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THE LAST LABYRINTHODONT? A NEW BRACHYOPOID (AMPHIBIA, TEMNOSPONDYLI) FROM THE EARLY JURASSIC EVERGREEN FORMATION OF QUEENSLAND, AUSTRALIA

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[Plates 1 and 2; pullouts 1 and 2; outrigger]

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Remains of a fossil amphibian have been recovered from an ironstone layer in the Upper Evergreen Formation, dated as late Liassic, of southeast Queensland. Extraction of the skeleton from the very hard matrix has presented a number of problems which are discussed.

The find is an almost complete skull and mandible connected to an articulated postcranial skeleton which is missing only some ribs, the right hind leg and the distal portions of the other limbs and tail. The remains are those of a temnospondyl labyrinthodont described as a new genus and species of the family Chigutisauridae. The new form is notable for its very large size (total length estimated to be in excess of 2.5 m), relatively large marginal dentition, with unique lance-shaped tooth tips, the presence of minute denticles associated with the palate and mandible, a well developed atlas showing a strong link with the axis, neorhachitomous vertebrae that lack ossified pleurocentra and have low, heavily built neural spines, a neck region and a narrow dermal pectoral girdle associated with unreduced limbs.

The discovery of this chigutisaur provides the first unequivocal evidence that labyrinthodonts survived beyond the end of the Triassic. The status of two previously described doubtful Jurassic forms is reviewed. *Austropelor* Longman, 1941, from the Early Jurassic Marburg Sandstone of southeast Queensland, is confirmed as a fragment of temnospondyl lower jaw, probably attributable to the superfamily Brachyopoidea, and there is no longer any reason to consider the earlier suggestion that it is a reworked Triassic fossil. *Cyrtura* Jaekel, 1904, from the Late Jurassic Solnhofen Shale of Germany, is considered not to be a labyrinthodont, but its exact relationships are uncertain.

The unsatisfactory nature of the higher taxonomy of the Temnospondyli is noted. The superfamily Brachyopoidea is reviewed and the family Kourerpetontidae is removed from it, membership of the superfamily thereby being restricted to the Brachyopidae (Late Permian to Middle Triassic) and Chigutisauridae (Early Triassic to Early Jurassic). Diagnoses for the superfamily and its two included families are provided. The relationships of the better characterized members of the two families are examined and a phylogeny based on shared derived character states is proposed. The analysis of relationships indicates that *Brachyops allos* Howie, 1972 shares few of the characters diagnostic of the type of *Brachyops* (*B. laticeps* Owen, 1855), and a new genus is proposed.

The diversity of Australia's brachyopoids, including the presence of the most primitive and earliest-known members of each of the included families, suggests that the superfamily originated in Australia.

INTRODUCTION

In the late 1960s Mr Colin Kehl recognized fossil bone and teeth in a piece of ironstone from his cattle station, 'Kolane', in southeast Queensland. This specimen (QM F7882) eventually found its way to the Queensland Museum. In 1975 an expedition led by Dr Mary Wade recovered some 50 blocks of ironstone from the site and a subsequent trip from La Trobe University nearly doubled this collection. The fossil site lies within the Evergreen Formation which has been dated as Late Liassic and this is thus the first undoubted Jurassic labyrinthodont. Although there have been two previous descriptions of Jurassic labyrinthodonts, authenticity of both has been questioned and will be further discussed below.

The new species is a temnospondyl, with a short deep skull, and was placed by Warren (1977) tentatively in the family Brachyopidae. Upon preparation, some parts of the skull show marked differences from other brachyopids, and affinities with a horned brachyopoid, *Keratobrachyops australis*, described by Warren (1981 *b*) as Australia's first member of the family

Chigutisauridae. Although the tabular area is missing, we have placed the new animal also in the family Chigutisauridae.

The fossil from the Evergreen Formation is significant as the last known labyrinthodont, because it is an almost complete individual, and because it indicates the presence of a terrestrial Early Jurassic fauna, few of which have been preserved.

Geology

The Upper Evergreen Formation at the site of recovery of QM F7882 is represented by ferruginous sandstone, thick seams of concretionary ironstone, and argillaceous oolites. These beds are probably an eastward extension of the Westgrove Ironstone member which is found towards the top of the Evergreen Formation in the western parts of the Surat Basin. Reiser & Williams (1969) conclude that most of the Evergreen Formation was laid down under continental conditions but that the lithology of the Westgrove Ironstone Member, and particularly the oolite band, may indicate a marine incursion. Two plesiosaurs recovered from the same site (Thulborn & Warren 1980) suggest that this part of the Evergreen Formation was marine: one of them was found within the oolitic member. Non-marine plesiosaurs are known, however, for example from the English Wealdon (Andrews 1922) and from the Early Jurassic Razorback Beds of Queensland (Bartholomai 1966; Molnar 1982); so no conclusions can be reached, at least on the evidence of its included vertebrates, as to the environment of deposition of the Evergreen Formation.

The age of the Evergreen Formation has been placed as Late Liassic based on the evidence of its plant microfossil assemblages (de Jersey & Paten 1964; Reiser & Williams 1969). In particular the appearance of *Tsugaepollenites segmentatus* and *T. dampieri* in the upper Evergreen clearly date this formation as Late Liassic. In addition, the possibility of a Late Triassic age for the lower Evergreen and underlying Precipice Sandstone is ruled out by the presence of *Classopollis classoides* which is not known from accurately dated pre-Jurassic sediments. The stratigraphic relationships of vertebrate-bearing Triassic and Early Jurassic sediments in Queensland are shown in table 1.

Associated fauna

Two partial plesiosaurs have been found close to the QM F7822 excavation. One is a dolichodeiran or long-necked plesiosaur while the other is indeterminate. When found, they represented the earliest adequate examples of plesiosaurs from Gondwana (Thulborn & Warren 1980), but subsequently Carroll (1981) has described a proto-plesiosaur from the Late Permian of Madagascar.

A single complete labyrinthodont intercentrum was found within the oral cavity of QM F7882. This element is less well preserved than most of the other skeletal elements and appears to have undergone more *post mortem* weathering. Although of a similar shape to some of the anterior presacral intercentra of QM F7882, it is markedly smaller and has better developed diapophyses. We think that it represents a second labyrinthodont at present not determinable.

Within the skull of QM F7822 near the iron–sandstone interface, which occurs just below the level of the palate, preparation under a binocular microscope revealed many small plates of bone bearing denticles (see *Dentition* below). At the same level were also uncovered several small segmented invertebrates. These have been described by Jell (1983) as *Decorotergum warrenae*, a millepede. *Decorotergum* is the only millepede known between the Carboniferous and

TABLE 1. STRATIGRAPHIC OCCURRENCE OF BRACHYOPOID FOSSILS IN THE JURASSIC AND TRIASSIC OF SOUTHEAST QUEENSLAND

(Compiled from Banks (1978), Foster (1979), Hill *et al.* (1966), Jensen (1975), de Jersey (1963), de Jersey & Paten (1964) and Mollan *et al.* (1972).)

GEOLOGICAL PERIOD			IPSWICH-MORTON BASIN	SURAT BASIN	BOWEN-GALILEE BASIN	
JURASSIC	Middle	Bajocian	Marburg Sandstone *Austropelor*	Hutton Sandstone		
	Early	Lias		W Westgrove Ironstone E 'oolite member' *Siderops*		
				Evergreen Formation		
			Wivenhoe Sandstone	Precipice Sandstone		
TRIASSIC	Middle	Ladinian			Moolayember Formation	
		Anisian			CLEMATIS GROUP	Expedition Sandstone
						Glenidal Formation
	Early	Scythian			REWAN GROUP	Arcadia Formation *'Brachyops' allos* *Keratobrachyops*
						Sagittarius Sandstone
PERMIAN	Late	Chhidruan			BLACKWATER GROUP	

the Oligocene, and its presence indicates a terrestrial period during the time that the body of QM F7882 was decaying.

Unionid molluscs have been collected from the site but their precise relationships are unknown.

Collection and preparation

The specimen was preserved partly in concretionary banded ironstone and partly in ferruginous sandstone. Its skeleton was fossilized in an articulated state, but when found had broken up into blocks which had rolled down the side of a low flat-topped ridge. While a few blocks were found on the surface, most were buried, the deepest lying approximately 1 m below the surface. Some adjacent blocks fitted together well, having broken recently, whereas others had extensive surface weathering, indicating they had been separate for some time. The bone was well preserved but softer than the surrounding ironstone, and had completely weathered away from some of the exposed blocks. Most of the blocks were eventually pieced together to form one 2.2 m unit.

Most of the preparation was done with a Chicago Pneumatic Airscribe after initial trimming of the blocks. In parts of the skeleton the ironstone made preparation difficult as bands of dense iron ran through matrix and bone alike. A Stensio mallet and airbrasive made little impression on the ironstone, but were used to clean up the ornament. Thioglycollic acid as used by Howie (1974) but had no effect on the iron matrix and no protective coating substance available in Australia would adhere to the bone in the presence of the acid.

Some blocks from the skull table were found with the ornament embedded and the ventral surface of the bone exposed. These were set in a Dow Corning Silastomer (3120 RTV), and that in turn was embedded in a plaster jacket. The Silastomer absorbed vibrations from the Airscribe while the plaster prevented distortion of the Silastomer. In this way ironstone could be removed from sheets of bone in some cases as thin as 2 mm.

In some instances, for example, parts of the left maxilla and pectoral girdle, bone had weathered almost away leaving a thin remnant only. In these cases a North Hill Plastics mounting plastic (NHP 2031/19) filled with glass microspheres was poured onto the part bone, part natural mould. This adhered to the bone which could then be prepared from the other side. The finished preparation thus consists in part of what little bone remained and in part of a cast in plastic of the bone concerned.

A dilute solution of Butvar B98 in alcohol was used as a bone impregnator, while a concentrate of the same proved an adequate glue.

Description

Order Temnospondyli
Superfamily Brachyopoidea Säve-Söderbergh, 1935
Family Chigutisauridae Rusconi, 1951

Siderops n.gen. (figures 1–23, 28–31, 33–34)

Etymology. From the Greek *sideros* (iron) and *ops* (face), alluding to the ironstone bed in which the type species was preserved. The suffix *-ops* is also commonly used in temnospondyl nomenclature and echoes the name *Brachyops*, the type genus of the superfamily to which the new form belongs.

Diagnosis. A large chigutisaurid amphibian with small anterolaterally situated orbits and distinguished from all other members of the family by its much larger marginal dentition and by the structure of its teeth, which are incurved with lancet shaped tips.

It is distinguished from *Pelorocephalus* by its coarse ridge–groove ornamentation, by its large pineal opening, by its reduced postparietals and tabulars and by the presence of a coronoid process on the mandible.

It differs from *Keratobrachyops* by the wide contact between the exoccipital and the pterygoid and by the ventral exposure of the cultriform process of the parasphenoid ending posterior to the anterior borders of the interpterygoid vacuities.

Siderops kehli n.sp.

Etymology. This species is named after the Kehl family of 'Kolane', Wandoan, Queensland where the fossil was found.

Type specimen. Holotype, QM F7882. An almost complete skull with attached mandible and a postcranial skeleton.

Type locality. The specimen was found on 'Kolane', 25° 49′ S, 150° 18′ E, approximately 65 km east northeast of Wandoan, southeast Queensland. The site is a little north of due west of Kennedy Peak which can be seen from the excavation.

Horizon. Upper Evergreen Formation, late Early Jurassic.

Diagnosis. As for the genus.

Skull

Preservation

The skull is incomplete posterodorsally especially on the left side, while its anterior rim is also missing. Posteriorly the skull has broken on a line from midway along the left postorbital to just behind the centre of ossification of the right squamosal. It appears that the posterior block then weathered dorsally, so that none of the posterior skull table is preserved. The ventral parts of this block did survive, including both stapes. An interface between iron and sandstone passes through the skull just below the palate. The only bones not represented at least in part on either right or left side are the tabulars and postparietals, and the quadratojugals are present only on the occipital surface. The bone is well preserved. Although in some places it is thick (a maximum of about 25 mm is reached just anterior to the orbits), for most of the skull table the bone is surprisingly thin, less than 10 mm on average. This gives an overall impression of a light skull compared with other large labyrinthodonts such as the massive metoposaurs. Dimensions of the skull are given in table 2.

TABLE 2. MEASUREMENTS AND RATIOS (WELLES & ESTES 1969) OF SKULL PROPORTIONS

(All taken from skull reconstruction.)

(*a*) measurements/mm

interorbital breadth, A	255
breadth of skull roof across quadratojugals, B	648
midline postorbital length, D	261
length of vomers, E	72
midline distance between nostrils and orbits, F	174
breadth across vomers, G	123
height at parasphenoid, H	135
internarial breadth, J	72
length of skull roof, L	489
midline preorbital length, O	141
distance behind orbits of parietal foramen, P	159
length of body of pterygoid, Q	87
breadth across pterygoids at concavity, R	369
distance of parietal foramen in front of end of skull table, T	93
midline orbital length, U	87
length of interpterygoid vacuity, Y	276
breadth of interpterygoid vacuity, Z	141

(*b*) ratios

B/L	J/L	A/L	O/L	U/L	D/L	P/A	T/A	G/E	Q/R	Y/L	Z/Y
133	15	52	29	18	53	62	36	171	24	56	51

Reconstruction

The skull as preserved is shown in plates 1 and 2 and figures 1, 3, 8 and 12, and reconstructions are presented in figures 2, 4, 9, 11 and 13. Dorsal views have been drawn normal to the midline of the skull table while ventral views are normal to the parasphenoid. This means that, in a deep-skulled form, the outlines of dorsal and ventral views will not coincide in the occipital area.

Although a substantial length of skull margin was not preserved, there is little room for error in the reconstructed outline. Anteriorly the curvature of the snout can be deduced from the lower jaw. In the anterior midline marked ventral curvature of the premaxillae external to the mandibular teeth shows that little of this area is missing.

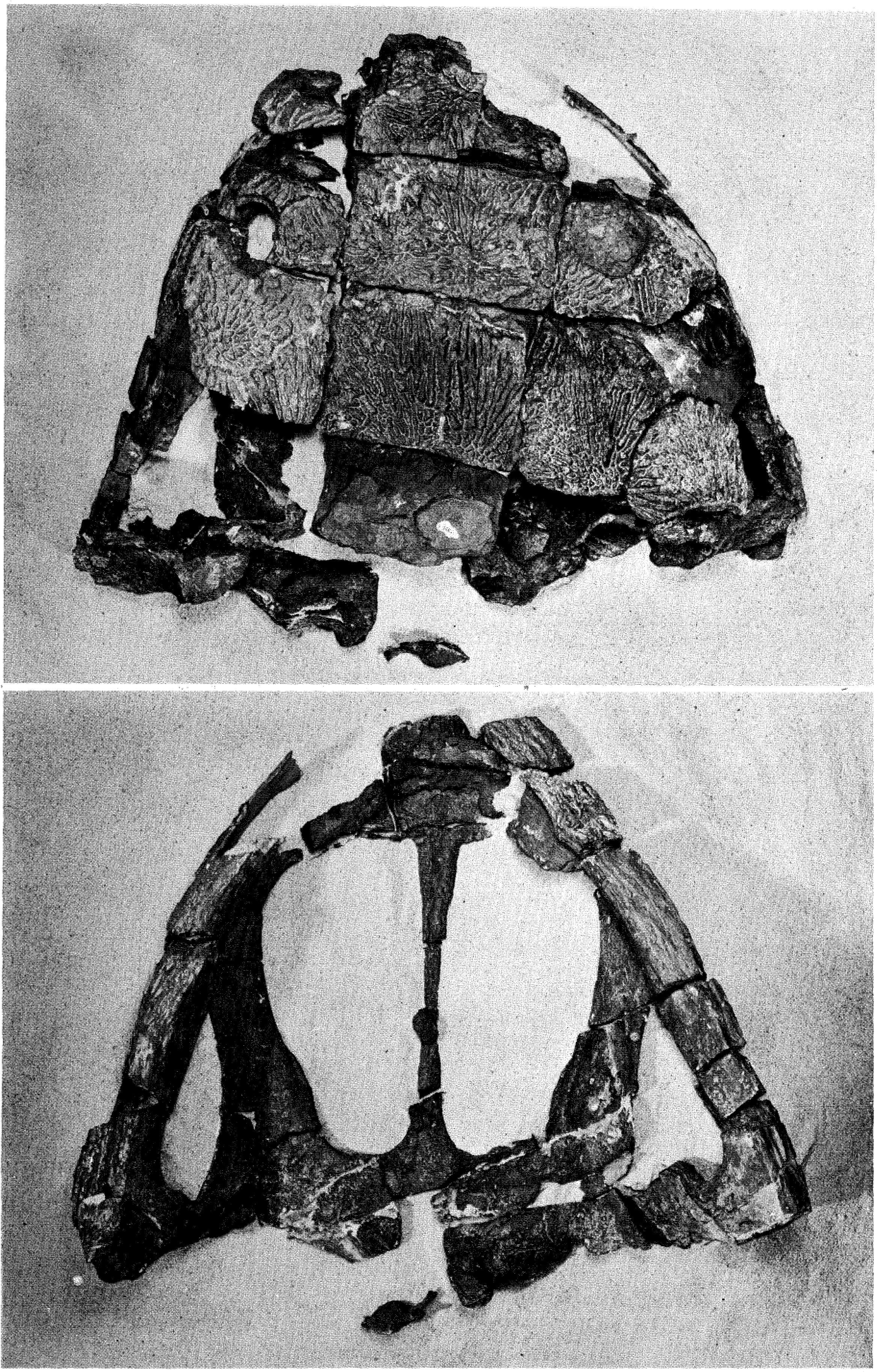


PLATE 1. *Siderops kehli* n.gen. n.sp. Dorsal and ventral views of the skull. (Approximately one-fifth actual size.)

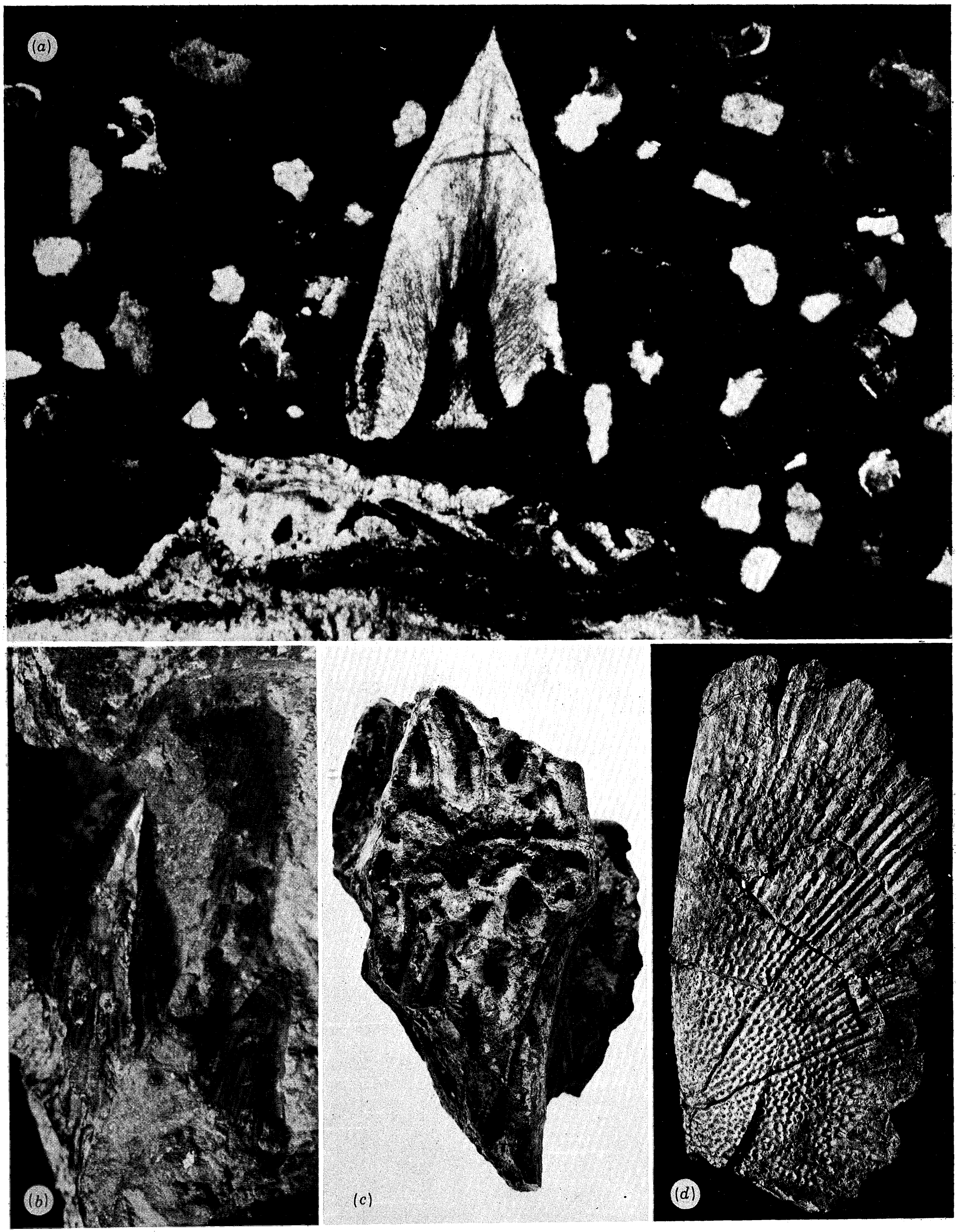


Plate 2. *Siderops kehli* n.gen. n.sp. (*a*) Photomicrograph of a section of a denticle attached to a plate. (Magn. × *ca.* 110.) (*b*) Oblique view of mesial side of right mandibular tusk. (Magn. × *ca.* 2.5.) (*c*) Ventral view of healed break in the left mandible. The lingual side of the jaw is towards the right. (Actual size.) (*d*) Ventral view of QM F10123, an Early Triassic clavicle, to show ornamentation. (Actual size.)

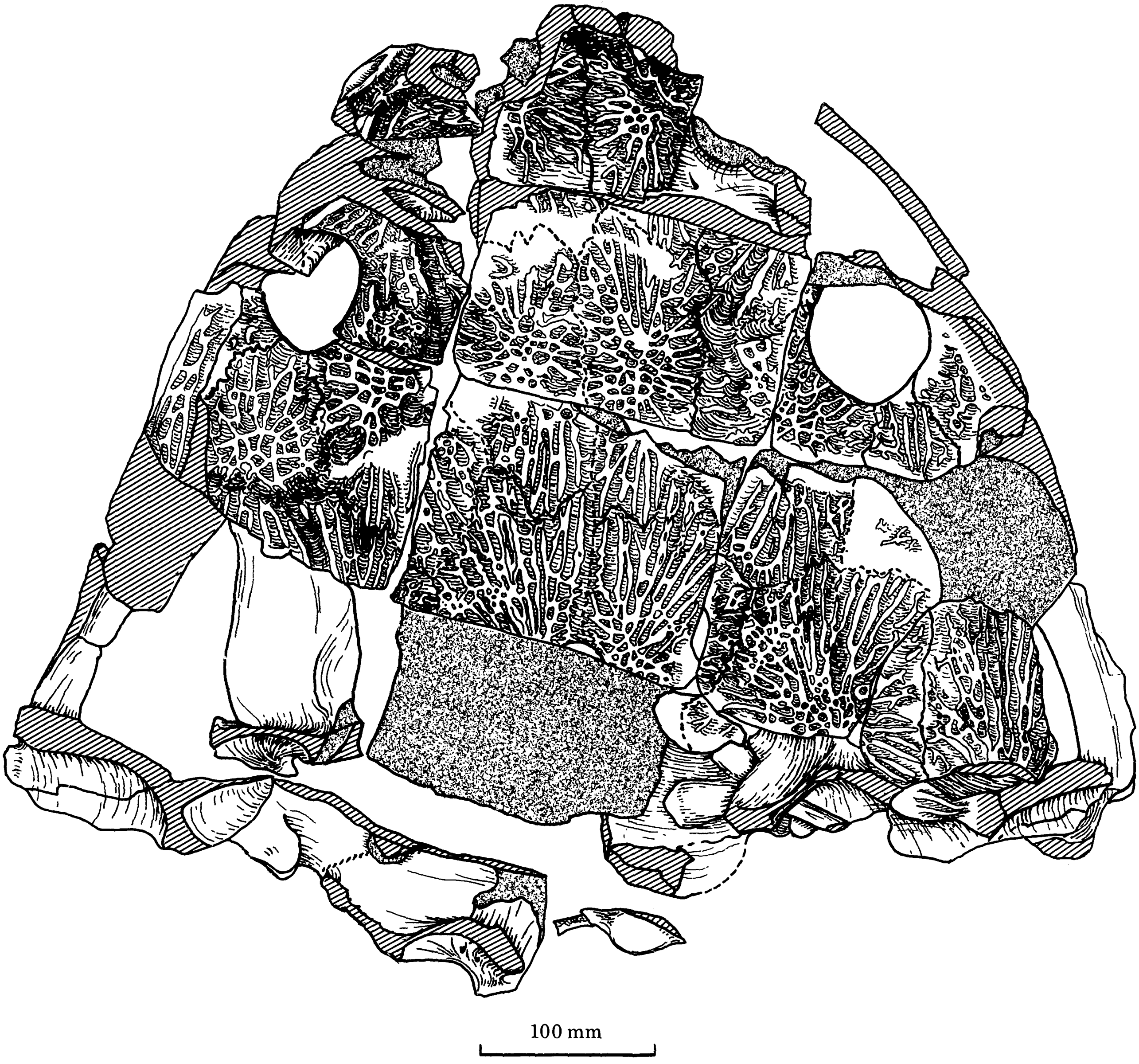


Figure 1. *Siderops kehli* n.gen. n.sp. Dorsal surface of the skull as preserved.

The presence of both mandibles also gives the shape to the posterolateral skull borders. While the entire posterior margin of the skull is restored there can be little doubt that the figured shape is close to the actual one.

The skull midline length, the position of the otic notch and tabular horns, and the shape of the latter, were determined by extrapolation from the palate and occiput. The right exoccipital has been preserved in articulation with the pterygoid and parasphenoid and determines the position of the posterior border of the postparietal, which has been restored just posterior to the vertical column of the exoccipital. Lateral to this, the paroccipital process projects posteriorly from the body of the exoccipital, indicating the presence of a tabular horn. In the family Brachyopidae, which lacks tabular horns, the paroccipital process of the

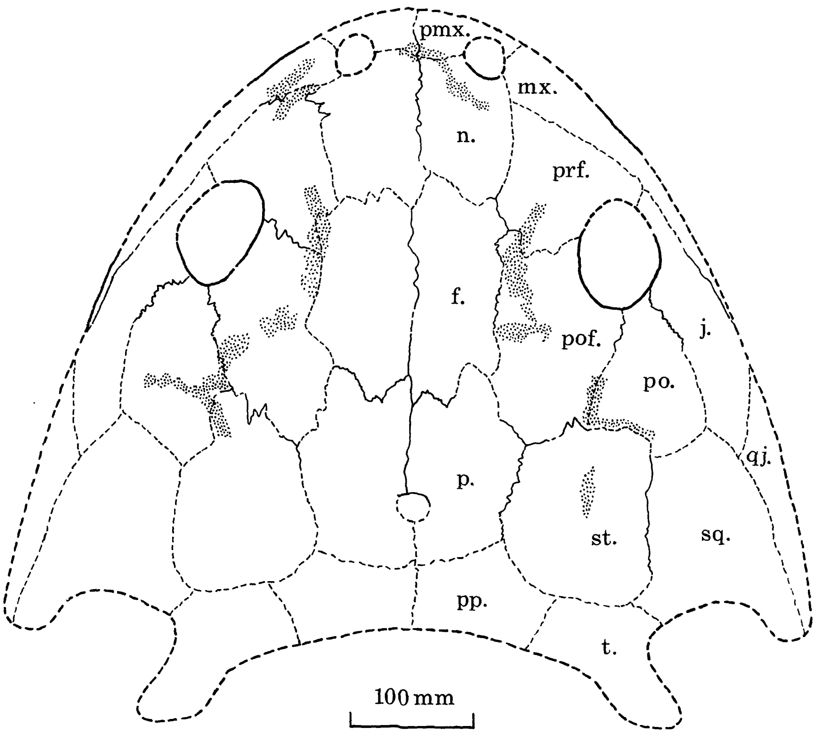


FIGURE 2. *Siderops kehli* n.gen. n.sp. Reconstruction of the dorsal surface of the skull. Abbreviations for this and subsequent figures appear on an outrigger at the end of the paper.

