A JUVENILE PLIOSAUROID PLESIOSAUR (REPTILIA: SAUROPTERYGIA) FROM THE LOWER CRETACEOUS OF SOUTH AUSTRALIA

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ABSTRACT—A partial skeleton tentatively referred to the Lower Cretaceous pliosauroid genus *Leptocleidus* is described from predominantly Aptian (Lower Cretaceous) opal-bearing deposits of the Bulldog Shale near Andamooka in South Australia. Small size coupled with incomplete fusion of the basicranial elements, vertebral centra, neural arches and cervical ribs, and incomplete ossification of the articular surfaces on the propodials and distal limb bones, indicate that the specimen was at an early stage in its ontogeny. Comparison with more mature specimens attributed to *Leptocleidus* spp. highlights several growth-related differences, particularly a marked disparity in proportions of the humerus and femur relative to the estimated maximum body length. Changes in the cranial skeleton during growth are harder to document because of the fragmentary nature of the skull. Nevertheless, fusion of some cranial sutures and well-developed cranial joint surfaces suggest that extensive ossification may have taken place in parts of the skull during early ontogeny. The potential implications of these findings for feeding, locomotion, and behavior in juvenile plesiosaurs are discussed.

INTRODUCTION

IN 1967 the partial skeleton (SAM P15980), including some cranial elements, of a very small-bodied juvenile plesiosaur was acquired by the South Australian Museum. The specimen had been discovered during mining operations in the predominantly Aptian (Alexander and Sansome, 1996) opal-bearing deposits of the Bulldog Shale (Eromanga Basin) near Andamooka in South Australia (Fig. 1). Recent assessment of the remains suggests potential attribution to the pliosauroid genus *Leptocleidus* Andrews, 1922. At around 700 mm in total length, the specimen represents by far the smallest and most immature exemplar yet discovered.

The current taxonomic disposition of *Leptocleidus* is controversial, as are its relationships (see O'Keefe, 2004 for summary). However, traditionally the taxon is regarded as a small to medium-sized (up to 3 m) pliosauroid plesiosaur occurring in the Lower Cretaceous (Valanginian–Upper Aptian/Lower Albian) freshwater and nearshore marine deposits of England (Andrews, 1922), South Africa (Andrews, 1911; Strömer, 1935; Cruickshank, 1997), and Australia (Cruickshank and Long, 1997; Kear, 2003). Another specimen representing a closely related genus was also recently discovered in Canada (P. Druckenmiller, personal commun., 2005; see Druckenmiller, 2002). *Leptocleidus*-like remains have been reported from the Lower Jurassic of Queensland, Australia (Bartholomai, 1966); however, reinterpretation suggests that the material might instead represent a late surviving pachypleurosaur (Cruickshank et al., 1999). Typically, three species of *Leptocleidus* are recognized: *L. superstes* Andrews, 1922, *L. capensis* (Andrews, 1911), and *L. clemai* Cruickshank and Long, 1997, with a possible fourth (as yet unnamed) identified from the Lower Aptian–Lower Albian Bulldog Shale deposits of South Australia (Kear, 2003, 2006). Cruickshank (1997) and Cruickshank and Long (1997) suggested a close, potentially direct ancestor-descendant relationship between *Leptocleidus* and the European Lias (Early Jurassic) taxon *Rhomaleosaurus* Seeley, 1874 based on synapomorphies in the cranial skeleton. This is consistent with the cladistic analysis of O'Keefe (2001), which grouped both *Leptocleidus* and *Rhomaleosaurus*, together with the middle Jurassic taxon *Simolestes* Andrews, 1913, in the monophyletic family Rhomaleosauridae. However, O'Keefe (2004) subsequently revised this classification, recognizing only *Rhomaleosaurus* and the Early Jurassic *Macroplata* Swinton, 1930 as members of Rhomaleosauridae: *Simolestes* and *Leptocleidus* were considered more derived sister taxa.

Ontogenetic development in plesiosaurs has been discussed by numerous authors (see below) but remains poorly understood in comparison to other sauropterygian groups (e.g., Carroll and Gaskill, 1985; Sander, 1988, 1989; Rieppel, 1989, 1994; Storrs, 1993; Lin and Rieppel, 1998; O'Keefe et al., 1999). Some notable accounts include Andrews (1910, 1913), who recorded aspects of ontogeny in plesiosauroid and pliosauroid specimens from the middle Jurassic (Callovian) Oxford Clay of England. Brown (1981) described growth-related changes in the cranial and postcranial skeleton of the middle-Late Jurassic plesiosauroids *Cryptoclidus* Philips, 1871 and *Muraenosaurus* Seeley, 1874. Storrs (1993) examined the potential for skeletal paedomorphosis in plesiosaurs and suggested that delayed ossification in the limb bones might have played a key role in the group's adaptation to an aquatic lifestyle. Caldwell (1997a, 1997b) and Maisch (1998) observed additional ontogenetic features in *Cryptoclidus* and *Muraenosaurus*, including modification of periosteal bone and variable ossification in the basicranial and dermatocranial elements. Similar developmental features have been reported in other plesiosaur taxa, including the enigmatic Early Jurassic (Liassic) pliosauroid *Eurycleidus* Andrews, 1922 (see Cruickshank, 1994), and several upper Maastrichtian elasmosaurids/pliosauroids from New Zealand (Wiffen et al., 1995) and Patagonia (Gasparini et al., 2003a).

