

The Triassic reptiles *Brachyrhinodon* and *Polysphenodon* and the relationships of the sphenodontids

N. C. FRASER*

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ

AND

M. J. BENTON†

Department of Geology, The Queen's University of Belfast, Belfast BT7 1NN

Received May 1988, accepted for publication December 1988

Two Triassic sphenodontid reptiles, *Brachyrhinodon taylori* and *Polysphenodon mulleri*, are redescribed. Both genera are blunt-snouted forms but, as a result of distortion in the original fossils, the degree to which the snouts are shortened has previously been over-elaborated. An elongate temporal region and an interorbital width exceeding that of the parietal table are both derived characters in sphenodontids. *Polysphenodon* is plesiomorphic for both conditions, whereas *Brachyrhinodon* displays the derived states. Therefore, it is assumed that the reduced snout has been independently derived in each genus. The limb elements of *Polysphenodon* are long relative to the size of the skull and are similar in proportions to some species of *Homoeosaurus*. This resemblance is considered to be indicative of similar locomotory requirements rather than close evolutionary relationships. Cladograms showing possible interrelationships within the Sphenodontida are based on twenty-nine character states.

KEY WORDS:—Reptilia – Sphenodontida – *Brachyrhinodon* – *Polysphenodon* – Triassic – skeletal morphology.

CONTENTS

| | |
|--------------------------------------------------------|-----|
| Introduction | 414 |
| Material | 414 |
| <i>Brachyrhinodon</i> | 414 |
| <i>Polysphenodon</i> | 416 |
| Description of <i>Brachyrhinodon taylori</i> | 416 |
| Skull | 417 |
| Mandible | 419 |
| Postcranial skeleton | 420 |
| Body proportions | 422 |

*Present address: Virginia Museum of Natural History, 1001 Douglas Avenue, Martinsville, Virginia 24112, U.S.A.

†Present address: Dept. of Geology, University of Bristol, Queens Road, Bristol, BS8 1RJ.

| | |
|-------------------------------------------------------------------------------|-----|
| Description of <i>Polysphenodon mülleri</i> | 425 |
| Skull | 425 |
| Postcranial skeleton | 429 |
| Taphonomy | 431 |
| Discussion | 432 |
| The relationship of <i>Polysphenodon</i> with <i>Brachyrhinodon</i> | 432 |
| Systematic analyses of sphenodontians | 436 |
| Summary | 442 |
| Acknowledgements | 443 |
| References | 443 |
| Abbreviations used in the figures | 444 |

INTRODUCTION

At the end of the Triassic and during the Jurassic sphenodontids were widespread in the Northern Hemisphere, with representatives known from England, Scotland, Germany, North America and Russia. The recent description of the exceptional sphenodontid material from the Mesozoic fissure deposits of southwest Britain have contributed to our knowledge of the early radiation of this group. The late Triassic genera *Polysphenodon* Jaekel 1911 and *Brachyrhinodon* Huene 1910 have been cited as evidence for regarding the living *Sphenodon* Gray 1872 as a relict that has changed little since the Mesozoic, and yet their descriptions remain incomplete and conflicting.

Brachyrhinodon taylori is known from a number of specimens recovered from the Lossiemouth Sandstone Formation of N.E. Scotland (Huene, 1910b, 1912b; Benton & Walker, 1985). As with the majority of the Elgin fossils, the specimens are preserved as natural moulds with very few remnants of the original bone. They have not been studied since the early 20th century and the descriptions remain incomplete.

Walker (1966) expressed an opinion that *Brachyrhinodon* and *Polysphenodon* might be congeneric, and it is therefore desirable to describe both genera together.

MATERIAL

Repository abbreviations are: BMNH—British Museum (Natural History); MB—Museum für Naturkunde der Humboldt Universität zu Berlin; SM—Royal Museum of Scotland; ELGNM—Elgin Museum.

Brachyrhinodon

There are at least twelve specimens of *Brachyrhinodon* available for study. These are in various states of preservation and completeness, yet the original papers by Huene (1910b, 1912b), based on just three individuals, remain as the only published descriptions of this early sphenodontid.

Collection data are rather vague and consequently it is possible that fragments of some specimens have been separated and are now housed in more than one institution. Nevertheless, a minimum of ten individuals are collectively represented in the material, since non-matching skull remains are present in ten specimens. Although the fossils are mostly preserved as natural moulds, fragments of bones and teeth do remain. Much of the following description is based on synthetic casts, and on occasion it has been found necessary to dissolve

remnants of bone to improve the quality of these casts. Dr A. D. Walker made PVC casts of many of the Elgin Museum specimens using the technique described in Benton & Walker (1981). One of us (NCF) made rubber casts of the specimens housed in the British Museum and Royal Museum of Scotland using Wacker Silicone RTV M531 and catalyst T33.

BMNH R 3559. Type. Small skeleton with well preserved skull. Figured Huene, 1910b. From Lossiemouth West Quarry; collected by William Taylor, purchased from the British Museum 1907.

BMNH R 3364. Part of a skull showing details of the palate in two main blocks plus two smaller pieces. From West Quarry, Lossiemouth; collected by W. Taylor, purchased 1905.

BMNH R 3913. Part of the caudal series of vertebrae from a small animal which might be *Brachyrhinodon*. Figured by Huene, 1912b. From Lossiemouth.

BMNH R 3921. Palate exhibiting tooth rows, a large maxillary tooth and part of the left lower jaw in two small blocks. Figured by Huene (1912a: fig. 21) as *Telerpeton*. From Lossiemouth; collected by W. Taylor, purchased 1911.

BMNH R 3929. Portion of mandible together with part of the palate preserved in three pieces. From Lossiemouth; collected by W. Taylor, purchased 1911.

BMNH R 4776. Part and counterpart blocks containing the majority of one individual. The skull is poorly preserved, but the vertebral column remains uncurled. Figured by Huene, 1912b (pls IV & V). From West Quarry, Lossiemouth; collected by W. Taylor, purchased 1912.

BMNH R 4777. A well preserved, but curled postcranial skeleton with counterpart slab. The skull is not well represented. From Lossiemouth; purchased from W. Taylor, 1915.

BMNH R 4778. Tightly curled skeleton contained in part and counterpart blocks together with two smaller pieces. From Lossiemouth; purchased from W. Taylor, 1915.

RSM 1966.43.6A & B. Two small counterpart blocks enclosing four vertebrae and ribs. Possibly part of one of the other individuals, although it does not obviously fit any of the BMNH or ELGNM specimens. Locality unknown; ex-Stollery collection.

RSM 1966.43.8A & B. Small skull in two counterpart blocks and bearing an almost complete palate. From West Quarry, Lossiemouth; ex-Stollery collection.

ELGNM 1978.569. 1A, B & C. (listed as EM Y24–27 by Benton and Walker (1985)). A reasonable postcranial skeleton, but a poorly preserved skull in two main blocks and two smaller fragments. From ?Lossiemouth; collected by ?W. Taylor.

ELGNM 1978.569. 2A, B & C (EM Y19–21). Part of a reasonably preserved skull together with the cervical vertebrae in three pieces. From ?Lossiemouth; collected by ?W. Taylor.

ELGNM 1978.874. 1A & B. (EM Y30–31). Two fragments bearing a small forelimb. It may belong to ELGNM 1978.569.2, but there is no obvious fit between the preserved blocks. Locality unknown; collected by ?W. Taylor.

ELGNM 1978.874.2–7, 9–12. Small sandstone fragments bearing faint traces of bone impressions. Although 1978.874.5, 6 & 7 are most probably from *Leptopleuron*, others may be fragments from *Brachyrhinodon* and could therefore be parts of individuals already listed.

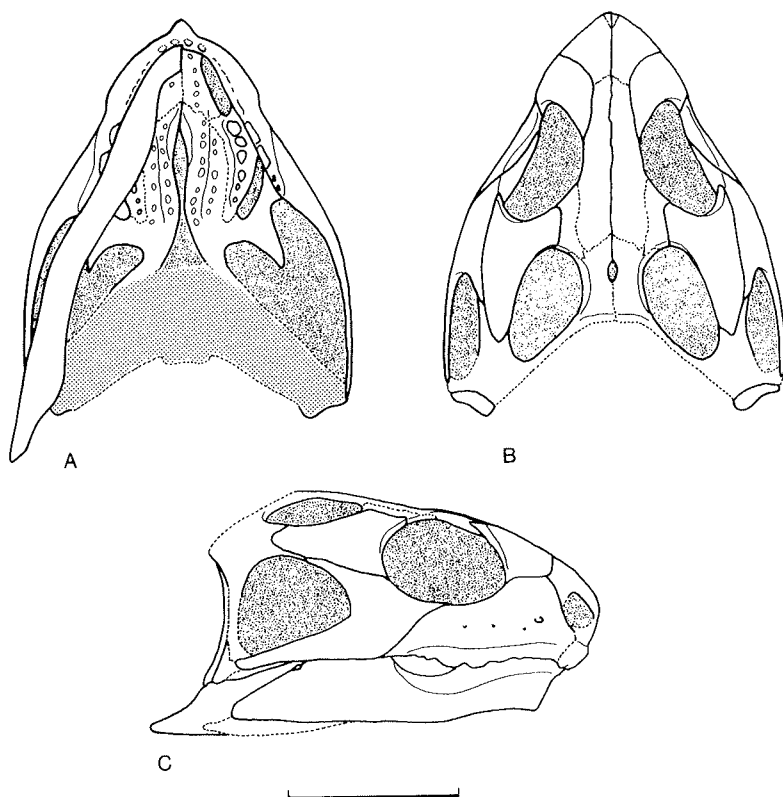


Figure 1. *Brachyrhinodon taylori*. Restoration of the skull in A, ventral, B, dorsal and C, lateral views. Scale bar = 1.0 cm.

Polysphenodon

The only known specimen of *Polysphenodon* was found in a borehole at a depth of 775 m in beds of Middle Keuper (Carnian or Lower Norian) in the vicinity of Hannover (Hoffmannsthal near Fallersleben). The skull and part of the left appendicular skeleton are preserved as natural casts in counterpart blocks. Unfortunately the original material has been missing since the 1930s, but four gutta percha casts and two plaster moulds are still available for study. MB. R. 1032. 2. Cast showing the skull, limbs and vertebral column partially preserved. MB. R. 1032. 6. Counterpart block.

DESCRIPTION OF *BRACHYRHINODON TAYLORI*

The first documentation of vertebrate fossils in the Lossiemouth Sandstone Formation dates back to the 1840s, when scutes of the aetosaur *Stagonolepis* Agassiz 1844 were interpreted as scales of a ganoid fish (Agassiz, 1844). Between then and 1920 a number of other reptilian genera were described (Mantell, 1852; Huxley, 1869, 1877; Newton, 1894; Woodward, 1907; Huene, 1910a, 1912a, 1920), but the end of commercial quarrying operations also effectively halted the recovery of new specimens. Since then the larger reptiles, including *Stagonolepis* (Walker, 1961), *Ornithosuchus* Newton 1893 (Walker, 1964) and *Hyperodapedon* Huxley 1859 (Benton, 1983), have been described in great detail,

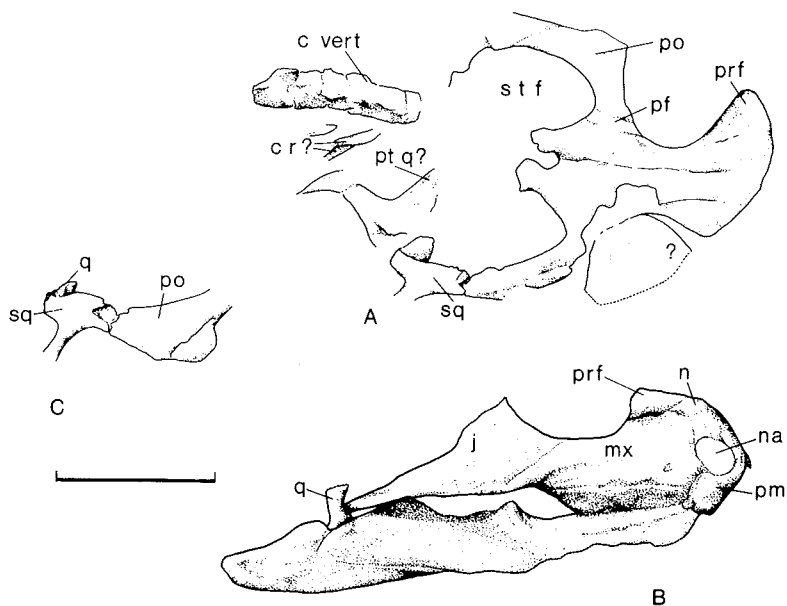


Figure 2. *Brachyrhinodon taylori*. The type, BMNH R 3559. The skull in A, dorsal and B, lateral views. C, Lateral view of the upper temporal arcade. Scale bar = 1.0 cm.

but the smaller genera, including *Brachyrhinodon*, have received much less attention.

