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POSTCRANIAL REMAINS OF FABROSAURIDAE (REPTILIA : ORNITHISCHIA) FROM THE STORMBERG OF SOUTHERN AFRICA

by

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ABSTRACT

The postcranial skeletons of three fabrosaurids from the upper Elliot Formation "Red Beds" of the Stormberg Group in southern Africa are described. The material demonstrates details of fabrosaurid anatomy previously unknown, particularly a short, deep prepubic process which is undoubtedly primitive for the Ornithischia. Besides the short prepubis, fabrosaurids are characterized by 1) a reduced manus; 2) an ilium having a lateral extension of the supra-acetabular margin and a deep nearly vertical brevis shelf; and 3) an elongated hindlimb. Postcranial morphology excludes the fabrosaurids from the ancestry of the contemporaneous heterodontosaurids. Neither can the fabrosaurids be considered ancestral to the 'juvenile scelidosaurid' (BMNH R6704) as has been suggested. On the contrary, the 'scelidosaurid' is more primitive in structure than fabrosaurids. The assignment of *Nanosaurus agilis* Marsh to the Fabrosauridae is not substantiated after morphological comparisons between the postcranial material of both. The taxonomic status of *Scutellosaurus lawleri* is regarded as uncertain. The fabrosaurids are more similar to the Morrison Formation camptosaurids, than to *Hypsilophodon*. Finally, it is argued that ornithopods were not a basal stock for the phylogenesis of non-ornithopods but represent an independent radiation comparable to the other ornithischian suborders. The fabrosaurids were an early development of the ornithopod radiation itself.

CONTENTS

	Page
INTRODUCTION	151
DESCRIPTION	153
DISCUSSION	167
ACKNOWLEDGEMENTS	176
REFERENCES	176
APPENDICES	178

INTRODUCTION

For many years it was thought that ornithischian dinosaurs appeared late in the Mesozoic since few unequivocal skeletal remains were known from earlier than the late Jurassic. This was in marked contrast to the saurischians which were relatively common in the later Triassic. The eventual recovery of early ornithischian material from late Triassic/early Jurassic deposits (Bonaparte 1976; Casamiquela 1967; Colbert 1981; Crompton and Charig 1962; Ginsburg 1964; Santa Luca, Crompton and Charig 1976; Simmons 1965; Thulborn 1970a, b, 1972. 1974) has disproven the notion of late evolving ornithischians. The next development in the assessment of early ornithischians was the recognition that they could not all be accommodated within the conservative ornithopod family Hypsilophodontidae; as a direct result the families Heterodontosauridae (Kuhn 1966; Romer 1966) and Fabrosauridae (Galton 1972) were erected to contain much of the new material. Finally, after a detailed analysis of some of the heterodontosaurid material, it became apparent that the morphological diversity displayed by the early ornithischians even went beyond the limits of the suborder Ornithopoda (Santa Luca Crompton and Charig 1976; Santa Luca 1980).

At the present time most early ornithischian dinosaurs known are classed either as Fabrosauridae or as Heterodontosauridae (the status of the 'juvenile scelidosaurid, BMNH R6704, remains uncertain). The fabrosaurids represent an early lineage in the ornithopod radiation; they were small, around a metre in length, and probably obligate bipeds in locomotion. They were also fairly widely distributed geographically: they are known from the Stormberg localities in southern Africa, from the Kayenta formation of western North America, from the Jurassic of Portugal (Thulborn 1973) and

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perhaps the Jurassic-Cretaceous of England (*Echinodon*).

The heterodontosaurids represent an early radiation of non-ornithopods; they were also small, the only complete postcranial skeleton giving a length of one metre. However, *Heterodontosaurus tucki* was certainly not an obligate biped and was capable of quadrupedal locomotion (Santa Luca 1980). The distribution of heterodontosaurids seems to be less widespread, from the Stormberg of southern Africa and perhaps from the Ischigualasto of Argentina (*Pisanosaurus:* Casamiquela 1967; Bonaparte 1976). The contemporaneity of these families, and the 'juvenile scelidosaurid' to be discussed later, suggests that diverging trends had become established quite early in ornithischian phylogeny.

CLASSIFICATION OF THE FABROSAURIDAE

Ginsburg (1964) described the first fabrosaurid, *Fabrosaurus australis*, on the basis of a fragmentary right dentary with several teeth. This specimen was found in 1959 in the Upper Red Beds of the Stormberg series of Lesotho Because the teeth were triangular in shape with small occlusal denticles and a basal cingulum he interpreted the specimen as a scelidosaur, comparing it with *Scelidosaurus harrisonii* Owen 1861 and interpreting the latter as a member of the suborder Stegosauria.)

Thulborn (1970) described the skull and dentitions of two more specimens from the Upper Red Beds of Lesotho which he believed were congeneric and conspecific with Ginsburg's specimens. One of these (University College, London B. 17) was collected from Likhoele Mountain, as was Ginsburg's; the other (UCL B. 23) was also collected from the Upper Red Beds but about 40 miles (c. 60 km) distant from the former. Specimen UCL B. 17 comprises cranial, dental and postcranial material but UCL B. 23 only cranial and dental material.

Thulborn (1970) disagreed with Ginsburg's assignment of *F. australis* to the Scelidosauridae and transferred both his and Ginsburg's specimens to the Hypsilophodontidae. The reason for doing so was the discovery that *F. australis* had a toothed premaxilla which Thulborn considered distinctive of hypsilophodontids. For the same reason he included *Echinodon* within the Hypsilophodontidae and interpreted it as an intermediate between *Fabrosaurus* and *Hypsilophodon* (1970:429–430).

Galton (1972) removed *F. australis*, both Ginsburg's and Thulborn's specimens, from the Hypsilophontidae; he reassigned them to the newly created family Fabrosauridae which was defined as "having marginally positioned maxillary and dentary teeth" (1972:464). At the same time *Echinodon* was transferred to this family because it also possessed this character, considered by Galton to be primitive for the Ornithischia. If in fact a marginal dentition is primitive, then the family Fabrosauridae would have been defined on the basis of a symplesiomorphy and the composition of the family (including *Echinodon* and *Nanosaurus agilis*) may be paraphyletic.

In a discussion of the supposed generic synonymy of *Lycorhinus* and *Heterodontosaurus*, Charig and Crompton (1974) briefly considered the dentition of the known fabrosaurids. In their opinion the dentition of these specimens may be primitive or plesiomorphous for ornithischians as a whole; the teeth would then not be diagnostic of a single genus or species but rather of a family or higher taxon. Consequently, they argued that the genus *Fabrosaurus* and the species *F. australis* were *nomina dubia* and that Ginsburg's and Thulborn's specimens were of an indeterminate genus and species of fabrosaurid.

Galton (1978) partially revised the Fabrosauridae to include *Nanosaurus agilis* Marsh 1877 (Marsh 1877, 1894) because the dentary is slender and had a marginal rather than inset dentition, the latter supposedly implying the presence of cheeks (Galton 1973). At the same time Galton removed Thulborn's University College, London specimens from *F. australis* Ginsburg and created a new genus as well as a new species for them, *Lesothosaurus diagnosticus* Galton 1978. He did not, however, follow Charig and Crompton (1974) regarding the invalidity of both the genus *Fabrosaurus* and the species *F. australis*, but accepted Ginsburg's assignment. In Galton's system then, *F. australis* refers only to the partial right dentary described by Ginsburg.

The only existing description of the fabrosaurid postcranial skeleton comes from Thulborn (1972). The specimens he described were fragmentary and many important structures were not preserved; in contrast the specimens to be described here, although also fragmentary, fortunately include details of postcranial anatomy not available from the UCL specimens. These details clarify the relative position of fabrosaurids to heterodontosaurids, the character-state of some important structural features in ornithschian phylogeny, and add considerably to the functional understanding of fabrosaurid anatomy.

The teeth of most early ornithischians are remarkably similar and primitive in character; in this case details of postcranial anatomy become all the more important in unravelling the evolutionary relationships of early ornithischians. Thus the goal of this paper is not merely to provide anatomical descriptions and functional interpretations of important osteological material, but to evaluate the evolutionary differences between the early ornithischians.

Material

The postcranial remains of three South African Museum specimens are described in this paper. SAM–K400 and K401 were recovered from Likhoele Mountain in Lesotho, the site of Ginsburg's original discovery of fabrosaurid remains and of the UCL B.17 specimen (for map see Thulborn 1972). SAM–K1106 was recovered at Dangershoek. In addition to the postcrania some dental remains

and fragmentary cranial material were recovered and are being described. An inventory of preserved material and a list of measurements are given in the Appendices.

The fabrosaurid specimens have been compared with a wide range of ornithischian postcranial material. This included ankylosaurs (Coombs 1978; Eaton 1960; Maryańska 1977); ceratopsians (Brown and Schlaikjer 1940; Hatcher, Marsh and Lull 1907; Maryańska and Osmólska 1975; Lull 1933; Osborn 1923, 1924); ornithopods (Galton 1974a, b, 1977, 1981; Galton and Jensen 1973; Gilmore 1909, 1915, 1924b, 1925; Hooley 1925; Janensch 1955; Lull and Wright 1942; Ostrom 1970; Marsh 1894; Parks 1920, 1926; Shepherd, Galton and Jensen 1977; Sternberg 1940); pachycephalosaurs (Gilmore 1924a Maryańska and Osmólska 1974), stegosaurs (Gilmore 1914) and *Heterodontosaurus tucki* (Santa Luca 1980).

DESCRIPTION

Vertebral Column

It is still not possible to determine the total number of vertebrae or the number of vertebrae in a particular region of the fabrosaurid vertebral column.

Cervical vertebrae (fig. 1–3).

The description of the cervical vertebrae must begin with a consideration of the cervical vertebrae preserved in the UCL B.17 specimen. Thulborn (1972:33, fig. 3) illustrated a fragment containing parts of three cervical vertebrae (the anterior two almost complete, the third represented only by the prezygapophyses) and attributed them to the middle cervical region but gave no evidence for this

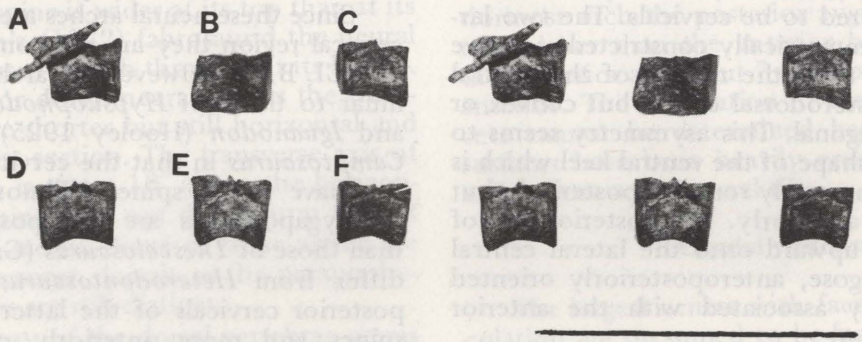

Fig. 1 SAM–K1106. A–C. Cervical centra. D–F. Dorsal centra. Right lateral view. Scale = 5 cm.

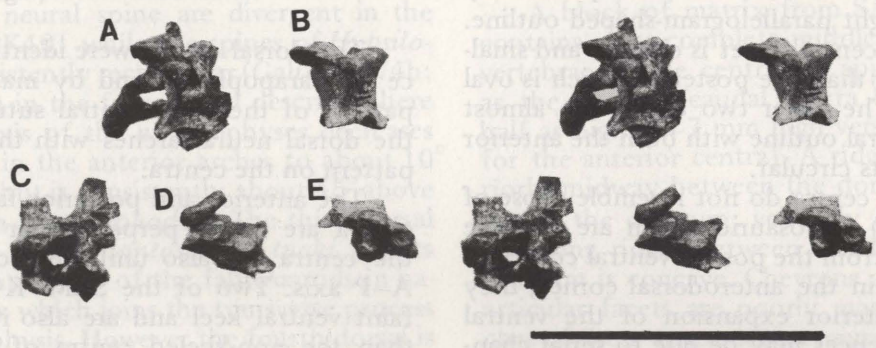

Fig. 2 SAM–K1106. A–B. Cervical neural arches. C–E. Dorsal neural arches. Right lateral view. Scale = 5 cm.

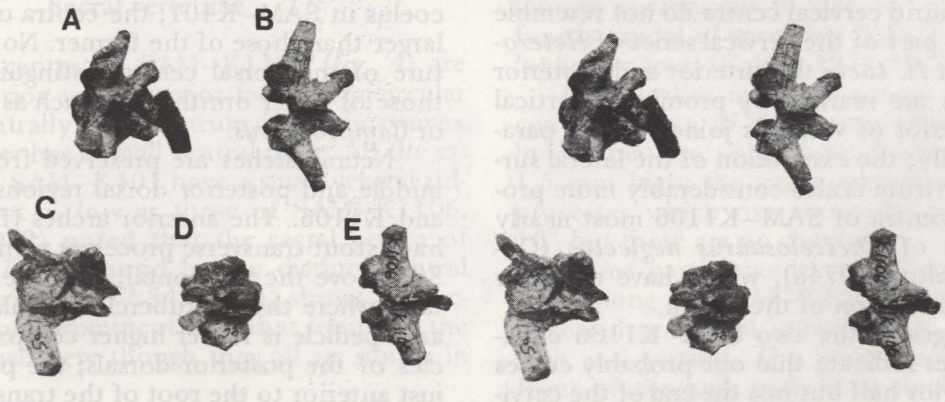

Fig. 3 SAM–K1106. A–B. Cervical neural arches. C–E. Dorsal neural arches. Dorsal view. Scale = 5 cm.

conclusion.