The present paper describes the partial skeleton of a juvenile plesiosaur from South Australia and discusses ontogenetically related features of the remains. This is intended to augment the current understanding of skeletal ontogeny in plesiosaurs, and specifically that of taxa allied to *Leptocleidus*.

Institutional abbreviations.—AM, Australian Museum, Sydney; BMNH, Natural History Museum (formerly British Museum [Natural History]), London; NTM, Museum and Art Gallery of the Northern Territory, Darwin; SAM-K, South African Museum, Cape Town; SAM P, South Australian Museum, Adelaide; WAM, Western Australian Museum, Perth.

GEOLOGICAL SETTING

Previous accounts of regional geology (including maps) and depositional environments for marine reptile fossil-bearing localities in the Bulldog Shale have been given by Johns (1968), Robertson and Scott (1990), Krieg and Rogers (1995), and Alexander and Sansome (1996).

The Bulldog Shale (Maaree Subgroup) comprises a continuous sequence of shallowly dipping epicontinental marine strata (mainly mudstones and claystones) that outcrop throughout the southwestern Eromanga Basin. They represent a predominantly transgressive shallow coastal-offshore marine depositional environment (Krieg and
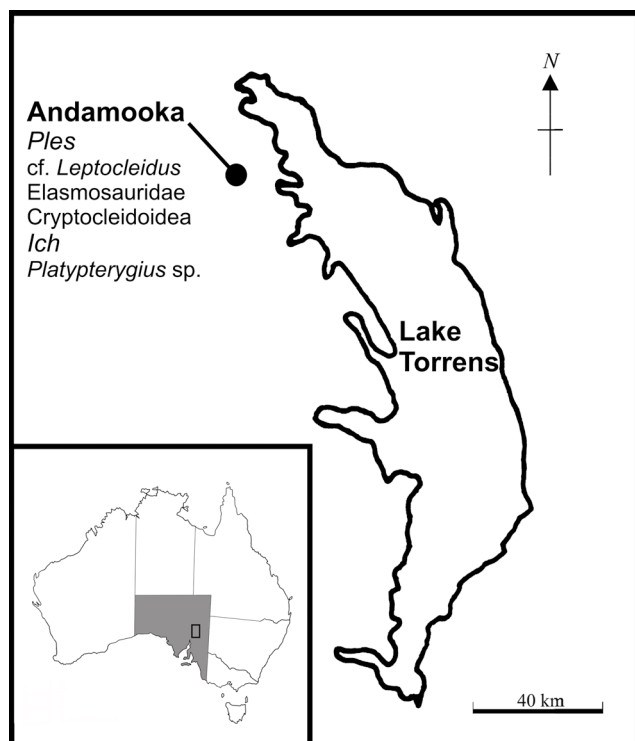
FIGURE 1—Map, showing geographic position of Andamooka, South Australia, and a list of marine reptile taxa recorded from the locality. Abbreviations: *Ples,* Plesiosauria; *Ich,* Ichthyosauria.

Rogers, 1995; Alexander and Sansome, 1996). Regular coquinoid layers (probably representing swell lags), isolated sandy deposits (Krieg and Rodgers, 1995), and disarticulated bones suggest deposition below normal wave base but probably within storm wave base. Some horizons in the Bulldog Shale (including Andamooka) are severely leached and bleached by weathering. This is typically associated with extensive deposits of opal (hydrated silica, $SiO_2 6H_2O$), occurring along cracks and faults, or within cavities left by fossil remains. The process of opal formation is poorly understood, although it may be linked to cyclical fluctuations in regional water tables (prompting dissolution of opal from silica-rich groundwater) during the middle to late Tertiary (Robertson and Scott, 1990).

Notably, some localities in the Bulldog Shale produce large (up to 3 m across) quartzite/porphyritic boulders (Frakes and Francis, 1988, 1990; Frakes et al., 1995) and glendonites (crystal aggregates pseudomorphing the calcium carbonate hexahydrate mineral ikaite, Sheard, 1990; De Lurio and Frakes, 1999). These are reliable indicators of paleoclimate, and suggest predominantly cool to very cold conditions, possibly with winter freezing (Frakes and Francis, 1988). Such interpretations are in keeping with determinations of paleolatitude, which place most of southern Australia at approximately 60°–70°S during the Early Cretaceous (Embleton and McElhinny, 1982; Embleton, 1984; Idnurm, 1985). Estimates of Cretaceous sea level isotopic paleotemperatures also indicate cool-cold conditions, with averages as low as 12.2°C (Stevens and Clayton, 1971; Dettmann et al., 1992).

Fossils are common in the Bulldog Shale. Ludbrook (1966) described a diverse range of microfossils, bivalve molluscs, gastropods, ammonites, and belemnites. The presence of large quantities of wood is consistent with an inferred proximity to land. Vertebrate remains are locally common and include ichthyosaurs, plesiosaurs (Kear, 2006), osteichthyan fish, chimaerids (Ludbrook,

1966; Alley and Pledge, 2000), and rare dinosaur (theropods, ornithopods) bones (Molnar, 1980; Molnar and Pledge, 1980; Alley and Pledge, 2000).

Rich macroinvertebrate (Ludbrook, 1966; Johns, 1968; Day, 1969) and palynomorph (Moore and Pitt, 1985; Moore et al., 1986; Krieg and Rodgers, 1995; Alexander and Sansome, 1996) assemblages have been used to determine the age of the Bulldog Shale as Lower Aptian to Lower Albian. Correlations based on the Australian Cretaceous palynological zonation of Helby et al. (1987) place the unit within the *Cyclosporites hughesii*, *Crybelosporites striatus* spore-pollen zones, and *Odontochitina operculata*, *Diconodinium davidii*, *Muderongia tetracantha* dinoflagellate zones. Because of severe weathering, most microfossil remains have been leached from the opal-bearing strata at Andamooka. Consequently, an accurate palynomorph zonation cannot be established for the deposits at this locality. A predominantly Aptian age can, however, be suggested based on representative macroinvertebrate taxa (see Ludbrook, 1966; Johns, 1968; Day, 1969; Henderson et al., 2000).

