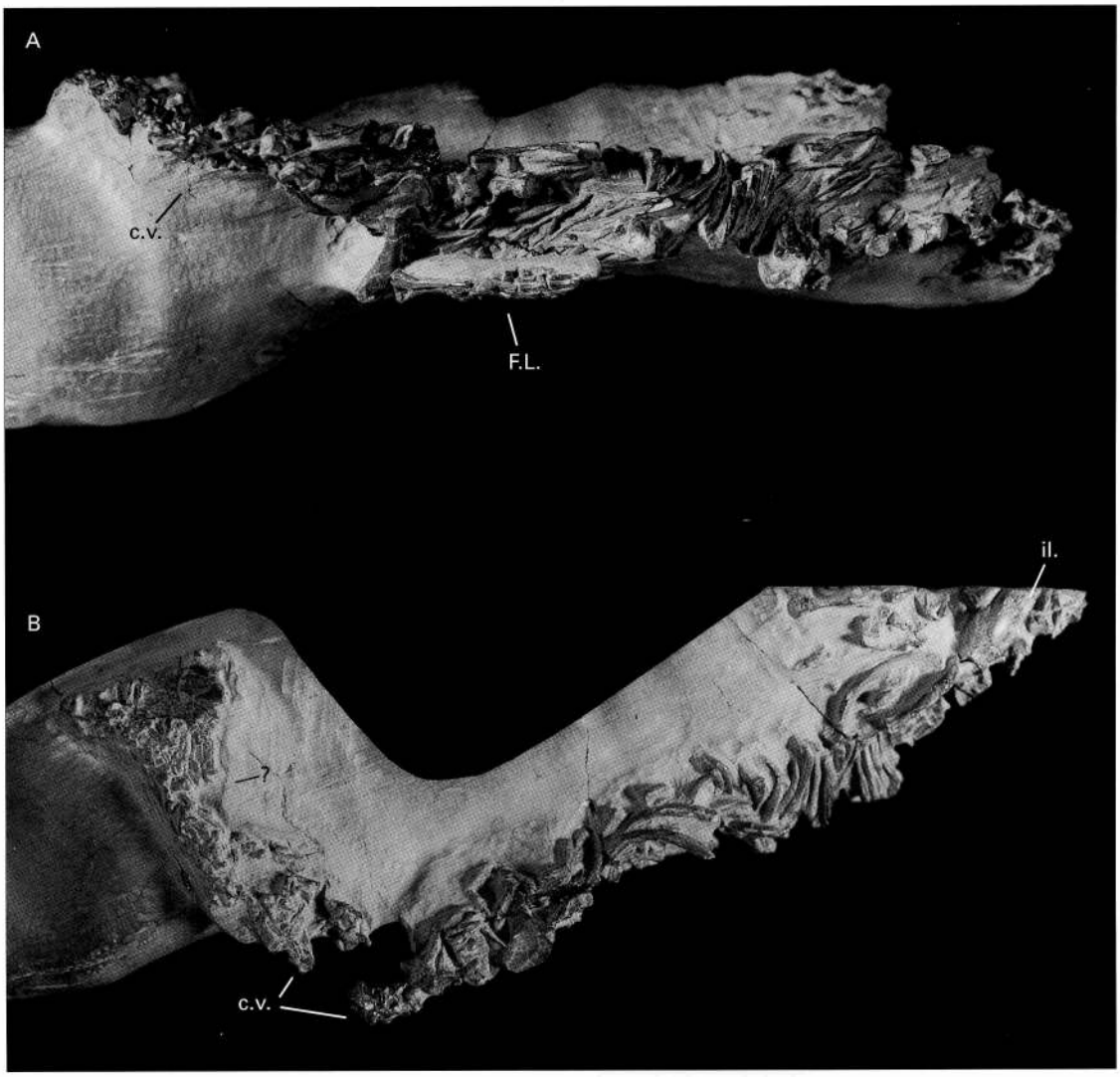


TEXT-FIG. 1. *Shokawa ikoi* gen. et sp. nov.; holotype, IBEF VP 3. A, left lateral view. B, dorsal view. Both ×0·8.

GEOLOGICAL BACKGROUND

The fossil material described here comes from a Lower Cretaceous fossiliferous horizon from approximately the middle of the basal member of the Okurodani Formation, in the Tetori Group of Central Honshu (Maeda 1961; Azumi and Tomida 1995; Hasegawa *et al.* 1995; Manabe and Hasegawa 1995; Unwin *et al.* 1996). It was collected by Mr Ikoi Shibata from a stream locality (designated KO2 by the collector) in the Kobudani Valley, near Shokawa village, Gifu Prefecture. The rock is a dark grey silty-sandstone which is partially metamorphosed, very hard and acid resistant. It requires painstaking preparation, and this was undertaken by the collector.

The bone bed horizon shows a coarse layering with plant macrofossils at the base, overlain by shell debris and isolated bones. Rare articulated specimens (turtles, choristoderes) are found above this detrital layer. Most of the vertebrate material is disarticulated, but is relatively unabraded

(Dr Liz Cook, Bristol University, pers. comm. 1997), suggesting deposition under relatively quiet conditions. Recent field work by Dr Chris Nicholas (University of Cambridge, Geology), suggests that the KO2 bone bed was deposited in a flood plain environment, possibly deltaic. The fact that most of the vertebrates recovered from this deposit are aquatic (fish, turtles, choristoderes and rare amphibians), is consistent with this model. Terrestrial vertebrates (dinosaurs, birds, pterosaurs and lizards) are rarer.

The fossiliferous horizon has been provisionally dated in relation to volcanic tuff layers above the bone bed, for which dates of 120–140 Ma were obtained by fission track dating (Gifu-Ken Dinosaur Research Committee 1993). Dr Nicholas' field work has identified a second underlying tuff and new analyses of the tuffs should help to constrain the date of the bone bed with greater accuracy.

Mr Shibata's collection has been deposited in the museum of the Visitors Centre, Izumi Board of Education, Izumi, Fukui Prefecture and all specimens carry the prefix IBEF VP.

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA Osborn, 1903
NEODIAPSIDA Benton, 1985
CHORISTODERA Cope, 1884

Genus SHOKAWA gen. nov.

Derivation of name. From the village of Shokawa, near the fossil locality.

Type species. Shokawa ikoi gen. et sp. nov.

Diagnosis. As for the type and only known species.

Shokawa ikoi gen. et sp. nov.

Text-figures 1–7

Derivation of name. To honour Mr Ikoi Shibata, the collector of the fossils.

Holotype. IBEF VP 3, a postcranial skeleton without skull.

Type locality and horizon. Stream section (KO2 locality), Shokawa village, Gifu Prefecture, Japan (36° 03′, 136° 53′ E); bone bed horizon in the Okurodani Formation, Lower Cretaceous (Valanginian) Tetori Group, Japan. To date, *Shokawa* is known only from this locality.

Referred specimens. The following specimens from KO2 are assigned to *Shokawa* on the basis either of their resemblance to elements of the holotype specimen (vertebrae, fore limb bones), or on a general resemblance to equivalent elements in other choristoderan taxa (hind limb, dentaries): IBEF VP 8, right dentary, IBEF VP 9, left dentary; IBEF VP 10, right distal humerus, forearm and part of hand; IBEF VP 11, an isolated right radius; IBEF VP 12, articulated caudal vertebrae; IBEF VP 13, associated limb bone fragments including a partial femur; IBEF VP 14, a caudal vertebra; IBEF VP 15, a series of associated caudal vertebrae; IBEF VP 16, associated hind limb (crus) and foot; IBEF VP 200, a dorsal vertebra.

Diagnosis. A small choristoderan reptile characterized by the following combination of features: at least 16 cervical vertebrae, of which most or all bear small bicapitate ribs; cylindrical vertebral

centra persistently separated from the neural arches except in the neck; caudal vertebrae with deep descending ventral flanges; anterior caudals with tall slender neural spines; interclavicle rhomboid with clavicles meeting at a strong angle in the ventral midline; strong quadrangular coracoids and reduced scapular blades; humerus, forearm and hand relatively short and broad; ilium with narrow vertical blade bearing strong vertical striations; ribs, limb bones and gastralia pachyostotic.

Remarks. *Shokawa ikoi* differs from *Lazarussuchus* and all known neochoristoderes in having at least 16 cervical vertebrae (the number of cervicals in *Cteniogenys*, *Pachystropheus* and *Khurendukhosaurus* is not known). It resembles *Pachystropheus*, but differs from *Cteniogenys*, in having very tall slender caudal neural spines, and differs from *Cteniogenys* in having more cylindrical dorsal centra (completely round in cross section). *Shokawa* differs from both *Khurendukhosaurus* and *Pachystropheus* in having a rhomboid rather than T-shaped interclavicle, and from *Khurendukhosaurus* in lacking the prominent muscle processes and tubercles on the scapulocoracoid (Sigogneau-Russell and Elfimov 1984; Efimov 1996). It resembles *Cteniogenys* and *Pachystropheus* in having a nearly vertical iliac blade, in contrast with that of neochoristoderes in which the blade is horizontal, and that of *Pachystropheus* which is strongly angled. These differences between *Shokawa* and other choristoderes justify the erection of a new genus for the Japanese form.

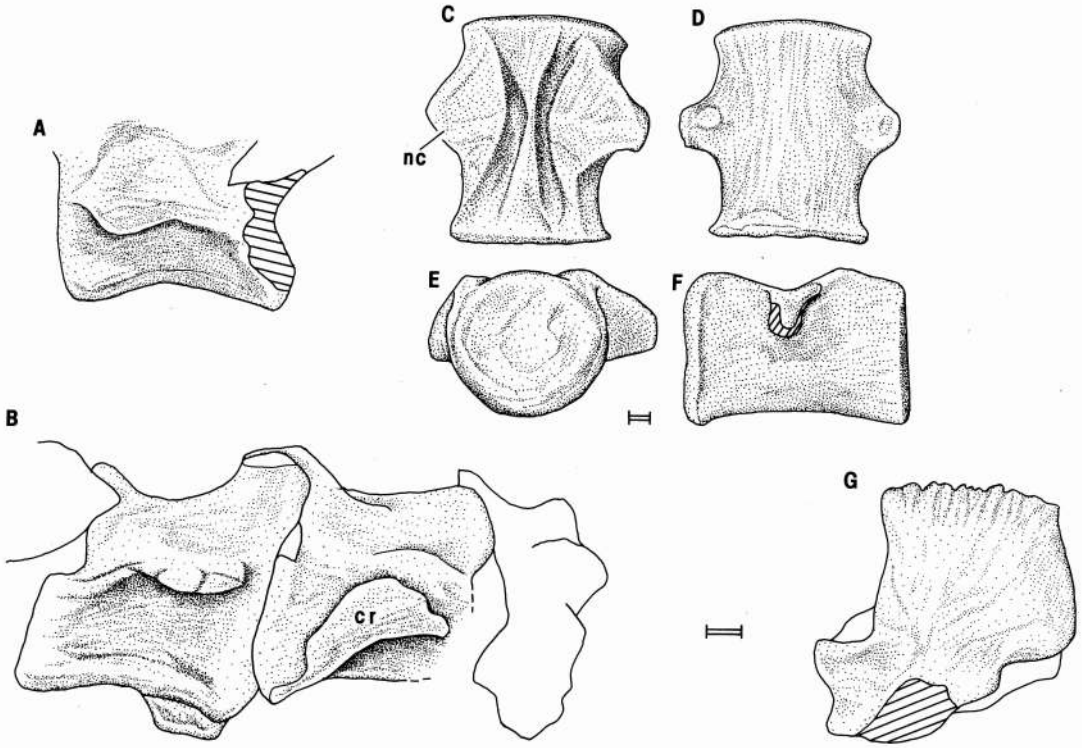
DESCRIPTION

Material. The material attributed to *Shokawa ikoi* consists of the holotype specimen, IBEF VP 3, and a series of isolated bones and partial skeletons, all from the KO2 locality. The material is generally well preserved and uncompressed, with little evidence of either rolling or abrasion, and most associated specimens retain their elements in either full, or partial, articulation. By far the most complete specimen is the holotype, IBEF VP 3, which comprises the presacral, sacral and anterior caudal vertebrae, associated ribs and gastralia, the pectoral girdle, a complete right forelimb and parts of the left forelimb, a left ilium and partial ischium, and fragments of one hind limb. The anterior cervical vertebrae have been disarticulated from the main skeleton and lie in a mass in front and slightly to the right of the main vertebral series. To the right of this cervical vertebral cluster is a mass of bone fragments, only partially exposed, which may contain part of the skull. However, no individual elements can be recognized and further preparation has proved impossible. Furthermore, neither an X-ray nor a CAT (Computerised Axial Tomography) Scan revealed any structure or depth to the bone mass. Apart from specimens in private hands, the only representative elements of the skull are two isolated dentaries, IBEF 8 and 9, which match the general morphology of choristoderan dentaries (those of *Cteniogenys*, for example; SEE, pers. obs.). With respect to the postcranial skeleton, the holotype specimen is supplemented by both isolated (IBEF VP 14, IBEF VP 200) and associated (IBEF VP 12, 15) specimens of dorsal and caudal vertebrae, by isolated (IBEF VP 11) and associated (IBEF VP 10) forelimb specimens, and by two associations of hindlimb bones (IBEF VP 13, 16). Thus the postcranial skeleton of *Shokawa ikoi* is well represented; the skull remains virtually unknown.

All the material here attributed to *Shokawa ikoi* represents individuals of comparable size, reaching *c.* 250 mm long from the skull tip to the junction of anterior caudal two and three (roughly equivalent to snout–vent length in a living animal). With the tail, the length would have been 370–400 mm. Whether the available material is representative of fully adult individuals (and therefore of full size) is difficult to establish, given that aquatic animals often show reduced ossification of vertebrae, joint surfaces and extremities. However, the fact that the cervical and caudal vertebrae show closed neurocentral sutures, and that the carpal and tarsal elements are fully ossified, suggests that the elements are not from young individuals.

Skull. Two dentaries (IBEF VP 8, IBEF VP 9) have been attributed provisionally to *Shokawa ikoi*. Each is extremely long and slender, and bears on its lateral aspect a double row of grooved sensory foramina as found in all choristoderes (Evans 1990). IBEF VP 8 has between 28 and 34 tooth positions, whereas IBEF VP 9 bears about 36. The teeth are homodont, resembling slender cones with slight anterior and posterior keels, and weak striae. The implantation is subthecodont, the tooth bases resting in shallow, rounded pits. Medially, there is a deep subdental shelf, but neither dentary has the medial surface fully prepared. In IBEF VP 8, the postdental part of the bone is preserved. It is quite long, tapering dorsally and apparently faceted laterally, perhaps for part of the coronoid.

Cervical vertebrae. The neck includes between 16 and 18 cervical vertebrae and is therefore unusually long for a choristoderan where the usual cervical count is nine. A group of disarticulated cervicals lies to the right of the holotype (Text-fig. 1), beginning with a rectangular bar of bone which may be either the atlas or the axis intercentrum. With this are at least seven disarticulated vertebrae, whilst at least a further eight are preserved in articulation on the main part of the specimen (Text-figs 1–3). All but the most posterior cervicals have closed neurocentral sutures, and all have a ventral keel, but none shows any trace of an intercentrum. The anterior vertebrae are not clearly visible, but those in the posterior part of the neck (CV10–16) resemble one another in being relatively long (i.e. longer than high), with a horizontally orientated overhanging diapophysis and a small ventral parapophysis (Text-fig. 2A–B). CV 10 has a small rib associated with it which is broad anteriorly,



TEXT-FIG. 2. *Shokawa ikoi* gen. et sp. nov.; presacral vertebrae. A, partial cervical vertebra of holotype, IBEF VP 3, in left lateral view. B, cervical vertebrae and reduced rib of holotype, IBEF VP 3, in right lateral view. C–F, dorsal vertebral centrum, IBEF VP 200, in C, dorsal, D, ventral, E, anterior, and F, left lateral views. G, dorsal neural arch from holotype, IBEF VP 3, in left lateral view. Scale bars represent 1 mm.

tapering slightly posteriorly, but not extending beyond the end of the centrum (Text-fig. 2B). The neural arches are not visible (and were probably low) except in posterior cervicals where they resemble the dorsal vertebrae in having strong rectangular neural spines with rugose tips. The last visible cervical is associated with a strongly bicapitate rib that has a short thick shaft. Since the last cervical of most neochoristoderes has a single head, the condition in *Shokawa* suggests that either: (1) bicapitate ribs extended into the anterior part of the dorsal series; or (2) one or more further cervical vertebrae are covered by the pectoral region.

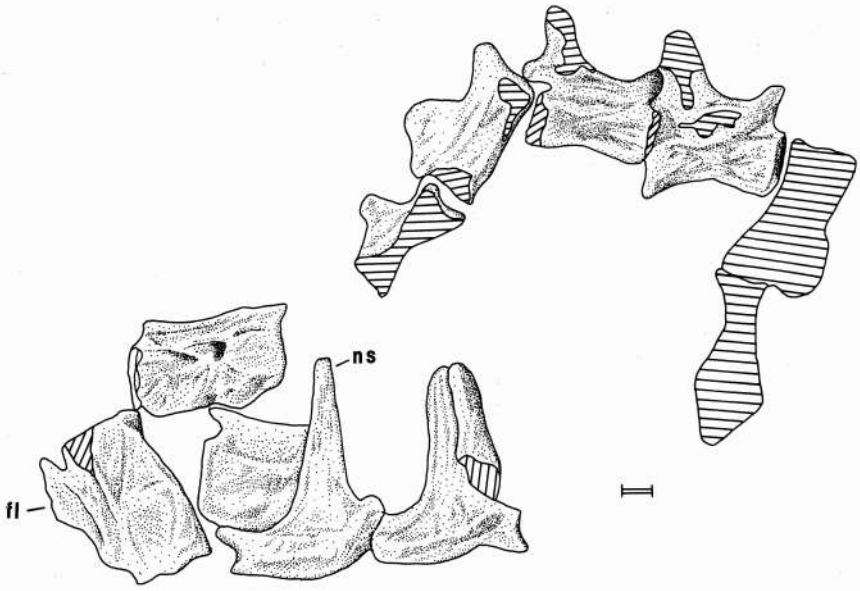
Dorsal vertebrae. In the holotype, the dorsal vertebrae are generally obscured by overlying girdles, thick ribs and gastralia, although the rugose tops of the neural spines are visible along the midline (Text-fig. 2G).

Supplementary information is available from isolated centra such as IBEF VP 200 (Text-fig. 2C–F). The centrum resembles that of typical choristoderans in being platycoelous and cylindrical. The open neurocentral sutures are broad and triangular (Text-fig. 2C), but differ from those of *Cteniogenys* in that the posterior part of the facet is a raised surface rather than a recess. Between the neural arch facets is a narrow central groove with a dorsal midline ridge which is squared off or rounded depending on vertebral position (Text-fig. 2C).

Dorsal ribs are thick and single-headed with carinae like those of other choristoderes (SEE, pers. obs.). There is also a set of very robust pachyostotic gastralia associated with the trunk region and partially responsible for obscuring the vertebrae (Text-figs 1, 4).

Sacral vertebrae. The sacral region is also somewhat obscured, but there are at least three sacrals which are characterized by broad rib facets and a rather depressed centrum shape. The sacral ribs are certainly not fused to the centrum, nor is the neurocentral suture closed.

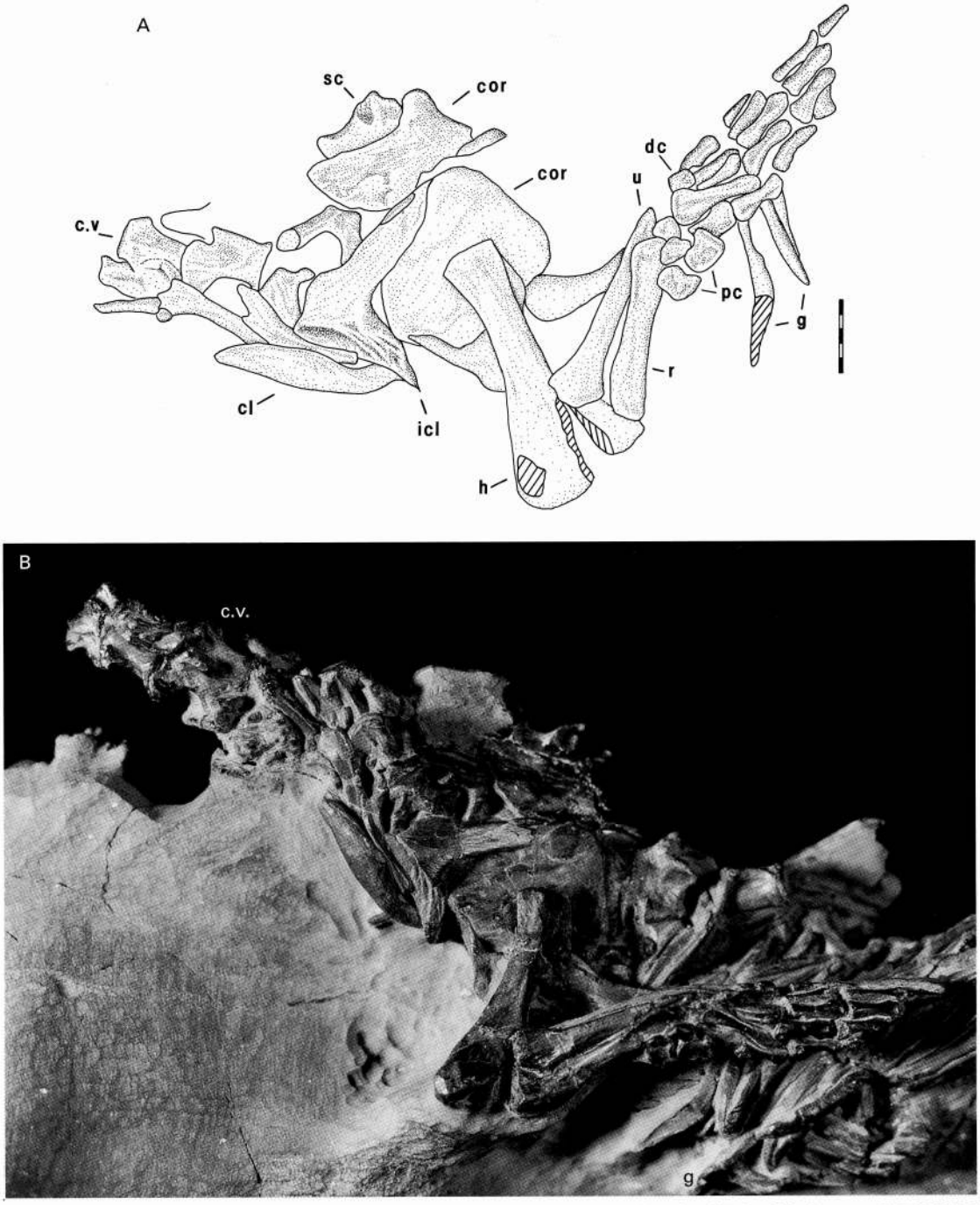
Caudal vertebrae. The anterior caudals have a shape similar to that of the sacrals, but bear a midline groove for the caudal vessels. The neurocentral suture is still not closed, but the first caudal ribs are fused to the centrum. The posterior caudals are not well preserved on the holotype block, but are seen as isolated elements (for example, IBEF VP 14) and in two separate associations (IBEF VP 12, IBEF VP 15; Text-fig. 3). In these



TEXT-FIG. 3. *Shokawa ikoi* gen. et sp. nov.; IBEF VP 15; series of caudal vertebrae. Scale bar represents 1 mm.

specimens, the neural arches are fused to the centra and the neural spines are tall and narrow, suggesting that the tail was particularly important in aquatic locomotion. In this feature, the caudals of *Shokawa* resemble those of *Pachystropheus* (Storrs *et al.* 1996). As in *Cteniogenys*, the posterior caudal centra have strong paired ventral flanges, but the presence of separate haemal arches establishes that the ventral flanges occurred in addition to, not instead of, the chevrons (Evans 1991).

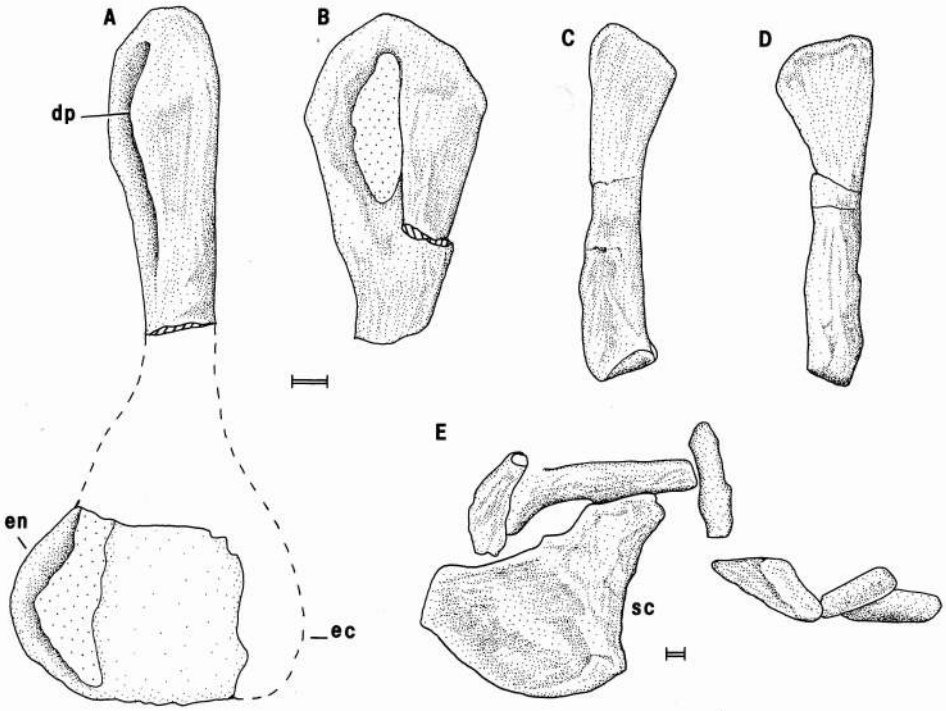
Pectoral girdle and forelimb. The pectoral girdle is represented by an interclavicle, clavicles and parts of the scapula and coracoid (Text-figs 1, 4–5). The interclavicle has a rhomboid shape, with large clavicular facets. The clavicles met in the midline and are expanded and very robust. The interclavicle also has a long, strong,



TEXT-FIG. 4. *Shokawa ikoi* gen. et sp. nov. A–B, pectoral girdle and right forelimb of holotype, IBEF VP 3. A, Scale bar represents 5 mm; B, ×2. The view in A is angled in comparison with B to show more detail of the left side of the pectoral girdle.

parallel-sided stem with a ridge and groove ornament (Text-fig. 4). The coracoid plates are square and robust, but the scapula appears relatively small and weak, with a narrow blade (Text-fig. 5E).

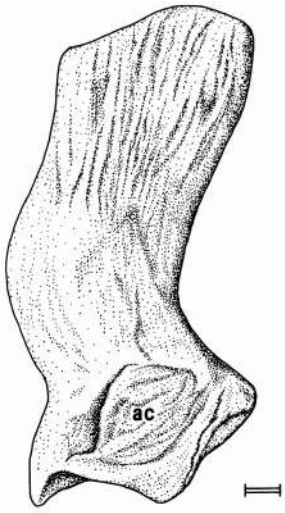
The right forelimb is almost complete in the holotype and is made up of short, thick elements. The right humerus is rather narrow proximally and expanded distally, but the articular surfaces are unclear (Text-fig. 4A–B). The left humerus has been dissociated (Text-fig. 5A–B). The proximal end is rather narrow, but bears



TEXT-FIG. 5. *Shokawa ikoi* gen. et sp. nov.; forelimb and girdle elements. A–B, holotype specimen, IBEF VP 3, left humerus, in A, ventral and B, partial anterior views. C–D, isolated right radius, IBEF VP 11, in C, posterior and D, anterior views. E, left scapula blade of holotype, IBEF VP 3, seen from the dorsal surface of the specimen. Scale bars represent 1 mm.

a strong deltopectoral expansion. The shape resembles that of *Champsosaurus albertensis* (Parks 1927) more than that of *Pachystropheus*, *Cteniogenys* or *Simoedosaurus*. There is a short, narrow shaft (shorter than in *Cteniogenys*), expanding into a broad distal head which is distinctly flattened dorsoventrally and is without developed articular condyles for either radius or ulna. The ectepicondylar region (ec) is damaged in the holotype, but is preserved in a specimen bearing a right distal humerus (IBEF VP 10) where there is, at best, a weak groove. The ulna is notched for articulation with the radius, but appears to show little or no development of the olecranon. However, the ulna of IBEF VP 10 has an expanded proximal end which looks as though a cartilaginous olecranon epiphysis may have been attached. The radius is preserved on the holotype, but also as an isolated element (IBEF VP 11, Text-fig. 5C–D). It is compressed, with a twisted shaft separating the relatively broad proximal end from the narrower distal one. The proximal surface is not expanded into a cotyle for the humeral capitellum, but this presumably reflects the very weak development of the distal humeral joint surfaces. The right wrist of the holotype preserves two large notched elements which must be proximal carpals (pc, Text-fig. 4A), probably the radiale and ulnare, but it is not possible to differentiate them. In addition, there are at least three smaller carpals, of which one or more must be distal carpals (dc). Elements of all five digits are preserved, but the phalangeal formula cannot be reconstructed with confidence. The phalanges and metacarpals are short and robust, but broadly similar to those of *Champsosaurus*.

Pelvis and hindlimb. Only the left ilium and a fragment of the ischium are preserved on the holotype block. The ilium (Text-fig. 6) makes a small contribution to the acetabulum (ac), but has a large blade with an essentially



TEXT-FIG. 6. *Shokawa ikoi* gen. et sp. nov., left ilium of holotype, IBEF VP 3, in lateral view. Scale bar represents 1 mm.

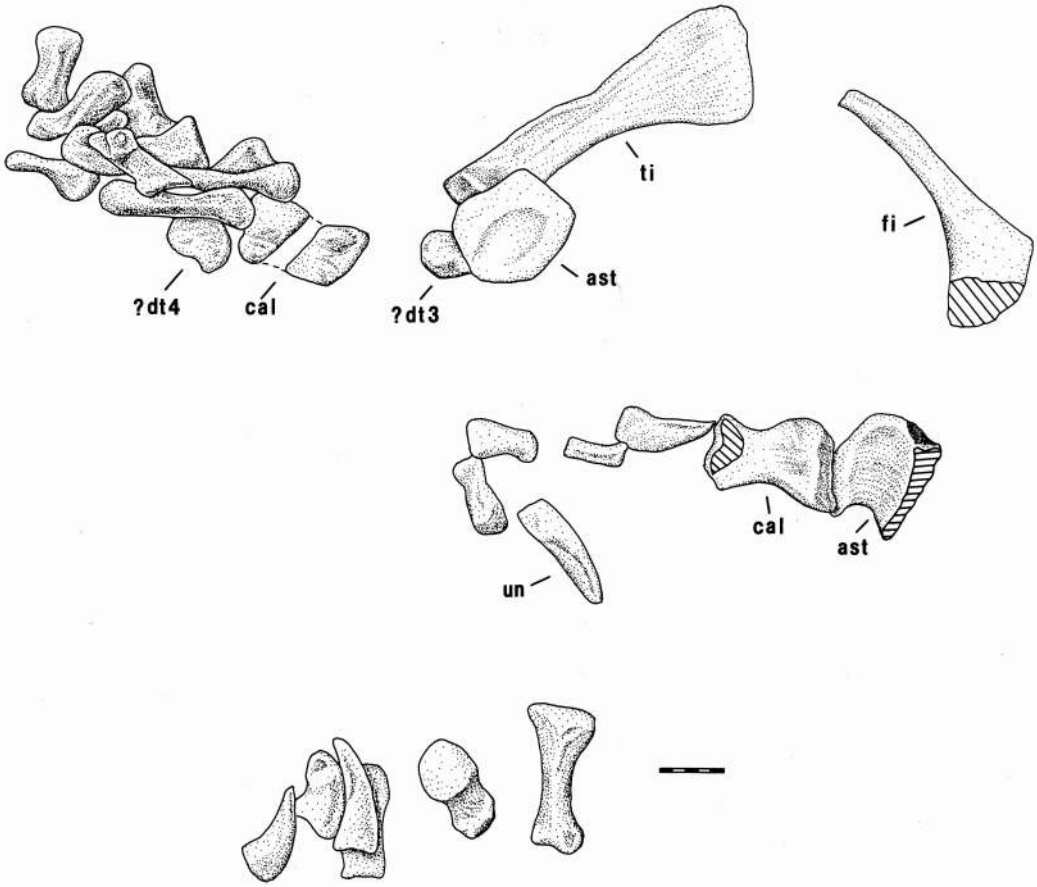
vertical, if sinuous, dorsal margin. The tip curves back slightly and has linear rugosites (like those of *Cteniogenys*, *Pachystropheus* and *Simoedosaurus*). In shape, and in the near vertical orientation of the blade, this ilium resembles those of *Cteniogenys* and *Lazarussuchus* more than those of neochoristoderes where the blade is horizontal and, in most genera, almost triangular (SEE, pers. obs.). That of *Pachystropheus* is intermediate in having a sharp angle between the acetabulum and the posteriorly directed blade. However, a growth series of *Champsosaurus* ilia figured by Erickson (1972) suggests that the orientation of the blade, at least, may change with age/size.

The hind limb is represented on the holotype by a small group of bones to the right of the specimen (part of the pes) and a detached femur. The latter, unfortunately, lacks the proximal and distal ends, and simply indicates that the femur of this form was similar to that of other choristoderes (and many other small reptiles) in being relatively long and slender with a sigmoid curvature. A separate right hind limb specimen (IBEF VP 16; Text-fig. 7) provides more information on the lower leg and foot. The tibia is a short robust bone with a broad proximal head, waisted shaft and little evidence of distal expansion. The bone is anteroposteriorly flattened and its medial border bears a raised crest. The fibula shows the typical choristoderan shape in having a narrow proximal part and an expanded distal end, although the distal expansion is particularly strong in this genus.

The astragalus and calcaneum are separate. Both astragali are preserved, but the right bone is more clearly visible. It forms a circular disc-like element with a concave surface. The tibial and calcaneal facets lie at roughly 45° and the outer border is thickened. Associated with the distal margin is a small rounded element which is probably distal tarsal (dt) 3. The calcaneum is displaced distally and rotated so that it cannot be seen clearly. It appears to be a roughly rectangular element. Close to it is a larger distal tarsal, probably dt4. The foot itself is composed of short strong metatarsals and short robust phalanges with strong claws which, as in other taxa, are elongate, ventrally expanded and lack a clearly developed flexor tubercle. The phalangeal formula cannot be reconstructed.

PHYLOGENETIC POSITION

Cope's (1884) name Choristodera reflected the separated, or unfused, state of the neurocentral sutures in the vertebrae, but today these reptiles are characterized principally by their elongated skulls with expanded temporal fenestrae. In the absence of skull material, attribution to the group

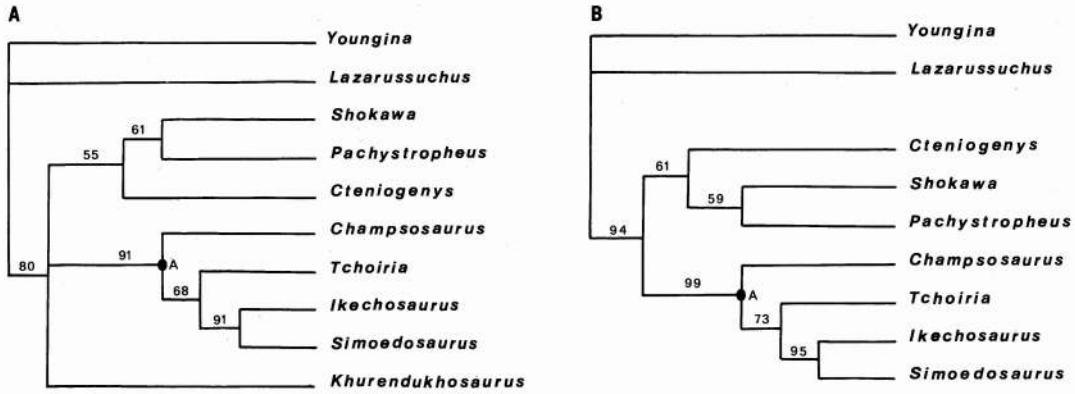


TEXT-FIG. 7. *Shokawa ikoi* gen. et sp. nov.; IBEF VP 3; block bearing elements of the hindlimbs and feet. Scale bar represents 5 mm.

relies on a small number of postcranial characters, at least some of which are present in other aquatic animals, and a less than satisfactory process of elimination. *Shokawa* lacks the derived character states of crocodiles (for example, osteoderms, ankle and pelvic structure), lizards and sphenodontians (for example, dental, vertebral and ankle characters), or sauropterygians (pectoral girdle characters). With choristoderes, *Shokawa* shares cylindrical, platycoelous vertebral centra, with open neurocentral sutures in the dorsal, sacral and anterior caudal regions; wide neurocentral articular surfaces which constrict the ventral surface of the centrum to a narrow groove; at least three sacral vertebrae; unfused sacral and anterior caudal ribs; short, rather robust fore- and hindlimbs with reduced numbers of carpal and tarsal elements; a fibula with a narrow proximal head, but an expanded distal head; and strong unguals lacking flexor tubercles, but with a broad ventral surface. Like neochoristoderes, the bone appears to be pachyostotic, and the recovered jaw material (IBEF VP 8, 9) matches that of other choristoderes quite closely (pattern of lateral foramina, tooth implantation, tooth form, elongated jaw shape).

Many of the most important characters for determination of relationships within the choristoderes are exhibited by the skull (Evans 1990) and this complicates discussion of the affinities of the Tetori choristodere. However, using 71 characters (Appendix 1) compiled partly from Evans (1990) and Hecht (1992) with additions and modifications by Gao and Fox (in press), and some new

postcranial characters, we investigated the relationships of the Tetori choristodere using PAUP 3.1 (Swofford 1993). In the absence of a clearly established outgroup for choristoderes, polarity was determined in relation to the Permian diapsid *Youngina*. Characters were run as unordered with polymorphic states treated as uncertainties. A run including all attributed choristoderan taxa, with *Youngina* as designated outgroup, PAUP 3.1 (Branch-and-Bound) yielded a single tree (length 105; Consistency Index, 0·93; Retention Index, 0·9; Rescaled Consistency Index, 0·84), in which *Champsosaurus*, and *Tchoiria* were consistently placed as consecutive sister taxa of *Simoedosaurus* + *Ikechosaurus* in a robust clade (Neochoristodera, Evans and Hecht 1993). *Shokawa* joined a small clade with *Pachystropheus* and *Cteniogenys*, emerging as the sister taxon of *Pachystropheus*. Text-figure 8A shows a 50 per cent. Majority-Rule Consensus tree with bootstrap values indicating the



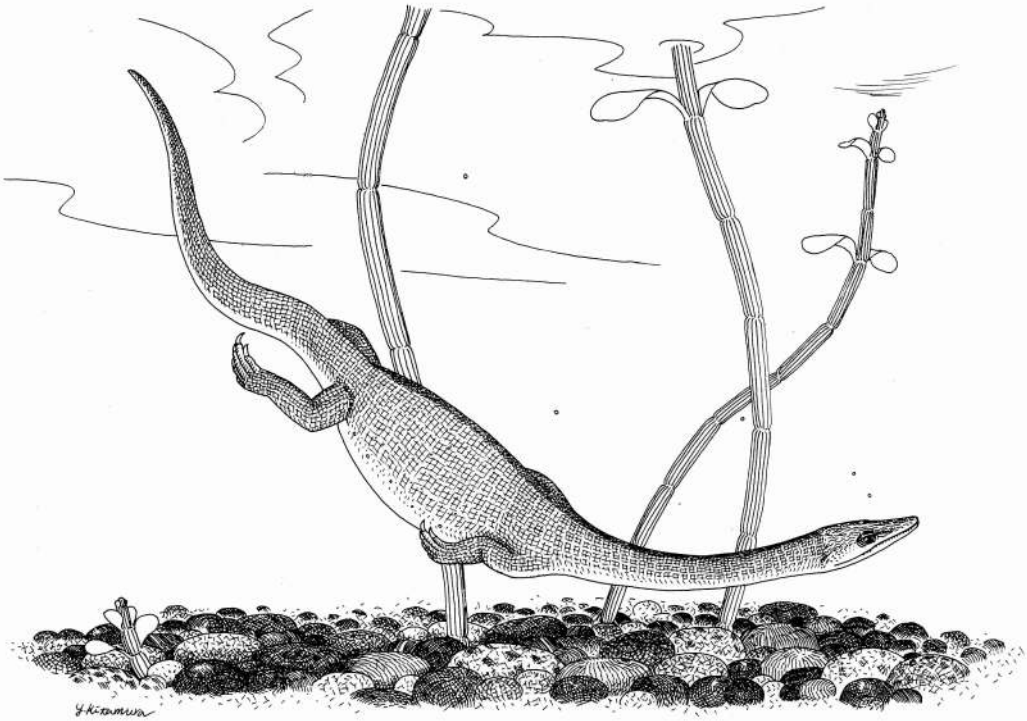
TEXT-FIG. 8. 50 per cent. Majority-Rule Consensus Trees generated by PAUP 3.1 (Swofford 1993) showing hypotheses of relationship for the Japanese (Tetori Group) choristoderan *Shokawa*. The numbers are the bootstrap values showing the support for the nodes, and the small A marks the base of Neochoristodera (Evans and Hecht 1993). A, a tree with all attributed choristoderan taxa included. B, tree after removal of the enigmatic Central Asian *Khurendukhosaurus*.

level of support for the various nodes. However, knowledge of *Khurendukhosaurus* is very limited (only 8 per cent. of characters coded). Its removal changes neither the length of the tree, nor the positions of the other taxa, but does change the bootstrap values slightly (Text-fig. 8B).

Within Neochoristodera, the placement of *Tchoiria* as the sister taxon of *Ikechosaurus* and *Simoedosaurus* agrees with Gao and Fox (in press), but differs from previous studies (e.g. Evans 1990; Evans and Hecht 1993) where it emerged as the sister taxon of *Champsosaurus*. The difference is due in part to the re-analysis and re-evaluation of characters by Gao and Fox, but also to the recovery of more complete material of *Tchoiria* from Mongolia. In all trees, the Oligocene *Lazarussuchus* (Hecht 1992) fell at the base of the clade, as shown also by Evans and Hecht (1993). Whether *Lazarussuchus* is genuinely a late surviving representative of a primitive choristoderan lineage, or a more derived form showing paedomorphic character reversal in some traits, is as yet unclear and needs further work. Similarly, the sister group placement of *Shokawa* and *Pachystropheus* should be considered as tentative, bearing in mind the amount of missing data (they are coded for only 35 per cent. and 25 per cent. of characters respectively) and the fact that their only certain synapomorphies are those of the tail (57, 71) which may simply reflect lifestyle. Clearly, the recovery of skull material of *Shokawa*, and of articulated material of *Cteniogenys*, *Khurendukhosaurus* and *Pachystropheus* is needed before the relationships of these genera can be fully resolved.

LIFESTYLE

Choristoderes are generally considered to be amphibious reptiles that spent some, possibly much, of their time in water. They are usually found in association with freshwater assemblages containing crocodiles, turtles, amphibians and rarer terrestrial elements (the exception being *Pachystropheus* which occurs in a marginal marine assemblage; Storrs *et al.* 1996). The freshwater KO2 assemblage fits the typical pattern, except for the rarity of crocodiles, and the relative abundance of choristoderan remains (with turtles and fish) provides indirect evidence of an aquatic lifestyle. Skeletal structure provides further support for this interpretation. As with most other choristoderes (except the primitive *Lazarussuchus*), and many other aquatic reptiles, the neurocentral suture remains open in all but the cervical vertebrae and distal caudals. Unlike *Cteniogenys* and *Lazarussuchus*, however, the ribs and gastralia of the Tetori choristodere are heavily ossified (pachyostotic), and, as in *Pachystropheus*, the caudal neural spines are tall and slender, suggesting a deep swimming tail. These two features suggest that the Tetori choristodere was more heavily committed to an aquatic lifestyle than was *Cteniogenys*. With the strong coracoid plate and weak scapula, long neck, and rather short limbs, the Tetori choristodere shows a superficial resemblance to the Triassic sauropterygian pachypleurosaurs and, in a freshwater context, may have had a similar lifestyle (Text-fig. 9).



TEXT-FIG. 9. Life reconstruction of the new Tetori choristodere, *Shokawa*.

The recovery of choristoderan fossils from the Lower Cretaceous of Japan extends the geographical range of the group overall (from the western to the extreme eastern margins of Laurasia) and extends the temporal range of the group in Eastern Asia from the Aptian/Albian

(*c.* 110 Ma, Mongolia, China) to the Neocomian (*c.* 135 Ma). The new specimens also add a new ecomorphotype to the choristoderan clade (Evans and Hecht 1993).

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REFERENCES

AZUMI, Y. and TOMIDA, Y. 1995. Early Cretaceous dinosaur faunas of the Tetori Group in Japan. 125–131. *In* AILING SUN and YUANQING WANG (eds). *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press, Beijing, vi + 250 pp.

BENTON, M. J. 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, **84**, 97–164.

BRINKMAN, D. B. and DONG ZHI-MING 1993. New material of *Ikechosaurus sunailinae* (Reptilia: Choristodera) from the Early Cretaceous Laohongdong Formation, Ordos Basin, Inner Mongolia, and the interrelationships of the genus. *Canadian Journal of Earth Sciences*, **30**, 2153–2162.

COPE, E. D. 1884. The Choristodera. *American Naturalist*, **17**, 815–817.

CURRIE, P. J. 1981. *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. *Paleontologia africana*, **24**, 99–168.

EFIMOV, M. B. 1975. [Champsosaurs from the Lower Cretaceous of Mongolia.] *Sovmestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya, Trudy*, **2**, 84–93. [In Russian].

—— 1979. [*Tchoiria* (Champsosauridae) from the Early Cretaceous of Khamarin-Khural, MNR.] *Sovmestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya, Trudy*, **8**, 56–57. [In Russian].

—— 1996. [Champsosaurid from the Lower Cretaceous of Buryatia (Russia).] *Paleontologicheskii Zhurnal*, **1996**, 123–124. [In Russian].

ERICKSON, B. R. 1972. The lepidosaurian reptile *Champsosaurus* in North America. *Monographs of the Science Museum of Minnesota* (*Paleontology*), **1**, 1–91.

—— 1985. Aspects of some anatomical structures of *Champsosaurus* Cope (Reptilia: Eosuchia). *Journal of Vertebrate Paleontology*, **5**, 111–127.

—— 1987. *Simoedosaurus dakotensis*, new species of diapsid reptile (Archosauromorpha: Choristodera) from the Paleocene of North America. *Journal of Vertebrate Paleontology*, **7**, 237–251.

EVANS, S. E. 1988. The early history and relationships of the Diapsida. 221–260. *In* BENTON, M. J. (ed.). *The phylogeny and classification of the Tetrapoda. Volume 1. Amphibians, reptiles, birds*. Systematics Association Special Publication. Clarendon Press, Oxford, vi + 377 pp.

—— 1990. The skull of *Cteniogenys*, a choristodere (Reptilia: Archosauromorpha) from the Middle Jurassic of Oxfordshire. *Zoological Journal of the Linnean Society*, **99**, 205–237.

—— 1991. The postcranial skeleton of the choristodere *Cteniogenys* (Reptilia: Diapsida) from the Middle Jurassic of England. *Geobios*, **24**, 187–199.

—— and HECHT, M. K. 1993. A history of an extinct reptilian clade, the Choristodera: longevity, Lazarus-taxa, and the fossil record. *Evolutionary Biology*, **27**, 323–338.

FOX, R. C. 1968. Studies of Late Cretaceous vertebrates. 1. The braincase of *Champsosaurus* Cope (Reptilia, Eosuchia). *Copeia*, **1968**, 100–109.

GAO KEQIN and FOX, R. C. in press. New choristoderes (Reptilia: Diapsida) from the Upper Cretaceous and Palaeocene, Alberta and Saskatchewan, Canada, and phylogenetic relationships of the Choristodera. *Zoological Journal of the Linnean Society*.

GIFU-KEN DINOSAUR RESEARCH COMMITTEE 1993. *Report on the dinosaur fossil excavation in Gifu Prefecture, Japan*. Gifu Prefectural Museum, Gifu, 46 pp. [In Japanese].

HASEGAWA, Y., MANABE, M., ISAJI, S., OHKURA, M., SHIBATA, I. and YAMAGUCHI, I. 1995. Terminally resorbed iguanodontid teeth from the Neocomian Tetori Group, Ishikawa and Gifu Prefecture, Japan. *Bulletin of the National Science Museum, Series C (Geology and Paleontology)*, **21**, 35–49.

HECHT, M. K. 1992. A new choristodere (Reptila: Diapsida) from the Oligocene of France: an example of the Lazarus effect. *Geobios*, **25**, 115–131.

HUENE, E. von 1935. Ein Rhynchocephale aus dem Rhät (*Pachystropheus* n.g.). *Neues Jahrbuch für Mineralogie, Geologie und Palaontologie, Abhandlungen*, **74**, 441–447.

MAEDA, S. 1961. On the geological history of the Mesozoic Tetori Group in Japan. *Journal of the Collections of Arts and Science, Chiba University*, **3**, 369–426. [In Japanese, with English abstract].

MANABE, M. and HASEGAWA, Y. 1995. Diapsid fauna and its palaeobiogeographical implication; the Neocomian section of the Tetori Group, Japan. 179. *In* AILING SUN and YUANQING WANG (eds). *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press, Beijing, vi + 250 pp.

OSBORN, H. F. 1903. The reptilian subclasses Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History*, **1**, 449–507.

PARKS, W. A. 1927. *Champsosaurus albertensis*, a new species of rhynchocephalian from the Edmonton Formation of Alberta. *University of Toronto Studies, Geological Series*, **23**, 1–48.

REISZ, R. R. 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Special Publication of the Museum of Natural History, University of Kansas*, **7**, 1–74.

ROMER, A. S. 1956. *The osteology of the reptiles*. University of Chicago Press, Chicago, xxi + 772 pp.

RUSSELL-SIGOGNEAU, D. and RUSSELL, D. E. 1978. Étude ostéologique du Reptile *Simoedosaurus* (Choristodera). *Annales de Paléontologie (Vertébrés)*, **64**, 1–84.

SIGOGNEAU-RUSSELL, D. 1981. Étude ostéologique du reptile *Simoedosaurus* (Choristodera). Iie partie: squelette postcranien. *Annales de Paléontologie (Vertébrés)*, **67**, 61–140.

—— and EFIMOV, M. 1984. Un Choristodera (Eosuchia?) Insolite du Crétacé Inférieur de Mongolie. *Paläontologische Zeitschrift*, **58**, 279–294.

STORRS, G. W. and GOWER, D. J. 1993. The earliest possible choristodere (Diapsida) and gaps in the fossil record of semi-aquatic reptiles. *Journal of the Geological Society, London*, **150**, 1103–1107.

—— —— and LARGE, N. F. 1996. The diapsid reptile *Pachystropheus rhaeticus*, a probable choristodere from the Rhaetian of Europe. *Palaeontology*, **39**, 323–349.

SWOFFORD, D. L. 1993. *PAUP: Phylogenetic Analysis Using Parsimony, version 3.1.1, documentation and software*. Illinois Natural History Survey, Champaign.

UNWIN, D. M., MANABE, M., SHIMIZU, K. and HASEGAWA, Y. 1996. First record of pterosaurs from the Early Cretaceous Tetori Group: a wing phalange from the Amagodani Formation in Shokawa, Gifu Prefecture, Japan. *Bulletin of the National Science Museum, Tokyo, Series C (Geology and Paleontology)*, **22**, 37–46.

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APPENDIX 1

Characters used in the analysis.

Characters 1–60 are taken from Gao and Fox (in press; modified from Evans 1990; Hecht 1992), with a few changes, characters 61–72 are new characters relating to the postcranial skeleton.

1. External nares: paired, oval, nearly terminal (0); paired, elongate and dorsally placed (1); terminal and confluent (2).
2. Prefrontals: anterolateral and separated by frontals (0); median contact limited to posterior half of length (1); median contact long, through entire length of element (2).
3. Parietal foramen: present (0); absent (1).
4. Preorbital skull proportions: moderately short and rounded (0); elongate but less than 50 per cent. of skull length (1), more than 50 per cent. of skull length (2) (Gao and Fox (in press) code *Tchoiria* as (1) on the basis of information from M. B. Efimov (pers. comm.), but a skull of *Tchoiria* (Geological Institute of the Mongolian Academy of Sciences, Ulan Bataar, 39-54-01) has a preorbital skull length of 54 per cent. of the total. In the matrix, *Tchoiria* has therefore been scored as variable (1/2)).
5. Dorsal flange of maxilla: high and vertical (0); low, with dorsal border inflected medially (1).
6. Lacrimal: enters external narial opening (0); retracted posteriorly from the opening, but remains elongate (1); further reduced as a small triangular bone (2).
7. Lacrimal perforation: perforated by one or two foramina (0); lacrimal foramen between lacrimal, prefrontal and palatine (1).
8. Nasals: short and paired (0); elongate and paired (1); elongate and fused (2). (In *Cteniogenys*, the nasals were paired, but their length is not known. In the matrix, the genus is scored 0/1).
9. Nasal/premaxilla contact: nasals contact but do not intervene between premaxilla (0); nasals intervene between premaxillae (1); nasals do not contact premaxillae (2).
10. Orbits: large and laterally directed (0); small and dorsally directed (1); large and dorsally directed (2).
11. Postfrontal/postorbital fusion: bones discrete and both enter orbital margin (0); bones discrete but postorbital excluded from orbital margin (1); postfrontal and postorbital fused (2) (on the basis of a pers. comm. from M. B. Efimov, Gao and Fox (in press) code *Tchoiria* as (2), but in specimen 39-54-01 (Geological Institute of the Mongolian Academy of Sciences), there appears to be a suture between the bones with the postorbital excluded from the orbit – the state has therefore been coded as variable (1/2)).
12. Dorsal process of squamosal: broad and short (0); slender and elongate to middle level of inferior temporal opening (1).
13. Upper temporal fenestra: smaller than orbit (0); roughly equal to size of orbit (1); posteriorly flared and substantially larger than orbit (2).
14. Parietal: having broad contact with the postorbital/postfrontal complex (0); reduced contact (1).
15. Squamosal/parietal suture in occiput: near posterior end of superior temporal fenestra (0); half way along fenestra (1).
16. Nasal/prefrontal contact: straightline contact dorsolateral on snout (0); broad V-shaped contact at dorsal midline (1); long, narrow wedge (2).
17. Vomer-maxilla contact: absent (0); present (1). (Gao and Fox (in press) use vomer-premaxilla contact here, but in a misunderstanding of character (8) in Evans 1990. Most diapsids have a vomer-premaxilla contact, it is the additional contact with the maxilla in an extended primary palate which is significant here. *Cteniogenys* has this contact and is thus coded (1)).
18. Location of choana: anteriorly, close to the premaxilla (0); retracted close to the midpoint of the marginal tooth row (1); displaced far back (2).
19. Palatal foramen: absent with vomer, palatine and pterygoid meeting at a closed three-point suture (0); opening at the junction between the three palatal bones (1); between pterygoid and palatine, without contribution from vomer (2).
20. Internarial: absent (0); present (1).
21. Pterygoid flange: consisting of pterygoid only and ventrally directed (0); consisting of pterygoid and ectopterygoid and having a horizontal overlap (1).
22. Basipterygoid/pterygoid joint: basipterygoid process articulates with pterygoid cotyle as part of a metakinetic joint (0); process and cotyle are reduced and the two bones are sutured (1); the two bones are fused (2).
23. Parasphenoid/pterygoid contact: no contact (0); clear sutural contact (1); tight contact or fusion (2).

24. Quadratojugal/quadrate articulation: having a simple overlapping facet for the quadrate (0); quadratojugal bears a cotyle meeting a rounded quadrate process (1).
25. Pterygoid process of quadrate: broad, vertically oriented with a large pterygoid facet (0); low, slender and horizontal, with a reduced pterygoid facet (1).
26. Dorsal process of jugal: as prominent as anteroventral process (0); prominent, but much shorter than anteroventral process (1); little or no process (2).
27. Nasopalatal trough: absent (0); present (1).
28. Palatal teeth: palate covered by shagreen of small teeth (0); paired pterygoid tooth batteries separated by nasopalatal trough (1); narrow rows of palatal teeth separated by nasopalatal trough (2).
29. Midline contact of pterygoids: separate or just touching in the midline anteriorly (0); long midline suture (1).
30. Size and location of interpterygoid vacuity: large and extends anterior to suborbital fenestra (0); small and near posterior border of the fenestra (1).
31. Enclosure of interpterygoid vacuity: enclosed anteriorly by pterygoids, but open posteriorly (0); enclosed anteriorly by pterygoid and posteriorly by parasphenoid (1); enclosed both anteriorly and posteriorly by pterygoids (2).
32. Shape of parasphenoid: isosceles triangle with long rostrum (0); broader anteriorly with short rostrum, moderate posterolateral expansion (1); slender anteriorly with long rostrum and strong posterolateral wing-like expansion (2).
33. Basal tubera of braincase: weakly developed (0); moderately expanded laterally (1); strongly expanded posterolaterally and wing-like (2).
34. Marginal tooth sockets: circular (0); transverse expansion occurs in anterior part of tooth row (1). (Based on a pers. comm. from M. B. Efimov, Gao and Fox (in press), code the teeth of *Tchoiria* (1), but the sockets appear circular in specimen 39-54-01 (Geological Institute of the Mongolian Academy of Sciences; SEE pers. obs.). The coding of ? in the matrix reflects this uncertainty.
35. Basal infolding of tooth enamel: absent (0); present (1).
36. Location of craniomandibular joint: roughly on a level with the occipital condyle (0); anterior to the condyle (1); posterior to the condyle (2). (Again based on a pers. comm. from M. B. Efimov, Gao and Fox (in press) code *Tchoiria* (2) for this character but in specimen 39-54-01 (Geological Institute of the Mongolian Academy of Sciences; SEE pers. obs.) the craniomandibular joint is roughly on a level with the occipital condyle [0]; the character is thus coded (0/2) to reflect the ambiguity).
37. Shape of suborbital fenestra: narrow, elongate (0); sub-triangular with straight medial edge (1); short, kidney-shaped (2).
38. Neomorph (*sensu* Fox 1968) in braincase: absent (0); present as part of external wall of braincase and medial wall of temporal fossa (1).
39. Pterygoquadrate foramen: absent (0); present and enclosed by neomorph and quadrate (1).
40. Paroccipital process/quadrate contact: only tip of process meets quadrate (0); elongated process lies in a trough formed by the quadrate and neomorph (1); elongated process lies in a trough of the quadrate that is lined by a thin sheet of the neomorph (2).
41. Mandibular symphysis: small and terminal (0); moderate elongation equalling length of one-third or less of the tooth row with little inclusion of splenial (1); strongly elongate, equalling at least half the length of the tooth row with longer inclusion of splenial (2).
42. Lateral exposure of splenial: splenial confined to medial side of mandible (0); exposed on ventrolateral surface of mandible (1).
43. Orientation of paroccipital processes: horizontal (0); slightly depressed (1); strongly deflected ventrally (2).
44. Supraoccipital/parietal contact: free from parietal (0); supraoccipital lightly arched, with sutural surfaces for parietal placed anteriorly (1); supraoccipital keeled, and parietal facets extend to posterior margin (2).
45. Posttemporal fenestra: present (0); absent through loss (1).
46. Pila antotica: remains unossified (0); ossified as part of the sphenoid (1).
47. Posterior opening of internal carotid artery: does not penetrate parasphenoid and opens ventrolaterally (0); penetrates parasphenoid and opens ventrally (1).
48. Atlas-axis complex: little or no development of anterior odontoid prominence of axis (0); free odontoid process unfused to axis (1).
49. Dorsal neurocentral sutures: closed in adult (0); remain open in adult (1). (Evans 1990, followed by Gao and Fox (in press) used the general character, neurocentral sutures, but there is variation in the cervical region (see 62)).

