THE SKULL OF *FABROSAURUS AUSTRALIS*, A TRIASSIC ORNITHISCHIAN DINOSAUR

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ABSTRACT. The skull of *Fabrosaurus australis* is described in detail. This study is based upon previously undescribed specimens from the late Triassic Red Beds of Lesotho.

The presence of a predentary bone at the mandibular symphysis substantiates Ginsburg's concept (1964) of *Fabrosaurus* as a member of the order Ornithischia—though there is no evidence for any close relationship between *Fabrosaurus* and the Liassic *Scelidosaurus*. Certain cranial features (the toothed premaxilla, the interparietal suture) indicate that *Fabrosaurus* should be referred to the family Hypsilophodontidae of the suborder Ornithopoda. Ornithischian origins and ornithopod phylogeny are re-examined in the light of new evidence from *Fabrosaurus*. *Fabrosaurus* seems to be a fairly direct antecedent of *Hypsilophodon* and appears to fulfil many of the requirements of a genuine 'archetypal' ornithischian.

PRIOR to this decade only a few and fragmentary fossils were available to permit of clarification of early ornithischian history. Faced with this lack of information several investigators tended to simplify the problem by selecting the well-known Wealden ornithopod *Hypsilophodon* as an ornithischian 'archetype' and by attempting to derive the varied ornithischian faunas of the later Mesozoic from similar hypothetical ancestors. This scheme, though useful, is unsatisfactory because of the late stratigraphic occurrence of *Hypsilophodon*—which appears later than stegosaurs and iguanodonts and is roughly contemporary with the earliest ankylosaurs and psittacosaurs. The anomalous situation of *Hypsilophodon* within such a scheme is quite clear—it is geologically younger than (or at least coeval with) those dinosaurs whose ancestry it is supposed to represent. It is in view of this unsatisfactory situation that adequate knowledge of early ornithischians, such as *Fabrosaurus*, becomes of critical importance.

The genus *Fabrosaurus* was established by Ginsburg (1964) on the basis of a tooth-bearing jaw fragment from the late Triassic Red Beds of Lesotho (then Basutoland). Ginsburg concluded, from the appearance of the teeth in the holotype, that *Fabrosaurus* was an ornithischian dinosaur related to the Liassic *Scelidosaurus*. Unfortunately the affinities of *Scelidosaurus* itself are far from clear. This large armoured dinosaur is often quoted as a fore-runner of the stegosaurs (e.g. Romer 1956); recent opinion tends, however, to confirm *Scelidosaurus* as an ankylosaur ancestor (Romer 1968).

The new materials described below considerably amplify knowledge of the *Fabrosaurus* skull and permit reconsideration of this reptile's affinities.

MATERIAL AND METHODS

Two specimens are described. These are listed below with brief notes on their preservation and contents; their original field numbers are given and will be used hereafter for reference.

Specimen B. 17. Three large blocks and numerous small pieces of matrix containing many cranial and post-cranial bones (though few are in natural articulation). At least two individuals are present —the smaller one being more complete.

Specimen B. 23. A well-preserved and slightly crushed skull (text-fig. 1) with parts of both mandibular rami. The snout is lacking and the teeth are poorly preserved.

These specimens were collected by Dr. K. A. Kermack and Mrs. F. Mussett during the 1963–4 expedition from University College, London, to Basutoland. Both specimens are preserved in the collection of the Zoology Department at University College, London.

Specimen B. 17 was collected from the Red Beds of the Stormberg Series on the northern flank of Likhoele Mountain, near the settlement of Mafeteng in western Lesotho, about 40 miles south-south-west of Maseru, the capital. Skull B. 23 was taken from a hillside exposure, also in the Red Beds, between Fort Hartley and Cutting Camp in south-west Lesotho, some 75 miles south of Maseru. The Red Beds are generally supposed to be of Upper Triassic age.

The bones, preserved in soft, white calcareous material, are enclosed in a tough medium-grained sandstone of bright red colour. The specimens were at first prepared by the use of acetic and formic acids (as described by Kermack 1956). It subsequently became clear that these acids, though effective, have certain disadvantages—they readily attack fossil bone, they have offensive smells and they may (if specimens are not very thoroughly washed after immersion) cause the formation of hard white efflorescences. Thus a saturated solution of sodium citrate in water was employed as an equally effective alternative. Since this solution does not attack bone as readily as formic or acetic acids the specimens were safely immersed in it for periods of up to 24 hours.

DESCRIPTION

General appearance of the skull. Specimen B. 23 is only slightly damaged and adequately demonstrates the general appearance of the *Fabrosaurus* skull (text-fig. 1). This incomplete skull has the following dimensions: maximum length, 94 mm.; maximum width (across frontals), 48 mm.; maximum height (with mandible), 40 mm. Fragments from assemblage B. 17 (text-figs. 2, 3) represent skulls of roughly similar size.

The skull is of typical archosaurian aspect—diapsid, with large circular orbits and extensive antorbital vacuities. The long and tapered snout affords the skull a triangular profile whilst the occipital surface, inclined at about 60° relative to the long skull axis, faces slightly in a dorsal direction. The small and elliptical upper temporal fenestra opens dorsally; the lateral fenestra is larger, faces laterally and is almost crescentic in outline due to the forwards extension of the quadrate.

Skull bones. To facilitate description the skull bones are considered in arbitrary groups (after Romer 1956).

(i) *Tooth-bearing bones.* The tip of the snout, formed by paired *premaxillae* (text-figs. 1, 6, 8), is laterally compressed and has a V-shaped outline in dorsal view. Each premaxilla is extended dorsally into two processes separated by the large and oval external naris. The broad pre-narial process is directed dorsally and slightly to the rear; its contact with the nasal cannot be observed—though it is likely (since the nasals are very extensive) that this process was not very tall. The long and acutely pointed post-narial process extends postero-dorsally at about 50° relative to the tooth row and is tightly sandwiched between the nasal and the maxilla on the side of the snout.

