

THE POST-CRANIAL SKELETON OF THE TRIASSIC ORNITHISCHIAN DINOSAUR *FABROSAURUS AUSTRALIS*

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ABSTRACT. The post-cranial skeleton of the ornithischian dinosaur *Fabrosaurus australis*, Ginsburg 1964, is described for the first time from material from the Upper Triassic Red Beds of Lesotho. Certain skeletal features (e.g. the tibio-femoral ratio) indicate that *Fabrosaurus* should be assigned to the family Hypsilophodontidae of the suborder Ornithopoda. *Fabrosaurus* is envisaged as a small, unarmoured and habitually bipedal dinosaur with distinct cursorial potential. Muscle scars on the femora and pelvic girdle bones point to a system of pelvic musculature not unlike that proposed by Romer (1927) for *Thescelosaurus* and by Galton (1969) for *Hypsilophodon*.

The problem of ornithischian origins is briefly examined. *Fabrosaurus* presents few primitive characters and is of little assistance in any attempt to locate the possible ancestors of the Ornithischia. It is concluded that *Fabrosaurus* represents the earliest known portion of a hypsilophodont stock which persisted through the greater part of the Mesozoic era and which gave rise, even if indirectly, to such varied ornithischian groups as the iguanodonts, hadrosaurs, and ceratopsians. Triassic relatives of *Fabrosaurus* may be discerned as far afield as China (*Tatisaurus*) and Argentina (*Pisanosaurus*). *Lycorhinus* [*Heterodontosaurus*], also from the Upper Trias of southern Africa, appears to represent an extremely early, rather specialized, and short-lived hypsilophodont divergence.

KNOWLEDGE of the earliest recorded (Upper Triassic) ornithischian dinosaurs is based upon rare and fragmentary fossils. In only two cases, *Lycorhinus* [*Heterodontosaurus*] and *Fabrosaurus*, are the skulls at all well known (Crompton and Charig 1962; Thulborn 1970a, 1970b). Post-cranial bones have been described only in the South American *Pisanosaurus* (Casamiquela 1967), and these are far from complete.

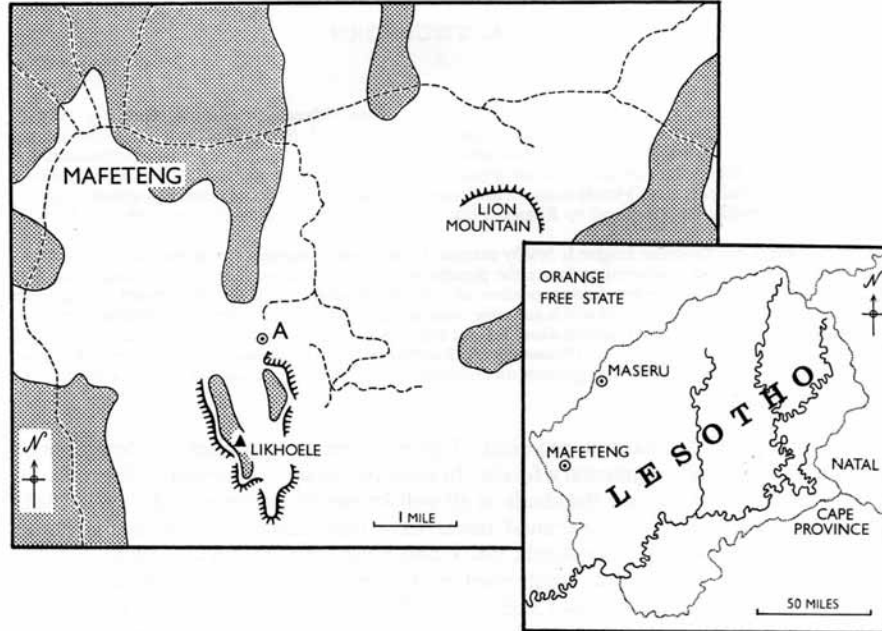
The genus *Fabrosaurus* was established by Ginsburg (1964) on the basis of a jaw fragment from the Upper Triassic Red Beds of Basutoland (now Lesotho). Subsequent discoveries have permitted description of the *Fabrosaurus* skull in near-entirety (Thulborn 1970a). This paper concerns the previously unknown post-cranial skeleton of *Fabrosaurus*. Hence *Fabrosaurus* becomes perhaps the best known pre-Jurassic ornithischian.

Material

The material described below is preserved in the collection of the Zoology Department at University College, London. It was collected by Dr. K. A. Kermack and Mrs. F. Mussett during the 1963–1964 expedition from University College to Basutoland. The material was obtained from the Upper Triassic Red Beds of the Stormberg Series on the northern flank of Likhoele Mountain, near the settlement of Mafeteng (see map, text-fig. 1). Greater stratigraphic precision is not possible for two reasons: firstly, because the classic subdivisions of the Trias, established upon marine faunas, cannot be extended into continental deposits such as the Red Beds, and secondly, because of the lack of suitable zone fossils within the Upper Trias of southern Africa. Such zonation as has been achieved in the late Trias of this area is not at all detailed and cannot be extended successfully over large areas.

The bones described below are all from 'assemblage B. 17' mentioned in separate accounts of the *Fabrosaurus* skull and dentition (Thulborn 1970a, 1971). This assemblage (text-fig. 2) contains at least [Palaeontology, Vol. 15, Part 1, 1972, pp. 29–60.]

two individuals of *Fabrosaurus*, the smaller one being the better represented. Assemblage B. 17 comprises: skull fragments (both individuals), numerous isolated teeth, 44 vertebrae or parts of vertebrae (? both individuals), rib fragments and ossified tendons (? both individuals), left and right scapulae, left scapula (larger individual), left humerus, left humerus (larger individual), right radius and ulna, left radius (larger individual), parts of right carpus and manus, paired ilia, ischia, and pubes, paired femora, tibiae, and fibulae, 2 left tarsal bones, left metatarsus and parts of right metatarsus, phalanges of left and right feet.



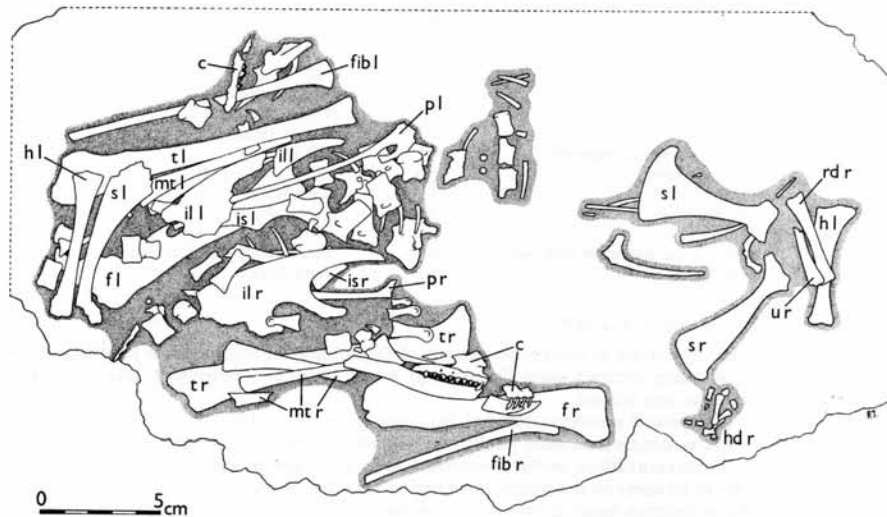
TEXT-FIG. 1. Maps showing provenance of assemblage B. 17 (*Fabrosaurus australis*). The material was collected at locality A, on the northern flank of Likhoele Mountain. Shaded areas (larger map) represent outcrops of Drakensberg volcanics overlying the Red Beds.

Preservation and preparation of material

The matrix is a tough medium-grained sandstone of bright red colour. The bones are preserved in grey or white calcareous material which is usually stained black, brown, or red. Nearly every bone is traversed by numerous fine cracks—the 'checkering' noted by Simmons (1965) in his account of reptiles from the Chinese Trias. These fissures doubtless represent sun-cracking acquired by the bones prior to burial. Similar effects may be observed at present in southern Africa, where even the stoutest bones (e.g. those of horses and oxen) are completely shattered after a few weeks' exposure. Each bone is enclosed within a coat of reddish-black ferruginous material. This coating is usually one or two millimetres thick and tends, where it is weathered, to part from the underlying bone very easily (a feature which is of considerable use in preparation). When freshly exposed, however, this encrustation adheres very firmly to the bone by virtue of innumerable intrusive veinlets. This is especially noticeable at the ends of the long bones and elsewhere at points of incomplete ossification (e.g. the dorsal margin of the scapula). It is also in these regions that the ferruginous cortex is thickest.

The material was prepared by both mechanical and chemical means. Soft or weathered matrix was

removed with a mounted needle. Tougher matrix was removed rapidly by the use of a light hammer with small cold chisels and straight dental probes. A variable-speed vibro-tool was used to the same effect; this lent itself to much finer control and was safely employed very close to the bone. Prior to chemical treatment all exposed bone was coated in a thin (1 part to 4) solution of polybutyl methacrylate in ethyl acetate. This protective coating, which also served to consolidate friable bone surfaces, may be removed at any time by washing in ethyl acetate. Subsequently the material was very thoroughly dried and then immersed in cold dilute (10–15%) solutions of either acetic or formic acids in water. The period of immersion varied between 30 minutes and 3 hours. After thorough washing and drying the material was further prepared mechanically. These processes were repeated until no more matrix could safely be removed (ideally until individual bones were freed from the matrix).



TEXT-FIG. 2. *Fabrosaurus australis*. Assemblage B. 17. $\times 0.38$. Several bones (mainly fragments of vertebrae) have been omitted for clarity. Two individuals are present, the larger one being represented by the humerus (*hl*) and the scapula (*sl*) at left.

DESCRIPTION

Explanation of abbreviations used in text-figures

<i>ac</i>	acetabular margin	<i>fc</i>	cleft between proximal trochanters of femur
<i>acet</i>	acetabulum	<i>fib</i>	fibula
<i>ae</i>	anterior embayment of ilium	<i>fib l</i>	left fibula
<i>apr</i>	anterior process	<i>fib r</i>	right fibula
<i>art</i>	proximal articular surface	<i>fl</i>	left femur
<i>c</i>	cranial fragments	<i>fr</i>	right femur
<i>c2</i>	second distal carpal	<i>g</i>	glenoid cavity
<i>c3</i>	third distal carpal	<i>gd</i>	grooved dorsal margin of ischium
<i>cap</i>	capitulum	<i>gt</i>	greater trochanter
<i>cf</i>	facet for chevron bone	<i>h</i>	head
<i>cg</i>	claw groove	<i>hd r</i>	bones of right hand
<i>cn c</i>	cnemial crest	<i>hl</i>	left humerus
<i>d</i>	diapophysis	<i>ig</i>	intermalleolar groove
<i>dc</i>	distal condyle		
<i>dpc</i>	delto-pectoral crest		

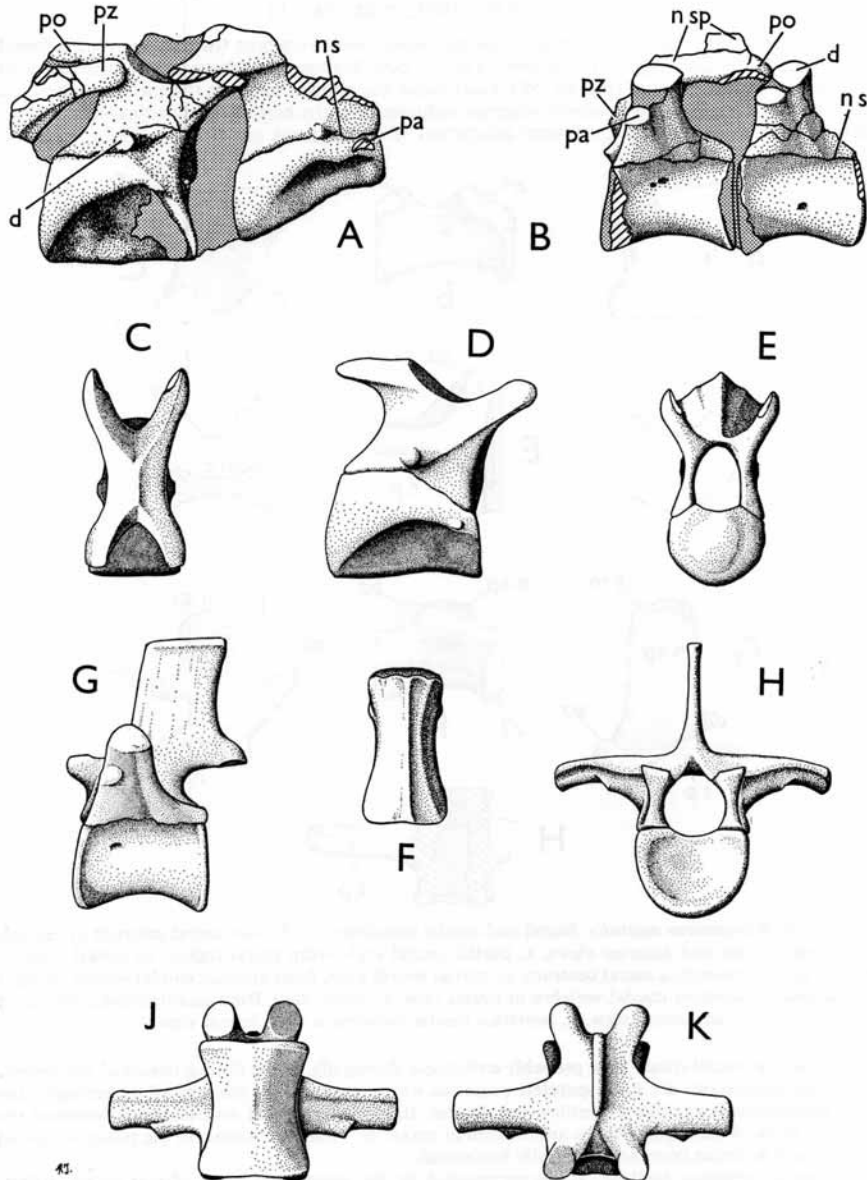
<i>il l</i>	left ilium	<i>p i f</i>	posterior intercondylar fossa
<i>il p</i>	iliac process of ischium	<i>p il</i>	posterior iliac shelf
<i>il r</i>	right ilium	<i>p l</i>	left pubis
<i>i m</i>	medial malleolus	<i>po</i>	postzygapophysis
<i>is l</i>	left ischium	<i>po p</i>	postpubis
<i>is p</i>	ischial peduncle of ilium	<i>p p</i>	prepubis
<i>is r</i>	right ischium	<i>p pd</i>	pubic peduncle of ilium
<i>l c</i>	lateral condyle	<i>p pr</i>	posterior process
<i>l t</i>	lesser trochanter	<i>p r</i>	right pubis
<i>m</i>	insertion of flexor tibialis (ischium)	<i>p t</i>	insertion of coccygeo-femoralis longus (femur)
<i>m c</i>	medial condyle	<i>pub p</i>	pubic process of ischium
<i>mc1 to mc4</i>	metacarpals i to iv	<i>pz</i>	prezygapophysis
<i>mt1 to mt4</i>	metatarsals i to iv	<i>r c</i>	radial condyle of humerus
<i>mt l</i>	left metatarsus	<i>rd</i>	radius
<i>mt r</i>	right metatarsus	<i>rd r</i>	right radius
<i>n</i>	notch in scapular margin	<i>s l</i>	left scapula
<i>n c</i>	neural canal	<i>s r</i>	right scapula
<i>n s</i>	neuro-central suture	<i>t f</i>	fourth trochanter
<i>n sp</i>	neural spine	<i>t l</i>	left tibia
<i>ob</i>	obturator process of ischium	<i>t p</i>	transverse process
<i>ob f</i>	obturator foramen	<i>t r</i>	right tibia
<i>o m</i>	lateral malleolus	<i>tub</i>	tuberculum
<i>o t</i>	ossified tendons	<i>u</i>	ulna
<i>pa</i>	parapophysis	<i>u c</i>	ulnar condyle of humerus
<i>p e</i>	insertion of ilio-femoralis externus (femur)	<i>u r</i>	right ulna

