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A REASSESSMENT OF *VULCANODON KARIBAENSIS* RAATH (DINOSAURIA:SAURISCHIA) AND THE ORIGIN OF THE SAUROPODA

by

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ABSTRACT

Vulcanadon karibaensis Raath is redescribed and figured in detail. It forms the basis of the new sauropod family Vulcanodontidae, to which the Indian *Barapasaurus* is also provisionally referred. The retention of numerous symplesiomorphies with the Prosauropoda leaves little doubt as to its ancestry. It is considered a primitive sauropod on account of its large size, columnar limbs, pelvic structure, reduced cnemial crest to the tibia, lack of distal tarsals, the length of its forelimbs and its quadrupedal gait. The post-cranial anatomy of *Vulcanodon* is sufficiently generalized for the Vulcanodontidae to have formed the ancestral stock of both the Camarasauridae and Diplodocidae.

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INTRODUCTION

Since Raath's (1972) original description of *Vulcanodon karibaensis* as a specialized melanorosaurid prosauropod, convergent towards the sauropod condition, a number of workers (Cruickshank 1975; Van Heerden 1978; Cooper 1980a) have discussed this species and concluded that it was, in fact, a primitive sauropod. As such, its significance takes on a whole new aspect and, in view of its early Jurassic age, its characters have considerable phylogenetic significance. Moreover, the subsequent description of the broadly contemporaneous *Barapasaurus tagorei* by Jain, Kutty, Roy-Chowdhury & Chatterjee (1975, 1979) from the Lower Jurassic Kota Formation of the Pranhita-Godavari valley, India, allows the comparison of *Vulcanodon* with a primitive sauropod *par excellence*.

The *Vulcanodon* material warrants re-evaluation because of the additional material now available, the recent misinterpretation of this species (Van Heerden 1978; Cruickshank 1979, 1980), the recognition of its phylogenetic importance, and because it is now clear that Raath's (1972) original description and illustrations are inadequate for the satisfactory interpretation of this species (*cf.* Jain *et al.* 1979). Moreover, it is apparent that the prosauropod origin of the Sauropoda (Romer 1956; Colbert 1964) is being disputed (Cruickshank 1979, 1981) because of unfamiliarity with the primitive representatives of this infraorder.

MS accepted February 1983

SYSTEMATIC PALAEONTOLOGY

The type material from the *Vulcanodon* site on Island 126/127, off Bumi Hills (fig. 1), is now housed in the National Museum of Zimbabwe, Bulawayo, and bears the catalogue number QG24. Much of the material was articulated or in close association and undoubtedly pertains to a single individual. However, bones collected subsequently by Professor G. Bond and the writer, indicate the presence of at least a second individual and hence this additional material is best regarded as topotype material; at least some of it could, however, belong to the holotype.

Class ARCHOSAURIA Watson, 1917

Subclass DINOSAURIA Owen, 1841

Order SAURISCHIA Seeley, 1888

Suborder SAUROPODOMORPHA von Huene, 1932

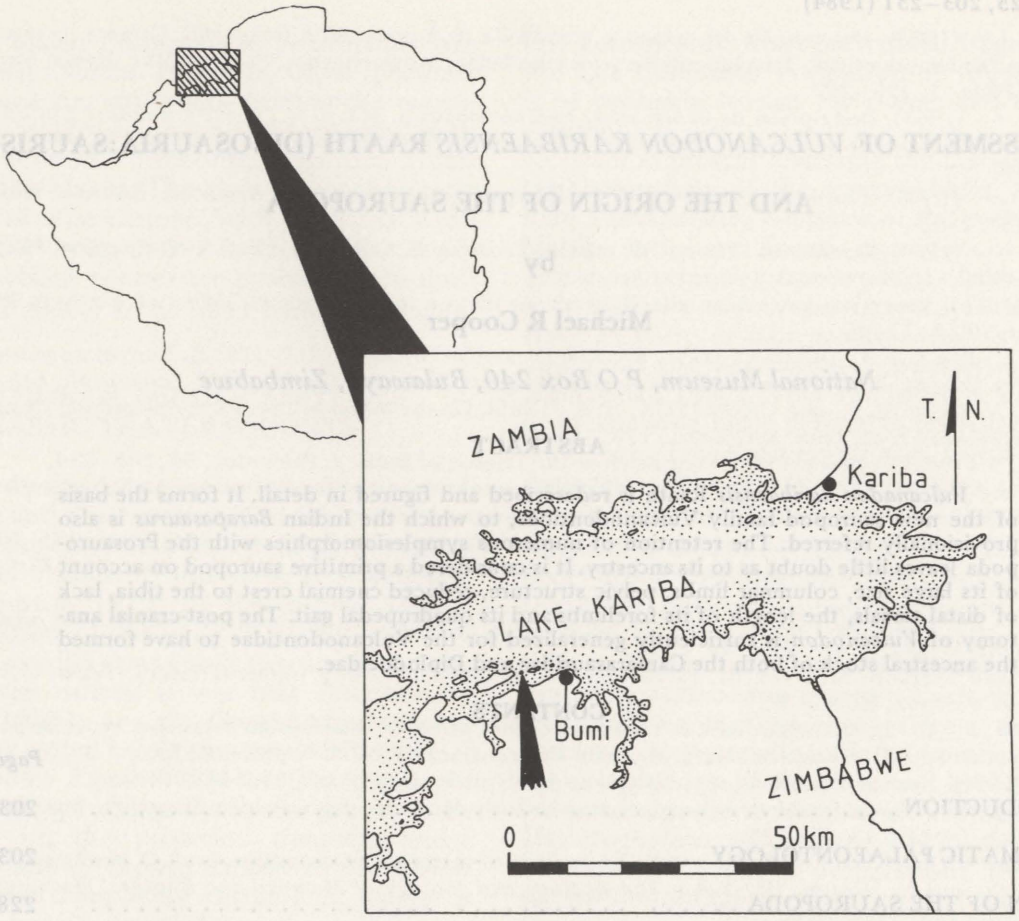


Fig. 1 Locality map, with the *Vulcanodon* site arrowed.

Discussion

Evidence presented here for the prosauropod ancestry of the Sauropoda establishes the Sauropodomorpha as a valid, monophyletic taxon. It may, therefore, be divided into two infraorders, the Prosauropoda and Sauropoda.

Infraorder SAUROPODA Marsh, 1878

Family VULCANODONTIDAE new family

Diagnosis

Primitive sauropods of early Jurassic age, retaining many characters which reflect ancestry. Skull, cervical and dorsal vertebrae unknown. Sacrum with 4 fused vertebrae. Pubis and ischium broadly articulated, the latter significantly longer than the former. Pubes form a prominent anteriorly facing, distal "apron", almost identical to the prosauropod condition, and lack a noticeable tubercle for the attachment of m.ambiens As in prosauropods, the ischia form the major parts of the lower acetabula. Ilium poorly known, but with very long pubic peduncle and very short ischiadic peduncle, suggesting comparison with *Barapasaurus*. Caudal vertebrae amphicoelous, lacking pleurocoels but with incipient cavitation and relict hyposphene/hypantrum articulations. Neural spines, simple, undivided. Humerus weakly flared proximally and distally, as in *Brachiosaurus* and about two-thirds the femoral length. Radius almost 60% of the humeral length and slightly longer than the tibia. Forelimb 78% of the length of the hindlimb. Femur straight, columnar, lacking sigmoid curvature. Tibia short, robust with strongly expanded proximal and distal ends and low cnemial crest; only 58% of the femoral length. Astragalus typically prosauropod, with a height: length ration of 1,18, and a prominent astragalar peg on the lateral surface. Calcaneum present but reduced. Metatarsals moderately short, subequal, with mtIII longest and 37% of the tibial length. Hallux ungual much enlarged, as in prosauropods. Distal nonungual pedal phalanges of digits III and IV stubby, wider than long.

Discussion

Since the writer would include provisionally also the Indian *Barapasaurus* within the Vulcanodontidae, it is worth noting the characters of this genus. No complete skeleton is yet known, but '... partial associations, and the wealth of individual bones available, provide detailed knowledge of the osteology of this dinosaur except for certain characters such as exact relative proportions of fore and hind limbs' (Jain *et al.* 1975: 223). It was diagnosed as follows:

'A large sauropod, but the limbs rather slender

in build. Teeth spoon-shaped, anterior and posterior keels bearing coarse denticles. Cervical and anterior dorsal centra opisthocoelous, all other centra approximately platycoelous. Hyposphene-hypantrum articulation present in middle and posterior dorsal vertebrae. Cervical centra probably a little less than twice the length of those of the middle dorsals. Centra not cavernous, but with oval or ovoidal depressions in the lateral or laterodorsal surface. Neural spine probably not bifurcate, those of the posterior dorsals fairly high. Sacrum of four co-ossified vertebrae, the centra amphiplatyan and 'waisted', the sacricostal yokes set close together, the neural spines fairly high. Scapula with tall narrow blade, its anterior border passing by a relatively shallow gradual curve into a moderately broad proximal expansion. Coracoid subcircular with coracoid foramen. Ilium with well-developed anterior process of the blade, rather deep medial wall of the acetabulum to which the sacricostal yoke does not contribute. Ischiadic peduncle of ilium short, pubic peduncle long and directed ventrally and slightly anteriorly. Ischium relatively slender and rod-like distally, slightly expanded distally, longer than pubis but exact proportions of these two bones not certainly established. Pubis usually rod-like distally, with well-developed terminal expansion which may contact its fellow of opposite side, a prominent symphyseal facet more proximally, a relatively large obturator foramen. Femora retaining a central cavity; lesser trochanter absent, fourth trochanter well-developed, ridge-like, may bear an acute and declined tip; the shaft straight and the head approximately at right angles. Tibia rather short, stout, cnemial crest fairly well developed, distal face with pronounced notch on lateroposterior side for ascending process of astragalus, as in other sauropods. Humerus almost equally expanded at proximal and distal ends, with prominent deltopectoral crest. Ulna stouter than radius, but slender in shaft, proximal end with typically sauropod shape in cross-section' (Jain *et al.* 1975: 225–226).

The Vulcanodontidae are here proposed as a family taxon because they are sufficiently generalized to be difficult to place as a subfamily either in the Camarasauridae or the Diplodocidae. The Diplodocidae, as diagnosed by Berman & McIntosh (1978), may be distinguished by their cleft mid-presacral spines, the fore and aft directed processes to the midcaudal chevrons, cervical centra which are 2,5 times the length of the dorsals, lack of a pubic "apron", tarsi reduced to a single element, the development of a process on the posteroventral edge of the lateral face of metatarsal I, and a radius shorter than the tibia. Moreover, the femur of diplodocids is more robust than in *Vulcanodon* and *Barapasaurus,* the astragali are very different, the ischia are relatively much shorter, the humeri are more robust, and the scapulae are more strongly expanded distally.

Camarasaurus, the only genus within the Camarasaurinae, differs from the Vulcanodontidae in possessing well-developed pleurocoels to the dorsal vertebrae, lacking an anteriorly directed pubic "apron", with very different astragalus and metatarsals, its femur has a proportionately much larger femoral head and the 4th trochanter is not declined and acuminate, its fibula lacks a proximal anteromedial crest, whilst its ischia, radii and ulnae are all rather different (cf. Ostrom & McIntosh 1966). Vulcanodontids differ from the subfamily Brachiosaurinae in having the forelimb only three-quarters of the length of the hindlimb, lacking the strong distal and proximal expansions of the scapula, lacking the well-developed pleurocoels seen in the dorsal vertebrae of *Brachiosaurus,* retaining a prosauropod-like astragalus and with the radius longer than the tibia.

The subfamily Euhelopodinae may be distinguished by having much longer cervical vertebrae, with rather different humeri and fibulae, whilst the femora are more robust, with less inturned heads and poorly developed 4th trochanters. In addition, the ischia of this group are only slightly longer than the pubes which do not form an apron distally, and the posterior dorsal vertebrae are opisthocoelous and with deep lateral pockets.

It is clear, therefore, that in many respects the family Vulcanodontidae is sufficiently generalized and primitive to be regarded as the rootstock for both the later camarasaurids and diplodocids.

Genus *Vulcanodon* Raath, 1972
Type species *Vulcanodon karibaensis* Raath, 1972; by monotypy.

Vulcanodon karibaensis Raath, 1972
Figs 2–9, 12-19, 21-36, 40

Vulcanodon karibaensis Raath, 1972: 4, pls 1-8, text-figs 3b, e, g, 4a–b, 5–8, 9b, e-f, 10b, 11b–f, 12–13. Cruickshank, 1975: 89.
Vulcanodon. . . . . , Jain *et al.,* 1975: 226; 1977: 205. Van Heerden, 1978: 187. Cruickshank, 1979: 177. Cooper, 1980a: 176, text-fig. 3.

Skull

Raath (1972) recorded parts of at least 9 carnivorous teeth found in the vicinity of the pubes of *Vulcanodon* and thought to pertain to this taxon. All the teeth are typically 'carnosaur', flattened labiolingually and more or less recurved, with the distal third of the anterior margin and the entire surface of the hind margin finely serrated. These dental characters are virtually identical to those of *Sinosaurus* (fig. 2) and the ubiquitous carnosaur teeth associated with melanorosaurid remains (Charig *et al.* 1965; Cooper 1980b). Doubt as to this association is, however, cast by the spatulate teeth associated with *Barapasaurus,* and the carnivorous teeth, may, therefore, have been lost during predation.

PECTORAL GIRDLE

Scapula

QG152, a topotype example (fig. 3), displays

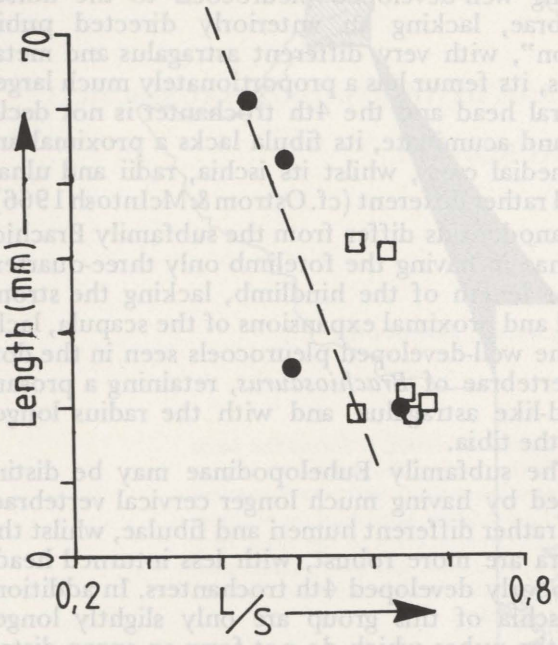


Fig. 2 Relative dimensions of teeth associated with *Vulcanodon*, compared with those of *Sinosaurus triassicus* Young (squares). L = labiolingual width, s = sagittal thickness at the base of the tooth. Data from Raath 1972.

the main features of the scapula of this species. It is a relatively long bone, more so than in *Barapasaurus*, showing only the slightest longitudinal curvature, and with a planoconvex cross-section at midlength. At this point it has a transverse thickness: width ratio of 1: 4,6. The blade expands both proximally and distally, and gives the impression of having been relatively more slender and prosauropod-like than that of *Barapasaurus*. There is a well-developed acromion but the glenoid region is not preserved.

Coracoid

Unknown.

FORELIMB

Humerus

Both humeri are preserved, but incomplete. The left humerus (fig. 4) is a strong robust bone which unfortunately lacks both distal and proximal ends. However, the distal end of the somewhat flattened right humerus is preserved (fig. 5), and allows a reasonable estimate for the humeral length of 700 mm, or 64% of the femoral length. In palmar view the humerus shows a gradual proximal and distal expansion which is strongly reminiscent of both *Plateosaurus* and *Brachiosaurus* with the deltopectoral crest extending *c.* 43% of the humeral length down the lateral side. Distally, the right humerus is crushed, but gives the impression of having relatively flat palmar and anconal surfaces, with little evidence for the palmar depression which, in prosauropods, marks the insertion of m. brachialis. In lateral view the twist of the shaft is particularly noticeable, whilst there is no evidence for a strong anteroposterior expansion of the distal end of the humerus, again recalling the prosauropod condition. The lateral surface of the deltopectoral crest is shallowly concave, with a deep, narrow longitudinal groove anteriorly, as in *Apatosaurus* (Ostrom and McIntosh 1966, pl. 48, fig. 2), and separated from the main portion of the proximal head by a prominent ridge.

Radius

The radius is long and thin (fig. 6), with an oval proximal articular surface (fig. 8) and subtrigonal cross-section at midshaft. Viewed medially, it is

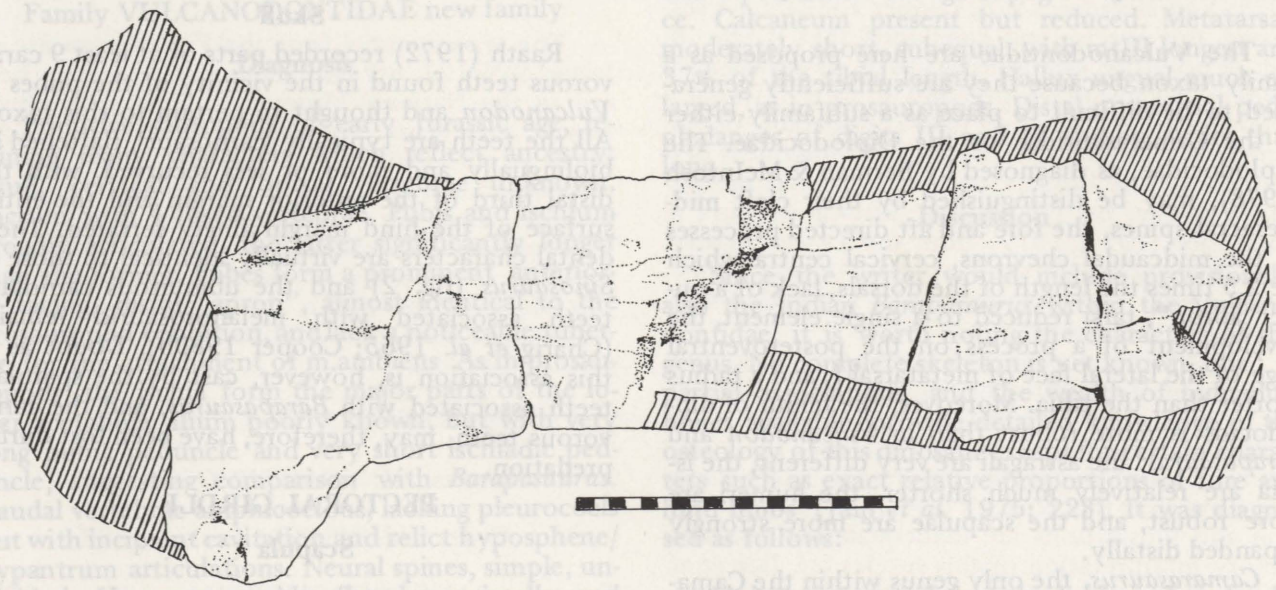


Fig. 3 *Vulcanodon karibaensis* Raath. Right scapula of QG152, a topotype example. The bar scale is 20cm.