On the basis of serial changes in cervical vertebrae (e.g., see *Hypsilophodon foxii,* Galton 1974b or *Heterodontosaurus tucki,* Santa Luca 1980) those of the UCL B.17 specimen can only be anterior cervicals First, the diapophyses are very small and set on the pedicles of the neural arch near the neurocentral suture as in anterior cervical vertebrae; in middle cervicals the diapophysis would be at the end of a small transverse process. Second, the parapophyses on the centra are poorly developed and lie below the neurocentral suture, also as in anterior cervical centra; in middle cervicals the parapophyses would be larger and would be bisected by the neurocentral suture. The three vertebrae Thulborn (1972) illustrated are more likely to be either the axis, C3 and C4 or C3, C4 and C5, rather than middle cervicals.

The three centra described here are from SAM–K1106 (fig. 1A–C); each has a ventral keel and were thus considered to be cervicals. The two larger centra are asymmetrically constricted: concave above a diagonal from the middle of the ventral margin to the posterodorsal corner but convex or flat below this diagonal. This asymmetry seems to be related to the shape of the ventral keel which is wide, low and transversely rounded posteriorly but narrow and sharp anteriorly. The posterior part of the keel extends upward onto the lateral central surface; it has rugose, anteroposteriorly oriented striations probably associated with the anterior vertebral musculature.

The remaining centrum (fig. 1C) is smaller, not asymmetrically constricted and does not have an expanded and flattened ventral keel; posteriorly it does have a slight parallelogram-shaped outline. The anterior intercentral facet is circular and smaller (7,3 mm high) than the posterior which is oval (8,7 mm high). The other two centra are almost rectangular in lateral outline with both the anterior and posterior facets circular.

These cervical centra do not resemble those of Thulborn's (1972) fabrosaurid which are concave below a diagonal from the posteroventral corner to the parapophysis in the anterodorsal corner; they also lack the posterior expansion of the ventral keel. These differences may be due to serial changes, but at the present no data are available to settle the question.

The fabrosaurid cervical centra do not resemble those from any part of the cervical series of *Heterodontosaurus.* In *H. tucki* the anterior and posterior central margins are marked by prominent vertical ridges, the anterior of which is joined to the parapophysis dorsally; the excavation of the lateral surfaces of the centrum is also considerably more pronounced. The centra of SAM–K1106 most nearly resemble those of *Thescelosaurus neglectus* (Gilmore 1915; Galton 1974a), which have a similar asymmetric constriction of the centra.

Serial changes in the two SAM–K1106 cervical neural arches indicate that one probably comes from the posterior half but not the end of the cervical series (fig. 2A, 3A); in this specimen only the uppermost part of the parapophysis is on the arch pedicle; the transverse process is about 8 mm long and arises just below the prezygapophysis; the transverse axis of the zygapophyses is about 60° to the horizontal; the distance between the anterior and posterior margins of the zygapophyses is 15,4 mm; the postzygapophyses lie on the same level as the prezygapophyses; and the neural spine is a small nubbin. The other cervical neural arch probably comes from nearer the end of the cervical series (fig. 2B, 3B); here the parapophysis lies almost entirely above the neurocentral suture; the transverse process is 9 mm long and arises at the level of the prezygapophyses; the transverse axis of the zygapophyses is about 45° ; the distance between the anterior and posterior margins of the zygapophyses is 16,7 mm; the pre- and postzygapophyses lie on the same level; the neural arch, while broken off, is still quite small.

Since these neural arches are from the posterior cervical region they are not comparable with those of UCL B.17. However the arches are generally similar to those of *Hypsilophodon* (Galton 1947b) and *Iguanodon* (Hooley 1925); they differ from *Camptosaurus* in that the cervicals of the latter do not have neural spines (Gilmore 1909) and their postzygapophyses are less posteriorly projecting than those of *Thescelosaurus* (Galton 1947a). They differ from *Heterodontosaurus* only in that the posterior cervicals of the latter have larger neural spines and more anteriorly projecting, tongue-shaped prezygapophyses.

Dorsal vertebrae (fig. 1–3)

The dorsal centra were identified by the absence of parapophyses and by matching the typical pattern of the neurocentral suture on the base of the dorsal neural arches with the negative of that pattern on the centra.

The anterior and posterior facets of the dorsal centra are nearly perpendicular to the A–P axis; the centra are also uniformly concave about the A–P axis. Two of the SAM–K401 centra have a faint ventral keel and are also relatively narrower than the non-keeled centra of SAM–K401. The centra are amphiplatyan or very slightly amphicoelus in SAM–K1106 but are more generally amphicoelus in SAM–K401, the centra of which are also larger than those of the former. No remarkable feature of the dorsal centra distinguishes them from those of other ornithopods such as *Hypsilophodon* or *Camptosaurus.*

Neural arches are preserved from the anterior, middle and posterior dorsal regions in SAM–K401 and K1106. The anterior arches (fig. 2C,D; 3C,D) have stout transverse processes rising at about 20°–30° above the horizontal; they are subcircular distally where the rib tubercle articulates. The neural arch pedicle is rather higher compared to the pedicles of the posterior dorsals; the parapophysis lies just anterior to the root of the transverse process in

SAM–K401 and immediately underneath the process in SAM–K1106. In this feature the SAM–K1106 arches resemble the third dorsal of *Camptosaurus* (Gilmore 1909:232, fig. 15). The transverse axis of the zygapophyses is also about 20°– 30° above the horizontal. The neural spine arises from a short base on the arch behind the prezygapophyses.

In the middle dorsal vertebrae (fig. 2E, 3E) the transverse processes are horizontal and rectangular in cross section at their distal end. The processes are also lower relative to the neurocentral suture as the pedicles are shorter. The parapophysis is closer to the anterior margin of the centrum, anterior and just inferior to the root of the transverse process and lateral to the prezygapophysis. The base of the neural spine is more extensive, since the distance between the pre- and postzygapophyses has increased. In SAM–K401 the anterior and posterior margins of the spine are somewhat divergent toward its extremity so the spine is wider at its top than at its base. In Thulborn's (1972) fabrosaurid the neural spine was of consistent width throughout its height.

In the posterior dorsal neural arches the transverse processes are shorter but still horizontal and rectangular in cross section. The transverse axis of the zygapophyses is about 10° above the horizontal. The neural spine does not differ from that of the middle dorsal arches. None of these arches are from the posteriormost dorsals as the parapophysis and diapophysis are still distinct.

The morphology of the dorsal vertebrae seems to have been quite conservative within the Ornithopoda. Only two differences separate those just described from the dorsals of *Hypsilophodon:* 1) the margins of the neural spine are divergent in the arches of SAM–K401 while the spines of *Hypsilophodon* are consistently rectangular (Galton 1974b: 55, fig. 22); 2) in the fabrosaurid described here the transverse axis of the zygapophyses decreases from about 45° in the anterior arches to about 10° in the posterior but is consistently about 45° above the horizontal in *Hypsilophodon.* The third dorsal neural arch of *Heterodontosaurus tucki* differs from the anterior arches of the fabrosaurids in having a small ridge which joins the transverse process and the parapophysis. However the fourth dorsal is a typical middle dorsal without a ridge.

Sacral vertebrae

The two centra of SAM–K1106 (fig. 4) are low, the anterior and posterior facets semicircular in shape. Ventrally one centrum is gently convex while the other has a small ventral ridge. All the sacral centra of SAM–K401 have a small ventral ridge but are not as low as those of SAM–K1106. Thulborn (1972) noted that the sacral centra of the UCL B.17 fabrosaurid bore a distinct ventral keel; his drawing (1972:34, fig. 4) shows a structure much more prominent than that found on the centra described here though they all are similar in absolute size.

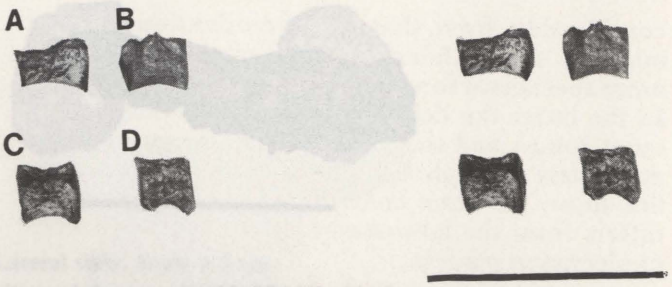

Fig. 4 SAM–K1106. A–B. Sacral centra. C–D. Caudal centra. Left lateral view. Scale = 5 cm.

The four sacral neural arches of SAM–K401 seem to represent a single series; the neural spines change from the dorsal type which are narrower at the base than distally, to the caudal type which are taller and uniform in anteroposterior width throughtout. A similar series of changes is noted in the level of the pre- and postzygapophyses. In the anteriormost arch the posterior zygapophyses are 2–3 mm higher than the anterior but in the last arch the posterior are about 7 mm above the level of the anterior. The orientation of the zygapophyseal facets cannot be determined because the articular surfaces have been heavily eroded. Each of these arches bore a true sacral rib.

Caudal vertebrae

The largest centra with facets for chevron articulation are presumed to be from the anterior caudal region. They are strongly convex along the A-P axis with anterior and posterior facets much wider than the centrum in mid-length.

A block of matrix from SAM–K1106 (fig. 5) contains eight complete middle-to-posterior caudal vertebrae. These centra are approximately as long as the anterior caudal centra but are only about half as high (5–7 mm high versus 10–15 mm high for the anterior centra). A ridge runs anteroposteriorly midway between the dorsal and ventral margin of the centrum; ventrally each centrum bears two long ridges between which the surface of the centrum is concave. Chevrons are present but their articular facets are poorly marked. The neural arches of these centra lack a neural spine and any trace of a transverse process; the arms of the zygapophyses lay 45° or less to the horizontal. These vertebrate correspond in size to about the twenty-fourth caudal of specimen BMNH R5830 of *Hypsilophodon foxii* (Galton 1974:70, fig. 32).

One further matrix fragment of SAM–K1106 contains three of the posteriormost caudal vertebrae. They are only about 5 mm long and about 1,5 mm high; the zygapophyses are still borne on processes which rise above the centrum at about 10°, but there are no chevrons.

Three partial caudal neural arches were identified among the SAM–K401 material. Only one has a complete neural spine which is narrow-based, high and vertical. The prezygapophyses extend in front of the arch pedicle on small horizontal pro-



Fig. 5 SAM–K1106. Matrix containing articulated caudal vertebrae. Left lateral view. Scale = 5 cm.

cesses just below the base of the spine; the posterior zygapophyses are 5 mm above the level of the anterior. The transverse axis of the pre- and postzygapophyses is about 45° in one arch and about 70° in the other two.

Thulborn (1972:35) speculated that the postzygapophyses were weakly developed or absent in the single posterior caudal neural arch from the UCL B.17 specimen. This is highly unlikely since even the smallest caudals of SAM–K1106, much smaller than that illustrated by Thulborn (1972: 34, fig. 4K), bear the anterior and posterior arms for both sets of zygapophyses. The middle and posterior caudals illustrated by Thulborn have no transverse process, as in the specimens here. In this they resemble the posterior caudals of *Hypsilophodon* but differ from those of *Heterodontosaurus,* in which the posterior caudals bear a small nubbin of a transverse process.

PECTORAL GIRDLE AND FORELIMB

Two fragmentary scapular blades are preserved in the matrix block of SAM–K1106 (fig. 6). At their posterior and inferior margin they bear a prominent expansion exactly like that found on the UCL B.17 scapula. This projection resembles that of *Camptosaurus* (except possibly *C. medius* Marsh) more than that of either *Hypsilophodon* or *Thescelosaurus* in which the process is less pronounced because the scapula of these latter expands in width gradually toward the vertebral border. An acromial process was present but its size is indeterminate since the distal end has been broken away. The narrowest part of the scapular shaft is about 11 mm wide and about 6,5 mm thick; thus the shaft is rectangular and never becomes circular in cross section. The glenoid surface of each scapula is covered with matrix.

Two unfused coracoids of SAM–K1106 are completely prepared (fig. 7). They are rectangular, about 27 mm dorsoventrally (from glenoid to acromial end) and about 21 mm anteroposteriorly (from scapular to free end). A large foramen pierces the external surface about 5 mm from the sutural attachment to the scapula. The course of the foramen is perpendicular to the plane of the coracoid and so pierces the deep surface of the bone also about 5 mm lateral to the scapular attachment. In the UCL B.17 fabrosaurid the coracoid surface of the scapula has a distinct notch whose mirror image in the coracoid would have created a foramen (the coracoids are not preserved in the UCL B.17 specimen). The coracoid is much thicker at the glenoid end than at the dorsal margin. The glenoid margin makes an angle of only about 20° with the scapular edge, creating a deep and narrow glenoid fossa. The coracoid of SAM–K1106 differs from that of *Hypsilophodon* BMNH R5830 (Galton 1974b) only in that the coracoid of *Hypsilophodon* has a pronounced concave ventral border while that of the fabrosaurid is nearly straight, marked only by a groove near the glenoid lip.

The scapulocoracoid of SAM–K1106 differs in several respects from that of *Heterodontosaurus:* 1) the hook-like process of the scapular blade at the posterior-ventral margin is much more prominent; 2) the shaft of the fabrosaurid scapula becomes rectangular in cross section but not circular; 3) the glenoid fossa is probably deeper than in *H. tucki.*

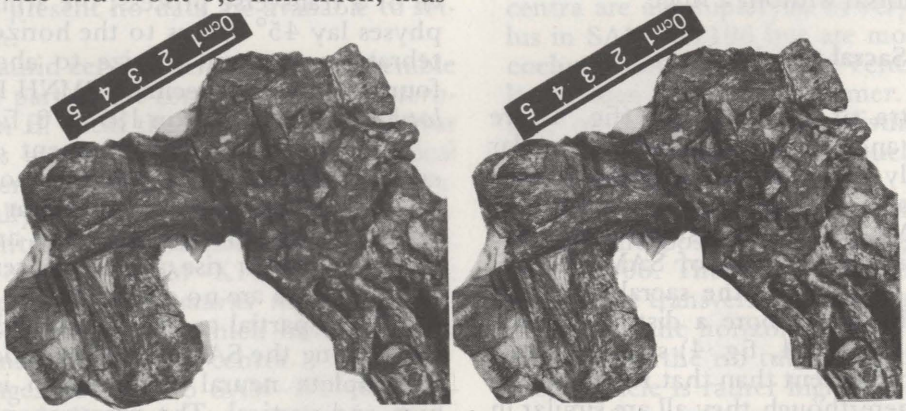

Fig. 6 SAM–K1106. Anterior portion of matrix block, left side. Note scapular blades and proximal humeral shaft.