Vertebral column (text-figs. 3, 4, and 5)

The material includes vertebrae from most regions of the column. It is impossible to estimate the vertebral formula with any accuracy since the material, which is rather fragmentary, may have been derived from more than one animal.

The best-preserved *cervical vertebrae* (text-fig. 3A) come from the middle of the neck. Their long and narrow centra have deeply excavated flanks and give the impression, in ventral view, of having been 'pinched in'. These excavations probably represent areas of origin for the rectus capitis musculature (running forwards to insert on the occiput) and serve to distinguish the neck vertebrae from others in the column. Each centrum bears a prominent median keel on its ventral surface. The terminal articular faces of the centra are in most cases obscured by thick crusts of haematite; these faces are shield-shaped, wider than high. The foremost centrum shown in text-fig. 3 tends slightly to the opisthocelous condition; the succeeding cervical centra are distinctly amphicoelous. The parapophysis is a poorly defined rugosity near the antero-dorsal corner of the centrum; it occurs at successively higher levels as it is traced back through the neck vertebrae. The other area of rib attachment, the diapophysis, is a small rounded eminence situated on, or slightly above, the mid-point of the persistent neuro-central suture. In the hindmost neck vertebrae the diapophysis is at a somewhat higher level and is extended into a short ventro-lateral process. The neural arch is about as high as the centrum whilst the neural spine is merely an insignificant median ridge. The rounded and tongue-like prezygapophyses overhang the front of the centrum; the postzygapophyses are shorter and are rather angular in outline. The articular faces of the zygapophyses are inclined at about 15° from vertical.

The *dorsal vertebrae* (text-figs. 3 and 5) are distinguished from the neck vertebrae by virtue of their more robust construction, principally through their broad centra and stout transverse processes. Each spool-shaped centrum has smoothly rounded flanks and bears a very faint median keel on its ventral surface. At their extreme anterior and posterior ends the lateral and ventral faces of the centra bear traces of wrinkling and weak longitudinal fluting. This ornament probably marks the former attachment of hypaxial trunk muscles. All of the dorsal centra are amphicoelous and have terminal articular faces of sub-circular outline. The very distinctive transverse processes are remarkably thick and massively constructed where they merge with the neural arch. Each process extends horizontally and terminates in an elliptical and convex facet (the diapophysis) for the attachment of the tuberculum from the associated rib. The facet for the capitulum of the rib (i.e. the parapophysis) is located on the

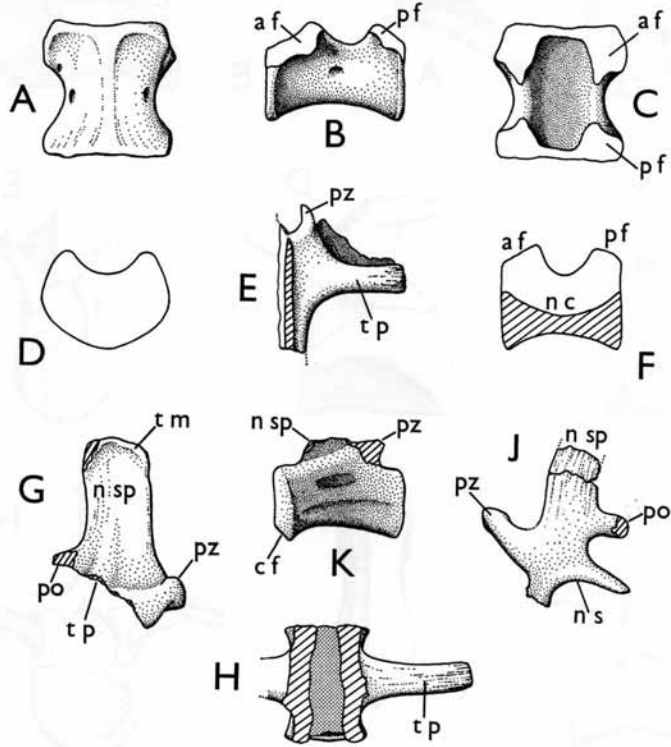


TEXT-FIG. 3. *Fabrosaurus australis*. Cervical and dorsal vertebrae, $\times 1.5$. A, parts of three cervical vertebrae in right lateral view. B, two dorsal vertebrae in left ventro-lateral view. C-F, reconstructed cervical vertebrae in dorsal, right lateral, anterior, and ventral views. G-K, reconstructed dorsal vertebra in left lateral, anterior, ventral, and dorsal views.

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anterior edge of the transverse process. In the hindmost dorsal vertebrae the parapophysis is found much closer to the diapophysis. The neural spines are best illustrated by three examples together with a number of ossified tendons (text-fig. 5F). Each blade-like spine arises from the entire length of the neural arch and is of consistent antero-posterior width for its entire height. Faint vertical striae on the flanks of these spines indicate the former attachment of epaxial trunk muscles. The thickened dorsal



TEXT-FIG. 4. *Fabrosaurus australis*. Sacral and caudal vertebrae, $\times 1.5$. A-D, sacral centrum in ventral, left lateral, dorsal and anterior views. E, partial neural arch, from sacral region, in dorsal view. F, sagittal section through a sacral centrum. G, partial neural arch, from anterior caudal region, in right lateral view. H, anterior caudal vertebra in dorsal view. I, neural arch, from middle caudal region, in left lateral view. J, neural arch, from middle caudal region, in right lateral view. K, posterior caudal vertebra in right lateral view.

margins of the neural spines were probably embedded, during life, in the fibrous tissues of the dermis. The postzygapophyses are stout spatulate processes which overhang the rear end of the centrum; the prezygapophyses are similar in outline, but shorter. In the anterior and middle dorsal vertebrae the articular faces of the zygapophyses are inclined at about 20° from horizontal; in the posterior dorsal region these articular faces are practically horizontal.

The *sacral vertebrae* (text-fig. 4) are represented by five centra and parts of two neural arches. Attachment scars on the ilium (text-fig. 8C) suggest that the *Fabrosaurus* sacrum incorporated five vertebrae. The sacral centra are distinguished by their remarkable width. Each one is constricted in the middle and bears a distinct median keel on its ventral surface. The terminal articular faces of the

centra are quite flat, crescentic in outline, and wider than high. There are no indications of any fusion between the centra. The dorsal view of a centrum (text-fig. 4C) shows four large facets for neural arch attachment and the deep basin-like excavation which represents the floor of the neural canal. A fortuitous sagittal section through one centrum (text-fig. 4F) reveals the full extent of the ventrally inflated neural canal. The neural arches of the sacral series are represented by fragments found at some distance from the nearest centrum. Depressed areas flanking the extremely thin neural spine merge imperceptibly with the flat dorsal surfaces of the transverse processes. Each stout and horizontal transverse process is some 7 mm long and is of uniform width to its free end. The prezygapophyses are situated close to the midline, indicating that the postzygapophyses (not preserved) must have been very close together. Each prezygapophysis has a sub-rectangular profile and bears an articular face which is almost vertical.

The *caudal vertebrae* (text-fig. 4) are rather poorly represented. The anterior tail vertebrae are distinguished by their long and extremely thin transverse processes. These processes are directed laterally and slightly to the front. The spool-shaped centra have flat terminal faces of sub-circular outline. At its postero-ventral margin each centrum is bevelled to form a crescentic facet for the attachment of a chevron bone (haemal arch); a similar, though smaller, facet is present at the antero-ventral margin. Each tall and blade-like neural spine is inclined to the rear and arises only from the posterior half of the neural arch. The bluntly rounded prezygapophyses overhang the front of the centrum; the postzygapophyses are represented merely by raised areas flanking the postero-ventral part of the neural spine. The articular faces of the zygapophyses are inclined at about 20° from vertical.

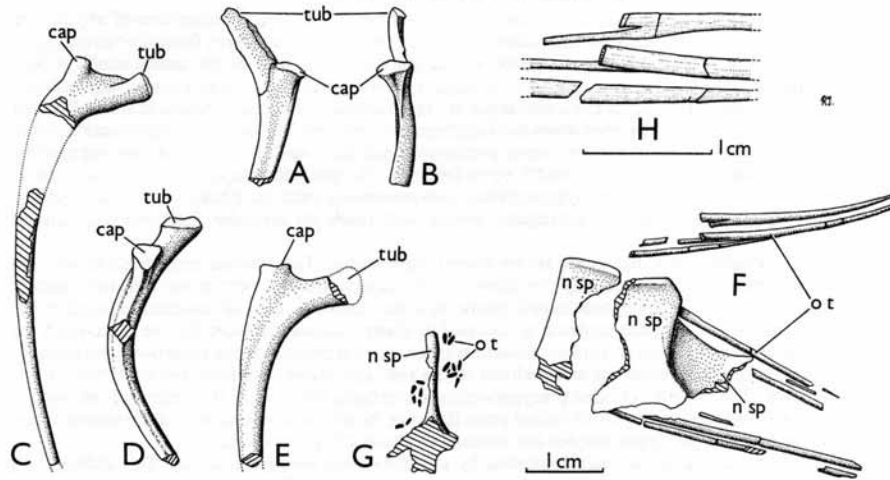
The middle caudal vertebrae are represented by a single neural arch (text-fig. 4J). This differs from the neural arches of the anterior tail vertebrae in lacking any trace of the transverse processes.

The distal parts of the *Fabrosaurus* tail are represented by a single vertebra (text-fig. 4K). Its slender and constricted centrum terminates in flat circular surfaces and bears distinct facets for the attachment of chevron bones. The neural arch consists of little more than a small pyramidal eminence. The slender and finger-like prezygapophyses are situated close to the mid-line; the postzygapophyses appear to have been very weakly developed or absent.

The *ribs* (text-fig. 5) are represented by numerous fragments. One rib appears to have come from the posterior cervical region (text-fig. 5E). The proximal part of this rib is flattened and rather plate-like. Capitulum and tuberculum are both well defined (the latter being distinctly the longer) and enclose an angle approaching 90°. More distally the antero-lateral edge of the rib tends to a definite sharpness whilst the postero-medial margin remains thicker and well rounded. The dorsal ribs are also two-headed (dichocephalous), though the hindmost ones show a tendency to the single-headed (holocephalous) state. The posterior dorsal region is, however, rather poorly known and there is no incontrovertible evidence that any of the ribs ever fully attained the holocephalous condition. In the larger ribs from the front of the thorax (text-figs. 5A-C) capitulum and tuberculum are both well developed and diverge at somewhat less than a right angle. The expanded proximal part of each rib passes distally into a long, slender, and rod-like portion. The entire rib is arched to the exterior (the greater part of this flexure occurring in the proximal one-third of the bone) and the antero-lateral edge is noticeably thinner and sharper than the postero-medial edge. In the posterior dorsal ribs (text-fig. 5D) the capitulum and tuberculum are situated closer together. These ribs are distinguished from those at the front of the thorax by being shorter, thicker, and more obviously arched to the exterior. The delicate transverse processes of the anterior tail vertebrae (text-fig. 4H) probably represent caudal ribs which are fused on to the vertebrae.

Fragments of *ossified tendons* (text-fig. 5F-H) are preserved alongside the neural spines of the dorsal and caudal regions. It is probable that the tendons originally extended to cover much of the tail in *Fabrosaurus*. Each slender, compressed, and rod-like tendon is applied to the flanks of up to five successive neural spines. At one end (anterior or posterior) the tendon tapers to a point; towards the other end it gradually widens and splays out into several narrow rays. Each tendon is about a millimetre wide and is marked with fine longitudinal striae. The tendons are grouped in definite bundles and in lateral view (text-fig. 5F) there is a slight suggestion of these bundles being disposed in a lattice-like pattern with diamond-shaped interstices.