LEGEND FOR ABBREVIATIONS

ac	—	distal anterior crest to fibula
ae	—	anterior excavation to proximal head of fibula
ap	—	astragalar peg
am	—	anteromedial crest to fibula
b	—	boss for muscle insertion
c	—	chevron facet
cn	—	cnemial crest
d	—	deltopectoral crest
dp	—	dorsal ascending process to astragalus
fib	—	fibula
ft	—	4th trochanter
h	—	femoral head
i	—	surface for articulation with ili ı
ic	—	inner condyle of femur
it	—	groove for origin of m. ischifemoralis
ivf	—	intervertebral fenestration
k	—	neural canal
l	—	lateral condyle of humerus
lc	—	lateral crest of tibia
lg	—	lateral groove to deltopectoral crest
lt	—	lesser trochanter
n	—	neural spine
oc	—	outer condyle to femur
p	—	surface for articulation with pubis
pf	—	posterior tongue or pfeiler
pm	—	posterior malleolus
po	—	posterior overhang of dorsal ascending process
poz	—	postzygapophysis
pz	—	prezygapophysis
r	—	distal roller
sr	—	sacral rib
sub	—	subacetabular buttress
su	—	suture
t	—	transverse process
tib	—	tibia
vg	—	ventral groove to caudal centrum

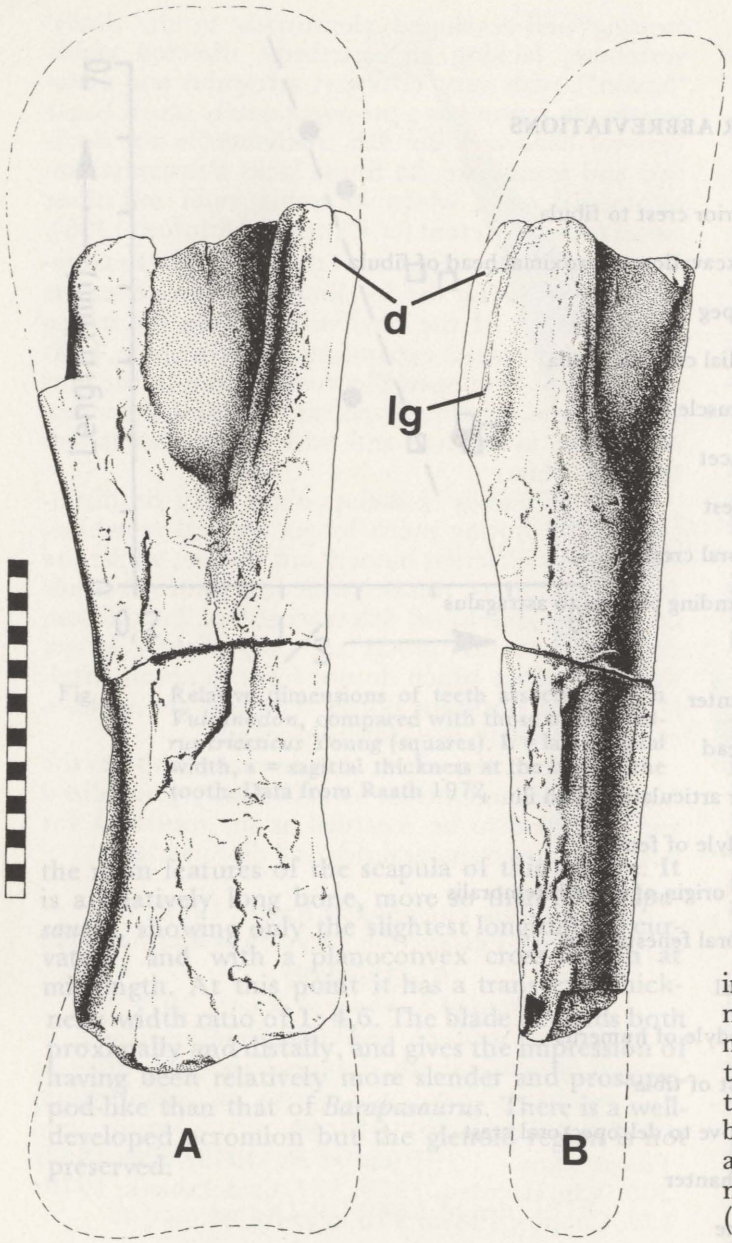


Fig. 4 *Vulcanodon karibaensis* Raath. Left humerus of the holotype, QG24, in (A) palmar and (B) lateral views. The bar scale is 20 cm.

bowed posteriorly, with a shallow groove extending from about midlength to the distal head, the latter strongly compressed transversely. There is a prominent excavation, immediately below the proximal head on the lateral surface, for receipt of the ulna. The anterior edge of the extreme distal end is turned outwards to form a weak, laterally directed crest. Viewed posteriorly the radius is straight.

Ulna

The ulna is a strong robust bone (fig. 7 A–B,D) with a crescentic proximal articular surface (fig. 8) and transversely compressed cross-section at midshaft. It is broadest proximally and tapers regularly to the poorly preserved distal head. Much of the posterior portion of the lateral surface, immediately below the proximal head, is deeply excavated, leaving a thick anterior rim to the bone. The significance of this hollow is unknown. On the anterior margin of the lateral surface, a short distance from the distal termination, is a distinct boss which relates to muscle insertion. An even more prominent boss is present on the medial surface of the ulna, at about midlength, and perhaps marks the origin of m. flexor digitorum profundus. Viewed posteriorly (fig. 9), the ulna shows a significant distal expansion, as well as curving away slightly from the radius. In posterior view its most noteworthy feature is a sharp rim formed by the proximal third of the bone. As preserved, the ulna is only slightly longer than the radius (Table 1) but its distal extremity seems to have been eroded away.



Fig. 5 *Vulcanodon karibaensis* Raath. Distal end of the right humerus of QG 24. The bar scale is 20 cm.

Carpals

Unknown.

Metacarpals

Although Raath (1972: 24) records the presence of 3 metacarpals in his original description, I have been unable to locate these bones and his original description is, therefore, repeated here:

'Three metapodials are preserved which are presumed to be metacarpals III, IV, and V. IV and V were articulated, and V also bore a phalanx in articulation.

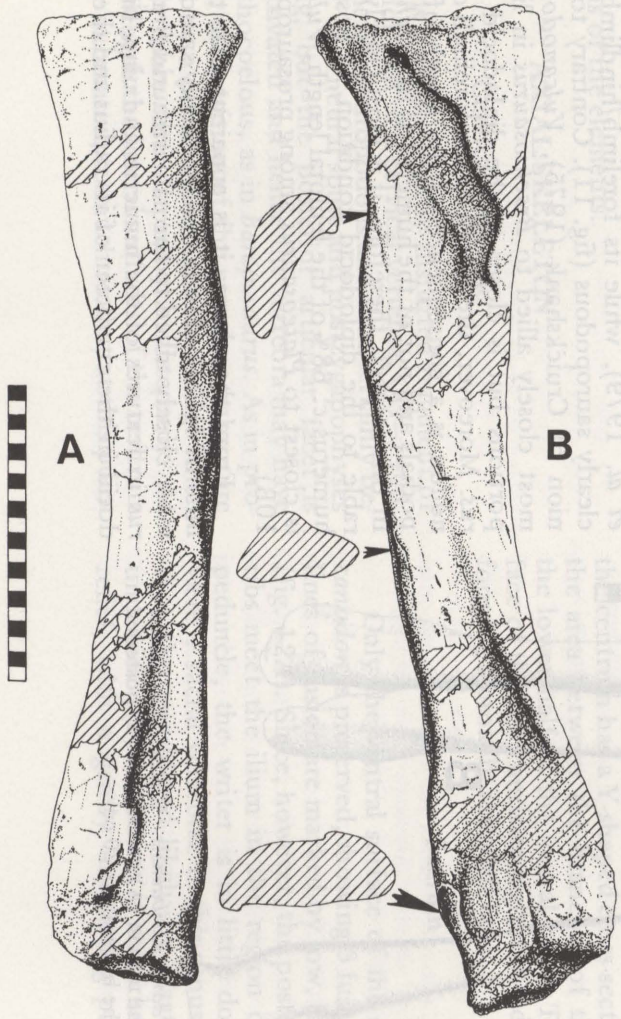
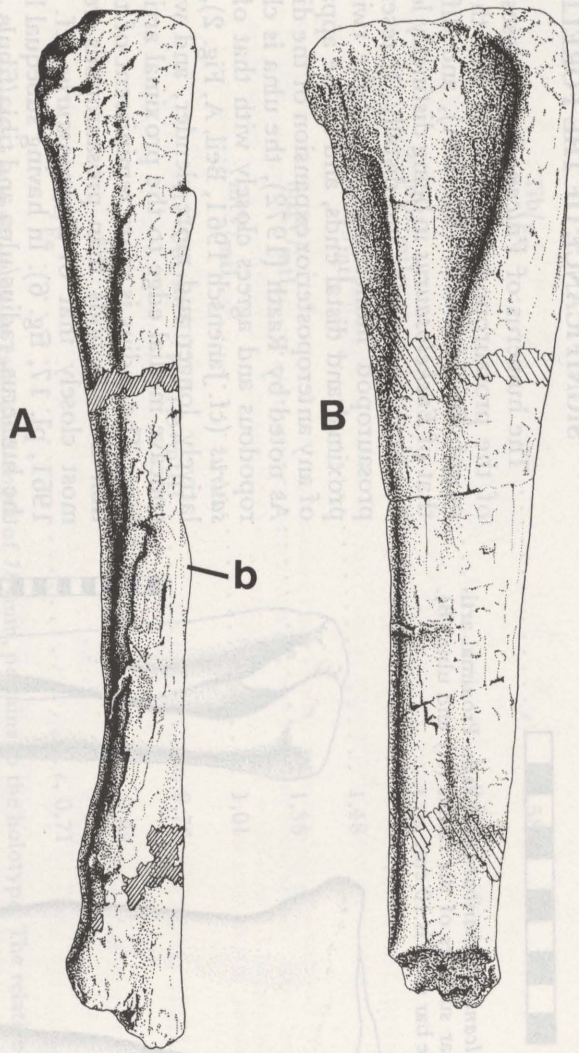


Fig. 6 *Vulcanodon karibaensis* Raath. The right radius of QG24 in (A) lateral and (B) medial views, with various cross-sections. The bar scale is 20 cm.



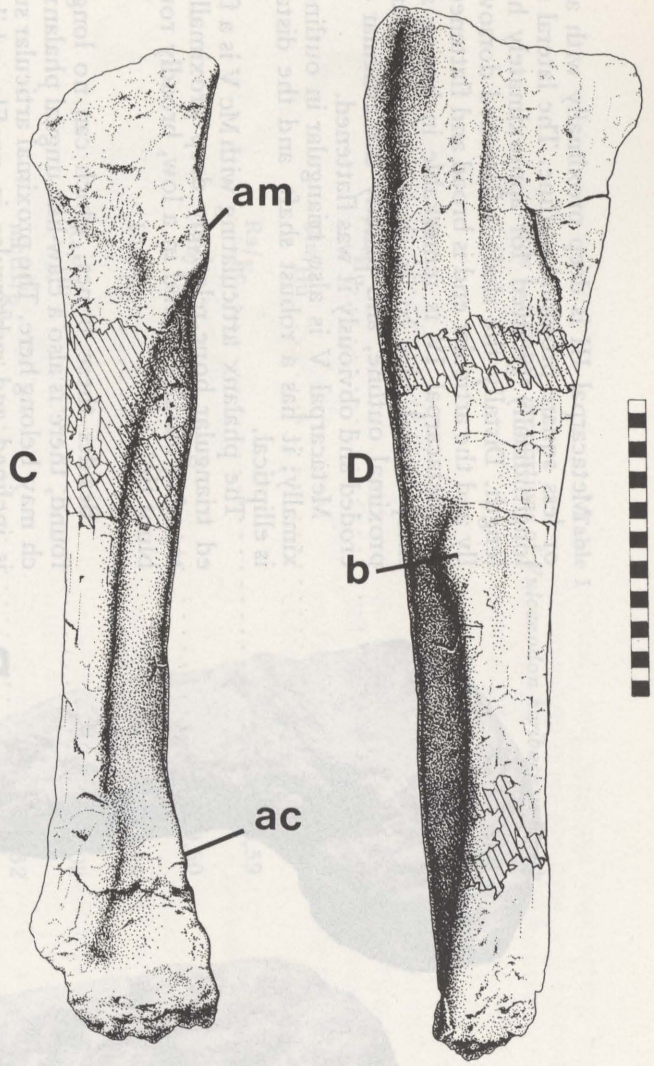


Fig. 7 *Vulcanodon karibaensis* Raath. A–B, D. Right ulna in anterior, lateral and medial views. C. Left fibula in medial view.

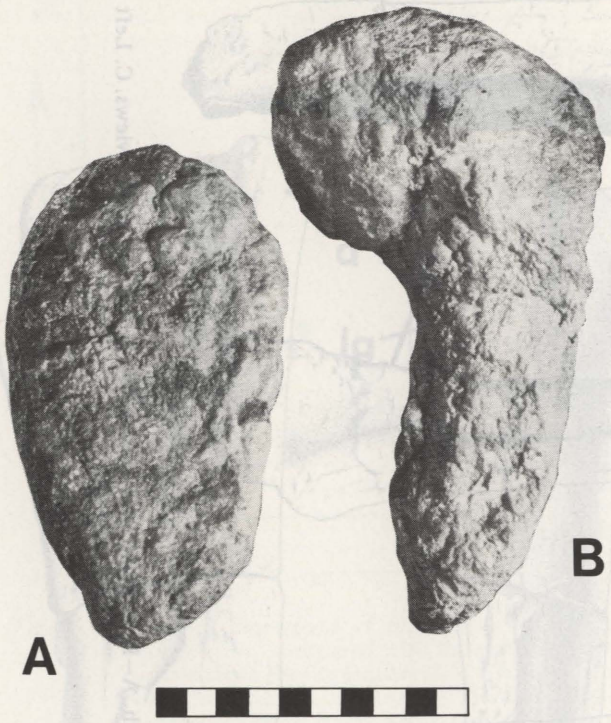


Fig. 8 *Vulcanodon karibaensis* Raath. Proximal articular surfaces of the radius (A) and ulna (B). The bar scale is 10 cm.

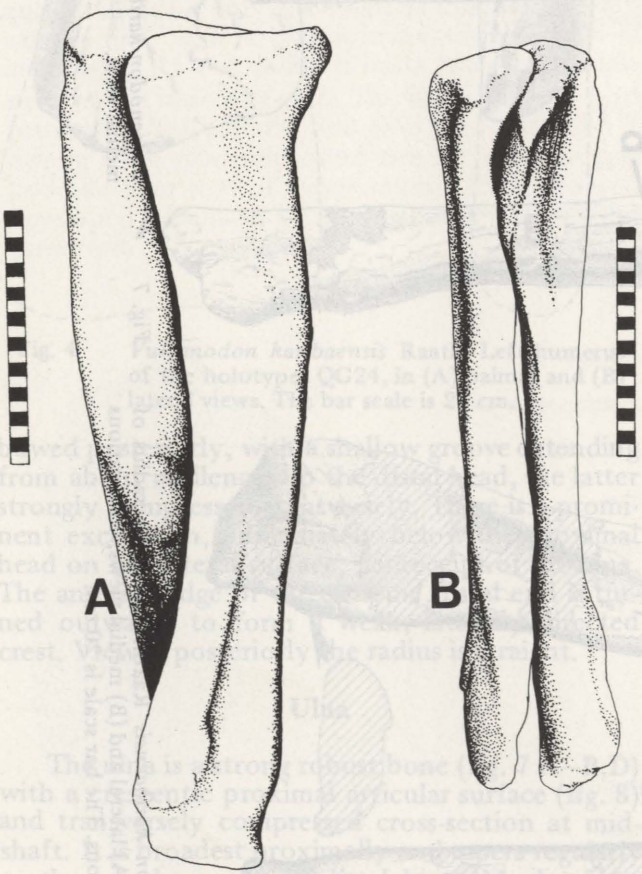


Fig. 9 *Vulcanodon karibaensis* Raath. Conjoined radius and ulna in (A) medial and (B) posterior views. The bar scale is 20 cm.

Metacarpal III is deep proximally with a more or less square proximal outline. The lateral side is longitudinally grooved for approximately half its length. Distally the shaft is flattened dorsoventrally and the articular end is broad and flattened.

Metacarpal IV is remarkable in having a very sharp lateral edge to its shaft. It has a triangular proximal outline, and distally the articular end is eroded and obviously it was flattened.

Metacarpal V is also triangular in outline proximally; it has a robust shaft and the distal end is elliptical.

