A new Jurassic pliosaur from Melville Island, Canadian Arctic Archipelago

Tamaki Sato and Xiao-chun Wu

Abstract: A partial skeleton of a plesiosaur (Reptilia: Sauropterygia) from the Hiccles Cove Formation (Middle Jurassic: Callovian) of Melville Island, Canadian Arctic Archipelago, is the first marine reptile fossil with well-preserved skull from the Canadian Arctic and represents a new genus and species of Rhomaleosauridae (*Borealonectes russelli*). The Rhomaleosauridae are a problematic group, and a review of the current status of included taxa is given prior to the description of the Canadian material. The holotype and only known specimen of the new species consists of the skull, anterior cervicals, and right forelimb. The new taxon is characterized by the large prefrontal and the configuration of the postorbital bar in which the postfrontal is excluded from the supratemporal fenestra; these are potentially unique features among rhomaleosaurids. It exhibits a combination of primitive and derived characteristics that are variable among rhomaleosaurids, such as the absence of the dorsomedian foramen and anterior pterygoid vacuity on the palate, and the presence of straight shaft of humerus. The occurrence of this specimen suggests a global distribution of rhomaleosaurids, and it is also significant as one of the few Jurassic plesiosaurs known from North America.

Résumé : Un squelette partiel de plésiosaure (Reptiles : Sauroptérygiens) de la formation de Hiccles Cove (Jurassique moyen : Callovien) de l'île Melville, dans l'archipel arctique canadien, est le premier fossile de reptile marin de l'Arctique canadien comprenant un crâne bien préservé; il représente également un nouveau genre et une nouvelle espèce de Rhomaléosauridés (*Borealonectes russelli*). Ces derniers constituant un groupe problématique, le statut actuel des taxons qu'ils renferment est examiné préalablement à la description du matériel canadien. L'holotype et unique spécimen connu de la nouvelle espèce comprend le crâne, les vertèbres cervicales antérieures et le membre antérieur droit. Le nouveau taxon est caractérisé par un gros os préfrontal et la configuration de la barre post-orbitale, dans laquelle l'os postfrontal est exclu de la fenêtre supratemporale. Il s'agit là de caractères potentiellement uniques parmi les rhomaléosaurides. Le spécimen présente une combinaison de caractères primitifs et dérivés dont la présence chez les rhomaléosaurides est variable, tels que l'absence de foramen dorsomédian et de vacuité ptérygoïde antérieure sur le palais, ainsi que la présence d'une diaphyse droite de l'humérus. L'existence de ce spécimen laisse croire à une distribution planétaire des rhomaléosaurides. Son importance découle également du fait qu'il s'agit d'un des rares plésiosaures jurassiques connus de l'Amérique du Nord.

[Traduit par la Rédaction]

Introduction

Previous studies on Cretaceous vertebrates in the polar region have provided important insights into the behavior and physiology of extinct animals in relation to the local climate (e.g., Brouwers et al. 1987; Tarduno et al. 1998; Rich et al. 1997). Such information is almost completely lacking for Jurassic reptiles due to a paucity of specimens. In this contribution, we provide a detailed description of a Middle Jurassic (Callovian) plesiosaur from Melville Island in the Canadian Arctic Archipelago, which was briefly reported by Russell (1993). The specimen includes the skull, and it is

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the best-preserved specimen of a marine reptile from the Jurassic of the Canadian Arctic to date. Detailed comparison reveals that it is a new taxon of rhomaleosaurid plesiosaur, rather than a cryptoclidid (Russell 1993) or *Simolestes* (Sato and Wu 2005), as previously reported.

Diversity of Rhomaleosauridae

The Arctic specimen has a triangular skull and short cervicals, traits that are typically seen in a group of plesiosaurs often referred to as Rhomaleosauridae (e.g., O'Keefe 2001, 2004a). Our study primarily employs the taxonomy of O'Keefe (2001, 2004a), in which Rhomaleosauridae includes *Rhomaleosaurus*, *Simolestes*, *Macroplata*, and *Leptocleidus*. Rhomaleosaurid taxonomy, however, has been chaotic, and the use of the term "rhomaleosaurid" requires explanation. First of all, Rhomaleosauridae is not universally recognized as a family (e.g., Brown 1981; Taylor 1992a, 1992b; Cruickshank 1994, 1997). There are several recent and ongoing research projects on rhomaleosaurids, involving revision of known taxa, description of new taxa, and (or) phylogenetic analysis (e.g., Noè 2001; Smith 2006; Druckenmiller 2006; Druckenmiller and Russell 2006). Their preliminary results often conflict with each other and with O'Keefe (2001, 2004a). For example, Druckenmiller (2006) (also Druckenmiller and Russell 2006) supports monophyly

of the traditional pliosauroids, including the Polycotylidae, and paraphyly of the rhomaleosaurid taxa, whereas Noè's (2001) extensive review of selected Jurassic pliosaurs classified *Simolestes* Andrews, 1909 as a pliosaurid. This situation suggests instability and the likelihood of significant taxonomic changes in the near future. We focus on the morphological characterization of the Canadian taxon in comparison with known rhomaleosaurids, which are briefly reviewed here.

Cruickshank (1994) gave the most recent generic diagnosis of *Rhomaleosaurus*. The genus includes up to six species: the type species *R. cramptoni* (Carte and Baily, 1863), *R. megacephalus* (Stutchbury, 1846), *R. propinquus* (Tate and Blake, 1876), *R. thorntoni* (Andrews, 1922*b*), *R. victor* (Fraas, 1910), and *R. zetlandicus* (Philips in Anonymous, 1854; see Taylor 1992*a*). A recent redescription of the skull was published for *R. megacephalus* (Cruickshank 1994), *R. thorntoni* (Cruickshank 1996), and *R. zetlandicus* (Taylor 1992*b*). The holotype of *R. cramptoni* is currently undergoing preparation and restudy (Smith 2006). Cruickshank (1996) considered *R. cramptoni*, *R. thorntoni*, and *R. zetlandicus* (all of which are from the Toarcian in Yorkshire) synonymous, making the first two species subjective junior synonyms of *R. zetlandicus*. *R. propinquus*, also from the Toarcian of Yorkshire, is a problematic taxon with a confusing nomenclatural history, and the holotype is a composite skeleton (Benton and Taylor 1984; Taylor 1992*a*). Previous studies distinguished it from other species of the genus in the structure of the lower jaw (Taylor 1992*a*; Cruickshank 1994). *R. megacephalus* is known from the Hettangian in Leicestershire, and *R. victor* is from the Toarcian of Germany. Recent phylogenetic studies (e.g., O'Keefe 2004*a*; Smith 2006; Druckenmiller and Russell 2006) agree on the paraphyly of *Rhomaleosaurus*.

Simolestes has been more often classified as a pliosaurid than a rhomaleosaur (e.g., Tarlo 1960; Noè 2001). Noè (2001) provides the most recent revision of the genus. The type species *S. vorax* is known from the Callovian of Europe, and *S. keileni* Godefroit, 1994 is represented by a fragmentary specimen from the Bajocian of France. Noè (2001) suggested *Eurysaurus raincourti* Gaudry, 1878 from the Aalenian–Bajocian of France and *Maresaurus coccai* Gasparini, 1997 from the Bajocian of Argentina might be congeneric. The holotype of *E. raincourti* was a fragmentary specimen and is now lost (Noè 2001), making it unavailable for detailed comparison.

Leptocleidus includes the type species *L. superstes* Andrews, 1922*a*, *L. capensis* (Andrews, 1911), and *L. clemai* Cruickshank and Long 1997, all known from the Lower Cretaceous. Druckenmiller (2006) and Druckenmiller and Russell (2006) are the most recent systematic studies of *Leptocleidus*, and they demonstrate that at least two species (*L. superstes*, *L. capensis*) are more closely related to the Polycotylidae than to *Rhomaleosaurus*. *L. clemai* is represented by fragmentary postcranial material and is distinguished from the other two species by its larger size and the proportions of the epipodials (Cruickshank and Long 1997).

Macroplata is known from the Lower Jurassic of England. A short report and description by Swinton (1930*a*, 1930*b*) are the only published accounts on *M. tenuiceps*, and redescription of this taxon is in preparation (A. Smith,

personal communication, 2007). The holotype of another species, "*M.*" *longirostris* (Blake in Tate and Blake, 1876), is a composite (White 1940). O'Keefe (2001) realized these two species (*tenuiceps* and *longirostris*) are not congeneric, and later (O?Keefe 2004*a*) noted that "*M.*" *longirostris* (not *M. tenuiceps* as in O'Keefe 2001) requires a new generic designation (also see Druckenmiller 2006). "*M.*" *longirostris* is a basal pliosaurid (O'Keefe 2001, 2004*a*) and is referred to as "Yorkshire taxon" in O'Keefe (2004*a*) and in this study. This taxon is also currently being redescribed (L.F. Noè, personal communication, 2007).

Yuzhoupliosaurus chengjiangensis Zhang, 1985 from the Middle Jurassic of China is the only rhomaleosaurid reported from Asia to date. The type and only known specimen consists of an incomplete mandible and fragmentary postcranial material and is in need of taxonomic reassessment. To our knowledge it has never been included in phylogenetic studies.

Umoonasaurus Kear, Schroeder, and Lee, 2006 includes only the type species, *U. demoscyllus* from the Lower Cretaceous of Australia and shows a mixture of primitive and derived characters. The holotype was originally referred to *Leptocleidus* (Schroeder 1998; Kear 2003), but Kear et al. (2006) formally described this taxon as a new genus of the Rhomaleosauridae. It is the sister-taxon of the group if the phylogenetic definition of the Rhomaleosauridae sensu O'Keefe (2001) is strictly applied to the phylogeny in Kear et al. (2006).

"*Plesiosaurus*" *macrocephalus* Conybeare, 1824 from the Lower Jurassic of England is a problematic taxon in need of revision. Some specimens once referred to this species are possibly referable to *Thalassiodracon hawkinsi* (Owen, 1838) or vice versa (Watson 1911; O'Keefe 2002). The well-preserved skull of "*P.?* *macrocephalus* described by Andrews (1896) is currently under study (P. Vincent, personal communication, 2007). This skull shares several characteristics with our Canadian specimen and is included in the comparison as a potential rhomaleosaurid.

Institutional abbreviations

CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; LEICT, New Walk Museum, Leicester, UK.; NHM, Natural History Museum, London, UK.; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; YORYM, Yorkshire Museum, York, UK.

Material and methods

Our specimen from Melville Island was collected by a CMN party led by D.A. Russell in 1985 (Russell 1993). Fine preparation has revealed details of the palate and braincase. Mechanical separation of the matrix and a coating of secondary minerals (calcite, gypsum) from the bones was difficult, because the bone surface was often poorly defined, and the secondary minerals commonly crystallized within the pore spaces of the bones. Many loose bone fragments were bound within the soft sediments that were solidified by the secondary minerals and glue, and some elements could only be partially prepared. Cross-sections of teeth were prepared by embedding each tooth in epoxy resin and sectioning it using a Buehler Isomet Low Speed Saw. The surface was first polished with 280, 400, and 600 grits using

a Boehler Metaserv 2000, then hand-polished with 1.0 Buehler Micropolish alpha alumina and 0.05 Buehler Micropolish II deagglomerated gamma alumina.

Specimens of *R. megacephalus* (LEICT G221.1851), *R. victor* (SMNS 12478), *R. zetlandicus* (YORYM G503), *S. vorax* (NHM 3319, R3170), and *L. superstes* (NHM R4828) were personally examined for comparison.

Systematic paleontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Pliosauroidea Seeley, 1874

Rhomaleosauridae Kuhn, 1961

Genus *Borealonectes*, gen. nov.

TYPE AND ONLY SPECIES: *B. russelli*, sp. nov.

Borealonectes russelli, sp. nov. (Figs. 1–9)

SYNONYMY: cf. *Cryptoclidus richardsoni* (Lydekker 1889); D.A. Russell, Geological Survey of Canada, Bulletin 450, p. 195 (1993)

HOLOTYPE AND ONLY KNOWN SPECIMEN: CMN 40729, skull, cervical vertebrae, and right forelimb. Collected in 1985.

