A NEW RHYNCHOCEPHALIAN FROM THE BRITISH UPPER TRIAS

by N. C. FRASER

ABSTRACT. The skull of a new fossil reptile, *Planocephalosaurus robinsonae* gen. et sp. nov., is described and its affinities discussed. The description is based on approximately 750 isolated skull bones recovered from Triassic fissure infills in Carboniferous Limestone in the Bristol Channel area. The skull is diapsid, although there is usually a small gap present in the lower temporal bar. Further evidence that an incomplete lower temporal bar is not a uniquely squamate character is provided. The new reptile is compared with the eosuchians and the taxonomic position of the family Sphenodontidae is reviewed.

CROMHALL QUARRY is one of several localities in the Bristol Channel area that yielded a fauna of Triassic terrestrial vertebrates (Robinson 1957). The fossils mostly occur in the sediment fills of karstic fissures and cave systems close to the Carboniferous Limestone/Triassic unconformity. The sediments consist of marls, sand, and recemented limestone debris, and most research has hitherto been directed towards articulated specimens of reptiles that have been recovered from the marls. More recently, however, Halstead and Nicoll (1971) drew attention to dissociated material within the recemented debris, and it is this that is now being re-investigated.

The recemented material consists mainly of derived crinoid ossicles and fine limestone debris which has been washed into solution features from the surrounding limestone surface. The vertebrate bones have been incorporated into this debris and cemented along with the limestone residues.

Cromhall is the type locality for the sphenodontid *Clevosaurus* (Swinton 1939; Robinson 1973) and reptilian faunas have now been described from six other similar localities in the Bristol Channel area (Robinson 1957). Halstead and Nicoll (1971) listed five groups of reptile from Cromhall, and whilst the present study involving some 1000 identifiable skull elements has revealed only three such groups, at least eight species are represented, of which six may be new. The present paper is a preliminary description of the commonest of these.

Work on the new genus and other genera from the Triassic fissure deposits is now continuing at Aberdeen University funded by a Research Grant through the NERC.

METHODS

Blocks of bone-bearing fissure limestone up to 6 kg are placed on trays within standard washing-up bowls and covered with 5% acetic acid. The acid neutralizes within two to three days and the bowls are then gently flushed with tap water for at least two hours to remove any salts from the residues. Most bones recovered are less than 15 mm long and need no protective treatment during solution. Residues are separated through sieves, dried, and then sorted by hand using fine sable brushes. Plate 69, fig. 5 illustrates a partially developed block and an archosaurian tibia revealed within the matrix.

Whilst a small degree of breakage occurred during recovery, this was insignificant and assemblages reveal that the more delicate elements such as nasals and prefrontals are under-represented in comparison with the robust bones, for example the principal jaw elements (Appendix 1). The size range of the bones is considered to be representative of both juveniles and adults. Some maxillae no longer than 3 mm have been recovered showing well-preserved unworn teeth, whilst the largest maxillae are over 12 mm long. In these specimens the teeth are worn and covered by secondary

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dentine. The various skull dermal bones have a corresponding size range, from juvenile stages through to mature forms. In dealing with a mixed assemblage of dissociated bones belonging to several species two lines of approach have been used. First, due note has been paid to the ratios of abundance of the individual skull elements when attempting to identify skull associations for individual species. Whilst variations in these ratios occur from locality to locality and level to level, which may reflect sorting patterns in water or other factors, the overall ratios of skull bones certainly reflect the original relative abundances of the species concerned. The validity of these statistically implied skull associations is then checked by a careful examination of the articulation facets between adjacent elements. This work is now complete for the most abundant skull element association, and these bones have been combined in a reconstruction (text-fig. 1). The association represents a new species of sphenodontid, which, although similar in some respects to *Clevosaurus*, is quite distinct and merits the erection of a new genus.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA
Subclass DIAPSIDA
Infraclass EOSUCHIA
Order RHYNCHOCEPHALIA
Family SPHENODONTIDAE
Genus *PLANOCEPHALOSAURUS* gen. nov.
Species *P. robinsonae* sp. nov.

The generic name refers to the characteristic flat parietal table which is in contrast to the median ridge often found in other genera of the family. The specific name is a testimonial to the work of Dr. Pamela L. Robinson.

Diagnosis. A small sphenodontid, skull approximately 2 cm long; temporal region diapsid but with a small gap normally present in the lower temporal bar, cf. *Clevosaurus*; frontals and parietals fused; a broad and flat parietal table with a large central pineal foramen; no supratemporal or lacrimal; deep overlap of the pterygoid and quadrate; quadrate and quadratojugal fused with a quadratojugal foramen present; premaxillae paired; vomers bear small scattered teeth; the pterygoids typically display two tooth rows; no teeth on the pterygoid flange; palatines bear two rows of obtusely conical teeth parallel to the marginal dentition; dentition acrodont; all teeth are radially ribbed; dentary has a posterior process articulating with the articular complex; no splenial.

Material. The description is based on a collection of approximately 750 catalogued skull elements that are housed in the geology department of the University of Aberdeen.

Holotype. Left maxilla. No. 11061 in the University of Aberdeen Palaeontology collection. Plate 69, figs. 1–4.

Type locality. Karstic fissures in Dinantian Limestones. Cromhall quarry, south Gloucestershire.

Horizon. Upper Triassic.

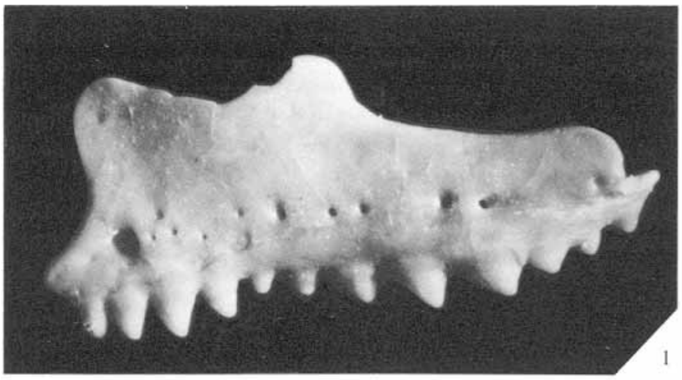
EXPLANATION OF PLATE 69

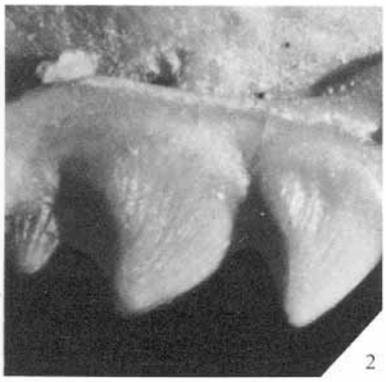
Figs. 1–4. *Planocephalosaurus robinsonae* gen. et sp. nov. Holotype, left maxilla, No. 11061, Aberdeen University Palaeontology collection. 1, lateral view, × 10. 2, detailed lingual view of the flanged tooth series, × 15. 3, lingual view, × 10. 4, detailed lingual view of the anterior dentition, × 15.

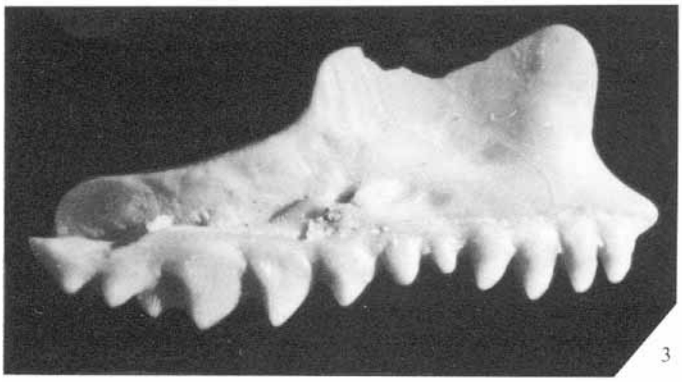
Fig. 5. Archosaurian tibia exposed from a partially developed block of fissure material, × ⅔.