No *chevron bones* are preserved in assemblage B. 17. But this is not surprising in view of the paucity of tail bones in general. Chevron bones were clearly present since the caudal centra bear prominent facets for their attachment.



TEXT-FIG. 5. *Fabrosaurus australis*. Ribs and ossified tendons, $\times 1.2$ (except figure H). A-B, anterior thoracic rib in anterior and medial views. C, middle thoracic rib in anterior view. D, posterior thoracic rib in medial view. E, posterior cervical rib in posterior view. F, ossified tendons associated with neural spines from three dorsal vertebrae. G, anterior view of a neural spine (from dorsal region) to show arrangement of the ossified tendons. H, detail of ossified tendons, $\times 2$.

Pectoral girdle (text-fig. 6)

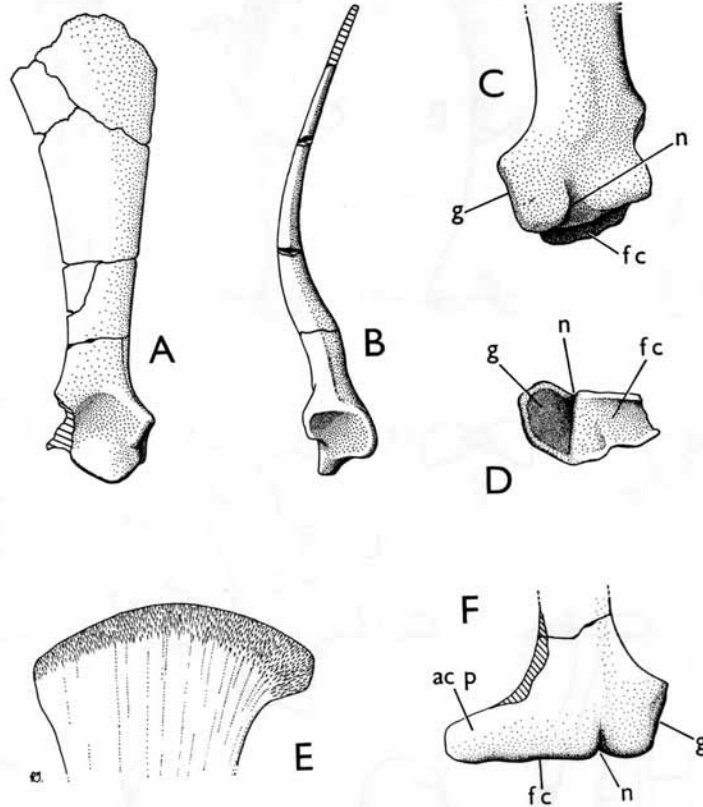
The *scapula* (text-fig. 6) is a tall, blade-like bone which is roughly triangular in lateral profile. The widely expanded dorsal margin is less solidly constructed than the rest of the bone and has a distinctly porous texture. This porous zone (text-fig. 6E) represents a region of transition between the scapula proper and a cartilaginous supra-scapula. At its postero-dorsal corner the bone is extended into a short tongue-like process; the antero-dorsal corner is obtusely angular. Vertical striae on the dorsal and central parts of the lateral scapular surface doubtless mark the origin of a broad sheet of muscle (the scapular deltoid) running down to insert at the proximal end of the humerus. The ventral part of the scapula is rather 'foot-like' in profile due to the presence of a salient and forwardly projecting 'acromial' process. In this region the depressed lateral face of the scapula probably bore the origin of a second shoulder muscle (scapulo-humeralis anterior) which inserted, like the deltoid, on the proximal part of the humerus. The posterior view (text-fig. 6B) demonstrates the strong latero-medial compression affecting the dorsal half of the scapula and also shows that the bone is elegantly curved so as to follow, in life, the convexity of the underlying rib cage. The glenoid cavity is roughly oval in plan, higher than wide, and opens postero-ventrally; it is confluent antero-ventrally with a shallow trough which received the dorsal margin of the coracoid. This trough is not as broad as the glenoid but is considerably longer owing to its anterior prolongation beneath the 'acromial' process.

No *coracoid* has been recovered from the material. Since the scapula bears a salient 'acromial' process (which lengthens the region for coracoid attachment) it is reasonable to infer that the coracoid was of considerable size. A distinct notch in the ventro-medial margin of the scapula (text-fig. 6C) indicates that the coracoid was perforate. In related genera (such as *Hypsilophodon*) this scapular notch is continuous with a coracoidal foramen which served to transmit the supratoracoid nerve and small blood vessels.

Fore limb (text-fig. 7)

The slender and columnar *humerus* (text-fig. 7A-E) is expanded at each end and is almost imperceptibly arched to the front. In anterior view (text-fig. 7A) it may be seen that the proximal end is

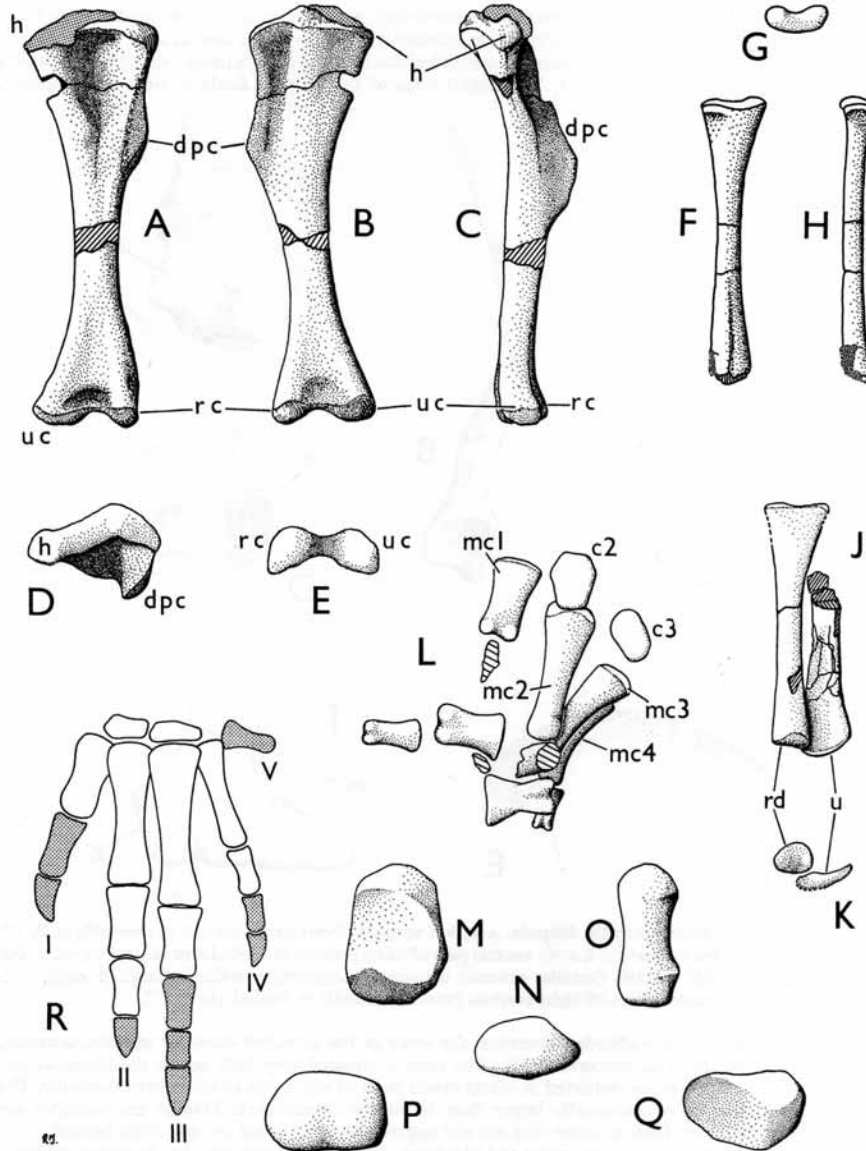
a little wider than the distal end and that the humeral shaft is narrowest at a point slightly distal to its centre. Both proximal and distal expansions are directed principally to the medial side. The blunt and slightly projecting proximo-medial corner constitutes the head of the humerus; the proximo-lateral corner is obtusely angular in profile. The lateral edge of the bone is fairly straight and the erect



TEXT-FIG. 6. *Fabrosaurus australis*. Scapula. A-B, left scapula (from larger animal in assemblage B. 17) in lateral and posterior views, $\times 1$. C-D, ventral part of same scapula in medial and ventral views, $\times 1.5$. E, dorsal part of left scapula (smaller animal) showing incompletely ossified marginal zone, $\times 2$. F, ventral part of right scapula (smaller animal) in medial view, $\times 2$.

delto-pectoral crest, which afforded insertions for some of the principal shoulder muscles, accounts for some 27% of the total humeral length. The crest is situated very high up on the humerus and appears, in fact, to be more restricted in distal extent than in any other ornithischian dinosaur. The medial distal condyle is fractionally larger than its lateral counterpart. Though the condyles are slightly expanded from back to front they are not appreciably attenuated or up-curved behind.

The *radius* (text-fig. 7F-K) is a slender rod-like bone, distinctly shorter than the humerus, which is expanded at both proximal and distal ends. It is quite straight and untwisted. Transverse sections near the middle of the shaft are of elliptical outline, widest antero-posteriorly. Similarly the convex and crescentic proximal surface is widest from front to back. Near the proximal end the anterior edge of



TEXT-FIG. 7. *Fabrosaurus australis*. Fore limb bones, $\times 1$ (except figures L or R). A-E, left humerus (from larger animal) in anterior, posterior, medial, proximal, and distal views. F-H, left radius (larger animal) in lateral, proximal, and anterior views. J-K, right radius and ulna (smaller animal) in antero-lateral and distal views. L, bones of right hand, as preserved, $\times 2$. M-O, right distal carpal (the second?) in proximal, palmar, and medial views, $\times 5$. P-Q, right distal carpal (the third?) in distal and proximal views, $\times 5$. R, reconstruction of left hand in dorsal view (reconstructed portions shaded), $\times 2$.

the radius tends to a definite sharpness. In lateral view (text-fig. 7F) the almost straight anterior margin contrasts with the concave rear edge. The distal articular surface is oval in plan and rather flat, though a shallow depression at the postero-medial margin lends it a 'saddle-shaped' appearance.

The sole example of the *ulna* (text-fig. 7J-K) is somewhat crushed and lacks the proximal end. At the middle of the bone, which is a little stouter than the radius, the shaft is elliptical in cross-section (widest from front to back). Anterior and posterior margins of the shaft are both quite thin, though the latter is distinctly the sharper. The distal articular surface has the outline of a narrow triangle with a width (latero-medial) of barely 2.5 mm. This incomplete ulna seems to be in natural relationship with the associated radius (text-fig. 7J); the ulna is situated lateral to the radius and slightly behind it, its concave medial face accommodating the rounded flank of the radius.

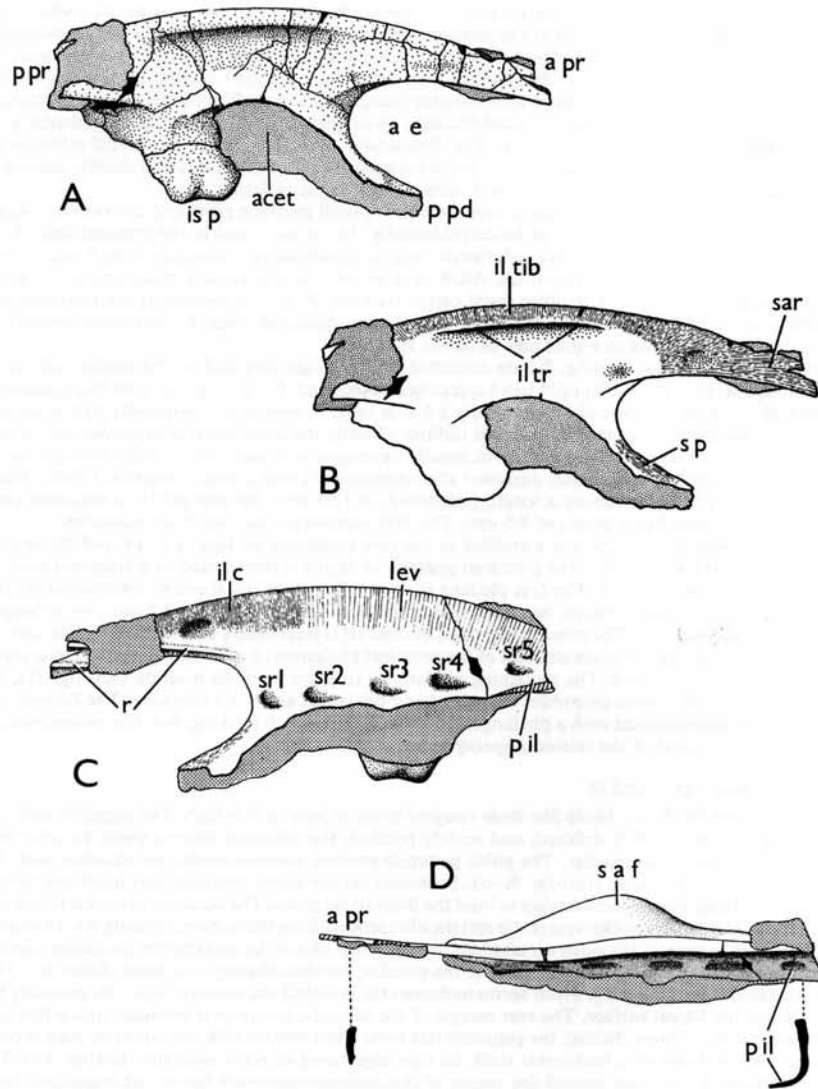
The *carpus* is represented by two distal carpal elements, both from the right fore limb of the smaller individual in assemblage B. 17. One distal carpal (text-fig. 7M-O) was found at the proximal end of the second metacarpal. This carpal bone is a flattened irregular quadrilateral measuring some 3 mm (latero-medial) by 4.5 mm. It is nearly 2 mm thick. All of its edges are thickened and rounded and its proximal surface is slightly depressed. The other distal carpal (text-fig. 7P-Q) was located at the proximal end of metacarpal III. This small and rectangular carpal bone measures some 4 mm (latero-medial) by 2.5 mm and is compressed to a thickness of about 1.5 mm.