TYPE LOCALITY: 76°09′04″N, 113°30′00″W, Cape Grassy, Melville Island, N.W.T., Canada (Russell 1993)

DISTRIBUTION: Hiccles Cove Formation, Callovian, Middle Jurassic of Melville Island, N.W.T., Canada (Russell 1993)

ETYMOLOGY: The generic name is based on Greek words and means "northern swimmer," in reference to the occurrence in the northern high latitudes. The species name is given in honor of Dr. Dale A. Russell for his contribution to the study of Mesozoic reptiles in the Canadian Arctic, including the collection of the holotype.

DIAGNOSIS: Differs from other known rhomaleosaurids in the following combination of character states: large prefrontal; exclusion of postfrontal from supratemporal fenestra; skull about twice as long as wide; absence of dorsomedian foramen; absence of crest along the dorsal midline or along premaxilla–maxilla suture; absence of anterior interpterygoid vacuity; presence of ventral crest on parasphenoid; at least six teeth in slightly expanded mandibular symphysis; shaft of humerus straight.

Description

For the details concerning the original condition of the specimen in the field, see Russell (1993). The skull and mandible are flattened and slightly displaced anteriorly and at the left jaw articulation. The left postorbital bar and cheek are fragmented and displaced. Many braincase elements are either lost or hidden under the collapsed skull roof. The left half of the posterior edge of the skull roof is missing, and the right half is severely damaged. See Appendix A, Table A1 for measurements of major skeletal elements.

Skull

The skull is subtriangular in dorsal view. The snout abruptly widens at about one third of the preorbital length near the premaxilla–maxilla suture. There are unusual paired elements, which are tentatively identified as "?nasals" ("n?" in Figs. 1, 2). These bones extend to the parietal, sep-

arating the frontals in dorsal view as the dorsal process of the premaxilla does in many plesiosaurs. The nasal in plesiosaur skulls, when recognizable, is a small and narrow strip of bone posterior to the external naris and does not reach the midline (e.g., O'Keefe 2001). However, the boundary between these bones and the premaxillae in the Canadian specimen are clear on the left side of our specimen and topographically lower than the neighboring bone surface (Fig. 2), leading us to conclude that there are separate paired elements although their identity remains uncertain.

The external nares are asymmetrical, most likely due to damage, but both are surrounded by the maxilla, "?nasal," and prefrontal. The posterior extension of the maxilla passes the anterior edge of the supratemporal fenestra, but it does not meet the squamosal, at least in the lateral view (Fig. 4). The prefrontal occupies the area between the external naris and the orbit, and its dorsomedial portion forms the anterodorsal edge of the orbit. It is much larger than the prefrontals in some other rhomaleosaurids (e.g., *Rhomaleosaurus*, *Leptocleidus*), in which the extent of this bone is limited to the narrow area at the edge of the orbit; the exact structure of this element is uncertain in many rhomaleosaurids (e.g., Taylor 1992b; Kear et al. 2006). Its posterior and ventral extents are unclear due to fusion with the maxilla. The lateral edge of the frontal is broken on both sides, and it cannot be confirmed whether the frontal was excluded from the orbit as in derived pliosauroids, such as *Peloneustes* (O'Keefe 2001) and *Brachauchenius* (Carpenter 1996).

The postorbital bar exhibits a mixture of non-rhomaleosaurid characteristics. The postorbital and postfrontal are arranged anteroposteriorly in *Borealonectes*, in contrast to the situation seen in *Rhomaleosaurus* (Taylor 1992b; Cruickshank 1994) and *Leptocleidus* (Cruickshank 1997), in which the postorbital is lateral or ventral to the postfrontal. We consider the posterior element the postorbital; it is larger, forms the anterior edge of the supratemporal fenestra, and overlaps the surrounding bones, but its medial portion is covered by the epipterygoid (Fig. 4). The smaller postfrontal forms the posterior edge of the orbit but does not enter the supratemporal fenestra. Both bones contact the frontal and jugal. The jugal contributes little, if at all, to the margin of the orbit, and it is excluded from the supratemporal fenestra by the posterior process of the postorbital. The relationships of the postorbital, postfrontal, and jugal vary significantly among the plesiosaurs (see section "Phylogenetic implications").

The parietal has a pair of short processes meeting the "?nasals" anterior to the pineal foramen, which is located at the base of the broken parietal crest. Although the right side of the parietal retains its connection with the squamosal, the suture with the latter cannot be located due to postmortem damage. The parietal forms the anteromedial edge of the supratemporal opening, and there is a sharp ridge that continues from the anterior end of the parietal crest to the postorbital at the anterior margin of the supratemporal fossa. The lateral extent of the parietal is unknown due to the overlapping postorbital (right) and damage (left).

The squamosal has the triradiate shape typical for plesiosaurs, but its relationship with the quadrate is unclear because of asymmetry on the left and right sides of the skull (Fig. 5). On the right side, the quadrate appears to form a

Fig. 1. *Borealonectes russelli* gen. et sp. nov.: dorsal view of the skull (A) and interpretation (B). Abbreviations for Figs. 1–5: a, angular; ar, articular; boc, basioccipital; co, coronoid; cp, coronoid process; d, dentary; dmt, dorsomedian trough; en, external naris; eo, exoccipital–opisthotic; ep, epipterygoid; f, frontal; h, hyoid; in, internal naris; iptv, interpterygoid vacuity; j, jugal; mx, maxilla; n, nasal; oc, occipital condyle; p, parietal; pfo, pineal foramen; pm, premaxilla; po, postorbital; pof, postfrontal; ppr, paroccipital process; pr, prootic; pra, prearticular; prf, prefrontal; ps, parasphenoid; pt, pterygoid; ptb, pterygoid boss; q, quadrate; qrpt, quadrate ramus of pterygoid; rg, ridge; sa, surangular; so, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; ste, subtemporal emargination.
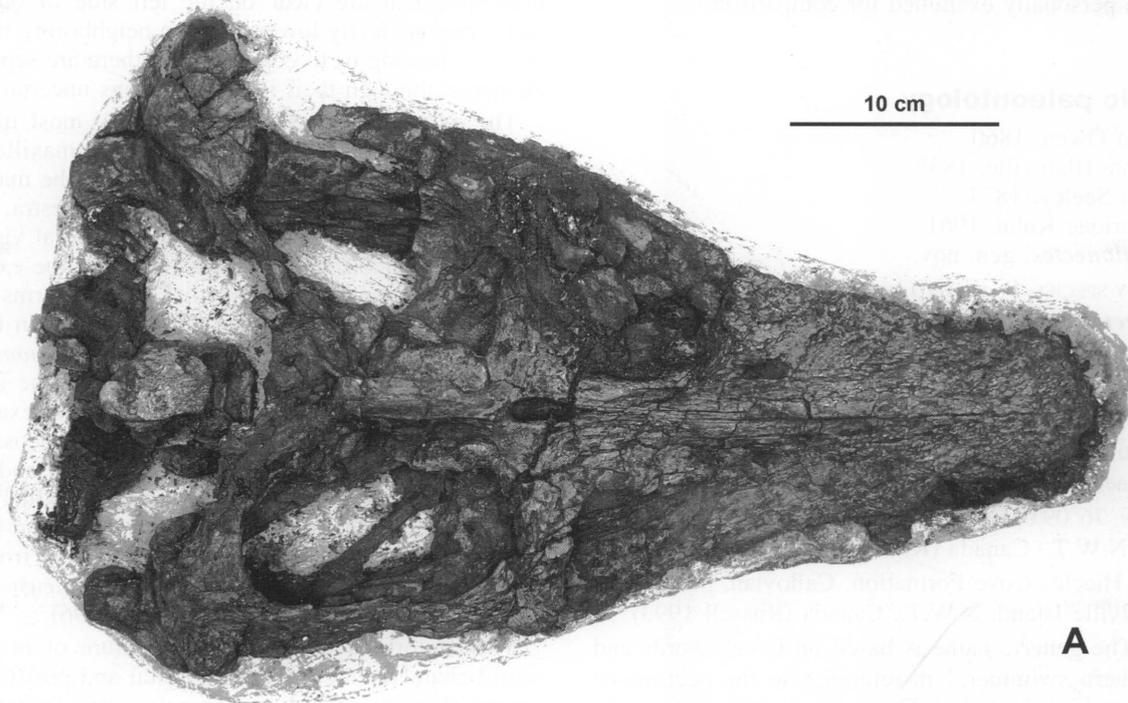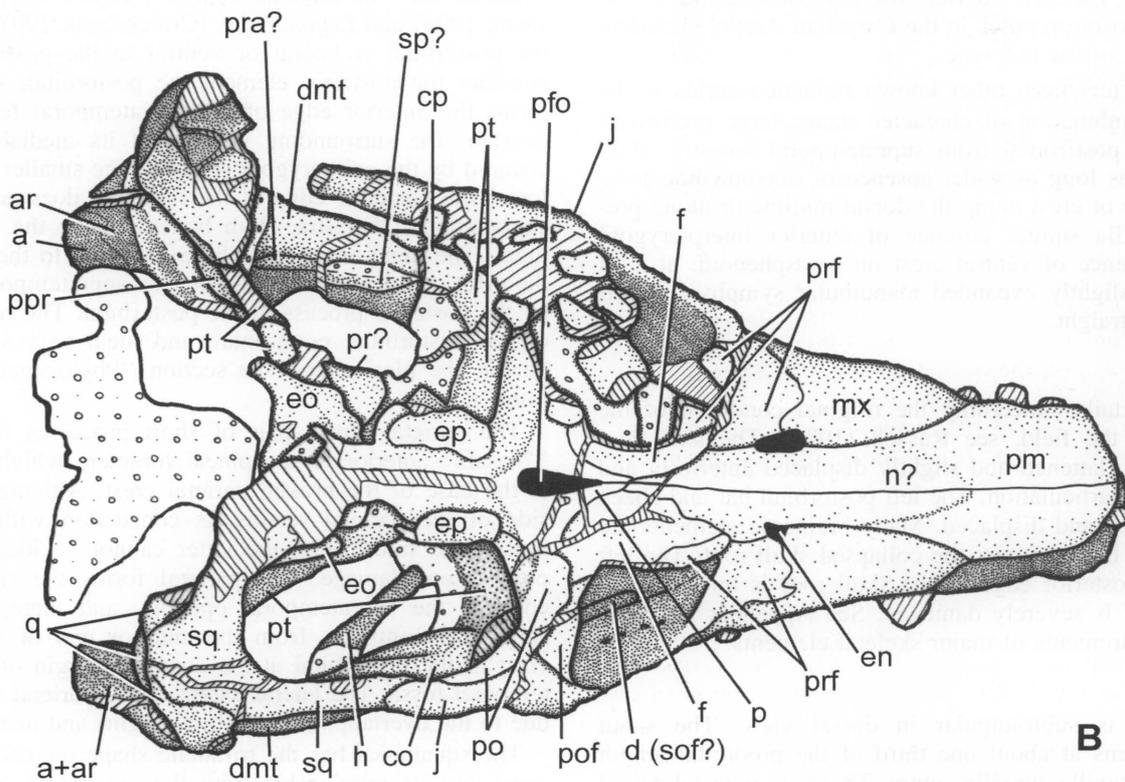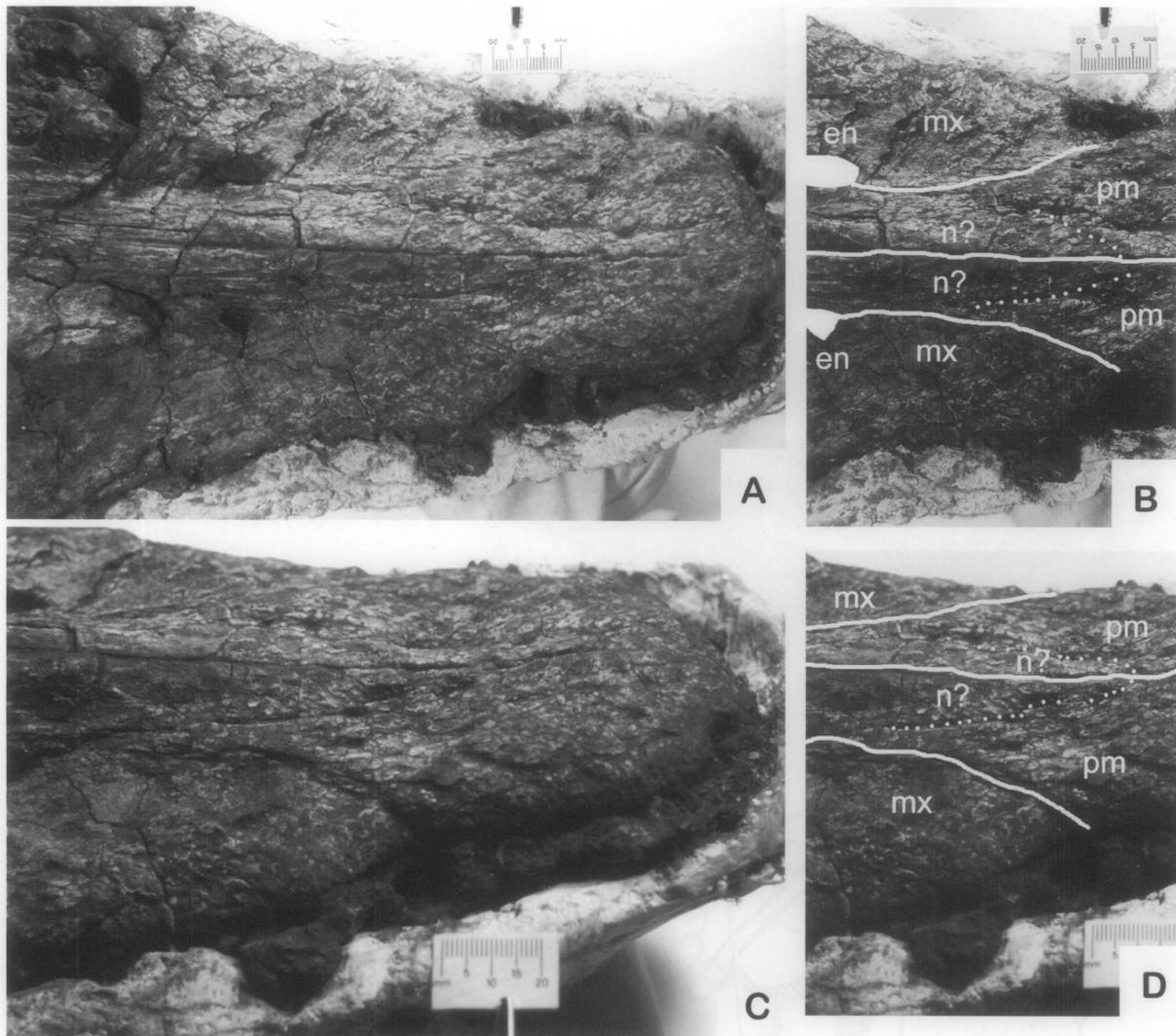
Fig. 2. *Borealonectes russelli* gen. et sp. nov.: close-up of the snout region in dorsal view (A) and interpretation (B), and oblique view (C) and interpretation (D). See Fig. 1 for abbreviations.