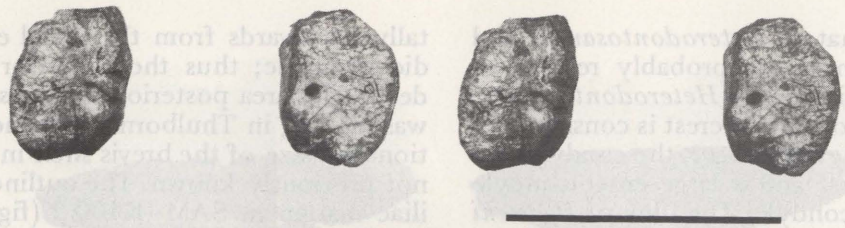

Fig. 7 SAM–K1106. Coracoids. Lateral view. Scale = 5 cm.

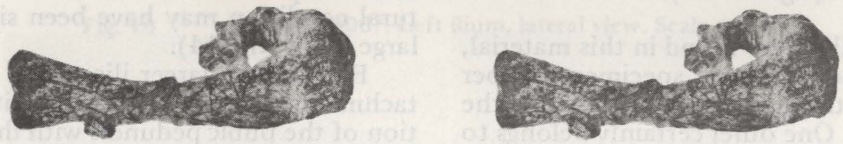

Fig. 8 SAM–K1106. Left humerus. Anterior view. A cervical neural arch is still attached by matrix. Scale = 5 cm.

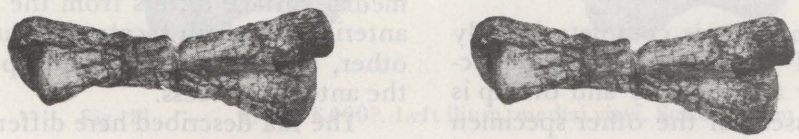

Fig. 9 SAM–K1106. Left radius (foreground) and ulna (background). Lateral view. Scale = 5 cm.

The proximal half of a right humerus (see fig. 6) and the entire left humerus (fig. 8) are preserved in SAM–K1106. The head is expanded (9 mm wide, considerably more than that of specimen UCL B.17) and convex both lateromedially and anteroposteriorly; it lies on the medialmost part of the proximal end and is not centrally placed. On the right humerus the medial side of the shaft below the humeral head is thickened into a ridge which continues inferiorly to the lower level of the deltopectoral crest opposite. A similar feature appears in Thulborn's (1972:38, fig. 7C) drawing of a humerus, but is not noted in the text. The surface of the left humerus is considerably damaged and consequently the ridge-like structure seems less well-developed. The deltopectoral crest projects from the humerus as a distinct process about 15 mm below the head; at its highest point is is about 5 mm above the humeral shaft and it is only about 15 mm long.

The radial condyle is anteroposteriorly longer than wide with the long axis directed anterolaterally; the ulnar condyle is more oval in section, the long axis transversely oriented. Consequently, the distal anteroposterior humeral width is greater laterally than medially. The distal posterior surface is slightly concave between the two condyles; the distal end of the shaft lacks both an ect- or entepicondylar process.

A left radius and ulna of SAM–K1106 (fig. 9) and a right radius of SAM–K400 were preserved but the articular surfaces and the cortical bone are so damaged that few details can be made out. The proximal end of the radius seems to be semicircular in cross-section, unlike the UCL B.17 radius which is kidney-shaped in proximal view, and the *Hypsilophodon* radius, which is rectangular in section (Galton 1974: 79, fig. 40E). Distally the radius of both specimens is subcircular in section. The ulna of SAM–K1106 lacks an olecranon process; the shaft is triangular in section at both extremities. These forearm bones are larger than those of the UCL B.17 fabrosaurid, but the humeroradial index is nearly the same: 1,49 in SAM–K1106 and 1,58 in the UCL B.17 specimen.

Two bones of the manus were found cemented by matrix to the radial margin of the left distal humeral shaft. The larger is 9,6 mm long, the smaller 6,3 mm long. By its rounded rather than concave proximal end the larger is probably a metacarpal and by its small size it could have been of digit 4, the smaller bone is the first phalanx of this metacarpal.

The SAM–K1106 humerus differs from that of the UCL B.17 specimen only in having a more concave posterior surface just above the distal condyles. However the SAM–K1106 humerus does differ

considerably from that of *Heterodontosaurus* and most of the differences are probably related to more specialised forelimb use in *Heterodontosaurus*. In the latter the deltopectoral crest is considerably more robust and somewhat larger, the condyles are much less amorphous, and a large entepicondyle lies above the ulnar condyle. The ulna of *H. tucki* differs from the fabrosaurid ulna in having a distinct olecranon process.

PELVIC GIRDLE AND HINDLIMB

Ilium (fig. 10–17).

Five fabrosaurid ilia were found in this material, but only one had been given a specimen number after preparation (the posterior process of the SAM–K1106 ilium). One other certainly belongs to SAM–K401 and another to SAM–K400, since their state of preservation and color match all the labelled SAM–K401 and SAM–400 material respectively. The remaining two ilia cannot be associated with any other postcranial material. Each of these ilia has the characteristic supra-acetabular flange which Thulborn (1972) described for his specimen.

The anterior iliac process is complete in only two specimens: in SAM–K401 (fig. 12) it is deflected somewhat ventrally and laterally and the tip is lateromedially compressed; in the other specimen (fig. 14) the anterior process is horizontal and approximately rectangular in cross-section at the tip. The difference in ventral deflection can probably be attributed to individual variation since Galton (1974b:83) noted similar variation in the various ilia of *Hypsilophodon*. The difference in cross-sectional shape may also be individual variation; Galton's illustrations do not show comparable variation in this character but Gilmore's (1909) study of *Camptosaurus* showed that the tip of the anterior process had different shapes in the various species of that genus.

In all specimens the pubic peduncle anteriorly is directed at about 35°– 45° to the horizontal long-axis of the ilium. The supra-acetabular flange is a laterally projecting ridge on the external acetabular margin of the pubic peduncle; it reaches its maximum lateral extent just above the junction of the peduncle and iliac blade. Posterior to this the flange is reduced until it disappears at the posterodorsal acetabular corner. The ischiadic peduncle is rectangular in cross-section, not an expanded bulbous process as seen in *Hypsilophodon*.

The posterior processes of the two more complete ilia (fig. 12, 14) are superficially somewhat different because of compression fractures to, and breakage of, the external surface of the SAM–K401 ilium. The most striking feature of the posterior process is the large brevis shelf which curves medially under the postacetabular process but then downward to form a nearly vertical wall. The inferior margin of the posterior process (the inferior margin of the brevis shelf) extends almost horizontally backwards from the distal end of the ischiadic peduncle; thus the posterior process is quite deep. The area posterior to the ischiadic peduncle was missing in Thulborn's specimen so the orientation and size of the brevis shelf in fabrosaurids was not previously known. The outline of the posterior iliac margin in SAM–K400 ? (fig. 10) and SAM–K401 is angular, but that of the other large ilium is smoothly convex. Careful examination of the former two under a low-power microscope indicates that the fragile bony margin of the posterior process had probably been broken away several millimeters proximal to its termination and in its natural condition may have been similar to the other large ilium (fig. 14).

Each of the larger ilia shows four sacral rib attachments; the most anterior is situated at the junction of the pubic peduncle with the anterior process rather than on the pubic peduncle itself as in the ilium of *Hypsilophodon*. A fifth sacral rib may have been attached to the posteriormost portion of the brevis shelf which is missing in each specimen.

The smallest ilium is only about half the size of the others (fig. 16–17), but even so it has a characteristic though smaller supra-acetabular flange. The medial surface differs from the others in that two anterior sacral rib facets are found, one above the other, at the junction of the pubic peduncle and the anterior process.

The ilia described here differ significantly from the UCL B.17 fabrosaur in the position of the sacral rib attachments. The latter has five facets beginning at the junction of the pubic peduncle and anterior iliac process. They extend backward and upward, each successive rib being attached closer to the dorsal iliac margin, the fifth rib being but about 7 mm below this edge. In all three specimens described here the fourth rib attached on the brevis shelf just posterior to the ischiadic peduncle, over 20 mm below the dorsal margin. A line through the sacral rib facets begins anteriorly at the junction of the pubic peduncle and anterior process, as in the UCL B.17 specimen, but then runs inferiorly through successive facets. This difference in sacral rib attachment finds no counterpart in the various *Hypsilophodon* specimens described by Galton (1947b).

In several important ways fabrosaurid ilia differ from that of *Heterodontosaurus:* in the latter, the anterior process is more robust; the pubic peduncle is more nearly perpendicular to the long axis of the ilium; the acetabular margin just above the ischiadic peduncle is not smooth but bears a strongly developed articular buttress; the posterior process is considerably shallower and the brevis shelf is narrow and horizontal.

Ischium

The proximal portions of both ischia, from the acetabular margin to the broken obturator process, are preserved in SAM–K401 (fig. 18) and SAM–K1106 (fig. 19). The concave acetabular margin has a chord of about 16 mm in all specimens and a



Fig. 10 SAM–K400?. Left ilium, lateral view. Scale = 5 cm.

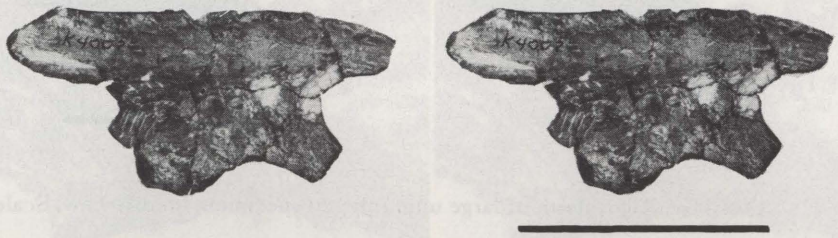

Fig. 11 SAM–K400?. Left ilium, medial view. Scale = 5 cm.

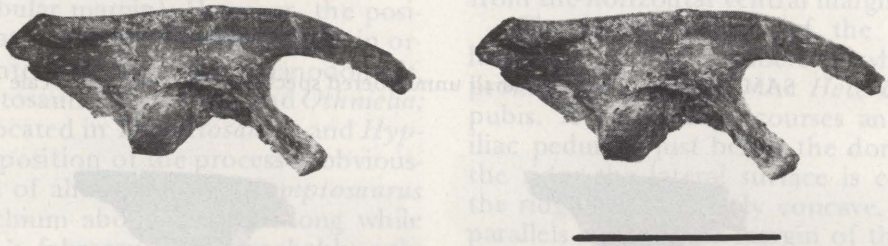

Fig. 12 SAM–K401. Right ilium, lateral view. Scale = 5 cm.

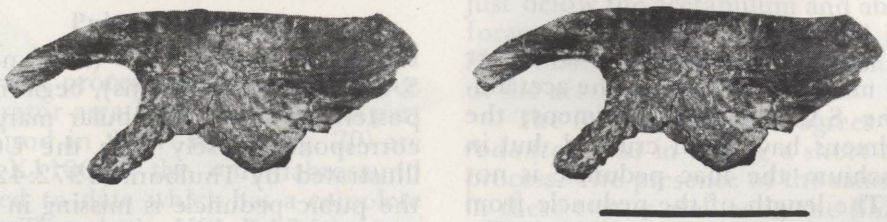

Fig. 13 SAM–K401. Right ilium, medial view. Scale = 5 cm.



Fig. 14 SAM–K?. Right ilium of large unnumbered specimen, lateral view. Scale = 5 cm.



Fig. 15 SAM–K?. Right ilium of large unnumbered specimen, medial view. Scale = 5 cm.

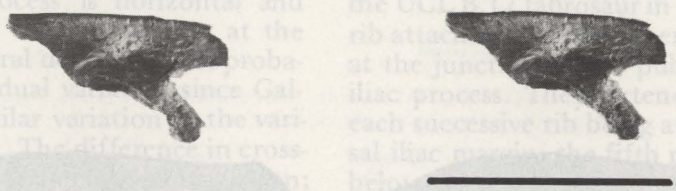

Fig. 16 SAM–K?. Right ilium of small unnumbered specimen. Lateral view. Scale = 5 cm.

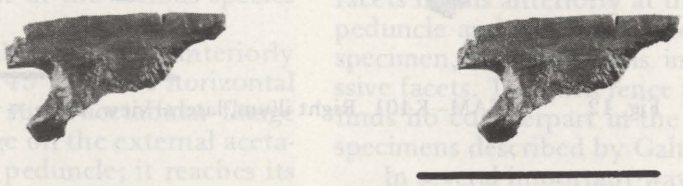

Fig. 17 SAM–K?. Right ilium of small unnumbered specimen. Medial view. Scale = 5 cm.

depth of about 5 mm. The iliac peduncle is thicker dorsally (about 8 mm) but thinner at the acetabular margin in the SAM–K1106 specimens; the SAM–K401 specimens have been crushed, but in the UCL B.17 ischium the iliac peduncle is not thicker dorsally. The length of the peduncle from dorsal to acetabular margin is about 12 mm. The pubic peduncle is rectangular in cross section, about 6 mm wide in both measurable specimens and about 14 mm high in SAM–K1106 (left) and 18 mm high in SAM–K401 (right).

The obturator process is anteriorly located in the SAM–K401 ischia (it is not visible in the SAM–K1106 specimens), beginning about 27 mm posterior to the acetabular margin. This position corresponds closely with the UCL B.17 ischium illustrated by Thulborn (1972:42, fig. 9). Most of the pubic peduncle is missing in Thulborn's specimen but present in those described here; most of the ischial rod posterior to the obturator process is present in Thulborn's specimen but absent in those described here. Consequently, more detailed comparisons are not possible.

