

THE POSTCRANIAL SKELETON OF THE UPPER TRIASSIC SPHENODONTID *PLANOCEPHALOSAURUS ROBINSONAE*

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ABSTRACT. The postcranial skeleton of the Triassic sphenodontid, *Planocephalosaurus robinsonae*, is described from dissociated remains recovered from the type locality at Cromhall Quarry, South Gloucestershire. A full reconstruction is outlined and its relationships within the Sphenodontidae are briefly discussed. A lower Jurassic eosuchian, *Gephyrosaurus bridensis*, is shown to share a number of characteristics with *P. robinsonae*, and *Gephyrosaurus* is consequently considered to be either a member of the Sphenodontidae or an offshoot from the stem Sphenodontidae.

ABUNDANT dissociated sphenodontid and archosaurian reptile remains are known from the Triassic fissure deposits of Cromhall Quarry, South Gloucestershire (Robinson 1973; Fraser 1982; Fraser and Walkden 1983). The skull of the most common of the sphenodontids, *P. robinsonae*, was recently described by Fraser (1982) and this paper deals with the postcranial skeleton of the same species.

Whilst a number of similar-sized reptiles are represented in the deposits the much greater preponderance of *Planocephalosaurus* elements (text-fig. 1) aids in their separation from the remaining material. However, because the Cromhall sphenodontids have similar postcranial structures, it is still possible to confuse some elements with juveniles of the larger *Clevosaurus hudsoni*, particularly in the more poorly preserved fossils. To avoid such difficulties only elements from a single site, where *Clevosaurus* is rare, have been considered. At this site (fissure four, text-fig. 1) archosaurs constitute the major percentage of the non-*Planocephalosaurus* material and are readily distinguished from sphenodontid elements.

Preservation of the bone is generally excellent although few bones are absolutely complete (Pls. 53 and 54 illustrate the typical nature of the material). The numbers of bones recovered which are more than half complete are shown in the Appendix. In addition, hundreds of smaller, yet still quite readily identifiable, fragments have been sorted from the residue and examined. In order that complete bones could be illustrated, most of the reconstructions have been based on more than one specimen, but the major part of any reconstruction is represented by a single specimen which is the one referred to in the legend.

Although most of the skeleton of *Planocephalosaurus* is represented some of the more fragile elements are either incomplete or not known at all. Despite this, a reliable reconstruction has been made which shows *Planocephalosaurus* as a lizard-like animal (text-fig. 2) with a lightly built skeleton indicating agility and swift action in prey capture and predator avoidance.

From a study of its dentition (Fraser and Walkden 1983), *Planocephalosaurus* was considered to have been primarily insectivorous, although possibly capable of taking newly hatched specimens of small sphenodontids if the opportunity arose.

AXIAL SKELETON

The vertebrae are generally quite well preserved although the articulation facets for both the ribs and the adjacent vertebrae are commonly a little eroded and the neural spines are usually incomplete.

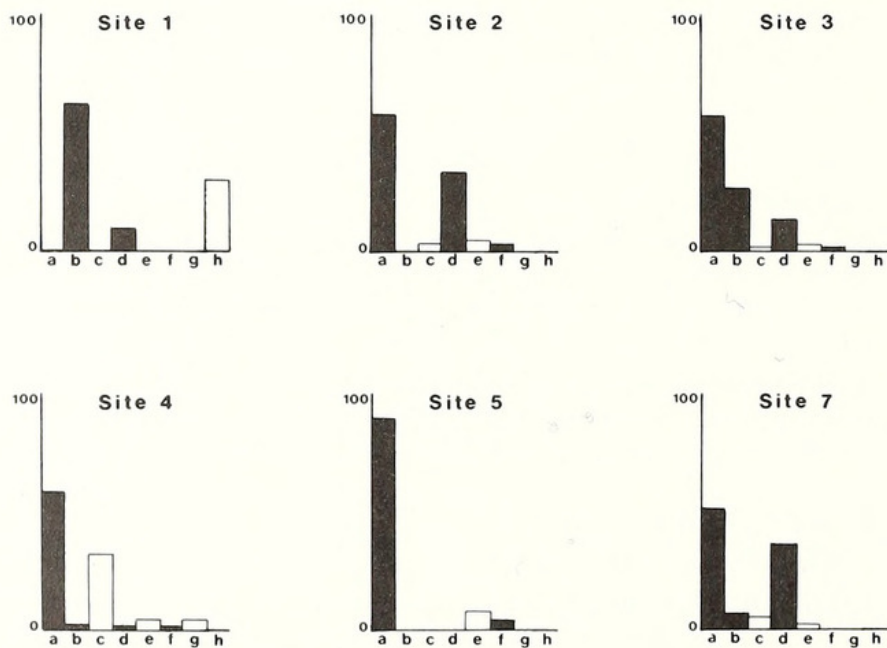
Amongst the vertebrae can be recognized the usual cervical, dorsal, sacral, and caudal elements,

but because the material is completely dissociated it is not possible to determine the exact number of vertebrae in each region. For the purposes of the reconstruction it has been assumed that there are twenty-five presacrals, two sacrals, and between thirty and thirty-six caudals corresponding to the distribution in the only extant spenodontid, *Sphenodon*. The centrum is of the notochordal amphicoelous type throughout. There is a rudimentary zygosphenic articulation (text-fig. 9a; Pl. 53, fig. 7) with the development of a zygosphen and zygtrum.

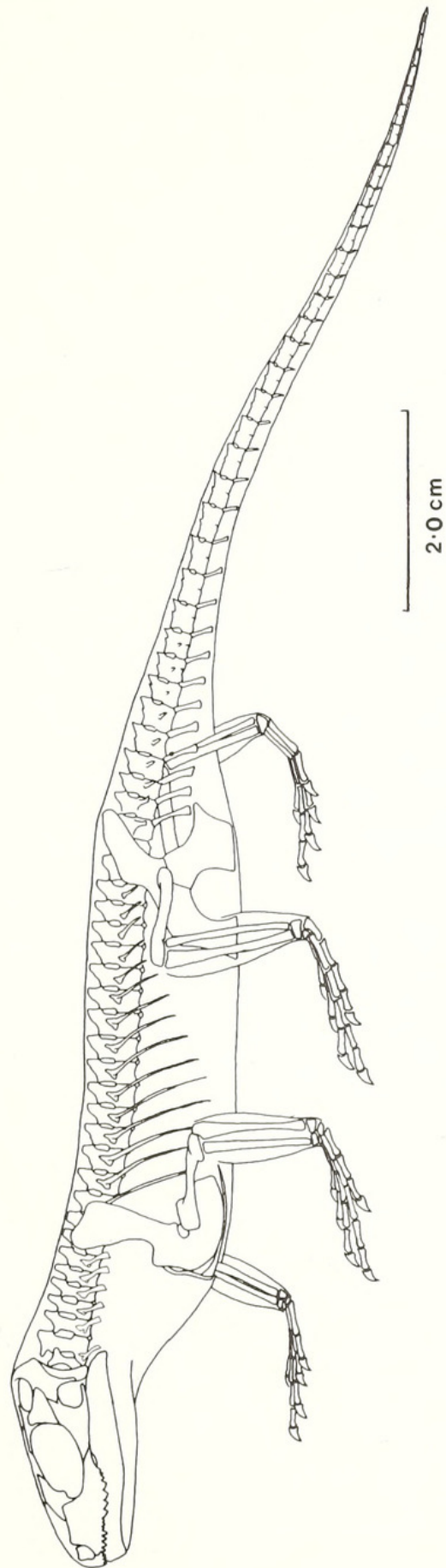
The element that was tentatively designated as the epipterygoid of *Planocephalosaurus* (Fraser 1982) is now known to be one of a pair of elements that met in the midline dorsal to the neural canal and together formed the atlas neural arch (text-fig. 3). A ventral process on each element articulated with the odontoid process medioventrally and with the atlas intercentrum ventrally. There is a postzygapophysial articulation with the axis, but the anterior process bears no facets and connective tissue probably attached it to the skull. The axis prezygapophysis takes the form of a simple circular facet that is directed dorsolaterally and overlapped by the atlas neural arch.

The odontoid process is formed by the fusion of the atlas and axis centra (text-fig. 4); a faint suture on the dorsal surface is the sole remaining evidence of their separate centres of ossification. The atlas intercentrum has not been positively identified but that of the axis has been fused to the centrum and bears a rib parapophysis on each side. The diapophyses for the axial ribs lie on the centrum.

As previously stated it is difficult to assess the precise number of cervical vertebrae; *Sphenodon* has eight, but the Jurassic spenodontids such as *Homeosaurus* and *Kallimodon* have just seven. In the reconstruction (text-fig. 2) *Planocephalosaurus* has been shown with eight. Excluding the atlas and axis, the cervicals are typically short with widely spaced zygapophyses angled at approximately 40° (text-fig. 5; Pl. 53, fig. 3). In the first one or two elements the parapophyses are situated on the edge of the intercentrum and separate diapophyses occur along the centrum/neural arch boundary, slightly posterior to the level of the parapophyses. The corresponding cervical ribs display separate capitula and tuberculae. The diapophyses on the more posterior cervical vertebrae show a tendency to form an elliptical-shaped facet that is elongated in a posterodorsal-anteroventral direction. These



TEXT-FIG. 1. The abundance of the predominant reptile genera at each of six fossiliferous fissure deposits at Cromhall Quarry. □—sphenodontid, □—non-sphenodontid, a—*Planocephalosaurus*, b—*Clevo-saurus*, c—a pseudosuchian, d—a small sphenodontid, e—a primitive crocodile, f—*Sigmala*, g—*Kuehneosaurus*, h—a pseudosuchian.

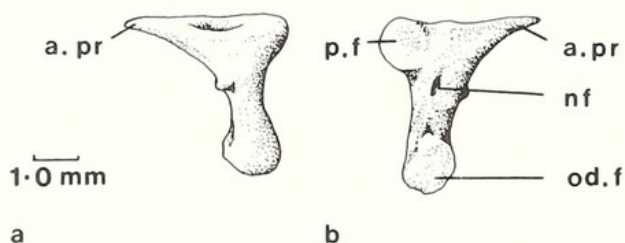


TEXT-FIG. 2. Restoration of the skeleton of *Planocephalosaurus robinsonae*.