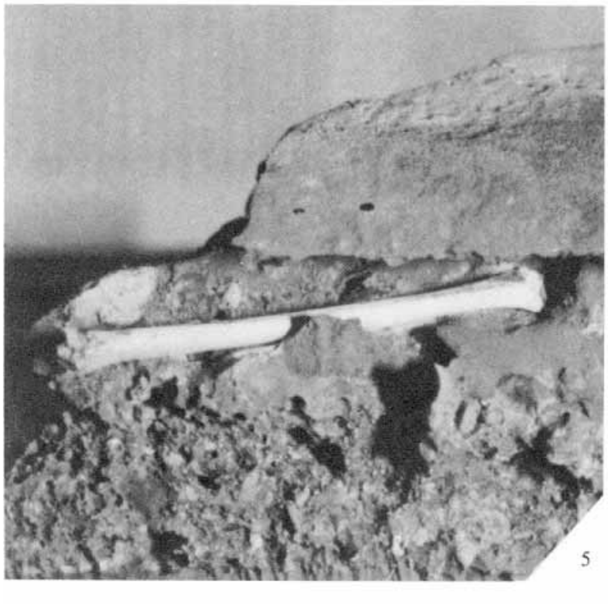
Fig. 6. *P. robinsonae* gen. et sp. nov. Detailed lateral view of a dentary, AUP No. 11062, and maxilla, AUP No. 11063, to show the wear facets on the lateral surface of the dentary caused by the maxillary dentition, × 10.

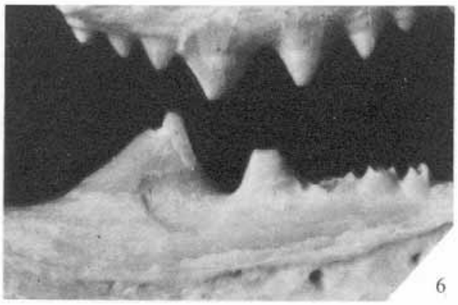
Fig. 7. *P. robinsonae* gen. et sp. nov. Lateral view of a left prefrontal, AUP No. 11064, × 10.

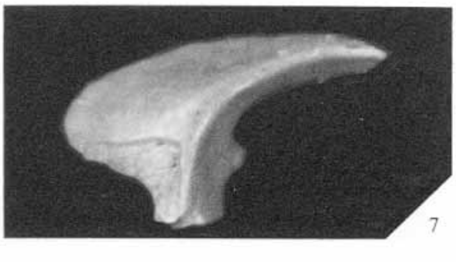




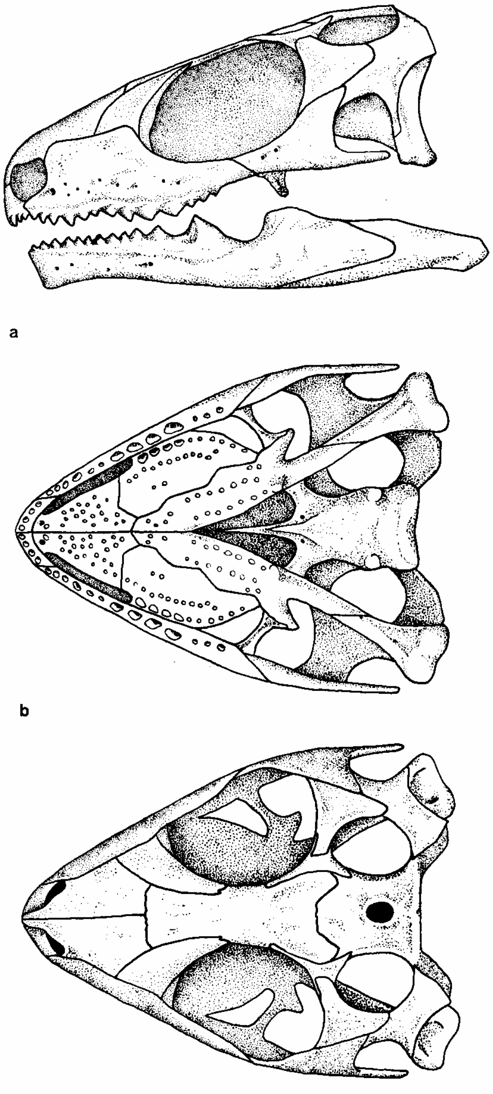








FRASER, *Planocephalosaurus*



TEXT-FIG. 1. *Planocephalosaurus robinsonae* gen. et sp. nov. Reconstruction of the skull in *a*, lateral, *b*, palatal, and *c*, dorsal view.

EXPLANATION OF PLATE 70

Figs. 1–12. *Planocephalosaurus robinsonae* gen. et sp. nov. 1, lateral view of a right premaxilla, AUP No. 11065, × 5. 2, a left dentary, AUP No. 11066, in lateral view, × 5. 3, a left postorbital, AUP No. 11067, in lateral view, × 5. 4, lingual view of a left dentary, AUP No. 11066, × 5. 5, a frontal, AUP No. 11068, in dorsal view, × 10. 6, the lingual aspect of a right jugal, AUP No. 11069, × 5. 7, dorsal view of the left side of a parietal, AUP No. 11070, × 5. 8, ventro-medial aspect of a right quadrate, AUP No. 11071, × 5. 9, lateral view of a right jugal, AUP No. 11069, × 5. 10, dorso-lateral view of a right nasal, AUP No. 11072, × 5. 11, dorso-lateral view of a right postfrontal, AUP No. 11073, × 10. 12, postero-lateral aspect of a right ectopterygoid, AUP No. 11074, × 10.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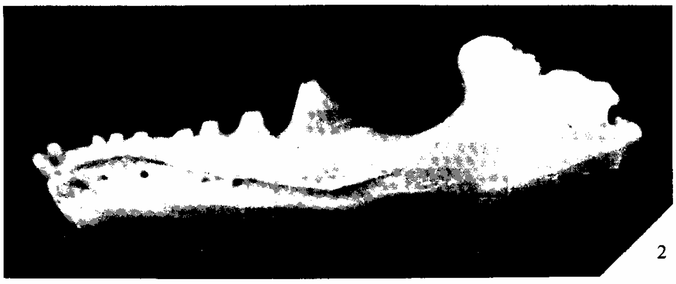
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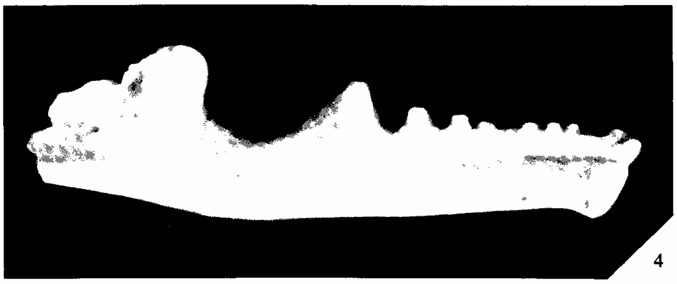
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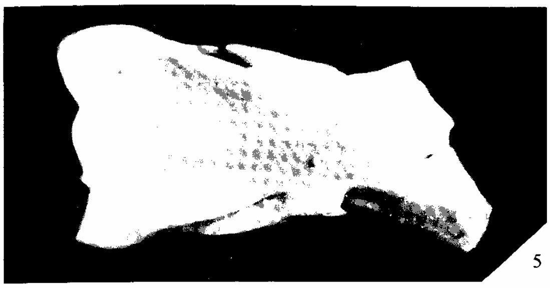
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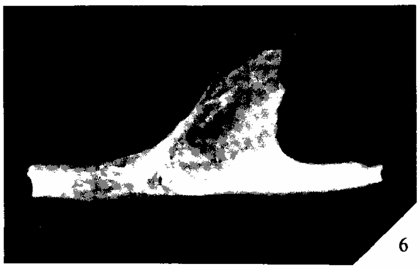
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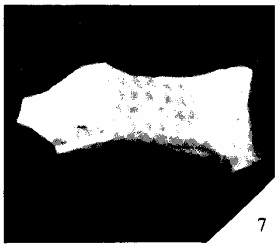
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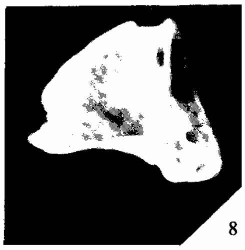
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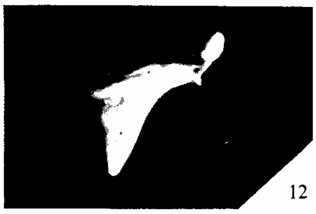
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FRASER, *Planocephalosaurus*

