

NEW TRIASSIC SPHENODONTIDS FROM SOUTH-WEST ENGLAND AND A REVIEW OF THEIR CLASSIFICATION

by N. C. FRASER

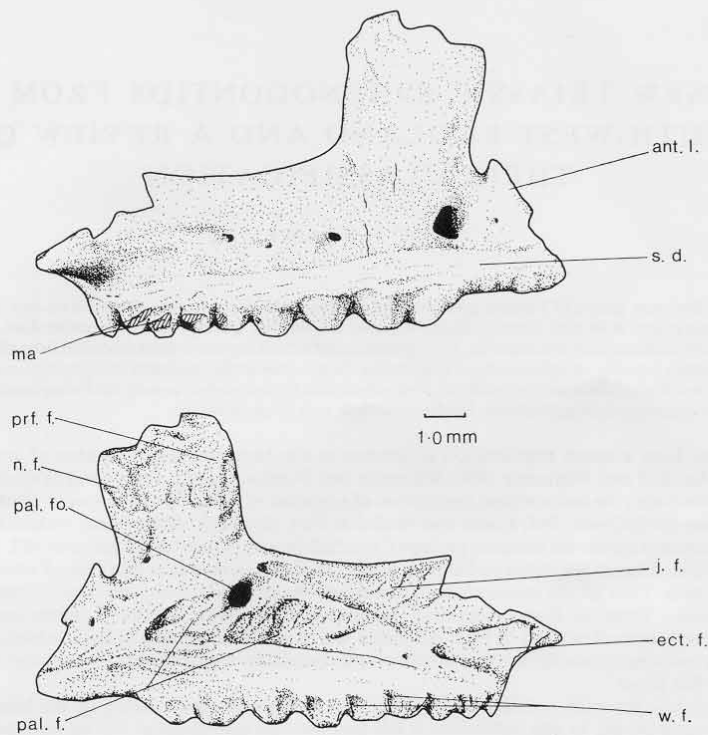
ABSTRACT. Two new genera of Triassic sphenodontid are described. *Sigmala sigmala* gen. et sp. nov. and *Pelecymala robustus* gen. et sp. nov. occur in fissure deposits in Cromhall Quarry, south Gloucestershire. They are based entirely on dissociated jaw elements. Five sphenodontid genera have now been described from this locality and they permit a review of sphenodontid systematics. Based principally on dental morphology, an updated classification of the Sphenodontidae is offered. Five subfamilies are recognized: namely the Polysphenodontinae, Brachyrhinodontinae, Sphenodontinae, Homoeosaurinae, and Eilenodontinae.

THERE has been a recent regeneration of interest in the Mesozoic herpetofaunas of south-west Britain (Marshall and Whiteside 1980; Whiteside and Robinson 1983; Fraser and Walkden 1983; Benton 1984a) with the concomitant description of a number of new genera and species (Evans 1980, 1981; Fraser 1982; Crush 1984; Fraser and Walkden 1984; Kermack 1984). Of the various localities known to contain vertebrate remains, perhaps Cromhall Quarry, south Gloucestershire (ST 704 916), has the largest range of tetrapods and at present the list of species stands at fourteen, of which six are sphenodontids. Four of the sphenodontids are relatively abundant and have been recorded from other localities. These are *Planocephalosaurus robinsonae*, *Clevosaurus hudsoni*, *C. minor*, and a third genus currently being described by D. I. Whiteside, which will be referred to as Sphenodontid X. The remaining two sphenodontids are known only from completely dissociated jaw bones and form the subject of this paper.

Although it is generally not desirable to erect new genera and species solely on the basis of one or two isolated bones, in this instance it is felt that little further material will be recovered from the Cromhall deposits, as a large quantity of sediment has already been systematically processed from all accessible levels of the fissure sediments. In addition one species has already been named in a previous discussion on the palaeoecology of the Cromhall assemblages (Fraser and Walkden 1983), and it is therefore necessary to document fully these forms and give them proper taxonomic treatment.

SYSTEMATIC PALAEOLOGY

The fifth most abundant sphenodontid in the Cromhall fauna was provisionally named *Sigmala sigmala* (Fraser and Walkden 1983). It will be formally described here as a new genus and species. Whilst not a common form the dentition is quite characteristic and has enabled the positive identification of the maxilla, dentary, and palatine, including juvenile specimens. No other elements have been recognized, probably for one or both of two reasons. First, the genus is in any case relatively rare; consequently only a few fragments of other bones are likely to be present in the residues: these may well be unrecognizably broken and worn. Secondly, since it would appear that skeletal morphology is quite uniform within the Triassic sphenodontids, the structure of other elements may resemble those of the similar-sized and much more abundant genus, *Clevosaurus*. In this case, polishing and general post-mortem attrition may have obliterated any distinguishing features that might be expected.



TEXT-FIG. 1. *Sigmala sigmala* gen. et sp. nov. Holotype, right maxilla, AUP no. 11083, in *a*, lateral and *b*, medial views.

Class REPTILIA
 Subclass DIAPSIDA Osborn 1903
 Order SPHENODONTIDA Cope 1890
 Family SPHENODONTIDAE Cope 1890
 Genus SIGMALA gen. nov.
 Species *Sigmala sigmala* sp. nov.

Etymology. Description of the flexure observed in the lower jaw when viewed dorsally (Gr. *Sigma*; L. *mala* jaw).

Diagnosis. A sphenodontid with maxilla approximately 13 mm long and bearing a distinct extension of bone on its anterior margin; all teeth acrodont with an approximate triangular form in lateral aspect; anteriorly the marginal teeth are small and alternate in size in the juvenile, but are entirely worn down to the bone in mature specimens; no successional teeth on either the maxilla or dentary; approximately eight to ten additional teeth in each jaw quadrant which bear rudimentary anterior and posterior flanges on the dentary, but only posterior flanges on the maxilla; all additional teeth generally of uniform size; both maxilla and dentary are broadened dorsoventrally; dentary exhibits

a distinct sigmoid flexure in dorsal aspect; discrete lateral wear facets on dentary; high coronoid process; palatine with a single row of seven or eight obtusely conical teeth.

Holotype. AUP no. 11083, right maxilla.

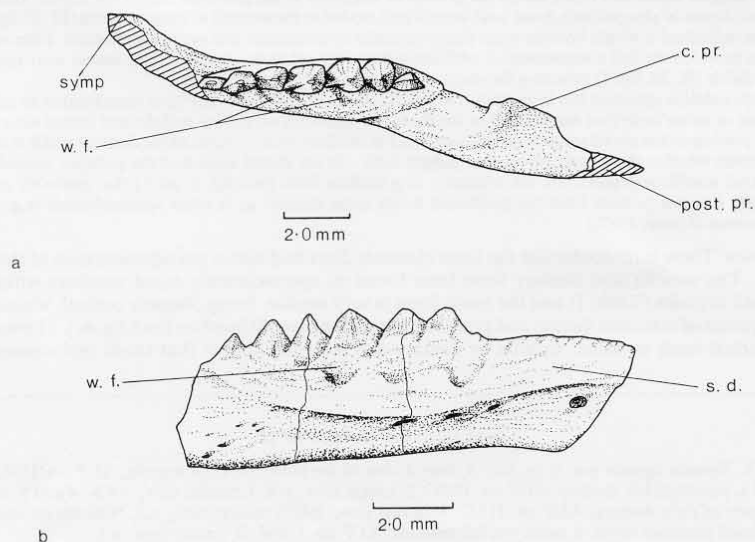
Paratypes. AUP no. 11082, left dentary; AUP no. 11084, left palatine.

Type locality. Karstic fissures in Dinantian limestones. Cromhall Quarry, south Gloucestershire.

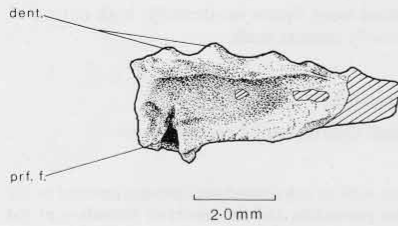
Horizon. Upper Triassic.

Description. The maxilla (Pl. 20, fig. 1; text-fig. 1) is a deep bone with an extensive dorsal process anterior to the orbit. A curious feature of the element is its contact with the premaxilla and the posterior boundary of the external naris. An examination of the medial surface of the bone (text-fig. 1*b*) reveals a pronounced facet for a premaxillary process just dorsal to the tooth row, but the elongated flap of bone immediately above the premaxillary facet has not been previously observed in any sphenodontid. This lappet (text-fig. 1*a*, ant.l.) of bone lacks any obvious facet either for the premaxilla or a descending process of the nasal. It seems unlikely that the posterior margin of the naris would have had such a complex outline; more probably either the premaxilla or nasal, or both, marked the posterior boundary of the external naris and were overlapped by this maxillary lappet. The dorsal process of the maxilla bears a well-defined medial facet where it overlapped the prefrontal. Mature individuals exhibit a broad flange of bone ventral to the orbit which on the medial surface displays facets for the jugal and palatine (text-fig. 1*b*, j.f. and pal.f.). The palatine facet is marked by the characteristic palatine foramen. Ventral to the extensive jugal facet is a further rugosity against which the ectopterygoid abutted.