SYSTEMATIC PALEONTOLOGY

Superorder SAUROPTERYGIA Owen, 1860
Order PLESIOSAURIA de Blainville, 1835
Superfamily PLIOSAUROIDEA Welles, 1943
(sensu O'Keefe, 2001)
Genus LEPTOCLEIDUS Andrews, 1922

Type species.—*Leptocleidus superstes* Andrews, 1922, p. 296, pls. 14, 15.

Diagnosis.—Cruickshank (1997), Cruickshank and Long (1997), and Kear (2003) have provided adequate diagnoses for *Leptocleidus*.

cf. LEPTOCLEIDUS sp.
Figures 2–6, Tables 1–3

Description.—SAM P15980 comprises a partial juvenile skeleton preserved entirely in honey-colored potch (nonprecious or common opal). Cranial skeleton severely crushed and very fragmentary, but potentially includes part of the exoccipital-opisthotic, parietals, and basioccipital. The recovered section of exoccipital-opisthotic (Fig. 2.1; Table 1) shows both the posterior and part of posterolateral surfaces. It is crushed onto the underside of an amalgamated potch shard also bearing the parietals and other indistinguishable, presumably cranial elements. The visible posterior surface of exoccipital-opisthotic bears the raised base of paroccipital process; this appears to have been slender and transversely compressed. A deep notch in the exoccipital-opisthotic's exposed outer margin might have formed part of the recess for the semicircular canal. This is bordered by a distinct groove (extending along posterior surface of exoccipital-opisthotic towards base of parroccipital process), potentially representing a remnant of the suture extending between the exoccipital and opisthotic.

Paired parietals (Fig. 2.2; Table 1) crushed but comprise posterodorsal region of braincase (missing both the anterior pineal region and posterior parietal-squamosal contact) and descending flanges (covering supraoccipital) visible in dorsal and left lateral aspects. Parietals weakly arched (having undergone compaction dorsoventrally), with dorsal midline forming base of sagittal crest (broken off along entire preserved length). This marks the position of the interparietal suture, which appears to have been well formed and at least partly fused.