Description. Dermal bones of the skull roof. The premaxillae extend a short distance ventrally to form a rudimentary beak. They separate the external nares and meet medially in long narrow vertical processes that extend into slot facets between the nasals. Below the external naris a posterior extension of the premaxilla is slightly overlapped by the maxilla and this fairly weak contact may have been strengthened by ligaments. Four teeth are characteristically present (Pl. 70, fig. 1), but they remained discrete throughout life and, unlike *Clevosaurus* and *Sphenodon*, did not tend to become worn into a single chisel-like structure in more mature individuals. Posterior to the teeth is a short palatal shelf.

The maxillae (Pl. 69, figs. 1 and 3) extend the full depth of the external nares defining the lower anterior quadrant of each orbit. They strongly overlap both the nasals and the prefrontals at their upper limits, thereby bracing the snout. Approximately two-thirds of the ventral border of either orbit is formed by the maxilla, and the jugal contact slopes posteroventrally from this border. Mesially there is a large foramen (Pl. 69, fig. 3) which was continuous with a similar foramen in the palatine contact and this carried the maxillary nerve and artery. The lateral surfaces of the maxillae are perforated by a series of small foramina which carried the nerves and blood vessels that supplied the skin. Usually each maxillae bears twelve to fourteen acrodont teeth, rarely up to seventeen. Four basic tooth categories can be recognized: the anterior three or four teeth are approximately 1·0 mm high, conical, and with a slightly recurved apex. These are followed posteriorly by a variable number of smaller conical teeth, usually three but up to seven, which in rare instances exhibit a slight alternation in size. These teeth never exceed 0·6 mm. The succeeding four teeth increase in size from about 0·6 mm anteriorly to over 1·0 mm in the most posterior member of the series. They are obtusely conical with broad bases and each bears a small posterolingual flange. The flange is comparable with those of *Sphenodon* and *Clevosaurus*, but less well developed. Three obtusely conical teeth approximately 0·5 mm high occur posterior to the flanged series. All teeth bear a distinct radial ribbing that is most prominent on the lingual surfaces (Pl. 69, figs. 2 and 4).

Anteriorly the paired nasals (Pl. 70, fig. 10) narrow to slender processes that descend ventrally and embrace the premaxillae. At their posterior limits there are transverse sutures with the frontal. The nasals descend partly over the sides of the skull and broad depressions receive the anterodorsal edges of the maxillae, so that jointly the maxillae and nasals form the posterior boundary of the external nares. The nasals also bear facets for the prefrontals.

The prefrontals overlap the nasals and form the anterodorsal quadrant of each orbit. At their posterior limits they extend to a point nearly mid-way along the supraorbital margin where there is a distinct interlocking of prefrontal with frontal (text-fig. 2*b*). A medial flange of the prefrontal descends along the anterior border of the orbit to articulate in a complex socket on the dorsal surface of the palatine (Pl. 71, fig. 4).

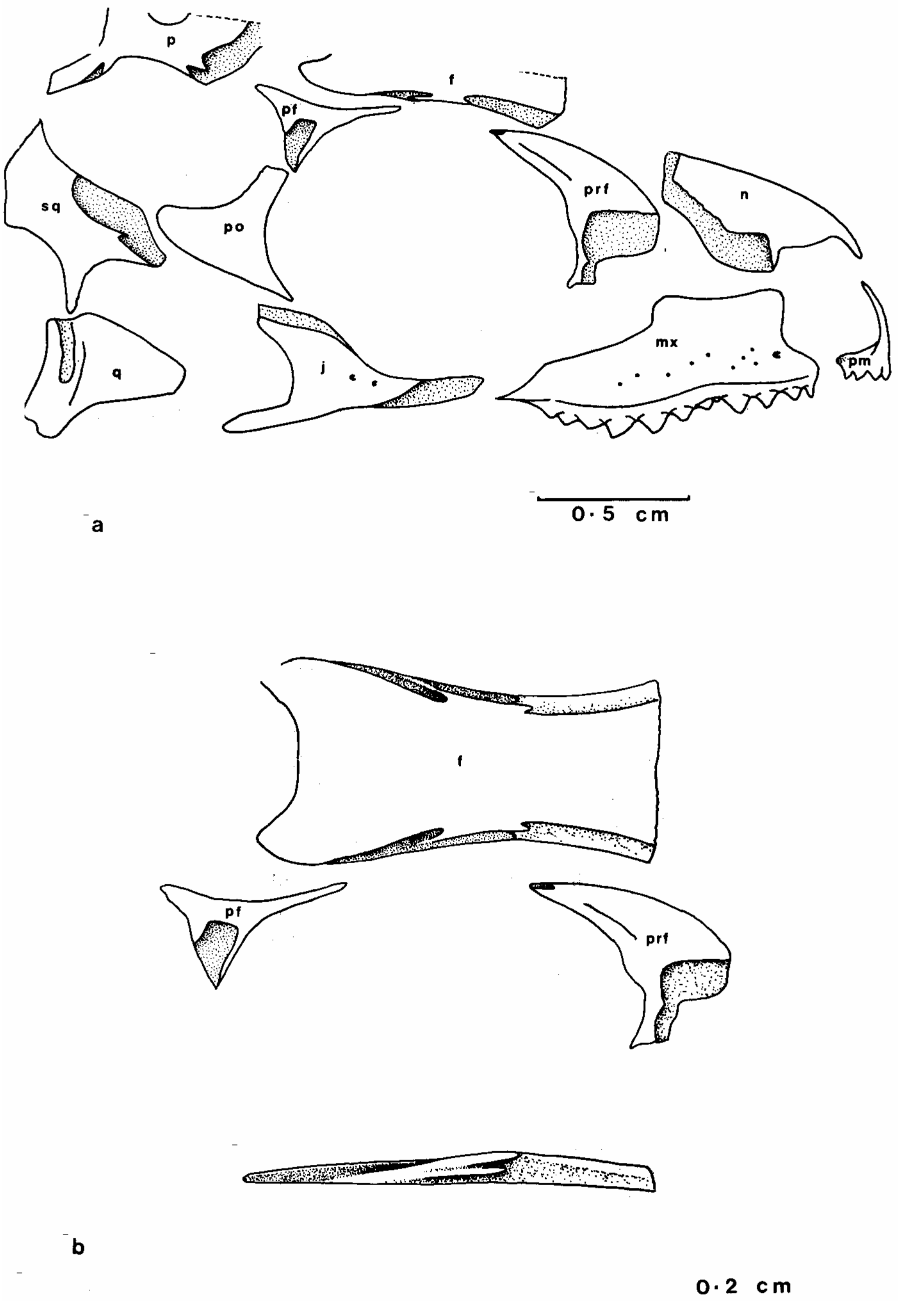
No lacrimals have been recognized and there are no facets on the prefrontals which might suggest their presence.