Anteriorly the maxilla bears approximately ten small teeth representing the remanent hatchling dentition. In the adult these teeth are invariably worn to the bone, but this series shows an alternation in tooth size in immature individuals. There were apparently no maxillary successional teeth. More posteriorly a mature individual normally has between eight and ten larger additional teeth which bear slight posterior flanges, but these are not as extensive as those of *Clevosaurus* and *Homoeosaurus*. The last three or four teeth of the additional series may be unflanged and somewhat smaller than the others. The additional teeth display extensive



TEXT-FIG. 2. *Sigmala sigmala* gen. et sp. nov. *a*, paratype, left dentary, AUP no. 11082, in dorsal view. *b*, right dentary, AUP no. 11364, in lateral view.



TEXT-FIG. 3. *Sigmala sigmala* gen. et sp. nov. Paratype, left palatine, AUP no. 11084, in dorsal aspect.

lingual wear facets and mature individuals have a broad layer of secondary dentine on the lateral surface of the maxilla (text-fig. 1a, s.d.).

The dentary (Pl. 20, figs. 2 and 3; text-fig. 2) is approximately 20 mm long, deep and with a high coronoid process. Anteriorly there is a stout jaw symphysis and posteriorly the element extends for some distance posterior to the coronoid process. Medially there is an open meckelian groove but with no indications of facets for a splenial. In dorsal view the dentary displays a slight S-shaped flexure (text-fig. 2a). There are approximately ten small teeth anteriorly which show some alternation in size. In mature individuals these teeth are completely worn to the bone and, as a result of the complete absence of successional teeth, there is an 'edentulous' anterior region. There are usually about eight additional teeth—each with small anterior and posterior flanges—and the posterior teeth are set slightly medial to the coronoid process (text-fig. 2a). Unlike other sphenodontids the additional teeth tend not to exhibit a progressive increase in size caudad. Well-defined lateral wear facets were caused by the precise occlusion of the maxillary dentition, and these facets extend well beyond the bases of the teeth and deep into the bone (text-fig. 2b). Wear facets on the lingual surfaces of the mandibular teeth are evidence of the influence of an enlarged tooth row on the palatine. In one example of a juvenile dentary (Pl. 20, figs. 4 and 5) an additional tooth shows the process of ankylosis at the posterior end of the ramus. This tooth displays a degree of pleurodonta, lying both ventral and medial to the summit of the jaw ramus (Pl. 20, fig. 5). In a mature individual it would become more firmly attached by cementum and secondary dentine. Even in those juveniles in which the full complement of additional teeth had yet to be attained, faint lateral wear facets are readily visible (Pl. 20, fig. 4) reflecting the shape of the individual maxillary teeth.

A single palatine specimen has been recovered (Pl. 20, fig. 6). This is a robustly built bone bearing an enlarged row of six or seven teeth that ran parallel to the maxillary dentition exhibiting well-defined lateral wear facets. A small portion of the maxillary process is preserved, but medially little remains of the element and it is difficult to determine whether there were any further palatal teeth. On the dorsal surface of the palatine, medial to the fragmented maxillary process, are the remnants of a shallow facet (text-fig. 3, prf.f.) that probably received a ventrally directed process from the prefrontal in the same manner as in other sphenodontids (e.g. *Planocephalosaurus* (Fraser, 1982)).

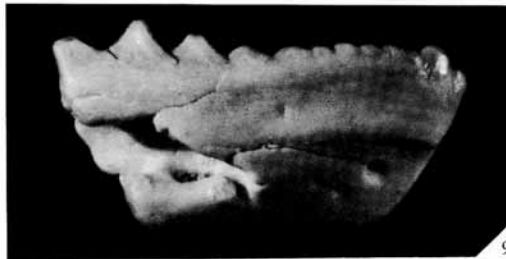
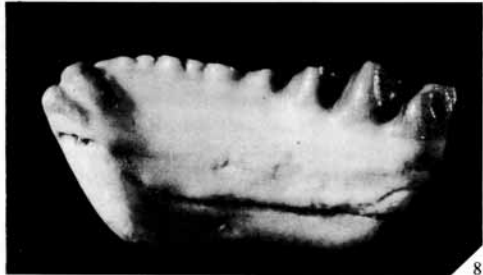
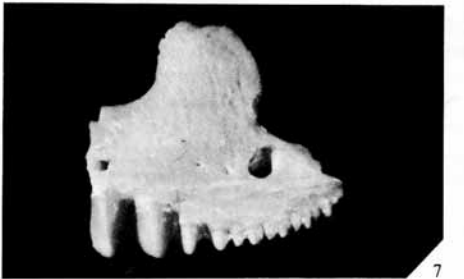
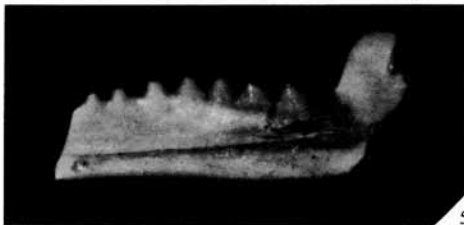
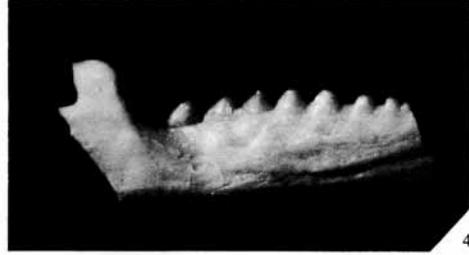
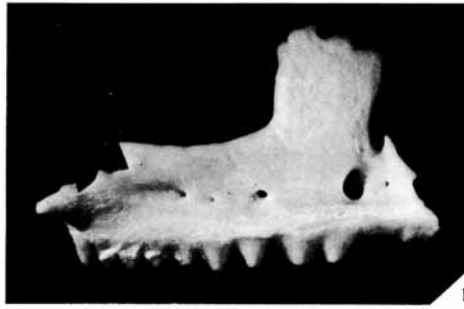
Discussion. There is no doubt that the three elements described above are representative of the same species. The maxilla and dentary have been found in approximately equal numbers within the Cromhall deposits (Table 1) and the tooth form is very similar, being obtusely conical, without the development of extensive flanges and generally not unlike that of *Opisthias* (text-fig. 4a). There are no successional teeth on either maxilla or dentary and it would appear that tooth replacement was

EXPLANATION OF PLATE 20

Figs. 1-6. *Sigmala sigmala* gen. et sp. nov. 1, lateral view of the holotype, right maxilla, AUP no. 11083, $\times 5$. 2 and 3, paratype, left dentary, AUP no. 11082. 2, lateral view, $\times 4$; 3, medial view, $\times 4.5$. 4 and 5, juvenile specimen of right dentary, AUP no. 11212. 4, lateral view, $\times 8$; 5, medial view, $\times 8$. Note the incompletely ankylosed posterior tooth. 6, paratype, left palatine, AUP no. 11084, in ventral view, $\times 8$.

Fig. 7. *Pelecymala robustus* gen. et sp. nov. Holotype, right maxillary fragment, AUP no. 11140, in lateral aspect, $\times 6$.

Figs. 8 and 9. *Pelecymala?* dentary specimen, AUP no. 11192. 8, lateral view, $\times 6$; 9, medial view, $\times 6$.



FRASER, *Triassic sphenodontids*

TABLE 1. Occurrence of *Sigmala sigmala* jaw-bone elements at each site in Cromhall Quarry.

Element	Site 2	Site 3	Site 4	Site 5
mx	1	4	4	
d		6	5	1
pal			2	

completely suppressed in this genus, although this cannot be verified at present as the premaxilla is unknown.

The enlarged tooth row on the palatine, posterior process on the dentary, acrodont marginal dentition, hatchling dentition showing an alternation in size, and the probable articulation of the prefrontal with the palatine form a suite of characters indicative of a sphenodontid. The morphology of the dentition is particularly diagnostic with the well-defined division of the marginal series into additional and hatchling dentitions. The additional teeth also bear rudimentary flanges, and medial wear facets on the maxillary teeth and lateral wear facets on the mandibular dentition are characteristic of the sphenodontid shearing bite. The wear facets reflecting the precise outlines of opposing dentitions is a feature shared with *C. hudsoni* and indicates a lack of propalinal movement. In contrast, *Sphenodon* and the Eilenodontinae (Rasmussen and Callison, 1981) are perhaps rather more advanced in that propalinal movements are incorporated into the shearing jaw action.