V-shaped socket in posterior view, in which the medial branch of the V is much longer than the lateral branch. The squamosal and quadrate are deformed and displaced at this joint, and the broken tip of the medial branch reaches close to the small ridge on the occipital surface of the squamosal ("rg" in Fig. 5). This branch overlaps the paroccipital process in posterior view. The lateral branch reaches above the level of the gentle notch in the squamosal ("subtemporal emargination" of Storrs and Taylor 1996), which is subtle when compared with that in some Early Jurassic pliosauroids (e.g., *Thalassiodracon* in Storrs and Taylor 1996; "*P.?macrocephalus*" in Andrews 1896). On the left side, there is no identifiable V-shaped joint. The left suspensorium is laterally displaced at the jaw joint and broken just above the mandibular condyle. The dorsal portion overlaps an upper part of the ventral portion, but the location of the small ridge of the squamosal ("rg" in Fig. 5), when compared with the right side, suggests that the overlap did not shorten the left suspensorium significantly. One of the fractures might represent the suture between the squamosal and quadrate, but none matches the pattern on the right side.

The epipterygoid has a broad contact with the parietal, overlapping the anterior portion of the parietal below the crest within the supratemporal fenestra (Figs. 1, 4). Both epipterygoids are broken at the edge of the skull roof, but the base of epipterygoid is visible on the dorsal surface of the palate in the right supratemporal fenestra. These conditions indicate a plate-like epipterygoid that occupies a considerable portion of the lateral wall of the braincase as in *R. megacephalus* (Cruickshank 1994) and differs from the relatively smaller structures in derived plesiosaurs, such as polycotylids or elasmosaurids (Carpenter 1997; Sato 2005).

Two elements under the collapsed skull roof may represent the supraoccipital and left prootic ("so?" and "pr?", Figs. 1, 4). The exoccipital–opisthotics are preserved on both sides. There is a long paroccipital process that extends to the quadrate on the right side, but the process on the left side is broken. The process is pressed against the posterior surface of the quadrate ramus of the pterygoid throughout its length. The cross-section of the shaft of the process is circular, and the shaft widens at the distal end (Fig. 5), presumably for the contact with the quadrate. In plesiosaur

Fig. 3. *Borealonectes russelli* gen. et sp. nov.: ventral view of the skull (A) and interpretation (B). See Fig. 1 for abbreviations.
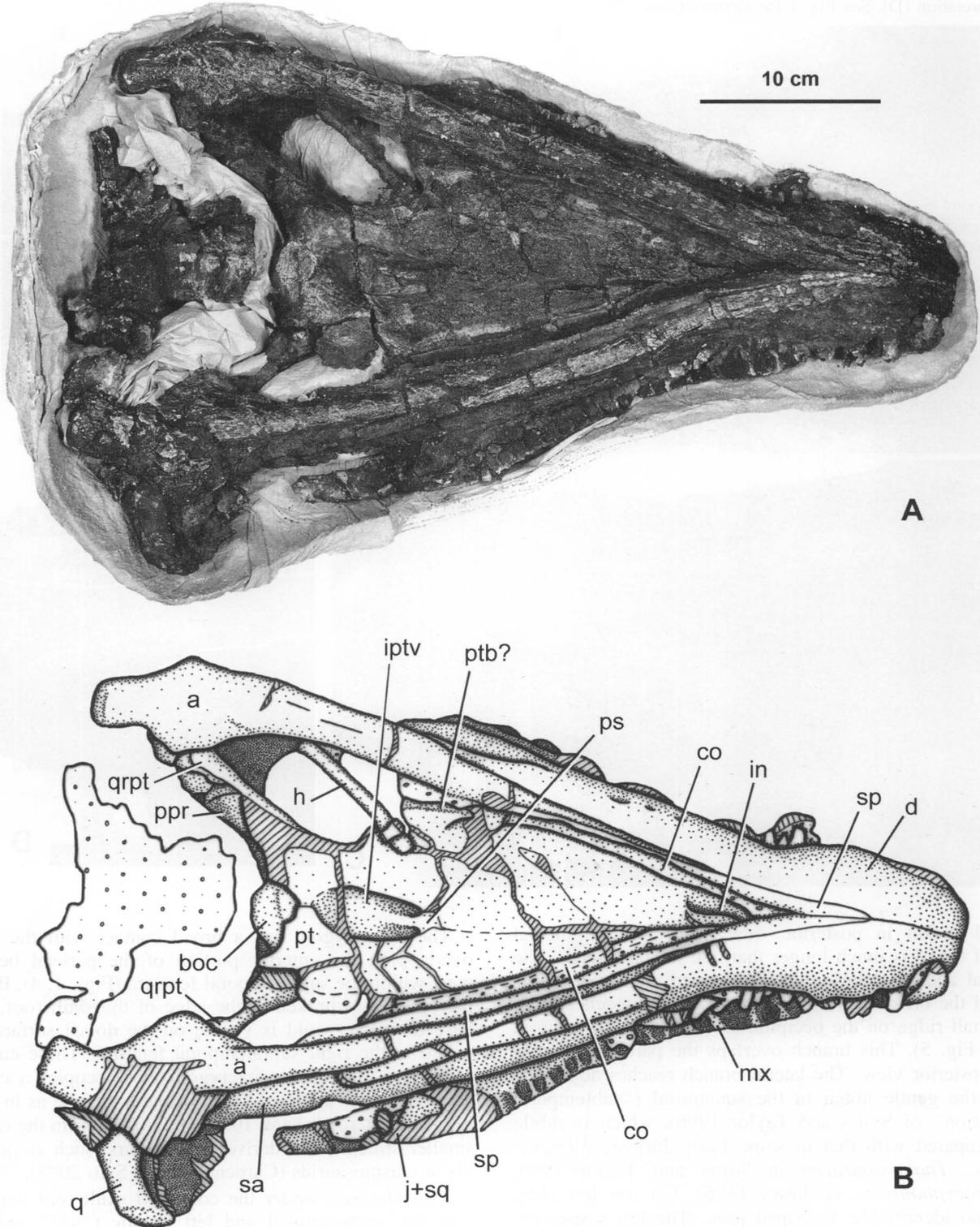

skulls, the paroccipital process is usually located above the quadrate ramus of pterygoid and there is a space between them. Our reconstruction suggests, however, that there was little, if any, space between the process and the ramus in this specimen (see section "Reconstruction of occiput").

Borealonectes lacks a ventral plate of the basioccipital below the occipital condyle. There is no distinct neck separat-

ing the condyle from the rest of the bone, and the ventral side of the condyle continues to the level of the palate. In other words, the palate is approximately at the same height as the ventral edge of the condyle. The height of the ventral plate varies among rhomaleosaurids; *Simolestes* (Noè 2001) has a condition similar to *Borealonectes*, in which the ventral plate is virtually absent, whereas it is high and distinct

Fig. 4. *Borealonectes russelli* gen. et sp. nov.: right side view of the postorbital region of the skull (A) and interpretation (B). See Fig. 1 for abbreviations.
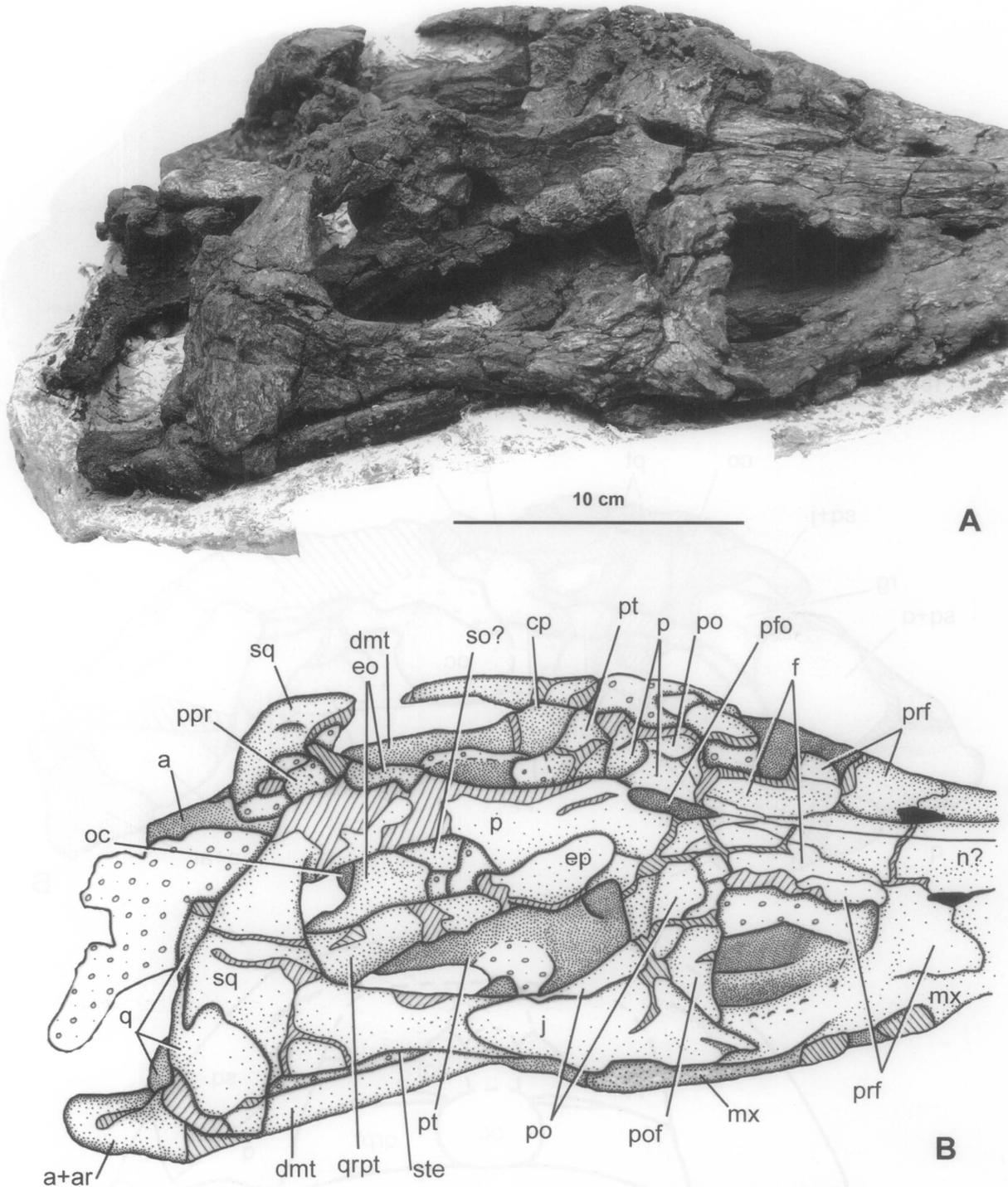

in *Maresaurus* (Gasparini 1997). The condition in *R. megacephalus* (Cruickshank 1994) is intermediate.

