

A LOWER CRETACEOUS PLIOSAUROID FROM SOUTH AFRICA

By

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(With 6 figures and 1 table)

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ABSTRACT

A revised account is given of the skull and partial skeleton of a small plesiosaur from the Lower Cretaceous (Upper Valanginian) Sundays River Formation of the Algoa Basin, South Africa. The specimen was originally described as *Plesiosaurus capensis* by C. W. Andrews in 1911, nominally as a 'small-headed' form of plesiosaurian, but is in fact a member of the 'large-headed', predaceous Pliosauroida. Its apparent closest relative is the English 'Wealden' (Barremian) species, *Leptocleidus superstes* Andrews, 1922. Both specimens seem to be very similar to, but smaller than, the Liassic genus *Rhomaleosaurus*. The Sundays River Formation is of shallow marine to estuarine-lagoonal provenance. A brief review is included of other, particularly Southern Hemisphere, occurrences of marginal and non-marine Plesiosauria.

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INTRODUCTION

The value of well-curated fossil collections is nowhere better displayed than in the specimen redescribed here. Very nearly one hundred years ago, Rogers & Schwarz (1901: 8–9) reported the recovery of the remains of a plesiosaurian

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reptile. It had been discovered by Schwarz in a cliff at the locality Picnic Bush, in the Zwartkops River Valley, south of Uitenhage. In the terminology of the day it was therefore ascribed to the Sundays River Beds of the Uitenhage Series. An age of Upper Valanginian to Lower Hauterivian was assumed, corresponding to the upper part of the 'Wealden' succession of England (Andrews 1911), but see below for further discussion. So far as is known this remains the only record of a plesiosaurian from southern Africa, although their remains are relatively common in Australia and New Zealand (Welles & Gregg 1971; Molnar 1982, 1984). The well-preserved, semi-articulated nature of this specimen encourages the hope that more may yet be found in the late Mesozoic rocks of Eastern Cape Province and KwaZulu-Natal.

Andrews (1911) assigned the specimen to a new species, *Plesiosaurus capensis*, and therefore by inference, to the small-headed superfamily Plesiosauroidea (Brown 1981). Several years later Andrews (1922) described a very similar specimen from the English Wealden (Berwick Brick Pit, Sussex) under the name of *Leptocleidus superstes*, and drew attention to close similarity of the Algoa Basin specimen to his new species, although the skull of *L. superstes* was lacking most of its structure anterior to the orbits. Strömer (1935) thought the South African specimen to be sufficiently different to warrant a distinct genus to itself, and created the genus *Peyerus* for it. However, Persson (1963) pointed out that Andrews original comparisons were sufficient to place *P. capensis* into the genus *Leptocleidus*, and that therefore Strömer's genus was effectively a subjective junior synonym for *Leptocleidus*. This course will be followed in this paper. The specimen is therefore *Leptocleidus capensis* (Andrews, 1911).

The specimen is of particular interest from several points of view. Firstly, it is a member of the superfamily Pliosauroidae, family Pliosauridae (Brown 1981)—aquatic animals showing extreme adaptations towards a predatory way of life, with skulls about half the length of the neck and large, conical, striated teeth adapted for piercing and tearing. It does not belong with the Plesiosauroidea, the contrasting group within the Plesiosauria, which show adaptations towards feeding on small or soft-bodied prey, and which possess heads very much less than half the length of the neck and slim elongate teeth. Secondly, the general structure of the skull of *Leptocleidus* is very close to that of the Liassic (Lower Jurassic) genus *Rhomaleosaurus* (Taylor 1992a, 1992b; Cruickshank 1994a). Thirdly, the palaeoenvironment of the sediments in which the specimen was found indicates close inshore, perhaps lagoonal, conditions (McLachlan & McMillan 1976; McMillan in press). A brief literature survey shows that several plesiosaurs, particularly those from southern continents, have originated from non-marine sediments, and hence a totally marine association of these predaceous aquatic reptiles is not necessarily to be expected (Bartholomai 1966; Molnar 1982, 1984; Rich *et al.* 1991). This paper will address these points, firstly by redescribing the specimen in the aftermath of further preparation, and by reviewing some occurrences of similar fossils.

Material referred to in the text is lodged in the following institutions: Palaeontology Department, Natural History Museum, Cromwell Road, London (BMNH); and Palaeontology Collections, Earth Sciences Division, South African Museum, Cape Town (SAM).

MATERIAL AND METHODS

LOCALITY AND GEOLOGICAL HORIZON

The specimen is recorded as having been discovered on the face of the cliff overlooking the farm Redhouse, in the Zwartkops (Swartkops) River Valley, from between the two upper mudstone beds, in a nodular clay limestone (Rogers & Schwarz 1901: 8–9; Rogers & Du Toit 1909). The locality is approximately 33°49'S 25°33'E (South African Topocadastral Series, sheet 3325). The specimen originally comprised 'portions of the shoulder girdle and some fifteen vertebrae, embedded in a nodule with the accompanying jaws (and ?skull), teeth, cervical vertebrae, hind limb bones and bones of the fore-arm and paddle loosely embedded in the dark grey clay' (Rogers & Schwarz 1901: 8–9).

The sediments are those of the Sundays River Formation, a lagoonal to shallow marine succession (McLachlan & McMillan 1976; McMillan in press), which forms the upper component of the Uitenhage Group of the Eastern Cape South Coastal Belt. The age of the Sundays River Formation has been variously reported as ranging from the 'Lower Greensand' to Liassic, but the general consensus of opinion holds that it is of Upper Valanginian–Lower Hauterivian age (Lower Cretaceous) (McLachlan & McMillan 1976: 205–206). This is confirmed by a recent analysis of the foraminiferans (McMillan in press), which shows that the Picnic Bush locality lies at the top of his new Biozone Bb, and is placed by him in the Uppermost Valanginian. From an associated palaeoecological study, McMillan shows that Biozone Bb equates with his Transgressive Zone. The entire Valanginian sequence of the Sundays River Formation is characterized, to a greater or lesser extent, by the presence of freshwater foraminiferans. The probability is that Biozone Bb was laid down under estuarine or marginal marine conditions. *Leptocleidus capensis* possibly lived, and was certainly preserved, in an inshore environment.

PRESERVATION

The remains of the shoulder girdle, forearm and teeth are no longer in the collections of the South African Museum. Nine posterior cervical and sixteen dorsal vertebrae run in an unbroken sequence but, at what appears to be the cervical–pectoral junction, there is a marked break in their line. Andrews (1911) recorded that the left side of the skull was obscured by the neural spines of six (?anterior) dorsal vertebrae—but which six is no longer clear, as they have all been cleared from the skull and may be among the several fragments that accompany the specimen.