The bones of the *manus* (text-fig. 7L) are described from the right fore limb of the smaller individual in assemblage B. 17. This partial right hand comprises metacarpals I to IV together with five phalanges. Metacarpal I is a slender rod-like bone nearly 6.5 mm long. It terminates proximally in a wide and slightly inflated articular surface of elliptical outline. Distally the metacarpal is expanded into a pair of small condyles. These condyles are about equally developed and each bears a faint circular pit on its flank. Metacarpal II is decidedly narrower than metacarpal I and is much longer (11 mm). Metacarpal III is even larger, attaining a length (estimated) of 12.5 mm. Metacarpal IV is narrower than any of the others and has a length of 8.5 mm. The fifth metacarpal has not been recovered.

The other bones of the hand are identified as the first phalanges in digits I to IV and the second phalanx in digit II (text-fig. 7R). The proximal phalanx of digit I is represented by a fragment close to the distal end of metacarpal I. The first phalanx in digit II lies at the distal end of metacarpal II; this short (5.5 mm) and stout phalanx has a maximum width of almost 4 mm and bears two sub-equal condyles at the distal end. The proximal phalanx of digit III is fractionally shorter than that of digit II. The first phalanx in digit IV is the smallest of the proximal phalanges; it is 3.5 mm long and has a maximum width of barely 2 mm. The remaining phalanx is, to judge from its position (text-fig. 7L), the second in digit II. This bone resembles the other hand phalanges and is 4.5 mm long. The *Fabrosaurus* hand is shown reconstructed with a phalangeal formula of 2:3:4:3:0 (text-fig. 7R); this reconstruction is based upon the hand of the related *Hypsilophodon*.

Pelvic girdle (text-figs. 8 and 9)

The *ilium* (text-fig. 8) is a blade-like bone roughly twice as long as it is high. The anterior iliac process is long, slender, slightly deflexed, and acutely pointed; the posterior process seems to have been considerably shorter and broader. The pubic peduncle extends antero-ventrally to articulate with the acetabular part of the pubis (text-fig. 9F-G). Striations on the pubic peduncle (*sp*) mark the former presence of cartilaginous tissues serving to bind the ilium to the pubis. The ischiadic peduncle is directed straight downwards; its swollen ventral tip met the iliac process from the ischium (text-fig. 9A-C) so as to define the rear margin of the open acetabulum. Immediately above the acetabulum the lateral surface of the ilium is strongly inflated (principally to the exterior, but also slightly in a dorsal direction). This supra-acetabular swelling (*saf*), which serves to deepen the acetabulum, contrasts with the generally flat remainder of the lateral surface. The rear margin of the ischiadic peduncle is extended into a thin and sharp-edged plate of bone. Behind the peduncle this bony sheet merges with the posterior iliac process and assumes the form of a horizontal shelf, its free edge being directed medially (text-fig. 8D). The ventral surface of this shelf carried the origin of the coccygeo-femoralis brevis, an important thigh muscle which inserted on the fourth trochanter of the femur (text-fig. 10) and functioned in drawing back the hind limb during locomotion. The lateral surface of the ilium bears a number of easily discerned markings (text-fig. 8B). A narrow striated zone at the dorsal margin (*il tib*) probably defines the origin of the posterior ilio-tibialis muscle; this muscle inserted on the front of the tibia and served to extend the knee joint. Directly beneath this striated zone, and immediately over the acetabulum, there



TEXT-FIG. 8. *Fabrosaurus australis*. Right ilium, $\times 1$. A, lateral view. B, lateral view with surface markings shown diagrammatically. C, medial view. D, dorsal view with transverse sections at the points indicated.

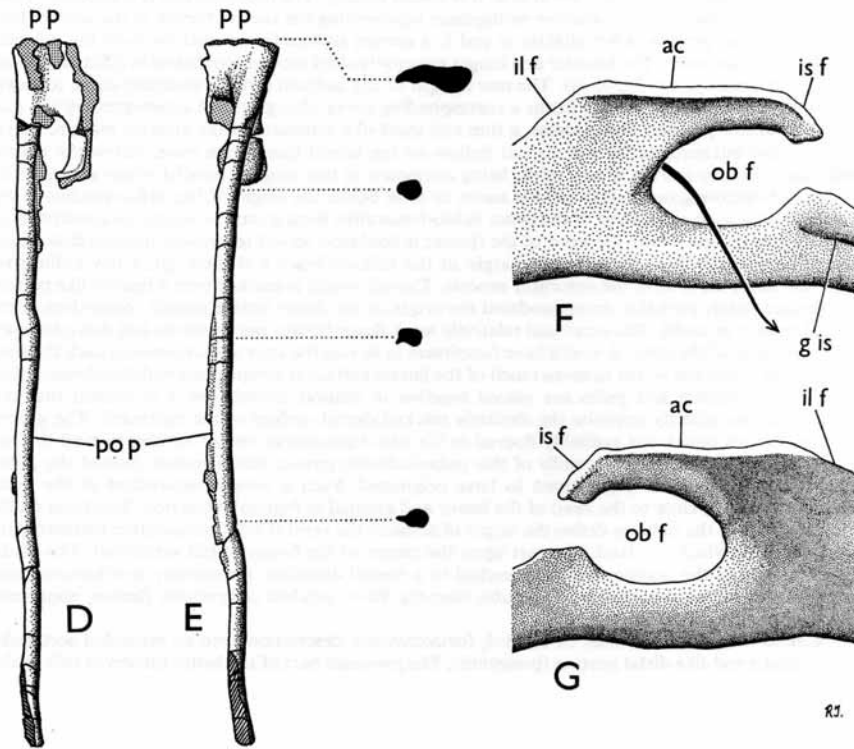
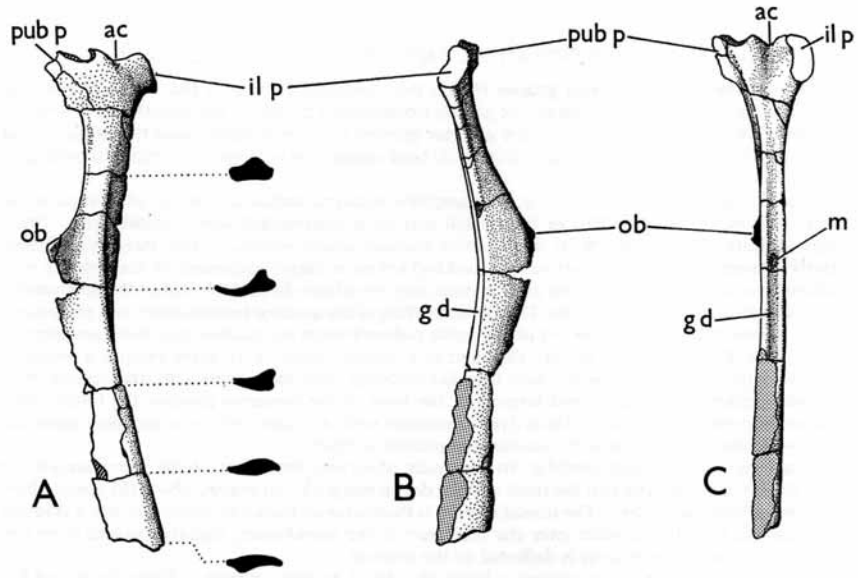
lies a long, shallow, and roughened groove (*il tr*); this doubtless represents the origin of the ilio-trochanteric muscle (which inserted on the greater trochanter of the femur and functioned in femoral protraction). The striated lateral face of the anterior process (*sar*) presumably bore the origin of the anterior ilio-tibialis muscle (or 'sartorius'); this would have assisted the posterior ilio-tibialis in extending the knee joint.

The medial surface of the ilium (text-fig. 8c) resembles its lateral surface in that the ventral parts are somewhat inflated. The dorsal half of the medial surface is ornamented with vertical striae. These markings indicate the attachment of dorsal axial muscles which would, in life, have run antero-posteriorly between the ilia. These striae (*il c* and *lev*) are most deeply impressed on the anterior half of the ilium—suggesting that the dorsal axial muscles may have been divided into anterior (ilio-costalis) and posterior (levator coccygis) groups. The medial surface of the anterior process bears two prominent and nearly horizontal ridges. At the top of the pubic peduncle there is a shallow and ill-defined depression in the medial iliac surface. Behind this, and at a slightly higher level, there extends a series of four similar depressions. The first of these four lies mid-way over the acetabulum, the second over the ischiadic peduncle, the third (and largest) at the base of the posterior process, the fourth (and faintest) on the posterior iliac shelf. These five excavations (*sr1*–*sr5*), representing attachment areas for the sacral vertebrae, are separated by smooth and convex surfaces.

The dorsal view of the ilium (text-fig. 8d) not only illustrates the extent of the supra-acetabular swelling but also demonstrates that the thick and flat dorsal margin is not everted above the acetabulum (i.e. there is no 'antitrochanter'). The dorsal margin is thickest over the acetabulum and has a sinuous course; it curves slightly outwards over the rear part of the acetabulum, slightly inwards over the anterior part. The anterior process is deflected to the exterior.

The *ischium* (text-fig. 9A–C) comprises a blade-like distal portion separated from the expanded proximal end by a long and weakly constricted 'neck'. Pronounced torsion of this 'neck' region causes the proximo-lateral face to turn forwards as it is traced distally. The proximal end is composed of two stout processes separated by a shallow embayment representing the ventral border of the acetabulum. The dorsal (iliac) process tapers slightly to end in a convex surface for articulation with the ischiadic peduncle from the ilium. The broader and longer anterior (pubic) process terminates in a flat face which meets the pubis (*is f*, text-fig. 9F–G). The rear margin of the ischium forms a sweeping curve (concave posteriorly); the anterior margin forms a corresponding curve, though this is interrupted by the projecting obturator process. This process, a thin and sheet-like extension of the anterior margin, curves forwards and outwards to form a distinct hollow on the lateral face of the bone. Below the twisted 'neck' the posterior margin is very thick, being composed of two roughly parallel ridges separated by a deep and narrow groove. This groove seems to have borne the origin of the ischio-trochanteric muscle (dinosaurian equivalent of the avian ischio-femoralis). Such a muscle would have extended up and forwards to insert near the head of the femur; it doubtless served to prevent femoral dislocation during locomotion. The grooved rear margin of the ischium bears a shallow pit, a few millimetres long, just below the level of the obturator process. This pit, which is marked with a feather-like pattern of divergent striae, probably accommodated the origin of the flexor tibialis muscle (equivalent of the ischio-flexorius in birds). The small and relatively weak flexor tibialis ran forwards and down to insert on the rear face of the tibia; it would have functioned in flexing the knee and in drawing back the hind limb. At the distal end of the ischium much of the lateral surface is ornamented with fine longitudinal striae. When ischium and pubis are placed together in natural articulation it is evident that this striated face lies directly opposite the similarly marked dorsal surface of the postpubis. The groove between the two bones was probably floored in life with ligamentous tissues serving to bind the two bones together. It is from both walls of this pubo-ischiadic groove that a muscle termed the pubo-ischio-femoralis externus is presumed to have originated. Such a muscle (equivalent of the avian obturator) inserted close to the head of the femur and assisted in femoral retraction. Striations on the medial surface of the ischium define the origin of some of the ventral axial musculature (probably the ischio-caudalis, which ran back to insert upon the centra of the foremost tail vertebrae). The blade-like distal part of the ischium is slightly arched in a medial direction, presumably to allow clearance for the femur during locomotion. The pubis (text-fig. 9D–E) exhibits comparable flexure, apparently with the same functional basis.

The *pubis* (text-fig. 9D–G) may be divided, for convenient description, into an expanded acetabular portion and a rod-like distal portion (postpubis). The proximal part of the better preserved (left) pubis



is damaged anteriorly (i.e. the prepubis is incomplete). The prepubis is twisted so that its lateral face is directed somewhat ventrally. A stout posterior process from the acetabular part of the pubis curves down towards the dorsal surface of the postpubis and defines the uppermost limit of the large obturator foramen (text-fig. 9F-G). The flattened dorsal surface of this process represents the pubic portion of the acetabular margin; anteriorly this same surface is modified into a facet (*il f*) to receive the pubic peduncle from the ilium. The deflexed tip of this sub-acetabular process lies some 2 mm away from the dorsal surface of the postpubis and defines the incomplete posterior margin of the elliptical obturator foramen. The postpubis is a long and slender bony rod, directed postero-ventrally away from the acetabulum. Its dorsal surface is slightly flattened, so that cross-sections are elliptical or oval. In lateral view (text-fig. 9D) the postpubis shows very slight ventral 'bowing' which is interrupted by a distinct dorsal kink about 25 mm behind the obturator foramen. Immediately behind the obturator foramen the dorsal surface of the postpubis bears a short and deep groove (*g is*, text-fig. 9F) which accommodated the ventral edge of the pubic process from the ischium. In its central and distal regions the postpubis is drawn out medially into a thin and sharp-edged flange nearly 2 mm wide. The striated dorsal face of the postpubis forms one side of the pubo-ischiadic groove and carried the origin (together with the adjacent part of the ischium) of the previously considered pubo-ischio-femoralis externus muscle. Striations on the ventral face of the postpubis indicate the former attachment of part of the ventral axial musculature (running forwards to the trunk region internal to the thigh).