The bar-like dentigerous part of the *maxilla* (text-figs. 1–4 and 8) is about 7 mm. deep (skull B. 23) and has a flat lateral surface. The maxilla extends posteriorly to under-lie the anterior ramus of the jugal—the two bones being separated by a long, straight, and oblique suture. A broad and flat process extends postero-dorsally from the front of
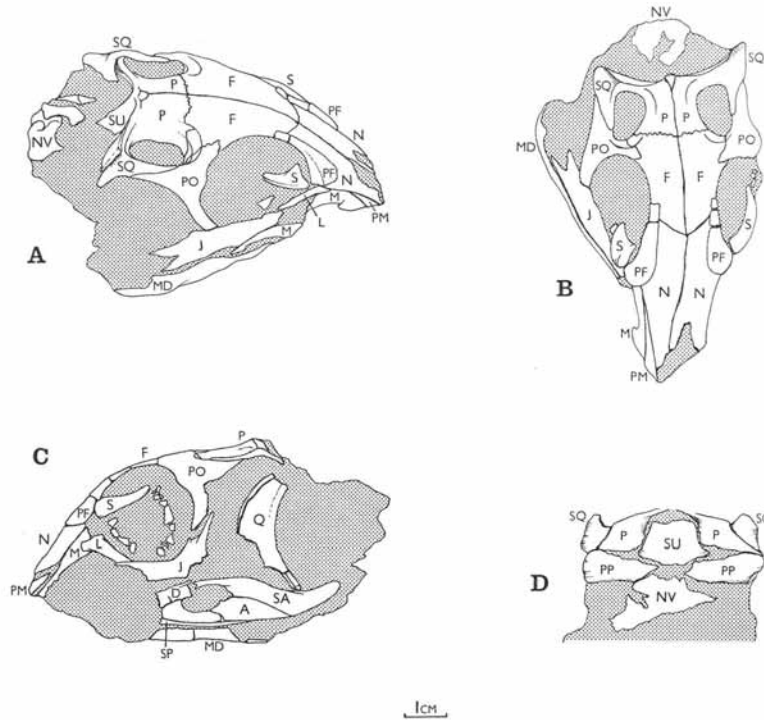
TEXT-FIG. 1. *Fabrosaurus australis.* Skull B. 23 as preserved. ×0·75. Matrix indicated by regular stip-pling. A, right dorso-lateral view; B, dorsal view; C, left lateral view; D, occipital view.

A, angular; D, dentary; F, frontal; J, jugal; L, lacrimal; M, maxilla; MD, mandible; N, nasal; NV, fragments of cervical vertebrae; P, parietal; PF, prefrontal; PM, premaxilla; PO, postorbital; PP, paroccipital process; Q, quadrate; S, supra-orbital; SA, surangular; SP, splenial; SQ, squamosal; SU, supra-occipital.

the maxilla so as to define the antero-ventral angle of the shallow, triangular antorbital vacuity. The thin bony wall medial to the vacuity is a simple sheet-like extension of the maxilla; this wall is gently convex in a vertical direction and is broken postero-ventrally by a small rounded notch.

(ii) *Skull roofing bones.* Paired *nasal* bones (text-figs. 1, 8) form the roof of the snout and meet in a long and straight median suture. The nasal is at least as long as the frontal and attains its maximum width (12 mm. in skull B. 23) close to the anterior tip of the

adjacent prefrontal. Anterior to the prefrontal the nasal curves down from the nearly flat skull roof to form part of the facial region. Posteriorly the nasal overlaps the frontal —the line of junction running postero-laterally from the mid-line.

Paired *frontal* bones (text-figs. 1, 8) form the skull roof between the orbits. Each frontal is roughly quadrilateral in outline, about 31 mm. long (skull B. 23) and is slightly arched in a longitudinal direction. At its postero-lateral corner the dorsal surface of the
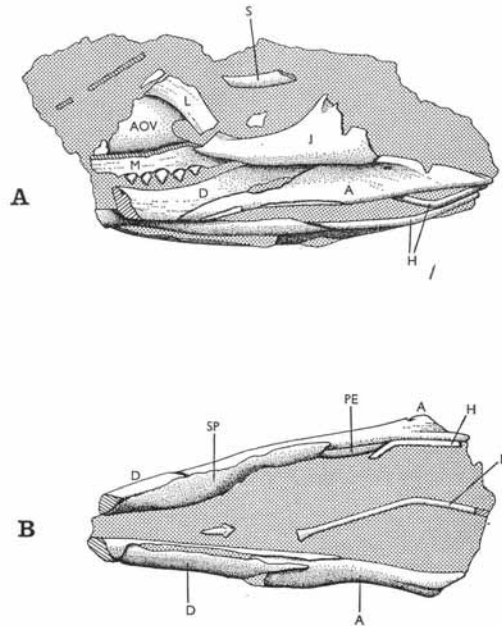
TEXT-FIG. 2. *Fabrosaurus australis*. Partial skull from assemblage B. 17. ×1.
Matrix indicated by regular stippling. A, left lateral view; B, ventral view.
AOV, antorbital vacuity; H, ossified first ceratobranchials; PE, pre-articular.
Other letters as for text-fig. 1.

frontal bears a deeply impressed crescentic pit which defines the anterior limit of the upper temporal opening. Anterior to this pit the dorsal tip of the postorbital is set into a deep V-shaped notch in the lateral edge of the frontal. The posterior tip of the prefrontal occupies a shallow groove in the antero-lateral corner of the frontal. The thin, sharp, and arched lateral edge of the frontal forms the overhanging upper rim of the orbit.

Paired *parietals* (text-figs. 1, 8) form the broadly convex zone of skull roof between the upper temporal openings. Each parietal is firmly joined to the frontal of the same side by a sinuous transverse suture and is extended postero-laterally as a vertical sheet of bone between the occipital surface and the upper temporal opening. The lateral tip

of this expanded portion is applied to the posterior face of the squamosal. The very distinct inter-parietal suture is quite straight and is confluent with that between the frontals.

(iii) *Circumorbital bones*. The *jugal* (text-figs. 1, 2, 8) is gracefully arched to the exterior and has slender processes directed anteriorly, posteriorly, and dorsally. The anterior branch, roughly circular in cross-section, extends to the postero-ventral angle of the antorbital vacuity; its rounded dorsal edge forms the lower rim of the orbit whilst its recessed ventral margin accommodates the postero-dorsal edge of the maxilla. The
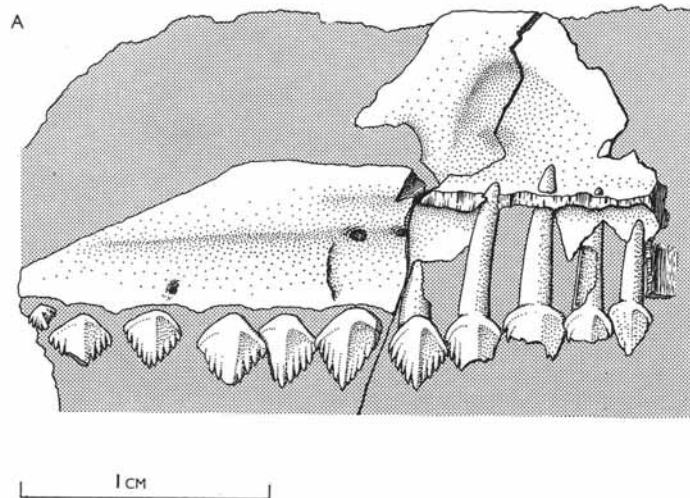
TEXT-FIG. 3. *Fabrosaurus australis*. Isolated right maxilla from assemblage B. 17. ×4. Matrix indicated by regular stippling. Lateral view.

broader posterior jugal ramus is damaged in all examples and its extent cannot be determined The tapered dorsal branch of the jugal is inclined slightly to the rear and is distinctly twisted (the lateral surface being turned to the front).