50. Vertebral centrum: amphicoelous and notochordal (0); amphiplatyan with notochordal canal closed (1).
51. Presacral vertebral centra: longer than wide (0); short and spool-like (1).
52. Ventromedial crest of dorsal vertebra: anterior dorsal vertebrae are strongly keeled like the cervicals (0); low or no keels (1).
53. Small spinous processes below the presacral postzygapophyses: absent (0); present but without accessory facets (1); present and bear accessory facets (2) (this character, originally from Hecht (1992), is also used by Gao and Fox (in press) in two states, with the derived state (2 here) found in *Simoedosaurus* and *Ikechosaurus*. This is modified here to include state 1, since Brinkman and Dong (1993), described the processes as present but without facets in *Ikechosaurus* and the same appears to be true for *Tchoiria* (specimen 39-54-31, Geological Institute, Mongolian Academy of Sciences; SEE pers. obs.)).
54. Number of sacral vertebrae: two sacrals (0); three sacrals (1); four sacrals (2).
55. Sacral and caudal ribs: fused to the vertebra in the adult (0); sacral ribs free, caudal ribs fused (1); sacral and caudal ribs free (2) (this character has been extended to include the intermediate (1) state found in *Shokawa*, other codings have been modified accordingly).
56. Caudal zygapophyses: lie at a small angle to the horizontal (0); nearly vertical (1).
57. Centra of caudal vertebrae: bears shallow ventral groove for caudal blood vessels (0); groove is flanked by deep ventral flanges (1). (N.B. – the key point here is that the flanges are deep; slight flanges border the caudal groove in many diapsid taxa).
58. Number of ossified carpal elements: at least nine (0); number reduced to, at most, seven (1).
59. Flexor tubercle or process on the ventral surface of the ungual: distinct and well developed (0); flexor tubercle low and reduced (1).
60. Bone structure: cancellous (0); having reduced medullary cavity (1); pachyostotic in adult (2). (In *Ikechosaurus* and *Shokawa*, the bone has not been sectioned. Elements such as ribs and gastralia are robust and appear pachyostotic, hence the coding of (1) or (2)).
61. Iliac blade, dorsal margin: essentially vertical or at a steep angle to the horizontal in adults (0); dorsal margin essentially horizontal, blade expanded, often triangular (1). (Primitively in diapsids the iliac blade is sub-rectangular and at an angle to the horizontal; adult neochoristoderes are characterized by a horizontal iliac blade, which may be expanded into a nearly triangular form (*Simoedosaurus*, *Ikechosaurus*, *Tchoiria*), although the blade can be narrower and angled in young individuals; Erickson 1972).
62. Cervical neurocentral sutures: closed (0); open (1). (Primitively, neurocentral sutures are closed throughout the column except in some aquatic taxa; in most neochoristoderes, the sutures are open throughout the column, but in some basal taxa, the cervical sutures remain closed although the dorsal sutures are open).
63. Interclavicle shape: rhomboid (0); T-shaped (1) (a rhomboid interclavicle occurs primitively in diapsids e.g. *Petrolacosaurus* [Reisz 1981], becoming T-shaped in some groups, e.g. younginids).
64. Interclavicle stem: long, slender and essentially parallel-sided (0); flask-shaped, broad in anterior and central portions, tapering distally (1); stem shorter than lateral processes (2) (a long slender interclavicle stem occurs primitively in diapsids (e.g. younginiforms); the neochoristoderan stem is typically flask-shaped, whereas that attributed to the Triassic *Pachystropheus* (Storrs *et al.* 1996) is unusually short-stemmed as figured).
65. Clavicular facets on interclavicle: meet at an angle in the midline (0); continuous across the midline in a smooth curve (1).
66. Cervical vertebral count: eight or nine (0); more than 16 (1) (in the cladograms shown in Text-fig. 8, this is an autapomorphy of *Shokawa*, but cervical numbers are unknown in *Cteniogenys* and *Pachystropheus*).
67. Cervical vertebral centra length: longer than high (0); shorter than high (1).
68. Dorsal vertebral centrum shape: sub-cylindrical (0); cylindrical (circular cross section) (1).
69. Fibula shape: proximal and distal ends of similar width, or proximally wider (0); proximal end narrow, distal end flared (1).
70. Gastralia thickness: thin, lightly built (0); robust, almost as thick as axial ribs and pachyostotic (1). (Thin gastralia are primitive for diapsids).
71. Caudal neural spines: low (0); long and narrow (1). (In most choristoderes, the caudal neural spines are like those of generalized diapsids; in *Shokawa* and the Triassic *Pachystropheus*, they are exceptionally long and slender).

APPENDIX 2

Data matrix of taxa and characters used in the parsimony analysis (PAUP 3.1).
Key: Y, *Youngina*; L, *Lazarussuchus*; CT, *Cteniogenys*; Sh, *Shokawa*; Ch, *Champsosaurus*; T, *Tchoiria*; I, *Ikechosaurus*; S, *Simoedosaurus*; P, *Pachystropheus*; K, *Khurendukhosaurus*.
Characters 1–71 are listed in full in Appendix 1. Data taken from personal observation (*Youngina*, *Cteniogenys*, *Shokawa*, *Champsosaurus*, *Tchoiria*, *Ikechosaurus*, *Simoedosaurus*), and from Sigogneau-Russell and Efimov (1984), Evans (1990), Hecht (1992), Storrs and Gower (1993), Efimov (1996), Storrs *et al.* (1996) and Gao and Fox (in press). The codings for *Tchoiria* are taken in part from Gao and Fox (in press) and in part from direct observations of new material from the Mongolian Academy of Sciences (specimen 39-54-01). Where the interpretation differs, this is reflected in the codings given (see under comments for individual characters in Appendix 1).

	Y	L	Ct	Sh	Ch	T	I	S	P	K
1	0	1	2	?	2	2	2	2	?	?
2	0	1	2	?	2	2	2	2	?	?
3	0	1	1	?	1	1	1	1	?	?
4	0	1	1	?	2	2	1	1	?	?
5	0	1	1	1	1	1	1	1	?	?
6	0	?	1	?	2	1	1	1	?	?
7	0	0	0	?	1	0	?	1	?	?
8	0	1	0/1	?	2	2	2	2	?	?
9	0	0	2	?	1	?	1	1	?	?
10	0	0	0	?	1	1	1	1	?	?
11	0	?	0	?	1/2	2	2	2	?	?
12	0	?	?	?	1	1	1	1	?	?
13	0	1	1	?	2	2	2	2	?	?
14	0	?	0	?	0	1	1	1	?	?
15	0	0	0	?	0	0	1	1	?	?
16	0	1	?	?	2	2	1	1	?	?
17	0	?	1	?	1	1	?	1	?	?
18	0	0	1	?	2	2	2	2	?	?
19	0	?	1	?	2	2	2	2	?	?
20	0	0	0	?	1	0	0	0	?	?
21	0	?	1	?	1	1	1	1	1	?
22	0	?	1	?	2	1	1	1	?	?
23	0	?	1	?	2	1	1	1	?	?
24	0	?	0	?	1	1	1	1	?	?
25	0	?	0	?	1	1	1	1	?	?
26	0	?	1	?	1	1	2	2	?	?
27	0	?	0	?	1	1	1	1	?	?
28	0	0	0	?	2	1	1	1	?	?
29	0	0	0	?	1	1	1	1	?	?
30	0	?	0	?	1	1	1	1	?	?
31	0	?	1	?	2	1/2	1	1	?	?
32	0	0	0	?	2	1/2	1	1	?	?
33	0	0	0	?	2	1	1	1	?	?
34	0	?	0	0	0	?	1	1	?	?
35	0	?	0	?	1	1	1	1	?	?
36	0	0	?	?	1	0/2	2	2	?	?
37	0	0	0	?	2	1	1	1	?	?
38	0	?	1	?	1	1	1	1	?	?
39	0	?	?	?	1	1	1	1	?	?
40	0	?	?	?	2	?	?	?	?	?
41	0	1	0	0	2	1	1	1	?	?
42	0	0	0	0	1	0	0	0	?	?
43	0	?	0	?	2	1	1	1	?	?

44	0	?	?	?	1	?	2	2	?	?
45	0	?	?	?	0	1	1	1	?	?
46	0	?	0	?	0	?	1	1	?	?
47	0	?	0	?	0	1	1	1	?	?
48	0	?	1	?	1	?	?	1	?	?
49	0	0	1	1	1	1	1	1	1	?
50	0	0	1	1	1	1	1	1	1	?
51	0	0	0	0	0	0	1	1	0	?
52	0	0	0	?	1	?	1	1	0	?
53	0	0	0	0	0	1	1	2	0	?
54	0	2	1	1	1	?	1	1	?	?
55	0	0	2	1	2	2	2	2	1/2	?
56	0	1	1	1	0	0	?	0	1	?
57	0	0	1	1	0	0	0	0	1	?
58	0	0	?	1	1	?	?	?	?	?
59	0	0	1	1	1	?	1	?	?	?
60	0	0	1	1/2	2	1/2	?	2	1	?
61	0	0	0	0	1	1	1	1	0	?
62	0	0	0	0	1	1	1	1	1	0
63	1	?	?	0	1	1	1	1	0	1
64	0	?	?	0	1	1	0	1	2	0
65	0	?	?	0	1	1	?	1	0	1
66	0	0	?	1	0	0	0	0	?	?
67	0	0	0	0	0/1	0	0	1	0	0
68	0	0	0	1	1	1	0/1	1	0	0
69	0	1	?	1	1	1	1	1	?	?
70	0	0	0	1	1	?	1	1	?	?
71	0	0	0	1	0	0	0	0	1	0

APPENDIX 3: ABBREVIATIONS USED IN THE TEXT-FIGURES

ac	acetabulum	fl	haemal flange
ast	astragalus	g	gastralia
cal	calcaneum	h	humerus
cl	clavicle	icl	interclavicle
cor	coracoid	il	ilium
cr	cervical rib	nc	neurocentral suture surface
cv	cervical vertebra	ns	neural spine
dc	distal carpal	pc	proximal carpal
dp	deltopectoral crest	r	radius
dt	distal tarsal 3, 4	sc	scapula
ec	ectepicondyle	ti	tibia
en	entepicondyle	u	ulna
fi	fibula	un	ungual
F.L.	forelimb	?	possible skull mass

THE CROCODILIAN *GONIOPHOLIS SIMUS* FROM THE LOWER CRETACEOUS OF NORTH-WESTERN GERMANY

by S. W. SALISBURY, P. M. A. WILLIS, S. PEITZ *and* P. M. SANDER

ABSTRACT. A re-evaluation of crocodilian material referred to *Goniopholis* from the Berriasian (Lower Cretaceous) of north-western Germany is presented, based on the description of a natural mould of a skull and mandible in the collections of the Institut für Paläontologie, Bonn. Along with other material from the Obernkirchen Sandstone of the Bückeburg Member of the German 'Wealden', the Bonn specimen is referred to *G. simus* Owen. Two previously recognized species of *Goniopholis* from Germany, '*G. pugnax*' Koken and '*G. minor*' Koken, are considered to be *nomina dubia*, because they are based on undiagnostic material, much of which can no longer be located. Two complete skeletons from the Hauterivian–Barremian of Bernissart, Belgium, previously assigned to *G. simus*, are considered to be representative of distinct species and should be redescribed and renamed. *G. simus* is restricted to the Berriasian of the Wessex-Weald Basin of southern England and the Niedersachsen Basin of north-western Germany. This is the first clear evidence of interchange between the non-marine vertebrate faunas of these two regions.

SPECIES of *Goniopholis* represent some of the northern hemisphere's most common and distinctive crocodilians during the Late Jurassic and Early Cretaceous. They are among the earliest crocodilians to resemble superficially the majority of living forms, with a broad, dorso-ventrally flattened rostrum, long tail and stout limbs; some species are estimated to have attained lengths in excess of 3 m (Hooley 1907). Unlike eusuchians, species of *Goniopholis* possess choanae secundare not completely contained within the pterygoids, amphicoelous vertebrae, a biserial paravertebral shield and a rigid gastral shield composed of interlocking, polygonal osteoderms. The type species, *Goniopholis crassidens*, was erected by Owen (1841) based on a partial, disarticulated skeleton from the Lower Cretaceous of Swanage, Dorset, southern England. The osteoderms from the paravertebral shield of this species are rectangular, with a well-developed processus articularis. Although now known to occur in many Mesozoic taxa, at the time of the specimen's discovery osteoderms such as these were not known for any other fossil crocodilian, and it was on the distinctiveness of this feature that Owen based the name *Goniopholis*, literally meaning 'angle scale' (Owen 1841, p. 72).

During the Late Jurassic and Cretaceous goniopholidids were widespread throughout the northern hemisphere, with abundant material being known from Europe, Asia and North America (Buffetaut 1982; Steel 1989). In Europe, the majority of *Goniopholis* species are known from the Wealden and Purbeck groups of southern England, where as many as five distinct species have been recognized (Owen 1841, 1849–84, 1878, 1879; Hulke 1878; Hooley 1907). With the exception of two nearly complete skeletons referred to *G. simus* from Bernissart, Belgium (Dollo 1883), the presence of *Goniopholis* in the Upper Jurassic and Lower Cretaceous of continental Europe, particularly in late Tithonian and Berriasian strata, has been uncertain. This is due primarily to the fragmentary nature of the material, which consists of isolated teeth, vertebrae, osteoderms, limb elements and, very rarely, skull fragments (Koken 1883, 1886, 1887, 1896; Edinger 1938; Jonet 1981; Huckriede 1982; von Oekentorp 1984; Buffetaut 1986*b*; Buscalioni and Sanz 1987*a*, 1987*b*; Norman 1987; Buffetaut *et al.* 1989; Cuny *et al.* 1991; Ortega *et al.* 1996).

In north-western Germany, material referred to *Goniopholis* was first discovered during the latter

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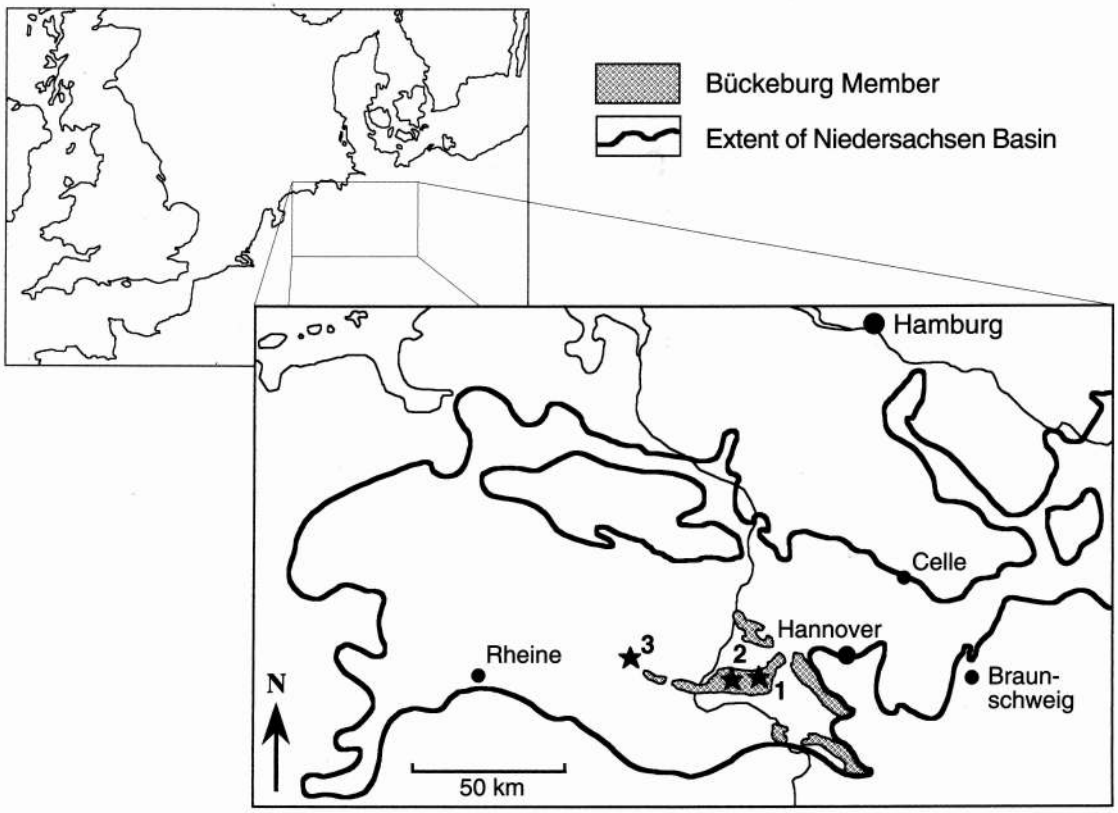
half of the nineteenth century. These specimens were collected from calcareous claystone units associated with coal seams in the Lower Obernkirchen Sandstone of the Bückeburg Member (Lower Cretaceous), at sites near Osnabrück, Wackerfield, Wendthagen and Obernkirchen (Text-fig. 1),



TEXT-FIG. 1. The Bückeburg Member of the 'Wealden' Formation of north-western Germany (after Pelzer 1988), and localities that have produced remains referable to *Goniopholis*. 1, Bückeburg; 2, Obernkirchen; 3, Osnabrück.

and were first described by Ernst Koken in 1887. Koken (1887) erected two species: '*G. pugnax*', based on a partial otoccipital, isolated teeth, vertebrae, rib fragments, a humerus, an ulna and several osteoderms from the gastral shield; and '*G. minor*', based only on cervical vertebrae and a partial osteoderm from the paravertebral shield.

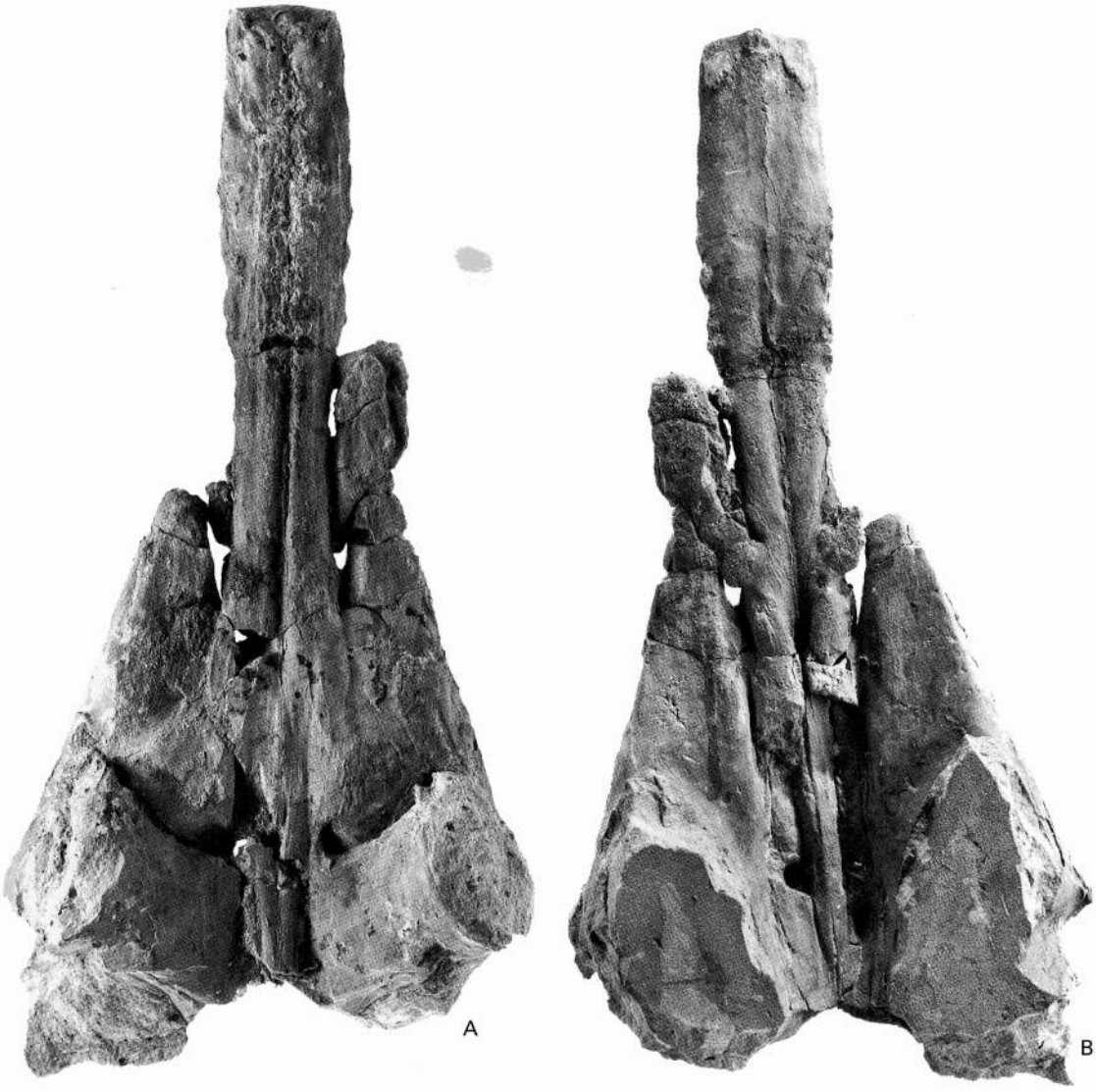
In 1896, Koken supplemented his original description of '*G. pugnax*' by referring a relatively complete rostrum maxillae and partial dentary, presented to him for study by the Bückeburg Natural History and Archaeology Society, to this species (Koken 1896). These specimens had been collected by the society from an exposure of 'Wealden Sandstone' in the vicinity of Bückeburg, and were apparently found in association, leading Koken to assume that they were from the same animal. Koken's reason for referring this material to '*G. pugnax*' was based on the stratigraphy of the site and the similarity of the teeth to those described in his original paper. Unfortunately, apart from the ulna (MB R2032), the corpus of a cervical vertebra (IGPMbg 1854) and three isolated teeth (MB R2077.1–3) referred to '*G. pugnax*', and the portion of an osteoderm from the paravertebral shield (IGPMbg V-Re-1-8) referred to '*G. minor*', all the material described by Koken (1887) can no longer be located and was presumably lost or destroyed during World War II.

TEXT-FIG. 2. *Goniopholis simus* (Owen, 1878); IPB R359 in dorsal aspect; ×0·2.

Between 1900 and 1930 additional crocodilian specimens, including natural moulds of as many as eight skulls, a right ramus mandibulae and isolated postcranial elements, were collected from an exposure of Obernkirchen Sandstone at a quarry near Obernkirchen by Max Ballerstedt of the Gymnasium Adolfinum, Bückeburg. Five of these specimens are missing, and are now represented only by photographs, held in the Georg-August-Universität, Göttingen, and four casts: BMNH R5262, a small (< 300 mm long) skull; GPIMü Pr. 280, another small skull; and BMNH R5260 and BMNH R5261, the two halves of a right ramus mandibulae. The three remaining specimens include natural moulds of the following material: the dorsal and ventral surfaces of a skull (IMGPGö 741-6); the ventral surface of a skull, minus the rostral half of the maxillae and premaxillae (GAB Sch. 1); and the dorsal surface of a skull (DFMMh Sch. 1a). Although the Ballerstedt skulls have never been studied, endocasts of the braincase and tympanic cavities obtained from two of these specimens were described by Edinger (1938) and referred to '*G. pugnax*' and '*G. minor*' respectively. Specimen numbers for these specimens were not cited by Edinger, and we have been unable to locate this material.

Crocodilian fragments from an Early Cretaceous (Aptian) site near Nehden, western Germany, originally noted by Huckriede (1982) and von Oekentorp (1984), were tentatively identified as *Goniopholis* sp. by Norman (1987). This material included two well preserved thoracic vertebrae, a number of osteoderms from the paravertebral shield, a partial left humerus and what may be the distal end of a left femur. Identification was based on direct comparison of the vertebrae with the specimens of *G. simus* from Bernissart (Norman 1987).

In 1992, during the re-organization and cataloguing of fossil collections in the Institut für Paläontologie, Universität Bonn, a large sawn block preserving the natural mould of the skull and mandible, and the endocast of the rostrum maxillae and orbital region of a species of *Goniopholis* was discovered (IPB R359; Text-figs 2–3). No information was associated with the specimen, so the



TEXT-FIG. 3. *Goniopholis simus* (Owen, 1878); IPB R359; endocast of the rostrum maxillae and orbital region in (A) dorsal aspect and (B) ventral aspect; ×0·35.

location from which it was collected along with the history of its discovery and acquisition by the Institut für Paläontologie are unknown. Nevertheless, the lithology of the matrix of the specimen suggests that it is derived from one of the calcareous claystones of the Upper Obernkirchen Sandstone of the Bückeburg Member of the north-western German 'Wealden' Formation. Only two specimens of the crocodilian *Pholidosaurus schauburgensis* and an isolated tooth, tentatively referred to *Goniophilis*, are recorded by Koken (1887) as coming from this unit.

The purpose of this paper is to review the taxonomic status of *Goniopholis* in north-western Germany based on the description of the Bonn specimen. This work forms part of a larger study on the taxonomy and evolutionary position of *Goniopholis* currently being undertaken by the first author.

Anatomical nomenclature

We have followed the anatomical terminology codified in *Nomina Anatomica Avium* (Baumel and Witmer 1993), and that outlined in Frey (1988), Rauhe (1993), Witmer (1995) and Rossman (1996). This terminology is used purely in a topographic sense and we do not imply any homology in the sense that it relates to common ancestry. Following Clark (1986), the fused exoccipital and opisthotic of crocodilians are referred to as the otoccipital. Cranial and caudal are used throughout in preference to anterior and posterior, except in the skull where rostral replaces cranial.

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; BMNH, The Natural History Museum, London (formally the British Museum (Natural History)); CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, USA; DFMMh, Dinosaurier-Freilichtmuseum, Münchehagen, Germany; GAB, Gymnasium Adolfinum, Bückeburg, Germany; GPIMü, Geologisch-Paläontologisches Institut der Universität Münster, Germany; IMGPGö, Institute und Museum für Geologie und Paläontologie der Georg-August-Universität, Göttingen, Germany; IGPMbg, Institut für Geologie und Paläontologie der Philipps-Universität, Marburg, Germany; IPB, Institut für Paläontologie der Universität Bonn, Germany; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MB, Museum für Naturkunde der Humbolt-Universität, Berlin, Germany; MHNBP, Natural History Museum, Boulogne-Sur-Mer, France; OMNH, Oklahoma Museum of Natural History, Oklahoma, USA; TMM, Texas Memorial Museum, University of Texas at Austin, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Abbreviations used in the figures are listed in the appendix.

SYSTEMATIC PALAEONTOLOGY

Order CROCODILIA Gmelin, 1788
Family GONIOPHOLIDIDAE Cope, 1875

Genus GONIOPHOLIS Owen, 1841

Goniopholis simus Owen, 1878

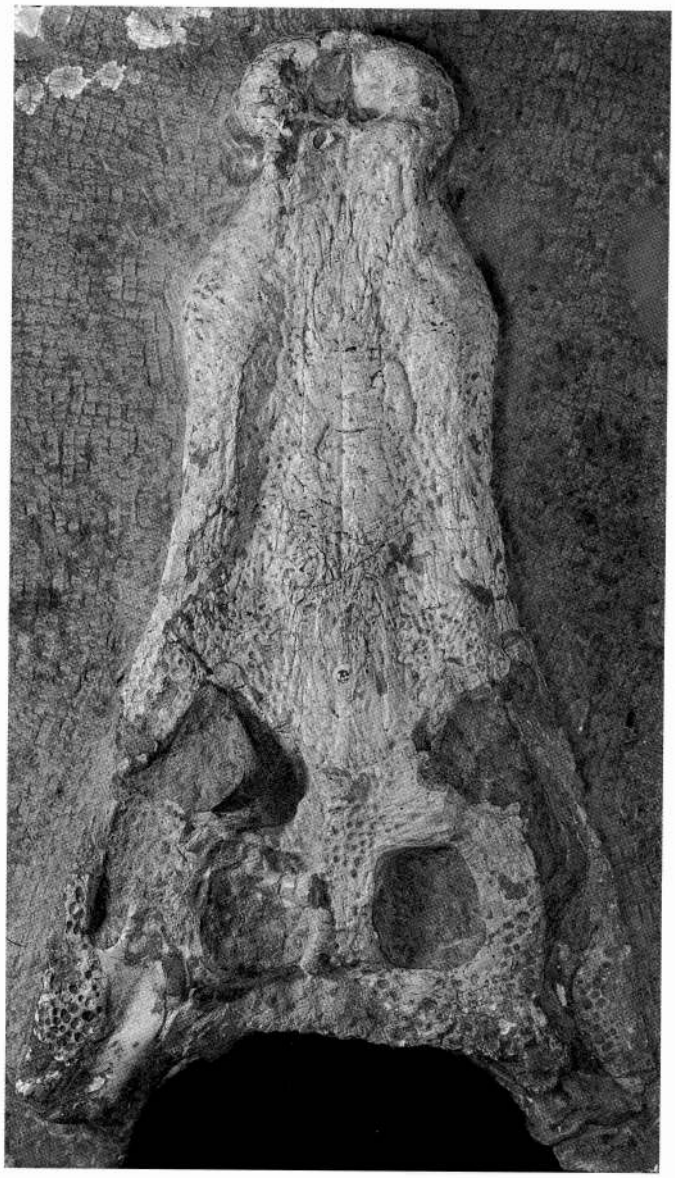
Text-figures 2–12

Holotype. BMNH 41098 and 41098a (the counter slab); a skull minus the mandible, along with two osteoderms from the paravertebral shield (Text-fig. 4).

Type locality. Collected some time during the late 1870s from the 'Middle' Purbeck of either the Lulworth or Durlston Formation, Swanage, Dorset, southern England (Owen 1878). The precise locality is unknown.

Stratigraphical range. Berriasian (Lower Cretaceous).

Distribution. Wessex-Weald Basin of southern England and Niedersachsen Basin of north-western Germany.



TEXT-FIG. 4. *Goniopholis simus* (Owen, 1878); BMNH 41098; holotype skull in dorsal aspect; ×0·35.

Revised diagnosis. Differing from all other crocodilian taxa in the possession of the following features: prefrontal contacts postorbital, excluding the frontal from the dorsal margin of the orbit; processus paroccipitalis and lamina ventrolateralis of the squamosal do not contact the quadrate; canalis quadratosquamosootoccipitalis exposed laterally, continuing caudally on the quadrate as a shallow sulcus; fenestra premaxillaris absent; diamond-shaped fossa premaxillaris on the rostral floor of the vestibulum nasi; transversely elongate foramen squamosootoccipitale.

G. simus also differs from other species of *Goniopholis* in the reduction of external sculpture on the nasal and maxilla.

DESCRIPTION OF THE BONN SPECIMEN

Preservation

The Bonn specimen is typical of the Obernkirchen Sandstone in being a natural mould. Impressions of the dorsal surface of the skull and portions of mandible are preserved (Text-fig. 2). Furthermore, the internal cavities of the rostrum maxillae and orbital region are preserved as a solid endocast (Text-fig. 3). No counter slab to the specimen has been found, so the nature of the ventral surface of the skull, lateral extent of the maxilla, jugal and quadratojugal, and caudomedial surfaces of each ramus mandibula cannot be commented on. Nevertheless, some aspects of the structure of the palate can be described from the impressions of the dorsal (internal) surfaces of the palatal elements preserved on the ventral surface of the endocast of the rostrum maxillae (Text-fig. 3B). The impressions of the mandible comprise a portion of left ramus rostral to the supraangular, and the lateral surface of the right ramus caudal to the end of the tooth row. Owing to the manner in which the slab was sawn, an impression of the articular region of the left ramus is missing. This permits a complete reconstruction of the mandible except for the portion of the rostrum rostral to a point level with the fourth dentary alveolus, the medial surface of the ramus caudal to the rostral limit of the fenestra mandibularis externa, and the dorsal surfaces of the supraangular and articular, including the fossa articularis quadratica and fossa retroarticularis. It is assumed, but cannot be demonstrated, that the impression of the lateral surface of the processus retroarticularis is preserved in entirety. No teeth were preserved in the mandible; however, a cut edge on the slab revealed a cross section through an isolated tooth. An endocast of the braincase was not present with the specimen when it was rediscovered. The broken surfaces along the caudal margin of the preserved endocast indicate that this part of the specimen may have been lost during collection. There is no evidence of any soft tissue elements on the endocast, and most of the sutures, foramina and fenestrae have close to what would be considered perfect definition had a cast of the skull been made without skin or tissue.

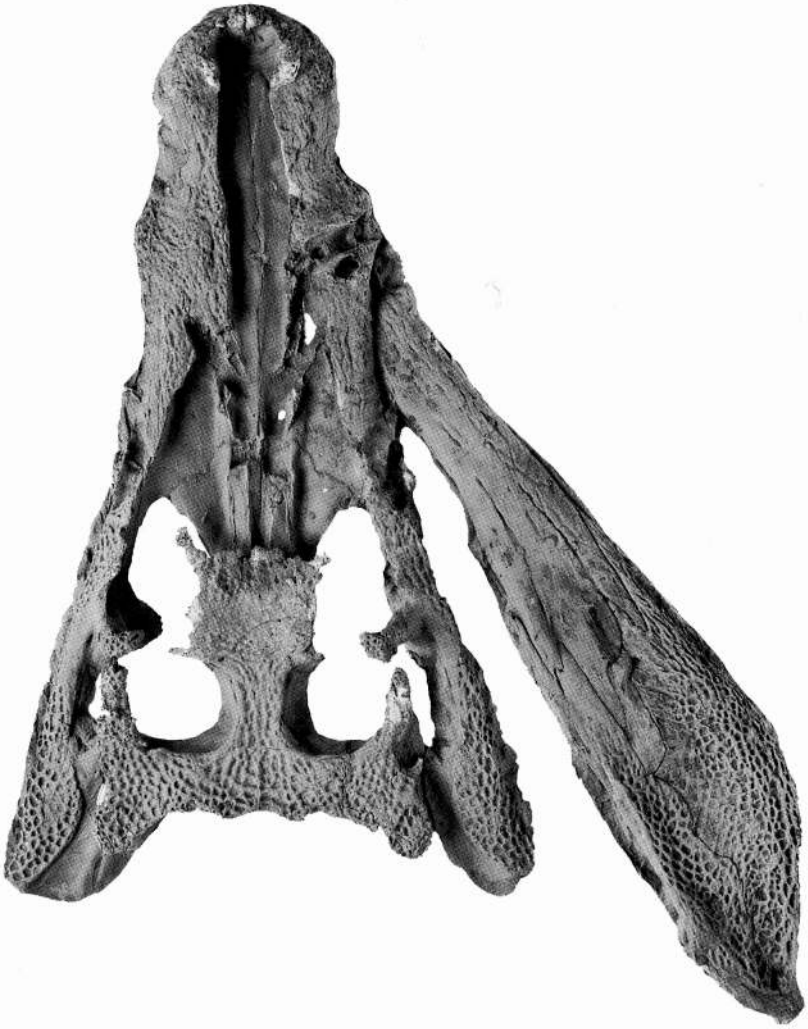
The mandible was not preserved in occlusion with the skull, nor were its rami in articulation. Assuming that the face on which the specimen is preserved (that shown in Text-fig. 2) represents the upper surface of the slab, the ramus mandibulae was preserved medial side up, sub-parallel to the right side of the skull. Hence, the portion of this ramus rostral to the end of the tooth row originally lay on top of the palate. The left ramus mandibulae was preserved lateral side up, on the same side as the right ramus mandibulae, but oriented perpendicular to it with the symphysial portion of the rostrum mandibulae alongside the right maxilla.

So that both the external and internal morphology of the bones could be examined, a series of silicon rubber casts were made using the specimen as a mould. These yielded a 'positive' copy of the skull and mandible. The first cast (Text-fig. 5) covered the entire skull and the caudal portion of the right ramus mandibulae. Before this cast was made the specimen received only basic cleaning, and the endocast of the rostrum maxillae and orbital region was left in place, preventing any replication of surfaces directly dorsal to these cavities. Due to the complexity of the caudal part of the skull, the portion of the cast that included the skull table could not be retrieved without damaging the specimen.

Prior to the making of the second cast, the endocast of the rostrum maxillae and orbital region was removed. As a result, the second cast duplicated the entire dorsal surface of the skull. Further silicon rubber casts were made of the left ramus mandibulae and the isolated tooth. During the removal of the former cast, the impression of the medial surface of the splenial was mostly destroyed.

Skull (Text-figs 6–9)

Form and proportions. The rostrum maxillae forms *c.* 60 per cent. of the total length of the skull, with the premaxillary portion being only slightly narrower than the maxillary portion, which, at its widest point, is still 20 per cent. narrower than the skull table. In dorsal aspect, the lateral margins of the rostrum maxillae are strongly concave for the reception of the mandibular pseudocanines at the suture between the premaxillae and maxillae. The rostrum maxillae is remarkably flat dorsoventrally, its maximum median depth being only 20 per cent. of its maximum width. The same is also true for the basicranium, where the height from the bottom of the foramen magnum to the horizontal plane of the skull table is less than 25 per cent. of the width of the latter. The skull table is 1·45 times broader than it is long, and in dorsal aspect the lateral margins are gently convex lateral to the foramina supratemporalia externa, but become concave caudally. In lateral aspect the skull table is only slightly elevated from the rostrum maxillae, the two regions being separated by a transverse, rostrally concave, crescent-shaped crista interobitalis. The medial margin of the orbit is almost level with the lateral margin of the foramen supratemporale externum, such that the interorbital plate is extremely broad. Sculpture on the skull consists of distinct, predominantly round, 2–4 mm wide pits, which are best developed on the skull



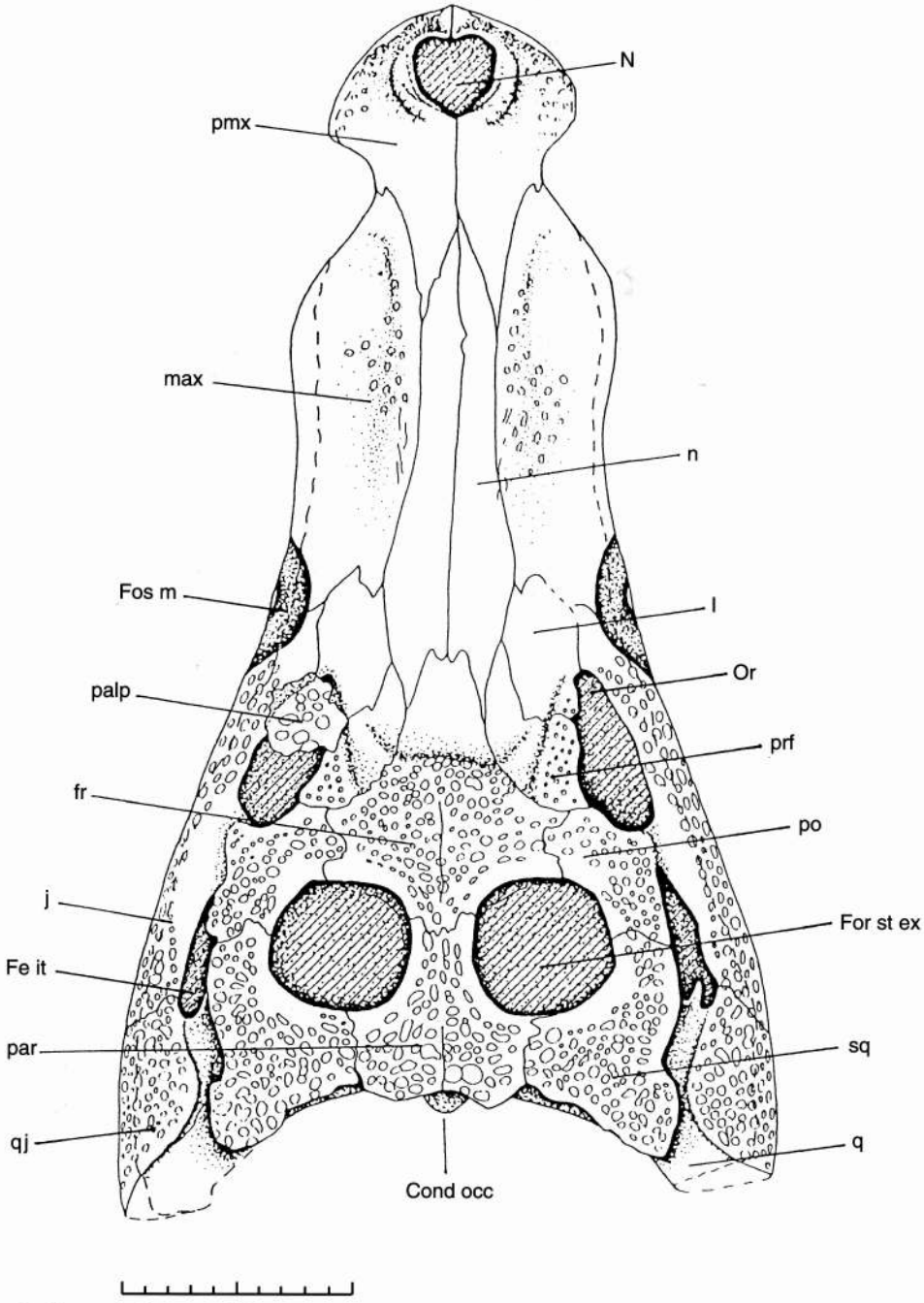
TEXT-FIG. 5. Silicon rubber cast of *Goniopholis simus* (Owen, 1878); IPB R359; cast made with the endocast of the rostrum maxillae and orbital region (Text-fig. 3) still in place; ×0·25.

table, quadratojugals and jugals. Similar sculpture on the rostrum maxillae is almost absent. Important cranial measurements are given in Table 1.

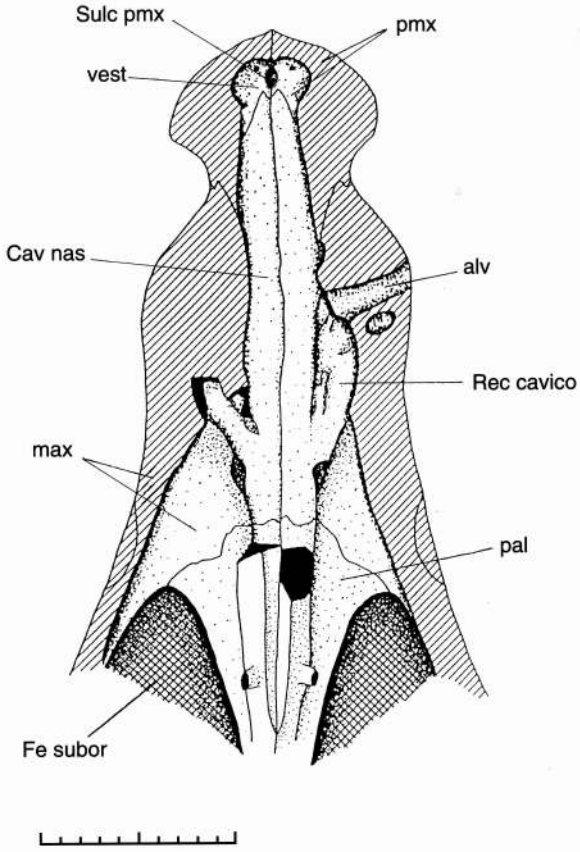
Foramen naris externum (Text-fig. 6). In dorsal aspect, this foramen is heart-shaped, with its axis aligned parallel to the median plane. It is directed dorsally and contained solely within the premaxillae. The rostral and lateral margins, the naris vallatus, are elevated above the level of the rostrum maxillae by a height of 10–15 mm.

Fenestra suborbitalis (Text-fig. 7). Only the rostral portions of each fenestra orbitalis are preserved. Each is broad and ovate, extending rostrally to a point beneath the caudal limit of the fossa maxillaris, and is bounded by the maxilla rostrally and the palatine medially.

Orbit (Text-figs 6, 8). In dorsal aspect, the orbit forms an ellipse that is elongated rostrocaudally with a slightly pointed rostral margin, being one-and-a-half times as long as it is wide. It is bounded by the lacrimal and prefrontal medially, the postorbital caudally and the jugal laterally.



TEXT-FIG. 6. *Goniopholis simus* (Owen, 1878); IPB R359; reconstruction of the skull in dorsal aspect. This view has been restored using details from two silicon rubber casts and the original natural mould (Text-fig. 2). The border of the second silicon rubber cast is shown as a dashed line. Scale bar represents 100 mm.



TEXT-FIG. 7. *Goniopholis simus* (Owen, 1878); IPB R359; reconstruction of the internal sinuses and cavities of the skull in dorsal aspect, based on the endocast of the rostrum maxillae and orbital region (Text-fig. 3) and first silicon rubber cast (Text-fig. 5), with the nasals, lacrimals, prefrontals and frontals removed. Single hatched areas indicate areas of external detail as seen in Text-figure 6. Scale bar represents 100 mm.

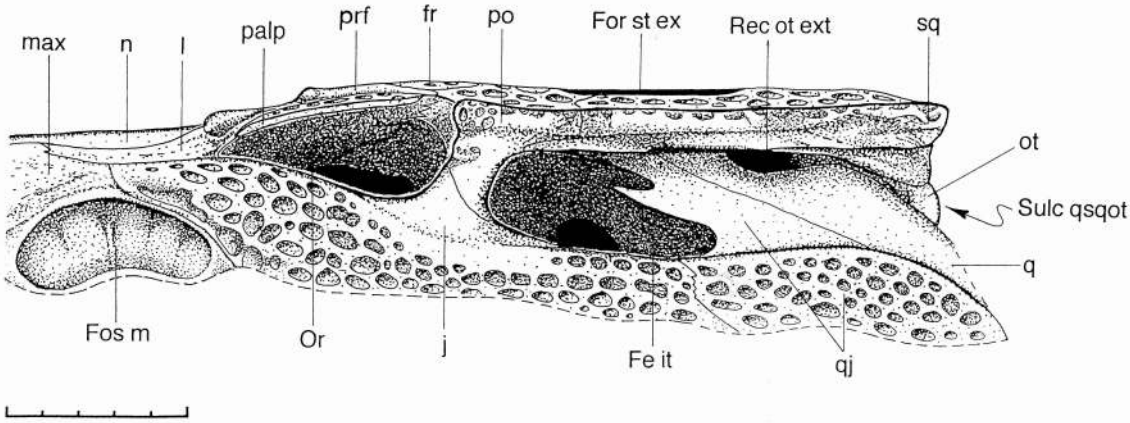
Foramen supratemporale externum (Text-fig. 6). This foramen is almost circular in outline, and is bounded by the squamosal caudolaterally, the parietal caudomedially, the postorbital rostrolaterally and the frontal rostromedially. The margins of the foramina are not elevated above the level of the rest of the skull table, and overhang only slightly the dorsal walls of the recessus supratemporales.

Fenestra infratemporalis (Text-figs 6, 8). This fenestra is slightly less than twice as long as it is high, and is bounded by the quadratojugal caudodorsally, the jugal laterally, the postorbital rostrally and a minor participation of the squamosal rostrodorsally. The processus infratemporalis of the quadratojugal enters the fenestra half way along its dorso-ventral margin.

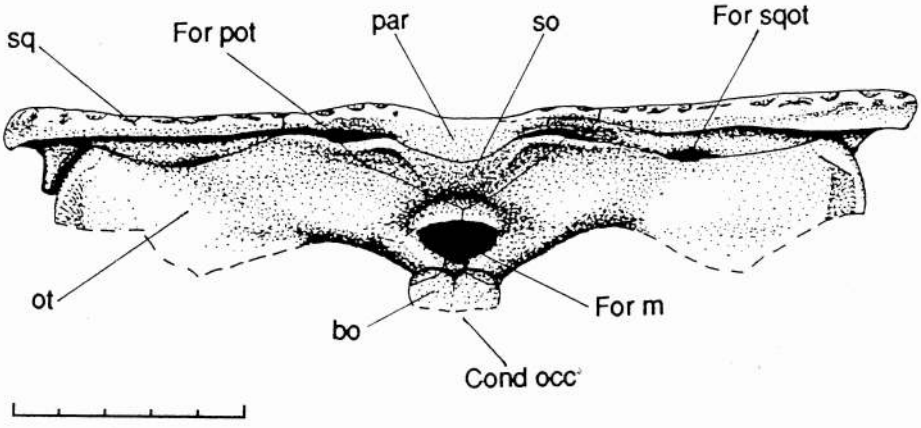
Foramen posttemporale (Text-fig. 9). This foramen is a wide, slit-like structure, eight times as long as it is high. It is bounded by the supraoccipital medioventrally, the parietal dorsally and a minor participation of the otoccipital lateroventrally. It is not visible in dorsal aspect.

Foramen squamosootoccipitale (Text-fig. 9). This foramen is approximately half the size of the foramen posttemporale, and is located mid way between the midline of the skull and the lateral margin of the skull table. It is bounded by the squamosal dorsally and the otoccipital ventrally.

Foramen magnum (Text-fig. 9). This foramen is transversely ovoid in shape, being two-and-a-half times wider than it is high. Apart from a small contribution the basioccipital ventrally, its margin is formed by the otoccipitals.



TEXT-FIG. 8. *Goniopholis simus* (Owen, 1878); IPB R359; reconstruction of the left rear of the skull in lateral aspect, based on the left and right sides of the first (Text-fig. 5) and second silicon rubber casts. The border of the first silicon rubber case is shown as a dashed line. Scale bar represents 50 mm.



TEXT-FIG. 9. *Goniopholis simus* (Owen, 1878); IPB R359; reconstruction of the occiput, based on the first (Text-fig. 5) and second silicon rubber casts, along with details from the original natural mould (Text-fig. 2). The border of the first silicon rubber cast is shown as a dashed line. Scale bar represents 50 mm.

Premaxilla (Text-figs 6–7). In dorsal aspect, the premaxillae are almost as broad as the maxillae and nasals, and, rostral to the suture with the maxillae, they have concave caudolateral margins. The foramen naris externum is located towards the rostral end of the premaxillae, 18·7 mm from the front of the skull. Rostral to this foramen, the premaxillae unite to form a rugose vertical crest. The premaxilla excludes the nasal from the foramen naris externum, and caudally, a long, broad process, which extends to a point level with the lateral swellings of the maxilla over the maxillary pseudocanines, also separates the nasal from the maxilla. External sculpturing is restricted to indistinct pits and rugosities on the medial and rostral surfaces.

The palatal surfaces of the premaxillae are not preserved; however, internally they form the dorsolateral walls of the cavitas nasalis. The internal rostral apex of the serrated, M-shaped suture between the premaxillae and maxillae is located just rostral to the caudal margin of the foramen naris externum. Two small pits, located rostrally within the vestibulum nasi, and 18·0 mm apart, are interpreted as the internal expression of tooth reception pits for the first dentary teeth. A fenestra premaxillaris is absent on this specimen, although on the rostral floor of the vestibulum nasi there is a small, median, diamond-shaped fossa, one-and-a-half times as long as it is wide, here termed the fossa premaxillaris.

TABLE 1. List of measurements for the Bonn specimen of *Goniopholis simus* (Owen, 1878); IPB R359.

Variable measured	Measurement (mm)
Skull	
1. Skull length, from tip of rostrum maxillae to condylus occipitalis	485·5
2. Skull width at lateral border of quadratojugals	290·5
3. Length of rostrum maxillae, from tip of premaxillae to rostral extent of orbits	301
4. Minimum width of rostrum maxillae	81
5. Maximum width of rostrum maxillae	161
6. Maximum width of premaxillae	116·7
7. Skull table width	197·6
8. Skull table length, from caudal limit of squamosals to caudal limit of orbit	137·6
9. Interorbital distance	106·1
10. Minimum distance between foramina supratemporalia externa	28·1
11. Foramen naris externum length	35·8
12. Foramen naris externum width	39·1
13. Fossa premaxillaris length	13
14. Fossa premaxillaris width	8·6
15. Fossa maxillaris length	57·0
16. Fossa maxillaris height	22·8
17. Fenestra infratemporalis length	73·8
18. Fenestra infratemporalis width/height	31·8
19. Foramen supratemporale externum length	59·1
20. Foramen supratemporale externum width	61·8
21. Orbit length	73·1
22. Orbit width	50
23. Fenestra suborbitalis maximum width	62·7
24. Foramen magnum height	10·1
25. Foramen magnum width	25·2
26. Foramen posttemporale height	2·4
27. Foramen posttemporale width	19·6
28. Foramen squamosootoccipitale height	1·8
29. Foramen squamosootoccipitale width	9·8
Mandible	
30. Mandible length (reconstructed)	540
31. Tooth row length (reconstructed)	300
31. Fenestra mandibularis externa length	70·6
32. Fenestra mandibularis externa height	18·7

Maxilla (Text-figs 6–8). The lateral margin of the maxilla is convex in the region that accommodated the maxillary pseudocanines, but becomes gently concave caudally. Caudomedially, a short, triangular caudal process separates the nasal from the rostral limit of the lacrimal. Apart from a slight dorsal swelling over the alveoli for the maxillary pseudocanines, external sculpture on the maxilla consists of indistinct scarring and small pits rostrally, which grade into rostrocaudal lineations caudally.

The fossa on the caudolateral margin of the maxilla is a deep, well-defined concavity, three times as long as it is high in lateral aspect, with a dorsally inflected ventral margin (Text-figs 6, 8). It is subdivided into five hemispherical concavities, positioned side by side in lateral aspect. There is a slight ridge between the second and third rostral-most of these concavities. The second concavity is slightly larger than the others, whilst the caudal-most (fifth) concavity is the smallest. The bone separating the fossa from the cavitas antorbitalis appears to have been extremely thin ($<$ 2–3 mm). There is no evidence of a fenestra antorbitalis in this region.

Internally, the maxilla forms the lateral and ventral enclosure of the rostral portion of the cavitas nasalis. Rostrally, this cavity is ovoid in section, being three times as wide as it is high, with slightly sinuous lateral margins, becoming higher and narrower with parallel sides caudally.

Only the right recessus caviconchalis is preserved (Text-fig. 7). It is contained wholly within the maxilla and is ovoid in outline, being three times as long as it is wide, with a rounded rostral margin that is level with the broadest lateral expansion of the maxilla. Caudally, this recess communicates with the cavitas antorbitalis through a nearly circular apertura caudalis, whilst medially it is connected to the cavitas nasalis by two apertures: a small, rostrocaudally ovate apertura rostromedialis, and a larger, near circular apertura caudomedialis.

The maxilla forms the ventral and dorsolateral walls of the rostrally pointed cavitas antorbitalis, which is 25·4 mm deep at its broadest point. The nature of the ventral suture between the maxilla and lacrimal, along with the position of the foramen caudal n. maxillaris cannot be determined.

The internal suture between the maxillae and palatines originates at the rostral apex of each fenestra suborbitalis, and is smooth and convex rostrally. Rostral to this suture, the maxillae enclose the ventral margins of the choanae primae, which appears to have been ovoid in transverse section.

Although the internal portions of two alveoli are preserved on the right maxilla (Text-fig. 7), these provide no information on the morphology of the alveolus or tooth.

Nasal (Text-fig. 6). In dorsal aspect, the nasals have subparallel sides between the maxillae, but widen caudally along their contact with the lacrimals. The rostral process of the nasals wedges out between the premaxillae, ending just caudal to a point level with the rostral-most extent of the maxilla. A wide, triangular, caudal process separates the rostral extent of the prefrontal from the rostral process of the frontals, and a second, much shorter process enters the rostral process of frontals. The nasals are devoid of external sculpture.

The nasals form the roofing bones of the cavitas nasalis. Rostral to the recessus caviconchalis, the suture between the two nasal bones is flat, but caudally it forms a deep (up to 10 mm), medial septum. The ventral contact with the frontal lies *c.* 18 mm rostral to a point level with the suture between the palatine and maxilla. From this point, the nasal extends caudolaterally before petering out just rostral to the orbits.

Lacrimal (Text-figs 6, 8). The lacrimal is twice as long as it is wide in dorsal aspect. The border with the jugal is lateral to the rostral angle of the orbit. Medially, a small wedge of the maxilla separates the rostral process of the lacrimal from the nasal; this wedge is slightly larger on the right hand side of the skull than it is on the left. A rostrolaterally aligned crest, beginning at the caudal end of the dorsal suture with the jugal, extends caudally over the lacrimal and continues onto the prefrontal. Although heavily sculptured laterally with well-defined, small pits (up to 2 mm in diameter), medial to this crest the lacrimal is unsculptured.

Prefrontal (Text-figs 6, 8). In dorsal aspect the prefrontal is crescent-shaped with a prominent lateral flexure, wedging out acutely between the lacrimal and nasal. Caudolaterally, the prefrontal contacts the postorbital approximately 20 mm from the caudal curvature of the orbit, excluding the frontal from participating in the orbital margin. The crest originating on the lacrimal continues for the full length of the prefrontal, and medial to it the prefrontal is devoid of sculpture. This crest is partly contiguous with the crista interorbitalis that extends across the rostral process of the frontals.

Ventrally, the processus ventralis ('prefrontal pillar' *sensu* Iordansky 1973) is round in section (up to 11 mm in diameter), and is located just caudal to the rostral extent of the fenestra suborbitalis. A bulbous, ventrally directed, medial process of this process forms a hood over the caudomedial corner of the recessus pneumaticus caudolateralis. Just caudal to the base of the processus ventralis, the prefrontal contacts the palatine. The caudal margin of the prefrontal extends ventrally for 10·4 mm within the orbit, before running diagonally towards the uppermost portion of the processus ventralis.