The break in the line of the vertebrae may indicate that the animal was essentially complete when its carcass came to rest on the bottom, only the head becoming detached and coming to lie alongside the vertebral column. One paddle must have been close by, as it donated a phalange to lie within the left temporal arcade, and a carpal(?) to lie inside the left orbit. The presence of hind limbs (two femoral shafts, two fibulae and a tibia) reinforces the idea that the skeleton was nearly complete at the time of burial, and had suffered minimal damage through scavenging and current action. A situation not unlike that reported by Taylor (1992a) for *Rhomaleosaurus zetlandicus* is a strong possibility for this specimen.

The skull has been symmetrically squashed dorso-ventrally, but mainly over the parietal region. The snout seems undistorted, but a pair of symmetrically placed depressions (dep) on either side of the mid-nasal ridge (dmc) might also be taphonomic damage, although not shown as such in the reconstructions (Figs 1, 2). As a result of the distortion of the parietal crest, the sidewall of the braincase is no longer easily interpreted (Fig. 2).

In summary, what is currently preserved of the specimen is as follows: an almost complete skull, portions of both jaws rami, but not the symphysis, 22 cervical and 16 dorsal vertebrae, two fibulae, one tibia, the remains of two femora, several carpals/tarsals and the bulk of a paddle.

SYSTEMATIC PALAEOLOGY

Class REPTILIA

Subclass SAUROPTERYGIA Owen, 1860

Order PLESIOSAURIA de Blainville, 1835

Superfamily PLIOSAUROIDEA (Grey, 1825) Welles, 1943

Family **Pliosauridae** Seeley, 1874

Genus *Leptocleidus* Andrews, 1922

Type species. *Leptocleidus superstes* Andrews, 1922: 285–298, pls 14–15, based on specimen BMNH R4824, from the Berwick Brick Pit, near Lewes, Sussex, United Kingdom, Upper Weald Clay (= Barremian), Lower Cretaceous.

Remarks

The classification of the Plesiosauria is at present in a state of flux. Hitherto, a clear-cut division of the order into two superfamilies, the Pliosauroidae and Plesiosauroidae, seemed to offer a stable solution to their classification (Brown 1981). However, recent descriptions of plesiosaurians from the Rhaeto-Liassic of England indicate that this simple relationship can no longer be held (Brown 1993; Storrs & Taylor 1993; Cruickshank 1994a, 1994b; Brown & Cruickshank 1995). In many of the characters of the skull, the genus *Leptocleidus* is very close to *Rhomaleosaurus* from the Liassic of Europe, but as the critical region of the lower jaw symphysis is not known with certainty in *Leptocleidus*, its final position must remain undecided for the present (see Table 1).

Leptocleidus capensis (Andrews, 1911)

- | | |
|------|---|
| 1911 | <i>Plesiosaurus capensis</i> Andrews, p. 309. |
| 1922 | <i>Leptocleidus capensis</i> Andrews, p. 291. |
| 1935 | <i>Peyerus capensis</i> Strömer, p. 44. |
| 1963 | <i>Leptocleidus capensis</i> Persson, p. 19. |

Material

SAM-K5822, from Picnic Bush site, Swartkops River Valley, Cape Province, overlooking Redhouse Farm, 33°49'S 25°33'E, Sundays River Formation (= Uppermost Valanginian).

Diagnosis

Pliosauroid plesiosaur very similar to, but smaller than, *Rhomaleosaurus*, having a subtriangular skull outline, possessing a dorsomedian foramen on the midnasal ridge of the premaxillae, dorsomedian troughs on the articulars and prearticulars, expanded lateral rami of the pterygoids, strong descending post-orbital flanges, a snout bearing a rosette of procumbent teeth; teeth conical, circular in section with striae and weak carinae. It differs from *Rhomaleosaurus* in having a relatively shorter snout, fewer teeth in both upper and lower jaws, and a recurved crest on the forward-facing part of the vertex.

Remarks

Strömer (1935) created the genus *Peyerus* to accommodate *Plesiosaurus capensis*, but Andrews (1922) had already strongly suggested that *P. capensis* and *Leptocleidus superstes* were congeneric. This route was followed by Persson (1963), who formally incorporated *P. capensis* into the genus *Leptocleidus*. The genus *Peyerus* therefore becomes a subjective junior synonym for *Leptocleidus*. Persson (1963: 19) also made the point that *L. capensis* was '... a Rhomaleosauroid genus', pointing out that the skull was well preserved, was comparatively large, and had a distinct constriction at the maxillo-premaxillary suture.

DESCRIPTION OF SPECIMEN

Skull (Figs 1–3)

The skull is that of an adult, the sutures being very difficult to distinguish in places and none of the bones show any sign of disarticulation (Cruickshank 1994b). This interpretation is reinforced by an examination of the vertebrae, where the neural arches are seen to be firmly fused to their centra, an accepted indication of adulthood (Brown 1981).

The skull is about 310 mm long on the dorsal midline, and 172 mm across the quadrates, giving a length : width ratio of 1.7 : 1. It appears little damaged, but some bone is missing from the lower rim of the right orbit (orb) and adjacent palate, and most of the right cheek-bar is reconstructed in plaster-of-Paris. The now fragile occiput has been strengthened by a layer of plaster-of-Paris, which has obscured its details. However, most of the 'fixed points' can be determined to give the outline as illustrated in the figures.

The bones of the left side and anterior of the palate are clear, although several of the sutures on the skull roof are not at all easily seen. In particular, it is not certain if there is a lacrimal in this species, and the outline of the frontals (fr) and postfrontals (pof), where they meet, has had to be interpreted. Andrews (1911, fig. 1) reconstructed the palate from information contained on the