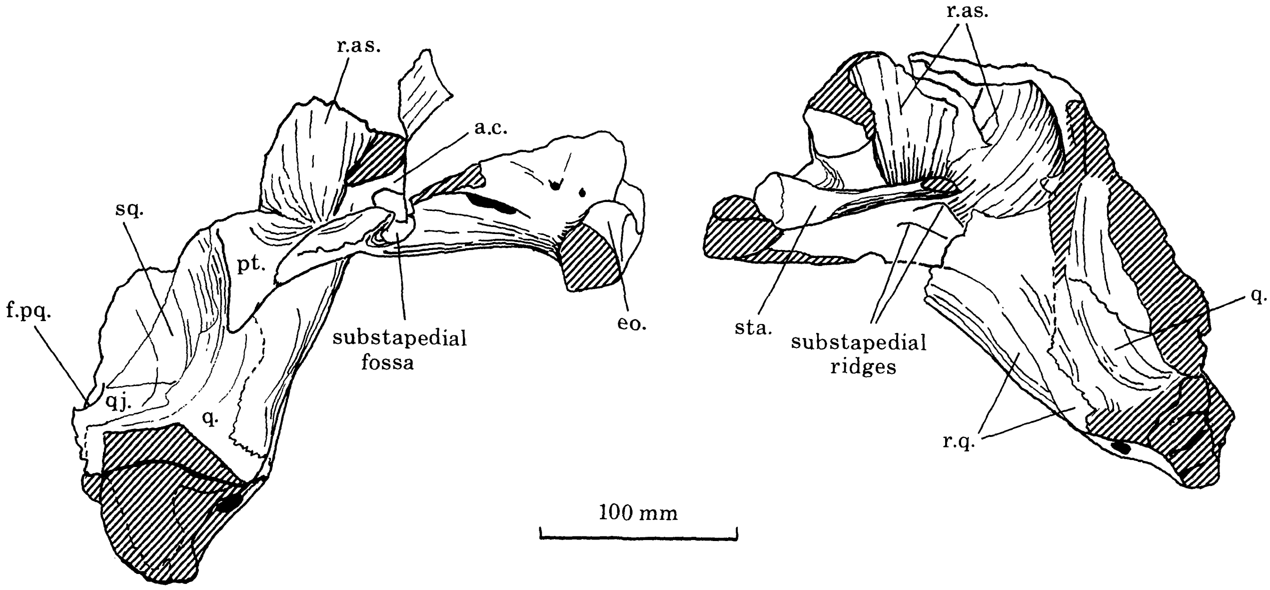


FIGURE 3. *Siderops kehli* n.gen. n.sp. Occipital surface of the skull as preserved.

exoccipital has an anterior slope. In *Siderops* the acute angle between this process and the palate also shows that the tabular horns must have been positioned relatively far to the side. This is confirmed by the right side of the occiput, where the junction of the ascending process of the pterygoid and the occipital part of the squamosal shows a concavity which must have been the border of the otic notch.

Nowhere is there any indication of an anteriorly inclined occiput as seen in all brachyopids and which is especially marked in the later ones such as *Hadrokkosaurus bradyi* (Welles & Estes 1969). An angle in the posterior border of the tabular midway along its length has been restored after *Keratobrachyops australis* (Warren 1981*b*) and *Pelorocephalus* (Rusconi 1951).

There is no evidence of post-quadratojugal, or post-squamosal processes as found in some specimens of *Pelorocephalus*.

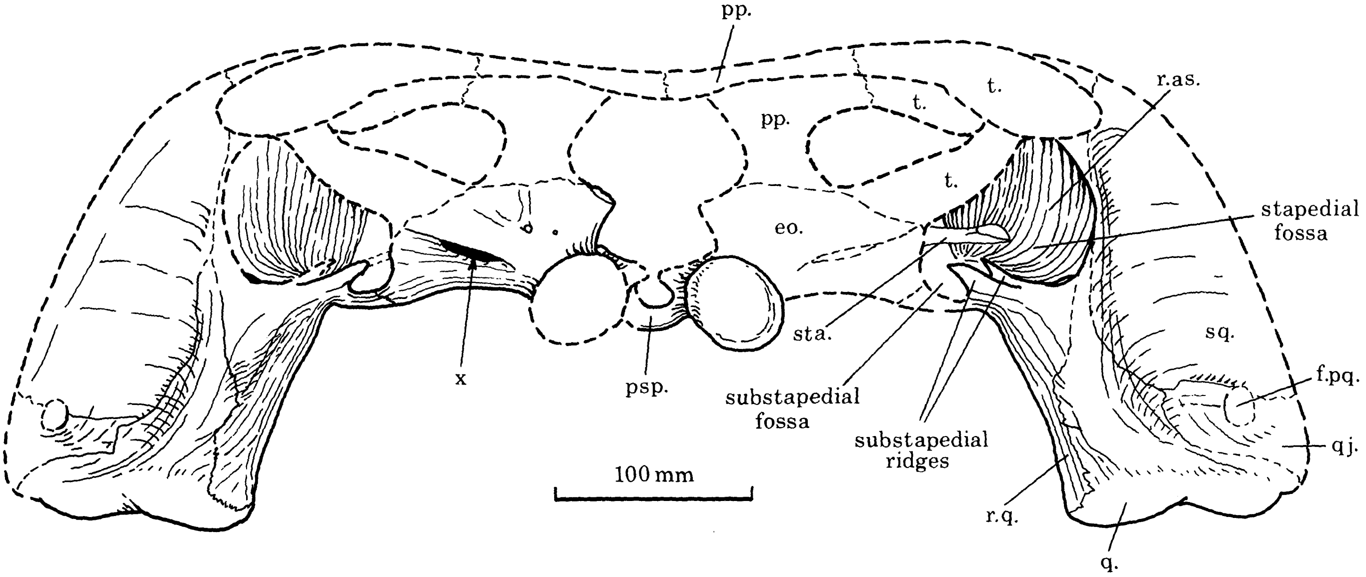


FIGURE 4. *Siderops kehli* n.gen. n.sp. Reconstruction of the occipital surface of the skull.

It was not possible to fully prepare the skull, large areas of matrix being left to support weak bone. In addition, the mandibles have been left in place as removing them would have destroyed the teeth. Hence much of the detail of the tooth row has been filled in by extrapolation.

In the reconstruction only those teeth preserved are drawn and all teeth are shown in outline only. The outline represents the size and shape of each tooth are the jaw level. The height of most teeth was estimated, although some were preserved intact. Presumed replacement teeth are represented by a V of approximately the correct size.

Skull roof

The dermal bones of the skull roof bear ornament which is coarsely pitted at the centre of each bone. Pits on the left postorbital average 8 mm in minimum diameter, but elsewhere they average 5 mm. Away from the bone's centre, pits lead to ridge groove sculpture on all bones preserved. Ridges are tallest towards the front of the skull, on the nasals and left prefrontal and maxilla.

Those sensory canals preserved are broad but irregular, their diameter varying from 8 mm behind the right nostril to 17 mm where they are shared by prefrontal and postfrontal on either side. They were not continuous canals: for instance the interruption seen on the more posterior part of the left postfrontal (figures 1, 2) is real although many of the apparent interruptions elsewhere are in places where the ornament was not preserved. The arrangement of those canals present is similar to that found in other brachyopoids.

Parts of both orbits are preserved. These are broadly oval and differ in shape, the left being larger and less regularly oval than the right. They are small, their $U{:}L$ ratio (midline orbital length/length of skull roof (Welles & Cosgriff 1965)) being 18 (table 2), and are placed laterally but face dorsally. Each is bordered by prefrontal, postfrontal, postorbital and jugal. Although the anterolateral corner of neither orbit is preserved, the angle of its sutures elsewhere indicates that the maxilla probably does not enter the orbital border.

Apart from a small portion of the posterior border of the right nostril, the shape and size of the nostrils are conjectural as is the distribution of sutures around them.

No interpremaxillary foramen was found.

The anterior edge of a large pineal foramen is preserved: in life this must have measured at least 17 mm in diameter. On the ventral surface of the parietal the bone tapers upwards towards the edge of the pineal foramen. Also on this surface two ridges lead anteriorly on slightly convergent courses from a position a few millimetres lateral to each side of the foramen's edge.

The skull roof shows the usual brachyopoid arrangement of dermal bones. In common with all Mesozoic temnospondyls there is no intertemporal, and the lacrimal is absent as in other brachyopoids.

The skull table posterior to the pineal opening is short, so that the postparietals must have been less than half as long as the parietals, and the body of the tabulars is also short. Although these areas are not preserved, there can be little doubt as to their real proportions. The position of the rear border of the postparietals is determined by the occiput (as shown on p. 7, and it would be most unusual to have the postparietal–parietal suture positioned nearer to the pineal foramen than it is in the reconstruction.

Occiput

In occipital view, the skull has the typical brachyopoid inverted U shape, formed chiefly by a downturning of the quadrate rami of the pterygoids. A well developed brachyopoid squamosal–quadratojugal trough is present. However, both sides are incomplete in this area and the sutures are indistinct. At the top of the trough on the medial side the squamosal sutures with the ascending process of the pterygoid, the suture continuing ventrally to the level of the palate. At this point a well ossified dorsal extension of the quadrate separates squamosal from pterygoid to form the median edge of the squamosal–quadratojugal trough. The suture between quadrate and pterygoid is anterior to the level of the trough, a condition typical of chigutisaurids in contrast to brachyopids where the quadrate ramus of the pterygoid extends as a flange posteriorly to the quadrate.

As the lower jaw of *Siderops* is in place the quadrate condyles are partly obscured by the articular. They can be determined to have the typical temnospondyl shape, that is a median, larger condyle with laterally a smaller condyle aligned with the posterior edge of the median condyle so that the two meet at an angle to form a screw-shaped articulating surface which projects little if at all below the level of the adjacent dermal bones. Internally the quadrate underlaps both the squamosal and pterygoid for several centimetres on either side, and extends a further 20 mm more dorsally to end at an 8 mm deep shelf. Just above the middle of the condylar area this internal surface of the quadrate has a well developed ridged muscle scar.

A small quadratojugal is partly preserved lateral to the quadrate. The suture between it and the squamosal above it runs horizontally across the squamosal–quadratojugal trough from the paraquadrate foramen. This foramen, the median edge of which is preserved on both sides of the skull, is thus shared by quadratojugal and squamosal.

The left exoccipital is almost complete but with most of the condyle missing; by contrast, the articular part of the condyle only is preserved on the right. As preserved, the right condyle is rounded, inclines a little towards the midline, and is continuous medially with a thin strip of parasphenoid which has just above it a small submedullar process. When the condyle is placed in articulation with the atlas, this process and the more ventral strip of parasphenoid neatly border the midline notochordal foramen between the two atlantal facets. The condyle proper is positioned just posterior to the parasphenoid.

The left exoccipital has a strongly developed lamellar process which is angled a little anterior of dorsal and is not delineated from the vertical column (Bystrow & Efremov 1940). The vertical column rises almost vertically from just behind the condyle, establishing the upright nature of the occiput. When viewed from above, the bone narrows to a ridge which in turn thickens laterally into the paroccipital process. Although the exoccipital part of the paroccipital process is incomplete, it can be seen to subtend an unusually acute angle with the palate, indicating that the tabular horn was placed well laterally.

The paroccipital process is directed a little posteriorly towards the position of the tabular horn. Lateral to the paroccipital process the palatal portion of the exoccipital terminates as the median border of a previously unreported structure, the substapedial fossa (see *pterygoid* below). Three foramina are visible in the exoccipital. Two lie in the V between the vertical column and the paroccipital process. The third, a much larger (21 mm × 4 mm) foramen, presumably for nerve x, lies below and parallel to the lower border of the paroccipital process. In internal view a round 14 mm foramen appears to be the entry of all three of these foramina into the exoccipital.

Both pterygoids are almost complete. From behind, their deeply downturned quadrate rami can be seen ending at marked interdigitating sutures with the quadrates. Each has a well developed ascending process which is best preserved on the right side (figures 5, 6). The process fans out dorsally from a base behind the distal end of the stapes. Its median edge is formed by a massive ascending column (dorsal column of the ascending process of Warren (1981 *b*) which increases in thickness from a 10 mm base to 30 mm before it reaches the level of the skull roof. In medial view it can be seen to continue anteriorly as a flange of bone which terminates just anterolaterally to the proximal end of the stapes. In anterior view this flange is seen to continue the convex rear margin of the ascending ramus as a concave curve, resulting overall in a sigmoid shape. The ascending column bulges out from the posteromedial corner of the posterior face of the ascending ramus so that the smoothness of the curve in this view is interrupted. In medial view it can be seen that the widest part of the ascending column may not have contacted the skull roof. Instead, a rounded area of apparently finished bone is directed medially from two-thirds of the way up the ascending column to the level of the skull roof. The dorsolateral edge of this rounded area forms a T with the main, lateral part of the ascending ramus. The area may have buttressed the pterygoid against the lateral wall of the braincase.

In posterior view it can be seen that the posterolateral edge of the ascending process curves down to meet the body of the pterygoid: this is the stapedial fossa (Colbert & Cosgriff 1974) (excavatio tympanica Bystrow & Efremov 1940). Here the pterygoid is drawn out into two parallel, previously undescribed substapedial ridges. The lower of these can also be seen partly preserved on the left hand side. Its lower edge is continuous with the ventral surface of the body of the pterygoid. Its upper edge rises as a flange which approaches the most ventrolateral part of the exoccipital (this detail is preserved on the left) to form the bottom and sides of a well defined hollow, the substapedial fossa. This fossa may have been functionally closed from above. The more dorsal of the substapedial ridges, which is only preserved on the right side, is separated from the ventral ridge by a deep posteriorly facing trough which we term the intertoral fossa. The dorsal surface of this ridge is a ventral continuation of the ascending process of the pterygoid and thus forms the floor of the stapedial fossa. Exiting from the postero-ventrolateral corner of the stapedial fossa, lateral to the upper substapedial ridge, is a half canal. This structure, which we have called the lateral pterygoid canal, in fact links the cavity of the stapedial fossa with the intertoral fossa. Both it and the intertoral fossa were undoubtedly enclosed in life. Medially the dorsal substapedial ridge ends 3 mm below the stapes, 10 mm from its distal end. On the dorsal surface of the body of the pterygoid is another smaller anteriorly directed ridge which also seems to end beneath the stapes but at the proximal end.

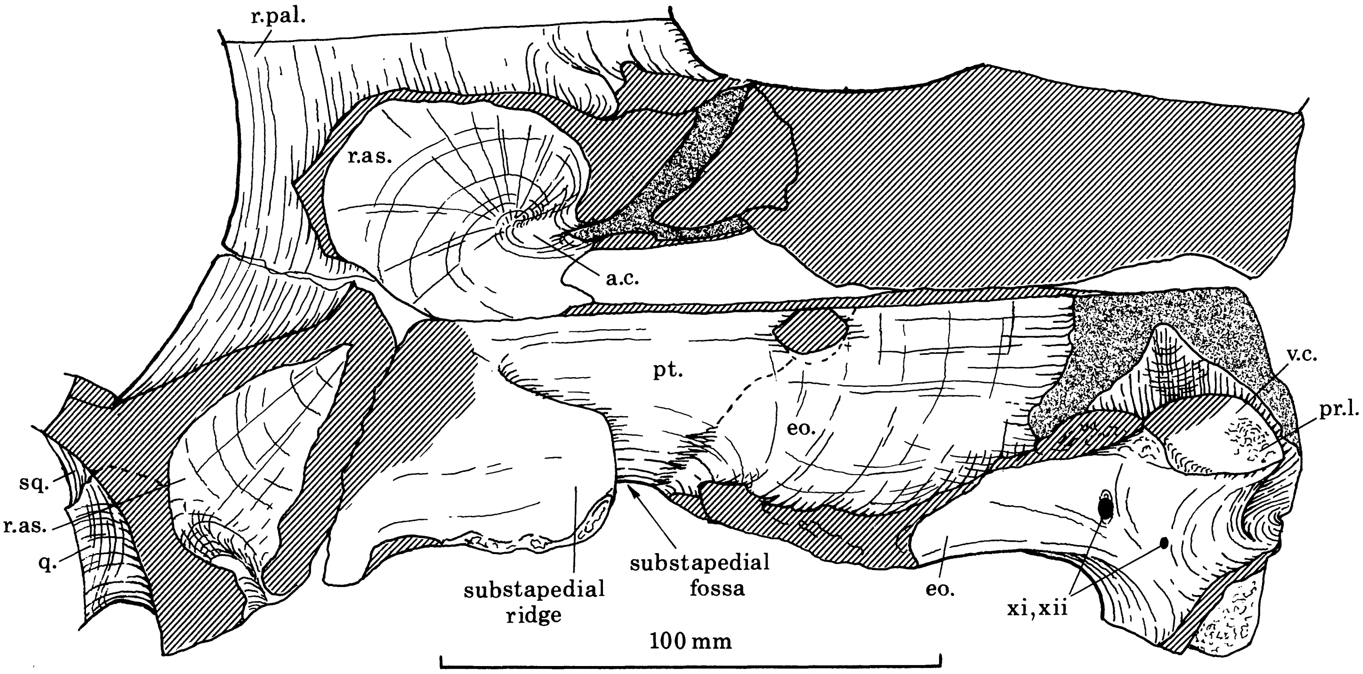


FIGURE 5. *Siderops kehli* n.gen. n.sp. Dorsal view of the left pterygoid and exoccipital.

The right stapes (figure 6) and a small part of the foot of the left stapes (figure 5) are preserved. Distally the stapes is narrow and oval in cross section. An elongate stapedial foramen enters the dorsal surface 30 mm from the distal end. Proximal to the foramen the bone expands in size and divides into two, forming a smaller lateral process and a massive medial process. The lateral process is equivalent to the processus basalis described by Bystrow & Efremov (1940) in *Benthosuchus sushkini* and the 'processus antero-interne ou accessoire' described by Dutuit (1976) in *Metoposaurus ouazzoui*. In *Siderops* this process lies just posteromedial to the anteromedial flange of the ascending process of the pterygoid. In anterior view the process is subtriangular with the apex of the triangle pointing ventrally. The second, medial process, is equivalent to the 'processus otique ou principal' of *M. ouazzoui*.

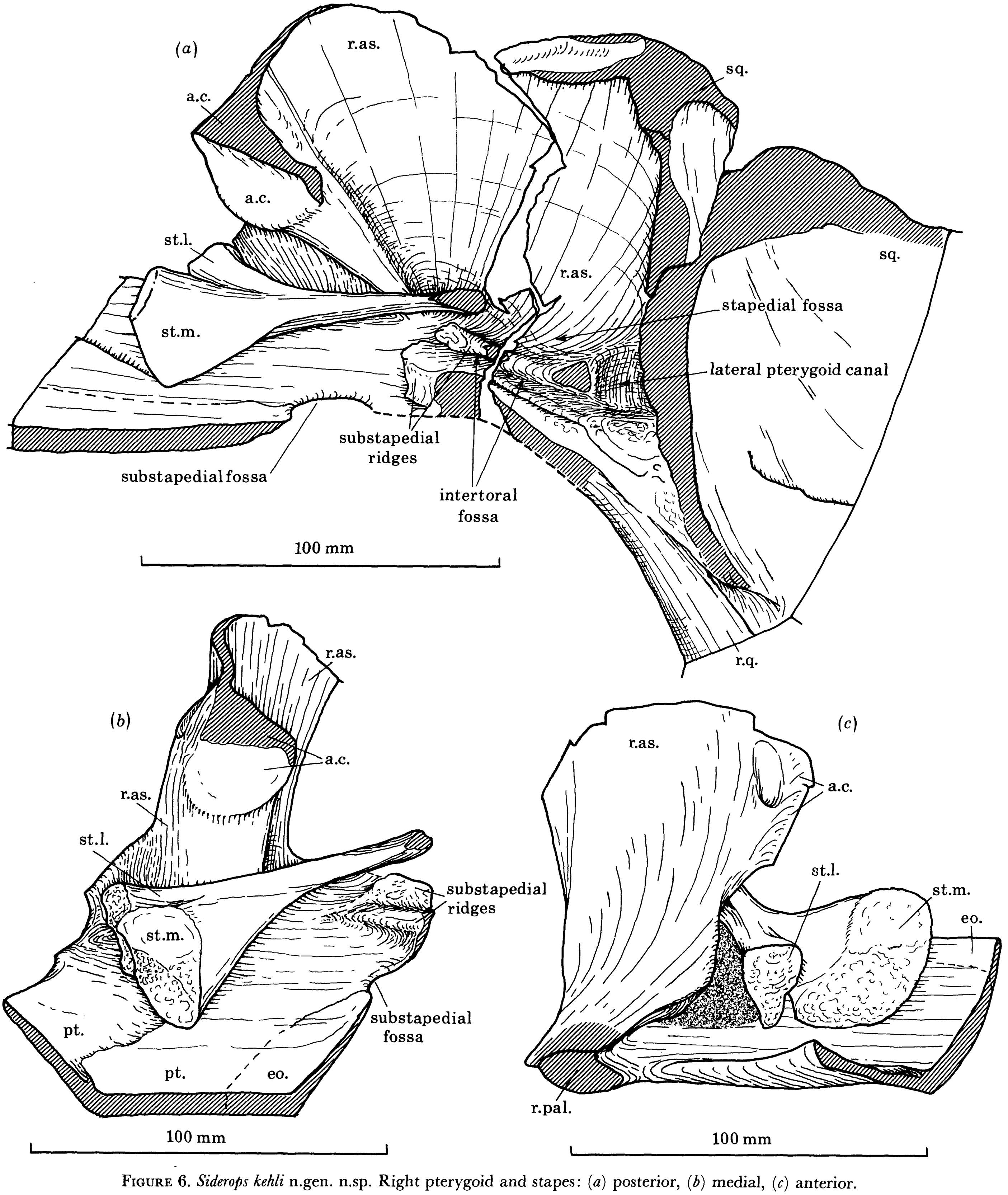


FIGURE 6. *Siderops kehli* n.gen. n.sp. Right pterygoid and stapes: (*a*) posterior, (*b*) medial, (*c*) anterior.

Both left and right epipterygoids were found but neither was in its natural position. The right epipterygoid (figure 7) consists of an ascending process and a stout triangular base. The former is dorsoventrally elongate where it arises from the basal process, narrows distally and then expands into a longitudinally oval surface which must have abutted the braincase. The base consists of three areas. Beneath the ascending process is a medial process whose articular surface curves dorsally away from the plane of the base. Posterolaterally there is a much narrower area, the lateral process, while between this and the medial process is a right-angled process which is directed anteriorly. The anterior and medial processes are separated by a deep epipterygoid notch.

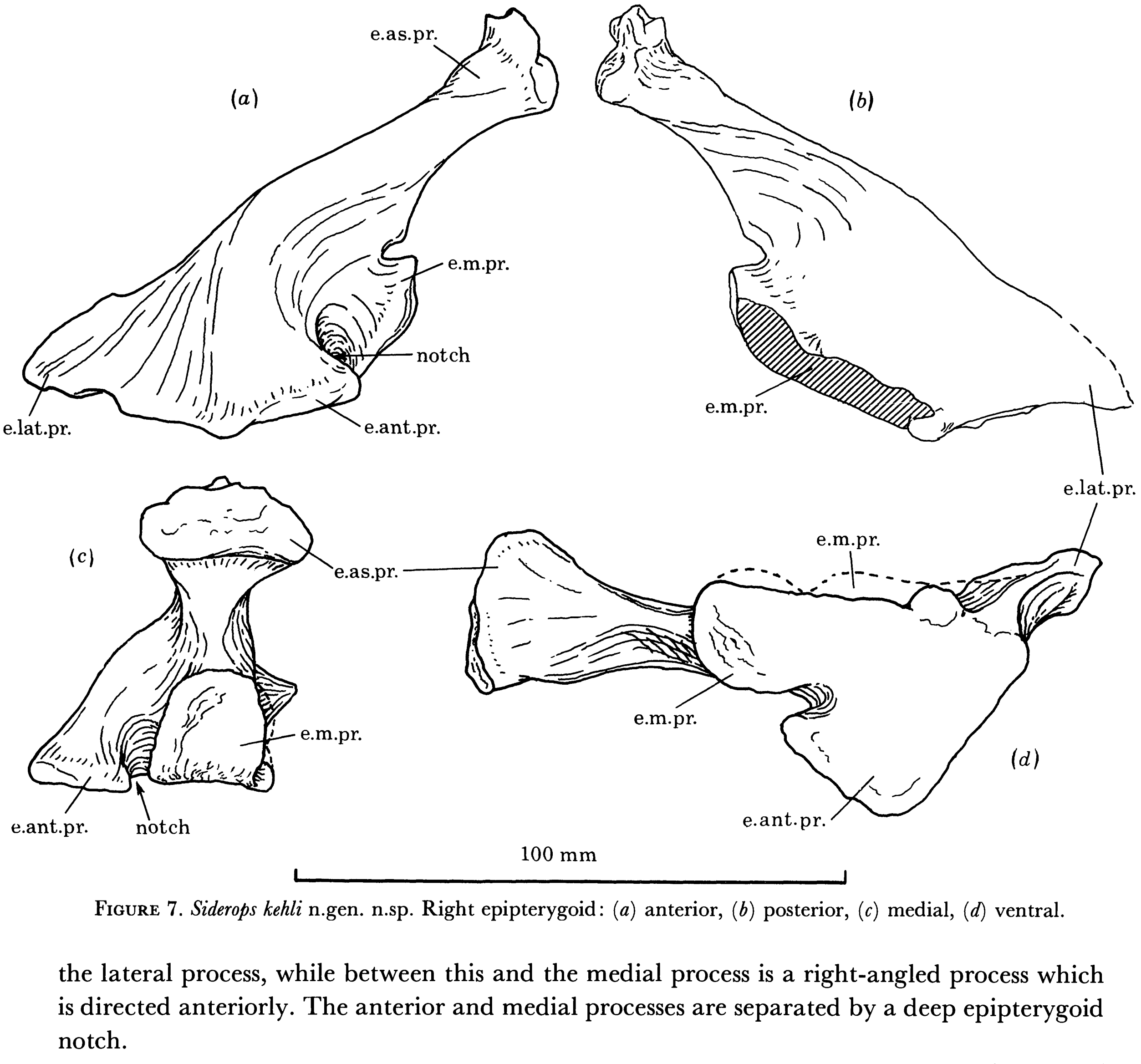


FIGURE 7. *Siderops kehli* n.gen. n.sp. Right epipterygoid: (*a*) anterior, (*b*) posterior, (*c*) medial, (*d*) ventral.

Two articulating bones forming a free-floating element were excavated from within the oral cavity (figure 10). We are unfortunately not completely certain of the orientation of these elements, but it is known that they were preserved in a transverse position with the larger subunit a little posterior to the smaller. These bones presumably represent some part of the visceral skeleton. They appear to be midline elements although they are not perfectly bilaterally symmetrical. Their combined longitudinal length is 170 mm or one-third of the midline skull length.

The larger element is broad but shallow at its free end, tapers towards its junction with the smaller unit and bears on one side in a medial position a deep longitudinal ridge. This ridge projects beyond the free edge of the bone. The smaller element is phalangeal in shape but with a slight ridge in the same position as the ridge on the larger bone.

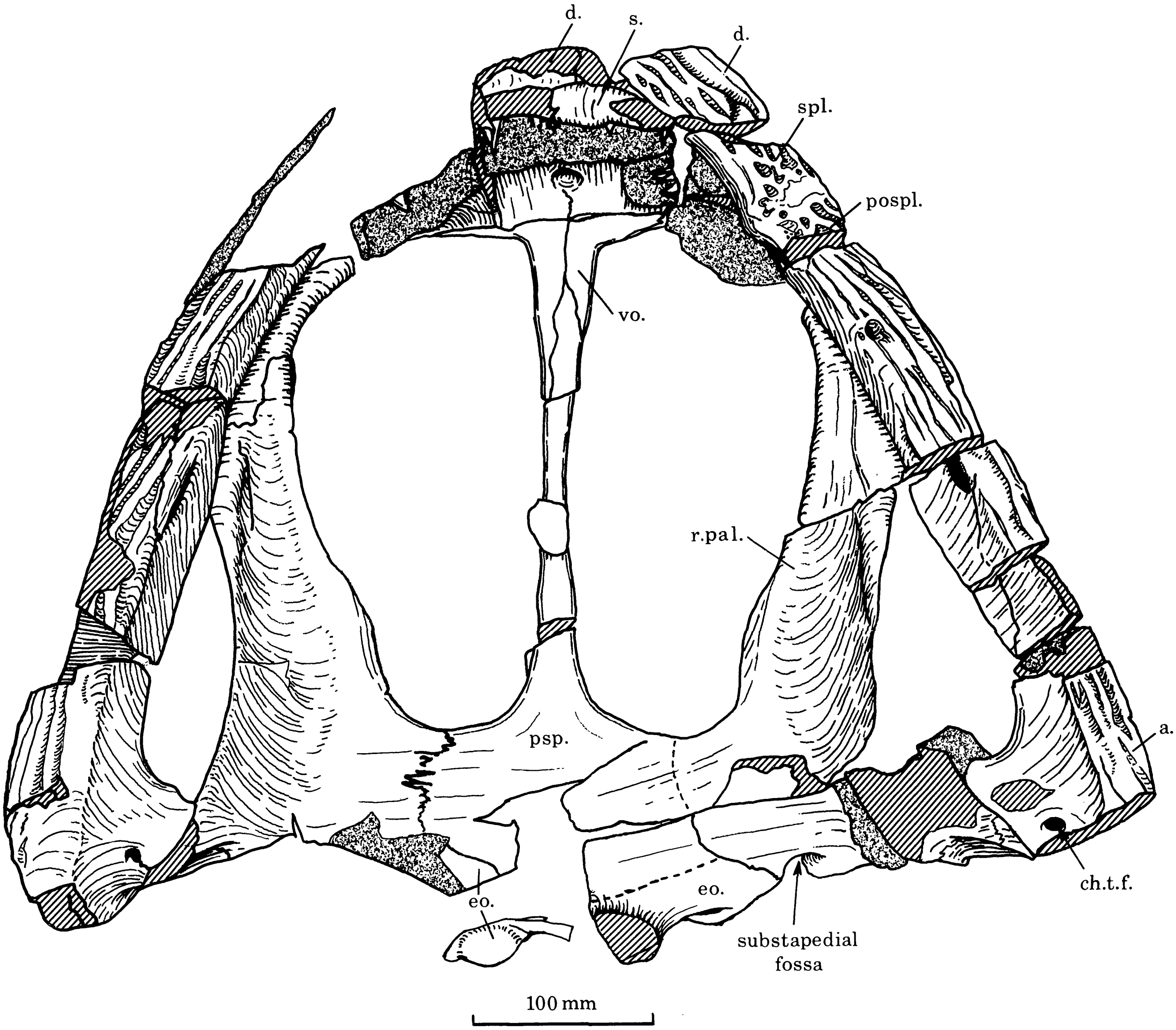


FIGURE 8. *Siderops kehli* n.gen. n.sp. Ventral view of the palate and mandible as preserved.