The sutures on the palate are unclear (Fig. 3). Most of the left internal naris is visible just behind the mandibular symphysis. The internal naris is located anterior to the external naris, but the presence of palatal grooves as in *R. megacephalus* (Cruickshank et al. 1991; Cruickshank 1994) was not confirmed in the exposed area. The anterior interpterygoid vacuity commonly occurs among most rhomaleosaur-

ids, but it is absent in our specimen. A small portion of the dentary is visible through the right orbit in dorsal view, which may indicate the presence of the suborbital fenestra ("d (sof?)", Fig. 1), although the fenestra may have been damaged by crushing of the mandible. In addition to a hyoid and a tooth remaining on the palate, there were two more teeth (near the internal naris) and another hyoid bone (right side of the posterior interpterygoid vacuity) on the palatal surface, but these were removed during preparation.
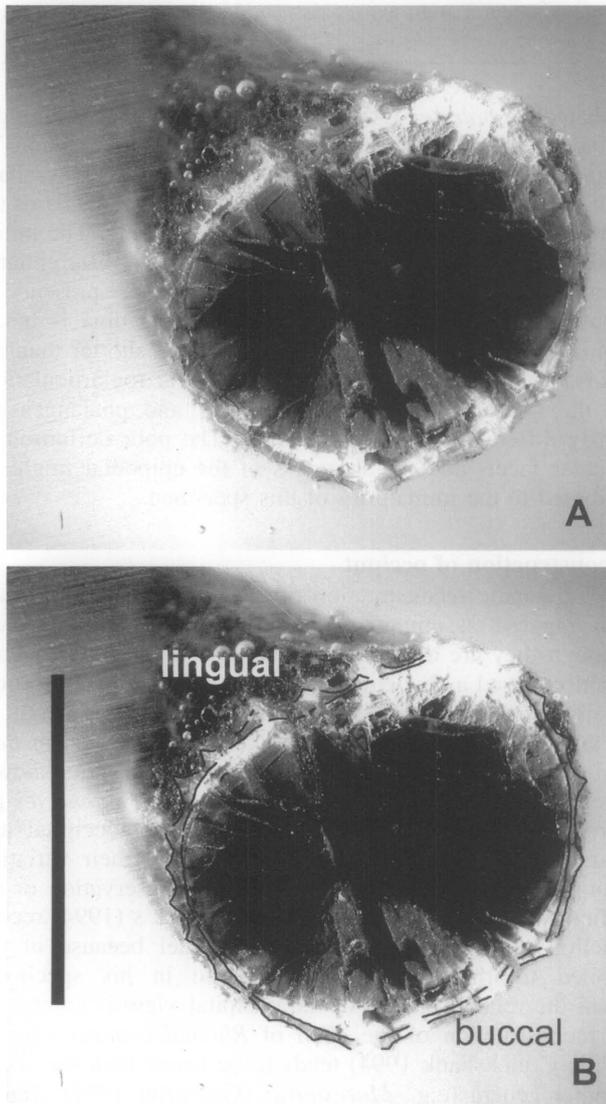
Fig. 5. *Borealonectes russelli* gen. et sp. nov.: occipital view of the skull (A), interpretation (B), and reconstruction (C). See Fig. 1 for abbreviations.
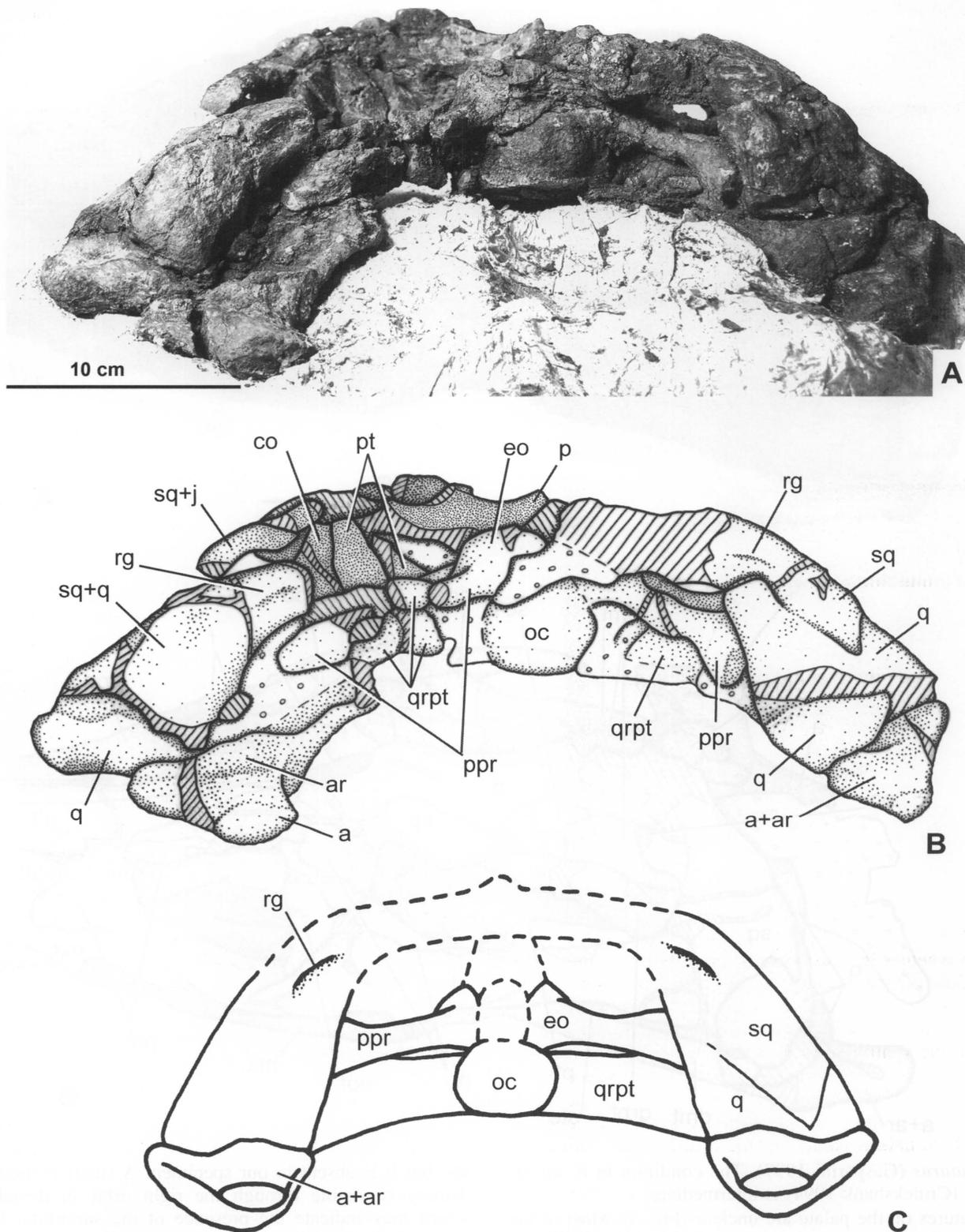
The overall structure of the posterior interpterygoid vacuity is most similar to that in *Leptocleidus* (Andrews 1922*a*; Cruickshank 1997) and *S. vorax* (Andrews 1913), although the arrangement of bones at the posterior end of the vacuity is not clear in the latter. A small portion of the parasphenoid is exposed between the pterygoids in front of the posterior interpterygoid vacuity, and a narrow ridge continues posteriorly into the vacuity for about a third of the vacuity. It is

Fig. 6. *Borealonectes russelli* gen. et sp. nov.: cross-section of a tooth (A) and the outline of enamel layer marked and superimposed (B). Scale bar = 1 mm.

L. capensis (Cruickshank 1997) or a portion of the ectopterygoid or pterygoid deformed by the thrust of the mandible.

The mandible is V-shaped, with nearly straight rami. The dentaries and splenials form the mandibular symphysis, which is relatively slender and long compared to those in *Rhomaleosaurus* and *Simolestes*, but much shorter than in *Macroplata* (Swinton 1930a) or the "Yorkshire taxon" (White 1940). There is a constriction of the mandible posterior to the symphysis and posterior to the notch at the premaxilla–maxilla suture. Both coronoids were pushed towards the palate post mortem; the anterior extent of these bones is unclear. The angular appears on the ventral surface between the dentary and splenial posterior to the internal naris.

Sutures between elements are unclear on the posterior portion of the mandible. The medial side of the left mandibular ramus is visible through the supratemporal fenestra. The coronoid process is low and pointed, and much taller than the surrounding area, a condition more similar to that in *R. zetlandicus* than in *L. capensis* or *S. vorax* (Taylor 1992b; Cruickshank 1997; Noè 2001). There is a dorsomedian trough (Cruickshank 1994) between the coronoid process and the anterior face of the mandibular cotylus. Two narrow strips of bone under the trough probably represent the prearticular and a posterior portion of the splenial, or possibly one of these split into two. The mandibular ramus widens at the cotylus because of the lateral flare (Taylor 1992b), but the width in the left ramus is exaggerated by deformation. There is a suture between the articular and angular on the dorsal surface of the left retroarticular process, suggesting the posterior extension of the articular was shorter than those reconstructed for *R. zetlandicus* and *L. capensis* (Taylor 1992b; Cruickshank 1997). Such a suture is not visible on the right side.

Only badly damaged teeth remain in the alveoli, and there are a number of isolated teeth that are poorly preserved. The exact number of teeth is unknown due to occlusion of the jaws, but we estimate five to six premaxillary teeth, at least 16 and possibly up to 25 maxillary teeth, and at least six teeth in the mandibular symphysis. The size of the sockets suggests that the sixth dentary and third maxillary teeth were larger than neighboring teeth. The mismatch of the constrictions in the upper jaw at the premaxilla–maxilla suture and in the lower jaw behind the symphysis indicates these large teeth (and possibly a few neighboring teeth) were visible when the mouth was closed, as in some crocodylians and *Simolestes* (Noè 2001).

Many isolated teeth retain their original gross morphology, but secondary minerals have grown on the surface and inside of the tooth, obscuring the original structure. We used the cross-sections of a few teeth to study the structure and ornamentation of the crown (Fig. 6). The ridges on the lingual side are more closely spaced than those on the labial side; in one tooth, the lingual half has 15 to 20 ridges, whereas the labial half has fewer than 10 ridges.

Vertebrae

The neural arches were only partially fused to the centra in the cervical vertebrae, indicating this is possibly a young adult (note the fusion of some skull elements mentioned in the "Skull" section). The first three vertebrae are preserved in one small block, along with at least four isolated, badly

unknown whether the basioccipital contributed to the posterior portion of the vacuity as in the "Yorkshire taxon" (White 1940). The pterygoids meet posterior to the posterior interpterygoid vacuity for a short distance, and only a small portion of the ventral surface of the basioccipital is exposed posterior to the united pterygoids. The ventral surface of the left quadrate ramus of the pterygoid is severely damaged, whereas the right ramus is damaged at the base on the dorsal surface of the palatal plane, making it difficult to outline the original posterior edge of the palate.