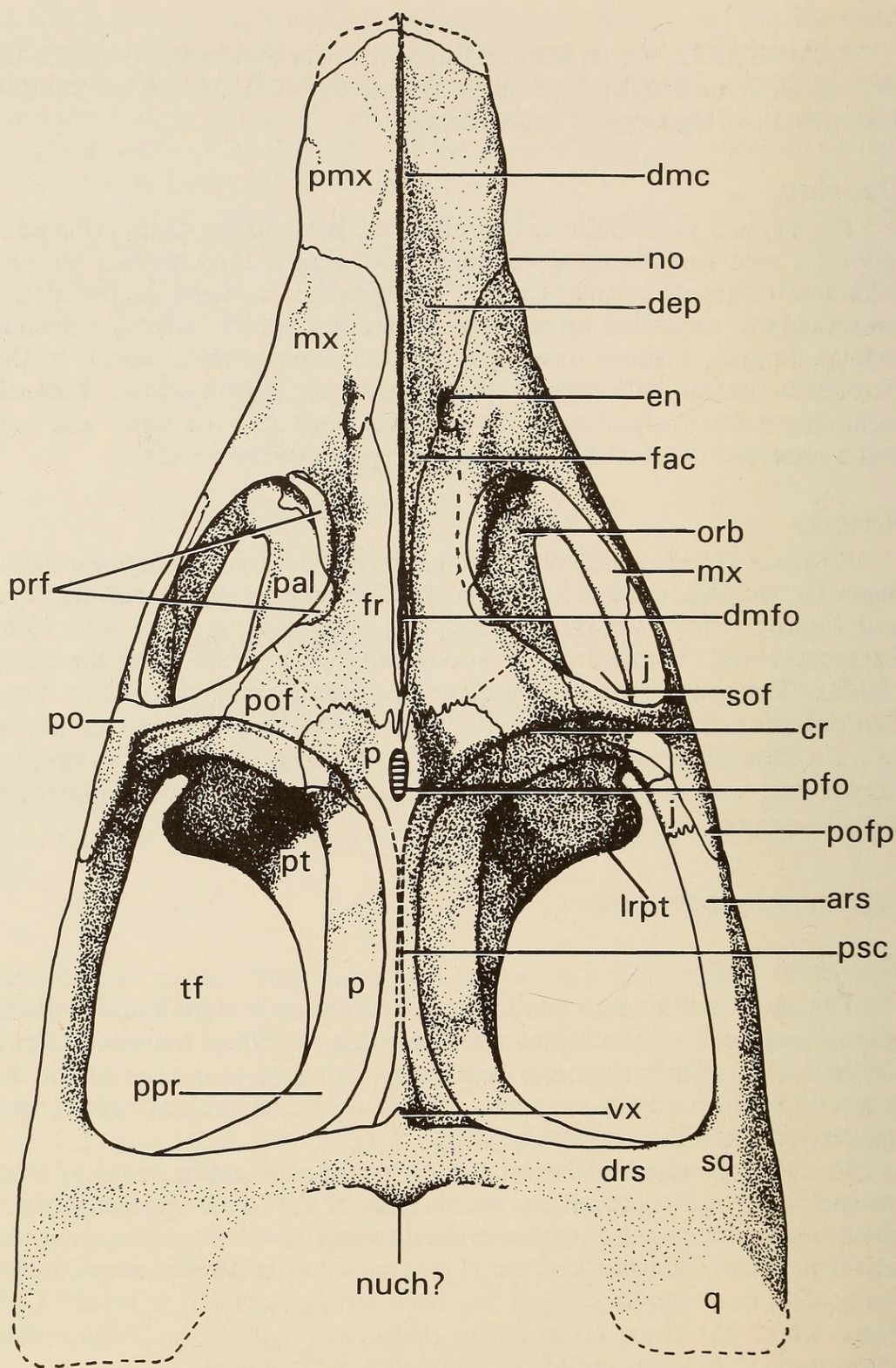


Fig. 1. Skull of *Leptocleidus capensis* (Andrews, 1911) in dorsal view.
For abbreviations to this and other figures see p. 225.
Scale bar = 50 mm.

damaged right side, and indicated that the ectopterygoid (ec) was an antero-posteriorly elongated bone. However, using the clear outlines of the bones now exposed on the left side of the palate, it is clear that the ectopterygoid is a leaf-like bone applied to the ventral surface of the lateral ramus of the pterygoid (lrpt), and elongated from side-to-side, with a connecting process linking it to the jugal (j).

The internal nares (in) are very similar to those of *Rhomaleosaurus*, having steeply-walled posterior limits, connected to a shallow channel (ch), which runs towards the diastema (dia) at the maxilla-premaxillary suture. Unlike *Rhomaleosaurus* and other pliosauroids, there do not seem to be any auxiliary foramina or channels associated with the narial system in this animal. The internal nares are positioned anterior to the external nares (en), and seem to have been part of an underwater olfactory system as described by Cruickshank *et al.* (1991) and Taylor & Cruickshank (1993).

A difference from the palates of species of *Rhomaleosaurus* is the proportion and placing of the parasphenoid (ps). In pliosauroids recently described (Taylor 1992b; Cruickshank 1994a), the parasphenoid is a relatively wide plate that spans the midline of the posterior interpterygoid vacuity (piv), and which effectively covers the bulk of the basioccipital and basisphenoid (bo, bs), with the exception of a small rim of basioccipital on the posterior limit of the palate, and the occipital condyle. In *Leptocleidus*, the parasphenoid is a narrow rod running back from a wedge inserted between the posterior portions of the anterior rami of the pterygoids, exposing the basicranium. In this specimen it is not possible to distinguish the suture between the basi- and parasphenoids, nor that between the basisphenoid and basioccipital in the region of the posterior interpterygoid vacuity. A similar structure of the rear of the palate is known in *Liopleurodon* and the plesiosauroid plesiosaurs (Andrews 1910–1913). The significance of this variation is not known at present.

The lateral ramus of the pterygoid descends below the line of the cheek bar, but is not at all robust, and does not have the 'boss' that is so strongly developed in *Rhomaleosaurus*. The postorbital bar (pob) has a very marked descending flange, very similar to that in *Rhomaleosaurus*, composed of elements of the parietals (p), postorbitals (po) and postfrontals (pof). However, the structure of this flange differs in two respects from that of *Rhomaleosaurus*. The postorbital itself has a very much reduced exposure on the descending flange, when compared with *Rhomaleosaurus* species (Taylor 1992a; Cruickshank 1994b), an area taken over by the postfrontal in *L. capensis*, but in turn the postorbital has a well-developed 'footplate' (pofp) running backwards over the junction of the jugal (j) and squamosal (sq). The descending flange also seems to be much deeper than in *Rhomaleosaurus*, closely approaching the dorsal surface of the palatal bones.

The articular surfaces of the quadrates (q) are missing, but the breaks seem to have been made only just above the joint surfaces, where the line of the medial surfaces of the quadrates start to turn outwards, as is indicated in the reconstructions (Figs 1–3).