The relationships of *Sigmala* within the Sphenodontidae are not so clearly defined. The teeth do not possess the enlarged flanges typical of *Homoeosaurus* and *Clevosaurus* and the jaws are much deeper and more robust than *Planocephalosaurus*. Unlike the other Triassic sphenodontids and *Sphenodon*, *Sigmala* does not possess an anterior successional dental series. However the tooth morphology is not unlike that of *Sphenodon* and *Opisthias*; all three genera exhibit an approximately triangular lateral aspect and rudimentary flanges (text-fig. 4). However, because of the occurrence of a propalinal jaw movement in *Sphenodon*, and possibly also in *Opisthias*, together with the reduction of marginal tooth numbers in *Sigmala*, the three genera cannot be unequivocally assigned to the same subfamily. It has been suggested elsewhere (Fraser and Walkden 1983) that *Sigmala* might have been herbivorous; the deep jaw outline and anterior 'edentulous beak' closely resemble those of a chelonian and the herbivorous agamid lizard, *Uromastix hardwickii*. In the same manner as in the Eilenodontinae the posterior mandibular teeth of *Sigmala* are set medial to the coronoid process (text-fig. 2a), but, unlike that particular group of herbivorous sphenodontids the teeth of *Sigmala* are not transversely broadened.

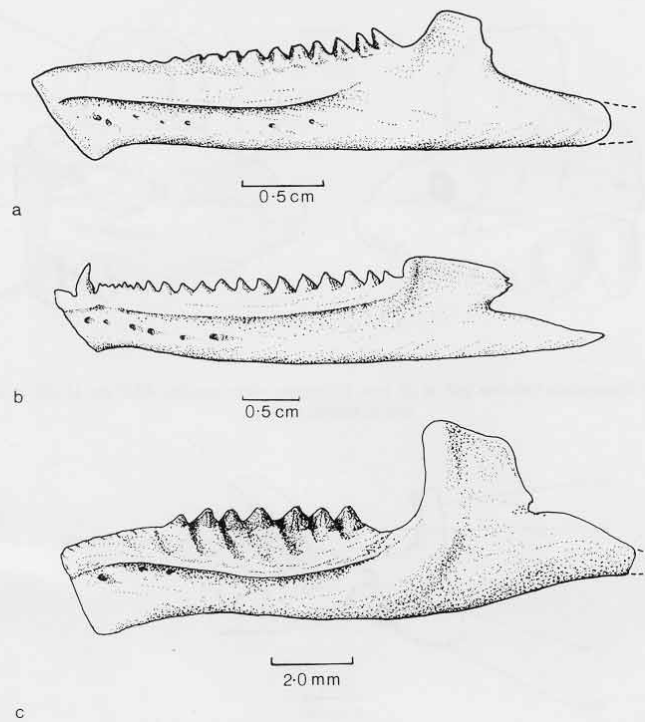
At this stage, without information regarding the skull and postcranial morphology of *Sigmala*, dental structure is the only taxonomic criterion available, and on this basis *Sigmala* is tentatively considered to be most closely related to *Sphenodon* and *Opisthias*.

Genus PELECYMALA gen. nov.
Species *Pelecymala robustus* sp. nov.

A sixth sphenodontid in the Cromhall fauna is represented by just four fragments of maxilla. On the basis of the quite distinctive additional teeth it is designated as a new genus.

Etymology. Derived from the hatchet-shaped appearance of the anterior region of the upper jaw and the strong robust nature of the additional teeth (Gr. *pelekys* (πέλεκυσ) hatchet; L. *mala* jaw).

Diagnosis. Sphenodontid reptile having a maxilla estimated to be approximately 15 mm long and bearing large transversely broadened additional teeth; maxillary hatchling teeth alternate in size; no



TEXT-FIG. 4. Reconstructions of the dentaries of *a*, *Opisthias rarus*, *b*, *Sphenodon punctatus*, and *c*, *Sigmala sigmala* gen. et sp. nov. All in lateral view. *a*, after Throckmorton *et al.* (1981).

successional teeth on the maxilla; additional teeth generally increase in size caudad; anterior region of the maxilla is hatchet-shaped.

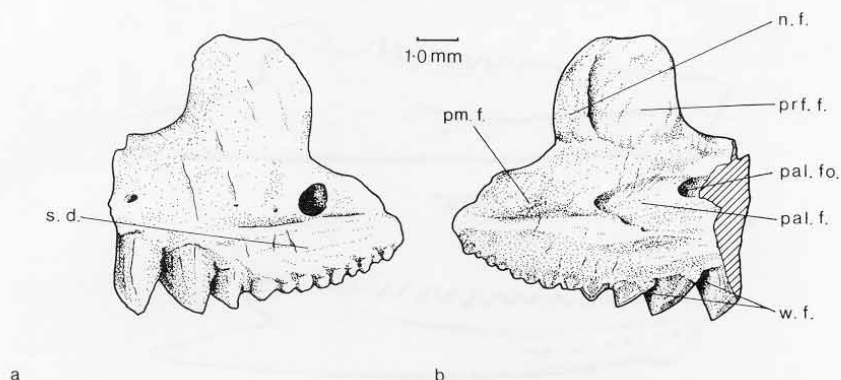
Holotype. AUP no. 11140, right maxilla.

Paratypes. AUP no. 11214, right maxillary fragment; AUP no. 11215, left maxillary fragment.

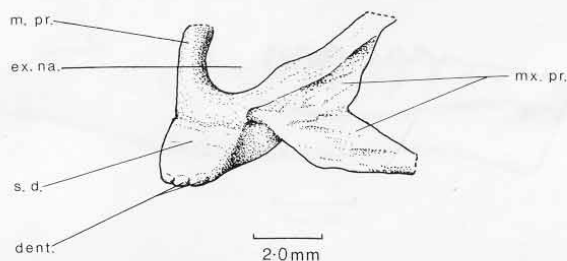
Type locality. Karstic fissures in Dinantian limestones, Cromhall Quarry, south Gloucestershire.

Horizon. Upper Triassic.

Description. Of the four maxillary fragments the most complete is AUP no. 11140, which represents the anterior portion of a right maxilla extending from the border of the external naris and the premaxillary contact to a point ventral to the anterior margin of the orbit (Pl. 20, figs. 7 and 8; text-fig. 5). The anterior border of the bone is concave and presumably marked the posterior boundary of the external naris in the same fashion as that observed in *Planocephalosaurus* (Fraser, 1982). A facet on the lingual surface of the bone immediately above the tooth row (text-fig. 5*b*, pm.f.) is similar to the arrangement in *Sigmala*, and probably received an extensive process from the premaxilla. In *C. hudsoni* the premaxilla possesses a forked maxillary process (text-fig. 6, mx.pr.) and the dorsal prong extends along the posterior boundary of the external naris, thereby excluding the



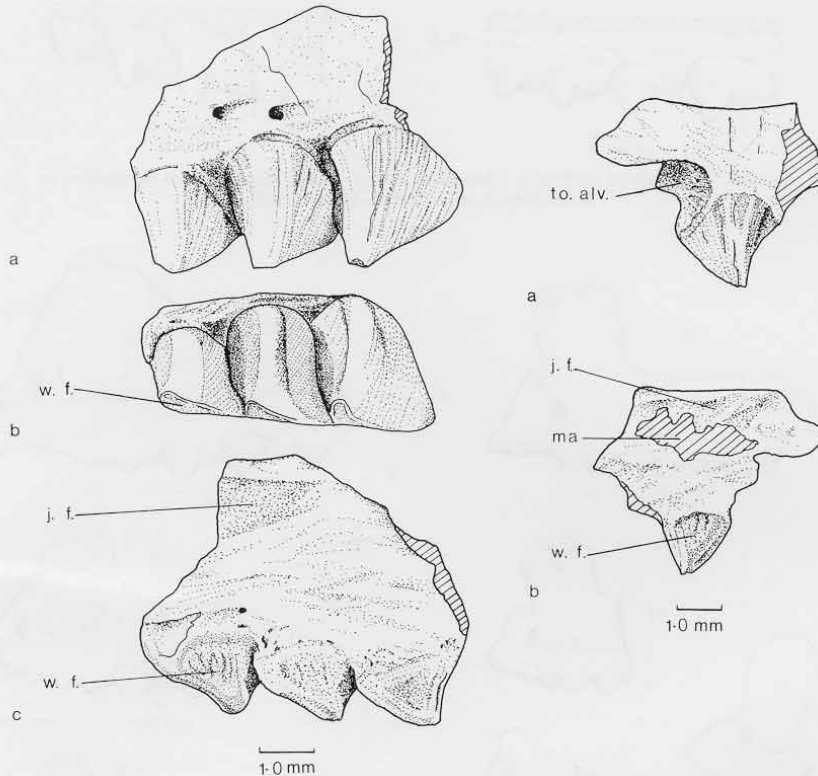
TEXT-FIG. 5. *Pelecymala robustus* gen. et sp. nov. Holotype, right maxilla, AUP no. 11140, in *a*, lateral and *b*, medial views.