Palate

The openings in the palate are not unusual. A well developed anterior palatal vacuity is present but its anterior border has been lost. At the back of this vacuity the vomers are swollen around the bases of the transvomerine teeth, the swelling projecting into the vacuity so that its ventral aspect is reduced in size. Laterally the walls of the vacuity slope upwards from a sharp ventral lip towards the swollen bone surrounding the vomerine tusks. The choanae are suboval in shape. On the animal's left side the presence of a well defined palatine–maxillary

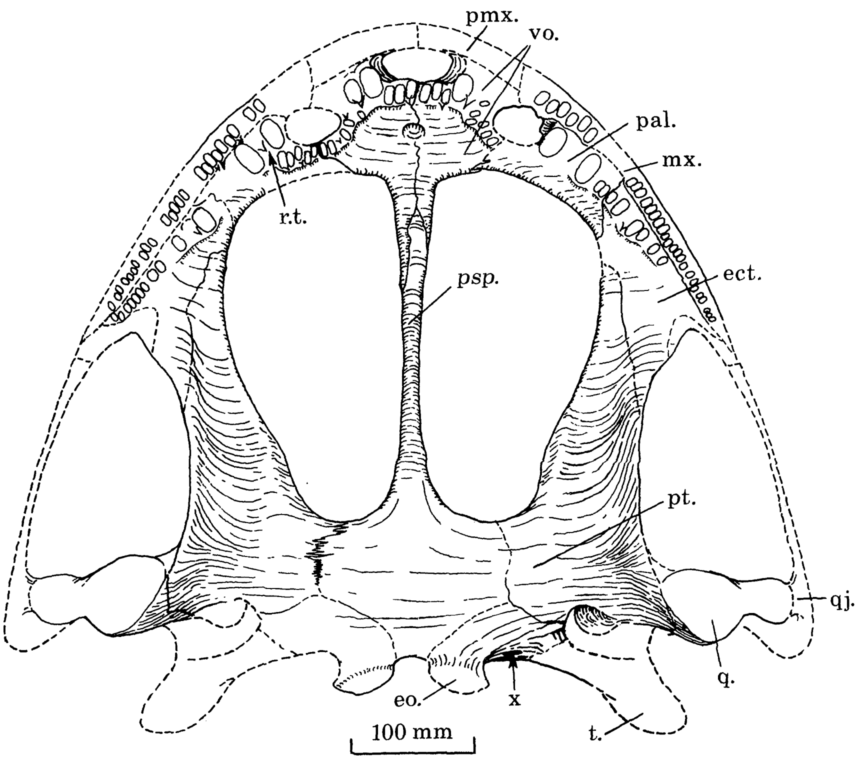


FIGURE 9. *Siderops kehli* n.gen. n.sp. Reconstruction of the palate.

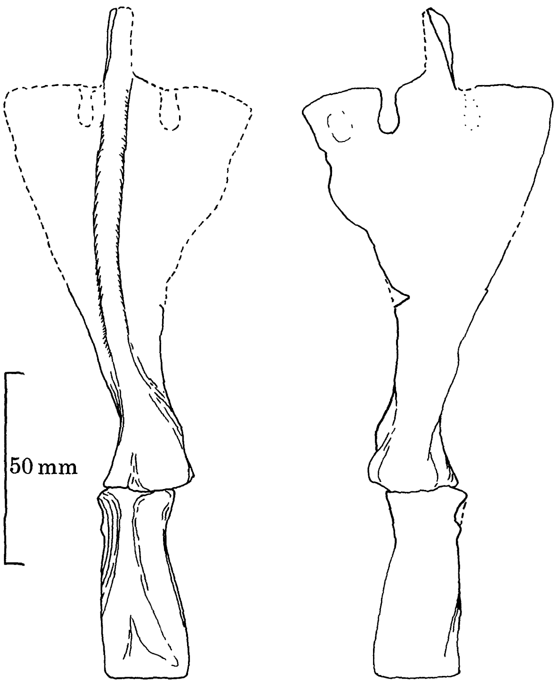


FIGURE 10. *Siderops kehli* n.gen. n.sp. Additional visceral elements.

suture shows that the maxilla formed a large part of the lateral border of the choana. In the midline between the vomers is a well developed pit in a similar position to the vomerine foramen figured by Chernin (1977) in *Batrachosuchus browni.*

The arrangement of the dermal bones of the palate is typical of brachyopoids: any points of interest are set out below. The exoccipitals form a broad suture laterally with the pterygoids, thus excluding the parasphenoid from contacting the rear margin of the palate at this point. However, the parasphenoid is exposed on the rear margin of the palate by the failure of the left and right exoccipitals to form a midline suture.

The cultriform process of the parasphenoid is extremely narrow. At its anterior end the ventral exposure of the cultriform process does not reach the level of the front border of the interpterygoid vacuities, but ends at a point between posteriorly directed processes of the left and right vomers. In cross section, the cultriform process is semicircular, the centre of the circle being dorsal. The bone of the process is extremely thin posteriorly (2 mm) but thickens anteriorly to 6 mm at the level of the most posterior vomerine projection. A more anterior section of the vomerine plate shows a broad re-expansion of the cultriform process. This expansion lies largery above the vomers but is overlapped laterally by thin vomerine processes. The anterior end of the cultriform process thus lies in a pocket of the vomer.

The ectopterygoids have a small exposure on the lateral margin of the interpterygoid vacuity. Although sutures in this area are not clear, it seems that a distinct process of the ectopterygoid extends posteriorly to form part of the border of the subtemporal vacuity. Beside this process there appears to have been an alar process of the jugal and this also borders the subtemporal vacuity.

Dentition

No premaxillary teeth are preserved.

On the maxilla, those teeth preserved vary in height (measured below the jaw line) from 7 mm near the back of the maxilla to approximately 27 mm lateral to the choana. Their bases are not arranged in a straight line, alternate teeth often being displaced lingually with respect to their neighbours.

Inside the maxillary tooth row is an almost continuous row of palatal teeth which are all embedded in a wide ridge of bone which projects below the level of the maxilla thus delineating the palatal tooth bearing area from the more medial parts of the palate (figures 9, 11).

The palatal teeth show a great range of sizes. Smallest are the most posterior ectopterygoid teeth, which are similar in height to the adjacent maxillary teeth (7 mm). Also quite small are the crescent of teeth bordering the median side of each choana; these vary in height from 14 to 20 mm. The other palatine teeth appear to have been much longer (around 30 mm), while some of the tusks are enormous. The smallest (ectopterygoid) tusk preserved is 39 mm tall, and the largest (vomerine) tusk measures an estimated 70 mm.

Despite the disparity in sizes, all teeth are remarkably uniform in shape (figure 14). In section, each is squarely elliptical at the base, the long axis of the ellipse being always perpendicular to the jawline or, in the case of the teeth bordering the choana, perpendicular to the choanal margin. A typical labyrinthodont convoluted pattern of dentine and enamel can be seen at this level, its complexity varying presumably with the age of the tooth (Bystrow 1938*b*). About two-thirds of its height above the base the tooth narrows and becomes circular in cross section. At this level the convolutions give way to an outer ring of enamel, overlying a thicker dentine layer, and an inner pulp cavity. Near the tip each tooth is solid in section. This structure is typical of teeth in the larger labyrinthodonts although these more often have tusks that are rounded at the base.

All teeth are curved, especially towards the tip, the direction of curvature being inwards (lingual) and thus in line with the long axis of their elliptical bases. In the teeth bordering the choana, the perichoanal teeth, this curvature is such that the tip of the tooth lies outside the limits of the tooth base when viewed from above. In addition, each tooth, including the tusks, has mesial and distal ridges running down the tooth from its incurved point and ending well above the base of the tooth. These ridges give a lance-like shape to the tip of the tooth.

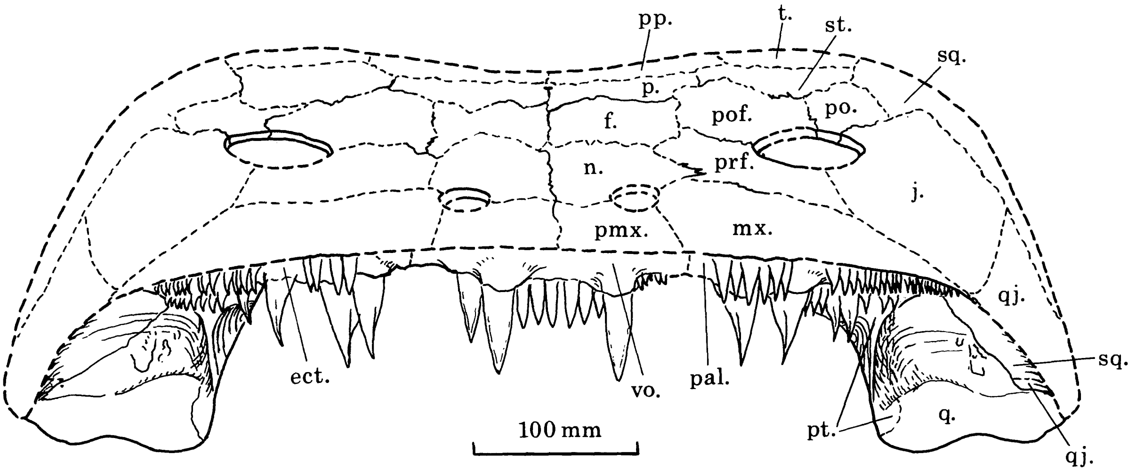


FIGURE 11. *Siderops kehli* n.gen. n.sp. Anterior view of the reconstructed skull.

In several places in the tooth rows apparent replacement teeth have been preserved. These appear as Vs of unconvoluted dentine and enamel usually lying in the same plane as the jaw. A few, however, have the same orientation as mature teeth although their bases are several millimetres above the jaw. Several of the smaller teeth are lying lingual to mature teeth, implying that they were in fact developing within the dental lamina, and had not yet moved labially onto a mature tooth locus.

During mechanical preparation a number of denticles often attached to thin bony sheets were found in the same area as the millepedes (see *Associated fauna* above), that is in the interface between sandstone containing little iron, and banded ironstone. Although no denticles were found attached to any skull bone they appear to be a part of *Siderops* rather than some animal preserved with the labyrinthodont. Denticle patches were found in several places lingual to the palatal rooth row and also associated with the left mandible above the middle coronoid bone. All denticles associated with the palate face ventrally while those associated with the mandible face dorsally, one reason that we consider them to be a part of *Siderops*.

Denticles that are well enough preserved to be measured average 1.4 mm in height and 0.7 mm in basal diameter; that sectioned was 0.8 mm tall (plate 2*a*).

Each denticle is conical, with the apex more acuminate than in denticles associated with the palate in other labyrinthodonts. In section it can be seen that the denticle is tooth-like, consisting of an inner pulp cavity, surrounded by dentine with an outer layer of enamel. All denticles arise from a thin sheet of bone which is separated from the underlying labyrinthodont bone by a variable amount of matrix. Sometimes this gap is a few millimetres, sometimes several centimetres. In places, for example behind the vomerine teeth bordering the anterior palatal vacuity, the sheet of bone bearing denticles appears to have been continuous rather than broken up into a series of denticulate plates. In other places its continuity cannot be determined.

In *Siderops*, then, there appears to have been a denticulate layer of bone, or several plates of bone, embedded in the skin of the palate beside the palatal teeth, and on the lingual side of the mandible.

Comparisons

Siderops's coarse ridge–groove ornament is of the commonest sort found in labyrinthodonts. In this it resembles *Keratobrachyops australis* (Warren 1981 *b*) although the *K. australis* ornament is much finer, but it differs markedly from the Argentinian chigutisaur *Pelorocephalus* (Rusconi 1951) whose ornament is uniformly pitted. The orbits are small as in all adult chigutisaurids, the large orbits of *K. australis* being considered to be a juvenile feature.

The pineal foramen in *Siderops* is larger relative to skull length than in the young specimen of *Keratobrachyops*, where a large pineal is not unexpected, and much larger than in *Pelorocephalus*. Especially large pineal foramina are also present in the brachyopids *Blinasaurus henwoodi* (Cosgriff 1965) and *Hadrokkosaurus bradyi* (Welles & Estes 1969). The position of the foramen well posterior to the orbits is typical of brachyopoids but *Siderops* shows the pineal foramen nearer to the posterior skull margin than in other genera. Ridges beneath the pineal in *Siderops* are similar to the situation described by Howie (1972 *a*) in '*Brachyops*' *allos*. They effectively delineate a pineal area in a manner similar to that found in many modern lizards.

The arrangement of the skull roofing bones is typically brachyopoid. The short postpineal skull table, while shared by *K. australis*, is not found in *Pelorocephalus*, where the postparietals are almost the same length as the parietals and the body of the tabulars is similarly long. On the only specimen of *Pelorocephalus* figured with sutures (Rusconi 1951, fig. 65), the arrangement of some skull roofing bones is unique and may need revision. For instance, in no other labyrinthodont does the postfrontal meet the postparietal or the tabular, the usual arrangement being the separation of these bones by a parietal–supratemporal suture.

The absence of the lateral parts of the quadratojugals in *Siderops* may be an accident of preservation. It is possible, however, that in some of the larger deep-skulled labyrinthodonts they were emarginated to accommodate adductor muscles. The area was not preserved in *Hadrokkosaurus bradyi* (Welles & Estes 1969) but is present in the Argentinian chigutisaurids which were also large.

The paraquadrate foramen, which is shared by the squamosal and quadratojugal in *Siderops*, in other labyrinthodonts is more often wholly contained by the quadratojugal: examples are *Dvinosaurus primus* (Bystrow 1938 *a*) and '*Brachyops*' *allos*. The foramen is not illustrated in other brachyopids but in the chigutisaurid *Pelorocephalus* it is figured by Rusconi (1951, fig. 68), who shows a suture between the foramen and the lateral skull border. This must be the squamosal–quadratojugal suture as it is in *Siderops*.

The well developed typical temnospondyl quadrate found in *Siderops* is also present in *K. australis* and *Pelorocephalus*. In the Brachyopidae, however, the quadrates are usually restored as a single subtriangular unit which projects well below the level of the quadratojugal and pterygoid. This is the case in the partly preserved quadrate of *Batrachosuchus concordi* described by Chernin (1977). '*Brachyops*' *allos* does not fit this brachyopid pattern, having a well developed double condyle like *Siderops*.

The occipital condyles do not project far behind the parasphenoid, so that the occiput lacks the anteriorly sloping vertical and paroccipital processes found in brachyopids. In this vertical occiput *Siderops* resembles the other chigutisaurs, the nature of the occiput presumably being correlated with the retention of the tabular horns.

Of the several ridges and grooves seen in the substapedial area of the occipital part of the pterygoid, only the more dorsal substapedial ridge has been seen elsewhere. It is in the same position as the thickening of the pterygoid described in *K. australis* (Warren 1981*b*, figs 5*A*, 7) and figured but not labelled by Rusconi (1951, fig. 68) in *Pelorocephalus*. It has not been recorded elsewhere.

The stapes itself is well developed in *Siderops*, the otic process in particular being more massive than in any other labyrinthodont.

The epipterygoid is also large and is closest in shape to that of *Metoposaurus ouazzoui* (Dutuit 1976) but lacks the otic process. The epipterygoid of *Keratobrachyops australis* is less robust than it is in *Siderops*, with an ascending process that is relatively more elongate with respect to the base.

The two articulating free-floating visceral elements cannot be identified with certainty. One is probably homologous with the copula and the other with the stile, both of these elements being found in a median position in the hyoid apparatus of urodeles. The single median element preserved in perennibranchiate labyrinthodonts is usually deemed to be the copula (Boy 1974). As far as we are aware, in no other temnospondyl have two median elements been preserved. Also, those with one element have in addition a series of basibranchials and ceratobranchials, confirming their perennibranchiate nature. The fact that median elements only were found in *Siderops* indicates that the animal was not perennibranchiate but may have had a well developed hyoid apparatus, functioning presumably to support a tongue.

The shape of the openings in the palate is similar to that found in *Keratobrachyops australis* except that the reniform shape of the anterior palatal vacuity cannot be established. Entry of the maxilla into the lateral border of the choana is found in the other chigutisaurs and paralleled by *Hadrokkosaurus bradyi* (Welles & Estes 1969) among the brachyopids.

The broad exoccipital–pterygoid suture seen on *Siderops's* palate parallels the situation in some brachyopids but is not found in *K. australis* and may be used as a character to separate the two Australian chigutisaurid genera.

Siderops has an extremely narrow cultriform process of the parasphenoid which differs from the wide processes seen in published illustrations of *Pelorocephalus* (see, for example, Rusconi 1951, figs 5, 6, 7) and the juvenile specimen of *K. australis* (QM F10115). In the larger specimen of *K. australis* (QM F10116) the cultriform process has narrowed and a similarly narrow process is seen in a specimen of *Pelorocephalus* at Harvard (MCZ 203.58m), and in the specimen of *Pelorocephalus* on loan to us (AMNH VP7606). *Siderops* and *Pelorocephalus* (MCZ 203.58m) are similar also in the relationship between the anterior end of the cultriform process and the vomers when seen in ventral view. *K. australis* differs from these specimens in that the cultriform process ends well anterior to the interpterygoid vacuities.

Lance-tipped labyrinthine teeth have been found in some anthracosaurs, for example *Anthracosaurus russelli* as described by Panchen (1977*a*), and in loxommatids (Beaumont 1977), and in some crossopterygian fish. Lance-shaped teeth apparently have not previously been described in Mesozoic temnospondyls. An exception is an isolated tooth of very similar shape, found associated with stereospondylous vertebrae, described as *Hercynosaurus carinidens* by Jaekel (1914). Similar curved teeth with longitudinal ridges are found in many amniote carnivores, notably varanid lizards, in gorgonopsids (Kemp 1969) and in mammals of the order Carnivora.

Although palatal denticles are commonly found in labyrinthodonts, none have been reported associated with but free from attachment to pterygoids, vomers, palatines or ectopterygiods as they are in *Siderops*. Also in no other labyrinthodont have such small denticles been found.

Van Hoepen (1915) has reported denticulate plates occupying the space between the pterygoids in *Uranocentrodon senekalensis*. These were not found above the bones of the palate, many of which bore denticles with a labyrinthine cross section. Van Hoepen describes the denticles as being 'about the same size as those on the pterygoids' (p. 135). Thus the denticles found in *Uranocentrodon* differ from those of *Siderops* in being much larger, and in their location in the interpterygoid vacuities rather than above the palatal bones. *Siderops* may have had interpterygoid denticulate plates as well as those associated with the ectopterygoids, palatines and vomers: if so they were not preserved, or were lost in preparation. Nevertheless these labyrinthodonts are the only two in which plates of thin bone free of attachment and bearing denticles have been found.

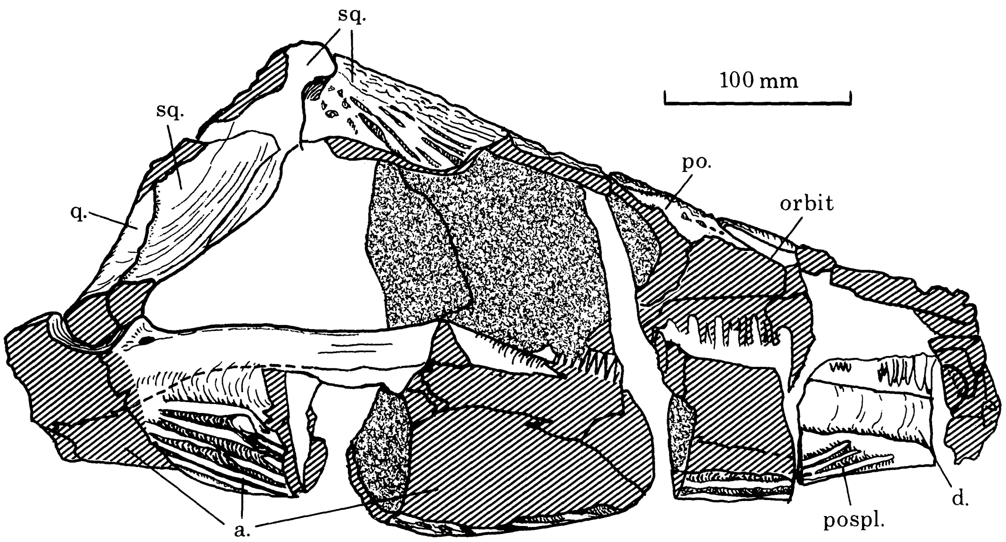


FIGURE 12. *Siderops kehli* n.gen. n.sp. Lateral view of the right side of the skull and mandible as preserved.

Jarvik (1954) described an extensive series of denticulate plates associated with the neural endocranium and other parts of the visceral skeleton of *Eusthenopteron* and compared them with similar plates found in the mucous membrane of the mouth and pharynx and of some extinct osteichthyes. The smaller among *Eusthenopteron's* plates look similar to those from *Siderops*.

Mandible (figures 8, 12, 15, 34)

Both mandibles are missing their retroarticular processes and a large part of their external, ornamented surfaces while the right mandible was only preserved posterior to the coronoid. By using left and right mandibles a fairly complete element could be assembled. As the jaws were preserved in articulation with the skull, much of their dorsal surfaces were not seen.

The left ramus is unusual in that it has been broken and then rehealed during the animal's

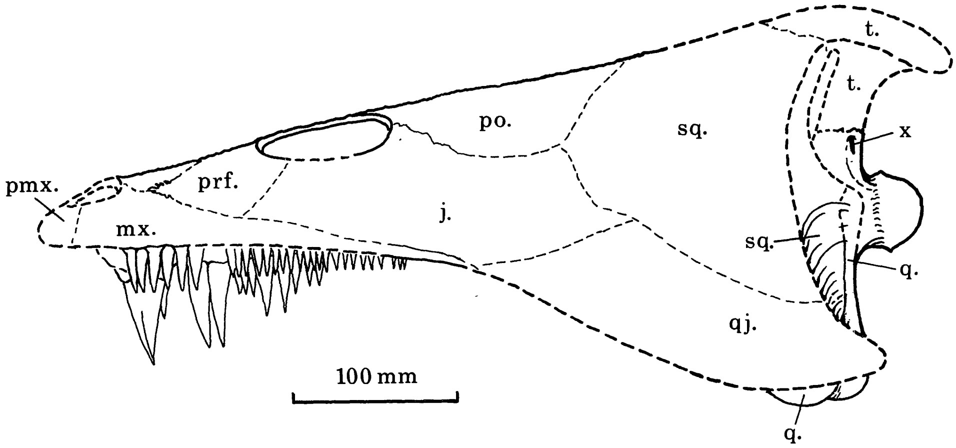


FIGURE 13. *Siderops kehli* n.gen. n.sp. Reconstruction of the skull in left lateral view.

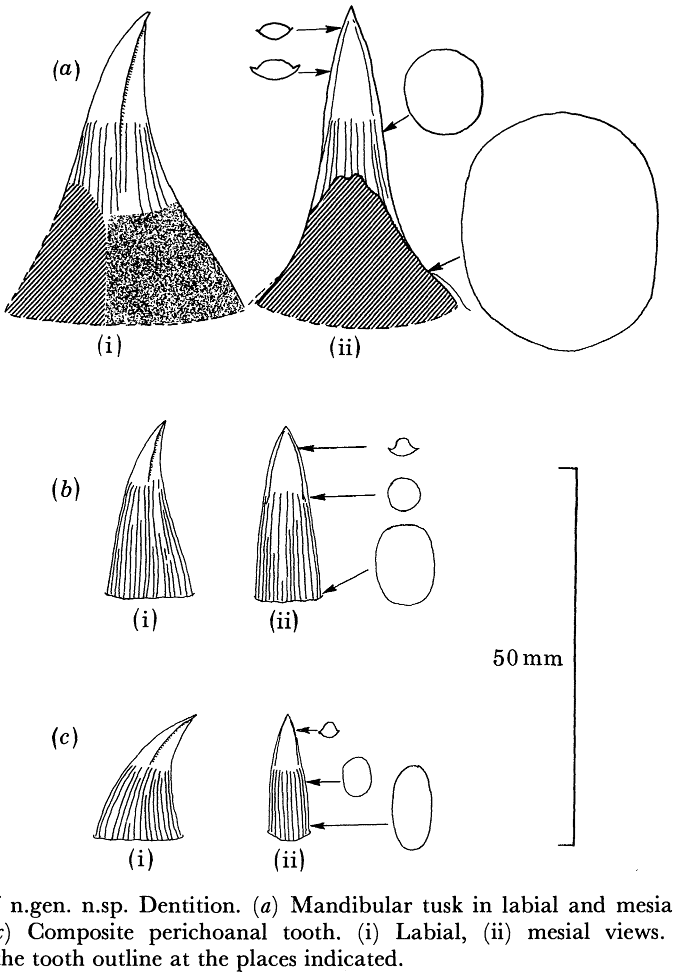


FIGURE 14. *Siderops kehli* n.gen. n.sp. Dentition. (*a*) Mandibular tusk in labial and mesial views. (*b*) Composite maxillary tooth. (*c*) Composite perichoanal tooth. (i) Labial, (ii) mesial views. Sections of teeth are approximations of the tooth outline at the places indicated.

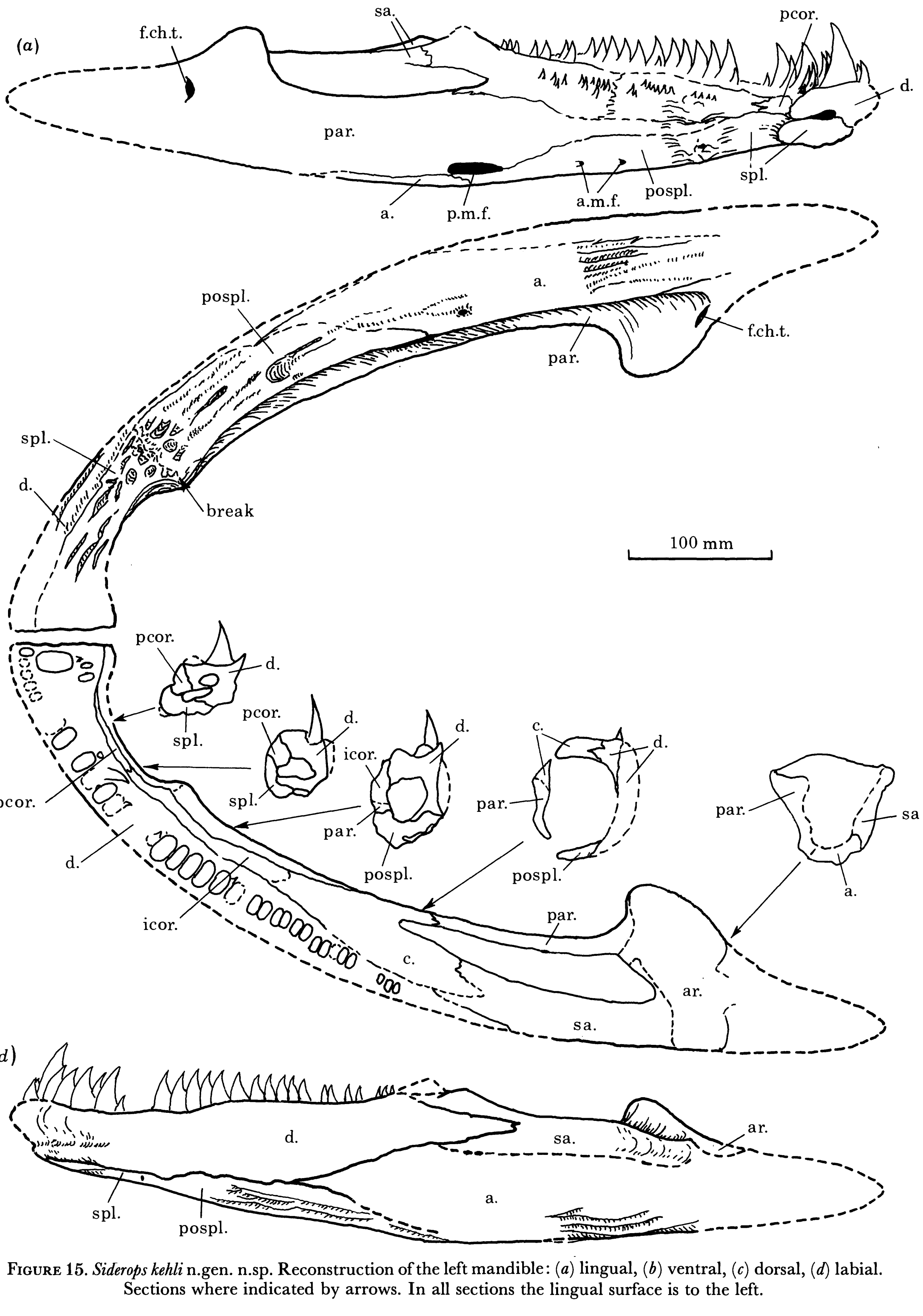


FIGURE 15. *Siderops kehli* n.gen. n.sp. Reconstruction of the left mandible: (*a*) lingual, (*b*) ventral, (*c*) dorsal, (*d*) labial. Sections where indicated by arrows. In all sections the lingual surface is to the left.

lifetime (plate 2*c*). This break has distorted the ornament on the ventral surface and has caused an irregular swelling on the lingual surface which at this point is largerly occupied by intercoronoid. Beneath the intercoronoid the break obscures the probable position of the splenial–postsplenial suture. This area is not preserved on the right mandible.

The dentary appears to have been unornamented above the mandibular sensory canal but shallowly ornamented below this. The ventral surface of the left splenial has a series of broad ridges with narrow grooves between them, and apart from a small area of pitted ornament in the region of the break (above) this ornament type continues on the ventral surface of all bones preserved. Towards the back of the part of the angular preserved the ornamental ridges become extremely tall and narrow; these enlarged ridges are present also on the labial side of the right angular and on the dermal pectoral girdle.

A small section of mandibular sensory canal is preserved on the left dentary, on a cast of the right dentary, and above the highest point of the right angular.

The adductor fossa is moderately developed and is bordered by the usual complement of dermal bones: that is, by the coronoid anteriorly, the surangular labially, and the prearticular lingually, with a narrow tongue of articular running vertically down its posterior edge between the dorsal process of the prearticular and an inturned flange of the surangular.