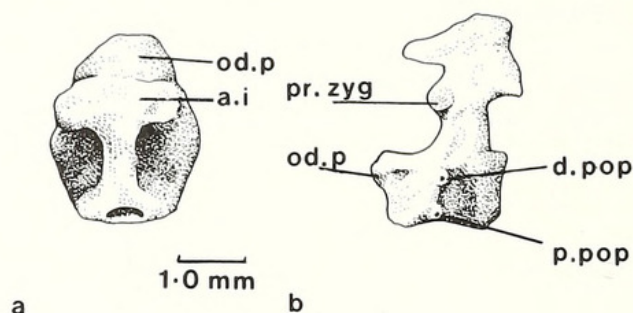
diapophyses articulated with enlarged tuberculae on the ribs but posteriorly the small capitulum soon becomes reduced until it fails to articulate with the parapophysis and both are subsequently lost. Hoffstetter and Gasc (1969) believe that in *Sphenodon* the parapophyses migrate dorsally to meet the diapophyses thereby forming elliptical-shaped synapophyses. For the posterior rib facets of *Planocephalosaurus* to be considered as true synapophyses, the diapophyses need to have enlarged at the same time as the parapophyses migrated dorsally; however, the evidence would suggest that the diapophyses enlarged to the exclusion of the parapophyses without any fusion of the two facets. In this way *Planocephalosaurus* apparently differs from *Sphenodon* in the formation of the elliptical-shaped dorsal rib facets.

Where the exact transition between cervical and dorsal vertebrae takes place is unknown, but the dorsal vertebrae are generally longer, with the elliptical facets for the rib articulation situated more dorsally on the neural arch (text-fig. 6). However, these rib facets become progressively smaller in the posterior members of the dorsal series (text-fig. 7). In comparison with the cervical vertebrae the zygosphenic articulation on the dorsals is slightly more pronounced.

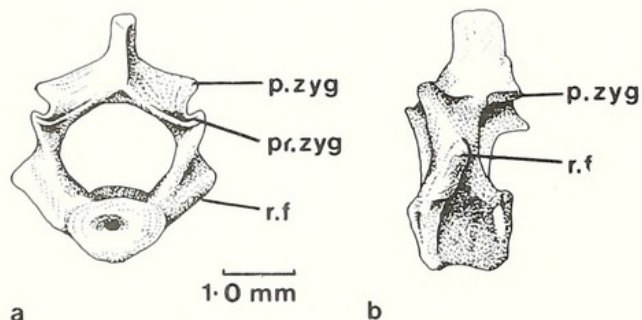
The two sacral vertebrae (Pl. 53, figs. 9, 10) have not been recovered in the fused condition. However, a clear distinction can be made between them (text-fig. 8). In both instances the very stout ribs are fused to the vertebrae with no trace of a suture, but in the first sacral these ribs are directed slightly ventrally, whereas in the second sacral each rib extends laterally and also bifurcates distally.



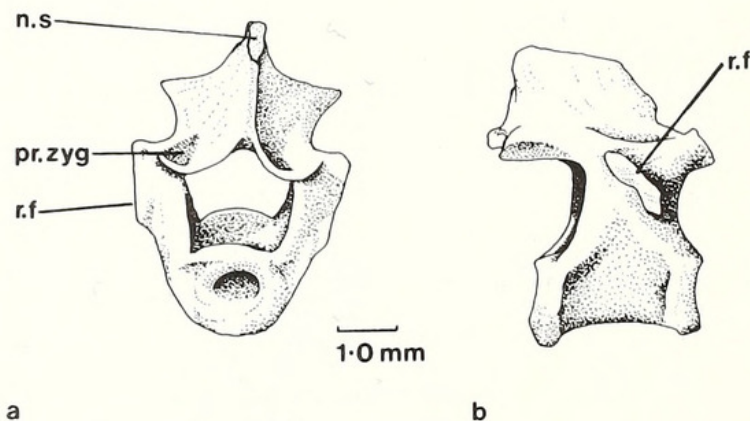
TEXT-FIG. 3. *Planocephalosaurus robinsonae*. Atlas neural arch, AUP No. 11136. *a*, lateral view and *b*, mesial view. See list of Abbreviations used in Text-figures, pp. 594-5.



TEXT-FIG. 4. *Planocephalosaurus robinsonae*. Reconstruction of the atlas/axis complex from AUP No. 11137. *a*, ventral and *b*, lateral aspects.

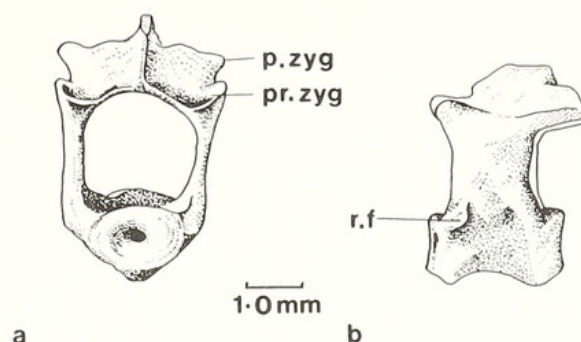


TEXT-FIG. 5. *Planocephalosaurus robinsonae*. Reconstruction of a cervical vertebra from AUP No. 11138. *a*, anterior and *b*, lateral aspects.



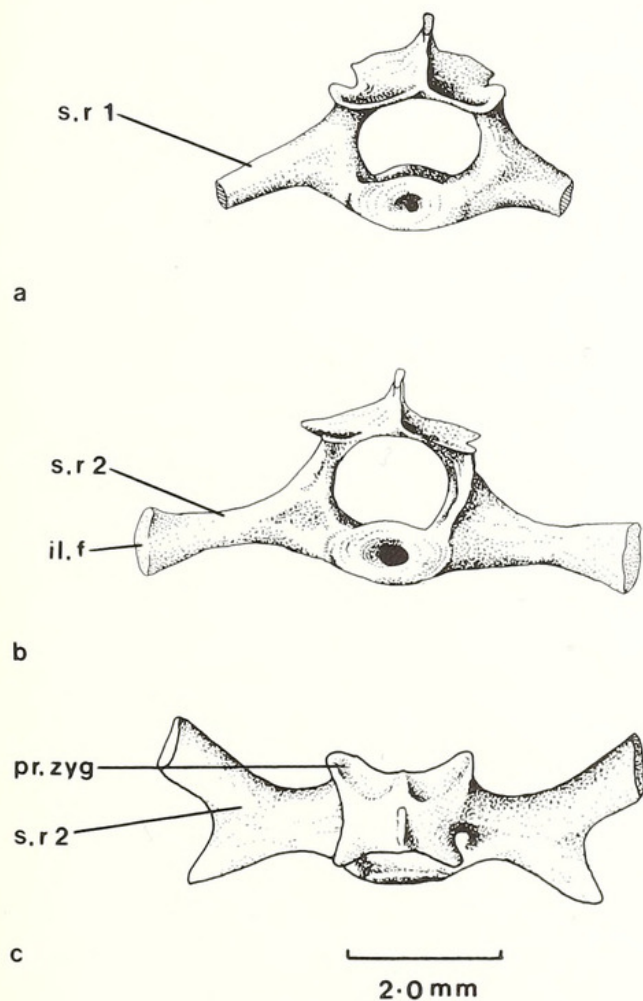
TEXT-FIG. 6. *Planocephalosaurus robinsonae*. Reconstruction of a mid-dorsal vertebra from AUP No. 11139. *a*, anterior and *b*, lateral aspects.

TEXT-FIG. 7. *Planocephalosaurus robinsonae*. Reconstruction of a posterior dorsal vertebra from AUP No. 11096. *a*, anterior and *b*, lateral views.

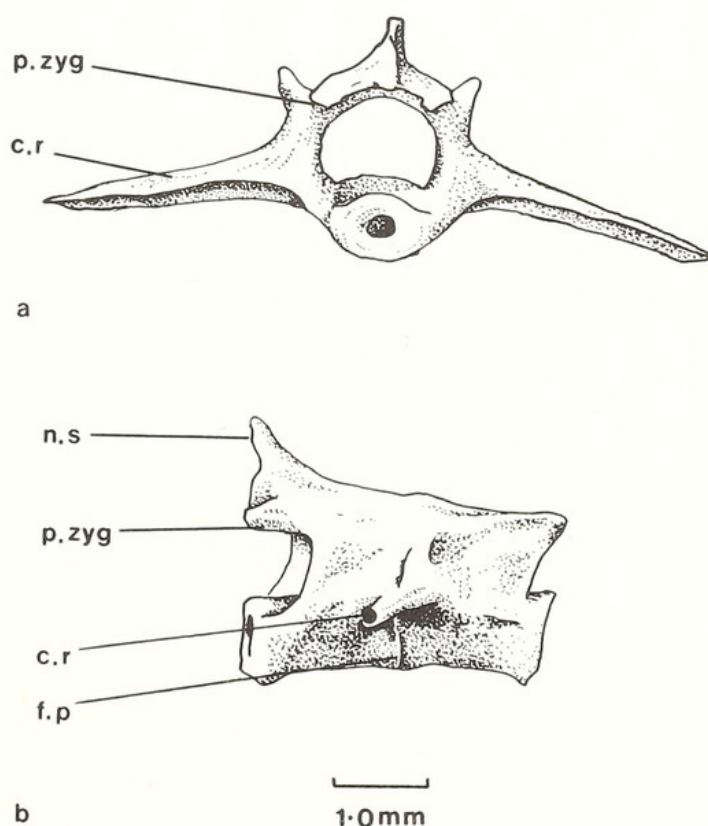


An anterior process extends both towards the rib of the first sacral and laterally to an articulation with the ilium. The posterior process bears no articulation facets and was presumably solely for muscle attachment. Such bifurcation of the second sacral ribs is also observed in the three Jurassic sphenodontid genera: *Homeosaurus*, *Kallimodon*, and *Sapheosaurus* (Hoffstetter and Gasc 1969), as well as in *Clevosaurus* (Swinton 1939).

The anterior caudal vertebrae are approximately equal in length to the posterior dorsals and they bear dorsoventrally compressed ribs projecting at right angles to the spinal cord (text-fig. 9*a*; Pl. 53, fig. 12). These ribs are fused to the neural arch and possess shallow ventral grooves. The neural spines



TEXT-FIG. 8. *Planocephalosaurus robinsonae*. Reconstructions of the sacral vertebrae. *a*, anterior view of the first sacral from AUP No. 11097. The second sacral in *b*, anterior view and *c*, dorsal view from AUP Nos. 11098 and 11099.



TEXT-FIG. 9. *Planocephalosaurus robinsonae*. Reconstructions of caudal vertebrae. *a*, posterior view of an anterior caudal from AUP No. 11100 and *b*, lateral view of a mid-caudal from AUP No. 11101.

are less elongated than in the dorsal series. Posteriorly the vertebrae become more elongate whilst the transverse processes become progressively shorter, more circular in cross-section, and directed posterolaterally rather than laterally (text-fig. 9*b*). They are eventually lost altogether (Pl. 53, figs. 13, 14). In the same way the neural spines become smaller and the zygapophyses converge until they form nothing more than rudimentary contact points. Fracture planes are present and these appear in the anterior members of the caudal series where the vertebrae are relatively short and still bear small transverse processes (text-fig. 9*b*): at an estimate between caudal 5 and caudal 10.

