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THE HEAD SKELETON OF THE RHAETIAN SPHENODONTID *DIPHYDONTOSAURUS AVONIS* GEN. ET SP.NOV. AND THE MODERNIZING OF A LIVING FOSSIL

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[Plates 1–7]

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The skull and lower jaw of a new sphenodontid reptile *Diphydontosaurus avonis* is described from disarticulated bones. The fossils were recovered from a detrital limestone of Rhaetian age deposited within solutional and tectonically formed fissures within the Carboniferous Limestone of Tytherington quarry near Bristol. The bone remains, numbering over 1000, are exquisitely preserved with intact facets.

Diphydontosaurus was the smallest member of an insular fauna, was primarily insectivorous, and probably formed locally high-density populations.

Uniquely for a sphenodontid, *Diphydontosaurus* had pleurodont teeth on the premaxilla and on the anterior regions of the dentary and maxilla. However, *Diphydontosaurus* also has the series of acrodont teeth alternating in size on the maxilla and dentary which is characteristic of the Sphenodontidae and particularly *Sphenodon*.

An analysis of 49 synapomorphs in the Diapsida emphasises the sphenodontid nature of *Diphydontosaurus*. A study of these synapomorphs among the other Triassic sphenodontids *Clevosaurus* and *Planocephalosaurus* and the eosuchian *Gephyrosaurus* suggests that the lack of a quadrate–quadratojugal conch and the complete lower temporal bar are secondarily derived in the 'living fossil' *Sphenodon punctatus*. The tuatara is therefore much less archaic than hitherto proposed. Functional reasons are advocated for the loss of the conch and the regrowth of a complete lower temporal bar. Transformation series are described which could have led to the shape of the maxilla, dentary, premaxilla, palatine and to the loss of the lacrimal in *Sphenodon*.

1. INTRODUCTION

A number of lepidosaurs have recently been described from the Mesozoic fissure fillings within the Carboniferous Limestone of the Bristol region and south Wales. The lepidosaurs include the gliding eolacertids *Kuehneosaurus latus* and *Kuehneosuchus latissimus* described by Robinson (1962, 1967); the eosuchian *Gephyrosaurus bridensis* (Evans 1980, 1981), and the sphenodontid

Planocephalosaurus robinsonae (Fraser 1982; Fraser & Walkden 1984*a*). Robinson (1973) has given the most complete account of the sphenodontid *Clevosaurus hudsoni* originally reported by Swinton (1939), and Fraser & Walkden (1983) have briefly described two other sphenodontids *Clevosaurus minor* and *Sigmala sigmala*.

The bones of a new lepidosaur were prepared from a detrital limestone recovered from a fissure in Tytherington quarry ST 660 890. One limestone block weighing 5 kg contained a minimum number of 40 individuals of this lepidosaur which constituted over 90 % of the fauna in the block. Many other bones have been prepared and the total number of bones of this species is over 1000. The majority of the skeletal elements have been identified but more preparation must be completed before the pro-otic, supraoccipital and opisthotic can be described.

The purpose of this paper is to describe the bony head skeleton of the new lepidosaur and to report some conclusions on the nature of the 'primitive' features of the extant tuatara, *Sphenodon punctatus* Gray. The bones are generally white although a few are pale yellow and the occasional brown bone is present. They exhibit exquisite preservation and the bones here described all derive from one site in fissure 2 of Whiteside (1983) and Whiteside & Marshall (1986). This site has since been destroyed by quarrying but unprepared rocks containing the lepidosaur are retained in the University of Bristol Geology department and bones of this species can currently be collected from fissure 16 although the bones at that locality are more fragmentary and are black or brown.

Tytherington quarry lies on the Lower Carboniferous Black Rock Limestone which forms part of the narrow western limb of a syncline of Palaeozoic rocks. These are over-stepped by Mesozoic beds principally of Triassic age (see figure 1). The fissures were formed in the Late Triassic by solutional and tectonic processes (Whiteside 1983) and were infilled by terrestrial deposits that derived from a small limestone island. These deposits were brought in by meteoric waters. Whiteside (1983) demonstrated that some fissures were infilled in a freshwater environment, some in brackish conditions and others in a mixed freshwater and marine régime.

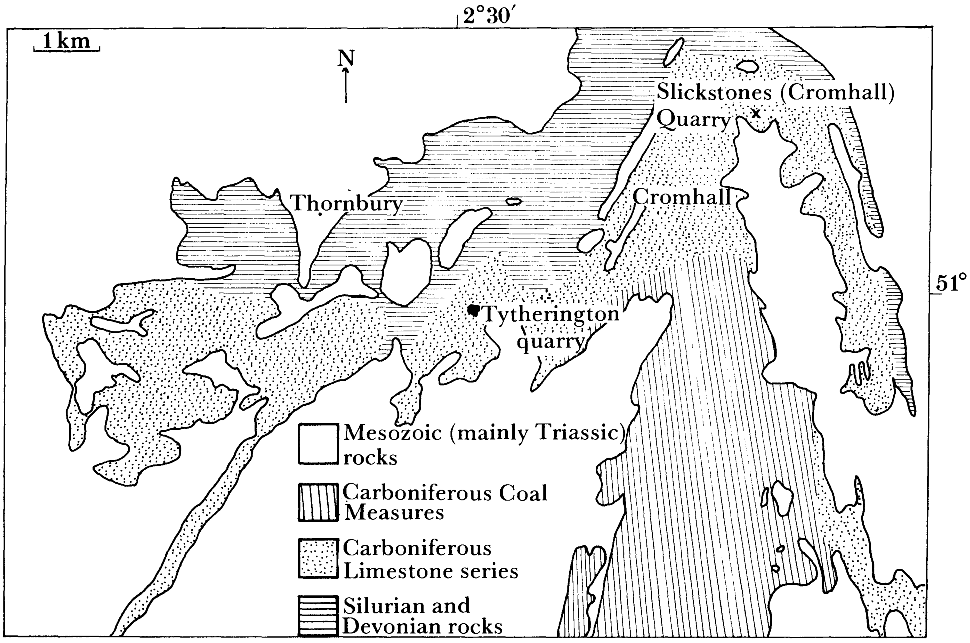

FIGURE 1. Areal relationship of the Triassic and Palaeozoic rocks in the region of Tytherington quarry.

Marshall & Whiteside (1980) on the basis of an assemblage of Rhaetian marine and terrestrial palynomorphs proposed that fissure 2 was infilled in a marginal marine location. Whiteside & Robinson (1983) expanded this model suggesting that this fissure was infilled in a fluctuating freshwater–saline environment which is compatible with their discovery of a glauconitic clay similar to others recorded from non-marine or brackish environments. A model for the filling of the Tytherington fissures is shown in figure 2.

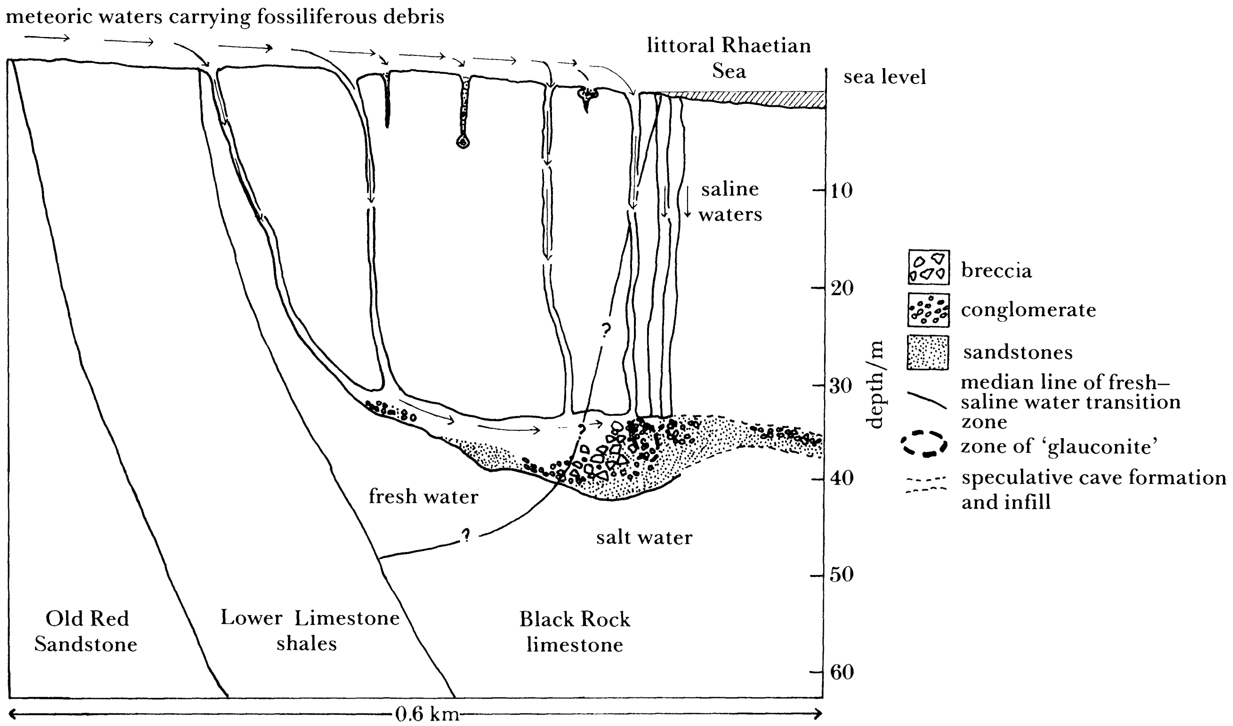

FIGURE 2. Suggested palaeoenvironment for the infilling of the Tytherington fissures in the Rhaetian. Modified from Whiteside & Robinson (1983).

In addition to other deposits the new lepidosaur has been found in two sediments, one from fissure 2 and one from fissure 1 which have yielded non-reworked palynomorphs. These palynomorphs and the lithology indicate a dating equivalent to the Late Westbury Formation (Lower Rhaetian) (Whiteside 1983; Whiteside & Marshall 1986). A similar palynomorph assemblage has been recovered from a fine-grained limestone in fissure 16 and this bed underlies conglomerates which contain fossils of the new lepidosaur. A blackened, reworked Rhaetian marine vertebrate fauna of *Gyrolepis*, *Hybodus* and *Saurichthys* have been found with white unreworked lepidosaur bones, including the new sphenodontid in fissures 1 and 2. In the detrital limestone from which the bones figured derive, there are a few scales of a fish, probably *Pholidophorus*, preserved in the same manner as the reptile bones. The fish scales are not in reworked clasts. All these features indicate that the new sphenodontid lived in the Rhaetian; probably in a time equivalent to the Late Westbury Formation, Penarth Group.

Fraser & Walkden (1983, 1984*b*) have dated a similar reptile assemblage which includes *Diphydontosaurus* from Cromhall quarry as Norian. This dating was based on the similarity of colour between the red and green sediment of the fissures and those of the Mercia Mudstone Group. They emphasised the absence of palynomorphs which they believed suggested that the

Cromhall sediments were not Rhaetian. However, during recent fieldwork with the author, the former manager of Cromhall quarry, Mr M. Curtis, discovered a dentary of *Clevosaurus* in horizontal sequences that overlay the Carboniferous Limestone surface. *Clevosaurus* is found in the same faunal assemblage as *Diphydontosaurus* in three fissure deposits at Tytherington. Later Mr Curtis discovered a nearly complete *Pholidophorus* in the same horizon as this reptile and fish teeth in the same matrix as the *Clevosaurus* dentary. *Pholidophorus* has not been recorded from beds below the Rhaetian in the United Kingdom. It would seem, therefore, that the Cromhall reptile assemblage is also of a similar Rhaetian age to that at Tytherington.

Therefore it is concluded that the new lepidosaur was a component of a Rhaetian insular fauna. The other faunal elements at Tytherington included the sphenodontids *Clevosaurus*, *Planocephalosaurus*, archosaurs such as *Thecodontosaurus* and a cursorial crocodile similar to *Terrestriosuchus* of Crush (1984).

2. Materials and methods

The bones were prepared by completely immersing 0.5 kg blocks of the limestone in 10% acetic acid at a temperature of 50 °C. Some blocks were stood on sieves but other residues were poured through a nest of sieves with a smallest mesh of 75 μm. The bones were then washed thoroughly with water for 24 h to eliminate any calcium acetate. The majority of the bones were found in the 500 μm mesh sieves and after drying all bones were hand-picked under a stereoscopic microscope by paint brush from the sieve. The bones are currently kept on a rubber base, which provides a non-adhesive friction surface, in small plastic trays at the University of Bristol Geology department.

3. Taxonomy

Class	Reptilia Laurenti 1768
Sub Class	Diapsida Osborn 1903
Order	Sphenodontoidea nom. transl., ex suborder Sphenodontoidea Lydekker 1888.
Family	Sphenodontidae Cope 1869
Genus	*Diphydontosaurus* gen.nov.
Species	*D. avonis* sp.nov.

3.1. *Holotype*: *a right dentary BU* 23760

Paratypes

Left premaxilla BU 23763, right maxilla BU 23764, left nasal BU 23842, frontal BU 23787, right parietal BU 23789, left postorbital BU 23785, left postfrontal BU 23781, right jugal BU 23790, left prefrontal BU 23780, left squamosal BU 23782, right quadrate with fused quadratojugal BU 23783, left epipterygoid BU 23784, right vomer BU 23772, left palatine 23776, left pterygoid BU 23768, left ectopterygoid BU 23774, basioccipital BU 23986, right exoccipital BU 23778, parabasisphenoid BU 23777, right articular complex BU 23761, left coronoid BU 23762.

3.2. *Diagnosis for genus Diphydontosaurus*

Temporal region diapsid with an incomplete lower temporal arcade in most specimens. Quadratojugal fused to quadrate forming a conch-like structure. Quadratojugal foramen present. Paired nasals. Single frontal. Paired parietals fused in larger specimens. Large parietal foramen present between fused parietals. Prefrontal with pronounced medial inflexion. Exoccipitals fused to basioccipital in adults. No foramen rotundum or ventral process of the opisthotic. Squamosal quadriradiate with lateral ventral ramus that holds the quadrate. Quadrate ramus of pterygoid deeply overlaps pterygoid ramus of quadrate. Teeth present on pterygoid, palatine and vomer. Enlarged lateral tooth row on palatine. Teeth on the anterior half of maxillary tooth row pleurodont. Teeth on the posterior half of maxilla tooth row acrodont, the anterior of these showing an alternation in size. Premaxilla with pleurodont teeth. Articular, pre-articular, surangular and possibly angular form fused unit. Dentary with long posterior process. Meckelian fossa narrowed in mid region by dentary. Teeth on the anterior and mid region of the dentary tooth row pleurodont. Posterior teeth of dentary tooth row acrodont with the anterior of these alternating in size.

Vertebrae amphicoelous. Atlantal centrum and axis intercentrum fused to the axis. Second sacral rib bifurcate. Caudal fracture plane present. Scapula and coracoid fused to form one unfenestrated bone. Supracoracoid foramen present. Humerus with ectepicondylar and entepicondylar foramen. Thyroid fenestra present in pelvic girdle. Hooked fifth metatarsal.

Derivation of name

Genus from Greek diphy (double (two types)), dont (tooth). Species from latinized version of Avon, the county in which the beast was found.

Type locality. Fissure 2 in Tytherington quarry, Avon, United Kingdom.

Diagnosis of type and only species D. avonis

A very small reptile with skull length less than 1.70 cm. Five to seven teeth in the premaxilla. The larger maxillae have usually 28 teeth, less than 75% of these being pleurodont, the rest acrodont. The larger dentary specimens with usually 24 but up to 28 teeth, less than 86% of these being pleurodont, the rest acrodont.

4. THE SKULL

Because the skull is reconstructed from isolated bones the reconstruction is necessarily of one composite individual. Other lepidosaurs from the fissure deposits of the Bristol region and South Wales such as *Kuehneosaurus*, *Gephyrosaurus* and *Planocephalosaurus* have also been reconstructed from entirely dissociated skull elements. Because the bones have well preserved facets the reconstruction given here is confidently presented as an accurate representation of the skull and lower jaw. Some bones such as the ectopterygoid and pterygoid have been fitted together mechanically.

4.1. *General description*

The skull is about 1.4 cm long (occiput to premaxillary tip), nearly 1.3 cm broad between the anterior processes of the quadratojugals and reaches a maximum of 0.6 cm high behind the orbits.

Viewed dorsally (figure 3*a*) the skull exhibits paired external nares, large orbits and prominent upper temporal openings. The pineal foramen is also large and positioned centrally just behind the mid point of the fused parietals. A supratemporal is absent, the single frontal has prominent posterior processes which preclude mesokinetic movement and a strongly marked ornament appears on the prefrontals, postfrontals and postorbitals.

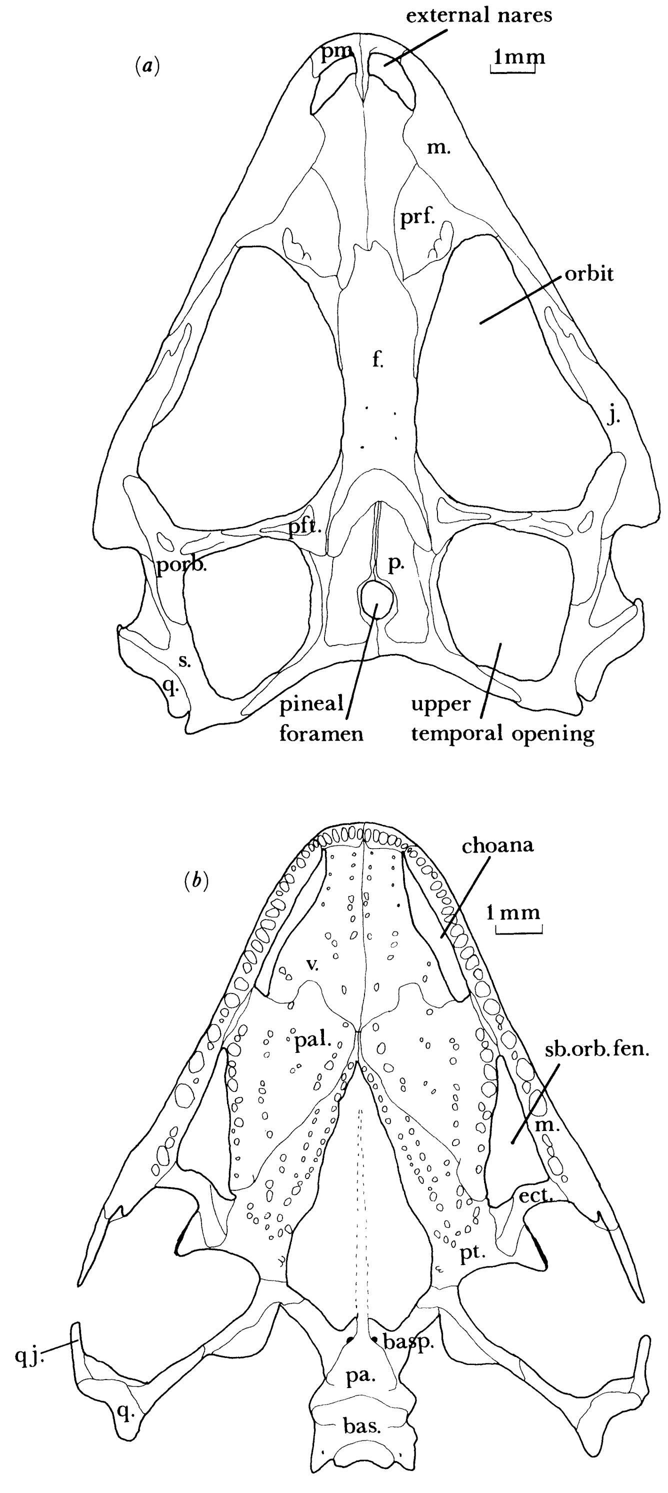

Figure 3. Reconstructed skull of *Diphydontosaurus avonis* (*a*) in dorsal view, (*b*)in palatal view.

The palatal reconstruction (figure 3*b*) displays extensive tooth formation on the maxillae, pre-maxillae, vomers, palatines and pterygoids. The largest of these teeth are positioned on the posterior part of the maxillae and juxtaposed with these are the large teeth of the lateral margin of the palatine. The interpterygoid vacuities are extensive and anteriorly the pterygoids thin and suture together, probably terminating in a contact with the vomers. Two prominent, suborbital fenestrae are displayed and posterior to these lie the large fossae containing the adductor musculature. An U-shaped suture unites the parabasisphenoid and basioccipital and fused to the latter are the two exoccipitals. Two prominent spheno-occipital tubercles are displayed on either side of the basioccipital. No vidian canals are present on the parabasisphenoid leaving the paired internal carotid foramina forming noticeable features. The nature of the basipterygoid processes suggest they formed movable joints with sockets on the pterygoids. The choanae are bounded by the maxillae, palatines and vomers and narrow in their mid region.

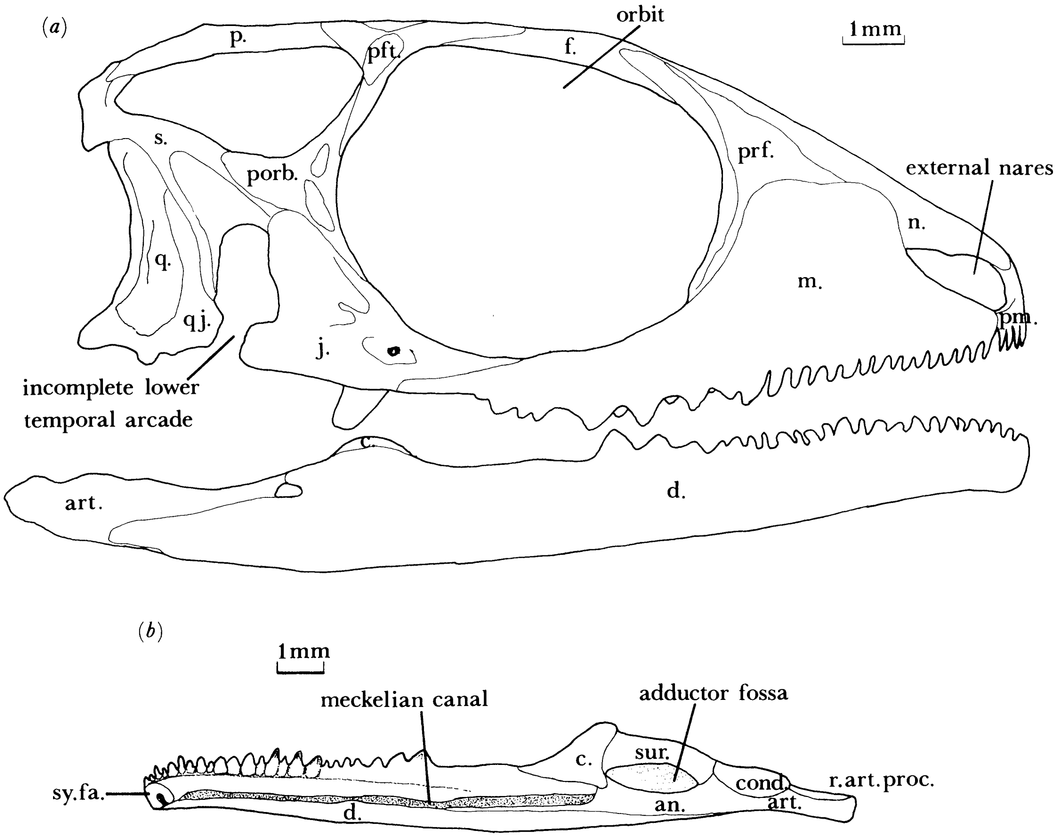

FIGURE 4. Reconstructed skull and lower jaw of *Diphydontosaurus avonis* (*a*) in lateral view; (*b*) lower jaw in medial view.

The lateral view (figure 4*a*) shows clearly the diapsid nature of the skull but the smaller lower temporal fossa is floored by an incomplete bar. A lacrimal is absent. The quadrate showing a pronounced conch (indicating a tympanum present), is strongly held by the descending process of the squamosal and the broad posterior pterygoid lamella; these prevented streptostylic movement. A deep pterygoid flange is indicated which serves as a strong guide for the lower jaw during occlusion. Prominent ornamentation is present on the jugal and some specimens have a more pronounced posterior process than is indicated in the figure. A foramen rotundum is absent, no large occipital recess being present in the basioccipital.

4.2. *Tooth-bearing marginal elements*

Premaxilla (*figures* 5 *and* 6*a*, *b*, *plate* 1)

Each of the paired premaxillae exhibits four facets. The expanded palatal shelf bears five to seven pleurodont replacement teeth (some specimens have gaps for absent teeth) with alternate lingual and labial placement. The shelf contacted the maxilla laterally and the vomer posteriorly by weak sutures.

On the posterodorsally recurved rostral process there is an extensive medial facet which contacted with the opposing premaxilla and there was a lateral tongue-in-groove suture with the nasal bone. On the posterodorsal surface of the palatal shelf, laterally positioned to the base of the rostral process, the bone is pierced by foramina which transmitted the subnarial branch of the maxillary artery and medial ethmoidal nerves.

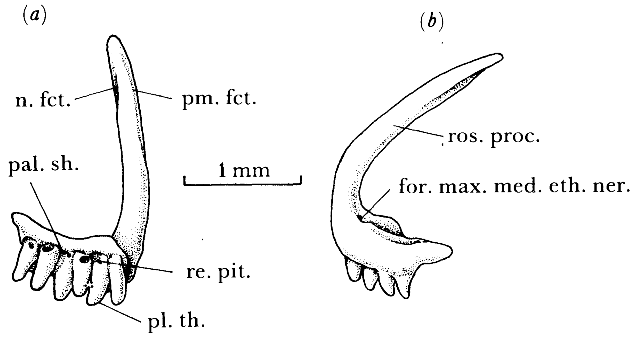

FIGURE 5. Left premaxilla, specimen no. 23763 in (*a*) ventromedial; (*b*) lateral view. (All specimen numbers in figures 5–32*i* refer to the Bristol University Geology Museum collection.)