The tri-radiate *postorbital* (text-figs. 1, 8) curves over from the side of the skull on to its dorsal surface, the dorsal and ventral branches of the bone defining the postero-dorsal corner of the orbit. In this region the rim of the orbit is thickened and bears, on the medial surface, a small cavity. The flat and slender ventral branch of the post-orbital occupies a long and shallow groove on the dorsal ramus of the jugal. The shorter and broader antero-dorsal branch is set into the postero-lateral corner of the frontal above whilst the third, posterior, branch meets an anterior extension of the squamosal to form the stout horizontal bar between superior and lateral temporal openings.

The *lacrimal* (text-figs. 1, 2, 8) is a small bar of bone, some 10 mm. long, which runs anteror-dorsally on the side of the skull from the anterior tip of the jugal. Its antero-ventral edge thus defines the posterior limit of the antorbital vacuity. The lacrimal is

inclined at about 45° relative to the line of the tooth row and is broader in front (6 mm.) than behind (4 mm.).

The *prefrontal* (text-figs. 1, 8) is a long, narrow, flattened, and strap-like bone forming the margin of the skull roof from a point midway over the orbit to the area where lacrimal, nasal, and maxilla all meet above the antorbital vacuity. Left and right prefrontals are completely separated by the frontals and nasals. The narrow posterior tip of the bone is set into a notch in the antero-lateral edge of the frontal whilst the broadly rounded anterior end overlies the nasal. The thin and sharp lateral edge of the prefrontal forms the antero-dorsal rim of the orbit; anteriorly this edge is thickened and planed off to form an attachment surface for the supra-orbital.

(iv) *Bones of the cheek region*. The *squamosal* (text-figs. 1, 8) forms the lateral and posterior margins of the upper temporal opening and is extended postero-laterally to overlap the upper end of the quadrate. A tapered triangular portion runs forwards to meet the posterior ramus of the postorbital—the two bones being separated above the lateral temporal opening by a long, straight, and oblique suture. Posteriorly the squamosal turns sharply in a medial direction to form the postero-lateral corner of the skull roof. This corner is acutely pointed and is ornamented with deeply incised transverse striae. The posterior face of the squamosal is overlain by a plate-like portion of the parietal forming the dorso-lateral part of the occiput. A very slender ventral process from the squamosal is applied to the anterior edge of the quadrate. Though the only example of this process (on the left side of skull B. 23) is damaged it is clear that it extended down the front of the quadrate for at least half the height of this latter.
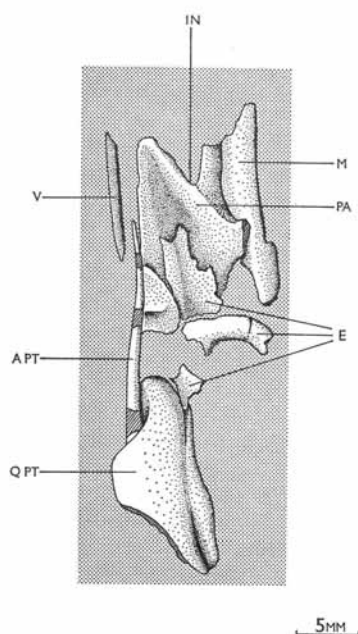
No *quadrato-jugal* has been recovered. Its probable form is indicated in the skull reconstruction (text-fig. 8).

A single *quadrate* is preserved (text-fig. 1). This example, on the left side of skull B. 23, is damaged antero-ventrally and has suffered slight displacement to the front. The quadrate is a latero-medially compressed plate of bone which is noticeably twisted—the lateral surface being turned to the rear at the ventral end. The thickened and buttress-like posterior margin is arched to the front; at its ventral end this buttress is transversely expanded to form a thick and roller-like condyle lying some 7 or 8 mm. below the level of the maxillary teeth. The sheet-like and slightly concave anterior part of the bone projects into the lateral temporal opening—accounting for the narrow outline of the opening. The dorsal tip of the quadrate fits tightly into a depression in the ventral surface of the squamosal.

(v) *Bones of the palate*. In the incomplete skull from assemblage B. 17 (text-figs. 2, 4) the right half of the palate is exposed in dorsal aspect. The bones displayed (pterygoid, ectopterygoid, palatine, and vomer) appear to have suffered little distortion or displacement. The palate seems to have been quite long, narrow, and moderately vaulted. A narrow inter-pterygoid vacuity is inferred whilst post-palatine fenestrae must (if present at all) have been very small.

The palatal (anterior) ramus of the tri-radiate *pterygoid* is a long, low vertical blade which runs forwards close to the mid-line. This paper-thin and sharp-edged process is 17 mm. long and nearly 3 mm. high. It is separated from the mid-line by the vomer—an arrangement which suggests that left and right palatal rami were not in contact and implies the existence of a narrow inter-pterygoid vacuity. Posteriorly the palatal ramus merges, by means of a sharp flexure, with the medial edge of the widely expanded quadrate

ramus of the pterygoid. This latter ramus, a triangular sheet of bone about a millimetre thick, presumably extended postero-laterally to meet the medial face of the quadrate in normal reptilian fashion. Anteriorly the quadrate ramus is constricted and runs into the third, transverse, ramus from the pterygoid. This transverse ramus is represented in specimen B. 17 only by a fragment of bone overlying the dorsal surface of the palatine. The dorsal surface of this constricted zone between quadrate and transverse rami bears a short and shallow longitudinal groove which doubtless accommodated a posterior extension of the ectopterygoid. The ectopterygoid is represented, in fact, by a small scale-like fragment of bone overlying the anterior end of this groove. An extremely similar arrangement is seen in a variety of reptiles—e.g. phytosaurs (Camp 1930), pelycosaurs (Romer and Price 1940), pseudo-suchians (Walker 1961).

The *ectopterygoid* lies anterior to the pterygoid and seems to be considerably smaller than this latter (though its full extent is not clear owing to breakage). Its posterior extension on to the pterygoid is described above. An equally thin anterior extension overlies the middle of the depressed dorsal surface of the palatine. In addition the ectopterygoid is produced laterally as a short (5 mm.), stout, and curved bar which serves to brace the medial surface of the maxilla.

The *palatine* is situated anterior to the pterygoid and antero-medial to the ectopterygoid. There is no trace of any (post-palatine) vacuity between palatine and ectopterygoid. A slender antero-lateral process from the palatine is applied to the medial surface of the maxilla; medial to this the deeply embayed anterior edge of the palatine represents the rear margin of the internal naris. Medial and posterior to the internal naris the palatine forms an extensive sheet of bone, some 9 mm. wide, which is flexed into a deep trough running postero-laterally. The floor of this trough contains the thin anterior part of the ectopterygoid whilst its medial edge meets the tip of the anterior pterygoid ramus.