With the exception of the fused atlas and axis there are small anteroventral and posteroventral facets on all the centra of the vertebral column which testify to the presence of intercentra throughout. Probably as a result of their small size and delicate nature none has been positively identified from the cervical region and only a few have been recovered representing the dorsal region. These dorsal intercentra are simple crescent-shaped bands of bone (text-fig. 10*c*), but the caudal intercentra take the form of chevron bones which possess a triangular fossa to allow for the passage of the caudal nerves and blood-vessels (text-fig. 10*a*). Below this fossa a medial ventrally directed process separated the muscle blocks on either side of the tail. The anterior chevron bones have a basal transverse bar at the point of attachment to the vertebral column, but in the posterior chevrons this bar is reduced so that the chevron is borne on two separate pedicels (text-fig. 10*b*; Pl. 53, fig. 18).

As already mentioned, the ribs were typically of the holocephalous type, the capitulum having been lost and the tuberculum expanded. However, in the first two or three cervical vertebrae there are small parapophyses and correspondingly the first three or four cervical ribs also possessed rudimentary capitula (text-fig. 11*a*). These may not necessarily have articulated with the parapophyses since ligaments could have completed the attachment where the capitula were reduced to mere protruberances. The posterior cervical ribs possess a short shaft that is expanded distally (text-fig. 11*b*; Pl. 53, fig. 17) whilst in the dorsal ribs the shaft is generally narrow and longer—particularly in the anterior dorsals (text-fig. 11*c*).

PECTORAL GIRDLE

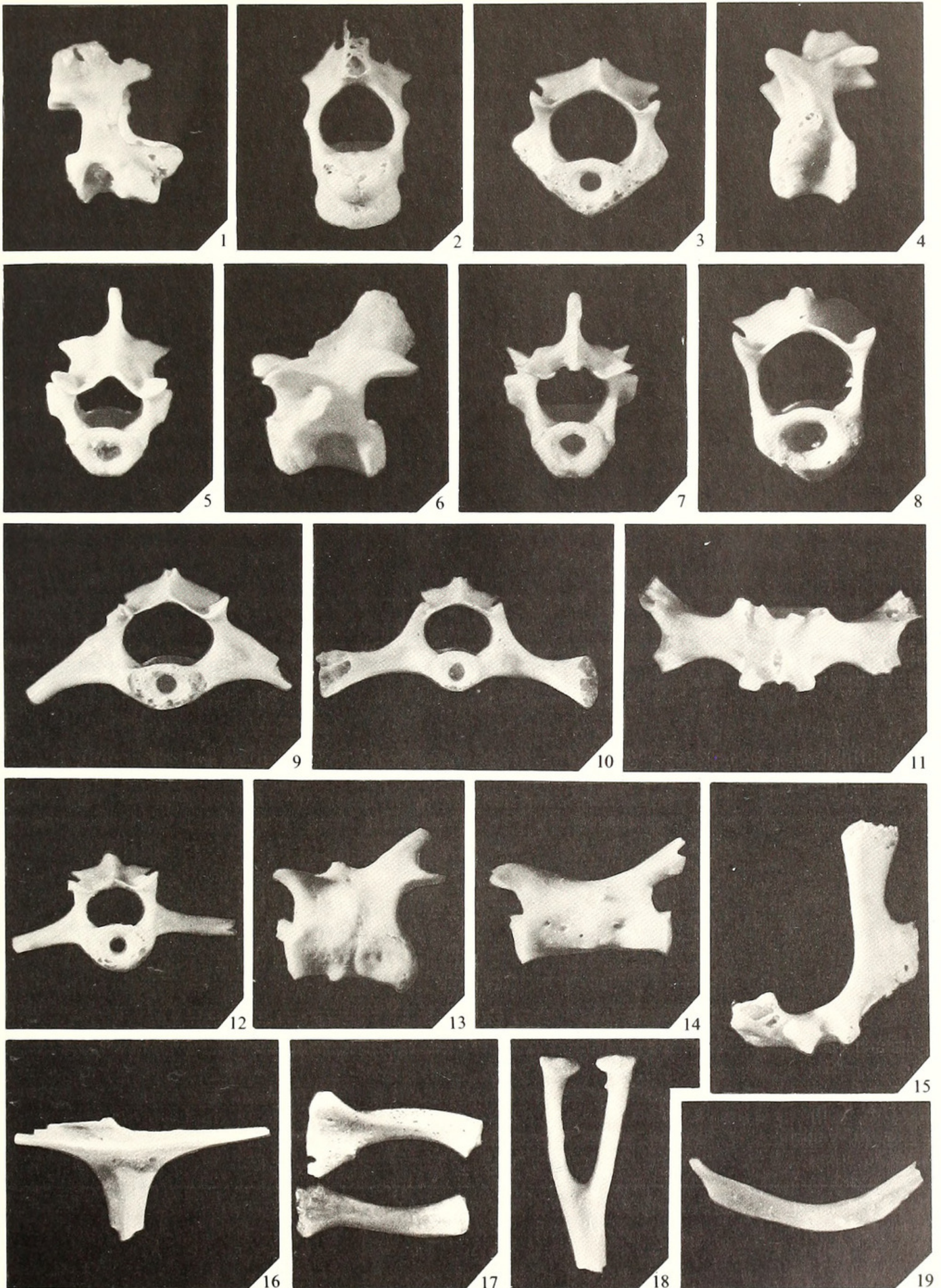
In total, five elements contribute to the pectoral girdle: one interclavicle, two clavicles, and two scapulocoracoids. There is no suture visible separating the scapula from the coracoid.

The interclavicle is a T-shaped bone with a slender anterior crossbar that supported the clavicles (text-fig. 12*a*; Pl. 53, fig. 16). This crossbar curves dorsally at its distal extremities. The facets for the clavicles are situated on the anteroventral edge of the bone and take the form of confluent grooves allowing the paired clavicles to meet at the midline.

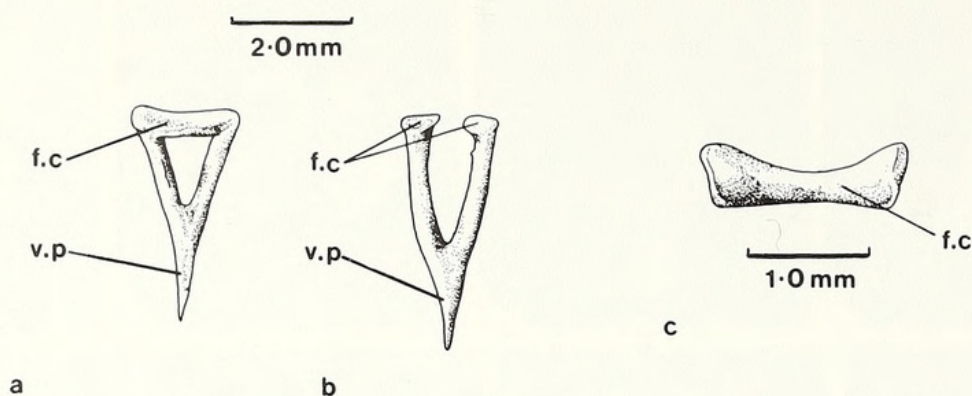
The clavicles are slender rod-like elements that curve dorsoventrally from their articulation with the interclavicle (text-fig. 12*b, c, d*). A long slender depression on the posteroventral surface represents the facet for the interclavicle and there is a small notch at the distal end where it makes contact with the scapulocoracoid. However, the posterolateral border of the clavicle possibly abutted against a cartilagenous zone of the scapulocoracoid for a short distance ventral to this notch.

EXPLANATION OF PLATE 53

Figs. 1–19. *Planocephalosaurus robinsonae*. 1, AUP No. 11093, atlas/axis complex, right lateral view, $\times 8$. 2, AUP No. 11123, atlas/axis complex, anterior view, $\times 9$. 3, AUP No. 11094, cervical vertebra, anterior view, $\times 9$. 4, AUP No. 11094, cervical vertebra in anterior, left lateral, and posterior views, $\times 6.5$. 5, AUP No. 11096, posterior dorsal vertebra, anterior view, $\times 10$. 6, AUP No. 11097, 1st sacral vertebra, anterior view, $\times 8.5$. 7, AUP No. 11098, 2nd sacral vertebra, anterior view, $\times 7$. 8, AUP No. 11098, 2nd sacral vertebra, dorsal view, $\times 7$. 9, AUP No. 11124, anterior caudal vertebra, anterior view, $\times 8$. 10, AUP No. 11125, mid-caudal vertebra, left lateral aspect, $\times 10$. 11, AUP No. 11126, caudal vertebra, left lateral aspect, $\times 7$. 12, AUP No. 11110, right scapulocoracoid, posterolateral view, $\times 5.5$. 13, AUP No. 11108, interclavicle, ventral aspect, $\times 8$. 14, AUP No. 11127 and 11106, cervical ribs, $\times 6$. 15, AUP No. 11104, chevron bone, $\times 8$. 16, AUP No. 11109, right clavicle, $\times 6.5$.