Skull

The most complete cranial specimens are BMNH R 3559, R 3364, RSM 1966.43.8 and ELGNM 1978.569.2, and much of the description is based on these.

The skull (Fig. 1) is approximately 25 mm long and, whereas Huene (1910b) emphasized the shortness of the snout, perhaps a more characteristic feature is the extent to which the narial region overrides the premaxillary teeth. This character is particularly well exhibited in the type, BMNH R 3559 (Fig. 2B), and BMNH R 4776 and, whilst *Leptopleuron* Owen 1851 (and procolophonids in general) also exhibit a similar condition, the premaxilla of *Brachyrhinodon* is instantly recognizable by its much smaller teeth. Each premaxilla bears two teeth on the downcurved rostrum which overhangs the tip of the lower jaw. But as in *Sphenodon*, there is a tendency for these teeth to coalesce and form a single structure through the growth of secondary bone. By contrast the teeth of *Leptopleuron* remain as separate entities and only the tooth apices are subject to extensive wear. In other details of the skull and postcranial skeleton *Leptopleuron* and *Brachyrhinodon* are quite distinct.

The laterally placed nares of *Brachyrhinodon* are bounded dorsally by the nasals and anteriorly and ventrally by the premaxilla. The configuration behind the naris is less clear, although BMNH R 3559 appears to show a short extension of the right premaxilla, forming part of the posterior boundary to the naris; but the maxilla also appears to make a contribution to this border.

The maxilla is clearly displayed in BMNH R 3559 (Fig. 2B), and its structure is also known from BMNH R 3364 and ELGNM 1978.569.2. Details of tooth

numbers and morphology are difficult to determine, partly because the particle size of the sandstone approaches the size of the smallest tooth, but in addition all the specimens appear to represent mature individuals in which extensive wear and deposition of secondary bone has tended to obscure the finer details. Anteriorly, there appears to be a short series of small teeth lying posterior to a single more prominent tooth. There are at least two larger teeth representing the additional series, and these are positioned towards the posterior end of the jaw ramus. They are obtusely conical and apparently each bears a posterolingual flange similar to those of *Homoeosaurus* Meyer 1847 and *Clevosaurus* Swinton 1939, but they are not as extensive. BMNH R 3921 indicates that at least two smaller teeth follow the flanged series. Overall the shape of the bone is similar to that of *Planocephalosaurus* (Fraser, 1982), but the depth of bone below the orbit is markedly greater. The element flares laterally away from the tooth row where it overlapped the leading process of the jugal and thereby assumed the bowing of the lower temporal arcade characteristic of other sphenodontids.

The dorsoventral compaction of specimens such as ELGNM 1978.569.2 and BMNH R 3364 has partially obscured the relationships between the nasals and adjacent elements, and in BMNH R 3559 the sutures are indistinct. Huene's short and blunt restoration of the snout appears to have been largely based on BMNH R 3559 as seen in dorsal aspect (Fig. 2A), but it should be noted that there is some damage to this specimen in that area, and the sediment covering the anterior end tends to enhance the illusion when viewed dorsally. Together with the prefrontals and frontals, the nasals combine to produce a somewhat overhanging, diamond-shaped pre-orbital region. The prefrontals largely contribute to the anterior margin of the orbit and there is nothing to suggest the occurrence of a lachrymal.

A suture defines the median articulation of the paired frontals. The articulations with the postfrontals and parietals are not as clearly marked, but faint hairlines suggest that the configuration conformed to the pattern seen in other sphenodontids. The ventral surface of the frontals, as seen in BMNH R 3559, shows a prominent ridge lying on either side of the orbital margin which presumably acted as a strengthening strut. Similar structures have been described in *Clevosaurus* (Fraser, 1988).

The parietals are displayed in BMNH R 3559 (Fig. 2A) and ELGNM 1978.569.2, although in both specimens they are incomplete posteriorly. Together they form a flat parietal table and the intertemporal width is approximately equal to that between the orbits. A prominent pineal foramen is situated almost mid-way along its length.

As seen in BMNH R 3559 (Fig. 2C) and R 3364, the postorbital is a large triangular shaped bone defining the posterior margin of the orbit and separating the two temporal fenestrae by a broad posterior process. It is not entirely clear whether the postorbital formed the entire superior temporal arcade, or if the dorsal process of the jugal met the squamosal in a limited contact below the postorbital and thereby also contributed to this arch. However, BMNH R 3559 and ELGNM 1978.569.2 suggest that the latter situation pertained, and this pattern is usual for sphenodontids.

BMNH R 3559, R 3921 and ELGNM 1978.569.1 clearly show the posterior ramus of the jugal extending to an articulation with the quadratojugal. Although the precise details of the sutures in this region are unclear, there is a

suggestion that a ventral ramus from the squamosal also makes contact with the posterior tip of the jugal. In ventral view, the lateral bowing of the arcade is clearly seen (Fig. 3). In lateral aspect the posterior process of the jugal starts off as a deep bar (Fig. 2B), but tapers away towards the quadratojugal. This contrasts with the condition in *Clevosaurus* and *Planocephalosaurus* where the bar is of a more uniform thickness.

The structure of the suspensorium is not apparent, but the shape and orientation of the squamosal appears to conform to the pattern seen in *Clevosaurus*. The parietal-squamosal articulation is not preserved in any of the specimens and there is nothing to indicate whether a supratemporal was present. The braincase is completely missing.

The palate (Fig. 1A) is particularly well exposed in BMNH R 3364 and RSM 1966.43.8. In addition to the enlarged tooth row on the palatine, which is characteristic of all sphenodontids, there are two tooth rows on each pterygoid and there also appear to be a variable number of small teeth scattered across the vomers. The palatine tooth row consists of six or seven teeth which posteriorly diverge away from the maxillary dentition. Since the pterygoidal tooth rows run parallel to the palatine teeth, progressing posteriorly they converge toward the midline. As a result, the interpterygoid vacuity is constricted at a point near the posterior limit of the pterygoid teeth, but it then widens again towards the basipterygoid articulations.

The internal nares, separated by the broad vomers, are elongate and laterally placed, lying immediately anterior to the palatine tooth rows. As a result of the posterior convergence of the palatine tooth rows towards the midline, the suborbital fenestrae are prominent. Each ectopterygoid, which is edentulous, articulates with the transverse flange of the pterygoid and together they sweep ventrally and laterally to form a deep pterygoid flange.

In cranial aspect the pterygoids, as seen in RSM 1966.43.8B, abut along the midline and continue dorsally for a short distance as a broad medial septum.

Mandible

Two bones can be distinguished in the mandible; namely the dentary and an articular complex. The dentary is a deep element bearing a high coronoid process. As in all sphenodontids the dentary continues as a well-developed process posterior to the coronoid (Fig. 2B). The tooth ramus, when compared with *Sphenodon*, is relatively short, and, although details of tooth numbers are not clear, the last tooth always appears to be the largest of the series. In all specimens in which this tooth is preserved it takes the form of an obtusely conical elongate crown. The anterior end of each dentary has a sharp almost rectangular lower angle and the jaw symphysis is recurved (Fig. 1C) in the same manner as *Sphenodon*. Huene (1910b) correctly identified some degree of compression in the type skull. However he incorrectly compensated for this by eliminating the angled recurvature of the lower jaw (Huene, 1910b: fig. 1b). In fact, crushing would tend to lessen the extent of the angulation, and not produce it. Therefore, if anything, the restoration should show a more exaggerated ventral angle than that seen preserved in the type. A prominent ledge below the tooth ramus marks the extent of secondary bone growth.

A faint notch at the base of the coronoid process in RSM 1966.43.8B may

represent the opening of the mandibular foramen between the dentary and articular complex. In lateral aspect the ventral edge of the mandible of BMNH R 3559 exhibits a shallow excavation where the dentary contacts the articular complex (Fig. 2B). Whether this represents the natural line of the mandible is not clear, but it is possible that at this point a separate angular extended around onto the lateral surface of the lower jaw in a similar fashion to *Clevosaurus*.

There are no indications of sutures on the articular complex and, as in *Planocephalosaurus*, it is assumed that it consists of the fusion of the articular, prearticular, surangular and maybe also the angular. As in other sphenodontids the splenial appears to have been lost and the meckelian canal persists as an open sulcus.

Postcranial skeleton

The postcranial skeleton is well represented in the type, BMNH R 3559 (Fig. 4), R 4776 (Fig. 3), R 4777 and R 4778, and they show that it departs little from the general sphenodontid pattern as displayed by *Clevosaurus*, *Planocephalosaurus* or *Sphenodon*.

As a result of breakages at critical points, the vertebral numbers are not readily apparent, but in BMNH R 3559 there are 24 preserved presacrals and this also appears to be true of BMNH R 4776 and R 4777. Because of the rather poor preservation of the area surrounding the pectoral girdle, the distinction between cervical and dorsal series is not clear but, following *Homoosaurus*, it is assumed that there are seven cervicals and 17 dorsals. The rib of the second of the two sacral vertebrae is bifurcated, but only the anterior ramus articulates with the ilium. The caudal series is incompletely represented in all specimens but

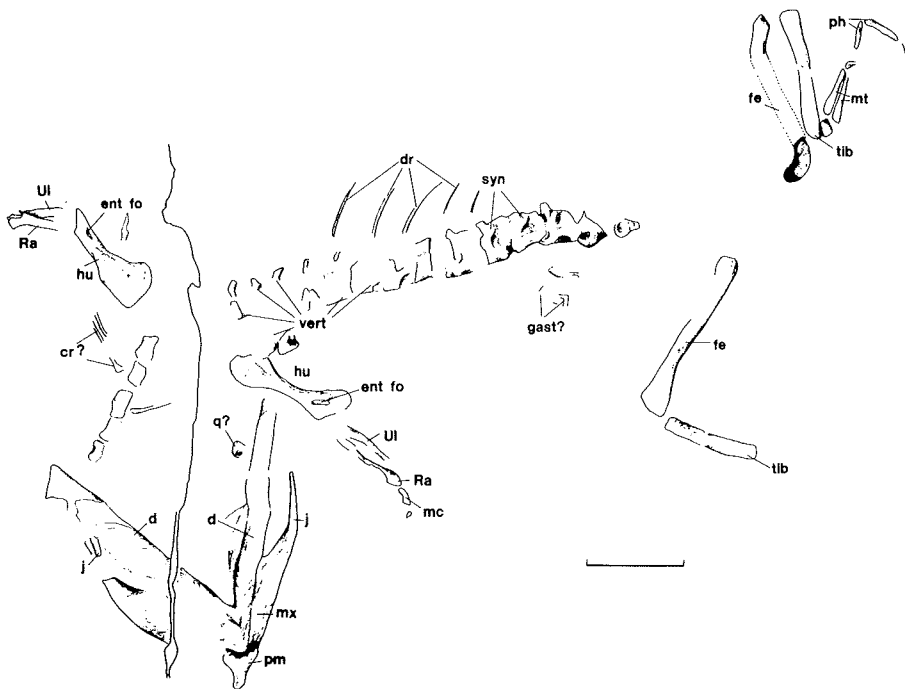


Figure 3. *Brachyrhinodon taylori*. Ventral aspect of BMNH R 4776. Scale bar = 1.0 cm.

there are at least 20 preserved in BMNH R 4776. Where preserved intact, all ribs are holocephalous. At least in one specimen, BMNH R 4777, there is evidence for the preservation of gastralia.

It would appear that the cervical vertebrae are somewhat shorter, and the neural spines taller than those of the dorsal series. In the latter the neural spines are generally rather low, and this conforms with the pattern described for other sphenodontids. In ventral view the centra are hourglass-shaped.

Intercentra may be present between some of the dorsal and cervical vertebrae, although this is by no means unequivocal. Certainly they are absent in some positions, but whether they were always missing or whether they were lost during burial cannot be determined. However, there is no uniform pattern to their apparent distribution, and it is assumed that they were present throughout.

None of the specimens clearly displays the intervertebral articulations, and consequently the presence or absence of a zygosphene/zygantrum cannot be commented upon.

Details of both limb girdles are poor. The structure of the pectoral girdle cannot be determined from the very small fragments that are preserved. Little more exists of the pelvis: part of the left ilium is preserved in the type, and this indicates that there was a posterodorsally directed blade with separate medial articulations for the two sacral vertebrae. The configuration of the ischium and pubis is unknown.

Both humeri of BMNH R 4776 are almost completely exposed in ventral aspect (Fig. 3). A prominent ventrally directed deltopectoral crest allowed for the attachment of the deltoid and pectoralis musculature. The extensive entepicondyle is pierced by a large foramen. The slender shafts of the right radius and ulna are also preserved in this specimen, but no details of the articulation surfaces are available for study. Similarly, details of the carpus and manus are sketchy, but there is no evidence to suggest that they differed greatly from *Sphenodon*.