Maxilla (*figures* 6*c*–*h and* 7)

An almost complete maxilla is represented by figure 7, the bone being broken across the midline in preparation. Anteriorly the maxilla contacted the premaxilla with that bone forming the ventral margin of the external nares.

Caudad the maxilla displays a quadrangular superior (or nasal) process whose steeply curved anterior margins formed the posterior rim of the external nares. Dorsally and anterodorsally the superior process sutured with the nasal bone by a weak overlapping contact. The posterodorsal and posterior border of the superior process forms the facet for the prefrontal and the lateral wall of the lacrimal canal.

The posterior process comprises more than half the length of the maxilla and the anterior dorsal rim, together with the jugal, formed the ventral orbital margin. The dorsal region contacted the jugal in a strong tongue-in-groove structure and on the medial surface there is an elongate facet for the lateral process of the ectopterygoid. Anteriorly there is the facet for the palatine. This region was one of the most rigid contacts between skull bones to resist the stresses produced during occlusion; the great intensity of force being indicated by bite marks on the opposing dentary produced by the posterior maxillary teeth. Posteriorly the maxilla formed the lateral margin of the suborbital fenestra and anteriorly the lateral rim of the choana.

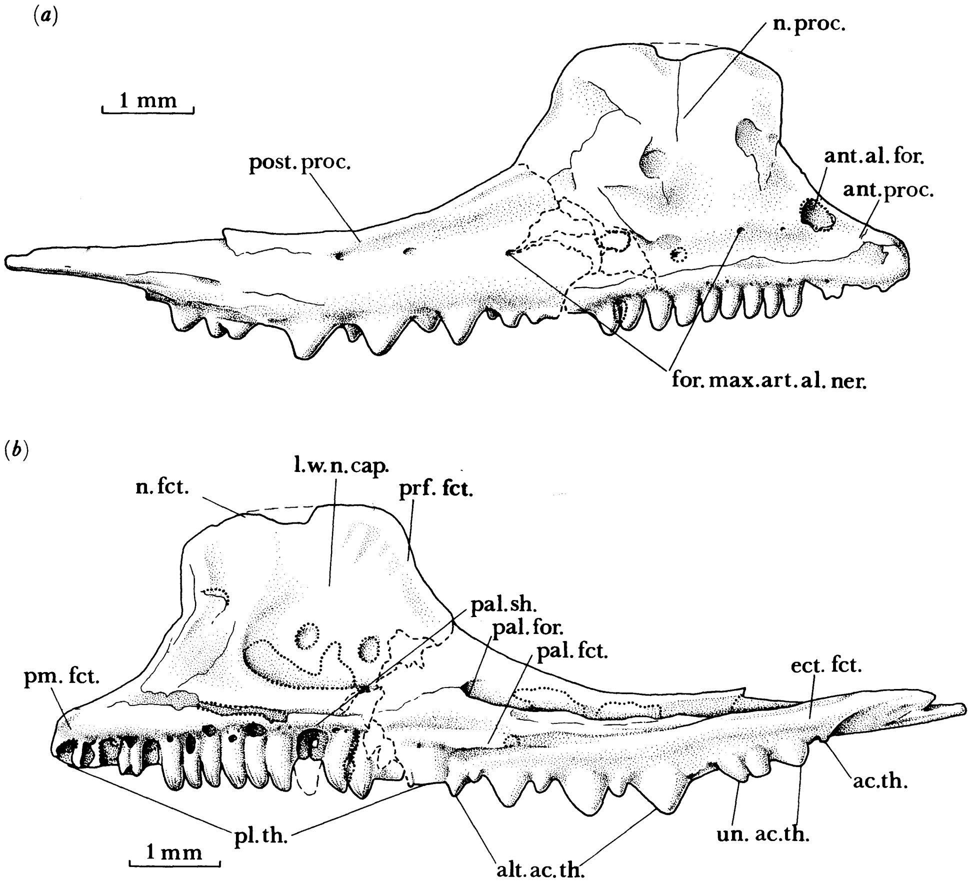

FIGURE 7. Right maxilla specimen no. 23764 (*a*) in lateral view; (*b*) in medial view.

DESCRIPTION OF PLATE 1

FIGURE 6. Tooth-bearing skull bones of *Diphydontosaurus* from fissure 2. (*a*) Specimen 23763. Left premaxilla posteroventral view (ammonium chloride coated) showing replacement pits at base of teeth. Magn. × 15.60. (*b*) Same anterolateral view (ammonium chloride coated). Magn. × 15.60. (*c*) Specimen 23764. Right maxilla, lateral view, small teeth of alternating series not conspicuous in photograph. Magn. × 6.15. (*d*) Specimen 23764. Anterior region of right maxilla, lateral view (ammonium chloride coated). Magn. × 15.15. (*f*) Same, medial view showing pleurodont emplacement of teeth and replacement pits. Magn. × 15.15. (*e*) Specimen 23765. Medial view right maxilla showing smaller replacement pits on posterior pleurodont teeth. Most posterior teeth below posterior border of nasal process have only tiny foramina at tooth base. Magn. × 11.10. (*g*) Specimen 23766. Medial view left maxilla showing typical water wear on the bone. Magn. × 18.08. (*h*) Specimen 23767. Medial view right maxilla with one tooth (in mid tooth row) growing medially. Magn. × 17.78.

DESCRIPTION OF PLATE 2

FIGURE 9. Skull bones of *Diphydontosaurus* from fissure 2. (*a*) Specimen 23842. Left nasal bone dorsal view. Magn. × 13.60. (*b*) Same, ventral view. Magn. × 13.60. (*c*) Specimen 23787. Dorsal view of frontal, posterior region missing in specimen (ammonium chloride coated). Magn. × 9.45. (*d*) Same, ventral view, ammonium chloride coated. Magn. × 9.45. (*f*) Specimen 23788. Dorsal view of frontal showing posterior process on right side (ammonium chloride coated). Magn. × 10.50. (*e*) Specimen 23789. Left parietal, dorsal view. Magn. × 15.23. (*g*) Same, ventral view, ammonium chloride coated bone. Magn. × 15.23. (*h*) Specimen 23790. Lateral view right jugal showing usual form. Magn. × 9.75. (*i*) Specimen 23791. Large, right jugal, lateral view with notch on posterior process for (?) suturing with quadratojugal and squamosal. Magn. × 11.93.

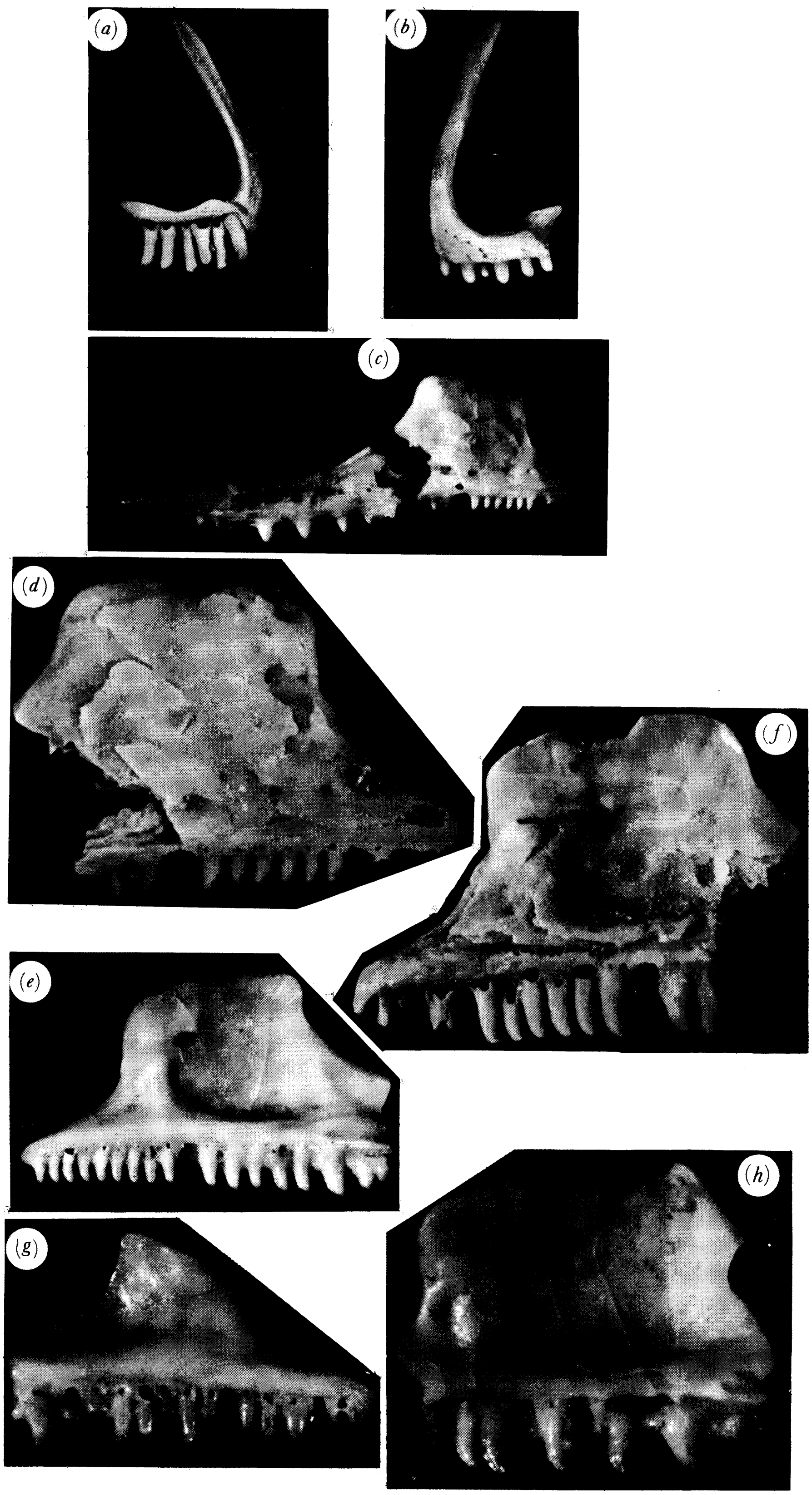

FIGURE 6. For description see opposite.

FIGURE 9. For description see p. 388.

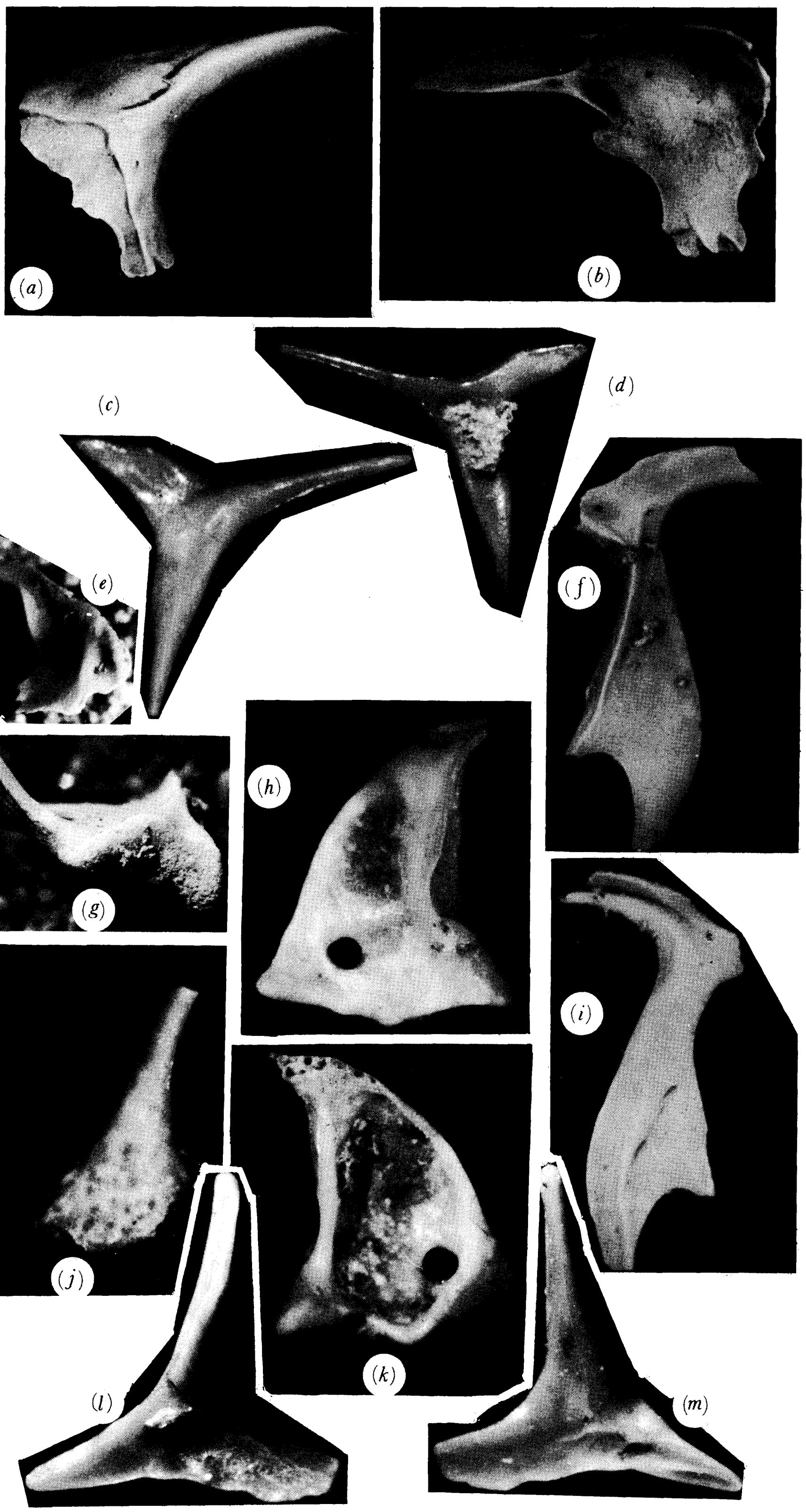

FIGURE 13. For description see p. 389.

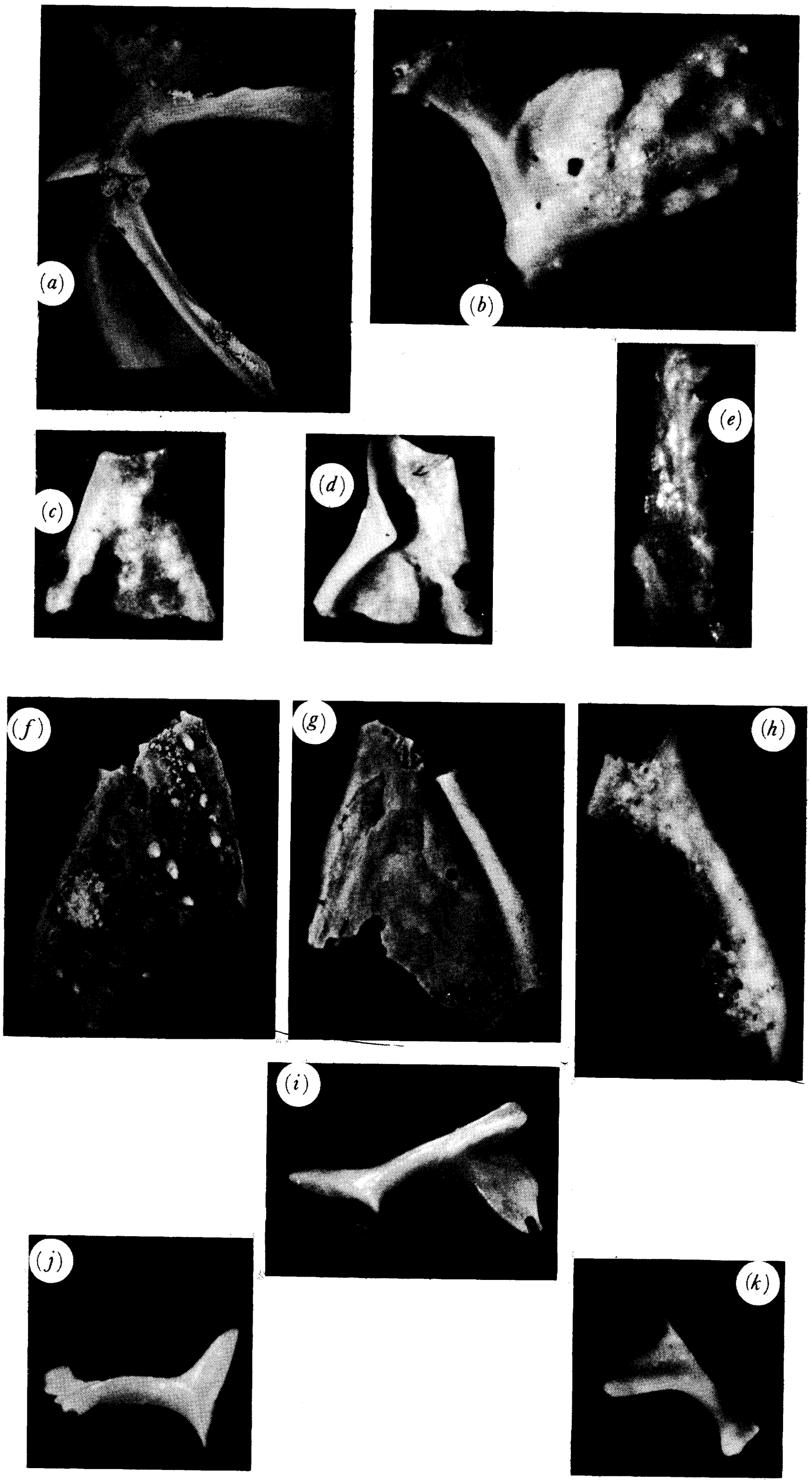

FIGURE 21. For description see opposite.

The inferior lateral region has nine foramina. The largest and most anterior, the anterior alveolar foramen, conveyed the terminal branches of the maxillary artery and superior alveolar nerve. Posteriorly the eight other foramina (five exiting anteriorly and three posteriorly) transmitted the cutaneous branches of the maxillary artery and superior alveolar nerve.

The ventral lip of the maxilla carried 28 teeth which form, together with those of the dentary, the most notable feature of *Diphydontosaurus*. On the paratype (BU 23764) the 17 anterior teeth are emplaced in pleurodont fashion as defined by Edmund (1969) with gaps for missing teeth; they are recurved with longitudinal ridges on their crowns. The last three or four of these teeth are more robust and do not display the larger replacement pits characteristic of the anterior group. Caudad to these large pleurodont teeth are 11 fully acrodont teeth, the first seven showing alternating size, both series, large and small, increasing in magnitude posteriorly. The base of the smaller teeth of the alternating series is always placed on the lingual side of the ventral margin of the maxilla. The three teeth lying immediately posteriorly to the alternating series are of uniformly small size and these are followed by the last and smallest tooth. In other specimens the alternating series varies from four to nine teeth and the uniform teeth reach a maximum of six.

The large medial depression on the nasal process of the maxilla formed the lateral wall of the nasal capsule.

4.3. *Median dermal roofing bones*

Nasal (*figures* 8 *and* 9*a*, *b*, *plate* 2)

The paired nasals formed the anterior roofing bones of the skull. There are four facets, two of these being on the medial edge, the more anterior is a slot structure for the premaxilla and behind this is the long facet for the opposing nasal.

Posteriorly the nasal formed an overlapping suture with the frontal and dorsolateral maxillary and prefrontal facets were present.

The anterior process of the nasal formed the superior rim of the external nares. On the ventral surface, as in *Gephyrosaurus bridensis* (see Evans 1980) the most prominent feature is a ridge that

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DESCRIPTION OF PLATE 3

FIGURE 13. Skull bones of *Diphydontosaurus* from fissure 2. (*a*) Specimen 23780. Left prefrontal in lateral view (ammonium chloride). Magn. × 9.75. (*b*) Same, in medial view. Magn. × 11.18. (*c*) Specimen 23781. Left postfrontal, medial view. Magn. × 6.38. (*d*) Same, lateral view. Magn. × 6.38. (*f*) Specimen 23782. Left squamosal in medial view. Magn. × 12.68. (*i*) Same, in lateral view. Magn. × 12.15. Both ammonium chloride coated. (*e*) Specimen 23783. Right quadrate view of dorsal head showing squamosal facet. Magn. × 10.28. (*g*) Same, in condylar view (ammonium chloride). Anterior at top. Magn. × 14.33. (*h*) Same, in anteromedial view. Magn. × 11.93. (*k*) Same, posterolateral view. Magn. × 11.93. (*j*) Specimen 23784. Left epipterygoid lateral view. Magn. × 20.25. (*l*) Specimen 23785. Left postorbital lateral view. Magn. × 11.18. (*m*) Same, medial view. Magn. × 11.18.

DESCRIPTION OF PLATE 4

FIGURE 21. Skull bones of *Diphydontosaurus* from fissure 2. (*a*) Specimen 23768. Left pterygoid, ventral view (bone coated in ammonium chloride) shows quadrate flange, and posterior part of anterior tooth-bearing ramus. Magn. × 12.38. (*b*) Specimen 23769. Right pterygoid mid region, ventral view showing notch for palatine and pterygoid flange. Magn. × 18.60. (*c*) Specimen 23770. Anterior part of left vomer ventral view. Magn. × 18.53. (*d*) Same, dorsal view. Magn. × 20.70. (*e*) Specimen 23771. Anterior part of tooth-bearing ramus of right pterygoid. Magn. × 20.93. (*f*) Specimen 23772. Right vomer, ventral view with anterior and posterior region missing. Magn. × 16.65. (*g*) Same, dorsal view. Magn. × 16.65. (*h*) Specimen 23773. Left vomer, most extensive specimen, ventral view. Magn. × 17.63. (*i*) Specimen 23774. Left ectopterygoid posterior view. Magn. × 13.56. (*h*) Same, ventral view. Magn. × 10.95. (*j*) Same, anterior view. Magn. × 10.95.

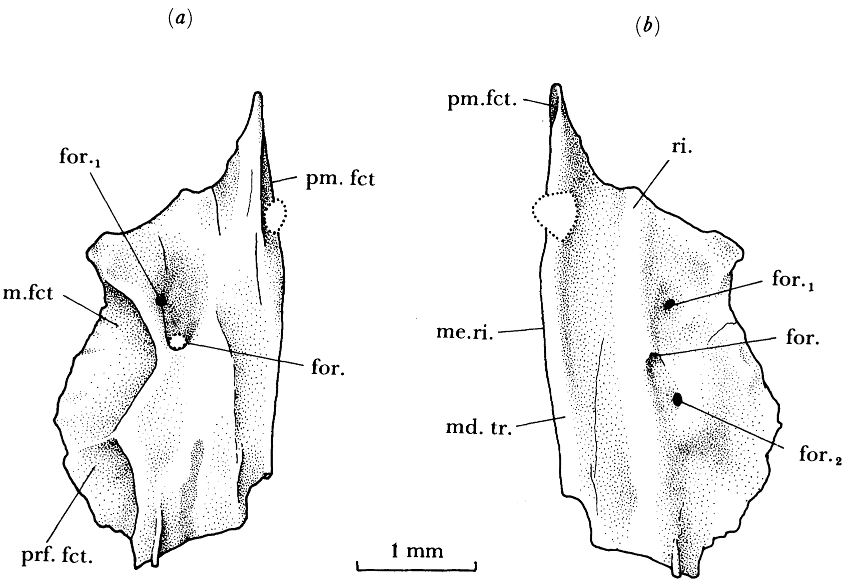

FIGURE 8. Left nasal, specimen no. 23842 in (*a*) dorsal and (*b*) ventral views.

runs anteroposteriorly. Medial to this ridge lies a trough which probably housed anteriorly the vestibulum and posteriorly the nasal chamber. As in *Gephyrosaurus bridensis* the posterior region of the trough is the deeper. A cartilaginous nasal septum was doubtless attached to the median ridge of the ventral surface.

The dorsal and ventral surface are perforated by foramina, through which, by comparison with the nasal of *Ctenosaura pectinata* (Oelrich 1956) branches of the lateral ethmoidal nerve would have exited. The larger of the two dorsal foramina is in the same position as a large foramen in the nasal of *Sphenodon*.

Frontal (*figures* 9*c*, *d*, *f and* 10)

The single frontal is the largest roofing bone and also one of the largest of the head bones. It lay astride the median plane and bridged the orbits forming part of their dorsal margins. The bone is slightly curved anteroposteriorly, and viewed dorsally is essentially rectangular with the long sides bowed inwards to form a narrow waist. The frontal forms bilaterally symmetrical posterior processes for facets of the postfrontal and parietal, the median excavation produced by these processes is thus deeply U-shaped. The lateral edges display the postfrontal facet posteriorly and a large prefrontal suture which formed a robust connection with the frontal process of that bone. Medially along the lateral region the bone has a medially indented ventral ridge with an overhanging dorsal lip. The medial hollow between the ventral ridges (the cristae cranii) was occupied by the olfactory canal. Anterodorsally, the frontal sutured to the nasal bones by means of a shallow under-lip with a raised area seperating the posterior ends of the nasals. The frontal has a number of foramina congregated particularly on the mid dorsal surface; these transmitted branches of the frontal ramus of the trigeminal nerve and the frontal artery.