The obturator process is considerably more



Fig. 18 SAM–K401. Proximal parts of ischia. Lateral view. Scale = 5 cm.

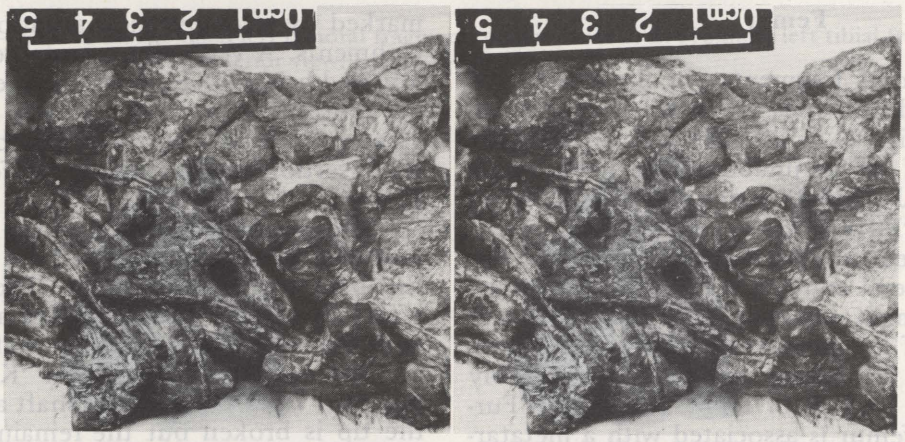

Fig. 19 SAM–K1106. Posterior portion of matrix block, left side. Note prepubic process and proximal part of left ischium.

posterior in *Hypsilophodon*, 53–63 mm behind the acetabular rim (in specimens comparable to SAM–K401, based on the size of the peduncles and of the acetabular margin). However, the position of the obturator process is quite variable in ornithopods: it is anteriorly located in iguanodontids, hadrosaurs, camptosaurs, *Dryosaurus* and *Othnielia;* it is posteriorly located in *Thescelosaurus* and *Hypsilophodon*. The position of the process is obviously not a function of allometry since *Camptosaurus dispar* had an ischium about 550 mm long while that of Thulborn's fabrosaurid was probably only about 100 mm long (based on the length of the postpubic rod which would have equalled the ischial rod in length). The fabrosaurid ischium differs significantly from that of *Heterodontosaurus* in that the latter does not have an obturator process.

Pubis

The left prepubic process of SAM–K1106 (fig. 19) and the obturator area with the proximal part of the postpubic rod in SAM–K401 (fig. 20) are preserved. SAM–K1106 is the only fabrosaurid specimen described to date which has a complete pre-pubic process. Though the UCL B.17 fabrosaurid lacked the prepubis, the pelvis has been reconstructed once with a long prepubic process (Thulborn 1972) and once with a short prepubic process (Thulborn 1971). The prepubis is a short stout process, 23 mm long from the anterior margin of the obturator foramen and 11 mm deep just anterior to the iliac peduncle. The anterior margin of the process is convex, sloping upward and backward from the horizontal ventral margin.

The lateral surface of the prepubic process lacks the muscular tubercles which were such a prominent feature of the *Heterodontosaurus* prepubis. A small ridge courses anteriorly from the iliac peduncle just below the dorsal margin; above the ridge the lateral surface is convex and below the ridge it is shallowly concave. A very low ridge parallels the inferior margin of the process; it continues posteriorly below the obturator foramen but fades away on the anterior part of the postpubic process. The acetabular margin is transversely thick in SAM–K401 (this area is not visible in SAM–K1106); it turns downward posteriorly to close the obturator foramen. One small muscle tubercle lies just below the acetabulum and above the obturator foramen; a similarly positioned larger tubercle in *Heterodontosaurus* presumably marked the position of the accessorius muscles.

The fabrosaurid pubis agrees with that of *Heterodontosaurus* in having a short but deep prepubic process. The presence of the same type of prepubis in these two as well as in the BMNH R6704 'juvenile scelidosaurid' indicates that this is the primitive ornithischian pattern. The prepubis of *Heterodontosaurus* is actually shorter (15,2 mm compared to 21 mm) than that of SAM–K1106, though total body size was probably not greatly different in the two specimens.

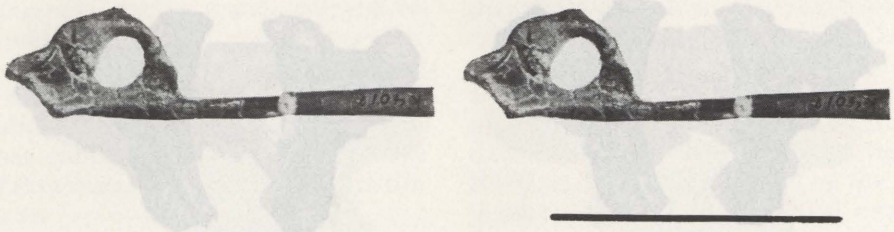

Fig. 20 SAM–K401. Fragmentary left pubis, lateral view. Scale = 5 cm.

Femur

Several femoral fragments are preserved: the proximal and distal ends of a left femur from SAM–K1106 (fig. 21A, 22, 23) and virtually the entire femur of an unnumbered specimen which matches the SAM–K400 material and will be referred to as the 'K400?' femur (fig. 24, 25).

This latter femur is partially reconstructed distally but the lateral condyle is sufficiently complete to give a length estimate of at least 147 mm (from the tip of the greater trochanter to the most distal point of the lateral condyle), considerably longer than the UCL B.17 femur (104 mm). Furthermore, this femur is associated with a metatarsal (probably the fourth) 82 mm long, much larger than that of UCL B.17 (67 mm). The length of this femur and metatarsal corresponds quite closely with that of the femur (151 mm) and third metatarsal (84 mm) of *Hypsilophodon foxii* (BMNH R196) (Galton 1974b) for which Galton gave an estimated body length of 1,36 metre. The 'K400' femur is also more curved than the UCL B.17 femur; measurement along the anterior surface of the former is 156 mm giving a curvature index (chord/arc) of 0,94.

In the 'K400?' femur a cleft separates the greater and lesser trochanters the long (dorsoventral) axis of the lesser trochanter makes an angle of 20° – 25° with the long axis of the greater trochanter. The tip of the lesser trochanter is incomplete in 'K400?' but its preserved length is 21 mm from the base of the cleft. The lateral surfaces of both trochanters and the medial surface of the lesser are marked by strong vertical striations for muscle attachments. A vertically oriented eminence just below and behind the intertrochanteric cleft seems to be continuous with the muscle markings on the greater trochanter and thus may be associated with the insertion of the pubo-ischio-femoralis externus 1.

The proximal portion of the SAM–K1106 femur (fig. 22A) retains part of the femoral head and the base of the trochanters. The head is 11 mm wide; its ventral outline makes about a 90° angle with the medial margin of the shaft.

The fourth trochanter in 'K400?' is pendant but rises from the femoral shaft along a wide base; the tip is broken but the remaining portion is 21 mm long. The depression for the coccygeofemoralis longus muscle (on the medial femoral surface anterior to the fourth trochanter) seems to be less pronounced than in the UCL B.17 femur; but the degree of development of this depression varies in Galton's *Hypsilophodon* femora (1974:96).

Distally the posterior intercondylar fossa of 'K400?' is much narrower and deepr than that of the UCL B.17 femur. The anteromedial condylar area is missing in 'K400?' but the distal end of the SAM–K1106 femur shows no anterior intercondylar fossa (fig. 23); the condylar surface of the latter is transversely flat perpendicular to the femoral long axis, indicating that the femur was held in a parasagittal plane. Thulborn (1972:44) notes that in UCL B.17 the outer femoral condyle is fractionally larger than the inner.

The fabrosaurid femora differ from those of *Hypsilophodon* only in having a more divergent les-



Fig. 21 SAM–K1106. A. Proximal left femoral fragment, anterior view; note base of lesser trochanter. B. Proximal left tibial fragment, lateral view. C. Fibular fragment, anterior view. Scale = 5 cm.

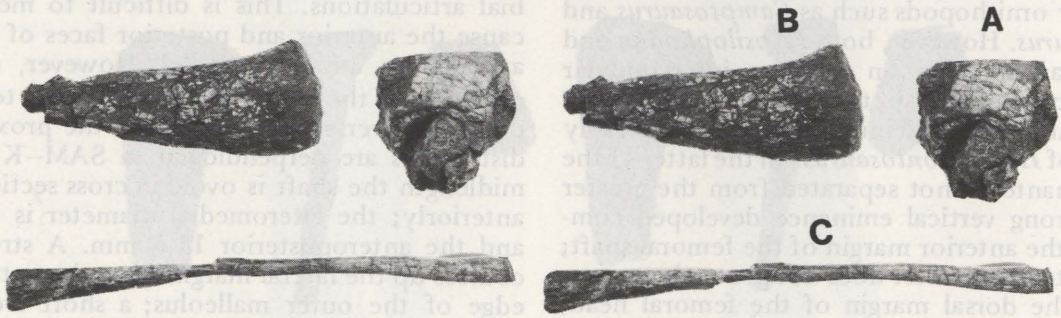

Fig. 22 SAM–K1106. A. Proximal left femoral fragment, posterior view. B. Proximal left tibial fragment, medial view. C. Fibular shaft, posterior view. Scale = 5 cm.



Fig. 23 SAM–K1106. Distal left femoral fragment. Scale = 5 cm.



Fig. 24 SAM–K401?. Left femur, lateral view. Scale = 5 cm.

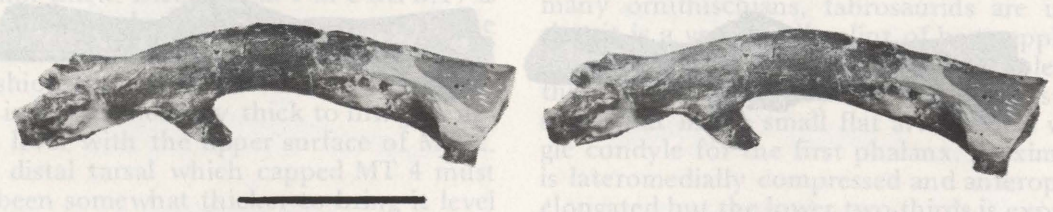

Fig. 25 SAM–K401?. Left femur, medial view. Scale = 5 cm.

ser trochanter. In this trait they resemble those of some larger ornithopods such as *Camptosaurus* and *Thescelosaurus*. However, both *Hypsilophodon* and the fabrosaurids lack an anterior intercondylar groove which is present in the latter two genera.

The fabrosaurid femur differs considerably from that of *Heterodontosaurus*. In the latter 1) the lesser trochanter is not separated from the greater but is a strong vertical eminence developed completely on the anterior margin of the femoral shaft; 2) the greater trochanter does not protrude vertically above the dorsal margin of the femoral head; 3) the lateral femoral condyle is the smaller, contrary to the fabrosaurid condition (however, most ornithopods had a larger inner condyle); 4) *H. tucki* lacks the well-developed posterior intercondylar fossa typical of most ornithischian femora; and 5) the terminal articular surface of the femur is obliquely oriented relative to the femoral long axis, giving the femur an abducted orientation. Significantly, neither *H. tucki* nor the fabrosaurids have an anterior intercondylar groove, so this trait is presumably primitive for ornithischians.

Tibia-Fibula

In SAM–K1106 a complete right tibia (fig. 26) with damaged condyles, a proximal left tibia (fig. 21B, 22B) and a single left fibula lacking the proximal end (fig. 21C, 22C) are preserved; the undamaged proximal portion of a left tibia and a distal right tibia were also found with the SAM–K400 material (fig. 27, 28).

The only well-preserved proximal tibial shaft is that of the SAM–K400 tibia: at 21 mm wide across the condyles it is more lateromedially compressed than the tibial head of *Hypsilophodon*. The inner tibial condyle is more protracted posteriorly though the lateral femoral condyle seems to have been the larger in fabrosaurids. As usual the medial margin of the head is convex and the lateral margin is marked by a deep concavity behind the cnemial crest and in front of the outer condyle. The length of the outer condyle behind this concavity is 16 mm. The transverse width of the cnemial crest, from the concavity to the medial margin, is 14 mm. The posterior intercondylar fossa is V-shaped and 7,5 mm wide. The proximal articular surface is horizontal, perpendicular to the tibial long axis.

Thulborn (1972:44) noted a torsion of 70° between the long axes of the proximal and distal tibial articulations. This is difficult to measure because the anterior and posterior faces of the distal articulation are not parallel. However, using the midpoint of the lateral and medial edges to give the distal transverse axis shows that the proximal and distal axes are perpendicular in SAM–K1106. At midlength the shaft is ovoid in cross section, wider anteriorly; the lateromedial diameter is 12,2 mm and the anteroposterior 11,5 mm. A strong crest courses up the lateral margin from the anterolateral edge of the outer malleolus; a short crest about 7 mm long lies along the medial margin above the inner malleolus. In the middle of the anterior surface a small vertical process divides the inner and outer malleolar areas

The SAM–K1106 tibia (144 mm) is larger than that of UCL B.17 (129 mm) but they do not differ in any morphological feature. It is also generally similar to that of *Hypsilophodon* except in having a narrower and deeper posterior intercondylar groove and a more lateromedially constricted cnemial crest. In the fabrosaurid the lengths and widths of the articular extremities are greater, the outer condyle is larger and the least shaft diameter is greater than they are in *Heterodontosaurus*. The most significant difference, however, is that the tibia of *Heterodontosaurus* forms a functional tibiotarsus with the fused tibula astragalus and calcaneum.