TEXT-FIG. 6. *Clevosaurus hudsoni*. Left premaxilla, AUP no. 11143, in lateral view.

maxilla from this opening. This condition did not occur in *Pelecymala*. However, in other respects the articulation facets of the maxilla in *Pelecymala* were similar to other Triassic sphenodontids with overlapping nasal and prefrontal contacts (text-fig. 5*b*, n.f., pr.f.). Thus, in medial aspect the flange of bone separating the external naris from the orbit has an anterodorsal facet for the nasal and a posterodorsal facet for the prefrontal. The prefrontal facet is markedly deeper than that for the nasal which suggests that the prefrontal also overlapped the nasal at this point providing a strong bracing contact between maxilla, nasal, and prefrontal.

The maxillary dentition is typically sphenodontid with an anterior series of ten small teeth that alternate in size. This alternation in tooth size is not as well marked as that normally seen in specimens of *Clevosaurus*, but this series is still assumed to be representative of the hatchling dentition. Whilst the most anterior tooth in AUP no. 11140 has broken off near its base there are no indications of the first two or three teeth being significantly larger than the subsequent ones in the hatchling series. Thus, like *Sigmala* and *C. hudsoni*, there appear to have been no replacement teeth on the maxilla in *Pelecymala*. There are only three additional teeth preserved on AUP no. 11140, but they show quite a remarkable form, displaying a slight tendency towards transverse broadening. This broadening of the additional teeth can be conveniently observed in AUP no. 11215 (text-fig. 7*b*). In both AUP nos. 11140 and 11215 the lingual surfaces of the additional teeth display well-defined wear facets (text-figs. 5*b* and 7*c*, w.f.) with grooves indicative of a precise occlusion with the dentary and no propalinal movement of the jaws.



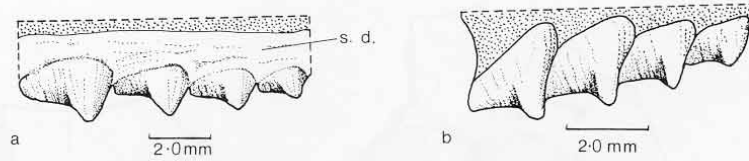
TEXT-FIG. 7 (left). *Pelecymala robustus* gen. et sp. nov. Paratype, left maxillary fragment, AUP no. 11215, in *a*, lateral, *b*, dorsal, and *c*, medial views.

TEXT-FIG. 8 (right). *Pelecymala robustus* gen. et sp. nov. Paratype, right maxillary fragment, AUP no. 11214, in *a*, lateral and *b*, medial views.

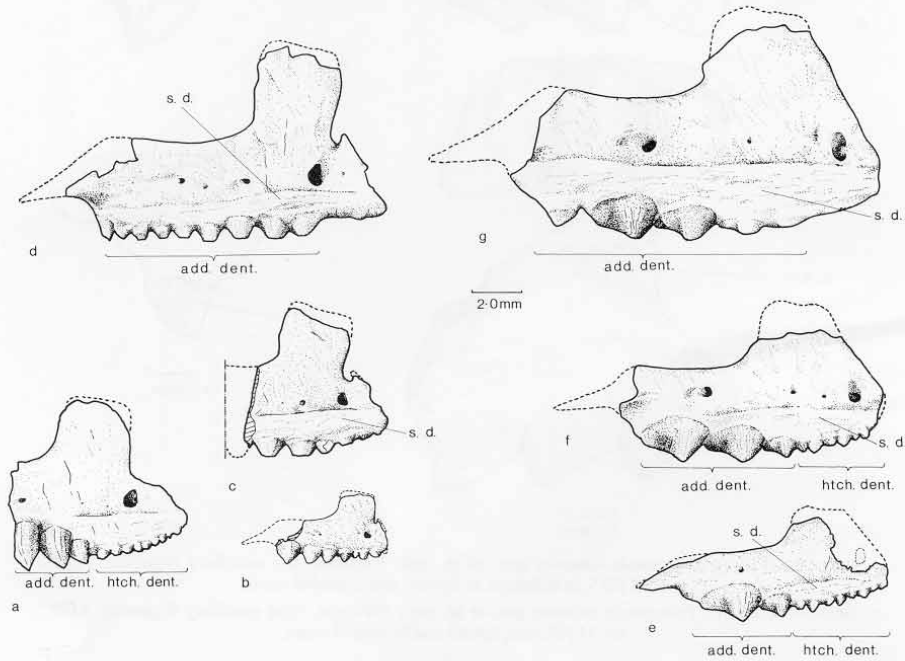
In AUP no. 11215 a short section of the ventral margin of the orbit is preserved, and below this on the medial side is a partially preserved articulation facet, which was in all probability for the jugal. Another fragment, AUP no. 11214, representing a more posterior section of the maxilla, illustrates this facet rather more clearly (text-fig. 8*b*, *j.f.*). This specimen is from a young individual and the full complement of additional teeth was not attained prior to death. Evidence for this is shown by the partly preserved excavation at the posterior end of the fragment where a tooth was not completely ankylosed (text-fig. 8*a*, *to.alv.*).

Although there is a rudimentary development of a posterolingual flange on the additional teeth of *Pelecymala*, this is not as extensive as that seen in the teeth of *Clevosaurus* (text-fig. 9*a*). Apart from the transverse broadening the additional teeth of *Pelecymala* are readily distinguished from *Sigmala* by their relatively larger size coupled with the progressive increase in their height caudad (text-fig. 10*a, b*). There is thus a unique set of dental characteristics serving to distinguish *Pelecymala* from the two other fissure sphenodontids that have a similar range in size.

There is also no question that any of the small fissure sphenodontids, such as *Planocephalosaurus* (Fraser,

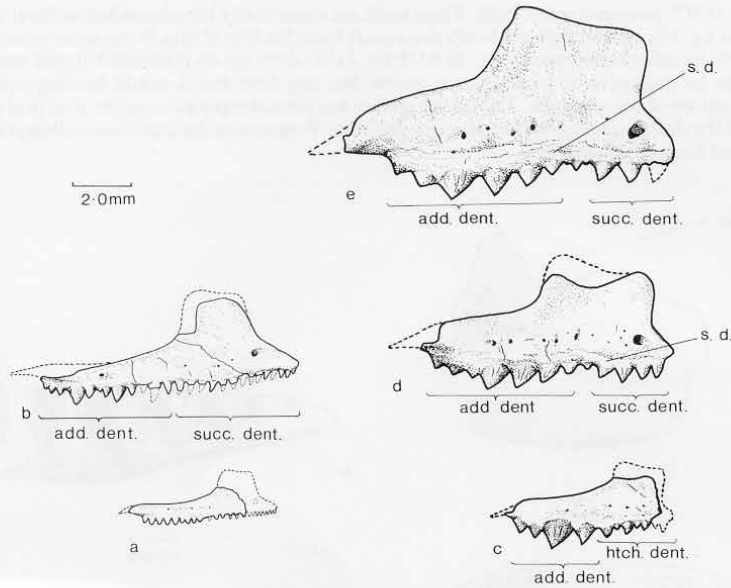


TEXT-FIG. 9. Additional teeth of *a*, *Clevosaurus hudsoni* and *b*, *Homoeosaurus maximiliani* in lateral view. *b*, after Cocude-Michel (1963).



TEXT-FIG. 10. Growth stages of Triassic sphenodontid maxillae. *a*, *Pelecymala robustus* gen. et sp. nov., AUP no. 11140. *b-d*, *Sigmala sigmala* gen. et sp. nov. *b*, AUP no. 11360; *c*, AUP no. 11361; *d*, AUP no. 11083. *e-g*, *Clevosaurus hudsoni*. *e*, AUP no. 11146; *f*, AUP no. 11187, reversed for comparative purposes; *g*, AUP no. 11144.