Some post-mortem damage to the parietal crest (psc) has caused the line of the crest to be depressed, which has also damaged the side-walls of the braincase. However, impressions of the jaw adductor muscles seem to be apparent on

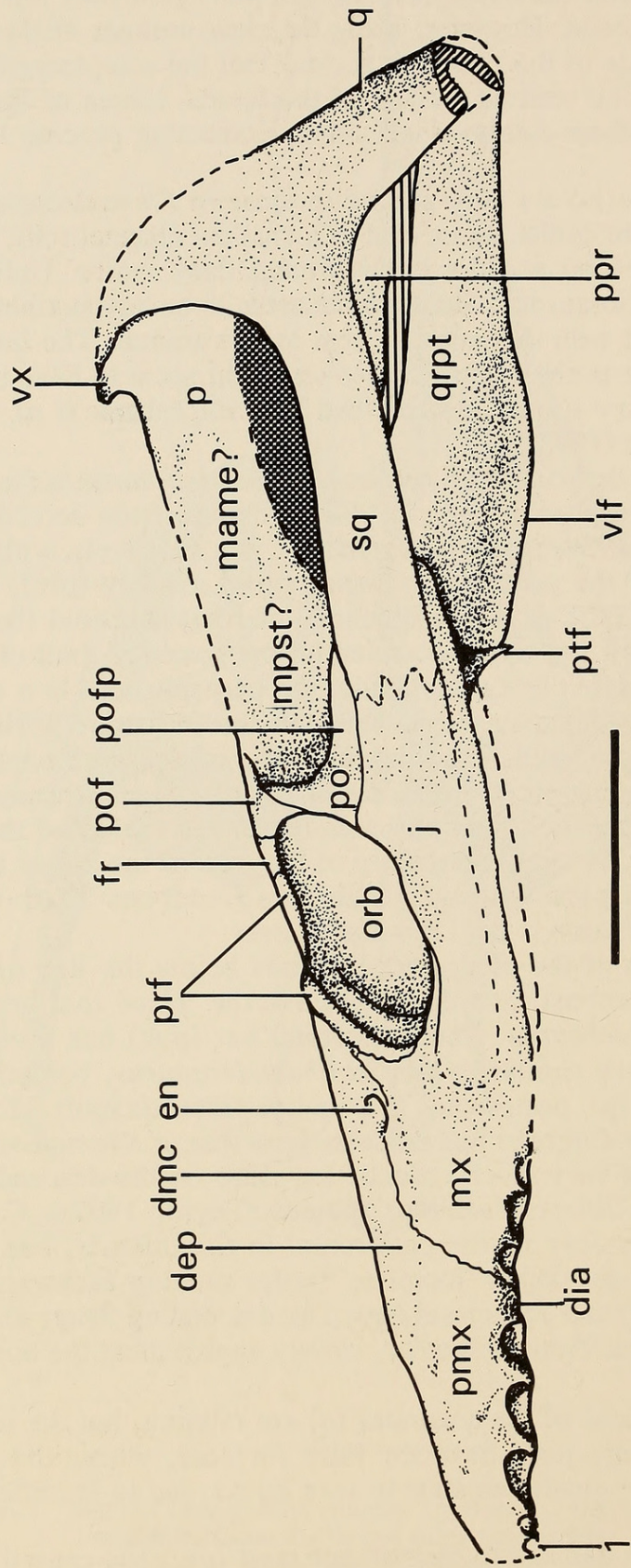


Fig. 2. Skull of *Leptocleidus capensis* (Andrews, 1911) in side view.
Scale bar = 50 mm.

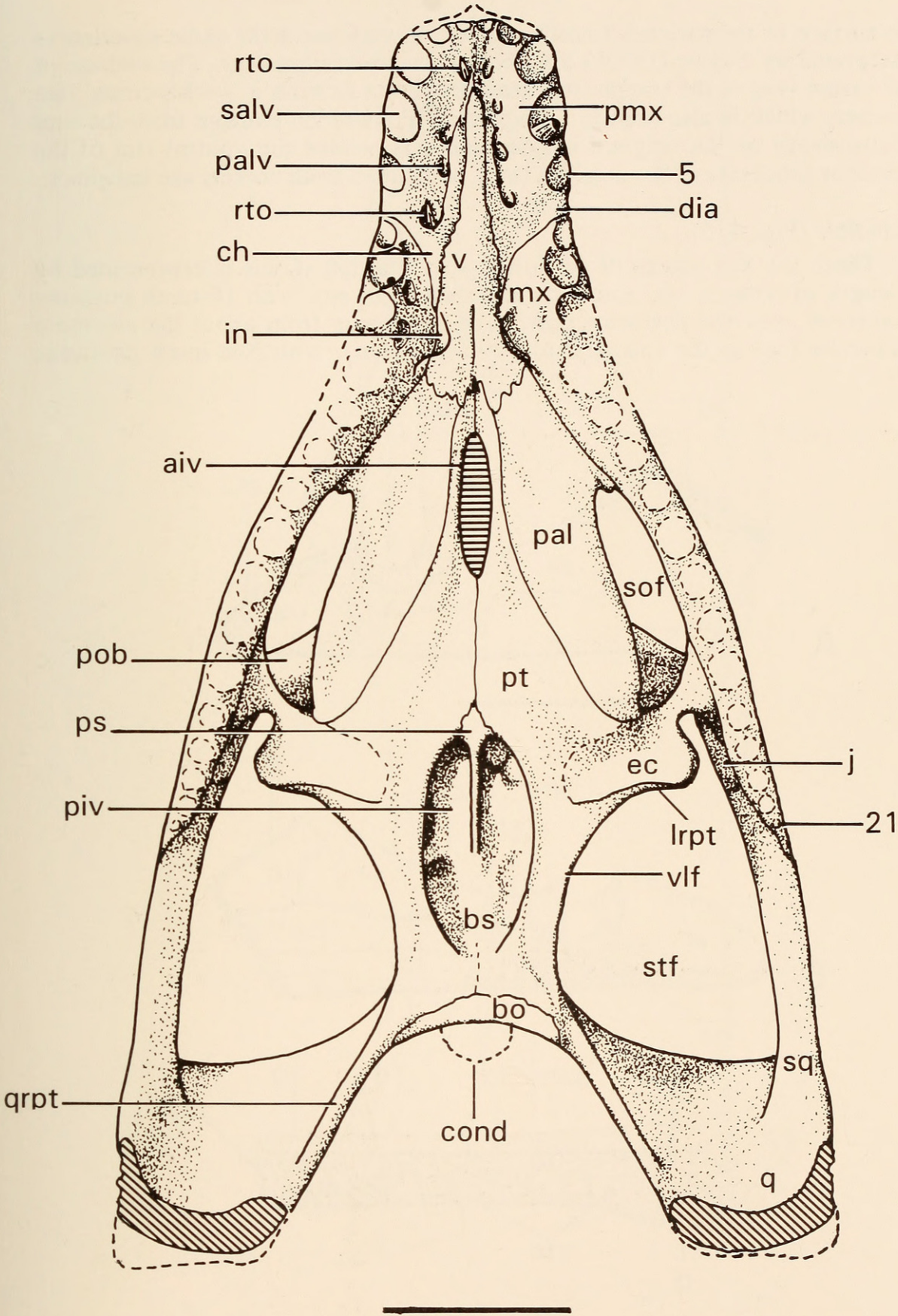


Fig. 3. Skull of *Leptocleidus capensis* (Andrews, 1911) in palatal view.
Scale bar = 50 mm.