The incomplete fibula of SAM–K1106 is 119 mm long; the distal malleolar end is semicircular in shape, 8 mm in anteroposterior dimension (from the flattened surface in contact with the tibia to the apex of the anterior rounded surface) and 10 mm in lateromedial width. The fibular head of SAM–K401 is much more expanded anteroposteriorly than that of UCL B.17.

Tarsus and Pes

The astragalus (fig. 26), calcaneum and the first distal tarsal capping MT 3 are preserved from the right hindlimb of SAM–K1106. The astragalus is 19,2 mm wide along the anterior margin; it tapers somewhat toward the posterior surface along which it is 17,6 mm wide. The anteroposterior length along the medial margin is 17,5 mm and along the lateral margin 13,6 mm. A strong ascending process marks the anteromedial portion; the height from the inferior surface to the tip of the

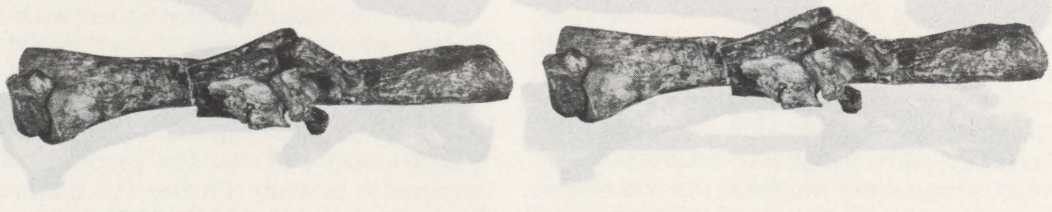

Fig. 26 SAM–K1106. Right tibia with astragalus anterior view. Note distal metatarsal fragments and proximal phalanges. Scale = 5 cm.



Fig. 27 SAM–K401. A. Proximal left tibia, lateral view. B. Proximal left fibula, lateral view. C. Distal right tibia, anterior view. Scale = 5 cm.



Fig. 28 SAM–K401. A. Proximal left tibia, medial view. B. Proximal left fibula, medial view. C. Distal right tibia, posterior view. Scale = 5 cm.

ascending process is 17,6 mm. The astragalus is attached to but not ankylosed with the inner malleolus. The calcaneum is crescentic in outline; the proximal surface for articulation with the fibula is flat, 8 mm long anteroposteriorly, 5,5 mm wide. Neither the astragalus nor the calcaneum are preserved in UCL B.17. The astragalus of SAM–K1106 most closely resembles small hypsilophodontids and *Pisanosaurus* in the presence of a well developed ascending process; this process is absent from larger ornithopods like *Thescelosaurus* and *Camptosaurus* but also the smaller *Othnielia* (= *Nanosaurus rex*) or *Laosaurus consors*). The calcaneum is more elongated proximodistally than it is in small hypsilophodontids.

Fabrosaurids possessed only two distal tarsals, one capping MT 3 and the other MT 4. Distal tarsal 1 in SAM–K1106 is elliptical in shape, 14,4 mm long anteroposteriorly and 10 mm wide lateromedially; it is flattened proximodistally and only about 3,5 mm thick. Distal tarsal 1 in UCL B.17 is disc-shaped and not elongated along any axis. The proximal surface of the metatarsals descends in stepwise fashion from MT2 to MT 3 to MT 4. Distal tarsal 1 is just sufficiently thick to bring its upper surface level with the upper surface of MT 2. The lateral distal tarsal which capped MT 4 must then have been somewhat thicker to bring it level with MT 2 and distal tarsal 1. The fabrosaurid distal tarsals generally resemble camptosaurids in that distal tarsal 1 covers only MT 3; in small ornithopods such as *Hypsilophodon, Othnielia (Nanosaurus), Laosaurus* and *Thescelosaurus,* distal tarsal 1 partially covers MT 2 as well as all of MT 3. The fabrosaurids differ considerably from *H. tucki* in tarsal structure. In the latter 1) the astragalus and calcaneum are indistinguishably fused to each other and to the tibia and fibula creating a bird-like tibiotarsus; 2) there are three distal tarsals, the medial caps both MT1 and MT 2 (the homologous bone in fabrosaurids was absent or present only in a cartilaginous state), the middle caps MT 3 and the lateral caps MT 4; and 3) the distal tarsals are fused to each other and to the metatarsals creating a tarsometatarsus.

Right metatarsals 1–4 and most phalanges are preserved from SAM–K1106, right metatarsals 2–4 (fig. 29,30) and most phalanges from SAM–K401 (fig. 31, 32). The following description of MT 2–4 applies to both specimens unless otherwise noted. Though MT 1 had become reduced in many ornithischians, fabrosaurids are unusual in that it is a very small splint of bone applied to the upper medial side of MT 2 (and completely fused there in SAM–K1106). The distal end is expanded somewhat into a small flat articulation with a single condyle for the first phalanx. Proximally MT 2 is lateromedially compressed and anteroposteriorly elongated but the lower two-thirds is expanded and subcircular in cross- section. The plane of the distal articular surface is inclined upward from the ante-

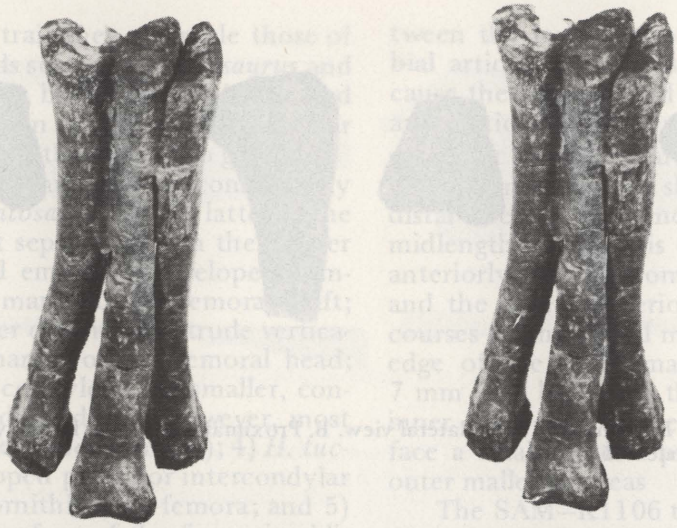

Fig. 29 SAM–K401. Right metatarsals 2,3,4. Oblique view. Scale = 5 cm.



Fig. 30 SAM–K401. Right metatarsals 2,3,4. Posterior view. Scale = 5 cm.

rior (dorsal) edge to the posterior (ventral) edge and in this it differs from MT 3 and 4 which are horizontal anteroposteriorly. The transverse axis of the metatarso-phalangeal joint deviated medially in digit 2.

Proximally MT 3 is also lateromedially compressed and anteroposteriorly elongated, though less so than MT 2; the anterior edge is wider than the posterior so that the shaft is triangular in cross-section. Metatarsal 1 and 3 were joined in their upper two-thirds but not in their lower third. The long axis of MT 2 (and of MT 4) courses slightly posterior to that of MT 3 which then lies anterior to the other two.

Unlike MT 2 and MT 3 the uppermost part of MT 4 is lateromedially expanded and anteroposteriorly compressed; in cross-section it is approximately triangular with the apex lateral. In SAM–K401 only the upper part of MT 4 is joined medially with the shaft of MT 3 but distally it deviates laterally to lie about 6 mm from the end of MT 3; in SAM–K1106 the long axis of MT 4 also curves laterally, but less so. In cross section the distal end of MT 4 resembles a right triangle, the base posterior and the hypotenuse, which is convex, lateral.

In comparison with the metatarsals of SAM–K401 and SAM–K1106 the first metatarsal of UCL B.17 is more robust and not completely fused along its entire length to MT 2, and the shaft of MT 4 is straight, contacting MT 3 along all its medial border. However, the lateral deviation of MT 4 in SAM–K401 and SAM–K1106 may be due to individual variation since the BMNH R5830 *Hypsilophodon* specimen described by Galton (1974b:99, fig. 57K) has a divergent MT 4 while that of BMNH R196 rests against MT 3 and is not divergent at all (1974b:100, fig. 58).

The fabrosaurid phalangeal formula is 2-3-4-5-? No identifiable digit 5 was found in either specimen described here but some indication of its attachment to the posterior upper surface of MT 4 was found in SAM–K401 (see fig. 30). The phalanges of digit 1 are reduced in size but are not atrophied or vestigial. The proximal surface of phalanx 1 bears a shallow subcircular depression for the flat, triangular-shaped distal end of MT 1. The distal end of phalanx 1 has a normal trochlea which accepts a small ungual phalanx.

In the remaining digits none of the first phalanges bears a projecting dorsal process but all the other phalanges do except the unguals. Phalanx 1 of digit 2 is longer and more slender than the first phalanges of digits 3 and 4; the proximal articular surface is very slightly concave. Several features of both phalanx 1 and 2 are associated with the medial deviation of digit 2: 1) the lateral condyle of the distal trochlea is larger than the medial; 2) the pits for the lateral collateral ligaments are

much larger than those for the medial collateral ligaments; 3) phalangeal length is greater along the outer margin than along the inner margin. No ungual phalanx can definitely be associated with digit 2 in either SAM– K401 or SAM–K1106.

The phalanges of digit 3 are not asymmetric like those of digit 2, indicating that digit 3 followed the midline long axis. Phalanx 1 of digit 3 is only 10% longer than that of digit 2 (22 mm to 20 mm) but it is 33% wider (12 mm to 9 mm); phalanx 2 of digit 3 is also wider than that of digit 2. The plantar surface of the ungual phalanx is a little flattened and a small ridge projects laterally below the grooves for the claw.

The lateral divergence of digit 4, necessary to produce the typical divergent three-toed stance, is accomplished primarily by the deviation of MT 4 from the midline axis. The lateral and medial phalangeal lengths are equal and the plane of the interphalangeal joints is flat, not oblique. The phalanges decrease rapidly in length: the fourth is only 6 mm long, though in a comparably sized *Hypsilophodon* (Galton 1974b:14–15, Table 111) it is 12 mm.

The phalanges of UCL B.17 were all dissociated and most had damaged articular surfaces. This may account for the major discrepancy between the specimens described here and the former: in SAM–K401 and SAM–K1106 the anterior surface of the phalanges of digit 1 face anteriorly just as in the other digits, but Thulborn reconstructed the first digit of UCL B.17 with the lateral surface of the phalanges anteriorly (1972:47, fig. 12R). The data from the specimens here shows that orientation to be incorrect.

The pedal phalanges of the fabrosaurids resemble those of small hypsilophodontids. Existing differences are minor: for example, the asymmetry in medial-lateral phalangeal length is not present in *Hypsilophodon*. The phalanges of digit 1 are not reduced compared to *Hypsilophodon*, though MT 1 is. Even by Stormberg times reduction of digit 1 in fabrosaurids had progressed beyond that seen in most ornithopods but had not reached the point seen in *Iguanodon* and *Dryosaurus altus* (both with rudimentary MT 1).

The fabrosaurid phalanges differ from *H. tucki* in that those of the latter had highly developed trochleas whose articular surfaces extended completely onto the dorsal (anterior) surface and permitted considerable hyper-extension of the interphalangeal joints. Thus the pes in the two Stormberg ornithischians with adequately known postcrania is functionally and structurally different: the fabrosaurid structure being fundamentally that of small hypsilophodontid ornithopods specialized in the reduction of digit 1; that of the heterodontosaurids being adapted to maximize metatarsal rigidity and hyperextension of the weight-bearing digits.

DISCUSSION

Diagnosis of the Fabrosauridae

Based on the postcranial material from southern Africa the following traits characterize the Fabrosauridae:

1) pelvis in which ischium and pubis are parallel and retroverted and in which the ilium has an elongated anterior process (features defining fabrosaurids as ornithischians);
2) an obturator process on the ischium (a feature defining fabrosaurids as ornithopods);



Fig. 31 SAM–K401. Phalanges of right pes, anterior view. A. Digit 1. B. Digit 3. C. Digit 4. Scale = 5 cm.



Fig. 32 SAM–K401. Phalanges of right pes, lateral view. A. Digit 1. B. Digit 3. C. Digit 4. Scale = 5 cm.

3) ilium with a brevis shelf which first turns medially and then downwards (probably a familial trait);
4) ilium with a supra-acetabular flange over the anterior half of the acetabulum (a feature of uncertain character-state and familial validity since it is also possessed by the 'juvenile scelidosaurid' which is not a fabrosaurid);
5) a short, deep prepubic process (a feature common to all early ornithischians in which this area has been preserved);
6) considerably reduced first metatarsal (probably a generic rather than familial trait; variation in degree of reduction may characterize different species; has parallels in genera of other ornithopod families);
7) reduced metacarpals and phalanges (lack of specimens prevents determining whether this is a generic or familial trait).

It has been difficult to judge the level of significance which should be attached to variations between the four fabrosaurid specimens available. When samples from other genera such as *Hypsilophodon* or *Camptosaurus* have been available for comparison, most of the differences between the various fabrosaurid specimens were resolvable into individual variation. Only in the case of the sacral rib facets does this not hold up; here the UCL B.17 specimen differs in an unusual way from the four South African Museum ilia. This warrants generic or at least specific distinction, much in the same way as variation in sacral articulation led Gilmore (1909:281) to distinguish species of *Camptosaurus*. However, no new genera or species of fabrosaurid will be named on the basis of this postcranial material until the related dental material is described and a total morphological assessment can be made.

The diagnosis given above, especially the pelvic features, clearly distinguishes fabrosaurids from other small ornithopods such as *Hypsilophodon* and *Dryosaurus*. It also provides the criteria against which proposed assignment to the Fabrosauridae should be judged. Later sections of this discussion will examine those specimens that have postcranial material and have been assigned to the Fabrosauridae. This includes *Nanosaurus agilis* Marsh 1877 and the 'juvenile scelidosaurid; unfortunately, *Echinodon* cannot be considered in this context.

The only other specimen assigned to the Fabrosauridae has been *Scutellosaurus lawleri* from the Kayenta formation of North America (Colbert, 1981). Of the diagnostic criteria given above, it has only the supra-acetabular flange which by itself is not diagnostic for the family Fabrosauridae. Its taxonomic status is thus uncertain.