The phalanx articulating with Mc V is a flattened triangular bone, relatively deep proximally but tapering distally to end in a low, broadly rounded blunt tip'.

Besides these bones, which can no longer be found, there is also a claw-like ungual phalanx which may belong here. The proximal articular surface is inclined and subcircular in profile, whilst the bone is only weakly curved and almost certainly terminated distally in a bluntly rounded tip.

SIGNIFICANCE OF THE FORELIMB

The humerus of *Vulcanodon* is closest to those of the prosauropod *Plateosaurus* and the camarasaurid *Brachiosaurus* (fig. 10A), and differs from that of *Euskelosaurus* in being distinctly less expanded both proximally and distally. It resembles the prosauropod humerus in the slight twist of the proximal and distal ends, and in the apparent lack of any anteroposterior expansion of the distal head. As noted by Raath (1972), the ulna is clearly sauropodous and agrees closely with that of *Brachiosaurus* (cf. Janensch 1961, Beil. A, Fig. 2), but is relatively longer and more slender, and with a less concave medial edge to the proximal articular surface. The radius is more reminiscent of the condition in sauropods than prosauropods, resembling most closely that of *Dicraeosaurus* (cf. Janensch 1961, pl. 17, fig. 6). In having subequal lengths of the humerus, radius/ulna and tibia/fibula, *Vulcanodon* is most closely allied to *Barapasaurus* (Yadagiri *et al.* 1979), while its forelimb/hindlimb ratio is clearly sauropodous (fig. 11). Contrary to the opinion of Cruickshank (1975), *Vulcanodon* is not most closely allied to *Brachiosaurus* in limb proportions but is closer to the diplodocid *Barosaurus*. Moreover, the length of the forelimb of *Vulcanodon* is a consequence of the length of the epipodials and not of the humerus as in *Brachiosaurus*. In this respect, therefore, it is most closely comparable to the diplodocid condition. In possessing a humerus *c.* 68% of the femoral length, *Vulcanodon* is closest to *Plateosaurus* among prosauropods (fig. 10B).

From the above, it is apparent that the forelimb of *Vulcanodon* is fundamentally sauropodous; most closely allied to the camarasaurid *Brachiosaurus* in features of the humerus and ulna, but diplodocid in the character of its radius and the relative

Table 1

Table 1. Relative proportions of *Vulcanodon karibaensis* Raath.

$Hu/_{Fe}$	*c.* 0,64
$Ra/_{Hu}$	*c.* 0,92
$Uln/_{Hu}$	*c.* 0,94
$Ra/_{Fe}$	0,59
$Uln/_{Fe}$	0,60
$Uln/_{Tib}$	1,04
$Ra/_{Tib}$	1,02
$mcIII/_{Ra}$	0,32
$Pu/_{Fe}$	0,52
$Isch/_{Pu}$	1,37
$Tib/_{Fe}$	0,58
$mtIII/_{Tib}$	0,32
$mtII/_{mtI}$	1,28
$mtIII/_{mtI}$	1,48
$mtIV/_{mtI}$	1,35
$mtV/_{mtI}$	1,01
$Hu+Uln+mcIII/_{Fe+Tib+mtIII}$	*c.* 0,78
$Sc*/_{Hu}$	*c.* 0,98
$Sc/_{Fe}$	*c.* 0,71

*Assuming the topotype scapula, with an estimated length of 784mm, pertains to the holotype. The relative proportions suggest this inference is reasonable.

proportions of the elements.

AXIAL SKELETON

Cervical vertebrae

There is a single, slightly distorted fragment of the posterior half of a cervical vertebra, QG–1406, which is clearly sauropodous and thus certainly belongs here. The neural spine and postzygapophyses are lacking, but the posterior articular facet is deeply excavated and hence the vertebra may have been opisthocoelous, as in *Barapasaurus*. As in prosauropods, the position of the neurocentral suture is marked by a pronounced horizontal ridge which presumably bore the diapophysis anteriorly. At about midlength the lateral surfaces of the centrum are deeply excavated, so much so that at this point the centrum has a Y-shaped cross-section (fig. 15C), the area between the branches of the Y filled by the lower half of the neural canal. The ventral surface of the centrum is strongly waisted at mid-length, forming a broadly rounded keel.

Sacrum

Only the ventral surface of the sacrum of *Vulcanodon* is preserved, showing 3 fused centra whose lines of fusion are marked by low, transverse ridges (fig. 12A). Since, however, the posterior two sacral ribs meet the ilium in the region of the ischiadic peduncle, the writer is in little doubt that there were 4 sacral vertebrae in this genus, an interpretation also considered likely by Raath (1972). The underside of the sacrum is remarkable for its low relief, with a gently undulating profile in lateral

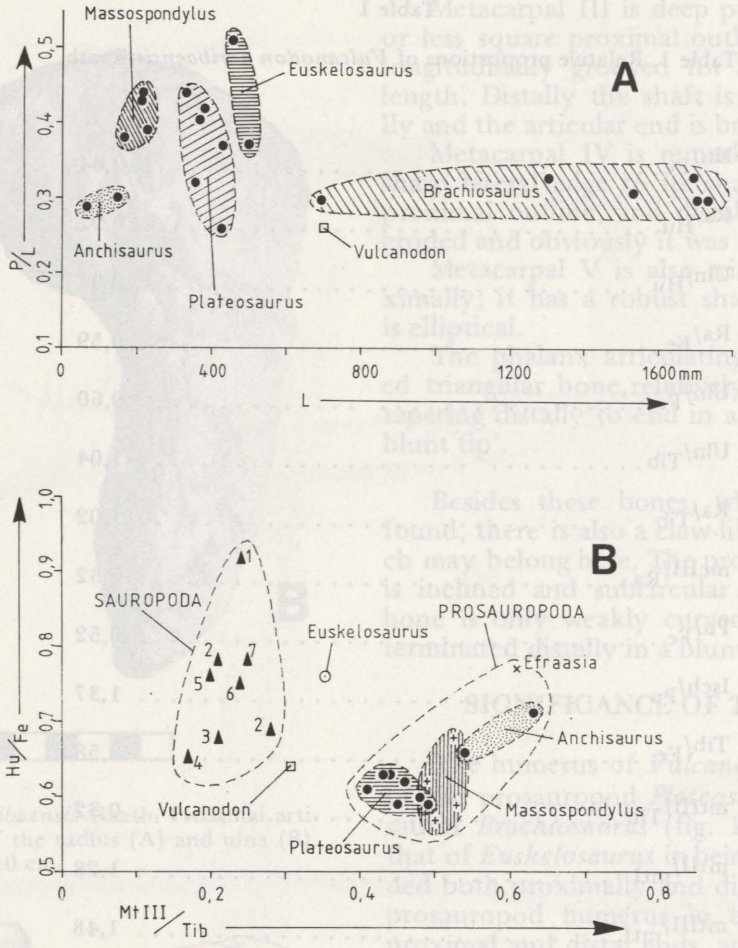


Fig. 10 (A) Comparison of humeri of various sauropodomorphs. L = length of humerus, P = transverse width of proximal head. (B) Relative proportions of various sauropodomorphs where Hu = humerus, Fe = femur, mt III = metatarsal III and Tib = tibia. 1 = *Astrodon*, 2 = *Cetiosaurus*, 3 = *Diplodocus*, 4 = *Laplatasaurus*, 5 = *Camarasaurus*, 6 = *Antarctosaurus*.

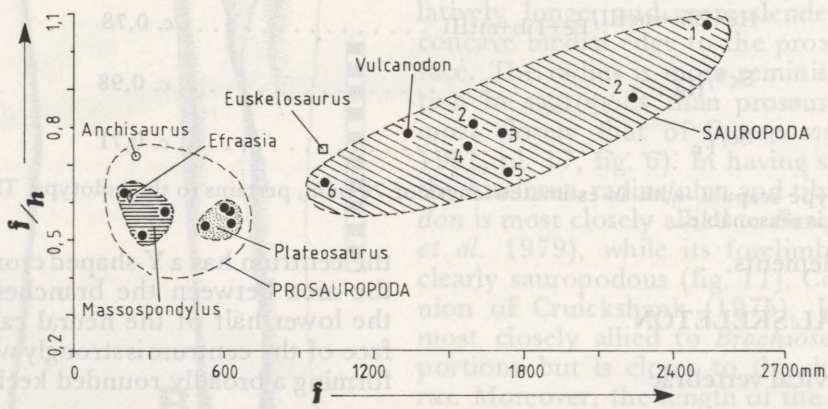


Fig. 11 Limb proportions for various sauropodomorphs, where f = length of forelimb (humerus + radius or h = length of hindlimb (tibia + femur), 1 = *Brachiosaurus*, 2 = *Cetiosaurus*, 3 = *Barosaurus*, 4 = *Tornieria*, 5 = *Diplodocus*, 6 = *Dicraeosaurus*.

view (Raath 1972). Only a short portion of the second centrum is preserved (the first is missing) but shows, as with the other sacrals, a strongly waisted outline in ventral view. The sacral ribs of the third and fourth vertebrae coalesce distally, as is typical of sauropods, to leave oblique, elliptical, intervertebral fenestrae. An isolated sacral rib, representing topotype material (fig. 12B), is remarkably similar to the second sacral rib of *Camarasaurus grandis* (Marsh) (Ostrom & McIntosh 1966, pl. 31, fig. 1) showing the same change in slope of the posterior edge (marked with an arrow in fig. 12B) as the centrum is approached. Viewed posteriorly the last sacral (fig. 13C) shows the centrum to have been wider than high, with a strongly flared, apparently platycoelous, posterior articular surface.

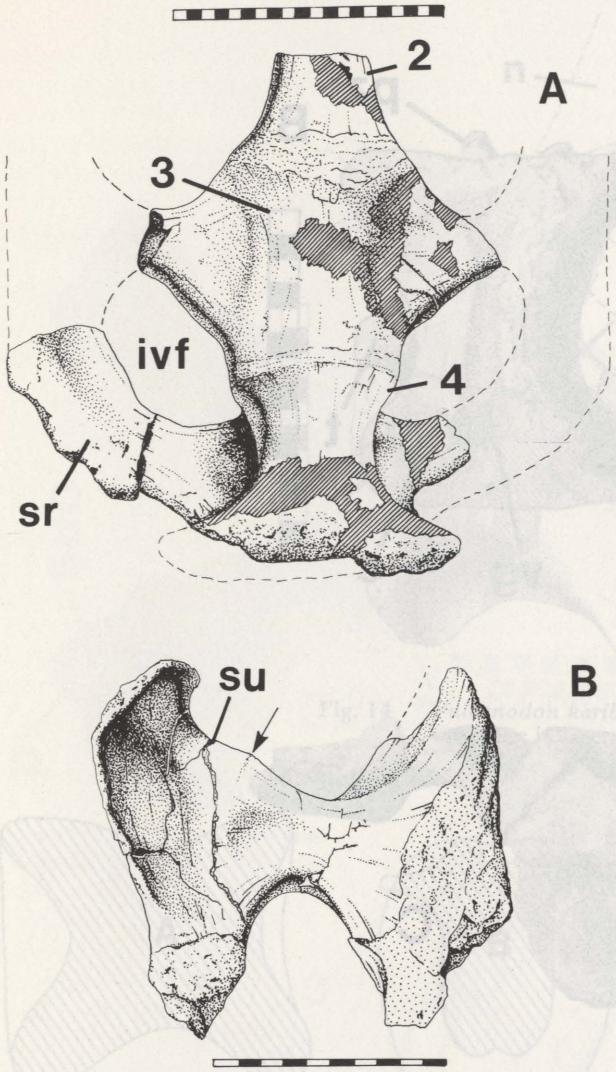


Fig. 12 *Vulcanodon karibaensis* Raath. A. Ventral view of fused sacram, where 2–4 = sacral vertebrae numbered from the anterior. The bar scale is 20 cm. B. A topotype example of a second rib in ventral view. The distinct geniculation in the anterior border is arrowed. The bar scale is 10 cm.

Caudal vertebrae

Most of the first 12 caudal vertebrae were articulated, although the majority lack transverse processes and all lack neural spines. The centra are about as high as long, amphicoelous, and strongly grooved ventrally (fig. 13B) for the guidance of the caudal blood vessels. Although pleurocoels are lacking, the caudal centra are excavated laterally (fig. 14–15), just below the transverse processes, giving them a strongly waisted appearance in ventral view (fig. 13B). This incipient cavitation may represent the forerunner of the lateral "pockets" seen in more advanced camarasaurids. The neural arch of the 11th caudal vertebra is high (fig. 14), laterally compressed, and with concave lateral surfaces. The neural canal is oval in outline, higher than wide, and cuts deeply into the dorsal surface of the centrum at midlength. The transverse processes of this vertebra are short, backwardly directed, and without supporting buttresses. The prezygapophyses are long and extend well beyond the anterior face of the centrum, with distal articular facets inclined at about 30° to the vertical. The postzygapophyses seem to represent, as in the prosauropod *Massospondylus* (Cooper 1981), merely the hyposphene articulations and do not protrude beyond the posterior margin of the centrum. The neural spine is not preserved but to judge from its broken base, was rather narrow anteroposteriorly.

Chevrons

The chevrons are virtually identical to the prosauropod condition, but very much larger. The transversely strongly compressed blade forms a Y proximally, joined by the dorsally concave intercentrum, leaving a prominent foramen for the caudal blood vessels. The chevrons are truncate distally, and seem to commence from the third caudal vertebra (Raath 1972).

Cervical ribs

Unknown.

Trunk ribs

Only short fragments of trunk ribs have been recovered, but none preserve the proximal head and hence are largely indeterminate.

Gastralia

Unknown.

FEATURES OF THE AXIAL SKELETON

What is known of the sacrum agrees closely with the condition in *Barapasaurus*, and *Vulcanodon* undoubtedly possessed 4 sacral vertebrae. As such, the sacral length was of the order of 550mm with a width of *c.* 400 mm, giving a length/width ratio of 1,39. The presence of 4 true sacrals is an advance over the prosauropod condition, and thus a sauropod character, while Raath (1972) has already remarked on the sauropod aspect of the ventral surface of the *Vulcanodon* sacrum. The apparent absence of sacricostal yokes suggests that *Barapasaurus* is somewhat more advanced than *Vulcanodon*. That the postzygapophyses of the caudal vertebrae seem to represent merely the hyposphene articulations tends to suggest that hyposphene/hypantrum articulations were present in the dorsal vertebrae, a condition found in *Barapasaurus* and all prosauropods.

The caudal vertebrae of *Vulcanodon* are also interesting in that in length, relative to the femoral length, they are intermediate between the condition in the prosauropod *Plateosaurus* and the sauropod *Rhoetosaurus*. This reflects a shortening of the caudal vertebrae relative to the femur.

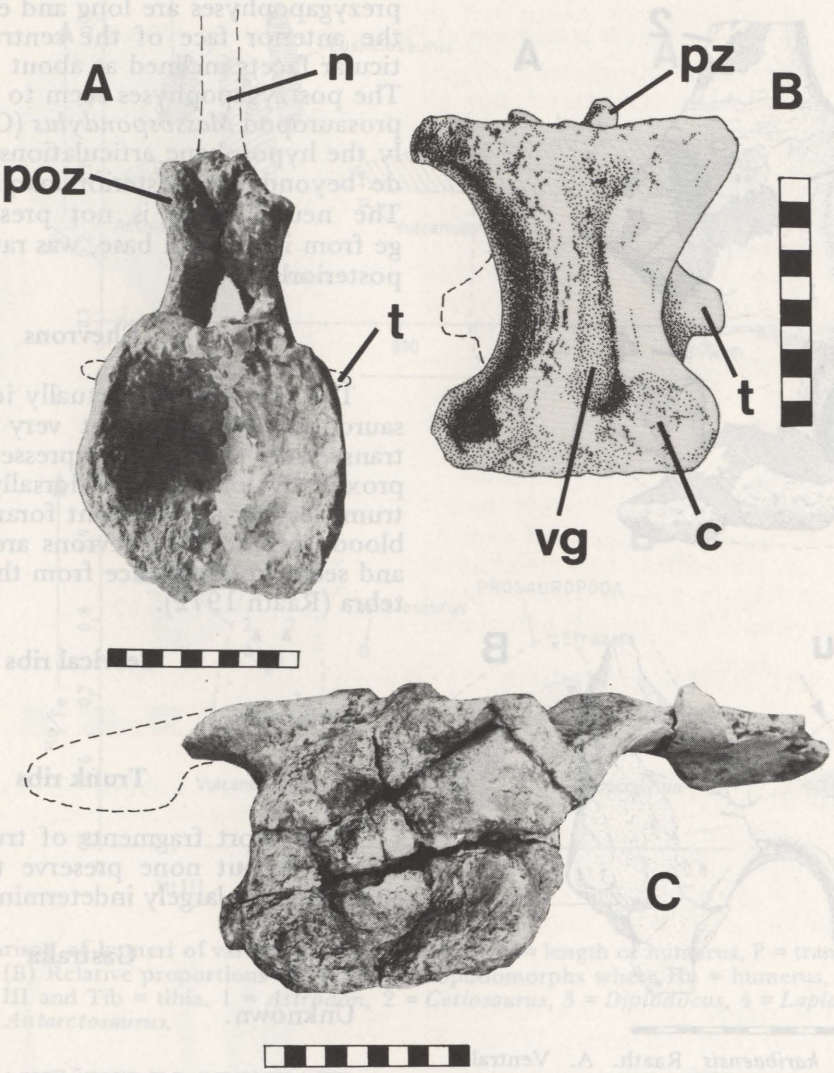


Fig. 13 *Vulcanodon karibaensis* Raath. A-B. Posterior and ventral views of the 11th caudal centrum. C. Posterior view of the 4th sacral vertebra. The bar scales are all 10cm.

In characters of its axial skeleton, therefore, *Vulcanodon* is intermediate between prosauropods and sauropods. Amongst the latter group, the incipient lateral cavitation of the caudal centra and the form of the second sacral rib most closely allies *Vulcanodon* to the camarasaurids.