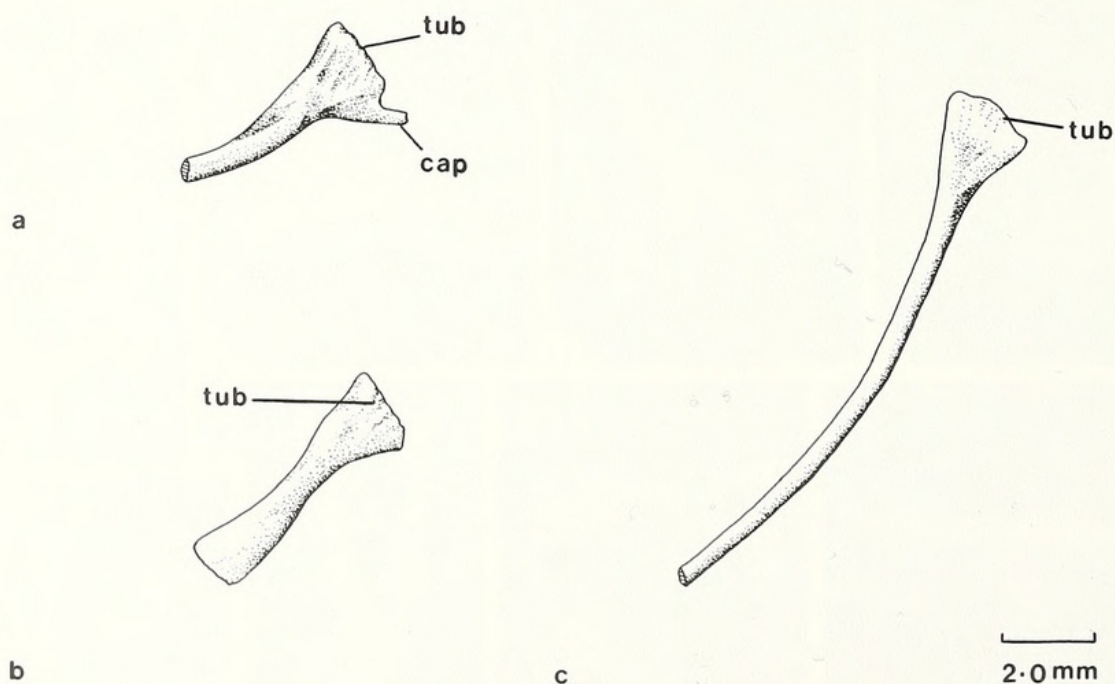


FRASER and WALKDEN, Upper Triassic sphenodontid

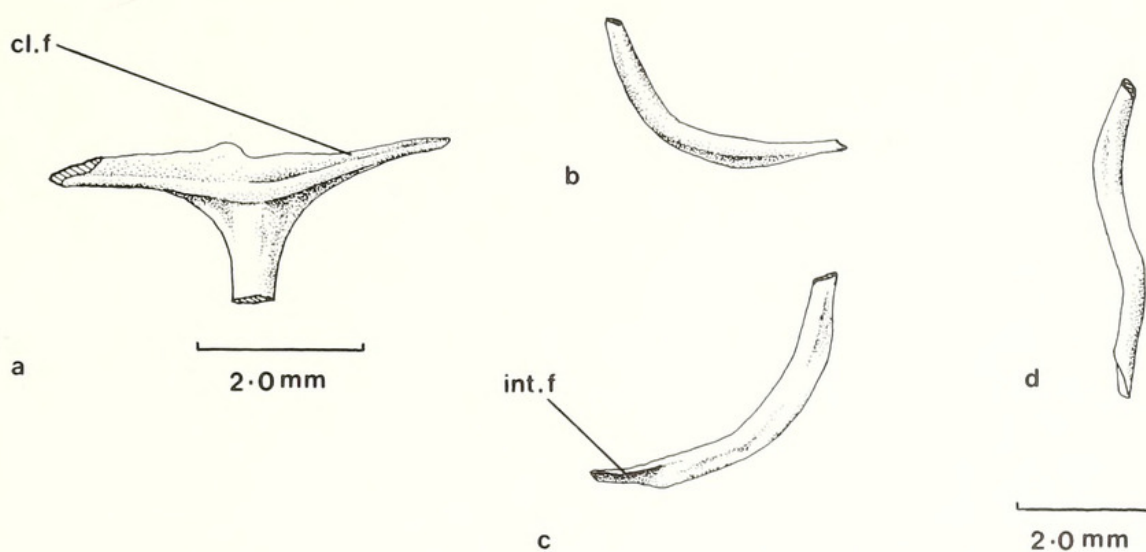


TEXT-FIG. 10. *Planocephalosaurus robinsonae*. Intercentra. *a*, anterior chevron bone, AUP No. 11103, in anterior view. *b*, posterior chevron, AUP No. 11104, anterior view. *c*, dorsal intercentrum, AUP No. 11102, dorsal view.

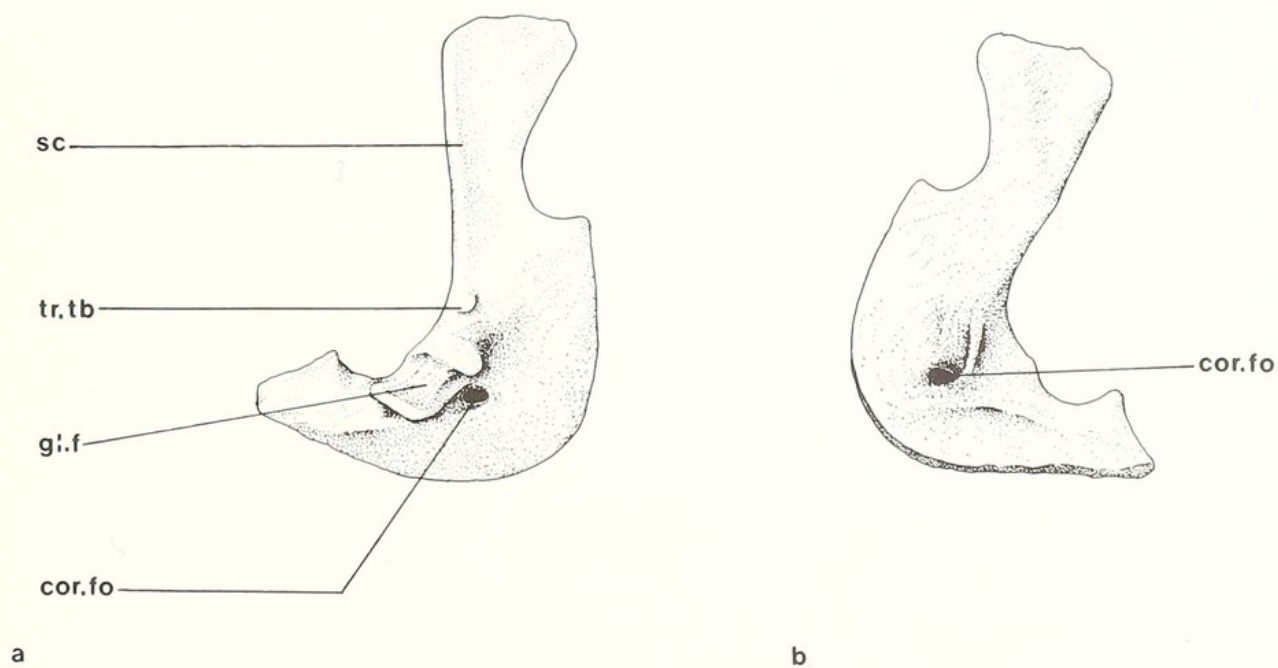
The scapulocoracoid is generally rather poorly preserved, but there are one or two almost complete specimens (text-fig. 13; Pl. 53, fig. 15). The glenoid fossa is the most robust part of the bone and consequently is more frequently preserved. It bears well-developed buttresses to support the proximal head of the humerus. Anterior to the glenoid is the supracoracoid foramen which carried the supracoracoid nerve and associated blood-vessels. Along the posterior margin of the bone, immediately dorsal to the glenoid, is a small tubercle to which the triceps tendon was attached. The element extends dorsally and there is a single fenestration entering into the anterior margin of the scapula blade which, as in the Lacertilia, probably related to the origin of the limb musculature (Romer 1956).



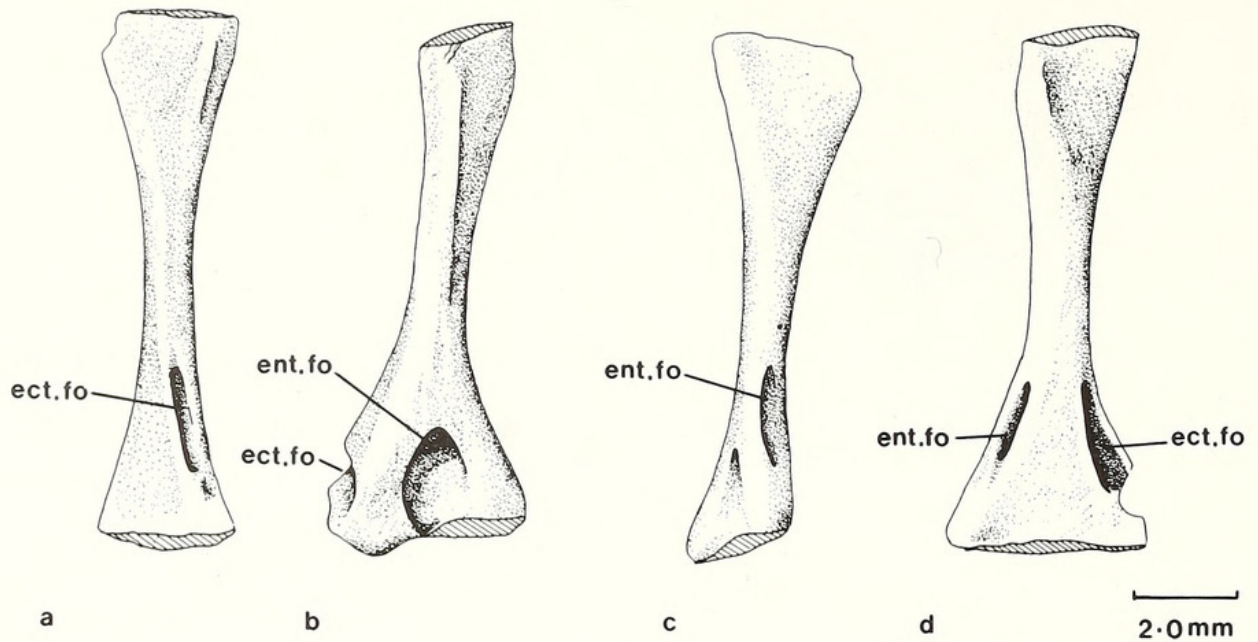
TEXT-FIG. 11. *Planocephalosaurus robinsonae*. Ribs. *a*, anterior cervical, AUP No. 11105. *b*, posterior cervical, AUP No. 11106. *c*, anterior dorsal, AUP No. 11107.



TEXT-FIG. 12. *Planocephalosaurus robinsonae*. Dermal elements of the pectoral girdle. *a*, an interclavicle, AUP No. 11108, in ventral aspect. Right clavicle, AUP No. 11109, in *b*, anterior view, *c*, posterior view, and *d*, dorsal view.



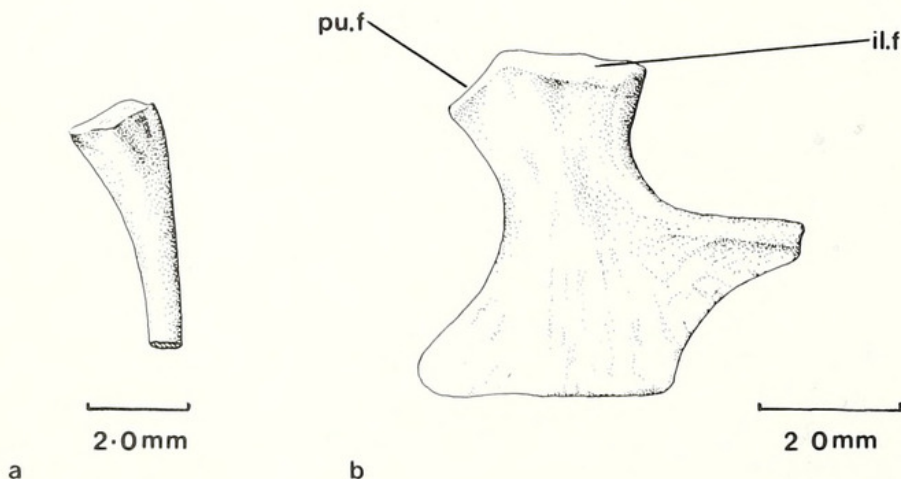
TEXT-FIG. 13. *Planocephalosaurus robinsonae*. Reconstruction of a right scapulocoracoid from AUP Nos. 11110 and 11111. *a*, lateral and *b*, mesial aspects.