The *vomer* is represented (specimen B. 17) by a sheet-like fragment of bone, 12 mm. long and 5 mm. high, which lies vertically in the mid-line between the palatines.

(vi) *Bones of the occiput* (text-figs. 1, 8). The account is based upon skull B. 23. In this skull the ventral parts of the occiput are obscured by fragments of cervical vertebrae and cannot (for the present at least) be described. The occipital surface is inclined, at

5MM

TEXT-FIG. 4. *Fabrosaurus australis*. Right half of palate in partial skull from assemblage B. 17 (see also text-fig. 2). Dorsal view, ×2. Matrix indicated by regular stippling.

APT, anterior (palatal) ramus of pterygoid; E, ectopterygoid (fragments); IN, rear margin of internal naris; M, maxilla; PA, palatine; QPT, quadrate ramus of pterygoid; V, vomer.

about 60° relative to the long axis of the skull, so that it faces dorsally as well as posteriorly. It is quite broad (44 mm. across the squamosals) and not exceptionally high (38 mm. including quadrate).

The dorsal part of the occiput is formed, in its central region, by the median *supra-occipital*. This transversely arched bone is of quadrilateral outline, some 15 mm. high, and attains a maximum width (ventrally) of 14 mm. Since its ventral margin is damaged it is difficult to estimate how far this bone contributed to the border of the foramen magnum. The lateral edge of the supra-occipital meets the posterior face of the *parietal* —forming the dorso-lateral part of the occiput. Towards the margin of the occiput the parietal overlaps the posterior face of the *squamosal*—which curves away on to the side of the skull. The intervening suture runs ventro-laterally, roughly parallel with that between supra-occipital and parietal. The ventro-lateral corner of the supra-occipital meets the dorsal edge of the *exoccipital*, which extends laterally away from the foramen magnum as the long (14 mm.) and stout paroccipital process. The expanded lateral tip of this process is doubtless composed of the *opisthotic* bone, though there is no suture serving to separate this from the confluent exoccipital. The paroccipital process is arched very slightly to the anterior; it is directed laterally, and almost imperceptibly in a ventral direction, to terminate in a vertically expanded sheet which is applied to the posterior face of the squamosal.

(vii) *Bones of the mandible* (text-figs. 1, 2, 5, 8). A composite description is derived from all available examples. Each long and slender mandibular ramus is slightly arched to the exterior in its middle and anterior regions. The jaw has a length of about 92 mm. (estimated for skull B. 23) and is latero-medially compressed—so that cross-sections are of elliptical outline. The retroarticular portion is extended as a salient finger-like process whilst the coronoid apophysis is little more than an indistinct rounded eminence on the dorsal surface. A widely open external mandibular fenestra lies at mid-height and just in front of the coronoid process. This opening is of lenticular outline, measuring 8 mm. (maximum length) by 3 mm. (maximum height). A similar, though larger, fenestra in the medial jaw surface is located slightly anterior to the external one.

The jaw rami are joined anteriorly by means of the median *predentary*. This scoop-shaped bone has the outline, in ventral view, of a blunt arrow-head—being composed of a large median portion bearing two smaller lateral processes or 'wings'. The median portion, some 10 mm. long and 4 mm. wide, extends posteriorly between the left and right dentary bones (though it is not clear if these were completely separated).

Behind the predentary the *dentary* bone forms the anterior two-thirds of the lateral jaw surface. This lateral surface is convex in a vertical direction and is confluent ventrally with the broadly rounded inferior margin of the jaw. Posteriorly the dentary ends in a wide V-shaped notch defining the anterior limit of the external mandibular fenestra. Above the fenestra the dentary overlies the surangular; below the opening it overlaps the angular and is drawn out posteriorly as a thin and flattened process applied to the thick ventral margin of the jaw. The dentary also forms the anterior third of the medial jaw surface. This surface is generally similar to the lateral surface just described and shows no indications of any foramina adjacent to the tooth row. Posteriorly this medial dentary surface is overlain by the paper-thin anterior part of the splenial.

The *splenial* forms the ventro-medial surface of the jaw behind the dentary and is extended posteriorly as a thin tongue-like process on the ventral surface of the

retro-articular process. In the middle of the jaw ramus the splenial is widely expanded to form the greater part of the medial surface—except dorsally, where a narrow zone of the underlying dentary is exposed adjacent to the tooth row. This central region of the medial jaw surface is generally flat; posteriorly it is depressed, leading down into the large inner mandibular fenestra.

The *angular* forms the postero-ventral part of the jaw, below the surangular and behind the dentary. The lateral surface of the bone is generally flat, curving round ventrally to merge with the thick inferior margin of the jaw. Angular and surangular are separated

5mm
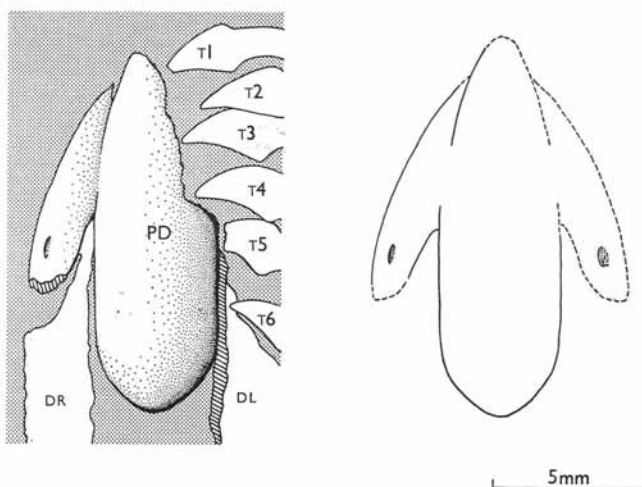
TEXT-FIG. 5. *Fabrosaurus australis*. Mandibular symphysis from assemblage B. 17. Ventral view, ×5. Matrix indicated by regular stippling, broken edges by diagonal shading.

DL, left dentary; DR, right dentary; PD, predentary; T1 to T6, left premaxillary teeth numbered from front.

by a distinct suture from the posterior angle of the external jaw fenestra. This suture runs obliquely in a postero-dorsal direction so that the angular and surangular appear to form roughly equal portions of the lateral jaw surface. Posteriorly this same suture is down-curved—so that a slender process from the angular underlies the retro-articular process (formed predominantly of the surangular).

The *surangular*, overlying the angular, forms the retro-articular process and the postero-dorsal limit of the external jaw fenestra. Since the retro-articular process is deflected medially the lateral surface of the surangular is convex from front to back. This lateral surface is demarcated from the dorsal margin of the retro-articular process by a thick and dorsally arched ridge. The long (10 mm.) and tapered retro-articular process has a bluntly rounded tip and is drawn out medially into a horizontal flange nearly 5 mm. wide. The ventral surface of this flange is gently excavated whilst its most medial tip is extended ventrally as a short and blunt projection.