the surface of the parietals (mpst?, mame?) in very much the same situation as interpreted by Taylor (1992b) for *Rhomaleosaurus zetlandicus*. The midline of the vertex (vx) of the occiput has been drawn out to form a 'cock's-comb'-like process, which is also seen in *L. superstes*. Preparation damage from the time of discovery or the original descriptions has eroded the ventral rim of the posterior processes of the maxillae (mx), so that the tooth sockets are indistinct.

Mandible (Figs 4, 5)

There are five pieces of the lower jaw. The left ramus is represented by a length of dentary (d), and associated bones (c, sp), with 16 tooth positions preserved, and the posterior portion of the ramus from about the coronoid eminence (ce) to the retroarticular process (rap), with five tooth positions

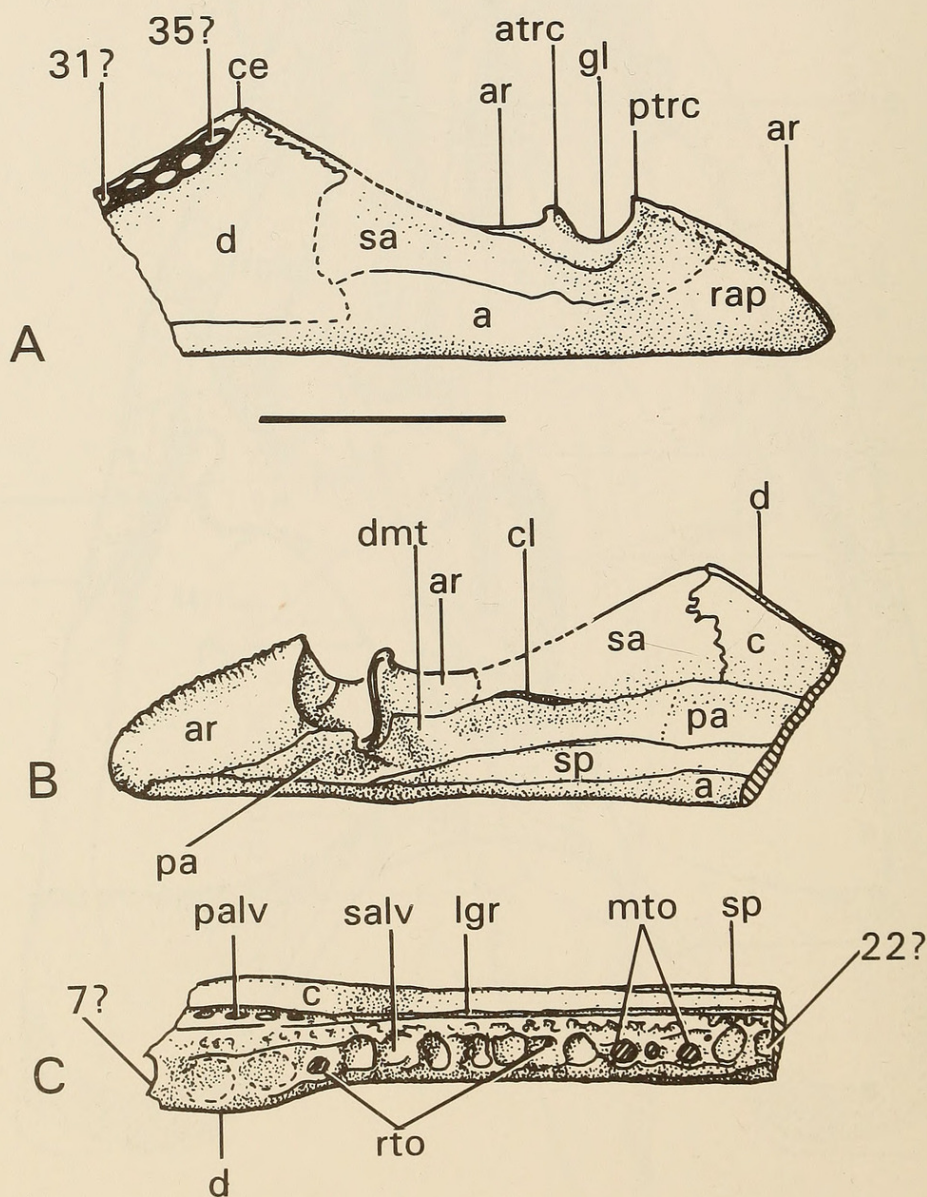


Fig. 4. *Leptocleidus capensis* (Andrews, 1911). A. Posterior portion of left ramus of lower jaw, outer view. B. Posterior portion of left ramus of lower jaw, inner view. C. Mid-region of lower jaw, dorsal view. Scale bar = 50 mm.

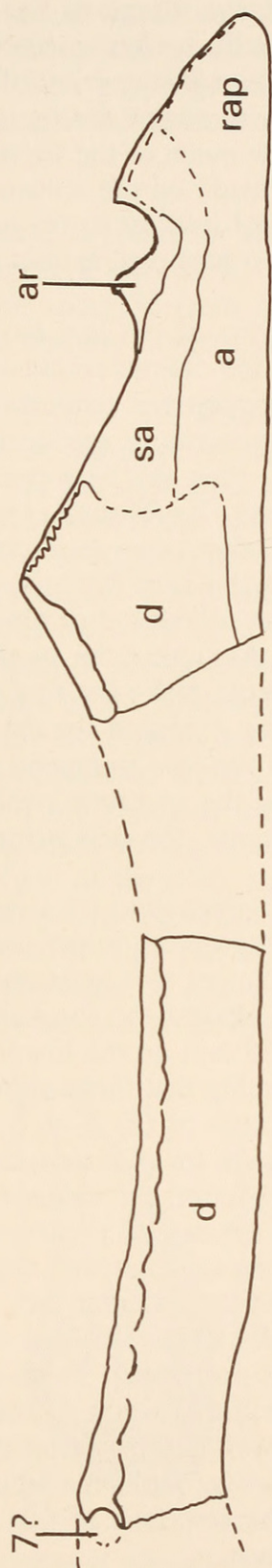


Fig. 5. Semi-diagrammatic reconstruction of left lower jaw of *Leptocleidus capensis* (Andrews, 1911) to show missing portions.
Scale bar = 50 mm.

preserved. The right ramus is represented by three portions: a short piece from just behind the symphysis (i.e. a mirror image of the very anterior of the anterior part of the other ramus); a badly broken piece from the mid-dentary region; and the very end of the ramus from just in front of the glenoid (gl) to the retroarticular process. Only the left jaw remnants are figured.

