A new species of mosasaur (Squamata: Mosasauridae) from the Pierre Shale (lower Campanian) of Manitoba

Robin S. Cuthbertson, Jordan C. Mallon, Nicolas E. Campione, and Robert B. Holmes

Abstract: *Plioplatecarpus nichollsae*, sp. nov., from the lower Campanian (Pembina Member, Pierre Shale Formation) is diagnosed by the following: a thickened ventral rim of the external naris, a short supratemporal fenestra, a frontal shield with well-developed posterolateral lappets that overlap the parietal dorsally, proximal rib shafts with an approximately circular (but not inflated) cross section, a scapula shaped as in other *Plioplatecarpus* species but approximately the same size (not larger) than the coracoid, and a moderately large parietal foramen that reaches the frontoparietal suture but does not invade the frontal. The last two characters require that the diagnosis of the genus *Plioplatecarpus* be emended. With other *Plioplatecarpus* species, *P. nichollsae* shares a robust humerus with a distal expansion at least as great as the total length of the bone, a rectangular preorbital frontal shield, a "peg and socket" postorbitofrontal–jugal articulation, a transversely directed ectopterygoid process of the pterygoid, a large, robust quadrate with a distinct eminence on the posterior surface of its shaft, an unossified gap in the ventral wall of the basioccipital, and at least 11 pygal vertebrae. *P. nichollsae* also shares primitive features with *Platecarpus*, as well as features apparently intermediate between *Platecarpus* and *Plioplatecarpus*. Revision of the genus *Platecarpus*, currently hypothesized to be both paraphyletic and polyphyletic, as well as a better understanding of the early Campanian mosasaur fauna from the Morden area, are necessary before the phylogenetic significance of some of these characters, and therefore the relationships of *Plioplatecarpus nichollsae*, can be fully resolved.

Résumé : La diagnose de *Plioplatecarpus nichollsae*, sp. nov., du Campanien inférieur (membre de Pembina, Formation du Pierre Shale) repose sur les caractères suivants : la bordure ventrale épaissie du naris externe, une courte fenêtre supratemporale, une plaque frontale présentant des barbes postérolatérales bien développées qui chevauchent dorsalement le pariétal, des diaphyses des côtes proximales de profil approximativement circulaire (mais non renflé), une scapula dont la forme est semblable à celle d'autres espèces de *Plioplatecarpus*, mais de dimensions environ semblables (et non supérieures) à celle de la coracoïde, et un foramen pariétal modérément grand qui rejoint la suture frontopariétale mais ne déborde pas sur le frontal. Ces deux derniers caractères nécessitent l'émendation de la diagnose du genre *Plioplatecarpus*. *P. nichollsae* partage avec d'autres *Plioplatecarpus* un humérus robuste présentant une expansion distale au moins aussi longue que la longueur totale de l'os, une plaque frontale préorbitale rectangulaire, une articulation postorbitofrontale-jugale en forme de « pivot et douille », un processus ectoptérygoïde du ptérygoïde orienté transversalement, un grand carré robuste présentant une éminence distincte sur la surface postérieure de sa diaphyse, une ouverture non ossifiée dans le mur ventral du basioccipital et au moins 11 vertèbres pygales. *P. nichollsae* présente également des caractères primitifs communs avec Platecarpus, ainsi que des caractères vraisemblablement intermédiaires entre *Platecarpus* et *Plioplatecarpus*. Une révision du genre Platecarpus, qui est, à l'heure actuelle, hypothétiquement présumé paraphylétique et polyphylétique, ainsi qu'une meilleure compréhension de la faune mosasaure du Campanien précoce de la région de Morden, sont nécessaires à l'établissement de la signification phylogénétique de certains de ces caractères et donc, des liens reliant *Plioplatecarpus nichollsae* à d'autres groupes.

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Introduction

Traditionally, the family Mosasauridae has been considered to comprise three subfamilies: Mosasaurinae, Plioplatecarpinae, and Tylosaurinae (Russell 1967). Although recent phylogenetic analyses (Bell 1997; Bell and Polcyn 2005) have required a reassessment of both their membership and interrelationships, all subfamilies remain meaningful taxonomic units within the family. The Plioplatecarpinae, minus *Prognathodon* and *Plesiotylosaurus* (both currently considered to be members of the Mosasaurinae), and its sister taxon Tylosaurinae, are grouped with the more basal taxa *Tethysaurus*, *Russellosaurus*, and *Yaguarasaurus* under the parafamily Russellosaurina (Polcyn and Bell 2005).

The plioplatecarpine mosasaur *Platecarpus* (Cope 1869–1870) is known from many specimens collected from Coniacian through Campanian-aged deposits, primarily from the Western Interior Seaway of North America (Russell 1967). Several species have been described (Cope 1874; Russell 1967), but some may be invalid (Everhart 2005). Recent phylogenetic analyses (Bell 1997; Bell and Polcyn 2005) have suggested that the genus is both paraphyletic and polyphyletic.

Plioplatecarpus, the sister group of *Platecarpus* (Bell 1997; Bell and Polcyn 2005), was first described from fossils found in deposits of late Maastrichtian age in Europe (Dollo 1882, 1890, 1905). It has since been recognized from mid-Campanian (Everhart and Bussen 2001) to late Maastrichtian (Russell 1967) deposits of North America. To date, the taxon has been reported from the Bearpaw Formation of Saskatchewan (Tokaryk 1993; Holmes 1996), the Saint Mary River Formation of Alberta (Holmes et al. 1999), the Pierre Shale of North Dakota (Hoganson et al. 1999), South Dakota (Russell 1967), and Kansas (Everhart and Bussen 2001), the Demopolis Chalk Formation of Alabama (Burnham 1991) and Mississippi (M.J. Everhart, personal communication, 2005), the Navesink Formation of New Jersey (Cope 1869–1870), and the Mason River Formation of the Northwest Territories (Holmes 1996).