In front of the retro-articular process, on the dorsal jaw surface, lies the glenoid fossa—a broad and shallow transverse groove. This region of the jaw is doubtless formed by an *articular* element, though the sutures which might define its limits cannot be discerned. Medial to the angular lies the *pre-articular* bone; little may be said of this apart from the fact that it seems to be of rather limited anterior extent.

(viii) *Accessory skull elements.* The partial skull from assemblage B. 17 (text-fig. 2) has a pair of slender rod-like bones preserved between the mandibles. That of the right side lacks only the posterior tip and has a length of 28 mm.; it is marked with fine longitudinal striae and has a diameter of 1·5 mm. Its anterior end is slightly inflated (to a diameter of 2·5 mm.) whilst the bone is sharply flexed in the middle—the ends diverging at about 150°. These curved bony rods are the ossified *first ceratobranchials*—which are, as Romer (1956) points out, the parts of the hyoid complex most frequently encountered in fossil reptiles.

The right orbit of skull B. 23 (text-fig. 1) contains a single undamaged *sclerotic plate*. This is paper-thin, roughly triangular (narrowest anteriorly) and is bent so that its lateral surface is concave from dorsal to ventral edges. It has a length of 4 mm. and a maximum width of 2·5 mm. The left orbit of the same skull contains fourteen similar plates (or parts of plates) which are disposed in overlapping arrangement to form a circle (mean diameter 12 mm.) ventral to the supra-orbital bone.

Each orbit of skull B. 23 also contains a long (20 mm.) and rod-like *supra-orbital* bone which is arched to the exterior. Anteriorly the bone is truncated by a facet for attachment to that part of the orbital rim formed by the thickened lateral edge of the prefrontal. The right supra-orbital has been displaced medially; that within the left orbit shows more clearly the natural relationships of the bone.

Dentition

The teeth are described from specimen B. 17 alone. Skull B. 23 contains teeth which are unmistakably those of *Fabrosaurus*, but these are so poorly preserved that they yield little useful information. In the following descriptions the terms used in dentistry will be employed. The tooth surface facing outwards, towards the lips, is termed *buccal*; the surface directed inwards, towards the tongue, is *lingual*. That surface facing the jaw symphysis is *mesial* whilst the surface facing the jaw articulation is *distal*. The tip of the root is defined as the *apex* of the tooth whilst the other, masticatory, end of the tooth is termed *occlusal*.

Premaxillary teeth (text-figs. 5, 6, 8). The left premaxilla from assemblage B. 17 bears six teeth (text-fig. 6), apparently the full complement. The most posterior tooth in this example displays a long and narrow root of circular cross-section and illustrates the thecodont mode of tooth implantation. Each crown appears in buccal profile as a tall (3·5 mm.) and slightly rounded triangle where the acute occlusal tip is slightly recurved. The last two premaxillary crowns are shorter than those in front and foreshadow the squat triangular crowns in the maxilla. At the alveolar margin the crown is distinctly inflated to the exterior and attains a maximum mesio-distal width of nearly 2 mm. The rest of the transversely convex buccal surface is perfectly smooth (save for an extremely faint vertical ridge near the occlusal end).

The smooth and convex lingual surface is marked, near the distal edge, with a distinct vertical furrow. The distal edge of the crown is considerably thinner and sharper than

the mesial edge. The fifth premaxillary crown (from the front) has its distal edge
ornamented with minute denticles; in the last (6th) crown both mesial and distal edges
are finely denticulate. These posterior teeth thus form a transition to the obviously
denticulate maxillary teeth.

Maxillary teeth (text-figs. 2, 3, 7, 8). The best-preserved example of the maxilla (text-
fig. 3) bears eleven teeth—so that their original number might be estimated at thirteen
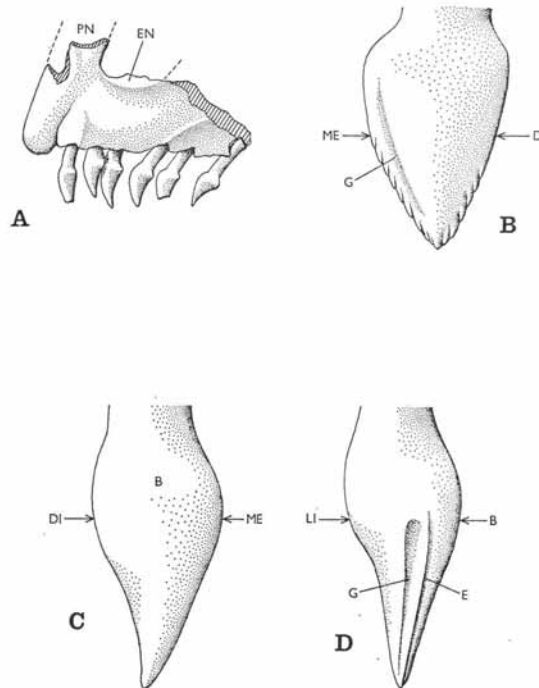
TEXT-FIG. 6. *Fabrosaurus australis*. The premaxilla and its teeth. A, Left premaxilla from assemblage
B. 17. Lateral view ×2·5. EN, inflected ventral margin of external naris; PN, pre-narial ramus.
B, Last (6th) crown in left premaxilla. Buccal view, ×10. DI, distal edge; G, furrow; ME, mesial edge.
c, D, Buccal and distal views of an anterior crown from the right premaxilla. Both ×10. B, buccal
surface; E, sharp distal edge; LI, lingual surface. Other letters as above.

or fourteen. In buccal (or lingual) profile each crown has the outline of a low and
symmetrical triangle where the occlusal tip is formed by the intersection of slanting
mesial and distal edges. The largest crowns, in the middle of the tooth row, are about
3 mm. tall and have similar mesio-distal widths; the smallest crowns, 1–1·5 mm. tall,
are situated at the rear of the maxilla and are perfect replicas of the larger ones.

Each crown is compressed in a bucco-lingual direction and has its inclined mesial and
distal edges ornamented with very characteristic denticles. These short and blunt
denticles are all parallel and none exhibits any curvature or 'hooking' at its tip. The

median denticle is similar to those flanking it and is not appreciably enlarged; there are about seven denticles to each side (mesial and distal) of the median one. The denticles are all of similar size—though locally a very small 'accessory' denticle may be intercalated between two otherwise normal ones.