TEXT-FIG. 14. *Planocephalosaurus robinsonae*. Partial reconstruction of the humerus from AUP Nos. 11112 and 11113. *a*, anterior, *b*, ventral, *c*, posterior, and *d*, dorsal aspects.

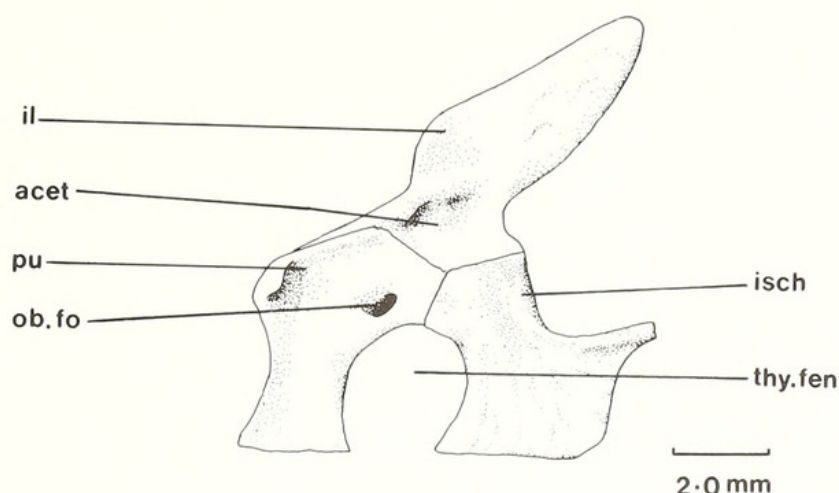
FORELIMB

The humerus (Pl. 54, figs. 1–4) is a slender element bearing expanded and compressed proximal and distal heads with an axial twist of the shaft so that the planes of the two heads are approaching 90° to each other (text-fig. 14). The proximal head is flattened anteroposteriorly with a ridge on the anteroventral edge marking the insertion of the latissimus dorsi muscle (text-fig. 14*a*). A similar ridge on the posteroventral edge was for the insertion of the deltopectoralis muscle (text-fig. 14*b*). The distal head is dorsoventrally compressed with the entepicondyle expanded slightly more than the ectepicondyle. The entepicondyle is perforated by a foramen (text-fig. 14*c*) which opens into a deep depression on the ventral surface (text-fig. 14*b*). The ectepicondyle foramen (text-fig. 14*d*), which allows for the passage of the radial nerve and blood-vessels, generally appears more as a groove than a foramen since the bone bridging across the canal is thin and membranous and thus prone to fragmentation. The articular surfaces on both proximal and distal heads have not been preserved in any of the specimens recovered.



TEXT-FIG. 15. *Planocephalosaurus robinsonae*. *a*, proximal head of an ulna, AUP No. 11114. *b*, lateral aspect of a left ischium, AUP No. 11115.

TEXT-FIG. 16. *Planocephalosaurus robinsonae*. Composite reconstruction of a left pelvic girdle in lateral aspect.

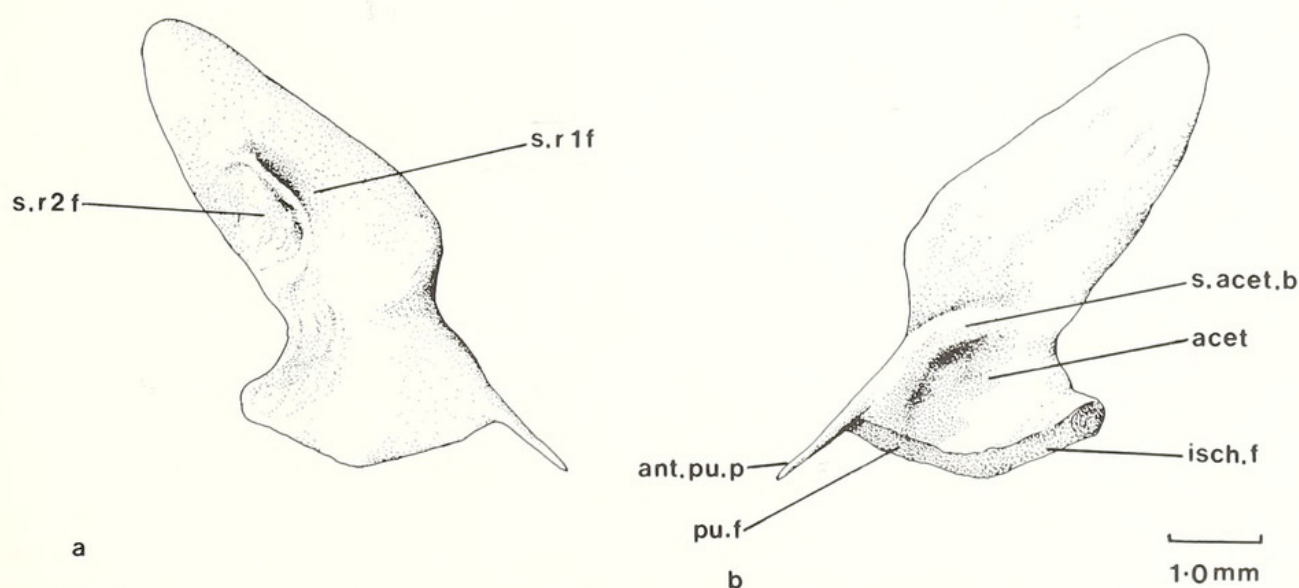


The epipodials are not as well represented being more slender and consequently rather more vulnerable to breakage. Only the proximal end of the ulna is completely known (text-fig. 15a). The expanded head is flattened anteroposteriorly and in all probability bore an olecranon epiphysis which is missing in all the recognizable specimens. There is a shallow depression on the posterior surface of the head outlining an area for muscle attachment. The shaft is narrow and circular in cross-section.

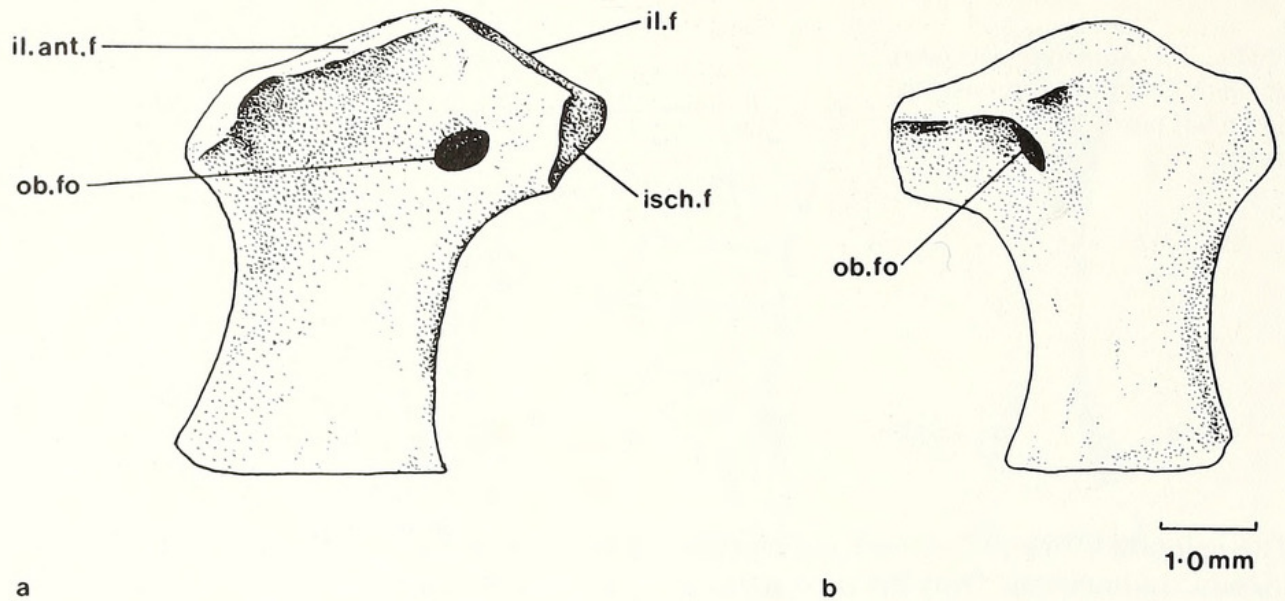
PELVIC GIRDLE

All three elements of the pelvic girdle are well represented in the deposits and a complete reconstruction is possible (text-fig. 16).

The ilium (Pl. 54, fig. 5) consists of a posterodorsally directed iliac blade which medially bears articular surfaces for the two sacral ribs (text-fig. 17a). The bone expands ventrally to form the major part of the acetabulum which is bounded dorsally by a well-defined supracetabular buttress (text-fig. 17b). On the anterior edge of the element, just dorsal to the buttress, is a small tuberosity for the attachment of the iliotibialis muscle. There are broad ventral contacts with the pubis and ischium and in addition an anterior process sheathed the anterior edge of the pubis thereby lending rigidity to the structure of the girdle.



TEXT-FIG. 17. *Planocephalosaurus robinsonae*. Reconstruction of left ilium from AUP No. 11116. a, mesial and b, lateral aspects.



TEXT-FIG. 18. *Planocephalosaurus robinsonae*. Left pubis, AUP No. 11117. *a*, lateral and *b*, mesial aspects.

The pubis (text-fig. 18*a*; Pl. 54, fig. 6) bears a dorsal facet for the ilium and a shorter posterior facet for the ischium. An obturator foramen is situated just anterior to the latter facet. The ventral plate of the bone is emarginated posteriorly by the thyroid fenestra which separates the pubis from the ischium ventrally.