PELVIC GIRDLE

Ilium

Only the base of the right ilium is preserved, showing a prominent curved pubic peduncle (fig. 16) and a very short, reduced ischiadic peduncle. The acetabular surface of the pubic peduncle is smoothly concave and the distal articular surface is subtrigonal in outline. There is a distinct rim to the lateral acetabular surface of the ischiadic peduncle, reminiscent of the condition in *Apatosaurus* (cf. Ostrom & McIntosh 1966, pl. 64). The ischiadic peduncle has a subtrigonal articular surface.

The very short and reduced ischiadic peduncle and long pubic peduncle are sauropod characters and, in view of what is now known of *Barapasaurus*, the writer is inclined to believe the ilium of *Vulcanodon* was sauropod-like. Certainly there is nothing to suggest that it was not very similar to the same bone in *Barapasaurus*.

Pubis

The pubes of *Vulcanodon* (fig. 17) are virtually identical to those of prosauropods, twisted proximally to form horizontal puboischiadic plates, each penetrated by a prominent obturator foramen, and forming a pronounced "apron" distally. The distal plates are thickest laterally and both clearly broken along their medial edges. As such, the sagittal fenestration of the pubic apron indicated by Raath (1972, fig. 5) is speculative. The distal ends of the pubes show a prominent expansion, most of which occurs posteroventrally. As in prosauropods, there

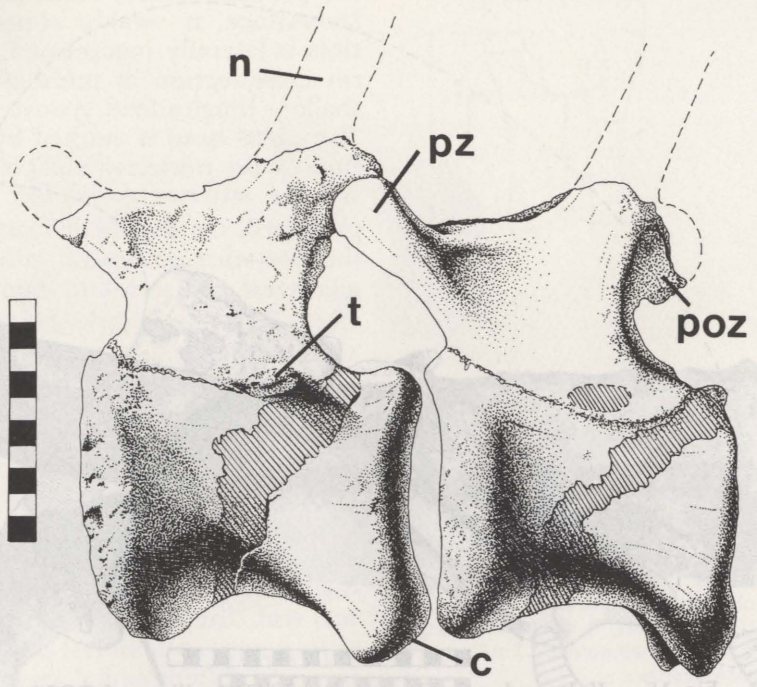


Fig. 14 *Vulcanodon karibaensis* Raath. 11th and 12th caudal vertebrae in lateral view. The bar scale is 10 cm.

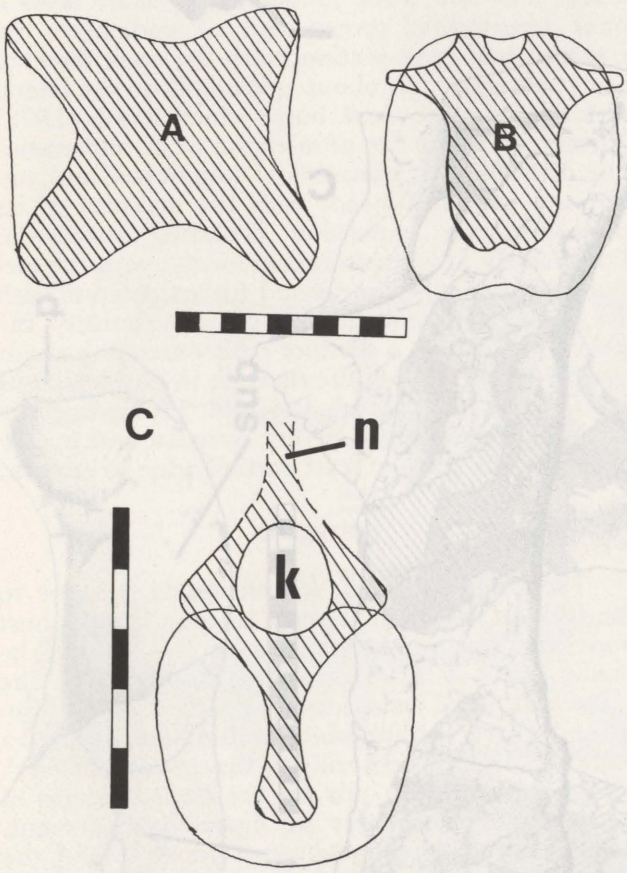


Fig. 15 *Vulcanodon karibaensis* Raath. (A) Sagittal and (B) transverse sections through the 11th caudal centrum (hatched), with centrum outline. The bar scale is 10 cm. (C) Transverse section through cervical vertebrae, with centrum outline. Corrected for slight distortion. The bar scale is 5 cm.

is no obvious tubercle for the attachment of m. ambiens and the pubes seem to have played subordinate parts in the formation of the acetabula. The pubis is 52% of the femoral length.

Ischium

The long, slender ischia (fig. 18–19) are reminiscent of the prosauropod condition, but unique in being considerably longer than the pubes (Table 1). Distally they are very irregular and perhaps pathologically malformed. While the distal rods are in contact for much of their lengths, they are only definitely fused for the distal 20%. The surface for articulation with the ischiadic peduncle of the ilium is suboval in outline, while the acetabular portion shows a well-developed subacetabular buttress. The proximal half of the ischia are strongly grooved dorsally for the insertion of m. ischiofemoralis, as in prosauropods.

FEATURES OF THE PELVIC GIRDLE

The pubes of *Vulcanodon* are typically prosauropodous and, as can be seen from Figure 20, are closest to the condition in *Plateosaurus*. This tends to suggest that *Barapasaurus* is slightly more advanced and hence, perhaps, somewhat younger. The ischia are also virtually identical to the prosauropod condition but are unique in being considerably longer than the pubes. In this respect they are closest to the camarasaurid *Haplocanthosaurus* in which the ischia are 114% of the pubic length (Raath 1972). The ilium of *Vulcanodon* is poorly known but what evidence there is favours a sauropod-type structure, perhaps very similar to that of *Barapasaurus*.

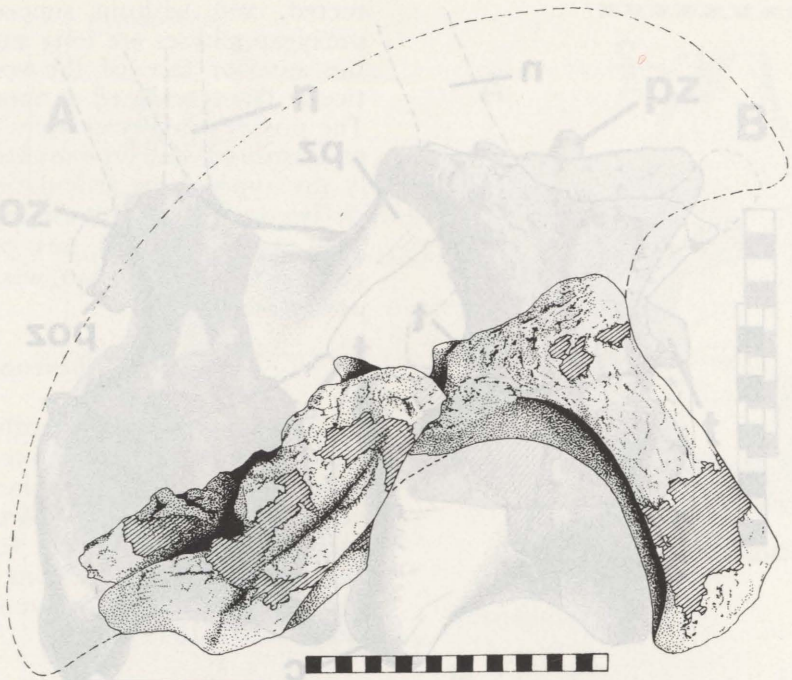


Fig. 16 *Vulcanodon karibaensis* Raath. Right ilium of QG24 in lateral view, reconstructed to the configuration of *Barapasaurus*. The bar scale is 20 cm.

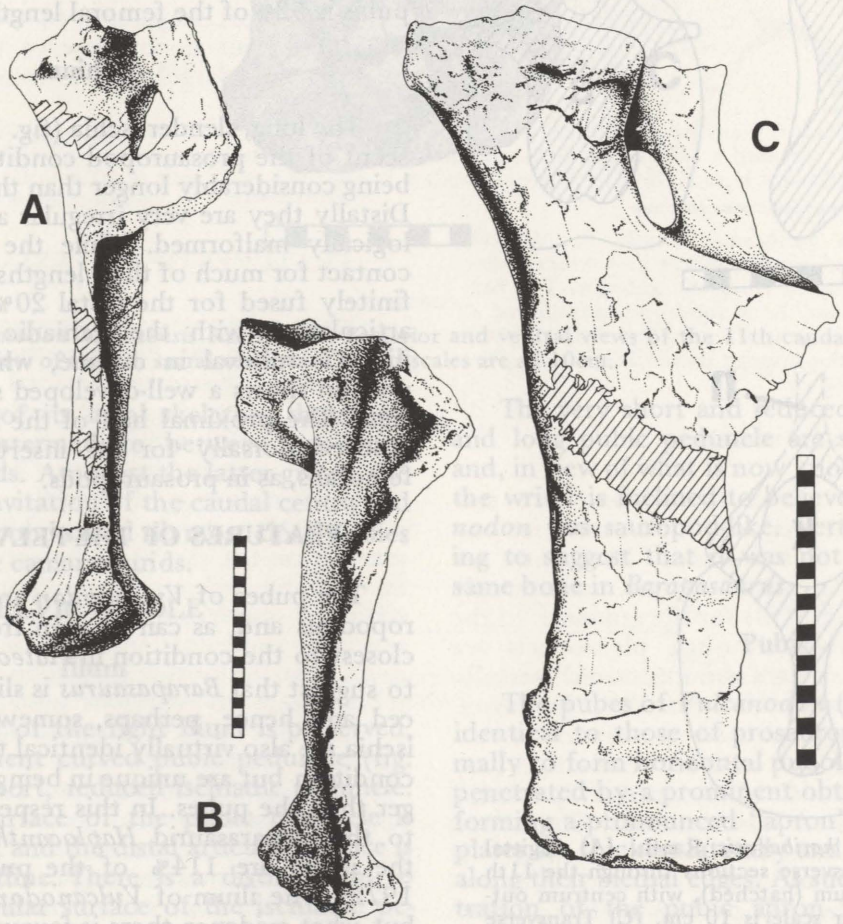


Fig. 17 *Vulcanodon karibaensis* Raath. Right pubis of QG24 in (A) medial, (B) lateral, and (C) anterior views. The bar scales are 20cm.

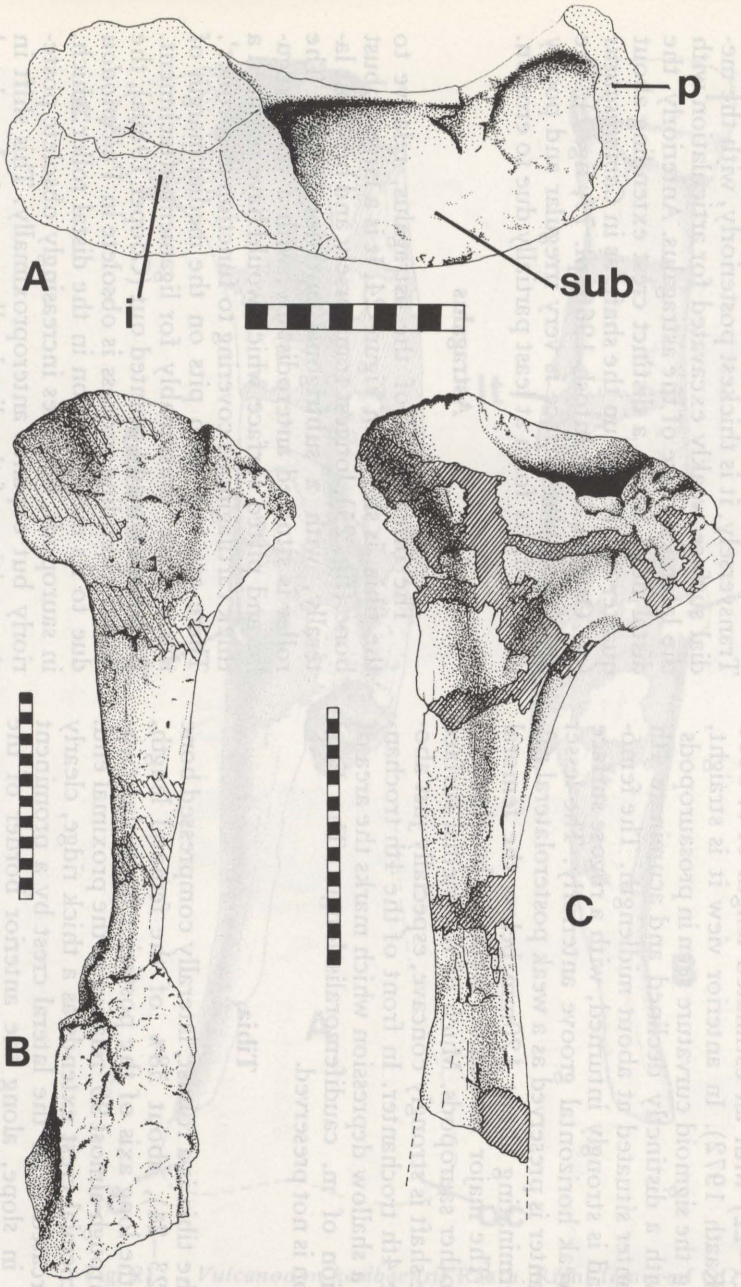


Fig. 18 *Vulcanodon karibaensis* Raath. The right ischium of QG24. (A) Proximal end. (B) Lateral view. (C) Medial view. The bar scales are in centimetres.
metres.

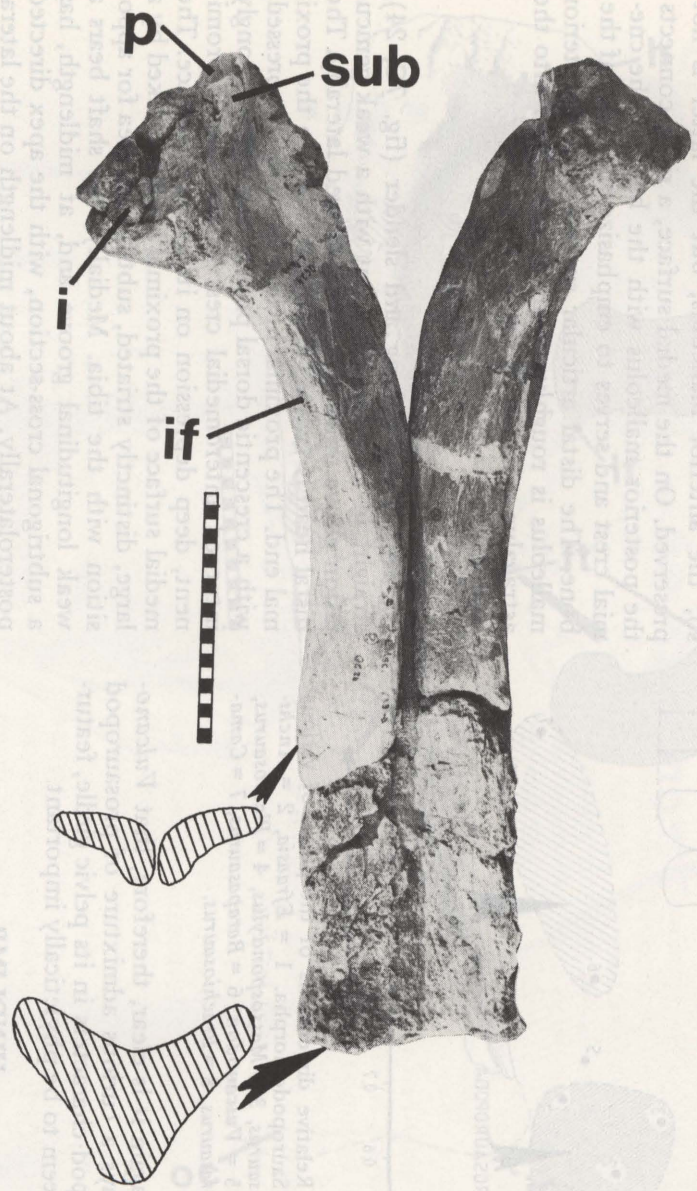


Fig. 19 *Vulcanodon karibaensis* Raath. Posterodorsal view of the conjoined ischia, with various cross-sections. The bar scale is 20 cm.

