THE POSTCRANIAL SKELETON OF THE UPPER TRIASSIC SPHENODONTID 
PLANOCERHOSAURUS ROBINSONAE

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ABSTRACT. The postcranial skeleton of the Triassic sphenodontid, Planocerasaurus 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 eusuchian, 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 Planocerasaurus 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 Cleidosaurus hudsoni, particularly in the more poorly preserved fossils. To avoid such difficulties only elements from a single site, where Cleidosaurus is rare, have been considered. At this site (fissure four, text-fig. 1) archosaurs constitute the major percentage of the non-Planocerasaurus 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 Planocerasaurus 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 Planocerasaurus 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), Planocerasaurus 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 sphenodontid, *Sphenodon*. The centrum is of the notochordal amphiocelous type throughout. There is a rudimentary zygosphenic articulation (text-fig. 9a; Pl. 53, fig. 7) with the development of a zygosphene and zygantrum.

The element that was tentatively designated as the epitypogoid of *Planoccephalosaurus* (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 postzygapophyseal 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 sphenodontids such as *Homeosaurus* and *Kallimodon* have just seven. In the reconstruction (text-fig. 2) *Planoccephalosaurus* 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 tubercula. 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
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 diapophyses 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. 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 *Cleveosaurus* (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. 9a; 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.

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. 9b). 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. 9b); 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. 10b), 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. 10a). 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 pedicles (text-fig. 10b; Pl. 53, fig. 18).

As already mentioned, the ribs were typically of the holoccephalous 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. 11a). These may not necessarily have articulated with the parapophyses since ligaments could have completed the attachment where the capitula were reduced to mere protuberances. The posterior cervical ribs possess a short shaft that is expanded distally (text-fig. 11b; Pl. 53, fig. 17) whilst in the dorsal ribs the shaft is generally narrow and longer—particularly in the anterior dorsals (text-fig. 11c).

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. 12b; 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. 12b, c, d). A long slender depression on the posteroverentral 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 cartilaginous 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, ×8. 2, AUP No. 11123, atlas/axis complex, anterior view, ×9. 3, AUP No. 11094, cervical vertebra, anterior view, ×9. 4, AUP No. 11094, cervical vertebra in anterior, left lateral, and posterior views, ×6.5. 5, AUP No. 11096, posterior dorsal vertebra, anterior view, ×10. 6, AUP No. 11097, 1st sacral vertebra, anterior view, ×8.5. 7, AUP No. 11098, 2nd sacral vertebra, anterior view, ×7. 8, AUP No. 11098, 2nd sacral vertebra, dorsal view, ×7. 9, AUP No. 11124, anterior caudal vertebra, anterior view, ×8. 10, AUP No. 11125, mid-caudal vertebra, left lateral aspect, ×10. 11, AUP No. 11126, caudal vertebra, left lateral aspect, ×7. 12, AUP No. 1110, right scapulocoracoid, posterolateral view, ×5.5. 13, AUP No. 11108, interclavicle, ventral aspect, ×8. 14, AUP No. 11127 and 11106, cervical ribs, ×6. 15, AUP No. 11127 and 11106, cervical ribs, ×6. 16, AUP No. 11104, chevron bone, ×8. 17, AUP No. 11109, right clavicle, ×6.5.
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. 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. 14a). A similar ridge on the posteroverentral edge was for the insertion of the deltopectoralis muscle (text-fig. 14b). The distal head is dorsoventrally compressed with the entepicondyle expanded slightly more than the ectepicondyle. The entepicondyle is perforated by a foramen (text-fig. 14c) which opens into a deep depression on the ventral surface (text-fig. 14d). The ectepicondyle foramen (text-fig. 14d), 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. 16. Planoccephalosaurus 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 GIRDLK

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

The pubis (text-fig. 18a; 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 thyroideus fenestra which separates the pubis from the ischium ventrally.