In her survey of the Pembina fauna of southern Manitoba, Nicholls (1988) recognized the presence of two plioplatecarpine mosasaurs: *Platecarpus tympaniticus* and *Platecarpus somenensis*. The latter, identified on the basis of tooth morphology (Thévenin 1896), was described as having a large parietal foramen extending to the frontoparietal suture, much as figured in *Platecarpus coryphaeus* (Baur 1892). However, a more recent assessment (Cuthbertson 2004) of the multitude of isolated elements from the same deposits suggested the presence of one or more additional plioplatecarpines closely comparable to *Plioplatecarpus*, although the evidence is also consistent with the presence of a taxon morphologically intermediate between *Platecarpus* and *Plioplatecarpus*. Unfortunately, the disarticulated and disassociated condition of the material made it impossible to discriminate between these two possibilities.

In July of 1934, C.M. Sternberg of the National Museums of Canada (now the Canadian Museum of Nature) collected two partial, semi-articulated mosasaur skeletons from the Pembina Member of the Pierre Shale Formation of southwest Manitoba, near the town of Morden. These specimens (CMN field numbers 1-1934 and 2-1934) were the first mosasaurs from Manitoba to be accessioned into a museum collection.

Fig. 1. Pierre Shale quarry sites in the proximity of Morden, Manitoba. Small map on the left represents, from left to right, the provinces of Alberta, Saskatchewan, and Manitoba. Arrow marks quarry #13, the site nearest the discovery location of CMN 52261. Redrawn from Nicholls (1988).
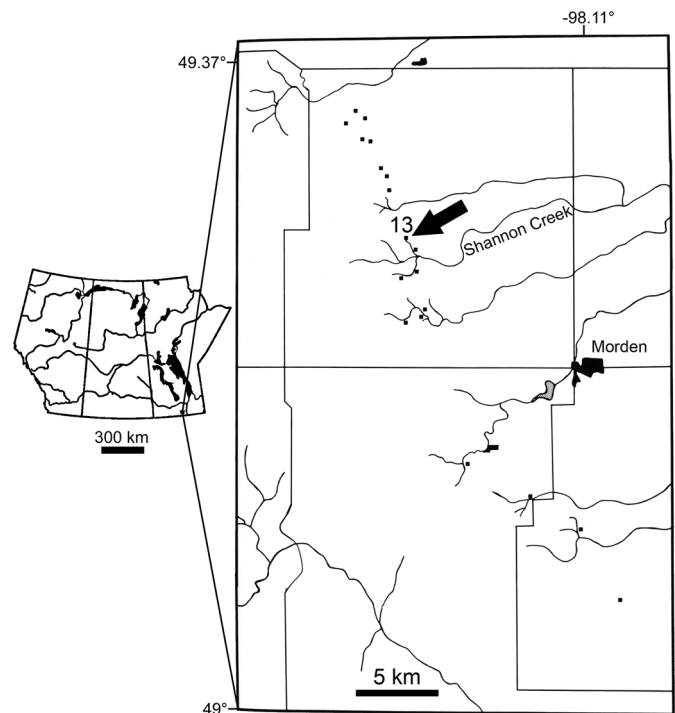
Preliminary announcements of their discovery were made within the year (Anonymous 1934; Kindle 1935). Shortly thereafter, the larger of the two skeletons (CMN field number 2-1934) was discarded from the museum collections because of its poor preservation. The specimens have since been mentioned only briefly in a summary of vertebrate fossils from Manitoba (Bardack 1968) and in Nicholls' (1988) review of the Pembina Member fauna, where they were referred to the genus *Platecarpus*. However, a phylogenetic analysis of mosasauroids that includes CMN field number 1-1934 (now designated CMN 52261) suggests that it is the sister taxon of *Plioplatecarpus primaevus*, and should be included in this genus.

Geology and type locality

The materials described here were collected from the Pembina Member of the Pierre Shale Formation—an upper Cretaceous marine unit that was deposited by the Western Interior Seaway (Nicholls 1988). The lower unit of the Pembina, known for its diverse marine fauna of fishes, birds, and reptiles (Bardack 1968; Martin and Stewart 1982; Nicholls 1988), is composed of black carbonaceous shales (Nicholls and Russell 1990) with numerous, nonfossiliferous bentonite seams occurring between beds. Selenite crystals commonly impregnate the fossils, reducing the quality of preservation (Martin and Stewart 1982; Nicholls and Russell 1990).

According to Sternberg's field notes, on file in the Sternberg Library of the CMN, CMN 52261 was collected from a bentonite mine ~19 km northwest of Morden, Manitoba at the

coordinates SE ¼, Section (Sec.) 31, Township (T) 3, Range (R) 6, west of the prime meridian (Fig. 1). It was found in a shale bed below the uppermost bentonite seam, which, according to Sternberg, is part of the lower lithologic unit of the Pembina Member (lower Campanian) of the Pierre Shale Formation (formerly Vermillion River Formation).

Although the collection site coordinates for CMN 52261 do not match any quarry locations that were mined between the mid-1970s and mid-1980s (see Nicholls 1988), it is very close to quarry 13 (NW ¼ Sec. 31, T 3, R 6). Potassium–Argon (K–Ar) dating of the uppermost bentonite seam in quarry number 13 gave an age of 81 (±3) million years (C. Roddick, personal communication in Nicholls 1988). Although we cannot be certain that this bentonite bed is the same as that of Sternberg's quarry, the close geographic proximity strongly suggests that we can accept this date for CMN 52261.