Palpebral (Text-figs 6, 8). A single bony element, polygonal in outline, is preserved over the rostral margin of the left orbit. This element is flat and heavily sculptured with large (2–3 mm diameter), well-defined pits. Although its caudal margin is irregular and probably broken, there is no indication of sutured margins or any other marks where this element could have been attached to the skull. This element is interpreted as a palpebral, since no other portion of the skull that could account for its presence appears to be missing. A second small bony element is present on top of the right quadratojugal (Text-fig. 2). Unlike the *in situ* palpebral, however, this bone has a 3–4 mm high spine or crest. There is no indication of any sutural contact on this bone and no other portion of the skull corresponds with it in any way. This element can be interpreted as: (1) a second, caudal, left palpebral; (2) the caudal portion of the single, *in situ* left palpebral; or (3) part of the right palpebral. Because of the close proximity of this element to the right orbit, the third possibility seems the most likely.

Frontal (Text-fig. 6). A smooth, median suture, extending from a point just caudal to the rostral limit of the foramina supratemporalia to the level of the junction between the frontal, prefrontal and postorbital, indicates that the frontals are only partially fused. Rostral to a distinct, transverse, crescent-shaped crista interorbitalis, the wedge-like rostral process of the frontals extends to a point level with the rostral margin of the orbits, but is squared off due to the presence of two small, caudal processes of the nasals. The contact with the prefrontal and nasal is a continuous, rostrolaterally concave, gentle curve. Laterally, the frontal flares slightly around a square, medial process of the postorbital. Caudally, the serrated contact with the parietals consists of a short, square, caudal process; two short, blunt processes of the parietals extend rostrally on either side. The frontal forms the rostromedial border of the foramen supratemporale externum, this border being sharp, but not elevated. Within the recessus supratemporalis, the frontal broadly separates the postorbital from the parietal.

The crista interorbitalis forms a distinct step-up on the frontals, sharply demarcating the almost smooth rostral region from the heavily sculptured skull table. The sculpturing on the caudal portion of the frontals consists of well-defined, 2–3 mm wide, circular or nearly circular pits, distributed in a reticulate pattern. Caudal to the orbits, there is a slight medial concavity.

Ventrally, the frontals underlap the nasals to a considerable degree, extending 52·3 mm rostral to their maximum dorsal extent. Caudally, each frontal flares a little laterally; the junction between the frontal, postorbital and laterosphenoid is 10·4 mm ventral to the dorsolateral contact between the prefrontal and postorbital on the skull table. From this point, the serrated suture between the frontal and prefrontal runs rostroventrally to the lateral wall of the dorsum sellae.

The cristae ventrales of the frontals are low, parallel structures, a maximum of 20 mm apart, that run close to the midline of the skull. They extend from the caudal border of the processus ventralis of the prefrontal to the rostromedial extent of the laterosphenoid. Caudal to this point, the ventral surface of the frontals is not preserved.

Postorbital (Text-figs 6, 8). In dorsal aspect, a small, rounded rostrolateral process of the postorbital forms the dorsocaudolateral border of the orbit, such that the rostrolateral angle of the skull table is almost square. Medially, it forms the rostrolateral corner of the foramen supratemporale externum, the edges along this margin being sharp, but not elevated. Although this area is poorly preserved, there does not appear to have been a vascular foramen on the lateral edge of the dorsal section of this postorbital. Sculpture on the dorsal surface of the postorbital continues down the columna postorbitales, which is circular in cross section, and terminates at a large, rounded, rostrolateral process. There is no caudal process of the postorbital extending beneath the squamosal at the rostrodorsal angle of the fenestra infratemporalis. Ventromedial and slightly caudal to the orbit, a blunt process of the postorbital extends between the frontal and the laterosphenoid.

Parietal (Text figs 6, 9). As is the case with the frontals, a smooth, median suture, extending from the caudal margin of the skull table to a point level with the caudal limit of the foramina supratemporalia externa, indicates that the parietals are only partially fused. Between the foramina supratemporalia externa, the dorsal surface of the parietals is slightly concave. The lateral margins, which are sharp, but not elevated, form the caudomedial third of the foramina supratemporalia externa. No foramen orbitotemporale is preserved along the caudal wall of the recessus supratemporalis. The suture with the squamosal is straight caudally, but flares laterally, just caudal to the foramen supratemporale externum. The parietals form approximately one-third of the caudal margin of the skull table, and two blunt, caudal projections overhang the foramina posttemporalia. Sculpture on the dorsal surface of the parietals is similar to that on the frontals, but with larger pits (up to 3–4 mm in diameter).

Squamosal (Text-figs 6, 8–9). The medial margin of the squamosal is concave, and forms the caudolateral border of the foramen supratemporale externum. Dorsal to the recessus oticus externus, the lateral margin is concave, whilst the border with the postorbital is transversely oriented. In lateral aspect, a thin rostral process of the squamosal underlaps the postorbital, extending almost to the columna postorbitalis. Dorsal to the recessus oticus externus, there is a shallow, rostrocaudally aligned sulcus that becomes deeper caudally and continues around the caudolateral corner of the squamosal onto the occiput, finally ending at the foramen posttemporale. Caudal to the recessus oticus externus, the lamina ventrolateralis of the squamosal does not contact the quadrate laterally, such that the canalis quadratosquamosootoccipitalis ('cranioquadrate canal' *sensu* Iordansky 1973) is exposed; the squamosal forming the roof of the resulting sulcus (Text-fig. 9). In occipital aspect, the squamosal overhangs the lateral extent of the otoccipital by 14·2 mm. Sculpture on the dorsal surface of the squamosal is similar to that on the parietal and frontal.

Supraoccipital (Text-fig. 9). The supraoccipital is a wide, but shallow, triangular bone that is inclined caudoventrally, and excluded from the skull table by the parietals. Two slight, lateral processes form the ventral margins of the posttemporal foramina. Ventrally, the supraoccipital forms a deep invagination dorsal to the contact with the otoccipital.

Otoccipital (Text-figs 8–9). Although wide, the otoccipital does not extend beyond the lateral margin of the squamosal in occipital aspect, and the processus paroccipitalis forms a laterally projecting, rounded flange that does not contact the dorsal surface of the quadrate. As a result, the foramen quadratosquamosootoccipitale is not enclosed laterally, and the otoccipital forms the medial wall of the sulcus quadratosquamosootoccipitalis. The positions of the foramina hypoglossali, foramen vagi and foramen caroticum caudale are not evident.

The dorsal contact with the squamosal forms a deep fold, and situated mid-way along this contact is the foramen squamosootoccipitale. Dorsomedially, the otoccipital forms only one-third of the ventrolateral border of the foramen posttemporale. Medially, the otoccipitals unite dorsal to the foramen magnum to form a small caudal projection or hood.

Basioccipital (Text-fig. 9). The only portion of the basioccipital preserved on the specimen is that which forms the dorsal surfaces of the condylus occipitalis. This is a hemispherical structure with a shallow median sulcus, which forms the ventral margin of the foramen magnum.

Laterosphenoid. Only the rostral half of the lateral surface of the laterosphenoid, preserved as an impression, is evident on the endocast of the rostrum maxillae. A shallow facet mid-way along the caudal suture between the postorbital and frontal, and medioventral to the orbit, indicates that the processus dorsalis was not firmly sutured to the base of the skull table. It is unclear whether this process contacted the quadrate.

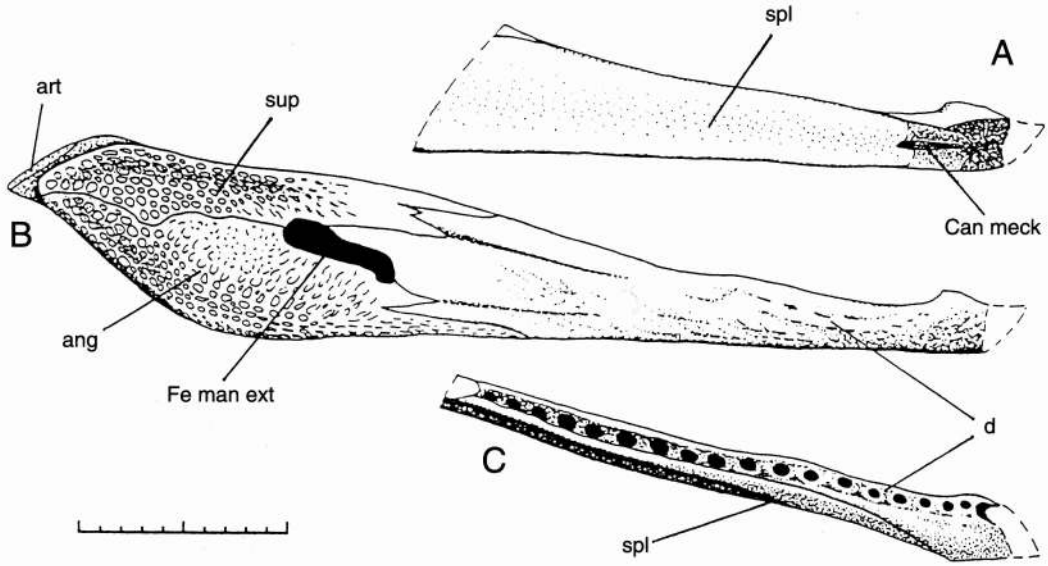
Jugal (Text-figs 6, 8). The jugal forms most of the ventral margin of the fenestra infratemporalis. Rostrally, it overlaps the maxilla, forming a shallow scarf joint, whilst dorsally it forms *c.* two-thirds of the rostral face of the columna postorbitalis, which is slightly inset medially from the lateral margin of the jugal. Lateral to this medial lip, the jugal is heavily sculptured to its rostral margin, with large, longitudinally ovoid, well-defined pits, aligned rostrocaudally into roughly linear patterns. The foramen ductus is located caudolateral to the columna postorbitalis, and is large and rostrocaudally elongate in outline. Caudally, the jugal contacts the quadratojugal in a straight, simple suture, which is located rostral to the caudolateral corner of the fenestra infratemporalis.

Quadratojugal (Text-figs 6, 8). The dorsal surface of the quadratojugal is clearly divided into two parts: a heavily sculptured lateral portion and a non-sculptured medial portion. These two regions are separated by a distinct, curved step that originates at the caudolateral corner of the fenestra infratemporalis, extending initially in a caudomedial direction and then curving caudolaterally, before ending lateral to the condylus mandibularis. Rostrally, the quadratojugal contacts the jugal 9·6 mm from the caudolateral corner of the fenestra infratemporalis. The triangular processus infratemporalis is situated midway along the caudodorsal margin of the fenestra infratemporalis. Rostrodorsal to the processus infratemporalis, the quadratojugal contacts the squamosal, broadly separating the quadrate from the fenestra infratemporalis.

Quadrate (Text-figs 6, 8). Unfortunately, only the dorsal surface of the left condylus mandibularis is preserved. Just medial to its midline, the caudal margin of the condyle is slightly inflected rostrally. The quadrate forms the ventral portion of the recessus oticus externus, and caudal to this region it does not contact the lamina ventrolateralis of the squamosal and processus paroccipitalis, such that the canalis quadratosquamoso-otoccipitalis is exposed laterally. The latter structure continues caudally on the quadrate as a shallow sulcus, terminating at a point level with the caudal margin of the squamosal in dorsal aspect. A foramen commune aerooticus is not evident on this specimen.

Vomer. Impressions of the vomer are preserved on the ventral surface of the endocast of the rostrum maxillae, medial to the choanae primae. The vomer is approximately five times as long as it is wide, and is 3–4 mm high. It does not appear to have been exposed ventrally on the palate.

Palatine (Text-fig. 7). Beyond a point level with the caudal extent of the orbits, the palatines are not preserved, so that their caudal contact with the pterygoids and the position of the choanae secundare cannot be



TEXT-FIG. 10. *Goniopholis simus* (Owen, 1878); IPB R359. Reconstruction of the mandible, in A, medial aspect; B, lateral aspect; C, dorsal aspect. Based on the first silicon rubber cast (Text-fig. 5), which included the caudal portion of the right ramus mandibulae, and the cast of the rostral portion of the left ramus mandibulae. Scale bar represents 100 mm.

determined. Internally, the processus rostralis flares laterally from a minimum width of 37·3 mm to a maximum of 113·3 mm, and has a broad, convex border with the maxillae. The palatines form the rostrodorsal and ventral walls of the ductus nasopharyngei.

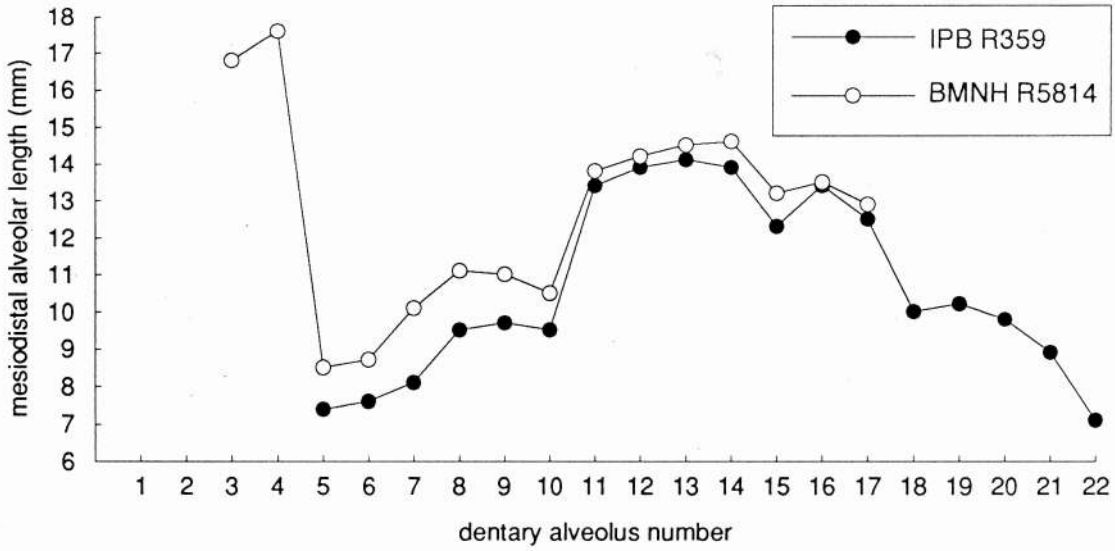
Pterygoid. Portions of the pterygoids forming the roof of the ductus nasopharyngei, caudal to the base of the processus ventralis of the prefrontal, are preserved as impressions on the ventral surface of the endocast of the rostrum maxillae. Dorsally they unite to form a narrow sulcus, which broadens rostrally to a maximum width of 2–3 mm at a point level with the processus ventralis of the prefrontals.

Mandible (Text-fig. 10)

Form and proportions. In lateral aspect, the ramus mandibulae is approximately four times deeper caudally than it is rostrally, with a short, caudoventrally directed processus retroarticularis. The caudodorsal margin of this process is slightly inflected dorsally. The tooth row forms approximately 55 per cent. of the reconstructed length of the ramus. In lateral aspect, the fourth and fifth dentary alveoli are raised above the rest of the tooth row, but the remainder of the dorsal margin of the dentary is only slightly festooned vertically, with a second, smaller peak between the 11th and 13th alveoli (see the following section on the dentary for the determination of alveolar numbers). If the missing portion of the dentary was reconstructed, in dorsal aspect the rostrum mandibulae would have been spatulate in outline, perhaps only slightly longer than it was wide. In dorsal aspect, the symphysial portion of the rostrum extends caudally to a point level with the sixth dentary alveolus. The lateral surface of each ramus mandibulae is heavily sculptured caudally and lightly sculptured or smooth rostrally and ventrally.

Fenestra mandibulae externa (Text-fig. 10). Contrary to previous descriptions of species of *Goniopholis*, for example those of Dollo (1883) and Hooley (1907), this specimen has a distinct external fenestra on the mandible. It is oblong, with its long axis aligned rostroventrally, being 3·7 times longer than it is high. The bottom rostroventral corner is slightly deflected ventrally. It is bounded rostrodorsally by the dentary, caudodorsally by the supraangular, and ventrally by the angular.

Dentary (Text-fig. 10). The exact number of dentary alveoli cannot be determined because the rostral-most portion of this bone is not preserved, nor can it be determined whether the third and fourth dentary alveoli were confluent. Nevertheless, if the sequence of dentary alveolar enlargement is similar to that seen in other platyrostral ('broad-snouted'), heterodont crocodilians (i.e. $1 = 4 \geqslant 3 \geqslant 2 = 5$), then it is likely that, as preserved, the rostral-most alveolus is the fourth in the series. If this is correct, there would have been 22 alveoli in the dentary. Mesiodistal alveolar lengths are shown in Text-figure 11. The caudal-most nine alveoli are set



TEXT-FIG. 11. Graph of mesiodistal alveolar lengths for the dentary of two specimens of *Goniopholis simus* (Owen, 1878); IPB R359 and BMNH R5814.

within a shallow alveolar groove. The dentary portion of the symphysis mandibulae extends caudally to a point level with the sixth alveolus. With the splenial *in situ*, the caudal limit of the sulcus associated with the canalis meckeli is level with the seventh dentary alveolus.

The dorsolateral contact between the dentary and the supraangular is 8·1 mm rostral to the caudal extent of the tooth row. Ventral to this contact, a thin, bipartite caudal process of the dentary underlaps the supraangular caudally to a point level with the rostral margin of the fenestra mandibulae externa. A triangular caudal process of the dentary wedges out between the two rostral processes of the angular, ventrorostral to the fenestra. Two converging sulci on the lateral surface of the dentary originate from a rostral process of the supraangular and a rostral process of the angular respectively, and extend rostrally to a point level with the 18th dentary alveolus. The external surface of the dentary is sculptured with small (1–2 mm diameter) pits and rostrocaudally aligned, 10–20 mm long lineations that are developed best on the ventral and ventrolateral surfaces.

Splenial (Text-fig. 10). The medial surface of the splenial is slightly concave, whilst caudal to the symphysial portion of the rostrum mandibulae, the dorsal surface forms approximately 50 per cent. of the width of the ramus along its length and the medial border of the tooth row from the 14th through to the 21st alveoli. In ventral aspect, it forms approximately 40 per cent. of the width of the ramus, but the extent of its caudal margin is not evident. Although the rostral extent of the splenial is not preserved, it does not appear to taper rostrally in medial aspect, and it is not clear whether it entered the symphysial portion of the rostrum mandibulae. Regardless, its rostral end appears to have been divided into two processes, one dorsal and one ventral to the sulcus associated with the canalis meckeli. There are no foramina on the preserved portions of the splenial.

Supraangular (Text-fig. 10). In lateral aspect, the supraangular bears a broad ridge parallel to its dorsal margin that extends from its caudal margin to a point above the fenestra mandibulae externa, of which the supraangular forms only a small portion (*c.* 13 per cent.) of the caudodorsal margin. Rostrally, a dorsal process overlaps the dorsal margin of the dentary. Ventral to this process, a second rostral process meets the dorsal sulcus on the external surface of the dentary. The supraangular does not contact the margin of the tooth row. Caudally, its lateral surface is covered in a reticulate pattern of well-defined, ovoid pits, 3–4 mm long, which degenerate into longitudinal lineations rostrally. Ventrally, these lineations are more vertically aligned. Caudally, the sculptured surface ends abruptly at a curved, caudoventrally aligned step.

Angular (Text-fig. 10). The angular has a broad ridge parallel to its ventral and caudoventral margins that fades out ventral to the fenestra mandibulae externa. Rostroventrally, a long, thin, rostral process overlaps the ventral margin of the dentary to a point level with the 20th dentary alveolus. Dorsal to this process, a second, shorter rostral process extends to the caudal end of the ventral sulcus on the external surface of the dentary. The angular alone forms the ventral and caudoventral margins of the fenestra mandibulae externa. Like the supraangular, it has a reticulate pattern of sculpturing on its external surfaces, consisting of well-defined, ovoid pits that degenerate rostrally into rostrocaudally aligned lineations. Rostrodorsally, these lineations are more vertically aligned. There is some rostrocaudal alignment of the caudal ovoid sculpturing on the ventral and caudoventral margins into chain-like lineations.

Articular (Text-fig. 10). Only a small impression of the lateral surface of the articular is preserved. It is unsculptured and forms the dorsocaudal surface of the processus retroarticularis.

Teeth

The single isolated tooth associated with the specimen is compressed buccolingually, with well-developed, closely spaced vertical striae that fade out at the base, and prominent, smooth, distal and mesial carinae.

DISCUSSION

Assignment of the Bonn specimen to Goniopholis

The anatomical construction of the skull and mandible of the Bonn specimen compares best to that of goniopholidid crocodilians, in particular those referable to *Goniopholis*. The characteristics of this genus are discussed in the works of Owen (1841, 1849–84, 1878, 1879), Hulke (1878), Lydekker (1890), Hooley (1907), von Nopsca (1928), Wiman (1931), Buffetaut (1982), Clark (1986) and Ortega *et al.* (1996), and in relation to the Bonn specimen include the following: at the suture between the premaxilla and maxilla, the lateral margin of the rostrum maxillae is strongly concave for the reception of the mandibular pseudocanines; short, broad premaxillae, with rostrally positioned, dorsally oriented, undivided foramen naris externum; exclusion of the nasals from the foramen naris externum by the premaxillae; broad interorbital plate, with the frontal forming only a small portion of the orbital margin; foramen supratemporale externum slightly larger than or of a similar size to the orbit, and nearly circular in outline; a flat skull table.

Another characteristic of the genus, not seen on the Bonn specimen, is the nature and position of the choanae secundare, which is situated mid-way between the palatines and pterygoid at a point level with the caudal margin of the fenestrae suborbitales, and is approximately three times longer than it is wide, and bipartite, with sharp palatal margins (see Buffetaut 1982, p. 31, fig. 7). An increase in the length of these choanae, combined with the presence of two smaller fenestrae between the palatines and maxillae, which are also connected to the ductus nasopharyngei, appears to be the main grounds upon which the American goniopholidid, *Eutretauranosuchus delfsi*, can be distinguished from *Goniopholis* (Mook 1967). A similar palatal construction in all the American species of *Goniopholis* (*G. stovalli*, *G. lucassi*, *G. gilmori* and *G.* (*Diplosaurus*) *felix*) may result in the referral of these taxa to *Eutretauranosuchus* (W. Langston Jr, pers. comm. 1996), but this possibility will not be discussed here.

In light of these similarities, in addition to the remaining natural moulds and casts of *Goniopholis* skulls and the ramus mandibulae from the Ballerstedt Collection (IMGPGö 741-6; GAB Sch. 1; DFMMh Sch. 1a; BMNH R5262; GPIMü Pr. 280; BMNH R5260; BMNH R5261), the Bonn specimen was compared with material of *G. crassidens* (BMNH 3798 and BMNH R3876), *G. simus* (BMNH 41098 and 41098a) and *Nannosuchus gracilidens* (BMNH 48217) from the Berriasian and lower Aptian of the Wessex-Weald Basin of southern England, and the skull and mandible of a relatively complete skeleton referred to *G. simus* (IRSNB R1537) from the Hauterivian–Barremian of Bernissart, Belgium. Further comparisons were made with specimens of *G. lucasii* (AMNH 5782) and *G. felix* (YPM 517 and YPM 986), *G. gilmorei* (CM 1339) and *G. stovalli* (OMNH 2392 and OMNH 2322) from the Tithonian Morrison Formation of Colorado, Wyoming and Oklahoma respectively, and an undescribed goniopholidid (TMM 4188-1) from the Lower Cretaceous of Arkansas. Skull fragments from the Lower Cretaceous of Galve, Spain, referred to *Goniopholis* cf. *G. crassidens* by Buscalioni and Sanz (1987*a*, 1987*b*) and two un-numbered specimens from the collections of the National Museum of Natural History, Washington and the American Museum of Natural History, New York were also examined. Comparisons with other taxa were made using illustrations and descriptions provided in the literature.

Comparison of the Bonn specimen with other Goniopholis *skulls from Germany*

The construction of the skull of the Bonn specimen agrees closely with that of the other *Goniopholis* specimens from the Ballerstedt Collection. Some variation in the overall size and proportions of the rostrum maxillae is evident: for example, the total cranial length of IMGPGö 741-6 is almost twice that of GPIMü Pr. 280, but this is by no means outside the range of variation exhibited by extant crocodilian species, and most probably relates to differences in ontogenetic stage or relative growth (Webb and Messel 1978; Hall and Portier 1994; Salisbury and Willis 1996; Monteiro *et al.* 1997). Although only two of the Ballerstedt *Goniopholis* specimens (IMGPGö 741-6 and GPIMü Pr. 280) show evidence of a palpebral, we do not consider this overtly significant in a taxonomic sense, since among living taxa these ossifications are free-floating elements, held in place only by thin integuments of tissue associated with the eye-lid (Wettstein 1937–54). As such, they could easily be lost during fossilization following the collapse of the eyeball. In the absence of any systematically variable characteristics, we therefore consider the Bonn specimen and other *Goniopholis* material from the Ballerstedt Collection to be representative of a single species.

Assignment of the German Goniopholis *material to* G. simus *Owen, 1878*

In all the crocodilians that we have examined, the prefrontal is excluded from contact with the postorbital by the frontal, which forms most of the dorsomedial margin of the orbit in those taxa lacking palpebrals. In species of *Goniopholis* and *Pholidosaurus*, the interorbital plate is extremely broad due to a more caudal position of the prefrontals. In both *G. simus* and the German *Goniopholis*, the condition is so extreme that the frontal is completely excluded from the orbital margin (or the medial edge of the palpebral) by a broad contact between the prefrontal and postorbital. This feature is particularly clear on the German specimens, but may have been overlooked on the holotype of *G. simus* since on both the left and right sides of the skull the rostrolateral portions of the skull table are broken. Examination of the counter slab associated with the holotype (BMNH 41098a) reveals an impression of the unbroken dorsal surface of the skull table. As in the German specimens, the suture between the frontal and prefrontal can be traced caudally to a contact with the postorbital, 3–4 mm medial to the orbital margin. This feature is also apparent on the dorsal surface of the right endocast of the orbit on the main slab (Text-fig. 12), and to our knowledge, is unique among crocodilians.

Clark (1986, p. 401) stated that the enclosure of the canalis quadratosquamosootoccipitalis was '...unique to mesoeucrocodylians [inclusive of thalattosuchians] among archosaurs.' However, a

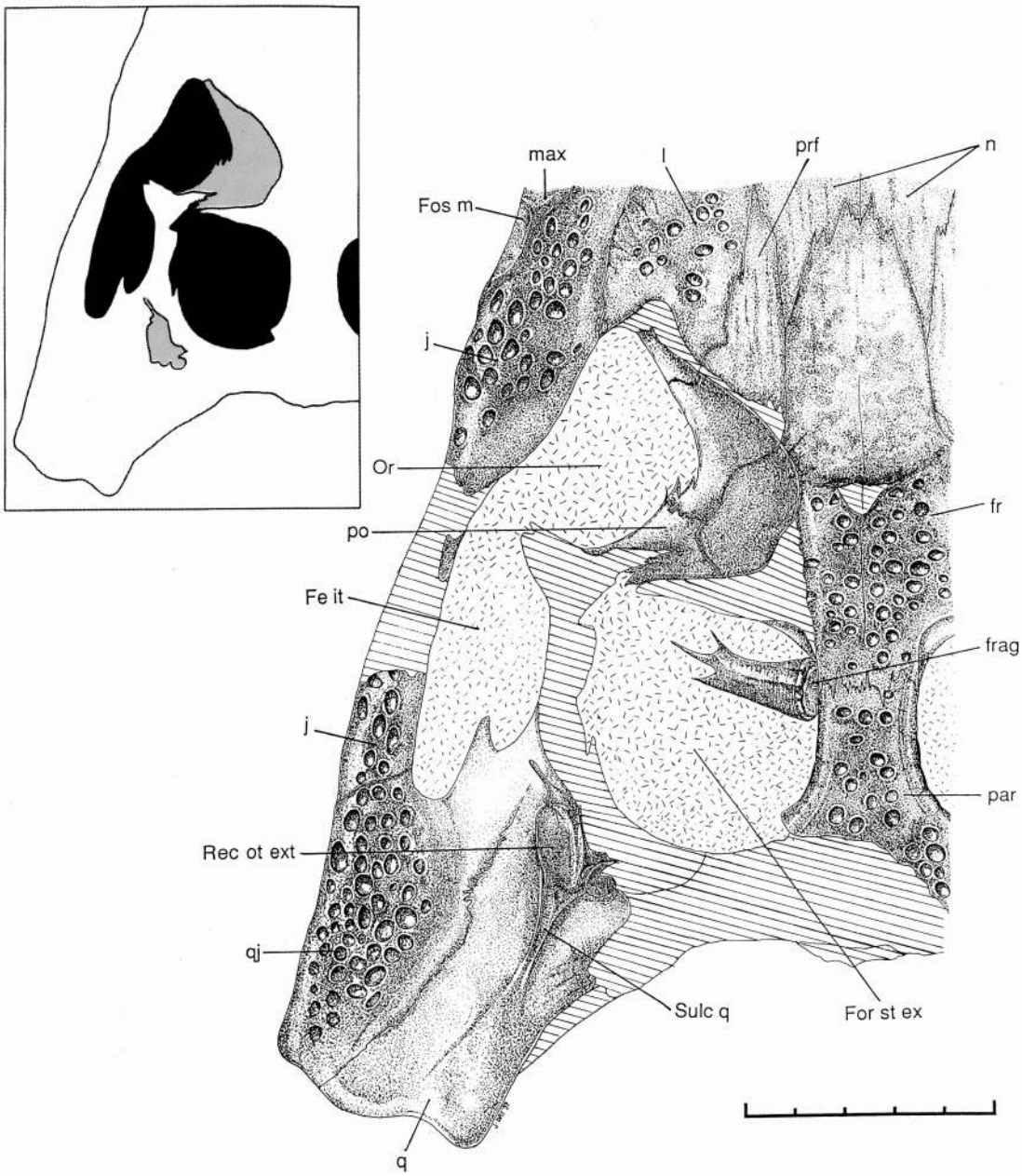
laterally exposed canalis quadratosquamosootoccipitalis is seen on the Bonn specimen and the cast of one of the missing Ballerstedt specimens (BMNH R5259). An examination of the holotype of *G. simus* reveals that, on the left side of the skull table, the slab and counter slab have been split along a horizontal plane that dissects the canalis quadratosquamosootoccipitalis. As a result, on the counter slab, as in the German specimens, it is possible to see that neither the lamina ventrolateralis of the squamosal nor the processus paroccipitalis contacted the dorsal surface of the quadrate caudal to the recessus oticus, and that the resulting sulcus is partially filled by sediment (Text-fig. 12). A longitudinal sulcus on the quadrate, which forms a causal continuation of the sulcus quadratosquamosootoccipitalis, is also apparent. A less laterally extensive processus paroccipitalis is also seen in *Hylaeochampsa vectiania* (Clark and Norell 1992) and many thallatosuchians, for example *Pelagosaurus typus* (illustrated by Koken 1887, p. 409, fig. 30a). However, in none of these forms is the canalis exposed laterally: in *P. typus* it is enclosed by a dorsal process of the otoccipital, and in *H. vectiania* by the lamina ventrolateralis of the squamosal. Unfortunately, the occipital and otic regions of many other Mesozoic crocodilians are poorly understood.

All crocodilians that we have examined thus far possess a fenestra premaxillaris. Koken (1896), illustrated and commented on the absence of this feature on the fragment of rostrum maxillae that he referred to '*G. pugnax*'. This is also clearly visible on IMGPGö 741-6 and the Bonn specimen. Although not commented upon before, the holotype of *G. simus* also lacks a fenestra premaxillaris (Text-fig. 4). Furthermore, as in the German specimens, in its place there is a small, diamond-shaped fossa premaxillaris, located just rostral to the ventral suture between the premaxillae and maxillae within the vestibulum nasi. Buscalioni and Sanz (1990) noted the extreme rostral position of the ventral suture between the premaxillae and maxillae in some American species of *Goniopholis*. This feature is apparent in *G. lucasii* (AMNH 5782), *G. stovalli* (OMNH 2392 and OMNH 2322) and *G. gilmorei* (CM 1339), and also appears to account for a correlated reduction in the size of the fenestra premaxillaris in these taxa (in *G. stovalli* there are two fenestrae, separated by a 3–4 mm broad septum), although in none of these taxa is the fenestra premaxillaris absent.

In comparison with other species of *Goniopholis*, in *G. simus* and the German *Goniopholis* material external sculpture is noticeably reduced on the nasal and maxilla, whilst the majority of other cranial bones are heavily sculptured with deep, circular pits, reticulations and ridges. Although differences in the size of sculpture pits can occur in living crocodilian taxa as a result of dietary deficiencies (C. A. Brochu, pers. comm. 1994), we are not aware of any cases where the actual pattern of pitting shows much variation.

Gomani (1997) illustrated, but did not comment upon, a foramen squamosootoccipitale on a specimen of *Malawisuchus mwakasyungutiensis* from the Lower Cretaceous of Malawi. Although this foramen is in the same position as that seen on the Bonn specimen and two of the Ballerstedt skulls (IMGPGö 741-6 and GPIMü Pr. 280), the absence of a foramen between the supraoccipital, otoccipital and squamosal in *M. mwakasyungutiensis* suggests that this is the foramen posttemporale, but in a more lateral position. Unfortunately, due to the poor preservation of the occiput, it cannot be determined whether such a foramen was present on the holotype of *G. simus*. In any case, the presence of a foramen squamosootoccipitale in addition to a foramen posttemporale in the German *Goniopholis* would appear to be unique among crocodilians. Considering its position and the lateral exposure of the canalis quadratosquamosootoccipitalis, it seems likely that this foramen represents the caudal opening of a subsidiary canal, which may have housed those structures that normally passed through the enclosed canalis quadratosquamosootoccipitalis in other species of *Goniopholis*.

Among the taxa referred to Goniopholididae, a fenestra mandibulae externa has only been described in *Eutretauranosuchus delfsi* (Mook 1967) and species of *Sunosuchus* (Young 1948; Buffetaut and Ingavat 1980; Buffetaut 1986*a*). This feature is clearly visible on both the Bonn specimen and a cast of one of the missing Ballerstedt specimens (BMNH R5260). Unfortunately, no mandibular material was associated with the holotype of *G. simus*. Nevertheless, another specimen, BMNH R5814, a partial skull from a quarry at Herston, near Swanage, Dorset, which can be referred to *G. simus* on the morphology of the interorbital plate (discussed above), does show



TEXT-FIG. 12. *Goniopholis simus* (Owen, 1878); BMNH 41098; drawing of the left rear corner of skull. Hatched areas represent broken bone and speckled areas matrix. Areas in grey shown on the inset diagram in the upper lefthand corner represent those surfaces of matrix endocasts that preserve bony impressions (illustrated on the main drawing). Scale bar represents 50 mm.

evidence of this fenestra, as does the holotype of *G. crassidens* (BMNH 3798) from Swanage; both specimens coming from either the 'Middle' or 'Upper' Purbeck Group. As to whether *G. crassidens* is distinct from *G. simus* cannot be determined until further examination and preparation of the

former holotype is completed. At present, comparisons between this specimen and material that can be referred to *G. simus* are limited to a second smaller slab that preserves an impression of skull table (Hooley 1907). However, the direct association of this slab with the main slab is still uncertain. Furthermore, we fail to see how Hooley (1907) was able to refer material from the Lower Aptian of the Isle of Wight (BMNH R3876) to this species based only on comparison with this specimen, which, in its current state of preparation, appears undiagnostic.

Although palpebral ossifications have never been described for any species of *Goniopholis*, our comparisons reveal that a single palpebral is present in *G. lucasii* (AMNH 5782), a specimen referred to *G. simus* from Bernissart (IRSNB R1537) and an undescribed goniopholidid from the Lower Cretaceous of Arkansas (TMM 41881-1). According to the figure published by Hulke (1878), the skull of a goniopholidid from the private collection of Mr Willett, may also have possessed a single palpebral. This bone is around the same size as the palpebral on the Bonn specimen. Unfortunately, the Willet specimen has thus far not been located, so further verification of the presence/absence of a palpebral is not possible. As first noted by Clark (1986), the type specimen of *Nannosuchus gracilidens* has what appears to be two palpebral ossifications in the orbit (Owen 1879, p. 10, pl. 3, fig. 1): a large bone, slightly smaller than the rostral palpebral of protosuchians, on the dorsomedial edge of the orbit, and possibly a second, smaller bone caudal to this in contact with the postorbital. In light of these observations, it would appear that palpebral ossifications are ubiquitous among goniopholidids, and that the taxonomic significance of this feature that has been stressed by previous authors, for example Clark (1986), may be unfounded.

Based on the peculiar morphology of the interorbital plate and otic region, the absence of a fenestra premaxillaris and the reduction of external sculpture on the maxillae and nasals, we refer the Bonn specimen and the skulls from the Ballerstedt Collection to *G. simus* Owen. Due to the outstanding preservation of the German specimens, we do not consider the fact that palpebral ossifications and a foramen squamosootoccipitale are unknown for the holotype of *G. simus* to be sufficiently significant to warrant non-referral of the German material to this species. The future collection of well-preserved material may verify this assumption.

The status of 'Goniopholis pugnax' *and* 'Goniopholis minor'

Koken (1887) used some characteristics of the dentition to distinguish '*G. pugnax*' from the other species of *Goniopholis* known at that time. According to Koken (1887), the teeth of '*G. pugnax*' are generally more robust than those of *G. simus* (the holotype) and in particular those of *G. tenuidens*. As a result, he noted that the vertical striations, often considered characteristic of the teeth of *Goniopholis* (following Owen 1841, 1878), are less closely spaced in '*G. pugnax*'. Koken also noted that on the lingual side of the teeth of '*G. pugnax*' there are approximately 22 vertical striations, whereas in *G. tenuidens* there are only 12. Koken (1887) used only size to differentiate between '*G. minor*' and '*G. pugnax*', specimens of the former being much smaller than those the latter.

Referring to Koken's original diagnosis for '*G. pugnax*', we have found that, as in living crocodilian taxa, dental characters such as the number of vertical striations are extremely variable for *Goniopholis*, and we agree with Hooley (1907, p. 53) that such features are insufficient to differentiate between species. Furthermore, we can find no additional characters in the description or illustrations provided by Koken (1887) that would allow '*G. pugnax*' to be differentiated from other species of *Goniopholis*. For taxonomic purposes Koken's (1887) definition is inadequate, and we propose that '*G. pugnax*' be considered a *nomen dubium*. Later referral of material to this taxon, for example, the fragments of rostrum maxillae and dentary described by Koken (1896), based purely on the characteristics of the dentition, should be considered invalid.

'*Goniopholis minor*' is even more poorly defined, and we can find no discrete characters in the definition of Koken (1887) that would allow this species to be differentiated from other Mesozoic crocodilians, let alone other species of *Goniopholis*. We therefore propose that this species should also be considered a *nomen dubium*.

The status of some other European goniopholidids

The two skeletons from Bernissart, Belgium, referred to *G. simus* by Dollo (1883), have never been described in detail, as Dollo's paper was intended only as a preliminary work. Although beyond the scope of the present paper, a preliminary examination of the skull and mandible of one of these skeletons (IRSNB R1537) – the other (IRSNB R1539) consisting of the postcranium only – indicates that several differences exist when compared with the English and German material of *G. simus*. For example, a fenestra mandibularis externa is absent, and the prefrontal does not contact the postorbital, such that the frontal contributes to the orbital margin. The outline of the skull table is also markedly different, due to the presence of a spine-like processus rostralis of the postorbital, forming the laterodorsal margin of the orbit, and a smooth, tuber caudolaterale of the squamosal. The fossa maxillaris is almost round in outline and does not have any internal divisions. A crista interorbitalis is also absent and the entire dorsal surface of the rostrum maxillae is uniformly sculptured with small, 2–3 mm wide pits (Hooley 1907). Thus, we consider that Dollo's (1883) assignment of this material to *G. simus* was incorrect, and that it most probably represents a distinct species of *Goniopholis*.

The material from Nehden, western Germany, tentatively identified as *Goniopholis* sp. by Norman (1987), is of approximately the same geological age as the Bernissart material (Norman and Weishampel 1990), although it is too fragmentary for detailed comparison with other European *Goniopholis*. Based on the form of the osteoderms from the paravertebral shield and vertebrae, we accept Norman's (1987) placement of this material in *Goniopholis*, but the species is indeterminate.

Buffetaut (1986*b*) described a left maxilla and premaxilla from the upper Tithonian of the Boulonnais, northern France (MHNBP 5.205), and based on comparison with drawings of the fragment of rostrum maxillae described by Koken (1896), assigned this specimen to '*G.* cf. *pugnax*'. We have not been able to examine this specimen, and although it is too incomplete to be referred confidently to *G. simus*, we agree with Buffetaut (1986*b*) that its overall proportions and the sequence of alveolar enlargement indicate that it is very similar to *Goniopholis* material from Germany, referred here to *G. simus*. Amending Buffetaut's (1986*b*) assignment of this specimen to *G.* cf. *pugnax*, in light of the present study we place it in *G.* cf. *simus*.

A small collection of postcranial material from the Isle of Wight and Ecclesbourne, Sussex, was assigned to *G. minor* by Lydekker (1890). The Isle of Wight material (BMNH R214) consists of osteoderms from the paravertebral shield, vertebrae, a coracoid, an articular and some fragmentary limb elements. A partial femur that also shares this number may belong to a small theropod dinosaur. The Ecclesbourne material (BMNH R608) consists of vertebrae and a femur. Excluding the osteoderms and a cervical vertebra, all of this material represents individuals probably no more than 1 m long, and it is likely that it was referred to *G. minor* only on the basis of its size. Pending further comparisons, we place this material in Crocodilia *incertae sedis*.

Biogeographical implications

Reference to some German Early Cretaceous strata as 'Wealden', for example by Dunker (1843–44), Koken (1883, 1886, 1887, 1896) and Edinger (1938), is misleading, since the majority of sediments are derived neither from the same basin, nor are they of an equivalent age to those of the English type sequence (Allen 1955, 1967; Kemper 1973*a*; Pelzer and Wilde 1987). During the Early Cretaceous two major depositional basins existed in what are now the Netherlands and north-western Germany: the West Netherlands Basin and the Niedersachsen [Lower Saxony] Basin (Allen 1967; Kemper 1973*a*; Ziegler 1990; Allen and Wimbledon 1991) (Text-fig. 1). Although the Niedersachsen Basin is dominated by muddy basin facies, the uppermost units contain some marginal limestones and fluvial-alluvial sandstones, accounting for the close resemblance to the Wealden of the English Weald (Allen 1962, 1967; Kemper 1973*a*, 1973*b*; Pelzer and Wilde 1987). However, unlike the type sequence of the Wealden, development of the Niedersachsen Basin largely

occurred during the Berriasian, and only the uppermost units (those of the Osterwald Member) are Valanginian (Allen 1955, 1967; Wolberg 1959; Kemper *et al.* 1981; Hoedemaeker 1987). Following the terminology of Clements (1993), sediments from the Bückeburg Member are now equated with those of the 'Middle' and 'Upper' Purbeck of the Lulworth and Durlston formations of the Purbeck Group (Martin 1940; Anderson 1962; Burger 1966; Kemper 1973*a*; Davey 1979; Herngreen *et al.* 1980; Allen and Wimbledon 1991).

The recognition of *G. simus* in the Niedersachsen Basin of north-western Germany during the Berriasian provides the first clear evidence of interchange between the non-marine vertebrate faunas of this region and those of the Wessex-Weald Basin of southern England. Up until now there has been little evidence of this, although this may have been due largely to a much less extensive knowledge of the German fauna, possibly as a result of the unusual preservation of much of the fossil material as natural moulds. Among the dinosaur taxa, material referred to the theropod *Altispinax* (*Megalosaurus*) *dunkeri* from both regions has recently been considered indeterminate by Molnar (1990). An isolated tooth (Dunker 1843–44), which was, unfortunately, lost, and a humerus, were assigned to *Iguanodon* by Koken (1887), but further comparisons with *I. mantelli* and *I. bernissartensis*, both known from the Wessex-Weald Basin, have proven inconclusive (Probst and Windolf 1993). Nevertheless, numerous three-toed footprints of the type usually attributed to *Iguanodon* in England (Benton and Spencer 1995 and references therein) have been found in the Obernkirchen Sandstone near Bückeburg (Probst and Windolf 1993). Other trackways also point to the existence of similar sized sauropods in each region: *Rotundichnus muenchehagensis*, from the upper Berriasian of Münchehagen (Hendricks 1981), and an as yet un-named ichnite from the Isle of Purbeck (Ensom 1987). Further track-ways in the Obernkirchen Sandstone, including those of a large carnosaur, *Bückeburgichnus maximus* (Kuhn 1958), and a nodosaur, *Metatetrapous valdensis* (Kuhn 1958), do not appear to be attributable to any ichnites or taxa based on skeletal material from the Berriasian Wessex-Weald Basin (Probst and Windolf 1993). The enigmatic ornithischian *Stenopelix valdenis* (Schmidt 1969; Sues and Galton 1982) and material referable to the pleurodire turtle *Plesiochelys*, both from the Obernkirchen Sandstone, are also not known from England.

The two other crocodilians from the Obernkirchen Sandstone, *Pholidosaurus meyeri* and *P. schauburgensis*, also appear remarkably similar to their counterparts in the Wessex-Weald basin, *P. decipiens* and *P. laevis*. Contrary to Andrews (1913), the only difference between the latter three forms relates to the size and density of sculpture pits on the skull table, a trait that often shows a high degree of intra-specific variation among extant crocodilian taxa (C. A. Brochu, pers. comm. 1994). It is likely that future work may show that this material can be referred to a single species. On the other hand, *Pholidosaurus meyeri*, originally based on a natural mould of a skull from Bückeburg, and described in detail by Dunker (1843–44), has been recorded from the lower Barremian of the Wessex Formation of Brook Bay, Isle of Wight (Lydekker 1887). However, Lydekker's assignment of this material (a partial skull; BMNH 28966) to *P. meyeri* is questionable, being based only on a comparison with Dunker's drawing (Dunker 1844, pl. 20, p. 74), which is not particularly informative. Our examination of Isle of Wight *Pholidosaurus* suggests that it may be distinct at the genus level, but, as with the other material, it needs to be re-examined and described in detail.

The presence of at least one, and perhaps even two, non-marine crocodilians in both the Wessex-Weald and Niedersachsen basins affords evidence of faunal continuity between these two regions during the Berriasian, and suggests that large-scale oceanic or orogenic separation was unlikely. The palaeogeographical reconstructions of Allen (1981) and Ziegler (1990) indicate that the basins were separated by a coastal expanse of approximately 500–700 km, and a shorter distance overland by the peneplained remains of the Variscan orogenic belt, which rose only a few hundred metres at most above sea level. Thus, for a crocodilian, dispersal could easily have occurred either along the coast or through inland fluvial systems.

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REFERENCES

ALLEN, P. 1955. Age of the Wealden in north-western Europe. *Geological Magazine*, **92**, 265–281.

—— 1962. The Hasting Beds deltas: recent progress and Easter field trip meeting report. *Proceedings of the Geologists' Association*, **73**, 219–243.

—— 1967. Origin of the Hastings facies in north-western Europe. *Proceedings of the Geologists' Association*, **78**, 27–105.

—— 1981. Pursuit of Wealden models. *Journal of the Geological Society, London*, **138**, 375–405.

—— and WIMBLEDON, W. A. 1991. Correlation of NW European Purbeck–Wealden (nonmarine Lower Cretaceous) as seen from the English type areas. *Cretaceous Research*, **12**, 511–526.

ANDERSON, F. W. 1962. Correlation of the Upper Purbeck Beds of England with the German Wealden. *Liverpool and Manchester Geological Journal*, **3**, 21–32.

ANDREWS, C. W. 1913. On the skull and part of the skeleton of a crocodile from the Middle Purbeck of Swanage, with the description of a species (*Pholidosaurus laevis*), and a note on the skull of *Hyalaeochampsa*. *Annals and Magazine of Natural History*, **8**, 485–494.

BAUMEL, J. J. and WITMER, L. M. 1993. Osteologica. 45–132. *In* BAUMEL, J. J. (ed.). *Handbook of avian anatomy: Nomina Anatomica Avium*. 2nd Edition. Nuttall Ornithological Society, Cambridge, Massachusetts, 779 pp.

BENTON, M. J. and SPENCER, P. S. 1995. *Fossil reptiles of Great Britain*. Chapman and Hall, London, 386 pp.

BUFFETAUT, E. 1982. Radiation évolutive, paléoécologie et biogéographie des Crocodiliens mésosuchiens. *Mémoires de la Société Géologique de France*, **60** (142), 1–88.

—— 1986*a*. Remarks on the anatomy and systematic position of *Sunosuchus miaoi* Young, 1948, a mesosuchian crocodilian from the Mesozoic of Gansu, China. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **11**, 641–647.

—— 1986*b*. Une Machoire de *Goniopholis* (Crocodylia, Meosuchia) dans le Portlandien supérieur du Boulonnais. *Mémoires de la Société Académique du Boulonnais*, **1**, 64–71.

—— and INGAVAT, R. 1980. A new crocodilian from the Jurassic of Thailand, *Sunosuchus thailandicus*, n. sp. (Mesosuchia, Goniopholididae), and the paleogeographic history of South East-Asia in the Mesozoic. *Géobios*, **13**, 879–889.

—— POUIT, D., RIGOLLET, L. and ARCHAMBEAU, J.-P. 1989. Poissons et reptiles continentaux du Purbeckien de la région de Cognac (Charente). *Bulletin de la Société géologique de France*, **5**, 1065–1069.

BURGER, D. 1966. Palynology of uppermost Jurassic and lowermost Cretaceous strata in the eastern Netherlands. *Geologische Medelingen*, **35**, 209–276.

BUSCALIONI, A. D. and SANZ, J. L. 1987*a*. Cocodrilos del Cretacio inferior de Galve (Teruel, España). *Estudios Geológicos, volumen extraodinario Galve-Tremp*, 23–43.

—— 1987*b*. Lista faunística de los Vertebrados de Galve (Teruel). *Estudios Geológicos, volumen extraordinario Galve-Tremp*, 65–67.

—— 1990. The small crocodile *Bernissartia fagesii* from the Lower Cretaceous of Galve (Teruel, Spain). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **60**, 129–150.

CLARK, J. M. 1986. Phylogenetic relationships of the crocodylomorph archosaurs. Unpublished Ph.D. thesis, Department of Anatomy, University of Chicago, Illinois.

—— and NORELL, M. A. 1992. The Early Cretaceous crocodylomorph *Hylaeochampsa vectiana* from the Wealden of the Isle of Wight. *American Museum Novitates*, **3032**, 1–19.

CLEMENTS, R. G. 1993. Type-section of the Purbeck Limestone Group, Durlston Bay, Swanage, Dorset. *Proceedings of the Dorset Natural History and Archaeological Society*, **114**, 181–206.

COPE, E. D. 1875. Check-list of North American Batrachia and Reptilia with a systematic list of the higher groups and an essay on geographical distribution based on the specimens in the U.S. National Museum. *Bulletin of the United States National Museum*, **1**, 1–104.

CUNY, G., BUFFETAUT, E., CAPPETTA, H., MARTIN, M., MAZIN, J. M. and ROSE, J. M. 1991. Nouveaux restes de Vertébrés du Jurassique terminal due Boulonnais (Nord de la France). *Neues Jahrbuch für Geologie and Paläontologie, Abhandlungen*, **180**, 323–347.

DAVEY, J. R. 1979. The stratigraphic distribution of dinocysts in the Portlandian (latest Jurassic) to Barremian (Early Cretaceous) of northwest Europe. *American Association of Stratigraphic Palynologists, Contributions Series*, **5B**, 49–81.

DOLLO, L. 1883. Première note sur les crocodiliens de Bernissart. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **2**, 309–338.

DUNKER, W. 1843–44. Über den norddeutschen sogenannten Wälderthon und dessen Versteinerungen. *Programm der höheren Gewerbschule in Cassel*, **1843–44**, 44.

EDINGER, T. 1938. Über Steinkerne von Hirn- und Ohr-höhlen der Mesosuchier *Goniopholis* und *Pholidosaurus* aus dem Bückeburger Wealden. *Acta Zoologie (Stockholm)*, **19**, 467–505.

ENSOM, P. C. 1987. A remarkable new vertebrate site in the Purbeck Limestone Formation of the Isle of Purbeck. *Proceedings of the Dorset Natural History and Archaeological Society*, **108**, 206.

FREY, E. 1988. Anatomie des Körperstammes von *Alligator mississippiensis* Daudin. *Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie)*, **424**, 1–106.

GMELIN, C. 1788. *Linnei Systema naturae*. 13th Edition. Leipzig, 1108 pp.

GOMANI, E. M. 1997. A crocodyliform from the Early Cretaceous Dinosaur Beds, northern Malawi. *Journal of Vertebrate Paleontology*, **17**, 280–294.

HALL, P. M. and PORTIER, K. M. 1994. Cranial morphology of New Guinea crocodiles (*Crocodylus novaeguineae*): ontogenetic variation in relative growth of the skull and an assessment of its utility as a predictor of the sex and size of individuals. *Herpetological Monographs*, **8**, 203–225.

HENDRICKS, A. 1981. Die saurierfährte von Münchehagen bei Rehburg-Loccum (Nordwest-Deutschland). *Abhandlungen des Landesmuseums für Naturkunde Münster*, **43**, 1–22.

HERNGREEN, G. F. W., HOEKEN-KLINKENBERG, P. M. J. VAN and BOER, K. F. DE 1980. Some remarks on selected palynomorphs near the Jurassic–Cretaceous boundary in the Netherlands. *IV International Palynological Conference 1976–1977*, Lucknow, 357–367.

HOEDEMAEKER, P. J. 1987. Correlation possibilities around the Jurassic/Cretaceous boundary. *Scripta Geologica*, **84**, 1–64.

HOOLEY, R. W. 1907. On the skull and greater portion of the skeleton of *Goniopholis crassidens* from the Wealden Shales of Atherfield (Isle of Wight). *Quarterly Journal of the Geological Society, London*, **63**, 50–63.

HUCKRIEDE, R. 1982. Die unterkretazische Karsthöhlen-Füllung von Nehden im Sauerland. 1. Geologische, paläozoologische und paläobotanische Befunde und Datierung. *Geologica et Palaeontologica*, **16**, 183–242.

HULKE, J. W. 1878. Note on two skulls from the Wealden and Purbeck formations indicating a new subgroup of Crocodilia. *Quarterly Journal of the Geological Society, London*, **34**, 377–382.

IORDANSKY, N. N. 1973. The skull of the Crocodilia. 201–262. *In* GANS, C. and PARSONS, T. S. (eds). *Biology of the Reptilia*, Academic Press, London, 539 pp.

JONET, S. 1981. Contribution à l'étude des Vertébrés du Crétacé portugais et spécialement du Cénomanien de l'Estremadure. *Commentares Servicio Geológico Portugal*, **67**, 191–3306.

KEMPER, E. 1973*a*. Das Berrias tiefe (Unterkreide) in NW-Deutschland. *Geologisches Jahrbuch*, **A9**, 47–67.

—— 1973*b*. The Valanginian and Hauterivian stages in northwest Germany. 327–344. *In* CASEY, R. and RAWSON, P. F. (eds). The boreal Lower Cretaceous. *Geological Journal Special Issue*, **5**, 1–448.

—— RAWSON, P. F. and THIEULOY, J. P. 1981. Ammonites of Tethyan ancestry in the early Lower Cretaceous of north-west Europe. *Palaeontology*, **24**, 251–311.

KOKEN, E. 1883. Die Reptilien der norddeutschen unteren Kreide. *Zeitschrift der Deutschen geologischen Gesellschaft*, **35**, 735–827.

—— 1886. Vorkommen fossiler Crocodiliden in den Wealdenbildungen Nord-deutschlands und über die Systematik der mesozoischen Crocodiliden. *Zeitschrift der Deutschen geologischen Gesellschaft*, **38**, 664–670.

—— 1887. Die Dinosaurier, Crocodiliden und Sauropterygier des norddeutschen Wealden. *Palaeontologische Abhandlungen*, **3**, 309–419.

—— 1896. Die Reptilien des norddeutschen Wealden. *Palaeontologische Abhandlungen*, **3**, 119–126.

KUHN, O. 1958. *Die Fährten der vorzeitlichen Amphibien und Reptilien*. Verlagshaus Meisenbach, Bamberg, 64 pp.

LYDEKKER, R. 1887. Note on the Hordwell and other crocodilians. *Geological Magazine*, **3**, 307–312.

—— 1890. *Catalogue of the Fossil Reptilia and Amphibia in the British Museum (Natural History). Part IV*. Trustees of the British Museum (Natural History), London, 295 pp.

MARTIN, G. P. R. 1940. Ostracoden des norddeutschen Purbeck und Wealden. *Senckenbergiana*, **22**, 275–361.

MOLNAR, R. E. 1990. Problematic Theropoda: 'carnosaurs'. 306–317. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 733 pp.

MONTEIRO, L. R., CAVALCANTI, M. J. and SOMMER, H. J. S. III 1997. Comparative ontogenetic shape changes in the skull of *Camain* species (Crocodylia, Alligatoridae). *Journal of Morphology*, **231**, 53–62.

MOOK, C. C. 1967. Preliminary description of a new goniopholid crocodilian. *Kirtlandia*, **2**, 1–10.

NOPSCA, F. von 1928. Palaeontological notes on reptiles. 7. On the classification of the Crocodilia. *Geologica Hungaria, Series Palaeonotologica (Budapest)*, **1** (1), 75–84, pl. 4.

NORMAN, D. B. 1987. A mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West Germany. *Proceedings of the Royal Society of London, Series B*, **230**, 215–255.

—— and WEISHAMPEL, D. B. 1990. Iguanodontidae and related ornithopods. 510–533. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. *The Dinosauria*. University of California Press, Berkeley, 733 pp.

OEKENTORP, K. von 1984. Die Saurierfundstelle Brilon-Nehden (Rheinisches Schiefergebirge) und das Alter der Verkarstung. *Kölner Geographische Arbeiten*, **45**, 293–315.

ORTEGA, F., MORATALLA, J. J., BUSCALIONI, A. D., SANZ, J. L., JIMÉNEZ, S. and VALBUENA, J. 1996. Sobre la presencia de un cocodrilo fósil (Crocodylomorpha: Neosuchia: *Goniopholis* sp.) en la Cuenca de Camerios (Cretăcico inferior: Vadillos-San Román de Cameros, La Rioja). *Zubia*, **14**, 113–120.