The smooth and transversely convex buccal crown surface is strongly inflated close to the junction with the root; ill-defined transverse ridges link this swollen area with the most mesial and distal of the marginal denticles. The lingual surface is noticeably flatter than the buccal surface and bears a very faint median ridge. In mesial or distal
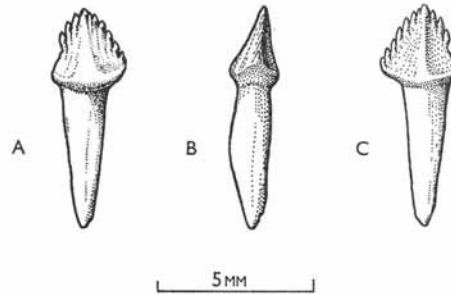
TEXT-FIG. 7. *Fabrosaurus australis*. Cheek tooth from assemblage B. 17.
A, buccal view; B, mesial or distal view; C, lingual view. All ×5.

view (text-fig. 7) it may be seen that the whole crown is slightly deflected in a lingual direction and that there is a weak constriction where the crown joins the narrower root.

Dentary teeth. These are identical to the maxillary teeth. They are of equivalent number and exhibit precisely comparable marginal denticles.

Arrangement of the teeth. Premaxillary, maxillary, and dentary teeth all have their crowns completely enamelled and are all disposed in simple marginal rows. Where the dentigerous bones are broken transversely small replacement teeth may be observed close to the lingual sides of the functional teeth.

Teeth extend right to the front of the premaxilla whilst the predentary is toothless. It may also be observed that the teeth in any jaw bone alternate both in size and in situation. The smaller crowns are regularly intercalated between larger ones (which are also located slightly nearer the lateral margin of the jaw).

The *Fabrosaurus* dentition is heterodont—the teeth in the premaxilla differing radically in appearance from the cheek teeth (i.e. those in maxilla and dentary). This change in form between the premaxillary and maxillary teeth is not abrupt but is marked by the appearance, at the rear of the premaxilla, of transitional crowns which are of intermediate shape and bear weakly developed marginal denticles.

DISCUSSION

The systematic position of Fabrosaurus

The materials described above may safely be referred to the genus *Fabrosaurus* since the teeth of this reptile are highly distinctive and are unlikely to be mistaken for those

of coeval ornithischians (or, for that matter, for those of Triassic saurischians). Gins-burg (1964) inferred ornithischian affinities for *Fabrosaurus* on the evidence of the cheek teeth alone. The identification (above) of a diagnostic predentary bone at the mandibular symphysis fully substantiates the concept of *Fabrosaurus* as an ornithischian dinosaur.

The next matter is to assign *Fabrosaurus* to a particular suborder (and, subsequently, to a family) within the Ornithischia. On the basis of dental similarities Ginsburg sug-gested that *Fabrosaurus* might be allied to the Liassic *Scelidosaurus*. There are, indeed, basic resemblances between the teeth in these two animals; in both cases the completely enamelled crown is compressed in a bucco-lingual direction and possesses an angular and denticulate occlusal margin formed by the intersection of inclined mesial and distal edges. Teeth conforming to this general description are, however, encountered through-out the order Ornithischia and cannot be taken as diagnostic of particular suborders or families. Such teeth are seen, for example, in ornithopods (*Hypsilophodon*), in stego-saurs (*Stegosaurus*), in ceratopsians (*Triceratops*), and in ankylosaurs (*Edmontonia*). These dental characters, though suggestive of ornithischian affinities for *Fabrosaurus*, do not provide sound evidence of any immediate relationship with *Scelidosaurus*. Further, there are numerous minor distinctions between the teeth in these two animals. The blade-like *Scelidosaurus* tooth is much taller than that in *Fabrosaurus* and tends to a distinct asymmetry; the marginal denticles of the *Scelidosaurus* tooth are much more variable in size, are distinctly 'hooked' at their tips, and are arranged in a divergent (rather than parallel) pattern. These differences are, however, of no real use in any attempt to assign the two animals to specific subordinal groups—a direct consequence of the basic conservatism of tooth structure within the Ornithischia.

Amongst ornithischian dinosaurs the skull of *Fabrosaurus* resembles most closely that of the Lower Cretaceous *Hypsilophodon* (as figured by Galton 1967). The pro-nounced similarities with *Hypsilophodon* indicate that *Fabrosaurus* should be placed alongside this former genus in the family Hypsilophodontidae of the suborder Ornitho-poda. *Fabrosaurus* falls naturally into this category (reserved for ornithopods of primi-tive aspect) when one considers that certain of its cranial features (e.g. the toothed pre-maxilla, the inter-parietal suture) are decidedly atypical of ornithischian dinosaurs and may best be matched in the thecodont reptiles—putative ancestors of the Ornithischia.

Though the skulls of *Fabrosaurus* and *Hypsilophodon* are essentially similar in con-struction there are several minor distinctions. The post-narial process of the *Hypsilopho-don* premaxilla separates the nasal from the maxilla on the side of the snout; in *Fabrosaurus*, in contrast, the maxilla is in contact with the nasal for a short distance in front of the orbit. Similar contact between maxilla and nasal is seen, incidentally, in thecodonts such as *Euparkeria* and *Sphenosuchus*.

The *Fabrosaurus* maxilla is distinguished from that of *Hypsilophodon* by its shallow-ness and by its lack of any longitudinal recess above the tooth row. The large and widely open antorbital vacuity is triangular in *Fabrosaurus*, sub-circular in *Hypsilophodon*. The *Fabrosaurus* lacrimal is straighter and is not arched over the antorbital vacuity.

The upper temporal openings of the *Fabrosaurus* skull are separated by a broad and flat zone of skull roof; in *Hypsilophodon*, and in most other ornithopods, there is only a very narrow zone between these skull openings. The *Fabrosaurus* parietals are divided by a distinct median suture. This very unusual feature, which cannot be matched in *Hypsilophodon* (where the parietals are fused in normal ornithischian fashion), is seen
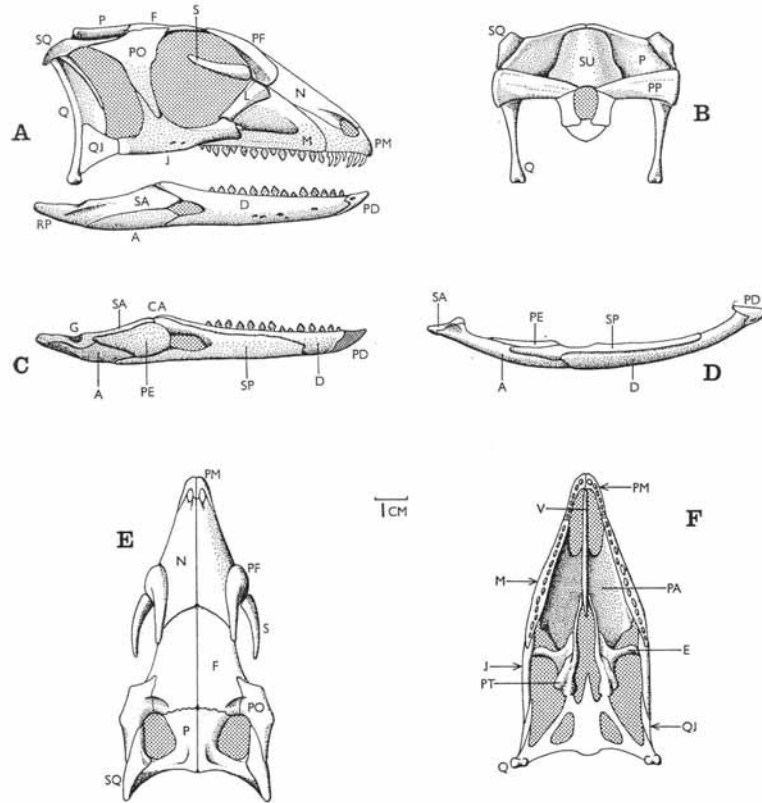
TEXT-FIG. 8. *Fabrosaurus australis*. Reconstruction of skull. All figures ×0·5. A, right lateral view of whole skull. B, occipital view. C, medial view of left mandible. D, ventral view of left mandible. E, dorsal view. F, palatal view.