Materials and methods

CMN 52261 was removed from the matrix and mounted as a plaster panel at some point after being transported to the museum. Several vertebrae, assorted limb elements, and numerous ichthyodectiform fish vertebrae, preserved in association with the skeleton, are currently held at the CMN with the loose elements of CMN 52261.

At the beginning of our study, a portion of the skeleton containing the skull roof and braincase was freed from the plaster using a PaleoTools microjack (# 6) to expose its dorsal surface. The microjack was then used to clean off as much of the remaining matrix as possible without damaging the underlying bone. The specimen was photographed, and important features were illustrated.

Institutional abbreviations

CMN, Canadian Museum of Nature (formerly National Museums of Canada), Ottawa, Ontario, Canada; UNO, University of New Orleans, New Orleans, Louisiana, USA.

Systematic paleontology

Squamata Oppel 1811
Mosasauridae Gervais 1853
Russellosaurina Polcyn and Bell 2005
Plioplatecarpinae (Dollo 1884) Williston 1897
Plioplatecarpus (Dollo 1882)

DIAGNOSIS: Emended from Holmes 1996. Anterior rim of large parietal foramen approaching or traversing the frontoparietal suture. Frontal plate widens anterior to orbits, forming rectangular or quasi-rectangular shield between orbits and external nares. Frontal plate forms acute process anteriorly slotting into posterior margin of internarial bar of the premaxilla. Otosphenoidal crest of prootic absent. Delayed or incomplete ossification of basioccipital exposing canal for basilar artery ventrally. Postorbital process of postorbitofrontal extremely short, forming a "peg-and socket" joint with jugal. Quadrate large (maximum height ~19% of total skull length). Tympanic ala greatly expanded to form conch. Prominent swelling of variable shape on posterior surface of quadrate shaft. Reduced infrastapedial process. 35–42 vertebrae ante-

rior to chevron bearing caudal vertebrae. At least 10 pygal vertebrae. Scapula with posteriorly expanded blade. Large radius with approximately circular humeral facet. Radius with mediolaterally expanded distal end. A transversely oriented ectopterygoid process of the pterygoid.

Plioplatecarpus nichollsae sp. nov.

ETYMOLOGY: The specific epithet is in honour of the late Dr. Elizabeth L. Nicholls, who greatly contributed to our knowledge of Mesozoic marine reptiles from Canada and did much to characterize the Pembina Member fauna of southwestern Manitoba.

HOLOTYPE: CMN 52261. Semi-articulated skeleton, arranged as a panel mount, consisting of the premaxillae, maxillae, mandibles, basioccipital, frontoparietal skull table, postorbitofrontals, partial left squamosal, partial left supratemporal, quadrates, pterygoids, complete cervical vertebral series, twenty-three dorsal vertebrae, eleven pygal vertebrae, five caudal vertebrae, ribs, scapulae, coracoids, humeri, radii, ulnae, left carpals and metacarpals (plus additional podials), left manual phalanges, left ilium, ?left ischium, ?left femur, left tibia and fibula, left astragalus, left calcaneum, left fourth distal tarsal, and left pedal phalanges.

DIAGNOSIS: Plioplatecarpine mosasaur exhibiting the following autapomorphies: thickened ventral (maxillary) rim of the external naris, short supratemporal fenestra, frontal shield with well-developed posterolateral dorsal lappets that severely restricts the dorsal exposure of the parietal in the portion of the skull table anterior to the supratemporal fenestrae and resulting in a frontoparietal suture of distinctive shape, scapula of the same shape as in other *Plioplatecarpus* species but approximately the same size (not larger) than the coracoid, moderately large parietal foramen that reaches the frontoparietal suture but does not invade the frontal, and proximal rib shafts with an approximately circular (but not inflated) cross section. With other *Plioplatecarpus* species, it shares the following derived features: robust humerus with a distal expansion, at least as great as the total length of the bone, rectangular preorbital frontal shield, "peg and socket" postorbitofrontal–jugal articulation, transversely directed ectopterygoid process of the pterygoid, large, robust quadrate with a distinct eminence on the posterior surface of its shaft, unossified gap in the ventral wall of the basioccipital, and at least 11 pygal vertebrae. With *Platecarpus*, it shares the following primitive features: long premaxillo-maxillary suture terminating posteriorly immediately dorsal to the gap between the second and third maxillary teeth, ventral quadrate condyle with a transversely oval outline, pointed suprastapedial process, and anterodorsally directed ilium.

Description

In the following description, the sources of comparative data, unless otherwise stated, are as follows: *Platecarpus* (Russell 1967), *Plioplatecarpus houzeaui* and *Plioplatecarpus marshi* (Lingham-Soliar 1994), and *Plioplatecarpus primaevus* (Holmes 1996). Measurements of selected elements are provided (Table 1).

Table 1. Measurements of selected skeletal elements of *Plioplatecarpus nichollsae*.

Element measured	Left	Size (mm)	Right
Skull			
Maxilla length	235		
Dentary length	270		
Mandible (maximum length)		470 (approximate)	
Quadrate (maximum height)	82		
Posterior condyle (height/width) of			
Seventh cervical vertebra		36/44	
Fourth thoracic vertebra		38/47	
Posterior thoracic vertebra		57/59	
Immediately post-pygal caudal		61/58	
Pectoral girdle and limb			
Scapula width (maximum)	137		151
Scapula height (maximum)	113		106
Coracoid width (maximum)	134		140
Coracoid height (maximum)	—		119
Humerus length	106		101
Humerus width (distal)	98		101
Radius length	74		75
Radius width (distal)	63		71
Ulna length	68		65
Pelvic girdle and limb			
Ilium	110		—
Ischium	88		—
Femur length	89		—
Femur proximal width (maximum)	50		—
Femur distal width (maximum)	62		—
Tibia length	56		—
Fibula length	55		—

Skull

The skull is partially disarticulated, but the elements remain in close association (Figs. 2–5). Although the bone surface is of poor quality as a result of selenite infiltration, the basic anatomy can be established and most of the sutures traced with reasonable confidence.