Basioccipital of SAM P15980 probably smashed during initial extraction and processing. However, a single opal shard (Fig. 3; Table 1) has been recovered, preserving (in oblique section) what appears to be the right basituber (to articulate with the pterygoid;
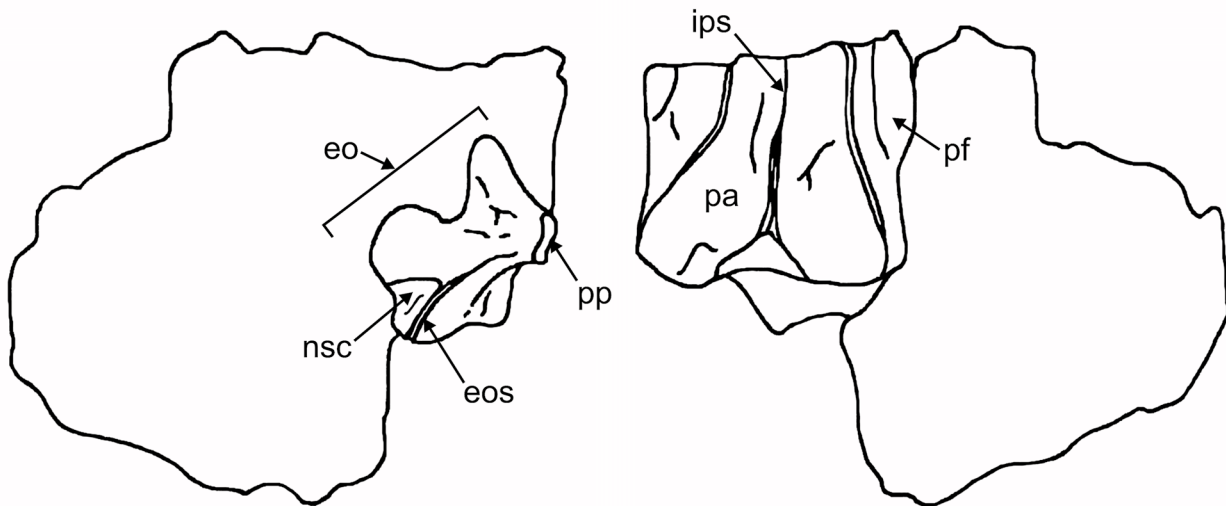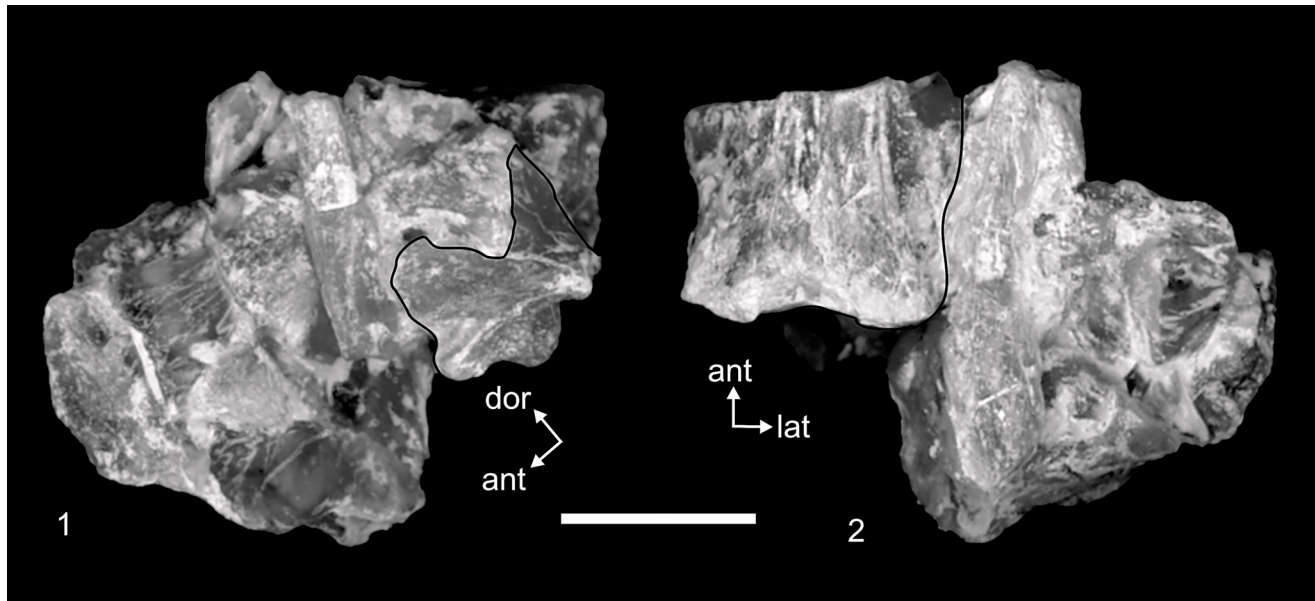
FIGURE 2—Cranial elements of cf. *Leptocleidus* sp. SAM P15980. Cranial fragment (with reconstructive drawing) showing *1,* exoccipital-opisthotic (outlined) in posterolateral view, and *2,* parietals (outlined) in dorsal view. Scale bar 20 mm. Abbreviations: eo, exoccipital-opisthotic; eos, exoccipital-opisthotic suture; ips, interparietal suture; nsc, notch for semicircular canal; pa, parietal; pf, parietal flange; pp, paroccipital process.
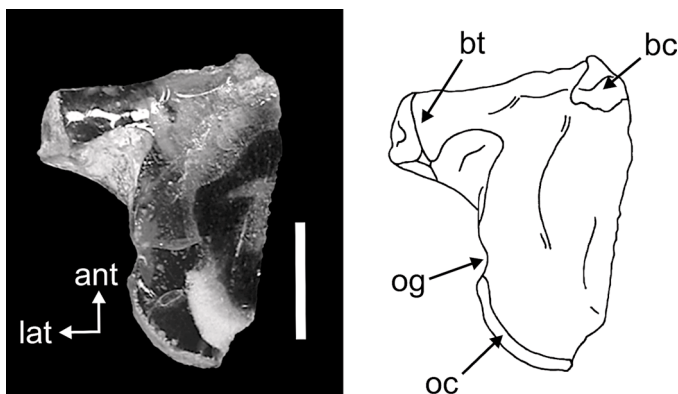

FIGURE 3—Basioccipital fragment of cf. *Leptocleidus* sp. SAM P15980 in ventral view. Scale bar 10 mm. Abbreviations: bc, basisphenoid contact; bt, basituber; oc, occipital condyle; og, occipital groove.

s. Carpenter, 1997) and part of the occipital condyle. No discernible sutures to suggest that other basicranial bones (e.g., exoccipital-opisthotic) are included in fragment. Anteroventral portion of basioccipital shard bears small section of the rugose basisphenoid facet; this shows no evidence of fusion with the basisphenoid. Ventrolaterally projecting basituber cylindrical and very prominent with smooth, well-ossified distal articular surface. Transverse width of basituber equivalent to over half the total preserved basioccipital length. Preserved segment of occipital condyle semicircular in cross section with well-ossified articular surface; its ridge-like anterior margin bordered by a prominent posterodorsally inclined condylar groove.