The frontal is a single element (Pl. 70, fig. 5) with transverse sutures separating it anteriorly from the nasals and posteriorly from the parietals. It forms the supraorbital margin for a short distance between the prefrontals and postfrontals and has rigid contacts with these elements (text-fig. 2*b*).

The parietals are fused, unlike the primitive situation, and form a broad and flat skull roof which is perforated by a well-developed parietal foramen. Anteriorly there are facets to receive the postfrontals and frontal (Pl. 70, fig. 7), and posteriorly lateral processes meet the squamosals.

Essentially triradiate bones, both postfrontals possess a long slender anterior process that slots into a narrow groove situated on the posterolateral margin of the frontal, and a shorter posterior process that articulates with the anterolateral edge of the parietal (Pl. 70, fig. 11). The third process is ventrolaterally directed and bears a depression to receive the postorbital; combined, these two elements jointly form the posterior border of the orbit. The postfrontals also enter into the anterior margins of the upper temporal fossae.

The postorbitals (Pl. 70, fig. 3) are approximately triangular bones that strongly overlap the squamosals posteriorly, and descend ventrally to meet and slightly overlap the jugals. A large area of contact between the postorbital and postfrontal is responsible for a rigid postorbital bar. There is no contact between the postorbital and the parietal.



TEXT-FIG. 2. *a*, The membrane bones of the skull indicating individual facets for articulation with adjacent elements. *b*, Detailed reconstruction of the articulation facets of the frontal, prefrontal, and postfrontal in dorsal view and the frontal in right lateral view.

Abbreviations used in figures. f = frontal; j = jugal; mx = maxilla; n = nasal; p = parietal; pf = postfrontal; pm = premaxilla; po = postorbital; prf = prefrontal; q = quadrate; sq = squamosal.

The maxillae overlap the anterior process of each jugal so that a combination of maxilla and jugal forms much of the ventral margin of each orbit. Posterior to the orbit the jugal slightly overlaps the anterior edge of the squamosal and thereby excludes the postorbital from the margin of the lower temporal fossa. A slender process extends posteriorly towards the quadratojugal and in the majority of specimens examined, including adults as well as juveniles, it tapers away to a rounded point so that the lower temporal bar is incomplete. However, of the fifty-one jugal specimens so far recovered, one exhibits notches at the posterior limit of this process that suggests an articulation with the quadratojugal and squamosal as reconstructed in text-fig. 3*b*. It would therefore appear that in one or two individuals at least the lower temporal bar was complete. The palatal borders of the jugals display raised facets for articulation with the ectopterygoids (Pl. 70, fig. 6).

The squamosals form the posterior region of the upper temporal arcades, extending anteriorly underneath the postorbitals and the jugals. All three bones contribute to the separation of the upper and lower temporal fossae. Posteromesially the squamosal narrows into a slender inwardly directed process that fits into a narrow slot on the lateral process of the parietal. There are no supratemporals and together the parietal and squamosals form the posterior margins of the upper temporal fenestrae. The ventral ramus of the squamosal is continuous with the lateral edge of the quadratojugal and may have provided a framework for a tympanic membrane. In most specimens this ventral ramus only extended part-way down the quadratojugal before tapering away, but in one specimen this ramus continues the full length of the quadratojugal and at the ventral extremity expands anteriorly to make a weak contact with the jugal (Pl. 71, fig. 8). This confirms the observation of the jugal specimen, which suggested that some individuals of *Planocephalosaurus* possessed a complete lower temporal bar with a weak articulation between jugal, quadratojugal, and squamosal. But more generally it seems likely that full ossification in this region did no occur in the embryo, thereby leaving a small gap in the lower temporal bar. The dorsal head of the quadrate was supported by a flange that extends mesially between the quadratojugal process and the posterolateral corner of the squamosal.

The quadrate and quadratojugal are fused with no visible sutures (Pl. 70, fig. 8). Generally this element has not been well preserved in the bone assemblages, particularly with respect to the quadratojugal region, and there is little evidence of the facet that articulates with the ventral ramus of the squamosal. The quadrate was clearly rigidly attached to the squamosal and the pterygoid, since its dorsal head was supported by a flange on the squamosal and a well-developed anteromesially directed lamina of bone broadly overlapped a posterolateral flange of the pterygoid. A lateral conch provided the support for a tympanic membrane.

The palate. The vomers extend from the premaxillae to the pterygoids, articulating with the latter bones by means of interlocking flanges. At their posterolateral edges they overlap the palatines and laterally they bound the internal nares. Small teeth are scattered across much of the ventral surface, but one or sometimes two teeth lying immediately posterior to the premaxillae and adjacent to the vomerine aperture are usually a little larger and more prominent than the rest.

The palatines extend from the posterior border of the internal nares to a point almost adjacent to the posterior limits of the maxillae, with which there are restricted contacts. Mesially they are bounded by the pterygoids and are thereby excluded from the interpterygoid vacuity. On the dorsal surface there is an anterior facet for the prefrontal (Pl. 71, fig. 4). On the ventral surface of the

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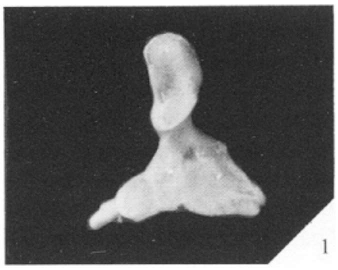
EXPLANATION OF PLATE 71

Fig. 1. An epipterygoid specimen, AUP No. 11075, considered to be *Planocephalosaurus robinsonae* gen. et sp. nov., × 10.