A large chorda tympanic foramen is present on the prearticular of both rami. Low on the lingual surface beneath the anterior end of the adductor fossa is a posterior meckelian fenestra. This lies on the suture between prearticular and postsplenial. Two smaller anterior meckelian foramina pierce the lingual surface of the postsplenial

The arrangement of the dermal bones of the mandible largely agrees with Warren's (1981*a*) description of the jaw of '*Brachyops*' *allos*.

On the lingual surface three coronoid bones are present, the most anterior of these being small. The coronoid itself forms a coronoid process above the anteriormost part of the adductor fossa. The exposure of the dentary above the coronoids is extremely narrow on the lingual surface which contrasts with the deeply developed dentary that can be seen in the labial view. The position of the splenial–postsplenial suture cannot be determined on either the lingual or the labial surface: it is presumed to be obscured by the break in the left mandible and the area is not preserved on the right.

An unusually large amount of prearticular is exposed in lingual view, with a narrow tongue of bone extending anteriorly almost to the level of the precoronoid. Posteriorly the prearticular occupies the entire lingual surface of the jaw so that the chorda tympanic foramen is contained wholly within it. This deep area of prearticular exposure may have extended posteriorly along the retroarticular process, but as both the left and right processes are missing this cannot be determined. In front of the articular area the prearticular bears a well developed dorsal process.

Although the upper surface of the articular is obscured by the quadrate it appears to have had the usual temnospondyl screw shape. An anterior view of the articular shows the tongue of bone between the dorsal process of the prearticular and the surangular mentioned above. From behind, a section of the jaw near the front of the retroarticular process has a large core of articular. This section also shows a part of the angular ventrally, indicating that the angular extended at least part of the way along the ventral surface of the retroarticular process. Just in front of the articular, on the labial side of the mandible, the surangular is expanded to form a wide shelf beside the adductor fossa. Anteriorly this shelf forms a small process similar in shape to the coronoid process, and just posterolabial to it.

Dentition

All teeth have the same unusual shape described above for those from the skull. They are distributed in a single row along the dentary except near the symphysis, where there is an outer row of teeth with, behind them, a large symphyseal tusk. Posterior to the tusk there is a further short tooth row. A number of well developed coronoid teeth form an irregular row along the dorsal surface of the coronoid and intercoronoid. The mandibular teeth vary in size. The coronoid teeth range from 4 to 7 mm in height and are more strongly curved than the other mandibular teeth, being equivalent in shape to the perichoanal teeth on the vomer. Dentary teeth average 8 mm posteriorly, increase in size to a maximum of 32 mm, and decrease in size again in front of the symphyseal tusk. The smaller teeth in front of and behind the symphyseal tusk are too incomplete to be measured. The right hand tusk measures 42 mm and is thus a good deal shorter than the larger vomerine tusks. As in the skull, replacement teeth were sometimes preserved, as was a patch of denticles associated with the intercoronoid.

Comparisons

Warren (1981*a*) described the mandible of '*Brachyops*' *allos*, a brachyopid, and later (1981*b*) compared it with the jaw of *Keratobrachyops australis*, a chigutisaur. *Siderops*'*s* jaw shares features of both these forms. Its teeth are particularly brachyopid in their large size and distribution, although no other labyrinthodont has similarly shaped teeth. In cross section *Siderops*'*s* jaw is broadly oval and shallows anteriorly as it does in brachyopids, in contrast to *Keratobrachyops*'*s* jaw, which is slimmer and deeper.

The retroarticular process of *Siderops* is more likely to have been covered lingually by prearticular (as in '*B.*' *allos*) than to have been formed by a lingual exposure of the articular (as in *Keratobrachyops*). On the other hand the jaw does not have the deeply bowed adductor region characteristic of brachyopids.

Siderops'*s* mandible differs from that of both '*B.*' *allos* and *Keratobrachyops* in the lesser lingual exposure of the dentary, in the greater anterior extension of the prearticular and in the better-developed coronoid process.

Vertebral column and ribs

Preservation

Although the vertebral column was collected preserved in numerous dissociated blocks, matching of the broken surfaces of both the vertebral elements and associated ribs has enabled the assembly of an apparently continuous series of 35 vertebrae (figure 33). There is little evidence of crushing or distortion of the individual vertebral elements. The neural arches are still articulated, but have dropped somewhat between the intercentra, so that the dorsal extremities of the intercentra are pushed up between successive transverse processes. This has caused the ribs either to disarticulate or to swivel upwards and backwards: such a superficial *post mortem* position may have been the reason that many of the ribs have been lost. The ribs are relatively well preserved in the vicinities of the pectoral and pelvic girdle, and to a lesser extent in the intervening area on the right side. Most of the ribs of the left side have, however, been lost. In the following discussion, the ribs are numbered according to the neural arch to which they are attached. Thus the first rib is numbered 2, since it is attached to the second vertebra (the axis), the first vertebra (the atlas) lacking a rib.

The vertebral series begins anteriorly with the atlas and the anterior half of the axis. There is a gap between this and the next vertebral block. This region is the most difficult to bridge, owing to extensive weathering of the exposed surfaces of the bones. An almost complete intercentrum has been identified, with some uncertainty, as intercentrum 3. Anteriorly it is attached to neural arch fragments, which appear to be part of the transverse process of the axial neural arch. The next most posterior vertebral block has a partial intercentrum anteriorly. This is not part of intercentrum 3 and is most probably intercentrum 4, the arrangement of ribs in this area making it unlikely than any more vertebrae are completely missing. There is a further gap between the back of neural arch 4 and the middle of neural arch 5, but this is bridged by ribs. From the middle of neural arch 5 to intercentrum 18 there is an uninterrupted sequence of neural arches and intercentra, mostly complete. The succeeding six vertebrae are more incomplete, but provide enough information to leave little doubt that they are continuous. The presacral vertebral count is 23, the sacral vertebra being the second to last of this continuous series. Following the first caudal (vertebra number 25) there is a gap, bridged by the displaced left ilium. Little remains of the second caudal. The following nine caudals are fairly complete and are continuous, although the elements are more compressed and displaced than is the case with the presacral vertebrae. The last four caudals (vertebrae 32–35) carry haemal arches. The tail is not complete as the most posterior caudal recovered is still quite deep. In summary, a probably complete presacral vertebral series, the sacrum and the anterior caudals have been recovered.

The persistent articulation of the vertebral elements, together with the collapsed and interlocked neural arches and intercentra and the extremely hard matrix have made preparation and observation of some regions of the column difficult. These regions include the posterior zygapophyses, the extremities of the transverse processes and the ventral surfaces of the neural arches.

Atlas–axis complex (figure 16)

The atlas is almost complete, with only some minor damage to the left side of the neural spine. It is followed by the intercentrum of the axis, still in articulation, to which is attached the anteriormost part of the axial neural arch, including much of the right and left transverse processes.

The atlas is similar in most respects to the same bone in other advanced temnospondyls (Sawin 1945; Welles & Estes 1969). Like these it is composed of an enlarged centrum bearing the two facets for the exoccipital condyles. Each facet is in the form of a shallow circular cup facing anterolaterally and separated from its pair by a medial vertical channel on the anterior face of the centrum. In anterior view there is a depression, indicating a hollow running anteroposteriorly through the atlantal centrum, between the articular facets. This presumably carried the notochord forward to the base of the skull. The neural canal is filled with a matrix which it has not been possible to remove, but appears to have been roughly diamond-shaped in anterior view.

The posterior face of the atlantal centrum is partly obscured by the axial intercentrum but is apparently in the form of a single concave excavation. In ventral view, the outline of the rear margin of the atlas is also concave.

The neural spine is fused to the centrum. In lateral view the spine flares out posteriorly towards its crest, but rises more or less vertically on its leading edge. In dorsal view it can be seen that the neural spine is wider posteriorly than anteriorly, and the posterior margin is notched medially, forming two posterolateral lobes. The atlas is in articulation with the axial neural arch via this posteriorly expanded neural spine, which appears to have borne postzygapophyses on its underside. Such a neural spine connection between atlas and axis has not been reported in other labyrinthodonts.

The intercentrum of the axis is similar to the more posterior presacral intercentra (see below), being crescentic with a relatively thick central region. It differs in that it is also crescentic (rather than parallel-sided) in dorsal view, with a convex anterior margin and a concave posterior margin. The anterior margin fits snugly into the back of the atlas. In the midline above the intercentrum but below the neural arch remnant is a mass of ossified material which might be the remains of the notochordal cartilage. On the right of the intercentrum can be seen a distinct parapophysis, which is raised above the surrounding bone to form a low boss. What remains of the axial neural arch is similar in shape to that of the following presacral arches (below).

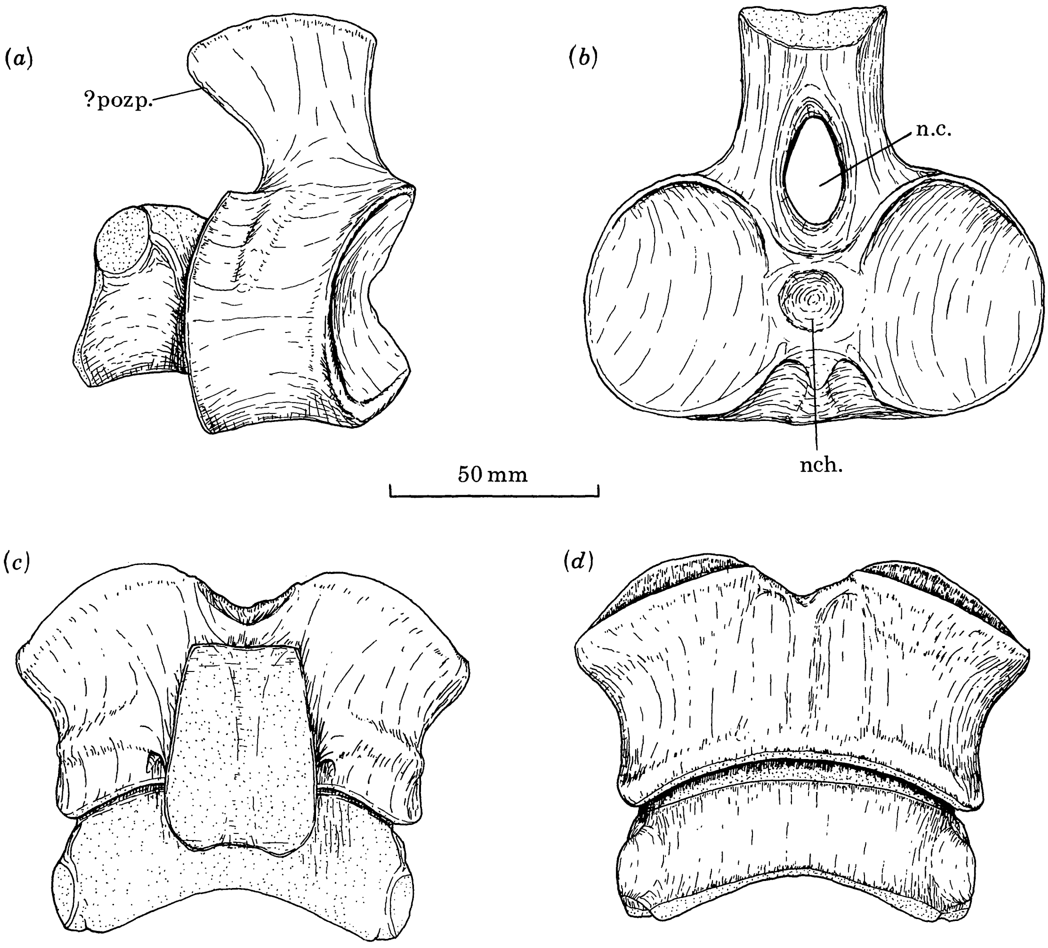


FIGURE 16. *Siderops kehli* n.gen. n.sp. Atlas–axis complex. Reconstruction of the atlas and the axis intercentrum (axis may be displaced dorsally): (*a*) left lateral, (*b*) anterior, (*c*) dorsal, (*d*) ventral.

Neural arches

The best-preserved of the more anterior neural arches are numbers 8 and 9 (figure 17). The dorsal surface of each transverse process extends at right angles from the body of the arch and the transverse process itself, when viewed dorsally, is also at right angles to the long axis of the body. The ventral surfaces of the processes arch downwards so that they are deeper distally than proximally. They also descend further on their anterior faces than on their posterior faces. This concave posterior region beneath the transverse process could have been the point of articulation of a cartilaginous pleurocentrum.

The diapophyses are apparently slightly angled posteriorly and slope anteroventrally when seen in lateral view. However, where the tips of the transverse processes are complete they are partially obscured by rib heads, and where ribs are absent the diapophyses also appear to be missing. Possibly these structures were mostly cartilaginous and have been lost.

The neural spine is situated well back on the neural arch, such that it lies almost completely posteriorly to the transverse processes. The spine is transversely thickened, being roughly square in cross section, and is rather low. The upper surface of the neural spine appears to be of unfinished bone, indicating the presence in life of a cartilaginous cap.

The prezygapophyses are well developed. In lateral view their anterior extremities are emphasized by the presence of a notch in the anterior edge of the arch on each side between the base of the transverse process and the prezygapophysis. The inner faces of the prezygapophyses are obscured by matrix beneath the postzygapophyses of the preceding neural arch. For the same reason the form of the postzygapophyses is not determinable. It can be seen on one of the caudal neural arches (see below).

The underside of the neural arch is difficult to observe and is completely obscured in most cases. Several cross sections show the form of the neural canal, and show that it was bordered ventrolaterally by a pair of longitudinal ridges which partially constrict its open ventral surface.

Progressing posteriorly the neural arches undergo marked changes in shape. These changes are illustrated in the measurements shown in table 3. Towards the posterior half of the presacral column the transverse processes become thinner dorsoventrally but broader anteroposteriorly. The angle between neural arch and transverse process increases so that the width of the vertebrae (between the extremities of the transverse processes) decreases. The neural spines become more massive and thicker dorsally, the thickness reaching a maximum in the middle of the presacral region. After this point the neural spines become progressively more laterally compressed. Another trend in the more posterior presacral vertebrae is for the neural spine to lengthen anteroposteriorly, the leading edge of the spine moving forward on the body of the neural arch. The expansion of the neural spine combined with the enlargement and posterior sloping of the transverse processes leads to the more posterior vertebrae having the neural spine positioned above rather than posterior to the transverse processes.

The compression of the neural spines evident in the posterior presacral vertebrae becomes more extreme in the caudal region, with the transverse processes also becoming greatly reduced in their lateral expansion, but extending further along the body of the neural arch in an anteroposterior direction. The caudal neural spines also develop a distinct posteriorly directed slope, which is not apparent in the presacral vertebrae.

The narrowness of the caudal neural spines emphasizes the position of the postzygapophyses,

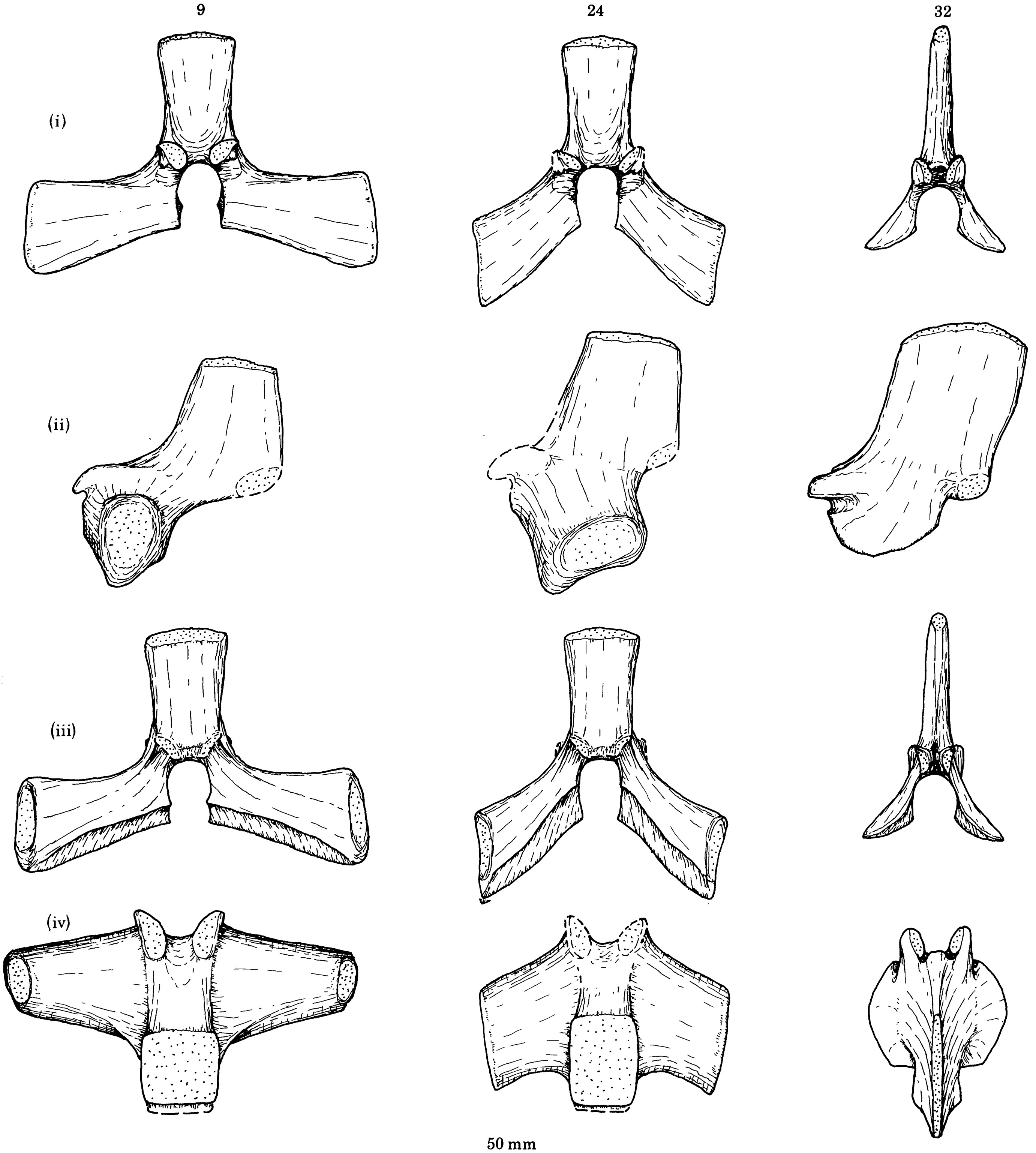


Figure 17. *Siderops kehli* n.gen. n.sp. Anterior presacral neural arch 9, sacral neural arch 24, and caudal neural arch 32; (i) anterior, (ii) right lateral, (iii) posterior, (iv) dorsal.

TABLE 3. MEASUREMENTS AND RATIOS OF REPRESENTATIVE NEURAL ARCHES SHOWING CHANGES IN THEIR PROPORTIONS

(*a*) measurements/mm

vertebra number	width across transverse processes, *a*	length of neural arch, *b*	width of top of neural spine, *c*	length of top of neural spine, *d*
9	102	61	26	23
17	84	56	30	25
24 (sacral)	74	56	22	28
32	42	53	11	38

(*b*) ratios

vertebra number	b/a	d/b	d/c
9	0.60	0.38	0.88
17	0.67	0.45	0.83
24 (sacral)	0.76	0.50	1.27
32	1.26	0.72	3.45

which cause noticeable bulges on the posteroventral margins of the spines. As reconstructed in figure 17, the postzygapophyses are ventrolaterally directed oval facets.

Intercentra

In contrast to the progressive changes in neural arch structure, the postaxial intercentra alter little in size or proportions (figure 18). Anteriorly they are crescentic, the lower surface being smoothly curved, but the upper surface showing much less curvature so that the central region of the intercentrum is relatively thick. All surfaces, except for a concave ventral strip, were finished in cartilage. The parapophyses, except that of the axis, are indistinct and must have been mainly cartilaginous. They lack the distinct rim around the facet seen in some other temnospondyl intercentra. The posterior presacral and anterior caudal intercentra become more flattened and narrower; their description is made difficult by the fact that most of the intercentra in the posterior half of the vertebral column are incomplete or partially obscured by other skeletal elements.

Haemal arches

Some haemal arches have been well preserved (e.g. on vertebrae numbers 32 and 34), permitting an accurate restoration of their structure (figure 18). The anteriormost haemal arch occurs on the eighth caudal (vertebra number 32) which is also the last rib-bearing vertebra. Thus the body of this intercentrum differs from the more posterior haemal arches because of the presence of a small parapophysis on each posterolateral corner. The intercentra of the haemal arches are much flattened compared with the presacral intercentra, have a shallow V-shape in anterior view and are quadrangular in dorsal view. The haemal arch is large, its depth being equivalent to the height of the neural spine, so that the distal portion of the tail is much deeper than broad. The haemal canal is large and vertically oval in anterior view. Ventral to the haemal canal the haemal spine is continued as a strong bony projection. It ends abruptly as an elliptical (in ventral view) plate of unfinished bone.

Pleurocentra

There are no traces of ossified pleurocentra associated with any of the vertebrae.

Ribs

As was mentioned above, the best-preserved ribs occur in the region of the girdles. In particular the anterior ribs of the left side include several that are virtually complete, and their preservation, lying side by side, has enabled them to be well prepared. The ribs of the left side from vertebra number 10 to vertebra number 18 are lost. The ribs of the right side are all present, although extensively broken and matted together by matrix. The ribs in the sacral region are well preserved, especially on the right side, where the last presacral, sacral and first caudal ribs have all been preserved and are apparently still in their normal positions with respect to the right ilium.

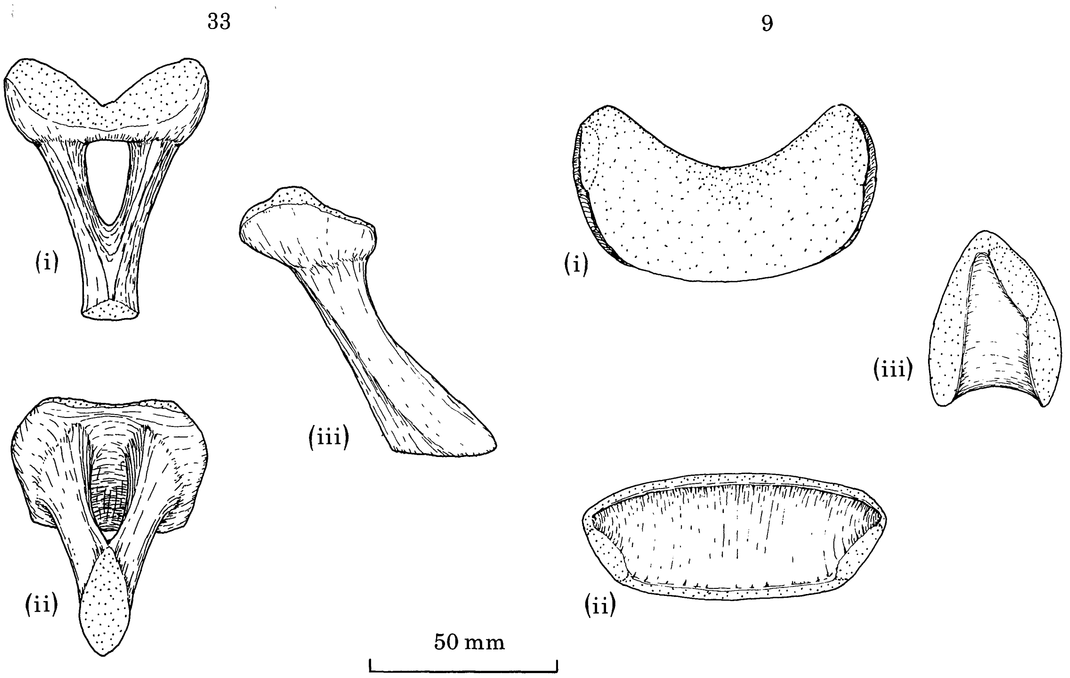


FIGURE 18. *Siderops kehli* n.gen. n.sp. Presacral intercentrum 9 and haemal arch 33: (i) posterior; (ii) ventral; (iii) left lateral.

The anteriormost (axial) rib is represented by its distal portion on each side as well as the head on the left side; it is apparently fairly short, although rather broad and flattened. Ribs 4 to 8 are large and broad, the trailing edges being markedly flattened and expanded, and bearing well developed uncinate processes (figure 19). The ribs are double-headed, but the area between the heads is filled in with bone. In a few cases, for example rib 4, two distinct heads are visible. Ribs 9 and 10 show a reduction in the size of the trailing-edge flange, and this structure has disappeared by rib 16 (figure 19), which has a flattened oval cross section. The ribs become progressively shorter towards the sacral region.

The sacral rib is markedly deeper and thicker than the ribs immediately preceding it (figures 30, 33). It has a pronounced bend halfway along its length, and the distal part is twisted so that the end of the rib is oriented with the dorsal surface facing outwards to contact the inner face of the ilium. The first caudal rib (rib number 25) is also relatively large and is twisted in a similar fashion so that the distal portion forms a laterally compressed blade. It is excluded from contact with the ilium by the sacral rib. The succeeding caudal ribs become rapidly smaller, but they too show the angular bend and longitudinal twisting seen in the sacral and first caudal ribs. Caudal rib number 29 (figure 19) is the most complete of the more posterior caudals.

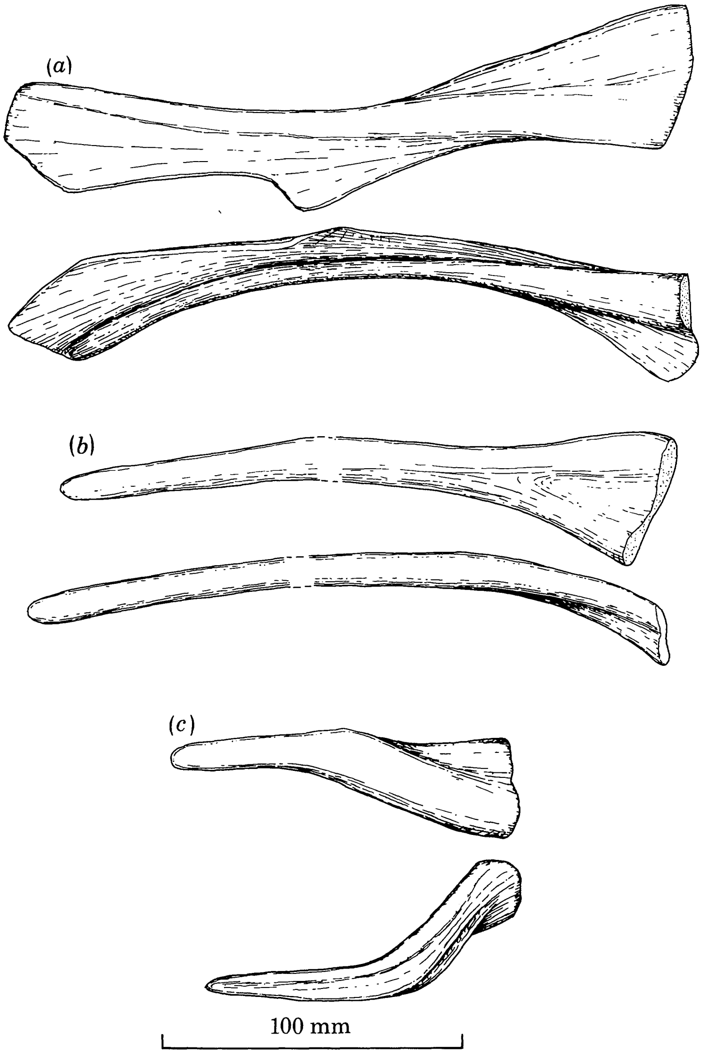


FIGURE 19. *Siderops kehli* n.gen. n.sp. Ribs shown as left elements: (*a*) rib 6 in anterodorsal and posterior views; (*b*) rib 16 (right side, reversed) in anterodorsal and posterior views; (*c*) rib 29 in anterolateral and dorsal views.

Comparisons

Very few vertebrae definitely attributable to brachyopoids have been described. One undoubted brachyopid, *Bothriceps major* has numerous articulated vertebrae preserved with the skull (Woodward 1909) but the state of preservation of the specimen makes it impossible to determine any detail of their structure or of the ribs, which appear uniform in size and shape, being simple prongs that are unusually short. Cosgriff (1974) described intercentra found with *Blinasaurus townrowi*, but in view of the conglomerate nature of the deposits the identity of these is not completely certain. The intercentrum figured by Cosgriff is much less massive than in *Siderops*, being thin and U-shaped in cross section. The atlas of *B. townrowi* described by Cosgriff is similar to that of *Siderops*, but the distinctive region for comparison, the neural spine, is largely missing.

The atlas referred by Welles & Estes (1969) to *Hadrokkosaurus bradyi* also lacks much of the neural spine. However, this appears to be the result of a naturally incomplete neural arch which is reduced to a pair of stout pedicels. In this genus therefore there is no possibility of the extra atlas–axis contact seen in *Siderops*. In other respects, the atlas of *H. bradyi* is similar to *Siderops*, although it is more dorsoventrally compressed. Welles & Estes also described an atlas and axis which they referred to *Batrachosuchus*. The atlas is similar in most respects to that referred to *H. bradyi*, and also has an incomplete neural arch. It is apparently unique in having the condylar facets confluent ventrally and in having a longitudinal midventral ridge. The axis referred to *Batrachosuchus* is remarkable in being 'essentially stereospondylous', being almost circular in anterior view, and is pierced medially by a large notochordal canal. In ventral view, its anterior and posterior margins are straight rather than convex and concave respectively as in *Siderops*. The trunk intercentra attributed to *Batrachosuchus* are rhachitomous, being crescentic in anterior view with a distinct notochordal notch, unlike the 'stereospondylous' atlas and axis. The notochordal notch and their dorsoventral flattening differentiate them at once from those of *Siderops*.