It is important to try to estimate how much of the front of the jaw is missing, as significant taxonomic decisions are made on the nature of the jaw symphysis (Tarlo 1960; Brown 1981). Also, it is of interest to try to calculate the amount missing from the ramus between the two portions, as this would help in arriving at a tooth-count for this species.

Neither of the anterior-most portions of the jaw have any indication of a symphyseal facet, but they both show the characteristic swelling that occurs in *Rhomaleosaurus* for at least two tooth positions behind the symphysis. Therefore, if the relationship with *Rhomaleosaurus* is appropriate and a symphyseal tooth-count of five is to be expected, then the first preserved tooth position cannot be more anterior than the sixth. In *Rhomaleosaurus*, the symphysis slopes backward ventrally and covers about one more tooth position after the fifth. Behind this the outer edges of the jaw rami are still parallel, to at least the seventh position, where the teeth start to reduce in diameter (Taylor 1992b, fig. 6; Cruickshank 1994a, figs 7, 9). Assuming the swelling to cover only one tooth position behind the symphysis would make the first preserved position the sixth, with an expectation of there being evidence for the remnants of the symphysis preserved on the lower edge of the jaw fragment; this is not evident. In order to be cautious, and assuming that the spatulate swelling of the anterior of the jaw covered more than seven positions, the first preserved tooth position is marked as the seventh.

Placing the jaw fragment in what appears to be a natural resting position against the upper jaw allows the swelling on the lower jaw to fit just behind the diastema (dia), leaving a distance sufficient to accommodate about five or six teeth to the front. Placing the glenoid against the (broken) end of the quadrate on the left side leaves a gap of about 75 mm on the lower edge of the jaw, into which about eight teeth could fit. Assuming that these approximations are nearly correct in their values, gives a tooth count of $(6) + 16 + (8) + 5 = 35$ for the lower jaw, a value within the known range for pliosauroids (Taylor 1992a).

The remainder of the jaw fits the general pliosauroid pattern, with, on the inner surface, a large coronoid (c) and substantial prearticular (pa) on each side. The splenial (sp) wedges between the prearticular and angular (a), and the prearticular runs under the medial flange of the articular (ar), to a point well behind the glenoid (Taylor 1992b; Cruickshank 1994a, 1994b).

No part of the Meckelian fossa is preserved, but a cleft (cl) between the prearticular and surangular (sa) marks the position of insertion of a portion of the jaw adductors (Taylor 1992b). A well-defined dorsomedian trough (dmt) is seen on the anterior faces of the articular and prearticular, as in *Rhomaleosaurus*, and which is believed to be characteristic of that genus (Taylor 1992a; Cruickshank 1994a) and its close relatives.

The mandible is a slender box-beam, with a low coronoid eminence lying fairly far back relative to the temporal fossa, just under the dorsally expanded vertex. A component of the external mandibular adductor muscles may have

originated in this pocket under the vertex and inserted in the cleft just in front of the glenoid. Such a muscle would act at its most efficient when the jaw was some way open, and enhance the speed at which it closed—a useful attribute in a generalized predator. This proposed muscle would be an addition to the main mass of the external mandibular adductor (mame?).

Dentition (Fig. 6)

In the upper jaw there is room for about 16 teeth in each maxilla, and five in each premaxilla, giving a total of 21 for the upper dentition. As calculated above, there seem to be about 35 teeth in each ramus of the lower jaw. These counts are within the known range for pliosauroids (Brown 1981; Taylor 1992a).

In the upper jaw, the first five teeth on each side commence with a very small tooth, which appears to have protruded almost horizontally, followed by four of increasing size, but also procumbent. In the upper jaw there is a diastema, at the maxilla-premaxilla junction, which is followed by a smaller tooth, behind which they enlarge again over two or three positions. However, damage to the maxillae behind this point has removed much information, and only what can be seen is indicated on the reconstruction—a run of substantial teeth extending to the limit of each maxilla. Little can be said of the mandibular dentition; the mesial part of the symphyseal region (in common with *Rhomaleosaurus*) shows several large tooth positions, followed by a marked decrease in size from about the postulated tenth position, to the end of the dentary. As judged from the visible replacement teeth (rto), each tooth is a substantial, slightly recurved cone, with strong striae on the lingual surfaces, and weak mesio-distal carinae. None of the teeth referred to by Andrews (1911) has survived, but he illustrated (pl. 18 (fig. 4)) a small (= ?posterior) tooth with a very much greater curvature to its tip. The implication is that the anterior teeth are simple cones, such as are found in *Rhomaleosaurus*, but that the posterior teeth were acting to help prey be swallowed, as is common in many modern reptiles,

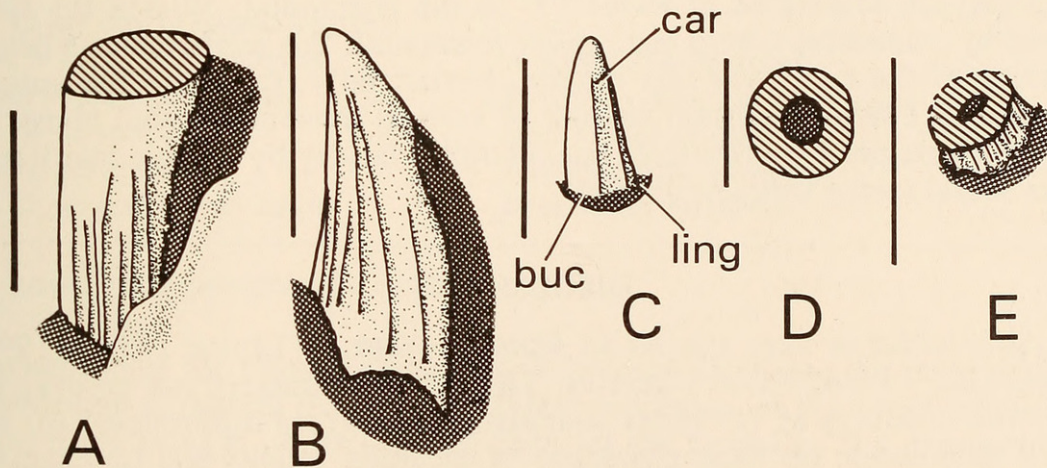


Fig. 6. Camera lucida drawings of selected teeth of *Leptocleidus capensis* (Andrews, 1911). A. Base of third left premaxillary replacement tooth. B. Apex of eighth right dentary replacement tooth. C. Apex of first right premaxillary replacement tooth. D. Cross-section of tenth right mature dentary tooth. E. ?Tenth left dentary mature tooth.