Lettering as for text-fig. 1, except for: CA, coronoid apophysis; E, ectopterygoid; G, glenoid fossa; PA, palatine; PD, predentary; PE, pre-articular; PT, pterygoid; QJ, quadrato-jugal; RP, retro-articular process; V, vomer.

Following parts are not known and are shown in generalized fashion—quadrato-jugal, bones around foramen magnum, prearticular, ventral surface of brain-case.

also in *Euparkeria* and, more unexpectedly, in *Protoceratops* (Brown and Schlaikjer 1940).

The *Fabrosaurus* mandible is generally similar to that of *Hypsilophodon* though the retro-articular portion is rather more prominent and the coronoid eminence is distinctly less well developed.

The 6 teeth in the *Fabrosaurus* premaxilla extend to the front of the snout; *Hypsilophodon* has 5 premaxillary teeth (Galton 1967) and these are preceded by a wide

edentulous space. The cheek teeth of *Hypsilophodon* (numbering 10 or 11 in maxilla or dentary) are distinguished from those of *Fabrosaurus* (numbering 13 or 14) by their greater height, their prominent surface ridging and the very marked variation in size of their marginal denticles.

Ornithischian origins

The presence of ornithischians in late Triassic sediments certainly suggests that the origins of the group are to be sought at some considerably earlier date. This concept of
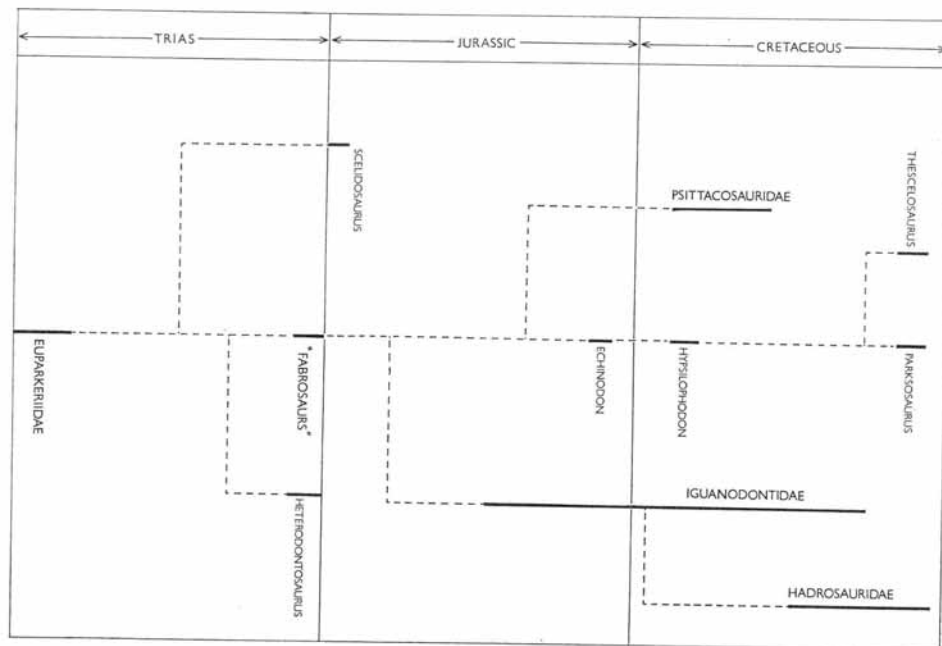
TEXT-FIG. 9. Suggested phylogeny for the Ornithopoda. The 'FABROSAURS' (*Fabrosaurus, Tatisaurus, Pisanosaurus*) are referred to the family Hypsilophodontidae together with *Heterodontosaurus, Echinodon, Hypsilophodon, Parksosaurus,* and *Thescelosaurus*.

a very early start to ornithischian history, whilst unsupported by fossil evidence, is reinforced simply by the geographic and structural diversity of the known Triassic ornithischians—*Fabrosaurus, Geranosaurus* (Broom 1911), and *Heterodontosaurus* (Crompton and Charig 1962) from southern Africa; *Tatisaurus* (Simmons 1965) from China; *Pisanosaurus* (Casamiquela 1967) from South America.

The skulls of *Geranosaurus, Pisanosaurus,* and *Tatisaurus* are known only from fragments; the better-known *Heterodontosaurus* skull has a remarkably specialized dentition including 'canine' teeth. Thus it is natural to turn to the relatively well-known and unspecialized *Fabrosaurus* skull in the search for persistent primitive features which

might be indicative of ornithischian ancestry. There are, in fact, only a few characters in *Fabrosaurus* which are noticeably atypical of later ornithischians and which might justifiably be termed primitive. Several cranial features, including the widely open antorbital vacuity, the large external mandibular fenestra and the weakly developed coronoid process, may be closely paralleled in a wide range of thecodont reptiles (e.g. *Ornithosuchus, Euparkeria, Stagonolepis*). It is immediately evident that such features are of no practical use in any attempt to locate the possible ancestors of the Ornithischia —simply because of their very frequent occurrence in diverse members of the Thecodontia. Similarly the inter-parietal suture of the *Fabrosaurus* skull is matched in numerous thecodonts (*Euparkeria, Ornithosuchus, Machaeroprosopus*, etc.) and gives no precise clue as to ornithischian origins.

Ewer (1965) supports the general contention advanced by Broom (1913) that the thecodont family Euparkeriidae probably includes the ancestors of all the major lineages of later archosaurs—including the Ornithischia. Whilst saurischian dinosaurs may be derived from hypothetical *Euparkeria*-like ancestors with no very excessive stretching of the imagination it is considerably more difficult to derive ornithischians from the same source—mainly because of irreconcilable differences in ankle and pelvis structure (see Ewer 1965). Whilst it is reasonable to assume that the ancestry of the Ornithischia extends back *ultimately* into the Euparkeriidae this still does not clarify the problem of ornithischian history between Lower and Upper Trias. The members of the Euparkeriidae exhibit no obvious trend towards the ornithischian state of organization whilst the earliest known ornithischians, such as *Fabrosaurus*, present very few primitive characters. Due largely to inadequacies of information concerning Middle Triassic archosaur faunas there is a very considerable hiatus between the Euparkeriidae and the earliest ornithischian dinosaurs. There are, in consequence, no apparent 'intermediates' between the Lower Triassic *Euparkeria* and the Upper Triassic *Fabrosaurus*.