Despite the availability of three reasonable postcranial skeletons (BMNH R 3559, R 4776, R 4778), details of the hindlimb are again rather poor.

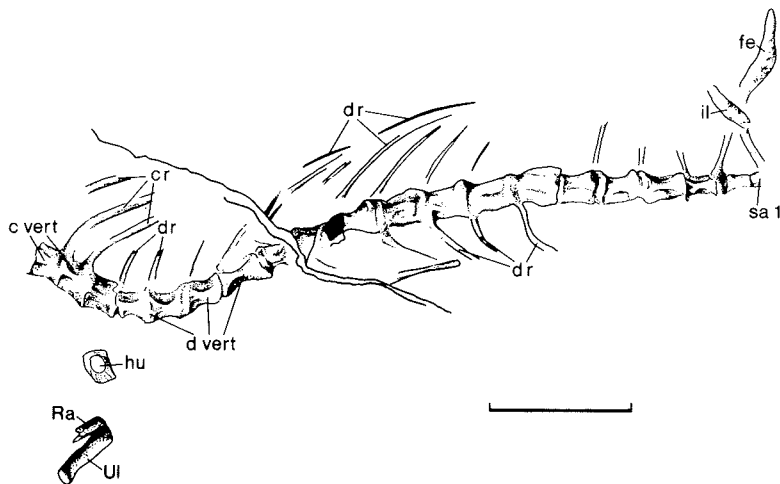


Figure 4. *Brachyrhinodon taylori*. The type, BMNH R 3559, showing the major part of the vertebral column in ventral view. Scale bar = 1.0 cm.

Frequently the bones are disrupted by the joints between sandstone blocks. It is apparent that the limb is slender, and BMNH R 3559 and R 4776 (Fig. 3) show that the sigmoid flexure of the femur is retained. Although much of the tarsus and part of the pes are preserved in R 4778, details are obscured by crushing of many of the bone fragments.

Body proportions

Wherever possible, measurements of the skull, axial skeleton and limb elements were made for each specimen (Table 1). Because of the difficulties in determining the absolute ends of the long bones, the measurements are only approximate. Nevertheless, estimates of various skeletal ratios have been made (Table 2) and it is immediately apparent that inconsistencies occur in the lengths of the long bones and vertebral column when compared with the skulls. Although the skulls of BMNH R 3559 and R 4776 are of similar dimensions, the postcranial skeleton of the type, BMNH R 3559, is noticeably smaller than R 4776. Whether this could be indicative of sexual dimorphism or possibly the occurrence of more than one species of *Brachyrhinodon* is unclear. However, in R 4776 there appears to have been a certain amount of disruption of the vertebral column in the vicinity of the pectoral girdle. Certainly the cervical vertebrae are not in natural association with the basicranium (Fig. 3), and they may have been displaced anteriorly. If this assumption is correct then the length of the presacral vertebral column may have been overestimated. Similarly, errors may be present in the estimated dimensions of R 3559. Although in this instance the entire presacral column is clearly exposed and can be readily measured, the

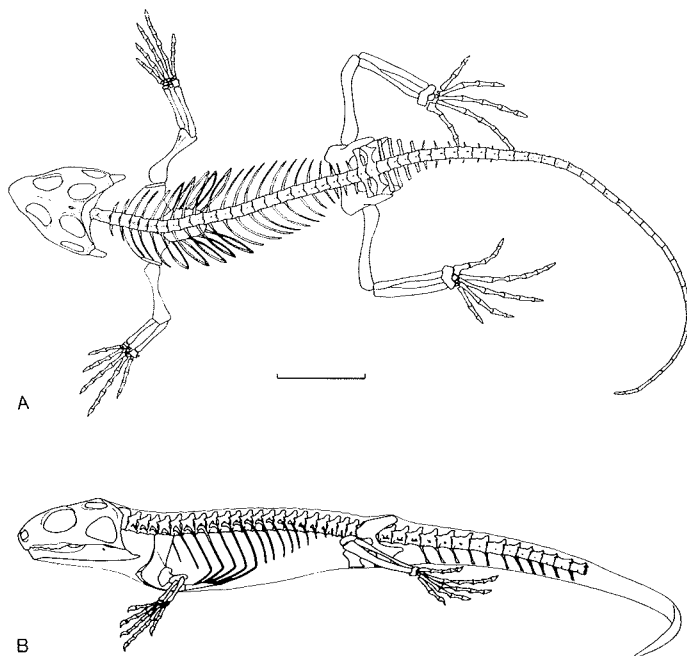


Figure 5. Restoration of *Brachyrhinodon taylori* in A, dorsal and B, lateral views. Scale bar represents 2.0 cm. Where unknown the reconstruction is based on the general sphenodontid body plan as typified by *Sphenodon* and *Clevoosaurus*.

TABLE 1. Key measurements (mm) of selected sphenodontids

| | Length between premaxillae and quadrate condyles | Length between premaxillae and the retroarticular processes | Width across the quadrate condyles | Length of the orbits | Interorbital width | Length of the superior temporal fenestrae (S.T.F.) | Width of the parietal table | Length of the humerus | Length of the radius | Length of the ulna excluding the olecranon process | Length of the femur | Length of the tibia | Length of the presacral vertebral column (PSC) | Length of the trunk between the pectoral and pelvic girdles | Source reference |
|----------------------------------------|--------------------------------------------------|-------------------------------------------------------------|------------------------------------|----------------------|--------------------|----------------------------------------------------|-----------------------------|-----------------------|----------------------|----------------------------------------------------|---------------------|---------------------|------------------------------------------------|-------------------------------------------------------------|------------------------|
| <i>Gephyrosaurus briedensis</i> | 30 | 34 | 18 | 9.6 | 4.6 | 6.1 | 4.2 | 16 | 12 | 12 | 22.5 | 18.5 | 68 | 54 | Evans, 1980; 1981 |
| <i>(Planocephalosaurus robinsonae)</i> | 19 | 21 | 14 | 6.7 | 2.5 | 3.5 | 3.5 | 11 | 9 | 9 | 16 | 13 | 68 | 54 | Fraser & Walkden, 1984 |
| <i>(Diphyodontosaurus avonis)</i> | 15 | 17 | 12.5 | 6.1 | 1.6 | 3.5 | 3.0 | | | | | | | | Whiteside, 1986 |
| <i>Polysphenodon mulleri</i> | 25 | | | 9.0 | 2.7 | 4.2 | 5.4 | 17 | 12 | 14 | 21.5 | 20 | 63 | | Cocude-Michel, 1967 |
| <i>Homoeosaurus maximiliani</i> | 21 | | | | | | | 13 | 13 | 14 | 16 | 14 | 55 | | Fabre, 1973 |
| <i>Homoeosaurus solnhofensis</i> | | | | 9.0 | | 4.0 | | 21 | 14 | | 26 | 19 | 80 | | Fabre, 1973 |
| <i>Homoeosaurus aff. solnhofensis</i> | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> | 21 | | | | | | | 12 | 8 | | | 12 | | | |
| ELGNM 1978.569.1 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> | 20 | 23 | 18 | | | | | | | | | | | | |
| ELGNM 1978.569.2 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> | 24 | 27 | | 8.0 | 3.5 | 7.5 | 3.5 | | | | 17 | | 74 | 49 | |
| BMNH R3559 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> | | | 18 | | | | | | | | | | | | |
| BMNH R3364 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> | 24 | 27 | 20 | | | | | 13 | 10 | | 18 | 15 | 81 | 56 | |
| BMNH R4776 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> | | | | | | | | 9 | 7 | | 13 | 11.5 | 56 | 44 | |
| BMNH R4777 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> | | 24 | | | | | | | | | 15 | 10 | | | |
| BMNH R4778 | | | | | | | | | | | | | | | |
| <i>Cleosaurus hudsoni</i> | 32 | 35 | | | | | | 20 | 18 | 18 | 28 | 23 | 98 | 74 | |
| UMZC T1271 | | | | | | | | | | | | | | | |
| <i>(Cleosaurus hudsoni)</i> | 36 | 40 | 24 | 11.0 | 4.8 | 11.0 | 4.0 | 20 | 20 | 18.5 | 29 | 22 | 100 | 75 | Fraser, 1988 |
| <i>Kallinodon pucheltius</i> | 35 | | 24 | 9.0 | 3.0 | 13.5 | 1.1 | 14.5 | 10.5 | | 21 | 16 | 86 | | Fabre, 1973 |
| <i>Picocormus laticeps</i> | 57 | 61 | 43 | 22.0 | 7.0 | 20.0 | 1.0 | 30 | 13 | 13 | 24 | 19 | 111 | 120 | Cocude-Michel, 1967 |
| <i>Sphenodon punctatus</i> | | | | | | | | | 19 | 19 | 39 | 27 | 160 | | |

The figures for the specimens in parentheses are based on disassociated elements and represent average estimates of the dimensions

TABLE 2. Main body proportions of selected sphenodontids

| | Length S.T.F. | | Forelimb Hindlimb | Hindlimb Trunk | Humerus | | Radius | | Ulna | | Femur | | Tibia | | Source reference |
|------------------------------------------------|---------------|--|----------------------|-------------------|---------|------|--------|------|------|------|-------|------|-------|------|------------------------|
| | Orbit | | | | PSVC | PSVC | PSVC | PSVC | PSVC | PSVC | PSVC | PSVC | PSVC | PSVC | |
| <i>Gephyrosaurus bridensis</i> | 0.63 | | 0.68 | | | | | | | | | | | | Evans, 1980; 1981 |
| <i>Planocephalosaurus robinsonianae</i> | 0.52 | | 0.69 | 0.54 | 0.16 | | | | 0.13 | | 0.23 | | 0.19 | | Fraser & Walkden, 1984 |
| <i>Diphydonosaurus avonis</i> | 0.57 | | | | | | | | | | | | | | Whiteside, 1986 |
| <i>Polysphenodon mulleri</i> | 0.46 | | | | | | | | | | | | | | MB R 1032 2/6 |
| <i>Homoeosaurus maximiliani</i> | | | 0.75 | | 0.27 | 0.21 | | | 0.22 | | 0.34 | | 0.31 | | Cocude-Michel, 1967 |
| <i>Homoeosaurus maximiliani</i> | | | 0.77 | | 0.26 | 0.21 | | | | | 0.32 | | 0.29 | | Fabre, 1973 |
| <i>Homoeosaurus solnhofensis</i> | | | 0.73 | | 0.24 | 0.16 | | | | | 0.29 | | 0.26 | | Fabre, 1973 |
| <i>Homoeosaurus aff. solnhofensis</i> | 0.44 | | 0.77 | | 0.26 | 0.18 | | | | | 0.33 | | 0.24 | | Fabre, 1973 |
| <i>Brachyrhinodon taylori</i> ELGNN 1978.569.1 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> ELGNN 1978.569.2 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> BMNH R3559 | 0.93 | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> BMNH R3564 | | | 0.70 | 0.59 | 0.16 | 0.12 | | | | | 0.22 | | 0.19 | | |
| <i>Brachyrhinodon taylori</i> BMNH R4776 | | | 0.65 | 0.56 | 0.16 | 0.13 | | | | | 0.23 | | 0.20 | | |
| <i>Brachyrhinodon taylori</i> BMNH R4777 | | | | | | | | | | | | | | | |
| <i>Brachyrhinodon taylori</i> BMNH R4778 | | | | | | | | | | | | | | | |
| <i>Clevoosaurus hudsoni</i> UMZC T1271 | | | 0.75 | 0.70 | 0.20 | | | | 0.19 | | 0.29 | | 0.23 | | |
| <i>Clevoosaurus hudsoni</i> | 1.0 | | 0.77 | 0.68 | 0.21 | | | | 0.18 | | 0.29 | | 0.22 | | Fraser, 1988 |
| <i>Kallimodon pulchellus</i> | | | 0.67 | | 0.16 | 0.12 | | | | | 0.24 | | 0.19 | | Fabre, 1973 |
| <i>Procomurus laticeps</i> | 1.5 | | 0.74 | 0.51 | 0.17 | 0.12 | | | 0.12 | | 0.21 | | 0.17 | | Cocude-Michel, 1967 |
| <i>Sphenodon punctatus</i> | 0.91 | | 0.74 | 0.55 | 0.18 | 0.12 | | | 0.12 | | 0.24 | | 0.17 | | UMZC R2572 |

limb bones are not particularly well represented. In addition the left femur may have suffered some damage so that the shaft is telescoped in the region of the acetabulum. This would have the effect of artificially lowering the apparent length of the bone. In view of these facts a conservative approach is adopted for the present, and only one species is assumed to occur in the Lossiemouth Sandstone Formation. Likewise, there is no firm basis for the recognition of sexual dimorphism. For the purposes of comparison with other sphenodontids the proportions of the postcranial skeleton are based on R 4777, since it is reasonably certain that in this specimen the vertebral column is intact and there is no obvious indication of compression in the long bones.