The ischium (text-fig. 15f; 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 thyroideus 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. 19a, 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, ×5-5. 5, AUP No. 11132, right ilium, lateral aspect, ×5-5. 6, AUP No. 11117, left pubis, lateral view, ×5-5. 7, AUP No. 11115, left ischium, lateral view, ×5-5. 8, AUP No. 11118, femur, ×4. 9, AUP No. 11128, femur, ×4-5. 10, AUP No. 11119, fibia, ×4. 11, AUP No. 11129, two tibias, ×4. 12, AUP No. 11120, astragalocalcaneum, ×9-5. 13, AUP No. 11121, tarsometatarsal, ×10. 14, AUP No. 11130, phalanges, dorsal, and planar views, ×10. 15, AUP No. 11131, ungual phalanges, ×9-5.
FRASER and WALKDEN, Upper Triassic sphenodontid
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. 19c, 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 
astragalo-calcaneum with no trace of sutures (text-fig. 20a; 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. 20c, 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. 20c, Pl. 54, fig. 15). These phalanges possess medial and lateral grooves which may have borne ducts supplying sebaceous 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:

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

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

\[
\begin{align*}
\text{Forelimb:} & \quad \text{Humerus 11 mm} \quad \text{Ulna 9 mm} \quad \text{20 mm} \\
\text{Hindlimb:} & \quad \text{Femur 16 mm} \quad \text{Tibia 13 mm} \quad \text{29 mm}
\end{align*}
\]

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 presacral, two sacral, and between twenty-nine and thirty-six caudal vertebrae.

<table>
<thead>
<tr>
<th></th>
<th><em>P. robinsonae</em> Level k, site 4</th>
<th><em>P. robinsonae</em> Level m, site 4</th>
<th><em>P. robinsonae</em> Total numbers at site 4</th>
<th><em>Sphenodon punctatus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Per cent cervical</td>
<td>13.3</td>
<td>12.8</td>
<td>12.5</td>
<td>12.7-14.3</td>
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<tr>
<td>vertebral</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per cent dorsal</td>
<td>25.7</td>
<td>26.5</td>
<td>26.2</td>
<td>27.0-30.4</td>
</tr>
<tr>
<td>vertebral</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per cent sacral</td>
<td>2.8</td>
<td>3.2</td>
<td>2.9</td>
<td>3.2-3.6</td>
</tr>
<tr>
<td>vertebral</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Per cent caudal</td>
<td>58.7</td>
<td>57.7</td>
<td>58.0</td>
<td>57.2-51.8</td>
</tr>
<tr>
<td>vertebral</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total number of</td>
<td>218</td>
<td>189</td>
<td>646</td>
<td></td>
</tr>
<tr>
<td>vertebrae in the</td>
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<td>sample</td>
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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 69-69%, but this disparity is in common with other eouschians and is not as great as that generally seen in bipedal reptiles such as *Malerisaurus*, *Saltroposuchus*, *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 eouschians, 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 eousuchian, *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 eouschians 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 ento- 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 puboischadic 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 Cleurosaurus (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–quadratoidugal 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 sphenodontids. Whilst there is a general tendency in *Clebosaurus* and *Sphenodon* to show a reduction in the number of small teeth scattered across the palatal elements, *Planoecephalosaurus*, 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 eousuchian genera such as *Youngina*, *Tanystropheus*, and *Kuehneosaurus*, but it is known in other sphenodontids such as *Planoecephalosaurus* and *Clebosaurus* and is also seen in *Gephyrosaurus*. Evans (1980) notes the overall similarity of the *Gephyrosaurus* lower jaw to that of the sphenodontids, 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 sphenodontids. However, one major difference does exist and that is the attachment of the marginal dentition. Whereas *Gephyrosaurus* has a pleurodont attachment the sphenodontids 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 sphenodontids and some other eousuchians.

<table>
<thead>
<tr>
<th></th>
<th>Sphenodon</th>
<th>Clebosaurus</th>
<th>Planoecephalosaurus</th>
<th>Kuehneosaurus</th>
<th>Tanystropheus</th>
<th>Gephyrosaurus</th>
<th>Rhynchosaurus</th>
<th>Youngina</th>
<th>Prodaectera</th>
<th>Macrocerus</th>
<th>Palaeogama</th>
<th>Akepyrosaurus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fusion of the frontals</td>
<td>0</td>
<td>0</td>
<td>x</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>o</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fusion of the parietals</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>o</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lachrymal small or absent</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>o</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>o</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lower temporal arcade incomplete</td>
<td>o</td>
<td>x/o</td>
<td>x/o</td>
<td>o</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Enlarged palatine tooth row</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>o</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dentary with pronounced posterior process</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>o</td>
<td>0</td>
<td>x</td>
<td>x</td>
<td>o</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Splenial absent</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>o</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Acrodont dentition</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>o</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Zygosphene/zygantrum</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>o</td>
<td>o</td>
<td>0</td>
<td>o</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Caudal fracture planes</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>o</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Most presacrals with single headed ribs</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>o</td>
<td>x</td>
<td>o</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Vertebrae amphicoelous and notochordal</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Scapulocoracoid a single bone</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>o</td>
<td>0</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Scapulo coracoid fenestrated</td>
<td>0</td>
<td>o</td>
<td>x</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Humerus with two distal foramina</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>0</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Thyroid fenestra</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>o</td>
<td>o</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hooked fifth tarsometatarsal</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>o</td>
<td>x</td>
<td>o</td>
<td>x</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