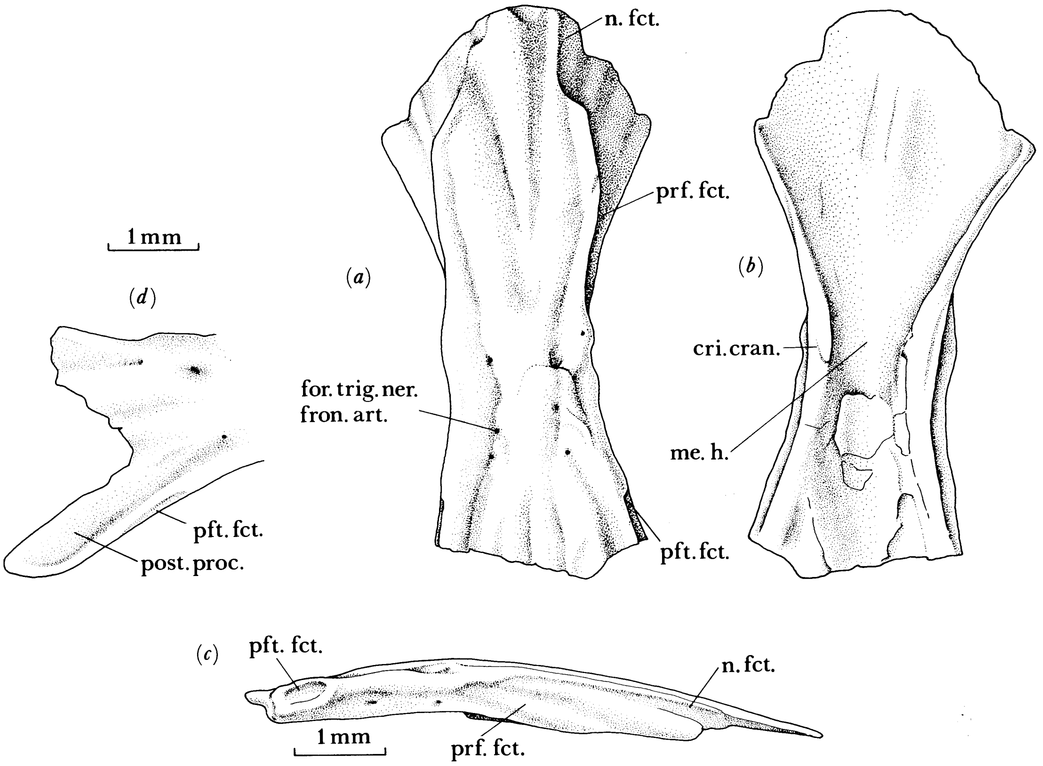

FIGURE 10. Frontal, specimen no. 23787 in (*a*) dorsal, (*b*) ventral, (*c*) right lateral view, (*d*) specimen no. 23788, showing posterior process.

Parietal (*figures* 9*e*, *g and* 11)

A dorsoventrally flattened paired bone fused along the midline. A prominent feature of the parietal is a large pineal foramen placed centrally. Anteriorly there are facets that underly the posterior processes of the frontal and, laterally, the postfrontal. A ridge runs around the lateral and posterior borders of the dorsal surface and this continues posterolaterally on the elongated posterior process. The lateral part of this ridge is continued anteriorly on the posterior process of the frontal.

The ventral surface forms two troughs either side of the median line separated by a ventral ridge which is formed from the fusion of the two bones. Below this region lay the optic lobes and part of the cerebral hemispheres.

The posterior process sutured into a slot formed on the parietal process of the squamosal and the posterior margins of both these bones formed the origin for the depressor mandibulae. The lateral region of the parietal formed the site of origin for some of the major adductor musculature.

4.4. *Circumorbital series*

Postorbital (*figures* 12 *and* 13*l*, *m*, *plate* 3)

This is a robust, T-shaped bone which formed the junction between the orbits anteriorly and the supratemporal fossa posteriorly. The dorsal postfrontal process was joined laterally by a strong twisting suture to the descending postorbital process of the postfrontal. Posteriorly the

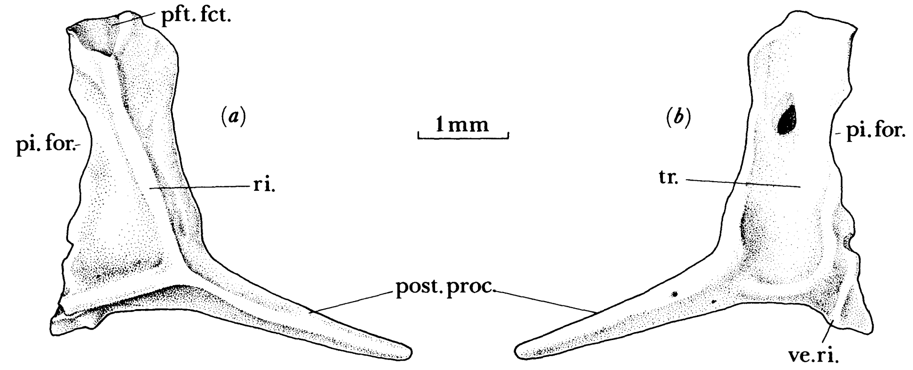

FIGURE 11. Right parietal, specimen no. 23789 in (*a*) dorsal (*b*) ventral view.

postorbital expands to form medially an extensive facet which overlay a corresponding region on the squamosal. Also medially, and posteroventrally directed, is a ridge suture which fitted in a reinforcing tongue-in-groove fashion onto the dorsal area of the jugal. The postorbital is thickened anteriorly, this region attached to the connective tissue of the orbital fascia. On the lateral surface, the central regions are indented to form two depressions, this being a feature only represented in larger specimens such as that figured. Medially and centrally placed is a small nutrient foramen.

Postfrontal (*figures* 13*c*, *d and* 14)

The postfrontal is of triradiate form with curved margins and bears three facets. The posterior process is the shortest and displays a medial parietal facet. The long, thin anterior process exhibits a long facet which was the tongue for a corresponding groove of the frontal. The stout ventral postorbital process sutures to the postorbital medially and ventrally and features a slight ridge which terminates midway and greatly strengthened the connection. This was important in bracing the temporal region between the orbits and upper temporal fossa. On the lateral surface at the junction of the three processes and covering part of the ventral process the bone is excavated to form a shallow sulcus. In some large specimens the bone is markedly bowed outwards dorsoventrally but this is not a consistent feature.

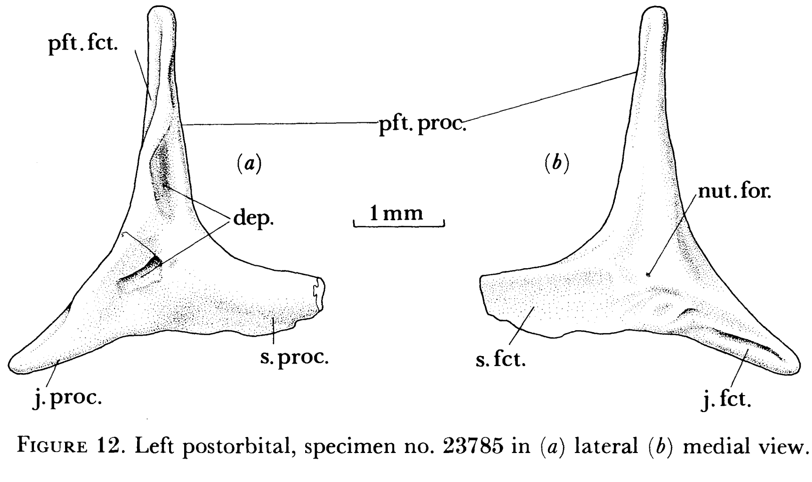

FIGURE 12. Left postorbital, specimen no. 23785 in (*a*) lateral (*b*) medial view.

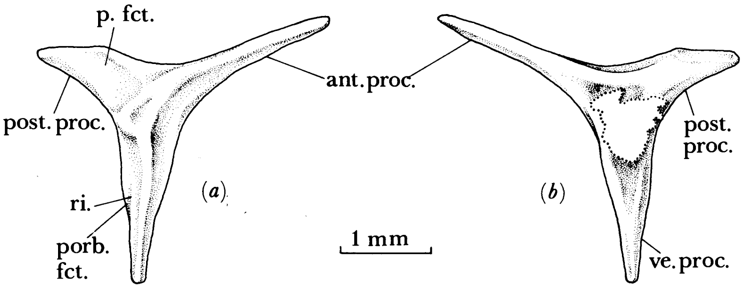

FIGURE 14. Left postfrontal specimen no. 23781 in (*a*) medial (*b*) lateral view.

Jugal (*figures* 9*h*, *i and* 15)

The jugal is a triangular bone with an extended anterior process bearing two facets, one along its lateral and ventral surface for the maxilla and, on the medial side, another sutured with the lateral flange of the ectopterygoid. The entire posterior lateral surface is ornamented. A large central foramen and a number of smaller ones are present, these transmitted the cutaneous branches of the maxillary nerve.

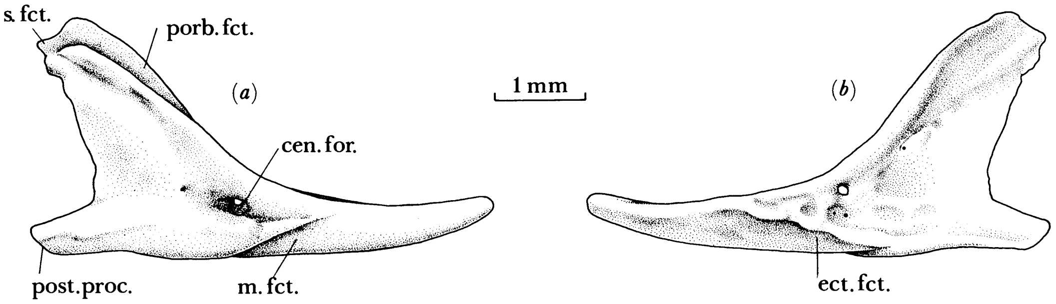

FIGURE 15. Right jugal, specimen no. 23790 in (*a*) lateral (*b*) medial view.

On the dorsal and anterodorsal surface there is a deep slot facet for the postorbital, this facet is sometimes inflected laterally especially in larger specimens. The posterior process is truncated in smaller specimens and has no facets which would have made a connection with the quadratojugal, however, one very large specimen (figure 9*i*) bears a distinct terminal fork which suggests a suture with the quadratojugal. As there is no equivalent facet for the jugal on any specimen of quadratojugal it seems likely that generally the lower temporal bar is incomplete, but that in very old animals a complete bar may be present, formed perhaps by ossification of a ligament between the posterior process of the jugal and anterior process of the quadratojugal.

On the posterodorsal surface is a slot (continuing the postorbital facet) which was the facet for the squamosal.

The jugal is concave on the posterior medial surface and formed the lateral wall of the coronoid recess; anterodorsally the thickened jugal margin formed part of the inferior rim of the orbits.

Prefrontal (*figures* 13*a*, *b and* 16)

This is a large, pyramid-shaped bone whose curved anterior region formed the anterior and part of the superior rim of the orbit. The bone displays an ornamented depression on the dorsal lateral surface above the pyramid apex. The anterior lateral area forms a large facet, which underlay the maxilla, forming an extensive, though shallow, suture and there is an anterodorsal contact for the nasal which is not well known from any specimen.

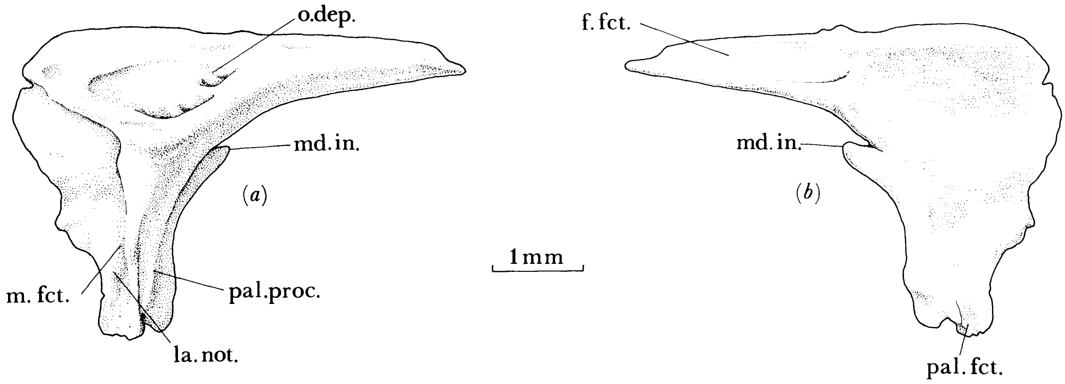

FIGURE 16. Left prefrontal, specimen no. 23780 in (*a*) lateral (*b*) medial view.

The distinct posteriorly oriented frontal process manifests an elongated medial groove facet that sutured with the frontal forming a rigid connection that strengthened the superior orbital margin. There is a pronounced ventrally directed palatine process which is strongly inflected dorsomedially forming possibly the site of attachment for tissue holding the sclerotic ossicles. The lower lateral margin of the palatine process is bowed inwards for the lacrimal canal and the process terminates with the palatine facet that would have filled a depression on the dorsal palatine surface thus reinforcing the joint and preventing the dissipation of forces during biting.

4.5. *Cheek bones*

Squamosal (*figures* 13*f*, *i and* 17)

The squamosal is a tetraradiate bone with four facets. The dorsal parietal process carries a deep groove which accepted the long posterior process of the parietal. The very slender curved ventral process (which is not shown on specimen BU 23782) firmly sutured around the anterolateral edge of the quadrate and the quadratojugal. Anteriorly the bone is emarginated dorsally and formed the superior border of the infra-temporal fossa. The anterior process exhibits on its dorsal surface an extensive facet for the postorbital and anteriorly fitted into a posterodorsal notch on the jugal. The posterior process is not complete in any specimen; this region overlay the cephalic head of the quadrate.

Quadratojugal (*figures* 13*g*, *h*, *k and* 18)

Fused to the lateral margin of the quadrate and forming the lateral rim of the tympanic crest the quadratojugal is a small bone whose suture line is only marked in some specimens. The most persistent part of the suture line occurs above the quadratojugal foramen. Medially the

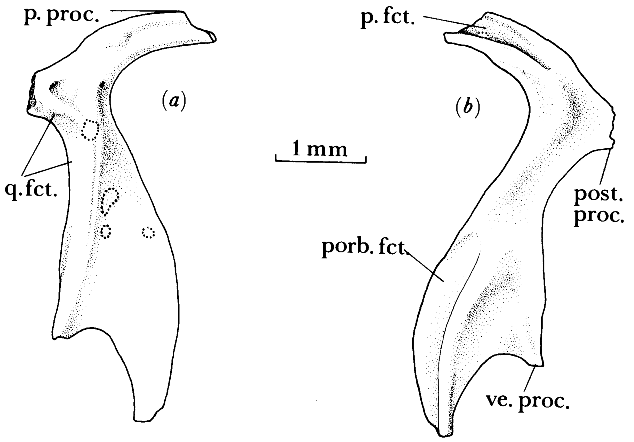

FIGURE 17. Left squamosal, specimen no. 23782 in (*a*) medial and (*b*) lateral view.

bone skirts the lateral margins of the quadratojugal foramen and anteriorly forms a triangular extension with no facet which is the remnant of the posterior part of the lower temporal bar (see the description of the jugal). The medial surface of the quadratojugal provided the origin of small muscles of the external superficial adductor complex, the retractor anguli oris by analogy with *Sphenodon* (Hass 1973), that flexed the rictal plates.

4.6. *Palatoquadrate group*

Quadrate (*figures* 13*e*, *g*, *h*, *k and* 18)

Ventrally the quadrate forms a double condyle (the larger being the more medial) and this region articulated with a corresponding region on the articular complex of the lower jaw. Posteriorly a large basin, the conch (*sensu* Robinson 1973) is bordered laterally by a rim, the tympanic crest formed by the quadrate and fused quadratojugal, and medially by a posterior crest which runs from the cephalic head and expands ventrally into the double condyle. A large foramen pierces the conch and is partly bounded laterally by the quadratojugal; this is the quadratojugal foramen (*sensu* Robinson 1973) which probably carried, as in *Sphenodon* (see O'Donoghue 1920 plate 7, figure 2), the vena mandibularis. Medially a broad pterygoid flange had a deep overlap with the posterior process of the pterygoid thus producing a strong

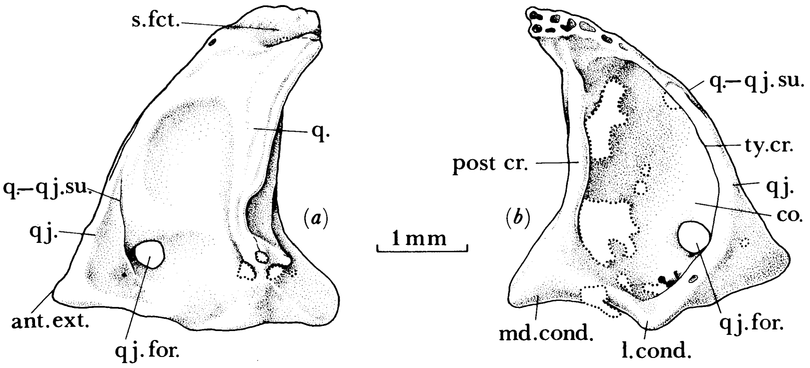

FIGURE 18. Right quadrate, specimen no. 23783 in (*a*) anteromedial and (*b*)posterolateral view.

reinforcing structure and rendering the quadrate largely immobile. Dorsally the cephalic head displays a depression and medially a broad facet for reception of the squamosal. As in *Sphenodon* (Haas 1973) the walls of the pterygoid lamella of the quadrate probably sited the origins of some fibres of the M. pterygoideus typicus and the posterior adductor musculature. The prominent tympanic crest probably formed the anterior base for the tympanum.

Epipterygoid (*figures* 13*j and* 19)

Only known from one specimen, the ventral region of a left bone, the epipterygoid, is rod-shaped dorsally and sutured medially to the pterygoid and the anterior lamella of the quadrate. The region of contact with the pterygoid and quadrate is expanded into a dish which forms a stout basal support for the extended dorsal process. The dorsal head of the epipterygoid presumably formed as in *Sphenodon* (see Haas 1973) part of the origin of the pseudotemporalis profundus which inserted onto the medial surface of the coronoid and the anterior region of the prearticular.

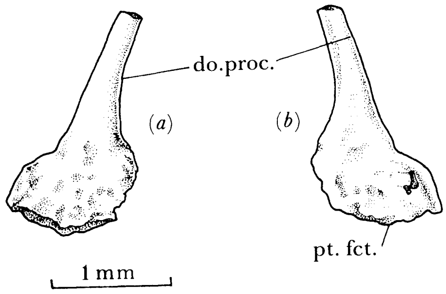

FIGURE 19. Left epipterygoid, specimen no. 23784 in (*a*) lateral and (*b*) medial view.

4.7. *Palatal complex*

Vomer (*figures* 20 *and* 21*c, d, f, g, h, plate* 4)

The vomer is a paired triangular bone forming the anterior part of the palate. The lateral border is rolled dorsomedially forming a tube which rimmed the choanae medially. Medially the vomer displays a straight-edged tongue-and-groove structure for the opposing vomer. The anterior facet for the premaxilla and the posterior facets for the palatine and (presumably) the pterygoid are not preserved. Ventrally the vomer exhibits a number of small ridged teeth, the most prominent row being near the median suture.

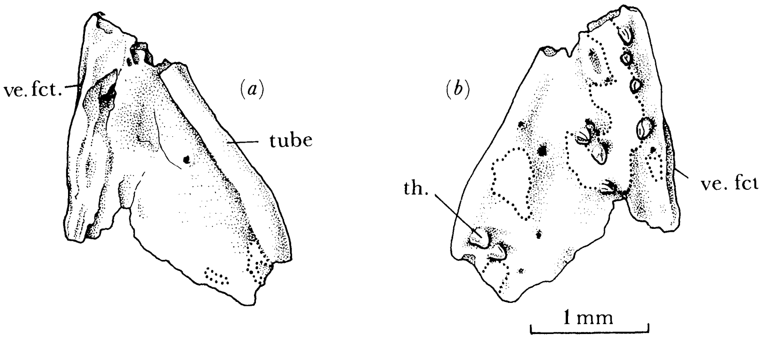

FIGURE 20. Right vomer, specimen no. 23772 in (*a*) dorsal and (*b*) ventral view.

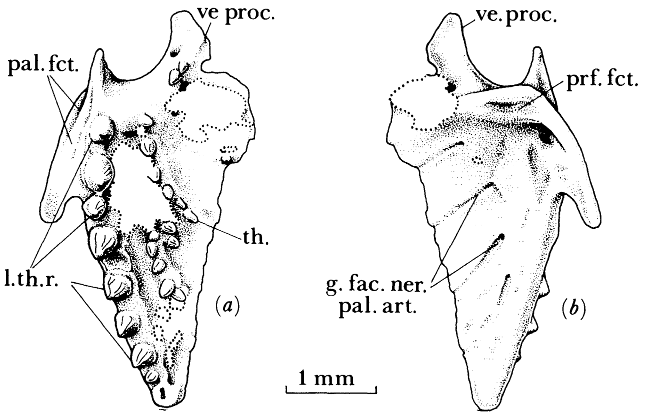

FIGURE 22. Left palatine, specimen no. 23776 in (*a*) ventral and (*b*) dorsal view.

Palatine (*figures* 22 *and* 23*a–d*, *plate* 5)

The palatine bears four facets. The most prominent is on the maxillary process developed laterally; this is a robust double shelf structure which slotted into the maxilla and reinforced the main region of occlusion between the acrodont maxillary teeth and the enlarged palatine tooth row. The maxillary process is pierced by a large foramen, the infra-orbital canal, which carried the superior alveolar nerve and large maxillary artery; these vessels continued in a counterpart foramen in the maxilla abutting against the infraorbital foramen. The anterior region lateral to the vomerine suture formed the posterior border of the choana. The vomerine suture is not well known but appears to have overlain the palatine facet of the vomer; dorsally a foramen transmitted the medial palatine nerve. Just posterior to the palatine margin of the choana a dorsal ridge is formed which is the medial continuation of the dorsal maxillary process. This ridge carries the facet that sutured with the ventral process of the prefrontal. The whole medial margin of the palatine contacted the pterygoid by a shallow facet (the contact may have been very weak as in some specimens of *Sphenodon*). The medial dorsal surface of the palatine carries four grooves for the palatine ramus of the facial nerve and palatine artery. The ventral surface displays four rows of radially ridged teeth, the most prominent being a series of eight or nine enlarged teeth on the lateral edge juxtaposed with the acrodont maxillary teeth. Although one specimen displays a series of five alternating-sized teeth the lateral tooth row does not generally display alternating size. The medial rim of the suborbital fenestra was formed by the lateral lip of the palatine.

Pterygoid (*figures* 21*a*, *b*, *e and* 24)

Six facets connected the pterygoid to other bones, the most extensive being the palatine process which extended anteriorly and sutured with the palatine. A space between the palatine processes of the two pterygoids is known as the pyriform recess and was filled by part of the pharyngeal membrane. Laterally, midway along the bone, a prominent pterygoid flange terminates in an oval flattened surface that guided the lower jaw during occlusion. The anterior part of the flange displays a complex socket which interlocked with the medial process of the ectopterygoid forming one of the strongest of all the skull connections; the fitting of these bones has been successfully attempted by using actual specimens confirming the rigidity of the structure. Slightly anterior and medial to the ectopterygoid facet the pterygoid formed the posterior rim of the suborbital fenestra and a deep incision marks the posterior boundary of the palatine suture. As in *Sphenodon* (Haas 1973; Gorniak *et al.* 1982) the M. pterygoideus typicus doubtless orginated from the medial, lateral and ventral aspect of the pterygoid process, from the ectopterygoid and from the anterodorsal part of the medial surface of the posterior pterygoid flange.

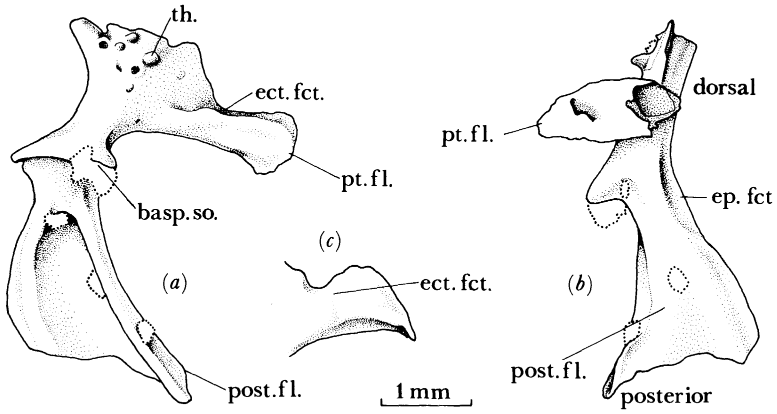

FIGURE 24. Left pterygoid, specimen no. 23768 in (*a*) ventromedial (*b*) lateral view and (*c*) pterygoid flange, anteroventral view showing ectopterygoid facet.

The large posterior flange of the pterygoid is a broad, convex-lateral trough that covered the equally prominent pterygoid lamella of the quadrate and sutured dorsally with the epipterygoid. Into the medial surface of the posterior process inserted the protractor pterygoideus muscle.

Between the posterior flange and the posterior teeth the bone is principally a solid cylinder but on the medial side a pocket is formed and this allowed a movable articulation with the basipterygoid process. The anterior ventral surface (except the extremity of the lateral flange) is covered by three rows of small robust conical teeth reducing to two rows on the non-faceted part of the palatine process.

Ectopterygoid (*figures* 21 *i*, *j*, *k and* 25)

This is a twisted H-bar which braced the palate between the pterygoid, jugal and maxilla. Medially a posteroventral flange is largely occupied by the double pterygoid facet which is formed by an extensive posteroventral area and, set at right angles, the smaller dorsal region. The facet is finely ridged which would have damped any dorsoventral movement during occlusion.

The mid region of the bone is cylindrical and slightly convex anteriorly, the rim marked the

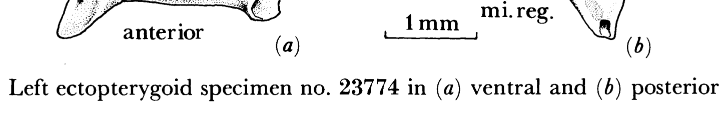

FIGURE 25. Left ectopterygoid specimen no. 23774 in (*a*) ventral and (*b*) posterior view.

posterior boundary of the suborbital fenestra. The concave posterior margin formed the anterior boundary of the coronoid recess. The expanded lateral flange has two facets; one above for the jugal and the other below for the maxilla.

4.8. *The braincase*

The pro-otic, opisthotic and supraoccipital are not preserved excepting one fragmentary specimen and will not be described here.

Basioccipital (*figures* 23*g and* 26)

Caudad and posteroventrally the basioccipital forms the major part of the occipital condyle, the remaining part being formed by the exoccipitals which are fused laterad. The point of fusion is marked by a pronounced ventrolateral ridge.