DESCRIPTION OF *POLYSPHENODON MÜLLERI*

The specimen was originally described by Jaekel (1911), and Huene (1929) added further information. Most recently, Carroll (1985) extended the descriptions and corrected certain misinterpretations made by the former authors, although without providing a detailed account of the specimen. In the light of the comparison made between *Brachyrhinodon* and *Polysphenodon* by Walker (1966), a re-examination of *Polysphenodon* is called for and, at the same time, certain discrepancies in the early descriptions can be fully rectified.

Skull

An initial inspection of the casts (Fig. 6) suggests that *Polysphenodon* possessed a very short snout. However, a closer examination shows that the nasals and premaxillae have been displaced downwards and backwards with respect to the palate and the sides of the skull. The effect of this has been to displace the maxillae laterally (and possibly also the prefrontals to some extent), which thereby gives the effect of a broad, blunt snout. The full extent of this compression is not clear, but the transverse line separating the nasals from the frontals and prefrontals is considered most unlikely to represent a natural suture. In all other sphenodontids an irregular suture separates these elements, with the frontals extending much further forwards towards the midline. In *Polysphenodon* it seems likely that the crushing of the snout has resulted in the nasals partially overriding the frontals so that the transverse crack is most satisfactorily explained as post mortem damage. In this case the natural articulation between the nasals and frontals is not exposed. If this is correct, then, like *Brachyrhinodon*, the shortness of the snout has been exaggerated. Nevertheless, the nasal rostrum was probably still relatively shorter in these two genera than in other known sphenodontids.

Carroll (1985) estimated the length of the nearly complete skull to be 25 mm. It is not clear what points of reference Carroll used, nor whether this was a restoration which took into account the degree of distortion in the specimen. Measuring from the anterior tip of the nasal, as exposed in dorsal view, to the back of the quadrate gives a minimum measurement of 20 mm. But the telescoping of the snout makes this an artificially low reading and 25 mm is probably a more realistic value (Fig. 7). This adjustment takes into account the fact that the walls of the skull have been deflected posteriorly, and that as a result the quadrate may lie somewhat further back from its original position.

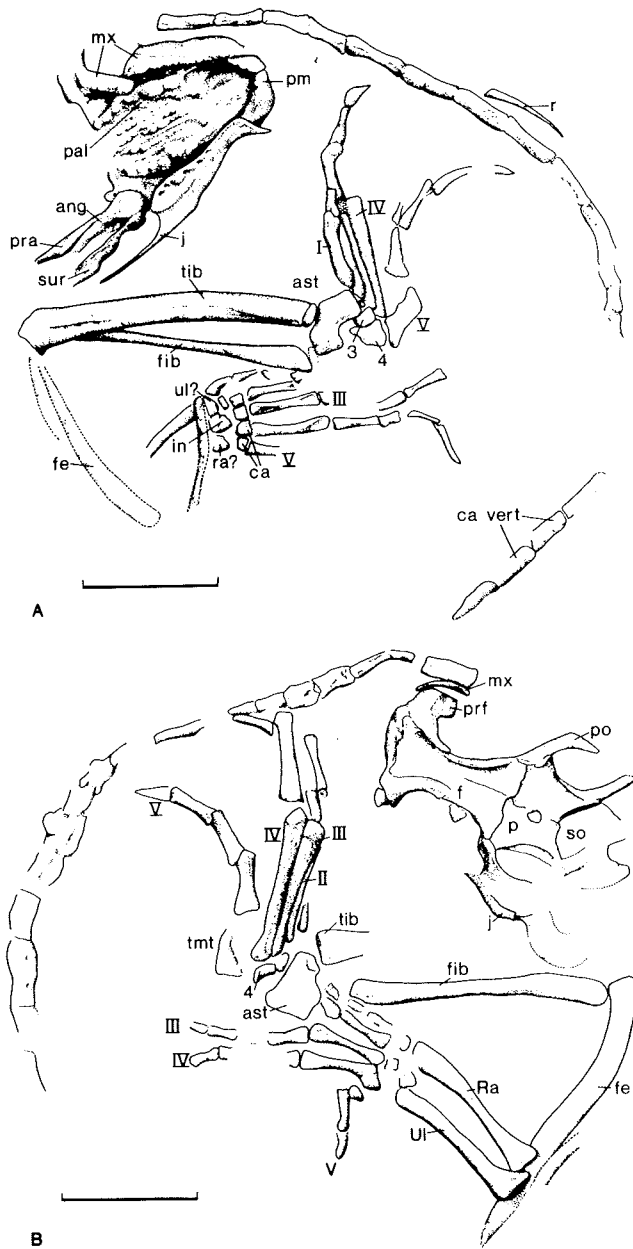


Figure 6. *Polysphenodon milleri*. The sole specimen, MB R 1032. A, 'ventral' and B, 'dorsal' blocks. Scale bar = 1.0 cm.

The paired premaxillae are only exposed in ventral view and consequently it is difficult to determine whether the internarial bar projects anteriorly in the same fashion as *Brachyrhinodon*. However, even in the limited material available it would be expected that there might be some indication of this feature if it were present. When seen anteriorly, a small notch on the right side may mark the dorsal margin of the external naris, but this is not clearly defined. Jaekel (1911)

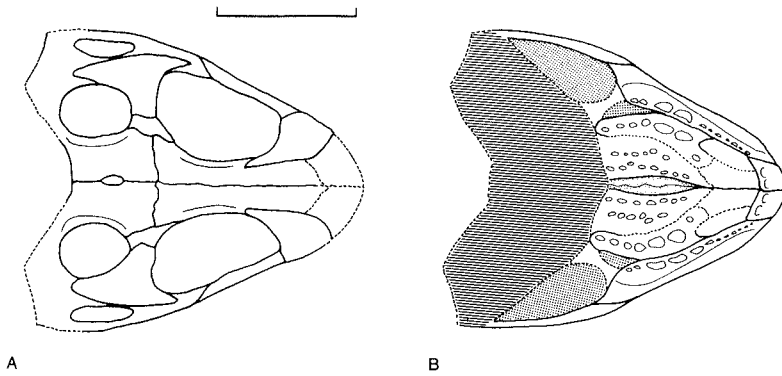


Figure 7. *Polysphenodon mülleri*. Reconstruction of the skull in A, dorsal and B, ventral aspects. Scale bar = 1.0 cm.

showed two teeth on each premaxilla. On the other hand Huene (1929) suggested that there is but a single cutting edge on each element, a view shared by Carroll (1985), who compares it with the condition in *Sphenodon*. Details of the dentition are difficult to perceive, but on the right side there appear to be two distinct teeth, whereas on the left side such a distinction is less apparent. There is no indication of the broad posterior process which in *Clevosaurus* extended beyond the external nares and under the leading edge of the maxilla.

Both maxillae are preserved in ventral aspect, and on the dorsal slab the ascending process of the right element is exposed as a splinter of bone which has been displaced laterally and lies adjacent to one of the caudal vertebrae. The dorsal margin of this process is similar to that of *Planocephalosaurus* and indicates a broad separation between the external naris and the orbit. Carroll (1985) states that the maxilla of *Polysphenodon* is approximately the same length as that of *Planocephalosaurus*, although, at 11.0 mm, it is, if anything, slightly larger in *Polysphenodon*. There are at least eight teeth on the left side and possibly as many as ten, but the anterior teeth are rather worn and indistinct. The posterior half of the jaw ramus bears a series of four teeth which increase in size posteriorly. They are elongated anteroposteriorly so that there is at least a suggestion of a posterolingual flange on each tooth. Behind these four teeth are two smaller ones which have reverted to the obtusely conical shape of the anterior teeth. A clear lateral ridge marks the growth of secondary bone, and adjacent to the posteriormost three teeth the maxilla bulges laterally, thereby marking the bowing of the lower temporal arcade. The individual teeth are not clearly defined on the right side, and the posterior end of the ramus is broken and lies at an angle to the normal axis of the marginal dentition.

Paired frontals are separated by a faint suture which is most readily apparent posteriorly. Together the elements form a fairly narrow interorbital shelf. The dorsal margin of each orbit is marked by a pronounced bony ridge.

The prefrontals are large bones forming the entire anterior margins of the orbits. They appear to have been rotated slightly about the anterior edge of the frontals so that the broad strut running ventrally and medial to the anterior edge of each orbit is somewhat displaced laterally; this is particularly pronounced on the right side. Presumably this ventral strut articulated with the palatine in the manner seen in all other sphenodontids.

An almost transverse but somewhat irregular suture separates the parietals from the frontals. This contrasts with the general condition in sphenodontids where the suture is concave from front to back or even V-shaped. The parietals are paired elements forming a flat table which is broader than the interorbital width. A moderate sized pineal foramen is situated at the centre of the parietal table.

Sutures defining the limits of the postfrontal bones are not readily apparent. The lateral walls of the skull have been deflected backwards, and in addition the left side has also been somewhat compressed medially. As a result the dorsal processes of the postorbitals may have obscured the postfrontals in dorsal aspect. Whether, in addition to facets for the frontals, there were separate facets on the parietals for the postfrontals is not clear. Certainly, as Carroll (1985) remarks, there does not appear to be a long anterior ramus of the postfrontal. However, a short groove in the posterolateral edge of the left frontal probably received a reduced anterior process. By contrast the postfrontal of *Sphenodon*, *Planocephalosaurus*, *Clevosaurus*, etc. has an extensive contact with the frontal immediately above the orbit.

Only the postfrontal process remains of the right postorbital, the remainder being lost in the cast of the matrix, but on the left side the element is almost complete. It is a large triangular bone with a broad posterior process extending towards the squamosal and separating the temporal fenestrae. Along its ventral edge the dorsal process of the jugal contacted the squamosal, but further details of these elements are lost in the matrix.

The suspensorium is preserved on the left side, but the boundaries between the squamosal, quadrate, and quadratojugal are not at all clear. The quadrate seems to form a deep pillar, but the pterygoid wing and surface details are not preserved. There is no indication of a quadratojugal foramen, but this region does appear to have been partially covered with matrix. The squamosal has been displaced and as a result the upper temporal fenestra has been distorted. The posterolateral process of the parietal, which would normally be expected to contact the squamosal behind the upper temporal fenestra, has been damaged on the left side and the natural configuration of the neighbouring elements has been altered. On the right side the suspensorium is not displayed at all, although the lateral wall of the temporal region has not been compressed as much as the left side, and the small, oval upper temporal opening probably reflects the original orientation.

Behind the parietals, Carroll (1985) described the presence of a broad supraoccipital, and tentatively identified part of the left exoccipital. However, this region is very poorly defined and there are various fractures and protruberances which may simply represent missing fragments and breaks in the original sediment rather than structural details of the skull. Although there are traces of a flat plate-like supraoccipital, the surface detail is very indistinct and the supposed exoccipital could just as equally represent the anterior part of the axial skeleton or even nothing more than small depressions in the matrix.

In the ventral aspect the skull is only preserved from the premaxillae as far back as the pterygoid flanges. There are no details of the braincase nor of the jaw articulations. Part of the left mandible is preserved, but many of the sutures are indistinct.

The maxillae and premaxillae appear to have been pushed down with respect to the palate, and this displacement together with the compression of the snout

has probably resulted in the fragmentation of the vomers. Certainly there is no clear indication of the vomers and, contrary to Carroll's (1985) description, the full extent of the internal nares is unknown. The 'row of teeth' he describes bordering the medial margin of the naris is probably little more than small fragments of the broken palate. Only the posterior border of the right choana is preserved where it emarginates the palatine.

The palatines are typical in possessing a single row of enlarged teeth running the length of the lateral margin. The right palatine bears seven teeth in this row; the first two of which are larger than the rest. The posterior teeth diverge away from the maxillary tooth ramus and there would appear to be an extensive suborbital fenestra between the palatine and the maxilla which was presumably bounded on the posterior side by the ectopterygoid. Just anterior and slightly medial to the palatine tooth row is an isolated tooth. This is presumably also borne on the palatine, and, as in *Clevosaurus*, aligned with the more lateral of the pterygoid tooth rows. Probably as a result of uncleared bone and matrix the teeth on the right palatine are less distinct, but there do appear to have been at least six teeth in the lateral row.

Although Carroll (1985) states that there is nothing of the palate visible behind the palatines, a transverse ridge on each side lies in the expected positions of the pterygoid flanges. Jaekel (1911) reconstructed the palate without a suborbital fenestra and with a large ectopterygoid bearing a single tooth row. The casts suggest that that was incorrect and it seems likely that Jaekel mistakenly identified the displaced posterior fragment of the left maxilla with the ectopterygoid: this fragment lies in approximately the same position as Jaekel's reconstructed ectopterygoid.