Axial skeleton represented by 20 partial cervical and the first pectoral centrum, nine associated fragmentary neural arches, and numerous ribs. Neural arches (Fig. 4.1; Table 2) fragmentary with only the smallest anterior cervical having part of arch in direct association with centrum. Neural spines posteriorly inclined with flattened dorsal margin. Prezygapophyses (where preserved) large
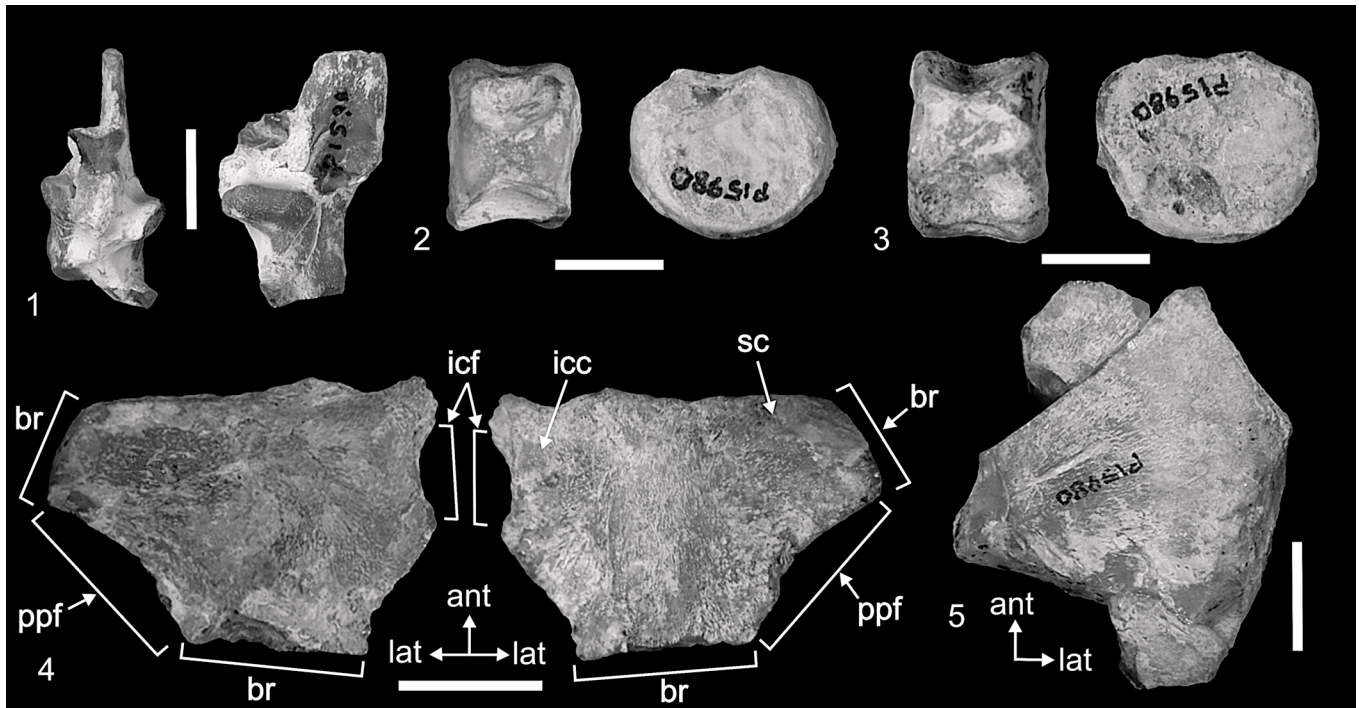
FIGURE 4—Postcranial elements of cf. *Leptocleidus* sp. SAM P15980. *1,* Neural arch in anterior and lateral views. *2,* Anterior cervical centrum (C10) in lateral and anterior views. *3,* Posterior cervical centrum (C14) in lateral and anterior views. *4,* Clavicle in dorsal and ventral views. *5,* Coracoid fragment in dorsal view. Scale bar 10 mm in *1* and 20 mm in *2–5.* Abbreviations: br, broken edge; icc, interclavicle contact; icf, position of interclavicle foramen; ppf, position of pectoral fenestra; sc, scapular contact.

and lobate with ovoid articular surfaces oriented approximately 45° to horizontal axis. Postzygapophyses similar in shape and orientation, but slightly narrower transversely. Both cervical (Fig. 4.2, 4.3; Table 2) and pectoral (Table 2) centra short and amphicoelous with a shallow central notochordal pit. Articular surface margins raised into a prominent convex rim, giving centra a conspicuous spool-shaped outline. Neural arch and rib facets deeply excavated and rugose, suggesting the presence of cartilage.

All recovered ribs fragmentary and lack unequivocal associations with centra. Both cervical and dorsal ribs single headed with poorly ossified articular surfaces.

Appendicular skeleton represented by left clavicle, glenoid portions of left and right coracoid, left humerus, and left femur. Numerous fragments, probably comprising other elements of the pectoral and pelvic girdles, have been recovered but are too incomplete for unequivocal identification.

Left clavicle (Fig. 4.4; Table 3) nearly complete, missing only its posterior and lateral extremities. In overall form, large and plate-like with a dorsally inclined lateral margin for contact with scapula. Concave posterolateral edge would have formed the anteromedial margin of the pectoral fenestra (see Andrews, 1922, pl. 15.1). Similarly, the notched anteromedial margin probably represents part of border for the interclavicle foramen (s. Andrews, 1922, p. 293, pl. 15.1). Ventral surface of clavicle bears broad median ridge separating the scapular contact from the excavated medial margin, which overlapped the interclavicle.

Coracoid (Fig. 4.5; Table 3) fragments dorsoventrally flattened with medial section oriented approximately 10° ventral relative to a horizontal plane through the rugose glenoid articular surface. Glenoid facet anteroposteriorly elongate and separated from triangular scapular facet (offset approximately 120° medial to the longitudinal axis to the glenoid facet) by a prominent vertical ridge.

Recovered left humerus (Fig. 5.1; Table 3) complete but has suffered some damage to the shaft midsection. Large in proportion to other skeletal elements with the exception of femur. Anterior humeral margin nearly straight with posterior margin being strongly concave. Articular surfaces of humeral head and prominent dorsal tuberosity poorly formed and composed entirely of cancellous endochondral bone. Humeral shaft slender and ovoid in cross section becoming dorsoventrally flattened distally. Distal humeral extremity fan-shaped in dorsal outline with rugose articular surface showing no clear differentiation between the radius and ulna facets.