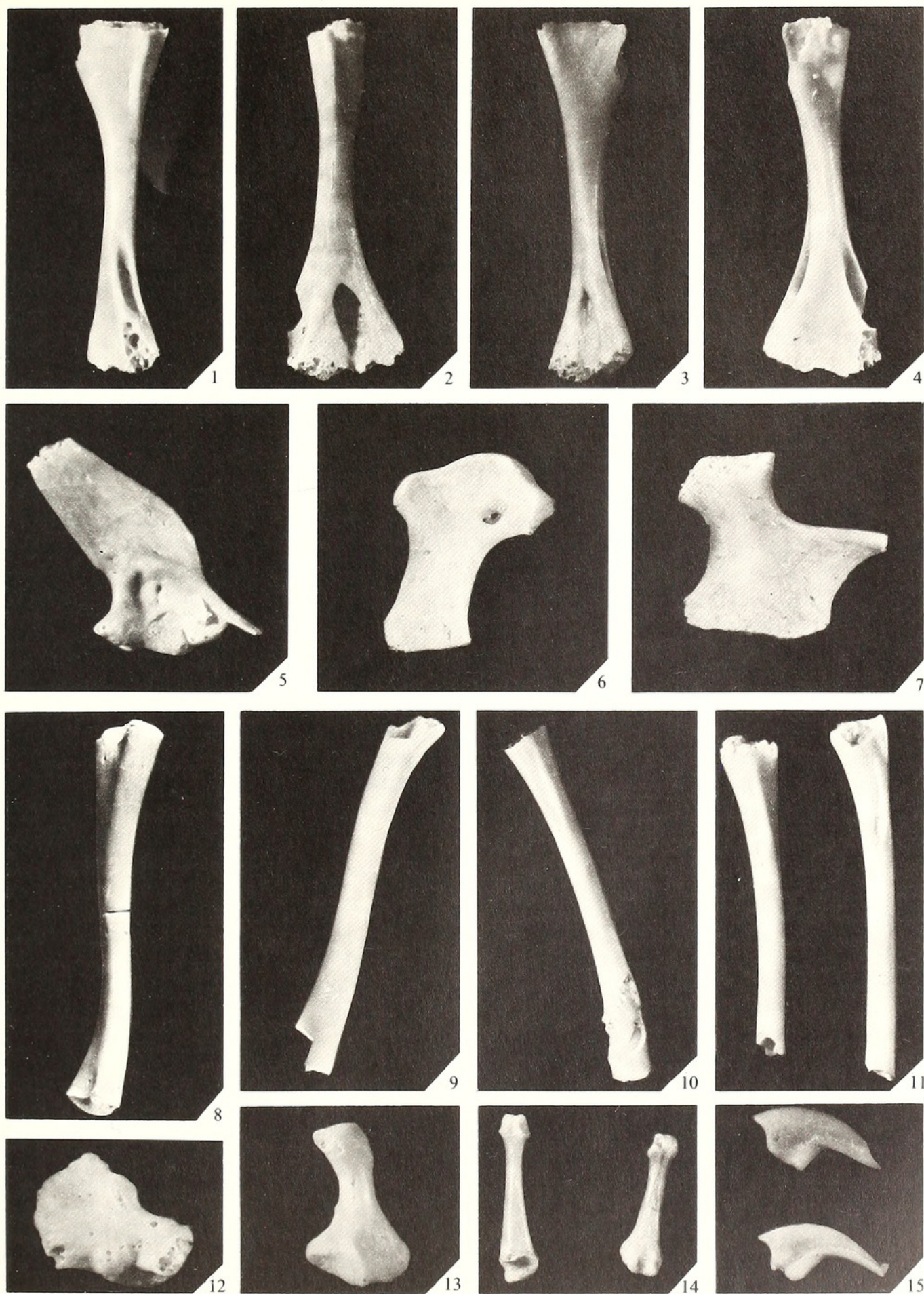
The ischium (text-fig. 15*b*; Pl. 54, fig. 7) formed the posterior half of the puboischiadic plate. The anterior edge has a short facet for the pubis and ventral to this there is a concave margin marking the posterior boundary of the thyroid fenestra. The posterior margin of the bone is extended backwards into a prominent tubercle for the attachment of ligaments and tendons of the tail musculature.

HINDLIMB

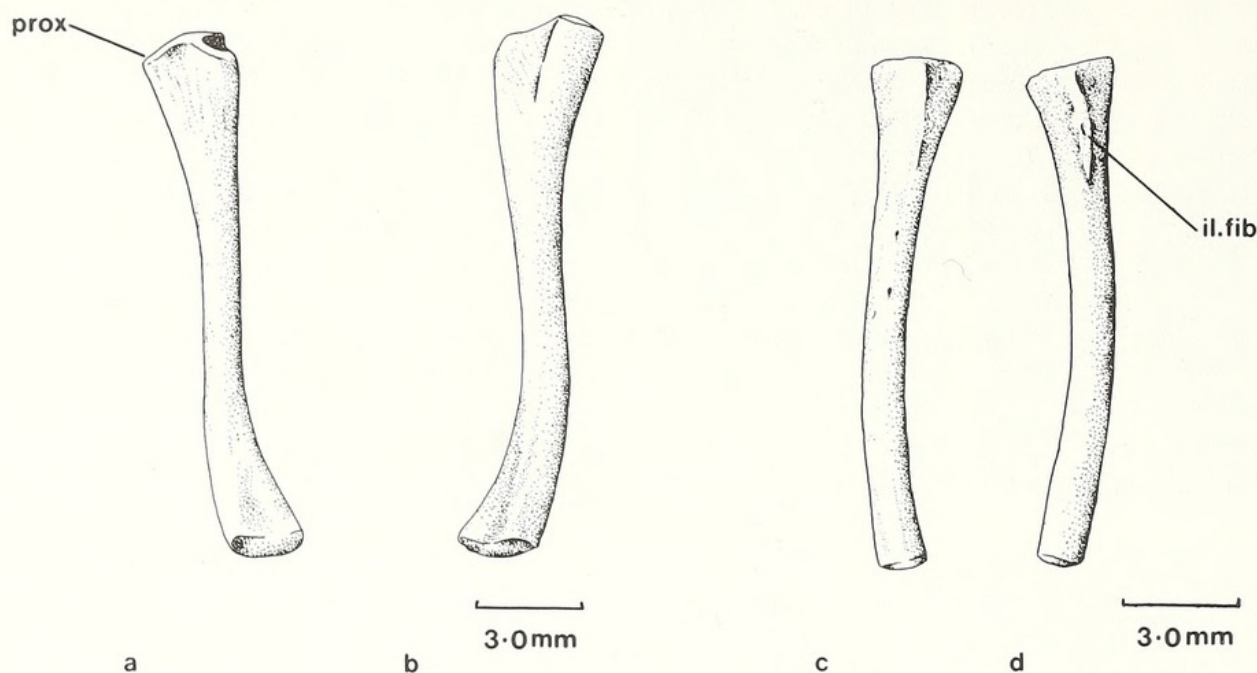
The femur (Pl. 54, figs. 8, 9) is a long slender bone with a sigmoid flexure along the length of the shaft (text-fig. 19*a, b*). The proximal expansion bears a well-developed internal trochanter situated ventral to the articulation head. Lying on the anterior surface, positioned between the internal trochanter and the head, is an area for the attachment of the puboischiofemoralis internus. Unfortunately, the epiphyses of the element are missing in all instances and thus other details of muscle attachment are unknown.

EXPLANATION OF PLATE 54

Figs. 1–15. *Planocephalosaurus robinsonae*. 1–4, AUP No. 11112, humerus in anterior, ventral, posterior, and dorsal aspects, $\times 5.5$. 5, AUP No. 11132, right ilium, lateral aspect, $\times 5.5$. 6, AUP No. 11117, left pubis, lateral view, $\times 5.5$. 7, AUP No. 11115, left ischium, lateral view, $\times 5.5$. 8, AUP No. 11118, femur, $\times 4$. 9, AUP No. 11128, femur, $\times 4.5$. 10, AUP No. 11119, fibia, $\times 4$. 11, AUP No. 11129, two tibias, $\times 4$. 12, AUP No. 11120, astragalocalcaneum, $\times 9.5$. 13, AUP No. 11121, tarsometatarsal, $\times 10$. 14, AUP No. 11130, phalanges, dorsal, and planar views, $\times 10$. 15, AUP No. 11131, ungual phalanges, $\times 9.5$.



FRASER and WALKDEN, Upper Triassic sphenodontid



TEXT-FIG. 19. *Planocephalosaurus robinsonae*. Reconstruction of a femur from AUP No. 11118. *a*, anterior and *b*, posterior aspects. Reconstruction of a tibia from AUP No. 11119, *c*, anterior and *d*, posterior aspects.

Of the two epipodials only the tibia (text-fig. 19*c, d*; Pl. 54, figs. 10, 11) has been confidently identified, but again the articulation surfaces themselves have been poorly preserved. It is a long slender bone that is concave towards the fibula. The posterior surface of the proximal head bears a slight ridge and rugosity for insertion of the iliofibularis musculature.

MANUS AND PES

A variety of small carpals, tarsals, and metapodials have been recovered from the residues at all the sites, but these have proved difficult to separate into distinct forms and it is likely that the structures of the manus and pes are quite uniform in all the Triassic sphenodontids; varying only in size.

The manus and pes of *Planocephalosaurus* are described from elements recovered solely from site four, but the following comments also serve as an outline for the generalized sphenodontid structure.

The small bones of the carpus are difficult to determine since many of their distinguishing characteristics are obscured by erosion and polishing. The astragalus and calcaneum are fused into an astragalocalcaneum with no trace of sutures (text-fig. 20*a*; Pl. 54, fig. 12). It is a relatively flat bone-bearing articulation facets on its dorsomedial surface for the tibia and fibula, and a well-defined concavity for the fourth distal tarsal. The distal tarsals themselves are unknown.

With the exception of the fifth metatarsal, the metapodials are all similar, varying only in size and slight details of the proximal head. Each metapodial has a long slender shaft with the proximal head slightly expanded and usually bearing small tuberosities for the attachment of the digital extensor and flexor muscles. The fifth metatarsal (text-fig. 20*c, d*), which should more accurately be termed the fifth tarsometatarsal, since it is a fusion of the fifth distal tarsal with the fifth metatarsal, is easily recognized as a small robust bone that is clearly 'hooked' and very similar to that observed in *Sphenodon*. The proximal head has a broad facet for the fourth distal tarsal, and tuberosities on the

plantar surface were for the attachment of flexor muscles such as the gastrocnemius. Robinson (1975) discussed the role of the hooked fifth metatarsal in the functioning of the hind limb and concluded that it was of major importance in allowing for the opposition of the first digit to the fifth, and thereby increasing the gripping powers of the foot. It also had a role to play in bringing the crus and pes musculature to bear in the locomotor effect of the hind limb.