In addition to the palatine tooth rows described above there are the remains of four additional palatal tooth rows. Although there are no obvious sutures, it is assumed that the configuration adheres to the pattern described in *Clevosaurus* (Fraser, 1988) and that there are two tooth rows on each pterygoid. In general these pterygoid teeth are smaller than those borne on the palatines.

The long posterior process of the jugal is preserved on the left side and bows laterally away from the maxillary tooth row. Although its length suggests that the lower temporal arcade was complete, the evidence for this is equivocal. Part of the lower jaw overlies much of the adductor fossa on the left side. The dentary is entirely absent, but exposed in lateral view are parts of the surangular, angular and prearticular. The extent of the retroarticular process is unknown.

Postcranial skeleton

The precise numbers and structure of the preserved vertebrae are not clear. Carroll (1985) believed that approximately 21 caudal vertebrae could be seen and that no autotomic septa were preserved. However, the casts only show 16 obvious vertebrae. It is possible that two or three autotomic septa are preserved and that Carroll may have mistaken these for the divisions between separate centra. Very little structural detail can be perceived, but two vertebrae lying adjacent to the tarsal bones reveal outlines of a low neural spine and zygapophyses.

Huene considered the narrow, tapering bone fragment, which lies outside the vertebral column on the ventral slab, to be an isolated dorsal rib. It is certainly too long to be a distal haemapophysis.

Much of the left fore and hindlimbs are preserved, but some of the detail is poor. In the dorsal block Huene (1929) identified a fragment of bone lying along the shaft of the femur as the remnant of the left humerus. It is certainly in the expected position, lying adjacent to the radius and ulna, but the outline is not at all clear and it may just represent a small channel in the original matrix. The ulna and radius are completely exposed on the ventral block. Both bones are long and narrow, with the radius slightly the longer of the two. There is no evidence of an ossified olecranon.

The bones of the carpus are rather better exposed in the ventral block, although details are sketchy (Fig. 7A). There appear to be traces of distal carpals 2-5, and possibly the ulnare, radiale, the intermedium and two centrales. A curved ridge overlying the proximal end of the carpus may be part of a rib shaft or merely indicate a crack running through the block. All the metacarpals are at least partially exposed as well as many of the phalanges, including the ungual phalanx of the third digit. Although the phalangeal formula cannot be accurately counted, the preserved elements do not conflict with the numbers found in *Sphenodon*.

Part of the left femur is exposed, but the full dimensions of the element are unknown. The sigmoidal flexure of the slender shaft is still apparent. Both the tibia and fibula are well represented. The fibula is a long slender element with a compressed shaft which exhibits a slight kink towards the proximal end. The tibia, as seen in the ventral slab, is the stouter of the two epipodials and bows away from the fibula (Fig. 7A). The proximal end is broader than the distal articulation surface and its posterior surface bears a prominent ridge on which the puboischiotibialis musculature was inserted. Although neither end has a pronounced expansion, the distal head is the least prominent, although there does appear to be an incompletely ossified epiphysis articulating with the astragalus. The presence of this discrete epiphysis, together with the absence of an olecranon on the ulna, led Carroll (1985) to the opinion that the specimen was not quite fully mature, although he did note the high degree of ossification of the tarsals which does suggest a fairly mature individual. In animals with determinate growth the epiphyses of adults may not be completely distinct from the shaft once the epiphyseal plates have ossified (Haines, 1969). However, in many mature lepidosaurians the epiphyses remain separate (Carroll, 1977). In view of this variability in the ossification of the epiphyses, the high degree of ossification of the *Polysphenodon* tarsals may be of more significance in determining the maturity of the specimen.

The tarsus is particularly well exposed in the ventral block, which shows the astragalus and distal tarsals four and three in palmar view (Fig. 7A). There are separate facets on the astragalus for the tibia and fibula. A recess in the distal margin of the astragalus received distal tarsal four which itself bears a medial notch for distal tarsal three. Although Carroll (1985) believed the calcaneum was not represented, the element on the dorsal block which he labelled as the astragalus very probably consists of a fused astragalocalcaneum. Certainly the entire facet for the fibula is displayed, together with a short lateral expansion of the bone and this would almost certainly consist largely of the calcaneum. But, in contrast to *Homoiosaurus*, there is no suture demarcating the calcaneum from the astragalus. Presumably only a small part of the astragalus contributes to the bone in dorsal view.

All five metatarsals are present, but only III and IV can be clearly seen. Carroll noted that the fourth is longer than the third and suggested that the reverse holds true for *Sphenodon*. However, an examination of dried skeletons of *Sphenodon* suggests that the feature is variable: normally there is little difference in their length, and IV may sometimes be the longer of the two. Metatarsal V is broader and shorter than the others and it clearly shares the 'hooked' configuration observed in other sphenodontids and lizards (Robinson, 1975). A number of phalanges are also preserved, but, although digit V is complete, the phalangeal formula cannot be accurately estimated. Nevertheless, as in the manus, there is nothing to suggest a radical departure from *Sphenodon*.

TAPHONOMY

The specimens of *Brachyrhinodon taylori* were nearly all collected by William Taylor (BMNH, ELGNM?) from quarries at Lossiemouth. Lossiemouth West Quarry (NJ 231 704) is specified for some, while others are labelled merely 'Lossiemouth' (see Materials, above). The latter may refer to the larger Lossiemouth East Quarry (NJ 236 707). These quarries were the most prolific source of the associated reptilian fauna (Benton & Walker, 1985). There is no evidence for finds of *Brachyrhinodon* from the Spynie or Findrassie Quarries nearby, which yielded other reptilian taxa.

The Lossiemouth Sandstone Formation is a white or buff-coloured, medium-grained sandstone. The sands are well sorted and they display large-scale cross-bedding. They have been interpreted as aeolian deposits laid down over fluvial units beneath (Peacock *et al.*, 1968). The reptiles seem to have been found predominantly at the foot of the dunes which suggests that they may have occupied a well-vegetated lowland which was overwhelmed by the advancing dune field. The Lossiemouth Sandstone Formation contains no fossils of plants or invertebrates, and it represents an environment that would seem to have been inimical to vertebrate life.

The skeletons of *Brachyrhinodon* are generally preserved fairly completely. Where major elements are absent, such as the skull, or the posterior half of the skeleton, this is the result of collection failure rather than failure of preservation. The skeletons are generally in articulation, with little sign of post mortem disturbance by scavengers, or by sedimentary movements.

As with the other reptiles of the Lossiemouth Sandstone Formation the skeletons of *Brachyrhinodon taylori* are mostly flattened and spread out on a single bedding plane (Benton & Walker, 1985). However, in the type (BMNH R 3559) the right forelimb is flexed and orientated vertically. The vertebral column may be straight (BMNH R 4776), flexed (BMNH R 3559, R 4777) or very tightly curled in a C-shape as in BMNH R 4778. In BMNH R 4776 the skull has been slightly displaced, but in other specimens the skull lies in natural articulation with the backbone. The limbs may be extended to the sides or folded in a 'frog-like' arrangement. There are no records of isolated elements from *Brachyrhinodon*, and the animals appear to have been rapidly covered by sand with a minimum of pre-fossilization damage.

Much less is known of the taphonomy of *Polysphenodon* since the single specimen is now lost, and because it came from a borehole. Remarkably, the borehole coincided with a large part of the skull and skeleton, but much of the

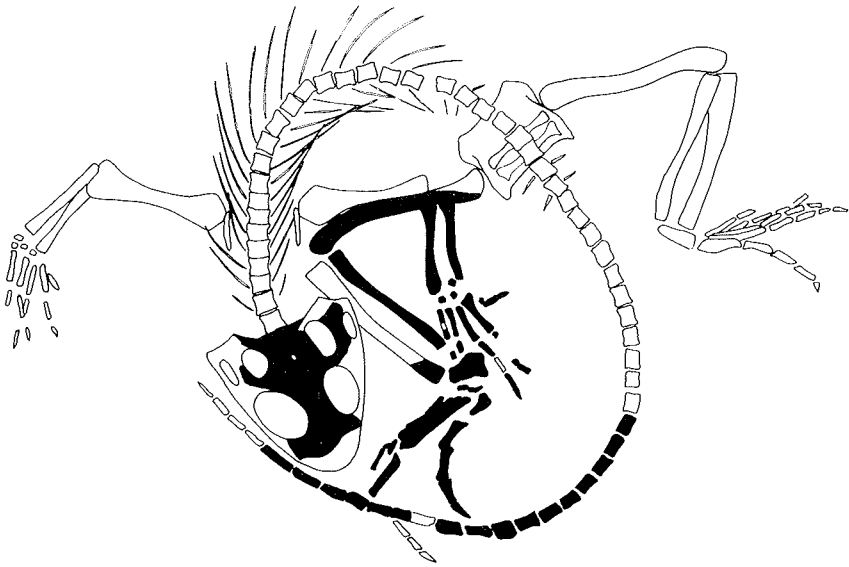


Figure 8. Suggested configuration for the single specimen of *Polysphenodon mülleri* as originally preserved. The shaded elements are those which were actually recovered from the borehole.

right hand side of the body lay outside, and is now lost. The entire remains are regarded as a single specimen in which the vertebral column has curled tightly around the skull and the left side of the appendicular skeleton (Fig. 8). It is assumed that originally the curvature of the backbone was considerable, far greater than in the majority of the preserved *Brachyrhinodon* specimens, and even a little more than BMNH R 4778, with the tip of the tail lying beside the head. As with *Brachyrhinodon*, the skeleton seems to have been preserved nearly fully articulated (even the carpals and tarsals are only slightly spread out) and with no signs of post mortem disturbance. Although it is remotely possible that there is more than one individual in the block, this seems highly unlikely.

DISCUSSION

The relationship of Polysphenodon with Brachyrhinodon

The similarity between the palates of *Polysphenodon* and *Brachyrhinodon* has largely gone unrecognized because a description of the palate of *Brachyrhinodon* has not been previously published. Huene (1956) even went so far as to place *Polysphenodon* in the Rhynchosauridae even although he had originally recognized its true status as a sphenodontid. Despite such inconsistencies, *Polysphenodon* and *Brachyrhinodon* are normally grouped together as primitive blunt-snouted sphenodontids, and Walker (1966) even suggested that they might be congeneric.

It has been shown above that a certain amount of compaction of the snout has occurred in the single specimen of *Polysphenodon*. This has also occurred to a similar extent in the *Brachyrhinodon* fossils, and yet it has not been adequately corrected for in previous restorations. Nevertheless, the nasal rostrum is shorter in both these genera than in *Clevosaurus*, *Homoosaurus*, and *Sphenodon*, and very

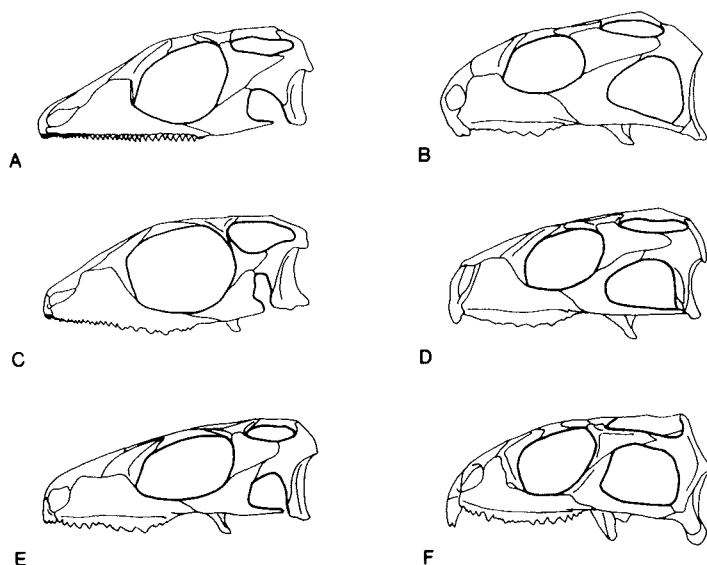


Figure 9. Lateral views of the skulls of A, *Gephyrosaurus*, B, *Brachyrhinodon*, C, *Diphydontosaurus*, D, *Clevosaurus*, E, *Planocephalosaurus* and F, *Sphenodon*. (A, after Evans, 1980; C, after Whiteside, 1986; D, after Fraser, 1988; E, after Fraser, 1982).

much shorter than *Gephyrosaurus* and *Kallimodon* Cocude-Michel 1963 (Figs 9, 10). *Polysphenodon* and *Brachyrhinodon* both possess a single enlarged tooth row on the palatine and double pterygoidal tooth rows (a condition shared by *Clevosaurus* (Fraser, 1988)), and in terms of overall size the two genera are very similar with skulls between 20 and 25 mm in length.