Scale bars (all to left of figure) = 5 mm.

and which condition has been described in the Upper Jurassic pliosauroid, *Pliosaurus brachyspondylus* (Taylor & Cruickshank 1993).

The form of the teeth corresponds closely to Massare's (1987) 'generalist' predator type, being adapted to apprehending active, struggling prey (Taylor 1992b), or being capable of dismembering large carcasses by gripping strongly, and wrenching out mouthfuls by 'twist-feeding' (Taylor 1987), each mouthful being swallowed whole.

Postcranial skeleton

Andrews (1911) described the postcranial elements very well, and no further attempt will be made here to amplify his comments, except to note some items regarding the vertebrae.

A total of 38 vertebrae have been identified during this study, one more than originally described, but which can be accounted for by taking into account half centra on the ends of the preserved sequences. They comprise 22 cervicals and 16 dorsals (which is where the count differs from that of Andrews). Eleven of the cervicals occur in four dissociated groups, and two single, damaged vertebrae. Nine posterior cervicals are articulated with the 16 dorsals. All vertebrae show their neural arches firmly fused to their centra and are, therefore, from an adult animal (Brown 1981). All the centra are as long as they are wide, an unusual state for a Cretaceous pliosauroid (Brown 1981).

Leptocleidus capensis had at least 22 cervicals but, as neither atlas nor axis are represented here, the count must rise to a minimum of 24. The known range of cervicals for *Rhomaleosaurus* is 28–32, and hence a value within that range is possible for *Leptocleidus capensis*. This is unusual to say the least, as it is assumed that within the Pliosauroida, by the Cretaceous, the cervical count has diminished to about 13 highly compressed vertebrae (Brown 1981). It is impossible to see whether the rib-heads are single or double.

The smallest (anterior) cervical vertebrae have zygapophyses orientated almost horizontally. The larger, posterior, cervicals and the dorsals have their zygapophyses orientated at about 50° to the horizontal. Within the limits allowed by connective tissues and similar constraints, this might indicate that the posterior of the neck was less mobile, horizontally, than was the anterior (Evans, MS 1993). A certain amount of vertical movement, both above and below the horizontal is presumed, but controlled largely by relative interference by the neural spines with one another.

DISCUSSION

Leptocleidus is very similar to *Rhomaleosaurus* (Taylor 1992a, 1992b; Cruickshank 1994a; Table 1 herein). Twenty-six characters can be evaluated under the headings of (a) gross similarities, (b) gross differences, (c) size-related differences, (d) those characters of uncertain validity and (e) characters not known or which are unpreserved in *Leptocleidus*.

(a) Head shape, the expanded lateral ramus of the pterygoid, the snout with rosette of intermeshing teeth, and the general tooth shape and character are all probably plesiomorphic and therefore not significant. What may prove to be

TABLE 1

Comparisons of *Rhomaleosaurus* and *Leptocleidus*. Similarities: head subtriangular; dorsomedian foramen between facial processes*; dorsomedian trough on anterior face of articular and prearticular*; expanded lateral ramus of pterygoid; strong descending flange on postorbital bar*; snout with rosette of intermeshing teeth; teeth conical, circular in section; teeth with weak caninae.

<i>Rhomaleosaurus</i>	<i>Leptocleidus</i>
GROSS DIFFERENCES	
Lower Jurassic age	Lower Cretaceous age
Skull profile smooth	Vertex with dorsal notch
Boss on lateral ramus of pterygoid	No boss
Postorbital = postfrontal on postorbital bar	Postorbital smaller than postfrontal
Wide exposure of parasphenoid on palate	Narrow parasphenoid
Postorbital lacks ventral footplate	Postorbital with footplate
Teeth uniform shape	Posterior teeth slightly recurved
Teeth striated all round	Buccal surface of teeth smooth
Accessory grooves on anterior of palate	No accessory grooves on palate
SIZE-RELATED DIFFERENCES	
Skull length-to-width ratio—2 : 1	1.7 : 1
Tooth count in upper jaw—30	21
A DIFFERENCE OF UNCERTAIN VALIDITY	
Lacrimal present	Lacrimal absent
UNPRESERVED OR NOT KNOWN FOR <i>LEPTOCLEIDUS</i>	
Moderately large; > 5 m	Overall length of 2 m, based on skull length 310 mm
Head 15 per cent of overall length*	
5 teeth in lower jaw symphysis	< 7 teeth in symphysis*
Symphysis spatulate/elongate	Symphysis shape not known
Neck 28–32 vertebrae	Neck at least 24 vertebrae
Presacral vertebrae 58	Presacral count not known
Neck 25 per cent overall length	Neck length not known

*—possible autapomorphies for rhomaleosaurids

autapomorphies for *Rhomaleosaurus* and its close allies are the possession of dorsomedian foramina between the facial processes of the premaxillae and dorsomedian troughs on the anterior faces of the articulars and prearticulars, allied with strong descending flanges on the postorbital bars.