Hind limb (text-figs. 10, 11, and 12)

The *femur* (text-figs. 10, 11H-M) is a stout columnar bone which is expanded both proximally (to form the head and the proximal trochanters) and distally (to form the condylar region). The femoral shaft is not perfectly straight but is slightly arched to the front. In its central regions the latero-medially compressed shaft is elliptical in cross-section. A faint vertical ridge down the front of the shaft probably marks the line of division of the femoro-tibialis musculature into lateral and medial portions. These muscles, extending over the front of the knee to insert upon the tibia, served to open the knee.

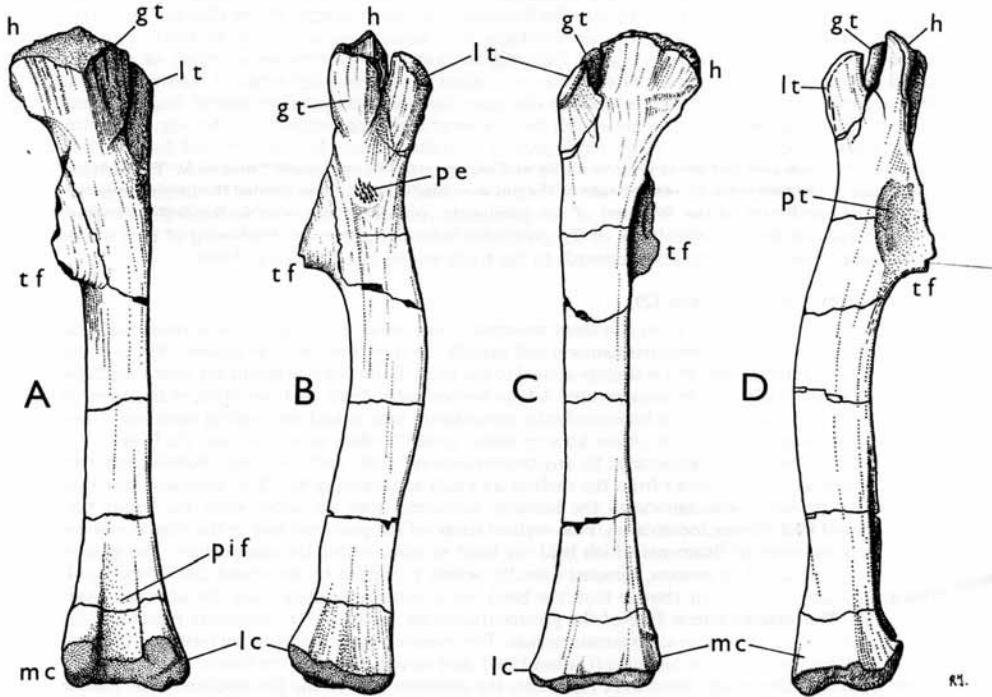
The femoral head is not demarcated by any constriction or 'neck' and is a simple bulb-like process which is directed medially away from the shaft at an angle approaching 90°. The depressed rear face of the head probably accommodated the ischiadic peduncle from the ilium when the femur was drawn up and back during locomotion. Fine vertical striae on the posterior face of the head doubtless mark the attachment of ligaments which held the head in place within the acetabulum. The greater trochanter is a blade-like process, directed dorsally, which is applied to the lateral face of the head. This trochanter is somewhat shorter than the head but is noticeably taller than the adjacent lesser trochanter. The striated lateral face of the greater trochanter (text-fig. 11H) probably represents the insertion area of the ilio-femoralis internus muscle. This muscle originated from the posterior thoracic region, and possibly from the prepubis (Galton 1969), and served to extend the femur. The roughened upper surface of the greater trochanter represents the insertion area of the ilio-trochanteric muscle (see description of ilium for details). The lesser trochanter is an erect finger-like process which diverges antero-laterally from the region where the head and the greater trochanter meet anteriorly (text-fig. 11H-I). The lesser trochanter lies antero-medial to the greater trochanter and is separated from it by a deep vertical cleft. Just below this cleft, on the lateral surface of the femoral shaft, there lies a small, rounded, and conspicuously pitted eminence (text-fig. 10B). This pitted area, together with the striated lateral face of the lesser trochanter, seems to have borne the insertion of the ilio-femoralis externus muscle (see description of ilium for details).

The fourth trochanter arises from the rear face of the shaft and is entirely confined to the proximal half of the femur. This trochanter is a triangular and blade-like structure with an acute and declined tip (i.e. it is of 'pendent' type). The surface of the fourth trochanter bore the insertion of the large coccygeo-femoralis brevis muscle (see account of ilium for details). Medial to the fourth trochanter there lies a prominent roughened depression (text-fig. 10D). This excavation doubtless marks the

TEXT-FIG. 9. *Fabrosaurus australis*. Ischium and pubis, $\times 1$ (except figures F and G). A-C, left ischium in antero-lateral, postero-medial, and posterior views. D-E, left pubis in lateral and ventral views. F-G, acetabular portion of left pubis (reconstructed) in lateral and medial views, $\times 3$. The arrow indicates the probable course of the obturator nerve and associated blood vessels.

insertion of the occygeo-femoralis longus (which originated from the anterior tail vertebrae and served to retract the femur).

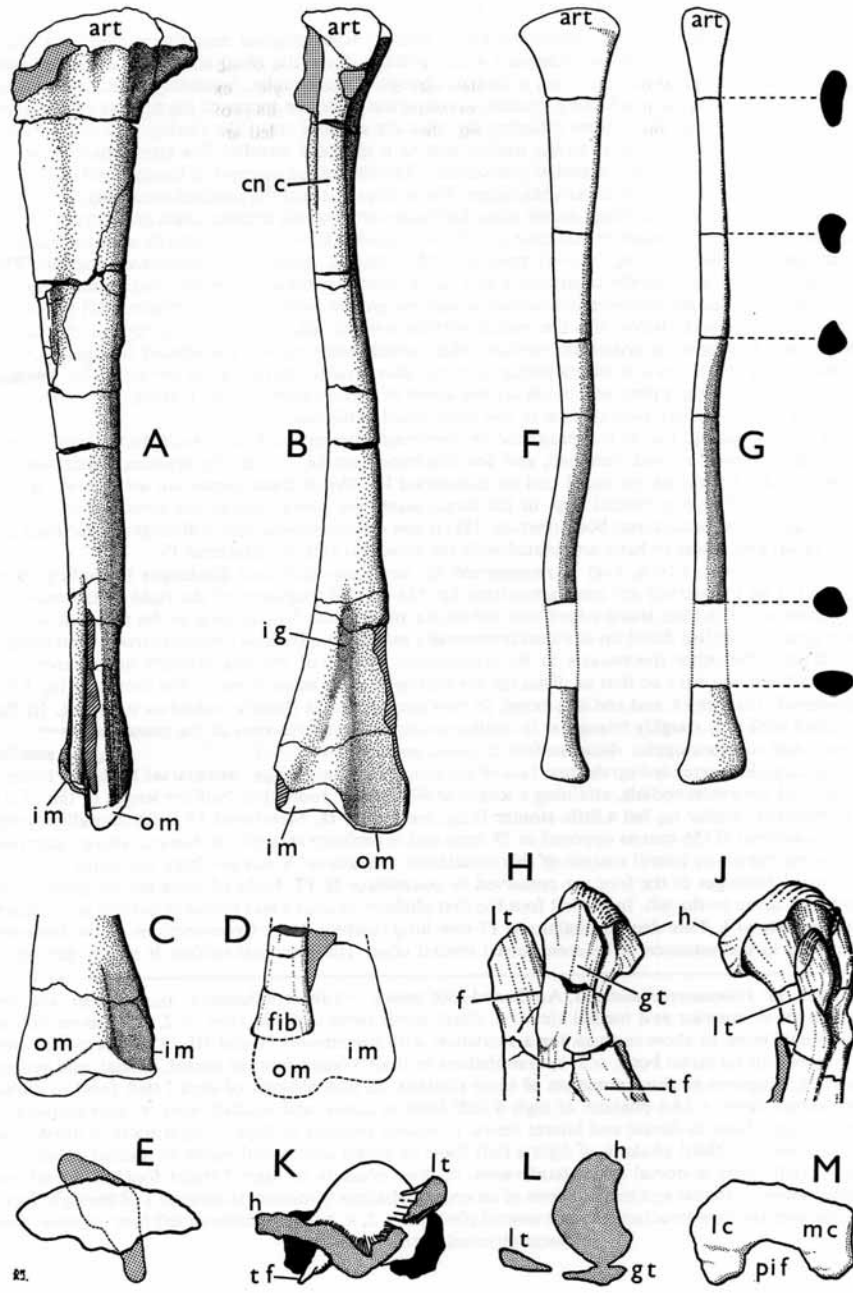
The shaft is widest just above the distal end. The lateral distal condyle is fractionally larger than its medial counterpart; these condyles are not appreciably attenuated behind and are separated by the wide and deep posterior intercondylar fossa. There is no trace of any anterior intercondylar fossa.



TEXT-FIG. 10. *Fabrosaurus australis*. Right femur, $\times 1$. Posterior (A), lateral (B), anterior (C), and medial (D) views.

The *tibia* (text-fig. 11A-E) is considerably longer than the femur. Its proximal end is widest from front to back whilst its distal end is expanded latero-medially. These differing directions of expansion lend the tibia a decidedly twisted appearance, the proximal view of the bone (text-fig. 11E) showing that this torsion ranges through some 70° . The anterior view (text-fig. 11B) shows that the bone is also affected by a weak sinuous flexure, the proximal half being arched medially whilst the distal half is arched to the exterior. The convex and roughened proximal surface is crescentic in outline. At the proximal end of the tibia the antero-medial surface is transversely convex whilst the postero-lateral

TEXT-FIG. 11. *Fabrosaurus australis*. Tibia, fibula, and femur, $\times 1$. A-B, left tibia in lateral and anterior views. C, distal part of same tibia in posterior view. D, distal parts of right tibia and fibula in natural juxtaposition (anterior view). E, proximal outline of left tibia (thick line) superimposed upon distal outline (shaded) to illustrate torsion affecting the bone. F-G, right fibula in lateral and anterior views. H-J, proximal part of left femur in lateral and anterior views. K, proximal view of right femur. L, plan of head and proximal trochanters in the left femur. M, distal view of right femur.



face is generally depressed. This postero-lateral concavity is interrupted near the middle by a blunt triangular projection (the 'lateral condyle') which extends down the tibial shaft as a thick and well rounded rib. Anterior to this there lies a similar, though rather smaller, 'accessory condyle' (text-fig. 11A). The 'inner condyle' is a blunt projection forming the posterior corner of the tibia at its proximal end. In consequence of the torsion affecting the tibia the cnemial crest (the thickly rounded anterior margin of the bone) shifts over to the medial side as it is traced distally. The lateral malleolus is a little broader and longer than its medial counterpart. The sharpened margins of the malleoli extend for a short distance up the tibial shaft as weak ridges. The anterior faces of the malleoli are almost flat. There are few obvious surface markings on the tibia. Indistinct striae on the cnemial crest probably mark the insertion of part of the extensor musculature (the femoro-tibialis and the ilio-tibialis or parts thereof).

The slender *fibula* (text-fig. 11F-G) resembles the tibia in displaying pronounced torsion. The proximal tip is latero-medially compressed and has its posterior corner extended into a short process. From the depressed proximo-medial surface a shallow groove runs down the fibular shaft for about a quarter of its length. Below this the medial surface is nearly flat. In its central regions the lateral face of the bone bears a prominent vertical ridge (which accounts for the almost triangular cross-sections of the shaft). As it is traced proximally this lateral ridge shifts over to the posterior margin. Distal parts of the right tibia and fibula are preserved in natural relationship (text-fig. 11D); the tip of the fibula lies on the flat anterior face of the outer tibial malleolus.