On the other hand, a number of differences can be listed. Firstly, the superior temporal fenestrae of *Polysphenodon* appear to be markedly shorter than the orbits. Although the temporal openings have been distorted to some extent, this has probably affected the length much less than the width. Likewise, because the postorbital bar has been deflected backwards, the length of the orbit as it is preserved is probably greater than in its natural orientation. But, even allowing for these distortions, the length of the upper temporal fenestrae in *Polysphenodon* is approximately 46% that of the orbits, whereas in *Brachyrhinodon* the length of the temporal fenestrae and the orbits is approximately equal (Table 2). Thus it is apparent that the temporal region of *Polysphenodon* is relatively shorter than in *Brachyrhinodon*, and therefore more like *Planocephalosaurus* and *Homoeosaurus*.

The parietal table in both *Polysphenodon* and *Brachyrhinodon* is broad and flat, and therefore similar to *Homoeosaurus* and *Planocephalosaurus*. In common with *Homoeosaurus* and *Planocephalosaurus*, the width of the parietal table in *Polysphenodon* is greater than the interorbital distance (interorbital distance approximately 60% of the parietal table width), whereas in *Brachyrhinodon* the interorbital width is equal to that of the parietal table (Table 2).

The short temporal region, together with a parietal table that is broader than the interorbital distance, suggests that *Polysphenodon* may be more closely related to *Homoeosaurus* than it is to *Brachyrhinodon*. In this respect *Brachyrhinodon* shows a greater affinity to *Clevosaurus*; and both possess relatively long temporal arcades. However, although the widths of the parietal table and interorbital bar are

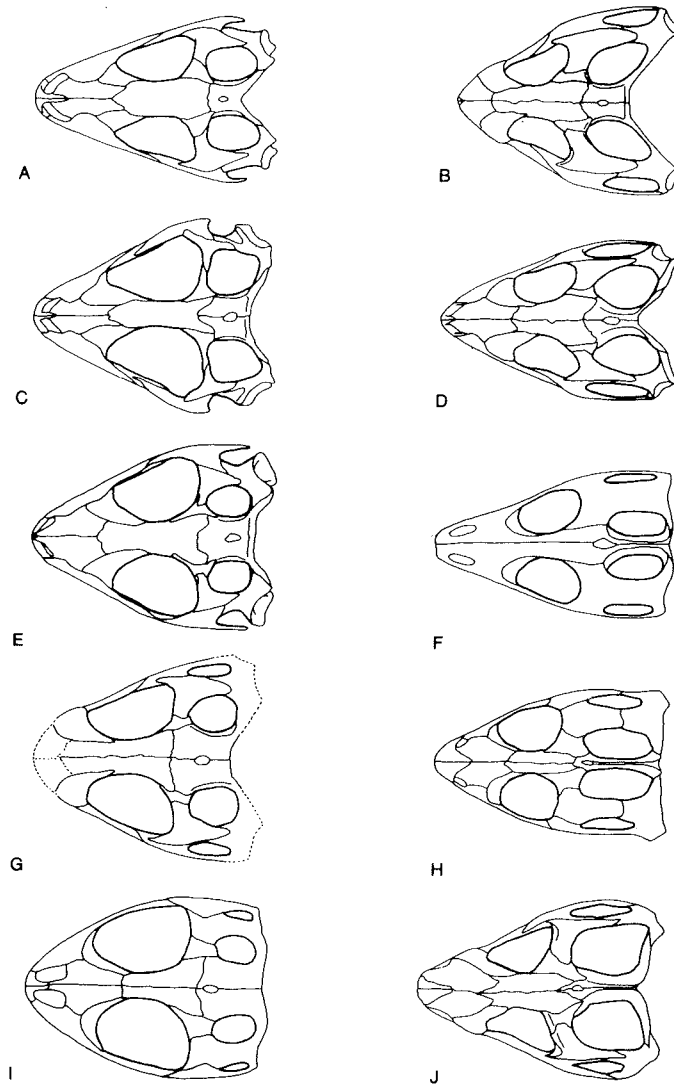


Figure 10. Dorsal views of the skulls of A, *Gephyrosaurus*, B, *Brachyrhinodon*, C, *Diphydontosaurus*, D, *Clevosaurus*, E, *Planocephalosaurus* F, *Kallinodon*, G, *Polysphenodon*, H, *Sapheosaurus* Meyer 1850, I, *Homoeosaurus*, J, *Sphenodon*. (A, after Evans, 1980; C, after Whiteside, 1986; D, after Fraser, 1988; E, after Fraser, 1982; F,H & I, after Cocude-Michel, 1963).

approximately equal in both *Brachyrhinodon* and *Clevosaurus*, only *Clevosaurus* possesses the derived condition of a median ridge, albeit rather broad. *Brachyrhinodon* retains the plesiomorphic condition of a flat parietal table.

As Carroll (1985) demonstrates, the lengths of the limb bones relative to the skull are assumed to be greater in *Polysphenodon* than in *Sphenodon* and many other fossil forms (including *Brachyrhinodon*). This discrepancy is particularly noticeable in the tibia, and only *Homoeosaurus maximiliani* Meyer 1847 has relatively larger epipodials (Cocude-Michel, 1967). Perhaps a more valuable estimate of the relative lengths of the limb bones can be obtained by comparing the ratios of the

various limb elements to the length of the presacral vertebral column. Unfortunately, these cannot be estimated for *Polysphenodon*, but it is interesting to note that where such measurements have been possible only *Clevosaurus* approaches the high values calculated for the various species of *Homoeosaurus* (Table 2). *Polysphenodon* might also be expected to have shown similar high ratios. It is assumed that any such similarities between *Polysphenodon*, *Homoeosaurus*, and *Clevosaurus* more accurately reflect locomotory functions than close evolutionary relationships.

Carroll (1985) stated that, in contrast to the basically primitive pattern of the skull roof, *Polysphenodon* was advanced in having a laterally bowed lower temporal arcade, a condition which he asserted was also present in *Sphenodon*, but not in the Upper Jurassic sphenodontids, nor *Palaeopleurosaurus* Carroll 1985. Whiteside (1986) has suggested that the lower temporal arcade has been secondarily derived in sphenodontids and that the lateral temporal bowing was acquired in conjunction with the greater development of the adductor musculature, which in turn is associated with the development of the sphenodontid shearing jaw action. The bowing of the temporal arcade in mammal-like reptiles similarly provides space for the superficial layers of the jaw adductor musculature (Barghusen, 1968).

Contrary to Carroll's assertion, the lower temporal bar is bowed in the Upper Jurassic sphenodontids, but this character would appear to have been overlooked as a result of the consistent crushing of the skull in these Jurassic fossils. A specimen of *Kallimodon pulchellus* Zittel 1887 in the collections of the Universitätsinstitut für Paläontologie und historische Geologie, Munich illustrates this point. In this specimen, No. 1887/IV/I, the temporal arcade has been compacted against the sides of the lower jaw as seen in ventral aspect, but it is also apparent that there has been a certain amount of dorsoventral compression. This has resulted in the lower temporal arcade rotating downwards and medially about its long axis, thereby giving the impression of a straight temporal arcade continuous with the tooth ramus. However, the preservation of a raised flange lying posterolateral to the last three maxillary teeth indicates that the jugal did indeed bow away from the tooth ramus in this specimen. Although the specimen of *Palaeopleurosaurus* has not been examined at first hand, the plates in Carroll (1985) indicate a similar arrangement to No. 1887/IV/I, a condition which can be seen to be repeated in many other sphenodontid specimens recovered from the Solnhofen limestones. *Brachyrhinodon* is no exception, and it too exhibits the bowed lower temporal arcade.

Amongst sphenodontids a reduction in the length of the snout is unique to *Brachyrhinodon* and *Polysphenodon*. However, *Polysphenodon* apparently lacks the anterior projection of the internarial bar that characterizes the snout of *Brachyrhinodon*. The notable differences in other cranial characters clearly show *Brachyrhinodon* and *Polysphenodon* to be quite distinct genera and a short snout should probably be viewed as a convergence.

The teeth of *Polysphenodon* and *Brachyrhinodon* as shown by Jaekel (1911) and Huene (1929), are small and obtusely conical, and consequently little different from those of *Planocephalosaurus*. However, the present study suggests that at least small posterolingual flanges may have been present on some of the additional maxillary teeth of *Brachyrhinodon*. These are most clearly seen in BMNH R 3364. Although by no means unequivocal, there also seems to be evidence supporting

the occurrence of flanges on certain maxillary teeth in *Polysphenodon*. Therefore, contrary to previous opinion, these two genera may exhibit certain derived character states of the dentition. Taken together with the variation in cranial dimensions this suggests that their position within the Sphenodontida needs to be revised from Fraser (1986).

Systematic relationships of sphenodontians

The relationships of sphenodontians are hard to assess, and several schemes have been published recently (Evans, 1984, 1988; Benton, 1985; Fraser, 1986; Whiteside, 1986). The different conclusions reached in these studies have been caused by the use of different character sets, the existence of many non-congruent postulated synapomorphies, and the incompleteness of data sets—certain taxa are so poorly known that it is not possible at present to determine all of the relevant character states.

Carroll (1985) indicated that the Sphenodontida shared a close relationship, not only with the Squamata, but also with the Pleurosauridae. However, the question of these relationships is outside the scope of the present work. Therefore, in our cladistic analyses of sphenodontid interrelationships *Youngina*, a typical plesiomorphic lepidosauromorph (Evans, 1984; 1988; Benton, 1985) is selected for outgroup comparison.

The most detailed recent cladistic analysis of sphenodontians (Evans, 1988; Fig. 11 here) was based on an analysis of 29 characters (closest outgroup of Sphenodontida is the Squamata). We question the validity of eight of her characters as potential synapomorphies.

(9) All teeth acrodont in adult. It is very hard to distinguish acrodonty clearly from pleurodonty (Fraser & Shelton, 1988). Both conditions may occur in one sphenodontian taxon, and they approach each other closely in, for example, *Planocephalosaurus*.

(13) Prominently flanged and striated teeth on posterior region of the maxilla. This is partly a repeat of Evans' character (7).

(15) Short scapula, reduced coracoid. This is hard to establish in those sphenodontians in which the shoulder girdle is known. There seems to be little difference between *Planocephalosaurus*, *Clevosaurus*, and *Sphenodon* in these proportions.

(16) Narrow, elongated, waisted pubis. This character seems to apply equally to *Clevosaurus*, *Planocephalosaurus*, and all other sphenodontians in which it can be determined.

(19) Elongation of temporal and antorbital regions. The antorbital region becomes shorter in derived sphenodontians, so the polarity reverses.

(25) No pterygoid teeth. In certain genera there may be some variation in the occurrence of pterygoid teeth. In addition this character cannot be satisfactorily evaluated in many other genera, and it is therefore not considered here.

(28) Teeth circular to square in cross-section. In part, this is possibly the primitive condition of Evans' character (27).

(29) Narrow parietal. A repeat of character (17). Seven of these characters have been omitted from our analyses, while (19) has been modified. The distribution of the derived states in Evans' characters 6, 7, 8, 10, 17, 18 and 23 is also questioned, and different results are given here.

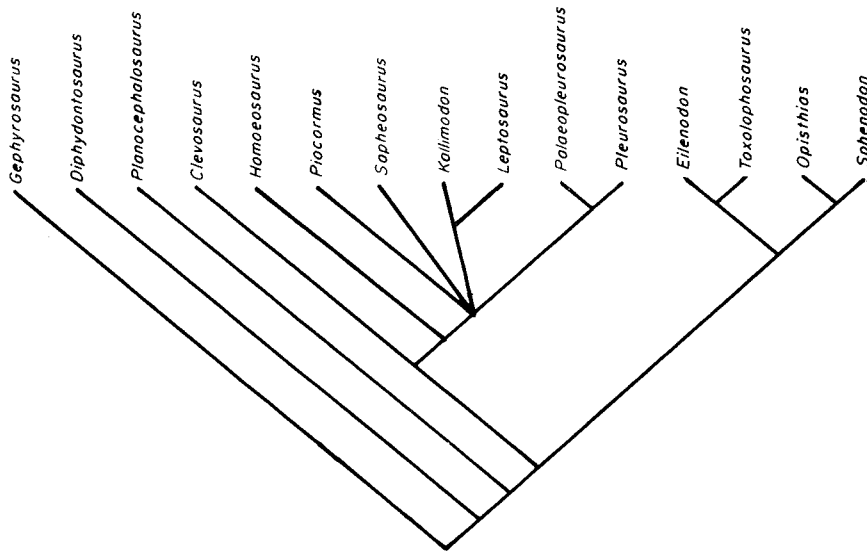


Figure 11. Cladogram for the sphenodontids based on 29 characters according to Evans (1988).