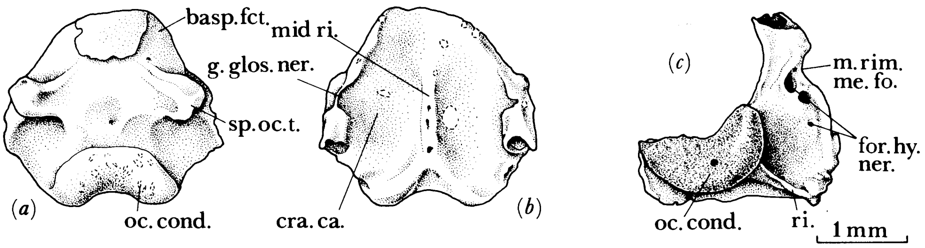

FIGURE 26. Basioccipital, specimen no. 23986 in (*a*) ventral and (*b*) dorsal view. (*c*) Specimen no. 23778 in posterior view showing right exoccipital.

Viewed dorsally the bone is circular with two smooth basins either side of a midline ridge and formed the posterior floor of the braincase. The lateral rim of the dorsal surface is raised but slightly indented midway, this indentation represents the ventral margin of the metotic fissure and possibly allowed the glossopharyngeal nerve to exit. On the mid ventral surface are the large paired sphenooccipital tubercles which probably formed the insertion of the flexor muscle, longissimus capitis. Anterior to the sphenooccipital tubercles the basioccipital sutured with the basisphenoid, overlapping that bone and producing an open U-shaped facet, the median part of that pointing anteriorly.

Para-basisphenoid (*figures* 23*e*, *f and* 27*a*, *b*)

This fused unit is formed by the basisphenoid dorsally and parasphenoid (including the rostraparasphenoid) ventrally. The parabasisphenoid is faceted dorsally for the pro-otic and was connected caudad by an underlying suture for the basioccipital. The ventral region is trapezium-shaped posteriorly (the main part of the parasphenoid) and a long thin projection, the cultriform process (rostraparasphenoid) extends anteriorly and dorsally along the median line. Laterad to the base of the cultriform process there lies the crista trabecularis ridge and dorsally, in a lateral angle between those and the main part of the parasphenoid, is a large foramen which transmitted the internal carotid artery. Prominent anteroventral basipterygoid processes extend from the mid lateral margin of the basisphenoid and terminate in a condyle which formed a movable articulation with the pterygoid. A groove for the internal carotid artery and palatine nerve ran laterally and dorsal to the main part of the parasphenoid before the artery gave off a dorsal branch at the internal carotid foramen and continued as the palatine artery. The groove is the equivalent of the squamate vidian canal which is entirely enclosed by a complete fusion of the lateral edges of the parasphenoid to the basisphenoid. In *Sphenodon* an analogous situation occurs where the osseous groove is transformed into a canal by tough connective tissue (Save Soderburgh 1947) and such a situation may have existed in this case.

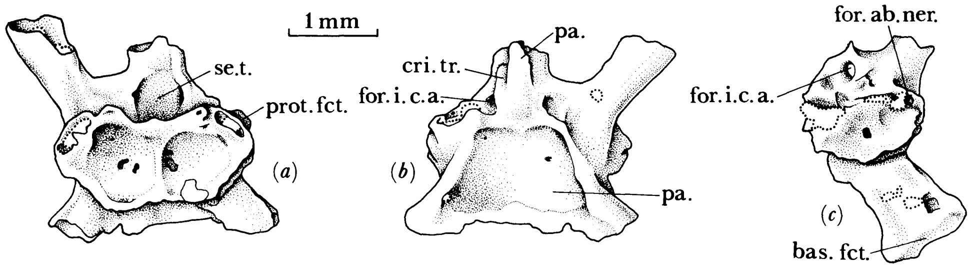

FIGURE 27. Parabasisphenoid specimen no. 23777 in (*a*) dorsal and (*b*) ventral view. (*c*) specimen no. 23792 in dorsal view showing posterior process.

On the dorsal surface the basisphenoid formed part of the floor of the cranial cavity, this region consisting of paired depressions separated by a median ridge. The lateral anterior rim of this region has a canal which transmitted the abducens nerve. The transverse wall that forms the anterior part of the basisphenoid is the dorsum sella that anchored the origin of the retractor bulbi. The foramina of this region have been described above but in the median space between the internal carotid arteries there lay the sella turcica which contained the pituitary body.

Laterad between the anterodorsally situated alar process and basipterygoid process is a groove, this was the pathway for the internal jugular vien.

Exoccipital (*figures* 23*g and* 26*c*)

These are paired bones that are fused to the posterolateral margins of the basioccipital and form the lateral part of the occipital condyle. Medially the bones formed the lateral margins of the foramen magnum and anterodorsally at the end of the dorsal process there is a flattened facet for the opisthotic. Laterad just below the opisthotic facet the exoccipital formed the posterior boundary of the metotic foramen. Near the lateral margin the bone is perforated by two large and one smaller foramina which transmitted the hypoglossal nerve. The medial surface forms the posterolateral walls of the cranial cavity and is perforated by two hypoglossal foramina.

5. THE MANDIBLE

The lower jaw (figure 4*a*, *b*) was relatively robust and was braced by the dentary which occupied 90 % of the length. Teeth occupy the anterior part of the jaw but an edentulous region (indicated by some specimens of dentary, for example BU 23760) occurs anterior to the

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DESCRIPTION OF PLATE 5

FIGURE 23. Skull bones of *Diphydontosaurus* from fissure 2. (*a*) Specimen 23775. Large left palatine ventral view. Magn. × 19.50. (*c*) Same, dorsal view. Magn. × 19.50. (*b*) Specimen 23776. Right palatine (ammonium chloride) ventral view showing radially ridged teeth on lateral row. Magn. × 13.20. (*d*) Same, (ammonium chloride) dorsal view showing prefrontal facet. Magn. × 12.68. (*e*) Specimen 23777. Parabasisphenoid ventral view. Magn. × 14.40. (*f*) Same, (ammonium chloride) dorsal view. Magn. × 12.90. (*g*) Specimen 23778. Posterior view of basioccipital and exoccipital. Magn. × 19.13.

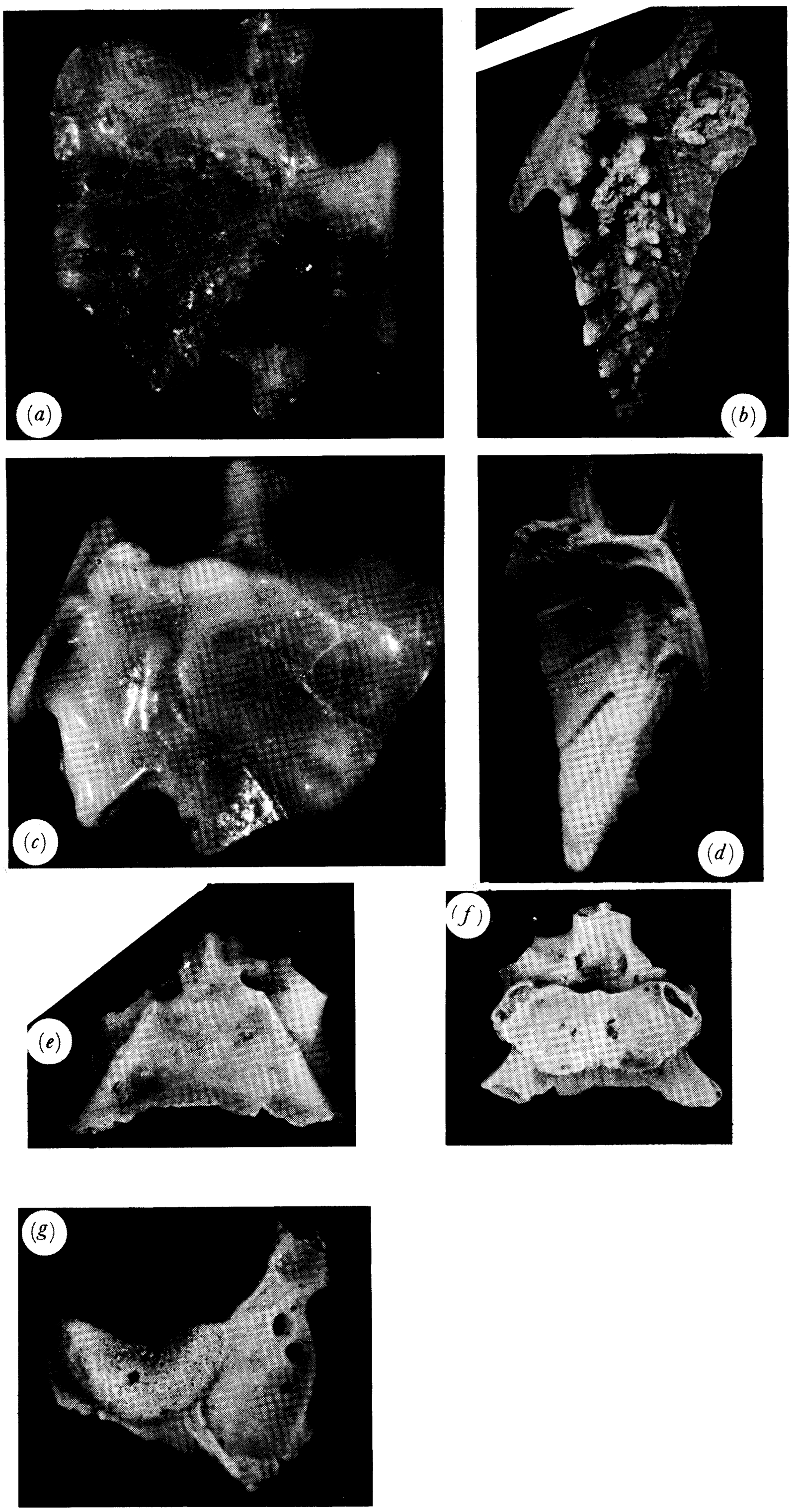

Figure 23. For description see opposite.

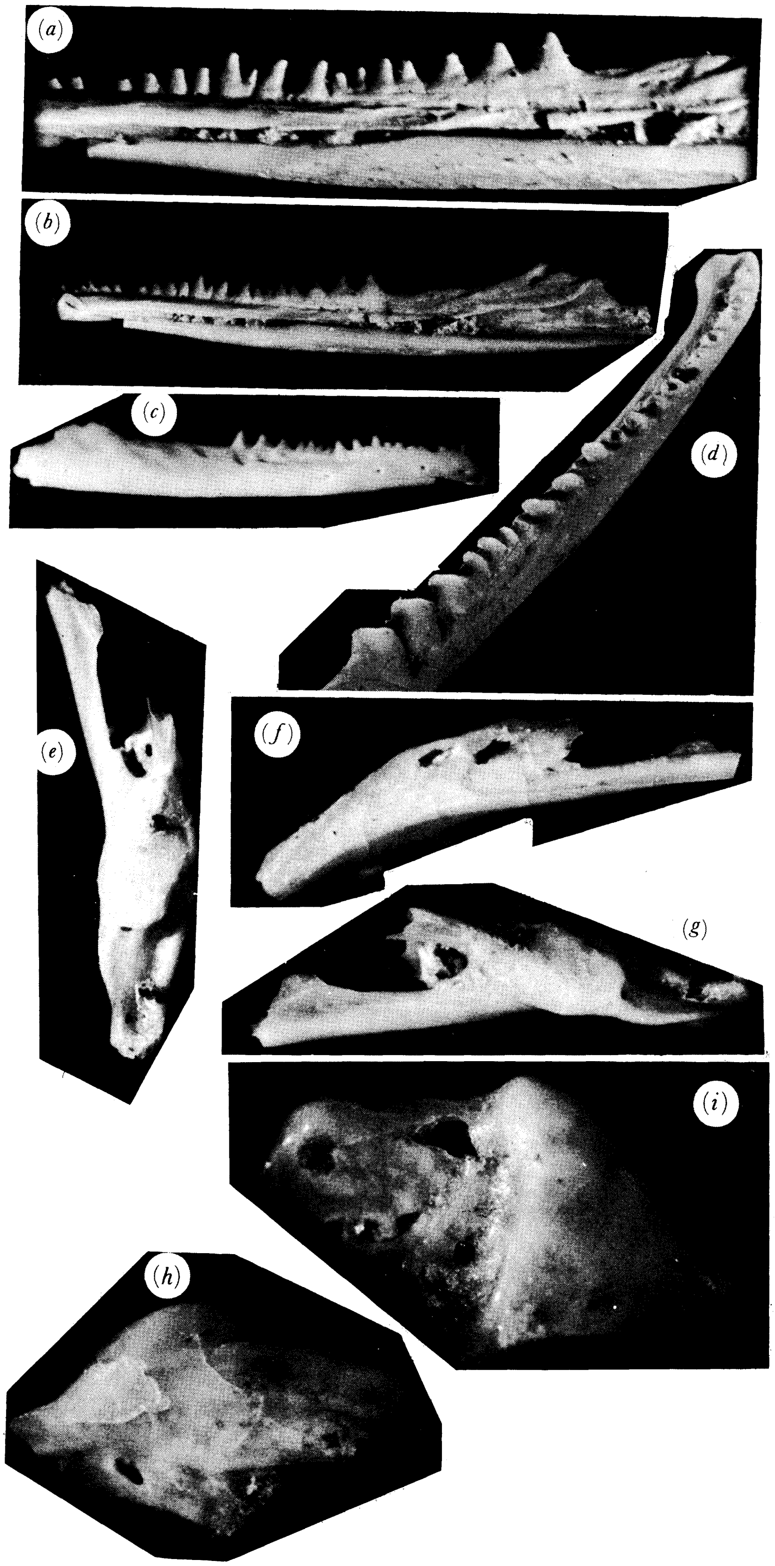

FIGURE 29. For description see opposite.

DESCRIPTION OF PLATE 6

FIGURE 29. Bones of the lower jaw of *Diphydontosaurus* from fissure 2. (*a*) Specimen 23760. Close up of holotype right dentary with near closure of meckelian groove in middle of photograph cf. *Gephyrosaurus bridensis*. Medial view (ammonium chloride coated). Magn. × 11.18. (*b*) Specimen 23760. Complete medial view of holotype right dentary. Magn. × 6.08. (*d*) Same, dorsal view of complete tooth row (ammonium chloride coated). Magn. × 11.10. (*c*) Same, complete lateral view showing wear facets caused by maxillary teeth. Magn. × 4.80. (*e*), (*f*) and (*g*) Specimen 23761. Articular complex in (*e*) dorsal view, (*f*) ventrolateral view and (*g*) laterodorsal view. Magn. × 10.50. (*h*) Specimen 23762. Left coronoid bone, lateral view. Magn. × 19.20. (*i*) Same, medial view. Magn. × 23.03.

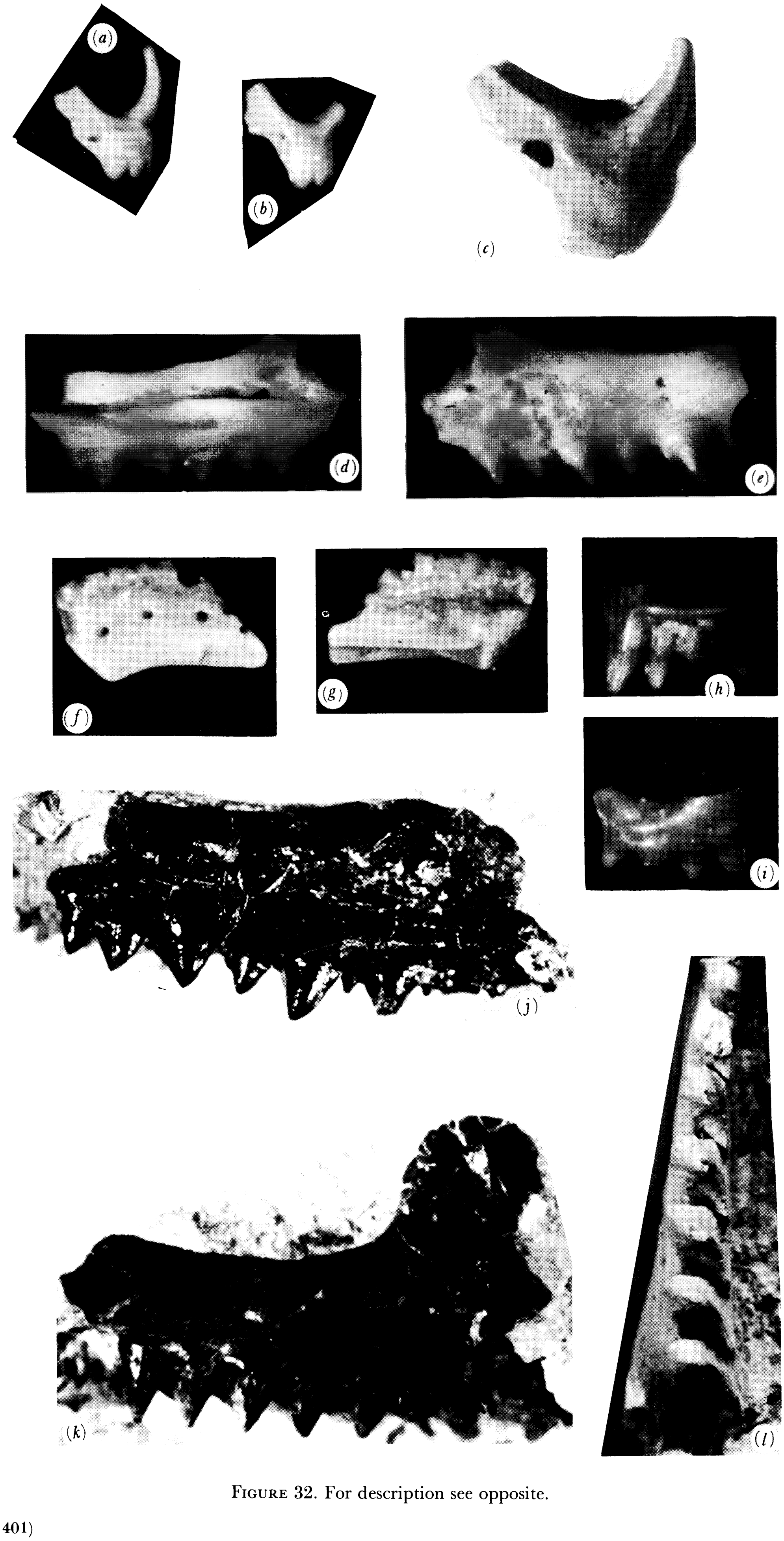

FIGURE 32. For description see opposite.

coronoid process. A syndesmotic symphysis was present which allowed an asymmetric occlusion of the jaws. The coronoid process was relatively undeveloped (compared with *Clevosaurus*, for example). A retroarticular process was well developed and to the lateral rim of this structure probably attached the ventral margin of the tympanum.

5.1. *Bone descriptions*

The dentary (figures 28 and 29*a–d*, plate 6) is robust, mediolaterally flattened posteriorly and rounded anteriorly terminating in an oval facet. This formed an attachment to the other dentary by means (presumably) of strong ligaments as in *Sphenodon*. The medial surface is characterized by the open meckelian canal which runs throughout the length of the bone; this canal is nearly enclosed by the medial wall in the region underlying the third and fourth most caudad teeth. Anterior to this part the canal becomes more ventrally situated and posteriorly the medial wall is bounded by the anterior part of the angular that contacted the dentary. In

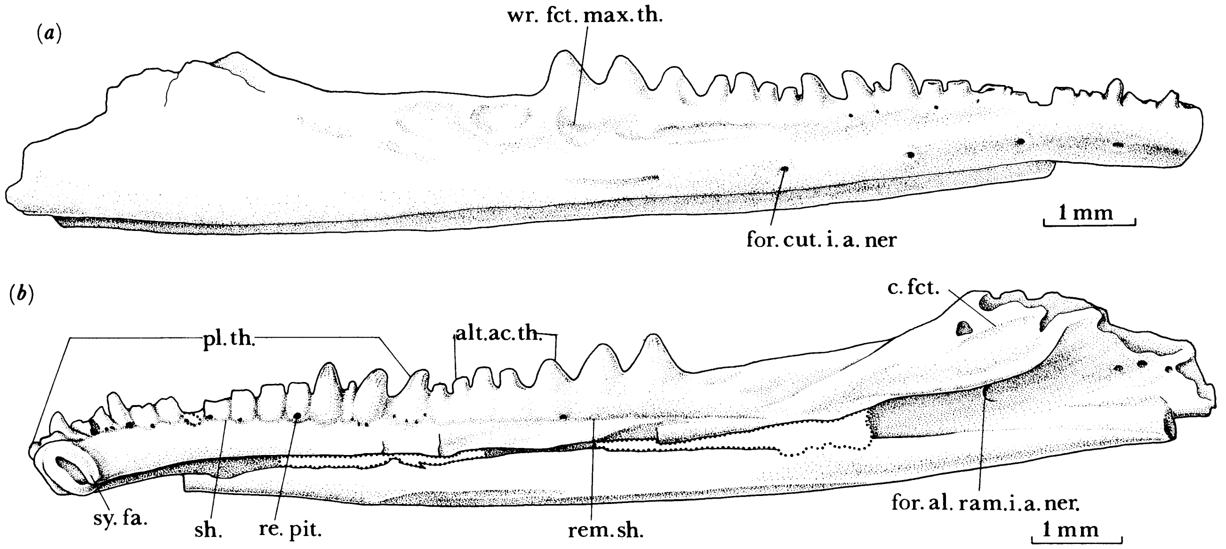

FIGURE 28. Right dentary, specimen no. 23760 holotype (*a*) in lateral view; (*b*) in medial view.

DESCRIPTION OF PLATE 7

FIGURE 32. Skull bones of *Clevosaurus* and *Planocephalosaurus* from Tytherington quarry. Maxillae of *Homoeosaurus* from the Beckles collection. (*a*) Specimen 23705. Right premaxilla of a juvenile *Clevosaurus* in anterior view showing the merging of teeth at the base leaving three cusps. Fissure 8 at Tytherington. Magn. × 8.40. (*b*) Specimen 23706. Right premaxilla of a juvenile *Clevosaurus* in anterior view showing the merging of teeth at the base leaving two cusps. Fissure 8 at Tytherington. Magn. × 8.40. (*c*) Specimen 23708. Right premaxilla of *Clevosaurus* showing a single chisel like tooth. In anterior view. From fissure 2 at Tytherington. Magn. × 12.10. (*d*) Specimen 23703. A medial view of the mid part of the left maxilla of a juvenile *Clevosaurus* showing alternating sized teeth. The posterior three teeth are noticeably flanged. From fissure 2. Magn. × 17.60. (*e*) Same as (*d*) in lateral view. Magn. × 17.60. (*f*) Specimen 23719. A medial view of the anterior region of the left dentary from a juvenile *Planocephalosaurus*. The anterior is to the left. From fissure 4 at Tytherington. Magn. × 10.70. (*g*) Same as (*f*) viewed laterally. Magn. × 10.70. (*h*) Specimen 23751. The right premaxilla of *Planocephalosaurus*, posterior view. Note foramina at tooth base. From fissure 4 at Tytherington. Magn. × 10.70. (*i*) Same as (*h*) in anterodorsal view. Magn. × 10.70. (*j*) BMNH 48255. A lateral view of a juvenile *Homoeosaurus* right maxilla from the Beckles collection. Note alternating sized teeth. Magn. × 7.90. (*k*) BMNH 48255. A lateral view of the right maxilla from an adult *Homoeosaurus*. Beckles collection. Magn. × 6.30. (*l*) Same as (*k*) in ventral view showing the lingual flanges on the teeth. Magn. × 5.80.

the holotype the anterior dorsal surface exhibits 24 teeth of which the first 17 are pleurodont. These pleurodont teeth lie, as a result of the recessed lingual wall, on a shelf and bear replacement pits at their base (see figure 23*b*). The most caudad of these pleurodont teeth are replaced infrequently, few specimens showing other than minute replacement pits and none showing teeth missing. The seven posterior teeth are truly acrodont with four of these showing a noticeable alternating size. In other specimens up to eight teeth alternate in size and in all dentaries there is a groove below the base of all the acrodont teeth. This groove is a continuation of the anterior shelf underlying the anterior pleurodont teeth and probably represents the remnant of a posterior shelf. Thus there is a strong indication that the acrodont teeth were converted from a pleurodont emplacement during ontogeny. The three most caudad teeth are the largest and triangular in vertical section. All teeth, both pleurodont and acrodont, display radial ridges on the medial wall. On the lateral dentary surface below the acrodont teeth and also slightly caudad there are deep wear marks formed by the larger maxillary acrodont teeth during full occlusion (see figure 28*a*). The anterior lateral wall is pierced by six equally spaced mental foramina which transmitted cutaneous branches of the inferior alveolar nerve. Posteriorly the dentary was sutured to lateral facets of the articular complex and dorsomedially, behind the tooth rows, to the coronoid and surangular. Also medially the dentary doubtless contacted the angular but a facet is not observed in any specimen. Medially, below the coronoid facet the meckelian fossa is pierced by a large foramen which transmitted the alveolar ramus of the inferior alveolar nerve. The inferior alveolar canal which lies laterally to the meckelian fossa transmitted the chorda tympani, the lingual branches of the inferior alveolar nerve, the internal mandibular artery and posteriorly the internal mandibular vein.

Presumably as in *Sphenodon* (see Haas 1973) the ventral surface of the dentary would have sited the origin of the intermandibular muscles. The posterolateral surface of the dentary doubtless provided the site of insertion for the superficial adductor musculature.

Coronoid (*figures* 29*h*, *i and* 30)

The coronoid overlapped the dentary dorsally and formed most of the medial face of the coronoid process (the major part of the lateral wall being formed by the dentary). The lateral surface of the coronoid, lying below the most dorsal extremity, bears a large facet for the dentary.