OWEN, R. 1841. On British fossil reptiles. *Report of the British Association for the Advancement of Science*, **11**, 60–204.

—— 1849–84. *A history of British fossil reptiles*. Cassell and Company Limited, London, 1625 pp.

—— 1878. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Supplement No VIII. Crocodilia (*Goniopholis*, *Petrosuchus* and *Suchosaurus*). *Monograph of the Palaeontographical Society*, **32** (149), 1–15, pls 1–6.

—— 1879. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Supplement No IX. Crocodilia (*Goniopholis*, *Brachydectes*, *Nannosuchus*, *Theriosuchus* and *Nuthetes*). *Monograph of the Palaeontographical Society*, **33** (155), 1–15, pls 1–4.

PELZER, G. 1988. Sedimentologie und Palynologie der Wealden-Fazies in Hannoverschen Bergland. Unpublished Ph.D thesis, Matthematischer-Naturwissenschaftlicher Fachbereich, Universität Gottingen.

—— and WILDE, V. 1987. Klimatische Tendenzen während der Ablagerung der Wealden-Fazies in Nordwest Europa. *Geologisches Jahrbuch*, **A96**, 239–263.

PROBST, E. and WINDOLF, R. 1993. *Dinosaurier in Deutschland*. Bertelsmann, Munich, 316 pp.

RAUHE, M. 1993. Postkranialskelett und Taxonomie des Alligatoriden *Allognathosuchus haupti* (Mitteleozän von Messel, Darmstadt) unter Berücksichtigung der Anatomie und Altervariationen von *Allognathosuchus* cf. *haupti*. Unpublished Ph.D. thesis, Johannes Gutenberg Universität Mainz.

ROSSMAN, T. 1996. Anatomische konstruktionsmorphologische und systematische Bearbeitung, sowie palökologische Interpretation des aberranten Krokodiliers *Pristichampsus rollantii* (Grey, 1831) Gervais, 1853 aus dem Tertiär von Europa und Nordamerika. Unpublished Ph.D. thesis, Johannes Gutenberg Universität Mainz.

SALISBURY, S. W. and WILLIS, P. M. A. 1996. A new crocodylian from the Early Eocene of southeastern Queensland and preliminary investigation of the phylogenetic relationships of crocodyloids. *Alcheringa*, **20**, 179–226.

SCHMIDT, H. 1969. *Stenopelix valdensis* H. v. Meyer, der kleine Dinosaurier des norddeutschen Wealden. *Paläontologische Zeitschrift*, **43**, 194–198.

STEEL, R. 1989. *Crocodiles*. Christopher Helm, London, 198 pp.

SUES, H.-D. and GALTON, P. 1982. The systematic position of *Stenopelix valdensis* (Reptilia: Ornithischia) from the Wealden of north-western Germany. *Palaeontographica, Abteilung A*, **178**, 183–190.

WEBB, J. W. and MESSEL, H. 1978. Morphometric analysis of *Crocodylus porosus* from the north coast of Arnhem Land, northern Australia. *Australian Journal of Zoology*, **26**, 1–27.

WETTSTEIN, O. von 1937–54. Crocodilia. *Handbuch der Zoologie*, 7, **1** (2) 236–424.

WITMER, L. M. 1995. Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. *Journal of Morphology*, **225**, 269–327.

WIMAN, C. 1931. *Goniopholis kirtlandicus* n. sp. aus der oberen Kreide in New Mexico. *Bulletin of the Geological Institute of Upsala*, **23**, 181–190, pls 4–5.

WOLBERG, J. 1959. Die Cyprideen des NW-deutschen Wealden. *Senckenbergiana Lethaea*, **40**, 223–315.

YOUNG, C. C. 1948. Fossil crocodiles in China with notes on dinosaurian remains associated with the Kansu crocodiles. *Bulletin of the Geological Society of China*, **28**, 255–288.

ZIEGLER, P. A. 1990. *Geological atlas of western and central Europe*. Shell Internationale Petroleum, Maatschappij BV, 239 pp.

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APPENDIX: ABBREVIATIONS USED IN THE TEXT-FIGURES

alv	alveolus maxillaris
ang	os angulare
art	os articulare
bo	os basioccipitale
Can meck	canalis meckeli
Cav nas	cavitus nasalis
Cond occ	condylus occipitalis
d	os dentale
Fe it	fenestra infratemporalis
Fe man ext	fenestra mandibulae externa
Fe subor	fenestra suborbitalis
For m	foramen magnum
For pot	foramen posttemporale
For sqot	foramen squamosootoccipitale
For st ex	foramen supratemporale externum
Fos m	fossa maxillaris
fr	os frontale
frag	indeterminate fragment of bone
j	os jugale
l	os lacrimale
max	os maxillare
n	os nasale
N	foramen naris externum
Or	aditus orbitae
ot	os otoccipitale
pal	os palatinum
palp	os palpebrale
par	os parietale
pmx	os premaxillare
po	os postorbitale
prf	os prefrontale
q	os quadratum
qj	os quadratojugale
Rec cavico	recessus caviconchalis
Rec ot ext	recessus oticus externus
so	os supraoccipitale
spl	os spleniale
sq	os squamosum
Sulc pmx	sulcus premaxillaris
Sulc q	sulcus quadratus
Sulc qsqot	sulcus quadratosquamosootoccipitalis
sup	os supraangulare
vest	vestibulum nasi

AN ENIGMATIC NEW CROCODILE FROM THE UPPER CRETACEOUS OF MADAGASCAR

by GREGORY A. BUCKLEY *and* CHRISTOPHER A. BROCHU

ABSTRACT. Material of a new mesoeucrocodylian, *Mahajangasuchus insignis* gen. et sp. nov. from the Late Cretaceous Maevarano Formation, Mahajanga Basin, of north-western Madagascar includes a complete left and partial right mandible, several isolated teeth, much of the postcranial skeleton, and numerous osteoderms. *M. insignis* differs from all known non-crocodylian crocodyliforms in possessing a broad, rounded anterior portion of the dentary with a very short mandibular symphysis, superficially resembling the condition found in nettosuchid crocodylians. Many features of the postcranial skeleton are concordant with those of other known Gondwanan crocodyliforms, whilst features of the teeth and mandible indicate close affinity with *Trematochampsa* and the South American peirosaurids. Indeed, a weakly supported sister-group relationship between *M. insignis* and Peirosauridae raises interesting questions regarding the biogeographical history of Madagascar. The potential non-monophyly of the trematochampsids, the sparse material by which they are known, and several unique features of *M. insignis*, combine to preclude assignment of *M. insignis* to a particular mesoeucrocodylian lineage.

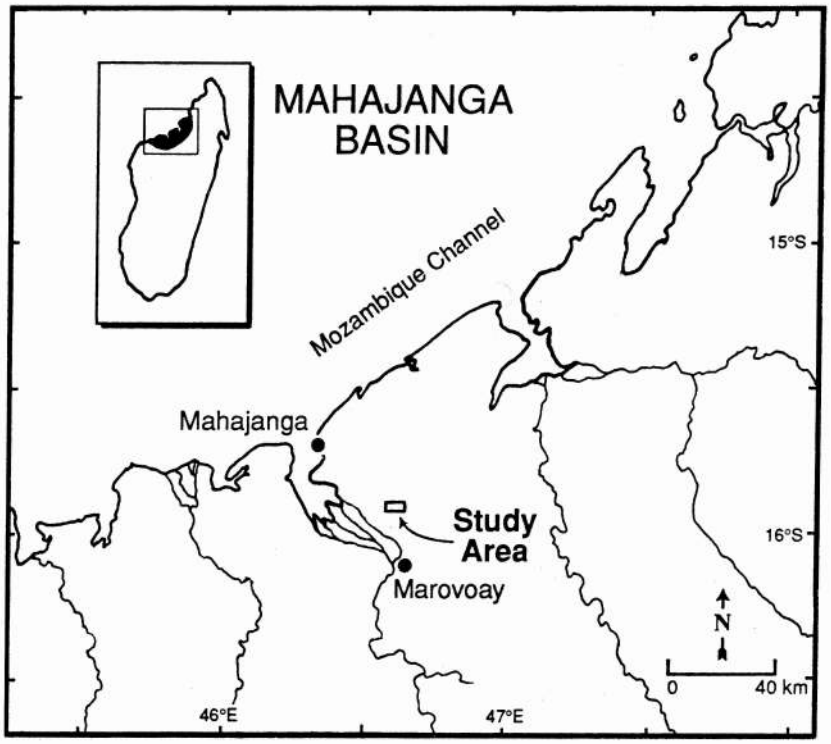
THE Mahajanga Basin of north-western Madagascar has long been known as a source of Late Cretaceous vertebrate fossils. Beginning more than a century ago, brief French, Madagascan, and Japanese expeditions discovered and described a number of Late Cretaceous taxa from terrestrial freshwater deposits of the Maevarano Formation (e.g. Boule 1896; Depéret 1896*a*, 1896*b*; Russell *et al.* 1976; Obata and Kanie 1977). Study of Cretaceous Madagascan vertebrates suggested strong faunal similarities with older African faunas (Buffetaut and Taquet 1979; Buffetaut 1985) and contemporaneous South American and Indian faunas (Russell *et al.* 1976; Sues 1980), but the mostly fragmentary material collected by these expeditions provided few insights into the biogeographical origins of either the Cretaceous or modern Madagascan vertebrate assemblages.

More recent palaeontological fieldwork conducted by joint SUNY-Stony Brook/University of Antananarivo expeditions in the region (Text-fig. 1) has dramatically increased known diversity of the Late Cretaceous vertebrate fauna of Madagascar, quadrupling the number of known species. New discoveries include the first Late Cretaceous mammals known from Africa (Krause *et al.* 1994; Krause and Grine 1996), lepisosteid and other bony fishes (Gottfried and Krause 1994), frogs (Asher and Krause 1994), turtles, lizards, and snakes (Krause *et al.* 1997*a*). Among the more notable fossils recovered are remains of archosaurs, including the oldest known bird material from Africa (Forster *et al.* 1996*a*, 1996*b*), new material of titanosaurid sauropods (Sampson *et al.* 1996*a*), the theropod *Majungatholus* (Krause and Dodson 1994; Sampson *et al.* 1996*b*, 1996*c*, 1998), and a surprising diversity of crocodyliforms (Buckley and Brochu 1996).

Russell *et al.* (1976) noted three crocodyliform taxa from the Upper Cretaceous Maevarano Formation: a large 'mesosuchian' (based on amphicoelous vertebrae), an indeterminate eusuchian (based on procoelous vertebrae), and fragmentary remains of a smaller species. Buffetaut and Taquet (1979) described a large species of crocodyliform from the region, *Trematochampsa oblita*, on the basis of three fragments of a mandible. Recent field work has further expanded our knowledge of crocodyliforms in the Maevarano Formation vertebrate assemblage, revealing the presence of at least six and possibly seven species (Buckley and Brochu 1996), rendering crocodyliforms the most diverse component of the fauna.

Previously unrecognized crocodyliforms recovered from the Maevarano Formation since 1993

[Special Papers in Palaeontology, No. 60, 1999, pp. 149–175, 5 pls]

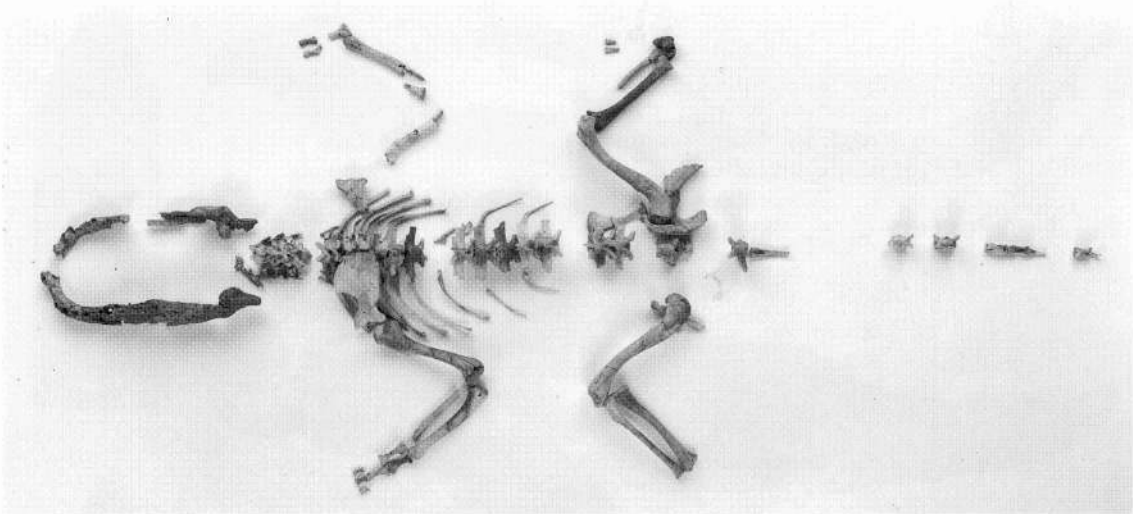


TEXT-FIG. 1. Map of the Mahajanga Basin, north-west Madagascar, showing the field area from which the skeleton of *Mahajangasuchus insignis* gen. et sp. nov. was recovered. Modified from Sampson *et al.* (1996*b*).

include a new species of the metasuchian *Araripesuchus*, a possible peirosaurid, a longirostrine form of uncertain affinities, one other species of indeterminate suborder, and the species described herein. Only *Araripesuchus* and the species described here are represented by fairly complete material, including postcranial remains. Remains of the other taxa are fragmentary, precluding a more definitive assessment of their affinities.

The material described here was discovered in 1995 and consists of a large portion of a disarticulated but associated postcranial skeleton, both mandibles, isolated teeth, and numerous osteoderms (Text-fig. 2). It was originally supposed that the specimen represented *T. oblita*, based primarily on the large size of the specimen, its ziphodont teeth, and fossa on the surangular for reception of a quadratojugal condyle, as well as numerous postcranial features concordant with those of metasuchian crocodyliforms in general (Buckley and Brochu 1996). Evaluation of the lower jaws, following preparation, indicates that although probably related to *T. oblita*, this is a previously unknown taxon.

'Trematochampsidae' is an enigmatic assemblage of deep-snouted ziphodont crocodyliforms from the Upper Cretaceous of Africa, South America, and Madagascar, and (questionably) the Cretaceous and Tertiary of Europe (Buffetaut 1974, 1982, 1985, 1988, 1989, 1991, 1994; Buffetaut and Taquet 1979; Chiappe 1988; Gasparini *et al.* 1991; Vasse 1995). The monophyly of this group has been disputed (Gasparini *et al.* 1991; Ortega *et al.* 1996), and the relationships of its various taxa are poorly known (Buffetaut 1982). Most described material consists of fragmentary cranial and mandibular material and, with the exception of *T. taqueti* (Buffetaut 1976), most 'trematochampsid' taxa are very poorly known. Examination of the postcranial skeleton of the new taxon reveals striking similarities to *T. taqueti* and other Gondwanan 'mesosuchian' taxa, such as *Araripesuchus* and *Uruguaysuchus*.



TEXT-FIG. 2. Photograph of partial skeleton of *Mahajangasuchus insignis* gen. et sp. nov., in dorsal view; UA 8654, holotype; ×0·06.

The palaeobiogeographical history of Madagascar has been difficult to reconstruct from the fossil record. Several taxa recovered by earlier expeditions to the Mahajanga Basin were known to have Gondwanan distributions, but closer faunal similarities to one particular landmass over others had not been established. The timing of the break-up of Gondwana and the isolation of Madagascar from other landmasses (particularly the Indian subcontinent and Antarctica) limit the number of probable (or possible) dispersal routes for Mesozoic faunal components reaching Madagascar. The new species described here provides an additional element to be considered in suggesting possible origins for the Late Cretaceous fauna of Madagascar. The biogeographical distributions of many of the faunal elements, including the species described here, suggest that vicariant origins may predominate.

Institutional abbreviation. UA, University of Antananarivo, Madagascar.

SYSTEMATIC PALAEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Hay, 1930
MESOEUCROCODYLIA Whetstone and Whybrow, 1983
Family *incertae sedis*

Genus MAHAJANGASUCHUS gen. nov.

Derivation of name. From the Mahajanga Basin, referring to the provenance of the type species.

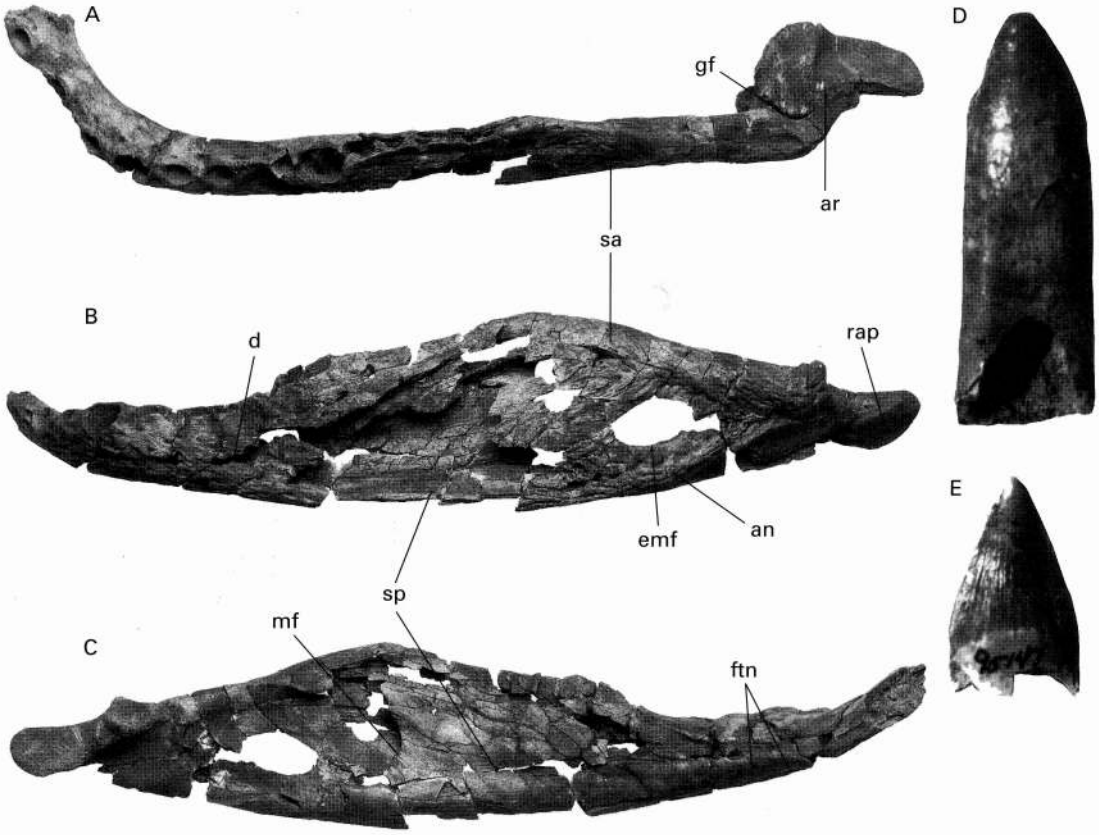
Type species. Mahajangasuchus insignis gen. et sp. nov.

Diagnosis. As for the type and only known species.

Mahajangasuchus insignis sp. nov.

Plates 1–5; Text-figures 2–3

Derivation of name. Latin: *insignis* (extraordinary, singular); referring to the morphology of the mandible as well as the preservation of the type material.



TEXT-FIG. 3. *Mahajangasuchus insignis* gen. et sp. nov.; UA 8654, holotype. Left mandibular ramus in A, dorsal, B, lateral, and C, medial views; ×0·25. D–E, isolated teeth; ×1·35. Abbreviations: an, angular; ar, articular; d, dentary; emf, external mandibular fossa; ftn, foramina for the ramus intermandibularis oralis of the trigeminal nerve; gf, glenoid fossa; mf, anterior margin of the Meckelian fossa; rap, retroarticular process; sa, surangular; sp, splenial.

Holotype. UA 8654, a skeleton including a nearly complete left mandible and anterior and posterior portions of a right mandible, partial postcranial remains, and numerous osteoderms.

Locality and Horizon. Approximately 1 km south-east of the village of Berivotra, near the top of the Upper Cretaceous (Campanian?), Maevarano Formation, Mahajanga Basin, north-west Madagascar. Exact locality coordinates are filed at the Field Museum of Natural History, Chicago.

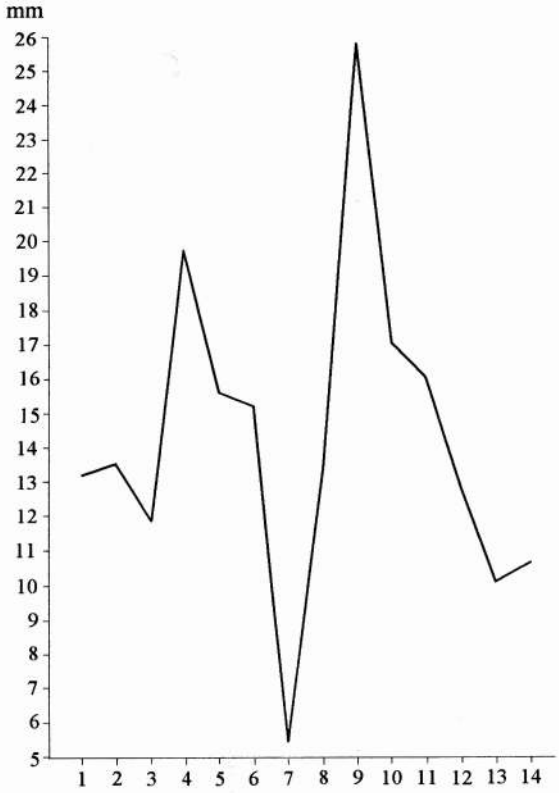
Diagnosis. A medium-sized to large, broad-snouted crocodyliform differing from known 'trematochampsids' in possessing a lower jaw with an extremely short mandibular symphysis extending posteriorly only to the posterior margin of the second alveolus, and a splenial that extends significantly onto the ventral surface of the dentary.

This species shares with *Trematochampsa oblita* and *T. taqueti* a deep fossa on the surangular, continuous with the glenoid fossa of the articular, for reception of a quadratojugal condyle. It shares with *Hamadasuchus rebouli* a dorsally arched dentary and surangular, enlarged fourth and ninth lower alveoli separated by a series of small alveoli from enlarged posterior alveoli, interalveolar distances in the posterior lower dentition reduced to only a few millimetres, and teeth laterally compressed with lanceolate crowns and serrated anterior and posterior carinae.

DESCRIPTION

Mandible

The mandible is represented by a nearly complete left ramus and an incomplete right ramus (Text-fig. 3A–C). The anterior portions of both dentaries are damaged, but small sutural remnants indicate that the break includes a small portion of the symphysis. The mandibular symphysis was apparently extremely short, extending only to the posterior margin of the second alveolus. There are 14 alveoli in the dentary, with the fourth and ninth significantly enlarged (Text-fig. 4). The first alveolus is



TEXT-FIG. 4. Lower alveolar pattern of *Mahajangasuchus insignis* gen. et sp. nov.; UA 8654, holotype. Anteroposterior diameters of alveoli (vertical scale) are plotted against the serial numbers of the alveoli (horizontal scale).

elevated above the level of the second. The lateral positions of the first four alveoli indicate that the teeth were moderately procumbent. The fifth through ninth alveoli are near the midline of the dentary, whilst the posterior alveoli are positioned toward the dorsolingual margin. An extremely small seventh alveolus is present on the internal margin of a large concavity that accommodated a large maxillary tooth that occluded external to the lower teeth. Posterior to the eighth alveolus, the distances between alveoli are reduced to only a few millimetres.

The lateral surface of the dentary is heavily sculpted with deep pits and grooves. In lateral view the dorsal margin of the dentary extends obliquely upward in a nearly straight line from the small seventh alveolus to the suture between the dentary and surangular. The dentary does not extend beneath the external mandibular fenestra.

In dorsal view the most striking aspect of the mandible is the straight lateral profile with a marked medial curvature of the dentary anteriorly, approaching a very narrow mandibular symphysis. There is very little dorsal exposure of the dentary lingual to the alveoli, contrary to the condition seen in alligatorids with a short mandibular symphysis. The extremely short symphysis gives the jaws a peculiar aspect, superficially resembling the anterior mandibular regions of nettosuchids (Langston 1965).

The splenials are preserved up to the anterolingual portions of both mandibles, but damage precludes assessment of whether or not they participated in the mandibular symphysis. The splenial apparently lay along the ventral face of the dentary for part of its length. In all other crocodyliform taxa in which this region is known, the splenial lies along the medial face of the dentary. Two foramina for the ramus intermandibularis oralis of the trigeminal nerve are anteriorly positioned on the ventrolingual surface of the splenial.

The external mandibular fenestra is fairly small and ovate (41 mm anteroposterior diameter). It is bounded anteriorly by the dentary, ventrally by the angular, and dorsally by the dentary and surangular. Medially, the splenial and angular form the anterior and ventral margins of the large Meckelian fossa.

The anterior portion of the surangular is arched dorsally. The surangular also has a pronounced concavity on its posterodorsal surface, separated by a sharp ridge from the glenoid fossa, of which it forms a significant portion with the articular. This suggests that the quadratojugal participated significantly in the jaw articulation, as indicated by the wide glenoid fossa that extends considerably on to the surangular. A large, spatulate, posteroventrally directed retroarticular process is preserved. Several small foramina are present on the mediodorsal surface of the articular. The foramen aërum is closed, but was apparently positioned on the medial edge of the retroarticular process.

Dentition

Several isolated teeth that were found near the mandibles are attributed to the specimen (Text-fig. 3D–E). They vary in size, but all are typically ziphodont (laterally compressed with serrated carinae). The crowns are separated from the roots by a slight constriction, and the crowns of the smaller teeth are lanceolate in lateral profile.

Postcranial skeleton

The extraordinary preservation of the specimen and the number of postcranial elements recovered makes this one of the most complete non-eusuchian metasuchians known. Nearly all of the skeleton has been recovered, including vertebral elements (although most of the caudal vertebrae are missing), ribs, both limb girdles, and limbs (although only the distal portions of both radii and a few distal limb elements are preserved). Measurements of selected postcranial elements are given in Table 1.

Vertebrae. The vertebral column is represented by the first intercentrum, five cervicals, 14 dorsals, one sacral, and seven caudals (Pl. 1, figs 1–14). All vertebral centra are amphicoelous to slightly amphiplatyan. The intercentrum is wider than it is long.

The cervical vertebrae are presumed to be the first through fourth and sixth postaxials. The neural spine of the first postaxial is short and anteroposteriorly broad relative to those of the rest of the cervical series. In all cervical vertebrae the neural spine is posteriorly positioned, with the anterior edge of the neural spine aligned with the midpoint of the centrum, behind the posterior ends of the prezygapophyses. Throughout the cervical

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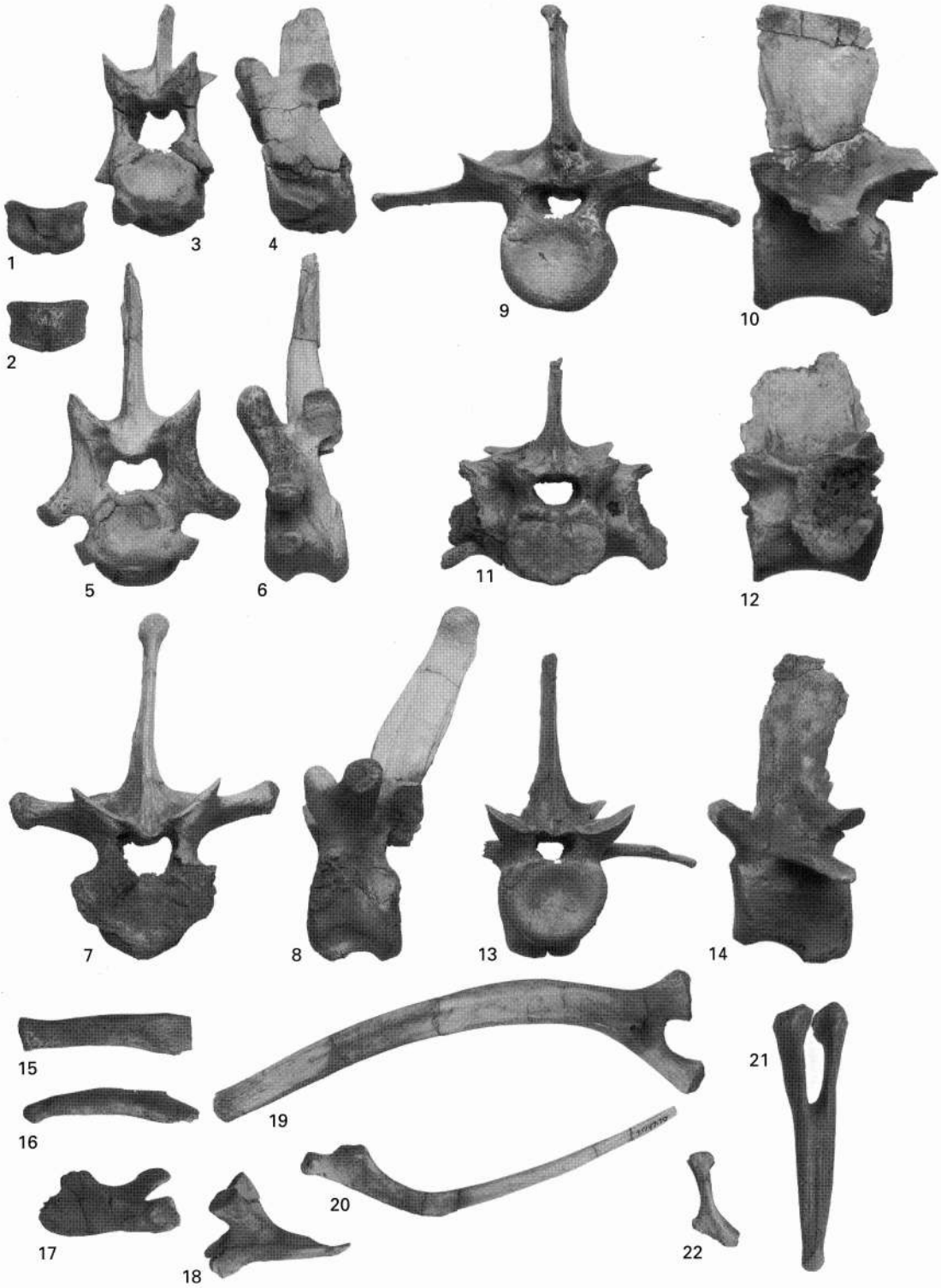
EXPLANATION OF PLATE 1

Figs 1–22. Elements of the axial skeleton of *Mahajangasuchus insignis* gen. et sp. nov.; UA 8654, holotype. 1–2, intercentrum in dorsal and ventral views. 3–4, first postaxial vertebra in anterior and left lateral views. 5–6, posterior cervical vertebra in anterior and left lateral views. 7–8, anterior dorsal vertebra in anterior and left lateral views. 9–10, posterior dorsal vertebra in anterior and left lateral views. 11–12, second sacral vertebra in anterior and left lateral views. 13–14, anterior caudal vertebra in anterior and left lateral views. 15, first cervical rib, ventromedial view. 16, second cervical rib, ventromedial view. 17, right cervical rib, right lateral view. 18, posterior right cervical rib, ventral view. 19, anterior right trunk rib, anterior view. 20, posterior left trunk rib, dorsolateral view. 21, anterior haemal arch, anteroventral view. 22, posterior haemal arch, left lateral view. All ×0·48.



BUCKLEY and BROCHU, *Mahajangasuchus*

TABLE 1. Measurements (in mm) of selected girdle and limb elements of *Mahajangasuchus insignis* gen. et sp. nov.; UA 8654, holotype.

Feature	Measurement (mm)	Feature	Measurement (mm)
Max. D-V length, left scapula	109	Max. D-V length, right ilium	76
Max. A-P width, left scapula	162	Max. A-P width, right ilium	142
Length, left humerus	245	Max. length, right ischium	152
Length, left ulna	210	Length, left femur	293
Length, left radiale	66	Length, left tibia	226
Length, left ulnare	51	Length, left fibula	216

series, the neural spines become progressively taller, more anteroposteriorly compressed, and more posteriorly inclined. The pre- and postzygapophyses are dorsally elevated well above the level of the neural canal, and have steeply inclined, subvertical articular facets. In the first through third postaxial vertebrae the neurocentral suture divides the diapophysis into two facets: a dorsal facet directed ventrolaterally and a ventral facet directed laterally. The diapophyses of the posterior cervical vertebrae are above the neurocentral suture and become more rounded and knob-like. The parapophyses of the anterior cervicals are short and ventrolaterally directed, with anteriorly expanded articular facets. The parapophyses of the posterior cervicals are positioned nearer to the dorsoventral midline of the centrum and are laterally directed, with no anterior expansion of the articular surface. All of the cervical vertebrae possess a moderately sized, knob-like hypapophysis on the anteroventral surface of the centrum, with a more pronounced keel present in the anterior cervicals.

The next two vertebrae, interpreted as D1 and D2, are very similar to the posterior cervical vertebrae. The neural spines are strongly compressed anteroposteriorly, but, unlike the posterior cervicals, the zygapophyseal articular surfaces are oriented nearly horizontally. Additionally, the diapophyses extend laterally from the neural arch. The parapophyses have a long vertical axis and are bisected by the neurocentral suture at their dorsal margin. Both possess knob-like hypapophyses.

The third dorsal vertebra is similar to the first two dorsals in the position of the parapophyses, but the neural spine is more blade-like. The dorsal tip of the neural spine bears a prominent knob. A smaller, less distinct knob is present in the same position on D2 and is completely absent in all other vertebrae. D3 possesses a prominent hypapophysis and a stronger keel than is seen in any of the other vertebrae, including the cervicals.

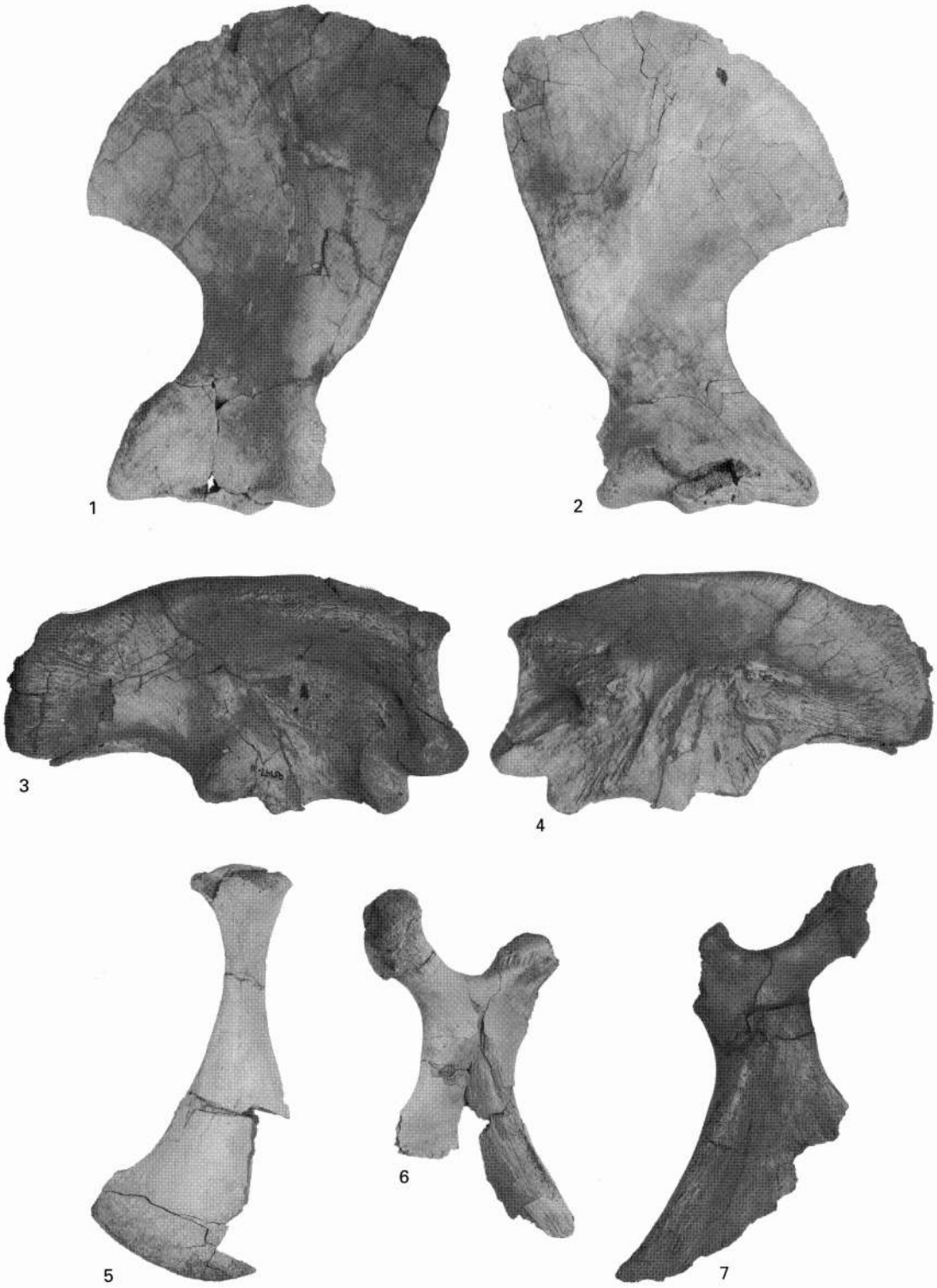
D4 is the last dorsal vertebra to display a distinct hypapophysis. It is also the first vertebra in which the parapophyses are entirely upon the neural arch. Moving caudad through the dorsal series, the parapophyses migrate dorsally onto the transverse process, closer to the diapophyses, until they fuse into a single synapophysis in the posterior dorsals. The posterior neural spines become dorsoventrally shorter and anteroposteriorly elongate, and the articular surfaces of the zygapophyses become shallower and approach a horizontal position near the level of the top of the neural canal. The posterior trunk vertebrae possess massive centra, short transverse processes, and anteroposteriorly elongate neural spines that lean strongly anteriorly.

The single preserved sacral vertebra, S2, possesses a stout centrum with a slightly concave posterior surface and a nearly flat anterior surface. The ventral surface lacks a hypapophysis. The neural spine is anteroposteriorly broad and the zygapophyses are small. A pair of sacral ribs are fused to the centrum and ventrolateral surface of the neural arch.

Seven caudal vertebrae have been recovered. The first caudal vertebra lacks a neural arch, but the amphicoelous centrum has two well-defined lateral facets on the anterior surface for articulation with the sacral ribs. It also bears a distinct medial concavity toward the posterior end of its ventral surface and lacks a haemal arch. A second vertebra represents the anterior portion of the series, with the remaining five from the middle to posterior region. The anterior caudal has a tall neural spine and very small transverse processes. A deep

EXPLANATION OF PLATE 2

Figs 1–7. Elements of the pectoral and pelvic girdles of *Mahajangasuchus insignis* gen. et sp. nov.; UA 8654, holotype. 1–2, left scapula in lateral and medial views; 3–4, right ilium in lateral and medial views. 5, left pubis in dorsal view. 6, left ischium and 7, right ischium, both in lateroventral view. All ×0·5.



BUCKLEY and BROCHU, *Mahajangasuchus*

longitudinal groove extends along the ventral surface of the centrum, separating two robust ridges that terminate posteroventrally in large knobby surfaces that articulated with a haemal arch. In the more posterior caudal vertebrae, the centra become more elongated relative to their lateral width, and there is a markedly concave bowing of the ventral surface in lateral view. The neural spines are relatively tall in the mid-caudals. The most posterior caudal recovered lacks the transverse groove on the ventral surface of the centrum seen in the anterior and mid-caudals.

In both anterior and posterior view, the openings of the neural canal are round in the sacral and posterior caudal vertebrae. In the presacral and anterior caudal vertebrae the openings are compressed dorsoventrally with a strong incursion of the neural arch into the dorsal region of the canal.

Ribs and haemal arches. Many of the ribs are remarkably well preserved, with ten cervical, 16 dorsal, and two sacral ribs recovered (Pl. 1, figs 15–20). The first two cervical ribs are flat and holocephalous, with the first being slightly larger and having a large, flat surface for articulation with the atlas intercentrum. The second is smaller, has a more knob-like head, and fits neatly on the dorsal side of the first rib.

The remaining cervical ribs are paired, and are assumed to be the fourth, fifth, sixth and eighth pairs. The anterior cervical ribs have a short cranial process and a much longer, medially concave posterior body that overlies the cranial process of the following rib. The bodies of the fourth and fifth ribs are bifurcated, with posteriorly and posteroventrally expanded branches. The tubercula of ribs five and six are also bifaceted, reflecting the bifaceted nature of the diapophyses of their corresponding vertebrae. Cervical rib six is distinct in that it possesses a dorsal protuberance at the lateral base of the tuberculum. The lateral surface of the body is strongly concave and the cranial process is very short and rugose. The eighth cervical rib has a very small cranial process and a narrow, pointed body. The medial surface of the body is not concave, suggesting that it did not overlap with the next rib in the costal series. The articular surfaces of the tuberculum and capitulum are cupped, corresponding to the rounded, knob-like parapophysis and diapophysis of the eighth cervical vertebra.

The anterior trunk ribs have a strong anterior flange near the conjunction of the tuberculum and capitulum, as well as a knob on the end of the costal shaft that at one time probably articulated with a cartilaginous intercostal element. The third, fourth and fifth trunk ribs also possess a distinct posterior flange that extends further down the costal shaft. The more posterior costal elements decrease in size, and the tubercula and capitula become flatter and, ultimately, join into a single articular surface in the same plane as the transverse processes of their corresponding vertebrae.

The pair of sacral ribs is fused to the body of the second sacral vertebra (Pl. 1, figs 11–12). The ribs are wider posteriorly where they form a surface that articulated with the centrum of the first caudal vertebra. The lateral ends of both ribs are damaged, precluding assessment of the length of their posterior expansion.

Three haemal arches have been recovered, one from the anterior end of the series and two from a more posterior location (Pl. 1, figs 21–22). The anterior arch is long and robust, with a central ridge descending down the anterior face and a concave trough down its posterior face, terminating ventrally in a distinct knob. The base where it attaches to the caudal vertebra is paired, with the two branches barely contacting each other, and the right side has a pyramidal protuberance on the medial side of its dorsal articular surface that fits into a pit on the posteroventral articular surface of the caudal vertebra. The more posterior arches have a completely paired base with branches that do not contact each other and a blade-like ventral keel with short anterior and long posterior expansions.

Pectoral girdle and forelimbs. A complete left scapula and distal end of the right scapula are preserved (Pl. 2, figs 1–2). Neither of the coracoids has been recovered. The scapula is characterized by an extremely broad scapular blade with a high, convex dorsal edge, strongly concave anterior edge, and nearly straight posterior edge. In the distal region of the scapula, the lateral margin is concave, ascending anteriorly to a strong distolateral acromial crest. On the posterolateral edge is a rugose knob for the insertion of the scapular head of *M. anconaeus scapularis lateralis externus*. Ventral to that, on the ventral surface of the bone, is the scapular

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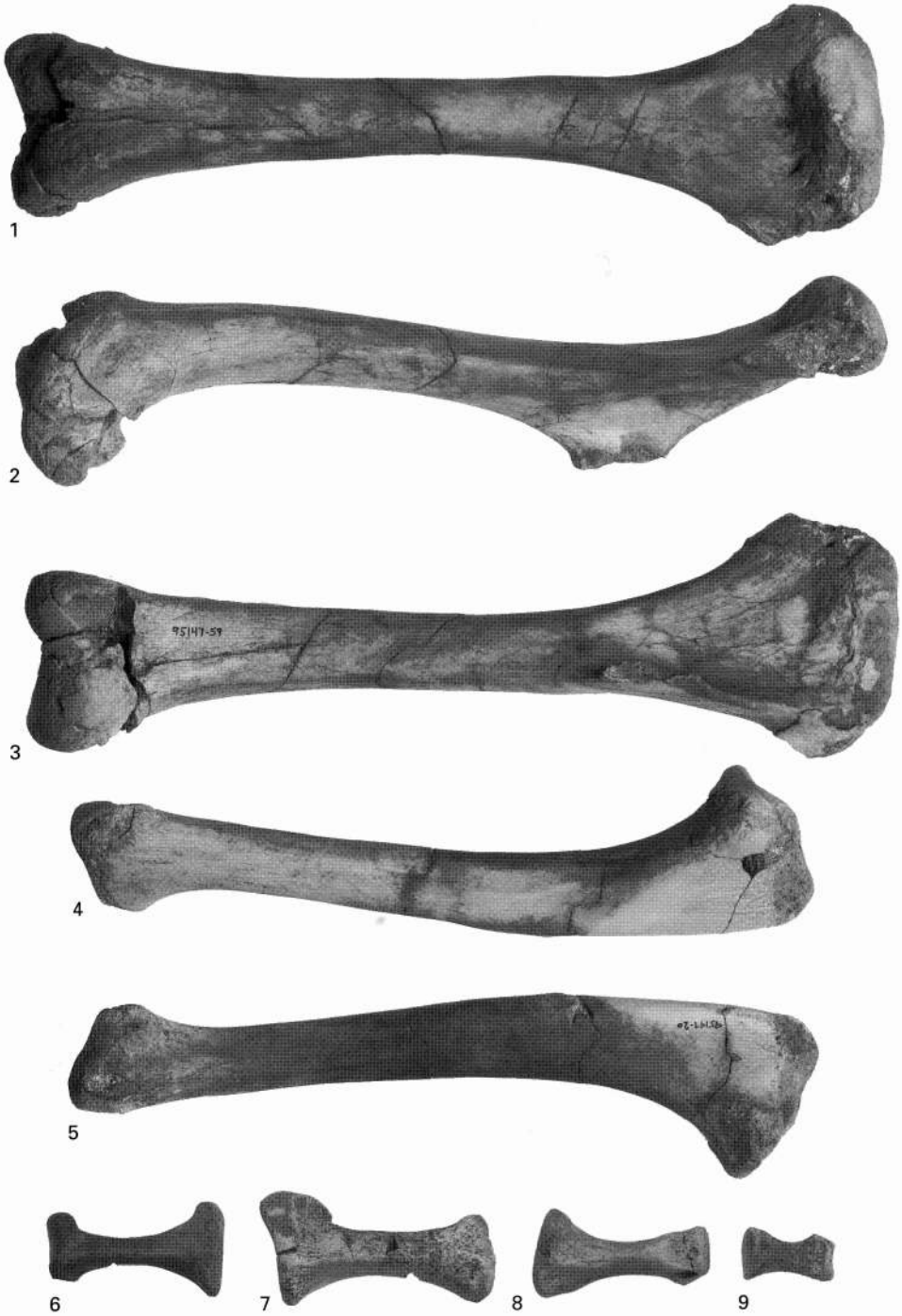
EXPLANATION OF PLATE 3

Figs 1–9. Elements of the forelimb of *Mahajangasuchus insignis* gen. et sp. nov.; UA 8654, holotype. 1–3, left humerus in anteroventral, posteromedial, and posterodorsal views. 4–5, left ulna in lateral and medial views. 6, left ulnare in anterodorsal view. 7, left radiale in anterodorsal view. 8, left metacarpal in dorsal view. 9, distal phalangeal element in dorsal view. All ×0·5.



BUCKLEY and BROCHU, *Mahajangasuchus*

margin of the glenoid fossa. The scapular articulation with the coracoid occurred upon a long, rough medioventral surface, with the coracoid contributing to the glenoid.

A complete left humerus and shaft of a right humerus are preserved (Pl. 3, figs 1–3). The humerus is slender and approximately seven-eighths the length of the femur. The shaft is nearly straight, but the curvature of the proximal head and the distal condylar region results in an overall sigmoidal shape in lateral and medial views. The articular head is broadly convex and transversely expanded. There is a shallow fossa on the anteroventral surface of the shaft near the head, and a much stronger fossa with prominent muscle scars on the posterodorsal surface for the insertion of *M. dorsalis scapulae*. A short protuberance extends from the posterolateral margin of the head. The deltopectoral crest expands distally along the anterolateral margin of the shaft, extending from the articular head to nearly the midpoint of the shaft, with greatest expansion occurring at approximately one-third of the shaft length. Distal condyles separated by a ligamental groove are moderately expanded, with prominent rugose ridges extending proximally from the posterior margins of the condyles onto the shaft.

A complete left ulna and the distal three-quarters of a right ulna are preserved (Pl. 3, figs 4–5). The proximal head is thickened and possesses a medially extensive olecranon. The shaft of the bone is compressed anteroposteriorly and is slightly curved inward. The distal end of the bone is only slightly expanded with well developed articular surfaces for the radiale, ulnare and pisiform. Only the proximal portion of the right radius and the shaft of the left is preserved. The proximal head is damaged, but is very similar to that of living eusuchians. The shaft is slender, with robust ridges and extensive muscle scarring, indicative of extremely muscular forearms.

Preserved carpal elements include a complete left radiale and ulnare (Pl. 3, figs 6–7) and the proximal end of the right radiale. Both elements are elongated, with the ulnare slightly shorter than the radiale. The proximal end of the radiale has a broad convex surface for articulation with the distal end of the radius and a medial face that contacted the distal margin of the ulna. The distal end is expanded with a shallow articular surface. The proximal end of the ulnare possesses a small concave articulation, whilst the distal end is greatly expanded.

One complete left and two partial right metacarpals were recovered (Pl. 3, fig. 8). The longest is approximately the same length as the ulnare. Two distal phalangeal elements were also recovered (Pl. 3, fig. 9). The terminal phalanges are unknown.

Pelvic girdle and hind limbs. A complete right ilium is preserved (Pl. 2, figs 3–4). The preacetabular process is small but prominent, whilst the postacetabular blade is somewhat narrow ventrodorsally. The acetabulum is large and perforated medially between the anterior and posterior peduncles, both of which are twinned. The supra-acetabular crest is robust and lacks a prominent ridge demarcating the dorsal margin of the acetabulum. The supra-acetabular region and the posterolateral, posteromedial, anteromedial and dorsal surfaces of the iliac blade are heavily scarred for the attachment of muscle and connective tissue. The anteroventral margin of the blade, the surface of the acetabulum, and the dorsomedial surface above the sacral rib articulations are smooth. Smooth articular facets are present on the ventral portions of the peduncles and on the lateral acetabular surface of the posterior peduncle.

Portions of both ischia are preserved, although both are damaged (Pl. 2, figs 6–7). The anterior process contacting the ilium is long and enlarged toward the dorsal end. A well-developed articular face is present on the ventromedial surface of the anterior process for the pubis, indicating that the pubis did not participate in the acetabulum. The posterior ischiadic process is damaged in both the left and right elements, but was apparently much shorter than the anterior process. The ischiadic blade is anteroposteriorly broad. The posterior margin of the blade is thick, with blade thickness diminishing anteriorly.

Only the right pubis is preserved (Pl. 2, fig. 5). The articular surface for the ischium is teardrop-shaped, and a distinct process extends laterodorsally. The distal end is expanded and blade-like.

Both femora are completely preserved (Pl. 4, figs 1–3). The bone is large, robust and sigmoidally curved. The proximal end is compressed dorsoventrally with a large articular surface. A shallow ventral fossa is present

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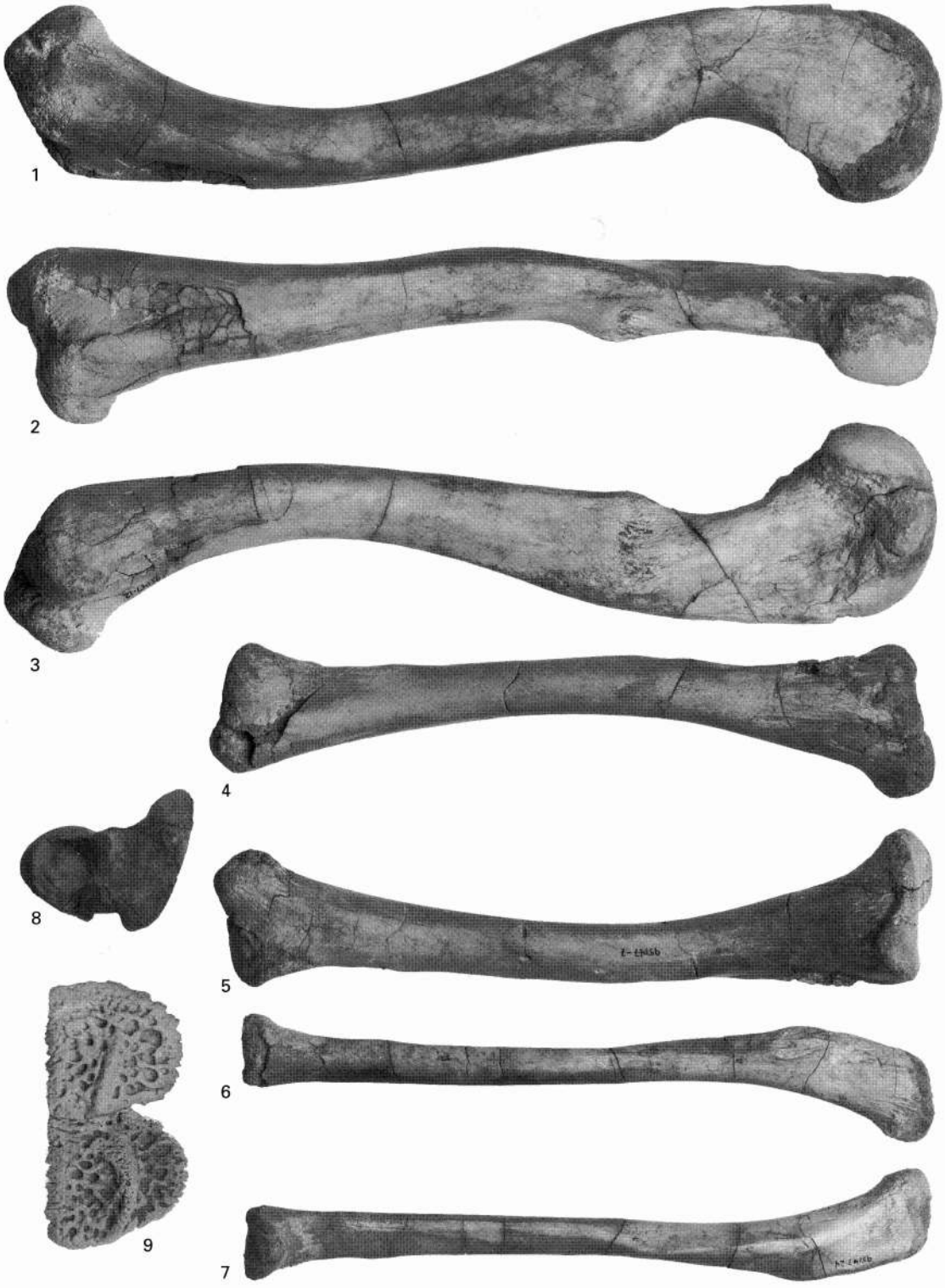
EXPLANATION OF PLATE 4

Figs 1–8. Elements of the hind limb of *Mahajangasuchus insignis* gen. et sp. nov.; UA 8654, holotype. 1–3, right femur in posterolateral, mediodorsal, and anteromedial views. 4–5, right tibia in anteromedial and posterolateral views. 6–7, left fibula in lateral and medial views. 8, right calcaneum, medial view. All ×0·48.

Fig. 9. Two dorsal trunk osteoderms (in imbricated position) of *Mahajangasuchus insignis* gen. et sp. nov.; UA 8654, holotype; ×0·48.



BUCKLEY and BROCHU, *Mahajangasuchus*

below the femoral head. There is a noticeable constriction of the shaft between the head and the moderately developed fourth trochanter. A prominent process for the insertion of the *M. coccygeofemoralis* extends medially at the level of the fourth trochanter. Several strong ridges extend distally down the length of the shaft. The condyles are strong, with a small sulcus on the laterodistal condyle for the proximal end of the fibula. The crista tibiofibularis is well defined.

Both the left and right tibiae as well as a complete left and distal portion of a right fibulae are preserved (Pl. 4, figs 4–7). The tibia is robust with a broad proximal surface for articulation with the femoral condyles and a large facet on the distal end for the astragalus. There is a ridge along the posterior face of the shaft for *M. flexor tibialis interior*. Behind this, there is a longitudinal ridge for the long digit flexors. The fibula is slender and slightly shorter than the tibia. Both the fibula and tibia strongly resemble those of modern crocodylians.

A complete right calcaneum represents the tarsal complex (Pl. 4, fig. 8). Notable features include the presence of a robust calcanear tuber and a deep socket for articulation with the astragalus. The calcaneal tuber does not turn laterally outwards relative to the body of the bone, but rather retains the orientation that Parrish (1987) identified as the primitive crocodylomorph tarsal pattern.

The distal ends of two metatarsals have been recovered. Both are slender and elongated. Distal elements of the hind foot are unknown.

Osteoderms

Numerous osteoderms were recovered along with the postcranial remains (Pl. 4, fig. 9). These are all deeply and irregularly pitted, except on the anterior margins where each was overlapped by the preceding osteoderm. Strong keels are present, extending anterolaterally to the posteromedial margin. The larger dermal scutes are sub-quadrangular to ovate, with rounded lateral edges and straight medial edges with a pronounced sutural surface. The rounded lateral margins of the larger osteoderms suggest the presence of no more than two longitudinal rows of dermal armour.

PHYLOGENETIC RELATIONSHIPS

Methods

To explore further the phylogenetic implications of the morphology and systematic relationships of *Mahajangasuchus*, a matrix of 110 characters was subjected to a maximum parsimony analysis using PAUP, version 3.0s (Swofford 1991). Most of the characters were derived from Clark (1994) or Ortega *et al.* (1996), but a few others were added to reflect information derived from *Mahajangasuchus* and other Madagascan crocodyliforms, as indicated in Table 2. *Orthosuchus*, *Hemiprotosuchus*, and *Protosuchus* were used as outgroups.

We added three crocodyliform taxa not considered by Clark (1994): *Trematochampsa*, Peirosauridae and *Hsisosuchus*. Crocodylidae, *Gavialis*, Alligatoridae and *Leidyosuchus* were collapsed into a single terminal taxon (Crocodylia) with primitive character states for the root of this group derived following the tree topology of Norell (1989), Clark and Norell (1992) and Brochu (1997).

Buffetaut (1988, 1989) has argued that Peirosauridae Gasparini, 1982 should be considered a junior synonym of Trematochampsidae Buffetaut, 1974 at the familial level. This assertion cannot be tested by this analysis for the simple reason that only a single recognized 'trematochampsid', *Trematochampsa*, was included. Later analyses might find the peirosaurid taxa to be nested within a monophyletic Trematochampsidae, at which point strict adherence to Linnaean ranks would require the suppression of Family Peirosauridae in favour of Family Trematochampsidae.