In our analyses of sphenodontian relationships, we excluded *Opisthias* since it is so poorly known, *Leptosaurus* (? = *Kallimodon*), and *Pleurosaurus*. The characters used in our studies are listed in Table 3, and the distribution of the primitive and derived states is listed in Table 4. This latter clearly shows the incompleteness of certain taxa—fewer than 50% of characters could be determined in *Sappeosaurus*, *Plocormus*, *Eilenodon*, and *Toxolophosaurus*.

The first analyses were carried out using the PAUP (Phylogenetic Analysis Using Parsimony) package (Version 2.4) developed by David L. Swofford (1985) on an IBM-PC. The trees were rooted with *Youngina* defined as the ancestor, and the GLOBAL branch-swapping, and MULPARS options were invoked. The first analysis, with all 15 taxa included, yielded 82 different equally parsimonious trees. The four poorly-represented taxa (listed above) were then omitted, and the program yielded two equally parsimonious trees for the 11 remaining taxa. Then, *Brachyrhinodon* and *Polysphenodon* (each with 15–20% incomplete data) were omitted, and the remaining nine taxa were arranged in four different equally parsimonious trees. Finally, when four more taxa which had one or two missing items of data (*Gephyrosaurus*, *Diphydontosaurus*, *Homoeosaurus*, *Kallimodon*) were deleted, the remaining five taxa were arranged into a single most-parsimonious tree (Fig. 12D). In all cases, the consistency index (CI), a measure of the congruence of the data, was relatively high, ranging from 0.871 to 0.931. However, the high values for the first two analyses described above (CI = 0.879, 0.875 respectively) probably relates to the assumption of congruent values by the program for the relatively large amount of missing data (i.e. the program substitutes 0 or 1 for missing data points, and it will tend to select congruent values).

The multiple most-parsimonious trees were summarized by application of the CONTREE program (Swofford, 1985). This yields single trees that take account of different branching patterns, and thus inevitably contain one or more

TABLE 3. Characters used in the cladistic analyses. Primitive states are indicated by 0, derived states by 1. Evans' (1988) character numbers are indicated in parentheses after our numbers

-
- 1 (1). Palatine tooth row: small (0), enlarged (1).
 - 2 (2). Posterior process of dentary: ends anterior to, or beneath, the coronoid (0), ends behind the coronoid (1).
 - 3 Lower temporal arcade: aligned exactly with the maxillary tooth row (0), bows away laterally from the line of the maxillary tooth ramus (1).
 - 4 (14). Ischium: uninterrupted posterior edge extending from the acetabulum to the median symphysis (0), prominent posterior tubercle on posterior margin (1).
 - 5 (3). Lachrymal: present (0), absent (1).
 - 6 Frontals and parietals: separate (0), fused (1).
 - 7 (4). Dentition: pleurodont (0), a degree of acrodonity and some alternation in tooth height (1).
 - 8 (5). Premaxillary teeth: more than seven (0), seven or fewer (1).
 - 9 (11). Premaxillae: individual teeth remain discrete in adult (0), premaxillae developed into chisel-like structures in mature individuals (1).
 - 10 (7). Posterior maxillary teeth: simple conical structures (0), presence of a posteromedial ridge or flange (1).
 - 11 Lateral and medial wear facets on marginal teeth: absent or poorly defined (0), well established on both maxillary and mandibular teeth (1).
 - 12 (6). Ridges and flanges on dentary teeth: absent (0), anterolabial ridge or flange on at least one dentary tooth (1).
 - 13 (8). Premaxillary tooth numbers: more than four (0), four or fewer (1).
 - 14 (10). Premaxillary teeth: more than three (0), three or fewer (1).
 - 15 (12). Flanges or ridges on palatal tooth row: absent (0), posterolateral ridges or flanges present on some palatine teeth (1).
 - 16 Palatine tooth rows: more than one (0), a single tooth row (1).
 - 17 (19 pars). Antorbital region: elongate (0), shortened (1).
 - 18 (19 pars). Temporal region: short (0), elongate (1).
 - 19 (17, 29). Parietal table: broader than interorbital width (0), narrow (1).
 - 20 Parietal crest: absent (0), present (1).
 - 21 (21). Numbers of presacral vertebrae: 24 or 25 presacrals (0), additional presacrals (1).
 - 22 (29). Caudal autotomy: present (0), absent (1).
 - 23 (22). Metatarsals: I–IV longer than V (0), all of similar length (1).
 - 24 (26). Jaw movements: precision-shear bite (0), propalinal action (1).
 - 25 (24). Retroarticular process: pronounced (0), reduced (1).
 - 26 (23). Quadrate/quadratojugal conch: pronounced (0), reduced (1).
 - 27 (27). Breadth of marginal teeth: approximately equal to the length (0), greatly expanded mediolaterally (1).
 - 28 Extensive posterolingual flanges on some maxillary teeth (at least as long again as the main tooth cone): absent (0), present (1).
 - 29 (18). Limb proportions with respect to the presacral vertebral column (PSVC): humerus less than or equal to 0.20 PSVC, tibia less than or equal to 0.25 PSVC, femur less than 0.30 PSVC, radius less than 0.15 PSVC (0), all measures greater than these values (1).
-

multichotomies. The trees for all 15 taxa (Fig. 12A), 11 taxa with more than 50% information (Fig. 12B), and nine taxa with more than 80% information (Fig. 12C), show broadly similar patterns to the single most-parsimonious tree produced from the five taxa which had complete character information (Fig. 12D). These resemblances include:

(1) the broad sequence of outgroups from *Youngina*, through *Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*, (*Polysphenodon* + *Homoeosaurus*), and *Brachyrhinodon*, to the crown group;

(2) the probable pairing of *Polysphenodon* and *Homoeosaurus*;

(3) the pairing of *Kallimodon* and *Palaeopleurosaurus*. However, some key differences exist. The five-taxon tree (Fig. 12D) shows a clear pairing of *Clefosaurus* and *Sphenodon* with *Palaeopleurosaurus* as their closest outgroup. However, these three taxa form part of an unresolved multichotomy in the analyses that contain additional taxa (Fig. 12A–C). The interesting question of

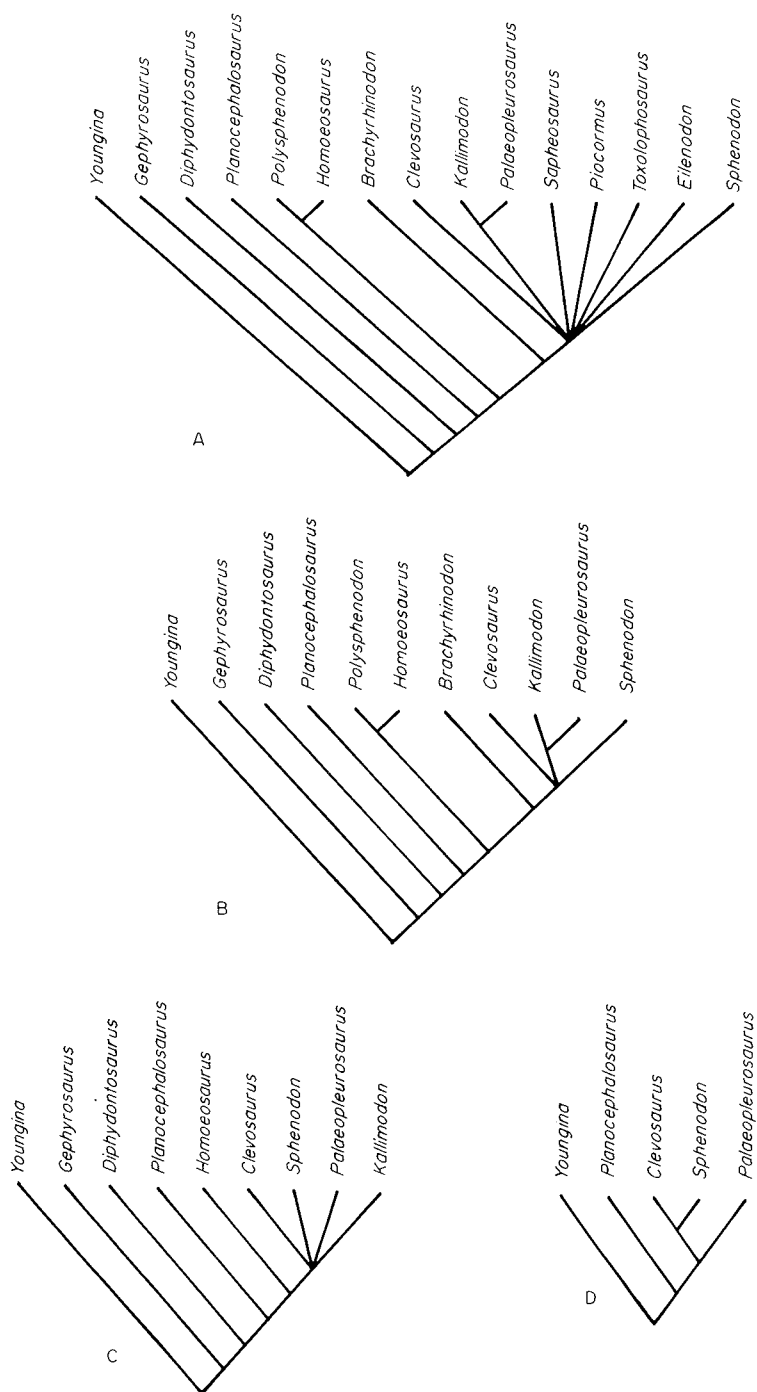


Figure 12. Results of PAUP (version 2.4) computer analyses based on data presented in Tables 3 & 4. Summaries of multiple most-parsimonious trees by the CONTREE program. A, All 15 sphenodontid taxa (trees: 82, Consistency Index: 0.879, steps: 33). B, 11 taxa with more than 50% information (trees: 2, C.I.: 0.875, steps: 32). C, Nine taxa with more than 80% information (trees: 4, C.I.: 0.871, steps 31). D, Five taxa with complete information (trees: 1, C.I.: 0.931, steps 29). See text for full explanation.

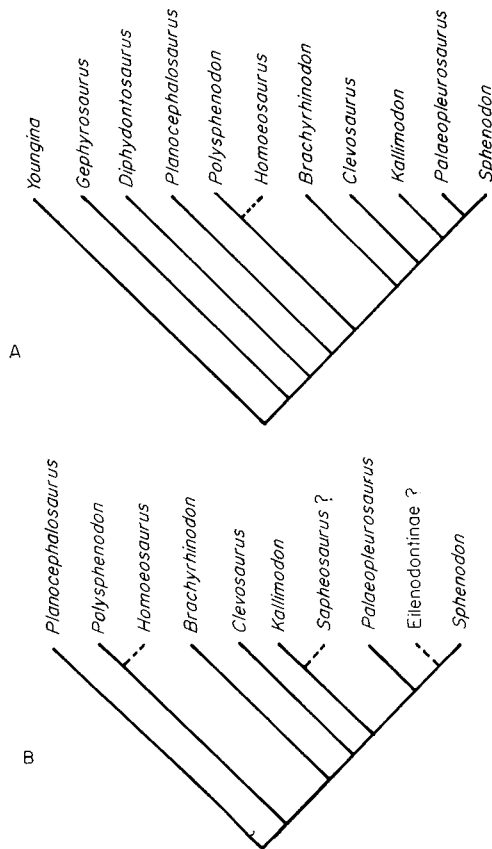


Figure 13. Results of CLINCH (Version 3.1) computer analysis based on data presented in Tables 3 & 4. A, Tree for 11 taxa by 16 characters. B, Tree for eight taxa by 13 characters. See text for full explanation.

the relationships of taxa within the crown group multichotomy of eight taxa (Fig. 12A) cannot be resolved by PAUP with the present data set.

An alternative analytical approach was attempted in order to try to resolve the crown-group multichotomy. The CLINCH program (Cladistic Inference by Compatibility of Hypotheses, Version 3.1; K. L. Fiala & G. F. Estabrook) compares the compatibility of all characters with each other, and aims to produce the tree(s) with highest compatibility values. The CLINCH program does not permit incomplete data, so the four very poorly known taxa (*Sapheosaurus*, *Piocormus*, *Eilenodon*, *Toxolophosaurus*) were omitted, as were characters 4, 7, 12–14, 16, 20–22, and 26–29 (Table 1). This gave a complete data matrix (11 taxa by 16 characters). The resulting cladogram (Fig. 13A) confirmed the broad sequence of stem taxa discovered by the PAUP analyses, as well as the possible pairing of *Polysphenodon* and *Homoeosaurus*, and it sorted out four of the crown-group taxa, with *Clevosaurus*, *Kallimodon*, and *Palaeopleurosaurus* as successively closer outgroups of *Sphenodon*.