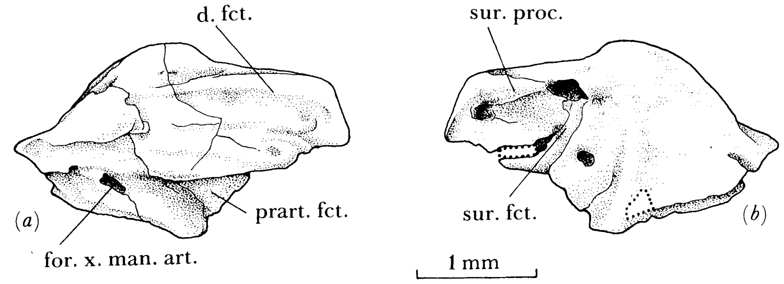

FIGURE 30. Left coronoid, specimen no. 23762 in (*a*) lateral and (*b*) medial view.

Ventrally the coronoid sutured with the surangular. Medially the coronoid is divided into an anterior smooth surface, to which inserted (by comparison with *Sphenodon* (Haas 1973) the pseudotemporalis profundus muscles (the lateral dorsal surface sited the attachment of the bodenaponeurosis), and the prearticular process which sutured with that bone.

The coronoid is pierced medially by a foramen for the external mandibular artery which emerged on the surangular facet and continued in the meckelian canal. The bone formed the anterior margin of the adductor fossa.

Articular group (figures 29*e, f, g and* 31)

This bone is formed by the fusion of the articular, prearticular, surangular and probably the angular. Dorsally the most striking feature is the condylar surface which articulated with the quadrate. This condyle is divided by a ridge which runs diagonally and separates the medial and deeper fossa from another lying laterad. Posteriorly and also posterolaterally to the condyle is the pronounced retroarticular process which displays a central basin rimmed by a raised margin. The lateral margin forms the tympanic crest to which the fibres of the tympanic membrane attached, posteriorly the rim is enlarged to form a boss for the depressor mandibulae muscle. Medially the rim displays a slight subarticular process to which inserted the M. pterygoideus typicus (this also probably inserted onto the retroarticular basin). At the junction of the retroarticular process and posterior part of the condyle a prominent foramen is present which transmitted the chorda tympani nerve. Anterior to the condyle two processes, the medial formed from the angular and prearticular and the other lateral formed by the surangular, surrounded the adductor fossa. The floor of the adductor fossa was formed mainly by the dentary but the posterior region was underlain by the angular. A large facet for the dentary is formed on the surangular, the posterior extent of the suture being ventrolateral to the mid point of the condyle. As in *Gephyrosaurus bridensis* (see Evans 1980) the angular may also form part of this facet; however, the suture between the angular and surangular is not marked. Laterally the surangular is pierced by a foramen (supra-angular) which transmitted a cutaneous branch of the inferior alveolar nerve.

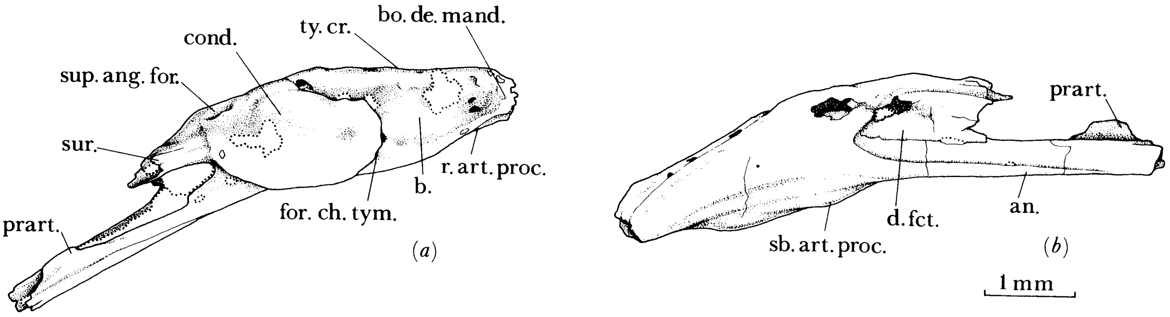

FIGURE 31. Right articular complex, specimen no. 23761 in (*a*) dorsal and (*b*) ventral view.

The prearticular–angular process extended anteriorly and underlay the coronoid and sutured to it dorsally before terminating in a weak contact with the dentary forming part of the medial wall of the meckelian groove.

6. THE RELATIONSHIPS OF *DIPHYDONTOSAURUS AVONIS*

6.1. *Method*

The technique used here is derived from the methodological approach of Hennig (1966). Hennig defined a number of character states that are pertinent in considering the taxonomic position of a particular species or group (Kavanaugh 1972). These character states are: (i) plesiomorph, the original state from which a transformation begins; (ii) apomorph, which is the derived state.

To discover whether a group of species is monophyletic we can only consider (i) synapomorphy, the common occurrence of a derived state and more particularly; (ii) autapomorphy, which is a derived character state unique to that group. It is not possible to conclude on the basis of a shared original state, or symplesiomorphy that a group is monophyletic.

In accordance with the procedure used by Evans (1980, 1981) for non-archosaurian diapsids a matrix of derived characters was compiled (table 1). The reason for deciding if a character is derived is based on a threefold approach.

(i) One character is considered as derived from another if change in that direction seems functionally more likely than in reverse.

(ii) Studying the *development* of a species. As an example, in *Sphenodon* non-successional teeth appear later in ontogeny than successional forms (Harrison 1901). Thus the former are considered to be derived.

These first criteria are considered justifiable in deciding polarity of the transformation by Underwood (1982). The last criterion (iii) is based on the assumption that the state of a character with a greater incidence in, or unique to, early forms rather than later species, is likely to be primitive.

Underwood (1982) rejects the use of the fossil record as a criterion for adjudging polarity since there may be derived characters unique to fossil forms. He does, however, admit that the state of a character unique or in a higher proportion in early species is likely to be primitive. It should be noted here that Bishop (1982) rejects all criteria used above except comparative functional anatomy but other authors, for example Nelson (1973) support the use of ontogeny and Marx & Rabb (1970) support the use of the fossil record.

The data for the matrix was abstracted from described or figured material in the accounts of Benton (1983), Carroll (1975, 1976*a*, *b*, 1977), Chatterjee (1980), Cocude-Michel (1963), Edmund (1969), Evans (1980, 1981), Fraser (1982), Gow (1975), Hoffstetter (1955), Howes & Swinnerton (1903), Jollie (1960, 1962), Kuhn (1969), Malan (1963), Parker (1885), Robinson (1962, 1967*b*, 1973, 1976), Romer (1956, 1966), and Watson (1957). Original data from fossils came from the Tytherington collection of *Diphydontosaurus*, *Clevosaurus* and *Planocephalosaurus* and the Bristol University geology collection of *Gephyrosaurus bridensis* from Pont Alun and *Planocephalosaurus robinsonae* from Slickstones. The extant species used were principally, *Sphenodon* skulls and skeletons BMNH 1972.1499, 97 2–6 10, 65.5.4.3, 44.10.29.11 and Bristol University zoology department H3b.I, agamid skulls BMNH 90.9.22.22 (*Phrynocephalus*) and personal collection, *Chamaeleo* skull BMNH 93.10.26.32 and personal collection.

6.2. *Analysis*

Of the derived features of the skull and lower jaw found in *Diphydontosaurus* it can be certain that 16 are shared by *Planocephalosaurus*, 14 by *Gephyrosaurus*, *Clevosaurus*, *Sphenodon* and by agamids and 11 by *Chamaeleo*.

From a study of the synapomorphs it would appear therefore that the affinities of *Diphydontosaurus* lie either with *Sphenodon*, *Clevosaurus*, and *Planocephalosaurus* which are all classified in the Sphenodontidae Cope 1869 (respectively Kuhn 1969; Robinson 1973; Fraser

Table 1. Showing the distribution of apomorphic characters in the skull and lower jaw of a number of extant and fossil lepidosaurs

	Sphenodon	*Clevosaurus*	*Homoeosaurus*	*Planocephalosaurus*	*Diphydontosaurus*	*Gephyrosaurus*	*Malerisaurus*	*Palaeagama*	*Paliguana*	*Youngina*	*Prolacerta*	*Chamaeleo*	agamids	*Tupinabis*	*Elachistosuchus*	*Kuehneosaurus*	rhynchosaurs
a series of regularly alternating sized acrodont teeth on part of the dentary	×	×	—	0	×	0	0	0	—	0	0	0	0	0	—	0	0
a series of regularly alternating sized acrodont teeth on part of the maxilla	×	×	×	?	×	0	0	0	0	0	0	0	0	0	—	0	0
non-replacement teeth posteriorly on maxilla	×	×	×	×	×	?	0	—	—	0	0	×	×	0	—	0	0
non-replacement teeth posteriorly on dentary	×	×	×	×	×	?	0	—	—	0	0	×	×	0	—	0	0
all maxillary teeth acrodont	×	×	×	×	0	0	0	—	0	0	0	×	0	0	×	0	0
all dentary teeth acrodont	×	×	×	×	0	0	0	0	—	—	0	×	0	0	×	0	0
caniform anterior dentary tooth	×	0	0	0	0	0	0	—	—	—	0	0	×	0	0	0	0
posterior maxillary teeth with prominent posteromedial flanges	×	×	×	×	0	0	0	—	0	0	0	0	0	0	0	0	0
anterolabial flanges on some dentary teeth	×	×	—	×	0	0	0	—	—	0	0	0	0	0	0	0	0
a lateral row of enlarged teeth on palatine	×	×	—	×	×	×	0	—	—	0	0	0	0	0	—	0	0
pre-maxilla bears acrodont chisel tooth	Λ	Λ	×	0	0	0	0	—	—	0	0	0	0	0	—	0	0
battery of teeth on maxilla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	×
palatine teeth with posterolateral flanges	×	×	—	0	0	0	0	—	—	0	0	0	0	0	—	0	0
no teeth on vomer	Λ	0	—	0	0	0	×	—	—	0	0	×	×	×	—	0	×
no teeth on palatine	0	0	—	0	0	0	0	—	—	0	0	×	×	×	—	0	0
no teeth on pterygoid	×	0	—	0	0	0	0	—	—	0	0	×	×	×	—	0	×
no teeth on parabasiphenoid	×	×	—	×	×	×	×	—	—	×	×	×	×	×	—	0	×
no teeth on pterygoid flange	×	×	—	×	×	×	×	—	—	0	0	×	×	×	—	0	×
well developed coronoid process of dentary	×	×	×	×	0	0	0	—	—	—	—	0	0	0	—	0	×
posterior process of dentary underlies glenoid fossa	×	×	×	×	×	×	0	—	—	—	0	0	0	0	—	0	0
dentary with meckelian canal anteriorly overlayed by downgrowth of bone	×	×	—	×	0	0	—	—	—	—	0	×	×	0	0	—	?
lateral side of dentary with prominent longitudinal lip	×	×	—	×	0	0	0	—	—	—	0	0	0	0	0	0	?
medial process developed on pre-articular	0	0	—	0	0	0	—	—	—	—	×	0	×	×	—	×	—
retroarticular process present	×	×	—	×	×	×	—	0	×	0	×	0	×	×	?	×	×
splenial absent	×	×	×	×	×	×	0	0	0	0	0	×	×	0	—	—	0
foramen rotundum present	0	0	—	—	—	0	—	—	—	0	0	0	×	×	—	0	0
quadrate conch	0	×	—	×	×	×	—	—	×	0	×	0	×	×	—	×	0
incomplete lower temporal bar	0	×	0	×	×	×	—	?	?	0	×	×	×	×	—	×	0
no extended posterior process on jugal	0	0	0	0	0	0	0	?	?	0	0	×	×	×	0	×	0
parietal foramen at frontoparietal border	×	0	0	0	0	0	0	0	0	0	0	0	×	0	—	×	0
no parietal foramen	0	0	0	0	0	0	?	0	0	0	0	0	0	×	—	0	×
single parietal	0	0	0	×	A	×	×	0	0	0	0	×	×	×	—	0	×
superior process under half maxilla length	×	×	×	×	×	×	0	0	0	0	0	×	×	0	?	×	0
superior border of orbit fiormed by prefrontal and post orbital	0	0	0	0	0	0	0	0	0	0	0	×	0	0	—	0	0
single frontal	0	0	0	×	×	×	0	0	0	0	0	×	×	×	—	0	0
single external nares aperture	0	0	0	0	0	0	0	—	—	0	0	0	0	0	—	×	×
single premaxilla	0	0	0	0	0	0	0	—	—	0	0	0	×	×	—	0	0
pterygoid not contacting vomers	0	—	—	0	0	0	×	—	—	0	0	×	×	×	—	0	0
supratemporal absent	×	0	×	×	×	×	×	—	—	?	0	×	×	×	—	×	0
lacrimal small or absent	×	×	×	×	×	×	0	—	—	0	0	0	×	0	×	0	0
quadratojugal absent	0	0	0	0	0	0	0	—	—	0	0	×	×	×	—	×	0
paroccipital process, squamosal and supratemporal form quadrate facet	0	0	—	0	0	0	0	—	—	0	0	×	×	×	—	0	0
exoccipital overlies mid condylar region of basioccipital	0	—	—	0	0	0	0	—	—	—	—	×	0	0	—	0	—
exoccipital fused to opisthotic	Λ	—	—	—	0	0	×	—	—	0	0	×	×	×	—	0	0
ventral ramus to opisthotic	0	0	—	0	0	0	0	—	—	—	×	0	0	0	0	×	0
parabasisphenoid with tripartite basioccipital suture	0	0	—	0	0	0	×	—	—	×	×	0	0	0	—	×	0
complete abducens canal	×	—	—	—	×	×	—	—	—	0	0	×	×	×	—	0	—
complete parabasal canal	0	—	—	0	0	0	?	—	—	0	0	×	×	×	—	—	—
medial inflexion of prefrontal	0	—	—	×	×	0	0	—	—	—	—	0	0	0	—	—	0

×, character present; 0, character absent; ?, character possibly present; —, insufficient information; Λ, character present in adult.

1982); *Gephyrosaurus* Evans 1980, an eosuchian, and sole member of the Gephyrosauridae; *Chamaeleo* and agamids of the lacertilian families Chamaeleonidae and Agamidae.

Although this quantitative assessment of synapomorphs is a useful guide to affinities it is important to examine qualitatively some of the derived characters for autapomorphy, reversal or parallellism.

6.3. *Assessment of the principal synapomorphs*

In table 1 none of the derived characters exhibited by *Diphydontosaurus* is unique to that genus but one feature, the medial inflexion of the prefrontal, is only shared with *Planocephalosaurus*. The series of alternating sized acrodont teeth on the dentary is only certainly found in two other taxa and the alternating series of acrodont teeth on the maxilla is shared with three other taxa. These three characters are considered in more detail below.

6.3. *The medial inflexion on the prefrontal*

This feature is best developed in *Diphydontosaurus* (see figure 16) but is also present in *Planocephalosaurus* in the Cromhall collection at Bristol University and in that illustrated by Fraser (1982, plate 69, figure 7).

The function of this inflexion is not known but it probably served as an anchorage for tissues of the orbital fascia and possibly those of the sclerotic ossicles.

6.3.2 *A series of alternating sized acrodont teeth on the dentary*

This feature is generally lost in the adults of *Sphenodon* and *Clevosaurus* (owing to wear in occlusion) but not in *Diphydontosaurus*. There is not sufficient information to be certain of its presence or absence in *Homoeosaurus* and *Planocephalosaurus* juveniles but it is not reported in the descriptions of either of these two genera, Cocude-Michel (1963) and Fraser (1982) respectively. The character is present, however, in the sphenodontid *Theretairus antiquus* Simpson 1926, which Kuhn (1969) regards as a juvenile of *Opisthias* Gilmore 1909 where the feature is absent (Throckmorton *et al.* 1981). It has also been noted that the alternating series is not recorded on the sphenodontid *Toxolophosaurus cloudi* although Throckmorton *et al.* (1981) state that the feature may have been worn away. The alternating series of acrodont teeth on the dentary is a derived character unique to the Sphenodontidae and previously known for certain only in *Sphenodon*, *Clevosaurus* and *Theretairus*. The presence of this sphenodontid autapomorph in *Diphydontosaurus* is therefore a very strong indication of affinity with that group.

6.3.3. *A series of alternating sized acrodont teeth on the maxilla*

Diphydontosaurus shares one other advanced character, a series of alternating sized acrodont teeth on the maxilla, previously only known in the sphenodontids *Sphenodon*, *Clevosaurus* and *Homoeosaurus*. Cocude-Michel (1963) stated that the alternating size dentition does not occur in *Homoeosaurus* but a juvenile specimen BMNH 48255 (figure 32, plate 7) from the Beckles collection (cf. adult BMNH 48255 (figure 32*k*, *l*)) shows that the phenomenon is present in the genus. Fraser (1982) notes that the character is rare in *Planocephalosaurus* and is much less extensive than in other genera being composed of three teeth whereas the others display at least four. It is thus not certainly included as a *Planocephalosaurus* feature in table 1. In *Sphenodon*, *Clevosaurus* (figure 32*d*, *e*), *Homoeosaurus* (figure 32*j*) and *Diphydontosaurus* (figure 7) it can be seen that both series increase in size caudad and that the base of the smaller series always lies at the lingual side of the ventral margin of the maxilla.

The alternating series lie at different places in the maxillary tooth row within the five genera. This is partly because of the posterior extension of the tooth row with 'additional teeth' (*sensu* Robinson 1976) that vary in number depending on genus and partly because of the number of replacement teeth in the anterior position. Edmund (1960) believed that in *Sphenodon* the two series represent the last two replacement waves of alternately erupting sequences. The reason for the two sizes of teeth and the lingual placement of the smaller series can be explained by their differing ontogenetic history. Although Harrison (1901) believed that the older teeth are the smaller series it seems more likely that the larger series teeth are older, having been laid down on the free margin of the dental lamina, later moving labiad (occlusad) as the tooth grows. The smaller series of newer teeth are in an arrested stage of development because the free margin has become covered by an operculum restricting their attainment of full size and the labiad movement (Edmund 1960, p. 160).

6.4. *Other important synapomorphs*

6.4.1. *A lateral row of large teeth on the palatine*

With the exception of the described sphenodontids a lateral row of large palatine teeth is only found in *Gephyrosaurus* and *Diphydontosaurus* (see figure 22*a*). Chatterjee (1980) describes two large teeth on the lateral region of the palatine of *Malerisaurus* but the term row or series is used here to signify three or more teeth. Thus the mandibular tooth row in occlusion passes between two rows of upper teeth, laterally the maxillary series and medially the enlarged palatine tooth row. Throckmorton *et al.* (1981) believed this to be a unique sphenodontid pattern. Its presence in *Diphydontosaurus* is therefore again a strong indication of affinities with the sphenodontids. Evans (1980) did not emphasize the taxonomic significance of the enlarged palatine tooth row in *Gephyrosaurus*, stating only that it was one of only two features (the other being loss of teeth on the pterygoid flange) that distinguished the bones and palatal teeth of this genus from the eosuchians *Youngina*, *Heleosaurus* and *Prolacerta*. She did not remark on the fact that this feature was otherwise an autapomorph of the Sphenodontidae.

6.4.2. *Non-replacement teeth on the posterior part of the maxilla and the dentary*

These apomorphs are shared by *Sphenodon*, *Clevosaurus*, *Homoeosaurus*, *Planocephalosaurus* (all sphenodontids) and *Diphydontosaurus*. Non-replacement (additional *sensu* Robinson 1976) teeth are also probably present on the posterior part of the dentary of the sphenodontids *Toxolophosaurus* and *Opisthias* (Throckmorton *et al.* 1981) and *Eilenodon* (Rasmussen & Callison 1981). The two synapomorphies of non-replacement posterior teeth are also recorded in *Chamaeleo* and *Agama* (Cooper *et al.* 1970). However, *Phrynocephalus* BMNH 90.9.22.22 displays small, probably erupting teeth in the middle of a row of generally large teeth on both maxillae and Carlsson (1893) (in Edmund 1969) recorded tooth replacement in various parts of the jaw of an *Agama agama* individual of 100 mm. In the agamid *Uromastyx hardwickii* tooth replacement is completely absent (Robinson 1976). Although Edmund (1969) stated that there is no evidence of replacement in the Chamaeleontidae except very young specimens, an individual *Chamaeleo* BMNH 93.10.26.32 displays smaller, therefore probably erupting, teeth among larger teeth in both maxillae and mandibles. These small teeth are lingually placed on the maxillae suggesting that replacement is occurring.

Evans (1980) stated that tooth replacement in *Gephyrosaurus* is of the iguanid type (Edmund 1960). This is certainly true of the anterior and mid region teeth on both maxilla and mandible.

On the maxilla, gaps can be seen in the anterior and mid region (Evans 1980, figures 31 and 32) which indicate the recent loss (at the time of death) of old teeth in a replacement wave. However, in over 30 specimens of the posterior part of the *Gephyrosaurus* dentary and maxilla held in the Bristol University geology museum collection there are only a few with a gap not caused by *post mortem* breakage. Evans (1980) figures three replacement pits, one on the anterior and two on the mid region of the posterior part of the maxillary tooth row. Two of these pits may be no more than nutrient foramina but at the very least, replacement, if it occurred, must have been rare in the posterior part of the maxilla and in the posterior part of the dentary.

6.4.3. *The posterior process of the dentary extending below the glenoid fossa*

In *Planocephalosaurus*, *Sphenodon* and *Diphydontosaurus* the posterior suture of the dentary with the articular complex occurs in a region underlying the glenoid fossa. In all other sphenodontids where the suture position is known it appears always to underlie the glenoid fossa. This is the case in *Eilenodon robustus* (Rasmussen & Callison 1981) and *Kallimodon* (Cocude-Michel 1963). However, this suture position also occurs in *Gephyrosaurus bridensis* (see Evans 1980, figure 45A). Of other lepidosaurs Romer (1956, figure 60D) has illustrated *Pleurosaurus* with a suture in a very similar position. No squamate or eosuchian has such a posteriorly extended dentary. Among lacertilians the most extreme case occurs in *Anolis* (Jollie 1960) where the suture is posterior to the coronoid but anterior to the glenoid.

6.5. *Other synapomorphs*

The incidence within other taxa of the seven major synapomorphs of *Diphydontosaurus* considered in 6.3. and 6.4. are shown in table 2.

TABLE 2. THE SEVEN MAJOR DERIVED CHARACTERS OF THE SKULL AND LOWER JAW OF *DIPHYDONTOSAURUS* WITH THEIR DISTRIBUTION IN OTHER TAXA

taxon	shared	possibly shared	not shared	unknown
Clevosaurus	6	0	0	1
Sphenodon	6	0	1	0
Planocephalosaurus	5	1	1	0
Homoeosaurus	4	0	0	3
Gephyrosaurus	2	2	3	0
agamids	2	0	5	0
Chamaeleo	2	0	5	0
Tupinabis	0	0	7	0
rhynchosaurs	0	0	7	0
Kuehneosaurus	0	0	7	0
Malerisaurus	0	0	7	0
Prolacerta	0	0	6	1
Youngina	0	0	5	2
Palaeagama	0	0	2	5
Paliguana	0	0	1	6
Elachistosuchus	0	0	0	7

The 12 other derived characters exhibited by *Diphydontosaurus* are shared by genera of two or more families. All of these features are found within the combined four sphenodontid genera named in table 1. Thus *Diphydontosaurus* is not uniquely linked by a synapomorph feature to the eosuchians *Malerisaurus*, *Prolacerta*, *Paliguana*, *Palaeagama* and *Youngina*. Nor is it uniquely linked synapomorphically with the lacertilians as exemplified by *Chamaeleo*, agamids and *Tupinabis*, the eolacertilian *Kuehneosaurus*, the rhynchosaurs or the possible sphenodontid *Elachistosuchus* described by Walker (1966). The relationship with the eosuchian *Gephyrosaurus* which shares all 12 of the synapomorphs considered in this section and 14 of the total number of derived characters seen in *Diphydontosaurus* is worthy of note and the taxonomic position of *Gephyrosaurus* is considered in more detail later.

6.6. *Taxonomic position of* Diphydontosaurus

On the evidence presented in the preceding analysis there seems no doubt that *Diphydontosaurus* can be ascribed to the Sphenodontidae on the following autapomorphic characters.

(i) The presence of a series of alternating sized acrodont teeth on the maxilla. In particular, as in the anterior additional series in *Sphenodon* the teeth in both the large and small series become larger caudally.

(ii) The series of alternating sized acrodont teeth on the dentary.

The large lateral tooth row on the palatine is also in accord with a placing in the Sphenodontidae since it is only found in *Gephyrosaurus* outside of this family.

In addition *Diphydontosaurus* also displays the following features, both apomorphic and plesiomorphic, which are exhibited by sphenodontids (data from Whiteside 1983).

Plesiomorphs

Large parietal foramen. Long posterior process of the jugal. Fixed quadrate. Quadratojugal present. Parabasal canal absent. Humerus with entepicondylar and ectepicondylar foramina. Supracoracoid foramen present. Pronounced posterior tubercle on the ischium (not emphasized in *Diphydontosaurus*).

Apomorphs

Abducens canal present in parabasisphenoid. Posterior process of dentary extends beneath glenoid fossa. Splenial absent. Atlas centrum and axis intercentrum fused to axis. Vertebrae exhibit rudimentary zygantrum–zygosphene articulations. Caudal fracture plane present. Thyroid fenestra present. Fifth metatarsal hooked.

6.7. *A reconsideration of the taxonomic position of* Gephyrosaurus bridensis *Evans* 1980

Evans (1980, 1981) placed *Gephyrosaurus bridensis* as the only species of the eosuchian family Gephyrosauridae. However, Evans (1980) did remark on a number of presumed convergent features with the skull and lower jaw of the sphenodontids. These features included the extended posterior process of the dentary and a lack of a splenial, but in particular the presence of a lateral row of enlarged palatine teeth, otherwise an autapomorph of the Sphenodontidae. Evans (1980) also speculated that the lower jaw moved with a propalinal action like *Sphenodon* a 'food handling system unique among the vertebrates' (Gorniak *et al.* 1982). Of all the 25 derived characters, cranial and postcranial exhibited by *Gephyrosaurus* (Evans 1980, table 1; 1981, table 2) 22 are found in *Sphenodon* or *Clevosaurus* or both, (19 being present in *Sphenodon* alone) and all bar one of the cranial features are certainly shared by *Diphydontosaurus*.