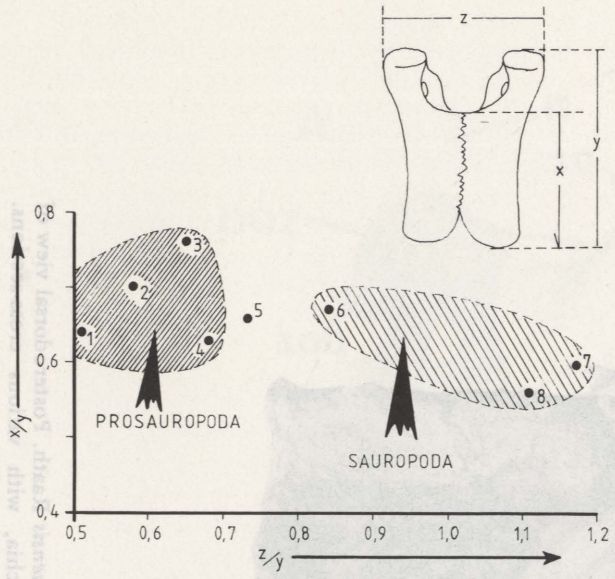


Fig. 20 Relative dimensions of the pubes of various Sauropodomorpha. 1 = *Efraasia*, 2 = *Anchisaurus*, 3 = *Massospondylus*, 4 = *Plateosaurus*, 5 = *Vulcanodon*, 6 = *Barapasaurus*, 7 = *Camarasaurus*, 8 = *Brachiosaurus*.

Once again it is clear, therefore, that *Vulcanodon* displays a curious admixture of prosauropod and sauropod characters in its pelvic girdle, features which seem to be phyletically important.

HINDLIMB

Femur

The femur is a relatively narrow, columnar bone (fig. 21–22) with an estimated length of *c.* 1100 mm (Raath 1972). In anterior view it is straight, lacking the sigmoid curvature seen in prosauropods and with a distinctly declined and acuminate 4th trochanter situated at about midlength. The femoral head is strongly inturned, with a rugose surface and weak horizontal groove anteriorly. The lesser trochanter is preserved as a weak posterolateral ridge, terminating about 120mm below the femoral head. The major trochanter seems to be obsolete, as in other sauropods. Much of the medial surface of the shaft is strongly concave, especially just above the 4th trochanter. In front of the 4th trochanter is a shallow depression which marks the area of insertion of m. caudifemoralis longus. The distal portion is not preserved.

Tibia

The tibia is a robust, laterally compressed bone (fig. 23–24), about 58% of the femoral length, with the long axis of the posterior malleolus twisted through almost 90° relative to the proximal end. The cnemial crest extends as a thick ridge, clearly demarcated from the lateral crest by a prominent break in slope, along the anterior border of the proximal head, but fails to reach the level of the proximal articular surface. The medial surface of the proximal head, immediately below the articular surface, is weakly concave. The shaft of the tibia is laterally compressed, with a weakly reniform cross-section at midshaft due to a prominent shallow longitudinal groove on its lateral surface. The distal head is marked by the transverse expansion of the posterior malleolus and, presumably also, the anterior malleolus, but the latter is not preserved. On the medial surface, a ridge connects the posterior malleolus with the base of the cnemial crest and serves to emphasize the twist of the bone. The distal articular surface of the posterior malleolus is roughly rounded, and inserts into the astragalus as shown in Figure 23D.

Fibula

The fibula is long and slender (fig. 7C, 24), straight in anterior view, but with a weak geniculation above midlength when viewed laterally. The distal head is twisted slightly relative to the proximal end. The proximal head is laterally compressed, with a crescentic dorsal profile, due to the strongly inturned anteromedial crest which bears a prominent, deep depression on its anterior surface. The medial surface of the proximal head is marked by a large, distinctly striated, subtrigonal area for apposition with the tibia. Medially, the shaft bears a weak longitudinal groove and, at midlength, has a subtrigonal cross-section, with the apex directed posterolaterally. At about midlength on the lateral surface is a large weak bulge which Raath (1972) interpreted as the site of insertion of m. anconaeus. The distal head is transversely compressed and, unlike the proximal head, with the majority of its anteroposterior expansion occurring anteriorly. Transversely, it is thickest posteriorly, with the medial surface weakly excavated for articulation with the lateral surface of the astragalus. Anteriorly, the distal head forms a distinct crest extending about quarter of the way up the shaft, as in *Camarasaurus* (cf. Ostrom & McIntosh 1966, pl. 77, fig. 1). The distal articular surface is very irregular and poorly preserved, its form at least partially due to erosion.

Astragalus

The orientation of the astragalus, relative to the tibia, is shown in Figure 24. It is a large, robust bone (fig. 25), longest transversely and broadest laterally, with a subtrigonal anterior profile. The roller is situated anterodistally, with a very irregular and pitted surface which would have required a thick cartilaginous covering to function as a 'roller'. There are two deep pits on the medial margin of this surface, presumably for ligament attachment. As I have already pointed out (Cooper 1980a), the dorsal ascending process is obsolete in *Vulcanodon* due to its incorporation in the distal roller which, in sauropods, becomes increasingly obsolete posteriorly but expands anteroproximally. This shift in the position of the distal roller seems to be related to the change from a digitigrade to a semi-planti-

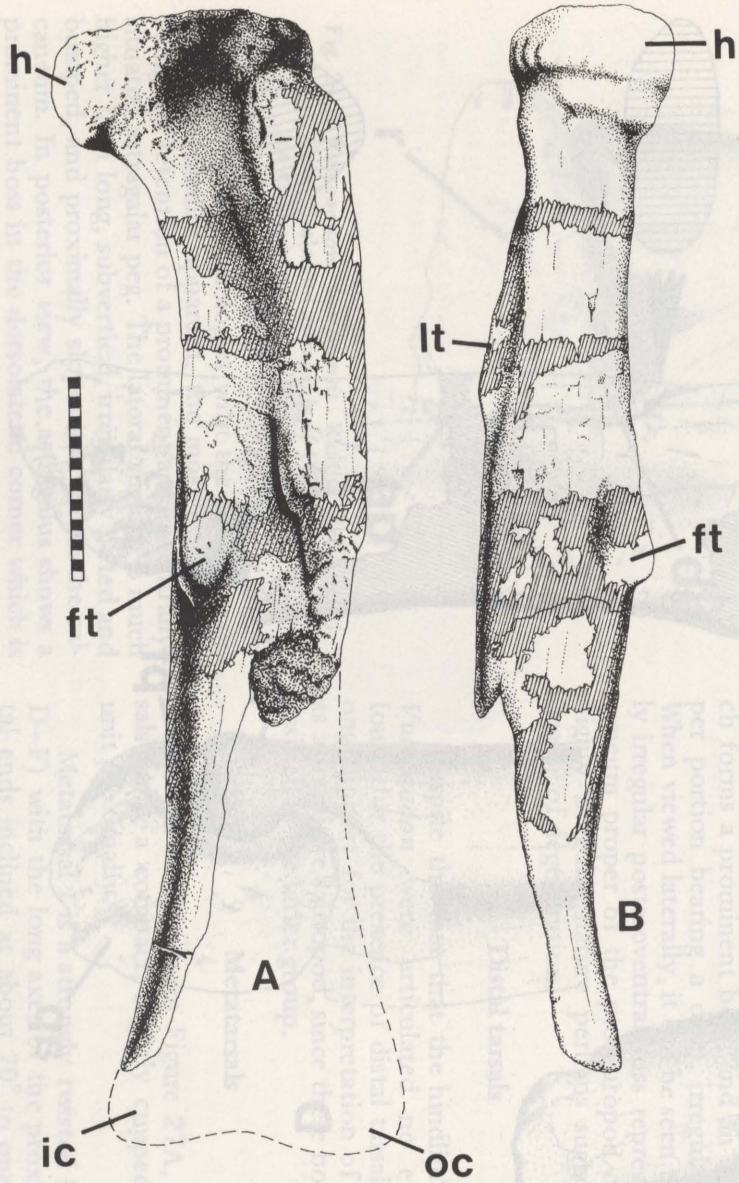


Fig. 21 *Vulcanodon karibaensis* Raath. Right femur of QG 24 in (A) medial and (B) anterior views (with respect to the prosauropod condition). The bar scale is 20 cm.

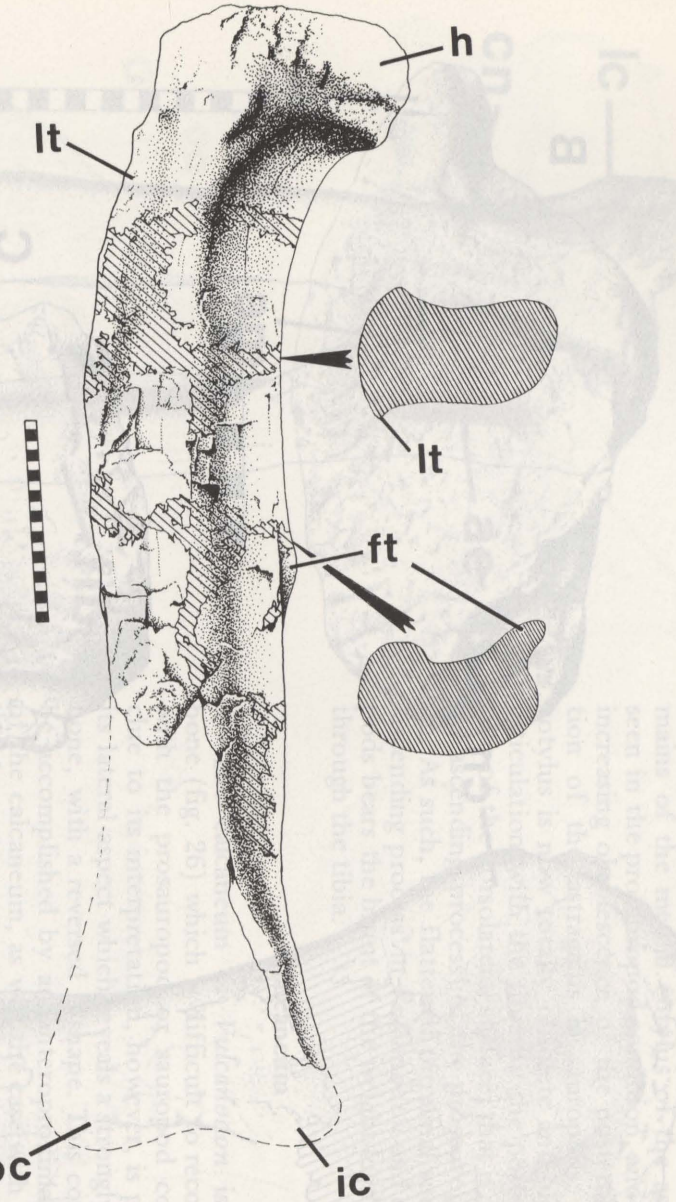


Fig. 22 *Vulcanodon karibaensis* Raath. Right femur of QG 24 in lateral view, with various cross-sections. The bar scale is 20 cm.

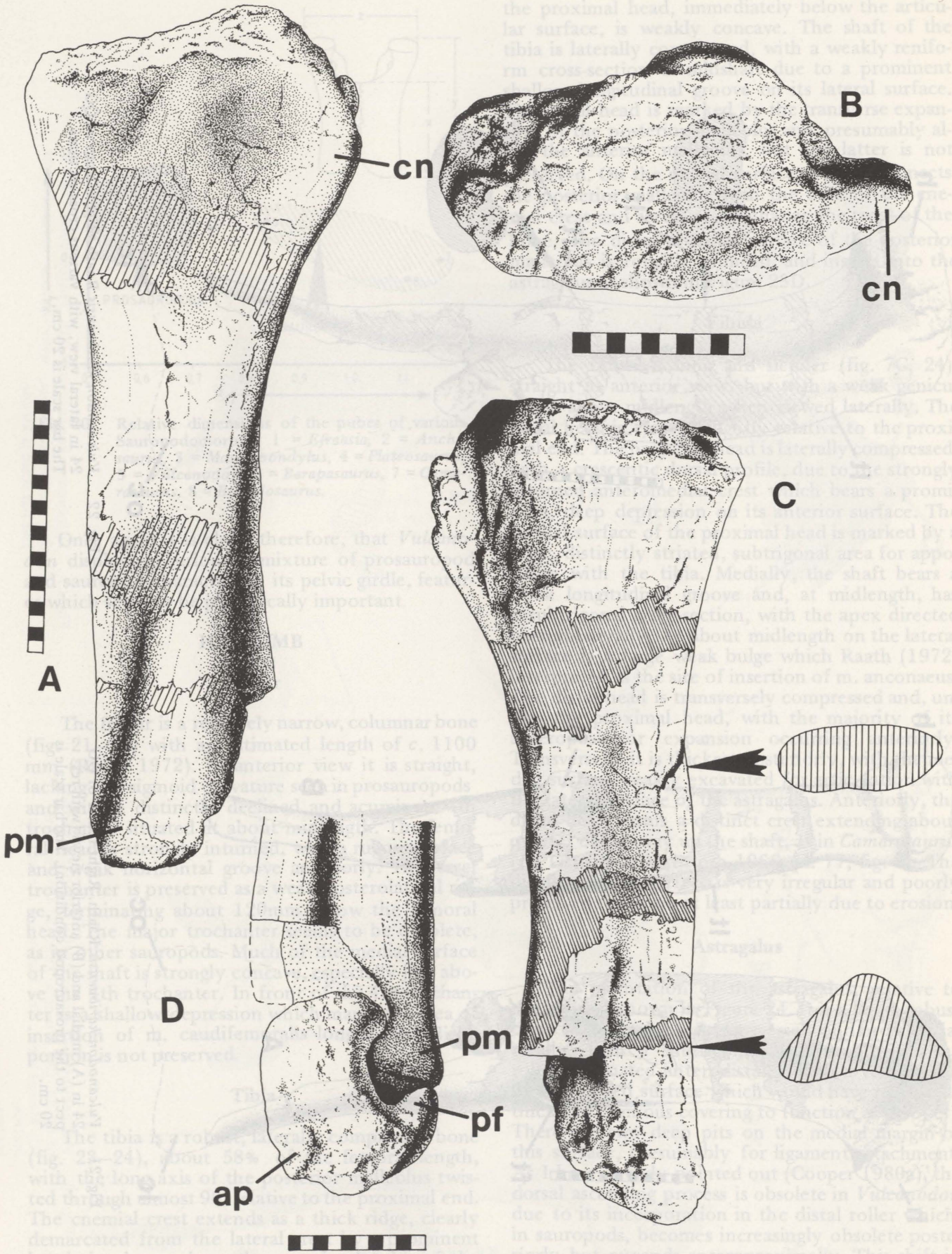


Fig. 23 *Vulcanodon karibaensis* Raath. The left tibia of QG24. A. Medial view. B. Proximal articular surface. C. Lateral view with various cross-sections. D. Lateral view of distal end to show articulation with the astragalus. The bar scales are in centimetres.

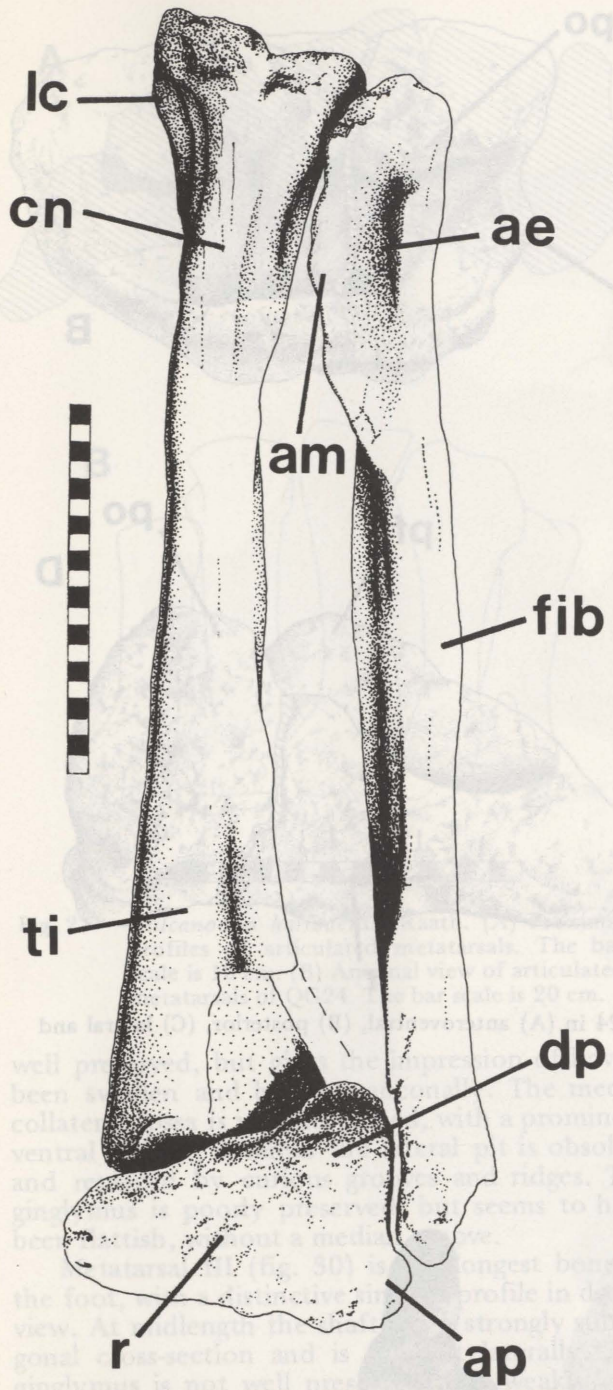


Fig. 24 *Vulcanodon karibaensis* Raath. Articulated tibia, fibula and astragalus of QG24 in anterior view. The bar scale is 20 cm.

grade stance brought about by weight stress. Viewed laterally, the homologies with the prosauropod ankle are readily apparent, the most noteworthy being the retention of a prominent anteroventrally-situated astragalar peg. The lateral surface is much higher than long, subvertical, irregularly pitted and bumped, and proximally slopes away from the calcaneum. In posterior view, the astragalus shows a prominent boss in the dorsolateral corner which is homologous to the posterior overhang of the dorsal ascending process in the prosauropod condition (Cooper 1980a). This is connected by a weak, oblique ridge of bone, which divides the posterior surface into two concave hollows, to the posterior tongue or pfeiler. The latter represents all that remains of the medial cotylus of the astragalus, as seen in the prosauropod condition, and reflects the increasing obsolescence of the posteroventral portion of the astragalus in sauropods. The lateral cotylus is now totally obsolete and blocked from articulation with the tibia by the posterior expansion of the dorsolateral surface; that is, of the 'dorsal ascending process' of the prosauropod condition. As such, the flattened proximal surface of the 'ascending process' in *Vulcanodon* and other sauropods bears the brunt of the weight-load transferred through the tibia.