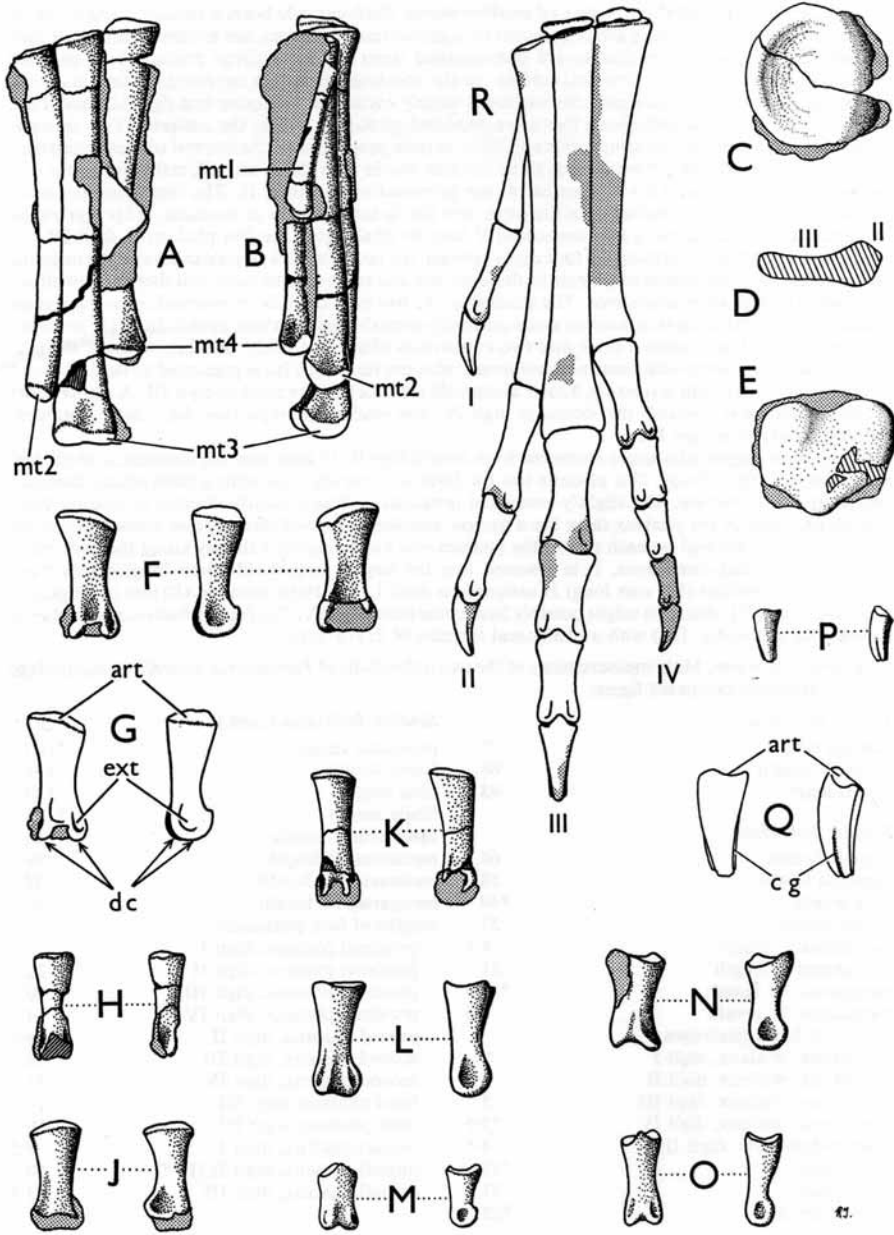
The *tarsus* (text-fig. 12C-E) is represented by two poorly preserved distal tarsals, both from the left side. One of these is a small, flattened, and disc-like bone (text-fig. 12C-D); its depressed distal surface accommodates the raised proximal end of metatarsal III. When these bones are articulated in this fashion the overhanging medial edge of the tarsal meets the lateral half of the proximal surface of metatarsal II. The other tarsal bone (text-fig. 12E) is less well preserved; this is slightly thicker than the other tarsal and seems to have articulated with the proximal end of metatarsal IV.

The *pes* (text-fig. 12A-B, F-E) is represented by numerous scattered phalanges (including three unguis), a well preserved left metatarsus (text-fig. 12A-B) and fragments of the right metatarsus.

Metatarsal I is a thin, sharp-edged, and splint-like bone about half as long as the adjacent second metatarsal. Its swollen distal tip is widest transversely and bears a shallow median furrow. Metatarsal I differs from the other metatarsals in its orientation; instead of running straight downwards it is directed down and back so that its distal tip lies well behind the other bones of the foot (text-fig. 12B). Metatarsal II is a thick and rod-like bone, 58 mm long, which is slightly arched to the front. Its flat proximal surface is roughly triangular in outline owing to the narrowness of the posterior margin. Its convex and sub-rectangular distal surface is developed into two small condyles; the slightly smaller medial condyle is extended up the rear face of the bone as a sharp ridge. Metatarsal III is the longest of the hind limb metapodials, attaining a length of 67 mm (i.e. more than half the length of the tibia). It is basically similar to, but a little stouter than, metatarsal II. Metatarsal IV is fractionally shorter than metatarsal II (56 mm as opposed to 58 mm) and is perfectly straight. A thin and sharp ridge persists along the entire lateral margin of this metatarsal. Metatarsal V has not been recovered.

Fifteen phalanges of the foot are preserved in assemblage B. 17. Eight of these are assigned to the right foot, seven to the left. In the left foot the first phalanx in digit I was found in natural articulation with metatarsal I. This slender phalanx is 17 mm long (text-fig. 12H). Cross-sections of the bone are triangular in consequence of its compressed medial edge. The proximal surface is nearly flat whilst

TEXT-FIG. 12. *Fabrosaurus australis*. Ankle and foot bones, $\times 1$ (except figures C, D, E, and Q). A-B, left metatarsus in anterior and medial views. C, distal tarsal bone in distal view, $\times 2$. D, cross-section of same tarsal bone to show surfaces for articulation with metatarsals II and III, $\times 2$. E, proximal view of a second distal tarsal bone, $\times 2$. F, first phalanx of digit 3 (right foot) in dorsal, medial, and ventral views. G, diagrams to show structure of same phalanx. H, first phalanx of digit I (left foot) in dorsal and lateral views. J, first phalanx of digit 4 (left foot) in dorsal and medial views. K, first phalanx of digit 2 (right foot) in dorsal and lateral views. L, second phalanx of digit 2 (right foot) in dorsal and medial views. M, third phalanx of digit 4 (left foot) in dorsal and lateral views. N, second phalanx of digit 3 (left foot) in dorsal and lateral views. O, third phalanx of digit 3 (right foot) in dorsal and medial views. P, dorsal and medial views of an unguis phalanx (probably from digit I of the right foot). Q, diagrams to show structure of same unguis phalanx, $\times 2$. R, reconstruction of left foot in dorsal view (reconstructed portions shaded).



the distal end is elaborated into a pair of small condyles. Each condyle bears a shallow circular pit on its flank; similar pits, marking the attachment of digital extensor muscles, are evident in the other foot phalanges. The proximal phalanges are distinguished from the more distal phalanges of the foot through the structure of the proximal surface; in the proximal phalanges the proximal face is almost flat whilst in the distal phalanges this surface is deeply excavated (compare text-figs. 12F and 12L). This criterion serves to distinguish five more proximal phalanges within the material. Two of these are merely fragments; the remaining three all differ in their proportions. The stoutest of these phalanges (text-fig. 12F) would seem, from its size, to be the first one in digit III. A second, rather narrower and longer phalanx (text-fig. 12K) is regarded as the proximal one in digit II. The remaining proximal phalanx (text-fig. 12J) is shorter than the other two but is intermediate in stoutness. This represents, by elimination (and assuming that metatarsal V bore no phalanges), the first phalanx in digit IV.

The distal phalanges, forming the foot digits between the proximal row of phalanges and the unguis, are represented by six examples. A pair of these are left and right counterparts and there are, in effect, only five examples to be considered. The stoutest of the five (text-fig. 12N) is assumed to be the second phalanx in digit III since it articulates quite agreeably with the first phalanx in this digit. Its proximal surface is divided by a vertical ridge into two concavities which receive the distal condyles of the preceding phalanx. A somewhat narrower and longer phalanx (text-fig. 12L) is presumed to be the second in digit II. A third example (text-fig. 12O) is tentatively identified as the third in digit III. A rather short (11 mm) phalanx is probably the second in digit IV. The smallest example (text-fig. 12M) is doubtless the third phalanx in digit IV.

Of the three unguis phalanges recovered from assemblage B. 17 only one, the smallest, is at all well preserved (text-fig. 12P-Q). This phalanx has the form of a curved cone with a transversely flattened ventral (palmar) surface. The slightly excavated proximal surface is nearly circular in outline. Half way up each side of the phalanx there lies a narrow and deeply incised claw groove; these grooves are about equally developed on each side of the phalanx and extend nearly half way along the bone from its bluntly rounded distal apex. It is assumed that the largest unguis (13.5 mm long) comes from digit III. The smallest (8.5 mm long) is assigned to digit I. The third example (10 mm in length) is assigned to digit II, though it might possibly have come from digit IV. The foot of *Fabrosaurus* is shown reconstructed (text-fig. 12R) with a phalangeal formula of 2:3:4:5:0.

Measurements in mm. Main measurements of the two individuals of *Fabrosaurus australis* in assemblage B. 17. *Indicates estimated figure.

<i>Larger Individual</i>		<i>Smaller Individual (cont.)</i>	
scapula height	75	postpubis length	*100
humerus length	68	femur length	104
radius length	43	tibia length	129
		fibula length	*123
<i>Smaller Individual</i>		metatarsal I length	*30
scapula height	66	metatarsal II length	58
humerus length	58	metatarsal III length	67
ulna length	*40	metatarsal IV length	56
radius length	37	lengths of foot phalanges:	
metacarpal I length	6.5	proximal phalanx, digit I	17
metacarpal II length	11	proximal phalanx, digit II	22
metacarpal III length	*12.5	proximal phalanx, digit III	20
metacarpal IV length	8.5	proximal phalanx, digit IV	14
lengths of hand phalanges:		second phalanx, digit II	18.5
proximal phalanx, digit I	*4	second phalanx, digit III	15.5
proximal phalanx, digit II	5.5	second phalanx, digit IV	11
proximal phalanx, digit III	5	third phalanx, digit III	14
proximal phalanx, digit IV	*3.5	third phalanx, digit IV	10.5
second phalanx, digit II	4.5	unguis phalanx, digit I	8.5
ilium length	*85	unguis phalanx, digit II (IV?)	10
ilium height	31	unguis phalanx, digit III	13.5
ischium length	*95		

DISCUSSION

Systematic position of Fabrosaurus

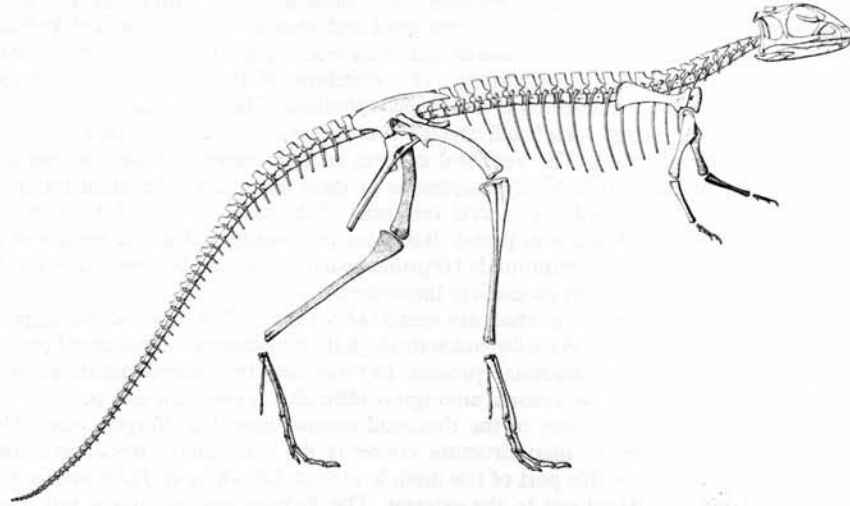
In his original account of the genus, based upon a jaw fragment, Ginsburg (1964) recognized the ornithischian status of *Fabrosaurus* and suggested that it might be closely related to the Liassic *Scelidosaurus*. In a subsequent description of the skull (Thulborn 1970a) this alliance with the armoured and somewhat problematical *Scelidosaurus* has been refuted and *Fabrosaurus* has been referred to the family Hysilophodontidae of the suborder Ornithopoda. The structure of the post-cranial skeleton endorses this concept of *Fabrosaurus* as a hysilophodont. The *Fabrosaurus* skeleton is very like that of *Hysilophodon* itself, though it is distinguished through its noticeably more delicate construction. The vertebral column of *Fabrosaurus*, though it remains poorly known, matches that of *Hysilophodon* in most essentials. The main point of difference concerns the number of sacral vertebrae; *Fabrosaurus* has 5 whilst *Hysilophodon* typically has 6 (Galton in press). But since the number of sacral vertebrae is slightly variable within the ornithopods (*Hysilophodon*, for example, sometimes has 5) this distinction does not seem excessively important.

The limb girdles of the two animals are remarkably similar. The *Fabrosaurus* scapula is distinguished from that of *Hysilophodon* through its projecting postero-dorsal corner and through its prominent 'acromial' process. In possessing this salient 'acromial' process *Fabrosaurus* is somewhat unusual amongst ornithischians (with the exception of the stegosaurs) and resembles some of the theropod saurischians (e.g. *Gorgosaurus*). The most obvious difference in iliac structure concerns the immediate supra-acetabular region; in *Hysilophodon* this part of the ilium is almost flat whilst in *Fabrosaurus* it is strongly inflated and flared out to the exterior. The *Fabrosaurus* ischium is not quite as straight as that of *Hysilophodon* and has the obturator process situated rather nearer the acetabulum. The *Fabrosaurus* pubis is very similar to that of *Hysilophodon*; the postpubis demonstrates none of the shortening seen in later and larger ornithopods.

The humerus is remarkably like that figured for *Hysilophodon* by Swinton (1936); in both cases the free edge of the delto-pectoral crest accounts for roughly one third of the total humeral length. The fore arm bones and the diminutive manus of *Fabrosaurus* are quite comparable with those of *Hysilophodon*. The femora of the two animals are both characterized by a large fourth trochanter of 'pendent' type which is located unusually high up on the shaft. In both cases there is no anterior intercondylar fossa and the proximal trochanters are divided by a deep cleft. Within the *Fabrosaurus* hind limb, the tibia is considerably longer than the femur; this unusual tibio-femoral ratio is quite typical of members of the family Hysilophodontidae. The *Fabrosaurus* metatarsus is equally as long and as narrow as that of *Hysilophodon*. In both animals the phalangeal formula for the foot appears to be 2:3:4:5:0 and the digits terminate in slender claws. Finally *Fabrosaurus* resembles *Hysilophodon* in possessing a system of ossified tendons along the rear parts of the vertebral column and in having hollow and thin-walled limb bones.

There can be no doubt, in view of this evidence, that *Fabrosaurus* is a genuine ornithischian dinosaur of Triassic age. This is amply demonstrated by its possession of a predentary bone at the mandibular symphysis (Thulborn 1970a) and by the tetra-radiate plan of its pelvic girdle. Certain structural peculiarities, such as the toothed

premaxilla (Thulborn op. cit.) and the unusual tibio-femoral ratio, indicate that this genus should be included within the family Hypsilophodontidae. It is proposed, in view of these findings, to remove *Fabrosaurus australis* from the Scelidosaurinae (Ginsburg's assignment, 1964) and to place it within the family Hypsilophodontidae of the suborder Ornithopoda. Ginsburg's original diagnosis is greatly amplified.