1982) and Sphenodontid X, represent juvenile stages of larger genera, such as *Pelecymala* and *Sigmala*. Fairly complete ontogenetic series are known for *Planocephalosaurus*, Sphenodontid X, *Sigmala*, and *Clevosaurus*, and the juvenile stages of each form are quite different from each other (text-figs. 10 and 11) and instantly recognizable. Indeed, for the following reasons, it is very likely that all the known material of *Pelecymala* represents immature individuals. First, all the specimens have additional teeth of approximately equal height, yet in the most complete specimen the anterior hatching teeth are still distinct and not worn to the bone. Secondly, as mentioned previously, AUP no. 11214 indicates that ankylosis of the full complement of additional teeth was incomplete, at least in this specimen. Thirdly, the depth of bone between the orbit and the base of the



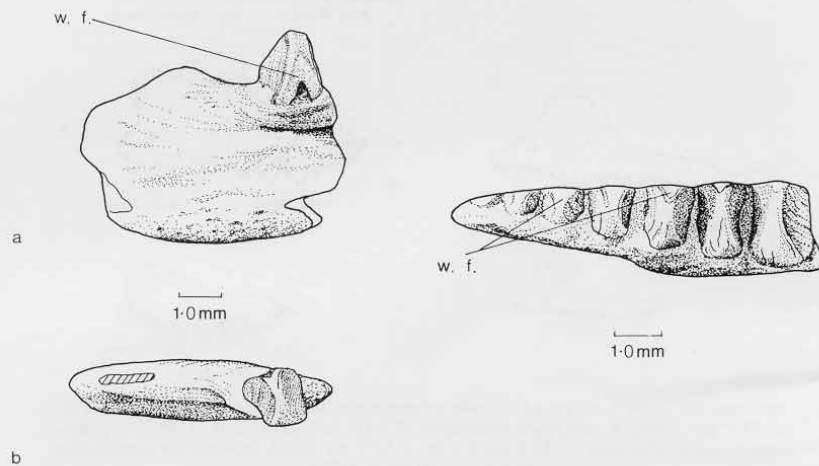
TEXT-FIG. 11. Growth stages of Triassic sphenodontid maxillae. *a, b*, Sphenodontid X. *a*, AUP no. 11196; *b*, composite restoration of AUP nos. 11194 and 11195. *c-e*, *Planoccephalosaurius robinsonae*. *c*, AUP no. 11359; *d*, AUP no. 11061, reversed for comparative purposes; *e*, AUP no. 11093.

teeth is relatively very narrow in proportion to the height of the teeth; this suggests incomplete ossification. Finally, and perhaps of most significance, is the underdevelopment, or complete absence, of secondary dentine in any of the specimens. Secondary dentine is a characteristic feature of all mature individuals of the other fissure sphenodontids (text-figs. 10*b*, *e* and 11).

Dentary fragments possibly attributable to Pelecymala. Because of the paucity of recognizable jaw bones, it has proved almost impossible to indubitably identify elements, other than the maxilla, with the genus *Pelecymala*. In attempts to establish relationships between various problematic elements, very little useful data can be produced by assessing relative abundances of particular bones when the initial sample size is very small. However, within the Cromhall deposits, there are numerous fragments of acrodont jaw bones bearing teeth that are transversely broadened, some of which are likely to represent the new genus *Pelecymala*: in particular there are three dentary fragments and one palatine fragment possessing a very similar dentition.

Two of the dentary fragments are highly polished, but retain sufficient detail to merit description. The smallest of these, AUP no. 11216, bears a single tooth which displays wear facets on both the lingual and labial surfaces and is slightly broadened transversely (text-fig. 12). Posterior to the tooth the bone expands dorsoventrally towards a coronoid process; the full extent of which is impossible to restore owing to fragmentation and polishing. There would also appear to have been a posterior process, but this too has been broken and subject to a great deal of attrition. However, from the nature of the tooth wear facets it is reasonable to assume that the jaw occlusion was similar to that in known sphenodontids and that an enlarged tooth row existed on the palatine. A second specimen,

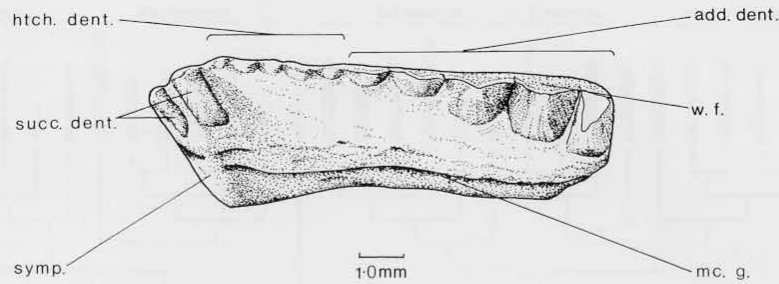
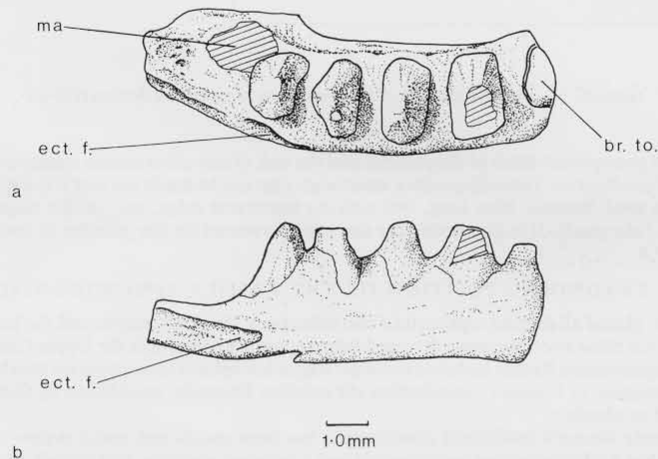
AUP no. 11217, possesses seven teeth. These teeth are transversely broadened but without a central ridge (text-fig. 13); instead they gradually slope away from the lateral edge in the same manner as the *Pelecymala* maxillary additional teeth. In AUP no. 11217 there are no prominent lingual wear facets that might be indicative of palatal tooth action, but any faint facets would be obscured by the polished nature of the specimen. The lateral surface has been sharply cut away in a vertical plane as a result of the shearing action of the maxillary dentition. Posterior to the tooth row nothing further of the element has been preserved.



TEXT-FIG. 12 (left). *Pelecymala?* dentary fragment, AUP no. 11216, in *a*, lateral and *b*, dorsal views.

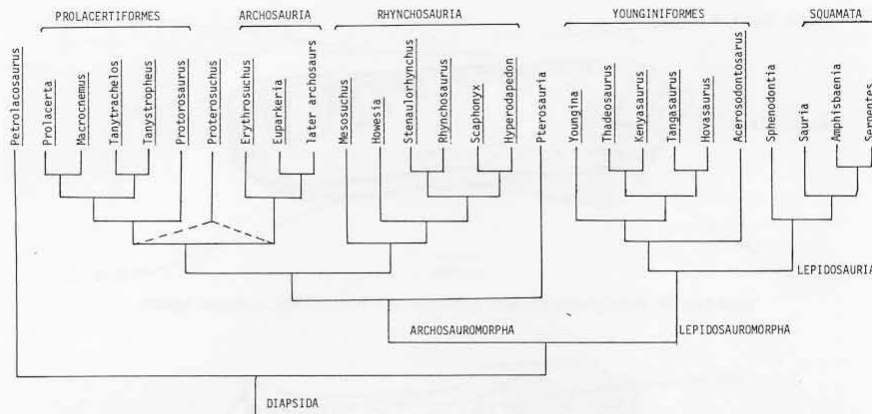
TEXT-FIG. 13 (right). *Pelecymala?* dentary fragment, AUP no. 11217, in dorsal aspect.

The most complete of the three dentary specimens, AUP no. 11192, represents the anterior section of a right element, extending from the symphysis to a point assessed to be mid way along the tooth ramus (Pl. 20, figs. 8 and 9; text-fig. 14). Like *Clevosaurus* and *Sphenodon* (Robinson, 1976), the teeth can be categorized into three distinct series: successional, remanent hatchling, and additional. The first two teeth are transversely broadened, but again without a transverse ridge. The bases of these teeth are set deeper than the succeeding teeth and are therefore considered to represent the only tooth positions at which replacement has occurred: the bone having been eroded and reabsorbed to accommodate the larger replacement teeth. Following the two successional teeth are six or seven smaller teeth which are the remnants of the hatchling dentition. They exhibit alternation in size, but like the *Pelecymala* type specimen, this is not accentuated to the extent of *Clevosaurus*. Posterior to the remanent hatchling series are three or four larger teeth which show a trend to increase in size posteriorly. These represent part of the additional series and they are transversely broadened in an identical fashion to the two successional teeth. Thus the highest point of each tooth is at the lateral edge where the maxillary teeth made their shear contact. The additional teeth also have a small anterolateral flange and possibly a rudimentary posterolateral one. These are best observed in lateral view (Pl. 20, fig. 9). The overall shape of AUP no. 11192 is not dissimilar to the dentary of *C. hudsoni* and both have a prominent jaw symphysis. But whilst apparently of a similar length, AUP no. 11192 is perhaps somewhat deeper than the typical *C. hudsoni* dentary.