Excepting *Diphydontosaurus*, which also exhibits pleurodonty, *Gephyrosaurus* only significantly differs from the sphenodontids by the attributes of a pleurodont dentition and a small ('reduced' (Evans 1980)) lacrimal. It is demonstrated later that both these features are probably primitive within transform series.

The transformation series described in § 6.9 and the presence of two characteristic sphenodontid synapomorphs (the lateral row of enlarged palatine teeth and the extended posterior process of the dentary) suggest that *Gephyrosaurus* is morphologically similar to an eosuchian stage that is monophyletically and immediately ancestral to the sphenodontids.

6.8. *Other Triassic sphenodontids*

The sphenodontids (and the near sphenodontid *Gephyrosaurus*) from the Mesozoic fissure deposits of the Bristol area and South Wales are by far the best preserved and best known of the early Sphenodontidae. Besides these forms, a nearly complete skull of an undescribed American species similar to *Sphenodon* is recorded from the upper division of the New Haven Arkose (Norian–Rhaetian) by Olsen (1980). Of described genera, *Palacrodon* (Broom 1906) displays an acrodont dentition, but it as likely to be a lizard or procolophonid as a sphenodontid (Malan 1963), and *Brachyrhindron* from the Triassic of Elgin is classified as a sphenodontid by Huene (1910) principally on the basis of similar temporal openings and jaw shape. *Brachyrhinodon* has an acrodont dentition and may have lost the lacrimal but otherwise is poorly known and shows no derived characters that can be especially ascribed to the Sphenodontidae. Kuhn (1969) suggests that the subfamily Brachyrhinodontinae may merit independent family status. *Polysphenodon* does show a large row of teeth on the lateral side of the palatine (Kuhn 1969), but it also displays teeth on what may be the ectopterygoid (Hoffstetter 1955) and the orbits are set far forward. The temporal region is incomplete posteriorly but the upper border of the lower temporal opening seems to slope obliquely downwards. The skull structure thus deviates considerably from that of *Sphenodon* and following Kuhn (1969) is not considered here as a member of the Sphenodontidae. Walker (1966) believes *Polysphenodon* is very closely related to *Brachyrhindon* if not actually congeneric.

Gow & Raath (1977) describe a few jaws of a sphenodontid from the Rhaetian of Zimbabwe, which they suggest is similar to *Clevosaurus*.

6.9. *Transform series*

Because the fissure sphenodontids are so well preserved and are autapomorphically linked to *Sphenodon* it is possible to suggest some of the transformation steps by which a number of features displayed by *Sphenodon* have been derived.

6.9.1. *Maxilla*

Considering the change in the shape of the maxilla from a series using *Youngina* (as a generalized eosuchian), *Gephyrosaurus*, *Diphydontosaurus* and *Sphenodon*, the transformation sequence follows (figure 33).

Youngina has an essentially triangular shaped maxilla with no pronounced superior (nasal) process and the teeth are of thecodont implantation with continual replacement (Gow 1975).

Gephyrosaurus has a noticeably tripartite bone with distinct anterior and posterior regions on either side of the mid area that bears the superior process. This pronounced superior process displays a steeply sloping posterior margin and only slightly less steeply sloping anterior aspect. The dentition is pleurodont with the relatively slender anterior teeth rapidly replaced. The

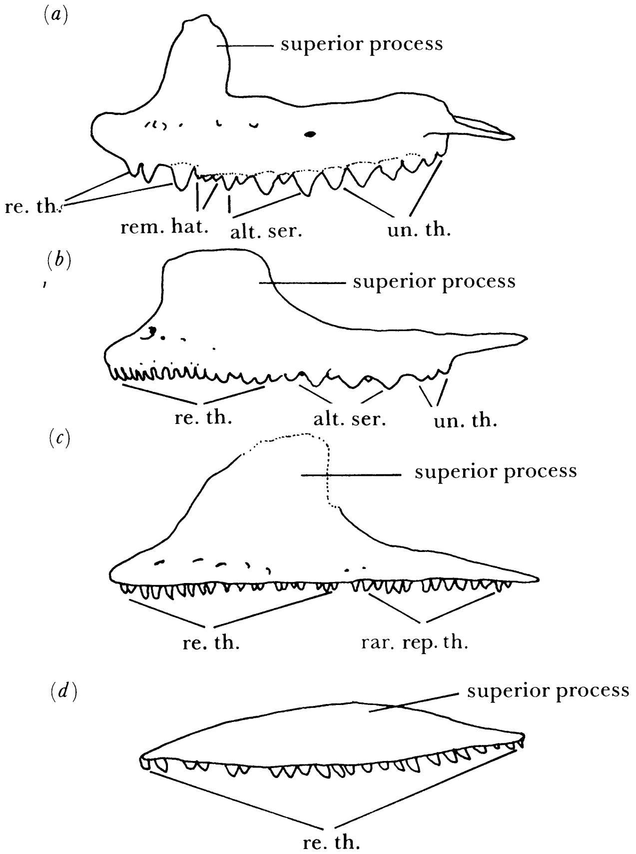

FIGURE 33. Showing suggested transformation steps towards the *Sphenodon* maxilla drawn to same size. (*a*) *Sphenodon* (after Robinson 1976); (*b*) *Diphydontosaurus* (original); (*c*) *Gephyrosaurus* (after Evans 1980); (*d*) *Youngina* (after Gow 1975).

posterior teeth that lie immediately behind the posterior slope of the superior process are broader and have much less frequent (very rare?) replacement.

In *Diphydontosaurus* the maxilla displays a well developed superior process that occupies about one third of the total length of the bone (the corresponding figure for *Gephyrosaurus* is over 40 %) and has steeply sloping anterior and posterior margins. The anterior teeth are pleurodont, slightly more dorsally based (see figure 7*b*) than the posterior series and rapidly replaced. However, the teeth lying immediately posterior to the posterior margin of the superior process are acrodont in a row of alternating sizes, both sizes becoming larger posteriorly. The larger teeth in the series are broad and conical, much larger, but of lower height than anterior pleurodont forms. It is noticeable that in many specimens a groove marks a continuation of the palatal shelf. It seems likely that very young *Diphydontosaurus* had a pleurodont dentition in this region.

Sphenodon has a very short superior process which occupies less than 25 % of the maxilla in adults and displays almost vertical anterior and posterior margins. The anterior teeth are successional (Harrison 1901), of slender conical form, and their bases lie dorsally to the posterior series. In unworn specimens the lingual side of their bases appear to be slightly more dorsally placed than the labial. When not worn down they include forms that are as high as or higher than any of the posterior teeth. Lying below and just anteriorly to the posterior margin of the superior process (for example, BMNH 1972, 1499) are the remnant hatchling teeth which alternate in size (Robinson 1976). These teeth are in the equivalent position to the few teeth that lie in the transition zone between the markedly pleurodont and markedly acrodont series of *Diphydontosaurus*. As in the hatchling teeth of *Sphenodon* these forms are more ventrally based than the anterior successional teeth. This abrupt change in tooth base from the dorsal position of the successional dentition to the noticeably more ventral position of the acrodont teeth occurring in a region below the posterior margin of the superior process is an important feature common to both *Sphenodon* and *Diphydontosaurus*.

The teeth that lie behind the posterior margin of the superior process (additional teeth of Robinson 1976) alternate in the anterior part of the row and are followed by uniformly sized forms.

From this transformation series it is therefore proposed that the reduction in the superior (nasal) process of the maxilla is related to an adaptation of a shearing dentition. The teeth that lie caudally to the posterior margin of the nasal process are non-successional (or very infrequently replaced as in *Gephyrosaurus*) and are acrodont in *Diphydontosaurus* and *Sphenodon*. Robinson (1976) suggested that acrodonty was related to a precise occlusion and shearing bite but suggested that the advanced shear (propalinal action) of *Sphenodon* seemed to contradict this idea. However, acrodonty would appear to be even more necessary in a propalinal action (some iguanids, for example, have a shearing action with a pleurodont dentition, see Throckmorton (1976)) since the anterior movement of the jaw after occlusion would tend to rip out replacement teeth (such as the typical pleurodont form) causing gaps in the tooth row that would disrupt the shearing action.

In the growth of the maxilla *Sphenodon* appears to maximize the proportion of the additional flanged teeth that form the cutting device of the maxilla. The posterior part of the nasal process and the region directly below and anterior to this area (bearing the hatchling dentition) grows very little or not at all after birth. However, the anterior part of the maxilla does grow about twice in length from a specimen of skull length 35 mm to one of 64 mm, whereas the posterior part of the maxilla shows an even bigger increase of 2.20 times the length for the same skulls (figures taken from Robinson (1976)). The change in the proportions of the maxilla during the ontogeny of *Sphenodon* seem, therefore, to mirror the phylogenetic change proposed in the transformation series.

6.9.2. *Premaxilla*

The series *Gephyrosaurus–Diphydontosaurus–Planocephalosaurus–Clevosaurus* and *Sphenodon* shows a reduction in the number of teeth, restriction of replacement to very young or embryonic stages, and the merging of two or three teeth to form a single chisel tooth on each premaxilla. *Gephyrosaurus* displays eight to ten pleurodont teeth (Evans 1980) which exhibit replacement. The same type of teeth occur in *Diphydontosaurus* but it is noticeable in that genus that each alternate tooth is more lingually based (figure 5) and there are only five to seven teeth in each premaxilla. In *Planocephalosaurus* there are only four premaxillary teeth which although occasionally showing small foramina at their bases (figure 32*h*) do not seem to show replacement. The implantation is apparently that of a semi-pleurodont form with the lingual side of the tooth base sitting on a shelf (see figure 32*h*, *i*). In *Clevosaurus* three teeth in subadults and juveniles became merged to form a chisel shape structure in the adult (figure 32*a*, *b*, *c*). In *Sphenodon* the same acrodont chisel structure is formed from the merging at their base of two or three teeth (Harrison 1901; Robinson 1973) but replacement activity occurs in the embryo.

6.9.3. *Dentary*

The dentary of *Gephyrosaurus* has pleurodont teeth which are seemingly replaced far more frequently anteriorly than posteriorly (see earlier comments). The posterior teeth are broad, and have a bony layer around their lingual bases rather than sitting on a shelf (see Evans 1980, figure 2A).

Diphydontosaurus displays slender conical pleurodont teeth on the anterior part of the dentary. These show signs of active replacement. These are followed by a transition area of larger, infrequently replaced, pleurodont teeth and behind these are a sequence of alternating sized acrodont forms which sit on the crest of the dentary. The last two teeth on the dentary may not be part of the alternating series but uniform additional teeth as in *Sphenodon*. A shallow groove below the acrodont teeth is probably a remnant shelf (see figure 28*b*) and is a continuation of the anterior shelf that bears the pleurodont dentition.

The anterior part of the lower jaw of *Planocephalosaurus* bears simple conical semi acrodont teeth which in some specimens have a markedly recessed lingual base (see figure 32*f*, *g*) and sit on a remnant shelf whereas the posterior teeth sit on the crest of the mandible.

In *Sphenodon* the anterior part of the dentary bears teeth that are successional and these are followed by a short series of an alternating sized acrodont dentition. The greatest part of the tooth row of the jaw is occupied by additional teeth. Indeed the jaw grows mainly posteriorly, the anterior region (with the successional and alternate dentition) showing little or no growth (Robinson 1976). This differential growth is indicated by the congregation of small foramina for the cutaneous branches of the alveolar nerve that lie on the extreme anterior lateral side of the dentary of *Sphenodon*. In *Diphydontosaurus* these foramina are evenly spread.

In this suggested transition from the *Diphydontosaurus* type stage to the condition seen in *Sphenodon* it is postulated that this differential growth rate of the *Sphenodon* dentary, as in the maxilla, maximizes the area of the non-successional acrodont teeth (and minimizes that of the successional forms) which are of great importance in shearing and particularly propalinal shear.

6.9.4. *Lacrimal*

The lacrimal of *Gephyrosaurus* (Evans 1980, figure 1C) shows a marked reduction in size compared with earlier eosuchians such as *Youngina* or *Prolacerta* (see Gow 1975).

It seems likely that this very small lacrimal was lost in the evolution of the *Diphydontosaurus* stage where a small notch is present on the ventral process of the prefrontal. This embayment probably represents the medial wall of the lacrimal canal.

The lacrimal canal is present in *Sphenodon* between the prefrontal and the maxilla and the prefrontal bone appears *not* to be a compound element in embryological development (Howes & Swinnerton 1903). This suggests that the lacrimal was lost and not fused to the prefrontal in phylogeny.

6.9.5. *Palatine*

A noticeable feature of *Sphenodon* is the extensive bony palate whereas *Diphydontosaurus*, *Planocephalosaurus* and *Gephyrosaurus* have large suborbital fenestrae. The posterior region of the palatine in *Sphenodon* has expanded laterally bringing the marginal tooth row much closer to, and in parallel with, the large acrodont maxillary teeth. In the ontogeny of *Sphenodon* the anterior region of the sub-orbital fenestra narrows and there is a relative lateral expansion of the posterior part of the palatine as development proceeds (see the stages R and S, plates III and IV of Howes & Swinnerton (1903)). This feature is undoubtedly an adaptation to the propalinal shearing action used by *Sphenodon*. Any food material is held by the closely adjoined palatine and maxillary teeth and this permits the mandibular teeth to achieve a short elastic strain shear.

7. PALAEOBIOLOGY OF *DIPHYDONTOSAURUS*

7.1. *Mode of life*

The simple conical pleurodont puncturing teeth in the anterior part of the jaws of *Diphydontosaurus* indicate an insectivorous diet. The robust acrodont teeth worked in a strong shearing action which left prominent tooth wear features on the lateral aspect of the dentary (see figure 28*a*). These acrodont teeth would have reduced the invertebrate prey into manageable pieces that could be swallowed.

Pough (1973) has demonstrated that small lizards of snout-vent length 5–20 cm have relatively high metabolic rates and thus require high energy foods such as insects. Plant material has a lower energy content per unit mass and also produces a lower assimilation efficiency than insect tissue. The snout-vent length of *Diphydontosaurus* would have been only a little above 5 cm and is equivalent to the smallest body size of lizards studied by Pough. This seems to confirm that *Diphydontosaurus* was insectivorous. The large orbits and prominent quadrate–quadratojugal conch structure suggest that the animal had well developed sight and hearing for detecting arthropod prey.

It should be noted, however, that *Diphydontosaurus* was an insular lizard-like reptile. It has been shown by Sadek (1981) that *Lacerta dugesii*, a very small lacertilian lizard which lives on the Madeiran Archipelago, consumes plant material as part of its diet. Other small insular lizards also have a partly herbivorous diet. It seems quite likely therefore that *Diphydontosaurus* although primarily insectivorous also ate some plant material. In fact, an expanded niche would be expected in an insular species such as *Diphydontosaurus* where an impoverished arthropod fauna would be likely because of the small land area.

It should also be noted that modern day insular lizards tend to live in very high population densities, much higher than their mainland equivalents. *Diphydontosaurus* would have only met direct competition from the young of the other sphenodontids *Clevosaurus* and *Planocephalosaurus*, mammals being absent in the fissures. The main predators would have been *Clevosaurus* and the cursorial crocodile. We can therefore envisage that *Diphydontosaurus* lived in high population densities among the weathered Carboniferous Limestone blocks and with a high congregation around the entrances to dolines and other fissures where the local climate and soils may have been more moist. In those areas insect prey would have been abundant, possibly scavenging on dead remains of animals washed in.

7.2. *Mode of death*

The palaeoecological reconstruction, based on Whiteside & Robinson (1983) is of a high water table at deposition with a nearby sea. Any major rainfalls would have tended to fill rapidly the dolines and could have drowned the lepidosaurs living at the entrance, particularly if the rain occurred at night when the body temperatures of these small reptiles would be low. The dead bodies would have become bloated and beached, their decomposition possibly being executed by arthropods. The bones together with those of individuals that had died from other natural causes would have been washed into the fissures by further subsequent rainfall.

The high population density and localized doline congregations would have given rise to the remarkable abundance of the fossils in fissure 2.

8. THE MODERNIZING OF A 'LIVING FOSSIL'

The autapomorphs, the high proportion of shared synapomorphs, and the detailed and plausible transformation series described above strongly suggest that *Gephyrosaurus* (or a form morphologically similar) and *Diphydontosaurus* (and also possibly *Clevosaurus* and *Planocephalosaurus*) are linked monophyletically to *Sphenodon*.

The author has applied the Le Quesne test (Le Quesne 1982) which suggests that two independent characters cannot be uniquely derived if all four combinations (or only three excepting the primitive combination) are found in the species being studied.

The major incompatibilities within the skull and lower jaw of the group *Gephyrosaurus*, *Diphydontosaurus*, *Clevosaurus*, *Planocephalosaurus*, *Homoeosaurus* and *Sphenodon* are the presence of the quadrate (plus quadratojugal) conch, the incomplete lower temporal bar, single parietal, lack of a supratemporal and the single frontal. Also incompatible is the autapomorph alternating sized acrodont teeth on the dentary, this incompatibility being entirely caused by the lack of this character in *Planocephalosaurus*. As mentioned previously this latter feature could well be present in juveniles (in the Tytherington *Clevosaurus* for example, this feature is only observed in juveniles) and is thus not excluded here.

The single parietal and single frontal displayed by *Gephyrosaurus*, *Diphydontosaurus and Planocephalosaurus* may well be related to strengthening of the skull roof in these small species (maximum length of 3 cm in *Gephyrosaurus* Evans 1980). A fused parietal, for example, is a species characteristic among geckos and fused frontals are related to the narrow interorbital cranial roof in some lizards (Jollie 1960). Also considering the problem of fused median elements in lizards, Camp (1923) recorded Mehely's suggestions that ancestors with fused elements can give rise to descendants with paired elements either in the embryo or post-embryonic condition.

The quadrate conch, lower temporal bar and supratemporal present different problems. Kuhn (1969) reports that the supratemporal is absent in the Sphenodontidae but later Robinson (1973) recorded its presence in *Clevosaurus*. In figure 4A of Robinson (1973) the supratemporal of *Clevosaurus* is in the same equivalent position as the posterior part of the squamosal that sutures to the parietal and contacts the head of the quadrate in *Gephyrosaurus*, *Diphydontosaurus* and *Sphenodon*. It may be, as suggested by Baur (1896), that the squamosal in *Sphenodon* (and by analogy *Gephyrosaurus* and *Diphydontosaurus*) is the fused tabular (= supratemporal) and prosquamosal (squamosal). There is no supporting evidence for this suggestion in the embryological studies of Howes & Swinnerton (1903) but as pointed out by Camp (1923) presumed 'recently united bones such as the paired postfrontals and postorbitals are fused in the embryo of (the scincid) *Lygosoma*'.

It is plausible, therefore, that fusion of the two elements of the squamosal occurred ontogenetically late in the fossil forms. The *Clevosaurus* figured by Robinson (1973) is a juvenile (demonstrated by the three-crowned premaxilla) and it can be postulated that in adults or larger individuals the element was fused to the squamosal *sensu stricto*. An alternative to this suggestion is that fusion of the two squamosal elements in *Gephyrosaurus*, *Planocephalosaurus* and

Diphydontosaurus occurred to strengthen the skull temporal region in these small forms and that it was from this group that *Sphenodon* derived. It must be admitted, however, that none of these suggestions seem probable and the supratemporal in *Clevosaurus* represents a considerable problem.

The occurrence of the two advanced features of an incomplete lower temporal bar and a conchlike structure on the quadrate and quadratojugal of the Triassic *Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus* and *Clevosaurus* seems paradoxical when considering that these characters are absent in the extant *Sphenodon*.

However, it appears that at least some individuals of *Planocephalosaurus* had a complete lower temporal bar (Fraser 1982), this was also apparently the case in some specimens of *Clevosaurus* (T. Kemp, personal communication) and probably in larger *Diphydontosaurus* individuals. Moreover, a comparison between the position of the posterior process of the jugal suture in *Sphenodon* and early eosuchians such as *Youngina* suggests that they are not homologous. In lateral view the jugal sutures with the quadratojugal below the middle of the lower temporal opening in *Youngina* (figure 34). However, in *Sphenodon*, viewed laterally, the suture is much more posteriorly positioned laying directly below the posterior margin of the lower temporal opening and the structure is with the quadrotojugal *and* the squamosal. Also in the embryo skull the jugal–quadratojugal–squamosal connection is one of the last to form (see Howes & Swinnerton 1903, plate 3, figure 10, 11 and 12) (figure 34).

If, as suggested, *Gephyrosaurus*, with an incomplete lower temporal bar, is of an ancestral type to the fissure sphenodontids in which all species show some (larger?) individuals with complete bars, and if, as indicated, the suture position of the bar is not homologous in *Sphenodon* and eosuchians it seems likely that the complete lower bar is secondarily acquired in the phylogeny

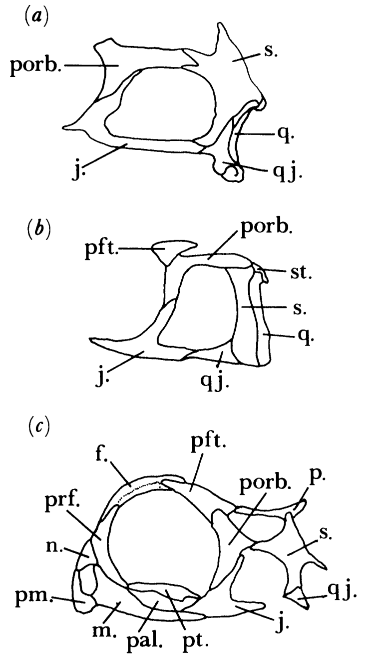

FIGURE 34. Temporal region of (*a*) *Sphenodon* and (*b*) *Youngina* in lateral view drawn to the same size to illustrate the position of the jugal suture on the lower temporal bar. From Gow (1975). (*c*) Embryo of *Sphenodon* illustrating the late stage of contact between the jugal and quadratojugal and squamosal. Modified from Howes & Swinnerton (1903).

of *Sphenodon*. Functional reasons why this should be the case are argued below, together with an explanation of the degenerate tympanic membrane (Baird 1970) in *Sphenodon*.

8.1. *Opening of the lower temporal bar*

Romer (1956) stated that the opening of the lower temporal arcade in squamates allowed the attainment of the streptostylic condition with the quadrate freely movable. However, in *Clevosaurus* the incomplete lower bar was not related to streptostyly since the quadrate was still firmly sutured to the squamosal and pterygoid in a monimostylic condition. Robinson (1973) suggested that the opening of the lower temporal arcade was possibly related to reducing the influence of bone-conducted sounds from the upper jaw made during biting. This was in addition to other acoustic barriers formed by the synovial joint with the lower jaw, and the intercalary cartilage that lies on the cephalic condyle of the quadrate. Evans (1980), however, pointed out that feeding noises would have passed through the pterygoid–quadrate contact and that without a streptostylic condition the tympanic membrane would have been repeatedly deformed during feeding. She also doubted the effectiveness of synovial joints as acoustic barriers since substrate vibrations are picked up through these joints in, for example, snakes.

Rieppel & Gronowski (1981) argued that from the fossil record the loss of the lower temporal arcade is not necessarily correlated with streptostylic development. They suggested what appears to be a much more plausible hypothesis; that the opening of the lower temporal bar allowed an expansion onto the lateral parts of the dentary by the posteroventral 1b part of the superficial adductor mandibulae externus.

In accordance with this hypothesis the small gap in the lower temporal arcade such as that seen in *Gephyrosaurus* and *Prolacerta* is suggested by the current author to relate to a lepidosaurian puncturing dentition (thecodont, subthecodont or pleurodont) for food capture where, as suggested by Robinson (1973), a relatively weak but fast snapping action is required. The posterior position of the lower temporal bar opening in these forms is commensurate with this suggestion since the moment arm of the expanded lower jaw musculature would be relatively small giving a rapid weak action.

8.2. *Regrowth of the lower temporal bar*

The posterior teeth of *Gephyrosaurus* are large and apparently adapted to an incipient shearing action (Evans 1980). In *Diphydontosaurus* the trend continues and strong wear facets are present on the posterior lateral part of the dentary caused by the posterior maxillary teeth during a precision shear. In response to this precise shearing action large pterygoid flanges are developed (see figure 4) which guided the lower jaw into exact occlusion. It seems likely, however, that because the quadrate (via the quadratojugal) had lost the complete lower bar as a bracing structure a torque would have developed on the quadrate during movement of the lower jaw.

In a hard biting movement (particularly in adult sphenodontids consuming large invertebrate or small vertebrate prey) when the jaw elevator muscles are in maximum contraction the muscles tend to pull backwards as well as upwards. The resultant of these forces could effect a posterior rotation of a quadrate. However, a fused quadrate and quadratojugal held firmly on the medial side by the pterygoid and on the dorsal head by the squamosal, but not as strongly on the lower lateral side as in sphenodontids with an incomplete lower temporal bar, could have resulted in a torque developing on the quadrate condyles with the lateral side being twisted posteriorly. Also any movable joint such as that indicated for *Diphydontosaurus*, between the basipterygoid process and the pterygoid will, during biting stresses, push the pterygoids apart (Frazzetta 1962) and this movement will translate to the quadrates causing them in turn to move apart also.

Such movements of the quadrate would cause disruption of the lower jaw–quadrate joint and lead to imprecise occlusion.

It is therefore suggested that the lower bar reconnected with the quadratojugal and the squamosal thus holding the articular condyles of the quadrate completely fixed as a necessity for precision shearing.

In *Sphenodon* the fixed nature of the quadrate becomes very important in guiding the anteroposterior line of action of the M. pterygoideus typicus during the propalinal shearing phase (Gorniak *et al.* 1982). It is also interesting to note that the skull of *Sphenodon* seems to have secondarily lost the basipterygoid–pterygoid joint because although the constrictor internus dorsalis complex is relatively well developed (Haas 1973), strong ligaments bind the palate with the braincase (Evans 1980).