The pterygoid boss at the anterior edge of the subtemporal fenestra is known in some species of *Rhomaleosaurus* (Taylor 1992b; Cruickshank 1994). There is a narrow projection on the palatal surface on the right side of our specimen ("ptb?" in Fig. 3). It may represent a boss, but its elongate shape does not match the boss in *Rhomaleosaurus*. Other possible interpretations of this feature include the edge of the lateral ramus of the pterygoid similar to that in

Fig. 7. *Borealonectes russelli* gen. et sp. nov.: atlas, axis, and third cervical vertebrae, photographs (A to D) and interpretations (E to F) in anterior (A, E), dorsal (B, F), left lateral (C, G), and ventral (D, H) views. Scale bars = 5 cm. 3c, third centrum; 3na, third neural arch; 3ns, third neural spine; 3prz, third prezygapophysis; 3r, third rib; 3rf, third rib facet; atc, atlas centrum; atic, atlas intercentrum; atna, atlas neural arch; atns, atlas neural spine; axc, axis centrum; axic, axis intercentrum; axna, axis neural arch; axns, axis neural spine; axpoz, axis post-zygapophysis; axr, axis rib; axrf, axis rib facet; t, tooth; tub, tuberosity.

weathered teeth (Fig. 7). Although the three anterior centra are in articulation, their neural arches and ribs are slightly displaced and damaged. The atlas and axis are not completely fused. Unlike *Cryptoclidus* and related taxa, the atlantal centrum is not hypertrophied (Bakker 1993), and the neural arches and intercentrum form a complete atlantal cup. There are no facets for atlantal ribs, but there is a tubercle on either side of the intercentrum ("tub", Fig. 7). The relationships of the components of the atlas–axis complex are not clear in ventral view. In our interpretation, the posterior portion of the atlantal intercentrum is asymmetrical, and there is a separate axial intercentrum ("second subvertebral wedge-bone" of Andrews 1913) exposed on the ventral side of the block and dorsal to the tubercle on the right side of the atlantal intercentrum. The intercentra of atlas and axis exclude the atlantal centrum from the ventral surface of the complex. The neural spine of the atlas–axis complex is broken at the base and lies with its left side facing up. Its ventral half weakly projects laterally, and we tentatively identify this portion as the atlantal neural spine ("atns?", Fig. 7). The probable atlantal neural spine extends posteriorly, and there is no evidence of a gap between the atlantal and axial neural arches.

There are seven isolated cervical vertebrae, labeled A (anterior) to G (posterior); they were collected from the middle of the cervical series (Russell 1993). Only the base of the neural arch is preserved in three of the seven; the neural arch is completely missing in the rest (Fig. 8). The rib facet occupies most of the lateral surface of the centrum. Vertebra B has a rib facet that is weakly constricted in the middle, suggesting the presence of a double-headed rib, whereas the other vertebrae have round facets. Double-headed cervical ribs are common in Jurassic plesiosaurs including rhomaleosaurs (*Simolestes*, Andrews 1913; *Rhomaleosaurus zetlandicus*, personal observation, 2005), whereas Cretaceous forms including *Leptocleidus superstes* (Andrews 1922a) and *Umoonasaurus* (Schroeder 1998) have single-headed ribs (see section "Phylogenetic implications"). The centra are deeply amphicoelous. There is a weak ventral ridge between the foramina subcentralia, a common feature for many rhomaleosaurids.

Forelimb

The forelimb exhibits a mixture of primitive and derived features. The preserved forelimb includes the humerus, epipodials (Fig. 9), five carpals, two supernumeraries, four metacarpals, and 15 phalanges. A photograph of the specimen in situ (Russell 1993, Fig. 2) indicates that the limb was articulated but that there was a wide space between the elements, suggesting the presence of a considerable amount of intervening cartilage. The humerus is badly weathered and contained in a jacket, and only the ventral view is visible. Unlike *R. victor* (Fraas 1910) and other primitive plesiosaurs, in which the humeral shaft is curved (e.g., Storrs 1997); the humerus of *Borealonectes* is straight and similar

to that of *Simolestes* (Andrews 1913), likely representing a derived feature (see section "Phylogenetic implications"). Epipodial facets are differentiated and form a wide V-shape with the apex at the distal end of the humerus. Details of the bone surface are not available due to weathering. The radius is slightly longer than wide, with a poorly differentiated facet on the posterolateral corner indicating the presence of an unpreserved supernumerary element. The ulna is lunate (a primitive feature), shorter than wide, and shorter than the radius. The carpals have no defined facets for articulation, but the articular facets in metacarpals and phalanges are clearly differentiated from the shaft. The poor definition of articular facets and the shortness of the epipodial might be attributed to the immaturity of this specimen.

Reconstruction of occiput

A schematic reconstruction of the skull in posterior view was prepared, assuming bones were not severely deformed, although they are displaced or rotated (Fig. 5C). The reconstruction posed a challenge, especially for the dorsal portion, because of the difficulty in estimating the original height of the skull. The suspensorium is broken and displaced in *Borealonectes*, and the height of the supraoccipital is unknown. A reliable estimate of the skull height for *Borealonectes* requires an estimate of the height of the supraoccipital and foramen magnum, but little is known about their variation among rhomaleosaurids because of poor preservation or insufficient preparation. We used Cruickshank's (1994) reconstruction of *R. megacephalus* as a model because of the detailed information on the braincase in his specimen. When the relative height of the occipital view is compared, the reconstruction of the skull of *Rhomaleosaurus* (Taylor 1992b; Cruickshank 1994) tends to be lower than the skulls of other genera (e.g., *Maresaurus* (Gasparini 1997); *Leptocleidus* (Cruickshank 1997); *Simolestes* (Noè 2001)). Our choice of the model may explain the relatively low skull height in our reconstruction.

We believe that there was little, if any, space between the paroccipital process and quadrate ramus of the pterygoid prior to postmortem crushing. The quadrate ramus of the pterygoid of *Borealonectes* measures 28 and 35 mm tall at the proximal and distal ends, respectively. The maximum height of the paroccipital process near its distal end is about 20 mm, and the narrowest part of the process is near the braincase, with a diameter of about 10 mm. The right exoccipital–opisthotic has been slightly rotated clockwise in posterior view. To accommodate the long paroccipital process under the sloping suspensorium, we believe that the paroccipital process was only slightly oblique to the quadrate ramus of the pterygoid. Such an arrangement results in a slit-like space between the bones, or possibly the absence of such an opening as indicated in the reconstruction of the skull of the pliosaurid *Pliosaurus brachyspondylus* by Taylor and Cruickshank (1993).
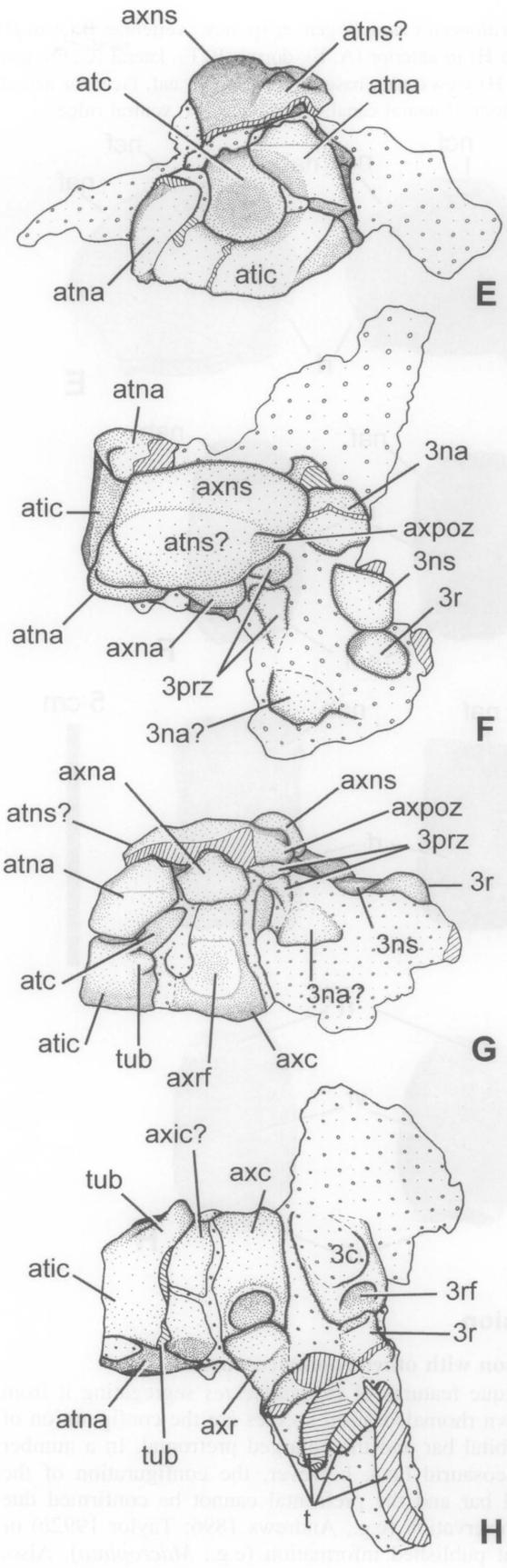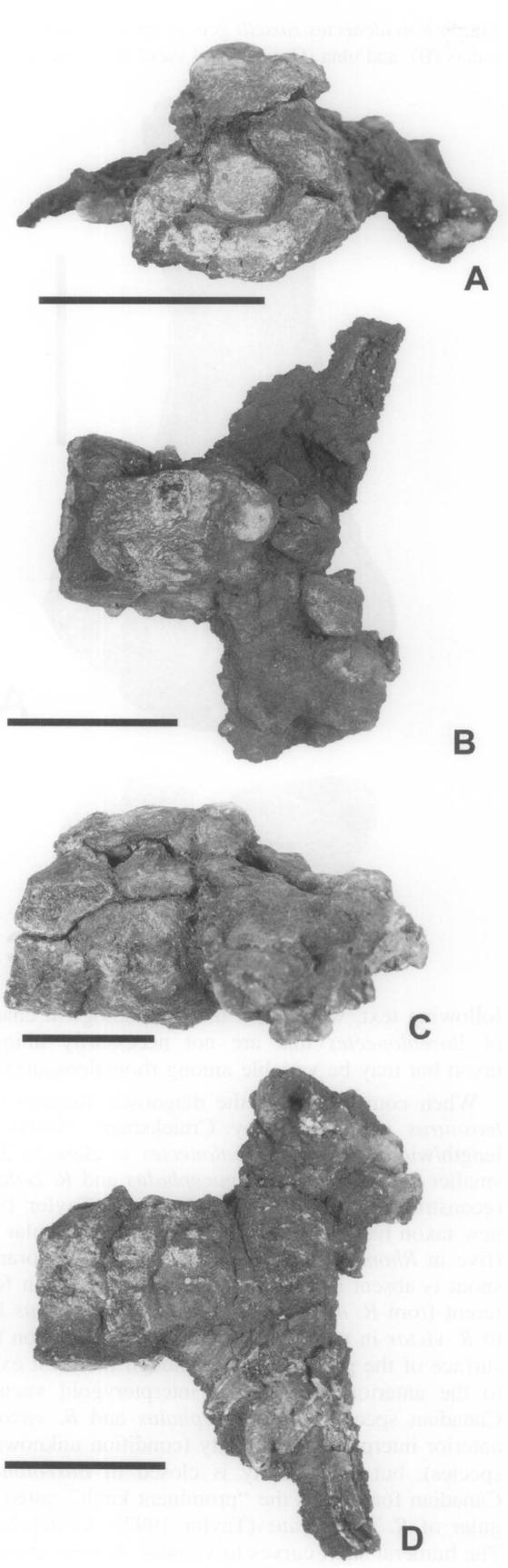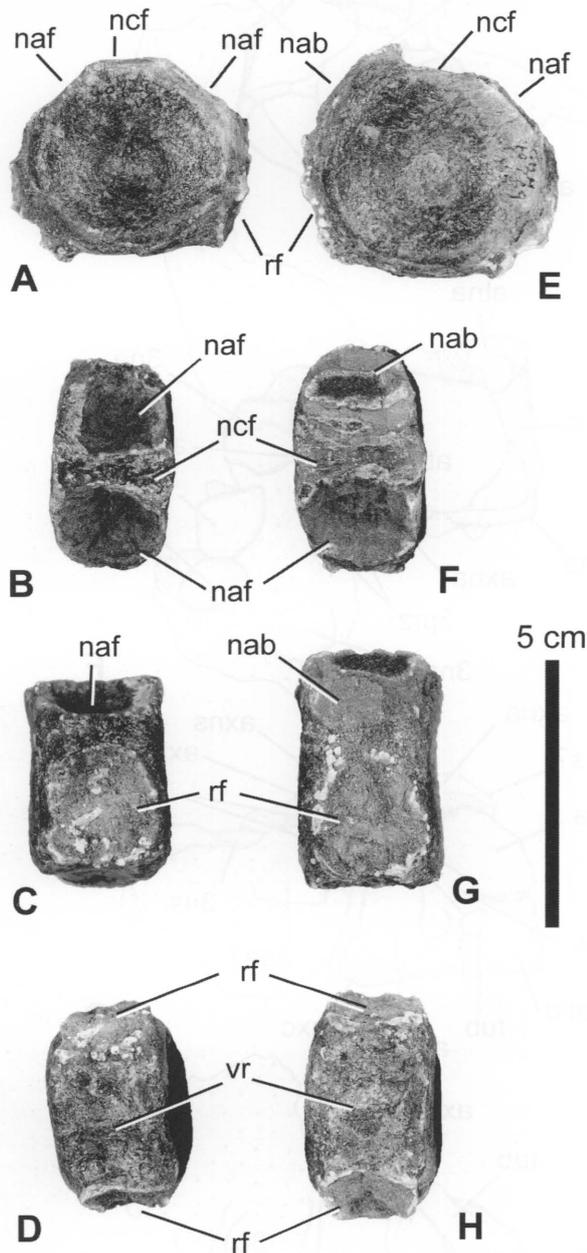
Fig. 8. *Borealonectes russelli* gen. et sp. nov.: vertebrae B (A to D) and D (E to H) in anterior (A, E), dorsal (B, F), lateral (C, G), and ventral (D, H) views. nab, base of neural arch; naf, facet for neural arch; ncf, floor of neural canal; rf, rib facet; vr, ventral ridge.