Figs. 2–9. *P. robinsonae* gen. et sp. nov. 2, a parabasisphenoid, AUP No. 11076, in ventral view, × 5. 3, ventral view of a basioccipital, AUP No. 11077, × 5. 4, dorsal view of a left palatine, AUP No. 11078, × 10. 5, ventral view of a left palatine, AUP No. 11078, × 10. 6, lateral aspect of a left squamosal, AUP No. 11079, × 10. 7, dorsal view of a left pterygoid, AUP No. 11080, × 10. 8, lateral aspect of the single squamosal specimen, AUP No. 11081, possessing a jugal contact, × 10. 9, a left pterygoid, AUP No. 11080, in ventral view, × 10.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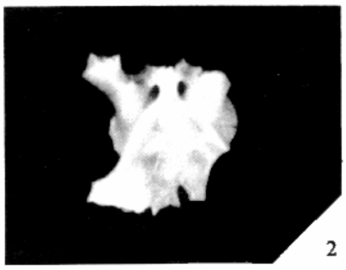
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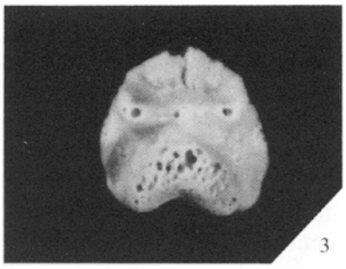
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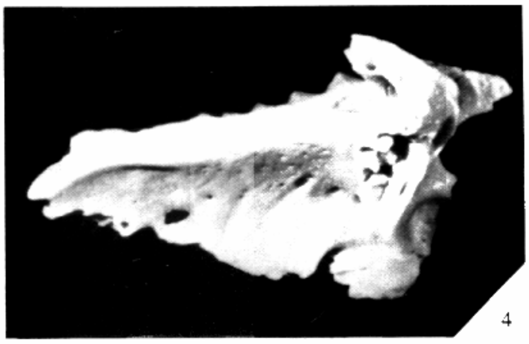
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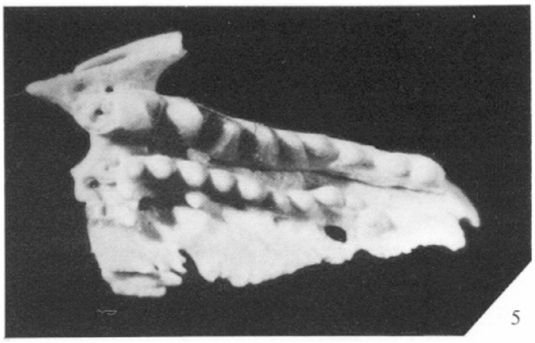
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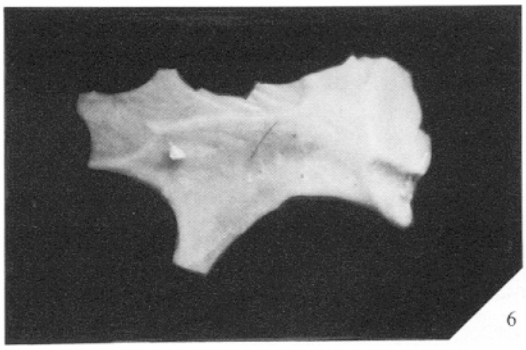
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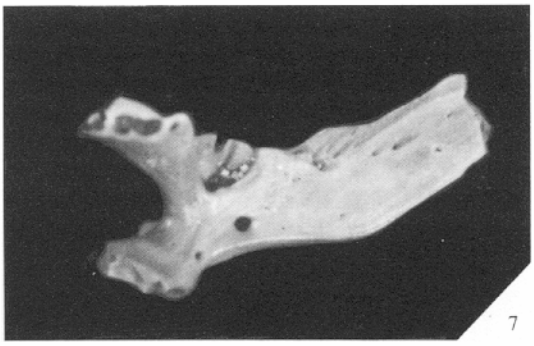
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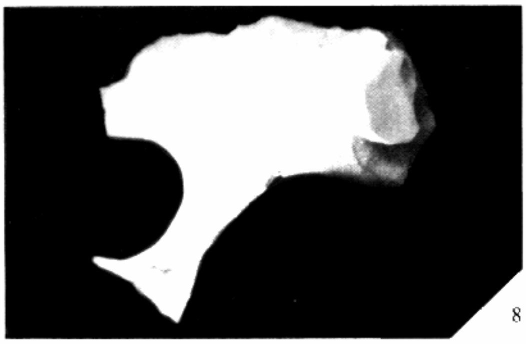
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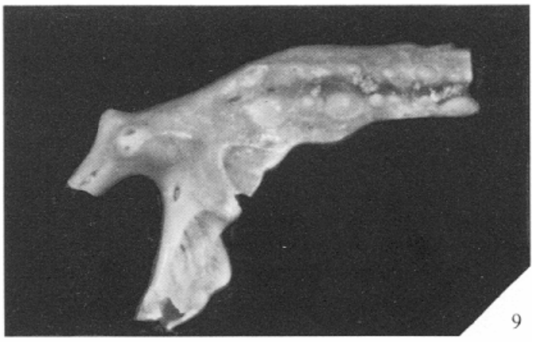
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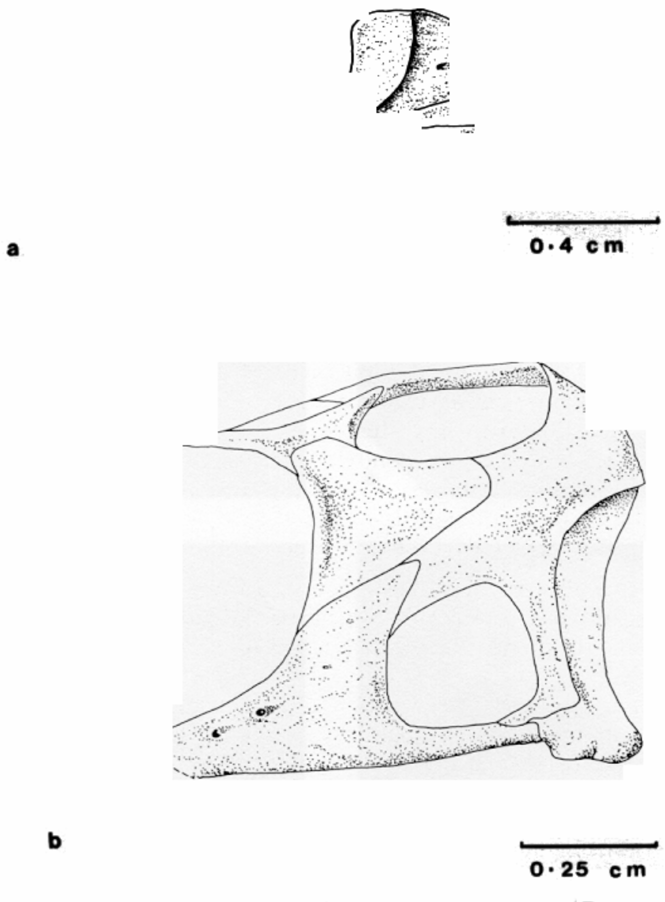
FRASER, ***Planocephalosaurus***

palatines there are characteristically two tooth-rows, which anteriorly run parallel to the marginal dentition but diverge somewhat mesially in the posterior part of the element (Pl. 71, fig. 5). Additional teeth may form a third row. The most lateral tooth-row typically bears ten teeth; the anterior four or five being similar to the maxillary teeth to which they lie adjacent, and displaying labial facets reflecting wear through shearing movements. The remaining five or six teeth in this row are smaller and do not exhibit such labial facets. The second row usually consists of twelve to fourteen uniform teeth similar to the posterior teeth of the most lateral row. A rudimentary third row is normally marked by only two anterior teeth, but up to six may be present. All palatal teeth are marked by the radial ribbing pattern characteristic of the marginal dentition.

Anteriorly the pterygoids meet along the midline by means of interdigitating facets, but more posteriorly they diverge to form a narrow interpterygoid vacuity. As described above the pterygoids reach forward to the vomers and lateral facets on their dorsal surfaces provide broad contacts with the palatines (Pl. 71, fig. 7). The palatal ramus of each pterygoid bears a number of radially ribbed teeth that are roughly arranged into two rows (Pl. 71, fig. 9), although in some specimens there is also



TEXT-FIG. 3. *Planocephalosaurus robinsonae* gen. et sp. nov. *a*, Reconstruction of the dentary and articular complex in lingual view, and *b*, an alternative structure of the temporal region of the skull where the lower temporal bar is complete.

evidence of a third row situated just anterior to the pterygoid flange. The quadrate process is a deep, mesially concave flange that passes posterolaterally and broadly overlaps a similar-shaped process on the quadrate. The basipterygoid process of the parabasisphenoid articulates in a mesial depression situated anterior to the quadrate ramus, and on the ventral surface immediately anterior to this depression there is a small protuberance. Laterally the pterygoids have broad contacts with the ectopterygoids and together they form a deep pterygoid flange to guide the action of the lower jaw.

Laterally the ectopterygoids are expanded anteroposteriorly and there is a notch facet on this surface for the jugal. Passing posteromesially the ectopterygoids expand dorsoventrally to the contacts with the pterygoids.

Thirteen '*Sphenodon*-like' epipterygoids provisionally attributed to *Planocephalosaurus* have been recovered (Pl. 71, fig. 1). However, the pterygoid and quadrate specimens of *Planocephalosaurus* that have been recorded do not bear detailed epipterygoid articulation facets, so that some doubt remains regarding the origin of the epipterygoids; nevertheless, their abundance and size indicates that they are representatives of *Planocephalosaurus*. They have an expanded ventral head which presumably articulated with the quadrate and pterygoid. The shaft is expanded dorsally and fibrous tissue probably attached it to the parietal and supraoccipital.