Premaxilla

The premaxillae are coossified, as in all mosasaurs, except *Plioplatecarpus houzeaui* and *P. marshi*. The foramina for the facial branch of the trigeminal nerve are preserved on the dorsal surface. Two teeth and two alveoli are preserved on the premaxillae for a total of four teeth. There is no predental rostrum anterior to the procumbent teeth. Other than the area around the tooth bases, the ventral surface is not exposed.

Maxilla

The left maxilla is more complete than the right, which is missing its posterior end. The bone surface is badly damaged, but a few foramina are visible on its lateral aspect. Eight teeth and four alveoli are present in the left element. All of the teeth are posteromedially recurved. As in *Platecarpus*, the dorsal end of the premaxillo-maxillary suture terminates at the anterior extremity of the external naris directly above the gap between the second and third maxillary teeth. This is distinct from the condition in *Plioplatecarpus houzeaui*, in which the suture terminates above the midpoint of the second maxillary tooth, and *P. primaevus*, in which it terminates above the gap between the first and second maxillary teeth. Immediately posterior to this point, the narial margin of the maxilla is both thickened and convex mediolaterally (Fig. 6). The dorsal lamina is best preserved on the right maxilla. Its maximum height is 21% that of the total maxillary length, slightly less than the 25% seen in *Platecarpus ictericus* (Russell 1967, fig. 38) and all species of *Plioplatecarpus*, except *P. marshi*. The medial surfaces of the maxillae are not exposed.

Frontal

The interorbital width of the frontal shield is considerably greater than in *Plioplatecarpus primaevus* or *P. houzeaui*, and is more comparable to *Platecarpus* (e.g., Russell 1967, fig. 83). Although incomplete anteriorly, what remains of the preorbital region indicates that it was relatively rectangular in outline, as in *Plioplatecarpus*, rather than triangular, as in *Platecarpus* and most other mosasaurs. The frontal plate is divided by a straight, sagittal furrow. Although it may repre-

Fig. 2. *Plioplatecarpus nichollsae* CMN 52261. Photograph of disarticulated skeleton.

Fig. 3. *Plioplatecarpus nichollsae*. Drawing of disarticulated skeleton. bo, basioccipital; cav, caudal vertebra; cev, cervical vertebra; cor, coracoid; dv, dorsal vertebra; f, femur; fi, fibula; h, humerus; il, ilium; is, ischium; lj, lower jaw; mx, maxilla; op, opisthotic; pm, premaxilla; pt, pterygoid; pv, pygal vertebra; q, quadrate; r, radius; sc, scapula; t, tibia; u, ulna. Prefixes l and r designate left and right, respectively.
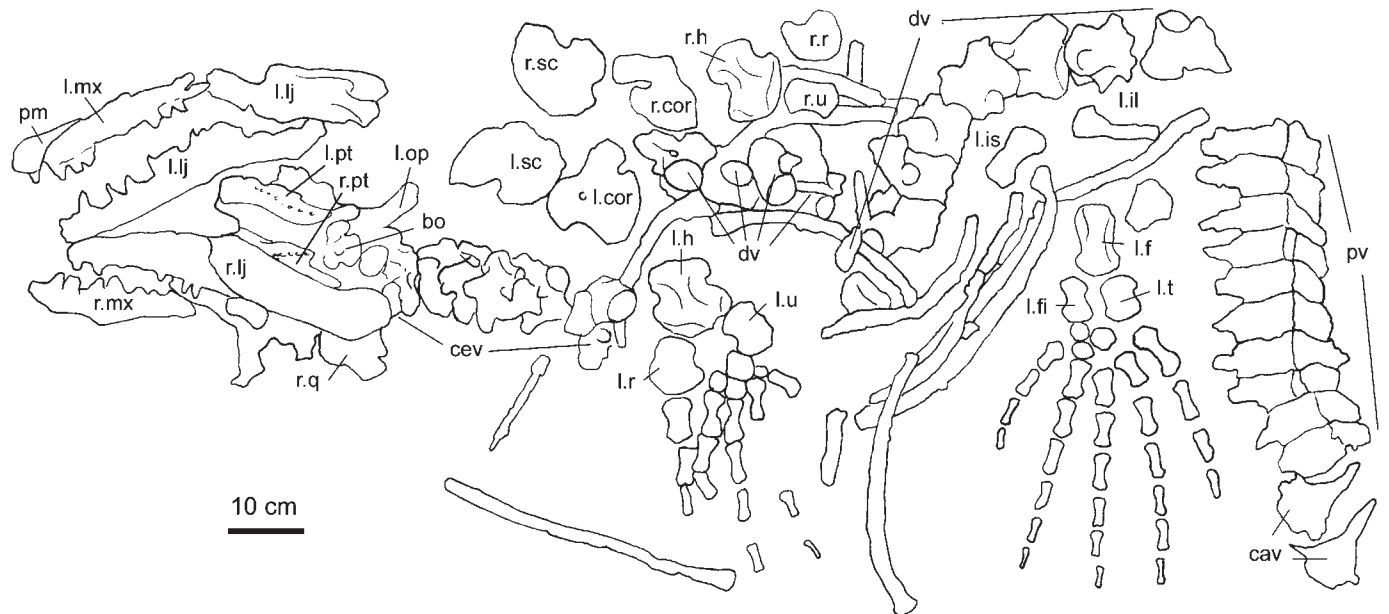