TEXT-FIG. 14. *Pelecymala?* dentary specimen, AUP no. 11192, in dorsal aspect.TEXT-FIG. 15. *Pelecymala?* palatine specimen, AUP no. 11218, in *a*, ventral and *b*, lateral views.

These three dentary specimens apparently represent a single species, and, although generally not well preserved, they represent a sphenodontid of similar proportions to, and a dentition comparable with, *Pelecymala*.

A solitary palatine fragment has been identified which bears an enlarged row of transversely broadened teeth (text-fig. 15). Unfortunately the specimen is rather fragmentary and worn, but it bears the remnants of five teeth forming the posterior end of a single tooth row. Posterolaterally the element has a grooved facet for the ectopterygoid (text-fig. 15*b*, ect.f.) which conforms to the typical sphenodontid pattern. Much of the medial and anterior portions of the element are missing, including the maxillary and pterygoid facets. The teeth display lateral wear facets, but their full extent has been obscured by degradational polishing, so that although there is no indication of grooved facets that would infer a precise occlusion with the dentary, such an occlusion with no propalinal movement cannot be discounted.



TEXT-FIG. 16. The classification of the diapsids as proposed by Benton (1984b).

The overall poor preservation of the palatine and the lack of any other similar elements restricts the discussion of its affinities. The only positive statements that can be made are that it is a sphenodontid palatine with teeth broader than long, but with no transverse ridge, and in this respect it is not dissimilar to *Pelecymala*. It is also within the size range expected for the palatine of that genus.

THE TAXONOMIC POSITION OF THE FAMILY SPHENODONTIDAE

Romer (1966) placed all diapsid reptiles into two subclasses: the Archosauria and the Lepidosauria. He believed that these two subclasses diverged from separate ancestors in the Upper Carboniferous. Within the Lepidosauria Romer included the order Rhynchocephalia to incorporate the rhynchosaur and sphenodontids. In Romer's classification the subclass Diapsida, established by Osborn (1903), was regarded as obsolete.

More recently Romer's traditional classification has been questioned and it is now more widely believed that the Archosauria and Lepidosauria had a common ancestry, and that all diapsid reptiles can be derived from a form similar to *Petrolosaurus*—a primitive Carboniferous eosuchian (Reisz 1977, 1981). Evans (1980) subsequently outlined a new classification incorporating the concept of the diapsids as a monophyletic group and reinstated the subclass Diapsida.

In the most recent work on the Diapsida, cladistic analyses have produced classifications (Benton 1984b; Evans 1984; Gauthier, in press) which suggest that two main lineages diverged during Permian times: namely the Archosauromorpha and the Lepidosauromorpha (text-fig. 16). However, further discussion of this concept is beyond the scope of the present paper, suffice to say that the sphenodontids are incorporated into the Lepidosauromorpha, probably as the sister group of the Squamata.

Recent work has also questioned the affinities of the rhynchosaur and sphenodontids. Carroll (1976) showed that the ankle joint of *Noteosuchus*, a primitive rhynchosaur, is in fact similar to that of the thecodont, *Proterosuchus*, and that supposed shared characters of rhynchosaur and sphenodontids are either primitive features of diapsids generally or have been wrongly interpreted. To take an example of the latter, the supposed acrodont teeth of rhynchosaur have now been shown to possess deep roots (Chatterjee 1974; Benton 1983). Following Romer (1956), I initially (Fraser, 1982) recognized the order Rhynchocephalia to consist of the rhynchosaur and sphenodontids, but, since

it is apparent that they share only a very few primitive characters, they should now be separated. The complex concave-convex ankle joint is a feature shared by archosaurs, prolacertiformes, and rhynchosaurs (Thulborn 1980; Brinkman 1981), but not sphenodontids. This, together with other synapomorphies (for list see Benton (1984b)), shows that the rhynchosaurs belong to the Archosauromorpha assemblage.

The name Rhynchocephalia was erected for the genus *Sphenodon* by Günther (1867) and the rhynchosaurs were added later. Now that it is deemed necessary to separate the two groups, the order Rhynchocephalia should strictly be applied to *Sphenodon* and its allies. However, as a result of the past association of the rhynchosaurs with the Rhynchocephalia, Estes (1983) suggested that the sphenodontids should be placed in a new order, the Sphenodontida. Carroll (in press) adds the pleurosaurs to this order.

INTER-RELATIONSHIPS WITHIN THE SPHENODONTIDAE

S. punctatus Gray 1832 is the sole surviving member of a family that flourished in the Triassic and Jurassic. Previously the lack of abundant fossil representatives of the family has led to our knowledge of the Sphenodontidae being rather restricted. Just as the affinities of the family have been questioned, the history of the taxonomy at subfamilial level has been varied. Some classifications, such as that of von Huene (1956), placed particular emphasis on temporal relationships. Thus von Huene recognized three subfamilies of the Sphenodontidae: the Brachyrhinodontinae (Triassic), the Monjurosuchinae (Jurassic), and the Sphenodontinae (Jurassic to Recent). Other recent classifications (Table 2) have been based primarily on structural morphology but each has used slightly different criteria, and are incomplete. To update the classification of the Sphenodontidae, so that all recently described forms are included, I have adopted an eclectic approach and used a combination of the most recent classifications. Because tooth morphology is the only character that can be satisfactorily examined in many of the known sphenodontids, I have relied mostly on Rasmussen and Callison's (1981) (Table 2) classification system.

One of the most primitive sphenodontids is probably *Polysphenodon* from the Trias of Hanover which possesses numerous rows of teeth on the palate, including an ectopterygoid dentition. Jaekel (1911) restored the palate of *Polysphenodon* with no subtemporal fossa between the palatine and the ectopterygoid, but this is apparently incorrect and the typical subtemporal fossa does exist (R. L. Carroll, pers. comm.). Bearing this in mind the palate of *Planocephalosaurus* is not dissimilar to that of *Polysphenodon*, although the ectopterygoid is not dentigerous in the former genus (Fraser 1982). Sphenodontid X also possesses the vast majority of sphenodontid characteristics, yet it too has a number of palatal teeth and in addition part of the marginal dentition has a pleurodont implantation (Whiteside 1983). Even more primitive in this respect is the Jurassic genus *Gephyrosaurus* (Evans 1980, 1981) which possesses a totally pleurodont marginal dentition. Evans (1984) believed *Gephyrosaurus* to be the sister group of the squamates and that the sphenodontids formed the sister group of *Gephyrosaurus* and the squamates together. She considered (Evans 1980, 1981, 1984) that the similarities between *Gephyrosaurus* and the sphenodontids resulted from homoplasy. However, some characters which she cited as evidence for a *Gephyrosaurus*-squamate sister grouping separate from the sphenodontids are to be found in some sphenodontids. These include the fusion of the frontals and parietals and a concavity in the astragalocalcaneum for the reception of a process on the fourth distal tarsal. Whiteside (1983) has offered strong evidence to suggest that *Gephyrosaurus* is a sphenodontid and Fraser and Walkden (1984) also believed this to be the case. *Elachistosuchus*, originally described by Janensch (1949) as a pseudosuchian, was concluded by Walker (1966) to be a primitive sphenodontid with numerous marginal teeth.

It is therefore proposed that *Planocephalosaurus*, Sphenodontid X, *Gephyrosaurus*, and *Elachistosuchus* are placed together with *Polysphenodon* in the subfamily Polysphenodontinae. All are characterized by numerous palatal teeth and a relatively large number of approximately conical marginal teeth which are mostly acrodont. The pleurodont dentition that occurs in some forms probably recalls the occurrence of an intermediate pleurodont stage in the evolution of acrodonty

TABLE 2. Outline Classification of sphenodontids according to various authors.