The braincase. The braincase is not as well represented in the assemblages as the skull roof elements, and only the parabasisphenoid, basioccipital, and exoccipitals are present in sufficient numbers and with sufficient detail to make any comment. Different hydrodynamic properties may partly account for this poor representation of the braincase, but, because of the greater complexity of the braincase, fragmentary specimens are also more difficult to interpret than those from the skull roof.

The parasphenoid has become fused to the ventral surface of the basisphenoid to form a single unit, the parabasisphenoid (Pl. 71, fig. 2). Posteriorly the parabasisphenoid has a broad overlapping contact with the basioccipital, and laterally there are facets for the prootic bones. The basipterygoid processes arise laterally to the carotid foramina and, diverging slightly, extend forward into sockets in the pterygoids. Anteriorly the lateral margins of the parabasisphenoid converge to form a narrow cultriform process that extends an unknown distance into the interpterygoid vacuity.

Exoccipitals are occasionally recovered fused to the basioccipital, but usually they are separate as a result of the disintegration of the narrow exoccipitals, which are extremely vulnerable and fragile. A well-marked facet on the anterior ventral surface of the basioccipital receives the parabasisphenoid, and a pair of well-developed basal tubera situated more posteriorly (Pl. 71, fig. 3) were for the attachment of neck muscles. The occipital condyle forms the posterior limit of the basioccipital.

The exoccipitals are slender columnar structures fused to the posterior dorsal surface of the basioccipital, forming the lateral margins of the occipital condyle. They are pierced by foramina that accommodated branches of the hypoglossal nerve. Their facets for the opisthotics are unknown.

The lower jaw. Only two elements have been identified from the lower jaw, the dentary and an articular complex. The articular complex is considered to be a fusion of the articular with the overlying dermal elements: the prearticular, angular, and surangular. Neither splenial nor coronoid bones have been identified.

The dentaries meet anteriorly at the jaw symphysis and extend posteriorly to the articular complex. Posterior to the tooth ramus the dentaries expand dorsoventrally to form at least part of the coronoid process, extending slightly higher than the most posterior tooth. Mesially there is thought to have been no splenial and the Meckelian canal apparently remained open. Normally there are thirteen or fourteen radially ribbed teeth, of which the anterior eight or nine are generally of a uniform size, approximately 0·4–0·6 mm high. The four or five remaining teeth progressively increase in size posteriorly and the last often exceeds 2·0 mm. This most posterior tooth is characteristic and bears a rudimentary anterolabial flange. In labial view it has a relatively elongate base and marked anteroposterior asymmetry; the anterior edge is slightly concave, but owing to a slight shoulder the posterior edge is convex. All teeth are laterally compressed, but less so in anterior members. Only the posterior tooth bears a flange of any description.

Since no sutures define the limits of the articular, prearticular, angular, and surangular, this group of elements is best described as a single unit. The most prominent features are the glenoid fossa, which receives the condyles of the quadrate, and, anterior to this fossa, the adductor fossa. The lateral surface of the complex bears a large facet for the posterior ramus of the dentary, which provided a rigid bond between the two major elements of the lower jaw.

Postcranial elements. The bone assemblages contain a number of dissociated postcranial elements that include abundant pelvic and pectoral girdle fragments, vertebrae, ribs, epipodials, propodials, and phalanges. They represent a reptile of similar size to the new species and bear many sphenodontid characters. It is hoped that these specimens will be used in future work to make a full reconstruction of the postcranial skeleton of *Planocephalosaurus*.

DISCUSSION

Certain features of *Planocephalosaurus*, in particular the temporal region and the roof of the skull, raise important questions concerning the classification of some of the smaller diapsids. The first modern attempt to organize the taxonomy of these diapsids was by Romer (1966), who classified the eosuchians, squamates, and rhynchocephalians as separate orders within the subclass Lepidosauria, and considered the subclasses Archosauria and Lepidosauria as having separate ancestries (Appendix 2). Kuhn (1969) modified the subclass Lepidosauria to include the orders Rhynchocephalia, Squamata, and Protorosauria. As he defined the order Rhynchocephalia it incorporated eight suborders including the Eosuchoidea, Rhynchosauroidea, and Sphenodontoidea. The order Protorosauria incorporated four suborders, and these included the Protorosauroidea, Prolacertoidea, and the Tanysitracheloidea (Appendix 2). Like Romer, Kuhn believed the Kuehneosauridae to be true lacertilians.

More recently the eosuchians have been accredited with rather more significance than an assorted assemblage of primitive diapsid genera since Cruickshank (1972) and Carroll (1976) argue the case for the eosuchians as the ancestors to both the Squamata and Archosauria as well as other diapsids. Taking this latter viewpoint, the taxonomic position of the rhynchocephalians, including the Sphenodontidae, is called into question.

In a further review of diapsid classification Evans (1980) recognizes a subclass Diapsida within which there are three infraclasses; the first is the Eosuchia, which gave rise to the remaining two; the Archosauria and the Squamata. The term Lepidosauria becomes redundant, and as she defines the Eosuchia it contains sixteen families, including the Sphenodontidae and the rest of the rhynchocephalians (Appendix 2).

Planocephalosaurus possesses a number of features in common with *Sphenodon*, *Clevosaurus*, *Homeosaurus*, and others, including acrodont dentition, pterygoids reaching forward to the vomers, and absence of the tabulars, postparietals, and lacrimals. These characteristics clearly indicate that the genus belongs to the family Sphenodontidae. However, it also shares a number of characteristics with the eosuchians and some lizards, and is therefore important in considering the taxonomic position of the Sphenodontidae.

Perhaps the most advanced feature of *Planocephalosaurus* is the presence of fused frontals and parietals, a characteristic shared by *Gephyrosaurus* and lizards, but not seen in either *Clevosaurus* or *Sphenodon*. An essentially primitive feature, however, is the retention of a large central parietal foramen shared with *Youngina*, *Tanystropheus*, *Gephyrosaurus*, *Clevosaurus*, and others. Thus, with respect to the skull roof *Planocephalosaurus* exhibits both primitive and advanced characteristics and is very similar to *Gephyrosaurus*.

The absence of a lacrimal in *Planocephalosaurus* is a characteristic shared by *Sphenodon*, but many eosuchians, including *Gephyrosaurus*, *Youngina*, and *Tanystropheus*, retain a lacrimal. However, with respect to other features of the circumorbital elements, *Planocephalosaurus* is similar to *Gephyrosaurus*, *Youngina*, and *Tanystropheus* as well as *Sphenodon* and *Clevosaurus*. All these species possess a triradiate postfrontal that enters the border of the upper temporal fenestra, and this is in contrast to

Icarosaurus, *Kuehneosaurus*, and *Prolacerta*. In *Gephyrosaurus* and *Clevosaurus* the postorbital is excluded from the boundary of the lower temporal fenestra by the apposition of the jugal and squamosal; this is also the condition observed in *Planocephalosaurus*.

No supratemporal bone is present in *Planocephalosaurus*, *Sphenodon*, or *Gephyrosaurus*, but *Clevosaurus* retains this element. However, all four genera possess a similar squamosal with a ventral ramus attached firmly to the quadratojugal and the squamosal forming the sole support for the head of the quadrate. These four genera also have a deep overlap between pterygoid and quadrate, which would have inhibited any streptostylic movement.