To assess support for groups in this analysis, a set of 100 bootstrap replicates was generated, and trees one step longer were also examined. For the purposes of this particular study, trees longer than one step from optimal were considered irrelevant. A list of apomorphies for the analyses conducted in this study is given as an appendix. The specific fully-resolved trees used to generate them are shown in Text-figure 5.

General results

A heuristic search of this matrix recovered 17 equally most parsimonious trees. The strict consensus

TABLE 2. Character matrix. Characters 1 through 101 are from Clark (1994), and were used without modification. The only changes to Clark's matrix involved revisions for *Sebecus*, *Baurusuchus* and *Araripesuchus* based on new material. The following characters were added to the matrix: 102, surangular forms only the lateral wall of glenoid fossa (0), surangular forms approximately one-third of the glenoid fossa (1); 103, anterior margin of femur linear (0), anterior margin of femur bears flange for coccygeofemoralis musculature (1); 104, teeth without carinae, or with smooth carinae (0), teeth serrated (1); 105, dentary smooth lateral to seventh alveolus (0), dentary with large occlusion pit lateral to seventh alveolus (1); 106, scapular blade no more than twice the length of the scapulocoracoid articulation (0), scapular blade very broad and greater than twice the length of the scapulocoracoid articulation (1); 107, dorsal edge of dentary straight (0), dorsal edge of dentary sinusoidal, with two concave waves (1); 108, compressed dentary (0), transversely expanded dentary, almost as wide as high (1); 109, lateral surface of dentary continuous, without longitudinal groove (0), lateral surface of dentary with longitudinal groove (1); 110, splenial thin posterior to symphysis (0), splenial robust dorsally posterior to symphysis (1). Characters 107 through 110 are modified from Ortega *et al.* (1996). On the matrix, Peirosauridae is based largely on *Lomasuchus* (Gasparini *et al.* 1991), although some details were extracted from Ortega *et al.* (1996). *Hsisosuchus* was scored based on Li *et al.* (1994) and Wu *et al.* (1994), and further details for *Araripesuchus* were taken from Hecht (1991) and undescribed material from the Mahajanga Basin (Buckley and Brochu 1996).

	10	20	30	40	50	60	70	80	90	100	110
Protosuchus	000?000010	0000?00011	00?0000001	0111?00000	0000000?00	0000000??0	?0?0?001?0	10000?0000	000??00100	000??????	?000000000?
Hemiprotosuchus	?00??0?1??	?????10010	?0??00?001	0011????01	??0020?00?	11?1100101	??1?1?10??	2?11????01	????????0	????1?00?1	?000000000?
Orthosuchus	100?000110	1?00010010	0011000001	0001000?00	0000001100	1111100??1	?1?01010?0	?000?00100	0100011100	000?110010	000000000?
Notosuchus	?12?001101	0100111010	11?110?011	0000002??0	?000201120	11?1000?10	?110??10??	5?010?110?	0??1?????0	0?0???????	?0??0?0000
Baurusuchus	0000001111	??00?11010	1??110?011	0?????2?10	11??111120	11?1000??0	?11??03?01	5?01011101	0????????	0????????	?0?1??0011
Libycosuchus	?10?001101	??00?11010	10?110?011	000?002???	??00?11120	11?1010??0	???0?0?0??	5?0001?000	0???????0	0?0???????	???1??00??
Sebecus	1000?01101	0000?11000	11?111?0?1	0001012110	1100?11120	1111000??0	?1??103000	5100011000	0???????0	?00???????	?0010?001?
Araripesuchus	1121011121	0100211010	1011110014	0001?02110	100011112?	11?1000??0	?11?101000	5?00011010	1111111?0	10002?0???	?010011100
Alligatorium	112101?03?	0000?10000	101111?00?	100?10???0	??00??11??	1??1000???	????10?0??	4?00101?10	1101111100	????1?0010	0000001100
Theriosuchus	112101?131	0100110000	1101111001	1001102110	10001?11?0	1111000???	??1?10200?	4?00101010	1101111?0	011?110010	0000001100
Pelagosaurus	111?011101	0011020101	0000000000	0001012110	1000000110	1111001001	?10001210?	3000012000	0110111?00	0000110001	1000000100
Teleosauridae	011?011101	0011010100	1000000000	0011002110	1000?00110	1111001011	?1?001210?	3?00012000	0010111?0	000?110001	0000000100
Metriorhynchidae	011?011101	0011?20101	1000000000	0011002110	?000?00110	1111001011	?1?001210?	3000112000	00101?11?0	000??????0	?000000100
Pholidosaurus	101??11101	??11?11101	100111?001	000100211?	1000011120	11?101??10	?100?1300?	300????2?0?	??11?1???0	?0?0??1?0??	?0000?0100
Sokotosuchus	111?111101	??10????00	1001???101	001?012?1?	?????1112?	11?1?11??0	???1?1?1??	???????01?	?????????	?????????	?0000?0100
Dyrosauridae	011??1?101	?010?11?00	100011?101	0011012?10	1010011120	11?1011?10	?10101311?	3?00??2?00	0????????0	100??????1	?100000100
Eutretauranosuchus	112??11101	0010211000	100111?00?	0001001110	?000?11120	11?1010??0	?1?0?12010	4?00001010	111???1?0	??0?1?????	?0000001100
Goniopholis	112?11?131	?010?11000	101111?001	0001002?10	1000?11120	11?1010?10	?1?011301?	4?001?1010	11?1??1?0	?00?1100?1	1000001100
Bernissartia	112?111131	??00?11000	10?111?001	000?002???	??00011112?	11?10100?0	?1???130??	4?0010?010	11?1?11??0	0002101011	0000001100
Crocodylia	1120111131	0000211000	1001111001	0001002110	1011011120	1111010010	1110013100	3100011010	1111111101	1111101011	1000001100
Mahajangasuchus	1????????	????????	????????	????????	????????	????????	????????1	51010????0	11?1111?01	1000010??	?111111001
Peirosauridae	112?111121	1?002?10?0	100111?011	0001012110	11001?112?	1111000?00	?1?0??2000	????0?1?1?	????????	????????	??????11?1
Hsisosuchus	100??????1	1?00?00010	100111?011	0001012110	1000101?11	11?1000?0?	?1?02?1001	1?000?1?10	010?01????	????1?0011	00?000000??
Trematochampsa	112?0011?1	00??211??0	100111?011	000101????	????111112?	11????0000	?1?0??10??	5?0???1???	????????	100020?0??	?1111?1100

of these trees (Text-fig. 6A) is broadly congruent with the tree recovered in Clark (1994), although some of the resolution found by Clark at the base of Mesoeucrocodylia was not supported by this analysis, and it failed to support the monophyly of a clade including Atoposauridae (*Alligatorium* + *Theriosuchus*) and Neosuchia. This analysis supports the contention of Wu *et al.* (1994) that *Hsisosuchus* is a basal member of Mesoeucrocodylia.

Notably, Thalattosuchia is most parsimoniously seen as a derived member of Neosuchia. We share Clark's concern over the departure this represents from previous hypotheses (e.g. Buffetaut 1982; Benton and Clark 1988), and agree with him that there is no means of rejecting this tree without more character evidence. When *Pholidosaurus*, *Sokotosuchus* and Dyrosauridae were removed, Thalattosuchia was most parsimoniously seen as a very primitive mesoeucrocodylian lineage, in accord with earlier hypotheses (Text-fig. 6B). Analyses excluding *Pholidosaurus*, *Sokotosuchus*, and Dyrosauridae also resulted in support for Atoposauridae + Neosuchia.

Because Thalattosuchia is most parsimoniously viewed as a close relative of other long-snouted crocodyliforms, we strongly suspect that characters correlated with longirostry are responsible for this anomaly. Nevertheless, whilst we find the tree in Text-figure 6B more intuitively satisfying, we view this not as a basis for rejecting the tree in Text-figure 6A, but as an indication that more attention should be paid to resolving the issue of longirostrine crocodyliform relationships.

Relationship of Mahajangasuchus *to other Gondwanan crocodyliforms*

Our analysis discovered a strongly supported clade including *Mahajangasuchus*, *Araripesuchus*, *Trematochampsa*, Peirosauridae, Atoposauridae and Neosuchia (with or without Thalattosuchia), but most of the characters diagnosing it are not known in *Mahajangasuchus*. A rostrum that is wider than high, premaxillae that are dorsally horizontal, enlargement of maxillary teeth toward the middle of the toothrow, and a pubis with an expanded distal end all diagnose this clade. The pubic character ceases to diagnose this node when Thalattosuchia is constrained as a basal crocodyliform. Rostral shape diagnoses this clade, in part, because we have reassessed the character states in *Sebecus* and *Baurusuchus* relative to their codings in Clark (1994).

Two diagnostic characters for this node can be assessed in *Mahajangasuchus*: a laterally undulating dentary with two concave waves and a transversely expanded dentary. Both were used to diagnose a similar monophyletic group by Ortega *et al.* (1996).

A monophyletic group including *Araripesuchus*, *Trematochampsa*, Peirosauridae and *Mahajangasuchus* was weakly supported in this analysis. It only occurred in 94 per cent. of trees when trees one step longer than the most parsimonious set were considered, and was not supported by 50 per cent. of bootstrap replicates. None of the putative synapomorphies for this group was preserved in all members.

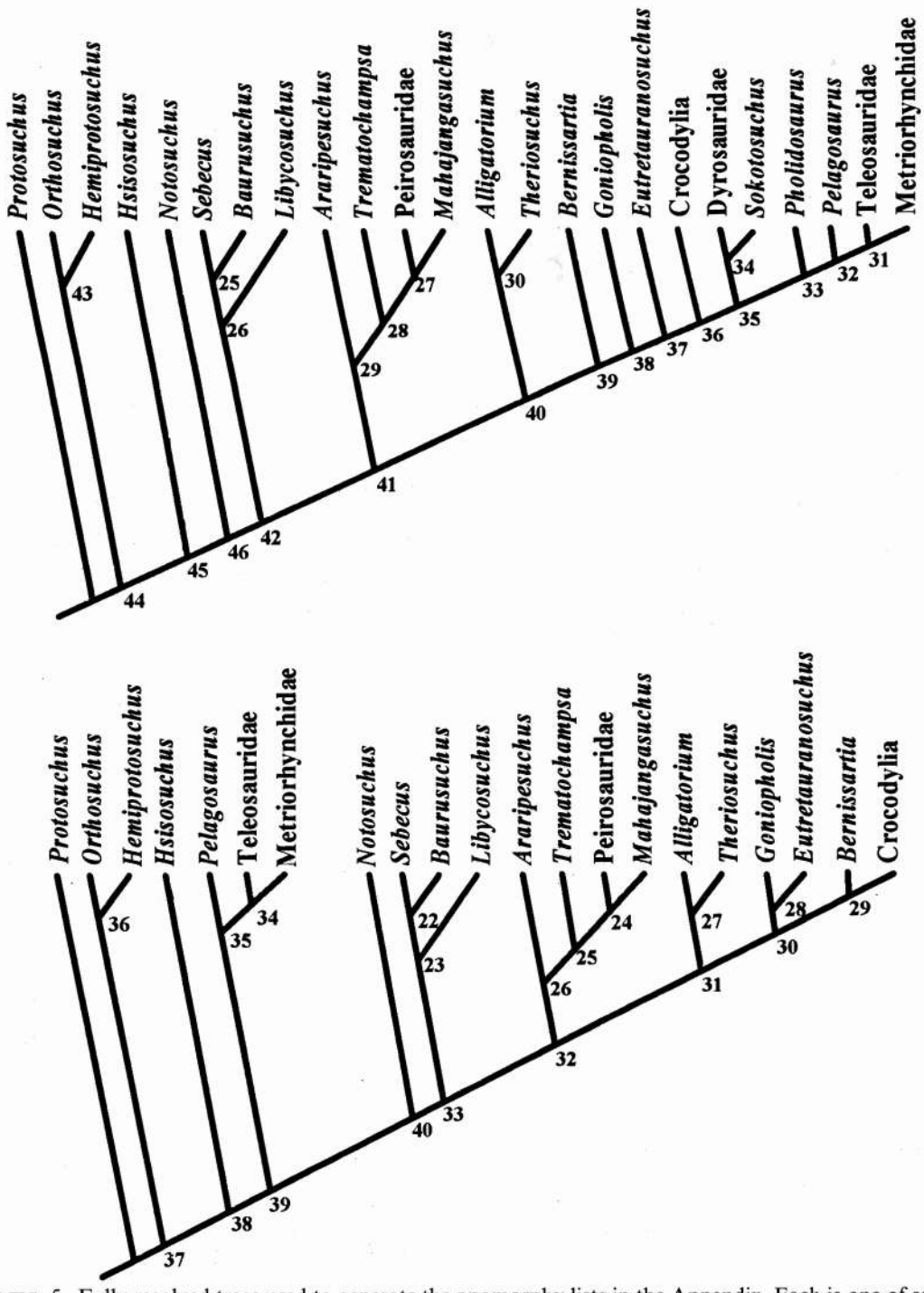
This group is diagnosed by the presence of an anterior expansion on the femur for the insertion of the coccygeofemoral musculature. Femora of *Araripesuchus*, *Trematochampsa taqueti* and *Mahajangasuchus* all show this feature, but the femur is not known in peirosaurids. *Araripesuchus* and *Mahajangasuchus* also have an unusually wide scapular blade.

Three characters used by Clark (1994) potentially diagnose this group. There is a narrow slit at the constriction between the premaxilla and maxilla in *Araripesuchus* and Peirosauridae; the cervical vertebrae have well-developed hypapophyses in *Araripesuchus*, *Mahajangasuchus*, and *T. taqueti*; and the dorsal osteoderms are rectangular in *Araripesuchus* and *T. taqueti*. This last character potentially unites *Araripesuchus* and *T. taqueti*, because the dorsal osteoderms of *Mahajangasuchus* are more equilateral, although at present the most parsimonious optimization indicates a secondary transformation in *Mahajangasuchus*.

EXPLANATION OF PLATE 5

Restoration of *Mahajangasuchus insignis* gen. et sp. nov. Original illustration by Carolyn McKee-Freese.

BUCKLEY and BROCHU, *Mahajangasuchus*



TEXT-FIG. 5. Fully resolved trees used to generate the apomorphy lists in the Appendix. Each is one of several equally most parsimonious trees recovered in a strict parsimony analysis. A, tree with all ingroup taxa included. B, tree with Dyrosauridae, *Sokotosuchus*, and *Pholidosaurus* excluded from the analysis. Numbers at nodes are assigned by PAUP.

Several characters potentially diagnose a monophyletic group including *Trematochampsa*, Peirosauridae and *Mahajangasuchus*. The most robust synapomorphy for this group is the presence of an occlusion pit near the seventh alveolus of the dentary in *Mahajangasuchus* and *T. taqueti*. In *T. taqueti* and Peirosauridae (e.g. *Lomasuchus*) the squamosals bear long processes at their posterolateral corners, a character seen also in *Sebecus*, *Hsisosuchus*, some long-snouted crocodyliforms, and derived crocodylians. The glossopharyngeal nerve exits through a separate foramen medial to that for cranial nerves X and XI in *T. taqueti* and Peirosauridae and, although all three nerves pass through a common opening in *Araripesuchus*, the state of this character is not known in Atoposauridae, *Bernissartia*, *Sebecus*, *Baurusuchus* or *Libycosuchus*. Separate foramina are known in *Hsisosuchus* and the outgroups in this analysis. *Mahajangasuchus* and *T. taqueti* bear modest anterior processes on the anterior edges of the dorsal osteoderms, but this character could not be assessed in most non-neosuchian taxa in this analysis. *Mahajangasuchus* and *T. taqueti* both bear well-developed articular facets on the surangular for the quadratojugal, a character also found in dyrosaurids; and along with *Sebecus* and *Baurusuchus*, they both have ziphodont dentition.

Mahajangasuchus and Peirosauridae share a single synapomorphy: a splenial that is mediolaterally thick dorsally. This character state is also seen in *Baurusuchus*, but is unknown in *Sebecus*.

Comparison of Mahajangasuchus *with* '*trematochampsids*'

Several features, not all of which were included in our phylogenetic analysis, preclude the assignment of this specimen to *Trematochampsa oblita* (known from the same strata) or, for that matter, any other known 'trematochampsid'. The symphysis of *Mahajangasuchus insignis* is much shorter than in any other known 'trematochampsid', in which the symphysis typically extends to the sixth or seventh alveolus. In addition, *T. oblita* has enlarged first, fourth and tenth mandibular teeth, whereas *M. insignis* has enlarged fourth, ninth and tenth teeth.

An enlarged fourth mandibular tooth, followed by a succession of smaller teeth and another enlarged tooth (or teeth) is a condition shared by *Mahajangasuchus* and other known 'trematochampsids'. Other features suggesting a relationship between *M. insignis* and other 'trematochampsids' (not necessarily to the exclusion of other groups) include: a large, robust dentary, ziphodont dentition; a fossa on the dorsolateral surface of the dentary behind the fourth alveolus to accommodate a large maxillary tooth in occlusion; and a jaw articulation incorporating the quadratojugal and surangular.

There are striking similarities between the mandibular profile of *M. insignis* and that of the 'trematochampsid' *Hamadasuchus rebouli*, described on the basis of an incomplete left dentary from the upper Albian or lower Cenomanian of Morocco (Buffetaut 1994). *H. rebouli* and *M. insignis* share a high, convex posterodorsal mandibular profile, very narrow interalveolar spaces in the posterior portions of the dentition, strong lateral tooth compression, and serrated lanceolate-type teeth. The extremely short mandibular symphysis and different positions of tooth enlargement distinguish *M. insignis* from *H. rebouli*.

DISCUSSION

Reconstructing the biogeographical origins of the Late Cretaceous Madagascan biota remains challenging, as the fauna may reflect vicariance as well as Late Cretaceous immigration events. Whilst it is imperative to base biogeographical hypotheses upon a framework of phylogenetic taxonomic relationships, it is also necessary to examine the palaeogeographical history of a region. In doing so, it may be possible to recognize both the opportunities for faunal interchange between landmasses, as well as the constraints that may have existed during a particular time period.

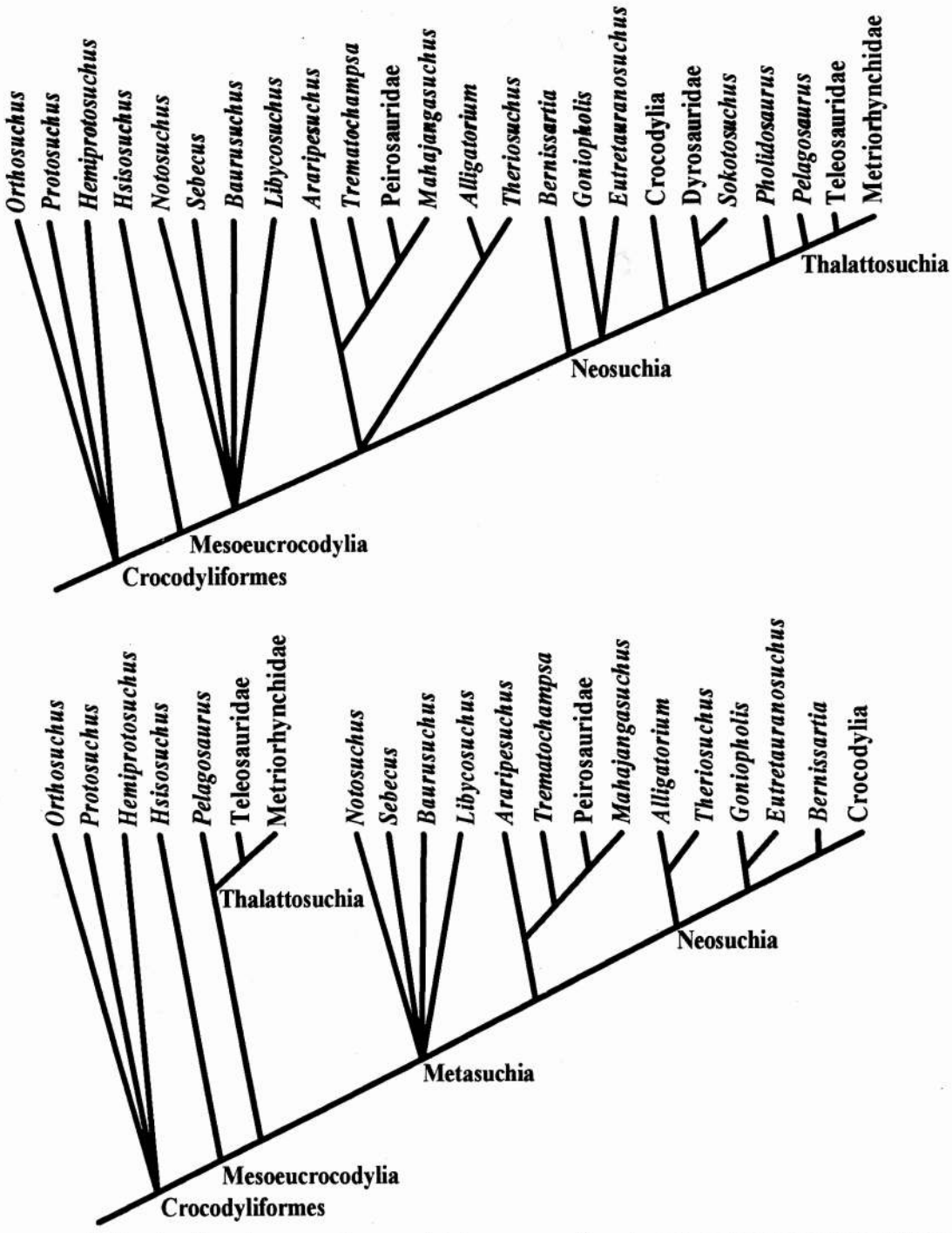
Current geophysical evidence indicates that south-eastern Gondwana (Antarctica, Australia, the Indian subcontinent, and Madagascar) separated from the African mainland during the Jurassic, although Antarctica remained in contact with or was in close proximity to the southern tip of South

America through the Cretaceous and into the Tertiary (Lawver *et al.* 1992; Shen 1995; Livermore and Hunter 1996). Madagascar and the Indian subcontinent, coupled as a single landmass, have been presumed to have separated from Antarctica during the Barremian–Aptian, between *c.* 120–110 Ma (Roeser *et al.* 1996), although a much later date, perhaps well into the Late Cretaceous, has been suggested based on revised palaeogeographical reconstructions of the region (Hay *et al.* in press). Geophysical evidence also indicates that the Indian subcontinent rifted from Madagascar *c.* 88 Ma (Storey *et al.* 1995).

The palaeogeographical distributions of crocodyliforms closely related to those recovered from the Upper Cretaceous of Madagascar (*Araripesuchus*, *Trematochampsa*, peirosaurids and *Mahajangasuchus*) seem to reflect this palaeogeographical history. *Araripesuchus* Price, 1959 is known from the Cretaceous (Albian–Aptian) Santana Formation of the Araripe Basin, Brazil and from the Aptian Elrhaz Formation of Niger (Buffetaut 1979, 1981). The earliest known crocodyliforms that have been regarded as 'trematochampsids' occur in the Albian–Cenomanian of Morocco (*Hamadasuchus rebouli* Buffetaut, 1994); occurrences in the Hauterivian–Barremian of Argentina have been reported (*Amargasuchus minor* Chiappe, 1988), but the assignment of this form to Trematochampsidae has been questioned (Gasparini *et al.* 1991). Other 'trematochampsids' occur in the lower Senonian of Niger (*Trematochampsa taqueti* Buffetaut, 1974), Maastrichtian of Brazil (*Itasuchus jesuinoi* Price, 1955), and the Eocene of Algeria (*Eremosuchus elkoholicus* Buffetaut, 1989) and Europe (*Bergisuchus dietrichbergi* Kuhn, 1968 and *Iberosuchus macrodon* Antunes, 1975), although some recent authors (e.g. Rauhe and Rossmann 1995; Ortega *et al.* 1996) have supported earlier assessments (e.g. Berg 1966; Antunes 1975) that the Tertiary European 'trematochampsids' are actually sebecosuchians. Both genera currently included within Peirosauridae, *Lomasuchus* and *Peirosaurus*, are known from the Senonian of South America. As mentioned previously, Buffetaut (1988, 1989) regards both of these taxa as constituents of Trematochampsidae.

The phylogeny recovered in this analysis, as well as the palaeogeographical history of Gondwana and the stratigraphical and geographical distributions of relevant taxa, is consistent with vicariance as a model for the origin of the Late Cretaceous Madagascan crocodyliform fauna. Sister-group relationships among *Mahajangasuchus* and its closest relatives indicate increasing provincialism in a crownward direction, with *Mahajangasuchus* at the crown. Its closest relative, Peirosauridae, is currently known only from the Upper Cretaceous of Madagascar and South America. These two landmasses, according to some palaeogeographical reconstructions, were connected by way of Antarctica well into the Late Cretaceous, but were isolated from Africa by the Mozambique Channel and a widening southern Atlantic Seaway by this time. The cosmopolitan distribution of 'trematochampsids' and *Araripesuchus* on Gondwana, now known from Madagascar, South America and Africa, is consistent with the advent of these taxa near the end of the Early Cretaceous when physiographic connections between these three landmasses (through Antarctica and the Indian subcontinent) were still present. The predecessors of the Madagascan crocodyliforms of the Late Cretaceous may then have become isolated on the island by the break-up of southern Gondwanan land-routes. The isolation of Indo–Madagascar from all other Gondwanan landmasses, whether it was during the late Early Cretaceous, or even much later as proposed by Hay *et al.* (in press), may have contributed to the survival of the crocodyliform taxa in Madagascar by impeding the later immigration of competitive forms that may have led to the decline of their relatives in South America and Africa.

The crocodyliform fauna of the Maevarano Formation partially mirrors the biogeographical signals found in other faunal lineages that have been recovered from the same lithological horizon. Gondwanatherian mammals, represented in Madagascar by *Lavanify miolaka* (Krause *et al.* 1997*b*), are elsewhere known only from the Upper Cretaceous of India and the Upper Cretaceous and Paleocene of Argentina (Krause and Grine 1996). The abelisaurid theropod dinosaur *Majungatholus crenatissimus*, also present in the Maevarano Formation of Madagascar, is a closely related sister taxon to *Indosuchus* from the Upper Cretaceous of India and *Carnotaurus* from the upper Lower Cretaceous of Argentina (Sampson *et al.* 1996*a*, 1997, 1998).



TEXT-FIG. 6. Results of parsimony analyses. A, strict consensus of most parsimonious trees when all taxa are considered. B, strict consensus of most parsimonious trees when *Pholidosaurus*, Dyrosauridae and *Sokotosuchus* are excluded from analysis.

These faunal distributions necessitate the assumption that members of these lineages were present on an intervening landmass between South America and Madagascar during the Late Cretaceous. The only possibilities are Africa and/or Antarctica, both of which, unfortunately, have yielded a depauperate Late Cretaceous fossil record. Based on current palaeogeographical reconstructions of southern Gondwana, we favour a scenario in which Antarctica persisted as a faunal corridor between South America and a Madagascar/Indian subcontinent landmass well into the Late Cretaceous.

A notable difference pertaining to the crocodyliform palaeogeographical distributions, as compared with those of non-crocodyliform lineages, is that there are definitely shared faunal elements between the Late Cretaceous Madagascar and Early Cretaceous African assemblages, specifically *Araripesuchus* and *Trematochampsa*. As mentioned above, the presence of *Araripesuchus* and Trematochampsidae in South America as well leads us to favour a vicariant origin for the taxa in Madagascar. The fragmentary nature of the Cretaceous African fauna renders this conclusion very tentative, and hence the likelihood of crocodyliform dispersal across the Mozambique Channel from Africa to Madagascar cannot be completely discounted. Several terrestrial and freshwater species have made the crossing during the Cenozoic, including the extinct '*Crocodylus*' *robustus* (Grandidier and Vaillant 1872; Barbour 1918; Mook 1921; Brochu and Storrs 1995) and the modern Nile crocodile, *Crocodylus niloticus*. Future discoveries in older deposits of Madagascar as well as in Upper Cretaceous deposits of sub-Saharan Africa are necessary to confirm or refute any biogeographical hypothesis.

Our conclusions are also limited by the incomplete preservation of most other 'trematochampsid' taxa. Most are too poorly known to include in a phylogenetic analysis. Similarities between *Mahajangasuchus* and *Hamadasuchus* have been noted, and a close relationship between them would support a different biogeographical scenario than a *Mahajangasuchus*-peirosaurid relationship. Such a grouping, however, cannot be proposed in the absence of a parsimony analysis. Until the phylogenetic relationships of all relevant taxa are better understood, the Late Cretaceous crocodyliform fauna of Madagascar will remain enigmatic.

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REFERENCES

ANTUNES, M. T. 1975. *Iberosuchus*, crocodile Sébécosuchien nouveau. L'Eocène ibérique au nord de la Chaîne centrale, et l'origine du canyon de Nazaré. *Comunicaçoes dos Serviços Geologicos de Portugal*, **59**, 285–330.

ASHER, R. J. and KRAUSE, D. W. 1994. The first pre-Holocene (Cretaceous) record of Anura from Madagascar. *Journal of Vertebrate Paleontology*, **14**, 15A.

BARBOUR, T. 1918. Vertebrata from Madagascar, 2. Amphibia and Reptilia. *Bulletin of the Museum of Comparative Zoology*, **14**, 479–489.

BENTON, M. J. and CLARK, J. M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. 295–338. *In* BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods, volume 1: amphibians, reptiles, birds*. Systematics Association Special Volume 35A. Clarendon Press, Oxford, 377 pp.

BERG, D. E. 1966. Die Krokodile, insbesondere *Asiatosuchus* und aff. *Sebecus*? aus dem Eozän von Messel bei Darmstadt/Hessen. *Abhandlungen des Hessischen Landesamtes für Bodenforschung*, **52**, 1–105.

BOULE, M. 1896. Note préliminaire sur les débris de Dinosauriens envoyés au Muséum par M. Bastard. *Bulletin du Muséum National d'Histoire Naturelle, Paris*, **2**, 347–351.

BROCHU, C. A. 1997. Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. *Systematic Biology*, **46**, 479–522.

—— and STORRS, G. W. 1995. The giant dwarf crocodile: a reappraisal of "*Crocodylus*" *robustus* from the Quaternary of Madagascar. 6. *In* PATTERSON, B. D., GOODMAN, S. M. and SEDLOCK, J. L. (eds). *Environmental change in Madagascar*. The Field Museum, Chicago, 143 pp.

BUCKLEY, G. A. and BROCHU, C. A. 1996. Campanian (Upper Cretaceous) crocodyliforms from Madagascar and their biogeographic implications. *Journal of Vertebrate Paleontology*, **16**, 24A.

BUFFETAUT, E. 1974. *Trematochampsa taqueti*, un Crocodilien nouveau du Sénonien inférieur du Niger. *Comptes Rendus de Séances de l'Académie des Sciences (Paris), Série 2*, **279**, 9–472.

—— 1976. Ostéologie et affinités de *Trematochampsa taqueti* (Crocodylia, Mesosuchia) du Sénonien inférieur d'In Beceten (République du Niger). *Géobios*, **9**, 3–198.

—— 1979. An early Cretaceous terrestrial crocodilian and the opening of the South Atlantic. *Nature*, **280**, 486–487.

—— 1981. Die biogeographische Geschichte der Krokodilier, mit Beschreibung einer neuen Art, *Araripesuchus wegeneri*. *Geologische Rundschau*, **70**, 611–624.

—— 1982. Radiation évolutive, paléoécologie et biogéographie des crocodiliens mésosuchiens. *Mémoires de la Société Géologique de France*, **142**, 1–88.

—— 1985. Zoogeographical history of African crocodilians since the Triassic. 53–469. *In* SCHUCHMANN, K.-L. (ed.). *Proceedings of the International Symposium on African Vertebrates: systematics, phylogeny and evolutionary ecology*. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, 585 pp.

—— 1988. The ziphodont mesosuchian crocodile from Messel: a reassessment. *Courier Forschungsinstut Senckenberg*, **107**, 211–221.

—— 1989. A new ziphodont mesosuchian crocodile from the Eocene of Algeria. *Palaeontographica, Abteilung A*, **208**, 1–10.

—— 1991. *Itasuchus* Price, 1955. 348–350. *In* MAISEY, J. G. (ed.). *Santana fossils: an illustrated guide*. TFH Publications, Neptune City, 459 pp.

—— 1994. A new crocodilian from the Cretaceous of southern Morocco. *Comptes Rendus de Séances de l'Académie des Sciences (Paris), Série 2*, **319**, 1563–1568.

—— and TAQUET, P. 1979. Un nouveau Crocodilien mésosuchien dans le Campanien de Madagascar: *Trematochampsa oblita*, n. sp. *Bulletin de la Société Géologique de France*, **21**, 183–188.

CHIAPPE, L. M. 1988. A new trematochampsid crocodile from the Early Cretaceous of north-western Patagonia, Argentina and its palaeobiogeographical and phylogenetic implications. *Cretaceous Research*, **9**, 379–389.

CLARK, J. M. 1994. Patterns of evolution in Mesozoic Crocodyliformes. 84–97. *In* FRASER, N. C. and SUES, H.-D. (eds). *In the shadow of the dinosaurs: early Mesozoic tetrapods*. Cambridge University Press, Cambridge, 435 pp.

—— and NORELL, M. A. 1992. The Early Cretaceous crocodylomorph *Hylaeochampsa vectiana* from the Wealden of the Isle of Wight. *American Museum Novitates*, **3032**, 1–19,

DEPÉRET, C. 1896*a*. Sur l'existence de Dinosauriens, Sauropodes et Théropodes dans le Crétace supérieur de Madagascar. *Comptes Rendus de Séances de l'Académie des Sciences (Paris), Série 2*, **122**, 483–485.

—— 1896*b*. Note sur les Dinosauriens Sauropodes et Théropodes du Crétace supérieur de Madagascar. *Bulletin de la Société Géologique de France*, **21**, 176–194.

FORSTER, C. A., CHIAPPE, L. M., KRAUSE, D. W. and SAMPSON, S. D. 1996*a*. The first Cretaceous bird from Madagascar. *Nature*, **382**, 532–534.

—— —— —— —— 1996*b*. The first Mesozoic avifauna from eastern Gondwana. *Journal of Vertebrate Paleontology*, **16**, 34A.

GASPARINI, Z. 1982. Una nueva familia de cocodrilos zifodontes cretácicos de América del Sur. *Actas V Congreso Latinoamericano de Geología, Buenos Aires*, **4**, 317–329.

—— CHIAPPE, L. M. and FERNANDEZ, M. 1991. A new Senonien peirosaurid (Crocodylomorpha) from Argentina and a synopsis of the South American Cretaceous crocodilians. *Journal of Vertebrate Paleontology*, **11**, 316–333.

GOTTFRIED, M. D. and KRAUSE, D. W. 1994. Late Cretaceous fishes from Madagascar: a first look. *Journal of Vertebrate Paleontology*, **14**, 27A.

GRANDIDIER, A. and VAILLANT, L. 1872. Sur le crocodile fossile d'Amboulintsatre (Madagascar). *Comptes Rendus de Séances de l'Académie des Sciences (Paris)*, **75**, 150–151.

HAY, O. P. 1930. *Second bibliography and catalogue of the fossil Vertebrata of North America*, Volume 2. Carnegie Institution of Washington, Washington, D.C., 1074 pp.

HAY, W. W., DECONTO, R., WOLD, C. N., WILSON, K. M., VOIGT, S., SCHULZ, M., WOLD-ROSSBY, A., DOLLO, W.-C.,

RONOV, A. B., BALUKHOVSKY, A. N. and SÖDING, E. in press. An alternative global Cretaceous paleogeography. *In* BARRERA, E. and JOHNSON, C. (eds). *The evolution of Cretaceous ocean/climate systems*. Special Publication of the Geological Society of America.

HECHT, M. K. 1991. *Araripesuchus* Price, 1959. 342–347. *In* MAISEY, J. G. (ed.). *Santana fossils: an illustrated guide*. TFH Publications, Neptune City, 459 pp.

KRAUSE, D. W. and DODSON, P. 1994. The premaxilla of *Majungasaurus* (Theropoda), Late Cretaceous, Madagascar: implications for relationships. *Journal of Vertebrate Paleontology*, **14**, 32A.

—— and GRINE, F. E. 1996. The first multituberculates from Madagascar: implications for Cretaceous biogeography. *Journal of Vertebrate Paleontology*, **16**, 46A.

—— HARTMAN, J. H. and WELLS, N. A. 1997*a*. Late Cretaceous vertebrates from Madagascar: implications for biotic change in deep time. 3–43. *In* PATTERSON, B. and GOODMAN, S. (ed.). *Natural change and human impact in Madagascar*. Smithsonian Institution Press, Washington, D.C.

—— —— —— BUCKLEY, G. A., LOCKWOOD, C. A., WALL, C. E., WUNDERLICH, R. E., RABARISON, J. A. and RANDRIAMIARAMANANA, L. L. 1994. Late Cretaceous mammals. *Nature*, **368**, 298.

—— PRASAD, G. V. R., KOENIGSWALD, W. von, SAHNI, A. and GRINE, F. E. 1997*b*. Cosmopolitanism among Gondwanan Late Cretaceous mammals. *Nature*, **390**, 504–507.

KUHN, O. 1968. *Die vorzeitlichen Krokodile*. Verlag Oeben, Munich, 124 pp.

LANGSTON, W. JR 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *University of California Publications in Geological Sciences*, **52**, i–viii, 1–169.

LAWVER, L. A., GAHAGAN, L. M. and COFFIN, M. F. 1992. The development of paleoseaways around Antarctica. 7–30. *In* KENNETT, J. P. and DETLEF, A. W. (eds). *The Antarctic paleoenvironment: a perspective on global change*. Antarctic Research Series, American Geophysical Union, Washington, D.C., 385 pp.

LI JINLING, WU XIACHUN and LI XUANMIN 1994. New material of *Hsisosuchus chungkingensis* from Sichuan, China. *Vertebrata PalAsiatica*, **32**, 107–126.

LIVERMORE, R. A. and HUNTER, R. J. 1996. Mesozoic seafloor spreading in the southern Weddell Sea. 227–241. *In* STOREY, B. C., KING, E. C. and LIVERMORE, R. A. (eds). *Weddell Sea tectonics and Gondwana break-up*. Geological Society Special Publication Number 108, London.

MOOK, C. C. 1921. Description of a skull of the extinct Madagascar Crocodile, *Crocodilus robustus* Vaillant and Grandidier. *Bulletin of the American Museum of Natural History*, **44**, 25–33.

NORELL, M. A. 1989. The higher level relationships of the extant Crocodylia. *Journal of Herpetology*, **23**, 325–335.

OBATA, I. and KANIE, Y. 1977. Upper Cretaceous dinosaur-bearing sediments in Majunga region, northwestern Madagascar. *National Science Museum Bulletin, Series C (Geology)*, **3**, 161–172.

ORTEGA, F., BUSCALIONI, A. D. and GASPARINI, Z. 1996. Reinterpretation and new denomination of *Atacisaurus crassiproratus* (Middle Eocene; Issel, France) as cf. *Iberosuchus* (Crocodylomorpha, Metasuchia). *Geobios*, **29**, 353–364.

PARRISH, J. M. 1987. The origin of crocodilian locomotion. *Paleobiology*, **13**, 396–414.

PRICE, L. I. 1955. Novos crocodilídeos dos Arenitos da Série Baurú, Cretáceo do estado de Minas Gerais. *Anais da Academia Brasileira Ciências*, **27**, 487–498.

—— 1959. Sôbre um crocodilídeo notossúquio do Cretácico Brasileiro. *Divisao de Geologia e Mineralogia Boletim*, **188**, 7–55.

RAUHE, M. and ROSSMAN, T. 1995. News about fossil crocodiles from the middle Eocene of Messel and Geiseltal, Germany. *Hallesches Jahrbuch für Geowissenschaften*, **17**, 81–92.

ROESER, H. A., FRITSCH, J. and HINZ, K. 1996. The development of the crust off Dronning Maud Land, East Antarctica. 243–264. *In* STOREY, B. C., KING, E. C., and LIVERMORE, R. A. (eds). *Weddell Sea tectonics and Gondwana break-up*. Geological Society Special Publication Number 108, London.

RUSSELL, D., RUSSELL, D., TAQUET, P. and THOMAS, H. 1976. Nouvelles récoltes de Vertébres dans les terrains contintaux du Crétacé supérieur de la région de Majunga (Madagascar). *Compte Rendu Sommaire des Séances et Bulletin de la Société Géologique de France*, **5**, 205–208.

SAMPSON, S. D., FORSTER, C. A., KRAUSE, D. W., DODSON, P. and RAVOAVY, F. 1996*a*. New dinosaur discoveries from the Late Cretaceous of Madagascar: implications for Gondwanan biogeography. *North American Paleontological Convention, Washington, D.C., Paleontological Society Special Publication*, **8**, 336.

—— KRAUSE, D. W., DODSON, P. and FORSTER, C. A. 1996*b*. The premaxilla of *Majungasaurus* (Theropoda, Ceratosauria), with implications for Gondwanan paleobiogeography. *Journal of Vertebrate Paleontology*, **16**, 601–605.

—— —— FORSTER, C. A. and DODSON, P. 1996*c*. Non-avian theropod dinosaurs from the Late Cretaceous of Madagascar and their paleobiogeographic implications. *Journal of Vertebrate Paleontology*, **16**, 62A.

—— WITMER, L. M., FORSTER, C. A., KRAUSE, D. W. and O'CONNOR, P. M. 1997. Discovery of a complete theropod skull from the Late Cretaceous of Madagascar yields new information on *Majungasaurus*, *Majungatholus*, and Abelisauridae. *Journal of Vertebrate Paleontology*, **17**, 73A.

—— —— —— —— —— DODSON, P. and RAVOAVY, F. 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science*, **280**, 1048–1051.

SHEN, Y. 1995. A paleoisthmus between southern South America and Antarctic Peninsula during Late Cretaceous and Early Tertiary. *7th International Symposium on Antarctic Earth Sciences*, 345.

STOREY, M., MAHONEY, J. J., SAUNDERS, A. D., DUNCAN, R. A., KELLEY, S. P. and COFFIN, M. F. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. *Science*, **267**, 852–855.

SUES, H.-D. 1980. A pachycephalosaurid dinosaur from the Upper Cretaceous of Madagascar and its paleobiogeographical implications. *Journal of Paleontology*, **54**, 954–962.

SWOFFORD, D. L. 1991. *PAUP: Phylogenetic Analysis Using Parsimony version 3.0*. Illinois Natural History Survey.

VASSE, D. 1995. *Ischyrochampsa meridionalis* n. g. n. sp., un crocodilien d'affinité gondwanienne dans le Crétacé supérieur du Sud de la France. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1995**, 501–512.

WALKER, A. D. 1970. A revision of the Jurassic *Hallopus victor* (Marsh) with remarks on the classification of crocodiles. *Philosophical Transactions of the Royal Society of London, Series B*, **257**, 323–372.

WHETSTONE, K. N. and WHYBROW, P. J. 1983. A "cursorial" crocodilian from the Triassic of Lesotho (Basutoland), Southern Africa. *Occasional Papers of the Museum of Natural History, University of Kansas*, **106**, 1–37.

WU XIAO-CHUN, LI JINLING and LI XUANMIN 1994. Phylogenetic relationship of *Hsisosuchus*. *Vertebrata PalAsiatica*, **32**, 166–180.

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APPENDIX

Apomorphy lists for parsimony analyses conducted in this study. These lists are based on one of the fully resolved most parsimonious trees from the total analysis (Text-fig. 5A) and the pruned analysis, with *Sokotosuchus*, Dyrosauridae, and *Pholidosaurus* removed (Text-fig. 5B). In both cases, the number in parentheses indicates the derived character state for that node; characters with one asterisk (*) are diagnostic for that node only under ACCTRANS optimization; those with two asterisks (**) are diagnostic only under DELTRANS optimization. Numbers adjacent to nodes in Text-figure 5 were assigned by PAUP.

A: Total Analysis

node 44: 1(1), 8(1), *11(1), *16(1), 20(0), 24(1), 32(0), *33(0), *38(1), 47(1), 51(1), 52(1), 53(1), 54(1), 62(1), 67(1), 68(0), *78(1), 82(1), 86(1), 87(1)
node 43: **16(1), *23(1), 55(1), *58(1), 60(1), *71(2)
Hemiprotosuchus: *33(1), 40(1), 45(2), 48(0), **58(1), **71(2), 73(1), 74(1), 80(1)
Orthosuchus: **11(1), **23(1), **33(0), **78(1), 100(0)
node 45: *7(1), *9(0), 10(1), *15(1), 21(1), 25(1), 29(1), **33(0), 37(2), **38(1), 39(1), 41(1), 45(1), *49(1), *72(1), *76(1), 77(1), *84(1)
Hsisosuchus: **11(1), *16(0), 36(1), **49(1), 50(1), 65(2), 70(1), 79(1)
node 46: 2(1), *3(2), **7(1), **9(0), *11(0), **16(1), 17(1), 49(2), *59(1), 71(5), *83(1), **84(1), *85(1)
Notosuchus: **3(2), 12(1), **15(1), 22(1), 34(0), 45(2), **59(1), 74(1), **78(1)
node 42: *15(2), 46(1), *67(3), **72(1), *78(0)
node 26: *3(0), *42(1), **76(1), 104(1), *109(1), *110(1)
node 25: 2(0), *22(1), *36(1), **42(1), **67(3), **109(1)
Baurusuchus: 1(0), 9(1), 70(1), 74(1), 78(1), 80(1), **110(1)
Sebecus: 19(0), **22(1), 26(1), **36(1)
Libycosuchus: 56(1)
node 41: **3(2), *4(1), 6(1), *9(2), **15(2), 26(1), 79(1), 81(1), **85(1), 107(1), 108(1)
node 29: **9(2), *59(0), *67(1), 91(1), 95(2), *96(0), 103(1), 106(1)

Araripesuchus: **4(1), 12(1), 23(1), **76(1), **83(1)
node 28: 36(1), *42(1), *74(1), *90(1), **96(0), *97(1), 102(1), 104(1), 105(1)
node 27: *5(1), *11(1), *67(2), *95(0), 110(1)
Mahajangasuchus: 70(1), **74(1), **90(1), **95(0), **97(1), 108(0)
Peirosauridae **5(1), **11(1), **42(1), **67(2)
Trematochampsa: 6(0)
node 40: 9(3), 19(0), *27(1), 29(0), 71(4), 75(1), *76(0)
node 30: **4(1), *15(1), 17(0), 31(1), 35(1), *67(2), *83(0), *92(1), *93(1), 100(0)
Alligatorium: 8(0), 23(1)
Theriosuchus: 12(1), **15(1), 22(1), **27(1), **67(2), **92(1), **93(1)
node 39: *4(0), 5(1), 45(0), 56(1), 66(1), **67(3), *69(1)
node 38: 13(1), **59(1), *91(1), 101(1)
node 37: *9(0), *65(0), 75(0), **83(1)
node 36: *43(1), **65(0), 68(1), *69(0), 71(3), 76(1)
node 35: 3(1), **9(0), *15(0), *18(1), *27(0), 57(1), 63(0), *72(0), 77(2), *79(0), 81(0), *99(0), 107(0)
node 33: *5(0), 14(1), **18(1), 20(1), *43(0), **72(0), **79(0), *91(0)
node 32: **5(0), **15(0), *16(2), 17(0), 24(0), 25(0), 26(0), 30(0), 46(0), 47(0), 49(1), 56(0), 60(1), 67(2), 84(0), **99(0)
Pelagosaurus: **16(2), 21(0), 36(1), 59(0)
node 31: 1(0), 33(1), 82(0), *101(0)
Teleosauridae: *16(1), 20(0), **101(0)
Metriorhynchidae: **16(2), 75(1), 100(0)
Pholidosaurus: 2(0), 68(0)
node 34: 28(1), 33(1), 36(1), 64(1), *69(1)
Sokotosuchus: *79(1)
Dyrosauridae: 1(0), 24(0), **43(1), **69(1), **79(0), **91(1), 102(1)
Crocodylia: *9(3), 13(0), **27(1), **43(1), 44(1), 90(1), **91(1), 92(1), 93(1), 94(1), 96(0), 97(1)
Eutretauranosuchus: **9(0), 37(1), 67(2), **69(1)
Goniopholis: 23(1), **69(1)
Bernissartia: 94(2), 96(0), 97(1)

B: Pruned Analysis

node 37: 1(1), 8(1), *11(1), *16(1), 20(0), 24(1), 32(0), *33(0), *38(1), 47(1), 51(1), 52(1), 53(1), 54(1), *60(1), 62(1), 67(1), 68(0), 82(1), 86(1), 87(1)
Hemiprotosuchus: *33(1), 40(1), 45(2), 48(0), **58(1), **71(2), 73(1), 74(1), 80(1)
Orthosuchus: **11(1), **23(1), **33(0), **78(1), 100(0)
node 36: **16(1), *23(1), 55(1), *58(1), **60(1), *71(2), *78(1)
node 38: *7(1), *9(0), 10(1), 21(1), *25(1), *29(1), **33(0), 37(2), **38(1), 39(1), 41(1), *45(1), 49(1), *76(1), 77(1)
Hsisosuchus: **11(1), *16(0), **25(1), **29(1), 36(1), **45(1), 50(1), 65(2), 70(1), 79(1)
node 39: 2(1), *3(1), **7(1), **9(0), *11(0), *59(1), *71(3), **76(1), 83(1), 85(1)
node 40: *3(2), *15(1), **16(1), 17(1), **25(1), **29(1), 49(2), *60(0), 71(5), *72(1), 84(1)
Notosuchus: **3(2), 12(1), **15(1), 22(1), 34(0), 45(2), **59(1), 74(1), 78(1)
node 33: *15(2), **45(1), 46(1), *67(3), **72(1)
node 23: *3(0), *42(1), 104(1), *109(1), *110(1)
node 22: 2(0), *22(1), *36(1), **42(1), **67(3), **109(1)
Baurusuchus: 1(0), 9(1), 70(1), 74(1), 78(1), 80(1), **110(1)
Sebecus: 19(0), **22(1), 26(1), **36(1)
Libycosuchus: 56(1)
node 32: **3(2), *4(1), 6(1), *9(2), **15(2), 26(1), 79(1), 81(1), 107(1), *108(1)
node 26: **9(2), *59(0), *67(1), 91(1), 95(2), *96(0), 103(1), 106(1)
Araripesuchus: **4(1), 12(1), 23(1)
node 25: 36(1), *42(1), *74(1), *90(1), **96(0), *97(1), 102(1), 104(1), 105(1)
node 24: *5(1), *11(1), *67(2), *95(0), 110(1)
Mahajangasuchus: 70(1), **74(1), **90(1), **95(0), **97(1), 108(0)
Peirosauridae: **5(1), **11(1), **42(1), **67(2)

Trematochampsa: 6(0)
node 31: 9(3), 19(0), 27(1), 29(0), 71(4), *75(1), 76(0), *94(1)
node 27: **4(1), *15(1), 17(0), 31(1), 35(1), *67(2), **75(1), 83(0), *92(1), *93(1), 100(0)
Alligatorium: 8(0), 23(1)
Theriosuchus: 12(1), **15(1), 22(1), **67(2), **92(1), **93(1)
node 30: *4(0), 5(1), *45(0), 56(1), **59(1), 66(1), **67(3), *101(1)
node 28: 13(1), 69(1)
Eutretauranosuchus: 9(0), 37(1), 67(2), *75(0)
Goniopholis: 23(1), **75(1), **101(1)
node 29: **45(0), *65(0), 96(0), 97(1)
Bernissartia: **75(1), 94(2), *101(0)
Crocodylia: 43(1), 44(1), **65(0), 68(1), 71(3), *75(0), 76(1), 90(1), 91(1), 92(1), 93(1), **94(1), **101(1)
node 35: **3(1), 6(1), 13(1), 14(1), 16(2), 18(1), 19(0), *20(1), 24(0), *25(0), *29(0), 30(0), *45(0), 47(0), *57(1), **60(1), *63(0), 65(0), 66(1), 67(2), 68(1), **71(3), 77(2), 99(0), 108(1)
Pelagosaurus: **20(1), 21(0), 36(1), *59(0), **63(0), 101(1)
node 34: 1(0), 33(1), **59(1), 82(0)
Teleosauridae: 16(1), *20(0)
Metriorhynchidae: **20(1), 75(1), 100(0)

A SYSTEMATIC REVIEW OF ANKYLOSAURIAN DINOSAUR REMAINS FROM THE ALBIAN–CENOMANIAN OF ENGLAND

by XABIER PEREDA SUBERBIOLA *and* PAUL M. BARRETT

ABSTRACT. Ankylosaur material from the upper Lower Cretaceous to lower Upper Cretaceous (Albian–Cenomanian) of south-eastern England is reviewed systematically. '*Acanthopholis horridus*' from the Lower Chalk of Folkestone (Kent) is regarded as a *nomen dubium*. A re-evaluation of the ankylosaur specimens from the Cambridge Greensand (mostly probably reworked from the underlying Gault Clay) suggests that all of the species of '*Acanthopholis*' erected by Seeley, on the basis of fragmentary, and often composite, non-diagnostic material, are invalid. *Anoplosaurus curtonotus* Seeley is removed from the Ornithopoda, and provisionally regarded as a valid taxon of nodosaurid ankylosaur. A lectotype, a partial scapula, is designated for this species. *Anoplosaurus* appears to be a relatively primitive nodosaurid which retains several plesiomorphic features in the lower jaw, sacrum and appendicular skeleton.

THE ankylosaurs are quadrupedal ornithischian dinosaurs characterized principally by extensive dermal armour (e.g. Coombs and Maryanska 1990). Two families are currently recognized: Nodosauridae and Ankylosauridae (Coombs 1978*a*), although several authors have suggested that this dichotomy may be misleading (Kirkland and Carpenter 1994; Carpenter *et al.* 1996). Ankylosaurids appear to have been restricted to Asia and North America, and most are Late Cretaceous in age, but recent work may extend their temporal range into the Jurassic (e.g. Dong 1993). By contrast, nodosaurids had a broader distribution in both time and space. They first appear in the Middle Jurassic of Europe and achieved an almost global distribution by the late Early Cretaceous. Most of our knowledge of nodosaurid anatomy and palaeobiology is based on specimens from the Wealden of Europe (*Hylaeosaurus*, *Polacanthus*), and from the upper Lower Cretaceous and Upper Cretaceous of North America (e.g. *Sauropelta*, *Edmontonia*).

The study of armoured dinosaurs began in England with the description of the nodosaurid ankylosaur *Hylaeosaurus armatus* from the Hastings Beds (Upper Berriasian–Valanginian) of Sussex (Mantell 1833). This was followed by the discovery of the basal thyreophoran *Scelidosaurus harrisonii* from the Lower Jurassic of Dorset (Owen 1861), and the description of *Polacanthus foxii*, a nodosaurid from the Wessex Formation (Barremian) of the Isle of Wight (Anonymous 1865). In 1867, another English dinosaur was placed in this group when Huxley erected the binomen '*Acanthopholis horridus*' on the basis of fragmentary remains from the Lower Chalk of Folkestone, Kent. This material, poorly illustrated by Huxley (1867, pl. 5), includes parts of a basicranium, isolated teeth, vertebrae and dermal plates. Huxley's preliminary description was supplemented with a note on the stratigraphical position of the remains (Etheridge 1867). Huxley (1867) regarded '*Acanthopholis*' as a close relative of *Scelidosaurus*, *Hylaeosaurus* and *Polacanthus*.

During the mid to late nineteenth century, the Cambridge Greensand of Cambridgeshire and surrounding areas was worked extensively, resulting in the recovery of abundant vertebrate remains (Seeley 1879). Seeley (1869) erected three additional species of '*Acanthopholis*' ('*A. platypus*', '*A. macrocercus*' and '*A. stereocercus*') and several other taxa on the basis of this material. Several syntypes of '*A. platypus*' were subsequently referred to the sauropod *Macrurosaurus* (Seeley 1876). Later, Seeley (1879) revised the dinosaur material from the Cambridge Greensand, and erected several new taxa, including '*Acanthopholis eucercus*', *Anoplosaurus curtonotus*, '*Anoplosaurus*

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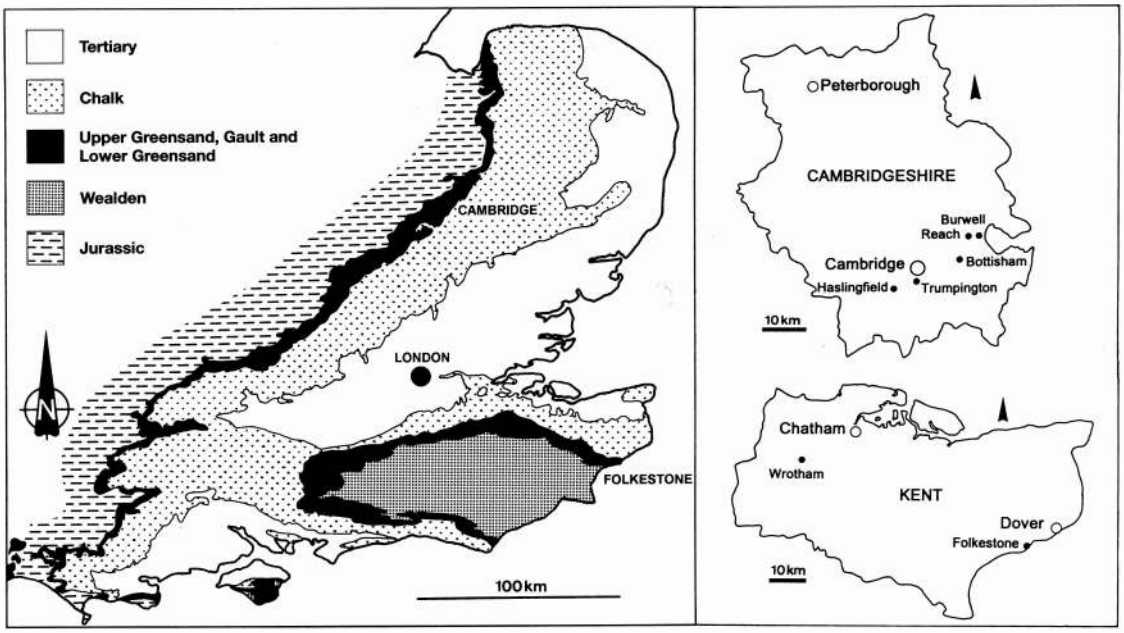


TEXT-FIG. 1. Geological map of south-eastern England and the Albian–Cenomanian localities of Cambridgeshire and Kent that have yielded ankylosaur material.

major' (based, in part, on material formerly described as '*Acanthopholis stereocercus*'), '*Eucercosaurus tanyspondylus*' and '*Syngonosaurus macrocercus*'. The last was established on several of the syntypes of '*Acanthopholis macrocercus*' (Seeley 1879). Systematic criteria used by Seeley (1879) included vertebral characteristics, size differences and the presence or absence of dermal armour. With the exception of '*Eucercosaurus*', regarded by Seeley (1879) as an iguanodontid-like dinosaur, all of these taxa were simply referred to as 'dinosaurs'.