Calcaneum

The calcaneum of *Vulcanodon* is a curious bone (fig. 26) which is difficult to reconcile either with the prosauropod or sauropod condition. A clue to its interpretation, however, is provided by its lateral aspect which reveals a strongly crescentic bone, with a reversed L shape. This condition can be accomplished by an anteroproximal expansion of the calcaneum, as was the case with the astragalus, from the prosauropod condition. Functionally, this change would again reflect the shift of the distal roller to a more anterior position.

In anterior view, the calcaneum has an oval outline with a strongly convex medial margin and a convexoconcave lateral edge. Its anterior surface is rough and pitted and must have borne a cartilaginous covering to function as a roller. The posterior surface is divided horizontally into two parts, a lower portion of very irregular and pitted bone which forms a prominent boss, and an almost flat upper portion bearing a deep, irregular excavation. When viewed laterally, it can be seen that this highly irregular posteroventral boss represents the calcaneum proper of the prosauropod condition, its highly irregular nature perhaps suggesting a high degree of degeneration.

Distal tarsals

Despite the fact that the hindlimb and pes of *Vulcanodon* were articulated no evidence was found for the presence of distal tarsals This is strong support for the interpretation of *Vulcanodon* as a primitive sauropod, since these bones were not ossified in the latter group.

Metatarsals

As can be seen from Figure 27A, the metatarsals form a compact, slightly cupped metapodial unit proximally.

Metatarsal I is a strongly twisted bone (fig. 28 D–F) with the long axes of the proximal and distal ends inclined at about 70° to one another. At midlength the shaft of the bone is trigonal in cross-section and thickest medially. The distal ginglymus is well-developed, asymmetrical, with a much enlarged lateral condyle and an oblique anterior groove. The lateral collateral fossa is the more strongly

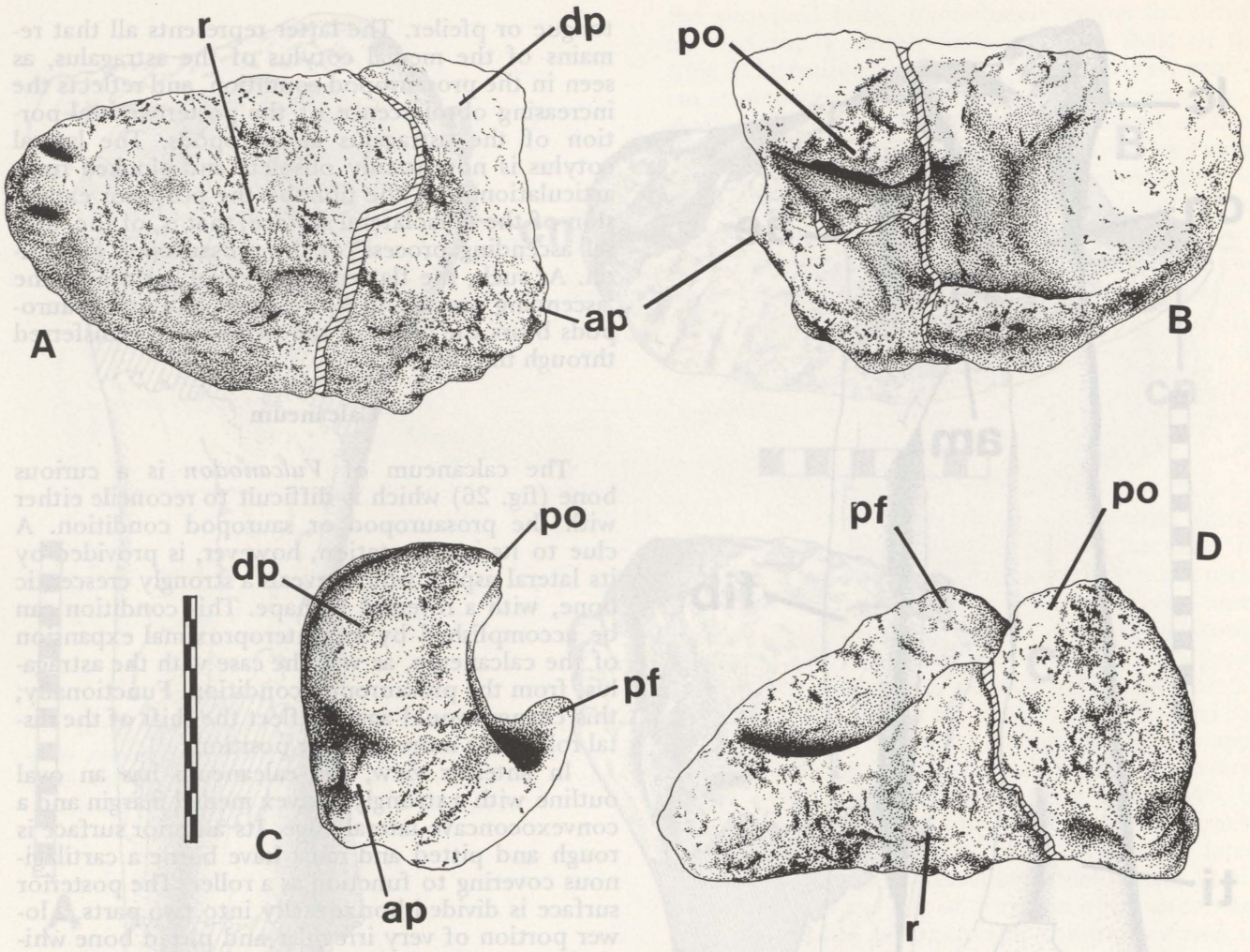


Fig. 25 *Vulcanodon karibaensis* Raath. Astragalus of QG24 in (A) anteroventral, (B) posterior, (C) lateral and (D) dorsal views. The bar scale is 10cm.

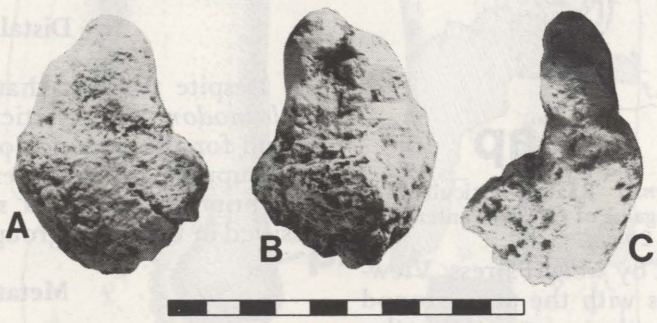


Fig. 26 *Vulcanodon karibaensis* Raath. The left calcaneum of QG24 in (A) anterior, (B) posterior and (C) medial views. The bar scale is 10 cm.

developed of the two, with a distinct ventral selvage.

Viewed dorsally, mtII is narrowest proximally (fig. 29) with a weakly concave proximal head, and expands towards the distal ginglymus. The lateral, medial and ventral surfaces of the proximal head are all concave, while the shaft has a laterally compressed, subrectangular cross-section at midlength, with a weakly concave medial surface. The distal head is irregular and not easy to interpret; it is not

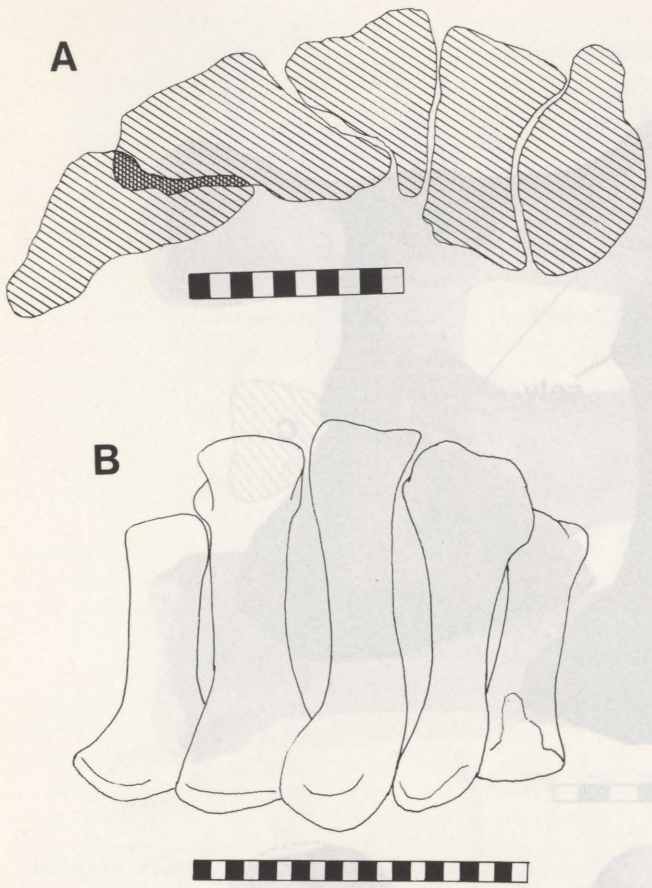


Fig. 27 *Vulcanodon karibaensis* Raath. (A) Proximal profiles of articulated metatarsals. The bar scale is 10 cm. (B) Anconal view of articulated metatarsals of QG24. The bar scale is 20 cm.

well preserved, but gives the impression of having been swollen and bulbous anconally. The medial collateral fossa is well developed, with a prominent ventral selvage, whereas the lateral pit is obsolete and replaced by curious grooves and ridges. The ginglymus is poorly preserved, but seems to have been flattish, without a median groove.

Metatarsal III (fig. 30) is the longest bone in the foot, with a distinctive sinuous profile in dorsal view. At midlength the shaft has a strongly subtrigonal cross-section and is thickest laterally. The ginglymus is not well preserved; it is weakly concave anteriorly and bordered posterolaterally, on the dorsal surface, by an arcuate pit. The collateral fossa of the lateral side is poorly preserved, while the whole medial surface of the distal head is deeply concave, with a bounding rim dorsally and anteriorly. In palmar view, the distal head is strongly concave and, like mtIV, shows little expansion of the ginglymus onto this surface.

Metatarsal IV is a long bone (fig. 31) with a strongly expanded, asymmetrical proximal head in dorsal view. Its palmar surface is excavated laterally to accomodate mtV. At midlength the shaft has an oval cross-section, and is thickest laterally. The distal ginglymus is poorly preserved but apparently lacked a pulley-like groove. The collateral pits are well-developed, especially the lateral fossa, and are bounded by flared selvages, of which the lateral is the more prominent.

Metatarsal V is a relatively large bone (fig. 28A) with a strongly flared proximal end which gives it a funnel-shaped outline in dorsal view. The proximal head is thickest laterally, with a median dorsal ridge, whilst the palmar surface is concave medially. The shaft of the bone is oval, broadest transversely and thickest laterally. The distal condyle is a rugose knob, with an irregular, flattened anterior surface. The medial and lateral collateral fossae are obsolete, although the medial surface retains the selvage which bounded this pit ventrally in the primitive condition. As such, my earlier comment (Cooper 1980a: 178) that ' . . . . metatarsal V of *Vulcanodon* is every bit a reduced as in *Massospondylus*' was over-zealous and erroneous.

Pedal phalanges

Phalanx 1 of the first digit is a prominent asymmetric bone (fig. 32) with a pronounced expansion of the proximal head in medial view. Although it is not preserved, there was clearly a well-developed dorsal lappet proximally and a pronounced flexor tubercle on the palmar surface. The proximal articular surface shows no clear vertical division; it is concave dorsally and convex ventrally. Immediately behind the distal head, the shaft has an oval cross section, and is thickest medially. In medial view, there is a prominent collateral fossa from which runs, along the dorsomedial edge of the bone, a deep groove to guide the collateral ligament. The lateral surface of this phalanx is not well preserved, and it is not certain whether the collateral pit is absent because of erosion or because it had become obsolete. The poor development of the lateral condyle of the distal ginglymus might also be attributable to erosion, since the ginglymus is asymmetrically grooved to produce an oblique arc of rotation.

The ungual phalanx of digit I is a clear relict of the prosauropod condition. It is an enormous, laterally compressed bone (fig. 33), with an asymmetrically biconcave proximal articular surface and a poorly developed flexor tubercle. The flattened lateral surface is marked by a deep groove extending from the region of the flexor tubercle almost to the tip of the claw. The convex medial surface is irregular and difficult to interpret, as in *Camarasaurus* (cf. Ostrom & McIntosh, 1966, pl. 63, fig. 2). Viewed ventrally, it can be seen that the medial edge of the ungual was sharpened. The distal tip of ungual I is bluntly rounded.

Phalanx 1 of the second digit (fig. 34 E–H) was found articulated to the metatarsal and hence there is no doubt as to its identity. It shows a distinct twist of the distal condyles relative to the long axis of the proximal end. Viewed dorsally the bone is trapezoidal in outline, tapering slightly to the anterior, and with a distinct pit behind the lateral condyle of the ginglymus. If present, a dorsal lappet was only poorly represented. The shaft has

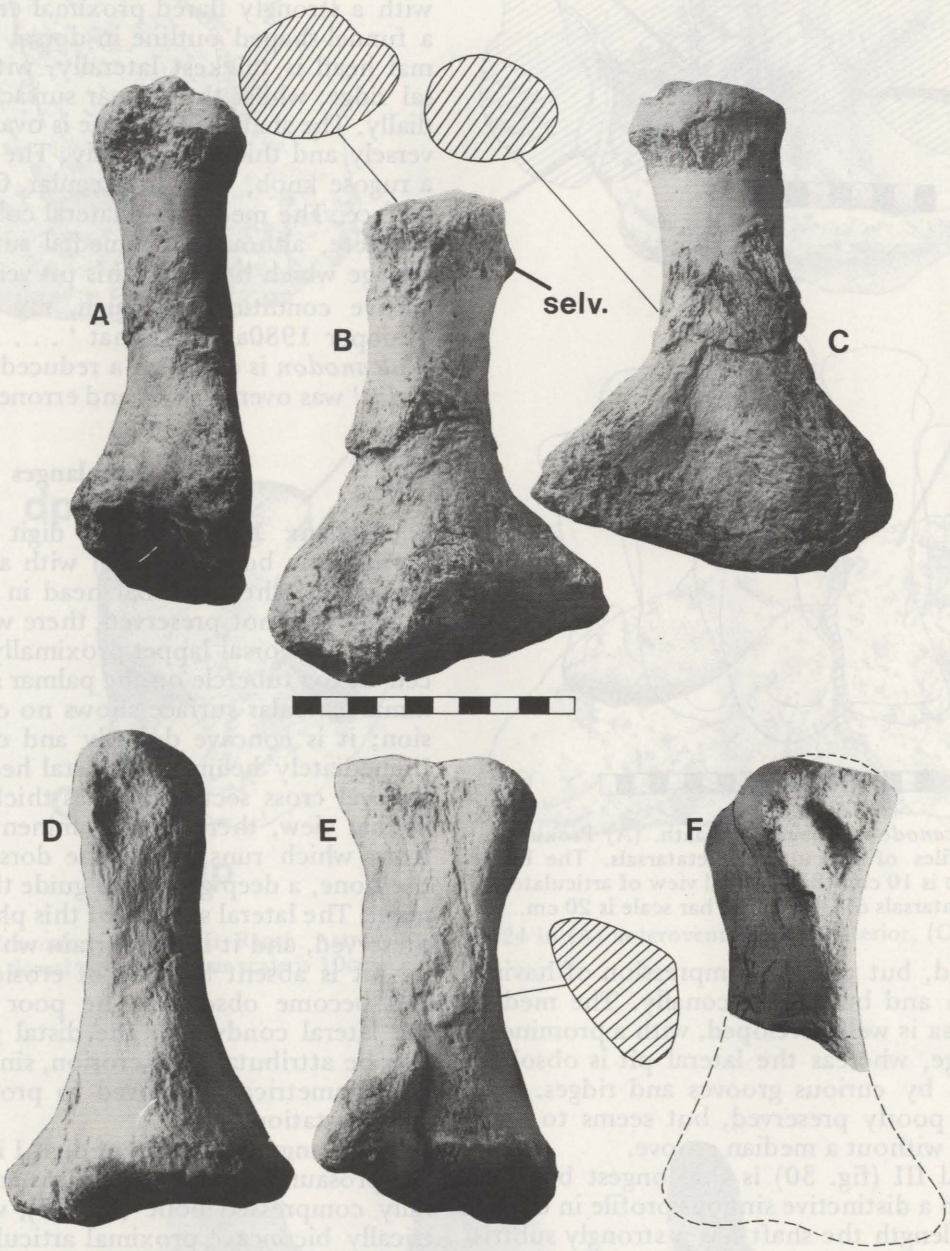


Fig. 28 *Vulcanodon karibaensis* Raath. A–C. Medial, anconal and palmar views of metatarsal V, with various cross-sections. selv. = selvage. D–F. Metatarsal I in medial, anconal and lateral views. The bar scale is 10cm.

a suboval cross-section at midlength, with the lateral portion of the ventral surface weakly concave. Both collateral fossae seem to be naturally absent. The distal ginglymus is evenly convex, without a dividing groove.

What is taken to be Phalanx 2 of the second digit (fig. 35A–D) is very similar to the first, apparently also with obsolete collateral pits and an undivided distal ginglymus. In this bone, however, there is a weakly developed, laterally situated dorsal lappet, with the dorsal depression proximal to the ginglymus deepest medially.

Ungual 2 is a diagnostic bone, curiously asymmetrical and with a strongly sharpened medial edge (fig. 36D–F). The dorsomedial surface is inclined at *c.* 45° to the long axis of the concave proximal articular surface, and bears a prominent longitudinal groove. The ventrolateral surface is rough and irregular with no sign of a groove.