The arrangement of the acrodont teeth in *Planocephalosaurus* is similar to *Sphenodon* and *Clevosaurus*, with the largest biting teeth occurring at the back of the jaw ramus and the possession of enlarged palatine tooth rows. In *Sphenodon* the articular surface for the quadrate is elongated, thereby allowing for antero-posterior movement at this articulation, and, as Robinson (1976) has shown, the wear facets on the lateral surface of the dentary show that propalinal movement occurs whilst feeding. Evans (1980) postulated that *Gephyrosaurus* may have had a similar feeding action to *Sphenodon*, as it too has an elongated articular surface on the lower jaw. There is also an enlarged tooth row on the palatine of *Gephyrosaurus*, and Evans believes that propalinal feeding movements best explain this character. However, *Clevosaurus* also bears an enlarged palatine tooth-row and, as Robinson (1976) states, in this species there was a precise occlusion of the teeth, as indicated by the impression of the individual maxillary teeth that have been scored on the dentary; therefore no propalinal movement of the jaw was involved in the feeding action. Thus, the enlarged palatine tooth-row is not necessarily a feature solely associated with propalinal jaw movements, but may have aided with the grasping and crushing of relatively large prey.

In *Planocephalosaurus* the articular surface for the quadrate is somewhat elongated and there are faint scoring marks on the lateral surface of the dentary, which suggest that small propalinal movements occurred, but not to the same extent as *Sphenodon*. Individual maxillary tooth impressions are still recognizable on the *Planocephalosaurus* dentary (Pl. 69, fig. 6), but these are not as precisely defined as those of *Clevosaurus*.

Like *Gephyrosaurus*, the snout region of *Planocephalosaurus* is well braced, with firm contacts between the nasals, prefrontals, maxillae, and palatines that would resist pressures resulting from feeding on relatively difficult material, and as Evans (1980) indicates the single frontal and parietal may be regarded as a further adaption in the general strengthening of the skull.

The reduction of the lower temporal bar in such forms as *Kuehneosaurus*, *Icarosaurus*, and *Prolacerta* has been accepted in the past as an essentially squamate or 'presquamate' character. In some instances the lower temporal bar is complete in *Planocephalosaurus* (text-fig. 3*b*), but generally it is very similar to *Clevosaurus* and *Gephyrosaurus* in this respect and is incomplete. This gap in the lower temporal bar is therefore no longer acceptable as a uniquely squamate or 'presquamate' condition, and reasons other than streptostyly must be looked for to account for the appearance of this character in a variety of genera. Although Robinson (1973) suggested that in *Clevosaurus* this feature might improve the reception of airborne sound, it would seem unlikely to be effective in completely isolating the tympanic membrane from feeding sounds transmitted from the dentition, and, as Evans (1980) proposed, it was more likely to have occurred as a result of a change in the action and arrangement of the jaw adductor musculature.

Haas (1973) reports that in *Sphenodon* the origins of the adductor mandibulae muscle complex are variable. Very little of this complex is actually attached to the lower temporal bar, with the exception of the M. Levator anguli oris, which in some instances has been found to originate from the medial surface of the quadratojugal ramus of the jugal, while in others it may originate as high as the anteromedial surface of the postorbital. The M. Levator anguli oris is also present in lizards, but as a result of the loss of the lower temporal bar, the origins of the muscle have moved entirely to the upper temporal arch. If for some reason it became advantageous for a diapsid with both temporal bars complete to have a longer M. Levator anguli oris then its origin might move to a higher position on the upper temporal arch, and consequently the lower temporal bar would be made completely redundant for muscle attachment and might therefore fail to ossify fully. In lizards the loss of the lower temporal bar is associated with the highly kinetic skull, but this is not an explanation for the atrophy observed in the lower temporal bar of *Planocephalosaurus*, since in this species the pterygoid and quadrate are firmly attached and kinesis is restricted. If in *Planocephalosaurus* the M. Levator anguli oris originated exclusively on the postorbital, then a reduction in ossification of the lower temporal bar might be expected. The consequent increase in length of the M. Levator anguli oris may have been coupled with an increase in length of other adductor muscles, a change which could result in greater speed of adduction. This might be of value in facilitating quick snapping movements of the jaws when taking small insects. *Planocephalosaurus* is considered likely to have had a very varied diet, having been equipped with large shearing teeth at the posterior end of the jaw, enabling large insects with resistant cuticles and maybe the occasional small vertebrate to be masticated, while the sharper more pointed teeth on the premaxilla and anterior regions of the maxilla and dentary would have been capable of snapping and impaling smaller insects and grubs. Both the speed of contraction and the force of contraction of the jaw adductor musculature may well have been important in such a varied diet.

Whilst *Planocephalosaurus* closely resembles *Gephyrosaurus* in the structure of the skull roof and the temporal region, the acrodont implantation of the dentition contrasts markedly with the pleurodont insertion displayed by *Gephyrosaurus*. Similarly, *Planocephalosaurus* has close affinities with *Clevosaurus* and *Sphenodon*, and these three genera are considered to be members of the family Sphenodontidae. The affinities of *Planocephalosaurus* and *Gephyrosaurus* are probably due to the relationship of the two families Gephyrosauridae and Sphenodontidae; both are included within the infraclass Eosuchia as outlined by Evans (1980).

Appendix 2 illustrates three different classifications of some diapsid reptiles, and it is clearly seen how confusion has arisen regarding the systematics of many diapsid genera; often this has resulted in the different usage of similar terms. The current belief that *Petrolacosaurus* is an early Carboniferous diapsid (Reisz 1977) lends support to the Evans classification with an infraclass Eosuchia giving rise to the Archosauria and Squamata, but the arrangement of orders within the Eosuchia remains a problem. In Romer's (1966) classification those diapsids with an acrodont dentition, but which in other respects may be quite different, have unfortunately been grouped together in one order, the Rhynchocephalia. Kuhn (1969) partly solved this problem by favouring the use of a number of suborders within each order, but his use of the term Rhynchocephalia is rather misleading in that it includes the suborder Eosuchoidea. Whilst Evans (1980) does not arrange the families of the infraclass Eosuchia either into orders or suborders, she admits that an order Rhynchocephalia may be useful, and I propose that such an order could be structured as in Table 1, consisting of forms derived from the eosuchians of the Permian and Lower Triassic (Hoffstetter 1955). The four suborders are all characterized by an acrodont dentition, or are toothless and evidently derived from the acrodont condition.

The Sphenodontoidea is a clearly characteristic suborder incorporating the only living genus, *Sphenodon*. Diagnostic features of the family Sphenodontidae include a diapsid skull, acrodont dentition, pterygoids elongated anteriorly to meet the vomers, an immobile quadrate firmly overlapping the pterygoid, amphicoelous vertebrae, 23-25 presacral vertebrae, 2 sacral vertebrae, and autotomy septa present in the caudal vertebrae. *Monjurosuchus* was classified as a member of the

TABLE 1. Classification of the order Rhynchocephalia

Infraclass	Order	Suborder	Family	
Eosuchia	Rhynchocephalia	Sphenodontoidea	Monjurosuchidae	e.g. *Monjurosuchus*
			Sphenodontidae	e.g. *Sphenodon*, *Clevosaurus*
		Sapheosauroidea	Sapheosauridae	e.g. *Sapheosaurus*
		Rhynchosauroidae	Mesosuchidae	e.g. *Mesosuchus*
			Rhynchosauridae	e.g. *Rhynchosaurus Scaphonyx*
		Clarazisauroidea	Claraziidae	e.g. *Clarazia*

family Sphenodontidae by Romer (1966), but differences, including the presence of 3 sacral vertebrae, indicate a separation from the Sphenodontidae and, following Hoffstetter (1955) and Kuhn (1969), *Monjurosuchus* is assigned to a separate family, the Monjurosuchidae.