Fig. 9. *Borealonectes russelli* gen. et sp. nov.: right humerus (A), radius (B), and ulna (C) in ventral view. Scale bar = 10 cm.

Discussion

Comparison with other rhomaleosaurids

The unique features of *Borealonectes* segregating it from other known rhomaleosaurid species are the configuration of the postorbital bar and the enlarged prefrontal. In a number of rhomaleosaurid taxa, however, the configuration of the postorbital bar and the prefrontal cannot be confirmed due to poor preservation (e.g., Andrews 1896; Taylor 1992*b*) or insufficient published information (e.g., *Macroplata*). Also, the enlarged atlantal neural spine may be unique to *Borealonectes*, but little is known about this structure in other plesiosaurian taxa due to preservation and fusion. In the

following text, we discuss the morphological characteristics of *Borealonectes* that are not necessarily unique to this taxon but may be variable among rhomaleosaurids.

When compared with the diagnostic features of *Rhomaleosaurus* summarized by Cruickshank (1994), the skull length/width ratio of *Borealonectes* is close to 2, which is smaller than that of *R. megacephalus* and *R. zetlandicus* (as reconstructed by Cruickshank 1994 and Taylor 1992*a*). The new taxon has five or six teeth in the mandibular symphysis (five in *Rhomaleosaurus*). The dorsomedian foramen of the snout is absent in *Borealonectes*. The Canadian form is different from *R. megacephalus* and *R. zetlandicus* but similar to *R. victor* in possessing a longitudinal crest on the ventral surface of the parasphenoid, although the crest extends only to the anterior third of the interpterygoid vacuity in the Canadian species. *R. megacephalus* and *R. victor* have an anterior interpterygoid vacuity (condition unknown for other species), but this vacuity is closed in *Borealonectes*. The Canadian form lacks the "prominent knob" noted on the angular of *R. propinquus* (Taylor 1992*b*; Cruickshank 1994). The humeral shaft curves to variable degrees among the species of *Rhomaleosaurus*, and the condition in *Borealonectes* is at one end of a continuum; *R. victor* is at the other end with the most prominent curvature of the shaft, in which

the preaxial edge of the shaft is convex. The shaft is curved and the preaxial edge is nearly straight in *R. zetlandicus* and its potential synonyms (*R. cramptoni* and *R. propinquus*; Cruickshank 1996), but it is clearly concave in *Borealonectes*.

Simolestes and the possibly congeneric *Maresaurus* (Noè 2001) differ from *Borealonectes* in having a much wider mandibular symphysis. In *S. vorax* and *Maresaurus*, the palatal space posterior to the posterior interpterygoid vacuity is much longer than in *Borealonectes*, and the Arctic taxon lacks the deep embayment in the tooth row at the suture between the premaxilla and maxilla. *Maresaurus* is distinguished from *S. vorax* and *Borealonectes* by the absence of a ventral ridge on the parasphenoid and by the presence of three sagittal crests on the rostrum (Gasparini 1997).

The poorly preserved skull of *Leptocleidus superstes* allows only a limited comparison. *L. superstes* lacks the large epipterygoid attached to the parietal, as well as the sharp ridge at the anterior edge of the supratemporal fenestra (personal observation, 2002). Cruickshank (1997) noted the similarity between *Leptocleidus* and *Rhomaleosaurus*, including the dorsomedian foramen that is absent in *Borealonectes*. The anterior interpterygoid vacuity is present in *L. capensis* (Cruickshank 1997) but not in the Canadian specimen. *L. clemai* is represented by a fragmentary postcranial skeleton, and it is impossible to make a detailed comparison. Noted differences include the straight to slightly convex anterior edge of the humeral shaft in *L. clemai* (Cruickshank and Long 1997) and in *L. superstes* (Andrews 1922a), in contrast to the concave edge in *Borealonectes*. The epipodials are wider than long in *L. clemai* (Cruickshank and Long 1997) but the radius is longer than wide in the Canadian species.

The "Yorkshire taxon" is easily distinguished from other rhomaleosaurids, including *Borealonectes*, by its elongated snout and the perforation in the basisphenoid (White 1940). *Macroplata* also has a relatively long mandibular symphysis that occupies nearly one third of the skull length, and the preaxial margin of the humerus is convex (Swinton 1930a). *Yuzhoupliosaurus* obviously had a higher skull length/width ratio than most rhomaleosaurids, including *Borealonectes* (Zhang 1985), although the exact extent of the anterior portion of the skull is unknown due to damage. *Umoonasaurus* and *Borealonectes* differ in the snout (presence of the midline crest and absence of the constriction in the former) and palate (short ventral keel of the parasphenoid and lack of the dished pterygoid in the latter) morphology. The skull of "*Plesiosaurus*" *macrocephalus* described by Andrews (1896) is distinguished from the Canadian taxon by the prominent notch in the squamosal and a short mandibular symphysis.

Phylogenetic implications

So many rhomaleosaurids are currently under study or revision by other researchers (see previous section) that a cladistic analysis at this stage is deemed premature. Instead, our discussion will focus on several features that may be significant for assessing the phylogenetic relationships of *Borealonectes*.

The large prefrontal extending to the external naris is unexpected for a rhomaleosaurid, because it is a diagnostic

feature of the Plesiosauroidea sensu O'Keefe (2001) and known in plesiosauroids such as *Plesiosaurus*, elasmosaurids, and polycotylids (Storrs 1997; Sato 2003; O'Keefe 2004b). It contrasts with the prefrontals in pliosauroids and Triassic pistosauroids (the closest relatives of the Plesiosauria), in which the bone does not reach the external naris (e.g., Carpenter 1996; Noè 2001; O'Keefe 2001; Rieppel et al. 2002).

The polarity of the anterior interpterygoid vacuity is unclear among basal plesiosaurians, and it is unknown whether the absence in *Borealonectes* represents a primitive or derived condition within the Rhomaleosauridae. Among the Triassic pistosauroids, the vacuity is completely closed (Sues 1987; Rieppel 2000; Rieppel et al. 2002), except for one species in which there is a very narrow space (Cheng et al. 2006). The vacuity is present in basal plesiosauroids (Storrs 1997; O'Keefe 2004a) and in at least one specimen of the basal pliosauroid *Thalassiodracon* (O'Keefe 2001). It should be noted, however, that the condition is variable among the specimens referred to *T. hawkinsi*; for example, the vacuity appears absent in the specimen figured by Owen (1865, pl. 716). Andrews (1896) argued that the palate of the specimen of "*Plesiosaurus*" *macrocephalus* studied by him was originally closed. The condition in other basal pliosauroids, such as *Eurycleidus*, and the pliosaurid *Attenborosaurus* (Cruickshank 1994; Bakker 1993; O'Keefe 2001) is unknown due to the lack of adequate materials. Among the derived plesiosaurians, the presence of the vacuity is confirmed for the Polycotylidae (e.g., Druckenmiller 2002; O'Keefe 2004b) and its absence for most elasmosaurids (e.g., Carpenter 1997; Sato 2003) and the pliosaurid *Brachauchenius* Williston 1903. The distribution of this character requires homoplasies in all previously proposed hypotheses of phylogenetic relationships (O'Keefe 2001, 2004a; Druckenmiller 2006).

The configuration of the postorbital bar varies significantly within the Plesiosauria, but the anteroposterior arrangement of the postorbital and postfrontal in *Borealonectes* is unusual. The postfrontal and postorbital equally contribute to the orbit and supratemporal fenestra in Pliosauridae and Rhomaleosauridae (e.g., Taylor and Cruickshank 1993; Cruickshank 1994; O'Keefe 2001). This is likely the case also in polycotylids, although it is often obscured due to poor preservation and fusion (O'Keefe 2004b). Among the Early Jurassic non-rhomaleosaurid plesiosaurs (Storrs and Taylor 1996; Storrs 1997; Grossmann 2007), the postorbital is slightly larger than the postfrontal, and the former forms most of the anterior edge of the supratemporal fenestra, whereas the latter contributes to the posteromedial corner of the orbit. The postorbital is the major component of the postorbital bar in elasmosaurids and the cimoliasaurid (sensu O'Keefe 2001) *Kimmerosaurus*; the small postfrontal is confined within the supratemporal fenestra in elasmosaurs (O'Keefe 2001; Sato 2003), whereas this bone in *Kimmerosaurus* is as yet unknown (Brown et al. 1986). The postorbital is posterior to the postfrontal in *Cryptoclidus*, and the suture suggests that the postorbital "may have had only a small exposure to the orbit" (Brown and Cruickshank 1994, p. 946); the postfrontal was, however, only tentatively identified, and its relationships remain unclear.

Borealonectes lacks the anterior process of the jugal that

excludes the maxilla from the orbit in many pliosauroids, such as *Rhomaleosaurus*, *Peloneustes*, *Pliosaurus*, and possibly *Leptocleidus* (Taylor and Cruickshank 1993; Cruickshank 1994, 1997; O'Keefe 2001). The relationship of the orbit and jugal in *Borealonectes* is likely plesiomorphic, because it is comparable to those in basal plesiosaurs and plesiosauroids (e.g., *Plesiosaurus*, polycotylids, elasmosaurids: Storrs 1997; O'Keefe 2001, 2004*b*; Sato 2003). Another possible plesiomorphy is the large postorbital with a posterior extension, excluding the jugal from the supratemporal fenestra, because this is also common in Early Jurassic plesiosaurs (Andrews 1896; Storrs and Taylor 1996; Storrs 1997; Grossmann 2007). The jugal does not enter the supratemporal fenestra in the Cryptocleidoidea sensu O'Keefe (2001), such as *Cryptoclidus*, *Kimmerosaurus*, and *Dolichorhynchops* (Brown et al. 1986; Brown and Cruickshank 1994; O'Keefe 2004*b*), but the postorbital does not have a significant posterior extension in these forms.

The detailed structure of the atlas–axis complex is unknown for most rhomaleosaurids due to preservation and (or) incomplete preparation. When compared with non-rhomaleosaurids, the atlas–axis complex of *Borealonectes* is most similar to those in polycotylids, such as *Dolichorhynchops* Williston, 1903 and *Edgarosaurus* Druckenmiller, 2002 in the relationship of the atlantal and axial centra, the lack of the gap between the neural arches, and lack of the hypertrophied atlantal centrum (Andrews 1910, 1913; Bakker 1993; O'Keefe 2001).