TEXT-FIG. 13. *Fabrosaurus australis*. Restoration of skeleton. Approximately $\frac{1}{3}$ natural size.

Class REPTILIA
 Order ORNITHISCHIA
 Suborder ORNITHOPODA
 Family HYSILOPHODONTIDAE
 Genus FABROSAURUS Ginsburg 1964
 Monotypic species *F. australis* Ginsburg 1964

Diagnosis (for genus and sole known species): unarmoured ornithischian, about 1 metre long, with slender and hollow limb bones. Skull* about 10 cm long, triangular, diapsid, with extensive circular orbits at sides. Antorbital vacuity triangular, widely open. Premaxilla extended behind naris but does not reach lacrimal. Maxilla flat above tooth row; jugal slender, without ventral flange. Parietals separate, forming broad and flat zone between upper temporal openings. Frontal with transverse crescentic depression marking front limit of upper temporal opening. Quadrate tall, extended anteriorly, with front edge overlain by slender descending process from squamosal. Mandible slender, with salient finger-like retroarticular process and weak coronoid apophysis. Small median edentulous preentary at mandibular symphysis. Dentition heterodont; implantation thecodont; teeth in simple marginal row. Premaxilla with up to 6 acute,

* Details of skull construction from Thulborn 1970a.

smooth, recurved teeth, last 2 bearing minute marginal denticles. About 14 teeth in maxilla; equivalent number in dentary. Crowns of cheek teeth squat, triangular, inflated buccally, flattened lingually; mesial and distal edges of crowns with small erect denticles of unvarying size. Replacement from lingual side, alternate; wear affects mesial and distal edges of cheek teeth separately.* About 15 dorsal vertebrae; sacrum of 5 vertebrae, with neural canal expanded ventrally within centra. Scapula tall, with projecting postero-dorsal corner and prominent 'acromial' process. Fore limb much smaller than hind limb. Humerus slightly shorter than scapula, with delto-pectoral crest confined to upper third. Radius and ulna slender, roughly equal in length, shorter than humerus. Manus diminutive, with probable formula of 2:3:4:3:0. Pelvis tetra-radiate; ilium long, low, with pointed and deflexed anterior process, without 'antitrochanter'. Postpubis long, narrow, rod-like, fairly straight; prepubis short, blade-like, twisted. Obturator process very high up on ischium. Acetabulum open, roofed above by lateral extension of ilium. Femur twice as long as humerus, with pendent fourth trochanter confined to proximal half; greater and lesser trochanters divided by deep cleft; distal condyles sub equal, not drawn out behind. Tibia stout, twisted, longer than femur; fibula slender, rod-like, slightly shorter than tibia but longer than femur. Metatarsus long and narrow; metatarsal I reduced, splintlike; metatarsal III equivalent to 55% of tibia length. Phalangeal formula of foot 2:3:4:5:0; digits clawed.

Size

It seems likely that *Fabrosaurus australis* is a dinosaur which did not attain any great size (rather than a form represented by immature specimens). All known specimens are of much the same size; the list includes the holotype (Ginsburg 1964), a nearly complete skull (Thulborn 1970a), the two individuals in assemblage B. 17 and parts of two undescribed individuals in the British Museum (Natural History).

In his discussion of *Hypsilophodon*, Swinton (1936) implied that the length of the humerus, relative to that of the scapula, might indicate the maturity of individual hypsilophodonts:

'... scapula and humerus ... are almost equal in length in the new young specimen, but the former is definitely shorter than the latter in the adult, so that generally it may be said that this somewhat unusual condition in dinosaurian osteology is common to *Thescelosaurus neglectus* and *Hypsilophodon*.'

If scapula and humerus lengths really are equal in immature hypsilophodonts, whilst the humerus is longer in adults, comparisons of these bones should provide a rough working guide to the maturity of individual specimens. Table 1 shows that in *Fabrosaurus* the scapula is longer than the humerus, an arrangement which is totally irreconcilable with Swinton's hypothesis. The scapula-humerus ratio in *Fabrosaurus* is comparable with that in the Upper Cretaceous hypsilophodont *Parksosaurus* (Sternberg 1940) and in the iguanodont *Camptosaurus* (Gilmore 1909). It is clear that this skeletal ratio is no sound criterion upon which to establish the relative maturity of hypsilophodont specimens. This ratio is rendered even more suspect when one considers that the dorsal margin of the scapula may, since it passes into the supra-scapula, be ossified to very different degrees in different individuals.

* Details of tooth wear and replacement from Thulborn 1971.

Galton (in press) maintains that in *Hypsilophodon* the humerus displays greater torsion with greater maturity of the individual. This seems to imply that the straight and untwisted humerus of *Fabrosaurus* signifies immaturity. Alternatively the lack of torsion affecting the *Fabrosaurus* humerus might well be interpreted as a primitive character, especially since this bone is only slightly twisted in pseudosuchians such as *Euparkeria*.

Since all the known specimens are of roughly similar size it seems reasonable to assume that *Fabrosaurus* was, in fact, a rather small ornithischian dinosaur. It is estimated that the smaller (more complete) individual in assemblage B. 17 had a maximum length (from snout to tail tip) of slightly less than one metre. The hind limb is comparable in size with that of a living chicken (*Gallus*). The fore limb is very much shorter than the hind limb whilst the neck, which was relatively short, carried a quite large skull (perhaps 10 cm long). The tail is not well represented in the material but is shown in the reconstruction (text-fig. 13) as roughly equivalent in length to head, neck, and trunk combined (i.e. much as in other hypsilophodont ornithopods).

Locomotion

It is important to recognize that there are no specific features of skeletal construction which might serve as absolutely reliable criteria in distinguishing between bipedal and quadrupedal dinosaurs. A comparable situation exists in living lizards, where bipeds are indistinguishable from quadrupeds through examination of the skeleton alone. There are, however, numerous osteological characters in *Fabrosaurus* which are distinctly suggestive of bipedalism and which, in conjunction, render the concept of *Fabrosaurus* as a biped quite acceptable. These adaptations for bipedalism are evident in almost every part of the skeleton. The entire skeleton is very lightly built. The slender, hollow and thin-walled limb bones resemble those of birds and of pterosaurs, where weight reduction would have been of critical importance. Lightening of the skeleton is most marked in advance of the hips—in the fenestrated skull (Thulborn 1970a), in the relatively short neck, in the small fore limbs and in the rather delicate construction of the presacral vertebrae. Such weight reduction in front of the hips is explicable when one considers that in a biped the whole body must be pivoted over the hips and that, in consequence, the tail alone must counter-balance the weight of the trunk, fore limbs, neck, and head. Further, the lack of dermal armour in *Fabrosaurus* would have contributed to the reduction of total body weight.

The almost horizontal zygapophysial faces of the vertebrae immediately preceding the sacrum would have prevented undue sagging of the vertebral column whilst the animal was in a bipedal pose. The 'lumbar' vertebrae of large and undoubtedly bipedal theropods (*Tyrannosaurus*, *Allosaurus*, and the like) frequently show traces of fusion, presumably with a similar functional basis. The lattice of ossified tendons, attached to the neural spines in front of and behind the sacrum, seems to have a similar purpose. Ostrom (1964) suggests that such a tendon system would have effected resistance to any sagging of the vertebral column.

The zygapophysial faces of the caudal vertebrae are practically vertical, indicating that flexures of the tail took place mainly within a vertical plane. Snyder (1949) has emphasized the importance of the tail in the bipedal locomotion of lizards such as *Basiliscus* and has shown that their bipedal faculties are seriously impaired when the tail is even partially amputated. This author points out that the tail is held clear of the

ground (i.e. elevated in a vertical plane) during bipedal running. Snyder (1962) further makes it clear that such tail movements serve to counter-balance the weight of those parts of the body in advance of the hips. Vertical tail movements, in every way comparable to those of bipedal lizards, would seem to have been of fundamental importance in *Fabrosaurus*. These tail flexures would not have been impaired by the ossified tendons since individual bundles of tendons would have 'slipped' relative to those crossing above and below.

The five centra of the *Fabrosaurus* sacrum are distinguished through the great enlargement of the neural canal within them. Ewer (1965) noted similar inflation of the neural canal in the whole 'lumbar' region of the pseudosuchian *Euparkeria* (from the 13th dorsal vertebra to the 1st caudal). It is evident that this peculiarity affects similar zones in *Euparkeria* and *Fabrosaurus* but that owing to the shortness of the sacrum in the former (only two vertebrae) it extends to include both posterior dorsal and anterior caudal vertebrae. The functional significance of the dilated neural canal is debatable. Ewer (op. cit.) maintains that these dilations in the centra might have been filled with non-nervous tissue intimately associated with the nerve cord (rather than with any expansion of the spinal cord itself). Such an arrangement might be paralleled in birds, where the sinus lumbosacralis is the associated tissue (Terni 1924). This hypothesis suffers, however, from some difficulties. Firstly, the avian sinus lumbosacralis lies dorsal to the nerve cord whilst the excavations in the *Fabrosaurus* vertebrae (and those of *Euparkeria*) are situated ventrally. Secondly, the function of the glycogen-filled sinus lumbosacralis is not readily apparent. It is unlikely that such glycogen-rich tissues could have provided fuel for muscular energy since (in birds at least) the main locomotor muscles derive fuel from deposits of fat, which provides twice the energy that glycogen does (George and Berger 1966). It is suggested here, in contrast, that the inflated neural canal in the sacral region did in fact accommodate nervous tissue—a genuine ganglionic expansion of the nerve cord. Dilations of the spinal cord have long been quoted in a variety of dinosaur sacra (e.g. see Marsh 1881; Seeley 1882) and Romer (1956) suggests that this local refinement of the central nervous system is to be related directly to the size of the hind limbs. In both *Euparkeria* and *Fabrosaurus* the hind limbs are considerably larger than the fore limbs. Yet sheer relative size of the hind limbs alone would not seem to account for any local expansion of the nerve cord in these animals, particularly when their over-all small size is recalled. It is important to recognize, however, that *Fabrosaurus* is presumed to have been an habitual (if not obligatory) biped. When not running this animal must have walked slowly on the hind limbs alone. In such slow bipedal progression there regularly comes a point when contact with the ground is maintained by one foot alone (assuming that the tail would have been nearly clear of the ground). Thus for short periods, perhaps a second or so in duration, the animal must be poised on one foot and must, as a result, be prone to simply topple over. The only way in which this tendency can be counteracted is through delicate shifts of body weight so as to maintain equilibrium. This, in turn, demands perfect muscular control within and between the hind limbs and the major organ of balance, the tail. Such sophisticated muscular control might well have been governed by a local dilation of the nerve cord which, logically, would have been situated close to both hind limbs and the base of the tail (i.e. in the sacrum).

The proximal end of the humerus bears an extensive articular surface but lacks any

salient 'head'. This indicates that the humerus had significant freedom of movement within the glenoid cavity. Many earlier dinosaur reconstructions have the proximal end of the humerus set firmly in the glenoid; in consequence the humerus is directed horizontally at right angles to the line of the vertebral column (see Casier 1960, for restorations of *Hypsilophodon* and *Megalosaurus*). Whilst this attitude was undoubtedly possible it seems more likely that in normal circumstances the humerus would have been closely applied to the side of the thorax and directed down and forwards. In this position the projecting proximo-medial corner of the humerus would have served as the functional 'head'. Such humeral mobility suggests that the fore limb had no very great positive locomotor function; the humerus would surely have been too prone to dislocation for the fore limb to have sustained any sizeable proportion of the body-weight. This, once again, is indirectly suggestive of habitual bipedalism.

The *Fabrosaurus* hand, in relation to the foot in the same animal, is diminutive (compare text-figs. 7R and 12R). None of the bones of the hand shows the elongation which characterizes the foot bones. It is clear that this delicate hand could have had no significant locomotor function. In quadrupedal archosaurs (e.g. *Alligator*, *Stegosaurus*) the hand is generally only slightly smaller than the foot, despite a startling size-difference between the entire fore and hind limbs. It appears that the span of the hand relative to that of the foot (rather than the length of the fore limb against that of the hind limb) is of some use in deducing the probable mode of locomotion.

Strong pelvic and thigh muscles have been inferred for *Fabrosaurus* on the evidence of muscle scars on the femora and pelvic girdle bones. These muscles are matched in the related dinosaurs *Thescelosaurus* (Romer 1927) and *Hypsilophodon* (Galton 1969) and are comparable, in general terms, with those of birds and lizards. The principal locomotor agent in *Fabrosaurus* was doubtless a strong backwards thrust of the hind limb, generated by contraction of the powerful femoral adductor muscles. These adductor muscles (the coccygeo-femorales) extended from the fourth trochanter of the femur to areas of origin on the rear part of the ilium and the anterior tail vertebrae. During femoral adduction there would necessarily have been some tendency for the base of the tail to bend into a kink towards the approaching femur. This is admirably shown by Snyder (1962) in a figure of the lizard *Crotaphytus*. Such tail flexure would have affected the efficiency of the adductor muscles to a considerable degree. It is likely that the vertical zygapophysial faces of the caudal vertebrae served to brace the tail in order to resist such lateral flexure.