sent postmortem damage, it appears to be an open suture. A median ridge is present, but preservation of the bone surface is too poor to determine if it is as developed as in *Plioplatecarpus primaevus*. The frontoparietal suture extends laterally from the midline for about 18 mm, at which point it is deflected posteriorly. Immediately anterior to the rim of the upper temporal opening, it angles laterally, and can be traced to the posterolateral corner of the skull table (Figs. 4A, 5A). This highly distinctive suture shape approximates most closely the pattern seen in *Platecarpus tympaniticus* (Russell 1967, fig. 83).
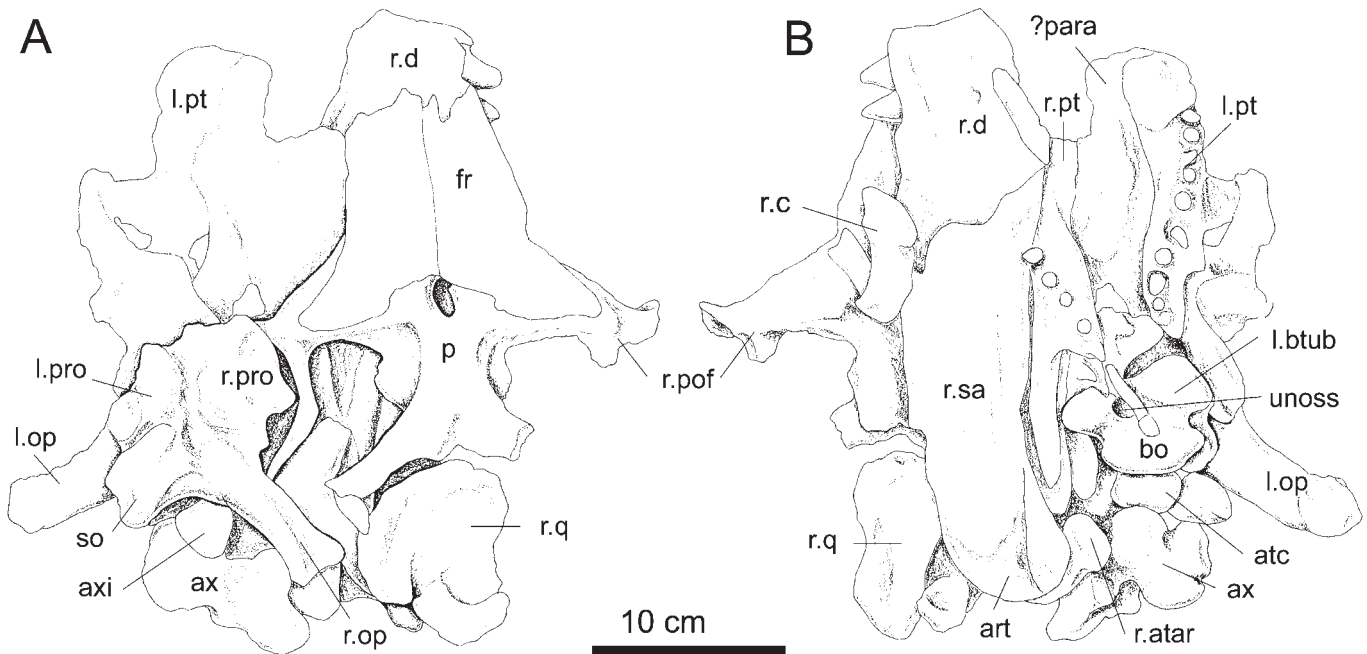
Parietal

As in *Platecarpus* and most other mosasaurs (Bell 1997, fig. 6), the exposure of the parietal on the posterodorsal surface of the skull table is severely limited by posterolateral lappets of the frontal. This is distinct from the condition in *Plioplatecarpus* where the parietal contributes significantly to the dorsal surface of the skull roof immediately anterior to the supratemporal fenestra (Lingham-Soliar 1994, fig. 17; Holmes 1996, fig. 3A). Although these variations in the superficial pattern of the frontoparietal suture may correlate with underlying differences in the structure of the articula-

Fig. 4. *Plioplatecarpus nichollsae* CMN 52261. Photograph of disarticulated skull. (A) dorsal and (B) ventral views.
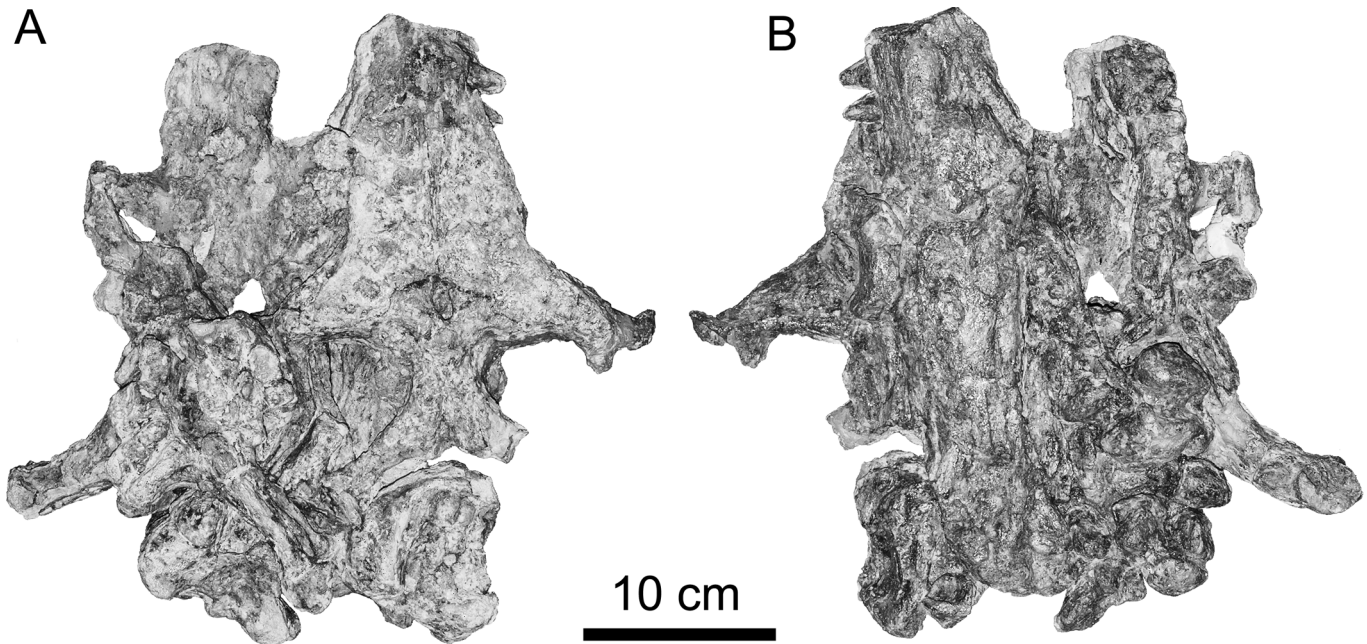
Fig. 5. *Plioplatecarpus nichollsae* CMN 52261. Drawing of disarticulated skull in (A) dorsal and (B) ventral views. art, articular; atar, atlas arch; atc, atlas centrum; ax, axis; bo, basioccipital; btub, basal tuber; c, coronoid; d, dentary; fr, frontal shield; op, opisthotic, p, parietal; para, parasphenoid; pof, postorbitofrontal; pro, prootic; pt, pterygoid; q, quadrate; sa, surangular; so, supraoccipital; unoss, unossified gap in the floor of the basioccipital.