The virtually complete left femur (Fig. 5.2; Table 3) slightly longer than humerus and large in proportion to rest of skeleton. Like the humerus, it has a straight anterior, and concave posterior margin; the articular surfaces of both the femoral head and broad dorsal trochanter are poorly formed and composed entirely of cancellous endochondral bone. Shaft of the femur anteroposteriorly broad relative to that of humerus and markedly dorsoventrally compressed. Distal extremity fan-shaped and slightly posteriorly offset. Distal articular face upturned and rugose with no clear differentiation between tibia and fibula facets.

An isolated mesopodial element and two phalanges have been recovered. Because all are incompletely ossified, the exact positioning of the elements and identity of the mesopodial is unknown. Mesopodial (Table 3) trapezoidal in outline and proximodistally compressed. Lateral margins lack any trace of periosteal bone and bear slightly raised angular edges. Phalanges (Table 3) dumbbell-shaped and proximodistally elongate. Both the proximal and distal articular surfaces poorly ossified and bordered by a continuous flange-like margin.

Discussion.—SAM P15980 is regarded as being at an early stage in its ontogenetic development because of its small size,

FIGURE 5—Propodials of cf. *Leptocleidus* sp. SAM P15980. *1,* Humerus and *2,* femur in dorsal, proximal articular, and anterior views. Scale bar 80 mm.

coupled with incomplete fusion of the basicranial elements, vertebral neurocentral sutures, and cervical ribs, and poorly ossified articular surfaces on the humerus, femur, and other distal limb elements (s. Brown, 1981). Generic assignment of the specimen to cf. *Leptocleidus* sp. is suggested on the basis of morphology. The Bulldog Shale deposits have produced a range of plesiosaur taxa, including small pliosauroids (*Leptocleidus*), large pliosaurids (*Kronosaurus* Longman, 1924), indeterminate elasmosaurids, a 'cryptocleidoid-like' taxon, and a possible polycotylid (see Kear,
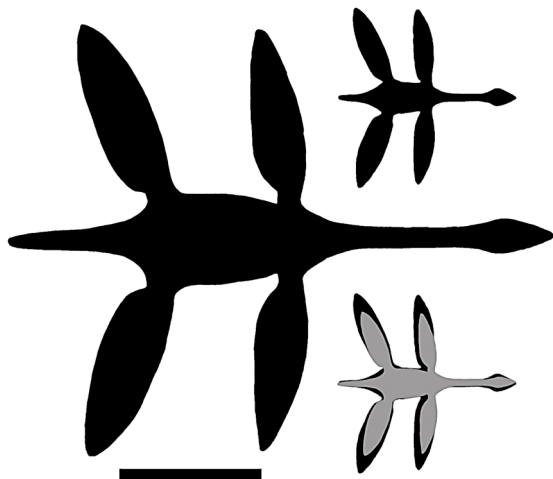

FIGURE 6—Reconstructed silhouettes of *Leptocleidus* individuals showing juvenile (top), adult (middle), and adult (gray) overlay on juvenile (black) to show proportional differences (bottom) in limb lengths. Relative dimensions based on a composite of specimens (AM F99374, SAM P15980, SAM P23841, SAM P31050, SAM P39915) in the Australian Museum, Sydney, and South Australian Museum, Adelaide. Scale bar 500 mm.

2003, 2006). Of these, SAM P15980 shares key traits with remains attributed to *Leptocleidus*: specifically a large, well-developed clavicle (also occurring in *L. superstes*, see Andrews, 1922); cervical vertebra count of at least 20, not including the atlas-axis (*L. capensis* has 22 cervical centra, not including the atlas-axis; Cruickshank, 1997); and anteroposteriorly compressed (length < width and height, see Table 2), amphicoelous cervical centra (common to all species of *Leptocleidus*; Andrews, 1922; Cruickshank, 1997; Cruickshank and Long, 1997; Kear, 2003). Notably, these features are comparable to some plesiomorphic Lower Jurassic pliosauroids (e.g., *Rhomaleosaurus*, which has similar cervical vertebral morphology but a slightly higher count of 28–32; Cruickshank, 1997); however, larger-bodied pliosaurids differ in having much fewer cervical vertebrae (only 12 have been reported in *Kronosaurus*; see Kear, 2003). Long-necked plesiosauroids (cervical count >35) such as elasmosaurids (e.g., Welles, 1962; Brown, 1981; Bardet et al., 1999; O'Keefe, 2001) and Cretaceous cryptocleidoids (O'Keefe, 2001, 2004) can also be distinguished from SAM P15980 on the basis of their cervical vertebra morphology. This characteristically includes in excess of 30 vertebrae (>40 in elasmosaurs; Bardet et al., 1999), which may be markedly elongate (length > width and height in elasmosaurs; length < width in Cretaceous cryptocleidoids; e.g., Gasparini et al., 2003b) and have platycoelous articular surfaces. Short-necked polycotylids (Plesiosauroidea) have between 19 and 26 cervical vertebrae (usually anteroposteriorly compressed and amphicoelous) but differ from SAM P15980 in their propodials, which tend to be more elongate and pendulous (see Carpenter, 1996; Adams, 1997).

The cranial remains of SAM P15980 exhibit several notable features:

1. The presence of a prominent groove incising the ventral and lateral margins of the occipital condyle. This potentially ontogenetically related state (see Brown, 1981; Maisch, 1998)

TABLE 1—Measurements (mm) of SAM P15980 cranial elements.