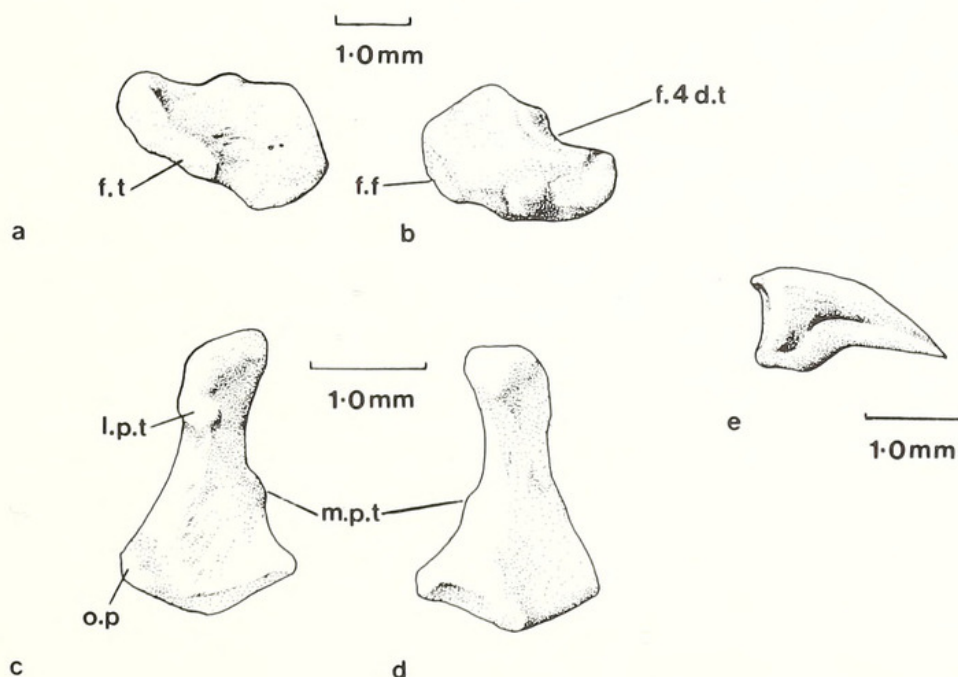
The phalanges (Pl. 54, fig. 14) bear deeply concave proximal articulation surfaces whilst the distal head is convex. There is some variation in the shape of the shaft—some have an almost circular cross-section whereas others exhibit a degree of dorsoventral compression and also on occasions possess a shallow ventral ridge. The latter were probably the most proximal in position (Evans 1981). A number of ungual phalanges are known which are mediolaterally compressed (text-fig. 20e; Pl. 54, fig. 15). These phalanges possess medial and lateral grooves which may have borne ducts supplying secretory glands.

As a consequence of the material being completely dissociated the phalangeal formula is unknown, but it may have been the same as *Sphenodon*, namely:

Hand 2, 3, 4, 5, 3
Foot 2, 3, 4, 5, 4

RECONSTRUCTION OF THE SKELETON

There is a complete absence of articulated material from which direct measurements of *Planocephalosaurus* could be taken. Thus to deduce the relative proportions of the body the mean sizes of the available completely ossified elements must be calculated. There are, however, only a few complete limb bones which do not provide satisfactory sample sizes from which to calculate means. To rectify this deficiency the full lengths of a number of incomplete bones were extrapolated by direct



TEXT-FIG. 20. *Planocephalosaurus robinsonae*. Reconstruction of a left astragalocalcaneum from AUP No. 11120, *a*, anterior and *b*, posterior views. Right tarsometatarsal, AUP No. 11121, in *c*, plantar and *d*, dorsal views. *e*, Ungual phalanx, AUP No. 11122, in lateral view.

comparison with intact representatives of each of the four relevant limb elements, and the following mean lengths were obtained:

Forelimb: Humerus	11 mm	} 20 mm
Ulna	9 mm	
Hindlimb: Femur	16 mm	} 29 mm
Tibia	13 mm	

With respect to the vertebrae, their numbers more than their individual sizes govern the relative proportions of the axial skeleton. With dissociated material it is very difficult to estimate the exact numbers of vertebrae in the column, but the relative abundance of each of the four vertebral types within the deposits (Table 1) suggests that it is perfectly acceptable to reconstruct *Planocephalosaurus* with the same vertebral count as *Sphenodon*.

TABLE 1. Relative abundances of the four major vertebral types of *Planocephalosaurus robinsonae* expressed as a percentage of the total vertebral count from two different strata at Site 4. The percentages for *Sphenodon* are obtained from data given by Hoffstetter and Gasc (1969) where *Sphenodon* is assumed to possess twenty-five presacials, two sacials, and between twenty-nine and thirty-six caudals.

	<i>P. robinsonae</i> . Level k, site 4	<i>P. robinsonae</i> . Level m, site 4	<i>P. robinsonae</i> . Total numbers at site 4	<i>Sphenodon</i> <i>punctatus</i>
Per cent cervical vertebrae	13.3	12.8	12.5	12.7–14.3
Per cent dorsal vertebrae	25.7	26.5	26.2	27.0–30.4
Per cent sacral vertebrae	2.8	3.2	2.9	3.2–3.6
Per cent caudal vertebrae	58.7	57.7	58.0	57.2–51.8
Total number of vertebrae in the sample	218	189	646	

The full reconstruction shows *Planocephalosaurus* having a snout-vent length of approximately 7.5 cm with an additional 7.0–8.5 cm of tail. The forelimb/hindlimb ratio is 69.6%, but this disparity is in common with other eosuchians and is not as great as that generally seen in bipedal reptiles such as *Malerisaurus*, *Saltoposuchus*, *Basiliscus*, etc. (Ewer 1965; Chatterjee 1980). In addition, the vertebral numbers suggest that the trunk of *Planocephalosaurus* was not reduced in length; the combined tibia and femur length being approximately 45% that of the trunk. In bipeds, on the other hand, the latter ratio is much higher: 75% for *Malerisaurus* and 100% in *Basiliscus* (Chatterjee 1980). The small limb disparity in quadrupedal eosuchians, such as *Planocephalosaurus*, may permit better acceleration and the ability to change direction quickly. This, coupled with opposable first and fifth digits would have enabled *Planocephalosaurus* to negotiate quite rough terrain at speed in its attempts to avoid danger and capture elusive prey.

DISCUSSION

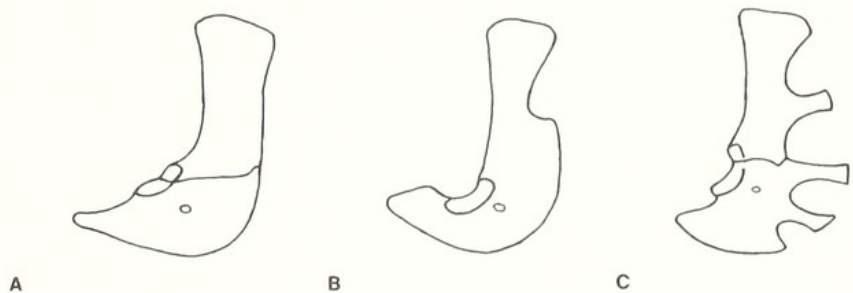
Following Evans (1980), the family Sphenodontidae is considered to lie within the infraclass Eosuchia. The following discussion concentrates on the affinities of *Planocephalosaurus* with a second eosuchian, *Gephyrosaurus*, and assesses the possibility of including the latter within the Sphenodontidae.

The rudimentary zygosphenic articulation of *Planocephalosaurus* (text-fig. 9a) is a character not reported amongst other fossil eosuchians with the exception of *Saurosternon* and *Gephyrosaurus*.

However, Evans (1981) points out the difficulties of observing such a feature in articulated skeletons and suggests that it might be more widespread than reported. Together with *Gephyrosaurus*, *Homeosaurus*, and *Sphenodon* strong fracture planes occur in the caudal vertebrae of *Planocephalosaurus*. These are absent in many other eosuchian genera. Evans (1981) suggests this may be the result of the functional importance of the tail in other groups (e.g. for swimming or as a counterbalance) and may not have any bearing on ancestral relationships.

In a similar fashion to *Sphenodon* the scapula and coracoid of *Planocephalosaurus* have fused into a single unit and the same is also true of *Gephyrosaurus*. But unlike *Sphenodon*, other sphenodontids, and *Gephyrosaurus*, *Planocephalosaurus* does possess a fenestrated scapulocoracoid. Compared with the lacertilians this fenestration is rudimentary as only one fenestra occurs in the scapula region of the bone compared to two in *Iguana* (text-fig. 21). *Iguana* also possesses two fenestra in the coracoid section of the bone whilst in *Planocephalosaurus* this region is unfenestrated. Evans (1981) believed that such fenestration is a uniquely lacertilian character, but the present evidence would suggest otherwise and further support is provided by Carroll (1975) who reported a similar condition in *Saurosternon*. Thus with regard to the pectoral girdle *Planocephalosaurus* would appear quite advanced, but with respect to the humerus it conforms to the pattern observed in *Sphenodon* and *Gephyrosaurus*, possessing both ent- and ectepicondylar foramina.

TEXT-FIG. 21. The scapulocoracoid ossification of A, *Sphenodon*, B, *Planocephalosaurus*, and C, *Iguana*.



The pelvic girdle of *Planocephalosaurus* is very similar to that of *Sphenodon* and *Homeosaurus* having a puboischiadic plate perforated by a well-developed thyroid fenestra. This condition is also seen in other advanced eosuchians such as *Kuehneosaurus* and *Gephyrosaurus*. The iliac blade of *Planocephalosaurus* is not as elongated as that of *Sphenodon* and resembles more closely that of *Gephyrosaurus*.

Thus the postcranial skeleton of *Planocephalosaurus* does not depart noticeably from the general sphenodontid structure. The main difference is in the structure of the scapulocoracoid where that of *Planocephalosaurus* exhibits fenestration, but this is atypical of the family. In all other respects, including the cranial morphology (Fraser 1982), *Planocephalosaurus* is a typical sphenodontid. At the same time it can be said that there are a number of similarities between *Planocephalosaurus* and *Gephyrosaurus*. However, *Gephyrosaurus* was assigned by Evans (1980) to a new family within the Eosuchia, the Gephyrosauridae. There is therefore reason to believe that there are some affinities between the Sphenodontidae and Gephyrosauridae and a brief résumé of cranial morphology would seem to strengthen the argument.

Evans (1980) commented on the fusion of both frontals and parietals in *Gephyrosaurus* and considered this to be unusual within the Eosuchia; however, *Planocephalosaurus* also shows this characteristic. The sphenodontids generally do not possess a lachrymal and whilst this element is present in *Gephyrosaurus* it is quite rudimentary. The incomplete lower temporal bar of *Gephyrosaurus* is a characteristic that also occurs in some members of the Sphenodontidae—including *Planocephalosaurus* and *Clevosaurus* (Robinson 1973). The quadriradiate shape of the squamosal is a feature shared with the sphenodontids and Evans herself (1980) noted the similarity of the quadrate–quadratojugal arrangement but concluded that it must be a result of convergence.