tion between these two bones (see character 19 in Bell 1997), this suture in both CMN 52261 and all available specimens of *Plioplatecarpus primaevus* is firmly coossified, preventing confirmation of this hypothesis.

The oval parietal foramen is slightly larger than in *Platecarpus*, but is considerably smaller than in *Plioplatecarpus*. Unlike *Platecarpus*, in which the foramen is typically enclosed by the parietal (e.g., Russell 1967, fig. 83; Bell 1997, fig. 6B), the rim of the foramen extends anteriorly to the

frontoparietal suture. A small piece of bone that bore the right anterolateral portion of the foramen border is missing (Figs. 4A, 5A), but it is clear that although the beveled rim of the foramen makes a slight impression on the postero-median edge of the frontal, the foramen itself is contained completely within the parietal. The ventral surface of the skull roof is not accessible, making it impossible to establish the mutual relationships of the frontal, parietal, and foramen from that aspect. The suspensorial rami project more directly

Fig. 6. *Plioplatecarpus nichollsae* CMN 52261. Reconstruction of the skull in dorsal view. bo, basioccipital; fr, frontal shield; mx, maxilla; op, opisthotic; p, parietal; pf, parietal foramen; pm, premaxilla; pof, postorbitofrontal; so, supraoccipital; sq, squamosal; st, supratemporal.
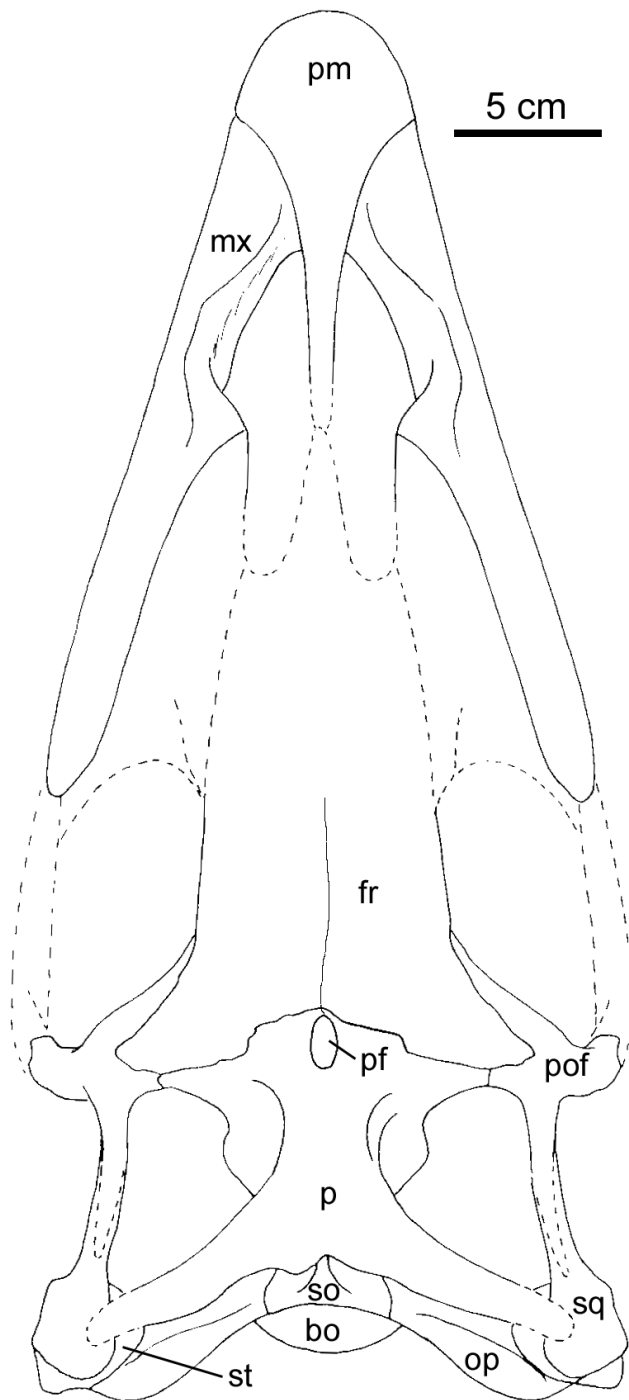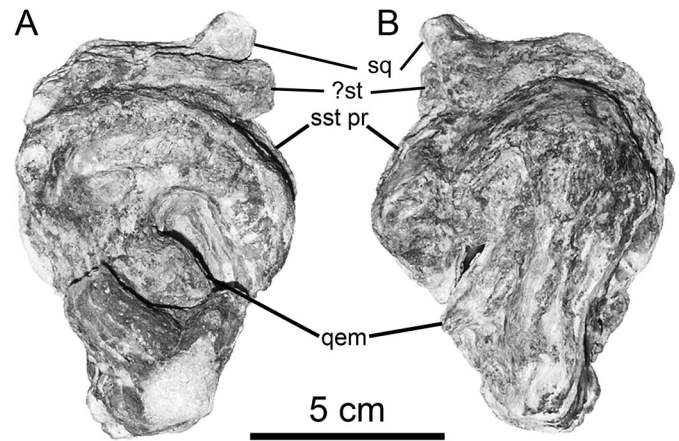