The number of cervical rib heads is a classic character for plesiosaur taxonomy, and the chronological trend in which the double-headed ribs are seen in early plesiosaurs and single-headed ones in later forms has been known for some time (e.g., Brown 1981). The cervicals in *Borealonectes* exhibit evidence for both conditions; one cervical has a constricted rib facet and suggests the presence of a double-headed rib, but others suggest single-headed ribs. Tarlo (1960) reported the presence of the two types of rib facets on a posterior cervical in the Late Jurassic *Pliosaurus*, and it is possible that this character could vary within one individual. Of the seven cervicals preserved in the holotype of *Borealonectes*, those with single-rib facets exceed the ones with double-rib facets in number, and it would be more natural to consider *Borealonectes* a taxon with single-headed ribs. The variation in rib head morphology is not well documented, and it is difficult to evaluate the significance of the condition in *Borealonectes* and *Pliosaurus*.

The curvature of the humeral shaft is a common feature among Triassic sauropterygians (e.g., Storrs 1991) and in many basal plesiosaurians (Storrs 1997; O'Keefe 2004*a*) and rhomaleosaurids. The lunate ulna and relatively long epipodials are also considered primitive for the Plesiosauria (O'Keefe 2001). Therefore, *Borealonectes* has a combination of derived (humerus) and primitive (epipodials) characters in one limb. The immaturity of the Canadian specimen complicates the interpretation of humeral character, because there are conflicting reports on the ontogenetic variability of this character in the related forms; the humeral curvature does not change ontogenetically in the pistosauroid *Corosaurus* or the plesiosaur *Cryptoclidus* (Storrs 1991; Caldwell 1997), whereas Grossmann (2007) noted a straighter humerus in the juvenile specimen of Jurassic plesiosauroid *Hydrorion* Grossmann, 2007.

In summary, *Borealonectes* has a combination of (potentially) derived and primitive features, as well as those not usual for a rhomaleosaurid or a pliosauroid. The anterior interpterygoid vacuity, dorsomedian foramen, and curved humerus are common features for basal rhomaleosaurids, such as *Rhomaleosaurus*, but *Borealonectes* lacks them, possibly suggesting the Canadian taxon is more derived than these basal rhomaleosaurids. Primitive features of *Borealonectes* shared with early plesiosaurs include the large posterior extension of the postorbital and the modest contribution of the jugal into the orbit. The large prefrontal, jugal, and possibly the structure of atlas–axis complex are more plesiosauroid than pliosauroid.

To be more precise about the phylogenetic relationships of *Borealonectes*, more anatomical information for a number of related taxa is needed. It is promising that there are so many ongoing projects on rhomaleosaurids for the further anatomical and taxonomic clarification of the taxa in this problematic group.

Biogeographic significance

Borealonectes is the first marine reptile fossil with a fairly well-preserved skull from the Canadian Arctic, and the oldest plesiosaur genus known from the circumpolar Arctic region. This region has shifted from mid to high latitudes during the Mesozoic (Scotese 2002), and plesiosaurs were obviously common inhabitants there. Although poorly preserved, plesiosaurian remains are known from various horizons ranging from the Middle Jurassic to latest Cretaceous in the Canadian Arctic (Russell 1967, 1990; Sato and Wu 2005). In the Arctic region outside of Canada, plesiosaurian remains are mostly known from the Upper Jurassic of Alaska (Weems and Blodgett 1996) and Scandinavia (Persson 1963). Indeterminate or potentially plesiosaurian remains have been reported from the Upper Triassic of Spitzbergen (Persson 1963; Cox and Smith 1973; Worsley and Heintz 1976).

A reliable estimate of the water temperature in which *Borealonectes* lived is not available, but previous studies on Jurassic climates suggest less equable climate when compared with the known greenhouse condition during the Cretaceous (Hallam 1993), including the possible presence of ice in polar regions in Middle to Late Jurassic time (Dromart et al. 2003). Similarly cold climate is also suggested for *Umoonasaurus* from the Early Cretaceous high-latitude region (Kear et al. 2006). There are two possible interpretations for the presence of plesiosaurs in such regions. One is that these plesiosaurs might have been capable of living in relatively cold water. Another possibility is that they were seasonal migrants, if they preferred warmer temperatures in winter. More information on the temperature of their living environment and reliable estimates of their temperature tolerance are needed to further explore these possibilities.

Plesiosaurs with rhomaleosaurid characteristics (*Borealonectes* and *Umoonasaurus*) had a global distribution, including the northern and southern high-latitude regions. The potential synonymy of *Maresaurus* and *Simolestes* (Noè 2001) suggests a wide geographic distribution of this rhomaleosaurid genus, because the former is from the Middle Jurassic of Argentina and the latter is from northwestern Europe. Should the rhomaleosaurid status of the fragmentary

known *Yuzhoupliosaurus* from the Middle Jurassic of China be confirmed, it would extend the biogeographic distribution of the group even further. The monophyly of the Rhomaleosauridae has been disputed, but it is fair to say that rhomaleosaurids are important in the study of biogeographic radiation of the Plesiosauria.

Borealonectes is also important as one of the few Jurassic plesiosaurs known from North America. The oldest plesiosaur in North America is an indeterminate plesiosauroid from the Lower Jurassic (Sinemurian) of Alberta (Nicholls 1976). The Middle Jurassic *Borealonectes* is the second oldest, followed by the Late Jurassic plesiosaurs from the Sundance Formation in Wyoming (Knight 1898; O'Keefe and Wahl 2003*a*, 2003*b*), the Alaskan record of *Megalneusaurus* (Weems and Blodgett 1996), and a few specimens of the Late Jurassic (Oxfordian) or younger age (Nicholls 1976).

Acknowledgements

References

Andrews, C.W. 1896. On the structure of the plesiosaurian skull. Quarterly Journal of the Geological Society (of London), **52**: 246–253.

Andrews, C.W. 1909. On some new Plesiosauria form the Oxford Clay of Peterborough. Annals and Magazine of Natural History, **8**: 418–429.

Andrews, C.W. 1910. A descriptive catalogue of the marine reptiles of the Oxford Clay, Part I. British Museum (Natural History), London.

Andrews, C.W. 1911. Description of a new plesiosaur (*Plesiosaurus capensis* sp. nov.) from the Uitenhage beds of Cape Colony. Annals of the South African Museum, **1**: 309–322.

Andrews, C.W. 1913. A descriptive catalogue of the marine reptiles of the Oxford Clay, Part II. British Museum (Natural History), London.

Andrews, C.W. 1922*a*. Description of a new plesiosaur from the Weald Clay of Berwick (Sussex). Quarterly Journal of the Geological Society (of London), **78**: 285–295.

Andrews, C.W. 1922*b*. Notes on the skeleton of a large plesiosaur (*Rhomaleosaurus thorntoni* sp. n.) from the Upper Lias of Northamptonshire. Annals and Magazine of Natural History, **9**: 407–415.

Anonymous. 1854. Report of the Council of the Yorkshire Philoso-

phical Society. Annual Report of the Yorkshire Philosophical Society, **1853**: 7–8.

Bakker, R.T. 1993. Plesiosaur extinction cycles—events that mark the beginning, middle and end of the Cretaceous. *In* Evolution of the Western Interior Basin. *Edited by* W.G.E. Caldwell and E.G. Kaufman. Geological Association of Canada, Special Paper 39, pp. 641–644.

Benton, M.J., and Taylor, M.A. 1984. Marine reptiles from the Upper Lias (Lower Toarcian, Lower Jurassic) of the Yorkshire coast. Proceedings of the Yorkshire Geological Society, 44, Part 4, No. 29, pp. 399–429.

Brouwers, E.M., Clemens, W.A., Spicer, R.A., Ager, T.A., Carter, L.D., and Sliter, W.V. 1987. Dinosaurs on the North Slope, Alaska: high latitude, latest Cretaceous environments. Science, **237**: 1608–1610. doi:10.1126/science.237.4822.1608.

Brown, D.S. 1981. The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauria. Bulletin of the British Museum (Natural History), Geology, **35**: 253–347.

Brown, D.S., and Cruickshank, A.R.I. 1994. The skull of the Callovian plesiosaur *Cryptoclidus eurymerus*, and the sauropterygian cheek. Palaeontology, **37**: 941–953.

Brown, D.S., Milner, A.C., and Taylor, M.J. 1986. New material of the plesiosaur *Kimmerosaurus langhami* Brown from the Kimmeridge Clay of Dorset. Bulletin of the British Museum (Natural History), Geology, **40**: 225–234.

Caldwell, M.W. 1997. Limb osteology and ossification patterns in *Cryptoclidus* (Reptilia: Sauropterygia) with a review of sauropterygian limbs. Journal of Vertebrate Paleontology, **17**: 295–307.

Carpenter, K. 1996. A review of short-necked plesiosaurs from the Cretaceous of the Western Interior, North America. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, **201**: 259–287.

Carpenter, K. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs. *In* Ancient marine reptiles. *Edited by* J.M. Callaway and E.L. Nicholls. Academic Press, San Diego, Calif., pp. 191–216.

Carte, A., and Baily, W.H. 1863. Description of a new species of *Plesiosaurus*, from the Lias, near Whitby, Yorkshire. Journal of the Royal Dublin Society, **4**: 160–170.

Cheng, Y.-n., Sato, T., Wu, X.-c., and Li, C. 2006. First complete pistosauroid from the Triassic of China. Journal of Vertebrate Paleontology, **26**: 501–504. doi:10.1671/0272-4634(2006) 26[501:FCPFTT]2.0.CO;2.

Conybeare, W.D. 1824. Additional notices on the fossil genera *Ichthyosaurus* and *Plesiosaurus*. Transactions of the Geological Society (of London), **1**: 103–123.

Cox, C.B., and Smith, D.G. 1973. A review of the Triassic vertebrate faunas of Svalbard. Geological Magazine, **110**: 405–418.

Cruickshank, A.R.I. 1994. Cranial anatomy of the Lower Jurassic pliosaur *Rhomaleosaurus megacephalus* (Stutchbury) (Reptilia: Plesiosauria). Philosophical Transactions of the Royal Society (of London), Series B, **343**: 247–260.

Cruickshank, A.R.I. 1996. The cranial anatomy of *Rhomaleosaurus thorntoni* Andrews (Reptilia, Plesiosauria). Bulletin of the British Museum (Natural History), Geology, **52**: 109–114.

Cruickshank, A.R.I. 1997. A Lower Cretaceous pliosauroid from South Africa. Annals of the South African Museum, **105**: 207–226.

Cruickshank, A.R.I., and Long, J.A. 1997. A new species of pliosaurid reptile from the Early Cretaceous Birdsong Sandstone of Western Australia. Records of the Western Australian Museum, **18**: 263–276.

Cruickshank, A.R.I., Small, P.G., and Taylor, M.A. 1991. Dorsal

nostrils and hydrodynamically driven underwater olfaction in plesiosaurs. Nature, **352**: 62–64. doi:10.1038/352062a0.

de Blainville, M.H. 1835. Description de quelques espèces de reptiles de la Californie precédée de l'analyse d'un système général d'herpétologie et d'amphibiologie. Nouvelles Annales du Muséum d'Histoire Naturelle, Paris, **3**: 233–272.

Dromart, G., Garcia, J.-P., Picard, S., Atrops, F., Lecuyer, C., and Sheppard, S.M.F. 2003. Ice age at the Middle–Late Jurassic transition? Earth and Planetary Science Letters, **213**: 205–220. doi:10.1016/S0012-821X(03)00287-5.

Druckenmiller, P.S. 2002. Osteology of a new plesiosaur from the Lower Cretaceous (Albian) Thermopolis Shale of Montana. Journal of Vertebrate Paleontology, **22**: 29–42. doi:10.1671/0272-4634(2002)022[0029:OOANPF]2.0.CO;2.

Druckenmiller, P.S. 2006. Early Cretaceous plesiosaurs (Sauropterygia: Plesiosauria) from northern Alberta: paleoenvironmental and systematic implications. Ph. D. thesis, University of Calgary, Calgary, Alta.

Druckenmiller, P.S., and Russell, A. 2006. A phylogeny of Plesiosauria (Sauropterygia) with emphasis on the systematic status of *Leptocleidus*, Andrews 1922. Journal of Vertebrate Paleontology, **26**: 57A.

Fraas, E. 1910. Plesiosaurier aus dem oberen Lias von Holzmaden. Palaeontographica, **57**: 105–140.