The skull structure of the Rhynchosauroidea is easily derived from that of the Sphenodontoidea with modifications associated with the specialized herbivorous diet. The suborder can be separated into two families. The Mesosuchidae, which are similar to the Sphenodontoidea in bearing teeth on the premaxilla and in having the parietal pierced by a pineal foramen, have acquired the single median nasal opening and the rudiments of lateral tooth-rows on the maxilla, so characteristic of the Rhynchosauridae. The Rhynchosauridae are heavily built forms with large and complex tooth batteries on the maxilla and dentary and a toothless premaxilla.

The two remaining suborders, the Sapheosauroidea and Clarazisauroidea, are not as well documented, much of the fossil material being fragmented and poorly preserved. The postcranial skeleton of the Sapheosauroidea is similar to that of *Homeosaurus* (Hoffstetter 1955, Romer 1956). The Clarazisauroidea was erected by Peyer (1936*a*, *b*) for two genera of aquatic reptiles—both with an acrodont dentition, an immobile quadrate, and amphicoelous vertebrae.

Pleurosaurus is a rather aberrant acrodont genus that was classified by Romer (1966) as a rhynchocephalian. However, it has an unusual temporal region that is euryapsid in nature, and Hoffstetter (1955), while recognizing some affinities to the rhynchocephalians, considers the differences to be sufficiently great to merit a separate order, the Pleurosauria; and this classification is followed here.

The Sphenodontoidea may include the family erected by Kuhn (1969) to incorporate the Lower Triassic acrodont genus *Palacrodon*. But, as Malan (1963) points out, this genus might just as easily be considered to be an aberrant procolophonid or lizard as an aberrant rhynchocephalian. Hoffstetter (1955) postulates that it may be a remote ancestor of the Pleurosauria or possibly at the evolutionary point of separation of the Rhynchocephalia and Pleurosauria. There is insufficient evidence to permit the inclusion of *Palacrodon* in the Rhynchocephalia and its position remains uncertain.

Because of insufficient evidence at present, the remaining Eosuchian families listed by Evans (1980) have not been assembled into larger units.

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APPENDIX

Total numbers of each skull element recovered from Cromhall Quarry

Element	pm	mx	n	prf	f	p	pf	po		sq	q	v	pal	pt	ps	bo	d
Number of *Planocephalosaurus* elements from a single site and stratum	19	61	18	21	27	17	17	18	36	8	7	5	42	18	6	6	99
Number of *Planocephalosaurus* elements recovered in total	46	115	32	30	36	27	33	28	51	24	18	17	93	49	19	23	146
Total number of elements of all species represented in the bone assemblages	61	161	37	32	45	30	51	36	69	33	18	17	112	50	19	23	232

Abbreviations	bo	basioccipital	p	parietal	ps	parabasisphenoid
	d	dentary	pal	palatine	pt	pterygoid
	f	frontal	pf	postfrontal	q	quadrate
	j	jugal	pm	premaxilla	sq	squamosal
	mx	maxilla	po	postorbital	v	vomer
	n	nasal	prf	prefrontal		

APPENDIX 2 *Three alternative classifications of the diapsid reptiles excluding details of the lizards and archosaurs*

	Subclass	Infraclass	Order	Suborder	Family	
ROMER (1966)	EURYAPSIDA		ARAEOSCELIDA		TANYSTROPHEIDAE	e.g. *Tanystropheus*
					PROTOROSAURIDAE and others	e.g. *Protorosaurus, Trachelosaurus*
	LEPIDOSAURIA		EOSUCHIA		YOUNGINIDAE	e.g. *Palaeogama, Paliguana, Youngina*
					TANGASAURIDAE	e.g. *Tangasaurus*
					CHAMPSOSAURIDAE	e.g. *Champsosaurus*
					THALATTOSAURIDAE	e.g. *Thalattosaurus, Askeptosaurus*
					PROLACERTIDAE	e.g. *Macronemus, Prolacerta*
			SQUAMATA		KUEHNEOSAURIDAE and others	e.g. *Kuehneosaurus, Icarosaurus*
			RHYNCHOCEPHALIA		SPHENODONTIDAE	e.g. *Clevosaurus, Homeosaurus, Sphenodon*
					RHYNCHOSAURIDAE	e.g. *Howesia, Mesosuchus, Scaphonyx*
					SAPHEOSAURIDAE	e.g. *Sapheosaurus*
					CLARAZIIDAE	e.g. *Clarazia*
					PLEUROSAURIDAE	e.g. *Pleurosaurus*
	ARCHOSAURIA					
KUHN (1969)	ARAEOSCELOMORPHA		ARAEOSCELIDA		PETROLACOSAURIDAE and others	e.g. *Petrolacosaurus*
	LEPIDOSAURIA		RHYNCHOCEPHALIA	EOSUCHOIDEA	YOUNGINIDAE	e.g. *Youngina*
					PALIGUANIDAE	e.g. *Paliguana, Palaeagama*
					TANGASAURIDAE	e.g. *Tangasaurus*
				SPHENODONTOIDEA	POLYSPHENODONTIDAE	e.g. *Polysphenodon*
					SPHENODONTIDAE	e.g. *Clevosaurus, Homeosaurus, Sphenodon*
				SAPHEOSAUROIDEA	SAPHEOSAURIDAE	e.g. *Sapheosaurus*
				PLEUROSAUROIDEA	PLEUROSAURIDAE	e.g. *Pleurosaurus*
				RHYNCHOSAUROIDEA	MESOSUCHIDAE	e.g. *Mesosuchus*
					RHYNCHOSAURIDAE	e.g. *Howesia, Rhynchosaurus, Scaphonyx*
				CLARAZISAUROIDEA	CLARASIIDAE	e.g. *Clarazia*
				THALATTOSAURDIDAE	THALATTOSAURIDAE	e.g. *Thalattosaurus*
					ASKEPTOSAURIDAE	e.g. *Askeptosaurus*
				CHORISTODEROIDEA	CHAMPSOSAURIDAE	e.g. *Champsosaurus*
			PROTOROSAURIA	PROTOROSAUROIDEA	PROTOROSAURIDAE	e.g. *Protorosaurus*
				PROLACERTOIDEA	PROLACERTIDAE	e.g. *Prolacerta, Macronemus*
				TANYSITRACHELOIDEA	TANYSTROPHEIDAE	e.g. *Tanystropheus*
			SQUAMATA		KUEHNEOSAURIDAE and others	e.g. *Kuehneosaurus, Icarosaurus*
	ARCHOSAURIA					
EVANS (1980)	DIAPSIDA	EOSUCHIA			PETROLACOSAURIDAE	e.g. *Petrolacosaurus*
					YOUNGINIDAE	e.g. *Youngina*
					TANGASAURIDAE	e.g. *Tangasaurus*
					ASKEPTOSAURIDAE	e.g. *Askeptosaurus*
					THALATTOSAURIDAE	e.g. *Thalattosaurus*
					PLEUROSAURIDAE	e.g. *Pleurosaurus*
					SPHENODONTIDAE	e.g. *Clevosaurus, Homeosaurus, Sphenodon*
					MESOSUCHIDAE	e.g. *Mesosuchus*
					RHYNCHOSAURIDAE	e.g. *Rhynchosaurus, Scaphonyx*
					CLARAZIIDAE	e.g. *Clarazia*
					DAEDALOSAURIDAE	e.g. *Daedalosaurus*
					PALIGUANIDAE	e.g. *Paliguana, Palaeagama*
					TANYSTROPHEIDAE	e.g. *Tanystropheus*
					PROLACERTIDAE	e.g. *Prolacerta, Macronemus, ?Protorosaurus*
					KUEHNEOSAURIDAE	e.g. *Kuehneosaurus, Icarosaurus*
					GEPHYROSAURIDAE	e.g. *Gephyrosaurus*
		SQUAMATA				
		ARCHOSAURIA				