Fig. 7. *Plioplatecarpus nichollsae* CMN 52261. Left quadrate in (A) lateral and (B) medial views. qem, eminence on posterior surface of the quadrate shaft; sq, squamosal; sst pr, suprastapedial process; st, supratemporal.

projecting jugal process are obscured. The jugal process of the right postorbitofrontal bears a deep groove on its posteroventral surface that suggests the presence of a "peg and slot" joint with the dorsal process of the jugal, resembling that in *Plioplatecarpus* rather than the simple overlapping joint seen in *Platecarpus*. The dorsal surface of the left postorbitofrontal articulates with the frontal and parietal medially, although the sutures cannot be traced throughout their entire extent. An anterior process of the left postorbitofrontal attenuates along the lateral margin of the frontal to form the lateral margin of the posterolateral skull roof and the posterodorsal orbital rim.

Pterygoid

The sigmoidal body of the pterygoid bears at least twelve teeth, although the anterior end of the better exposed left element is broken, so it is possible that more teeth were present. This falls within the range recorded for *Platecarpus* (10–12) and between that of *Plioplatecarpus houzeaui* (11) and *P. primaevus* (13). The tooth bases, circular in cross-section, are largest in the middle of the row, but decrease in size only slightly towards either end of the pterygoid. All are significantly smaller than the marginal teeth. The stout ectopterygoid process projects laterally at a right angle from the body of the pterygoid, as reconstructed in *P. primaevus* and *P. houzeaui*. This is in contrast to the condition in *Platecarpus*, in which the slender ectopterygoid process is directed anterolaterally at an acute angle. Posteriorly, the pterygoid divides into a short medial basisphenoid process and an elongate quadratic process, the details of which are obscured by the surrounding bones.

Quadrate

The quadrate (Fig. 7) is remarkably robust, as in *Plioplatecarpus*. Its maximum height is ~18% of the estimated total skull length. As in *Platecarpus* and *Plioplatecarpus*, the suprastapedial process is large, but unlike in *Halisaurus* (Holmes and Sues 2000), *Prognathodon* (Lingham-Soliar and Nolf 1989), and *Ectenosaurus* (R.H., personal observation), it does not articulate with the infrastapedial process. However, in contrast with *Plioplatecarpus*, in which the pro-

laterally than in either *Platecarpus* or *Plioplatecarpus*, resulting in a relatively short supratemporal fenestra (Fig. 6).

Postorbitofrontal

The slender squamosal process of the left postorbitofrontal is virtually complete, but is twisted laterally at its distal tip. Much of the medial and posterior surfaces of the ventrally

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cess is parallel sided with a blunt termination, the process of CMN 52261 tapers to a point distally, much as in *Platecarpus*. The ventral part of the tympanic ala, preserved on the left quadrate, indicates the presence of a deep conch-like intratympanic cavity, like that in other species of *Plioplatecarpus*. The posterior face of the quadrate shaft possesses a swelling that is larger than the incipient swelling reported in some specimens of *Platecarpus* (Russell 1967; Lingham-Soliar 1994; Holmes 1996). In size and shape, this eminence falls well within the range of variation exhibited by other species of *Plioplatecarpus*. The morphology of the stapedial pit is obscured by poor preservation. The ventral condyle is in the form of a transverse oval as in *Platecarpus*, and not "quasi-triangular," as described in *Plioplatecarpus* (Holmes 1996; Bell 1997). The posterior portion of the left squamosal and another bone, possibly a fragment of the left supratemporal, adhere to the dorsal surface of the quadrate (Fig. 7).

Braincase

The braincase (Figs. 4B, 5B) is essentially complete, but surface preservation is poor and much of the finer detail has been lost. The basioccipital and basal tubera are exposed in ventral view. As in other mosasaurs, the robust basioccipital condyle is crescent-shaped. It is slightly distorted and lacks the right dorsolateral margin that would have articulated with the exoccipital. The floor of the medullary cavity is obscured by matrix, as is the median canal for the basilar arteries. Nevertheless, it is clear that, as in *Plioplatecarpus*, a deep irregular opening is visible in the ventral wall of the braincase between the basal tubera (Figs. 4B, 5B). The short, robust basal tubera project laterally and slightly ventrally. The basisphenoid has been lost.

The left paroccipital process has been displaced slightly relative to the basioccipital. Although the left prootic and opisthotic–exoccipital are present, the suture separating these elements is not visible. A shallow stapedial sulcus is present on the posteroventral surface of the opisthotic–exoccipital, following the long axis of the paroccipital process. The proximal end of the stapedial sulcus is poorly preserved, and the precise position of the fenestra ovalis cannot be determined.