What is believed to be the first phalanx of digit III (fig. 34A–D) has a crescentic, concave, proximal articular surface, with a slight twist at midshaft

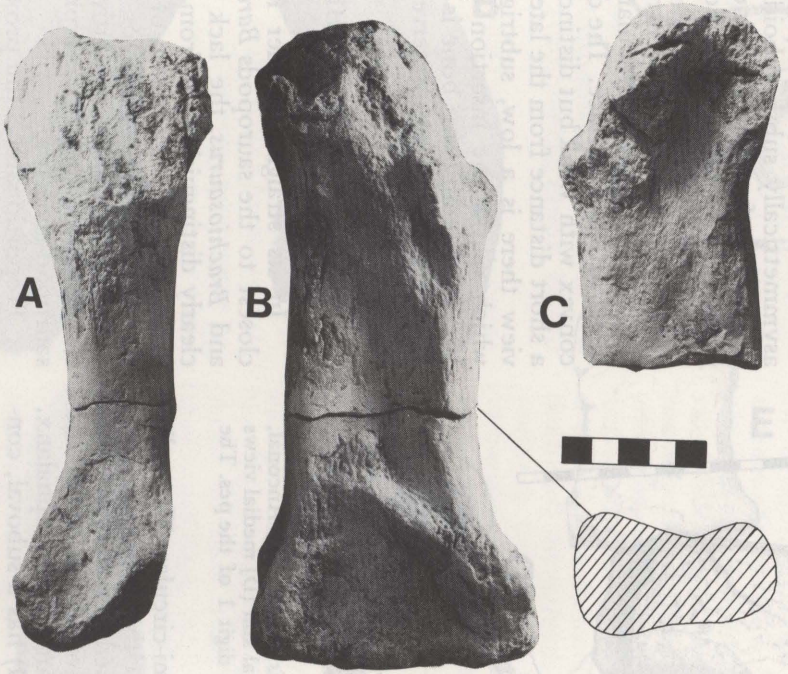


Fig. 29 *Vulcanodon karibaensis* Raath. (A) Anconal, (B) lateral and (C) medial views of metatarsal II of QG 24. The bar scale is 5 cm.

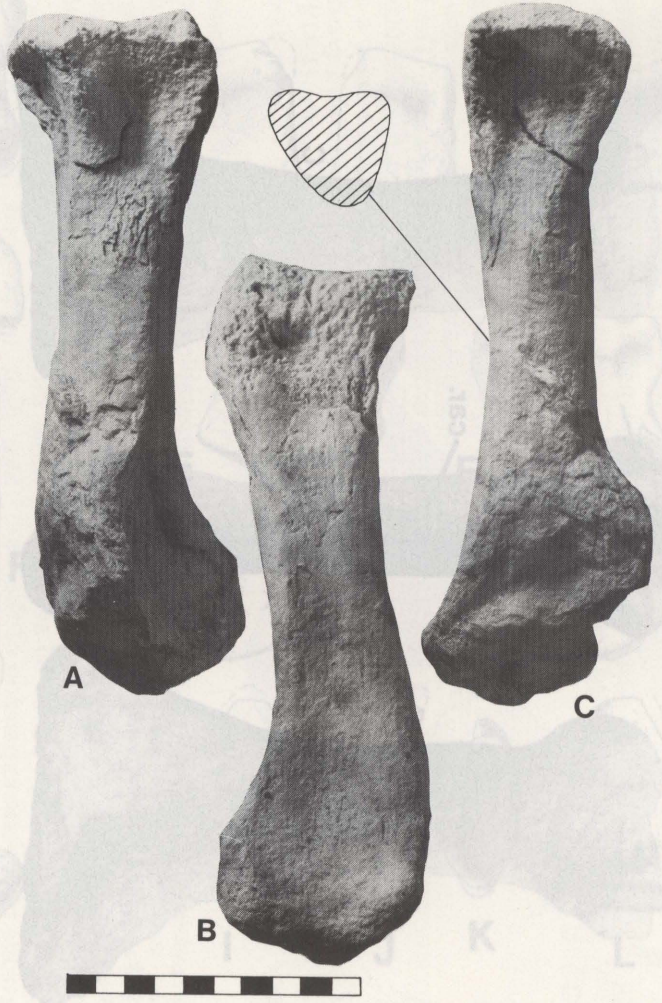


Fig. 30 *Vulcanodon karibaensis* Raath. (A) Palmar, (B) anconal and (C) medial views of metatarsal III. The bar scale is 10 cm.

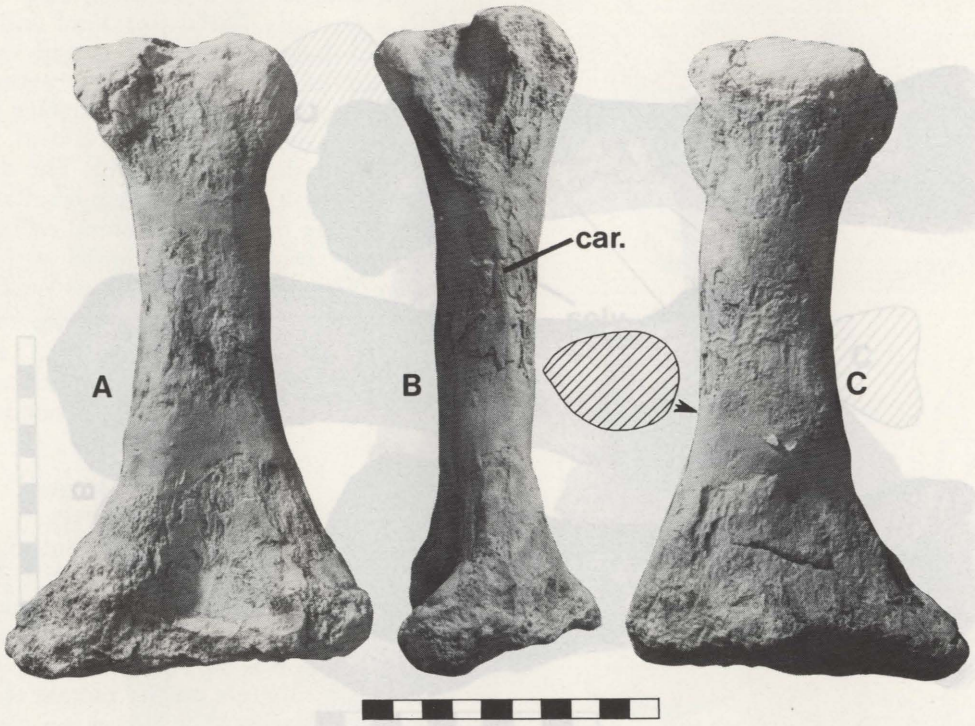


Fig. 31 *Vulcanodon karibaensis* Raath. (A) Palmar, (B) lateral and (C) anconal views of metatarsal IV of QG24. car = carina. The bar scale is 10cm.

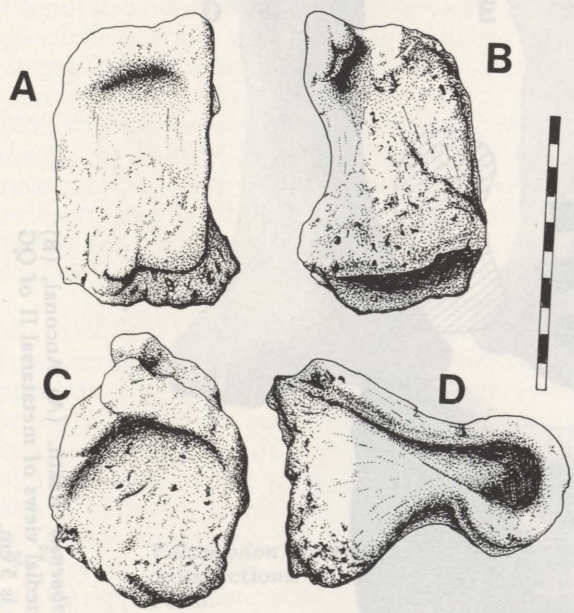


Fig. 32 *Vulcanodon karibaensis* Raath. (A) Anconal, (B) palmar, (C) proximal and (D) medial views of the first phalanx of digit 1 of the pes. The bar scale is 10 cm.

where the cross-section is semi-circular. The collateral pits are well developed, with a prominent ventral shelf, especially on the medial side. The distal ginglymus is asymmetrical, weakly grooved, and extends well onto the ventral surface of the phalanx.

Phalanx IIIii (fig. 35E–H) has a suboval, concave, proximal articular surface and a weakly grooved, asymmetrical, distal ginglymus, with the medial condyle the more swollen of the two. The collateral pits are moderately developed, opening outwards and upwards. Phalanx IIIiii could not be located, but a cast remains (fig. 36A–C). It shows an asymmetrically subrhomboidal, concave, proximal articular surface and a distinctly divided distal ginglymus. In dorsal view this bone has a subrhomboidal profile. Collateral pits are obsolete.

Ungual 3 is a dorsoventrally compressed bone (fig. 35I–L) with a lenticular, evenly concave, proximal articular surface. The dorsal surface is gently convex with weak but distinct longitudinal grooves a short distance from the lateral borders. In ventral view there is a low, subtrigonal area proximally which marks the insertion of the flexor tendon. Viewed laterally this bone is gently curved and, although the tip is not preserved, it was undoubtedly blunt.

FEATURES OF THE HINDLIMB

In its straight, slender femur, *Vulcanodon* is closest to the sauropods *Barapasaurus*, *Barosaurus* and *Brachiosaurus*, the lack of sigmoid curvature clearly distinguishing it from the prosauropod condition (fig. 37). The form of the 4th trochanter is also very similar to that of *Barapasaurus*, though *Vulcanodon* is more primitive in retaining a lesser trochanter, a symplesiomorphy shared with its prosauropod ancestor.

Proportionately, the proximal head of the tibia of *Vulcanodon* is closest to *Plateosaurus* (fig. 38), but distinctly sauropodous in that the cnemial crest

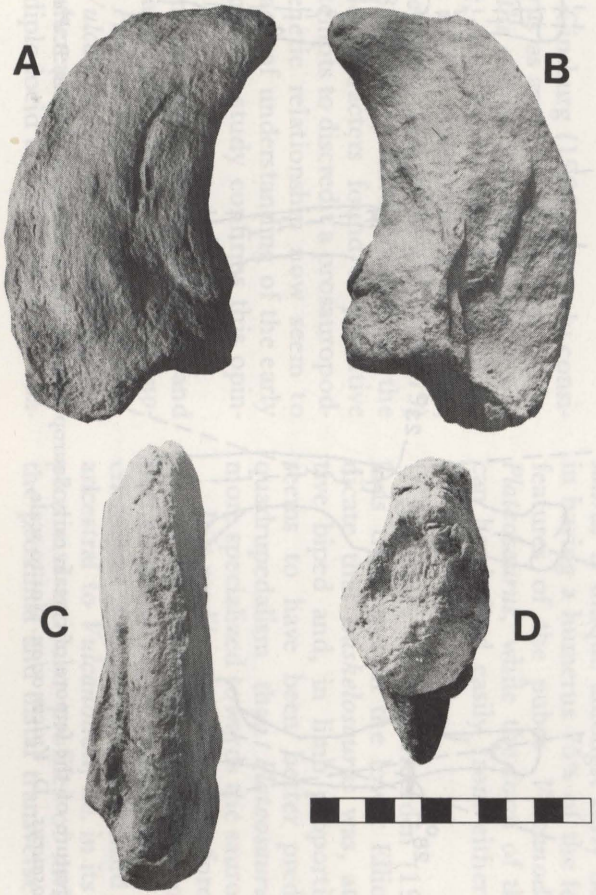


Fig. 33 *Vulcanodon karibaensis* Raath. (A) Medial, (B) lateral, (C) anconal and (D) proximal views of the ungual phalanx of the hallux of QG24. The bar scale is 10 cm.

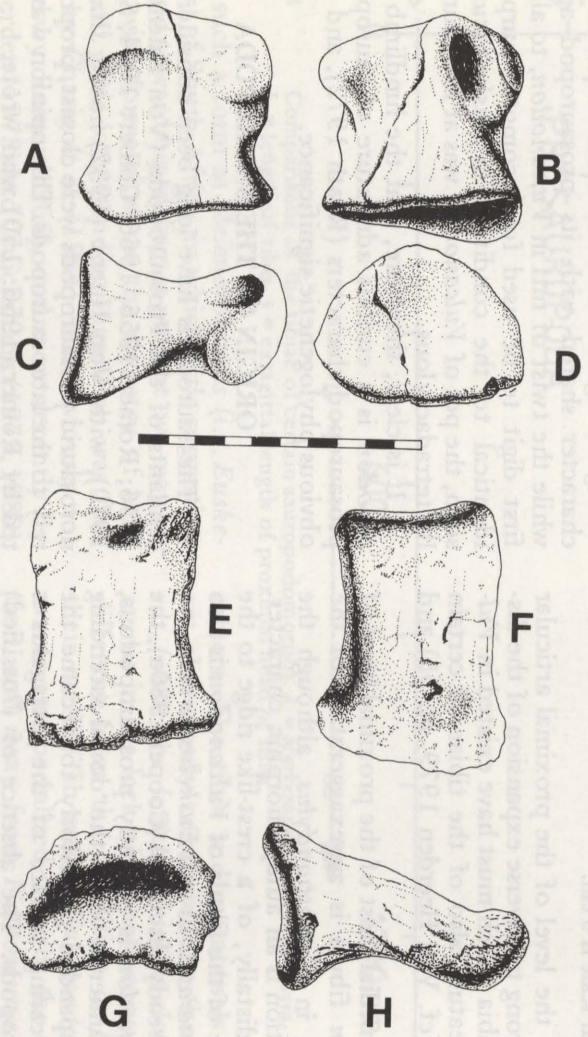


Fig. 34 *Vulcanodon karibaensis* Raath. A–D. Palmar, anconal, medial and proximal views of phalanx IIIi. E–H. Anconal, palmar, proximal and medial views of Phalanx IIi. The bar scale is 10 cm.

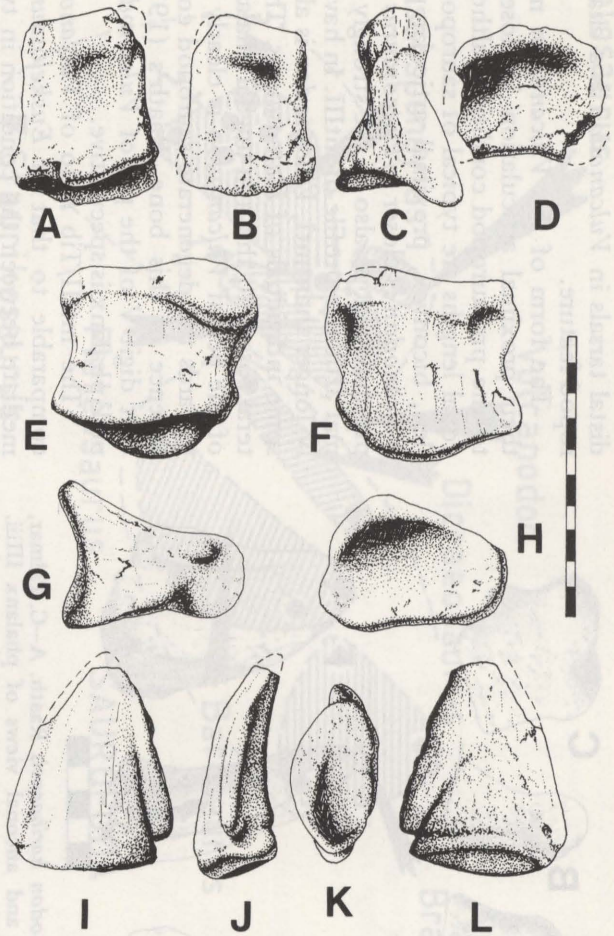


Fig. 35 *Vulcanodon karibaensis* Raath. A–D. Anconal, palmar, medial and proximal views of phalanx IIii. E–H. Palmar, anconal, medial and proximal views of phalanx IIIii. I–L. Anconal, medial, proximal and palmar views of the ungual of digit IV. The bar scale is 10 cm.

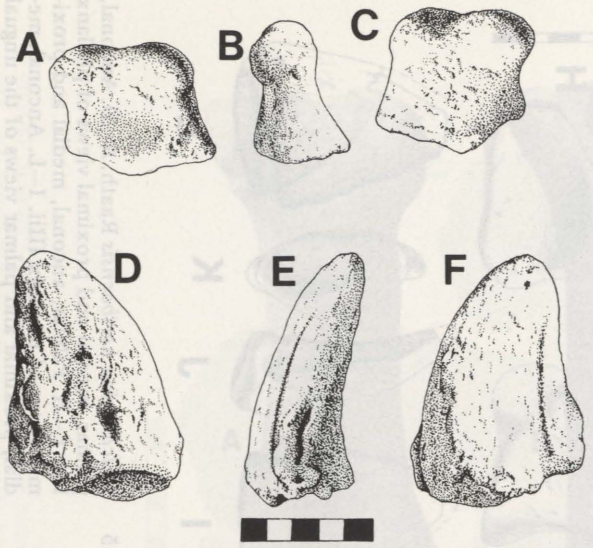


Fig. 36 *Vulcanodon karibaensis* Raath. A–C. Palmar, lateral and anconal views of phalanx IIIiii. D–F. Palmar, medial and anconal views of the ungual phalanx of digit II of the pes of QG24. The bar scale is 5 cm.

does not reach the level of the proximal articular surface. The strong transverse expansion of the distal end of the tibia which must have existed in *Vulcanodon* is a feature also of the tibiae of certain *Euskelosaurus* (cf. Van Heerden 1979, pl. 55) and *Barapasaurus.*

The anteromedial crest of the proximal head of the *Vulcanodon* fibula is an exaggeration of the condition seen in *Massospondylus,* although the anterior excavation is an autapomorphic character. The presence, distally, of a crest-like ridge to the anterior surface of the fibula of *Vulcanodon* is also a feature of *Camarasaurus* and *Euskelosaurus.*

As I have already discussed (Cooper 1980a), the ankle of *Vulcanodon* is patently prosauropodous, although the manner in which the 'dorsal ascending process' has expanded posteriorly to become the major weight-bearing surface of the astragalus is typical of sauropods. The absence of (?ossified) distal tarsals in *Vulcanodon* is a characteristic sauropod feature.