The closure of the lower temporal bar may be thought to have excluded or retracted the development of the posteroventral 1b of the superficial adductor muscle. Indeed in *Sphenodon* no separate posteroventral 1b is developed (Haas 1973) but the superficial muscle does reach the lateral surface of the jaw because the lower temporal bar is bowed outwards (Rieppel & Gronowski 1981). Therefore the loss of adductor force by the regrowth of the lower bar is minimized.

8.3. *Loss of the quadrate quadratojugal conch*

The early sphenodontids *Diphydontosaurus*, *Clevosaurus*, *Planocephalosaurus* and the near-sphenodontid *Gephyrosaurus* all display a quadrate–quadratojugal conch structure indicating that a tympanic membrane was attached in life. *Sphenodon* lacks a tympanic membrane but the aponeurosis that lies below the mass of the depressor mandibularis is regarded as a modified tympanic membrane by Huxley (1869), and Verluys (1898) argued in favour of this view.

It is therefore suggested here that the conch structure was lost in sphenodontid phylogeny as follows.

All the fissure sphenodontids and *Gephyrosaurus* display a marked retroarticular process. The attachment of the depressor mandibulae to the posterior of this process would have produced a relatively long effort arm which would have given a strong force in depressing the mandible. In small animals with a puncturing dentition (pleurodont or thecodont) this would have been of great use to retract the teeth from the puncture. The long retroarticular process would thus be expected in *Diphydontosaurus*, *Gephyrosaurus* and possibly *Planocephalosaurus*, which exhibits simple conical puncturing teeth in the anterior of both upper and lower jaws. The retroarticular process may have been present in *Clevosaurus* also, to provide the considerable force needed in depressing the lower jaw if elastic food such as fibrous plant matter or insect cuticles became trapped between the teeth. Furthermore, there may have been a positive selection pressure for retaining the efficient auditory system (and therefore tympanum) that has been described for this genus (Robinson 1973). The auditory system, for example, may have played an important role in locating insect prey. Presumably in the early sphenodontids as in the squamate *Ctenosaura pectinata* (Oelrich 1956) the ventral part of the tympanum would have been attached (possibly via a skin connection) to the lateral border and tip of the retroarticular process.

In *Sphenodon* there is a much smaller retroarticular process and the insertion of the depressor mandibulae is thus positioned anteriorly with respect to the earlier sphenodontids. With the evolution of the propalinal action (see figure 35) of *Sphenodon* the prey are more efficiently sheared and it became less important for a relatively great force in depressing the lower jaw. However, it may well have become important to have a faster (although weaker) jaw opening and the forward migration of the depressor mandibulae would have produced a short effort arm and consequent fast jaw opening action. Also, the actual gape of the jaw would have been increased. The reason why a faster mandible opening action and wider gape became important would have been related to the method of feeding seen in *Sphenodon*. *Sphenodon* everts the tongue to capture insects such as grasshoppers and cockroaches. Thus a quick jaw-opening action is required to enable the tongue to capture the agile prey in the shortest possible time. The fact that it is the anterior fibres of the depressor mandibulae that fire to maximum first in jaw opening (Gorniak *et al.* 1982) is in accord with a fast-opening hypothesis since these are the fibres closest to the fulcrum of the lower jaw–quadrate articulation. It is also perhaps no accident that of all lacertilian lizards only the chamaeleons (and two other genera) should not generally possess a retroarticular process since they also use tongue eversion as the principal form of prey capture and they also have a shearing dentition. The convergent similarities with *Sphenodon* can be carried further since chamaeleons also lack a tympanic membrane (Wever 1978) and, interestingly, also lack a foramen rotundum (Parker 1885), this latter feature not being recorded in any sphenodontid. Also a few agamids, iguanids and scincids lack a tympanic membrane.

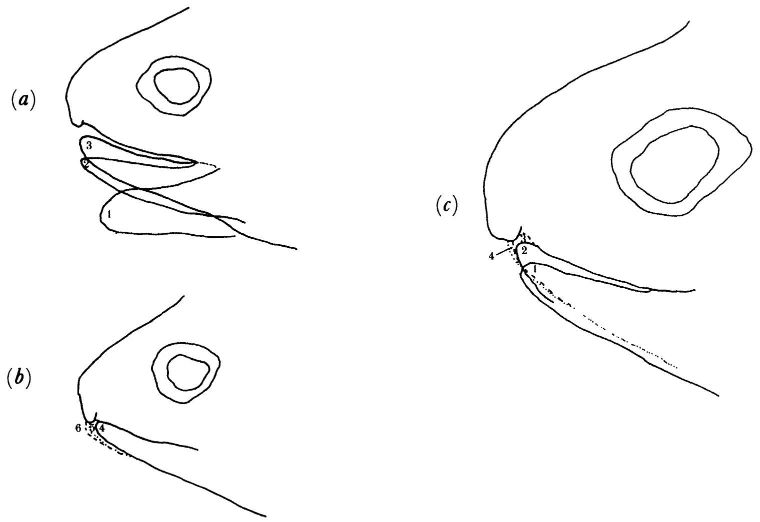

FIGURE 35. Jaw closing and propalinal movement in *Sphenodon*. Taken from BBC film. (*a*) Jaw closing; (*b*) same sequence propalinal movement; (*c*) slow motion separate sequence, propalinal movement. Number 1–6 indicate sequence from first to last.

The relatively wide gape suggested for *Sphenodon* would be useful in handling large vertebrate prey such as petrels (birds) which inhabit the areas with tuataras. These birds are often found decapitated (Crook 1975) which is commensurate with the dismemberment of mice caused by feeding tuataras in laboratory conditions (Gorniak *et al.* 1982).

The wear on the anterior mandibular teeth also effectively increases the vertical distance (gape) between the upper and lower tooth rows in the region (Gorniak *et al.* 1982). This wear on the mandibular teeth also produces a relatively greater height in the successional caniform teeth allowing larger prey to be impaled (Gorniak *et al.* 1982).

The loss of the tympanum in the evolution of *Sphenodon* is, therefore, suggested to be correlated with the relative anterior insertion of the depressor mandibulae and shortening of the retroarticular process compared with the early sphenodontids. The intrusion of the mass of the depressor mandibulae into the area formerly occupied by the tympanum and outer part of the middle ear, together with the loss of most of the retroarticular process that acted as the ventral support for the structure, would have made the tympanum useless. The consequent loss of the tympanum would have made the quadrate conch, which supported the anterior part of this structure, also functionless.

Finally the reduction of auditory sensitivity with the loss of the tympanum is not as severe as may be thought. The skin that lies over the depressor mandibularis acts as a sound receptive device. The re-entrant fluid circuit used by *Sphenodon* (and also by the chamaeleons in which, as in *Sphenodon*, the periotic sac exits with the glossopharyngeal nerve) is adequate for the detection of low frequency vibrations (Wever 1978). Indeed the ear can adequately receive warning cries, such as the harsh croaking sounds produced by *Sphenodon* and the cochlea in this genus is quite well developed having a hair population greater than in some lizards or amphisbaenids (Wever 1978).

It is therefore concluded, on the basis of the fossil record and functional morphology, that the lower temporal arcade is secondarily complete in *Sphenodon* and that the ear system is degenerative and has lost the quadrate conch. The loss of this latter feature was coupled with the more anterior position of the insertion of the depressor mandibulae and consequent reduction in the length of the retroarticular process.

8.4. *Alternative hypotheses*

The suggested derived condition of the complete lower temporal bar and the absence of a quadrate–quadratojugal conch in *Sphenodon* is here considered the most parsimonious hypothesis. However, other hypotheses are possible and three are now considered.

The first is that the four researchers working on *Clevosaurus*, *Gephyrosaurus*, *Planocephalosaurus* and *Diphydontosaurus* have failed to deduce correctly the true nature of the lower temporal bar in these genera. In many specimens minor abrasion of the jugal and quadrate–quadratojugal could have obscured the facets in the smallest specimens. However, it seems unlikely that these facets would have been uniquely abraded on this element in four genera leaving the facets on other bones clearly evident. A careful search for any such facet on *Diphydontosaurus* has indicated that such a feature is absent.

A second hypothesis is that the fissure sphenodontids were subject to severe genetic drift resulting in either repeated mutation of the lower temporal bar producing a gap, or endemic evolution deriving from one ancestor, for example *Gephyrosaurus*, with that mutation. However, multiple mutations of the same nature in four genera seems improbable and although the faunas are insular they were present on near-mainland continental and not oceanic islands. Endemism is much less prevalent on continental than on oceanic islands.

A third hypothesis is that the suggested transformations could have progressed in the opposite direction to that suggested. This would be important particularly if there were a change in the *Diphydontosaurus* morphology to that of *Gephyrosaurus*. This would mean that the posterior non-successional acrodont dentition of *Diphydontosaurus* would have given rise to the posterior, robust, pleurodont and possibly successional teeth in *Gephyrosaurus*.

A transformation from a *Diphydontosaurus* morphology to that seen in *Gephyrosaurus* would also imply a re-evolution of a 'lacrimal'. However, from the stratigraphical evidence such a transformation seems reasonable because it would appear that *Gephyrosaurus* is a Lower Liassic reptile (Evans 1980) whereas *Diphydontosaurus* is older, forming part of the Rhaetian terrestrial biota.

It is suggested here that *Gephyrosaurus* represented a 'living fossil' in the Lower Lias. We may postulate that the true sphenodontids with their shearing dentition were direct competitors for the insectivorous mammals such as *Morganucodon*. The ability to shear indicates that a relatively wide range of prey size could be tackled and reduced for swallowing. Moreover an endothermic mammal of the size of *Morganucodon* would have needed to feed at three hourly intervals and would thus have been doubtless in direct temporal competition with any insectivorous sphenodontid. It is perhaps significant to note that in New Zealand islands, where the extant *Sphenodon* occurs with the introduced partly carnivorous Polynesian rat, the tuatara shows indications of a population decline (Crook 1975). It is also significant that mammals are absent from the Cromhall and Tytherington faunas where sphenodontids are abundant.

Gephyrosaurus relied on an essentially puncturing and crushing pleurodont dentition and would have specialized in arthropod prey of a restricted size range and would therefore have avoided a direct competition with the mammals. It is noticeable that *Gephyrosaurus* seems to be by far the most numerous lepidosaur which was contemporaneous with the mammals in the slot fissures. Therefore it is suggested that where they co-occurred the mammals replaced the true sphenodontids on these islands and only *Gephyrosaurus* with a different niche survived.

9. Relationships of the Sphenodontidae

9.1. *Taxonomic relationships of the Sphenodontidae*

With the suggestion that the quadrate conch and the possession of a *secondarily* complete lower temporal bar are primitive the position of *Sphenodon* appears much less archaic. Romer (1956, 1966) classified the Sphenodontidae in the order Rhynchocephalia with the other acrodont families (and one edentulous family presumed derived from an acrodont group) Sapheosauridae, Rhynchosauridae, Pleurosauridae and Claraziidae. Kuhn (1969), pointing out that it was unnatural to separate the Eosuchia and Rhynchocephalia, grouped them together in the order Rhynchocephalia which also included the thallatosaurs and *Champsosaurus*. Evans (1980), on the basis of the presence of diapsids such as *Petrolacosaurus* in the Upper Carboniferous (Reisz 1977), suggested that the diapsids were monophyletic and grouped the earliest forms under the Eosuchia (which included the Sphenodontidae). Fraser (1982) suggested that the Rhynchocephalia should include forms derived from eosuchians of the Permian and Lower Triassic. The suborders in that classification all have an acrodont or edentulous dentition (presumably this should therefore include the chamaeleons and agamids?).

The current author suggests that the Sphenodontidae form a valid monophyletic group the member genera displaying some or all of the following advanced features, many of which were recognized by Robinson (1973).

(i) Alternating sized acrodont teeth on part of the dentary.
(ii) alternating size acrodont teeth on part of the maxilla.
(iii) A row of large teeth on the lateral ventral side of the palatine.
(iv) The presence of posteromedial flanges on the posterior acrodont teeth of the maxilla.
(v) The presence of anterolabial flanges on the posterior acrodont teeth of the dentary.

(vi) The presence of posterolabial flanges on the palatine lateral teeth.

(vii) The presence of chisel structures on the premaxillae formed by a number of teeth and which bear one compound tooth per bone.

(viii) The posterior process of the dentary extends to a region underneath the glenoid fossa of the articular complex.

This group derived from an eosuchian ancestor extremely similar to, or possibly actually, *Gephyrosaurus* in perhaps the late Triassic. The rhynchosaurs are not derived from the Sphenodontidae (nor vice versa) since, for example, the former family has a quite different dentition with the teeth ankylosed in sockets (Malan 1963). The Claraziidae are poorly known forms not known to show the features of the Sphenodontidae outlined above except acrodonty. The Pleurosauridae seem to show a number of the typical sphenodontid features outlined above but further study is needed to discover the nature of the features and the relationships of the family. The sapheosaurids do show great morphological similarity to the sphenodontids and the edentulous condition may indeed be derived from an acrodont dentition as suggested by Romer (1956). Cocude-Michel (1963) believed that with the exception of being toothless the sapheosaurids were near identical to *Homoeosaurus*.

In many features the sphenodontids resemble the lacertilian lizards and these have been outlined by Carroll (1977). Carroll (1977) distinguished the sphenodontids from the lizards by the following primitive characters of the Sphenodontidae.

(i) They exhibit an entepicondylar foramen on the humerus.

(ii) They have ventral dermal scales.

(iii) They display all the primitive elements in the carpus and distal carpal one is unmodified as an epiphysis.

Carroll (1977), however, suggested that the main difference lay in the complete diapsid condition of the skull shown by typical members of the Sphenodontidae. Even in the presumed atypical *Clevosaurus* he pointed out that the temporal region was relatively larger than in the paliguanids and kuehneosaurs, the postulated ancestors of the lizards. Also Carroll (1977) believed that the presence of the quadrate–quadratojugal conch in *Clevosaurus* was possibly separately developed from that of lizards.

It has been demonstrated by the author above that the opened lower temporal bar and the quadrate conch are primitive for sphenodontids. Also the early sphenodontids *Diphydontosaurus*, *Planocephalosaurus* and the near-sphenodontid *Gephyrosaurus*, have a temporal region which occupies about 30% of the total length of the skull. This is a higher figure than the *ca.* 25% of kuehneosaurs and paliguanids but less than the 35% and 41% of *Clevosaurus* and *Sphenodon*, respectively. It is thus tentatively suggested that the ancestors of the sphenodontids had a relatively short temporal region which would have been allied to the weak, fast bite expected in their pleurodont ancestors.

Sphenodon differs from the lacertilians in the absence of a copulatory organ (but these are suggested to be secondarily lost in some other tetrapod groups, for example, birds (Romer 1970) and, recently, Arnold (1984) suggested that *Sphenodon* has a copulatory organ precursor. *Sphenodon* also differs from the lacertilian in some aspects of the chondrocranium and development of the skull which include the presence of an egg-caruncle (as opposed to the true egg-tooth of lizards) and no concha for Jacobson's organ (Bellairs & Karmal 1981). However, El-Toubi & Karmal (1970) (in Bellairs & Karmal 1981) pointed out that the differences between *Sphenodon* and lizards in the development of the skull are little more than the differences between the various lacertilian families. In the osteocranium the sphenodontids possess a quadratojugal which is probably absent in lizards; this bone has been reported in the geckonnid *Lygodactylus* (Brock 1932) and in *Scincus* (El-Toubi 1938) but all these occurrences are doubted by Jollie (1960). The presence of a discrete supratemporal (or tabular) is a feature not generally found in sphenodontids except *Clevosaurus* and is present in the majority of lizards, the exceptions including *Lygodactylus* (Brock 1932).

In addition to the features of the skull bones, sphenodontids, with the exception of a rudimentary structure in *Planocephalosaurus* (Fraser & Walkden 1984*a*), do not show the fenestrated scapulacoracoid of lizards. The actual differences therefore appear to be rather small and there seems little problem therefore in the suggestion made by Carroll (1977) that the sphenodontids and lizards share a common ancestry from the eosuchians. It is suggested here that the ancestry would lie close to *Gephyrosaurus* (perhaps slightly earlier) with a similar type of pleurodonty and perhaps a discrete supratemporal. The dichotomy of lizards and sphenodontids would lie perhaps in the late Upper Triassic or the Lower Jurassic.

9.2. *Phylogeny of the Sphenodontidae*

A full phylogeny for the Sphenodontidae is not proposed here because there is insufficient data on the Jurassic and Cretaceous forms. However, a phylogeny is proposed for *Gephyrosaurus* and the sphenodontids considered in table 1; figure 36 depicts a summary cladogram for the relationships suggested in this paper.

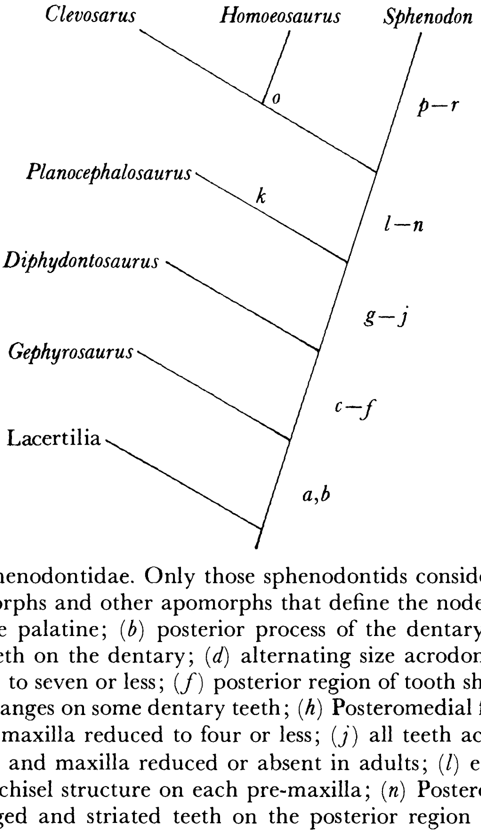

FIGURE 36. Phylogeny of the Sphenodontidae. Only those sphenodontids considered in table 1 and *Gephyrosaurus* are included. The autapomorphs and other apomorphs that define the nodes are (*a*) a row of enlarged teeth on the lateral margin of the palatine; (*b*) posterior process of the dentary underlies the glenoid fossa; (*c*) alternating size acrodont teeth on the dentary; (*d*) alternating size acrodont teeth on the maxilla; (*e*) teeth on each pre-maxilla reduced to seven or less; (*f*) posterior region of tooth shelf on dentary reduced to groove or absent; (*g*) Anterolabial flanges on some dentary teeth; (*h*) Posteromedial flanges on the posterior maxillary teeth; (*i*) teeth on each pre-maxilla reduced to four or less; (*j*) all teeth acrodont in adults; (*k*) alternating teeth series on both dentary and maxilla reduced or absent in adults; (*l*) each pre-maxilla with three teeth or less; (*m*) development of chisel structure on each pre-maxilla; (*n*) Posterolateral flanges on some palatine teeth; (*o*) prominently flanged and striated teeth on the posterior region of the maxilla; (*p*) reduction of quadrate–quadratojugal conch; (*q*) reduction of retroarticular process; (*r*) no teeth on the pterygoid. The lower temporal bar was incomplete in *Gephyrosaurus* but may have been complete in some specimens of *Diphydontosaurus*. A complete lower temporal bar was probably present in some specimens of *Clevosaurus* and *Planocephalosaurus*. In *Sphenodon* a complete lower temporal bar is present in all post embryonic stages.

Of the other known sphenodontids, *Opisthias* (and *Theretairus*) and *Toxolophosaurus* have a probable propalinal jaw action (Throckmorton *et al.* 1981) which suggests a particular affinity to *Sphenodon*, whereas the prominently flanged and striated teeth of *Kallimodon* (and *Leptosaurus*) ally that genus to *Clevosaurus* and *Homoeosaurus*.

10. Concluding discussion

The skull and lower jaw of *Diphydontosaurus avonis* has been described from disarticulated bony elements. These bones and the reconstructed osseous head skeleton are of a sphenodontid nature but the reptile had a pleurodont dentition on the premaxilla and on the anterior region of the maxilla and dentary.

If the condition of the complete lower temporal bar and the lack of a quadrate–quadratojugal conch are accepted as derived in *Sphenodon* then *Diphydontosaurus* or a morphological near-equivalent appears to represent a very plausible ancestral condition for that genus. The advanced features of *Diphydontosaurus* that may preclude any claim for true ancestral status are the medial inflexion of the prefrontal and the fused frontals and fused parietals (fused late in ontogeny in *Diphydontosaurus*). These latter features seem of doubtful status as important characters, as, for example, median bone fusion seems to be a species characteristic among some modern lepidosaurs and doubtless could also have been the case in early sphenodontids.

In favour of an ancestral position for *Diphydontosaurus* are a number of advanced features which are strikingly similar to those in *Sphenodon*. Such a feature is the relative position of the alternating series of acrodont teeth on the maxilla of *Diphydontosaurus* which commences in the region below the posterior margin of the nasal process. The position corresponds directly with the alternating additional teeth in *Sphenodon*. Also in both genera the individual teeth in both series become larger posteriorly and there are about seven such teeth in both genera (for *Sphenodon* see Robinson (1976, figure 3)). Both *Diphydontosaurus* and *Sphenodon* adults have anterior successional teeth and posterior uniform-sized acrodont teeth on the maxilla. It is true that in *Sphenodon* all maxillary teeth are acrodont whereas in *Diphydontosaurus* the anterior dentition is pleurodont. However, the presence of a groove at the base of the *Diphydontosaurus* acrodont teeth indicating a remnant shelf on both the maxilla and dentary are very strong indications that in the sphenodontids acrodonty has evolved from pleurodonty.

In *Sphenodon* and *Diphydontosaurus* there is a series of alternating sized teeth on the dentary preceded by successional teeth and followed by an acrodont dentition of near uniform-sized teeth. Again in *Sphenodon* the anterior teeth are acrodont whereas in *Diphydontosaurus* they are pleurodont. The position of the alternating sized series is much more anterior within the tooth row of *Sphenodon* but this situation is doubtless the result of the near lack of any growth of the anterior region of the dentary, the growth being essentially posteriorly oriented (Robinson 1976).

The quadratojugal of both *Diphydontosaurus* and *Sphenodon* is completely fused to the quadrate below the quadratojugal foramen but a suture line is evident in both genera above that feature. This partial ossification is also observed in *Clevosaurus* but its significance, if any, is not obvious.

All other features of *Diphydontosaurus* are the same as or could be primitive for *Sphenodon*. Of these characters the crested parietals of *Sphenodon* are quite different to the flattened forms in *Diphydontosaurus* but the former is probably an adaptation that increases the power of the adductor muscles possibly in relation to the propalinal action of feeding tuataras. The two other sphenodontids fully described from the fissure deposits *Clevosaurus* and *Planocephalosaurus* differ from *Sphenodon* in a number of ways. Both these Triassic genera have a well developed coronoid process of relatively greater development than in *Sphenodon* adults. Interestingly a coronoid bone has not been described for either genus (see Robinson 1973; Fraser 1982).

No successional teeth are recorded in the anterior of the maxilla or dentary of *Clevosaurus* by Robinson (1973). However, the presence of anterior alternating teeth resembles the condition present in *Sphenodon* hatchlings (see Robinson 1976, figure 3). A few other differences in tooth form between these genera are noted by Robinson (1973). However *Clevosaurus* does share 21 of the 28 derived characters present in *Sphenodon* (see table 1) and in a number of aspects, such as the paired frontals and parietals and the premaxillary chisel teeth, greatly resembles the tuatara. If *Clevosaurus* represented a group that gave rise to *Sphenodon* then the presence of a supratemporal in the former genus could be dismissed as primitive. However the supratemporal would still present a major problem in sphenodontid phylogeny.

Planocephalosaurus appears to be a very aberrant sphenodontid. There is either a lack or a poor development of the alternating series of acrodont teeth in both the maxilla and dentary and there may also have been a fenestrated scapulacoracoid (Fraser & Walkden 1984*a*), otherwise a unique lacertilian feature.

Of the genera considered here *Diphydontosaurus* seems to be the most plausible ancestral condition for the bony head morphology of *Sphenodon*. The major differences with the extant genus are all primitive in *Diphydontosaurus* excepting the fused median roofing bones and the prefrontal medial inflexion.

The advanced characters found in *Gephyrosaurus* also co-occur in *Diphydontosaurus* and the former genus, stratigraphical relationships notwithstanding, could well represent a plausible eosuchian or near-sphenodontid ancestral stage for a lineage leading to *Sphenodon*.

However, all the species *Clevosaurus hudsoni*, *Planocephalosaurus robinsonae*, *Gephyrosaurus bridensis* and *Diphydontosaurus avonis* are only known to occur on late Triassic or early Jurassic islands. Therefore it is improbable that they could represent any true ancestral populations for *Sphenodon* since these islands were all transgressed by the seas of the Jurassic and the terrestrial reptile biota would have been wiped out.

One final consideration in the relationships of *Sphenodon* needs to be outlined. All modern populations of the tuatara are insular, the species inhabiting small islands off the coast of North and South Island, New Zealand. The skull of *Sphenodon* seems to display a great variability in morphology. Among these variable features are a bony covering of both carotid arteries and facial nerves producing simple vidian canals in one specimen (OUM no.908 O-C. 5616). In another specimen described by Evans (1980) a vidian canal is present on one side of the skull. In most other specimens a vidian canal is absent, the carotid artery and facial nerve being covered by tough connective tissue (Save Soderburgh 1947). Other signs of this great morphological variability are found in the muscles of the head (see Haas 1973). In some specimens of *Sphenodon* the dentary completely encloses a region of the meckelian canal whereas in other individuals the canal is opened medially. These great differences between individuals could well be accounted for by the fact that the insular populations of *Sphenodon* are subject to pronounced genetic drift leading to considerable inter-island variation.

Finally the fact that *Sphenodon* lives in a biota where native mammalian competitors are absent may well explain the lack of selection pressures that may have allowed the loss of a tympanum and consequently the most efficient auditory system.