Bonaparte (1978, fig. 99) has illustrated the vertebral structure of the Argentinian chigutisaurid *Pelorocephalus*, which offers a number of similarities to *Siderops*, as well as some important differences. Chief among the latter are the persistent ossified pleurocentra and the much taller and strongly ridged neural spines. However, the shape of the transverse processes, which are rather long, almost perpendicular to the long axis of the body, and deeper at the ends than at their point of fusion with the body of the centrum, is very similar to that in *Siderops*. In addition, the intercentra appear to be identical in relative size and proportion to those of *Siderops*.

Kourerpeton bradyi, if indeed it is a brachyopoid, has a well developed rhachitomous vertebrae with large pleurocentra (Olson & Lammers 1976). Its ribs are similar to those of *Bothriceps*, being uniformly rather short and with little curvature. The shape, sculpturing and arrangement of intercentra, pleurocentra and neural arches are almost identical to those described by Chase (1965) for the trimerorhachoid *Neldasaursus*, and they bear no resemblance to the vertebrae of *Siderops*.

One other family, the Metoposauridae, has recently (Bonaparte 1978; Dutuit 1976) been suggested as a possible member of the Brachyopoidea. This is based on Romer's old (1947) scheme of labyrinthodont relationships, and no new evidence is offered for this suggestion. However, the metoposaurs are of interest because they are from the latest Triassic, and are therefore closest in time to *Siderops*. They are also well known and of unusually large size, and the latter feature might be expected to lead to similarities with *Siderops* brought about by the need to solve similar structural or mechanical problems. Major areas of difference between metoposaurs and *Siderops* are the extremely flat heads of the former and the construction of the vertebral column. Metoposaurs have long been regarded as stereospondylous, and all have spool-shaped rather than crescentic intercentra. The recent description of *Metoposaurus ouazzoui* (Dutuit 1976) shows that ossified pleurocentra were present in at least some metoposaurs, which would, strictly speaking, make the structure of their centra neo-rhachitomous rather than stereospondylous. In any case, in possessing spool-shaped intercentra and ossified pleurocentra, metoposaurs differ markedly from *Siderops*.

Nevertheless there are some close resemblances in other aspects of vertebral structure. The atlas of *Metoposaurus fraasi* (Sawin 1945) is strikingly similar to that of *Siderops*. The only point of difference is that no evidence of a medial notochordal canal is visible. The neural spine of *M. fraasi* is massive and has a posterior overhang similar to that seen in *Siderops*, which would, on the basis of Sawin's fig. 6*b*, appear to provide an articulating surface contacting the anterodorsal region of the atlas. The axial centrum, although it is 'stereospondylous' rather than rhachitomous, also appears to resemble that of *Siderops* in being convex anteriorly, enabling it to 'plug' itself into the back of the atlas.

Some features of the neural arch structure are also remarkably similar. *M. fraasi* and *M. ouazzoui* (Dutuit 1976) show the same low, 'swept-back' neural spines characteristic of the anterior presacral region of *Siderops*. The postzygapophyses are borne entirely on the undersides of these posteriorly projecting neural spines, as is thought to be the case in the Australian genus. The transverse processes of metoposaurs, however, are relatively dorsoventrally flattened, sharply downwardly angled, have very well marked diapophysial bosses, and do not closely resemble those of *Siderops*.

Pectoral girdle

A complete girdle has not previously been described for the Brachyopoidea. The dermal girdle was preserved almost complete. Missing are the tips of both dorsal (cleithral) processes of the clavicles, the dorsalmost portions of both cleithra, and a small block from the midline of the interclavicle. Part of the dorsal surface of the right clavicle and ventral surface of the left clavicle and the anterior tip of the interclavicle are preserved as impressions only. The scapulocoracoids are missing small areas of their ventral margins and the dorsal third of the left element. A vertical section through the right scapulocoracoid is absent because of weathering at a break in the bone.

Interclavicle

The interclavicle (figures 20–23) measures 350 mm long by 200 mm wide and is roughly diamond-shaped with the anterior half of the diamond a little smaller than the posterior. Both anterior and posterior projections are broadly rounded. All four borders of the bone curve inwards. On the dorsal surface tori are weakly developed, only being evident at the extreme lateral points. The ventral surface is covered with coarse ridge–groove ornamentation which radiates from a centre just posterior to the line of maximum width.

As the clavicles were preserved in articulation the articular facets for them on the ventral surface of the interclavicle are obscured. By comparison with the extent of the dorsal surface it can be seen that these were narrow strips of bone approximately 33 mm wide.

Clavicle (figures 20–23)

The left clavicle is the most complete. Its ventral plate is 170 mm long in its maximum dimension and 95 mm wide at the base of the dorsal (cleithral) process. The anterolateral margin is smoothly curved, while the posteromedial margin has a lesser curve except in the posterior quarter where the bone has a lateral dip. The centre of ossification is near the base of the cleithral process and an area of coarse pitted ornament extends from there 38 mm across

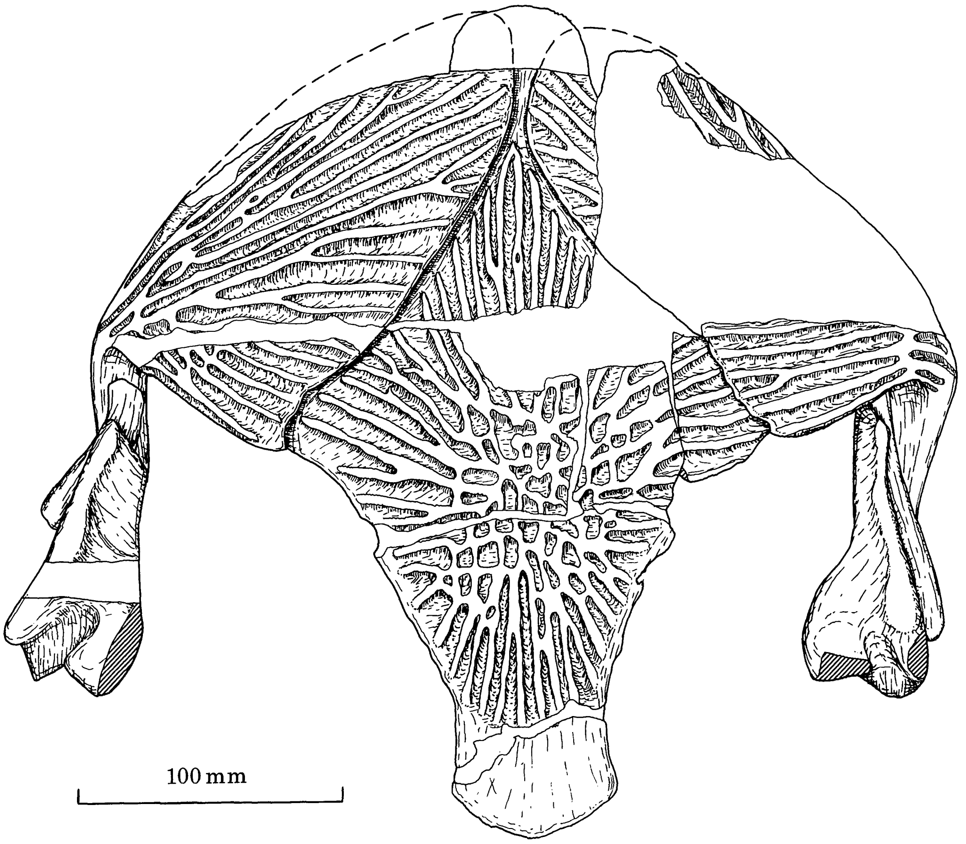


Figure 20. *Siderops kehli* n.gen. n.sp. Pectoral girdle as preserved in ventral view.

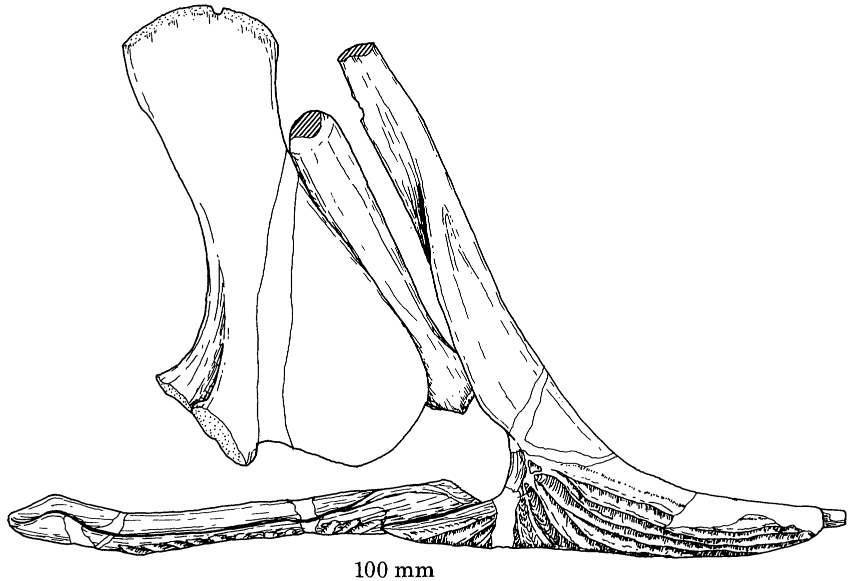


Figure 21. *Siderops kehli* n.gen. n.sp. Pectoral girdle as preserved in right lateral view.

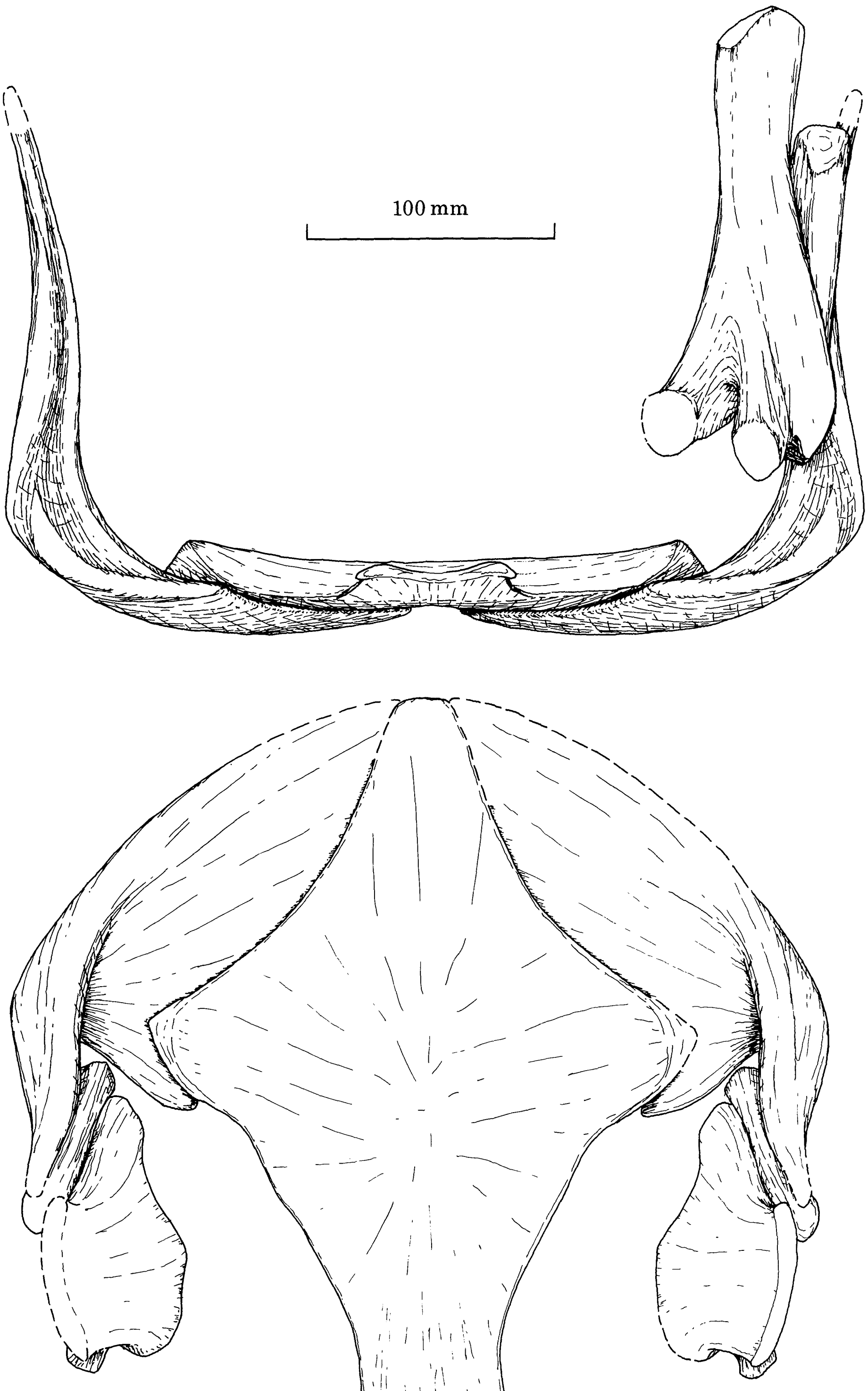


FIGURE 22. *Siderops kehli* n.gen. n.sp. Reconstruction of pectoral girdle: (*a*) posterior, (*b*) dorsal. In the posterior view the left scapulocoracoid and cleithrum have been removed to show the shape of the dorsal process of the clavicle.

the ventral surface. Otherwise a simple grooved type of ornament radiates to the edges of the bone on the ventral surface but barely extends on to the lateral surface.

The process is tall, extending 200 mm above the ventral surface of the girdle. It originates abruptly from the ventral plate, where its base is 63 mm anteroposteriorly, but it narrows rapidly only 60 mm above the ventral surface of the ventral plate. The process rises at an angle of 115° when viewed anterolaterally, but at 90° when viewed from behind. The tip of the process overhangs the posterior border of the ventral plate. A lateral twist to the process about two-thirds of its height above the ventral plate results in the dorsal tip also ending lateral to the limits of the rest of the girdle. Posteriorly the process is broadly grooved for the cleithrum, resulting in the posterolateral edge being extended as a ridge. There is no anterior scar for the cleidomastoideus muscle, the anterior border of the process is not drawn out into a ridge, and there is no sigmoid inturning of the process as a whole.

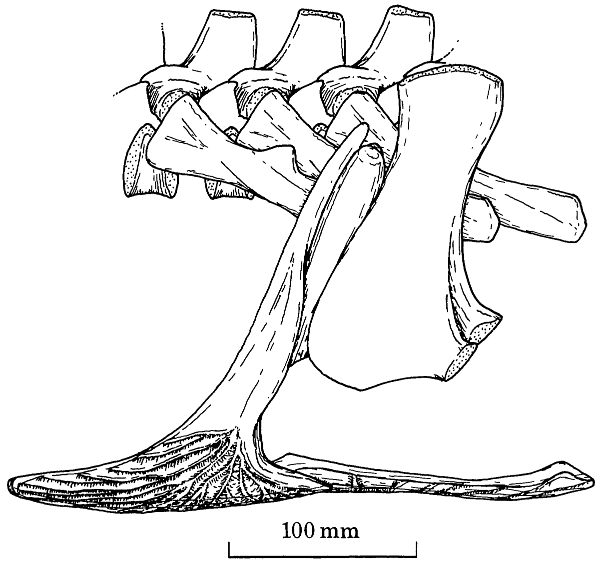


FIGURE 23. *Siderops kehli* n.gen. n.sp. Reconstruction of pectoral area in left lateral view.

The left clavicle is like the right in all respects except that the tip of the dorsal process lies just within the lateral border of the ventral plate. This is the position used in our restoration of the girdle.

Cleithrum (figures 20–23)

As the dorsal sections of both cleithra are missing, their total height is estimated as 170 mm. Each is a rod, triangular in cross section, which begins just above the centre of ossification of the clavicle as a blunt point, expands gradually dorsally and at its end, about 120 mm above its origin, is over twice the size of a section of the dorsal process of the clavicle. The posteromedial edge of each cleithrum has a more acute angle than the others. Although both cleithra are preserved in place between the scapulocracoid and clavicle their exact orientation is hard to determine.

Scapulocoracoid (figures 20–23)

The right scapulocoracoid is the more complete. It measures 180 mm in maximum height and 90 mm across the coracoid area, and 57 mm is the maximum dimension of the dorsal blade. It was finished in cartilage dorsally and also ventrally so that the supraglenoid buttress is not linked to the coracoid portion of the bone. This means that the large supraglenoid foramen is open ventrally.

The external surface of the coracoid plate is vertical. It is slightly bowed out anteriorly before merging smoothly with the dorsal part of the scapula. In internal view, however, the coracoid is recessed ventrally, the recess following the line of the supraglenoid foramen. As the scapulocoracoid is broken at this point, it cannot be determined if the coracoid recess and the supraglenoid foramen are confluent.

The shaft of the scapula is slender and tall with both anterior and posterior borders of finished bone.

Comparisons

In shape the interclavicle most resembles that of the Triassic capitosaurs, especially *Paracyclotosaurus* (Watson 1958).

While entire girdles have not been described in brachyopoids, the interclavicle and ventral plate of the clavicle are sometimes preserved. The interclavicle of the brachyopoid-like *Kourerpeton bradyi* is described as diamond-shaped by Olson & Lammers (1976). From their photograph it is apparent that the element is broader than in *Siderops*, with the centre of ossification further back. Cosgriff (1974, fig. 2) illustrated in ventral view two girdles attributed to *Blinasaurus townrowi*. His UTGD 87500 is of a much narrower diamond than *Siderops* and the centre of ossification is in the line of maximum width, not behind it as in *Siderops*. His second specimen, UTGD 87485, which has a broader diamond shape, has the centre of ossification well posterior, although as the specimen is incomplete its position is not certain.

The remaining brachyopid with interclavicle preserved is the juvenile *Blinasaurus wilkinsoni*. In this species the interclavicle has an extremely wide posterior border. It alone among the brachyopids has an interclavicle much narrower than the skull but this is not as marked as it is in *Siderops* (see below).

The interclavicle of the chigutisaurid *Pelorocephalus* is known but has not yet been fully described. Figure 97 in Bonaparte (1978) is a dorsolateral photograph of the whole animal and does not show the interclavicle.

The ventral plate of both clavicles is similar to that of many Triassic labyrinthodonts although it is shorter and broader than it is in *Lydekkerina* (UCMZ T243) and *Metoposaurus* (Sawin 1945) but not as broad as in *Pneumatostega potamia* (Cosgriff & Zawiskie 1979).

Compared with other brachyopoids it is also shorter than the fragmentary clavicles of *Blinasaurus henwoodi* and *B. wilkinsoni* (Cosgriff 1969, figs 3 and 11) but is approximately the same shape as *Blinasaurus townrowi* (Cosgriff 1974). The clavicle of *Hadrokkosaurus bradyi* (Welles 1947, fig. 8) is too incomplete to justify comparison.

It is the dorsal process of the clavicle that separates the clavicle of *Siderops* from all other clavicles found in the Mesozoic. This narrow dorsally directed rod is similar to that thought by Cosgriff (1974) to be typical of brachyopids and lydekkerinids. It differs from a specimen of *Lydekkerina* (UCMZ T243) in our collection in that in *Lydekkerina* the process does not slope posteriorly, and is drawn out to form a distinct ridge along its anterior border (see below). The only dorsal process to have been preserved in brachyopids is from the flattened *Blinasaurus wilkinsoni.* It was apparently rod-like but shows little else. Others such as *B. henwoodi* (Cosgriff 1965) and *B. townrowi* (Cosgriff 1974) have only the base of the process preserved. In *Pelorocephalus*, the process is preserved but has not been described.

The cleithra of *Siderops* cannot be compared satisfactorily with other cleithra, as the upper, more variable section of the cleithrum is missing. Their lower parts are typical of the few cleithra preserved, such as that of *Paracyclotosaurus davidi*, *Parotosuchus pronus* and *Metoposaurus fraasi* (see Howie 1970).

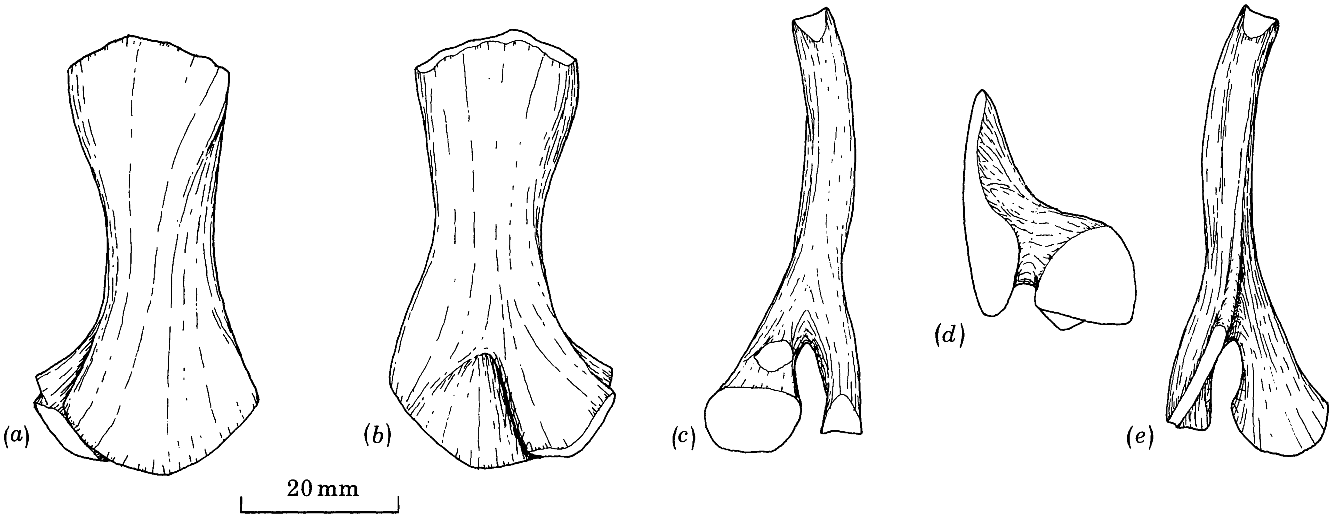


FIGURE 24. QM F10120. Early Triassic labyrinthodont right scapulocoracoid; (*a*) lateral; (*b*) medial; (*c*) posterior; (*d*) ventral; (*e*) anterior.

Compared with the scapulocoracoid of other Triassic labyrinthodonts, this element resembles only two described forms: *Rewana quadricuneata* (Howie 1972*b*) and *Paracyclotosaurus davidi* (Watson 1958). The resemblance is particularly noticeable in the tall slender shaft of the bone which is evident in *P. davidi.* It differs from *P. davidi* in that the supracoracoid foramen is open ventrally. The only two animals with this condition are *Siderops* and *R. quadricuneata.* Other described scapulocoracoids from the Triassic, such as *P. peabodyi* (Welles & Cosgriff 1965), *B. sushkini* (Bystrow & Efremov 1940) and *M. fraasi* (Sawin 1945), always have the supraglenoid buttress broadly joined to the coracoid (thus enclosing the supraglenoid foramen). Also in these forms the coracoid is broader and extends further anteriorly and dorsally, thus contributing to the thickness of the scapular shaft.

An isolated, almost perfectly preserved scapulocoracoid (QM F10120) (figure 24) from locality L78 in the Arcadia Formation is also very similar to *Siderops* and *R. quadricuneata.* No scapulocoracoid other than *Siderops*, however, has the deeply defined recess on the medial border of the coracoid plate.

The scapulocoracoids of Triassic labyrinthodonts may be divided into two classes: a better ossified group with enclosed supraglenoid foramen, enlarged coracoid plate and broad scapular blade, and a less well ossified group in which the supraglenoid foramen is usually open, with a narrow coracoid and a slender shaft. All Australian labyrinthodonts in which the scapulocoracoid is known belong to the latter group. One chigutisaurid, *Icanosaurus* (= *Pelorocephalus*) (Rusconi 1951), also shows this condition.

Discussion

From the above it is evident that, at least in the Mesozoic, few full descriptions of pectoral girdles exist. No attempt has been made to use the parts of the girdles taxonomically (except Cosgriff (1974), for the brachyopid clavicle, and Cosgriff & Zawiski (1979)) and no functional interpretation has been put on the separate types.

Often it appears that the dermal parts of the girdle vary according to skull type. Thus long-skulled trematosaurs have elongated diamond-shaped interclavicles with elongate, parallel-sided clavicles, while, at the opposite extreme, the short- and broad-skulled plagiosaurs have

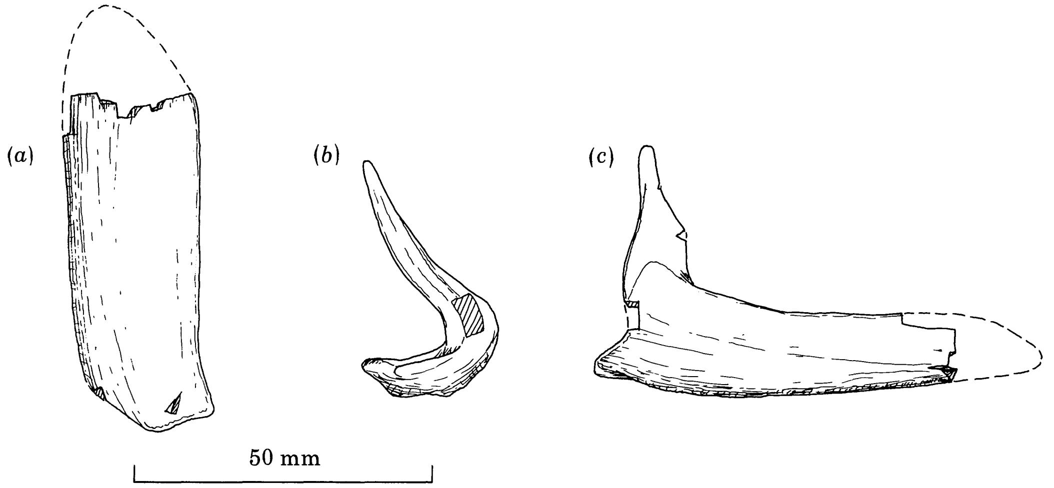


FIGURE 25. QM F10122. Early Triassic labyrinthodont clavicle associated with QM F10115, the holotype of *Keratobrachyops australis*: (*a*) right lateral; (*b*) dorsal; (*c*) posterolateral.

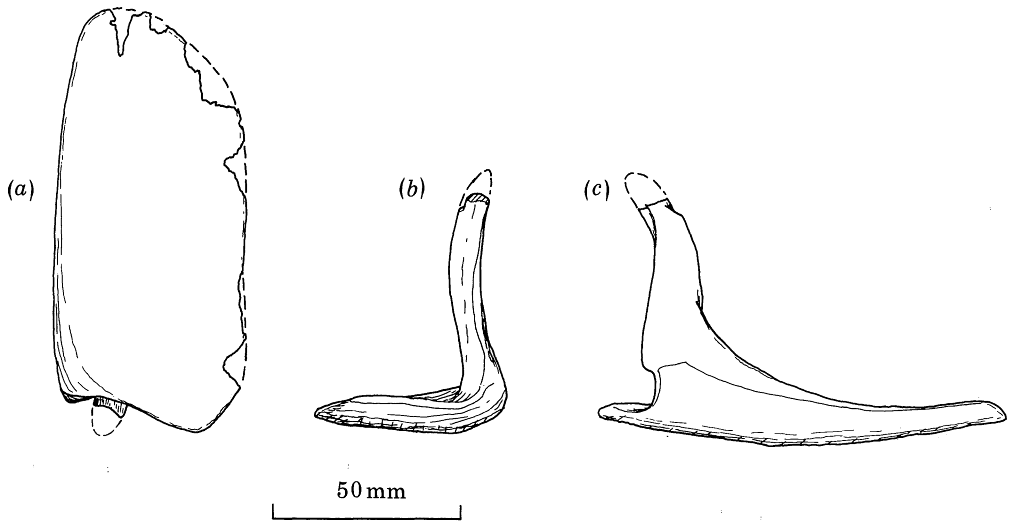


FIGURE 26. QM F10123. Early Triassic labyrinthodont clavicle from Queensland Museum field locality L78: (*a*) right lateral; (*b*) dorsal; (*c*) posterolateral.

short and broad interclavicles and fat, triangular clavicles. In between are the capitosaurs, brachyopids and rhytidosteids, where the body of the interclavicle is not markedly elongate, although the anterior and posterior extensions may be, and where the ventral plate of the clavicles is an elongate triangle. In this group, however, variation is found in the dorsal process of the clavicle. This also is dependent on the skull, but this time on its depth, the dorsal process tending to follow the outline of the back of the skull. In forms with flattened skulls (metoposaurs, *Parotosuchus pronus*), the dorsal process of the clavicle has a marked sigmoid curve and in the more extreme forms the anterior border is produced into an anteriorly directed ridge said to have been for insertion of the cleidomastoideus muscle (Watson 1958). Howie (1970) suggested that this assisted in raising the skull, the sigmoid bend of the clavicle bringing the insertion of this muscle in line with its origin on the tabular horn and paroccipital process. In forms with deep skulls, an extreme example being *Siderops*, the dorsal process of the clavicle arises vertically from the ventral plate and its anterior edge has no obvious muscle scar.

The Triassic clavicles with dorsal process intact that have been described can be arranged as follows and are shown systematically in figure 27.

> Brachyopoidea (based on *Siderops*). Dorsal process a rod of bone with posterodorsal slope, not drawn out anteriorly and not having a sigmoid curve. The position in the family brachyopidae is unclear. Although Cosgriff (1974) predicted from the shape of the base of the dorsal process that the brachyopids should have a rod-like cleithral process that sloped markedly backwards he had no actual specimen.
>
> Lydekkerinidae (based on *Lydekkerina huxleyi* UCMZ T243). Dorsal process a rod of bone without posterodorsal slope, drawn out anteriorly and not having a sigmoid curve.
>
> Rhytidosteidae (based on *Pneumatostega potamia* (Cosgriff & Zawiskie 1979)). Dorsal process a laterally compressed blade of bone which arises from a broad base and become progressively narrower anteroposteriorly, moving upwards towards its tip. It does not have a sigmoid curve.
>
> Capitosauridae and Metoposauridae (based on *Paracyclotosaurus davidi* (Watson 1958), *Parotosuchus pronus* (Howie 1970), *Metoposaurus fraasi* (Sawin 1945) and *M. ouazzoui* (Dutuit 1976). Dorsal process a laterally compressed blade of bone which arises from a broad base and becomes progressively narrower anteroposteriorly, moving upwards towards its tip. It has a marked sigmoid curve and a well developed cleidomastoideus scar along its anterior border.