The form of the *Vulcanodon* metatarsals and their proximal articulation is closely comparable to the prosauropod condition, although their subequal lengths are typical of sauropods. In the swollen, biconvex, proximal articular profile of mtI, *Vulcanodon* is closer to *Plateosaurus* than any other prosauropod, as also in the strongly trigonal proximal articular profile of mtIII. In having mtV slightly longer than mtI, *Vulcanodon* is also matched by some individuals of *Plateosaurus.* The loss of collateral fossae to the non-ungual phalanges of digit II of the pes of *Vulcanodon* is clearly a development towards the degenerate sauropod condition. In the absence of this bone, Raath's (1972) suggestion that digit V of the pes of *Vulcanodon* had a 'normal' phalanx is speculative.

The mtIII/Tib ratio of *Vulcanodon* is closely comparable to that of *Euskelosaurus,* and intermediate between the condition in typical sauropods and anchisaurid prosauropods (fig. 10B). The enlarged ungual to the hallux is a plesiomorphic character shared with its prosauropod ancestor, while the twist of mtI in *Vulcanodon,* to allow the first digit to be used for locomotor purposes, is identical to the condition in *Euskelosaurus.* As such, the pes of *Vulcanodon* was at least functionally tetradactylous.

It is clear, therefore, that the hindlimb of *Vulcanodon* is a curious admixture of sauropod and prosauropod characters (Raath 1972), and thus of obvious phylogenetic significance.

ORIGIN OF THE SAUROPODA

The sauropods have long been considered descendants of the Prosauropoda (Von Huene 1932, 1956; Romer 1956, 1966; Colbert 1964; Swinton 1970), with Von Huene (1932) noting that melanorosaurid prosauropods were closest, proportionately to the later sauropods. This opinion was accepted by Romer (1966: 150) who wrote, '. . . in the

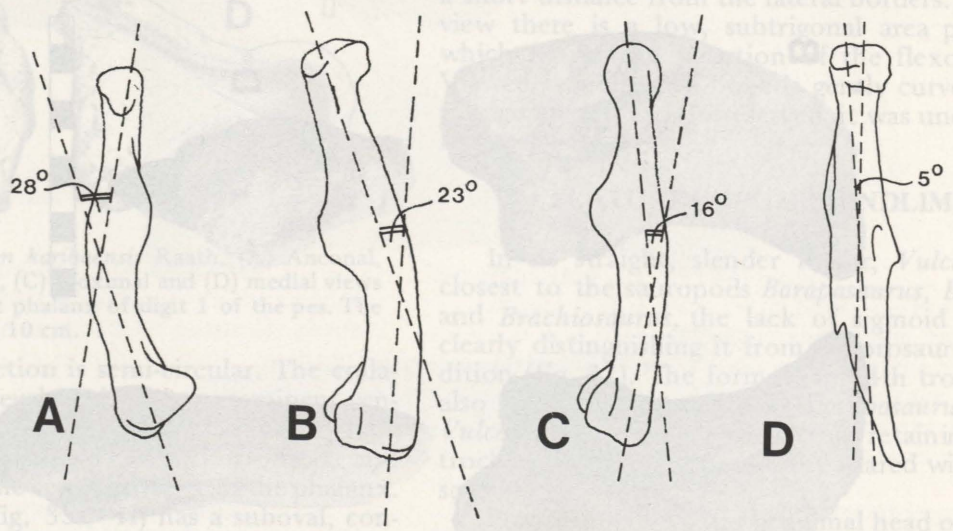


Fig. 37 Curvature of the femora of certain early Sauropodomorpha. A. *Massospondylus,* B. *Plateosaurus,* C. *Euskelosaurus.* D. *Vulcanodon.* Not to scale.

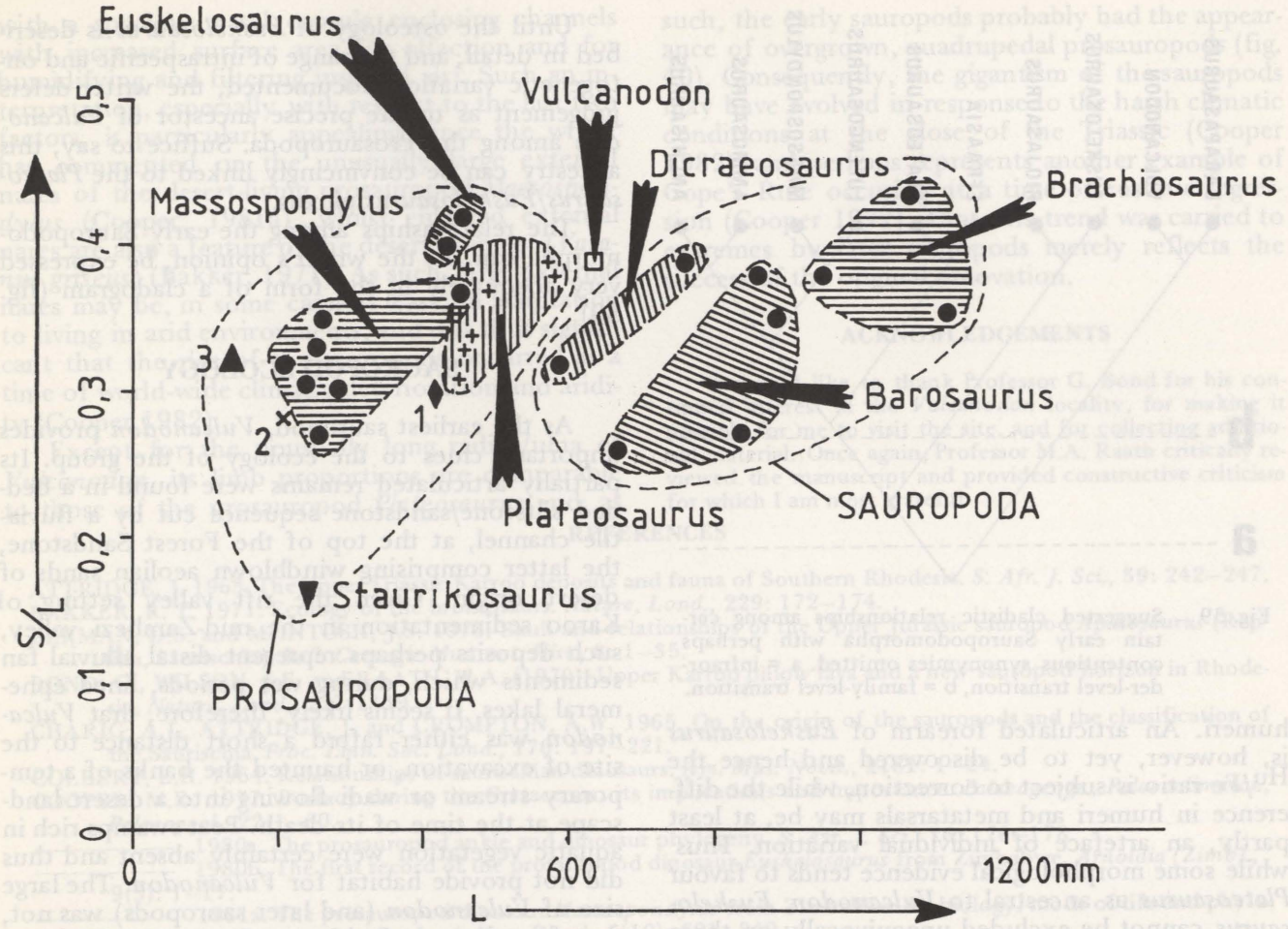


Fig. 38 Comparisons of the tibiae of certain sauropodomorphs. 1 = *Herrerasaurus*, 2 = *Efraasia*, 3 = *Anchisaurus*, L = length of tibia, s = exsagittal length of proximal head of tibia.

case of such a form as *Melanorosaurus* (i.e. *Euskelosaurus)* of South Africa, in which little suggestion of a trend toward bipedalism is present we may be dealing with forms close to the ancestry of later sauropods'. This long-standing suggestion was first refuted by Charig *et al.* (1964) (but obviously not accepted by Romer 1966), and more recently by Van Heerden (1978) and Cruickshank (1979, 1980).

Ellenberger & Ginsburg (1966) not only considered *Euskelosaurus* as ancestral to the Sauropoda, but considered it *the earliest sauropod.* This view is not accepted here, since *Euskelosaurus* is so obviously prosauropod in the characters of its femora, ilia and ischia. Recently, Jain *et al.* (1975, 1979) and Cooper (1980a, 1981) have pointed to the many prosauropod characters found in primitive sauropods, and attempts to discredit a prosauropod-sauropod phylogenetic relationship now seem to reflect merely a lack of understanding of the early Sauropoda. The present study confirms this opinion.

It is clear from the foregoing descriptions and discussions that, amongst prosauropods, *Vulcanodon* is closest to *Plateosaurus* and *Euskelosaurus.* The humerus of *Vulcanodon* is most similar to that of *Plateosaurus,* whereas the epipodials are a curious admixture of diplodocid and camarasaurid characters. The tibia and metatarsals of *Vulcanodon* are also closely comparable to those of *Plateosaurus,* while the femur, which is closest to *Euskelosaurus* in the lack of sigmoid curvature, is not very different from the condition in *Plateosaurus.* In their mt III/Tib ratios, *Vulcanodon* and *Euskelosaurus* are specialized towards the sauropod condition, and away from *Plateosaurus,* while *Euskelosaurus* is unique amongst early Sauropodomorpha in having a humerus 75% of the femoral length. In features of the pubes *Vulcanodon* is closest to *Plateosaurus,* while the form of the ilia and ischia can be derived easily from either *Plateosaurus* or *Euskelosaurus.*

Contrary to Van Heerden (1979), tetradactylous trackways in the lower Elliot Formation indicate that *Euskelosaurus* was, at best, a facultative biped and, in limb proportions it certainly seems to have been better predisposed towards quadrupedalism than *Plateosaurus,* and is thus more specialized towards the sauropod condition.

It is readily apparent, therefore, that while *Euskelosaurus* possesses adaptations towards the sauropod condition, in a number of (? relatively minor) characters it seems too specialized to be considered ancestral to *Vulcanodon,* i.e. in its $^{Hu}/_{Fe}$ ratio, the proximal articular profiles of mtI and mtIII, and the proximal and distal transverse expansion of its

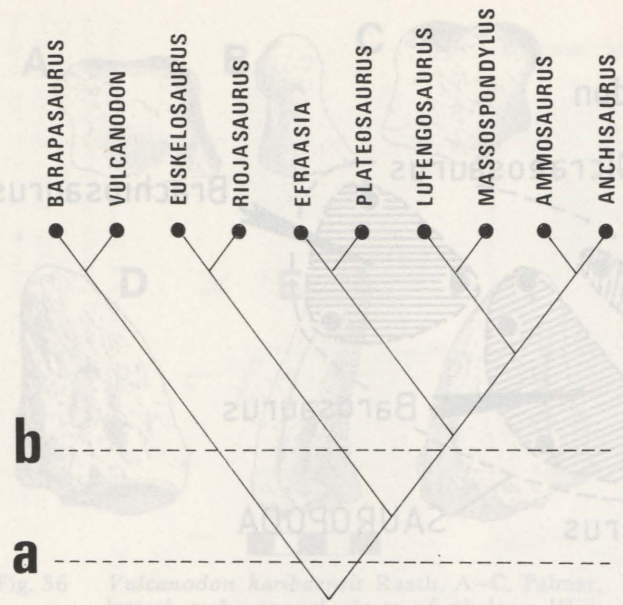


Fig. 39 Suggested cladistic relationships among certain early Sauropodomorpha with perhaps contentious synonymies omitted. a = infraorder-level transition, b = family-level transition.

humeri. An articulated forearm of *Euskelosaurus* is, however, yet to be discovered and hence the Hu/Fe ratio is subject to correction, while the difference in humeri and metatarsals may be, at least partly, an arteface of individual variation. Thus while some morphological evidence tends to favour *Plateosaurus* as ancestral to *Vulcanodon, Euskelosaurus* cannot be excluded unequivocally on these grounds, while geographic evidence as well as certain morphological characters, favours *Euskelosaurus* as the *Vulcanodon* ancestor. A feature which apparently mitigates against the latter relationship is the presence of alleged sauropod trackways contemporaneous with *Euskelosaurus* (Charig *et al.* 1965; Ellenberger *et al.* 1970; Ellenberger 1970).

Until the osteology of *Euskelosaurus* is described in detail, and the range of intraspecific and ontogenetic variation documented, the writer defers judgement as to the precise ancestor of *Vulcanodon* among the Prosauropoda. Suffice to say, this ancestry can be convincingly linked to the *Plateosaurus/Euskelosaurus* plexus.

The relationships among the early Sauropodomorpha can, in the writer's opinion, be expressed very adequately in the form of a cladogram (fig. 39).

SAUROPOD ECOLOGY

As the earliest sauropod, *Vulcanodon* provides important clues to the ecology of the group. Its partially articulated remains were found in a bedded siltstone/sandstone sequence cut by a fluviatile channel, at the top of the Forest Sandstone, the latter comprising windblown aeolian sands of desert origin. Given the rift valley setting of Karoo sedimentation in the mid-Zambezi valley, such deposits perhaps represent distal alluvial fan sediments which, during wet periods, lined ephemeral lakes. It seems likely, therefore, that *Vulcanodon* was either rafted a short distance to the site of excavation, or haunted the banks of a temporary stream or wadi flowing into a desert landscape at the time of its death. Peat swamps rich in aquatic vegetation were certainly absent and thus did not provide habitat for *Vulcanodon.* The large size of *Vulcanodon* (and later sauropods) was not, therefore, an adaptation to swamp dwelling and the buoyancy provided by water for the support of the skeleton.

The large external nares of sauropods have long been considered an aquatic adaptation, although this interpretation was challenged by Bakker (1971). According to Bakker (1971: 172), the large external naris of sauropods may have been filled '. . . .

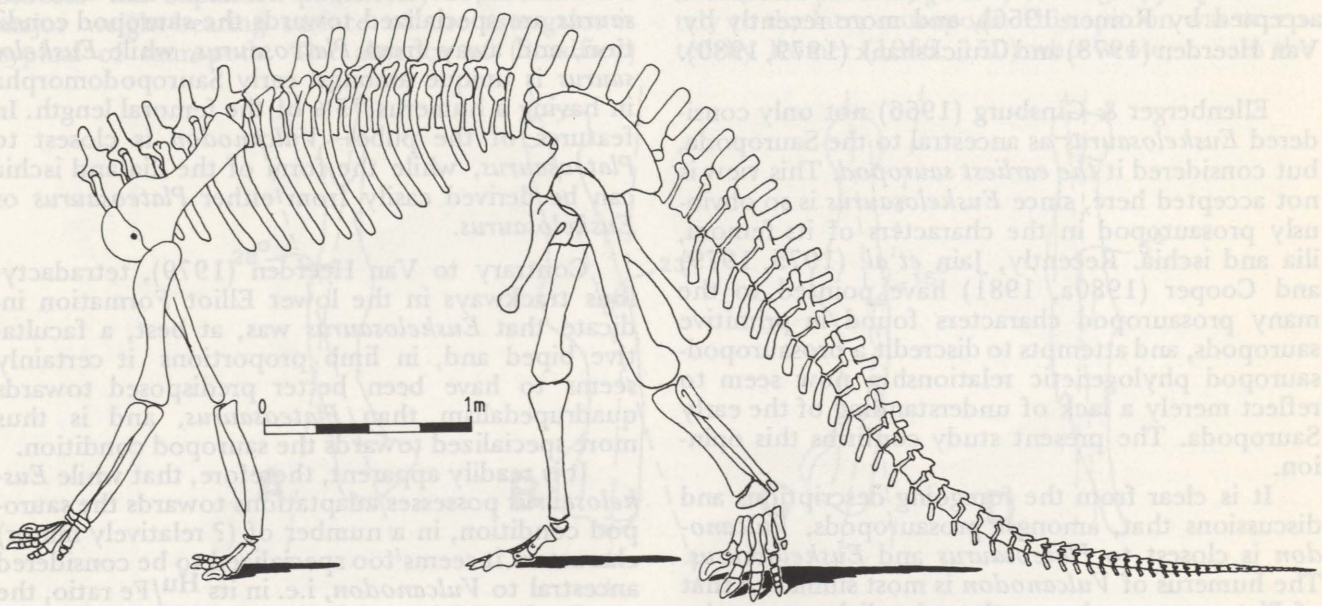


Fig. 40 Reconstruction of *Vulcanodon karibaensis* Raath. Trunk and ilium adapted from *Barapasaurus.*

with a spacious nasal capsule enclosing channels with increased surface area for olfaction and for humidifying and filtering inspired air'. Such an interpretation, especially with respect to the last two factors, is particularly appealing, since the writer has commented on the unusually large external nares of the desert-living prosauropod *Massospondylus* (Cooper, 1981a), whilst enlarged external nares are also a feature of the desert monitor (*Varanus griseus*) (Bakker, 1971). As such, large external nares may be, in some cases at least, an adaptation to living in arid environments, and it is thus significant that the rise of the sauropods occurred at a time of world-wide climatic deterioration and aridity (Cooper 1982).

Except for the unusually long radius/ulna of *Vulcanodon,* its limb proportions are comparable to those of the prosauropod *Plateosaurus* and, as such, the early sauropods probably had the appearance of overgrown, quadrupedal prosauropods (fig. 40). Consequently, the gigantism of the sauropods may have evolved in response to the harsh climatic conditions at the close of the Triassic (Cooper 1982), and perhaps represents another example of Cope's Rule occuring at a time of eustatic regression (Cooper 1977). That this trend was carried to extremes by later sauropods merely reflects the success of the original innovation.

ACKNOWLEDGEMENTS

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