Order Rhynchocephalia	
Suborder Sphenodontia	
Family Sphenodontidae— <i>Sphenodon</i> , <i>Homoeosaurus</i> , <i>Opisthias</i>	
(amphicoelous vertebrae, acrodont dentition)	
Family Sapeosauridae— <i>Sapeosaurus</i> , <i>Piocormus</i>	
(prococelous vertebrae?, edentulous, enlarged supratemporal?)	
Family Monjurosuchidae— <i>Monjurosuchus</i>	
(3 sacral vertebrae, 3 mandibular tooth rows)	(Hoffstetter 1955)
Family Polysphenodontidae— <i>Polysphenodon</i>	
Family Sphenodontidae	
Subfamily Brachyrhinodontinae— <i>Brachyrhinodon</i>	
Subfamily Sphenodontinae— <i>Sphenodon</i> , <i>Elachistosuchus</i> , <i>Opisthias</i> , <i>Clevosaurus</i>	
Subfamily Homoeosaurinae— <i>Homoeosaurus</i> , <i>Kallimodon</i> , <i>Leptosaurus?</i> (= <i>Kallimodon</i>)	
?Family Palacrodontidae— <i>Palacrodon</i>	(Kuhn 1969)
Family Sphenodontidae	
1. Triassic genera, e.g. <i>Polysphenodon</i>	
2. Broad parietal table, e.g. <i>Homoeosaurus</i>	
3. Narrow parietal table, e.g. <i>Kallimodon</i> , <i>Sapeosaurus</i> , <i>Sphenodon?</i>	(Cocude-Michel 1963)
Family Sphenodontidae	
Subfamily Brachyrhinodontinae, e.g. <i>Brachyrhinodon</i>	
(conical teeth, numerous palatal teeth)	
Subfamily Sphenodontinae, e.g. <i>Sphenodon</i> , <i>Opisthias</i> , ? <i>Clevosaurus?</i>	
(teeth circular or square in frontal section)	
Subfamily Homoeosaurinae, e.g. <i>Homoeosaurus</i> , <i>Kallimodon</i>	
(teeth elongated anteroposteriorly)	
Subfamily Eilenodontinae, e.g. <i>Eilenodon</i> , <i>Toxolophosaurus</i>	
(teeth elongated mediolaterally)	(Rasmussen and Callison 1981)

from a primitive protothecodont condition. As a result of grouping all the primitive forms together the possibility that the Polysphenodontinae is a paraphyletic group still remains, but with the data available it cannot be resolved any further.

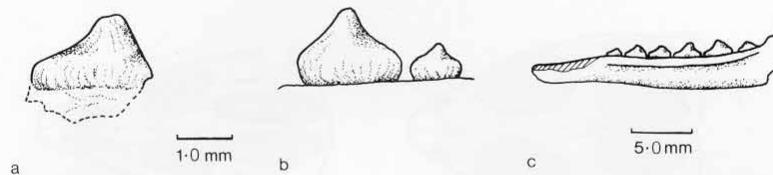
Fragmentary material of an unnamed sphenodontid from the Kirkwood Formation, South Africa (Rich *et al.* 1983), shows some similarities to the Polysphenodontinae. In addition the conical dentary teeth of *Theretairus*, described by Simpson (1926) from the upper Jurassic of Wyoming, also show some affinities to that subfamily. However, there is insufficient material to make a positive assertion with regard to their relationships.

The occurrence of *Brachyrhinodon* fossils as rather poorly preserved casts in the Elgin sandstone makes the material difficult to work with and the palate is undescribed. Consequently the affinities of *Brachyrhinodon* are difficult to assess. Following Kuhn (1969) it is here tentatively retained within the subfamily Brachyrhinodontinae, but with further study may be shown to be a member of the Polysphenodontinae. Walker (1966) thought *Brachyrhinodon* and *Polysphenodon* might be closely related, even possibly congeneric, although he offered little evidence to support this view.

With respect to the problematical Triassic genus, *Palacrodon*, it is very difficult to classify on the basis of a single fragment of lower jaw. Malan (1963) stated that it could be 'an aberrant procolophonid or lizard just as easily as an aberrant rhynchocephalian'. Whilst this is perhaps true, there are certain features of the teeth which are very similar to teeth recovered from the Cromhall fissure

deposits, as well as from deposits at Highcroft Quarry, Gurney Slade, Somerset (text-fig. 17), which I consider to be representative of the genus *Clevosaurus*. Thus, if *Palacrodon* were to be accepted as a sphenodontid it would seem reasonable to assign it to the same subfamily as *Clevosaurus*.

Kuhn (1969) included *Clevosaurus* in the subfamily Sphenodontinae along with *Sphenodon* and *Opisthias*; yet the teeth of the latter two are quite distinct from *Clevosaurus*, lacking the prominent flanges on the maxillary and mandibular additional teeth. Of the Cromhall sphenodontids *Sigmala* approaches most closely the *Sphenodon*/*Opisthias* tooth form, bearing approximately triangular teeth with anterior and posterior keels. At this point the little-known sphenodontids from the Upper Triassic Forest Sandstone of Rhodesia, briefly described by Gow and Raath (1977), will be mentioned. Whilst details of their tooth structure are unavailable, from what is known they are not unlike *Sigmala* and possess a short jaw ramus and no successional teeth. They are therefore tentatively placed in the Sphenodontinae.



TEXT-FIG. 17. *a*, isolated *Clevosaurus* tooth, AUP no. 11354, from Cromhall Quarry. *b*, acrodont tooth, BMNH R.6109, from Highcroft Quarry. *c*, dentary of *Palacrodon* (after Broom 1906).

The teeth of *Clevosaurus* are most like those of *Homoosaurus* (text-fig. 9) and the subfamily Homoeosaurinae is consequently taken to comprise *Clevosaurus*, *Kallimodon*, *Sapheosaurus*, *Homoosaurus* itself, and possibly *Palacrodon*. As Cocude-Michel (1963) pointed out, there may be evidence to suggest a further subdivision on the basis of the width of the parietal table, thereby separating *Kallimodon* and *Sapheosaurus* (text-fig. 18*b, c*) on the one hand from *Homoosaurus* (text-fig. 18*a*) and *Clevosaurus* on the other. Although *Sapheosaurus* is edentulous it has been placed within the Homoeosaurinae on the basis of its cranial similarity to *Kallimodon*.

The last of the five subfamilies is the Eilenodontinae which includes the highly specialized *Toxolophosaurus*, *Eilenodon*, and possibly also *Pelecymala*; the latter showing a tendency to transverse broadening of the additional teeth.

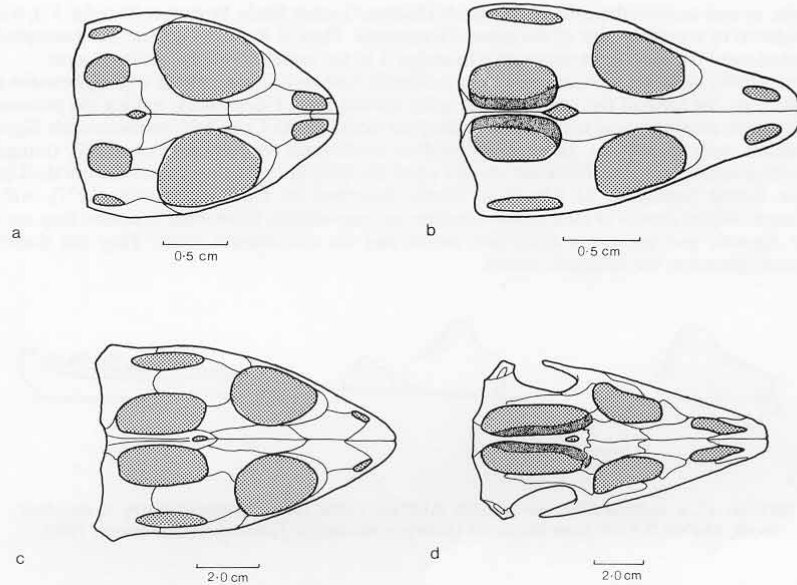
Outline of the proposed classification (text-fig. 19)

Family SPHENODONTIDAE

Diapsida with enlarged palatine tooth row running parallel or almost parallel to the maxillary dentition; prefrontal with ventral process articulating on the dorsal surface of the palatine; lachrymal characteristically absent; posterior process on the dentary; dentition usually acrodont, and hatchling dentition characteristically alternates in size; vertebrae notochordally amphicoelous; pelvic girdle with a large thyroid fenestra; posterior tubercle on the ischium; ent—and ectepicondylar foramina retained on the humerus; fused astragalocalcaneum.

(i) Subfamily POLYSPHENODONTINAE. Upper Triassic–Lower Jurassic. Sphenodontids possessing multiple tooth rows on the palate; marginal teeth approximately conical and usually acrodont although may show various degrees of pleurodonty.

(ii) Subfamily BRACHYRHINODONTINAE? Upper Triassic. The sole genus is *Brachyrhinodon* which bears a characteristically short snout. However other features include the numerous small teeth and broad parietal table which indicate some relationship to the Polysphenodontinae.