Additional clavicular material

Two clavicles from the Arcadia Formation (Early Triassic) of Queensland were collected in 1981. One of these QM F10122 (figure 25) was collected from within 1 m of the site of *Keratobrachyops australis* (Warren 1981*b*) and '*Brachyops*' *allos* (Howie 1972*a*). Although it is incomplete anteriorly the ventral plate can be seen to be narrow and elongate with parallel sides and a marked transverse curvature which is apparent in posterolateral view. The dorsal process in this view is intermediate between the markedly sigmoid capitosaur type and the process of most other labyrinthodonts which arises at right angles to the ventral plate. That is, it initially curves inwards but then inclines more dorsally. It is extremely tall in proportion to the narrow ventral plate. In anterolateral view the process rises from a fairly narrow base. In section this has a thickened rod anteriorly, with the breadth of the process being formed by a posterolateral ridge which must have lain lateral to the cleithrum. There is a very slight anterior ridge but otherwise this side of the dorsal process is rounded as it is in *Siderops*.

While the ornament on the ventral surface of QM F10122 is of a normal pit-and-groove form it is unusual in extending up the dorsal process of the clavicle for one-quarter of its height. There is no ridge marking the ornament off from the dorsal process as seen in *Pneumatostega* by Cosgriff & Zawiskie (1979). This ornament corresponds to that seen in *K. australis*, being finer than that of '*B.*' *allos*. If it is indeed the clavicle of *K. australis*, then the ventral plate is a very different shape from that of *Siderops*, although the dorsal process is similar, if a little more sigmoid near its base.

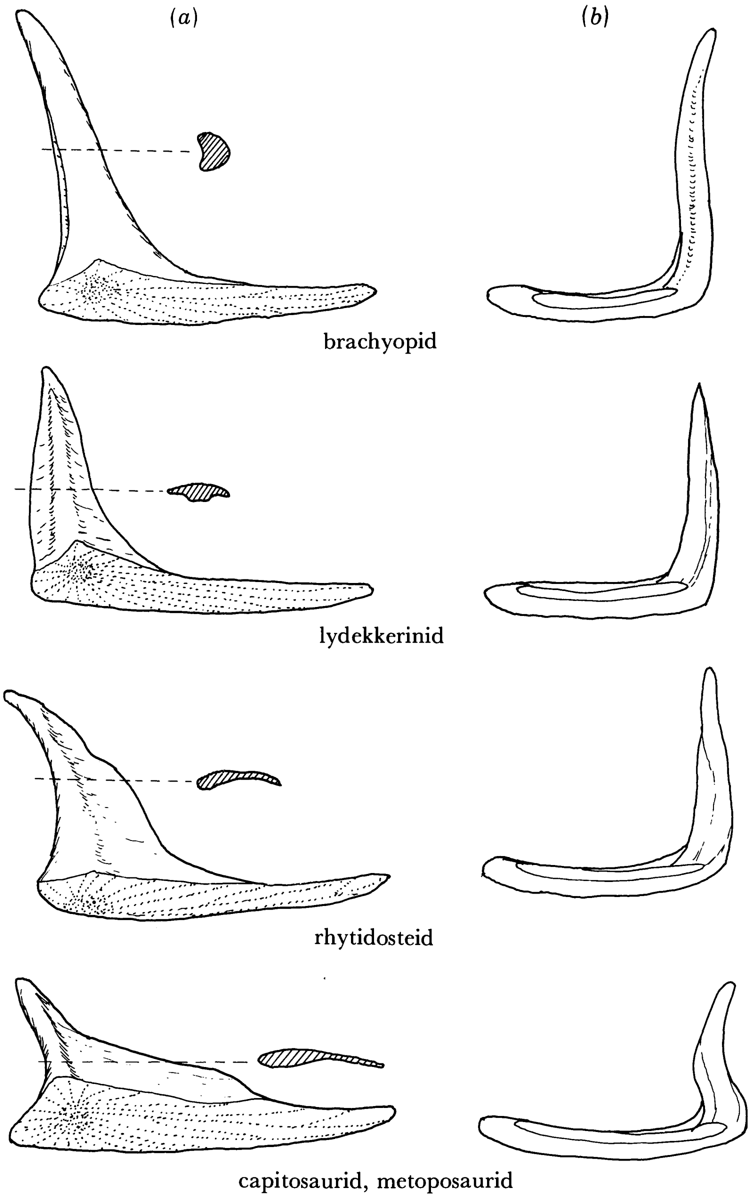


FIGURE 27. Schematic views of labyrinthodont clavicles: (*a*) anterolateral; (*b*) posterolateral.

The second clavicle QM F10123 collected from Queensland Museum field locality L78 is broader than QM F10122 but the sides are again almost parallel. Unlike QM F10122 the plate shows no transverse curvature (figure 26). Its ornament is very finely pitted near the centre of ossification, but about halfway along the length of the clavicle the pits give way to grooves which radiate to the edges of the plate (plate 2*d*).

The dorsal process of this clavicle is broader-based although its anterior border narrows rapidly to form a narrow process which rises vertically for some distance before turning backwards towards the tip. The anterior border is drawn out into a shallow ridge. Similarly, the posterolateral border forms a strong ridge lateral to a groove for the cleithrum. If this process had been broken off at the base a continuation of the cross section exposed would have resulted in a posterodorsally sloping rod as proposed by Cosgriff (1974) for brachyopids and lydekkerinids. However, as seen above, the process does not continue this slope, but turns vertically.

From the definitions of clavicle types above it appears that QM F10123 could be a rhytidosteid or a lydekkerinid although its dorsal process is not so drawn out anteriorly as in the described rhytidosteids. Its fine pitted and grooved ornament is found in both of these families, although Cosgriff (1974) notes that pits without grooves are characteristic of the ornament of lydekkerinid skulls. He does not extend this character to the girdles, however, and a specimen of *Lydekkerina huxleyi* (UCMZ T243) has both clavicles and interclavicle with pitting near the centre of ossification and ridges radiating therefrom, while the attached skull is pitted only. QM F10123 could thus be lydekkerinid although it is from an animal larger than any of that family yet described.

Forelimb

Humerus

Both of the humeri have been assembled from several blocks and are almost complete lacking only the ectepicondylar region. As prepared, the right humerus is 207 mm in length, the left humerus 214 mm.

The right humerus is shown in dorsal, lateral, anterior and posterior views in figure 28. It is lightly built compared with the same bone in many other labyrinthodonts, lacking extensively developed rugosities and projections. This 'streamlining' has been associated with a more strictly aquatic mode of life (see, for example, Watson (1958) on *Paracyclotosaurus*). A distinct pointed deltopectoral crest is situated on the leading edge of the humerus close to the proximal end. Although the relevant area is missing in both bones, it seems likely, from the shape of the broken area, that the supinator process was merged into the distal ectepicondylar flange of the humerus. The distal and proximal ends of the bone are twisted almost at right angles to one another, as is the case in many labyrinthodonts (Romer 1947).

No other forelimb elements have been recovered.

Comparisons

Among the Triassic labyrinthodonts for which the humerus is well known and that approach *Siderops* in size are the capitosaurs (e.g. *Paracyclotosaurus davidi* (Watson 1958) and *Parotosuchus pronus* (Howie 1970) and the metoposaurs (e.g. *Metoposaurus fraasi* (Sawin 1945) and *M. ouazzoui* (Dutuit 1976)). The metoposaur humeri are markedly different from those of *Siderops*, being broad and rather flattened, with well developed muscle attachment points. Those of the capitosaurs are more comparable, being without pronounced muscle scars or processes, apart from a modest-sized deltopectoral knob. However, these humeri are broader and thicker than in *Siderops*.

Few humeri attributable to members of the Brachyopoidea (in the restricted sense) have been described. When Welles & Estes (1969) transferred the lower jaw and postcranial material of the supposed plagiosaurid *Taphrognathus bradyi* Welles, 1947 to the new brachyopid genus *Hadrokkosaurus* they refigured a partial humerus. In the original paper the humerus had been compared with that of *Plagiosaurus* (figured in Nilsson (1939)) and the similarity noted. In the later revision, Welles & Estes (1969) compared this reconstruction with reconstructions of two incomplete humeri referred by them to *Batrachosuchus* sp., noting an even closer resemblance.

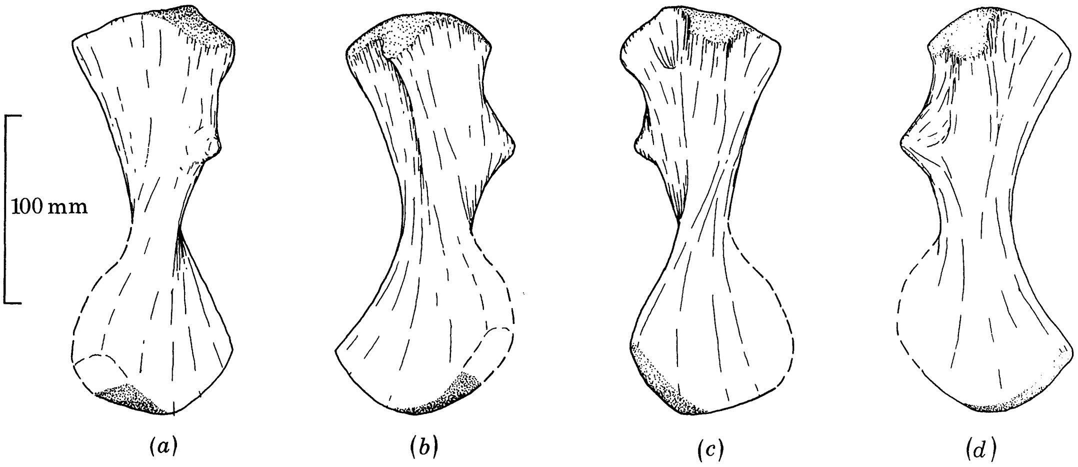


FIGURE 28. *Siderops kehli* n.gen. n.sp. Right humerus: (*a*) anterior; (*b*) dorsal; (*c*) posterior; (*d*) ventral.

Neither the humerus of *Hadrokkosaurus bradyi* nor that of *Batrachosuchus* sp. resembles that of *Siderops*. Both of the earlier genera show a much more robust form, with well developed supinator processes, deep strongly ridged distal expansions and the deltopectoral crest merging with the proximal articulating surface. The humerus of *Batrachosuchus* sp. actually resembles quite closely that of *Metoposaurus ouazzoui* (Dutuit 1976, fig. 58) in its rather flattened shape, broad distal expansion and very well developed supinator process.

Only two other brachyopoid genera have a humerus associated with them. The holotype of *Bothriceps major* (Woodward 1909) from the Newcastle Coal Measures (Lower Permian, New South Wales) has the right humerus, radius and ulna preserved with the skeleton. The specimen is unfortunately almost flattened but the humerus appears to be, as Woodward described it, quite slender and well capped with cartilage, so that it is not dissimilar to that of *Siderops*. The humerus of the Argentinian chigutisaur *Pelorocephalus* sp. (Bonaparte 1978, fig. 99) is very similar to that of *Siderops*. The two genera have in common a relatively smooth-surfaced humerus with an almost right-angled twist of the proximal and distal ends, a discrete pointed deltopectoral crest and a symmetrically fanned-out distal portion.

The brachyopoid-like *Kourerpeton*, which is extensively crushed, also has a humerus preserved. The drawing of the incomplete bone (Olson & Lammers 1976, fig. 3*c*) appears relatively more robust than that of *Siderops*, but little else can be said about it.

Pelvic girdle

Both ischia and both ilia have been recovered. The ischia are still in articulation and the right ilium is also apparently in its normal position with respect to the right ischium. However, there was some *post morten* damage to this area as the pelvis has been displaced to the animal's right, and the left ilium, although still contacting the left ischium, is pushed over onto its side and lies across the line of the vertebral column, which is interrupted at this point. The ischia are fairly complete except for the posterior end of the ischial assembly. The ilia lack both their upper portions and their posteroventral corners.

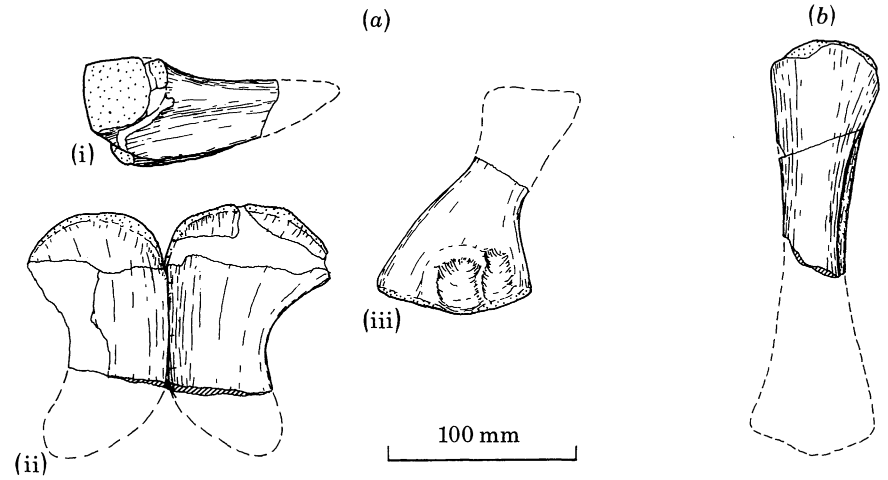


FIGURE 29. *Siderops kehli* n.gen. n.sp. (*a*) Pelvic girdle elements: (i) lateral view of left ischium; (ii) ventral view of ischia; (iii) lateral view of left ilium. (*b*) Femur in dorsal view.

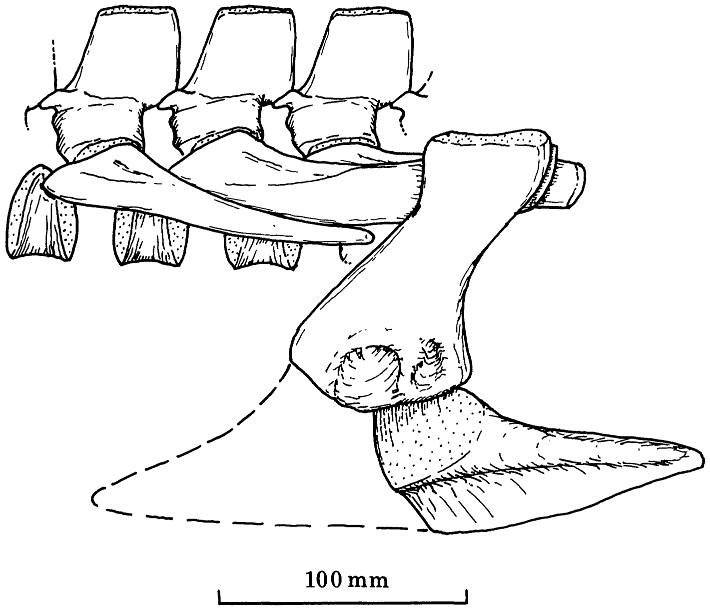


FIGURE 30. *Siderops kehli* n.gen. n.sp. Reconstruction of pelvic area in left lateral view.

Ilium (figures 29, 30)

The left ilium as reconstructed is 120 mm in maximum (dorsoventral) height and 82 mm along its base. The upper part of the acetabulum is preserved and merges with the unfinished bone of the ventral surface. A well defined recess can be seen between the posterior border of the acetabulum and the posterior margin of the iliac blade.

Ischium (figures 29, 30)

The left ischium measures 90 mm in maximum width near its anterior end and 50 mm at its narrowest, and is an estimated 120 mm long. The bone is thickest near its anterolateral margin (37 mm), thinning posteromedially to 7 mm. Its lateral border is strongly convex.

Comparisons

Compared with capitosaurs like *P. davidi* and *P. pronus*, the anterior and posterior borders of the iliac blade are less concave so that the base of the ilium is less expanded. It is, however, wider than in the metoposaurs (e.g. *M. fraasi* (Sawin 1945)).

All known ischia of Triassic labyrinthodonts are similarly shaped. In *Siderops* the ischia are more elongate than in all except *Paracyclotosaurus davidi* and have the greatest degree of convexity of the lateral margins.

Hindlimb

Femur

The proximal half of the left femur was found in two blocks, with its head still more or less in place lateral to the left ilium. As preserved, the femur is angled upwards and backwards. Besides the distal portion, the femur is also lacking the posterior part of the head (figure 29*b*). No other hindlimb elements have been found.

Enough of the femur remains to show that it is similar to femora of other temnospondyls. Unlike the humerus, the femur does not vary greatly in labyrinthodonts, any differences being in the slenderness of the shaft and the degree of development of the ventral adductor crest and the internal trochanter. Unfortunately these last areas are largely missing from this specimen, making comparisons difficult. It appears that the femur in *Siderops* may be rather more slender than in many labyrinthodonts such as capitosaurids (Watson 1958; Howie 1970), metoposaurids (Dutuit 1976), and indobrachyopids (Howie 1972*a*). It is noteworthy that two brachyopoids for which the femur has been figured, the brachyopid *Blinasaurus townrowi* (Cosgriff 1974) and the chigutisaur *Pelorocephalus* sp. (Bonaparte 1978), also have relatively slender femora.

Body reconstruction

The fact that the axial skeleton was preserved in articulation (figure 33) has enabled an accurate restoration to be made (figure 34). The position of the small dermal pectoral girdle was fixed by the connection, as preserved, of the fifth rib on each side with the ascending process of the clavicle. The size of the gap between a neural arch and its intercentrum is relatively large but was determined by the distance between the rib heads, and the position of the intercentrum well anterior to the neural arch was further established by the degree of curvature of the ribs. The distal limb bones have been restored on the basis of their structure in other temnospondyls, with use of a 4–5 digital formula (Romer 1947; Holmes 1980); the phalangeal counts of 2.2.3.3 and 2.2.3.4.3 are also usual in this group (Romer 1947). The tail has been restored as tapering fairly rapidly, and may have been somewhat longer. As restored to this minimum tail length, we estimate that the holotype of *Siderops kehli* had a total length from snout to tail tip of at least 2.60 m.

From the reconstruction of *Siderops* (figure 34) it is apparent that its body proportions, especially in the pectoral area, differ markedly from those of other labyrinthodonts (table 4). To formalize these comparisons, we took measurements of three parameters of girdle and limb size (length of humerus, maximum interclavicle width and width across ischia) and compared these, with the maximum width of the skull as denominator. For this study, only advanced temnospondyls were used. We have been able to find only a limited number of examples in which the postcrania are sufficiently well known and certainly associated with skulls. In some cases we have been able to make estimates. For example, for *Metoposaurus fraasi* the largest skull and interclavicle measurements given by Sawin (1945) were used, together with measurements of humerus and ischia taken from his drawings. For *Lydekkerina huxleyi* we were able to measure directly only relative interclavicle size, and obtained the other two measurements from the illustration in Watson (1919), which may be composite.

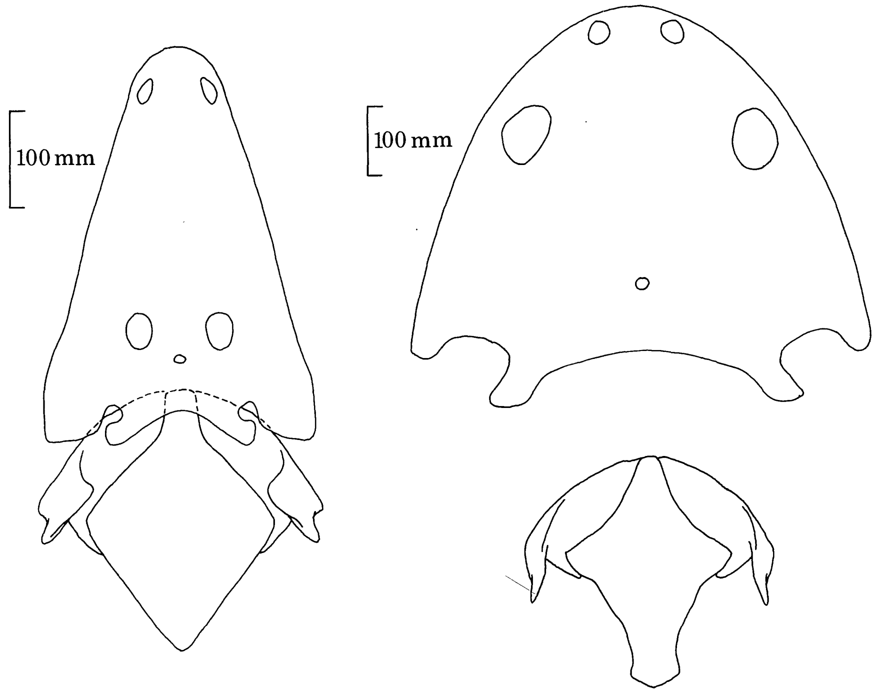


FIGURE 31. Dorsal views of *Siderops kehli* and of a capitosaurid based on *Parotosuchus pronus* (Howie 1967) to show the relative sizes of the pectoral girdles and the skulls.

TABLE 4. GIRDLE AND HUMERUS PROPORTIONS OF A VARIETY OF ADVANCED TEMNOSPONDYLS

(Sources of information: 1, present work; 2, Stephens (1887); 3, Woodward (1909); 4, Watson (1958); 5, Howie (1970) (specimen no. 481); 6, van Hoepen (1915) and Watson (1962); 7, Watson (1919) and personal observation of UCMZ T243; 8, Sawin (1945); 9, von Meyer (1857) (specimen nos 131 and 137). Symbols: B, maximum breadth of skull; L_h, length of humerus; W_{int}, width of interclavicle; W_{is}, width across ischia.)

source of information...	1	2	3	4	5	6	7	8	9
	Siderops kehli	*Blinosaurus wilkinsoni*	*Bothriceps major*	*Paracyclotosaurus davidi*	*Parotosuchus pronus*	*Uranocentrodon senekalensis*	*Lydekkerina huxleyi*	*Metoposaurus fraasi*	*Archegosaurus* sp.
L_h/B	0.33	—	0.34	0.38	0.33	0.41	0.46	0.29	0.27
W_{int}/B	0.33	0.36	—	0.81	0.79	0.74	0.40	0.88	0.33
W_{is}/B	0.27	—	—	0.30	0.35	0.25	0.31	0.37	0.23

From table 4 it can be seen that humerus and ischial width vary to a moderate degree in advanced temnospondyls, ranging between 0.27 and 0.46 of skull breadth for the humerus and

0.23 and 0.37 for the ischial width. *Siderops* falls well within these limits, with ratios of 0.33 and 0.27 respectively. By contrast, pectoral girdle width, as reflected by interclavicle size, varies much more. Most larger forms appear to have relatively large interclavicles, 0.7 to 0.9 times the width of the skull. *Lydekkerina* has a smaller interclavicle, its width less than half the breadth of the skull. *Blinasaurus* has a small interclavicle, possibly associated with its larval or neotenic condition, which would indicate an underdevelopment of the girdles. Finally, the smallest interclavicles are found in *Archegosaurus* and *Siderops*. In *Archegosaurus* there again seems to be evidence of underdevelopment of the limbs and girdles, since this elongate and slender form also has the shortest humerus and narrowest ischia of any of the taxa used in the comparisons.

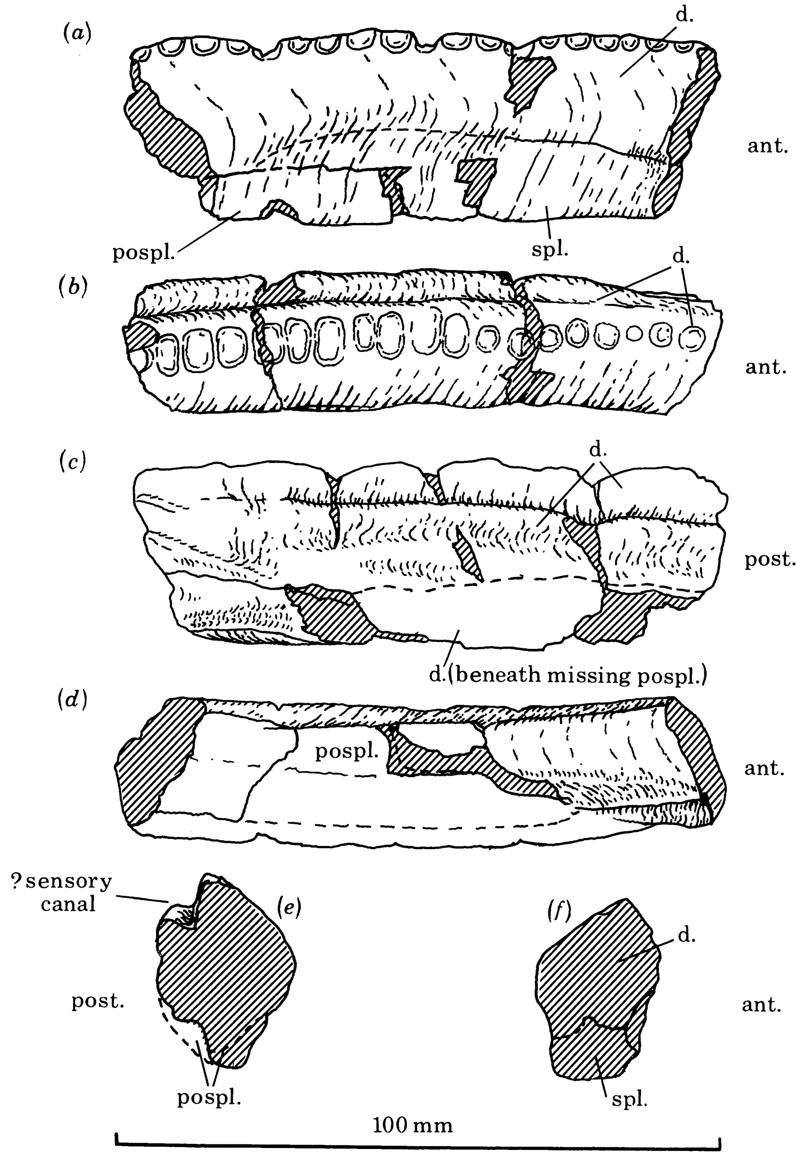


FIGURE 32. *Austropelor wadleyi* holotype QM F2628 left mandible: (*a*) lingual; (*b*) dorsal; (*c*) labial; (*d*) ventral; (*e*) posterior cross section; (*f*) anterior cross section.

In summary, table 4 shows that, compared with other advanced temnospondyls, *Siderops* had a remarkably narrow interclavicle, but that the humerus and pelvis were of average size.