Turning to the palate, the possession of an enlarged row of teeth on the palatine of *Gephyrosaurus* is another characteristic of the spenodontids. Whilst there is a general tendency in *Clevosaurus* and *Sphenodon* to show a reduction in the number of small teeth scattered across the palatal elements, *Planocephalosaurus*, in common with *Gephyrosaurus*, retains a number of small palatal teeth.

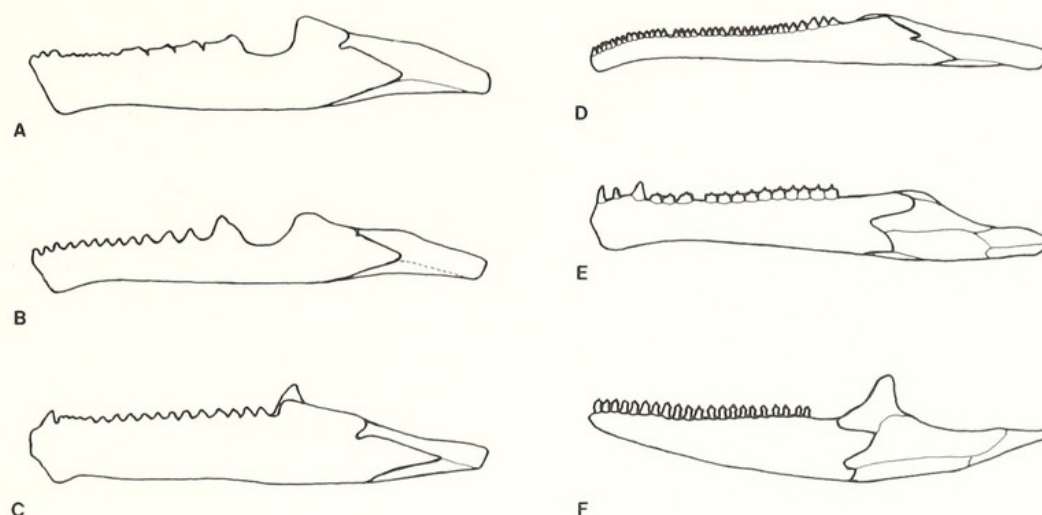
The posterior process of the dentary of *Sphenodon* meets the articular complex and braces the lower jaw (text-fig. 22). Such a process is not seen in other eosuchian genera such as *Youngina*, *Tanystropheus*, and *Kuehneosaurus*, but it is known in other spenodontids such as *Planocephalosaurus* and *Clevosaurus* and is also seen in *Gephyrosaurus*. Evans (1980) notes the overall similarity of the *Gephyrosaurus* lower jaw to that of the spenodontids, including the lack of a splenial, but again concludes that this must be the result of convergence.

The number of characteristics shared by *Gephyrosaurus* and the Sphenodontidae suggest a close relationship between the two (Table 2), the only obvious difference so far noted being the existence of a rudimentary lachrymal in *Gephyrosaurus*, and it is quite easy to see how this element could have been lost in the spenodontids. However, one major difference does exist and that is the attachment of the marginal dentition. Whereas *Gephyrosaurus* has a pleurodont attachment the spenodontids typically display an acrodont dentition. This difference does not necessarily rule out a close relationship between the two, however, since within the Lacertilia both acrodont and pleurodont forms are recognized.

TABLE 2. A comparison of spenodontids and some other eosuchians.

	<i>Sphenodon</i>	<i>Clevosaurus</i>	<i>Planocephalosaurus</i>	<i>Homoiosaurus</i>	<i>Kuehneosaurus</i>	<i>Tanystropheus</i>	<i>Gephyrosaurus</i>	<i>Rhynchosaurs</i>	<i>Youngina</i>	<i>Prolacerta</i>	<i>Macrocnemus</i>	<i>Palaeagama</i>	<i>Askeptosaurus</i>
Fusion of the frontals	o	o	x	o	o	o	x	o	o	o	o	o	o
Fusion of the parietals	x	o	x	o	o	x	x	x	o	o	o	o	o
Lachrymal small or absent	x	x	x	x	o	x	x	o	o	o	x	-	o
Lower temporal arcade incomplete	o	x/o	x/o	o	x	x	x	o	o	x	x	-	o
Enlarged palatine tooth row	x	x	x	x	o	o	x	o	o	o	o	-	o
Dentary with pronounced posterior process	x	x	x	x	o	o	x	o	o	x	o	-	o
Splenial absent	x	x	x	-	o	x	x	o	o	o	o	-	o
Acrodont dentition	x	x	x	x	o	o	o	o	o	o	o	o	o
Zygosphenes/zygantrum	x	x	x	-	o	o	x	o	o	o	o	o	o
Caudal fracture planes	x	x	x	x	o	x	x	o	o	o	o	o	o
Most presacrals with single headed ribs	x	x	x	x	o	o	x	o	o	x	o	o	o
Vertebrae amphicoelous and notochordal	x	x	x	x	o	o	x	o	x	x	x	x	x
Scapulocoracoid a single bone	x	x	x	x	o	o	x	x	o	x	o	o	o
Scapulo coracoid fenestrated	o	o	x	o	o	o	o	o	o	o	o	o	o
Humerus with two distal foramina	x	x	x	x	o	x	x	o	x	o	o	x	o
Thyroid fenestra	x	x	x	x	x	x	x	o	o	o	x	o	x
Hooked fifth tarsometatarsal	x	x	x	x	o	x	x	x	o	x	x	o	o

x—character present. o—character absent.



TEXT-FIG. 22. Lateral aspects of the dentaries of A, *Clevosaurus*, B, *Planocephalosaurus*, C, *Sphenodon*, D, *Gephyrosaurus*, E, *Tanystropheus*, and F, *Iguana*. (C after Robinson (1976), D after Evans (1980), E after Wild (1980), and F after Romer (1956)).

It might be postulated that intermediate forms would exist between sphenodontids and their eosuchian ancestors in which the marginal dentition displayed some degree of pleurodonty. The evidence presented suggests that *Gephyrosaurus* may be such an intermediate form. If it is not considered to be a 'true' sphenodontid then it probably represents an early offshoot from the stem Sphenodontidae.

It is also postulated that accompanying this trend towards a firmer anchorage of the marginal dentition, there is a tendency within the Sphenodontidae for a reduction in tooth numbers. Thus it is likely that within the Sphenodontidae and their ancestors there is a spectrum of forms ranging from small, relatively delicate individuals with numerous pleurodont teeth to more robust species possessing firm acrodon teeth with a marked decrease in their absolute numbers (Table 3). Such

TABLE 3. Tooth arrangement and insertion in three Triassic eosuchians indicating a probable trend towards acrodonity and a reduction of numbers in the Sphenodontidae.

	<i>Gephyrosaurus bridensis</i>	<i>Planocephalosaurus robinsonae</i>	<i>Clevosaurus hudsoni</i>
Palatal Dentition	Numerous teeth scattered across palatines, pterygoids, and vomers. Ordered into an enlarged tooth row on the palatine	Numerous teeth on palatines, pterygoids, and vomers. Predominantly arranged in rows with two enlarged tooth rows on the palatine	Reduction in palatal dentition. Teeth arranged in two rows on the pterygoids. A single enlarged tooth row on the palatine. Occasionally a few vomerine teeth
Insertion of marginal dentition	Pleurodont	Acrodon	Acrodon
Number of functional marginal teeth in the mature individual:			
(a) premaxilla	8-10	4	2-3
(b) maxilla	35-40	12-14	5-6
(c) dentary	30-40	13-14	5-6
			Juvenile teeth worn away to the bone anteriorly

ditional modifications are obviously associated with altered dietary habit, with the skull also becoming generally more robust and consequently capable of withstanding the greater stresses imposed upon it by more demanding diets.

Another species that occurs in the Cromhall fauna which is expected to substantiate the evolutionary trends outlined above, is presently being described by D. I. Whiteside (in prep.) from abundant remains occurring in Triassic fissure deposits at Tytherington Quarry (ST 660 890).

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APPENDIX

Total number of each postcranial element of *Planocephalosaurus robinsonae* recovered from fissure four, Cromhall Quarry.

Element	at.ar.	at/ax.	ce.v.	d.v.	1st s.	2nd s.	caud.	ch.	int.c.	ce.r.	d.v.	cl.
Numbers	17	12	69	169	8	11	377	147	87	61	150	13
Element	int.cl.	sc.	hum.	rad.	il.	isch.	pu.	fem.	tib.	5th met.	ast.	
Numbers	9	12	36	14	27	21	13	26	23	26	3	

ABBREVIATIONS

at.ar.	atlas arch	int.c.	intercentrum	il.	ilium
at./ax.	atlas/axis	ce.v.	cervical rib	isch.	ischium
ce.v.	cervical vertebra	d.r.	dorsal rib	pu.	pubis
d.v.	dorsal vertebra	cl.	clavicle	fem.	femur
1st s.	1st sacral vertebra	int.cl.	interclavicle	tib.	tibia
2nd s.	2nd sacral vertebra	sc.	scapulocoracoid	5th met.	5th tarsometatarsal
caud.	caudal vertebra	hum.	humerus	ast.	astragalocalcaneum
ch.	chevron bones	rad.	radius		

ABBREVIATIONS USED IN TEXT-FIGURES

acet.	acetabulum	f.t.	tibia facet
a.i.	axis intercentrum	f.4 d.t.	facet for 4th distal tarsal
ant.pu.p.	anterior pubis process	gl.f.	glenoid fossa
a.pr.	anterior process	il.	ilium
cap.	capitulum	il.ant.f.	anterior facet for ilium
cl.f.	clavicle facet	ilf.	facet for ilium
cor.fo.	coracoid foramen	il.fib.	insertion for iliofibularis muscle
c.r.	caudal rib	int.f.	facet for interclavicle
d.pop.	diapophysis	isch.	ischium
ect.fo.	ectepicondylar foramen	isch.f.	facet for ischium
ent.fo.	entepicondylar foramen	l.p.t.	lateral plantar tubercle
f.c.	facet for centrum	m.p.t.	median plantar tubercle
f.f.	fibula facet	n.f.	nutrient foramen
f.p.	fracture plane	n.s.	neural spine

Abbreviations used in text-figs. (cont.)

ob.fo.	obturator foramen	r.f.	rib facet
od.f.	odontoid facet	s.acet.b.	supracetabular buttress
od.p.	odontoid process	sc.	scapula blade
o.p.	outer process	s.r.1	sacral rib 1
p.pop.	parapophysis	s.r.2	sacral rib 2
p.f.	posterior facet	s.r.1f.	facet for 1st sacral rib
prox.	proximal head	s.r.2f.	facet for 2nd sacral rib
pr.zyg.	prezygapophysis	thy.fen.	thyroid fenestra
pu.	pubis	tr.tb.	tubercle for triceps attachment
pu.f.	facet for pubis	tub.	tuberculum
p.zyg.	postzygapophysis	v.p.	ventral process

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