Subsequently, Seeley (1881) described the basicranium of '*Acanthopholis horridus*' and discussed the relationships of this taxon to *Struthiosaurus austriacus* from the Late Cretaceous Gosau Formation of Austria. Nopcsa's (1923) revision of the Cambridge Greensand dinosaurs also included a discussion on the systematic position of '*Acanthopholis*', and considered the relationship between this taxon and *Anoplosaurus*.

'*Acanthopholis*' was originally placed within the Scelidosauridae (Huxley 1870; Seeley 1881; Lydekker 1888*a*), was later regarded as a stegosaur (Nopcsa 1901), and finally referred by Nopcsa (1923) to the family Acanthopholidae (currently regarded as a junior subjective synonym of Nodosauridae *sensu* Coombs 1978*a*). Most recent authors have followed Nopcsa's interpretation and listed '*Acanthopholis*' among the Ankylosauria (Romer 1956; Steel 1969). Coombs (1978*a*) regarded '*Acanthopholis*' as a *nomen dubium*, although he had previously noted that 'the remains indicate the presence of a nodosaurid as late as the basal Cenomanian of England' (Coombs 1971, p. 105). In the most recent review of the Ankylosauria, Coombs and Maryanska (1990) retained '*Acanthopholis horridus*' as a valid taxon, but noted that it may be a *nomen dubium*. Apart from some discussion of the systematic position of '*Acanthopholis*' and *Anoplosaurus* by Coombs (1971) and Brinkmann (1988) and further comments on Cambridge Greensand ankylosaurs (Coombs and Maryanska 1990), sauropods (McIntosh 1990), and ornithopods (Norman and Weishampel 1990), the dinosaurs from the Albian–Cenomanian of south-eastern England have not been extensively revised since the accounts of Seeley (1879) and Nopcsa (1923).

Therefore, the purpose of this paper is to review the ankylosaur material from the Albian–Cenomanian of England. Ankylosaur remains have been recovered from several deposits:

the junction between the Folkestone Beds and the Gault Clay (Kent), the Lower Chalk (Kent), and from the Gault Clay and the Cambridge Greensand of Cambridgeshire (Text-fig. 1). Stratigraphically, these formations range from the Lower Albian to the Lower Cenomanian (Rawson *et al.* 1978). The status of '*Acanthopholis horridus*', and of the other species referred to '*Acanthopholis*' and *Anoplosaurus*, is discussed in detail and a revised check-list of the Cambridge Greensand ankylosaurs is presented. A summary of the resulting taxonomy is presented in Table 1.

TABLE 1. Check-list of the '*Acanthopholis*' and *Anoplosaurus* species from the Albian–Cenomanian of England discussed in this paper.

Taxon	Status
Anoplosaurus curtonotus Seeley, 1879	Valid taxon of nodosaurid ankylosaur (Ankylosauria: Nodosauridae)
'*Anoplosaurus major*' Seeley, 1879	*Nomen dubium*, Ankylosauria indet. *partim*, Ornithopoda indet. *partim*
'*Acanthopholis horridus*' Huxley, 1867	*Nomen dubium*, Nodosauridae indet.
'*Acanthopholis eucercus*' Seeley, 1879	*Nomen dubium*, Ornithopoda indet.
'*Acanthopholis macrocerus*' Seeley, 1869	*Nomen dubium*, Ankylosauria indet. *partim*, Ornithopoda indet. *partim*
'*Acanthopholis platypus*' Seeley, 1869	*Nomen dubium*, Ankylosauria indet. *partim*, Sauropoda indet. *partim*, Dinosauria indet. *partim*
'*Acanthopholis stereocercus*' Seeley, 1869	*Nomen dubium*, Ankylosauria indet. *partim*, Ornithopoda indet. *partim*

Institutional abbreviations. BGS GSM, British Geological Survey, Keyworth, Nottingham; BMNH, The Natural History Museum, London; SMC, Sedgwick Museum, University of Cambridge, Cambridge.

LOWER CHALK (CENOMANIAN), KENT

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
ANKYLOSAURIA Osborn, 1923
Family NODOSAURIDAE Marsh, 1890

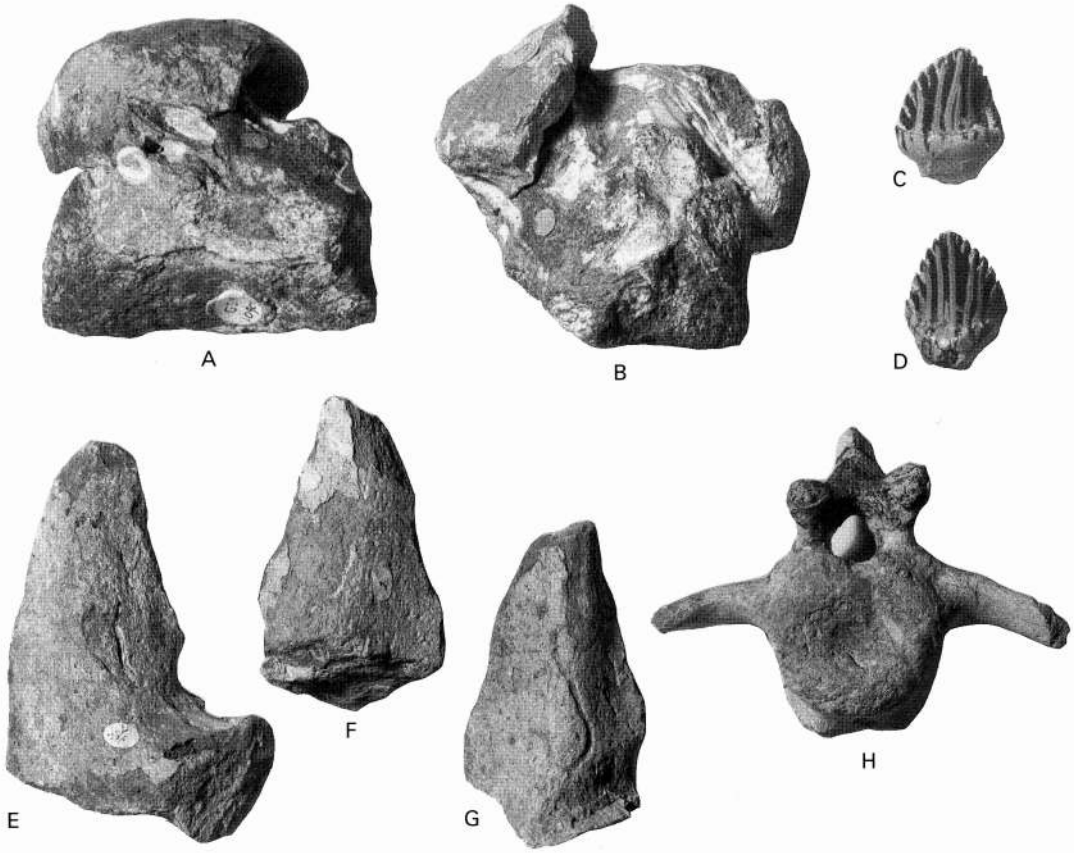
incertae sedis

Text-figures 2–3

1867 *Acanthopholis horridus* Huxley, p. 67, pl. 5.
1881 *Acanthopholis horridus* Huxley; Seeley, p. 634, pl. 27.
1923 *Acanthopholis* Huxley; Nopcsa, p. 193.
1969 *Acanthopholis horridus* Huxley; Steel, p. 54.
1971 *Acanthopholis horridus* Huxley; Coombs, p. 98.
1978*a* *Acanthopholis horridus* Huxley; Coombs, p. 169.
1990 *Acanthopholis horridus* Huxley; Coombs and Maryanska, p. 475.

Materials. BGS GSM 109057, fragmentary basicranium; 109045–109046 in part, 109051 in part, three isolated teeth; 109053, dorsal vertebra (doubtfully ankylosaurian); 109046–109052, 10955–10956, dermal armour, including spines and scutes. Several other elements listed by Huxley (1867), including a dorsal vertebra, a fragmentary humerus, and many scutes, could not be located during the course of this study.

The circumstances surrounding the discovery of '*Acanthopholis horridus*' are not clear. Huxley (1867) noted that the material was obtained from a Mr Griffiths, a collector from Folkestone, through a colleague called



TEXT-FIG. 2. Nodosauridae indeterminate (= '*Acanthopholis horridus*' Huxley) from the Lower Chalk (Cenomanian) near Folkestone, Kent, England. Original syntypes of '*Acanthopholis horridus*' Huxley (A–G) and referred specimen (H). A–B, BGS GSM 109057; basicranium in right lateral (A) and anterior (B) views; ×0·75. C–D, BGS GSM 109045; tooth in lingual? (C) and labial? (D) views; ×2. E, BGS GSM 109047; left cervical spine in dorsal view; ×0·3. F–G, BGS GSM 109050; right cervical spine in dorsal (F) and ventral (G) views; ×0·3. H, BMNH 44581; caudal vertebra in anterior view; ×0·3.

Dr Percy. The latter sent Huxley several fossils to be examined. Huxley recognized the large scutes and spines of an armoured reptile, and 'requested Mr Griffiths to procure for him every fragment of the skeleton' (Huxley 1867, p. 65). This request resulted in the recovery of 'three teeth, with a number of fragments of vertebrae, part of the skull and limb-bones, besides a large additional quantity of scutes' (Huxley 1867, p. 65). In total, 12 specimens, the syntypes of '*Acanthopholis horridus*' (BGS GSM 109045–109053, 109055–57), were obtained from three purchases of Chalk Marl reptile material from Mr Griffiths sometime between November 1866 and March 1867 (H. Ivimey Cook, pers. comm.). It is likely that Huxley had access to these specimens prior to 1867 as he published a brief account of the material in the January 1867 issue of the *Geological Magazine*. It seems that much more material was recovered by Mr Griffiths, but this material was never purchased and its whereabouts is currently unknown.

Huxley (1867, pl. 5) described a skull fragment, three teeth, two dorsal vertebrae, the distal end of a humerus, and several elements of the dermal armour, including conical spines and oval, keeled scutes, Unfortunately, the descriptions and illustrations provided by Huxley (1867) are inadequate to identify all of the material. Many of the individual elements lack definitive ankylosaurian features and their inclusion in the original type material of '*A. horridus*' seems to have been based on their presumed association with elements of dermal armour.

The original types of '*Acanthopholis horridus*' could belong to the same individual, but there is no accurate field information to confirm this hypothesis. When describing the dermal scutes, Huxley (1867, p. 66) suggested

that 'as they all came from one small area, they probably belonged to one animal'. However, two vertebrae from this assemblage are doubtfully ankylosaurian (BGS GSM 109053, 109058), and associated remains include the teeth and fragmentary sclerotic ring of a large ichthyosaur (BGS GSM 109059–109060). The occurrence of other disarticulated vertebrate remains in the same assemblage also casts doubt on the hypothesis that these remains belonged to a single individual, although this possibility cannot be completely excluded.

Additional ankylosaur remains, including caudal vertebrae and dermal scutes, recovered from the Lower Chalk near Folkestone, were purchased during the same period by the British Museum of Natural History, London (BMNH 44581, 47234, 49917). This material was also referred to '*Acanthopholis horridus*' (Seeley 1879; Lydekker 1888*a*). It seems likely that these specimens were obtained from the same (or a nearby) locality as the type material of '*A. horridus*', but the date of their recovery remains speculative. Seeley (1879, p. 596) stated that the remains were found at the same time as those described by Huxley (1867) and used this as a basis for suggesting that they belonged to the same individual. However, these specimens were obtained from three different collectors between 1873 and 1879 (S. Chapman, pers. comm.). This suggests that collection from the Folkestone site occurred over a period of several years and that the material represents a number of different individuals.

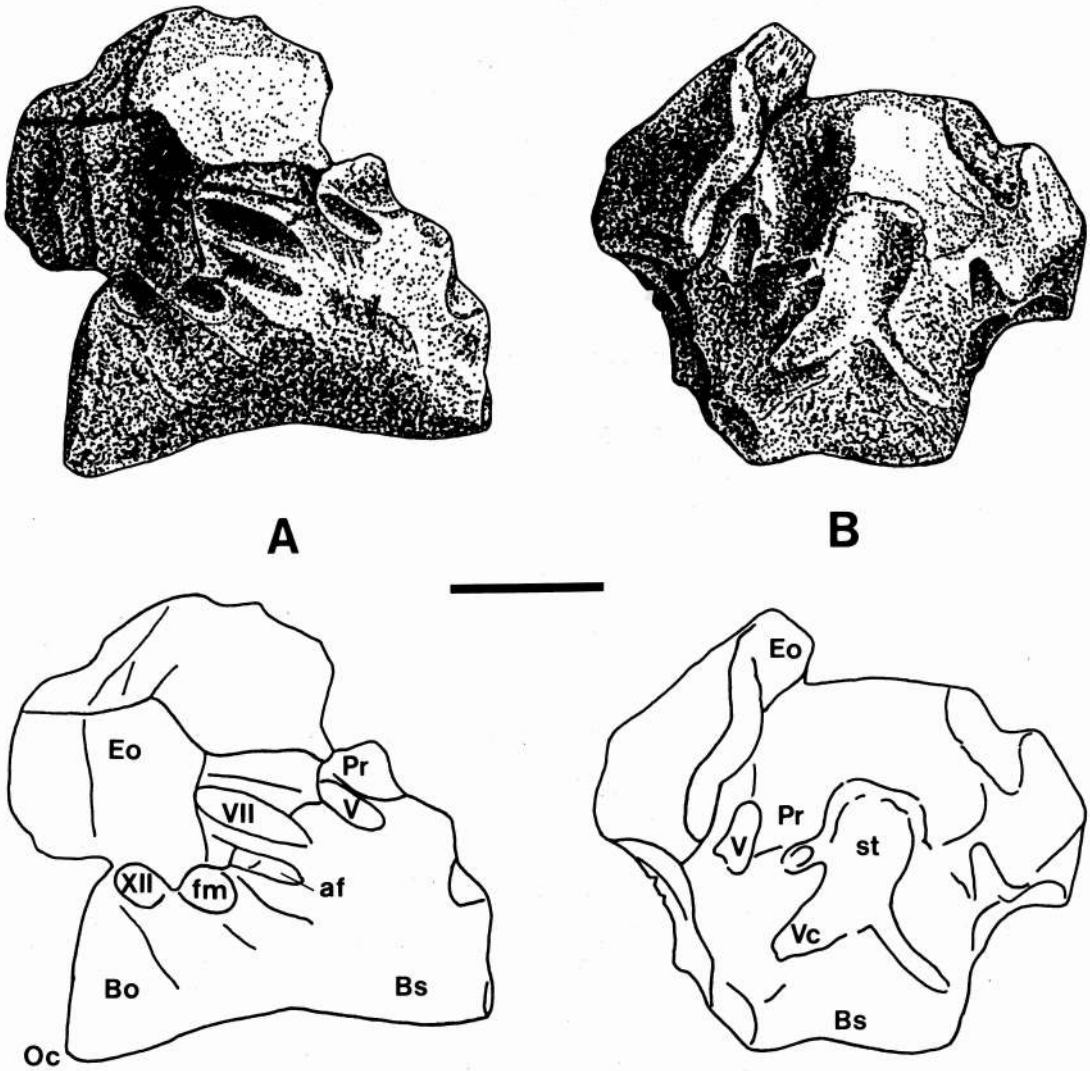
Locality and horizon. East of Copt Point, near Folkestone, Kent, England; Lower Chalk, Lower Cenomanian (Etheridge 1867; Rawson *et al.* 1978). The associated ammonite fauna suggests that the specimen is from the *Mantelliceras mantelli* Zone (lowermost Cenomanian; Rawson *et al.* 1978). Associated biota includes teleostean teeth, isolated ichthyosaur bones, and abundant invertebrate remains (Etheridge 1867).

Description

Skull (Text-figs 2A–B, 3A–B). A detailed description of the skull fragment was given by Seeley (1881, pl. 29, figs 7–8). The fragmentary basicranium (BGS GSM 109057) is small, massively built, and badly eroded. Most of the basioccipital and basisphenoid, and parts of the exoccipitals, opisthotics and prootics (some of them partially covered by a chalky matrix) are preserved. All braincase elements are fused and the sutures between the bones are obliterated, so that the recognition of the individual bones is based upon the position of the neurocranial foramina and other basicranial features. The endocranial cavity is filled with matrix.

The occipital condyle is composed of the basioccipital and is hemispherical in shape. The diameter of the occipital condyle (34 mm) is slightly longer than the maximal width of the circular foramen magnum (28 mm), a common condition in nodosaurid ankylosaurs. The occipital condyle is directed posteroventrally, as is characteristic of nodosaurid ankylosaurs (see below), and forms an obtuse angle with the ventral surface of the basisphenoid. The exact angle of downturn is difficult to establish, due to the fragmentary nature of the specimen, but the axis of the downturn appears to be angled *c.* 20–30° below the horizontal. The ventral surface of the basisphenoid is rugose and separated from the basioccipital by a small concavity. A number of large cranial foramina, five on the right side and six on the left side, is preserved (see interpretation in Text-fig. 3). On the posterior area of the basicranium, the hypoglossal nerve (XII) seems to be represented by two foramina on the left side and by a large foramen on the right side. In nodosaurids, the cranial nerve XII generally exits through two openings (e.g. *Silvisaurus*, Eaton 1960; *Struthiosaurus*, Pereda-Suberbiola and Galton 1994; cf. *Polacanthus*, Norman and Faiers 1996), but a single foramen is known in *Pawpawsaurus* (Lee 1996). Anterior to the XII cranial nerve, the braincase is perforated by a canal, the fenestra mitotica, for the exit of the jugular vein plus the foramen for the cranial nerves IX to XI. The fenestra mitotica is separated from the auditory foramen by a ridge of bone: the crista interfenestralis. A large depression situated anterolateral to the auditory recess may represent the foramen for the facialis nerve (VII) and the posterodorsal wall of the sella turcica is pierced by a foramen that appears to represent the external opening for the trigeminal nerve (V). The Vidian canal is visible in anterior view. As preserved, the floor of the braincase is 56 mm long and has a maximum width of 36 mm. The preserved height of the skull fragment is 58 mm and the maximum width between the exoccipitals is 67 mm. These measurements suggest a skull of about the same size as that of the nodosaurid *Silvisaurus condrayi* (length approximately 330 mm, BMNH R11189 [cast]).

Teeth (Text-fig. 2C–D). Three small isolated teeth are known (BGS GSM 109045, 109046 in part, 109051 in part), two of them still encased in matrix, and possibly belonging to the same individual. The teeth are typical of those found in ankylosaurs, with an asymmetrical, leaf-shaped, laterally compressed crown, and a basal cingulum on each side (Coombs 1990). However, these characteristics are primitive for Ornithischia (Sereno 1986) and, although they do not preclude the referral of these teeth to the Ankylosauria, they do not provide unequivocal ankylosaurian synapomorphies. The crown of the best preserved tooth (BGS GSM 109045) has



TEXT-FIG. 3. Nodosauridae indeterminate (= '*Acanthopholis horridus*' Huxley) from the Lower Chalk (Cenomanian) near Folkestone, Kent, England. A–B, drawings and interpretation of basicranium BGS GSM 109057 in right lateral (A) and anterior (B) views (modified from Seeley 1881, pl. 27, figs 7–8). Key: af, auditory foramen; Bo, basioccipital; Bs, basisphenoid; Eo, exoccipital; fm, fenestra mitotica; Oc, occipital condyle; Pr, prootic; st, sella turcica; Vc, Vidian canal; V, foramen for trigeminal nerve; VII, foramen for facial nerve; XII, foramen for hypoglossal nerve. Scale bar represents 20 mm.

eight denticles on the more convex side (?mesial margin) and seven on the other (?distal) margin. The mesial and distal edges of the tooth are separated by a large apical cusp; the height of the crown (9 mm) exceeds the maximum crown width (7 mm); the maximum labiolingual width of the tooth is 4 mm. The cingula are smooth and asymmetrically placed around the crown: thus, in mesial or distal view, one cingulum is significantly higher than the other as is more common in nodosaurids than in ankylosaurids or stegosaurs (Ostrom 1970; Carpenter 1990; Coombs 1990). There are no vertical ridges on the crown surface, and the 'coloured bands' described by Huxley (1867) are probably a taphonomic or diagenetic artefact. One of the teeth is broken longitudinally, exposing a small pulp cavity. The proximal part of the root is cylindrical in cross section and slightly curved.

Vertebrae (Text-fig. 2H). Huxley (1867) described two dorsal vertebrae, although only one of these (BGS GSM 109053) could be located. Coombs (1978*a*) listed two caudal vertebrae (BGS GSM 109054 and 109058) in the type series of '*A. horridus*', although these were not mentioned by Huxley (1867). As a result, these vertebrae cannot be regarded as syntypes of '*A. horridus*', although it is likely that they were recovered from the same locality. BGS GSM 109053 is rather fragmentary and possesses no unequivocal ankylosaurian characters, so we consider this vertebra to be doubtfully ankylosaurian.

BGS GSM 109054, an anterior caudal vertebra, is partially encased in matrix and few details are visible. The base of the centrum and most of the neural arch is missing. The centrum is slightly amphicoelous, and the neural canal is oval with the long axis extending vertically. The right transverse process projects laterally and slightly anteriorly and ventrally. There is no basis for the referral of BGS GSM 109054 to '*A. horridus*', as this material cannot be compared directly to the only vertebra that is known from the type series. However, BGS GSM 109054 is extremely similar to the anterior caudal vertebrae of other ankylosaurs, and can be regarded as Ankylosauria indeterminate. BGS GSM 109058 is too fragmentary for an accurate identification.

Seeley (1879, figs 2–3) described three additional ankylosaur vertebrae from the Lower Chalk of Folkestone (BMNH 44581, 47234) and referred them to '*Acanthopholis horridus*' (see also Lydekker 1888*a*). The anterior caudals have a short centrum which is wider than tall in anterior view. The centrum is reflected downwards posteriorly, so that the posterior articular surface is situated lower than the anterior surface. Chevron facets are present on the lateroventral margins of the posterior articular surface. The transverse processes are short and slender, directed laterally, and oriented slightly anteriorly and ventrally at the tip. The neural canal is oval, with the long axis of the oval extending vertically. The V-shaped prezygapophyses are widely separated from each other and overhang the anterior face of the centrum. The neural spine is oblique and directed posteriorly. The middle to posterior caudal centra are characterized by a deep ventral groove and longitudinal ridges along the lateral surfaces of the centra. Although this material was apparently recovered from the same site as the type material of '*A. horridus*' (see above), there are no characters which support the referral of BMNH 44581 and BMNH 47234 to '*A. horridus*', and they should be regarded as Ankylosauria indeterminate.

Dermal armour (Text-fig. 2E–G). The type species of '*Acanthopholis horridus*' includes three large spines and at least six oval keeled scutes (BGS GSM 109046–109052, 109055–109056). The most complete spine is approximately 180 mm long. The spines are conical, asymmetrical and tear-shaped in cross section. They can be divided into three sections: a basal region which was connected to the body of the animal, a shaft which makes up the pointed section of the spine, and a neck, which links the shaft to the base. These three sections are oriented at slightly different angles to each other. The basal region lies flat against the body, and the neck attaches perpendicular to the base. The shaft of the spine is offset from the perpendicular, continuing outward at an angle of *c.* 60° from the long axis of the neck region. The ventral surface is convex, whereas the dorsal surface is almost flat. A sharp keel extends from the base of the spine to the tip along both the anterior and posterior edges. The keel on the posterior edge is more prominent.

These spines closely resemble the cervical spines of the type specimen of *Hylaeosaurus armatus* (BMNH R3775; Owen 1858). Two of the spines, which are mirror-images of each other, may represent a pair of cervical spurs and the manner in which the basal region of the spines attached to the neck suggests that they projected anterolaterally.

The dermal scutes are variable in form and size (maximum length 65–105 mm). Some of the scutes are subcircular in dorsal view and have a low longitudinal keel, whereas others are narrower and the dorsal keel is more prominent. The ventral surfaces of the scutes are slightly excavated. Comparison with articulated ankylosaur material suggests that these scutes were probably attached to the trunk and the tail of the animal.

Several dermal scutes from the Lower Chalk of Folkestone (BMNH 47234, 49917) were referred to '*A. horridus*' by Lydekker (1888*a*). No characters support this referral, however, and this material should be regarded as Nodosauridae indeterminate. Lydekker (1888*a*, p. 184) noted that one of these scutes was illustrated by Huxley (1867, pl. 5, fig. 2), but the scute figured is actually one of the syntypes of '*Acanthopholis horridus*' (BGS GSM 109048).

Remarks. Coombs (1971, p. 105) noted that 'the genus [*Acanthopholis*] is clearly in a confused state. It is unlikely that any of the specimens upon which species have been established is adequate to allow definition and recognition of the taxon.' Consequently, Coombs (1971, 1978*a*) regarded '*Acanthopholis horridus*' as a *nomen dubium*, based on undiagnostic nodosaurid material. More recently, Coombs and Maryanska (1990) provisionally recognized the species, but noted that it may be a *nomen dubium*.

Comparison between the types of '*A. horridus*' and other nodosaurid taxa is difficult due to the incompleteness of the material, and only two or three skeletal elements can be compared in detail. The occipital condyle of nodosaurids is usually directed posteroventrally (Coombs 1978*a*), the axis of the downturn inclined at an angle of around 50° below the horizontal. This condition occurs in European nodosaurids, including *Struthiosaurus austriacus* and *Polacanthus foxii* (Pereda-Suberbiola 1994; Pereda-Suberbiola and Galton 1994; Norman and Faiers 1996), and in several North American forms (Coombs 1978*a*), including *Panoplosaurus* (BMNH unregistered cast [incorrectly labelled *Edmontonia*]), *Edmontonia* (Carpenter 1990, fig. 21.18C), and *Pawpawsaurus* (Lee 1996). In comparison with these taxa, the damaged occipital condyle of '*Acanthopholis horridus*' projects more posteriorly than ventrally (angled at 20–30° below the horizontal). However, a similar orientation of the basioccipital condyle (*c.* 30° below the horizontal) can be observed in *Silvisaurus condrayi* (Eaton 1960; BMNH R11189 [cast]) and in an undetermined juvenile nodosaurid from Texas (see Jacobs *et al.* 1994).

The morphology of the cervical spines of '*A. horridus*' suggest that they were oriented anterolaterally (see above). This feature contrasts with the laterally oriented cervical spines of *Struthiosaurus* (Pereda-Suberbiola *et al.* 1995), *Mymoorapelta* (Kirkland and Carpenter 1994), and *Polacanthus* (Blows 1987), and with the posterolaterally oriented cervical spines of *Sauropelta* (Carpenter 1984). However, *Edmontonia* (Carpenter 1990) and *Hylaeosaurus* possess anterolaterally directed cervical spines which are very similar to those of '*A. horridus*'. The remaining skeletal elements of '*A. horridus*' cannot be distinguished from those of other nodosaurids.

As the type material of '*Acanthopholis horridus*' has no unique diagnostic characteristics, we concur with the earlier view of Coombs (1971, 1978*a*) that '*A. horridus*' should be regarded as a *nomen dubium*. Moreover, as '*Acanthopholis horridus*' is the genotype of '*Acanthopholis*', which is, in turn, the type of the family Acanthopholidae, both of these taxa are now considered invalid.

The assignment of the material originally identified as '*A. horridus*' to the Nodosauridae is based on tooth structure (see above), and on the occurrence of long conical spines and solid keeled scutes (Coombs and Maryanska 1990). In addition, the posteroventral orientation of the occipital condyle also suggests nodosaurid affinities (Coombs 1978*a*; Sereno 1986; Coombs and Maryanska 1990). The significance of this character is not fully understood, but it may reflect differences in the way the head was carried in ankylosaurids and nodosaurids (Maryanska 1977; Pereda-Suberbiola and Galton 1994).

GAULT CLAY AND CAMBRIDGE GREENSAND (UPPER ALBIAN–LOWER CENOMANIAN), CAMBRIDGESHIRE

Geology

The Cambridge Greensand (or Phosphate Bed) is composed of glauconitic sandy marls. The lower layers of this deposit are rich in phosphatic nodules (formerly, and incorrectly, called 'coprolites'). These nodules were widely used as a fertilizer (see Penning and Jukes-Browne 1881). During the second half of the nineteenth century the surface exposure of the Cambridge Greensand was completely removed from large areas around the town of Cambridge. The deposits were worked by open-cast methods and the phosphatic nodules were extracted by washing. As a result of these open-cast workings, abundant fossil remains of invertebrates and vertebrates (mainly reptiles) were recovered from Cambridge and the surrounding area. The economical success of the 'coprolite diggings' led to further excavation and new discoveries. Sedgwick (*in* Seeley 1869) pointed out that a large collection of fossils was obtained from the 'phosphatite washings' of various localities. Seeley (1869) catalogued the vertebrate remains, including dinosaurs, crocodilians, pterosaurs, turtles, lizards, birds, ichthyosaurs, plesiosaurs and fishes, then housed in the University of Cambridge (SMC), and later published several works on this fauna (Seeley 1871, 1876, 1879).

The age, exact provenance and mode of preservation of the Cambridge Greensand vertebrate fauna have been debated for more than a hundred years. Age estimates based on the faunal content of the deposits have usually been founded on the foraminifera and other invertebrates present, with

little consideration of the vertebrates. At the time of the 'diggings' some authors considered the Cambridge Greensand to be a portion of the Upper Greensand, whilst others referred it to the uppermost part of the Gault Clay (see Hart 1973 for a historical summary). A re-investigation of the old Cambridge Greensand sites and collections has recently been undertaken in order to clarify their history of research (N. C. Fraser, pers. comm.). The precise age of the Cambridge Greensand remains unresolved, although recent work suggests a Late Albian or Early Cenomanian age for the deposits (Rawson *et al.* 1978; N. C. Fraser, pers. comm.). There is reason to suppose that the vertebrate remains are derived from the underlying Gault Clay (N. C. Fraser, pers. comm.) and are therefore Late Albian in age (Rawson *et al.* 1978). Consequently, it is probably inaccurate to refer to the vertebrate assemblage recovered during the 'coprolite mining boom' as a Cambridge Greensand fauna. In some pits nodule beds within the Gault Clay were excavated and the fossils from these levels were mixed with specimens recovered from the Cambridge Greensand at the washing and processing mills (N. C. Fraser, pers. comm.). As a result, the collections of Cambridge Greensand vertebrates from some localities presumably include material from the Upper Gault Clay.

Jukes-Brown (1875, pp. 274–275 and tables) distinguished two Cambridge Greensand faunas on the basis of their different states of preservation, and separated the dark, rolled, worn bones derived from the Gault Clay from those lighter in colour, recovered from the Chalk Marl. Jukes-Browne (1875) concluded that the Upper Gault Clay had been completely removed from the Cambridge area, and that the Upper Gault Clay fauna was reworked, in a phosphatized condition, in the Cambridge Greensand. However, Jukes-Browne (1903, appendix) later described (somewhat ambiguously) all of the reptilian remains from the Cambridge Greensand as indigenous to this deposit. Previously, Seeley (1879, pp. 591–593) had claimed that most of the specimens recovered occurred in large or small sets of naturally associated portions of skeletons of single individuals, and that scattered or isolated bones were comparatively rare. Moreover, Seeley (1879) stated that it was possible to identify the localities from which specimens were obtained on the basis of characteristic mineralization patterns peculiar to each different phosphatite digging. The generally worn condition of the fossils was explained by the exposure of the bones to the air and their subsequent maceration before burial (Seeley 1879).

Several of these suggestions are no longer tenable. Seeley (1876, 1879) admitted that fossils were occasionally purchased indiscriminately, and may have been mixed together by the quarrymen. In fact, most of the fossils collected from these deposits were obtained by purchase from collectors and labourers, rather than through the direct efforts of the scientists working on the fauna (see Sedgwick, *in* Seeley 1869, p. ix). Unfortunately, only a few exposures of the Cambridge Greensand are now available for study and most of the field data concerning the recovery of the vertebrate remains has been lost. As far as can be ascertained, most of the dinosaur remains were recovered from several of the pits around Cambridge, including Bottisham, Burwell, Haslingfield, Reach and Trumpington (Text-fig. 1; see also appendix 2 in Swinton 1970). The occurrence of associated vertebrate skeletons in the Cambridge Greensand is doubtful, although the syntypes of *Anoplosaurus curtonotus* may be an exception to the rule (see below). In most cases, it appears that the supposed series of bones are actually from different individuals, or even from different species (N. C. Fraser, pers. comm.).

Unusually, the type specimen of *A. curtonotus* consists of apparently associated remains. The 32 preserved centra probably represent more than half of the vertebral column of a single individual. The girdle and limb bones are proportional in size to the vertebrae and suggest that they belong to a small, immature individual *c.* 2 m long. If these remains are preserved in natural association, the specimens of *Anoplosaurus curtonotus* are quite exceptional among the Cambridge Greensand material. This taphonomic observation suggests the possibility that this material may have been recovered from the phosphate beds of the uppermost Gault Clay rather than from the Cambridge Greensand.

Many of the Cambridge Greensand dinosaurs described by Seeley (1869, 1871, 1879) include ankylosaur material in their type specimens. Here we present a revised summary of this material.

In addition to ankylosaurs, this dinosaur fauna also contains ornithopods, including one of the earliest recorded hadrosaurs ('*Trachodon cantabrigiensis*' Lydekker, 1888*b*), an iguanodontid ('*Eucercosaurus tanyspondylus*' Seeley, 1879) and a sauropod ('*Macrurosaurus semnus*' Seeley, 1876). In the following section, the only valid Cambridge Greensand ankylosaur, *Anoplosaurus curtonotus*, is discussed first. Other, invalid, taxa are dealt with subsequently. Many of the exact localities are unknown, and are listed in the Sedgwick Museum catalogue as 'from near Cambridge'.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
ANKYLOSAURIA Osborn, 1923
Family NODOSAURIDAE Marsh, 1890

Genus ANOPLOSAURUS Seeley, 1879

Type species. *A. curtonotus* Seeley, 1879.

Diagnosis. As for *A. curtonotus*.

Anoplosaurus curtonotus Seeley, 1879

Text-figures 4A–E, 5A–K

1879 *Anoplosaurus curtonotus* Seeley, pp. 600–603, pls 34–35.
1923 *Acanthopholis* Huxley; Nopcsa, p. 194.
1923 *Anoplosaurus* Seeley; Nopcsa, p. 194.
1969 *Anoplosaurus curtonotus* Seeley; Steel, p. 15.
1988 *Anoplosaurus curtonotus* Seeley; Brinkmann, p. 63.
1990 *Anoplosaurus curtonotus* Seeley; Norman and Weishampel, p. 531.

Designated lectotype. SMC B55731, a partial right scapula. *Anoplosaurus curtonotus* was erected on the basis of 77 syntypes (Seeley 1879). No holotype specimen was designated by Seeley (1879). In accordance with Article 74 of the International Code of Zoological Nomenclature (ICZN 1985) one of these syntypes (SMC B55731, a partial right scapula) has been designated the lectotype, and the remaining syntypes have been designated paralectotypes (see below). SMC B55731 was chosen as the lectotype as it had been figured previously (Seeley 1879, pl. 35, fig. 3; in accordance with ICZN Recommendation 74B), and as it possesses a distinctive morphology (see description below).

Paralectotypes. SMC B55670, partial left dentary; SMC B55671–55675, five cervical centra; SMC B55676–55688, thirteen dorsal centra; SMC B55689–55694, isolated neural arches; SMC B55695–55696, dorsal ribs; SMC B55697–55709, rib fragments; SMC B55710–55715, six unfused sacral centra; SMC B55716–55720, sacral ribs; SMC B55721–55728, eight caudal centra; SMC B55729–55730, coracoids; SMC B55732, fragmentary right humerus; SMC B55733, ?metacarpal; SMC B55734–55735 fragmentary left femur; SMC B55736–55737, fragmentary left tibia; SMC B55738–55741, ?metatarsals; SMC B55742, phalanx.

Type locality and horizon. The material was obtained in 1872 by Mr H. Keeping from a phosphatite-washing pit near Reach, a small village near Cambridge, Cambridgeshire, England; ?Upper Gault Clay or ?Cambridge Greensand, Upper Albian (Rawson *et al.* 1978; N. C. Fraser, pers. comm.).

Diagnosis. A small nodosaurid which can be distinguished from other nodosaurids by a thumb-like acromion process centrally placed on the scapula; an almost trapezoidal coracoid, wider anteroventrally than posterodorsally; and a finger-like lesser trochanter separated laterally from the femoral shaft by a shallow, but short cleft (a full discussion of these features can be found below).

Material. Seeley (1879) listed the material of *Anoplosaurus curtonotus* as follows: a fragmentary left lower jaw, five cervical, 13 dorsal, six sacral and eight caudal centra, four to six isolated dorsal neural arches, about 20 fragmentary dorsal and sacral ribs, incomplete right scapula, left and right coracoids (the latter very fragmentary), distal ends of a right humerus, fragmentary left femur and tibia, one metacarpal, four metatarsals and one phalanx (SMC B55670–55742). A fragment of ilium? (SMC B55743), apparently found with the other bones, was not described by Seeley (1879). There is no evidence of dermal armour in the assemblage. This material has been partially figured by Seeley (1879, pls 34–35) and Galton (1983, fig. 4D, O).

Description

Lower jaw (Text-fig. 4A). The lower jaw is represented by an incomplete left dentary (SMC B55670). No teeth are preserved. The tooth row is sinuous in dorsal and lateral views, a characteristic of thyreophorans (Sereno 1986). The first 13 alveoli and the replacement foramina for tooth numbers 1, 3, 6, 9, 11 and 12 are preserved. The tooth row extends almost to the symphysis (which is damaged). The splenial is missing and the Meckelian canal is visible as an open groove that tapers anteriorly (Seeley 1879). In lateral view, there is a buccal emargination, bounded ventrally by a moderately developed horizontal ridge. Two large nutrient foramina are situated in the buccal emargination. As Nopcsa (1923) noted, the small size (preserved length 60 mm) and the general form of the dentary are comparable to the nodosaurid *Struthiosaurus austriacus* (referred to as *Crataeomus* sp. in Seeley 1881).

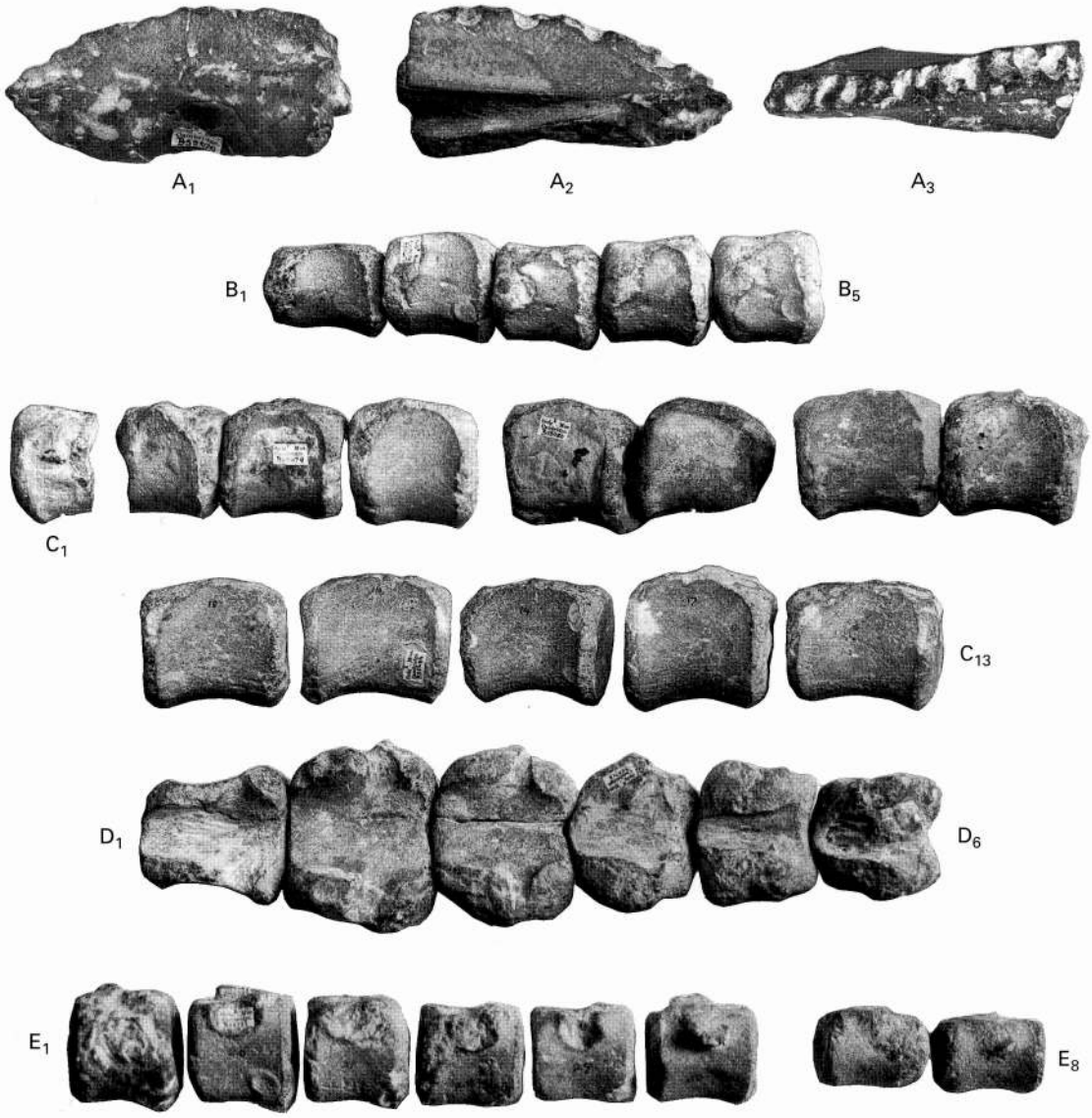
Axial skeleton (Text-fig. 4B–E). The axial skeleton of *A. curtonotus* is represented by 32 centra, including articulated portions of the cervical, dorsal, sacral and caudal series, with incomplete dorsal neural arches, and fragmentary dorsal and sacral ribs. The centra are acoelous to slightly amphicoelous.

Seeley (1879) identified five associated cervical centra (SMC B55671–55675) and, in the absence of the atlas and axis, interpreted them as a series from the 3rd to the 7th cervical vertebrae (total neck length *c.* 150 mm) (Text-fig. 4B). The first centrum is the longest and lowest of the series; the remaining centra become shorter and higher posteriorly. The parapophyses are situated laterally, near the anterior border of the centra, about half way down the height of the centrum in the anterior cervicals, but are placed higher in the posterior cervicals. The ventral surfaces of the centra are convex and lack basal keels. Since only one vertebra appears to be missing between the last cervical and the first dorsal of the series, Seeley (1879) suggested that *Anoplosaurus curtonotus* possessed at least seven and probably not more than eight cervical vertebrae.

Thirteen dorsal centra are present (SMC B55676–55688) and this number probably represents the complete (or almost complete) dorsal series of *A. curtonotus* (Text-fig. 4C). The centra are spool-shaped and increase in length slightly in the posterior part of the series. Seeley (1879) noted that, when placed together, the centra form an upward arch that measures *c.* 480 mm long. This pattern and the assumption that 'there would seem to be an approach towards a procoelus articulation in the lower part of the back' induced Seeley (1879, p. 603) to think that 'the body [of *Anoplosaurus curtonotus*] may have been carried in a semi-erect position, as was certainly the condition in so many of the Dinosauria'. The dorsal centra of *A. curtonotus* resemble larger ankylosaur vertebrae from the Cambridge Greensand (e.g. SMC B55746; Text-fig. 9D–F), but the articular faces are narrower. The best preserved dorsal neural arch was also described and figured by Seeley (1879). This specimen lacks most of the neural spine and the prezygapophyses. The postzygapophyses are set close together and have elongate, oval articular surfaces. The diapophyses project laterally and slightly dorsally, and are compressed anteroposteriorly. The basal part of the neural spine is laterally compressed and blade-like. The proximal end of each dorsal rib is T-shaped in cross section.

As preserved, the sacrum of *A. curtonotus* consists of six unfused vertebrae (SMC B55710–55715) (Text-fig. 4D). The total length of the sacral vertebrae is *c.* 220 mm. The lack of fusion between the centra, the neural arches, and the sacral ribs are juvenile features (see below). The first centrum is longer than wide and this condition also characterizes the last two centra. The mid-sacral centra are comparatively short and wide. The neural canal is very large in the second and third sacrals, as occurs in ankylosaurs and stegosaurs (Blows 1987). A shallow groove is present on the ventral surface of the anterior sacrals. The sacrum of *A. curtonotus* appears to be composed of four true sacral and two sacrocaudal vertebrae, a typical pattern among primitive nodosaurids (Pereda-Suberbiola 1994). The sacral vertebrae differ from the modified caudal vertebrae because the centra are comparatively wider, bear a more expanded neural canal, and have large surfaces for the ribs in an intervertebral position. The presacral rod is not preserved. Seeley (1879) suggested that at least one vertebra is missing between the last dorsal and the first sacral vertebra.

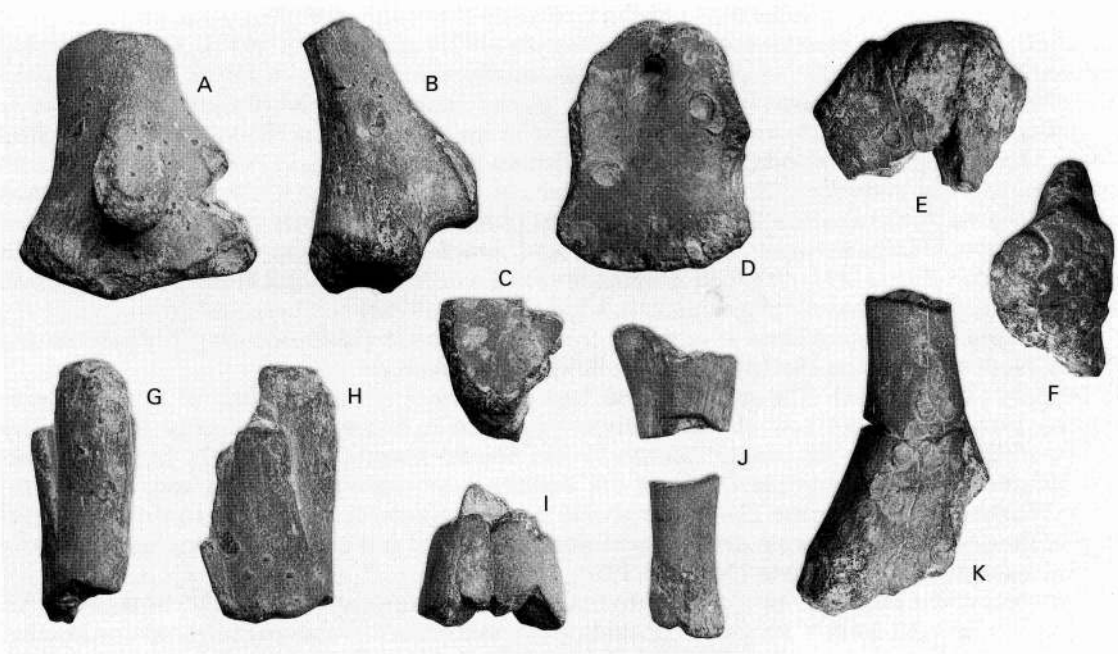
Eight caudal centra are preserved (SMC B55721–55728), six of which come from the anterior portion of the series (Text-fig. 4E). When arranged in sequence, the anterior caudals form a downwardly convex curve *c.*



TEXT-FIG. 4. *Anoplosaurus curtonotus*, a nodosaurid ankylosaur from the Gault Clay or Cambridge Greensand (Upper Albian) of Reach, near Cambridge, England. Paralectotypes: dentary and vertebral column. A_{1-3}, SMC B55670; left dentary in lateral, medial and dorsal views; ×0·75. B_{1-5}, SMC B55671–55675; cervical centra in lateral view; ×0·5. C_{1-13}, SMC B55676–55688; dorsal centra in lateral view; ×0·5. D_{1-6}, SMC B55710–55715; sacrum in dorsal view; ×0·5. E_{1-8}, SMC B55721–55728; caudal centra in lateral view; ×0·5.

160 mm long (Seeley 1879). The lateral surfaces for the transverse processes are well developed and there is some indication of the chevron facets near the posterior border of the centra. The articular faces occasionally display small notochordal processes.

Appendicular skeleton (Text-fig. 5A–K). The shoulder girdle is represented by an incomplete right scapula, a left coracoid and a fragmentary right coracoid (SMC B55729–55731). The scapula and coracoid are separate from



TEXT-FIG. 5. *Anoplosaurus curtonotus*, a nodosaurid ankylosaur from the Gault Clay or Cambridge Greensand (Upper Albian) of Reach, near Cambridge, England. Lectotype (A–B) and paralectotypes (C–K). A–B, SMC B55731; right scapula in lateral (A) and posterior views. C–D, SMC B55729–55730; right (C) and left (D) coracoids in lateral view. E–F, SMC B55732a; proximal portion of right humerus in posterior (E) and proximal (F) views. G–H, SMC B55734; proximal portion of left femur in lateral (G) and anterior (H) views. I, SMC B55735; distal portion of left femur in anterior view. J, SMC B55736–55737; two fragments of a left tibia in anterior view. K, SMC B55732b; distal portion of right humerus in posterior view. All ×0·4.

each other. The scapula is characterized by a central thumb-like acromion process, moderately displaced above the posterior edge of the glenoid (Text-fig. 5A–B). A small pre-spinous fossa is present anterior to the acromion process, as in derived nodosaurids (Coombs 1978*b*). An attempted reconstruction of the shoulder muscles of *A. curtonotus* made by Galton (1983, fig. 4) suggests that the origin of the M. supracoracoideus anterior was comparatively larger than that of *Struthiosaurus* and *Panoplosaurus*, but smaller than that of *Sauropelta*.

The coracoid is sub-rectangular or trapezoidal in shape, with the anterodorsal and anteroventral edges almost at a right angle (Text-fig. 5D). The anteroventral edge of the coracoid is wider than the posterodorsal edge (that which articulates with the scapula). The coracoid foramen is large, perforates the coracoid laterally, and opens on to the articular surface for the scapula (Nopcsa 1923).

The forelimb of *A. curtonotus* is known from two portions, one proximal and one distal, of a right humerus (SMC B55732a–b) (Text-fig. 5E–F, K). The humeral head is sub-oval and well separated from the triceps tubercle. The deltopectoral crest is broken. In proximal view, the bone is crescent-shaped. The distal end preserves a partial radial condyle. The reconstructed humeral length is *c.* 200 mm. Seeley (1879) also described a metacarpal and a phalanx (SMC B55733, B55742).

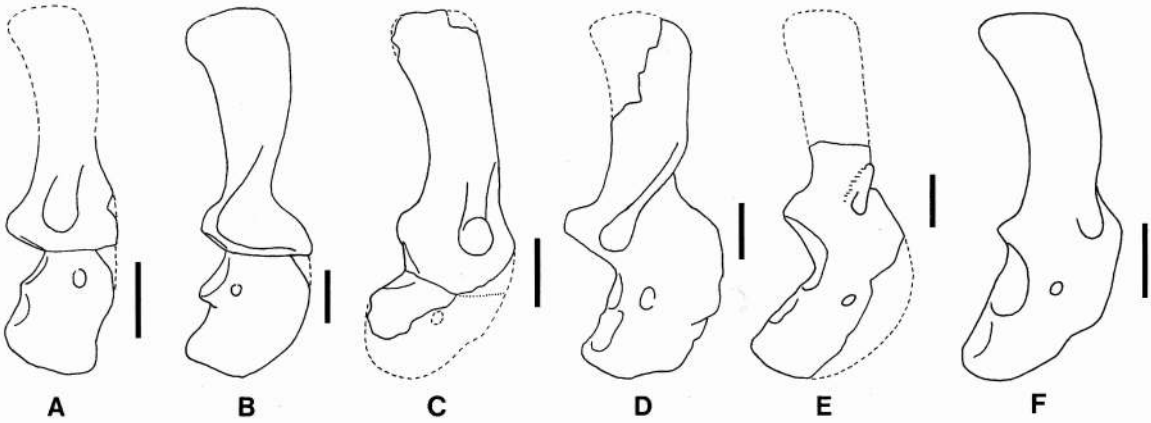
The hindlimb consists of the proximal and distal portions of a left femur (SMC B55734–55735), two sections of a left tibia (SMC B55736–55737), and four eroded metatarsals (SMC B55738–55741). The femur possesses a finger-like lesser trochanter, flattened anteroposteriorly, that is separated from the greater trochanter by a short, shallow cleft (Text-fig. 5G–H). Seeley (1879) estimated the total length of the femur as *c.* 300 mm. The left tibia is fragmentary, but appears to have been a slender bone bearing a prominent cnemial crest (Text-fig. 5J). The metapodials are too badly damaged to allow an accurate description.

Remarks. Seeley (1879, pp. 600–613, pls 34–35) described *Anoplosaurus curtonotus* in detail and regarded it as a small-sized, 'semi-erect' dinosaur. Nopcsa (1923) discussed the status of

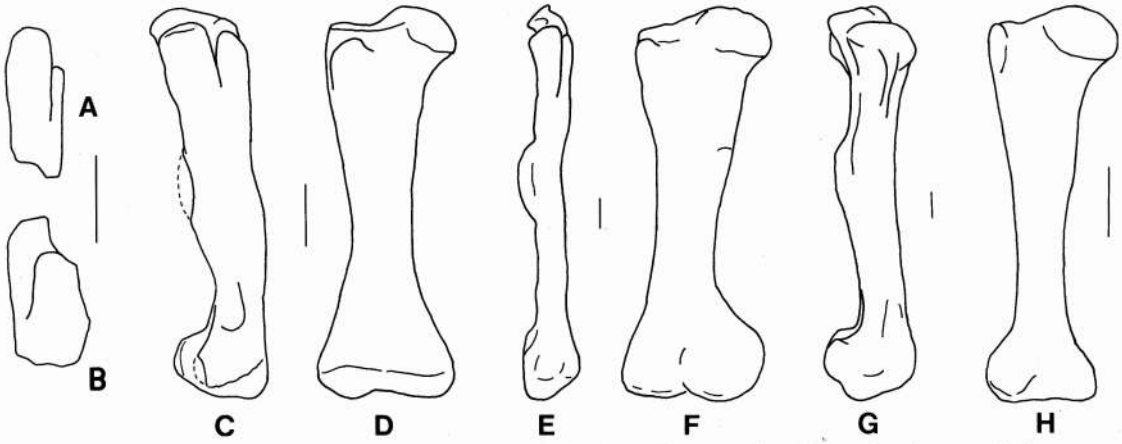
Anoplosaurus and removed some of the material to '*Acanthopholis*', including the dentary, scapula, coracoid, and femur, a practice followed by Coombs (1971) and Galton (1983). The relationship between *Anoplosaurus* and '*Acanthopholis*' was briefly discussed by Coombs (1971, p. 104). However, *Anoplosaurus curtonotus* is usually placed within the Ornithopoda, either as a camptosaurid (Nopcsa 1923; von Huene 1956), or as an iguanodontid (Kuhn 1936, 1964; Steel 1969). More recently, Brinkmann (1988) and Norman and Weishampel (1990) regarded it as an indeterminate iguanodontian. The original assignment of *A. curtonotus* to the Ornithopoda was probably based on the absence of associated dermal plates. However, these authors did not discuss either the relationships between '*Acanthopholis*' and *Anoplosaurus*, or the status of *Anoplosaurus curtonotus*. Von Zittel (1893) classified *Anoplosaurus* as a scelidosaurid, while Hennig (1915) referred it to the armoured dinosaurs (Ankylosauria *sensu* Coombs 1978*a*).

Here, *Anoplosaurus curtonotus* is removed from Ornithopoda (Iguanodontia) to Ankylosauria (family Nodosauridae) on the basis of the following eight features.

1. Dentary (Text-fig. 4A). The sinuous tooth row (see above) is characteristic of thyreophorans (Sereno 1986). The tooth row extends anteriorly, almost to the symphysis, as in the primitive nodosaurids *Sarcolestes*, *Silvisaurus*, *Sauropelta* and *Struthiosaurus* (Galton 1983). In iguanodonts and hadrosaurs, the anteriormost part of the dentary is edentulous (Norman and Weishampel 1990; Weishampel and Horner 1990). The alveoli in *A. curtonotus* form a single row on the dorsal edge of the dentary and show no development along the medial side of the lower jaw, as is common in *Iguanodon* and close relatives (Norman 1980, 1986).
2. Vertebral count (Text-fig. 4B–E). The vertebral series of *A. curtonotus* probably contained seven or eight cervicals, 13 dorsals, six sacrals (including two sacrocaudals) and an indeterminate number of caudals. This count is comparable to those of typical ankylosaurs, especially nodosaurids (Carpenter 1984; Coombs and Maryanska 1990), but differs from those of typical iguanodontians. In *Iguanodon* there are 11 cervicals, 17 dorsals (including one sacrodorsal), six or seven sacrals, and more than 30 caudals (Norman 1980, 1986).
3. Cervical vertebrae (Text-fig. 4B). The articular faces of the cervical centra are acoelous to slightly amphicoelous, as in ankylosaurs (Coombs 1978*a*; Coombs and Maryanska 1990). In ornithopods the cervical centra are opisthocoelous (e.g. Galton 1974; Norman and Weishampel 1990; Weishampel and Horner 1990).
4. Sacrum (Text-fig. 4D). The anterior sacral is longer than wide, as are the sacrocaudals. The mid-sacrals are shorter and wider in comparison. In *Iguanodon* the opposite arrangement occurs: the anterior and posterior sacrals are wider than long, whilst the mid-sacrals are longer than wide (Norman 1986). In addition, the general form of the sacrum is very similar to those of nodosaurid ankylosaurs such as *Polacanthus* (Blows 1987; Pereda-Suberbiola 1994).
5. Scapula (Text-figs 5A–B, 6A). The occurrence of a well developed pseudo-acromial process displaced towards the glenoid and the presence of a small pre-spinous fossa anterior to the scapular spine are considered to be derived conditions within the Nodosauridae (Coombs 1978*a*; Coombs and Maryanska 1990). These characters are absent in ornithopods.
6. Coracoid (Text-figs 5C–D, 6A). In nodosaurids the coracoid is relatively large compared with the scapula (scapula length being only around twice the length of the coracoid) (Coombs 1978*b*; Coombs and Maryanska 1990). By contrast, the coracoid of ornithopods is comparatively small, and the scapula is three to five times the length of the coracoid (e.g. Galton 1974; Norman and Weishampel 1990; Weishampel and Horner 1990). Although the scapula of *Anoplosaurus* is incomplete, the coracoid does seem to be relatively larger in this taxon than in ornithopods. Moreover, the coracoid of ornithopods possesses a hook-like sternal process (e.g. Galton 1974; Norman and Weishampel 1990; Weishampel and Horner 1990). A sternal process is also present in at least some ankylosaurids (e.g. *Euoplocephalus*, Coombs and Maryanska 1990; *Pinacosaurus* (= *Syrmosaurus viminicaudus*), Maleev 1954), but it is absent from the coracoids of *Anoplosaurus* (see above) and other nodosaurids (Coombs and Maryanska 1990).
7. Humerus (Text-fig. 5E–F, K). Nopcsa (1923) regarded this bone as camptosaurian-like but gave no characters to support this assignment. The humeral shaft of *Anoplosaurus curtonotus*, although



TEXT-FIG. 6. Comparison of the scapulocoracoids of nodosaurids in lateral view. A, *Anoplosaurus curtonotus*; B, *Hylaeosaurus armatus* (reconstructed using in part the holotype of '*Polacanthoides ponderosus*' [BMNH 2584]; C, *Struthiosaurus transylvanicus* (from Nopcsa 1929); D, *Sauropelta edwardsi* (from Coombs 1978*a*); E, *Texasetes pleurohalio* (from Coombs 1995); F, *Panoplosaurus mirus* (from Russell 1940). Scale bar represents 50 mm (A, C, E) or 100 mm (B, D, F).