Gasparini, Z. 1997. A new pliosaur from the Bajocian of the Neuquen Basin, Argentina. Palaeontology, **40**: 135–147.

Gaudry, A. 1878. Sur un grand reptile fossile (l'*Eurysaurus raincourti*). Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris, **86**: 1031–1033.

Godefroit, P. 1994. *Simolestes keileni* sp. nov., un pliosaure (Plesiosauria, Reptilia) du Bajocien Supérieur du Lorraine (France). Bulletin de l'Académie Lorraine des Sciences, **33**: 77–95.

Grossmann, F. 2007. The taxonomic and phylogenetic position of the Plesiosauroidea from the Lower Jurassic Posidonia Shale of south-west Germany. Palaeontology, **50**: 545–564. doi:10.1111/j.1475-4983.2007.00654.x.

Hallam, A. 1993. Jurassic climates as inferred from the sedimentary and fossil record. Philosophical Transactions of the Royal Society (of London), Series B, **341**: 287–296.

Kear, B.P. 2003. Cretaceous marine reptiles of Australia: a review of taxonomy and distribution. Cretaceous Research, **24**: 277–303. doi:10.1016/S0195-6671(03)00046-6.

Kear, B.P., Schroeder, N.I., and Lee, M.S.Y. 2006. An archaic crested plesiosaur in opal from the Lower Cretaceous high-latitude deposits of Australia. Biology Letters, **2**: 615–619. doi:10.1098/rsbl.2006.0504.

Knight, W.C. 1898. Some new Jurassic vertebrates from Wyoming. American Journal of Science, **4**(5): 378–381.

Kuhn, O. 1961. Die Familien der rezenten und fossilen Amphibien und Reptilien. Verlagshaus Meisenbach, Bamberg, Germany.

Lydekker, R. 1889. Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History). Part II. British Museum (Natural History), London.

Nicholls, E.L. 1976. The oldest known North American occurrence of the Plesiosauria (Reptilia: Sauropterygia) from the Liassic (Lower Jurassic) Fernie Group, Alberta, Canada. Canadian Journal of Earth Sciences, **13**: 185–188.

Noè, L.F. 2001. A taxonomic and functional study of the Callovian (Middle Jurassic) Plesiosauroidea (Reptilia, Sauropterygia). Ph.D. thesis, University of Derby, Derby, UK.

O'Keefe, F.R. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia: Sauropterygia). Acta Zoologica Fennica, **213**: 1–63.

O'Keefe, F.R. 2002. The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria (Reptilia: Sauropterygia). Paleobiology, **28**: 101–112. doi:10.1666/0094-8373(2002) 028<0101:TEOPAP>2.0.CO;2.

O'Keefe, F.R. 2004*a*. Preliminary description and phylogenetic position of a new plesiosaur (Reptilia: Sauropterygia) from the Toarcian of Holzmaden, Germany. Journal of Paleontology, **78**: 973–988. doi:10.1666/0022-3360(2004)078<0973:PDAPPO>2.0.CO;2.

O'Keefe, F.R. 2004*b*. On the cranial anatomy of the polycotylid plesiosaurs, including new material of *Polycotylus latipinnis*, Cope, from Alabama. Journal of Vertebrate Paleontology, **24**: 326–340. doi:10.1671/1944.

O'Keefe, F.R., and Wahl, W., Jr. 2003*a*. Current taxonomic status of the plesiosaur *Pantosaurus striatus* from the Upper Jurassic Sundance Formation, Wyoming. Paludicola, **4**: 37–46.

O'Keefe, F.R., and Wahl, W., Jr. 2003*b*. Preliminary report on the osteology and relationships of a new aberrant cryptocleidoid plesiosaur from the Sundance Formation, Wyoming. Paludicola, **4**: 48–68.

Owen, R. 1838. A description of Viscount Cole's specimen of *Plesiosaurus macrocephalus* (Conybeare). Proceedings of the Geological Society (of London), **2**: 663–667.

Owen, R. 1860. On the orders of fossil and recent Reptilia, and their distributions in time. Report of the British Association for the Advancement of Science, 29, pp. 153–166.

Owen, R. 1865. A monograph on the fossil Reptilia of the Liassic formations. Part I, Sauropterygia. Palaeontographical Society, Monograph 17, pp. 1–40.

Persson, P.O. 1963. A revision of the classification of the Plesiosauria with a synopsis of the stratigraphical and geographical distribution of the group. Lunds Universitets Arsskrift N.F., 59, pp. 1–60.

Rich, T.H., Gangloff, R.A., and Hammer, W.R. 1997. Polar dinosaurs. *In* Encyclopedia of dinosaurs. *Edited by* P.J. Currie and K. Padian. Academic Press, San Diego, Calif., pp. 562–573.

Rieppel, O. 2000. Sauropterygia I. Encyclopedia of Paleoherpetology, Part 12A. Verlag Dr. Friedrich Pfeil, Munich, Germany.

Rieppel, O., Sander, P.M., and Storrs, G.W. 2002. The skull of the pistosaur *Augustasaurus* from the Middle Triassic of northwestern Nevada. Journal of Vertebrate Paleontology, **22**: 577–592. doi:10.1671/0272-4634(2002)022[0577:TSOTPA]2.0.CO;2.

Russell, D.A. 1967. Cretaceous vertebrates from the Anderson River, N.W.T. Canadian Journal of Earth Sciences, **4**: 21–38.

Russell, D.A. 1990. Mesozoic vertebrates of Arctic Canada. *In* Canada's missing dimension: science and history in the Canadian Arctic Islands, *Edited by* C.R. Harington. Canadian Museum of Nature, Ottawa, Ont., Vol. 1, pp. 81–90.

Russell, D.A. 1993. Jurassic marine reptiles from Cape Grassy, Melville Island, Arctic Canada. Geological Survey of Canada, Bulletin, 450, pp. 195–201.

Sato, T. 2003. Description of plesiosaurs (Reptilia: Sauropterygia) from the Bearpaw Formation (Campanian–Maastrichtian) and a phylogenetic analysis of the Elasmosauridae. Ph.D. thesis, University of Calgary, Calgary, Alta.

Sato, T. 2005. A new polycotylid plesiosaur (Reptilia: Sauropterygia) from the Upper Cretaceous Bearpaw Formation in Saskatchewan, Canada. Journal of Paleontology, **79**: 969–980. doi:10.1666/0022-3360(2005)079[0969:ANPPRS]2.0.CO;2.

Sato, T., and Wu, X.-c. 2005. Plesiosaurs (Reptilia: Sauropterygia) from the Canadian Arctic: a preliminary report on their systematics and biostratigraphy. Journal of Vertebrate Paleontology, **25**: 109A–110A.

Schroeder, N. 1998. A review of Order Plesiosauria, and the description of a new, opalised pliosauroid, *Leptocleidus demoscyl-*

lus, from the Early Cretaceous of Coober Pedy, South Australia. M.S. thesis, Monash University, Victoria, Australia.

Scotese, C.R. 2002. Plate tectonic maps and continental drift animations by C.R. Scotese, Paleomap Project, http://scotese.com (last accessed December 2007.

Seeley, H.G. 1874. Note on some of the generic modifications of the plesiosaurian pectoral arch. Quarterly Journal of the Geological Society (of London), **30**: 436–449.

Smith, A. 2006. Cranial anatomy and systematics of Lower Jurassic plesiosaurs—new information from the National Museum of Ireland. Journal of Vertebrate Paleontology, **26**: 126A. doi:10.1671/0272-4634(2006)26[331:ANBTBF]2.0.CO;2.

Storrs, G.W. 1991. Anatomy and relationship of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. Bulletin of the Peabody Museum of Natural History, 44, pp. 1–151.

Storrs, G.W. 1997. Morphological and taxonomic clarification of the genus *Plesiosaurus*. *In* Ancient marine reptiles. *Edited by* J.M. Callaway and E.L. Nicholls. Academic Press, San Diego, Calif., pp. 145–190.

Storrs, G.W., and Taylor, M.A. 1996. Cranial anatomy of a new plesiosaur genus from the lowermost Lias (Rhaetian–Hettangian) of Street, Somerset, England. Journal of Vertebrate Paleontology, **16**: 403–420.

Stutchbury, S. 1846. Description of a new species of *Plesiosaurus*, in the Museum of the Bristol Institution. Quarterly Journal of Geological Society (of London), **2**: 411–417.

Sues, H.-D. 1987. Postcranial skeleton of *Pistosaurus* and interrelationships of the Sauropterygia (Diapsida). Zoological Journal of the Linnean Society, **90**: 109–131.

Swinton, W.E. 1930a. Preliminary account of a new genus and species of plesiosaur. Annals and Magazine of Natural History, **10**: 206–209.

Swinton, W.E. 1930b. A new plesiosaur from Warwickshire. Natural History Magazine, **2**: 271–275.

Tarduno, J.A., Brinkman, D.B., Renne, P.R., Cottrell, R.D., Scher, H., and Castillo, P. 1998. Evidence for extreme climate warmth from Late Cretaceous Arctic vertebrates. Science, **282**: 2241–2243. doi:10.1126/science.282.5397.2241.

Tarlo, L.B. 1960. A review of Upper Jurassic pliosaurs. Bulletin of the British Museum (Natural History), Geology, **14**: 147–189.

Tate, R., and Blake, J.F. 1876. The Yorkshire Lias. Van Voost, London, UK., pp. 25–252.

Taylor, M.A. 1992a. Taxonomy and taphonomy of *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) or the Yorkshire coast. Proceedings of the Yorkshire Geological Society, **49**(1): 49–55

Taylor, M.A. 1992b. Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. Philosophical Transactions of the Royal Society (of London), Series B Biological Sciences, **335**: 247–280. doi:10.1098/rstb.1992.0022.

Taylor, M.A., and Cruickshank, A.R.I. 1993. Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria). Philosophical Transactions of the Royal Society (of London), Series B, **341**: 399–418.

Watson, D.M.S. 1911. A plesiosaurian pectoral girdle from the Lower Lias. Manchester Memoirs, 15, pp. 1–7.

Weems, R.E., and Blodgett, R.B. 1996. The pliosaurid *Megalneusaurus*: a newly recognized occurrence in the Upper Jurassic Naknek Formation of the Alaska Peninsula. US. Geological Survey, Bulletin 2152, pp. 169–176.

White, T.E. 1940. Holotype of *Plesiosaurus longirostris* Blake and classification of the plesiosaurs. Journal of Paleontology, **14**: 451–467.

Williston, S.W. 1903. North American plesiosaurs, Part I. Field Columbian Museum, Publication 73, Geological Series 2, pp. 1–77.

Worsley, D., and Heintz, N. 1976. The stratigraphical significance of a marine vertebrate fauna of Rhaetian age, Kong Karls Land. Arbok – Norsk Polarinstitutt, 1976, pp. 69–81.

Zhang, Y. 1985. A new plesiosaur from Middle Jurassic of Sichuan Basin. Vertebrata PalAsiatica, **23**: 235–240.

Appendix

Table A1 appears on the following page.

Table A1. Measurements of CMN 40729 (in mm).

Skull, tip of snout to posterior end of quadrate condyle (deformed original length on left)	*455* (463)
Skull, tip of snout to posterior end of occipital condyle	393
Skull, tip of snout to anterior edge of orbit	189 (r, l)
Skull, longitudinal diameter of orbit	78 (r)
Skull, longitudinal diameter of supratemporal fenestra	125 (r)
Mandible, maximum length	496 (r), 512 (l)
Mandible, maximum width at cotylus (deformed original width)	*285* (292)
Mandible, length of symphysis	96
Mandible, maximum width of symphysis at 6th dentary tooth (deformed original width)	*82* (87)
Mandible, tip of coronoid process to anterior tip	328 (r)
Mandible, tip of coronoid process to center of cotylus	127 (r)
Cervical centrum A, L/H/W	25/37/43
Cervical centrum B, L/H/W	25/37/44
Cervical centrum C, L/H/W	25/37/45
Cervical centrum D, L/H/W	26/38/49
Cervical centrum E, L/H/W	28/40/48
Cervical centrum F, L/H/W	29/41/50
Cervical centrum G, L/H/W	*30/43/53*
Humerus (r), L/W	334/179
Radius (r), L/W	84/80
Ulna (r), L/W	73/80

Note: Italics indicate estimates. l, left; r, right; H, height; L, length; W, width.