Functional morphology of the fabrosaurid postcrania

The interpretation of the fabrosaurid postcrania is based on a joint consideration of anatomical structure and relative proportions of skeletal elements. Table 1 presents a sample of ornithischian limb proportions for comparison.

The general impression is that fabrosaurids had a diminutive forelimb, but this assumption can be refined by more complete data. The scapula (without coracoid) is about 78% of iliac length in the UCL B.17 specimen; this indicates no reduction in length relative to any of the later ornithopods. Fabrosaurid scapular morphology is relatively robust: the acromial process is well developed, minimum shaft width is large and the coracoids are 25% of the scapular length. Morphology and proportions both show that the scapula was not in any way reduced.

The proportion of fabrosaurid humeral to scapular length also shows no sign of forelimb reduction. The fabrosaurid ratios are all near 90%, slightly smaller than that for *Hypsilophodon* and *Thescelosaurus* (Galton 1974a), in which the humerus is as large as or larger than the scapula, but larger than that of *Iguanodon*, camptosaurids and hadrosaurids. Morphologically the humerus shows no signs of reduction: the deltopectoral crest rises about 5 mm above the humeral surface; a tubercle for muscle attachment lies opposite the base of the deltopectoral crest on the medial margin of the shaft, perhaps associated with the insertion of the coracobrachialis muscle (for humeral protraction) or the origin of the humero-radialis (brachialis) muscle (for forearm flexion). In the forearm the fabrosaurid radius is about 60% of scapular length, smaller than in the other ornithopods except camtosaurids and *Iguanodon*. Morphologically the radius shows no signs of robusticity as the humerus and scapula do.

The size of the manus can only be compared using metacarpal 3 since no single digit has all the phalanges and only UCL B.17 has a partial manus. The fabrosaurid third metacarpal is only 20% of scapular length; this is shorter than that of most ornithopods except *Iguanodon*, but that of *Hypsilophodon* is so close that the difference is probably insignificant. Compared to the radius, MC 3 is relatively larger than that of other ornithopods; but this is misleading because the fabrosaurid radius itself is relatively smaller as noted above.

Compared to a group of ornithopods the fabrosaurid forelimb is reduced in only its distal elements; the scapula and humerus are comparable in relative size or even larger than those of many later ornithopods. Only compared with *H. tucki* does the fabrosaurid forelimb show the degree of reduction already undergone in the ornithopod lineage by the late Triassic/early Jurassic. Each segment of the fabrosaurid anterior extremity is relatively shorter; culmulatively this results in a much shorter forelimb, both relatively and absolutely. When the measurements of humerus, radius and longest metacarpal (MC 2 in *H. tucki*) are added, the UCL B.17 specimen (107 mm) is just two-thirds that of *H. tucki* (154 mm). The difference would be greater if the entire fabrosaurid hand were preserved since phalanx 1 of its digit 3 is only 5 mm long but

TABLE 1. RELATIVE PROPORTIONS OF SKELETAL ELEMENTS IN EARLY ORNITHISCHIANS AND VARIOUS ORNITHOPODS

	Sc/II	H/Sc	R/Sc	R/H	MC3/Sc	MC3/R	Tr4	T/F	T+MT3/F	MT3/F	MT3/T
Fabrosaurids											
UCL B.17 (1)	0,78	0,88	0,56	0,64	0,19	0,34	0,37	1,24	1,89	0,64	0,52
SAM–K1106	—	0,91	0,62	0,68	—	—	(K400) 0,39	—	—	—	0,49
Heterodontosaurus tucki (2)	0,89	0,97	0,68	0,70	0,27	0,40	0,41	1,29	1,90	0,61	0,47
Hypsilophodon foxii (3)											
BM(NH) R 196	0,73	1,0	0,79	0,79	0,23	0,29	0,43	1,18	1,73	0,56	—
BM(NH) R 5830	—	—	—	—	—	—	0,42	1,17	1,79	0,62	0,53
Kritosaurus incurvimanus (4,3)	0,77	0,81	0,72	0,88	0,29	0,41	0,54	0,90	1,24	0,35	0,38
Parksosaurus warreni (5,3)	0,70	0,95	—	—	—	—	0,49	1,18	1,74	0,56	0,47
Camptosaurus nanus (6,3)	0,77	0,77	0,24	0,31	—	—	0,54	0,95	1,31	0,40	0,42
Microceratops gobiensis (7)	—	0,95	0,67	0,70	—	—	—	1,16	1,72	0,56	0,48
Iguanodon atherfieldensis (8,3)	0,85	0,67	0,47	0,71	0,20	0,42	0,48	0,88	1,23	0,35	0,40

Abbreviations: F, femur; H, humerus; Il, ilium; MC3, third metacarpal; MT3, third metatarsal; R, radius; Sc, scapula; T, tibia; Tr4, fourth trochanter index (length from femoral head to root of trochanter/femoral length). Sources of measurements: 1, Thulborn 1972; 2, Santa Luca 1980; 3, Galton 1974; 4, Parks 1920; 5, Parks 1926; 6, Gilmore 1925; 7, Maryańska and Osmólska 1975; 8, Hooley 1925.

phalanx 1 of digit 2 (the longest digit) in *H. tucki* is 16 mm long. Thus the shortness of the phalanges of the fabrosaurid manus indicates even more than metacarpal length that fabrosaurid and heterodontosaurid hands had quite different functions.

The fabrosaurid ilium differs in three essential respects from almost all other ornithopod ilia. The depth of the postacetabular process is relatively great due to the more vertical orientation of the brevis shelf; the supra-acetabular flange makes a bony hood over the acetabulum; and the medial acetabular border formed by the ilium was partially ossified.

The depth of the postacetabular process (measured at its midpoint) is 28% of iliac length, twice that of *Hypsilophodon* and more than three times that of *H. tucki* (8,3%). The postacetabular process is deep in camptosaurids, in which the brevis shelf also curves downwards to become more vertical, especially in *C. dispar* and *C. medius* (Gilmore 1909: Plates 15–16). Discounting the brevis shelf, the fabrosaurid postacetabular process is no deeper than that of *Hypsilophodon.*

The more vertically disposed brevis shelf does not necessarily mean a different fiber direction for the caudifemoralis (coccygeofemoralis) brevis muscle which attaches there. It does however give a larger attachment area for this muscle; the shelf is at least 13–15 mm in extent. If such a large shelf were horizontally disposed, then the medialmost fibers of caudifemoralis brevis would have a strong line of action medially (i.e. adduction) as well as posteriorly (i.e. retraction). The brevis shelf of *H. tucki* is horizontal and only 4–6 mm wide though the ilia of both are about the same absolute length.

The supra-acetabular flange must have affected femoral orientation, at least to the extent that the femur would be placed in some way so that the flange did not interfere with muscular attachments to the lesser trochanter. The femoral head may have articulated underneath the flange which would have transmitted weight between body and limb. Evidence for this is the allometric increase in lateral extent and in thickness of the flange with increasing iliac size. The distal femoral articular surface is horizontal, indicating a vertical orientation of the femoral shaft.

The medial acetabular wall formed by the ilium is more extensively ossified than in all other ornithopods, except perhaps camptosaurids. Normally the acetabulum is open medially to the level of the lateral upper acetabular margin. From the upper lateral margin the fabrosaurid acetabular surface turns inward to the cup-shaped undersurface of the flange and then downwards into a vertical wall; the ossification reaches almost to the lower ends of the ischiadic and pubic peduncles. This seems to be similar to the drawing of the 'juvenile scelidosaurid, given by Charig (1972:123, fig. 2). The partial ossification of the medial acetabular wall probably prevented the femoral head from seating directly underneath the body of the ilium; the supra-acetabular flange may have compensated for this by extending the acetabular articular surface laterally and allowing the direct transmission of weight and forces between the femur and the ilium.

Thus the three special morphological features of the ilium may all be functionally interrelated. The incompletely perforate acetabulum displaced a vertically oriented femoral shaft lateral to the main mass of the iliac blade; a supra-acetabular flange transmitted forces through the more laterally placed femoral shaft and a vertical brevis shelf kept the mass of the caudifemoralis brevis muscle more lateral and in the same parasagittal plane as the femur much more than a horizontal shelf would. While none of this can be proven, it is one logically and functionally consistent explanation of the morphological peculiarities seen in the fabrosaurid ilium.

The hindlimb ratios of fabrosaurids are in the high end of the range usually associated with rapid bipedal progression in ornithischians (see Table 1). The extent to which the distal hindlimb elements exceed the femur in length presumably indicates the extent to which the demand for rapidity of hindlimb stroke exceeds the demand for strength of hindlimb stroke.

The 4th trochanter is located higher on the femoral shaft than in any other ornithopod, in a position more advantageous for rapid than for powerful femoral retraction. The tibia/femur and tibia + MT3/femur ratios are also higher than in any other ornithopod; in the latter the tibia accounts for most of the difference and is relatively the most elongated while the relative length of MT 3 compares well with that of *Hypsilophodon* and does not demonstrate a greater degree of elongation.

The relative length of the tibia is even greater in *H. tucki* than in fabrosaurids, presumably indicating more highly developed bipedal capabilities. This is all the more remarkable since the forelimb of *H. tucki* is also relatively elongated and must have had a specialised function. The tibial ratios of *Microceratops gobiensis* also do not differ from those of *Hypsilophodon,* and the former must be considered to be as well adapted for rapid bipedal progression as the later. Thus both *H. tucki* and *M. gobiensis* demonstrate the existence of cursorial trends in non-ornithopod lineages.

Fabrosaurids and the ancestry of early ornithischians

The most important question for ornithischian phylogeny is whether a fabrosaurid could be ancestral to the early ornithischians *Heterodontosaurus* and the 'juvenile scelidosaurid'. A brief comparison of the postcrania of fabrosaurids and *H. tucki* appeared in the description of the latter specimen (Santa Luca 1980:199–200). The conclusions reached there, that fabrosaurids and *H. tucki* represent independent lineages and that the fabrosaurid lineage could not be ancestral to heterodontosaurids, are reinforced by further knowledge of fabrosaurid postcranial anatomy. Differences in structure are

TABLE 2. POSTCRANIAL SKELETAL DIFFERENCES BETWEEN FABROSAURIDS AND *HETERODONTOSAURUS TUCKI*

SKELETAL ELEMENT	FABROSAURIDS (UCL B.17, SAM–K400, K401 and K1106)	*H. tucki* (SAM–K1332)
cervical centra	asymmetric constriction of lateral surface	strong vertical ridges anteriorly and posteriorly
	small ventral keel wider posteriorly	prominent keel, ventral surface deeply concave
dorsal neural arch	spine wider at top than at base (in K401); constant in width (in UCL B.17)	spine rectangular
ossified tendons	in dorsal and caudal region	limited to dorsal region
scapula, distal end	hook-like process at ventral corner	smaller, attenuated process at ventral corner
scapula, shaft	rectangular in X-section above glenoid	circular in X-section above glenoid
glenoid cavity	deep (9 mm)	shallow (4 mm)
deltopectoral crest	gracile, smaller	robust, larger
distal humerus	entepicondyle absent	entepicondyle present
	anterior and posterior intercondylar grooves	no posterior intercondylar groove
ulna	no olecranon process	large olecranon process
metacarpals	I–III small, IV–V reduced	I–III large, IV–V reduced
ungual phalanges	unspecialized	prominent flexor tubercles
joints of manus	simple trochlea	specialized trochlea permitting hyperextension of digit I–III
ilium	supra-acetabular flange	no supra-acetabular flange
	brevis shelf deep and nearly vertical	brevis shelf small and horizontal
	no accessory articular surface at ischiadic peduncle	accessor 'avian-like antitrochanter' at ischiadic peduncle
anterior iliac process	about 1/3 total length, simple spine-like process	about 1/2 total length; thickened, terminating in knob-like process
acetabulum	medial iliac ossification	completely perforate
ischium	obturator process present	obturator process absent
prepubic process	relatively longer	relatively shorter
proximal trochanters	cleft separates greater and lesser	greater and lesser continuous
greater trochanter	extends above femoral head	level with femoral head
distal condyles	lateral larger	medial larger
intercondylar fossa	posterior only	none
transverse axis	distal almost horizontal	oblique
tibia-fibula	separate	fused tibiotarsus
astragalus-calcaneum	separate	fused; strong lateral and medial flanges
distal tarsals	2, unfused, flat	3, fused, lateral and medial flanges

found in all areas of the axial and appendicular skeleton; Table 2 presents a summary of these differences which, taken together, substantiate the existence of divergent structural patterns in early ornithischians. Some features listed in Table 2 do not preclude a fabrosaurid ancestry for heterodontosaurids and the condition in the latter could be derived from that of the former. For example, the olecranon process, entepicondyle, specialized interphalangeal joints and thickened anterior iliac process of heterodontosaurids could all be derived from the fabrosaurid condition. Of course, the heterodontosaurid features are probably all developed from primitive conditions and so do not prove a special phylogenetic relationship between fabrosaurids and heterodontosaurids.

However, primitive features aside, the structure of fabrosaurids is so ornithopod in its specializations that it cannot serve as a precursor for heterodontosaurids. The principal features excluding them from heterodontosaurid ancestry are: 1) the reduced manus; 2) the presence of an obturator process; 3) the presence of only two distal tarsals; and 4) the extreme reduction of metatarsal 1. If the Fabrosauridae, as the earliest well known ornithopod family, cannot be ancestral to the only other well known early ornithischian family, the Heterodontosauridae, then the concept of ornithopods as the basal stock for all other ornithischians radiations is questionable. Because the hypothesis has been so important in discussions of ornithischian evolution, it will be treated separately in a later section.