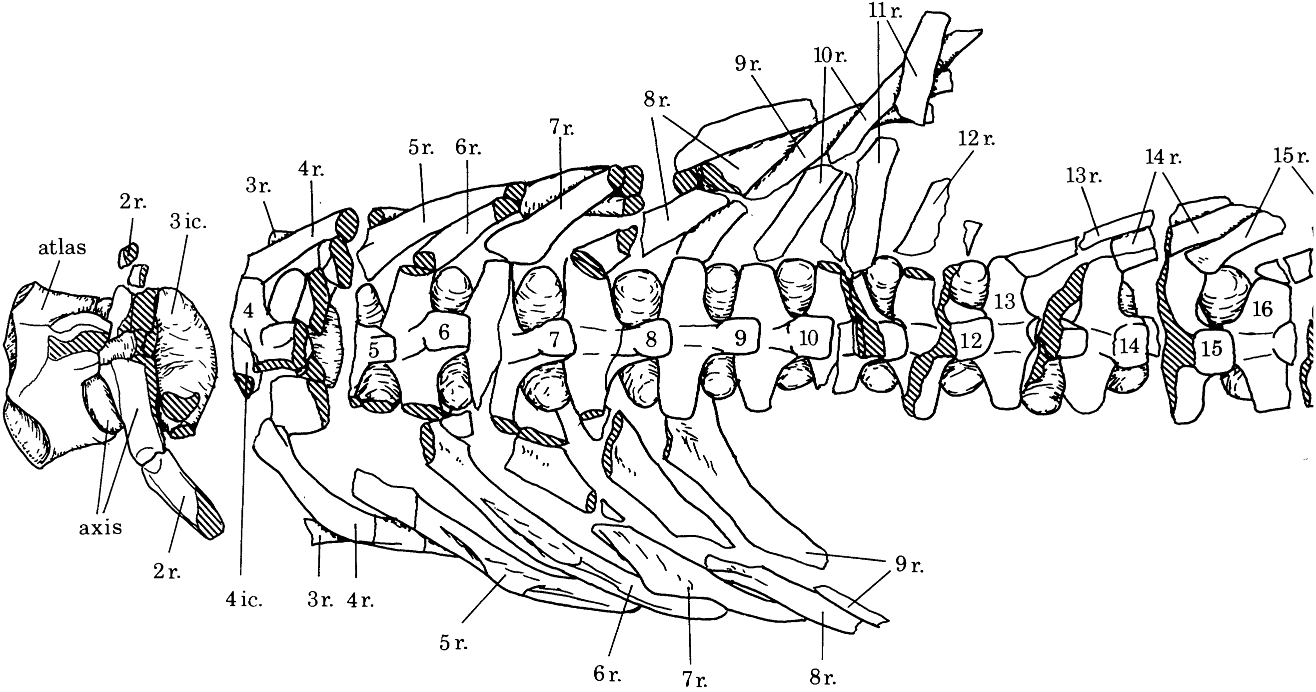
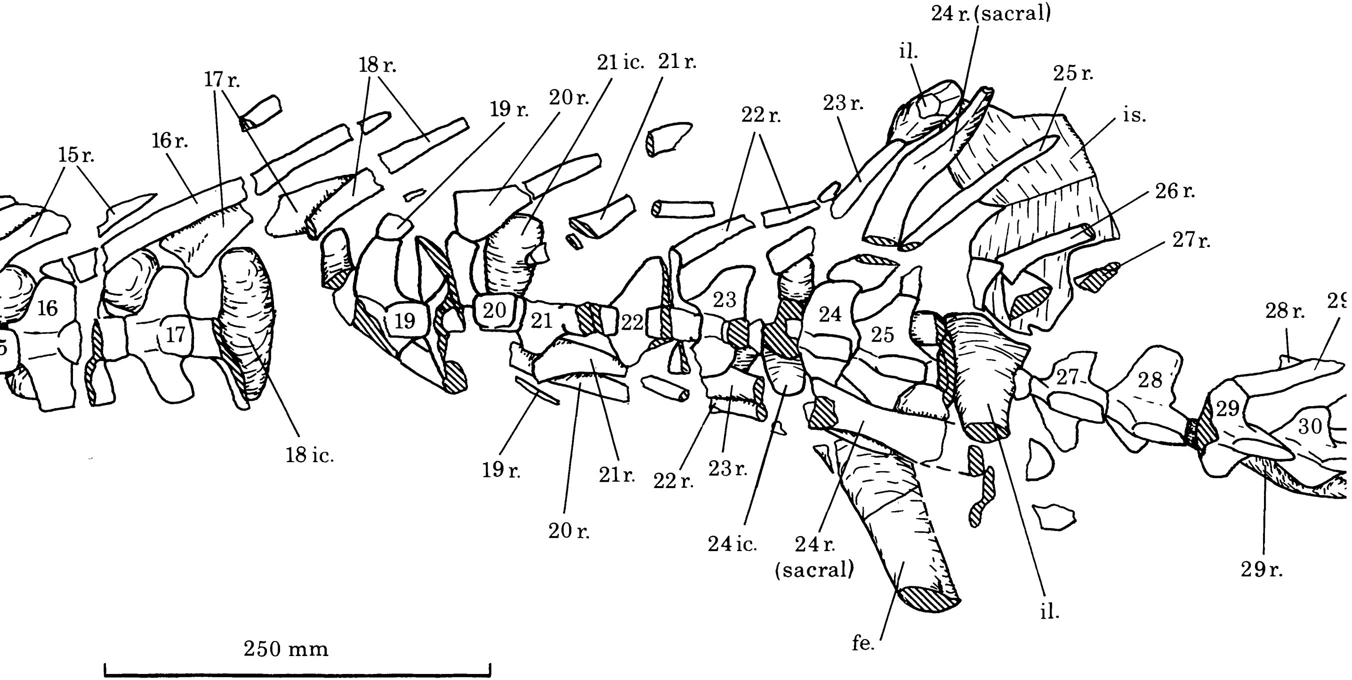
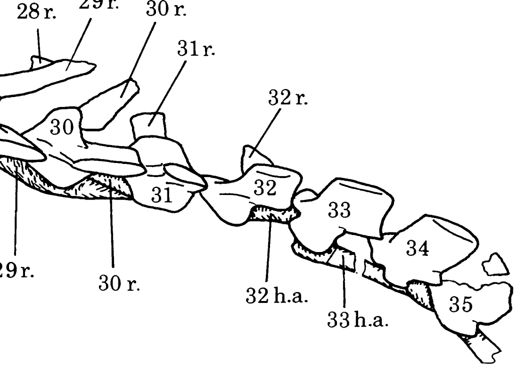


FIGURE 33. *Siderops kehli* n.ge



s *kehli* n.gen. n.sp. Dorsal view of the postcranial skeleton as preserved.



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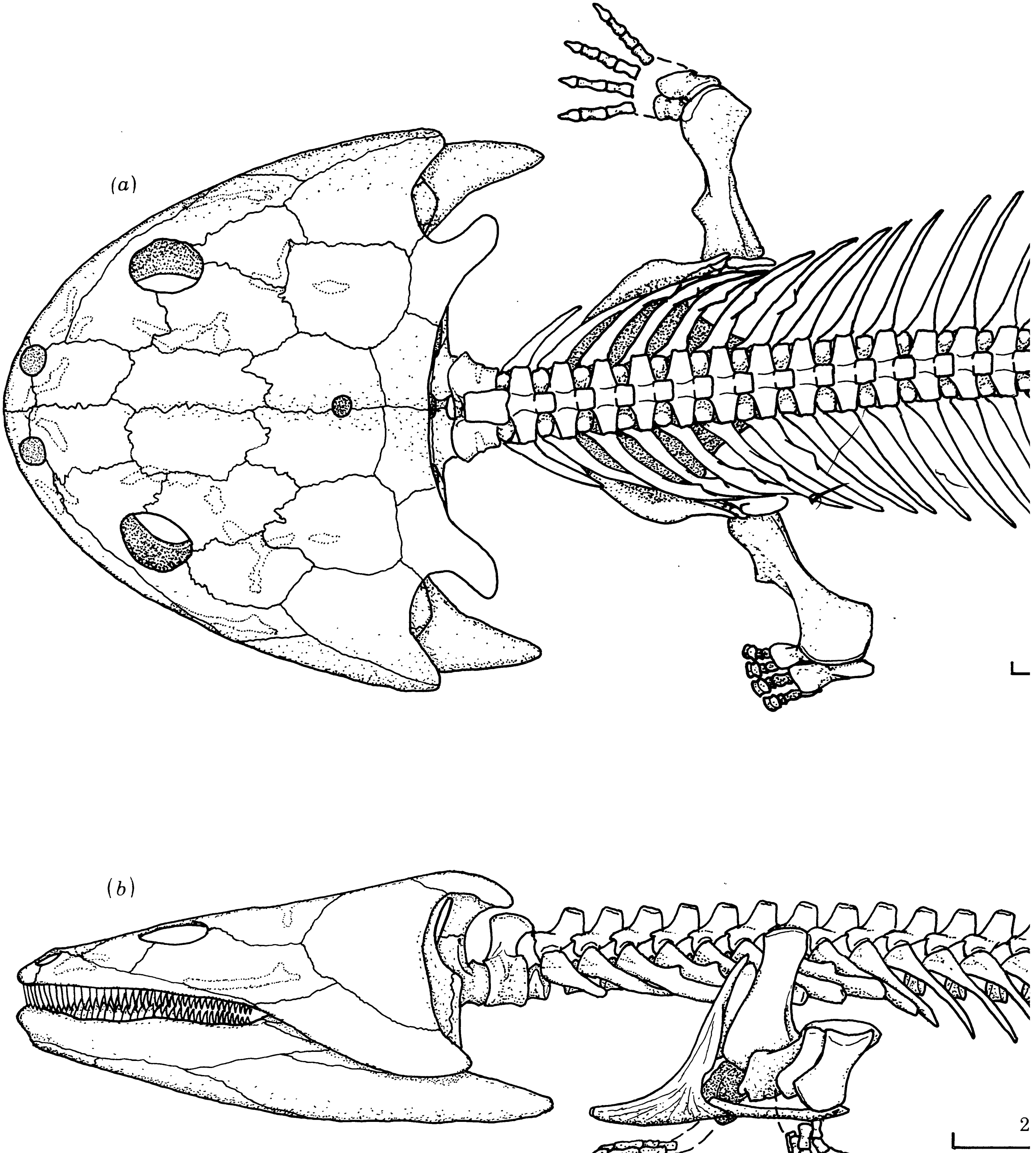
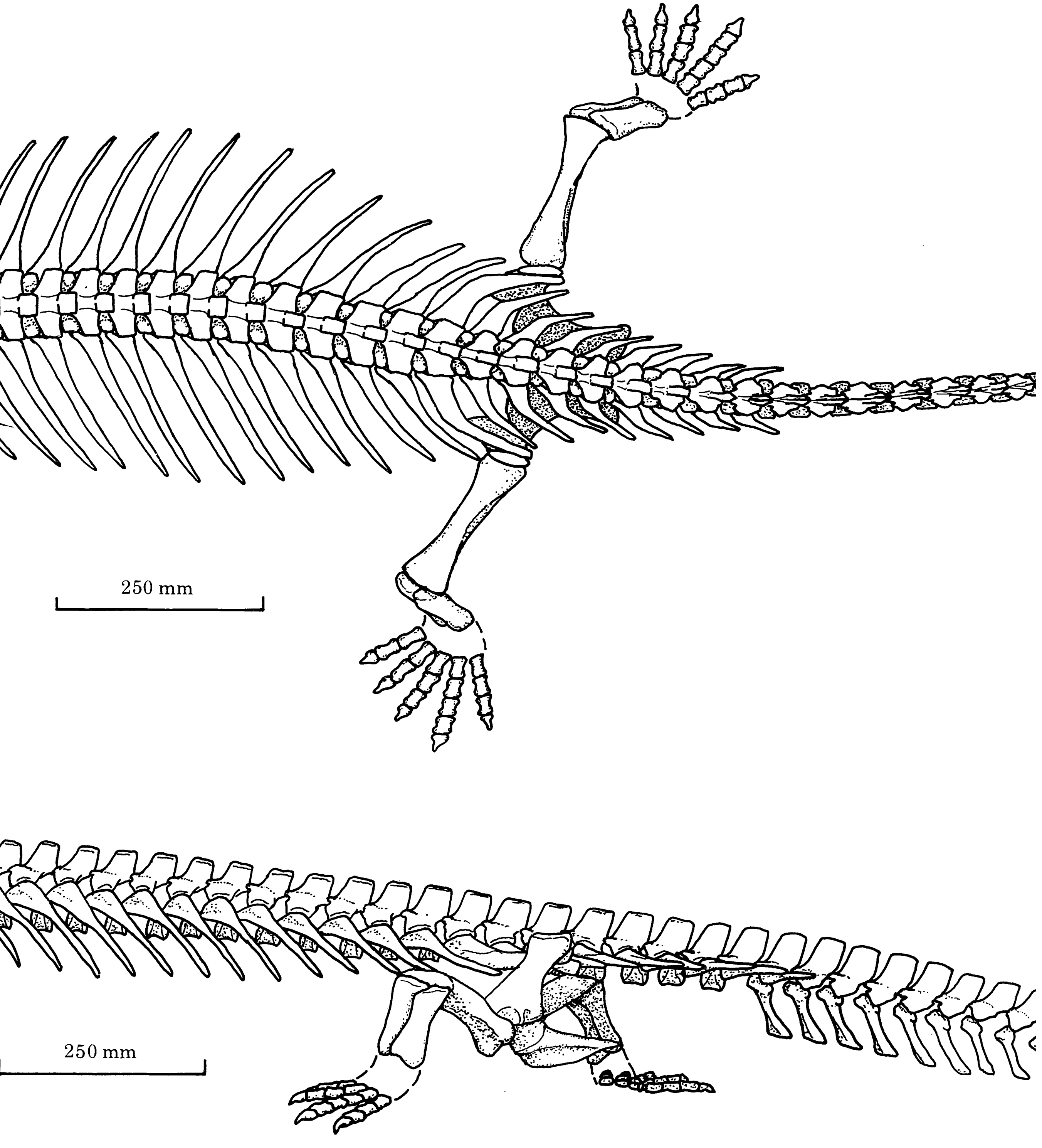
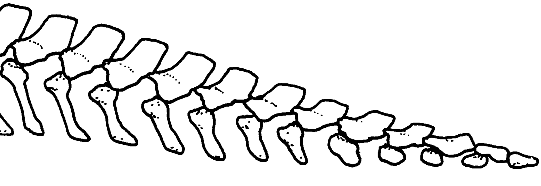


FIGURE 34. *Siderops kehli* n.g



s kehli n.gen. n.sp. Restoration of skeleton: (*a*) dorsal; (*b*) lateral.



As noted earlier, the humerus is similar to that of capitosaurs in its absence of enlarged rugosities and processes. The capitosaur humerus has been described (Watson 1958) as merely a paddle, incapable of significant weight-bearing function. The humerus of *Siderops* is, however, considerably more gracile in its proportions, and this, together with the unusual dermal girdle, indicates that its function may not have been comparable with that in capitosaurs. The narrowing of the clavicles and interclavicle results in the heads of the humeri being brought closer together to a position that would greatly improve the load-bearing abilities of the forelimbs. Such a reduction in interhumeral distance is seen in many terrestrial labyrinthodonts like *Eryops* which have humeri characterized by well developed articular and muscular processes. The lack, in *Siderops*, of the 'knobby' forelimb of the undoubtedly terrestrial eryopoids may reflect an improvement of the forelimb musculature, comparable perhaps with the situation in reptiles, rather than indicate poor terrestrial abilities.

The narrowing of the pectoral girdle has a further major effect in that it provides a reasonably well developed 'neck' region. This would have given greater manoeuvrability to the large head. At the same time, however, it would have reduced the supporting area for the head provided by the pectoral musculature in other labyrinthodonts (Howie 1970). This may have been compensated for by the unusual double articulation of the atlas and axis in *Siderops* providing a stronger mechanical link between the skull and vertebral column. Such mobility of the head, without loss of support, argues in favour of terrestrial adaptations.

Nevertheless it should be said that *Siderops* apparently spend an important part of its time in an aquatic environment. This is indicated by the persistence of well defined lateral line grooves on the skull and lower jaw bones, and by the strongly laterally compressed tail which may have provided most of the locomotory drive in water. The combination of limb and girdle structures discussed above suggests to us that, rather than being a simple paddler, *Siderops* was capable also of reasonably efficient terrestrial locomotion.

Other Jurassic labyrinthodonts

Austropelor wadleyi (figure 32)

This is a section of labyrinthodont mandible. It was originally described by Longman (1941) as part of a right maxilla.

The specimen was found in the bed of the Brisbane River near Lowood in a block of Marburg Sandstone which is now considered to be a lateral equivalent of the Evergreen Formation (table 1). The sandstone exposed at Lowood is near the base of the Formation which places *Austropelor* a little below *Siderops* stratigraphically. As no labyrinthodonts had previously been recorded from the Jurassic it was suggested by de Jersey (1963) that *Austropelor* was reworked from earlier rocks. Colbert (1967) concurred, remarking that 'there will have to be more definite evidence than is afforded by the single specimen of *Austropelor wadleyi* to justify the extension of the labyrinthodont amphibians into Jurassic sediments'. There is now every reason to suppose that *A. wadleyi* was indeed Jurassic.

We agree with Colbert's (1967) reassessment of *Austropelor* as a labyrinthodont mandible and with some reservations to its assignment to the left side. If the specimen is a left mandible, then the tooth alveoli decrease in size anteriorly and increase in size posteriorly. This situation is found in the Brachyopoidea, where the teeth are small anteriorly, increase in size and decrease again towards the adductor fossa (Warren 1981*b*), but rarely elsewhere in Mesozoic temnospondyls. The small anterior teeth in the brachyopoids are well forward towards the symphysis. In this region the curvature of the jaw is greatly increased, and the jaw becomes wider, at least dorsally, to accommodate the symphyseal tusk. *Austropelor*'s mandible exhibits little curvature, and is not markedly expanded at either end. The line of alveoli does approach the labial margin of the jaw more closely at the 'anterior' end so that the area between the alveoli and the lingual edge of the jaw is wider than it is 'posteriorly'. This may be the beginning of an expansion for the symphyseal tusk.

In labial view the jaw is heavily rugose (as pointed out by Colbert). However, in no other labyrinthodont is the dentary rugose except near the symphysis. The uppermost rugosity could be interpreted as the lower rim of a sensory canal. The main part of the labial surface is occupied by 'dentary', with a wedge of 'splenial' anteriorly. The 'splenial–dentary' suture runs from 10 mm below the tooth row anteriorly, on an oblique course to the ventral surface of the jaw. Thus the 'dentary' occupies the whole of the labial side of the jaw behind the splenial. Close examination of this area shows that the bone is roughened and also extremely thin. It is possible that a postsplenial may have overlain the dentary in this area. If so, about 20 mm of the dentary would be exposed between the 'postsplenial' and the tooth row, a more usual arrangement for temnospondyls. In this case the bone would appear less rugose (see above). The arrangement of bones is close to that shown in *Paracyclotosaurus* (Watson 1958) except that Watson does not label the postsplenial, and the dentary is deeper in *Paracyclotosaurus*. The only other interpretation, if this is a left mandible, is that the anterior bone is a postsplenial and the posterior an angular. The alveoli above the 'angular' seem too large for that.

In lingual view, exposure of the dentary is exceptionally deep. Below it an area of postsplenial is exposed posteriorly. Anteriorly one suture is clearly visible for 30 mm before it is lost at a break in the bone. At its most anterior point it sinks deep into the bone, perhaps at the origin of an anterior meckelian foramen. This must divide the dorsal dentary from the splenial below.

If the above sutural interpretation is true then Colbert's placement of the bone in the left mandible must be correct. In this position, the main anomaly is the absence of any coronoid bones. It is possible that an intercoronoid was present, and became detached before preservation.

In section, the jaw differs from all temnospondyls in that the lower splenial area is markedly delineated from the dorsal dentary area. This would be less marked in posterior view if the postulated missing area of postsplenial was added as in the posterior section of mandible in figure 32. Cross-sectional similarity is greatest to that of *Brachyops allos* (Warren 1981 *b*, fig. 9*B*) where the small precoronoid bears a similar bulge of dentary above. It is not close to the chiguitisaurid jaws illustrated by Warren (1981 *b*, figs 9 and 11) as these do not broaden dorsally until after they curve towards the symphysis. The *Siderops* jaw, described above, is wider in relation to depth than other chiguitisaurids and is thus closer to *A. wadleyi*. If the latter is drawn so that the tooth alveoli point directly upwards as they do in *Siderops* and the 'missing' bits of postplenial are added, its cross section more closely approaches *Siderops*.

We conclude with Colbert that *A. wadleyi* is closer to the brachyopids than the capitosaurs. While there is insufficient of the specimen to allocate it to a family within the Brachyopoidea, there is nothing to preclude it being a brachyopid or a chigutisaurid of the *Siderops* type.

Cyrtura temnospondyla

This specimen from the late Jurassic Solnhofen Limestone of Germany was described by Jaekel (1904) as a temnospondyl. It was subsequently placed in the Chelonia, apparently without discussion, by Romer (1966) and Orlov (1964). Kuhn (1964), however, supported its allocation to the Temnospondyli. *Cyrtura* consists of a series of 14 vertebrae. The basis for its inclusion in the Temnospondyli is that the intercentrum (hypocentrum) of the vertebra is larger than the pleurocentrum. This occurs in temnospondyls but not in reptiles.

We have located the specimen in the Museum für Naturkunde in East Berlin, and Dr Herman Jaeger has sent us a cast.

Jaekel (1904) and later Kühn (1964), who supported him, gave little evidence for their designation of the larger unit of the centrum as the hypocentrum (= intercentrum) and the smaller as the pleurocentrum. The evidence appears to us to indicate that the reverse is the case.

First, the small 'pleurocentrum' is unpaired, which would be exceptional for a rhachitomous temnospondyl. In some earlier rhachitomes the pleurocentra may fuse dorsally (e.g. *Eryops*) and in some dissorophoids a single pleurocentrum is the main central element (Bolt 1969). However, most rhachitomes have paired pleurocentra, situated dorsal to the intercentrum (Romer 1947), which become less important in Triassic forms, often failing to ossify as in *Siderops*. Thus it is only when the pleurocentra form a major component of the vertebra that they fuse to form a single unit, and the trend is for them to become smaller and more widely separated with time. If *Cyrtura* is to be treated as a temnospondyl, then its small yet fused and ventrally situated pleurocentra are quite contrary to the conditions that one would expect in a late member of that group.

Secondly, the haemal arch is always associated, both in amphibians and reptiles, with the intercentrum (Romer 1956, 1966), not the pleurocentrum as implied by Jaekel for *Cyrtura*. On both of these grounds, then, these caudal vertebrae would seem to us to have a centrum composed of a large pleurocentrum and a small intercentrum, which would indicate reptilian rather than amphibian affinities.

Our examination of the cast suggests to us that a further interpretation of the centrum is possible. The separation of the haemal arches from the caudal intercentra would, in our experience, be quite unusual, and it may be that the element preserved below the central elements represents the intercentrum plus haemal arch, the normal condition. If this is the case, then the bipartite body of the centrum observed in the specimen may reflect a normal, reptile-type centrum (i.e. pleurocentrum) divided by an area of incomplete ossification, such as an autotomy plane.

We thus consider *Cyrtura* to be a reptile but its exact relationships are not clear. Although *Cyrtura* has been placed in the Chelonia, Dr Eugene Gaffney (personal communication) has informed us that no chelonian of which he is aware possesses a caudal vertebral structure comparable to that of *Cyrtura*. We cannot say where *Cyrtura temnospondyla* has its closest affinities, and feel that it is best considered for the time being simply as Reptilia *incertae sedis*.

RELATIONSHIPS

Temnospondyl phylogeny

The higher classification of the Amphibia is still largely based on the scheme of Romer (1966). However, continuing research over the last 15 years has pointed out that all three of the subclasses employed by Romer, the Labyrinthodontia, Lepospondyli and Lissamphibia, may be artificial assemblages (see, for example: Bolt 1977; Carroll & Currie 1975; Carroll & Gaskill

1978; Carroll & Holmes 1980; Panchen 1977*b*; Panchen 1980). Panchen (1980) has revised the contents of Romer's Labyrinthodontia, placing anthracosaurs, seymouriamorphs and loxommatoids into the order Batrachosauria. The remaining labyrinthodonts he left in the orders Ichthyostegalia and Temnospondyli, although, as he pointed out, they are defined entirely by cranial and vertebral morphological characters which are primitive for all tetrapods. Apart from the presence of well developed interpterygoid vacuities (also found in some microsaurs and nectrideans) Panchen could find no other shared derived characters that would indicate that the Temnospondyli are monophyletic.

Smithson (1982) has recently pointed out that all temnospondyls have a unique relationship between the skull roof and braincase, with the latter region being supported by the suturing of the exoccipital bones to the postparietals and tabulars. This feature is clearly derived, as it replaces the fish-like hyomandibular support of the braincase, freeing the hyomandibula to 'become' the stapes. This arrangement of bones is also found in the lepospondyl order Microsauria. Thus microsaurs may be the sister group of temnospondyls, or may have been derived from them. In either case, this distinctive method of supporting the braincase is the best evidence yet presented that the temnospondyls form a natural group.

Within the Temnospondyli the two major suborders, the Rhachitomi and Stereospondyli, have been found to grade into one another (Panchen 1977*b*; Dutuit 1972) and do not appear to represent monophyletic units. The third suborder, the Plagiosauria (Panchen 1959), is a small group with highly characteristic vertebrae. Romer (1966) recognized nine superfamilies of temnospondyls. One of these, the Loxommatoidea, has recently been transferred, as mentioned above, to the Batrachosauria (Panchen 1980). Since Romer's work, two additional superfamilies, the Dissorophoidea (Bolt 1969) and the Rhytidosteoidea (Cosgriff 1965), have been defined, making a net total of ten (these are: Edopoidea, Eryopoidea, Dissorophoidea, Trimerorachoidea, Trematosauroidea, Rhytidosteoidea, Brachyopoidea, Rhinesuchoidea, Capitosauroidea and Metoposauroidea).

Numerous authors (for example: Romer 1947; Thomson & Bossy 1970; Howie 1970; Bonaparte 1978) have presented network diagrams expressing their views on relationships of these superfamilies within the Temnospondyli. Relationships have been based on the possession of both primitive and derived character states, and the monophyly (*sensu* Hennig) of some taxa must be doubtful since they are defined by the absence of shared derived character states (synapomorphies) possessed by their descendants. Examples include the edopoids and eryopoids.

No attempt has been made as yet to analyse the interrelationships of the temnospondyl superfamilies by cladistic methods, using shared derived character states to determine sister groups (Hennig 1966; Eldredge & Cracraft 1980). This is a powerful tool for establishing phylogenetic relationships, and we considered making such a study at a preliminary level. However, cladistic systematics is only as good as the basic data, the character state definitions and the distributions allow it to be. Boy (1981) has recently examined the problems inherent in applying Hennig's methods to phylogenetic studies of fossil groups, and particularly labyrinthodont amphibians. He emphasized the meagreness of the available characters and the difficulty of determining the evolutionary polarity of these characters. He further stressed the difficulties, under these circumstances, of detecting parallel evolution, noting that the results of purely cladistic approaches are likely to be biased by these deficiencies, and that phylogenies ought to be 'fleshed out' by the use of anagenetic characters (Mayr 1969). Nevertheless he stated his belief that Hennig's approach (based on synapomorphies) is the preferred method for establishing cladistic events since it 'works on logical reasonings and demands transparent documentation'. In fact this support of a basic cladistic analysis, to which is added information based on anagenetic and functional criteria, is similar to Eldredge's (1979) distinction between cladograms and phylogenetic trees, with the former being the basis of the latter.

For the temnospondyls we, like Boy, found it difficult to assemble from the literature a large enough number of character states for which the evolutionary polarity can reliably be inferred and that are observable throughout the groups under study. All too often one finds that the states of potentially useful characters in crucial taxa are simply not known or are based on someone's best guess. Moreover, we found that there is a disappointingly poor correlation between those characters that are available, leading to many alternative phylogenetic schemes, each of which is forced to include numerous hypotheses of convergent or parallel evolution. We were unable to choose between several equally unsatisfactory alternatives, and leave this problem unresolved.

It seems clear that the inadequacies of the higher classification of temnospondyls are a long way from resolution. In the absence of a detailed study of this problem, the course followed in this paper has been to accept the superfamilies as natural groups for the purpose of comparisons, even though the strict monophyly of several superfamilies remains to be demonstrated.

Brachyopoid phylogeny

The superfamily Brachyopoidea was most recently reviewed by Warren (1981 *b*). As defined by Warren, the superfamily consists of the Brachyopidae, the Chigutisauridae and the Kourerpetontidae. Warren presented a series of 12 character states said to define the Brachyopoidea. All of those would appear to be apomorphic with respect to other labyrinthodonts, although they are not all unique to brachyopoids. *Kourerpeton bradyi* (Olson & Lammers 1976), the only representative of its family, does not fit Warren's criteria in several respects, and retains a number of plesiomorphous character states that do not indicate a close relationship with the Brachyopoidea. Apomorphous character states shared by *Kourerpeton* and the Brachyopidae-Chigutisauridae group are the short broad skull, anteriorly situated orbits and the lack of zones of intensive growth. All of these occur in other temnospondyl taxa, and are linked in that all are juvenile characteristics (Bystrow & Efremov 1940) and may readily be produced by paedomorphosis.

Olsen & Lammers (1976) listed eight characters that could be used to compare *Kourerpeton* with the Trimerorhachoidea and the Brachyopidae. They contended that five of these linked *Kourerpeton* with the Brachyopidae, i.e. (1) basicranial joint fused, (2) loss of intertemporal, (3) quadrate well below level of occipital condyles, (4) quadrate ramus of pterygoid deep and reflected downward around adductor fossa, and extending posterior to quadrate, (5) palate 'arched to form a gently inverted U posteriorly'.

A number of comments may be made on this listing of character states. States 1–3 are found in a very wide variety of later temnospondyls and do not indicate any special relationship with brachyopoids. States 4 and 5 largely describe the same feature, i.e. the posteriorly deeply U-shaped palate is formed by well developed descending flanges of the pterygoid. Moreover, character 5 accurately describes the shape of the palate of *Kourerpeton*, but not of typical brachyopoids, which have very sharply downturned (almost 90°) and very deep pterygoid flanges. The only character state that appears to be a reliable brachyopid indicator is the posteriorly extended quadrate ramus of the pterygoid, and even this, as Olson & Lammers point out, is convergently present in the trimerorhachoid *Isodectes* (Chase 1965). It would seem that the available evidence is insufficient to permit the reliable allocation of *Kourerpeton* to the Brachyopoidea.

On the basis of the current superfamilial scheme, it would seem that the Kourerpetontidae are closest to the Trimerorhachoidea, a superfamily that includes other taxa combining brachyopid with eryopoid (i.e. primitive) characteristics. The lack of a moveable basicranial joint, however, makes it difficult to confidently assign *Kourerpeton* to this superfamily.

TABLE 5. MEMBERS OF THE SUPERFAMILY BRACHYOPOIDEA

Brachyopidae	
Austrobrachyops jenseni Colbert & Cosgriff, 1974	Antarctica (E. Triassic)
†*Batrachosuchus browni* Broom, 1908	S. Africa (E. Triassic)
†*B. concordi* Chernin, 1977	S. Africa (E. Triassic)
B. lacer (Shishkin, 1966)	Europe (E. Triassic)
†*B. watsoni* Houghton, 1925	S. Africa (E. Triassic)
†*Blinasaurus henwoodi* Cosgriff, 1969	Australia (E. Triassic)
†*B. townrowi* Cosgriff, 1974	Australia (E. Triassic)
B. wilkinsoni (Stephens, 1887)	Australia (E. Triassic)
†*Bothriceps australis* Huxley, 1859	Australia (L. Permian)
B. major Woodward, 1909	Australia (L. Permian)
†'*Brachyops*' *allos* Howie, 1972	Australia (E. Triassic)
†*B. laticeps* Owen, 1855	India (E. Triassic)
†*Hadrokkosaurus bradyi* (Welles, 1947)	N. America (M. Triassic)
Notobrachyops picketti Cosgriff, 1973	Australia (M. Triassic)
Chigutisauridae	
†*Keratobrachyops australis* Warren, 1981	Australia (E. Triassic)
†*Pelorocephalus mendozensis* Cabrera, 1944	S. America (M. Triassic)
†*Siderops kehli* n.gen. n.sp.	Australia (E. Jurassic)

† Only the species thus marked are represented by skulls sufficiently complete to allow detailed comparisons to be made. *B. wilkinsoni*, *B. major* and *N. picketti* are represented by skull roof impressions, *B. lacer* and *A. jenseni* by fragmentary cranial remains.

The superfamily Brachyopoidea is therefore limited here to the families Brachyopidae and Chigutisauridae. The Brachyopidae has been reviewed by several authors in recent years (Cosgriff 1969; Welles & Estes 1969; Cosgriff 1973; Chernin 1977), so that it is now limited to the genera and species shown in table 5. This table also includes the three chigutisaur taxa currently recognized (Warren 1981*b* and present work).