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Abbreviations used in figures

ac.th.	acrodont teeth
al.	alveolar
alt.ac.th.	alternating sized acrodont teeth
alt. ser.	alternating series
an.	angular
ant.	anterior
art.	articular complex
b.	basin
bas.	basioccipital
basp.	basisphenoid
bo.de.mand.	boss for depressor mandibularis
c.	coronoid
ca.	cavity
cen.	central
ch. tymp.	chorda tympani
co.	conch
cond.	condyle
cr.	crest
cra.	cranial
cri.cran.	crista cranii
cri.tr.	crista trabecularis
d.	dentary
dep.	depression
di.	distal
do.	dorsal
ect.	ectopterygoid
ep.	epipterygoid
ext.	extension
f.	frontal
fct.	facet
fl.	flange
for.	foramen
for.ab.ner.	foramen for the abducens nerve
for.al.ram.i.a.ner.	foramen for the alveolar ramus of the inferior alveolar nerve
for.cut.i.a.ner	foramen for the cutaneous branches of the inferior alveolar nerve

for.hy.ner.	foramen for the hypoglossal nerve
for.max.art.al.ner.	foramen for cutaneous branches of the maxillery artery and superior alveolar nerve
for.max.art.med.eth.ner.	foramen for the maxillery artery and medial ethmoidal nerves
for.trig.ner.front.art.	foramen for the trigeminal nerve and frontal artery
for.x.man.art.	foramen for the external mandibular artery
g.	groove
g.fac.ner.pal. art.	groove for facial nerve and palatine artery
g.glos.ner.	groove for glassopharyngeal nerve
h.	hollow
i.c.a.	internal carotid artery
in.	inflexion
j.	jugal
l.	lateral
la.	lacrimal
m.	maxilla
md.	medial
me.	median
met.	metotic
mid.	mid line
mi.reg.	mid region
n.	nasal
not.	notch
nut.	nutrient
o.	ornamented
oc.	occipital
p.	parietal
pa.	parasphenoid
pal.	palatine
pal.sh.	palatal shelf
pft.	postfrontal
pi.	pineal
pl.	pleurodont
pm.	premaxilla
porb.	postorbital
post.	posterior
prot.	pro-otic
prart.	pre-articular
prf.	prefrontal
proc.	process
pt.	pterygoid
q.	quadrate
qj.	quadratojugal
r.	row
ram.	ramus
rar.rep.th.	rarely replaced teeth
r.art.proc.	retroarticular process
rem.hat.	remnant of hatchling dentition
rem.sh.	remnant shelf
re.pit	replacement pit
re.th.	replacement teeth
ri.	ridge
ros.	rostral
s.	squamosal
sb.art.proc.	subarticular process
sb.orb.fen.	suborbital fenestra
se.t.	sella turica
sh.	shelf
so.	socket
sp.oc.t.	spheno-occipital tubercle
st.	supratemporal
su.	suture
sup.ang.for.	supra. angular foramen
sur.	surangular

sy.fa.	symphysial face
th.	tooth or teeth
tr.	trough
ty.cr.	tympanic crest
un.ac.th.	uniform sized acrodont teeth
un.th.,	uniform sized teeth
v.	vomer
ve.	ventral
w.n.cap.	wall of the nasal capsule
wr.fct.max.th.	wear facets caused by maxillary tooth
BMNH	British Museum Natural History
BU	Bristol University Geology Museum
OUM	Oxford University Museum

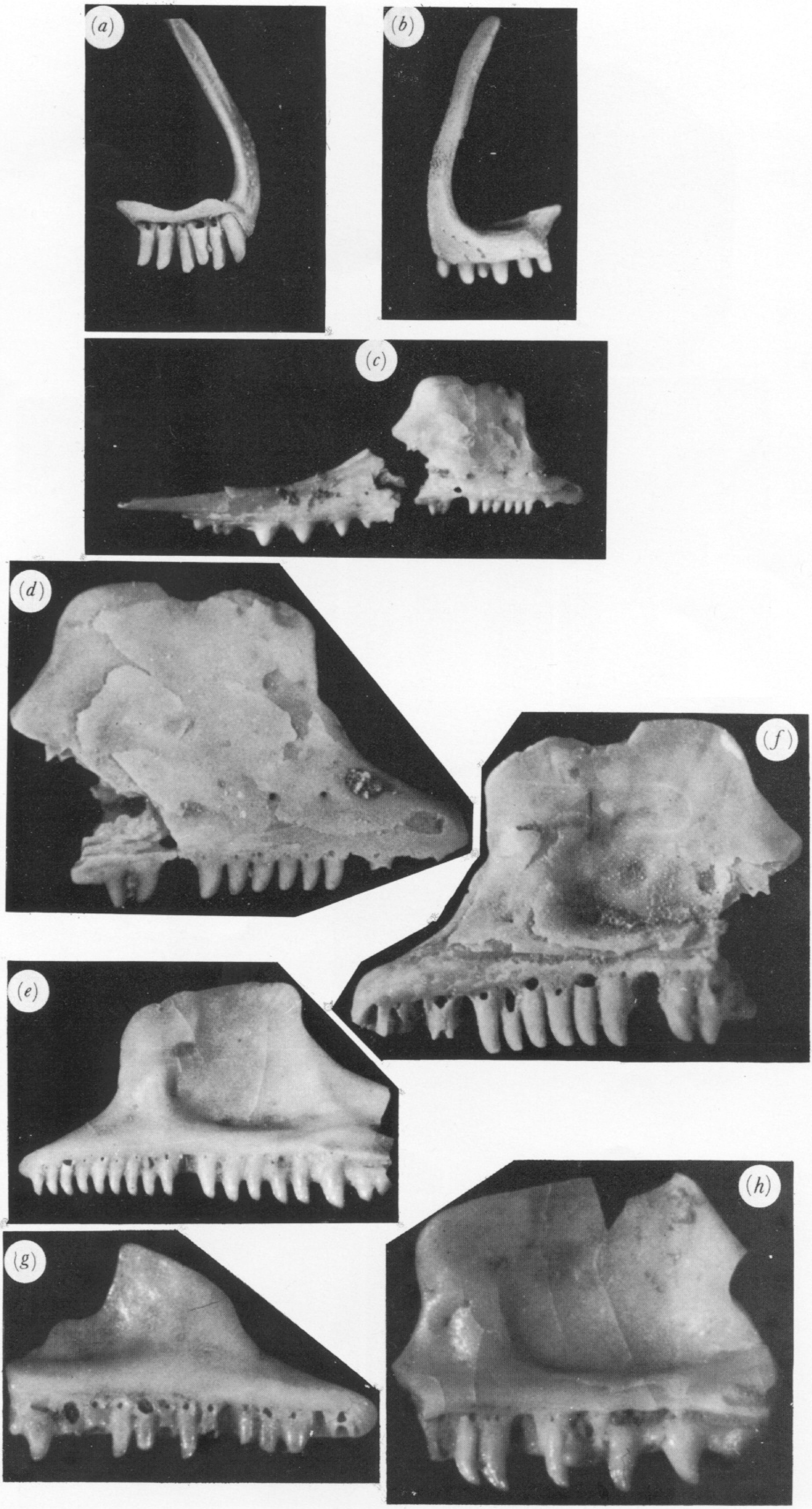

FIGURE 6. For description see opposite.

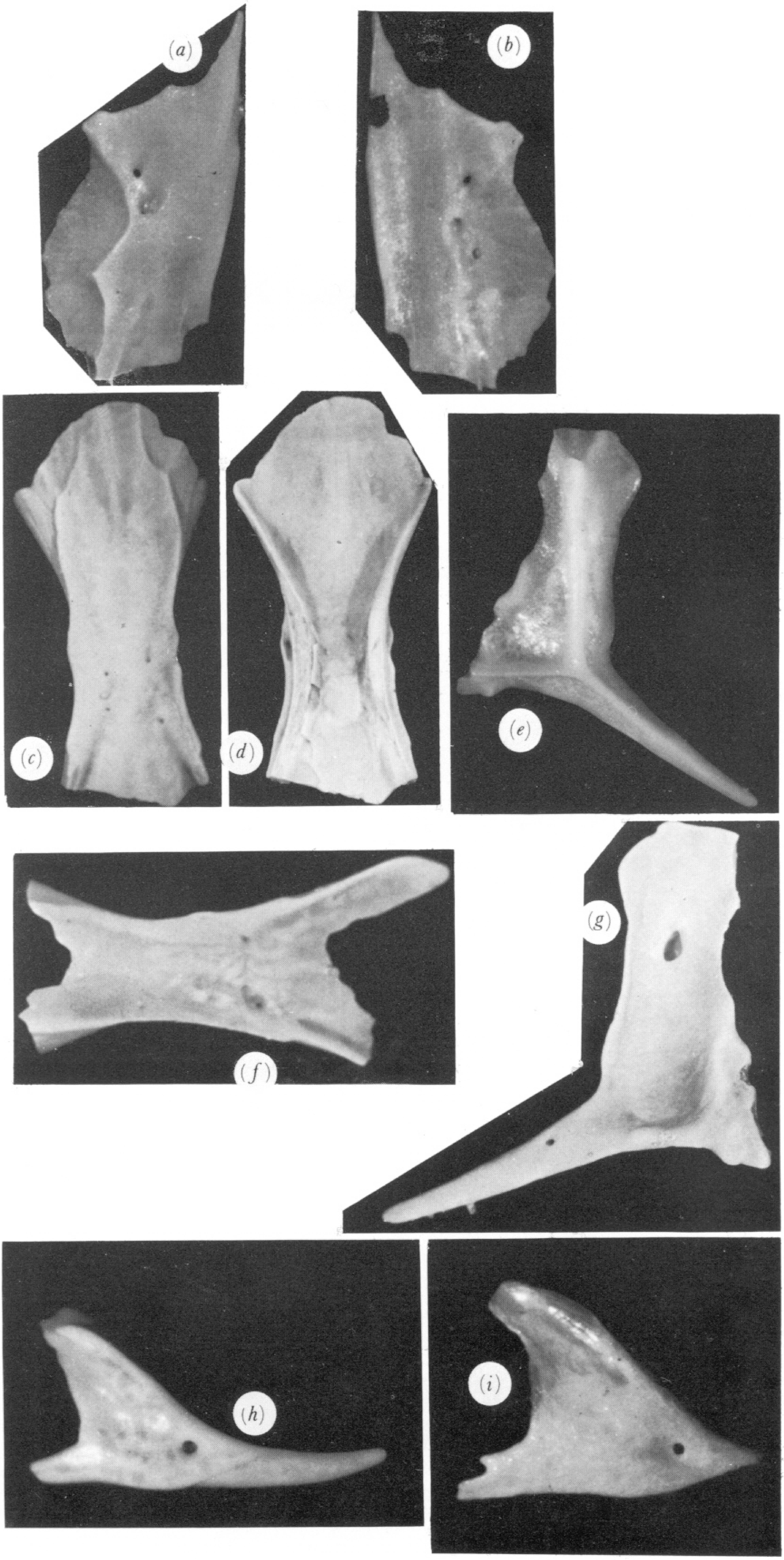

FIGURE 9. For description see p. 388.

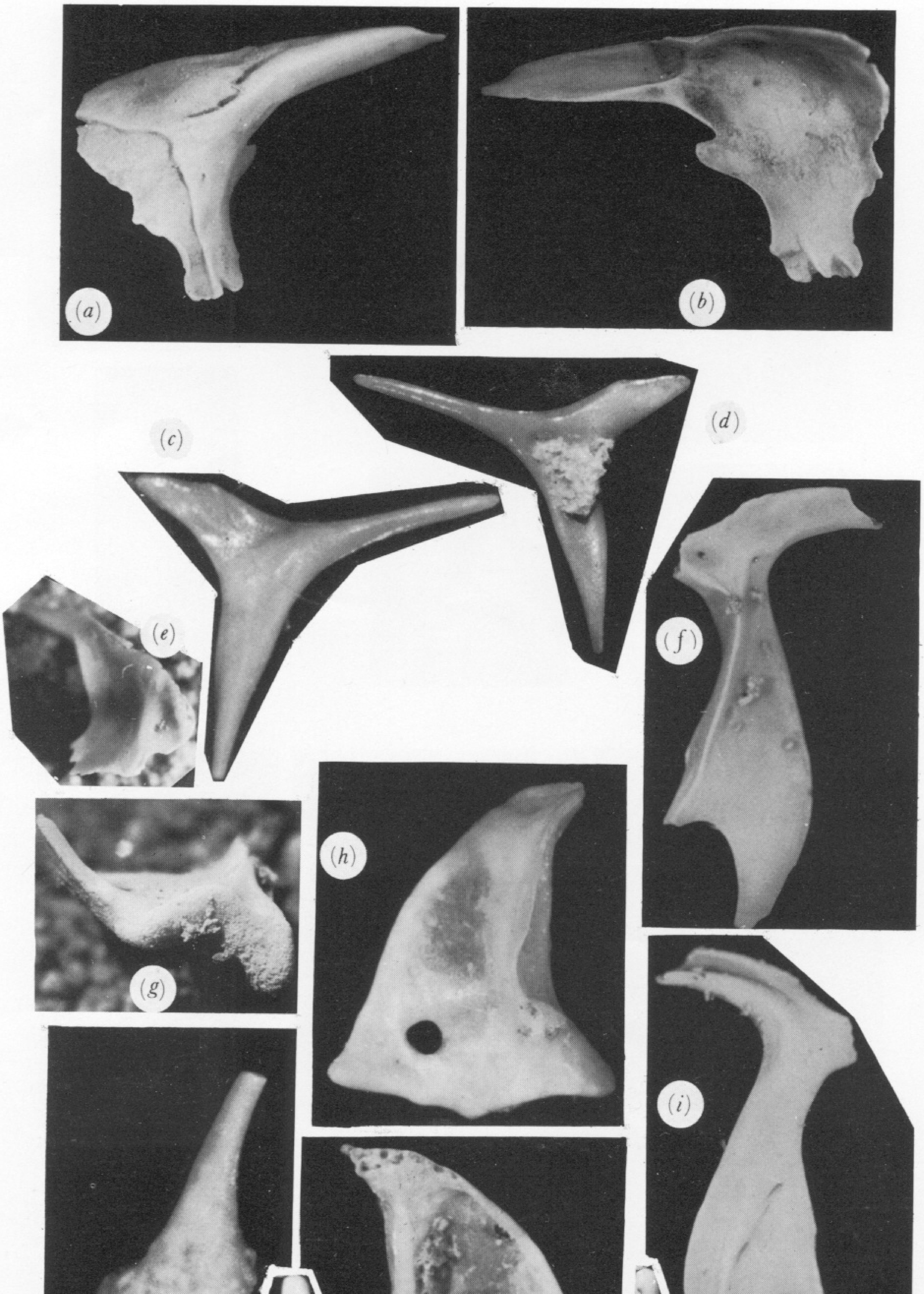

FIGURE 13. For description see p. 389.

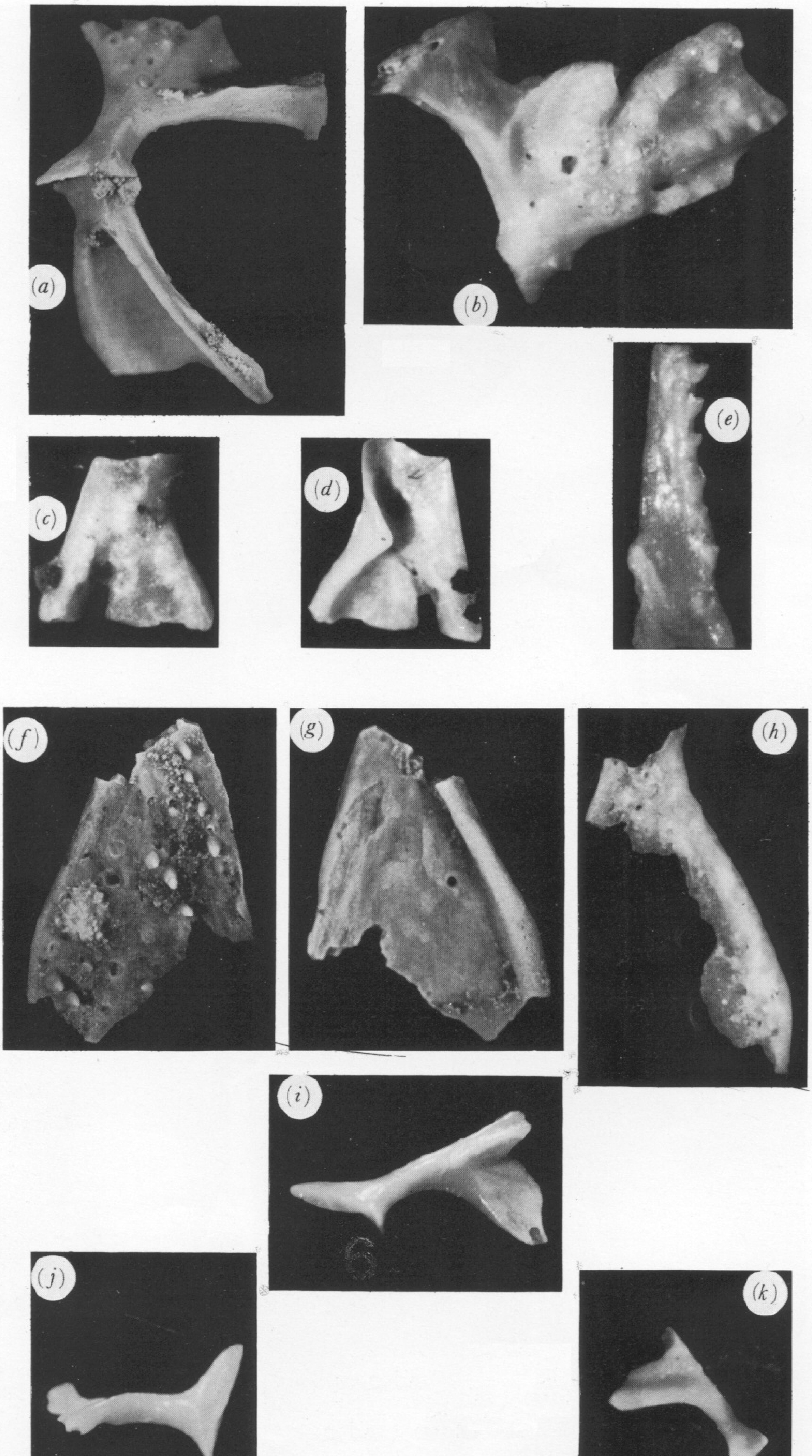

FIGURE 21. For description see opposite.

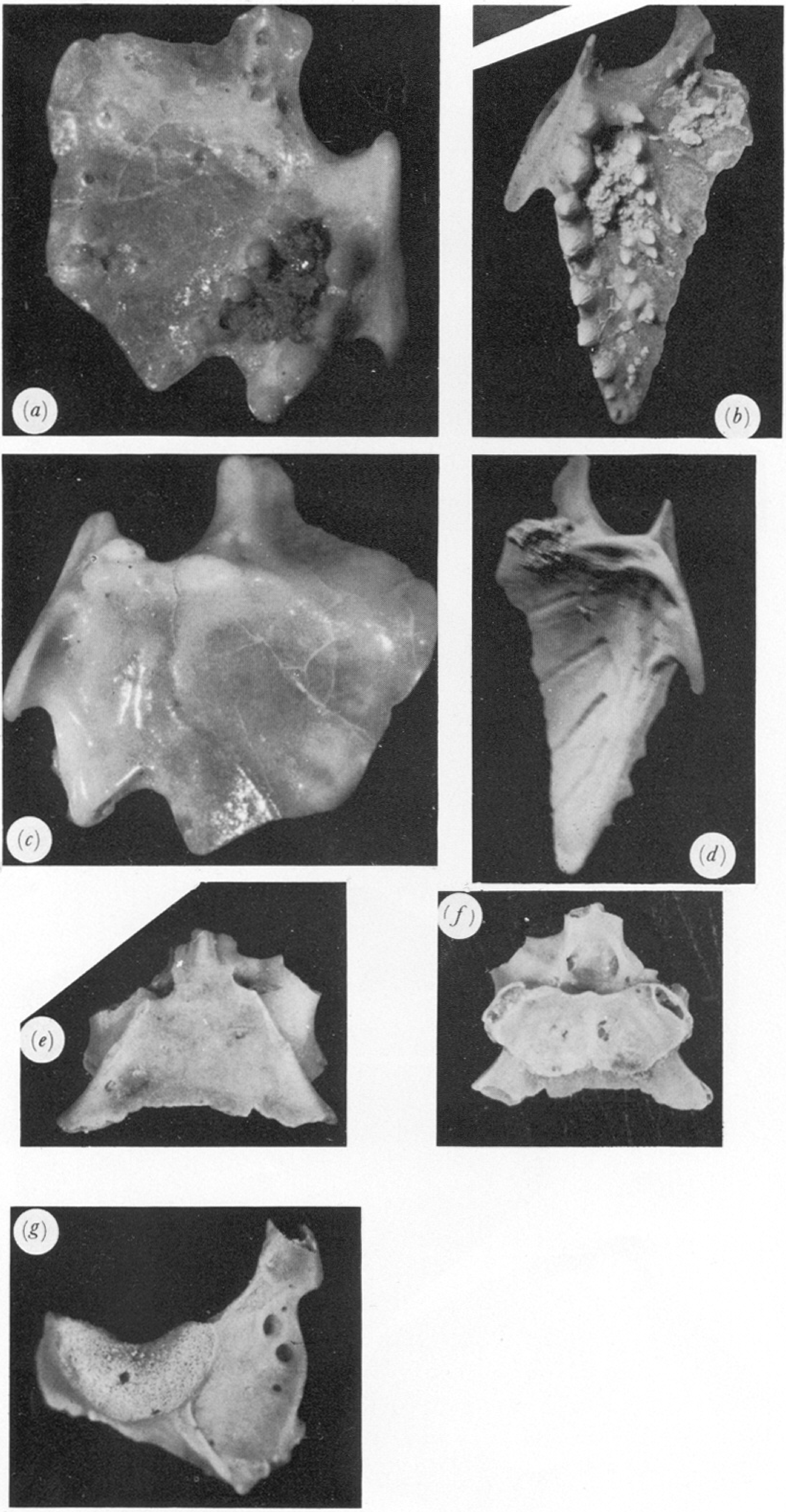

FIGURE 23. For description see opposite.

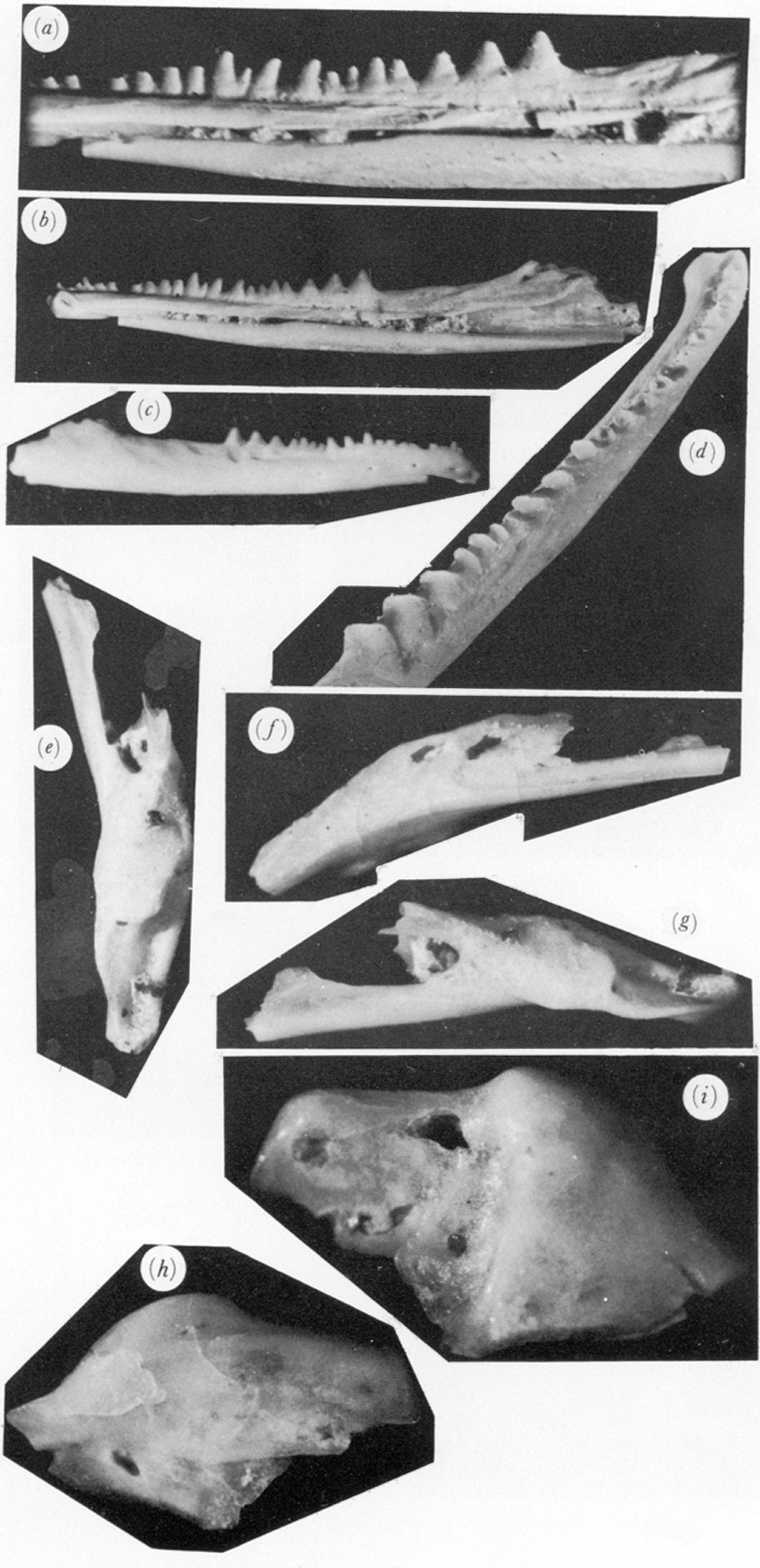

FIGURE 29. For description see opposite.

FIGURE 32. For description see opposite.