While the differences listed in Table 2 illustrate the existence of ornithopod and non-ornithopod lineages in Stormberg times, the similarities between fabrosaurids and *H. tucki* point out the most likely ancestral features for ornithischians as a whole. In the postcranial skeleton these are the scapular acromial process, a projecting spine-like anterior iliac process, a short but deep prepubis and a straight postpubic rod equal in length to the ischiadic rod. The presence of the same pelvic features in the 'juvenile scelidosaurid' (BMNH R6704; Charig 1972: 138, Plate VIA) reinforces their interpretation as ancestral traits.

Fabrosaurids have also been compared (Thulborn 1977) with the undescribed but illustrated (Newman 1968; Rixon 1968; Charig 1972) remains of the 'juvenile scelidosaurid' from the Lower Lias of England. Its systematic position is still uncertain but Thulborn (1977) argued that it is actually a cursorial ornithopod unrelated to *Scelidosaurus harrisonii* Owen 1861 (interpreted by Thulborn as an ankylosaur) and a direct descendant of the Stormberg fabrosaurids of southern Africa. Thulborn's method seriously biased the results of the comparisons since he only used two extremes in assessing the relationship of the 'juvenile scelidosaurid': the UCL fabrosaurids, and ankylosaurs. The fact that the 'juvenile scelidosaurid' did not resemble ankylosaurs at all is neither necessary nor sufficient reason to classify it in the only other group used for comparison. Thulborn also made the erroneous assumption that all bipedal ornithischians must be classified in the suborder Ornithopoda; this prejudiced the systematic and phylogenetic assessment of the specimen since many bipedal ornithischians are demonstrably not ornithopods (*Heterodontosaurus, Microceratops,* pachycephalosaurs, *Protiguanodon* and *Psittacosaurus*).

Thulborn cited eight traits shared by the UCL fabrosaurid and the 'juvenile scelidosaurid' to support his hypothesis that the former was ancestral to the latter: 1) scapula slender and constricted in midshaft; 2) femur with a pendent fourth trochanter, 3) greater and lesser trochanters divided by a cleft; 4) extensive postacetabular process; 5) ilium with a simple dorsal margin; 6) a distinctive swelling above the perforate acetabulum (presumably the supra-acetabular flange; 7) a short prepubis; and 8) postpubis equals length of ischial rod.

Most of these characters are not definitive for a systematic assignment and are widely distributed throughout the Ornithischia as primitive retentions. Character 1 is typical of small ornithischians and equally true for the non-ornithopods *Microceratops* and *Heterodontosaurus* as for fabrosaurids. Characters 2 and 3 are not restricted to ornithopods either but are present in, for example, *Leptoceratops, Protoceratops, Psittacosaurus* and *Protiguanodon.* Character 4 is present in pachycephalosaurs and the Ceratopsia as well as the Ornithopoda. Character 5, presumably meaning that the dorsal margin is not everted as in ankylosaurs, is also found in *Stegoceras* and the less modified ceratopsians such as *Leptoceratops.* Character 6 does not appear in other known ornithischians besides these two. Characters 7 and 8 are primitive for the order Ornithischia, characteristic of *Heterodontosaurus* as well as of primitive ornithopods. Therefore, of these 8 traits only one has any significance in comparing fabrosaurids with the 'juvenile scelidosaurid'.

Thulborn also noted four differences between the two specimens but dismissed them as irrelevant compared to the many similarities he listed. Since only one similarity of any consequence exists then these differences should be more carefully evaluated: 1) dermal armor, present in the 'juvenile scelidosaurid', but presumably absent in fabrosaurids; 2) sacral vertebrae, four in the 'scelidosaurid, five in the UCL fabrosaurid; 3) ischial rod and postpubis, concave ventrally in the 'scelidosaurid', convex ventrally in the fabrosaurid; and 4) obturator process, absent in the 'scelidosaurid', present in fabrosaurids.

Character 1 may not be a difference at all if the North American specimens (Colbert, 1981), which do indeed retain dermal armour, are actually fabrosaurids; otherwise it would be difficult to accept the reappearance of armour once it had been lost. Character 2 means very little since the number of sacral vertebrae, determined by the number of sacral ribs, is seen to vary when sufficient specimens of a single genus, or even species, are known. Character 3 is equivocal in meaning; a ventrally conca-

ve ischium and postpubis is common in quadrupedal ornithischians (*Ankylosaurus, Leptoceratops, Brachyceratops, Monoclonius*) but not universally (these elements are straight in stegosaurs). Character 4 is given much importance in this paper; in any single instance the loss of the obturator process during phylogenesis is possible. But its absence in the 'juvenile scelidosaurid' takes on another meaning once it is accepted that absence is the primitive ornithischian condition. Without strong evidence of derivation from the fabrosaurids (and one shared character of unknown character-state and functional significance is not strong evidence), absence could equally well mean retention of a primitive condition rather than a case of reduction and loss.

Two differences not noted by Thulborn make the derivation of the 'scelidosaurid' from the fabrosaurid less likely. First, the scapula is relatively larger in the 'scelidosaurid'; scapula length/femoral length is about 90% in the 'scelidosaurid', 63% in the smaller UCL fabrosaurid. Second, the fourth trochanter is more proximally located in fabrosaurids; the position index (length from level of femoral head to base of 4th trochanter ÷ femoral length) is 36,5% in the smaller UCL fabrosaurid, but 50% in the 'juvenile scelidosaurid'. These indices signify somewhat different adaptive strategies and it seems unlikely that the 'juvenile scelidosaurid' would be derived from a lineage committed to forelimb reduction and a rapid hindlimb stroke.

The only significant similarity which can be demonstrated between fabrosaurids and the 'juvenile scelidosaurid' is iliac structure, the everted dorsal acetabular margin and the dorsoventrally deep postacetabular process. To this is opposed differences in the ischium, prepubis, scapular size and fourth trochanter position. The data only partially resolve the question of fabrosaurid relationship to the 'juvenile scelidosaurid'. The only inference supported by the data is that the latter differs sufficiently from the former so as not to be classified within the Fabrosauridae (the absence of the obturator process is sufficient for that).

Before concluding this discussion, one viable alternative hypothesis deserves consideration. Instead of the Thulborn (1977) scenario discussed above, it is possible that the 'juvenile scelidosaurid' was ancestral to the fabrosaurids. The 'juvenile scelidosaurid' is a better structural precursor for the fabrosaurid than vice versa: the smaller prepubis (not the result of reduction but the absence of derived elongation common in ornithopods), the absence of the obturator process and the relatively larger scapula are probably all primitive relative to the fabrosaurids. The relatively lower 4th trochanter is also expected in the fabrosaurid ancestor, which had not yet become so specialized for bipedal locomotion. The supposed discrepancy in time between Stormberg and Lower Lias probably acted to formulate the hypothesized relationship as fabrosaurid – 'juvenile scelidosaurid'. However, the Lower Lias may not be any more recent than the Upper Red Beds (now Elliot Formation) of the Stormberg. Long ago Broom (1911:307) considered the Cave Sandstone (now Clarens Formation) to be Lower Jurassic in age and recently Olsen and Galton (1977; see also Olsen and Galton, this volume) have revised the correlations of the Newark, the Glen Canyon group and the Stormberg. They offered vertebrate paleontological, palynological and ichnological evidence that the upper part of the Newark (zone 3), the Glen Canyon group and the Upper Stormberg were all Liassic in age (Hettangian and Sinemurian). Since the scelidosaurids, both 'juvenile' and the 1861 type, were found in the Sinemurian of England and the fabrosaurids in the Upper Elliot Formation of the Stormberg they were probably contemporaneous. Thus there is no chronological or stratigraphic reason to reject an inversion of the hypothesized phylogenetic relationship and certainly no morphological reason to reject such a possibility.

Review of these three early ornithischians with good postcranial material has demonstrated a greater degree of evolutionary divergence than can be subsumed within the family Fabrosauridae and even within the suborder Ornithopoda. The 'juvenile scelidosaurid' cannot be assigned to the Fabrosauridae for the reasons noted above; since its pelvic structure differs from all other known ornithischians including *Heterodontosaurus* it probably belongs to an entirely new family. Its subordinal status is also indeterminate because, unlike the fabrosaurids, it cannot be associated with any late Jurassic/Cretaceous ornithischian suborder. Its status as an ornithopod is questionable since it lacks an obturator process. As with *Heterodontosaurus* its subordinal assignment must await further discoveries of early ornithischians. *H. tucki* cannot be assigned to the Fabrosauridae either for the many reasons noted above, nor can it be assigned to the Ornithopoda for reasons of pelvic structure.

The relationship between fabrosaurids and later ornithopods

The fabrosaurids have been offered as a model of the primitive, archetypical ornithopod from which all later ornithopods, particularly hypsilophodontids, could be derived (Galton 1978; Thulborn 1971. 1972). This proposition was supported primarily on the basis of shared primitive features of the skull and dentition but without detailed consideration of the postcranial material.

The fabrosaurids clearly belong to the ornithopod lineage but several features suggest that they were on an adaptive pathway different from that of the ancestors of the late Jurassic/Cretaceous ornithopods. Three features distinguish them from almost all later ornithopods: the supra-acetabular flange, the short prepubic process, and the partial acetabular ossification of the ilium. The short prepubic process is primitive for the Ornithischia, so its absence in later ornithopods does not automatically eliminate the fabrosaurids from their ances-

try. The phylogenetic significance of the supra-acetabular flange is more difficult to evaluate. Morphologically it is an accentuation of a ridge on the anterior acetabular margin which is typically present in many ornithischians. The flange could as easily be derived from the ridge as the ridge be derived by reduction of the flange. The flange seems to be present in the 'juvenile scelidosaurid' (Charig 1972:123, fig. 2, 1972:138, Plate VIA) but is clearly absent in *Heterodontosaurus.* The flange also seems to be present in the various species of camptosaurids. Gilmore (1909:257) noted that the pubic peduncle of the ilium was quite wide. His photographs (Gilmore, 1909:256, fig. 29; 257, fig. 30; Plate 16) show a flaring process over the anterior half of the acetabulum, though perhaps not as prominent as that seen in the fabrosaurids.

The one remaining feature of the fabrosaurid pelvis not easily matched in later ornithopods is the structure of the brevis shelf. In fabrosaurids it is deep and curves downward to become nearly vertical, and does not terminate by forming a horizontal shelf under the postacetabular process. The absence of a fabrosaurid-like brevis shelf in most later ornithopods seems to isolate the fabrosaurid lineage from any other except perhaps camptosaurids.

Finally, the first digit of the fabrosaurid pes is considerably reduced, much more so than that of *Hypsilophodon, Parksosaurus* and *Thescelosaurus,* but comparable to *Camptosaurus.* Such reduction by late Triassic/early Jurassic time may take known fabrosaurids outside the ancestral lineage of the three former ornithopods. The pes in *Dryosaurus/Dysalotosaurus* seems to have an even more reduced first metatarsal (Janensch 1955; Galton 1977), although Galton (1981) restored a large MT 1 to *Dryosaurus lettowvorbecki.*

On the basis of this postcranial survey fabrosaurids can be separated from the ancestry of some late Jurassic/Cretaceous ornithopods notably *Hypsilophodon.* In other cases the data are somewhat equivocal, especially when the structural differences pertain to probable ancestral traits in the fabrosaurids. However, fabrosaurids show more parallels with the various camptosaurids; iliac morphology in the latter is more similar to that of fabrosaurids (including the supra-acetabular flange and the brevis shelf) than to that of *Hypsilophodon,* which differs by having a horizontal brevis shelf and no development of a supra-acetabular flange. The most reasonable conclusion to be drawn is that fabrosaurids display some trends present in the later camptosaurids but the postcranial data are not sufficient to support the contention that known fabrosaurids were the common ancestors of all later ornithopods.

Fabrosaurids and *Nanosaurus agilis* Marsh

The only postcranial material outside of southern Africa assigned to the Fabrosauridae is that described as *Scutellosaurus lawleri* by Colbert (1981) and the very fragmentary remains of *Nanosaurus agilis* Marsh 1877 (Galton 1978). Amongst the latter is a matrix slab containing postcranial material, Yale Peabody Museum 1913 b–g, associated with a partial dentary in the same piece of matrix, YPM 1913a. Galton interpreted the dentary as a fabrosaurid since the dentition was marginally placed, a characteristic of his family Fabrosauridae (1972, 1973). The dentary teeth do not preserve any surface morphology and only their outline remains.

The postcranial material of *N. agilis* referred to comprises an ilium, two femora, two tibiae and a fibula, but none of it can unequivocally be assigned to the Fabrosauridae. The *Nanosaurus* ilium presumably had a well developed supra-acetabular flange, but it differs in structure from that of the fabrosaurids in which the flange is a lateral extension of the acetabular margin along the pubic peduncle and anterior half of the dorsal acetabular margin. The *Nanosaurus* fragment has a reflected margin over the entire dorsal acetabular area and not just the anterior half. In addition, nothing indicates that the presumed anterior iliac process was deflected inferiorly; in fact it is straight as figured by Huene and Lull (1908:fig. 4). The dorsal margin of the ilium seems to be broken, so it cannot be accurately reconstructed. Even as it is drawn in Huene and Lull (1908) and Galton (1978:148, fig. 4A), the depth of the ilium above the acetabular margin is deeper than in any of the known fabrosaurid ilia .

Several features of the posterior iliac process also separate *Nanosaurus* from the fabrosaurids. In the former an oblique ridge courses backwards and upwards to the dorsal corner of the process; in fabrosaurids this ridge, which divides the brevis shelf from the remainder of the posterior iliac process, is directed almost straight backwards and only slightly upwards, so that its highest point never reaches above the level of the superior acetabular margin. Finally, the posterior acetabular process of *Nanosaurus* is truncated, unlike any known ornithopod, comprising only 20% of iliac length; the process in fabrosaurids (the horizontal distance from the posterior edge of the ischiadic peduncle to the end of the ilium) is 33% of total iliac length.