Element	Dimension	Measurement
Basioccipital	Maximum length (whole fragment)	17.86
	Maximum width (whole fragment)	13.67
	Length (pterygoid process base)	7.5
	Width (pterygoid process)	5.08
	Length (condylar segment)	4.54
Exoccipital/opisthotic	Maximum height (whole element)	14.36
	Maximum width (whole element)	11.22
	Height (distal paroccipital process)	4.4
Parietal	Maximum length (along midline)	12.73
	Maximum width (posterior margin)	15.25

also occurs in some other pliosauroid taxa, including *L. superstes* (Andrews, 1922), the rhomaleosaurid *Rhomaleosaurus* (Taylor, 1992), and the pliosaurid *Liopleurodon* Sauvage, 1873 (Andrews, 1913). Traditionally, condylar groove development has been considered a diagnostic character for plesiosauroids (Welles, 1962; Brown, 1981; Bardet et al., 1999). However, in this group the groove is typically more dorsally continuous, completely circumscribing the occipital condyle and creating a pedunculate condylar neck. Despite this, some Jurassic plesiosaurids (Storrs and Taylor, 1996), cryptoclidids (Brown, 1981; Bardet et al., 1999), and Cretaceous elasmosaurids/cryptocleidoids (Chatterjee and Small, 1989; Kear, 2001; Gasparini et al., 2003b) exhibit a pliosaurid-like morphology with the dorsally incomplete condylar groove interrupted in some taxa (e.g., *Cryptoclidus*) by a posterior extension of the exoccipital-opisthotic facets onto the occipital condyle.

2. The presence of proportionately large, slender basitubera. This appears to be unique to SAM P15980, and differs from the common condition in other pliosauroid taxa (including *Leptocleidus* spp.), in which the basitubera tend to be short and stocky (Andrews, 1913; White, 1935; Cruickshank, 1994a). Cruickshank (1994a) suggested that the evolution of the basitubera in plesiosaurs might be related to a need for structural reinforcement of the posterior skull (through repositioning of the parasphenoid and particularly the pterygoids well beneath the basioccipital-basisphenoid complex)

TABLE 2—Measurements (mm) of SAM P15980 vertebral centra. Because the vertebral series was disarticulated when acquired, numbering of centra is based on rib facet position and relative size only. Abbreviations: C, cervical; P, pectoral (*centrum preserved as fragments only or † incomplete).

Vertebra	Length	Width	Height
C1	8.48	14.9	11.82
C2†	8.55	15.01	11.65
C3	8.99	16.06	11.78
C4*	—	13.7	10.19
C5*	9.44	—	—
C6†	9.27	14.88	12.67
C7†	9.48	13.32	12.87
C8	10.77	18.35	13.88
C9†	8.67	18.83	10.07
C10	11.16	19.39	14.9
C11†	12.12	13.5	15.88
C12†	10.22	13.53	20.37
C13†	11.9	19.65	15.65
C14†	14.05	19.67	15.15
C15	13.6	21.44	18.21
C16†	12.93	17.48	12.74
C17†	13.34	21.77	16.49
C18	12.63	14.17	12.92
C19	12.51	23.58	15.63
C20	12.63	25.25	17.38
P1	14.5	27.42	18.27

to resist loading forces encountered during active dismemberment of prey (Taylor, 1992; Taylor and Cruickshank, 1993; Cruickshank, 1994b). The relatively gracile structure in SAM P15980 could therefore reflect a system involving comparatively less stress dispersal through the basicranial region, and perhaps less vigorous processing of food items.

ONTOGENETIC FEATURES AND DISCUSSION

Comparison of SAM P15980 with more mature juvenile and adult specimens of *Leptocleidus* (AM F99374, SAM P24560, NTM P910, NTM P913–5, NTM P9606, NTM P9986; *L. capensis*, Andrews, 1911, Strömer, 1935, Cruickshank, 1997; *L. superstes*, Andrews, 1922; *L. clemai*, Cruickshank and Long, 1997) illustrates various types and degrees of ontogenetic change in the cranial and postcranial skeleton, and provides a model for understanding aspects of ontogenetic development in pliosauroids. For example, among the cranial elements the basioccipital shows a lack of fusion with the basisphenoid. This is a common trait in many juvenile and young adult pliosauroid (Andrews, 1913; Cruickshank, 1994a) and plesiosauroid (Andrews, 1910; Brown, 1981; Carpenter, 1997; Maisch, 1998) specimens. However, the exoccipital-opisthotic and interparietal sutures of SAM P15980 are apparently well ossified, suggesting commencement of fusion at an earlier growth stage. Similarly, some of the cranial joint surfaces show signs of advanced ossification (e.g., deposition of periosteal bone producing smooth, well-formed surfaces), particularly the articular surface of the basituber and occipital condyle.

The postcranium of SAM P15980 exhibits relatively limited ossification throughout most of its axial (e.g., unfused neural arches, cervical ribs, and centra) and appendicular elements (e.g., weakly developed articular surfaces on the pectoral girdle and limb bones). Interestingly, the angle of the anterior cervical prezygapophyses (oriented at approximately 45° relative to the horizontal axis) also differs from that recorded in some more mature *Leptocleidus* specimens (such as the holotype of *L. capensis*, SAM K5822). Here the anterior cervical prezygapophyses are oriented typically near horizontally, but become more obliquely angled (to 45°–50°) posteriorly (see Andrews, 1910; Cruickshank, 1997). Steeply angled zygapophyseal articulations on the cervical vertebrae suggest a capacity for vertical movement in the neck (taking into account the limitations imposed by connective tissue and interaction of the neural spines), and may reflect contrasting feeding techniques and prey types between taxa.