TEXT-FIG. 18. Reconstructions in dorsal view of the skulls of *a*, *Homoeosaurus maximiliani*, *b*, *Kallimodon pulchellus*, *c*, *Saphleosaurus thiollierei*, and *d*, *Paleopleurosaurus posidonieni*. *a-c*, after Cocude-Michel (1963); *d*, after Carroll (in press).

(iii) Subfamily SPHENODONTINAE. Upper Triassic?–Recent. Sphenodontids bearing a fully acrodont marginal dentition; usually a single tooth row on the palatine; marginal dentition approximately triangular in side view with small posterior and anterior keels.

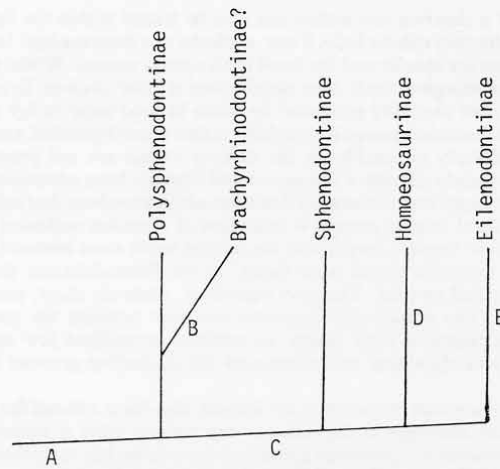
(iv) Subfamily HOMOEOSAURINAE. Upper Triassic–Upper Jurassic. Sphenodontids which characteristically have flanged additional marginal dentition so that the teeth are much longer than they are wide.

(v) Subfamily EILENODONTINAE. Upper Jurassic–Lower Cretaceous. Sphenodontids in which the marginal teeth are transversely broadened; wear facets on mandibular teeth characteristically approach the horizontal on the medial side.

CONCLUSIONS

Within the Sphenodontidae there is a broad evolutionary trend towards a reduction in tooth numbers coupled with a suppression of tooth replacement, not only in the marginal but also in the palatal dentitions. These changes are associated with the development of a powerful shearing bite.

The ancestral forms are likely to have been similar to *Gephyrosaurus* and Sphenodontid X, possessing numerous relatively small teeth with no flanges. The majority, if not all, the marginal teeth were probably pleurodont with some replacement occurring at each tooth position within the life of an individual. Numerous small palatal teeth would be expected in the ancestral form scattered across the vomers, palatines, pterygoids, and possibly the ectopterygoids. The advanced characteristics seen to occur in *Gephyrosaurus* and Sphenodontid X, such as the fused skull roofing elements, would not



TEXT-FIG. 19. The author's classification of the sphenodontids. A, diapsids with an enlarged palatal tooth row running parallel or almost parallel to the maxillary dentition; posterior process on the dentary; posterior tubercle on the ischium. B, much reduced snout region. C, fully acrodont marginal dentition; palatal dentition confined almost entirely to a single row on the palatine. D, additional teeth elongated anteroposteriorly. E, additional teeth elongated mediolaterally.

be expected in the stem sphenodontids, but would have been acquired later, possibly as a specialized offshoot.

The next evolutionary stage might have been similar to *Planocephalosaurus*, but again in all probability without the fusion of the frontals and parietals seen in this genus. In *Planocephalosaurus* all of the marginal dentition is acrodont, but in the adult all the premaxillary, the first four maxillary and the first five or six mandibular teeth are successional, having undergone a single tooth replacement soon after hatching. *Sphenodon punctatus* exhibits a reduction to two or three successional teeth on the maxilla and dentary, whilst in *Sigmala sigmala* and *C. hudsoni* the ultimate stage is reached with the absence of any successional teeth on either the maxillary or dentary. However, at present no sphenodontids are known in which tooth replacement is seen to have been suppressed completely. *C. hudsoni* bears at least one successional tooth on the premaxilla and *Sigmala* might yet be found to possess premaxillary successional teeth. Likewise the Jurassic genera *Homoeosaurus* and *Kallimodon* both possess successional teeth on the premaxilla: the former with two large teeth and the latter with apparently just one very large tooth. Cocude-Michel (1963) considered *Leptosaurus* Fitzinger 1837 to be a juvenile individual of *Kallimodon*. *Leptosaurus* displays two premaxillary teeth which could have been replaced by a single one in the adult. *Sapheosaurus* is a special case in being completely devoid of teeth and thus cannot be considered in the context of tooth replacement.

The number of palatal teeth have been gradually reduced in the evolutionary sequence until there is only the single enlarged tooth row remaining in *Sigmala*, *Homoeosaurus*, *Kallimodon*, and *Sphenodon*.

The development of a shearing jaw action can also be traced within the Sphenodontidae. The Polysphenodontinae generally exhibit little, if any, evidence of a shearing bite. In *Gephyrosaurus* and Sphenodontid X the jaws are slender and the small teeth acutely conical. Whilst there are wear facets on some of the posterior marginal teeth, their distribution is quite random. Evans (1980) concluded that such wear facets were probably produced by tooth to food wear rather than tooth to tooth occlusion. Although *Planocephalosaurus* does exhibit rather more organized wear facets (Fraser and Walkden 1983)—particularly noticeable on the dentary—these are not prominent and in some instances they are very poorly defined. *Clevosaurus* and *Sigmala* have advanced a stage further and display prominent wear facets on the marginal dentition which have been derived from tooth to tooth occlusion. The well-defined scoring pattern is indicative of a precise occlusion between upper and lower jaws. The jaws have become deeper and the palatal tooth rows assumed greater importance since they too exhibit extensive lateral wear facets. In the Eilenodontinae the development of a shearing jaw action reached its peak. The jaws were deep, relatively short, and with stout, closely packed marginal teeth. The mandibular dentition occluded between the maxillary and palatal tooth rows producing extensive wear facets. In addition pro-palatal jaw movements probably increased the efficiency of shredding and eliminated the distinctive grooved facets characterized by *Clevosaurus*.

In the Triassic genera in which the parietals are known, they form a broad flat table separating the supratemporal fenestrae, although in *Clevosaurus* this parietal table is somewhat narrower. The Jurassic genus *Homoeosaurus* also possesses a broad parietal table, but in *Kallimodon*, *Sapheosaurus*, and *Sphenodon* the parietals are much narrower and are raised to form a parietal ridge. This feature has resulted in the enlargement of the supratemporal fenestrae which, together with the ventral extension of the parietals, may have facilitated a greater development of the external jaw adductor musculature. Unfortunately the parietal region is not known in all sphenodontids and it is therefore difficult to assess whether the narrow parietal ridge is associated with the development of a powerful shearing bite.

Pleurosaurs such as *Paleopleurosaurus* (text-fig. 18d) also exhibit a narrow parietal table which, considering other sphenodontid affinities, may be indicative of origins from the same stock as *Kallimodon*, *Sapheosaurus*, and *Sphenodon*. If the structure of the parietal table is taken as a diagnostic derived character, then pleurosaurs, *Sphenodon*, *Kallimodon*, *Sapheosaurus*, and *Piocormus* may represent an advanced taxon separate from the Triassic sphenodontids and *Homoeosaurus*. On the other hand, *Polysphenodon* and *Brachyrhinodon*, which are primitive in most respects, share with *Sphenodon* the lateral bowing of the lower temporal arcade (Carroll, in press). This is almost certainly a derived character relative to other sphenodontids (D. I. Whiteside, pers. comm.). The situation is complicated further by the occurrence of a supratemporal in *Clevosaurus* (Robinson 1973). This element has not been reported in any other sphenodontid, but it is present in *Youginiiformes* and some squamates.

There is thus a mosaic of primitive and derived characters present in the various members of the Sphenodontidae which cannot be readily reconciled together. It is not possible at present to justify the separation of the Triassic sphenodontids and *Homoeosaurus* from *Sphenodon*, *Kallimodon*, and related forms and much more information is needed before the implications of parietal variation can be discussed relative to sphenodontid classification. However, it is hoped that future work on *Clevosaurus*, *Brachyrhinodon*, and *Polysphenodon* may go a long way to clarifying the situation.

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ABBREVIATIONS USED IN TEXT-FIGURES

add.	additional	m.	median
alv.	alveolus	ma.	matrix
ant.	anterior	mc.g.	meckelian groove
art.	articular	mx.	maxilla
br.	broken	n.	nasal
c.	coronoid	pal.	palatine
d.	dentary	pm.	premaxilla
dent.	dentition	post.	posterior
ect.	ectopterygoid	pr.	process
ex.na.	external naris	prf.	prefrontal
f.	facet	s.d.	secondary dentine
fo.	foramen	succ.	successional
frg.	fragmented	symp.	symphysis
htch.	hatchling	to.	tooth
j.	jugal	w.f.	wear facet
l.	lappet		

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