A second CLINCH run was attempted of eight of the better-known crown-group taxa, in which seventeen characters (1–5, 7, 10, 12–14, 16, 20–22, 26–28) had to be omitted in order to achieve a complete data set. One extra character

(snout: normal (0) or reduced (1)) was added. This yielded a cladogram (Fig. 13B) in which the sequence of ever closer outgroups to *Sphenodon* was *Planocephalosaurus*, *Polysphenodon* (+*Homoeosaurus*?), *Brachyrhinodon*, *Clevosaurus*, *Kallimodon* and *Palaeopleurosaurus*, as in the first CLINCH run.

All the PAUP and CLINCH analyses agree in:

(1) the sequence of sphenodontid outgroups from *Youngina*, through *Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus*, *Polysphenodon* (+*Homoeosaurus*) to *Brachyrhinodon*;

(2) the pairing of *Polysphenodon* and *Homoeosaurus*.

The PAUP analyses offered little resolution of the crown group, although *Kallimodon* usually paired with *Palaeopleurosaurus*. The CLINCH runs did not support this latter pairing, but did offer a possible resolution of the most derived sphenodontids, with *Clevosaurus*, *Kallimodon*, and *Palaeopleurosaurus* as progressively closer outgroups to *Sphenodon*. The position of *Sapheosaurus* and *Piocormus* (Sapheosauridae) and *Eilenodon* and *Toxolophosaurus* (Eilenodontinae) is hard to determine because of their incompleteness, but possible positions are indicated in Fig. 13B as sister-groups of *Kallimodon* and *Sphenodon* respectively.

Fraser (1988) suggested that together *Gephyrosaurus*, *Planocephalosaurus* and *Diphydontosaurus* might conceivably form a monophyletic assemblage constituting the sister group of all other sphenodontians. This suggestion was based on the following common characters: fused frontals, a relatively elongate snout, a short temporal region, little development of keels or flanges on the additional teeth, and more than one tooth row on the palate in addition to the numerous pterygoid and vomerine teeth. However, at present only the fused skull roofing elements can be viewed as a shared derived character, and neither the PAUP or CLINCH analyses supported the distinction. Therefore, the derived state of character 6 must be viewed at present as a homoplasy in *Gephyrosaurus*, *Diphydontosaurus* and *Planocephalosaurus*.

In the light of the accepted trees from both the PAUP and CLINCH analyses, the absence of flanged palatine teeth in *Palaeopleurosaurus* must be regarded as a reversal of character 15. In addition two other reversals must be assumed to have occurred. These are the elongation of the antorbital region in *Kallimodon* and *Palaeopleurosaurus* (a reversal of character 17), and the absence of extensive posterolingual flanges on the maxillary teeth of *Sphenodon* (a reversal of character 28).

SUMMARY

Polysphenodon from the middle Keuper of Hoffmannsthal near Hannover and *Brachyrhinodon* from the Lossiemouth Sandstone Formation are redescribed. Although the palate is very similar and the snout is reduced in both genera, the differing proportions of the orbits and temporal fossae indicate that they are not congeneric and that they should not be grouped as a single taxon within the Sphenodontida. Elongate temporal fenestrae and an interorbital width exceeding that of the parietal table are derived character states for sphenodontids. In both respects *Brachyrhinodon* is more derived than *Polysphenodon*. The proportions of limb bones seem to be variable throughout the Sphenodontida and no overall pattern is apparent. The lower temporal arcade is secondarily derived in sphenodontids and contrary to previous opinion it shows some degree of lateral bowing in all genera.

Analyses of sphenodontian relationships were carried out using PAUP and CLINCH programs on 29 character states. In general both analyses yielded a similar sequence of outgroups, but PAUP provided little resolution of the crown group.

ACKNOWLEDGEMENTS

We would like to express our thanks to A. C. Milner, British Museum (Natural History), S. M. Andrews, Royal Museum of Scotland, C. Sangster, Elgin Museum, H. Jaeger and W.-D. Heinrich, Museum für Naturkunde der Humboldt-Universität zu Berlin for permission to examine specimens in their care. A. D. Walker kindly provided casts of some of the *Brachyrhinodon* fossils, and also made his notes on these fossils available to us. We are also grateful to A. E. Friday and D. Jamison for assistance with computing. M. J. B. thanks H. Jaeger for kind hospitality during his stay in Berlin. This work was carried out whilst N. C. F. held a Research Fellowship at Girton College, Cambridge, and this is gratefully acknowledged.

REFERENCES

- AGASSIZ, L., 1844. *Monographie des poissons fossiles du vieux Grès Rouge ou système Devonien des Iles Britannique et de Russie*. Neuchâtel.
- BARGHUSEN, H. R., 1968. The lower jaw of cynodonts (Reptilia, Therapsida) and the evolutionary origin of mammal-like adductor musculature. *Postilla*, 116: 1-49.
- BENTON, M. J., 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, Series B*, 302: 605-720.
- BENTON, M. J., 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, 84: 97-164.
- BENTON, M. J. & WALKER, A. D., 1981. The use of flexible synthetic rubbers for casts of complex fossils from natural moulds. *Geological Magazine*, 118: 551-556.
- BENTON, M. J. & WALKER, A. D., 1985. Palaeoecology, taphonomy, and dating of Permo-Triassic reptiles from Elgin, North-east Scotland. *Palaeontology*, 28: 207-234.
- CARROLL, R. L., 1977. The origin of lizards. In S. M. Andrews, R. S. Miles & A. D. Walker (Eds), *Problems in Vertebrate Evolution. Linnean Society Symposia Series 4*: 359-396.
- CARROLL, R. L., 1985. A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. *Palaeontographica Abteilung A*, 189: 1-28.
- COCUDE-MICHEL, M., 1963. Les Rhynchocéphales et les sauriens des calcaires lithographique (Jurassique supérieur) d'Europe Occidentale. *Nouvelles Archives du Muséum d'histoire Naturelle de Lyon*, 7: 1-187.
- COCUDE-MICHEL, M., 1967. Revision des Rhynchocéphales de la collection du musée Teyler de Haarlem (Pays-Bas), II. *Proceedings of the koninklijke Nederlandse Akademie van Wetenschappen. Series B (Physical Sciences)*, 70: 547-555.
- EVANS, S. E., 1980. The skull of a new cosuchian reptile from the Lower Jurassic of South Wales. *Zoological Journal of the Linnean Society*, 70: 203-264.
- EVANS, S. E., 1981. The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. *Zoological Journal of the Linnean Society*, 73: 81-116.
- EVANS, S. E., 1984. The classification of the Lepidosauria. *Zoological Journal of the Linnean Society*, 82: 87-100.
- EVANS, S. E., 1988. The early history and relationships of the Diapsida. In M. J. Benton (Ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds. Systematics Association Special Volume, 35A*: 221-260. Oxford: Clarendon Press.
- FABRE, J., 1973. Un squelette d'*Homoosaurus* aff. *solnhofensis* (Rhynchocephalia) du Portlandien du Petit Plan de Canjuers (Var). *Comptes Rendus de l'Académie des Sciences Paris. Série D: Sciences Naturelles*, 276: 1139-1142.
- FRASER, N. C., 1982. A new rhynchocephalian from the British Upper Trias. *Palaeontology*, 25: 709-725.
- FRASER, N. C., 1986. New Triassic sphenodontids from South-west England and a review of their classification. *Palaeontology*, 29: 165-186.
- FRASER, N. C., 1988. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philosophical Transactions of the Royal Society of London, Series B*, 321: 125-178.
- FRASER, N. C. & SHELTON, C. G., 1988. Studies of tooth implantation in fossil tetrapods using high-resolution X-radiography. *Geological Magazine*, 125: 117-122.

- FRASER, N. C. & WALKDEN, G. M., 1984. The postcranial skeleton of *Planocephalosaurus robinsonae*. *Palaeontology*, 27: 575-595.
- HAINES, R. W., 1969. Epiphyses and sesamoids. In C. Gans *et al.* (Eds), *Biology of the Reptilia*, 1: 81-115. London: Academic Press.
- HUENE, F. VON, 1910a. Ein primitiver Dinosaurier aus der mittleren Trias von Elgin. *Geologische und Paläontologische Abhandlungen*. (N.F.), 8: 315-322.
- HUENE, F. VON, 1910b. Über einen echten Rhynchocephalen aus der Trias von Elgin, *Brachyrhinodon taylori*. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*. 1910 (2), 29-62.
- HUENE, F. VON, 1912a. Die Cotylosaurier der Trias. *Palaeontographica*, 59: 69-102.
- HUENE, F. VON, 1912b. Die zweite fund des Rhynchocephalen *Brachyrhinodon* in Elgin. *Neues Jahrbuch der Mineralogie, Geologie und Paläontologie*, 1912: 51-57.
- HUENE, F. VON, 1920. Ein *Telepeton* mit gut erhalten Schadel. *Zentralblatt für Mineralogie, Geologie und Paläontologie*, 1920: 189-192.
- HUENE, F. VON, 1929. Über Rhynchosaurier und andere Reptilien aus den Gondwana-Ablagerungen Sudamerikas. *Geologische und paläontologische Abhandlungen* (N.F.), 17: 1-62.
- HUENE, F. VON, 1956. *Paläontologie und Phylogenie der niederen Tetrapoden*. Jena: Gustav Fischer.
- HUXLEY, T. H., 1869. On *Hyperodapedon*. *Quarterly Journal of the Geological Society of London*, 25: 138-152.
- HUXLEY, T. H., 1877. The crocodilian remains found in the Elgin Sandstones, with remarks on the ichnites of Cummingstone. *Memoirs of the Geological Survey of the United Kingdom, Monograph*, 3: 1-52.
- JAEKEL, O., 1911. *Die Wirbeltiere*. Berlin: Borntraeger.
- MANTELL, G., 1852. Descriptions of the *Telepeton elginense*, and observations on supposed fossil ova of batrachians in the Lower Devonian strata of Forfarshire. *Quarterly Journal of the Geological Society of London*, 8: 100-109.
- NEWTON, E. T., 1894. Reptiles from the Elgin Sandstone. Descriptions of two new genera. *Philosophical Transactions of the Royal Society of London, Series B*, 185: 573-607.
- PEACOCK, J. D., BERRIDGE, N. G., HARRIS, A. L. & MAY, F., 1968. *The Geology of the Elgin District*. Edinburgh: Her Majesty's Stationery Office.
- ROBINSON, P. L., 1975. The function of the hooked fifth metatarsal in lepidosaurian reptiles. *Colloques internationaux du Centre National de la Recherche Scientifique*, 218: 461-483. In *Problèmes actuels de Paléontologie—Evolution des vertébrés*.
- SWOFFORD, D. L., 1985. *PAUP: Phylogenetic Analysis Using Parsimony, version 2.4*. Champaign, Illinois: Illinois Natural History Survey.
- WALKER, A. D., 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society of London, Series B*, 244: 103-204.
- WALKER, A. D., 1964. Triassic reptiles from the Elgin area: *Ormithosuchus* and the origin of Carnosaurs. *Philosophical Transactions of the Royal Society of London, Series B*, 248: 53-134.
- WALKER, A. D., 1966. *Elachistosuchus*, a Triassic rhynchocephalian from Germany. *Nature, London*, 211: 583-585.
- WHITESIDE, D. I., 1986. The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonis* gen. et sp. nov. and the modernizing of a living fossil. *Philosophical Transactions of the Royal Society of London, Series B*, 312: 379-430.
- WOODWARD, A. S., 1907. On a new dinosaurian reptile (*Scleromochlus taylori* gen. et sp. nov.) from the Trias of Lossiemouth, Elgin. *Quarterly Journal of the Geological Society of London*, 63: 140-146.

ABBREVIATIONS USED IN THE FIGURES

| | | | |
|---------|------------------------|-----|---------------------------------|
| ang | angular | mc | metacarpal |
| ast | astragalocalcaneum | mt | metatarsal |
| ca vert | caudal vertebra | mx | maxilla |
| cr | cervical rib | n | nasal |
| c vert | cervical vertebra | na | naris |
| d | dentary | p | parietal |
| dr | dorsal rib | pal | palatine |
| d vert | dorsal vertebra | pf | postfrontal |
| ent fo | entepicondylar foramen | ph | phalanx |
| f | frontal | pm | premaxilla |
| fe | femur | po | postorbital |
| fib | fibula | pra | prearticular |
| gast | gastralia | prf | prefrontal |
| hu | humerus | ptq | pterygoid ramus of the quadrate |
| il | ilium | q | quadrate |
| in | intermedium | r | rib |
| j | jugal | ra | radiale |

| | | | |
|------|------------------------|-------|-----------------|
| Ra | radius | syn | synapophysis |
| sa 1 | first sacral vertebra | tib | tibia |
| so | supraoccipital | tmt | tarsometatarsal |
| sq | squamosal | ul | ulnare |
| stf | supratemporal fenestra | Ul | ulna |
| sur | surangular | 4vert | vertebra |