The *Fabrosaurus* ilium is distinguished by its swollen and flared out acetabular margin. This forms, in effect, an overhanging roof above the acetabulum. In other hypsilophodonts the supra-acetabular part of the ilium is flat or only very slightly inflated. *Fabrosaurus* seems, in fact, to be unique amongst ornithischians in this portion of its iliac morphology. Such roofing-over of the acetabulum may be matched only in the coelurosaur *Coelophysis* and in the problematical reptile *Poposaurus* (Colbert 1961). These three reptiles have, moreover, certain other features in common; they are all of late Triassic age and they all appear (with the possible exception of *Poposaurus*) to have been habitual bipeds. The supra-acetabular expansion is probably a specialization related to bipedalism. In a biped much of the mechanical thrust affecting the femur is directed upwards; hence a deepened and partially roofed-over acetabulum would have assisted in retaining the 'head' of the femur in place during locomotion. This arrange-

ment may, in turn, be correlated with the rather weak development of the femoral 'head' in these forms.

The dorsal margin of the ilium is not at all everted or extended laterally and there is no trace of the 'antitrochanter' which occurs in larger ornithopods and in quadrupedal ornithischians. The functional significance of the 'antitrochanter' is obscure, though Romer (1927) suggests that its presence reflects some elaboration of the ilio-femoralis musculature. Lack of this structure from the *Fabrosaurus* ilium presumably points to an unspecialized arrangement of the ilio-femoralis (which holds the femoral 'head' in place and assists in elevating the thigh). The anterior process of the ilium is only slightly deflexed and has an acutely pointed tip (in contrast to the broadly spatulate tip observed in many iguanodonts). Most importantly the anterior process exhibits none of the arching seen in the ilia of hadrosaurs (e.g. *Hypacrosaurus*). Romer (op. cit.) relates such arching with reversion to quadrupedalism, suggesting that this flexure of the anterior process permitted passage for the ilio-femoralis internus muscle from the femur to the posterior thoracic region. Two ridges on the medial face of the anterior process (text-fig. 8c) seem to have strengthened this rather delicate structure. It may be noted, in this context, that the anterior process would have been subject to some lateral 'pull' through contraction of the attached 'sartorius' muscle.

The postpubis rivals the ischium in length and is also fairly straight; it lacks any of the downwards curvature which Romer correlates with quadrupedalism (1927). The large obturator foramen (text-fig. 9F-G) probably served as an exit for the obturator nerve and associated blood vessels. The foramen is very nearly encircled by bone and the small gap at the rear margin was doubtless filled with cartilage during life. This near-complete enclosure of the obturator foramen is characteristic of hypsilophodonts; in many other ornithopods the foramen is widely open at the back and is little more than a notch.

The prepubis is so poorly known (text-fig. 9D) that it cannot be discussed in detail. Hence it is impossible to reconsider Romer's hypothesis (1927) that the prepubis served principally as an abdominal support structure and that no musculature of any consequence was attached to it. Recently Galton (1969) has suggested that the prepubis did not provide the main support for the abdomen and that some muscle (the pubo-tibialis or part of the pubo-ischio-femoralis internus) originated from its lateral surface.

The elongated and thin-walled bones of the *Fabrosaurus* hind limb are not unlike those of birds in general appearance and are distinctly suggestive of bipedal potential. The hind limb is somewhat unusual in that the tibia is considerably longer than the femur. Comparable predominance of tibia over femur is seen in related hypsilophodonts, in some pseudosuchians (e.g. *Saltoposuchus*) and in many coelurosaurs (e.g. *Coelophysus*, *Ornithomimus*). The metatarsus of *Fabrosaurus* is similarly attenuated, the longest (third) metatarsal being equivalent to some 55% of the tibia length. Such elongation of the hind limb is almost certainly indicative of habitual bipedalism, though this does not imply that forms with a relatively short tibia and metatarsus (e.g. *Thescelosaurus*, *Euparkeria*) were precluded from a similar mode of locomotion. Lengthening of the hind limb probably served to increase potential for rapid acceleration. Hildebrand (1959, 1961) has shown that acceleration is achieved, in cursorial mammals at least, by lengthening of the stride rather than by any increase in the number of limb strokes per minute. This suggests that the long hind limbs of *Fabrosaurus* increased this animal's

ability to lengthen the stride and, in consequence, its capacity to achieve acceleration. It is probable that a dinosaur as small as *Fabrosaurus* could take off into rapid bipedal flight from a stationary position, much as the lizard *Basiliscus* (Snyder 1962) or the domestic chicken.

There is no trace of the fifth digit in the *Fabrosaurus* foot. In all probability digit V was represented only by a splint-like vestige of the fifth metatarsal (i.e. as in *Hypsilophodon* and *Thescelosaurus*). Digits II, III, and IV are the longest and stoutest and the *Fabrosaurus* foot may be considered as functionally tridactyl and rather bird-like (text-fig. 12R). The tridactyl foot would seem to have been a specialization related to bipedalism since it is encountered in other hypsilophodonts, in the pseudosuchian thecodonts (though digits I and V are not excessively reduced here) and in saurischian bipeds (e.g. *Allosaurus*, *Ornithomimus*). The second, third, and fourth digits of the *Fabrosaurus* foot were directed forwards and were somewhat splayed out whilst the shorter first digit was probably directed back and down as a heel-like 'prop'. This interpretation is borne out by the orientation of the first metatarsal when the metatarsus is preserved in an undisturbed state (text-fig. 12B).

In the saurischian dinosaurs Colbert (1964) has indicated some relationships between certain skeletal proportions and the presumed mode of locomotion. Some of the conclusions attained by this author may be extended to cover the early ornithischian now under consideration. Colbert correlates a 'dolichoiliac' type of pelvis (i.e. one with a long, low ilium) with the development of 'complete bipedalism', citing *Coelophysis*, *Compsognathus*, and *Ornithomimus* as examples. This author suggests that '... the dolichoiliac pelvis . . . would furnish the muscular base for an efficient bipedalism'. A similar argument might be applied to *Fabrosaurus*: a powerful pelvic musculature, well-suited for bipedal locomotion, has been inferred from the evidence of muscle scars whilst the long and blade-like ilium could be accommodated without difficulty in Colbert's 'dolichoiliac' category.

Colbert (op. cit.) also attempts to establish some line of distinction between saurischian bipeds and quadrupeds on the basis of disparity in size between the fore and hind limbs. Such an approach cannot, however, be utilized in the ornithischian dinosaurs; there are several cases where a limb ratio of bipedal aspect (with the fore limb very much shorter than the hind limb) is encountered within undoubted quadrupeds (e.g. *Stegosaurus*, *Nodosaurus*). Despite this difficulty it is still possible to distinguish purely bipedal ornithopods from those with a tendency to quadrupedalism—through comparisons of limb bone lengths within the hind limbs. In habitually bipedal types, such as the hypsilophodonts, the tibia is considerably longer than the femur and the metatarsus is equivalent to a significant proportion of the femoral length (66% in *Fabrosaurus*). In those ornithopods tending to quadrupedalism (notably iguanodonts and hadrosaurs) the tibia is not as long as the femur and the short, stout metatarsals constitute a foot of graviportal aspect.

It seems reasonable, in view of all this evidence, to envisage *Fabrosaurus* as a small and agile biped with distinct cursorial ability. In conclusion it may be pointed out that *Fabrosaurus* compares favourably with cursorial bipeds from elsewhere within the Reptilia—with *Basiliscus* and *Chlamydosaurus* (Snyder 1949, 1952, 1954, 1962), with *Coelophysis* (Colbert 1964), with *Euparkeria* (Ewer 1965) and with *Velocipes* (von Huene 1932).

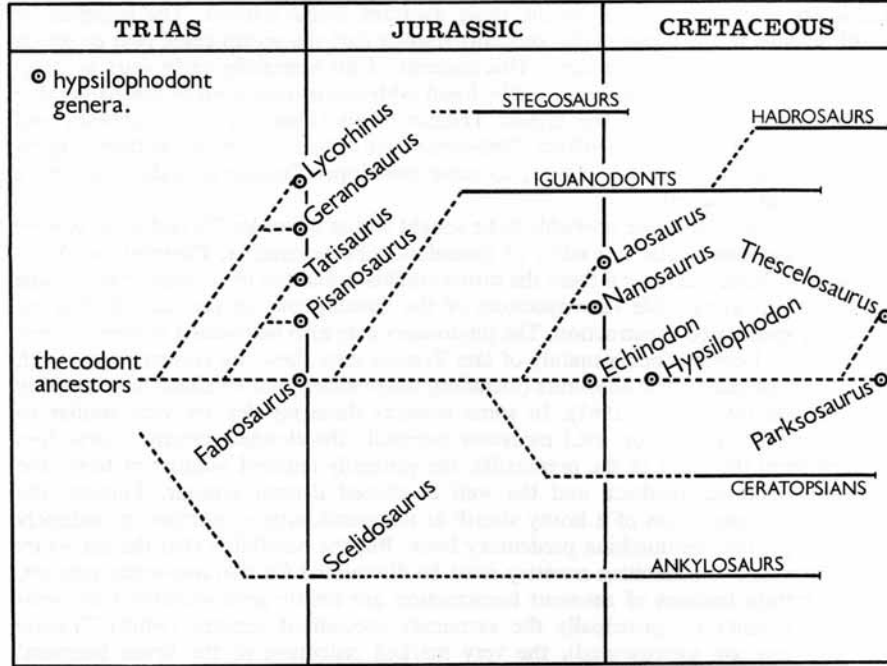
Ornithischian origins

Since all known Triassic ornithischians may be referred to the family Hypsilophodontidae it is clear that the whole question of ornithischian ancestry is bound up with the origin of this family in particular. This inferred monophyletic origin for the order Ornithischia is sustained by a remarkable homogeneity of structure throughout the group; important diagnostic features, such as the predeontary bone and the biramous pubis, are encountered in even the most aberrant ornithischians. The presence of ornithischians in the Upper Trias certainly implies that the group came into existence at some considerably earlier date. This concept of an extremely early start to ornithischian history, though unsupported by fossil evidence, is reinforced by the geographic and structural diversity of the known Triassic forms (*Fabrosaurus*, *Lycorhinus*, and *Geranosaurus* from southern Africa, *Tatisaurus* from China, *Pisanosaurus* from Argentina). Such diversity points, in turn, to some pre-Upper Triassic episode of adaptive radiation and dispersal.

Ornithischian origins are probably to be sought within the order Thecodontia. Romer (1966) distinguishes four suborders of thecodonts: Proterosuchia, Phytosauria, Aetosauria, and Pseudosuchia. Of these the proterosuchians and the phytosaurs may at once be discounted as possible near-ancestors of the Ornithischia on account of their remarkably specialized construction. The phytosaurs may also be rejected in view of their stratigraphic location (being mainly of late Triassic date these are contemporary with early ornithischians). The aetosaurs (including *Stagonolepis* and its allies) have recently been studied by Walker (1961). In some respects these reptiles are very similar to ornithischians; Walker (op. cit.) mentions especially the elongate external naris, loss of teeth from the front of the premaxilla, the generally reduced number of teeth, the forwardly inclined quadrate and the well developed dermal armour. Further, the existence in *Stagonolepis* of a horny sheath at the mandibular symphysis immediately calls to mind the ornithischian predeontary bone. But the possibility that the aetosaurs might represent ornithischian ancestry must be discounted for two important reasons. Firstly, certain features of aetosaur construction are totally irreconcilable with ornithischian conditions—principally the extremely specialized armour (whilst Triassic ornithischians are unarmoured), the very marked reduction of the lower temporal opening, the lateral situation of the upper temporal opening, and the typically thecodont pelvic girdle. Secondly, the aetosaurs are mainly of late Triassic age (i.e. contemporary with early ornithischians). It seems rather improbable, in view of these facts, that the aetosaurs could be involved in ornithischian history.

This leaves only the pseudosuchian thecodonts to be considered as possible ornithischian ancestors. In discussing the Lower Triassic pseudosuchian *Euparkeria* Ewer (1965) supports the suggestion, advanced by Broom (1913), that the family Euparkeriidae probably represents the ancestry of all the major groups of later archosaurs, including the Ornithischia. It is, however, rather difficult to imagine the derivation of ornithischians from hypothetical *Euparkeria*-like ancestors. This difficulty springs from fundamental differences in structure; Ewer (op. cit.) concludes that the Ornithischia arose '... from some form other than *Euparkeria*, differing from the latter in the structure of both pelvis and ankle...'. Whilst it may be inferred that ornithischian ancestry extends back ultimately into the Euparkeriidae this still does not clarify the problem of ornithischian history between Lower and Upper Trias. *Euparkeria* and its allies display

no obvious tendency towards the ornithischian state of organization whilst the earliest known ornithischians exhibit relatively few primitive characters and might be regarded as 'fully-fledged' members of the Ornithischia. There are, in consequence, no apparent 'intermediates' between the Lower Triassic *Euparkeria* and the Upper Triassic *Fabrosaurus*.



TEXT-FIG. 14. Outline of ornithischian phylogeny.

It has already been suggested that *Fabrosaurus* is a fairly direct antecedent of the hypsilophodonts of the Jurassic and Cretaceous (Thulborn 1970a). The structure of the post-cranial skeleton fully substantiates this assertion. So it is clear that *Fabrosaurus* represents the earliest known portion of a hypsilophodont stock which persisted through the greater part of the Mesozoic era. These hypsilophodonts appear to lie at the core of ornithischian history; they represent the ancestry, ultimately at least, of such groups as the iguanodonts, hadrosaurs, and ceratopsians (text-fig. 14). Hence there is some justification for regarding *Fabrosaurus* as a genuine 'archetypal' ornithischian. Amongst other Triassic ornithischians the Chinese *Tatisaurus* and the South American *Pisanosaurus* seem to be fairly close relatives of *Fabrosaurus*. The coeval *Lycorhinus* (*Heterodontosaurus*), from southern Africa, has a peculiar dentition which includes large 'canine' teeth (Crompton and Charig 1962; Thulborn 1970b, 1971). This genus appears to

represent an extremely early and rather specialized hypsilophodont divergence which failed to survive the changes concomitant with the close of the Triassic period.

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