The propodial elements of SAM P15980 are large, representing around 16% (Table 4) of the estimated 700 mm total body length (based on comparative estimates of vertebral column length with other specimens from the same deposits including AM F99374, see Fig. 6). This contrasts with more mature specimens of *Leptocleidus* spp., in which the propodials are comparatively smaller, representing only around 9%–12% (Table 4). Similarly, the relative proportions of the propodials to each other appears to vary with growth stage, juveniles showing very nearly equal humeral

TABLE 3—Measurements (mm) of SAM P15980 postcranial elements (*part of specimen incomplete).

Element	Dimension	Measurement
Cervical neural arch	Maximum height (incl. neural spine)	20.7, 23.72, 23.69, 17.97, 25
	Length (neural spine base)	10.76, 10.19, 10.64, 11.29, 9.02
	Length (most complete prezygapophysis)	6.81
	Width (most complete prezygapophysis)	5.92
	Length (most complete postzygapophysis)	7.06
	Width (most complete postzygapophysis)	6.68
Dorsal neural arch	Maximum height (incl. neural spine)	35.36
	Length (neural spine base)	11.08
	Height (neural arch)	8.58
Clavicle	Maximum length (whole fragment)	23.39
	Maximum width (whole fragment)	32.62
	Maximum depth (whole fragment)	7.91
Coracoids	Maximum length (whole fragment)	42.48, 30.52
	Height (articular surface)	17.94, 18.8
	Length (articular surface)	40.3, *30.03
	Length (scapular facet)	17.54, *14.29
	Length (glenoid facet)	27.67, *21.2
Humerus/femur	Maximum length (whole element)	122.53, 122.73
	Maximum width (distal extremity)	56.05, 62.02
	Height (proximal articular surface)	31.34, 29.74
	Length (proximal articular surface)	28.99, 26.38
Mesopodial	Maximum height	7.18
	Maximum width (mediolaterally)	11.34
	Maximum length (anteroposteriorly)	14.54
Phalanges	Maximum height	7.28, 6.9
	Maximum width (mediolaterally)	16.53, *10.52
	Maximum length (anteroposteriorly)	10.07, 9.04
	Length (at midsection)	7.66, *7.11

and femoral lengths (a condition also occurring in both juvenile and adult polycotylids, Adams, 1997), unlike more mature individuals, in which the femur is up to 6% larger (Table 4). The possible functional implications of this feature are manifold; however, one key aspect might have been locomotion and buoyancy. Indeed, larger limbs may have imparted effective maneuverability, and enabled maintenance of adequate propulsive thrust in spite of smaller body mass. This is potentially important given the suggestion that juvenile plesiosaurs might have specifically employed slower swimming speeds and a more hydrostatic (passive) regulation of body trim (a product of both their smaller body size and tendency towards pachyosteotic bone microstructure, see Wiffen et al. [1995]).

The high-latitude nearshore marine Bulldog Shale is an unusual deposit in which to find juvenile plesiosaurs. This is because it preserves paleoclimatic indicators (in association with the fossil remains), suggesting highly seasonal cool to very cold conditions with potential coastal ice buildup over winter. Such climate regimes are at odds with those typically tolerated by small-bodied

aquatic reptiles (which rapidly lose heat because of their large surface area to volume ratio), but do not appear to have affected these plesiosaurs, which are abundant in the Early Cretaceous low temperature marine deposits of southern Australia (Kear, 2003). Exactly what adaptations (if any) facilitated their survival is unknown. However, strategies—including elevated metabolic rates, rapid growth, and/or seasonal migration—may have enabled their exploitation of coldwater habitats along the southern coastal margin of the Australian Cretaceous epicontinental seaway. As an interesting aside, several studies (e.g., Wiffen et al., 1995; Case et al., 2000; Kear, 2006) have found that juvenile plesiosaur remains are particularly common in inshore marine/estuarine-freshwater depositional environments. Wiffen et al. (1995) suggested that this may represent age-related habitat partitioning, and was probably accompanied by segregation of available food resources (juveniles preferentially feeding upon easily caught slow swimming or benthic-oriented prey). However, this scenario may be difficult to apply to taxa such as *Leptocleidus*, in which both adult and juvenile individuals are currently thought to have frequented

TABLE 4—Body length estimates and propodial measurements (mm) for *Leptocleidus* spp. specimens. Dimensions for AM F99374 are taken directly from the remains. Source texts for measurements include: Andrews (1911[1], 1922[2]); Cruickshank (1997)[3]; Cruickshank and Long (1997)[4]; Kear (2002)[5]. Abbreviations: EBL, estimated body length; FL, femur length; HL, humerus length *element incomplete).

Specimen	EBL	HL	FL	HL/EBL	FL/EBL
Leptocleidus sp. indet.					
(SAM P15980)	700	112.5	112.7	0.16	0.16
(NTM-P913-5)[5]	—	—	260.8	—	—
Leptocleidus n. sp.					
(AM F99374)	2150	235	250	0.11	0.12
L. superstes[1, 4]					
(BMNH R4824)	<3000	245	—	0.08	—
L. capensis[2, 3]					
(SAM-K5822)	2000	—	*—	—	—
L. clemai[4]					
(WAM 92.8.1)	2500–3000	—	274	—	0.11–0.09
(WAM 94.1.6)	2500–3000	270	—	0.11–0.09	—

the same freshwater and nearshore marine habitats (Cruickshank, 1997; Cruickshank and Long, 1997). Small-bodied coastal forms such as this may have therefore employed alternative behavioral strategies (such as migration, differing prey preferences, and/or feeding zones within the water column) to effectively partition resources and avoid direct competition between sympatric age groups.

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