The two *Nanosaurus* femora are equally indeterminate in structure. The lesser trochanter does not seem to be separated by a cleft from the greater trochanter even though enough of the proximal end is preserved in both femora to have shown the cleft had it been there. The *Nanosaurus* tibiae and fibula also lack any diagnostic fabrosaurid character. Only one articular surface is preserved, the distal end of a tibia, and this is not diagnostic for fabrosaurids; the remaining bones are parts of the shaft and are not distinctive in any way.

In summary, the postcranial skeleton of *Nanosaurus agilis* offers no definitive evidence of fabrosaurid affinities; it does, on the other hand, have several features incommensurate with fabrosaurid postcranial anatomy: the structure of the posterior iliac process and the absence of a cleft between greater and lesser trochanters. Therefore, the postcranial material of *Nanosaurus agilis* Marsh 1877 should be removed from the family Fabrosauridae

and classified *incertae sedis.*

ORNITHISCHIAN EVOLUTION

It is generally assumed that ornithopods formed a basal ornithischian stock from which the other ornithischian suborders were derived. However, this hypothesis needs to be examined for several reasons: first of all, the definition of the Ornithopoda focuses on primitive ornithischian traits; second, since the Microceratopsidae were bipedally adapted and cranially similar to the Ceratopsia, there is no need to invoke the ornithopods as the structurally conservative ancestor of the ceratopsians; and last, the early ornithischians, the fabrosaurids and heterodontosaurids, are contemporaneous but structurally quite divergent, which points to a division in ornithischian evolution even at this early point.

For all practical purposes most bipedal ornithischians have been called ornithopod. Yet, placing all bipedal ornithischians within a single category makes the unwarranted assumption that bipedalism appeared only once in ornithischian phylogeny and that all bipedal forms are closely related. However, if bipedalism was the rule for the ancestral ornithischians, then bipedalism is a primitive character. And as a primitive character its appearance in different ornithischians is neither necessary nor sufficient evidence of phylogenetic relationship, nor is it evidence for the erection of a category based on this character.

Perhaps the best example of the difficulties caused by defining all bipedal ornithischians as ornithopods is presented by the genus *Microceratops* from Mongolia. This little ornithischian has a small cervical collar, or frill, characteristic of the Ceratopsia, but the skull is associated with a hindlimb adapted for bipedal locomotion. In this case, using the bipedal definition of ornithopods would lead to the inconsistency of classifying a form clearly related to the Ceratopsia in its specializations to the Ornithopoda, with which it shared the primitive ornithischian form of locomotion. To classify and to determine phylogenetic relationship on the basis of such a symplesiomorphy is certainly not valid.

Another reason for questioning the hypothesis that ornithopods form a basal ornithischian stock comes from the known early ornithischians themselves. If ornithopods were a basal stock, then the early ornithischians should show clear affinity to them; however, only fabrosaurids do so. But *Heterodontosaurus* is so divergent in structure that it cannot be derived from fabrosaurids or be ancestral to later ornithopods.

At this historical point in the study of the ornithischian phylogeny it seems necessary to revise the definition of the Ornithopoda to avoid these inconsistencies. A feature, or group of features, must be found which unites closely related forms--fabrosaurids, hypsilophodontids, thescelosaurids, camptosaurids, iguanodontids and the hadrosaurids--yet at the same time separates other forms which share with the former only primitive features such as bipedalism. The one postcranial feature which meets this criterion is the presence or absence of the obturator process of the ischium. This flange-like process which projects from the ventral surface of the ischium has a very limited distribution throughout the Ornithischia. It is present only in hypsilophodontids, thescelosaurids, camptosaurids, iguanodontids and hadrosaurids of the later ornithopods. That is, the process is present only in those forms which have always been grouped together. The process is absent, however, in every other ornithischian group: it is absent in all the other bipedal forms like *Protiguanodon,* psittacosaurids, pachycephalosaurs and *Heterodontosaurus,* and absent in all stegosaurs and ceratopsians. Consequently, ornithopods should be redefined on the basis of this character and should include only those ornithischians that have an obturator process on the ischium.

The real importance of this new definition of ornithopods depends, of course, on whether the obturator process is a primitive or derived feature. If it were primitive then nothing would be clarified in the analysis of ornithischian phylogeny since one primitive character would have been substituted for another and a paraphyletic grouping would have resulted again.

The data suggest that the obturator process is probably a derived feature while the absence of the process is primitive. Most importantly, the obturator process itself only appears in a group of closely related forms, those ornithopods noted above; thus, the feature seems to be circumscribed within a single lineage. Primitive traits, on the other hand, generally have a rather random distribution throughout unrelated genera. For example, the primitive and simple ornithischian tooth form is found in some ornithopods, stegosaurs and ankylosaurs. So the distribution of the obturator process conforms more closely to that expected of a derived trait. The pelvic morphology of the early ornithischians also lends support to this view. Pelvic structure is known well only in the early ornithischians discussed in this paper and only the fabrosaurids have an obturator process. Neither *Heterodontosaurus* nor the 'juvenile scelidosaurid' has one; the absence of the process in these two forms which are not themselves closely related, matches the distribution expected of a primitive trait. Similarly, a primitive ornithischian pelvic feature such as the short prepubic process appears in all three early ornithischians discussed here and fits the distributional pattern expected of a primitive trait. Also, presuming an ornithopod ancestry of non-ornithopods would have required losing the obturator process perhaps five different, independent times without any trace in the subsequent lineages.

By defining ornithopods as only those ornithischians having an obturator process and by accepting the obturator process as a derived trait, the standard scheme of ornithischian evolution changes in several important ways. For one, the ornithopods cannot be a basal stock in the phylogenesis of the other ornithischian suborders. They comprised an

independent, monophyletic diversifying lineage which alone was able to exploit bipedal adaptations over a long period of time and in a wide range of body sizes. In other words ornithopods are another branch of ornithischian evolution like the other suborders, not a basal stock. For instance, the hadrosaurids certainly rival the later ceratopsians in derived cranial specializations, while the more conservative ornithopods such as the Hypsilophodontidae are overall no more conservative or primitive in structure than the conservative Ceratopsia represented by the Microceratopsidae.

Finally, this reasoning leads back independently to the conclusion reached by comparison of early ornithischian postcrania: divergent ornithischian lineages had already become established by late Triassic/early Jurassic times. Thus the common ancestor of all the Ornithischia, its basal stock, was no more an ornithopod than it was a ceratopsian or a stegosaur. The ancestral ornithischians were pre-fabrosaurid, pre-heterodontosaurid and pre-scelidosaurid; the common ancestor of all three could not, structurally, belong to any of these families. Certainly this is the message that the ornithischians of the South African Stormberg are telling us.

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APPENDIX 1

Inventory of identifiable postcranial material, South African Museum fabrosaurids.

Skeletal Element	SAM–K400	SAM–K401	SAM–K1106
Vertebrae	1 dorsal centrum	2 cervical neural arches, partial	3 cervical centra
	2 dorsal neural arches	9 dorsal centra	3 cervical neural arches (one in matrix attached to humerus)
	1 sacral centrum, partial	7 dorsal neural arches	8 dorsal centra
	7 centra, indeterminate region	3 sacral centra (plus 4 sacral ribs)	4 dorsal neural arches
	2 neural arches, indeterminate region	9 caudal centra	2 sacral centra
		4 sacral arches	18 caudal centra
		3 caudal neural arches	
Pectoral girdle and forelimb	1 radius, right	————————————	2 scapula and coracoids
			2 humerus: left complete, right partial in matrix
			1 radius, left
			1 ulna, left
Pelvic girdle and hindlimb	1 ilium, left	1 ilium, right	1 posterior ilium, right
	1 pubis, partial	2 proximal ischia	1 prepubic process, left
	1 femur, left	1 pubis, left, minus prepubic process	2 ischia, proximal
	1 MT, 4th	1 tibia, left, proximal	1 femur, left, distal shaft
	1 phalanx	1 tibia, right, distal	1 femur, left, proximal end
		1 fibula, right, proximal	2 tibia, right; tibia, left, proximal
		3 MT, 2–4, right	1 fibula, right
		12 phalanges, right	1 astragalus, right
			1 calcaneum, right
			1 distal tarsal, right
			4 MT, 1–4, right
			14 phalanges, right
			– miscellaenous centra, neural arches and ribs in matrix

Fabrosaurid material not assignable to above specimen numbers:

-1 ilium, right large
-1 ilium, right, very small

APPENDIX 2

Measurements of fabrosaurid postcranial elements (in mm, figures in parentheses indicate approximate measurement)

SCAPULA (SAM–K1106, right)		
Maximum length	(81)	
Least dorsoventral shaft diameter	10,4	
Least lateromedial shaft diameter at above point	6,3	
Maximum distal breadth	30,5 (left)	
CORACOID (SAM–K1106)	Left	Right
Maximum length (on scapular axis)	21,3	21,2
Maximum length (perpendicular to scapular axis)	26,6	27,1
HUMERUS (SAM–K1106, left)		
Maximum length	74,2	
Proximal L–M width	21,8	
Proximal A–P width	9,8	
Distal L–M width	17,9	
Distal A–P width	9,5	
Least shaft diameter	8,2	
Distance to base of deltopectoral crest	31,1	
RADIUS (SAM–K1106, left; SAM–K400?, right)		
Maximum length	50,0	48,3
Maximum proximal L–M width	(5)	5,4
Maximum proximal A–P width	11,2	12,8
Maximum distal L–M width	8,7	8,8
Maximum distal A–P width	9,2	11,0
Least shaft diameter	4,8	5,0
ULNA (SAM–K1106)		
Maximum length	52,5	
Maximum proximal L–M width	9,2	
Maximum proximal A–P width	13,4	
Maximum distal L–M width	8,2	
Maximum distal A–P width	12,3	
Least shaft diameter	4,6	
PUBIS (SAM–K1106, left)		
Length from anterior margin of obturator foramen to end of prepubis	22,9	
Depth of prepubis	11,0	

ILIUM	Maximum length	Minimum height above acetabular rim	Maximum L–M width at supra-acetabular flange
SAM–K400?	NA	19,0	< 16
SAM–K401	(95)	17,3	14,7
SAM–K?, large	90,8	16,2	< 14
SAM–K?, small	NA	13,9	11,7

FEMUR	SAM–K1106, left	SAM–'K400?'
Maximum length	NA	156:arc along anterior curve 146,5:chord distance
Maximum proximal L–M width	26 (including head)	NA
Maximum proximal A–P width,		
excluding lesser trochanter:	11,3	(16)
at base of lesser trochanter:	16,4	19,7
Maximum distal L–M width	25,8	NA
Maximum distal A–P width	25,1	NA
L–M width, base of lesser trochanter	6,7	7,9
A–P width of lesser trochanter perpendicular to its long axis		(14)
Least shaft diameter	NA	13,2
Length of 4th trochanter (from middle of femoral attachment to extremity)	NA	(21)
Distance from tip of greater trochanter to distal attachment of 4th trochanter	NA	59,0

APPENDIX 2 (cont.)

TIBIA	SAM–K1106 Right	SAM–K1106 Left	SAM–K401 Proximal left, Distal right
Maximum length	143,7	NA	NA
Maximum proximal L–M width	(17)	(19)	20,8
Maximum proximal A–P width	(25)	(28)	34,9
Maximum distal L–M width	30,9	NA	32,2
Maximum distal A–P width	15,4	NA	13,2
Least shaft diameter	12,2	NA	NA

FIBULA (SAM–K401, right)

Maximum proximal L–M width	7,0
Maximum proximal A–P width	19,7

PES	Maximum length	Max. prox. L–M width	Max. prox. A–P width	Max. dist. L–M width	Max. dist. A–P width	Least shaft diameter
SAM–K401, right unless specified						
MT1	NA	NA	NA	5,4	6,2	NA
MT2	68,3	5,8	18,1	9,6	9,9	5,0
MT3	75,7	7,6	14,0	12,5	10,5	5,6
MT4	67,7	12,0	11,2	10,4	10,7	5,8
Ph1, digit 1	18,6	6,4	6,1	5,9	4,4	NA
Ph1, digit 3,						
right	22,9	13,6	11,4	10,5	8,5	5,6
left	23,0	12,8	11,2	10,8	8,2	5,9
Ph1, digit 4	16,7	10,8	8,5	NA	NA	4,9
Ph2, digit 3	15,9	10,4	9,0	9,8	5,1	4,9
Ph2, digit 4	NA	8,7	7,8	NA	NA	NA
Ph3, digit 3	12,8	7,8	7,5	7,0	4,6	3,9
Ph3, digit 4	13,0	8,2	7,6	6,7	4,6	3,8
Ungual, digit 3?	(15)	6,6	4,9			
Ungual, digit 4?	>9	5,4	4,9			
SAM–K1106, right						
MT1	36,9	2,0	5,8	5,1	6,0	(1)
MT2	63,8	6,2	19,2	NA	(8)	5,7
MT3	70,1	(7)	14,9	11,5	(13)	(6,5)
MT4	60,5	11,3	10,5	(11)	12,7	6,5
Ph1, digit 1	17,9	6,4	5,7	5,1	4,6	3,7
Ph1, digit 2	20,2	(9)	NA	9,0	6,9	NA
Ph1, digit 3	22,8	12,0	11,6	9,4	7,5	6,6
Ph1, digit 4	14,9	9,9	(9)	8,0	6,0	4,6
Ungual, digit 1	10,7	4,6	4,3			
Ph2, digit 2	15,2	7,5	7,5	6,8	4,6	3,9
Ph2, digit 3	15,2	9,2	8,3	7,7	6,6	4,1
Ph2, digit 4	11,4	7,8	7,2	6,4	5,0	3,8
Ph3, digit 3	12,1	7,6	6,8	6,6	4,2	3,6
Ph3, digit 4	8,6	6,3	6,1	5,7	4,1	3,5
Ungual, digit 3	12,6	5,8	5,4			
Ph4, digit 4	6,1	5,3	5,2	4,8	3,2	3,3
Ungual, digit 4	8,1	3,8	3,3			