Recently, Coldiron (1978) attempted a phylogenetic analysis of brachyopoid-trimerorhachoid relationships based entirely on synapomorphies. This study apparently followed Watson's (1956) suggestion that *Eobrachyops* (= *Isodectes*) formed a link between trimerorhachoids and the Brachyopidae. Coldiron's study had a number of shortcomings, including omission of significant taxa (Warren 1981*b*) and use of poorly defined character states. In fairness, however, it should be added that he, like us, was hampered by the lack of sufficient hard information concerning many characters.

Ingavat & Janvier (1981) have recently suggested that the Brachyopoidea might be included in their redefined Capitosauridae, based on the broad exoccipital–pterygoid contact. This view is not tenable in view of the fact that primitive brachyopoids (e.g. '*Brachyops*' *allos* and *Keratobrachyops australis*) lack such an extensive suture. Further, their concept of the Brachyopoidea is apparently based on that of Dutuit (1976), who, basing his scheme on that of Romer

(1947), included the Metoposauridae and Plagiosauridae in the superfamily. Ingavat & Janvier also referred to the brachyopoid affinities of *Almasaurus* noted by Dutuit, but again these affinities were with the 'brachyopoid' metoposaurs, and *Almasaurus* has nothing that allies it to the Brachyopidae or to our revised concept of the Brachyopoidea.

The wider relationships of the Brachyopoidea we leave open to question. The appearance of *Bothriceps* in the Australian Late Permian indicates that the superfamily was already recognizable and the chigutisaurid line had already split at this time. The plagiosaurs and metoposaurs, formerly related to this group by authors such as Romer (1947) and Watson (1956), lack too many brachyopoid features and possess too many specializations of their own to be considered close relatives. The superfamily Rhytidosteoidea, however, contains many relatively primitive Triassic temnospondyl genera, which also show a tendency to an anterior placement of the orbits, shortening of the face and reduction or even loss of the otic notch and tabular horns (Cosgriff & Zawiskie 1979). Many also lack the lacrimal bone, which is a further indication of brachyopoid affinities, and we should not be surprised if the rhytidosteoids prove to be the sister group of the brachyopoids.

We can now provide a redefinition of the superfamily Brachyopoidea, and its included families.

Superfamily Brachyopoidea Säve-Söderbergh, 1935

Temnospondyl labyrinthodont amphibians, typically with short broad parabolic skulls. Basicranial joint absent, pterygoids being broadly sutured to parasphenoid. Orbits in anterior half of skull. Otic notch weakly developed or absent. Tabular horns present or absent. Zones of intensive growth typically absent or confined to cheek region. Lacrimal bone absent. Quadrate condyles in same transverse plane as occipital condyles or (usually) well anterior to occiput. Palatal denticle layer generally absent (weakly present in *Siderops* and '*Brachyops*' *allos*). Anterior palatal vacuity unpaired. Pterygoid separated from vomer by palatine. Pterygoid with deep, vertical ventrally directed plate bordering subtemporal fossa, forming an inverted U-shaped palate. Quadrate condyles well below level of occipital condyles. Palatoquadrate fissure present or absent. Squamosal and quadratojugal with strong occipital flanges forming a vertical, transversely concave trough lateral to pterygoid. Retroarticular process long, with articular exposed on its dorsal surface. Posterior meckelian foramen and angular–prearticular suture on ventral surface or very low on lingual surface of lower jaw.

Family Chigutisauridae Rusconi, 1951†

Brachyopoids with tabular horns. A complete row of smaller teeth (as well as tusks) present on bones of palatal complex. Ascending ramus of pterygoid with column-like internal margin, the ascending column (but see comments on *Pelorocephalus* below). Infrastapedial process present on posterior margin of corpus of pterygoid. Quadrate ramus of pterygoid not extending posterior to quadrate. Quadrate sutured firmly to pterygoid and squamosal. Palatoquadrate fissure absent. Quadrate condyles markedly anterior to position of occipital condyles. Post-temporal fossa wider than deep.

Family Brachyopidae Broom, 1915

Brachyopoids lacking tabular horns. Tusks only on the bones of palatal complex, with scattered smaller teeth sometimes present, especially in region of anterior palatal vacuity and

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† Warren (1981*b*) erroneously attributed this family name to Bonaparte, 1978.

choanal margins. No column-like margin on ascending ramus of pterygoid. Pterygoid extends posteriorly to quadratojugal–squamosal trough, usually not sutured firmly to quadrate and separated from squamosal by a palatoquadrate fissure (not so in '*Brachyops*' *allos*). Occiput often extended posteriorly so that occipital condyles are well behind level of skull roof. Post-temporal fossa as wide as deep (usually circular) or deeper than wide.

TABLE 6. DERIVED CHARACTER STATES USED IN ESTABLISHING BRACHYOPOID PHYLOGENY

1 skull short, broad, parabolic
2 zones of intensive growth in cheek region only
3 lacrimal absent
4 basicranial joint firmly sutured
5 pterygoid with deep, vertical, ventrally directed plate forming inverted U-shaped palate; quadrate condyles well below level of occipital condyles
6 squamosal–quadratojugal trough present lateral to occiput
7 retroarticular process long
8 posterior meckelian foramen and angular–prearticular suture on ventral surface or very low on lingual surface of lower jaw
9 articular exposed on dorsal surface of retroarticular process
10 ascending column of pterygoid present
11 quadrate condyles markedly anterior to occipital condyles
12 complete row of small marginal teeth present on palatal complex
13 substapedial process of pterygoid present
14 postparietals shorter than parietals
15 lower jaw with distinct coronoid process
16 tabular horns absent
17 pterygoid extends posteriorly beyond squamosal–quadratojugal trough
18 post-temporal fossa about as deep as wide (rather than markedly wider than deep)
19 palatoquadrate fissure present
20 parasphenoid–exoccipital suture present, visible in ventral view
21 orbits very large (orbit length/skull length 0.29 or more, rather than 0.24 or less)
22 maxilla enters orbital border

The characters used by Coldiron (1978) and Warren (1981*b*) have been reviewed and condensed to exclude highly correlated character states and other characters difficult to define or of little diagnostic value. Table 6 lists 22 shared derived character states that form the basis of a cladogram (figure 34) illustrating a possible phylogeny for the Brachyopoidea. The derived condition of most of these character states can be readily inferred by using other amphibians, other temnospondyls and other Mesozoic temnospondyls as progressively less inclusive out-groups in which to observe character state distributions. The list was severely limited by the incomplete preservation of even some of the better known brachyopoid skulls, so that the resulting cladogram must be regarded as tentative. Some of the character states used require further discussion.

State 3, loss of the lacrimal, has not been used hitherto as a brachyopoid character. Only two of the species currently included in the Brachyopoidea have been reconstructed as possessing a lacrimal, these being *Blinasaurus henwoodi* and *Notobrachyops picketti*. In both cases, however, the outlines of these bones are entirely speculative since no sutures were preserved in the actual specimens. A third species, *Bothriceps australis*, was recently (Cosgriff 1973) said to possess a well developed lacrimal, and is so figured by Watson (1956). Welles & Estes (1969), however, figured *B. australis* without a lacrimal, this reconstruction being explicitly based on a careful re-examination of the type. Thus there seems no physical evidence that any brachyopoid possessed a lacrimal while, on the contrary, all brachyopoids in which the facial sutures are well preserved lack this bone. On this basis it seems reasonable to conclude that the superfamily as currently conceived may be characterized by the absence of the lacrimal bone.

The Chigutisauridae is at present incompletely known because the existing descriptions of the several skulls presently referred to *Pelorocephalus mendozensis* (Bonaparte 1978) are inadequate, but do indicate a large amount of variation within this supposed single species. We have based our phylogenetic analysis mainly on a *P. mendozensis* skull on loan from the American Museum of Natural History (AMNH VP7606) which we could examine at first hand. Unfortunately one of the most distinctive synapomorphies shared by the Australian chigutisaurs (character state 10) is not determinable in this specimen because of poor preservation of internal details, and previous descriptions do not mention this area. Future detailed revision of *Pelorocephalus* could well necessitate changes to the phylogeny presented here.

Character state 12 (presence of both tusks and a smaller tooth row on the palatal complex) is also problematical. Primitive temnospondyls and virtually all batrachosaurs had tusk pairs only on the vomers, palatines and ectopterygoids. In later temnospondyls, small teeth, similar in size to the maxillary teeth, are also present on these palatal bones, and the tusks become reduced or disappear, especially the ectopterygoid tusks. Thus the morphocline for this feature would be expected to be: tusks only, tusks plus marginal teeth, tusks reduced. On this basis, the brachyopids, which have few or no small palatal teeth, show a less derived condition than do the chigutisaurs, which have a complete row of small palatal teeth as well as tusks. We have accepted this hypothesis as the most likely one for our analysis. However, the dentition is specialized in brachyopids, which have unusually large teeth and tusks. The enlargement of brachyopid teeth combined with the shortening of the face may have caused the tusks to develop at the expense of the smaller palatal teeth, so that a possible alternative hypothesis is that the palatal teeth have been secondarily reduced or lost.

It will be noted that use has been made of only one of the skull proportion indices that have been much used in recent studies of labyrinthodont amphibians (see, for example: Welles & Cosgriff 1965; Welles & Estes 1969; Chernin 1977; Cosgriff & Zawiskie 1979). The single ratio chosen (U/L) reflects orbit size, proportional to the skull, and is employed because the extremely large orbits of *Blinasaurus* and *Hadrokkosaurus* are unusual in brachyopoids as well as in other temnospondyls and are likely to be derived with respect to the smaller orbits found in other brachyopids. We have not used other skull ratios in phylogeny reconstruction mainly because it is difficult to interpret the evolutionary polarity of each proportion measured, and moreover most ratios may not be treated as independent characters, since changes in one area of the skull are likely to cause changes in other areas. In addition, almost all brachopoids are known from single, usually partly incomplete, skulls, so that there is little information on ontogenetic variation in this family. Yet, as Bystrow & Efremov (1940) and Welles & Cosgriff (1965) have pointed out, large intrapopulation variations in many skull proportions can be observed when ontogenetic series of skulls are available. These proportions include those measured by the Welles & Cosgriff ratios. Thus, while the ratios may be useful in defining species or phenetically similar groups of taxa, the naturalness (i.e. monophyly of Hennig) of these groupings is not ascertainable from these ratios alone.

In the phylogeny of the Brachyopidae in figure 35, *Blinasaurus* refers to *B. henwoodi* and *B. townrowi* and not to the type species, *B. wilkinsoni*, which, because of its incomplete preservation of cranial characteristics (see footnote to table 4), could not be included in the analysis. A more important feature of the cladogram is the widely separated branching positions of *Brachyops laticeps* and '*B.*' *allos*.

In describing '*Brachyops*' *allos* as the second species of its genus, Howie (1972*a*) established that, based on the cranial indices of Welles & Estes (1969), this species was closest to *B. laticeps* (the type) and to *Batrachosuchus browni*. To some extent, her placement of '*B.*' *allos* in *Brachyops* was tentative, reflecting a desire not to indulge in excessive 'splitting' at the generic level until brachyopid relationships became better known. Certainly, she was reluctant to accept the cut-off point of a sum of differences (Welles & Estes 1969) score of 57 as grounds for the establishment of a new genus.

The analysis of synapomorphies done for the present study does, however, provide new grounds for examining the relationships of '*B.*' *allos*. As indicated in figure 35, '*B.*' *allos* has few of the characteristics that define most brachyopid genera, and is primitive in many respects.

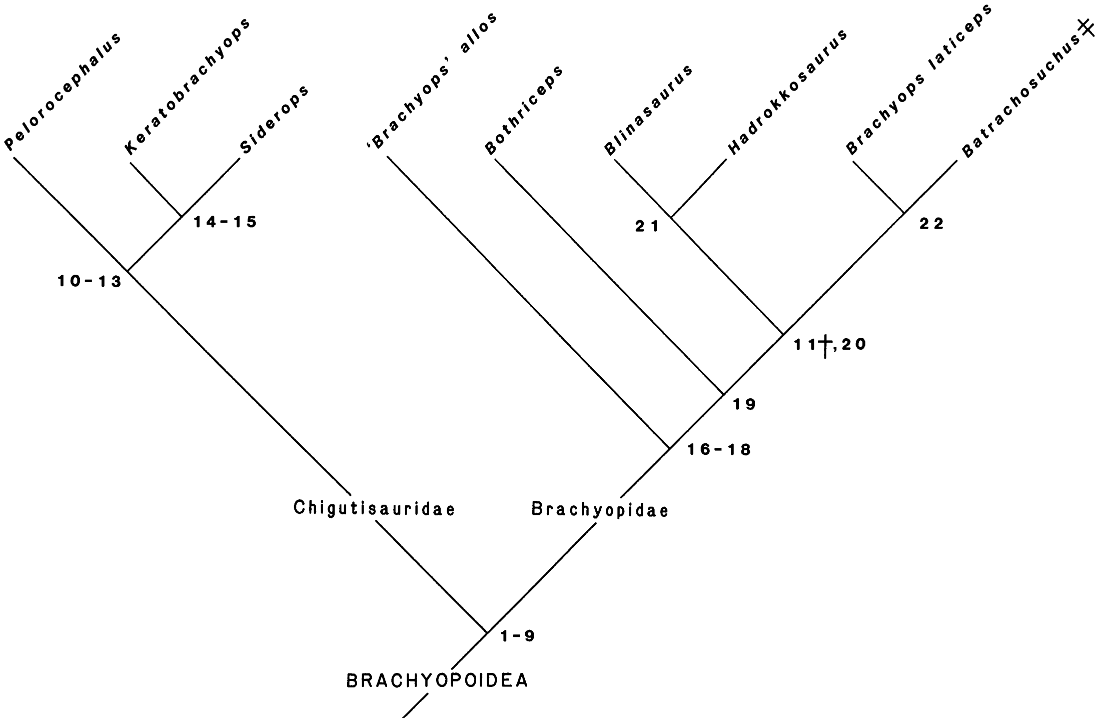

FIGURE 35. A hypothesis of relationships for the better-characterized brachyopoid taxa, based on the derived character states listed in table 6. †Character state 11 (anterior position of occipital condyles) convergently acquired by chigutisaurs and advanced brachyopoids. ‡Character state 22 (maxilla enters orbital border) not known in *B. concordi*.

Those derived character states that it does possess do not ally it with any other genus in particular, and it shows few of the several derived states that distinguish the type of *Brachyops*, *B. laticeps*. Specifically, '*B.*' *allos* lacks the anteriorly placed quadrates, a parasphenoid–exoccipital suture, a palatoquadrate fissure, and very short frontals (about half the length of the parietals), all found in *B. laticeps*. While *B. laticeps* can be derived from a form like '*B.*' *allos*, the same could be said of other advanced brachyopids such as *Blinasaurus henwoodi* or *Batrachosuchus* spp. '*B.*' *allos* appears to share a larger number of morphological similarities with *Bothriceps australis* but these are all plesiomorphies, and do not indicate special relationship.

The persistence of numerous primitive character states, combined with a few derived brachyopid states, indicate to us that '*B.*' *allos* is an early divergence from the brachyopid line, and warrant its removal from *Brachyops*. We therefore suggest that the peculiarities of '*Brachyops*' *allos* be expressed by its placement in a new genus, for which we propose the name *Xenobrachyops*.

Xenobrachyops n.gen.

Etymology. From the Greek *xenos* (strange, foreign) and the generic name *Brachyops*, drawing attention to the peculiarities of the new genus compared with the type of *Brachyops*, *B. laticeps*.

Diagnosis. A genus of brachyopid amphibians distinguished from all other members of the family by the presence of well ossified quadrate, absence of a palatoquadrate fissure, the presence of denticles on the parasphenoid and the base of the cultriform process, and a posteriorly expanded ectopterygoid which extends along the inner margin of the subtemporal fossa. Further distinguished from all except *Bothriceps* by the approximately linear (in dorsal view) arrangement of the occipital and quadrate condyles (i.e. quadrates not markedly anterior to occiput).

Included species. *Brachyops allos* Howie, 1972. Monotypic.

The complete listing of the characteristics of the genus would necessarily be the same as for the single included species, of which the holotype skull (QM F6572) is well described and figured by Howie (1972*a*), and the referred lower jaw (QM F10118, 10119) by Warren (1981*a*).

Zoogeography

The Brachyopoidea is predominantly a southern group, being especially diverse in Australia, which is the only continent to have yielded both chigutisaur and brachyopid remains. Australia has the oldest and most primitive members of both families, the former being *Keratobrachyops* and the latter *Bothriceps* and *Xenobrachyops*. Australia also has advanced members of both families (*Siderops* and *Blinasaurus*), which indicates a large amount of evolutionary divergence in this region. Other continents by contrast possess only limited generic-level diversity in their brachyopoid fauna. Thus southern Africa and India each have a single genus of advanced brachyopids (*Batrachosuchus* and *Brachyops* respectively), North America a distinctive, advanced brachyopid (*Hadrokkosaurus*) and South America a distinct local chigutisaur radiation (*Pelorocephalus*).

It is thus a reasonable hypothesis that the superfamily originated in East Gondwana, during the middle to late Permian, and subsequently dispersed, the chigutisaurs reaching 'South America' via the coast of 'West Antarctica', while the brachyopids spread to the rest of Gondwana and, to a limited extent, Laurasia, having traversed the other 'Antarctic' coastline. Welles & Estes (1969) also pointed out the distinctiveness of the Australian forms then known and their position at the base of the radiation of the Brachyopidae. Warren (1981*b*) has also suggested that Australia was the origin of the radiation of the superfamily.

The possible relationship between the Rhytidosteoidea and the Brachyopoidea suggested earlier would, if true, give added weight to these speculations, since Cosgriff & Zawiskie (1979) have suggested an Austral centre of origin for the rhytidosteoids. Australia's Permo-Triassic is remarkable for the absence, so far, of any synapsid reptile remains. Perhaps this absence created a vacuum, permitting an evolutionary radiation among the temnospondyl amphibians, resulting in the differentiation of two major assemblages, the superfamilies Brachyopoidea and Rhytidosteoidea.

We should like especially to thank the Kehl family of Kolane, Wandoan, Queensland, for their cooperation and hospitality during field work. Mary Wade of the Queensland Museum and Tony Thulborn of the Zoology Department, University of Queensland, made the initial excavations at Kolane, while many friends and colleagues helped with the subsequent field trips. The difficult job of extracting *Siderops* from its iron coat was undertaken principally by Jan Blinzler and Peter Crabb. Crabb was involved in much of the background work on matters geological and bibliographical that led to the production of this paper. Others involved with the preparation at various stages were Linda Bremner, Peter Mather, Pam Pittaway and Marlene Pugh. Wann Langston drew our attention to *Cyrtura* and we discussed its position with Gene Gaffney and Alec Panchen.

We are grateful to the Queensland Museum for parting with *Siderops* for so long, for casts of *Xenobrachyops allos* and *Austropelor wadleyi*, and for lending the holotype of *A. wadleyi*. We thank the American Museum of Natural History for the loan of *Pelorocephalus* (AMNH VP7606) and for casts of *Austrobrachyops jenseni*, the Museum of Paleontology at Berkeley for a cast of *Hadrokkosaurus bradyi*, the University Museum of Zoology, Cambridge, U.K., for *Lydekkerina huxleyi* (UCMZ T243), and Dr Herman Jaeger, Museum für Naturkunde, Humboldt Universität, Berlin, for a cast of *Cyrtura*.

Chuck Schaff of the Museum of Comparative Zoology gave technical advice on airscribes, Gordon Holmes of the Geology Department, La Trobe University, made the denticle sections and David Walsh showed endless patience with the photography as did Renee Alford and Trish Younger with the manuscript.

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Plate 1. *Siderops kehli* n.gen. n.sp. Dorsal and ventral views of the skull. (Approximately one-fifth actual size.)

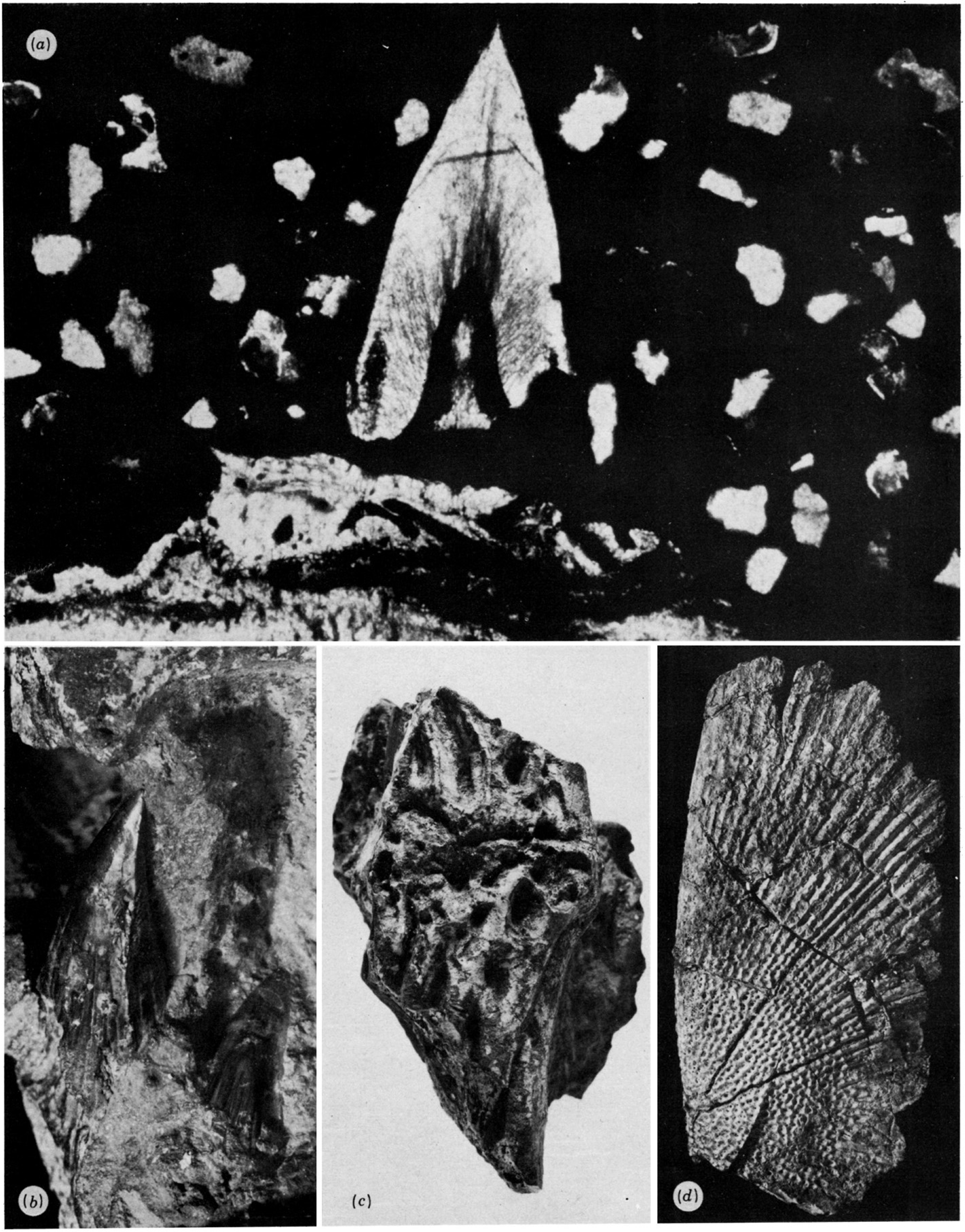

PLATE 2. *Siderops kehli* n.gen. n.sp. (*a*) Photomicrograph of a section of a denticle attached to a plate. (Magn. × *ca.* 110.) (*b*) Oblique view of mesial side of right mandibular tusk. (Magn. × *ca.* 2.5.) (*c*) Ventral view of healed break in the left mandible. The lingual side of the jaw is towards the right. (Actual size.) (*d*) Ventral view of QM F10123, an Early Triassic clavicle, to show ornamentation. (Actual size.)

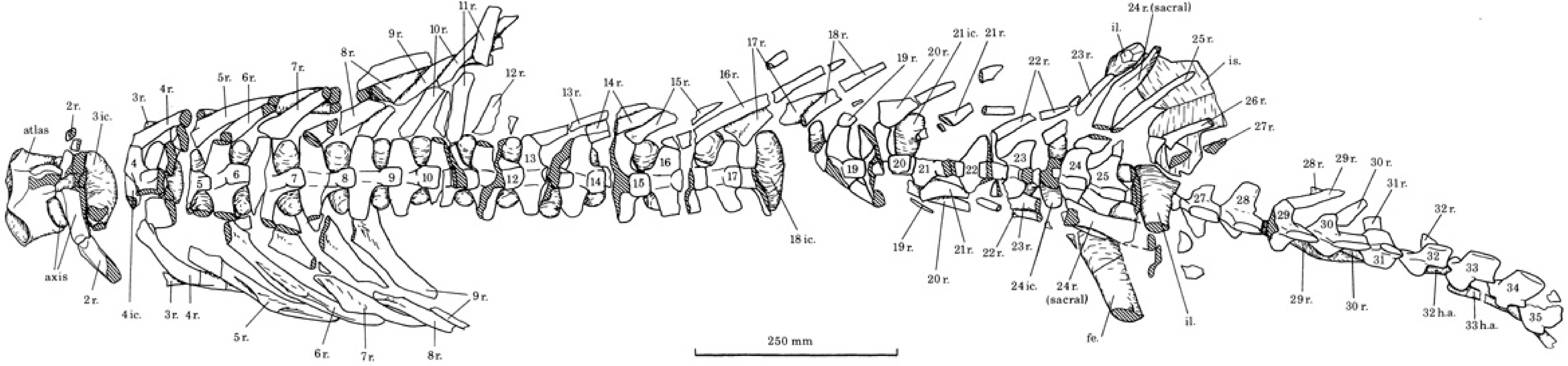

FIGURE 33. *Siderops kehli* n.gen. n.sp. Dorsal view of the postcranial skeleton as preserved.

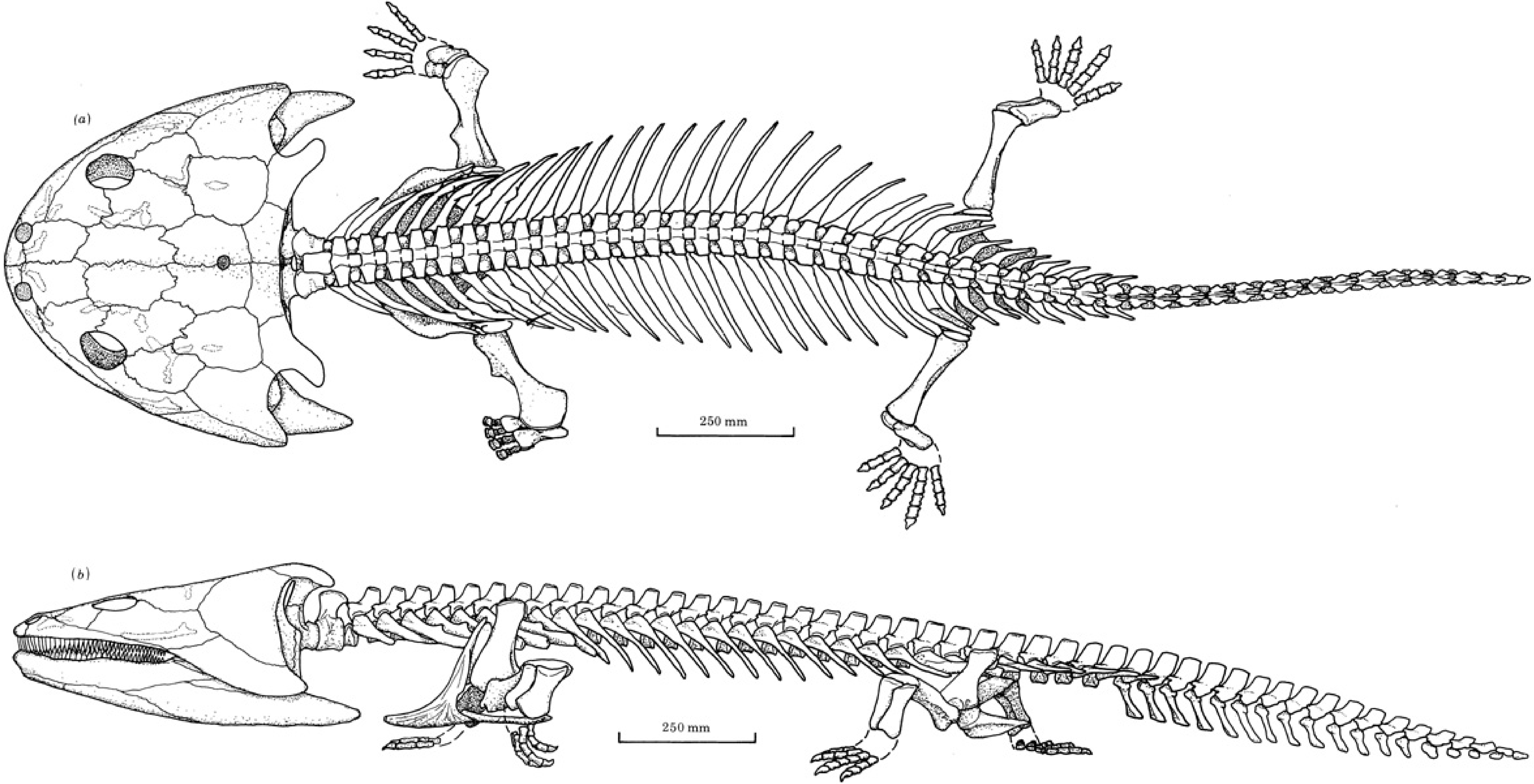

FIGURE 34. *Siderops kehli* n.gen. n.sp. Restoration of skeleton: (*a*) dorsal; (*b*) lateral.