TEXT-FIG. 7. Comparison of the femora of nodosaurids in lateral (A, C, E, G) and anterior (B, D, F, H) views. A–B, *Anoplosaurus curtonotus* (reversed drawing); C–D, '*Cryptodraco eumerus*' (from Galton 1983); E–F, *Polacanthus foxii* (from Pereda-Suberbiola 1994); G, *Sauropelta edwardsi* (from Coombs 1978*a*); H, *Struthiosaurus austriacus* (from Seeley 1881). Scale bars represent 50 mm.

fragmentary, does not show the sigmoidal curvature seen in ornithopods (Norman 1986), but is straight and more similar to the humerii of ankylosaurs (Coombs 1978*a*, 1978*b*) than to those of iguanodontids or camptosaurids.

8. Femur (Text-figs 5G–H, 7A). In '*Cryptodraco*' and *Polacanthus* (including *Hoplitosaurus*) the lesser trochanter is separated from the greater trochanter by a cleft which is deeper laterally than medially (Galton 1983) and the same is also true for *Texasetes* (Text-fig. 7). In other ornithischians (e.g. ornithopods and stegosaurs) the depth of the cleft is approximately the same both laterally and medially (Galton 1983). *Anoplosaurus* possesses the nodosaurid condition.

A number of other nodosaurid taxa are contemporary with *Anoplosaurus*, and are particularly well represented in North America. At least five nodosaurids are known from the upper Lower Cretaceous and lower Upper Cretaceous of North America: *Sauropelta edwardsi* from the Cloverly

Formation (Aptian–Albian) of Wyoming and Montana (Ostrom 1970; Carpenter 1984); *Silvisaurus condrayi* from the Dakota Formation (Cenomanian) of Kansas (Eaton 1960; Lund and Nelson 1990; J. J. Lund, pers. comm.); *Nodosaurus textilis* from the Mowry Shale or Thermopolis Formation (Albian) of Wyoming (Lull 1921); *Texasetes pleurohalio* and *Pawpawsaurus campbelli* from the Paw Paw Formation (Albian) of Texas (Coombs 1995; Lee 1996). In addition, Jacobs *et al.* (1994) described an undetermined juvenile nodosaurid from Texas that can be referred provisionally to *Texasetes* on anatomical (e.g. scapula and femur shape) and stratigraphical grounds. *Anoplosaurus curtonotus* may be distinguished from these other nodosaurids on the basis of the following characters.

1. A thumb-like acromion process centrally placed on the scapula, and moderately displaced toward the glenoid (Text-fig. 6). Within the Nodosauridae, the shape and position of the acromion process has taxonomic significance (Carpenter *et al.* 1995; Coombs 1995). *Anoplosaurus curtonotus* resembles *Texasetes pleurohalio* in the possession of a small acromion process that is directed toward the centre of the coracoid (Coombs 1995). However, the acromion of *Texasetes* is longer and more slender than that of *Anoplosaurus*. *Sauropelta edwardsi* possesses a short, compact acromion process, but, in comparison with *Anoplosaurus*, it is displaced posteriorly to lie above the glenoid (Ostrom 1970; Coombs 1978*a*). The acromion of *Panoplosaurus mirus* is blunt and knob-like, and almost continuous with the anterodorsal edge of the scapula (Sternberg 1921; Russell 1940; Carpenter 1990). In *Struthiosaurus*, the acromion is centrally located, but is an unusual hook-shaped structure (Seeley 1881; Nopcsa 1929). Finally, the scapulae of *Hylaeosaurus armatus* (including '*Polacanthoides ponderosus*'), *Polacanthus rudgwickensis* and *P. marshi* possess a transverse ridge-like acromion (Galton 1983; Pereda-Suberbiola 1993; Blows 1996). These latter forms, unlike the more derived nodosaurids, also differ from *Anoplosaurus* in lacking a pre-spinous fossa (Coombs 1978*a*, 1978*b*).

2. The coracoid of *Anoplosaurus curtonotus* differs in shape from those of other nodosaurids (Text-fig. 6). The anteroventral edge of the coracoid in *Anoplosaurus curtonotus* is wider than the posterodorsal one. Also, the sub-trapezoidal shape of the coracoid distinguishes it from the more rounded coracoids of other nodosaurids. The coracoid of *A. curtonotus* is longer (anterodorsal to posteroventral width) than wide (anteroventral to posterodorsal width), unlike the coracoid of most nodosaurids where it is approximately as long as it is wide (Coombs and Maryanska 1990). An isolated coracoid referred to *Edmontonia rugosidens* (Carpenter 1990) is sub-rectangular in shape and appears similar to that of *Anoplosaurus curtonotus*, but differs in the more pronounced curvature of the anteroventral edge, and the anterodorsal and posterovental borders run parallel to each other (whereas they are moderately concave in *Anoplosaurus curtonotus*).

3. Small, finger-like lesser trochanter, separated from the greater trochanter by a narrow, but short cleft (Text-fig. 7). The proximal end of the femur of nodosaurids is variable in form and this probably reflects slight differences in the way these taxa locomoted (*sensu* Galton 1983). In primitive nodosaurids the lesser trochanter is prominent and separated from the greater trochanter by a lateral groove. Unlike more derived nodosaurids (e.g. *Sauropelta*, *Edmontonia*) which have lost the lesser trochanter, the femora of '*Cryptodraco*', *Polacanthus*, *Texasetes*, *Struthiosaurus*, and *Anoplosaurus* retain a distinct lesser trochanter (Coombs 1978*a*, 1995; Galton 1983; Pereda-Suberbiola 1994). In *Anoplosaurus* this structure is a finger-like process that is comparatively smaller and more slender than that of '*Cryptodraco eumerus*', *Polacanthus foxii* or *P. marshi*. Also, the lateral cleft of *Anoplosaurus* is shallower than that of '*Cryptodraco*', and comparatively shorter than in the species of *Polacanthus*. In *Texasetes pleurohalio* and *Struthiosaurus austriacus*, the lesser trochanter is reduced and forms a splint-like projection (Coombs 1995).

The absence of armour in the type material of *Anoplosaurus* is surprising, as dermal armour is the most conspicuous feature of ankylosaurs (Coombs 1978*a*; Coombs and Maryanska 1990). However, the absence of osteoderms has been observed in juvenile nodosaurids (Jacobs *et al.* 1994) and juvenile stegosaurs (Galton 1982). This suggests that the ossification of scutes in thyreophorans occurs late in growth. We suggest that the absence of armour in the type material of *Anoplosaurus* may be explained by the juvenile status of the specimen. Considering the ontogenetic changes listed

by Galton (1982) and Coombs (1986), several other features of the type material support this contention, including: absence of fusion between the centra and the neural arches; the absence of fusion between the sacral ribs and the centra; articular faces of centra less expanded than in large vertebrae; coracoid and scapula not co-ossified; and the surfaces of the long bones are smooth. The lack of fusion of the splenial to the lower jaw, the unusual form of the coracoid foramen, and the small size of the specimens can also be interpreted as immature features (see Jacobs *et al.* 1994; Pereda-Suberbiola *et al.* 1995).

The rather fragmentary remains of *Anoplosaurus curtonotus* make the comparison of this form with other nodosaurids difficult. It is tempting to refer the other ankylosaur material from the Cambridge Greensand, and the other localities mentioned above, to *Anoplosaurus* due to the proximity of the localities, their similar ages, and the low range of variability seen in the material. This would also provide additional skeletal elements for comparison with other taxa. However, as the associations of this additional material are subject to some doubt, and none of this material shows any of the diagnostic characteristics of *Anoplosaurus*, we prefer to follow a more conservative approach, and limit our comparisons to the type material.

The lower jaw of *Anoplosaurus curtonotus* retains a tooth row that extends anteriorly almost to the symphysis. This condition is primitive for the Nodosauridae (Galton 1983). In *Silvisaurus* the extension of the tooth row to the anterior end of the mandible may be related to the occurrence of premaxillary teeth, and this may also be the case in some other nodosaurids (Ostrom 1970; Coombs 1971), although this suggestion cannot be confirmed at present.

The vertebral count of *Anoplosaurus* (as far as can be ascertained) is comparable to that of *Sauropelta edwardsi* (Carpenter 1984). The cervical series includes seven or, more probably, eight vertebrae. The dorsal count is not accurately known in nodosaurids: 13 free dorsal vertebrae were probably present in *Anoplosaurus*, whilst *Sauropelta* has been reconstructed with 12 (Carpenter 1984). As interpreted herein, the sacrum of *Anoplosaurus* is composed of six vertebrae, including four true sacrals and two sacrocaudals. *Sauropelta* (Ostrom 1970; Carpenter 1984), *Silvisaurus* (Eaton 1960; Lund and Nelson 1990; J. J. Lund, pers. comm.) and *Polacanthus* (Pereda-Suberbiola 1994) also possess four true sacrals. In more derived nodosaurids such as *Nodosaurus* (Lull 1921), *Niobrarasaurus* (Carpenter *et al.* 1995), and *Edmontonia* (Gilmore 1930; Carpenter 1990) the number of true sacrals is reduced to three. This suggests that there is an evolutionary trend toward a reduction in the sacral count in nodosaurids (Pereda-Suberbiola 1994; *contra* Coombs 1995).

The scapula of *Anoplosaurus* displays a caudally displaced knob-like acromion process with a small pre-spinous fossa anterior to it. This character is thought to unite the more derived nodosaurids (Coombs 1978*a*). *Hylaeosaurus* and *Polacanthus* retain the primitive condition: a transverse ridge-like acromion (Galton 1983). The sub-rectangular shape of the coracoid is unusual amongst nodosaurids, but a similar pattern has been described in *Edmontonia rugosidens* (Carpenter 1990). The humeral head in *Anoplosaurus* is not well differentiated from the shaft, a condition also seen in *Niobrarasaurus* and primitive nodosaurids (Carpenter *et al.* 1995). The femur of *Anoplosaurus* retains a distinct lesser trochanter, the primitive condition for the Nodosauridae (Galton 1983). The lesser trochanter appears to be more prominent than in *Sauropelta*, *Texasetes* and *Struthiosaurus*, but comparatively smaller than those of '*Cryptodraco*' and *Polacanthus*.

Anoplosaurus appears to be a relatively primitive nodosaurid, as indicated by the anterior extent of the dentary tooth row, the lack of differentiation of the humeral head from the shaft, the occurrence of four sacral vertebrae, and the presence of a distinct lesser trochanter on the femur. Some of these features are shared with other primitive nodosaurids, such as *Silvisaurus*. However, *Anoplosaurus* is distinct from, and more derived than, *Hylaeosaurus* and *Polacanthus* because its scapula has a prominent acromion process and a small pre-spinous fossa (features that are absent in *Hylaeosaurus armatus* and *Polacanthus marshi*). These scapular characters are also present in *Struthiosaurus*, but the latter appears to be more derived than *Anoplosaurus* because the M. scapulohumeralis anterior is further reduced (see Galton 1983, fig. 4). In addition, the lesser trochanter of the femur is less prominent (a more derived feature) in *Struthiosaurus* than in *Anoplosaurus*.

Anoplosaurus differs from *Sauropelta* in a number of features, especially in the morphology of the scapulocoracoid and femur (see above). *Texasetes* also retains several of the primitive characters seen in *Anoplosaurus*, but the two forms can be distinguished by the different morphologies of the acromion process of the scapula and the lesser trochanter of the femur (Coombs 1995). The similarities between *Anoplosaurus* and the juvenile nodosaurid from Texas (cf. *Texasetes*) may be due to the immature nature of the specimens, although the possibility of a close relationship should not be excluded. The type specimens of *Silvisaurus condrayi*, *Nodosaurus textilis* and *Pawpawsaurus campbelli* lack many of the elements that make up the type of *Anoplosaurus*, so a thorough comparison between these forms is not possible.

Anoplosaurus appears to be an intermediate taxon between very primitive nodosaurids such as *Hylaeosaurus* and *Polacanthus*, and a number of more derived representatives of the Nodosauridae, including *Struthiosaurus*, *Sauropelta*, *Edmontonia* and *Panoplosaurus*. However, further diagnostic material is needed to resolve the relationship of *Anoplosaurus* to other Albian–Cenomanian nodosaurids such as *Silvisaurus* and *Texasetes*.

ADDITIONAL NAMED ANKYLOSAUR MATERIAL FROM THE GAULT CLAY AND CAMBRIDGE GREENSAND

In addition to *Anoplosaurus curtonotus*, Seeley (1869, 1871) referred many more dinosaur remains from the Cambridge Greensand to the genera *Anoplosaurus* and '*Acanthopholis*', and he erected several new species names for the reception of this material. However, many of these species are based on composite, non-diagnostic material. This section lists those taxa which include some ankylosaur material in their type series. Additional ankylosaur material that was not formally described by Seeley is listed subsequently.

All known European ankylosaurs are referable to the family Nodosauridae (Coombs and Maryanska 1990). This would suggest that all isolated ankylosaur material from Europe is also referable to this family (W. T. Blows, pers. comm.). However, we prefer not to refer the following material to Nodosauridae, unless it bears diagnostic characters of this family, and follow the more conservative approach of referring to this material as Ankylosauria indeterminate.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA Owen, 1842
ORNITHISCHIA Seeley, 1887
ANKYLOSAURIA Osborn, 1923

incertae sedis

1869 *Acanthopholis macrocercus* Seeley *partim*, p. xvii, p. 24.
1879 *Syngonosaurus macrocercus* Seeley *partim*; Seeley, p. 621, figs 6–8.
1889 *Syngonosaurus macrocercus* Seeley *partim*; Lydekker, p. 41.
1969 *Anoplosaurus macrocercus* (Seeley) *partim*; Steel, p. 16.
1971 *Acanthopholis macrocercus* Seeley *partim*; Coombs, p. 99.
1978*a* *Acanthopholis macrocercus* Seeley *partim*; Coombs, p. 169.
1990 *Acanthopholis horridus* Huxley; Coombs and Maryanska, p. 475.

Material. SMC B55599–55609, dermal armour, e.g. keeled scutes.

Locality and horizon. Near Cambridge, Cambridgeshire, England; Cambridge Greensand, Upper Albian (Rawson *et al.* 1978; N. C. Fraser, pers. comm.).

Remarks. '*Acanthopholis macrocercus*' (Seeley 1869, pp. xvii, 24) was named on the basis of one cervical, nine dorsal, four sacral and five caudal vertebrae, a fragmentary humerus and tibia, four metatarsals, two phalanges, 11 osteoderms, and three undetermined bones (SMC B55570–55609), although many of these specimens, including vertebrae and metapodials (SMC B55588–55598) could

not be located during this study. Seeley (1879, p. 621, figs 6–8) later referred all of this material, with the exception of a single dorsal vertebra and a fragmentary tibia to the new genus '*Syngonosaurus*' as '*S. macrocercus*'. Seeley (1879, p. 622) noted that the specimens were obtained by a Mr Farren at the same time and from the same washing although 'there is no positive evidence that the armour was found with the bones'. The dorsal vertebra (SMC B55579) rejected from '*Syngonosaurus*' was referred to '*Acanthopholis*' by Seeley (1879, p. 623), who regarded it 'as... accidentally mixed with the other remains'. Seeley suggested that '*Syngonosaurus*' may have been armoured, but also stated that '*Syngonosaurus*' shared a close relationship with '*Eucercosaurus*', which was defined as a bipedal, unarmoured, iguanodontid-like dinosaur. Lydekker (1889, pp. 43–44) referred several vertebrae from the Cambridge Greensand (BMNH R460, four dorsal vertebrae and a sacral centrum) to '*S. macrocercus*' (also see Lydekker 1890, pp. 254–255), but this material is indeterminate, and cannot be assigned to the Ankylosauria with any confidence. Lydekker regarded '*Syngonosaurus*' as 'a dinosaur apparently allied to *Hylaeosaurus*' and provisionally referred it to the Scelidosauridae (Lydekker 1890, p. 254). Nopcsa (1923, p. 194) cast doubt on the validity of '*Syngonosaurus*' and considered that it 'certainly includes remains of *Anoplosaurus*, while the rest may belong to *Eucercosaurus*'.

'*Acanthopholis macrocercus*' is based on composite material; most of the vertebral remains (SMC B55571–55579, B55582–55586) belong to ornithopods, although the armour can be assigned to the Ankylosauria. Several other elements (SMC B55570, B55580–81, B55587) cannot be identified beyond the level of Dinosauria indeterminate. '*Acanthopholis macrocercus*' (*partim*), based on ornithopod material, was recently regarded as a *nomen dubium* represented by indeterminate iguanodontian material (Norman and Weishampel 1990), whilst '*Acanthopholis macrocercus*' (*partim*), based on ankylosaur material, was regarded as conspecific with '*A. horridus*' (Coombs and Maryanska 1990). We regard '*A. macrocercus*' as a *nomen dubium* based on indeterminate ornithopod and ankylosaur material. The ankylosaur material displays no diagnostic characters above the level of Ankylosauria indeterminate. Furthermore, none of that material can be assigned to '*A. horridus*' with any degree of confidence.

ANKYLOSAURIA Osborn, 1923

incertae sedis

1869	*Acanthopholis platypus* Seeley *partim*, p. xvii, p. 21.
1871	*Acanthopholis platypus* Seeley *partim*; Seeley, pp. 315–316.
1969	*Acanthopholis platypus* Seeley *partim*; Steel, p. 54.
1971	*Acanthopholis platypus* Seeley *partim*; Coombs, p. 99.
1978*a*	*Acanthopholis horridus* Huxley; Coombs, p. 169.
1990	*Acanthopholis horridus* Huxley; Coombs and Maryanska, p. 475.

Material. SMC B55454, phalanx; SMC B55455–55460, caudal centra.

Locality and horizon. Bottisham, near Cambridge, Cambridgeshire, England; Cambridge Greensand, Upper Albian (Rawson *et al.* 1978; N. C. Fraser, pers. comm.).

Remarks. Seeley (1869, pp. xvii, 21) erected '*Acanthopholis platypus*' on the basis of six caudal centra, one chevron, five articulated metapodials and one phalanx (SMC B55449–55461) from Bottisham, a small village east of Cambridge. The metapodials (SMC B55449–55453, metatarsals I–V) were described and figured by Seeley (1871, pl. 7), and later referred to the sauropod *Macrurosaurus* (Seeley 1876, p. 444). This interpretation was followed by Nopcsa (1923). However, in a hand-written note made by Seeley in his copy of the 1876 paper (document A.6.22: 20 in the library of the Department of Earth Sciences, University of Cambridge) he stated that 'this view cannot now be sustained' and regarded all of the material of '*Acanthopholis platypus*' as absolutely distinct from *Macrurosaurus semnus*. Coombs (1971, pp. 101–102) compared the metapodials of '*A. platypus*' to those of other dinosaurs and decided that the evidence for either referral was

inconclusive. More recently, McIntosh (1990) tentatively referred the metapodials to *Macrurosaurus semnus* (provisionally listing '*A. platypus*' as a junior synonym of *M. semnus*). The metapodials display a number of sauropod synapomorphies, including a short, robust metatarsal I and a 'funnel-shaped' metatarsal V (Upchurch 1993). Several other syntypes, a phalanx and several caudal vertebrae described by Seeley (1871), may belong to an ankylosaur, but are too incomplete for a definitive taxonomic designation, and a fragmentary neural spine (SMC B55461) cannot be identified beyond the level of Dinosauria indeterminate.

Coombs and Maryanska (1990) listed '*A. platypus*' as a junior synonym (*partim*) of '*Acanthopholis horridus*'. However, no diagnostic characteristics support this referral. Moreover, the type material displays no diagnostic characters and '*Acanthopholis platypus*' should be regarded as a *nomen dubium* based on indeterminate ankylosaur and sauropod material.

ANKYLOSAURIA Osborn, 1923

incertae sedis

1869 *Acanthopholis stereocercus* Seeley *partim*, p. xvii, p. 24.
1879 *Acanthopholis stereocercus* Seeley *partim*; Seeley, p. 628.
1923 *Acanthopholis* Huxley; Nopcsa, p. 7, figs 11–13.
1969 *Acanthopholis stereocercus* Seeley *partim*; Steel, p. 54.
1971 *Acanthopholis stereocercus* Seeley *partim*; Coombs, p. 99.
1990 *Acanthopholis horridus* Huxley; Coombs and Maryanska, p. 475.

Material. SMC B55560, B55562, B55566–55568, caudal vertebrae; B55569, dermal spine.

Locality and horizon. Near Cambridge, Cambridgeshire, England; Cambridge Greensand, Upper Albian (Rawson *et al.* 1978; N. C. Fraser, pers. comm.).

Remarks. The type specimen of '*Acanthopholis stereocercus*' consists of 11 fragmentary vertebrae and one dermal plate (Seeley 1869, pp. xvii, 24; SMC B55558–B55569). Seeley (1879) later used part of this material (SMC B55561, SMC B55563–55565) to erect '*Anoplosaurus major*' (see below). In the same paper, Seeley retained two dorsal and five caudal vertebrae, and a fragmentary spine (SMC B55558–55560, 55562, 55566–55569) under the name '*Acanthopholis stereocercus*'. The vertebrae were labelled '*Acanthopholis*' by Nopcsa during his visit to Cambridge in 1922, and one of them was figured in his article on '*Acanthopholis*' (Nopcsa 1923, pl. 7, figs 11–13). Some of these vertebrae and the dermal spine probably belong to Ankylosauria, although the possibility that some of the material represents ornithopods cannot be excluded (see Brinkmann 1988). The ornithopod material (SMC B55558–55559, dorsal vertebrae; '*A. stereocercus*' *partim*) has been listed as indeterminate iguanodontian (Norman and Weishampel 1990) whilst the ankylosaur material was regarded as conspecific with '*Acanthopholis horridus*' (Coombs and Maryanska 1990). We regard '*A. stereocercus*' as a *nomen dubium* based on indeterminate ornithopod and ankylosaur remains. No characters support the referral of the ankylosaur material to '*A. horridus*'.

ANKYLOSAURIA Osborn, 1923

incertae sedis

1879 *Anoplosaurus major* Seeley, p. 631.
1923 *Acanthopholis* Huxley; Nopcsa, p. 194.
1969 *Anoplosaurus major* Seeley; Steel, p. 15.
1988 *Anoplosaurus major* Seeley; Brinkmann, p. 67.
1990 *Anoplosaurus major* Seeley; Norman and Weishampel, p. 531.

Material. SMC B55561, cervical vertebra.

Locality and horizon. Near Cambridge, Cambridgeshire, England; Cambridge Greensand, Upper Albian (Rawson *et al.* 1978; N. C. Fraser, pers. comm.).

Remarks. Seeley (1879, p. 631) named a second and larger species of *Anoplosaurus* on the basis of one cervical and three caudal centra (SMC B55561, B55563–55565), that he removed from the original types of '*Acanthopholis stereocercus*' (Seeley 1869, pp. xvii, 24). Seeley (1879, p. 632) also mentioned that 'a small fragment of a nearly smooth dermal plate, probably referable to '*Acanthopholis*', was collected with these remains, but it is too imperfect to yield any useful characters'. This specimen (SMC B55569) was also a syntype of '*A. stereocercus*'. Nopcsa (1923) referred these vertebrae to a juvenile individual of '*Acanthopholis*'. The cervical centrum is amphicoelous and is more similar to the centra of ankylosaurs than to those of ornithopods. However, the caudal centra (SMC B55563–55565) are very elongate and may belong to an ornithopod. '*Anoplosaurus major*' has been listed as a *nomen dubium*, Iguanodontia indeterminate (Norman and Weishampel 1990), and we also regard this taxon as a *nomen dubium*, based on a mixture of ornithopod and ankylosaur remains.

ADDITIONAL ANKYLOSAUR MATERIAL FROM THE GAULT CLAY AND CAMBRIDGE GREENSAND

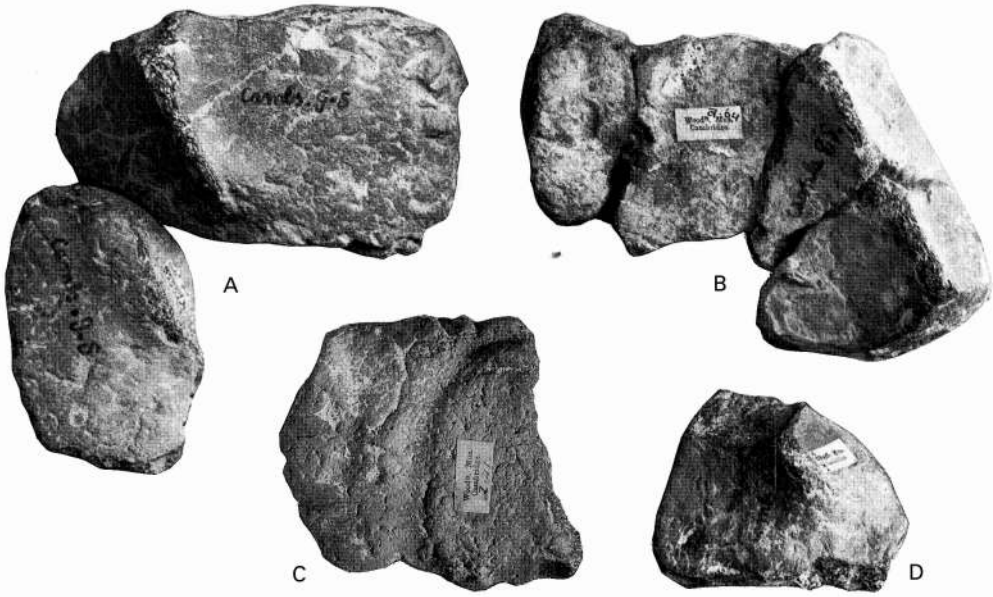
In addition to the remains described above, a number of other specimens from the Cambridge Greensand, including vertebrae, dorsal armour, and other elements, also pertain to the Ankylosauria and are listed and discussed below. Many of these specimens have previously been referred to '*Acanthopholis*'; however, as this taxon possesses no diagnostic characteristics and should be regarded as a *nomen dubium* (see above) we adopt a conservative approach to the identification of these remains and regard all of the following material as Ankylosauria or Nodosauridae indeterminate. Some of this material has been mentioned by previous authors (e.g. Seeley 1869; Nopcsa 1923; Coombs 1978*a*), but much is previously undescribed.

Seeley applied informal names to several collections of dinosaur material in the Sedgwick Museum. These names were never published, but were hand-written on the labels which accompany the material. Although these names were not formally proposed, they are mentioned here as Seeley obviously regarded this material as congeneric with '*Acanthopholis*'. Unless stated otherwise, the localities from which this material was recovered are unknown (listed simply as 'Cambridge Greensand, near Cambridge' in the alpha-numeric catalogue of the Sedgwick Museum).

A collection of bones listed (as 'Reptile – dinosaur') by Seeley (1869, p. 22), but not described, is labelled '*Acanthopholis hughesii*', but this binomen has never been formally proposed and should be disregarded. The material consists of vertebrae, including six dorsals, seven caudals and a transverse process, four metapodials, three phalanges and seven dermal plates (SMC B55463–55490). The phalanges were informally referred to *Anoplosaurus* by Nopcsa during his visit to Cambridge in 1922 (as recorded in the alpha-numeric catalogue of the Sedgwick Museum). Indeterminate ornithopod (SMC B55463–55467, dorsal vertebrae) and ankylosaur remains are present in this assemblage, in addition to a number of specimens which cannot be identified beyond the level of Dinosauria indeterminate (SMC B55476–55478, B55480–55483, metapodial bones). The specimens referable to the Ankylosauria include five keeled scutes and a pair of fragmentary spines (SMC B55484–55490) and, more tentatively, some vertebrae (SMC B55468–55475) and a metapodial bone (SMC B55479).

Seeley (1869, p. 23) catalogued a series of bones including five dorsal and six caudal centra (one caudal, SMC B55493, could not be located), three transverse processes, one rib, two chevrons, one metatarsal, two phalanges, a fragmentary ilium?, 13 dermal plates and two undetermined bones (SMC B55491–55526), which he referred to as a 'reptile – dinosaur' and labelled as '*Acanthopholis keepingi*'. However, this binomen has never been formally proposed and should be disregarded. Several different specimens appear to have been mixed together at the time of collection, and this assemblage contains the indeterminate remains of an ornithopod (SMC B55494, B55503, dorsal and caudal vertebrae), an ankylosaur, and a turtle (SMC B55509, undetermined limb fragment). A

number of other specimens cannot be identified beyond the level of Dinosauria indeterminate (SMC B55495–55496, B55501–55502, B55504–55508, B55510–55513, chevrons, rib remains, metapodial and phalanges). Ankylosaur remains in this assemblage include dorsal vertebrae (SMC B55491–55492), caudal vertebrae (SMC B55497–55500), and some elements of dermal armour: keeled scutes, polygonal plates and ossicles (SMC B55514–55526; Text-fig. 8A–D). A dorsal vertebra and 13 plates from this assemblage were provisionally referred to '*Acanthopholis*' by Coombs

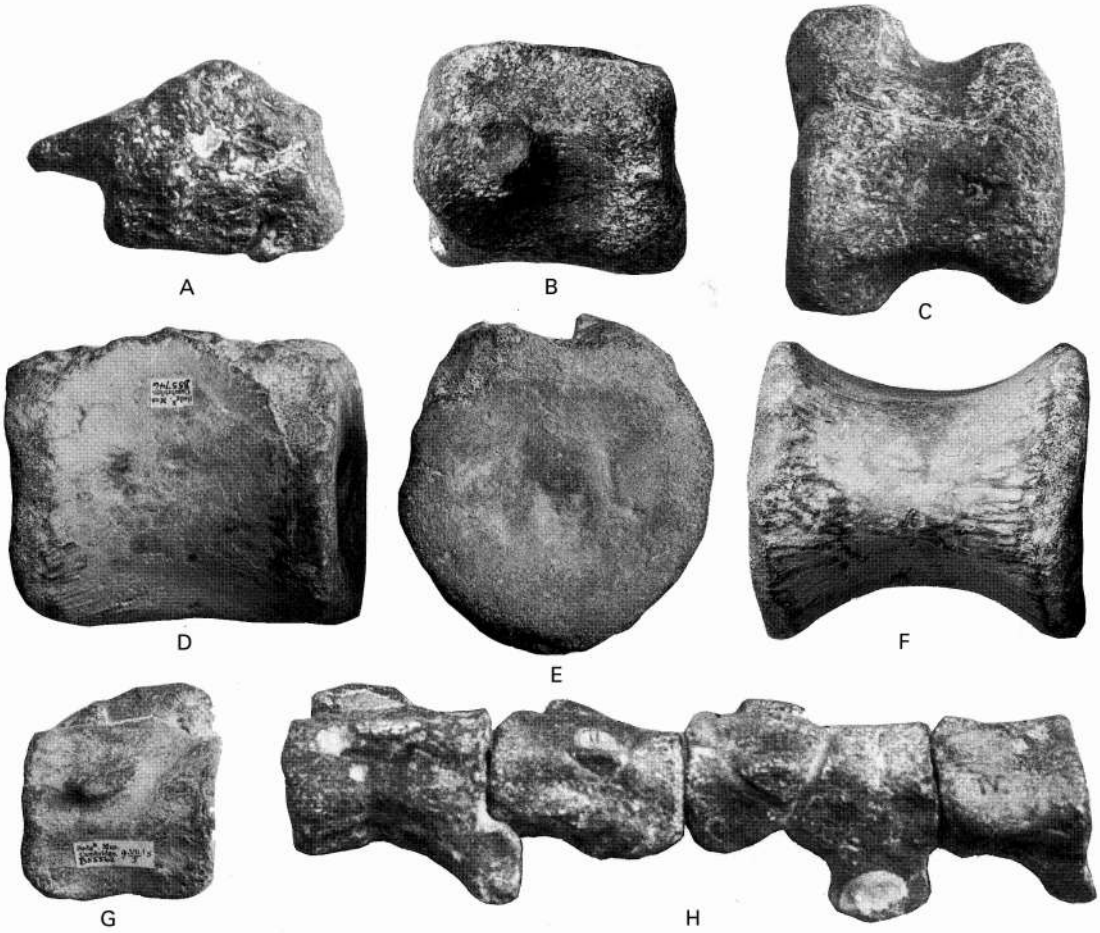


TEXT-FIG. 8. Indeterminate ankylosaur dermal armour from the Gault Clay or Cambridge Greensand (Upper Albian), near Cambridge, England. A, SMC B55522–55523; fragments of a polygonal, crested plate from the cervical? region. B, SMC B55525, a fragmentary, polygonal ?cervical plate. C, SMC B55517; mosaic fragment formed by the fusion of small ossicles and scutes. D, SMC B55526; armour fragment. All ×0·65.

(1978*a*), although there are no diagnostic characteristics to support this referral. Several fragmentary dermal elements are interesting as they appear to be portions of large polygonal, crested plates (SMC B55518–55520, B55522–55523, B55525–55526; Text-fig. 8A–B, D). These elements may represent fragments of one or more cervical rings similar to those of *Silvisaurus* (Eaton 1960, fig. 20), *Edmontonia* (Matthew 1922; Gilmore 1930, pl. 5), and some ankylosaurids (Carpenter 1982). Another fragmentary osteoderm (SMC B55517) consists of irregular ossicles and scutes co-ossified into a single plate. The scutes are separated from each other by a shallow groove (Text-fig. 8C) and the general morphology of the plate bears some resemblance to that of the cervical half-rings of *Struthiosaurus*, where the medial region of the cervical rings is made up of a fused mosaic of small, irregular ossicles (Seeley 1881; Nopcsa 1929). This specimen could be part of a cervical (or sacral?) plate, but is too fragmentary for an accurate identification.

Vertebrae (Text-fig. 9A–H). Most of the dinosaur vertebrae from the Cambridge Greensand consist of isolated centra. As Coombs (1971, p. 103) pointed out, the isolated and abraded vertebral centra of ankylosaurs and ornithopods are difficult to distinguish. Thus, the referral of these specimens to the Ankylosauria should be regarded as provisional.

Seeley (1879) referred a small isolated axis (SMC B55389) from the vicinity of Haslingfield, near Cambridge to '*Acanthopholis*' (Text-fig. 9A). The specimen is badly eroded, but preserves a long



TEXT-FIG. 9. Miscellaneous ankylosaur vertebrae from the Cambridge Greensand (Upper Albian) near Cambridge, England. A, SMC B55389; isolated axis in left lateral view. B–C, SMC B55745; cervical centrum in left lateral (B) and ventral (C) views. D–F, SMC B55746; dorsal centrum in left lateral (D), anterior (E), and ventral (F) views. G, SMC B55562; caudal centrum in left lateral view. H, SMC B55368–55371; four caudal vertebrae with fused chevrons in left lateral view. All ×0·65.

odontoid process fused to the axis centrum and the base of the neural arch. The articular surfaces for the ribs suggest that they were double-headed. The odontoid process is relatively long, projects forward a considerable distance, is triangular in dorsal view, and is separated from the centrum by a distinct 'neck' (Seeley 1879). Separation of the atlas and axis is common amongst primitive nodosaurids (Coombs 1978*a*), and, in general form, the axis is similar to that of *Polacanthus* (SMC B53371; Blows 1987). This specimen is thus probably referable to the Ankylosauria, although its fragmentary nature precludes unequivocal identification.

A few isolated ankylosaur cervical vertebrae and ribs are known from the Cambridge Greensand. The most complete vertebra (SMC B55745) was described and figured by Nopcsa (1923, pl. 7, figs 5–7; see Text-fig. 9B–C). The centrum is rounded, with the anterior articular surface flat and oval, and with well developed parapophyses placed laterally about the midline near the anterior border of the centrum: this vertebra is probably an anterior cervical. Nopcsa (1923, pl. 7, fig. 15) also

described a Y-shaped proximal portion of cervical rib (SMC B55391) and referred it to '*Acanthopholis*'.

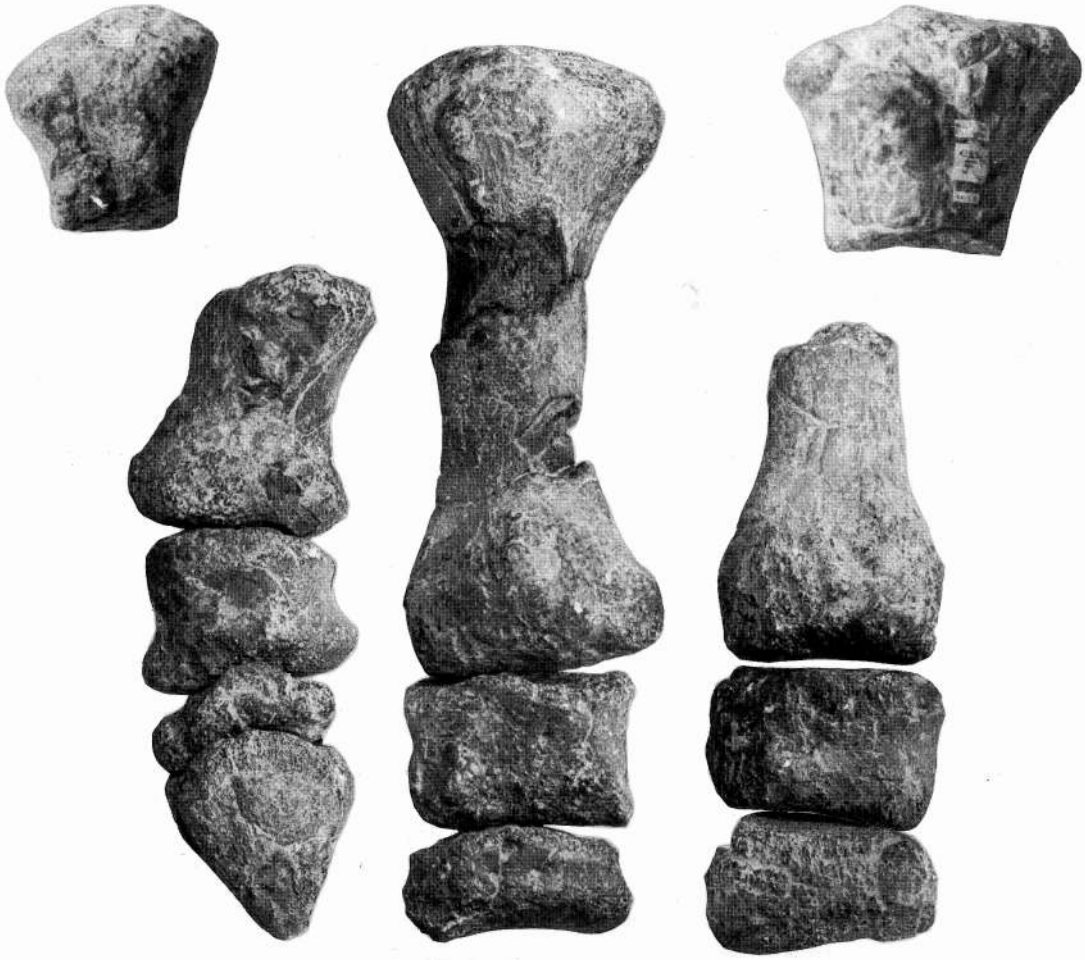
A number of large dorsal centra has also been recovered (Text-fig. 9D–F). These vertebrae were collected over several years by a number of different people and probably represent several different individuals (SMC B55746–55748, BGS GSM 114581–114583, JB.231). Nopcsa (1923, pl. 7, figs 8–10; pl. 8, fig. 1) described some of these centra, referring them to '*Acanthopholis*'. The centra are acoelous, hourglass-shaped in ventral view, and possess sub-circular articular faces, which may occasionally display small notochordal processes. A blunt keel is variably developed on the ventral surface of the centrum, and the neural canal is relatively small and circular. These vertebrae are similar to other ankylosaur dorsals collected from the junction of the Folkestone Beds and the Gault Clay of Kent (see below), but differ from those of *Polacanthus* and *Struthiosaurus* in that they are relatively shorter and more massively built. Moreover, the centra of the Cambridge form display less lateral compression and less excavation of the centrum by the neural canal than in *Polacanthus*. However, these features may be growth related or due to individual variation, and cannot be used as taxonomic characteristics with any degree of confidence.

During his visit to Cambridge in 1922, Nopcsa informally referred a portion of sacrum with two fused vertebrae (SMC B55752) to '*Acanthopholis*' (although he did not mention the specimen in his paper of 1923). However, this material is too fragmentary for accurate identification.

Ankylosaur caudal vertebrae are relatively common in the Cambridge Greensand (SMC B55356–55360, B55368–55371, B55754–55757; BMNH 35280–35282), and represented by material from many different individuals (Text-fig. 9G–H). As Nopcsa (1923) noted, the middle and posterior caudals have polygonal centra in cross section, with longitudinal ridges laterally and a narrow, deep groove on the ventral surface. Transverse processes are present on the caudal centra for almost the entire length of the tail and the chevrons are fused to the centra intervertebrally (Nopcsa 1923, pl. 7, figs 11–13). These last two characters also occur in *Struthiosaurus*, but are absent in *Hylaeosaurus* and *Polacanthus* (Pereda-Suberbiola 1994).

Pes (*or manus?*) (Text-fig. 10). Nopcsa (1923, pl. 7, fig. 4; pl. 8, fig. 2) described a collection of autopodial bones (SMC B55436–55448) from Haslingfield, near Cambridge, as a hind foot of '*Acanthopholis*'. The remains consist of one complete metapodial, four partial metapodials (some of which are almost certainly parts of the same element) and seven phalanges, including one ungual. These were formerly listed as metatarsals and phalanges of a dinosaur by Seeley (1869, p. 21), and referred to '?*Acanthopholis*' by Coombs (1978*a*, p. 169). One of the metapodials (SMC B55441) was not figured by Nopcsa (1923) and is currently missing. The bones were apparently found in association and may belong to the left foot of the same individual (see below). If so, the arrangement of the preserved metapodials and phalanges suggests that four, or perhaps five, digits were present. Three toes are relatively complete and probably represent digits II, III and IV. The complete phalangeal count cannot be determined, but digit II consists of three phalanges, and digits III and IV have at least three (and possibly more) phalanges. The most complete metapodial (digit III?) is elongate and slender, with expanded proximal and distal ends. The phalanges are short, massive disc-like bones; the only ungual phalanx is triangular, longer than wide and tapers distally to a rounded tip.

The structure of the autopodium indicates a mediportal to graviportal dinosaur, as in nodosaurids (stegosaurs and large ankylosaurids are regarded as fully graviportal by Coombs 1978*c*). In comparison with other nodosaurids the metapodials from Haslingfield are longer and more slender than those of *Sauropelta* (Ostrom 1970; Carpenter 1984), *Nodosaurus* (Coombs 1971), *Niobrarasaurus* (Carpenter *et al.* 1995), and *Edmontonia* (Lambe 1919) and are relatively gracile compared with those of ankylosaurids (Maleev 1956; Coombs 1986) and stegosaurs (Gilmore 1914). The elongated form and slenderness of the metapodials suggest that they are probably metatarsals, and not metacarpals (see Coombs and Maryanska 1990). On the other hand, the proximal phalanges are all similar in length, a character seen frequently in the ankylosaur manus, but rarely present in the pes (Carpenter 1984). These differences might imply that the phalanges were from the

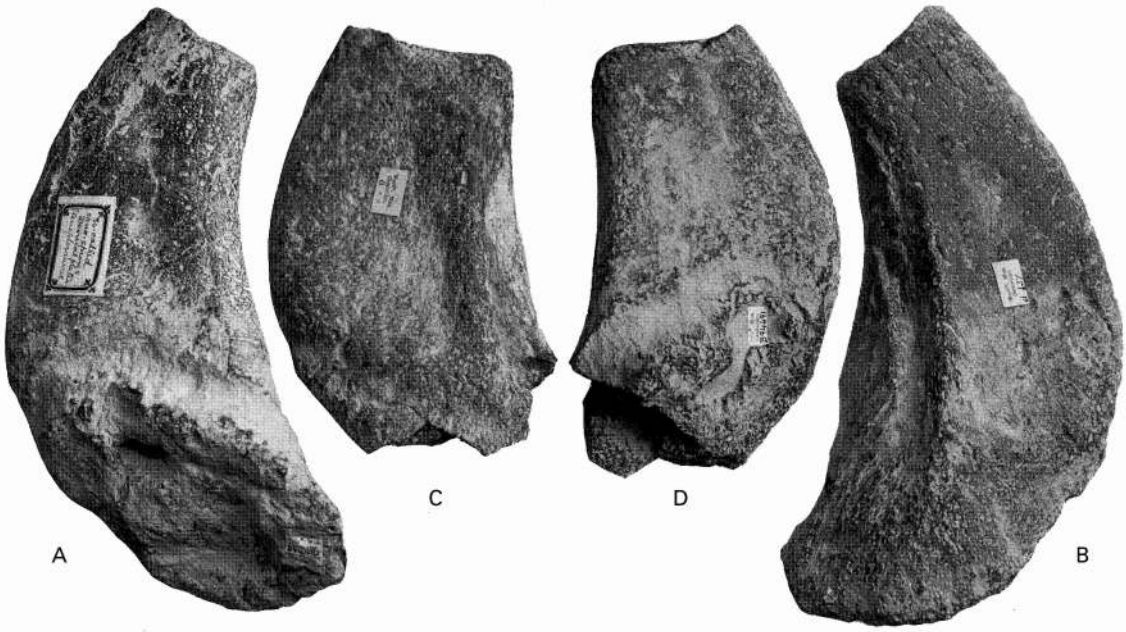


TEXT-FIG. 10. Associated autopodial bones (SMC B55436–55440, B55442–55448; metapodials and phalanges) of an indeterminate ankylosaur from the Cambridge Greensand (Upper Albian) of Haslingfield, near Cambridge, England, in dorsal view; ×0·5.

manus and the remaining elements from the pes; thus, the remains could come from either the same or different individuals. However, if the autopodial bones are from the same individual and the same foot, then the general form and proportions of the foot distinguish this pes from those of other ankylosaurs. Unfortunately, the referral of this pes to *Anoplosaurus* is not possible due to the lack of comparable elements in the two specimens. There is also a slight possibility that the pes is composed of elements from more than one individual. Although the foot is distinctive we feel that it is better to adopt a conservative approach and identify it as Nodosauridae indet.

Other isolated metapodials (SMC B55412, B55760–55763) from the Cambridge Greensand may be referable to the Ankylosauria and some phalanges regarded by Nopcsa (1923, pl. 7, fig. 3) as hadrosaurian may also belong to this taxon (SMC B55400, B55744; referred to as '*Acanthopholis*?' by Coombs 1978*a*, p. 169).

Armour (Text-fig. 11). The Cambridge Greensand has yielded numerous dermal elements, including four kinds of armour: conical scutes, low- and high-keeled scutes, and tall spines. A pair of large



TEXT-FIG. 11. Indeterminate nodosaurid spines from the Gault Clay or Cambridge Greensand (Upper Albian) near Cambridge, England. A–B, SMC B94492; in ventral (A) and dorsal (B) views. C–D, SMC B94491; in dorsal (C) and ventral (D) views. All ×0·5.

conical spines (SMC B94491–94492) represent some of the most complete armour elements to be recovered from this deposit (Text-fig. 11A–D). The spines are spur-shaped, compressed dorso-ventrally, and show sharp anterior and posterior edges. The solid basal region is strongly oblique to the shaft and separated from it by a constricted area forming a well-developed neck. The distal ends of the spines are missing, but their height (170 mm in the most complete specimen, as preserved) is almost twice the basal diameter (90 mm), a feature typical of nodosaurids (Coombs and Maryanska 1990). In overall morphology they resemble the shoulder spines of *Edmontonia* (Gilmore 1930; Carpenter 1990), and, more especially, *Sauropelta* (Carpenter 1984), although in contrast to those two taxa, the spines from the Cambridge Greensand are not straight, but strongly curved. We identify these spines as Nodosauridae indeterminate and assume that they were placed on the flanks of the trunk over the shoulder region and projected laterally.

A number of isolated scutes are known from the Cambridge Greensand including some that are flat, oval and bear an asymmetrical medial keel that extends longitudinally (SMC B55385–55386, B55540, B55544–55546, B55750, B55764–55766; Nopcsa 1923, pl. 8, fig. 3). These scutes are typical of thyreophoran dinosaurs and were arranged in transverse and longitudinal rows along the dorsal surface of the trunk (Coombs 1978*a*). Other scutes are conical, with a high dorsal keel (SMC B55387–55388, B55538–55539) and bear some resemblance to those of the basal thyreophoran *Scelidosaurus* (Owen 1863). These scutes are ventrally excavated and were probably located on the flanks of the body and tail. Finally, a few scutes are triangular, hollow-based and bear a high keel that projects distally, overhanging the posterior margin of the basal region (SMC B55384, B55541–55543, B55749, B55751, B55767; Nopcsa 1923, pl. 7, fig. 16; pl. 8, fig. 4). These plates probably come from the tail. The presence of high-keeled scutes on the tail is common in European nodosaurids, including *Polacanthus*, *Struthiosaurus* and possibly *Hylaeosaurus* (Pereda-Suberbiola 1994). Several other ankylosaur scutes from the Cambridge Greensand were collected by A. J. Jukes-Browne and associates, and they are currently housed at Keyworth (BGS GSM JB.201–203, 205–206; BGS GSM 114589).

NON-ANKYLOSAUR MATERIAL FROM THE GAULT CLAY AND CAMBRIDGE GREENSAND, PREVIOUSLY REFERRED TO 'ACANTHOPHOLIS'

'*Acanthopholis eucercus*' (Seeley 1879) was erected on the basis of six caudal centra (SMC B55552–55557) that were originally catalogued as 'reptile – dinosaur' by Seeley (1869, p. 24). Seeley (1879, p. 632) noted a close resemblance between these caudals and those of '*Acanthopholis horridus*', although he pointed out features that he believed distinguished the two taxa. Nopcsa (1923, p. 194) regarded the vertebrae as ornithopod-like and removed them to *Anoplosaurus*, whilst Coombs and Maryanska (1990) considered '*Acanthopholis eucercus*' to be doubtfully ankylosaurian. The caudal vertebrae appear to belong to an ornithischian, but are too fragmentary for accurate identification. They do not exhibit any diagnostic characteristics and thus the name '*Acanthopholis eucercus*' is a *nomen dubium*.

JUNCTION OF THE FOLKESTONE BEDS AND THE GAULT CLAY (LOWER ALBIAN), KENT

Casey (1961, p. 546) reported the discovery of dinosaurian remains, referred to as *Camptosaurus*, in the nodule beds at the junction of the Folkestone Beds and the Gault Clay (bed 8, upper *mammillatus* Zone; uppermost Lower Albian) at Wrotham, west Kent. The material (BMNH R6703) consists of three well-preserved dorsal vertebrae, rib fragments, and armour elements.

The dorsal centra are acoelous to slightly amphicoelous and have rounded articular faces (Text-fig. 12). The pedicels of the neural arches are robustly constructed, the neural canal is small, and the dorsal surface of the centrum (the ventral floor of the canal), is gently excavated. These vertebrae closely resemble the dorsal vertebrae from the Cambridge Greensand described above, and differ from those of *Polacanthus* and *Struthiosaurus* in the same ways: the centra are shorter and more massive than those of *Struthiosaurus*, and bear shorter and more robust neural pedicles, and the dorsal surfaces of the centra are not deeply excavated by the neural canal, whilst the reverse is true in *Polacanthus*. The dermal armour recovered from Wrotham is typically ankylosaurian, and consists of a very fragmentary hollow-based spine and the fragments of at least three small, oval, low-keeled scutes.

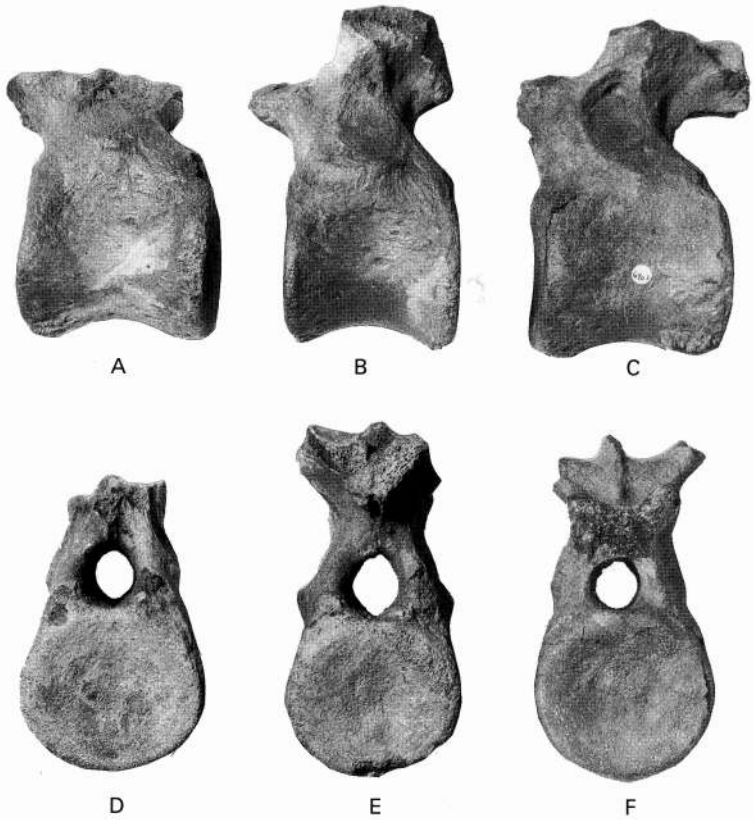
Casey (1961, p. 530) also mentioned the discovery of an isolated vertebra of '*Acanthopholis horridus*' in a glauconitic sand horizon within the Folkestone Beds (main *mammillatus* Zone; Lower Albian) at Copt Point, Folkestone, east Kent. The specimen (BGS GSM Zk 4775) closely resembles an anterior caudal referred to '*Acanthopholis horridus*' (Seeley 1879, fig. 2).

All of this material from Wrotham and Folkestone is referred to the Ankylosauria on the basis of the form of the vertebrae and the associated occurrence of dermal plates.

CONCLUSIONS

Revision of the ankylosaurian material from the Albian–Cenomanian formations of England suggests that: (1) *Anoplosaurus curtonotus* Seeley, 1879, usually regarded as a *nomen dubium*, represented by indeterminate iguanodontian material, can be referred to the Ankylosauria; *A. curtonotus* possesses several characters typical of the Nodosauridae and is provisionally regarded as a valid species, differing from other nodosaurids in the morphology of the pectoral girdle and the femur; (2) as previously suggested by other authors, the type material of '*Acanthopholis horridus*' Huxley, 1867 exhibits no unambiguous characteristics which support the validity of this taxon; hence, '*A. horridus*' should be regarded as a *nomen dubium*, and the type material identified as Nodosauridae indeterminate; (3) other species of '*Acanthopholis*' or *Anoplosaurus* erected by Seeley are based on indeterminate material and are considered in this work as *nomina dubia*.

No unequivocally ankylosaurid material could be identified from any of the Albian–Cenomanian localities mentioned above. This observation is consistent with existing palaeobiogeographical models of ankylosaur distribution, which suggest that ankylosaurids were restricted to Asia and North America (Maryanska 1977; Coombs 1978*a*; Coombs and Maryanska 1990). The absence of



TEXT-FIG. 12. Indeterminate ankylosaur dorsal vertebrae (BMNH R6703) from the nodule beds at the junction of the Folkestone Beds and the Gault Clay (Albian), Wrotham, Kent, England, in left lateral (A, C, E), posterior (B, D) and anterior (F) views. All ×0·4.

morphological variability in the ankylosaurian material from the Albian–Cenomanian of Kent and Cambridgeshire supports the suggestion that only a single species of nodosaurid was present in England at this time (e.g. Coombs 1971). This contrasts with the high diversity of nodosaurids (at least five species) known from the upper Lower and lower Upper Cretaceous of North America. Among European nodosaurids, *Anoplosaurus* occupies an intermediate phylogenetic position between the Wealden forms such as *Hylaeosaurus* and *Polacanthus* and the Late Cretaceous *Struthiosaurus*. The conservative character of *Anoplosaurus* relative to contemporary North American representatives, such as *Sauropelta*, may be explicable in terms of the geographical isolation of European faunas from the Albian (Le Loeuff 1991; Russell 1993), an event caused by the opening of the northern part of the North Atlantic Ocean (Doré 1991; Russell 1995).

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REFERENCES

ANONYMOUS 1865. A new Wealden dragon. Order, Sauria; Family, Dinosauria; Genus, *Polacanthus*; Species, *foxii*. *Illustrated London News*, **47** (no. 1334, Sept. 16th, 1865), 270.

BLOWS, W. T. 1987. The armoured dinosaur *Polacanthus foxii* from the Lower Cretaceous of the Isle of Wight. *Palaeontology*, **30**, 557–580.

—— 1996. A new species of *Polacanthus* (Ornithischia; Ankylosauria) from the Lower Cretaceous of Sussex, England. *Geological Magazine*, **133**, 671–682.