The outlines of ornithopod phylogeny

It is probable that all of the varied ornithischian types of the later Mesozoic have arisen from ancestors which are to be grouped, ultimately at least, within the Hypsilophodontidae. This scheme is quite reasonable since any later ornithischians (most particularly the iguanodonts and the hadrosaurs) may be derived from hypothetical *Hypsilophodon*-like ancestors without any great difficulty. This much, at least, of ornithischian history is fairly clear and has been adequately expressed by earlier authors (e.g. Romer 1945).

Pronounced cranial similarities between *Fabrosaurus* and *Hypsilophodon* have already been noted. *Fabrosaurus*, rather than *Hypsilophodon*, would seem to fulfil the requirements of a genuine ornithischian 'archetype'—simply by virtue of its much earlier stratigraphic location. The basic resemblances between these two dinosaurs also indicate that they are linked in an evolutionary sense—i.e. *Hypsilophodon* appears to be a fairly direct descendant of *Fabrosaurus*. *Echinodon*, a diminutive reptile from the British Purbeck, constitutes a very satisfactory intermediate between *Fabrosaurus* and *Hypsilophodon*, both in relative stratigraphic position and in morphology. *Echinodon* was originally described as a lizard (Owen 1861); it shows, however, thecodont implantation of the teeth (not acrodont or pleurodont as in true lizards), cheek teeth of ornithischian aspect,

and the 'special foramina' described by Edmund (1957) as characteristic of ornithischian dinosaurs. The premaxillary teeth of *Echinodon* point to hypsilophodont affinities.

These three dinosaurs (*Fabrosaurus*, *Echinodon*, *Hypsilophodon*) represent a hypsilophodont lineage persisting from the late Trias to the Lower Cretaceous. *Parksosaurus*, from the North American end-Cretaceous, appears to be the latest known representative of this lineage. These hypsilophodonts retain primitive features (e.g. the premaxillary teeth) which are not encountered in other ornithischians and which demonstrate the need for coherence of these forms in any evolutionary scheme. This same lineage is shown, in consequence, at the core of the 'evolutionary tree' of the ornithopods (text-fig. 9).

Heterodontosaurus, with its peculiarly specialized dentition, represents the earliest evolutionary divergence from the basic hypsilophodont stock. Since both *Fabrosaurus* and *Heterodontosaurus* are referred to the family Hypsilophodontidae it is probable that these two shared a common ancestry at some date earlier in the Trias, implying, in turn, that ornithischian origins were monophyletic. This latter inference is strengthened by the essential homogeneity of structure throughout the Ornithischia.

Tatisaurus and *Pisanosaurus* appear to have unspecialized dentitions and may be regarded as fairly close relatives of *Fabrosaurus*. The great geographic range of this 'fabrosaur' group points to some pre-Upper Triassic episode of migrations and dispersal. Since most known Triassic ornithischians come from southern Africa the centre of this hypsilophodont dispersal might reasonably be expected to occur in this region. This impression of a centre of origin might, however, merely reflect former intensity of interest, and of collecting, in the African Trias. At any rate the 'fabrosaurs' appear to have been much more adaptable and successful than *Heterodontosaurus* and the (perhaps) allied *Geranosaurus*, characteristics that one would naturally anticipate in the 'root-stock' of the ornithischian dinosaurs. *Heterodontosaurus* seems, in contrast, to have been a very specialized and localized (African only) off-shoot of the basic hypsilophodont lineage. Whilst the 'fabrosaurs' successfully faced the environmental changes concomitant with the close of the Triassic period, *Heterodontosaurus* did not, presumably because it was adapted for a very specific mode of life. There are no apparent post-Triassic derivatives of *Heterodontosaurus*.

The first armoured and quadrupedal ornithischians, exemplified by *Scelidosaurus*, appear at the beginning of the Jurassic. The disappearance at the end of the Trias of armoured, quadrupedal, and herbivorous pseudosuchians such as the aetosaurs (Walker 1961) might, in fact, be explained in terms of competition from similarly adapted ornithischians. The derivatives of *Scelidosaurus*, if there be any, cannot be determined at present.

At some date early in the Jurassic the *Fabrosaurus–Hypsilophodon* line of hypsilophodonts gave rise to the larger and more specialized iguanodonts. Known iguanodont remains extend from the Middle Jurassic (*Cryptodraco*) into the late Cretaceous (*Craspedodon*) and it is probable that there are several distinct evolutionary lines within this family itself—though these may not be discussed here. The arrangement shown (text-fig. 9) is in direct contrast to the scheme proposed by Colbert (1951)—where it is suggested that *Hypsilophodon* might have arisen from a 'camptosaurid stem'.

Ostrom (1961) has suggested that the hadrosaurs might have been derived from *Camptosaurus*-like iguanodonts by way of intermediates like the poorly known *Claosaurus*. This scheme is utilized here (see text-fig. 9).

Towards the close of the Jurassic period the basic hypsilophodont stock, exemplified at this point in time by *Echinodon*, gave rise to several small ornithopod types which are of decidedly primitive aspect (e.g. *Laosaurus*, *Nanosaurus*). At roughly the same time a number of diminutive forms (*Psittacosaurus*, *Protiguanodon*) emerged from a (presumably) similar source to become highly suggestive of ceratopsian ancestry.

The basic hypsilophodont stock persisted to the very end of the Cretaceous period with the appearance of *Parksosaurus*. The last divergence from this lineage, just before the extinction of dinosaurs in general at the end-Cretaceous, is represented by *Thescelosaurus*. *Thescelosaurus* possesses a femur which is longer than the tibia (the reverse being true in the otherwise comparable *Parksosaurus*); this feature suggests that *Thescelosaurus* might have filled an ecological niche similar to that previously exploited by the iguanodonts (which had a similar tibio-femoral ratio). If this is so it constitutes evidence that some form of iterative evolution (involving repeated divergences from a main stem towards a single goal) was an operative factor in ornithopod history.

It may be concluded that *Fabrosaurus* and its allies represent the earliest known portion of a hypsilophodont lineage which extended through the greater part of the Mesozoic era and which gave rise, even if indirectly, to well known and very specialized ornithischian groups—iguanodonts, hadrosaurs, ceratopsians, and the like. The 'fabrosaurs' appear, in fact, to fulfil the requirements of genuine ornithischian 'archetypes'. *Heterodontosaurus* seems, in contrast, to represent an early and rather specialized hypsilophodont divergence which failed to survive the close of the Triassic period.

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