(b) The eight gross differences noted between the two genera might all be considered the result of the time difference between the two; six of these are concerned with the reaction of the skull to feeding stresses (Taylor 1992b). In

Leptocleidus, the extension of the vertex is seen as allowing a slip of the external adductor muscles (mame) to grow slightly longer, and hence add to the speed of closure of the jaw. The lack of a boss on the lateral ramus of the pterygoid, and reduction of the pterygoid flange, indicates that the gullet was being opened up to enhance the speed of ingestion of food (cf. *Pliosaurus*—Taylor & Cruickshank 1993). The weakening of the skull in this region against lateral forces, as a result of that process, has been partially compensated for by the deepening of the ventral flange on the postorbital bar, and the change in proportions of the postorbital and postfrontal bones. This is associated with the development of the footplate on the postorbital, where it overlaps the jugal and squamosal; the maxilla is already known to have overlapped the jugal—squamosal junction by the Lower Jurassic (Cruickshank 1994a). As far as the teeth are concerned, there is a tendency for them to lose their ornament on the outer (buccal) surfaces, and to adopt a triangular section (Tarlo 1960). In addition the smaller, posterior teeth tend to become recurved, or hooked, to aid passing prey down the throat. *Leptocleidus* has teeth with unornamented buccal surfaces, and has slightly recurved small (?posterior) teeth, but they retain a circular section. In these ways it is advanced over *Rhomaleosaurus*, but only slightly. The lack of accessory grooves on the anterior palate—the significance of which is unknown—is a difference from *Rhomaleosaurus* (Cruickshank *et al.* 1991) and the reduced exposure of the parasphenoid on the palate is similar to the condition in the Plesiosauroidea, and may be a size-related factor.

(c) Other size-related factors are the skull length-to-width ratios and the number of teeth in the upper jaw. It is believed that the smaller animal would naturally have a relatively 'wider' skull than the larger, and with less space, the upper jaw at least would have fewer teeth.

(d) A character of unknown validity is the lack of an observed lacrimal in *Leptocleidus*, bearing in mind its occurrence even in late Jurassic forms (Taylor 1992b; Taylor & Cruickshank 1993; Cruickshank 1994a).

(e) Characters that cannot be commented on with certainty are those which are missing or which cannot be calculated, such as the relative size of the head in *Leptocleidus*, the number of teeth in its lower jaw symphysis, its count of neck vertebrae, the total number of presacrals and the relative length of its neck. However, circumstantial evidence can be brought to bear to indicate that all these characters are most likely to be 'rhomaleosaurid' in character.

Another point of significance is that *Leptocleidus capensis* was recovered from sediments with freshwater foraminifers—probably lagoonal or close inshore in character (McMillan in press). The animal was about the size of a seal, and may have lived very much in the same way, hunting fish and other modest-sized prey in the inshore zone of a shallow sea.

Other localities which have yielded 'non-marine' plesiosaurs include Berwick Brick Pit, Sussex, England, Wealden (= Barremian) (*L. superstes*—Andrews 1922), near Mount Morgan Copper Mine, Queensland, Australia, Lower Jurassic (*Leptocleidus* cf. *L. superstes*—Bartholomai 1966; Molnar 1982), south-eastern Australia, Lower Cretaceous (isolated teeth and ribs—Rich *et al.* 1989), Coober Pedy, South Australia, Lower Cretaceous (*Leptocleidus* cf. *L. superstes*—Ritchie 1991), Nanning, Kwangsi, China, Lower Cretaceous

(*Sinopliosaurus fustinensis*—Hou *et al.* 1975) and *Bishopliosaurus* also from the Chinese Lower Jurassic. The Antarctic record includes elasmosaurids and cryptoclidids from Late Cretaceous nearshore marine and coastal-deltaic sediments (Chatterjee & Small 1989).

The probability is that some pliosauroids, perhaps the smaller species at least, were exploiting the inshore habitat (Hudson 1966) and this would explain the apparent anomaly of a conventionally marine group having such a strong freshwater character. One can speculate that the (less advanced) representatives of the original pliosauroid stock were forced under competition to seek refuge in a relatively protected environment in the inshore shallows, whereas their replacements worked their way into the resulting vacant niches. One other area of mystery in the plesiosaurs is the lack of juveniles in the fossil record. Perhaps these inshore records reflect the result of unsuccessful egg-laying forays up rivers or on to sandbars?

SUMMARY & CONCLUSIONS

The skull of the pliosauroid plesiosaur *Plesiosaurus capensis* Andrews, 1911, from the uppermost Valanginian (Lower Cretaceous) Algoa Basin, South Africa, is figured and redescribed.

Plesiosaurus capensis shares many of its characters with *Leptocleidus superstes* Andrews, 1922, from the Barremian of the Weald Basin, England, and therefore can be ascribed to the latter genus, as suggested by Persson (1963). The name therefore becomes *Leptocleidus capensis* (Andrews, 1911).

Both these forms seem similar to undescribed Lower Cretaceous pliosauroids from Australia. *Leptocleidus* is close to and may be derived from the Lower Jurassic *Rhomaleosaurus* Seeley, 1874.

All three Lower Cretaceous forms come from lagoonal, or very shallow, close inshore, marine facies.

A brief review of the literature shows that several plesiosaurian finds are from freshwater facies in both Jurassic and Cretaceous age sediments.

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ABBREVIATIONS

(USED IN TEXT AND FIGURE CAPTIONS)

a	angular	gl	glenoid fossa
aiv	anterior interpterygoid vacuity	in	internal naris
ar	articular	j	jugal
ars	anterior ramus of the squamosal	lgr	longitudinal groove on dentary
atrc	anterior transverse crest of the glenoid fossa	ling	lingual surface of tooth
bo	basioccipital	lrpt	lateral ramus of pterygoid
bs	basisphenoid	mame?	m. adductor mandibulae externus
buc	buccal surface of tooth	mpst?	m. pseudotemporalis
c	coronoid	mta	mature tooth
car	carina of tooth	no	notch
ce	coronoid eminence	nuch?	origin of nuchal ligament
ch	channel	orb	orbit
cl	cleft	p	parietal
cond	occipital condyle	pra	prearticular
cr	crest	pal	palatine
d	dentary	palv	primary alveolus
dep	depression	pfo	parietal foramen
dia	diastema	piv	posterior interpterygoid vacuity
dmc	dorsomedian crest	pmx	premaxilla
dmfo	dorsomedian foramen	po	postorbital
dmt	dorsomedian trough	pob	postorbital bar
drs	dorsal ramus of the squamosal	pof	postfrontal
ec	ectopterygoid	poft	footplate to postorbital
en	external naris	ppr	paroccipital process
fac	facial process of the premaxilla	prf	prefrontal
fr	frontal	ps	parasphenoid
		psc	parasagittal crest

pt	pterygoid	salv	secondary alveolus
ptf	pterygoid flange	sof	suborbital fenestra
ptrc	posterior transverse crest to glenoid	sp	splénial
q	quadrate	sq	squamosal
qrpt	quadrate ramus of the pterygoid	stf	subtemporal fenestra
rap	retroarticular process	tf	temporal fenestra
rto	replacement tooth	v	vomer
sa	surangular	vx	vertex
		1-35	tooth positions

Mechanical stipple—matrix; horizontal lines—openings in skull; diagonal lines—broken or eroded bone.



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