x—character present. o—character absent.
It might be postulated that intermediate forms would exist between sphenodontids and their eusuchian 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 acrodont teeth with a marked decrease in their absolute numbers (Table 3). Such

<table>
<thead>
<tr>
<th></th>
<th>Gephyrosaurus bridensis</th>
<th>Planocephalosaurus robinsonae</th>
<th>Cleosaurus hudsoni</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palatal Dentition</td>
<td>Numerous teeth scattered across palatines, pterygoids, and vomers. Ordered into an enlarged tooth row on the palate</td>
<td>Numerous teeth on palatines, pterygoids, and vomers. Predominantly arranged in rows with two enlarged tooth rows on the palate</td>
<td>Reduction in palatal dentition. Teeth arranged in two rows on the pterygoids. A single enlarged tooth row on the palate. Occasionally a few vomerine teeth</td>
</tr>
<tr>
<td>Insertion of marginal dentition</td>
<td>Pleurodont</td>
<td>Acrodont</td>
<td>Acrodont</td>
</tr>
<tr>
<td>Number of functional marginal teeth in the mature individual:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a) premaxilla</td>
<td>8–10</td>
<td>4</td>
<td>2–3</td>
</tr>
<tr>
<td>(b) maxilla</td>
<td>35–40</td>
<td>12–14</td>
<td>5–6</td>
</tr>
<tr>
<td>(c) dentary</td>
<td>30–40</td>
<td>13–14</td>
<td>5–6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Juvenile teeth worn away to the bone anteriorly</td>
</tr>
</tbody>
</table>
dentitional 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 postcranal element of *Planoccephalosaurus robinsonae* recovered from fissure four, Cromhall Quarry.

<table>
<thead>
<tr>
<th>Element</th>
<th>at.art.</th>
<th>at/axs.</th>
<th>ce.v.</th>
<th>d.v.</th>
<th>1st s.</th>
<th>2nd s.</th>
<th>caud.</th>
<th>ch.</th>
<th>int.c.</th>
<th>ce.r.</th>
<th>d.v.</th>
<th>cl.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Numbers</td>
<td>17</td>
<td>12</td>
<td>69</td>
<td>169</td>
<td>8</td>
<td>11</td>
<td>377</td>
<td>147</td>
<td>87</td>
<td>61</td>
<td>150</td>
<td>13</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Element</th>
<th>int.cl.</th>
<th>sc.</th>
<th>hum.</th>
<th>rad.</th>
<th>il.</th>
<th>isch.</th>
<th>pu.</th>
<th>fem.</th>
<th>tib.</th>
<th>5th met.</th>
<th>ast.</th>
<th>astragalocalcaneum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Numbers</td>
<td>9</td>
<td>12</td>
<td>36</td>
<td>14</td>
<td>27</td>
<td>21</td>
<td>13</td>
<td>26</td>
<td>23</td>
<td>26</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

**ABBREVIATIONS**

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

**ABBREVIATIONS USED IN TEXT-FIGURES**

acet. acetabulum
a.i. axis intercentrum
ant.pu.p. anterior pubis process
a.pr. anterior process
cap. capitulum
c.l. clavicle facet
cor.f. coracoid foramen
c.r. caudal rib
d.p. diaphysis
ect.f. ectepicondylar foramen
ent.f. entepicondylar foramen
f.c. facet for centrum
f.f. fibia facet
f.p. fracture plane
f.t. tibia facet
f.4.d.t. facet for 4th distal tarsal
gl.f. glenoid fossa
il. ilium
il.ant.f. anterior facet for ilium
ill. facet for ilium
il.fib. insertion for iliofibularis muscle
int.f. facet for interclavicle
isch. ischium
isch.f. facet for ischium
l.p.t. lateral plantar tubercle
m.p.t. median plantar tubercle
n.f. nutrient foramen
n.s. neural spine
Abbreviations used in text-figs. (cont.)

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

REFERENCES


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