BRINKMANN, W. 1988. Zur Fundgeschichte und Systematik der Ornithopoden (Ornithischia, Reptilia) aus der Ober-Kreide von Europa. *Documenta Naturae*, **45**, 1–157, pls 1–8.

CARPENTER, K. 1982. Skeletal and dermal armour reconstruction of *Euoplocephalus tutus* (Ornithischia: Ankylosauridae) from the Late Cretaceous Oldman Formation of Alberta. *Canadian Journal of Earth Sciences*, **19**, 689–697.

—— 1984. Skeletal reconstruction and life restoration of *Sauropelta* (Ankylosauria: Nodosauridae) from the Cretaceous of North America. *Canadian Journal of Earth Sciences*, **21**, 1491–1498.

—— 1990. Ankylosaur systematics: example using *Panoplosaurus* and *Edmontonia* (Ankylosauria: Nodosauridae). 281–298. *In* CARPENTER, K. and CURRIE, P. J. (eds). *Dinosaur systematics: approaches and perspectives*. Cambridge University Press, Cambridge, 318 pp.

—— DILKES, D. and WEISHAMPEL, D. B. 1995. The dinosaurs of the Niobrara Chalk Formation (Upper Cretaceous, Kansas). *Journal of Vertebrate Paleontology*, **15**, 275–297.

—— KIRKLAND, J., MILES, C., CLOWARD, K. and BURGE, D. 1996. [Abstract] Evolutionary significance of new ankylosaurs (Dinosauria) from the Upper Jurassic and Lower Cretaceous, Western Interior. *Journal of Vertebrate Paleontology* (*Supplement*), **16**, 25A.

CASEY, R. 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology*, **3**, 487–621.

COOMBS, W. P. JR 1971. The Ankylosauria. Unpublished Ph.D. dissertation, Columbia University, New York. University Microfilms International no. 72-1291, Ann Arbor, Michigan.

—— 1978*a*. The families of the ornithischian dinosaur order Ankylosauria. *Palaeontology*, **21**, 143–170.

—— 1978*b*. Forelimb muscles of the Ankylosauria (Reptilia, Ornithischia). *Journal of Paleontology*, **52**, 642–658.

—— 1978*c*. Theoretical aspects of cursorial adaptation in dinosaurs. *Quarterly Review of Biology*, **53**, 393–418.

—— 1986. A juvenile dinosaur referable to the genus *Euoplocephalus* (Reptilia, Ornithischia). *Journal of Vertebrate Paleontology*, **6**, 162–173.

—— 1990. Teeth and taxonomy in ankylosaurs. 269–279. *In* CARPENTER, K. and CURRIE, P. J. (eds). *Dinosaur systematics: approaches and perspectives*. Cambridge University Press, Cambridge, 318 pp.

—— 1995. A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Lower Cretaceous of Texas. *Journal of Vertebrate Paleontology*, **15**, 298–312.

—— and MARYANSKA, T. 1990. Ankylosauria. 456–483. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 733 pp.

DONG, ZHIMING. 1993. An ankylosaur (ornithischian dinosaur) from the Middle Jurassic of the Junggar Basin, China. *Vertebrata PalAsiatica*, **31**, 258–265.

DORÉ, A. C. 1991. The structural foundation and evolution of Mesozoic seaways between Europe and the Arctic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **87**, 441–492.

EATON, T. H. JR 1960. A new armoured dinosaur from the Cretaceous of Kansas. *Paleontological Contributions from the University of Kansas, Vertebrata*, **25**, 1–24.

ETHERIDGE, R. 1867. On the stratigraphical position of *Acanthopholis horridus*, a new reptile from the Chalk Marl. *Geological Magazine*, **4**, 67–69.

GALTON, P. M. 1974. The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. *Bulletin of the British Museum* (*Natural History*), *Geology*, **25**, 1–152, pls 1–2.

—— 1982. Juveniles of the stegosaurian dinosaur *Stegosaurus* from the Upper Jurassic of North America. *Journal of Vertebrate Paleontology*, **2**, 47–62.

—— 1983. Armoured dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of Europe. *Palaeontographica, Abteilung A*, **182**, 1–25, pls 1–6.

GILMORE, C. W. 1914. Osteology of the armoured Dinosauria in the United States National Museum, with special reference to the genus *Stegosaurus*. *Bulletin of the United States National Museum*, **89**, 1–136, pls 1–37.

—— 1930. On dinosaurian reptiles from the Two Medicine Formation of Montana. *Proceedings of the United States National Museum*, **77**, 1–39, pls 1–10.

HART, M. B. 1973. Foraminiferal evidence for the age of the Cambridge Greensand. *Proceedings of the Geologists' Association*, **84**, 65–82.

HENNIG, E. 1915. *Kentrosaurus aethiopicus*. Die Stegosaurier-Funde von Tendaguru Deutsch-Ostafrika. II. Historisch-systematische Einführung. *Palaeontographica Supplement*, **7**, 103–253, pls 11–14.

HUENE, F. von 1956. *Paläontologie und Phylogenie der Niederen Tetrapoden*. Fischer, Jena, xii + 716 pp.

HUXLEY, T. H. 1867. On *Acanthopholis horridus*, a new reptile from the Chalk Marl. *Geological Magazine*, **4**, 65–67, pl. 5.

—— 1870. On the classification of the Dinosauria, with observations on the Dinosauria of the Trias. *Quarterly Journal of the Geological Society, London*, **26**, 32–51.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE 1985. *International Code of Zoological Nomenclature*. Third Edition. International Trust for Zoological Nomenclature/British Museum (Natural History)/University of California Press, London, Berkeley and Los Angeles, 338 pp.

JACOBS, L. L., WINKLER, D. A., MURRY, P. A. and MAURICE, J. M. 1994. A nodosaurid scutelling from the Texas shore of the Western Interior Sea. 337–346. *In* CARPENTER, K., HIRSCH, K. F. and HORNER, J. R. (eds). *Dinosaur eggs and babies*. Cambridge University Press, Cambridge, 372 pp.

JUKES-BROWNE, A. J. 1875. On the relations of the Cambridge Gault and Greensand. *Quarterly Journal of the Geological Society, London*, **31**, 256–315, pls 14–15.

—— 1903. *Memoirs of the Geological Survey of the United Kingdom. The Cretaceous rocks of Britain. Vol. II. The Lower Chalk and Middle Chalk of England*. HMSO, London, 568 pp., 1 pl.

KIRKLAND, J. I. and CARPENTER, K. 1994. North America's first pre-Cretaceous ankylosaur (Dinosauria) from the Upper Jurassic Morrison Formation of Western Colorado. *Brigham Young University, Geology Studies*, **10**, 25–42.

KUHN, O. 1936. Ornithischia (Stegosauriis excluses). *In* QUENSTEDT, W. (ed.). *Fossilium Catalogus, I. Animalia*, 78. Junk, 's-Gravenhage, 81 pp.

—— 1964. Ornithischia (Supplementum I). *In* WESTPHAL, F. (ed.). *Fossilium Catalogus, I. Animalia*, 105. Junk, 's-Gravenhage, 80 pp.

LAMBE, L. M. 1919. Description of a new genus and species (*Panoplosaurus mirus*) of armoured dinosaur from the Belly River Beds of Alberta. *Transactions of the Royal Society of Canada, Series 3*, **13**, 39–50, pls 1–12.

LE LOEUFF, J. 1991. The Campano-Maastrichtian vertebrate faunas from southern Europe and their relationships with other faunas in the world; palaeobiogeographical implications. *Cretaceous Research*, **12**, 93–114.

LEE YUONG-NAM 1996. A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Paw Paw Formation (Late Albian) of Texas. *Journal of Vertebrate Paleontology*, **16**, 232–245.

LULL, R. S. 1921. The Cretaceous armoured dinosaur *Nodosaurus textilis* Marsh. *American Journal of Science*, **1**, 97–127, pls 1–4.

LUND, J. J. and NELSON, M. E. 1990. Preliminary comparative analysis of two nodosaurid ankylosaurs (Ornithischia) from the Dakota Formation (Cenomanian) of Kansas. *Abstracts with Programs, South-Central Section, Geological Society of America*, **22**, 13–14.

LYDEKKER, R. 1888*a*. *Catalogue of the fossil Reptilia and Amphibia in the British Museum. Part I. Containing the orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, and Proterosauria*. British Museum of Natural History, London, xxviii + 309 pp.

—— 1888*b*. Note on a new Wealden iguanodont and other dinosaurs. *Quarterly Journal of the Geological Society, London*, **44**, 46–61, pl. 3.

—— 1889. On the remains and affinities of five genera of Mesozoic reptiles. *Quarterly Journal of the Geological Society, London*, **45**, 41–59, pl. 2.

—— 1890. *Catalogue of the fossil Reptilia and Amphibia in the British Museum. Part IV. Containing the orders Anomodontia, Ecaudata, Caudata, and Labyrinthodontia; and supplement*. British Museum of Natural History, London, xxiii + 295 pp.

McINTOSH, J. S. 1990. Sauropoda. 345–401. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 733 pp.

MALEEV, E. A. 1954. [Armoured dinosaurs from the Upper Cretaceous of Mongolia. Family Syrmosauridae.] *Trudy Paleontologicheskogo Instituta Akademie Nauk S.S.S.R.*, **48**, 142–170. [In Russian].

—— 1956. [Armoured dinosaurs from the Upper Cretaceous of Mongolia. Family Ankylosauridae.] *Trudy Paleontologicheskogo Instituta Akademie Nauk S.S.S.R.*, **62**, 51–91. [In Russian].

MANTELL, G. A. 1833. Observations on the remains of the *Iguanodon*, and other fossil reptiles, of the strata of Tilgate Forest in Sussex. *Proceedings of the Geological Society, London*, **1**, 410–411.

MARSH, O. C. 1890. Additional characters of the Ceratopsidae with notice of new Cretaceous dinosaurs. *American Journal of Science, Series 3*, **39**, 418–426, pls 5–7.

MARYANSKA, T. 1977. Ankylosauridae (Dinosauria) of Asia. *Palaeontologica Polonica*, **37**, 85–151, pls 19–36.

MATTHEW, W. D. 1922. A super-dreadnought of the animal world, the armoured dinosaur *Palaeoscincus*. *Natural History*, **22**, 333–342.

NOPCSA, F. 1901. Synopsis und Abstammung der Dinosaurier. *Földtani Közlöny*, **31**, 247–279, pl. 1.

—— 1923. Notes on the British dinosaurs. Part IV. *Acanthopholis*. *Geological Magazine*, **60**, 193–199, pls 7–8.

—— 1929. Dinosaurierreste aus Siebenbürgen. V. *Geologica Hungarica* (*ser. palaeontologica*), **4**, 1–76, pls 1–6.

NORMAN, D. B. 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* from the Lower Cretaceous of Bernissart (Belgium). *Mémoires de l'Institut royal des Sciences naturelles de Belgique*, **178**, 1–105.

—— 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **56**, 281–372.

—— and FAIERS, T. 1996. On the first partial skull of an ankylosaurian dinosaur from the Lower Cretaceous of the Isle of Wight, southern England. *Geological Magazine*, **133**, 299–310.

—— and WEISHAMPEL, D. B. 1990. Iguanodontid and related ornithopods. 510–533. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 733 pp.

OSBORN, H. F. 1923. Two Lower Cretaceous dinosaurs from Mongolia. *American Museum Novitates*, **95**, 1–10.

OSTROM, J. H. 1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. *Bulletin of the Peabody Museum of Natural History*, **35**, 1–234, pls 1–27, 7 charts, 1 map.

OWEN, R. 1842. Report on British fossil reptiles. Part II. *Reports of the British Association for the Advancement of Science*, **11**, 60–204.

—— 1858. Monograph on the fossil Reptilia of the Wealden and Purbeck formations. Part 4. Dinosauria (*Hylaeosaurus*). *Monograph of the Palaeontographical Society*, **10** (43), 8–26, pls 4–11.

—— 1861. Monograph on the fossil Reptilia of the Lias formations. Part 1. *Scelidosaurus harrisonii*. *Monograph of the Palaeontographical Society*, **13** (56), 1–14, pls 1–6.

—— 1863. Monograph on the fossil Reptilia of the Lias formations. Part 2. *Scelidosaurus harrisonii* Owen of the lower Lias. *Monograph of the Palaeontographical Society*, **14** (60), 1–26, pls 1–11.

PENNING, W. H. and JUKES-BROWNE, A. J. 1881. *Memoirs of the Geological Survey of United Kingdom. Geology of the Neighbourhood of Cambridge*. HMSO, London, 184 pp., 7 pls.

PEREDA-SUBERBIOLA, J. 1993. *Hylaeosaurus*, *Polacanthus*, and the systematics and stratigraphy of Wealden armoured dinosaurs. *Geological Magazine*, **130**, 767–781.

—— 1994. *Polacanthus* (Ornithischia, Ankylosauria), a transatlantic armoured dinosaur from the Early Cretaceous of Europe and North America. *Palaeontographica, Abteilung A*, **232**, 133–159, pls 1–5.

—— ASTIBIA, H. and BUFFETAUT, E. 1995. New remains of the armoured dinosaur *Struthiosaurus* from the Late Cretaceous of the Iberian peninsula (Laño locality, Basque-Cantabric basin). *Bulletin de la Société Géologique de France*, **166**, 207–211.

—— and GALTON, P. M. 1994. A revision of the cranial features of the dinosaur *Struthiosaurus* Bunzel (Ornithischia: Ankylosauria) from the Late Cretaceous of Europe. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **191**, 173–200.

RAWSON, P. F., CURREY, D., DILLEY, F. C., HANCOCK, J. M., KENNEDY, W. J., NEALE, J. W., WOOD, C. J. and WORSSAM, B. C. 1978. A correlation of Cretaceous rocks in the British Isles. *Special Report of the Geological Society of London*, **9**, 1–70.

ROMER, A. S. 1956. *Osteology of the reptiles*. University of Chicago Press, Chicago, xxi + 772 pp.

RUSSELL, D. A. 1993. The role of Central Asia in dinosaurian biogeography. *Canadian Journal of Earth Sciences*, **30**, 2002–2012.

—— 1995. China and the lost worlds of the dinosaurian era. *Historical Biology*, **10**, 3–12.

RUSSELL, L. S. 1940. *Edmontonia rugosidens* (Gilmore), an armoured dinosaur from the Belly River series of Alberta. *University of Toronto Studies, Geological Series*, **43**, 3–28, pls 1–8.

SEELEY, H. G. 1869. *Index to the Fossil Remains of Aves, Ornithosauria, and Reptilia from the Secondary Strata arranged in the Woodwardian Museum of the University of Cambridge*. Deighton, Bell and Co., Cambridge, x + 143 pp.

—— 1871. On *Acanthopholis platypus* (Seeley), a pachypod from the Cambridge Upper Greensand. *Annals and Magazine of Natural History*, **8**, 305–318, pl. 7.

—— 1876. On *Macrurosaurus* (Seeley), a long tailed animal with procoelous vertebrae from the Cambridge Upper Greensand, preserved in the Woodwardian Museum of the University of Cambridge. *Quarterly Journal of the Geological Society, London*, **32**, 440–444.

—— 1879. On the Dinosauria of the Cambridge Greensand. *Quarterly Journal of the Geological Society, London*, **35**, 591–635, pls 34–35.

—— 1881. The reptile fauna of the Gosau Formation preserved in the Geological Museum of the University of Vienna. *Quarterly Journal of the Geological Society, London*, **37**, 620–707, pls 27–31.

—— 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London*, **43**, 165–171.

SERENO, P. C. 1986. Phylogeny of the bird-hipped dinosaurs (Order Ornithischia). *National Geographic Research*, **2**, 234–256.

STEEL, R. 1969. Ornithischia. *Handbuch der Paläoherpetologie*, **15**, 1–84.

STERNBERG, C. M. 1921. A supplementary study of *Panoplosaurus mirus*. *Transactions of the Royal Society of Canada, Series 3*, **15**, 93–102.

SWINTON, W. E. 1970. *The dinosaurs*. Wiley, New York, 331 pp.

UPCHURCH, P. 1993. The anatomy, phylogeny and systematics of the sauropod dinosaurs. Unpublished Ph.D. Thesis, University of Cambridge.

WEISHAMPEL, D. B. and HORNER, J. R. 1990. Hadrosauridae. 534–561. *In* WEISHAMPEL, D. B., DODSON, P. and OSMÓLSKA, H. (eds). *The Dinosauria*. University of California Press, Berkeley, 733 pp.

ZITTEL, K. A. von 1893. *Traité de Paléontologie. III. Paléozoologie, Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. Doin, Paris, xii + 894 pp. [French edition by C. Barrois, original German edition published in 1890, Oldenbourg, Munchen and Leipzig].

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ICHNOLOGICAL EVIDENCE FOR THE USE OF THE FORELIMB IN IGUANODONTID LOCOMOTION

by JOANNA L. WRIGHT

ABSTRACT. Most modern reconstructions of iguanodontids in a quadrupedal walking posture show the forelimbs placed slightly closer to the midline than the hindlimbs, with the dorsal surface of the manus facing forwards. This posture is problematical because it would have required rotation of the radius around the ulna leading to distortion and dislocation of the joints at the wrist or elbow. Some unusual trackways from the Purbeck Limestone Group (Upper Jurassic–Lower Cretaceous, UK) which show manus impressions are attributed herein to iguanodontids, challenging previous ideas regarding placement of the manus during the locomotion of these dinosaurs. The manus impressions are oriented with the palmar surfaces facing inwards towards the trackway midline, thus digit I would have faced anteriorly rather than medially. This obviates the need for unnatural twisting of the bones of the lower forelimbs. In addition, these trackways show foot emplacement patterns characteristic of a facultative quadruped. The manus impressions lie in two lines on either side of the single line formed by the pes impressions, indicating that, when walking quadrupedally, the forefeet were placed in a wider trackway than the hindfeet.

THE Purbeck Limestone Group of Dorset, UK, has yielded one of the richest mid Mesozoic terrestrial biotas (Benton and Spencer 1995; Howse and Milner 1995). It also contains one of the most diverse dinosaur footprint assemblages in Britain (Ensom 1995), exposed largely in the numerous building stone quarries that formerly operated in this area. The great majority of documented finds of footprints are from the Middle Purbeck, from horizons now considered to be of earliest Cretaceous (Berriasian) age (Lake and Shepherd-Thorn 1987; Allen and Wimbledon 1991).

The first mention of dinosaur footprints in Dorset was as a footnote to an account of footprints in the Wealden of Sussex (Beckles 1854). Very few published reports on Purbeck footprints were made throughout the rest of the nineteenth century, but by the end of it footprints were known to occur at several horizons in the group (Mansell-Pleydell 1896). Occasional discoveries were made in the first half of this century (Ensom 1995), but it was in the 1960s that some of the most important dinosaur trackways were found. Delair (1960) recorded the first occurrence of a pentadactyl footprint, later recognized as being of pterosaurian origin (Wright *et al.* 1997). Also in this decade, several trackways of both theropods and ornithopods were discovered, five of which were collected by museums (Delair 1966; Ensom 1995). Important recent finds include 120^2 m of track-bearing limestone found at Townsend Road, Swanage (Ensom 1982), large quadrupedal tracks from Sunnydown Farm (Ensom 1987) and sauropodan tracks found at Keates Quarry in January 1997.

Ensom (1995) has recorded 148 separate dinosaur footprint occurrences, many of which are isolated prints found along the coast. Trackways of more than three or four consecutive prints are very rare, but tracks of all the major groups of dinosaurs known from the Lower Cretaceous – theropods, ornithopods, nodosaurids and sauropods – have been found. Trackways from the Purbeck Limestone Group are important because the uppermost Jurassic–lowermost Cretaceous is an interval from which track sites are scarce elsewhere. The fauna from the Purbeck Limestone Group is one of the richest mid Mesozoic continental tetrapod assemblages known (Howse and Milner 1995).

The trackways described in this paper were discovered in the summer of 1961 in Dorset, southern England (Charig and Newman 1962; Newman 1990) in rocks of the Intermarine Member of the

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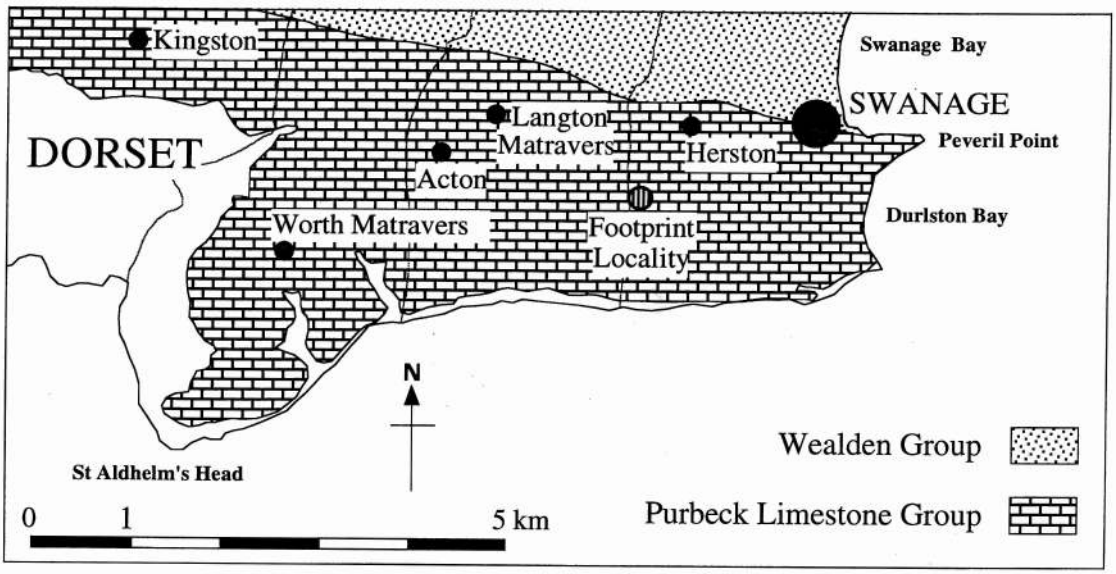


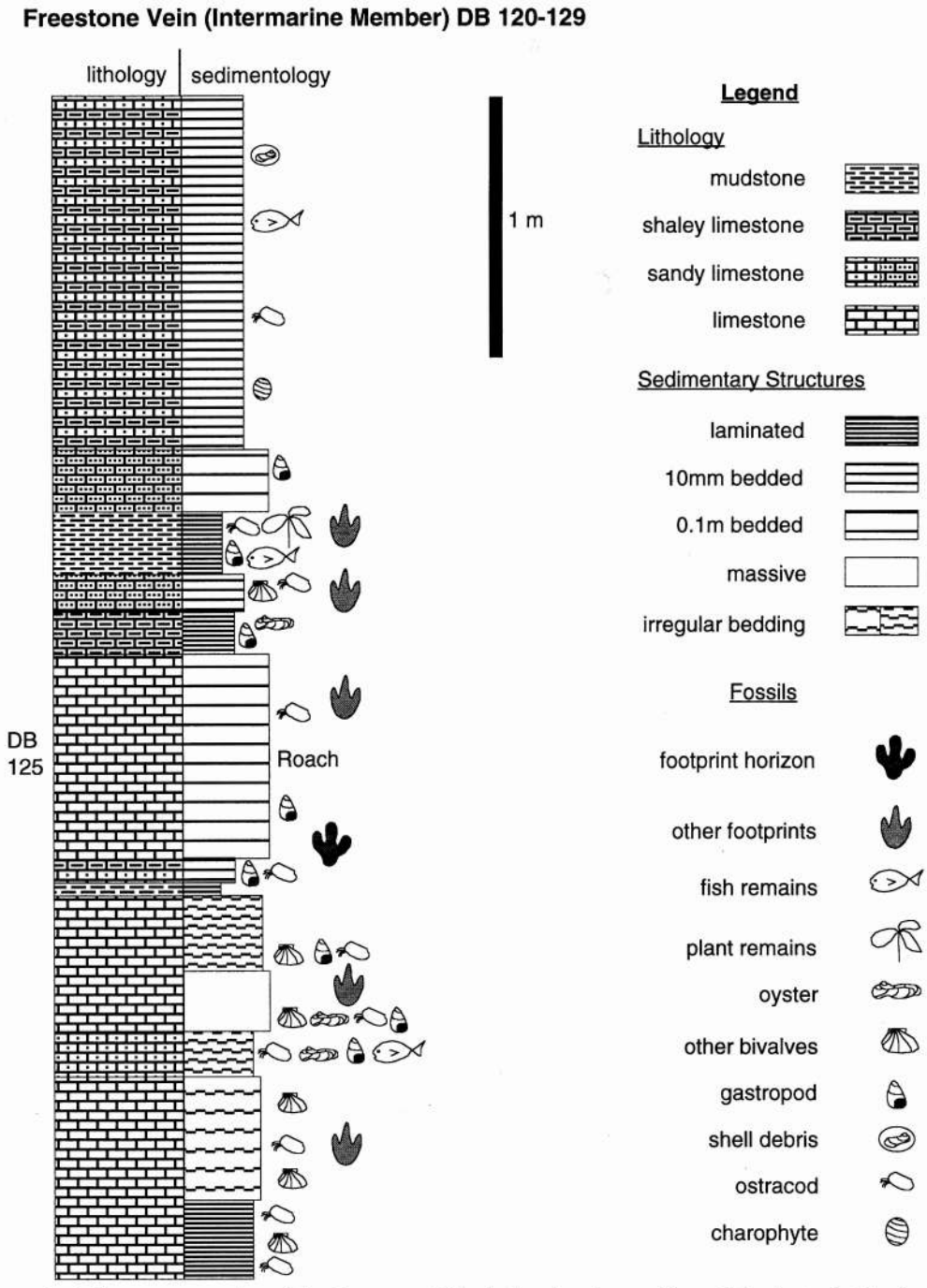
TEXT-FIG. 1. Simplified geology of the Isle of Purbeck showing the footprint locality (after Ensom 1995).

Purbeck Limestone Group (Early Cretaceous). They were preserved in the 'pink' bed of the 'roach' stone in Suttle's 'Mutton Hole' Quarry, south west of Herston (NGR SZ 022 782) (Text-fig. 1) (Charig and Newman 1962; Delair 1966; Delair and Lander 1973, fig. 1; Ensom 1995, Cat. No. 20). Thirteen pairs of prints (Trackway C) were reported, disposed in two parallel lines, and it was remarked that the dinosaur seemed to have been moving very slowly for such a large animal (Anon. 1962; Swaine 1962). There was another line of prints (Trackway A) parallel to the first set and *c.* 3 m away (Swaine 1962). Immediately adjacent to this line of prints, the surface in which the tracks were displayed was covered by overburden and it was thought that when this was removed the other half of the second trackway would be revealed. However, this was not the case, and further quarrying exposed the continuation of the double line of tracks and revealed that the two lines diverged 'at an appreciable angle'. This discovery, together with closer examination of the second trackway, clearly indicated that the first 'trackway' was actually two parallel trackways side by side. The footprints in these three trackways were attributed to theropods such as *Megalosaurus*, based on the narrow tapering nature of the digits and the wide digit divarification (Charig and Newman 1962; Newman 1990). Unfortunately, both of these features can be attributed to preservational conditions, and neither reflects distinctive morphological characteristics of the foot of the track-maker.

During June and July 1963, a party from The Natural History Museum (NHM) excavated a series of contiguous slabs bearing undamaged footprints amounting to a section *c.* 21 m long. Parts of all three trackways were collected and are now held in The Natural History Museum. Trackway A is on permanent display outside the museum (BM(NH) R 8643). Trackway C (two adjacent parallel trackways) is in the storage facility at Wandsworth (NHM R8643).

SEDIMENTOLOGY, STRATIGRAPHY AND PALAEOENVIRONMENTS

The Purbeck Limestone Group spans the Jurassic-Cretaceous boundary, but the position of the system boundary in the sequence remains uncertain. The boundary was previously thought to be at the base of the 'Cinder Bed' (DB 120) (Casey 1963), but the palaeontological evidence for this has been challenged by Wimbledon and Hunt (1983) who suggested that the 'Cinder Beds' of the



TEXT-FIG. 2. Sedimentary section of the Freestone Vein indicating the position of the footprint horizon (after Clements 1993). DB refers to the bed number at Durlston Bay, the type section of the Purbeck Limestone Group.

Wessex and Weald basins are not of the same age. Allen and Wimbledon (1991) have argued that the Jurassic-Cretaceous boundary is much lower in the sequence and just above the Portland Limestone Formation. However, charophyte evidence supports the view that the Wessex and Weald basins are roughly coeval and this evidence places the system boundary near the base of the Cypris Freestones Member (Feist *et al.* 1995). Either way, these trackways are preserved in rocks of earliest Cretaceous (Berriasian) age.

The sediments of the Purbeck Limestone Group were deposited in a very large, very shallow lagoon that partly dried out from time to time. The salinity in this lagoon was initially high, but later fluctuated from marine to fresh water (Sellwood and Wilson 1991). The middle Purbeck strata in which the trackways were found were deposited in predominantly brackish water (Arkell 1947; Allen and Keith 1965). The climate during the deposition of the lower Purbeck beds was seasonal and semi-arid (West 1975; Francis 1983). Later, during the deposition of the middle Purbeck beds, it was sub-humid and warm temperate.

A large proportion of the footprints found in the Purbeck Group occurs in the Intermarine Member (DB 112-145) (Clements 1993). These beds contain brackish water bivalves such as *Myrene*, *Liostrea* and *Protocardia*; the absence of cephalopods, brachiopods and corals also supports the conclusion that there was dilution of sea water by fresh water (Delair and Lander 1973). Thus, it is likely that all the footprints and trackways found in the Intermarine Member were made by animals moving across intertidal to supratidal flats, on the shores of a freshwater to brackish lagoon (El-Shahat and West 1983). The presence, in this member, of turtle and crocodile remains, now often found in similar environments, supports this general conclusion (Delair and Lander 1973).

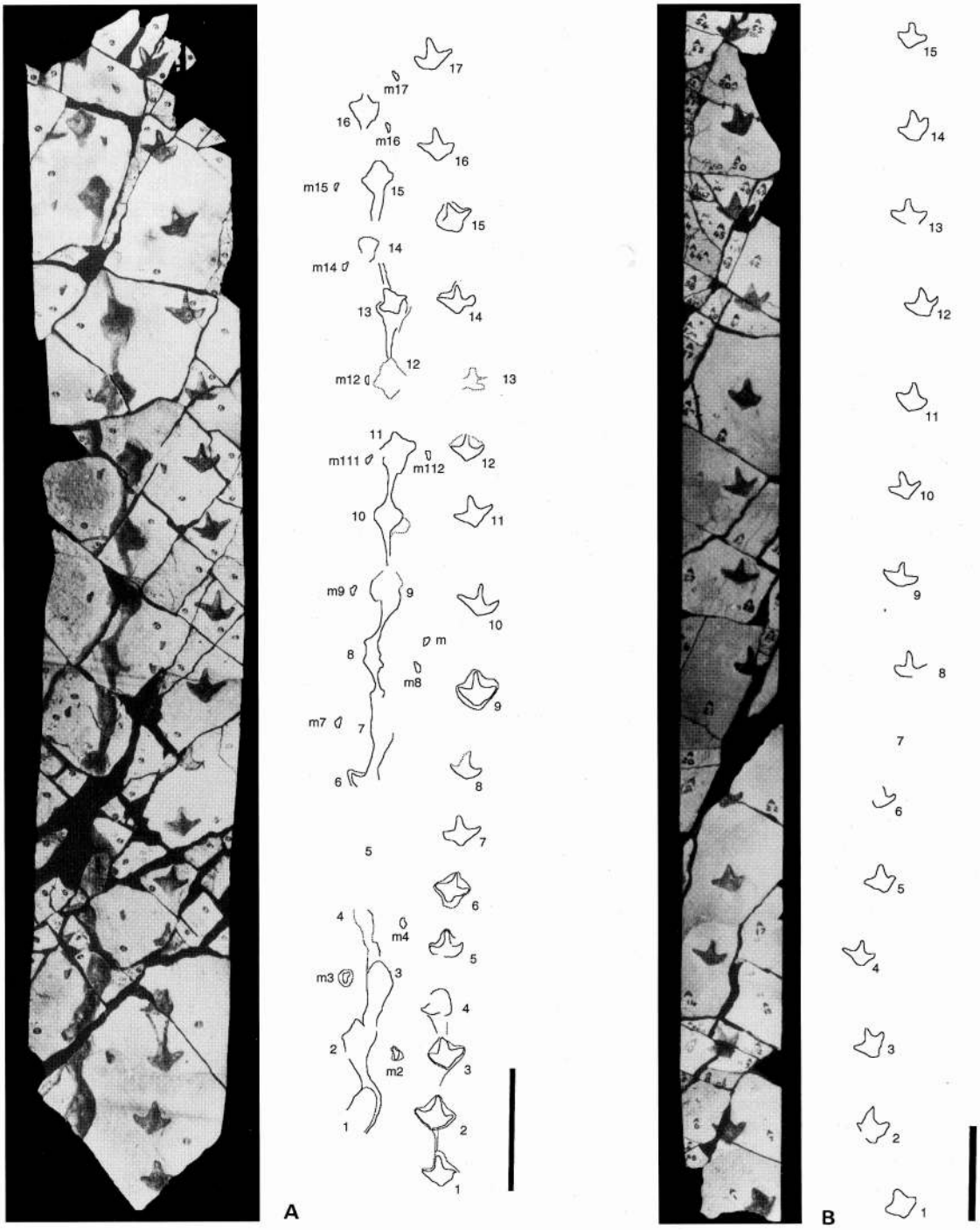
The trackways described here are preserved in the 'pink bed' of the 'roach stone' (Text-fig. 2) (Newman 1990) (DB 125) in the Intermarine Member. The footprint slabs are of a uniform thickness (*c.* 80 mm) and are composed of yellow-grey, bioclastic limestone. El-Shahat and West (1983) classified beds of this lithology as 'uncompacted biosparrudites'. They concluded that such rocks were deposited in a supratidal environment and were subject to early lithification. After deposition, such sediments were subjected to a high degree of subaerial exposure and often preserve vertebrate footprints.

The footprints are preserved as natural moulds; they are transmitted through the thickness of the slab and thus are visible on the top and bottom surfaces of the slabs. The impressions have a maximum depth of 50 mm. When the trackway was first discovered, it was reported that the strata beneath the footprints to a depth of up to 150 mm were bent down and distorted (Anon. 1962).

TRACKWAY DESCRIPTIONS

Trackway A (Text-fig. 3A) consists of 14 tridactyl pes prints averaging 294 mm long (range: 280–310 mm), 292 mm wide (range: 260–320 mm) and very similar in morphology to the pes prints of Trackway Cb; using the method of Alexander (1976) this results in a hip height of *c.* 1·2 m. The footprints represent a sequence of 15 footfalls, but one impression (No. 7) is not preserved. The average pace length of the footprints in this trackway is 729 mm (range: 660–784 mm). The average stride length is 1443 mm (range: 1330–1510 mm), with a pace angulation of 169° (range: 146–180°). Using the method of Alexander (1976) this can be calculated to correspond to a speed of about 2·8 kmh^{-1}.

Trackways Ca and Cb (Text-fig. 3B) contain 26 and 25 pes prints respectively. Trackway Ca also displays 16 manus prints. Trackway Cb has only one manus print. The pes prints of trackway Ca are ill-defined impressions (Text-fig. 3B); in only a few cases can a tridactyl outline be discerned. However, at the time of excavation and removal of these trackways, the pes print morphology of this trackway (Ca) was clearer, and closely resembled that of the other two trackways (Cyril Walker, pers. comm. 1995). This was because the clear pes impressions of trackway Ca were preserved in a layer of clay on the surface of the limestone that could not be collected and preserved (Cyril Walker, pers. comm. 1995). Thus, it seems that trackway Ca was either made at a slightly higher level, or

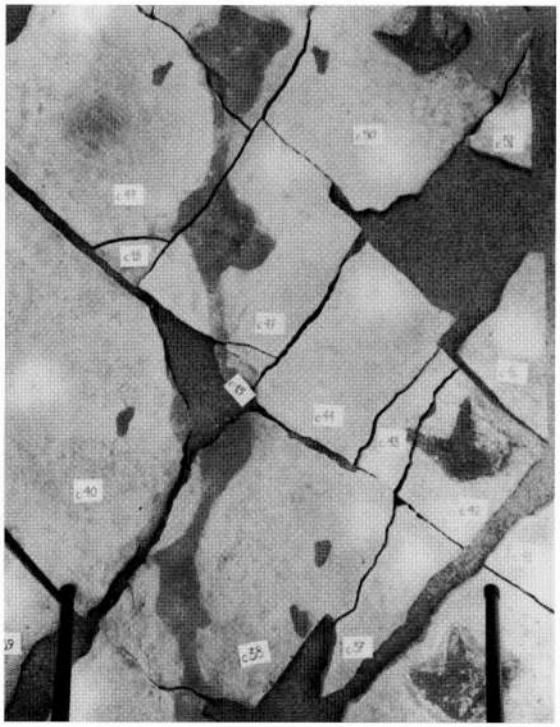


TEXT-FIG. 3. A, part of trackways Ca (left) and Cb. B, trackway A. Scale bars represent 1 m.

that the impressions of this trackway did not transmit as far as those of the other trackways through the layers of sediment above.

The pes prints of trackway Cb are tridactyl and show no internal detail (Text-fig. 3B). They average 278 mm long (range: 265–295 mm) and 321 mm wide (range: 280–356 mm); from this it can be calculated that the hip height of the track-maker was *c.* 1·1 m. The average pace length is 633 mm (range: 411–790 mm) and the average stride length is 1267 mm (range: 879–1467 mm) with a pace angulation of 169° (range: 148–180°). This corresponds to a speed of about 2·2 kmh^{-1}.

In addition to the tridactyl pes prints there are several other impressions on the trackway surface. These impressions are irregularly spaced on either side of Trackway Ca. They are very consistent in size and shape, averaging 96 mm long (range: 90–100 mm) and 48 mm wide (range: 44–50 mm). They have a curved, triangular or crescentic shape (Text-fig. 4) and are elongate parallel



TEXT-FIG. 4. Part of trackways Ca (left) and Cb; note the morphology of the manus impressions, the single manus print of trackway Cb and the irregular arrangement of the manus impressions of trackway Ca; ×0.042.

to the axis of the trackway, or with the long axis of the impression pointing obliquely inwards, making an angle of up to 30° with the trackway midline (Text-fig. 3). The narrow end of the triangle points posteriorly, with respect to the pes impressions, and the impressions are concave medially.

These impressions lie on either side of trackway Ca, at a consistent distance away from the tridactyl pes impressions, which suggests that they are associated with this trackway. Their placement along the trackway, however, is very irregular. The impressions on the opposite sides of the trackway are of the same shape, but are mirror images of one another. The most likely explanation is that they are associated manus impressions. Their morphology seems to show that they were made by three digits, set closely together, the largest in the centre and the smallest at the back or the outside. Thus it is possible to determine from the manus impressions alone both the direction in which the trackmaker was travelling and whether it is a right or a left manus impression.

All of the manus impressions were previously thought to belong to trackway Ca (Charig and Newman 1962; Norman 1980; Newman 1990). However, on closer examination it is clear that one

of the manus prints belongs to trackway Cb (Text-fig. 4). In this part of the trackway two manus impressions occur very close to one another on the right hand side of trackway Ca. The manus print closest to trackway Ca is the impression of a right manus; the other is the impression of a left manus. In addition, the long axis of the right manus impression is at an angle of 20° to the axis of trackway Ca, and the long axis of the left manus impression is inclined in the opposite direction, at an angle of 30° to the axis of trackway Cb. Thus, the left manus impression is in the correct position to have been made by the producer of trackway Cb and this interpretation is the most likely to be correct.

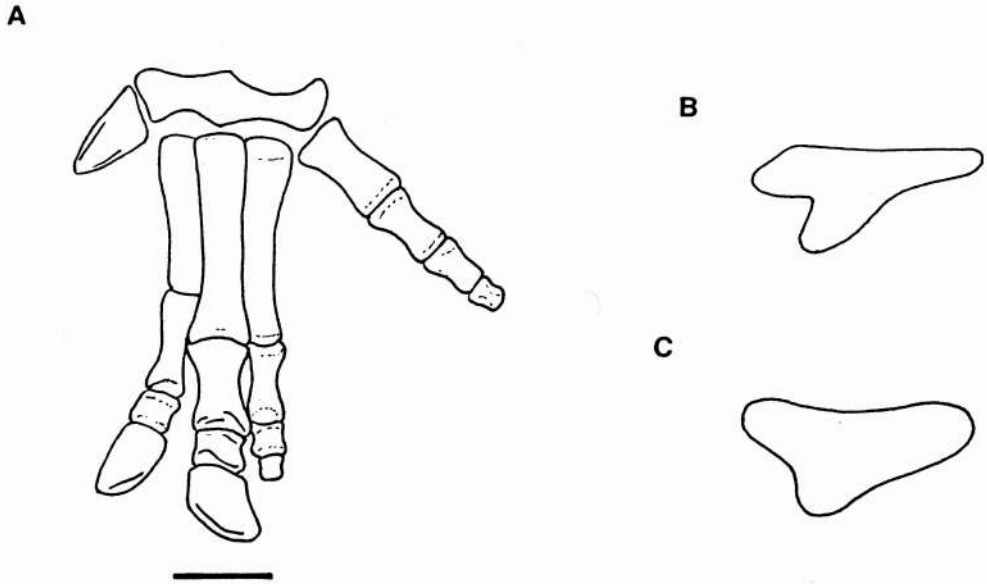
IDENTIFICATION OF THE TRACK-MAKER

Trackways Ca and Cb were both made by the same kind of track-maker. As the pes morphology of trackway A is so similar to that of trackways Ca and Cb it is most likely that trackway A was also made by a similar animal.

None of the pes impressions in any of the trackways is well enough preserved to determine the identity of the producer, thus track-maker identification must be based solely on the morphology of the manus impressions. Tridactyl pes impressions could have been made by theropods, ornithopods and stegosaurs. However, no theropods are currently thought to have been even facultatively quadrupedal, although it is conceivable that some long-armed theropods, such as *Baryonyx*, may have placed their hands on the ground from time to time. Moreover, the distinctive structure of the theropod manus (Paul 1988) would have produced manus tracks very different in morphology from those seen here. Stegosaurs can also be excluded as the trackmaker because the structure of the stegosaur manus indicates that they would have made a broader, crescentic impression showing five toes (Galton 1990). By contrast, some ornithopods could have placed just three manus digits on the ground and are thus the most likely producers of these tracks.

The large size of the tracks precludes a hypsilophodontid track-maker; hypsilophodontids were small animals, only 2–4 m long (Sues and Norman 1990). Hadrosaurs are of the right order of size to have produced these trackways, but are not known before the Cenomanian (Weishampel and Horner 1990), considerably later than the age of these ichnites. Iguanodontids, notably *Iguanodon atherfieldensis* and *I. bernissartensis*, are known from the nearby and slightly younger Wealden Group (Benton and Spencer 1994) and the poorly known *Iguanodon hoggii* has been found in the Purbeck Limestone Group (Benton and Spencer 1994). The only iguanodontids in which the manus is preserved are *Iguanodon atherfieldensis*, *I. bernissartensis*, *Ouranosaurus nigeriensis* and *Camptosaurus dispar* (Norman and Weishampel 1990). The manus of *Tenontosaurus tilletti*, a more primitive ornithopod from the Aptian of the United States (Sues and Norman 1990) is also known. However, the manus digits of *Camptosaurus* and *Tenontosaurus* were divergent and these two ornithopods would probably have made more elongate, and possibly five-fingered manus impressions.

The remaining iguanodontids all had a similar manus structure. The bones of the wrist were fused together in a manner indicative of a weight-bearing function (Norman 1980). Metacarpals II, III and IV were bound together by ligaments, and the joints of the phalanges enabled the digits to hyperextend, providing a stable walking surface similar to that of the pes (Norman 1980; Norman and Weishampel 1990). The size of the manus relative to that of the pes is different in these three dinosaurs, however. In *I. bernissartensis* the manus is about two-fifths the size of the pes (200/540 mm), in *I. atherfieldensis* it is one-fifth (90/480 mm) and in *Ouranosaurus* it is slightly less than one-half (153/333 mm). In the Purbeck trackways the length of the manus impression is about one-third the width of the pes impressions. This does not correspond exactly to any of the above proportions. It is difficult, however, to determine exact ratios from footprints, especially when they are not particularly well preserved. That the manus impressions in the trackways do not correspond closely to the foot proportions of European iguanodontid skeletons is not surprising because as weight was placed on the foot the digits would spread out to a greater or lesser extent, producing footprints of different sizes or proportions. The footprints in these trackways are of a relatively small size, and could have been made by a juvenile or an adult of a small and as yet unknown taxon.



TEXT-FIG. 5. A, Artificial manus of *Iguanodon atherfieldensis* (after Norman 1980). B, hypothetical manus impression based on skeletal morphology. C, outline drawing of manus impression m3. Scale bar represents 50 mm.

One way of testing whether large Early Cretaceous ornithopods, such as iguanodontids, could have made these tracks is to reconstruct the likely prints from skeletal morphology (Unwin 1989). This enables a comparison between the actual fossil footprint and the hypothetical footprint predicted by this method (Unwin 1989). The manus of *Iguanodon atherfieldensis* (Text-fig. 5A) was used as a basis for predicting footprint morphology. Studies of the skeletal structure of *Iguanodon*, and other advanced iguanodontids, such as *Ouranosaurus*, suggest that they placed three of their five manus digits (II–IV) on the ground when using their forelimbs for locomotion (Taquet 1976; Norman 1980; Text-fig. 5). These three digits ended in 'hooves' and had joints which allowed the digits to hyperextend and spread apart, like the bones of the foot, to provide a more stable base for walking (Norman 1980). Thus, digit II would have produced the anterior part of the manus impression and digit IV the posterior part (Text-fig. 5). The largest (digit III) made the widest part of the manus track.

The predicted footprint (Text-fig. 5B) is similar in overall morphology to the fossilized manus tracks (Text-fig. 5C). Thus, the shape of the manus tracks is consistent with the known skeletal morphology of the manus of *Iguanodon* and *Ouranosaurus* (Norman 1980). Therefore, although the preservational quality of the pes impression of trackways Ca and Cb is not high, they can be identified as iguanodontid based on the morphology of the associated manus prints.

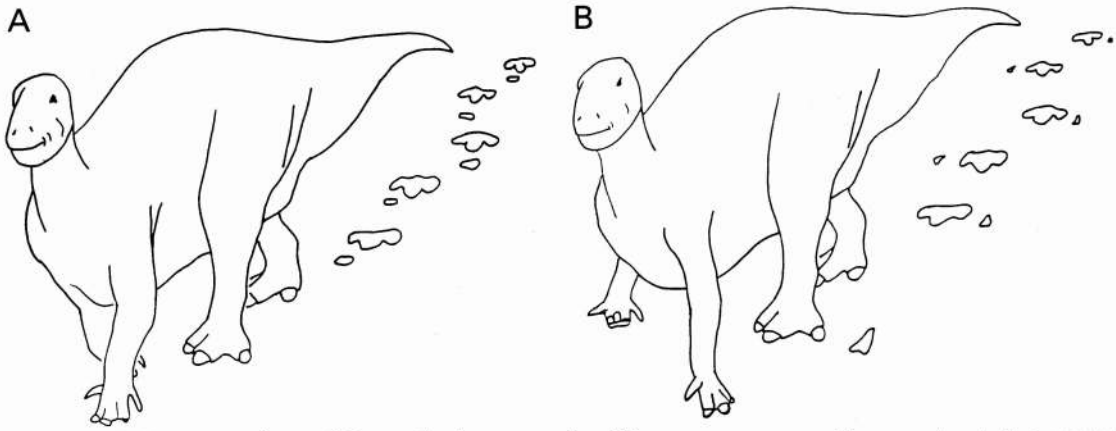
DISCUSSION

Trackway Ca displays far fewer manus prints than pes prints and they are not disposed in a regular pattern as would be expected from an obligate quadruped. For example, in the middle part of trackway Ca (prints 14–16), there are three pes prints and four manus prints (Text-fig. 4). The first manus print in this part of the trackway is m14, a left manus impression. This print is adjacent to (pes) print 14, a left pes impression. The right pes is the next print, and beside this is another left manus impression. This is followed by a right manus impression, then a right pes print and then a right manus impression again. By contrast, the pattern of the pes prints is very regular along the length of the trackway. There are two possible explanations for the irregular occurrence of the

manus impressions: (1) it may be an artefact due to the intermittent preservation of the much smaller manus prints; (2) the irregular placement may be a real feature of the way in which the track-maker walked. If the irregular placement of the manus print was a result of incomplete preservation, then the preserved manus prints would be expected to fit into an alternating pattern. The occurrence of two consecutive left manus impressions adjacent to a left and then a right pes impression belies this explanation, as does the occurrence of a left and right manus impression opposite one another on either side of (right) pes print 11. Thus it seems that the irregular and intermittent pattern of manus impressions is a real feature resulting from the way in which the animal walked. Hence, the forefeet were not essential for locomotion, and trackway Ca contains a print sequence that would be expected of a facultative quadruped.

The shape of the manus impressions is consistent with the interpretation of the middle three digits of the iguanodontian manus as a single structure with the distal part of the digits, including the 'hooves', capable of splaying out from one another, to form a more stable walking surface. The distinct trilobed shape of these manus tracks is in contrast to some bilobed tracks from the Hauterivian of Spain (Moratella *et al.* 1992). These much larger tracks are also interpreted as iguanodontian in origin, but may well have been made by a different taxon with a slightly different manus structure, where digits III and IV were much more tightly bound together. This parallels the situation in *I. atherfieldensis* and *I. bernissartensis*, where the digits in the latter, especially III and IV, show more evidence of ligamentous connections than in the former, and the digits seem to have had greater potential for independent movement (Norman 1980, 1986). The shape of ornithopod manus impressions seems to be quite variable, with those of some ichnotaxa being quite elongate, and others, such as *Caririchnium leonardii*, being rather more rounded (Currie *et al.* 1991).

The form of this trackway also shows that, when walking quadrupedally, iguanodontids, at least occasionally, placed their hands on the ground outside the line of tracks made by their feet, with the dorsal surface of the manus facing outwards parallel to the trackway midline (Text-fig. 6B). This



TEXT-FIG. 6. Reconstructions of *Iguanodon* in a normal walking pose: A, as usually reconstructed; B, posture as indicated by the footprints.

is in contrast to the way in which iguanodontids are often reconstructed, with their forelimbs placed slightly closer to the midline than the hindlimbs, and with the dorsal surface of the manus facing forwards (Paul 1987; Text-fig. 6A). This latter posture is problematical because it would necessitate rotation of the radius around the ulna leading to distortion and dislocation of the joint at the wrist or elbow. The posture indicated by the trackways obviates the need for unnatural twisting of the bones of the lower forelimbs, and is thus more compatible with what is known regarding the skeletal anatomy of these animals. This does not mean, however, that iguanodontids had a sprawling forelimb posture. The placing of the feet almost directly upon a single line is related to the location

of the centre of gravity near the pelvic girdle (Norman 1980), since, in a bipedal animal, the feet would need to be placed directly beneath the body midline to maintain balance, because these were the weight-bearing limbs. The forelimbs of this track-maker were not necessary for weight-bearing and balance in locomotion and thus did not have to operate under such constraints. The width of the angulation pattern of the manus tracks is *c.* 0·5 m (average 484 mm) which is about the width of the shoulder girdle of *I. atherfieldensis* (Norman 1986). These relative proportions suggest that the arms would have been held in a vertical position when the forefeet were in contact with the ground.

Although it is not possible to identify the makers of trackways to species level from their footprints alone, the morphology and proportions of the manus and pes impressions of these trackways fit the skeletal morphology of *I. atherfieldensis* more closely than that of *I. bernissartensis*. This is interesting in light of interpretations, based on skeletal morphology, of *I. bernissartensis* as an animal that typically spent more time walking quadrupedally than *I. atherfieldensis* (Norman 1980).

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REFERENCES

ALEXANDER, R. McN. 1976. Estimates of speeds of dinosaurs. *Nature*, **261**, 129–130.

ALLEN, P. and KEITH, M. L. 1965. Carbon isotope ratios and palaeosalinites of Purbeck–Wealden carbonates. *Nature*, **208**, 1278–1280.

—— and WIMBLEDON, W. A. 1991. Correlation of NW European Purbeck–Wealden (non-marine Lower Cretaceous) as seen from the English type-areas. *Cretaceous Research*, **12**, 511–526.

ANONYMOUS 1962. The slow march of the Purbeck *Iguanodon*. *New Scientist*, **271**, 186.

ARKELL, W. J. 1947. The geology of the country around Weymouth, Swanage, Corfe and Lulworth. *Memoir of the Geological Survey of Great Britain*. HMSO, 386 pp.

BECKLES, S. H. 1854. On the Ornithoidichnites of the Wealden. *Quarterly Journal of the Geological Society, London*, **10**, 456–457.

BENTON, M. J. and SPENCER, P. S. 1995. *British fossil reptile sites of Great Britain*. Geological Conservation Review Series. Chapman & Hall, London, 345 pp.

CASEY, R. 1963. The dawn of the Cretaceous period in Britain. *Bulletin of the South-Eastern Union of Scientific Societies*, **117**, 1–15.

CHARIG, A. J. and NEWMAN, B. 1962. Footprints in the Purbeck. *New Scientist*, **285**, 234–235.

CLEMENTS, R. G. 1993. Type section of the Purbeck Limestone Group, Durlston Bay, Swanage, Dorset. *Proceedings of the Dorset Natural History and Archaeological Society*, **114**, 181–206.

CURRIE, P. J., NADON, G. C. and LOCKLEY, M. G. 1991. Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Canada. *Canadian Journal of Eath Sciences*, **28**, 102–115.

DELAIR, J. B. 1960. The Mesozoic reptiles of Dorset: part 3. *Proceedings of the Dorset Natural History and Archaeological Society*, **81**, 57–85.

—— 1966. New records of dinosaurs and other fossil reptiles from Dorset. *Proceedings of the Dorset Natural History and Archaeological Society*, **87**, 57–66.

—— and LANDER, A. B. 1973. A short history of the discovery of reptilian footprints in the Purbeck Beds of Dorset, with notes on their stratigraphical distribution. *Proceedings of the Dorset Natural History and Archaeological Society*, **94**, 17–20.

EL SHAHAT, A. and WEST, I. M. 1983. Early and late lithification of aragonite bivalve beds in the Purbeck Formation (Upper Jurassic–Lower Cretaceous) of southern England. *Sedimentary Geology*, **35**, 15–41.

ENSOM, P. C. 1982. Dinosaur footprints at 19 Townsend Road, Swanage. *Proceedings of the Dorset Natural History and Archaeological Society*, **103**, 141.

—— 1987. A remarkable new vertebrate site in the Purbeck Limestone Formation on the Isle of Purbeck. *Proceedings of the Dorset Natural History and Archaeological Society*, **108**, 205–206.

—— 1995. Dinosaur footprints in the Purbeck Limestone Group (?Upper Jurassic–Lower Cretaceous) of Southern England. *Proceedings of the Dorset Natural History and Archaeological Society*, **116**, 77–104.

FEIST, M., LAKE, R. D. and WOOD, C. 1995. Charophyte biostratigraphy of the Purbeck and Wealden of southern England. *Palaeontology*, **38**, 407–442.

FRANCIS, J. E. 1983. Reconstruction of the dominant conifer of the 'Fossil Forests' of the Lower Purbeck Formation (Upper Jurassic) Dorset. *Palaeontology*, **26**, 277–294.

HOWSE, S. C. B. and MILNER, A. R. 1995. The pterodactyloids from the Purbeck Limestone Formation of Dorset. *Bulletin of the British Museum (Natural History), Geology Series*, **51**, 73–88.

LAKE, R. D. and SHEPHERD-THORN, E. R. 1987. Geology of the country around Hastings and Dungeness. *Memoir of the Geological Survey*. HMSO, 345 pp.

MANSELL-PLEYDELL, J. C. 1896. On the footprints of a dinosaur (?*Iguanodon*) from the Purbeck beds of Swanage. *Proceedings of the Dorset Natural History and Antiquarian Field Club*, **17**, 115–122.

MORATELLA, J. J., SANZ, J. L., JIMENEZ, S. and LOCKLEY, M. G. 1992. A quadrupedal ornithopod trackway from the Early Cretaceous of La Rioja (Spain): inferences on gait and hand structure. *Journal of Vertebrate Paleontology*, **12**, 150–157.

NEWMAN, B. H. 1990. A dinosaur trackway from the Purbeck Beds of Swanage, England. *Palaeontolographica africana*, **27**, 97–100.

NORMAN, D. B. 1980. On the ornithischian dinosaur *Iguanodon bernissartensis* of Bernissart (Belgium). *Mémoires de l'Institut Royal des Sciences Naturelle de Belgique*, **178**, 1–105.

—— 1986. On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin Institut Royal des Science Naturelle de Belgique: Sciences de la Terre*, **56**, 281–372.

PAUL, G. S. 1987. The science and art of restoring the life appearance of dinosaurs and their relatives: a rigorous how-to guide. 5–49. *In* CZERKAS, S. J. and OLSEN, E. C. (eds). *Dinosaurs past and present*. University of Washington Press, London.

—— 1988. *Predatory dinosaurs of the world*. Simon and Schuster, New York, 464 pp.

SELLWOOD, B. W. and WILSON, R. C. L. 1991. Jurassic sedimentary environments of the Wessex Basin. *Field Guide no. 7 for 13th International Sedimentological Congress, Nottingham*, 1990, 89 pp.

SWAINE, J. 1962. Iguanodont footprints. *New Scientist*, **13**, 520.

TAQUET, P. 1976. *Geologie et paleontologie du gisement de Gadoufaoua (Aptien du Niger)*. Cahiers Paleontologie C.N.R.S., Paris, 191 pp.

UNWIN, D. M. 1989. A predictive method for the identification of vertebrate ichnites and its application to pterosaur tracks. 259–274. *In* GILLETTE, D. D. and LOCKLEY, M. G. (eds). *Dinosaur tracks and traces*. Cambridge University Press, Cambridge.

WEST, I. M. 1975. Evaporites and associated deposits of the basal Purbeck Formation (Upper Jurassic) of Dorset. *Proceedings of the Geologists' Association*, **86**, 205–225.

WIMBLEDON, W. A. and HUNT, C. O. 1983. The Portland–Purbeck junction (Portlandian–Berriasian) in the Weald, and correlation of latest Jurassic–early Cretaceous rocks in southern England. *Geological Magazine*, **120**, 267–280.

WRIGHT, J. L., UNWIN, D. M., LOCKLEY, M. G. and RAINFORTH, E. C. 1997. Pterosaur tracks from the Purbeck Limestone Formation of Dorset. *Proceedings of the Geologists' Association*, **108**, 39–48.

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