The distal end of the left paroccipital process flares dorsoventrally, with the supratemporal forming its anterior face and the opisthotic–exoccipital the posterior face. The supratemporal exhibits a distinct anteroventrally directed squamosal facet, but its anterodorsal articulation with the prootic and opisthotic–exoccipital is unclear.

The underside of the skull block preserves the braincase elements in anterior view (Figs. 4B, 5B). The sagittal crest of a badly damaged and incomplete supraoccipital is partially preserved. Other than its anterolateral contact with the prootic, no details are visible. The left prootic is more complete than the right. The dorsal portion of the left prootic, forming the lateral half of the otic capsule, is mediolaterally thickened and thins ventrally to its approximate mid-height. Its anteroventral basisphenoid process and the basisphenoid have been lost.

Lower jaws

The slender lower jaws are exposed only in lateral view (Figs. 2–5). They are most similar to those of *Plioplatecarpus*. The dentary bears nine teeth and three alveoli. The teeth are similar in size and shape to those of the maxilla. Those in the posterior part of the dentary curve medially toward their tips. A few foramina are present on the lateral aspect of the dentary.

Most of the sutures are obscured by poor surface preservation. However, the intramandibular joint is clearly delineated, as is a small fenestra located midway up the suture. This likely marks the intersection of the dentary, splenial, angular, and surangular on the lateral surface of the lower jaw. The dentary–splenial contact is faintly visible as well. On the posterior end of the left half of the mandible, the poorly preserved surangular and prearticular can be identified on the lateral and medial surfaces, respectively, of the glenoid-bearing articular. The dorsal edge of the surangular ("surangular coronoid buttress") is incomplete in both jaws, but appears to have been straight and horizontal. The retroarticular process is moderately reflected, with its upper surface facing dorsomedially at an angle of ~45° to the parasagittal plane.

The coronoid resembles that of *Platecarpus* and *Plioplatecarpus* in possessing only a slight dorsal curvature, a rudimentary posterior wing, and lacking a posteromedial process. The medial wing is not exposed.

Dentition

Most of the teeth are missing from both upper and lower jaws, and those remaining are in poor condition. However, one isolated tooth shows that distinct facets or fluting are absent, they are not inflated, and that although carinae are well developed, serrations are absent (see Bell 1997, characters 85–89).
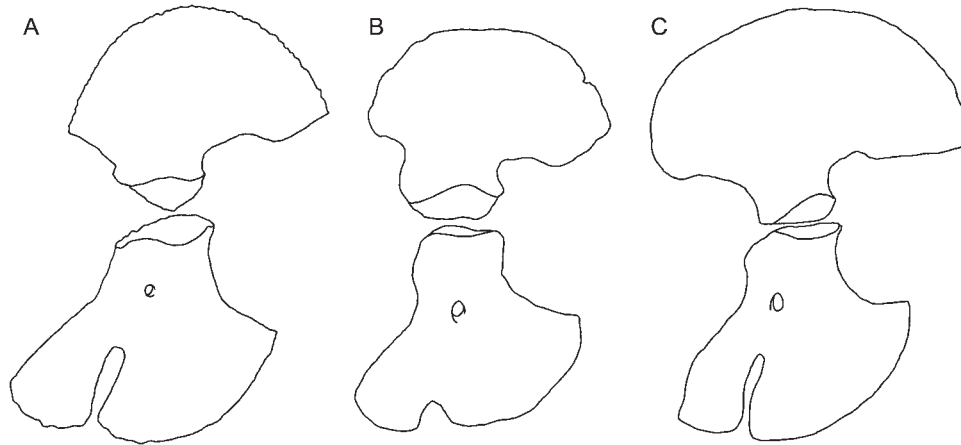
Vertebral column

The vertebral column of CMN 52261 is poorly preserved, and many of the fine details have been lost. The only segments of the column preserved in continuous articulation are the third to seventh cervical vertebrae (the axis and one atlas arch are preserved in association with the skull), five anterior dorsal vertebrae, seven posterior dorsal vertebrae, and 10 pygal vertebrae (Figs. 2, 3). Two proximal caudal vertebrae are preserved immediately posterior to the pygal series. Additional isolated vertebrae not incorporated in the panel mount, include 11 dorsal vertebrae (for a total of 30 presacral vertebrae), one pygal vertebra, and three caudal vertebrae. Zygosphenes and zygantra are lacking from all vertebrae.

Cervical vertebrae

The poorly preserved right atlas neural arch arises directly anterior to the axis, but the atlas is otherwise concealed by the surrounding bones. The axis bears a typical hatchet-shaped neural spine, "slightly flared" posteriorly, as in *Plioplatecarpus primaevus* (Holmes 1996, fig. 9A), and retains a prominent, rounded, dorsally flattened odontoid process (atlas intercentrum of Holmes 1996). All cervical vertebrae possess hypapophyseal facets on the ventral aspect of their centra. The hypapophyses have been lost. The distal facet on the axial synapophysis is horizontally oval in outline. These facets become longer and more diagonal in more posterior cervical vertebrae, and by the seventh cervical form a long, curved surface extending from the posterodorsal corner of the lateral surface of the

Fig. 8. *Plioplatecarpus nichollsae* CMN 52261. Lateral view of the left scapulocoracoid of (A) *Platecarpus tympaniticus* (modified from Russell 1967); (B) *Plioplatecarpus nichollsae*; and (C) *Plioplatecarpus primaevus* (modified from Holmes 1996). Scaled to the same coracoid height.

centrum anteroventrally almost to its anteroventral edge. The vertebral condyles are moderately dorsoventrally compressed, particularly toward the anterior end of the series, and each shows a horizontally oval outline with a slight excavation on the dorsal margin. Anteriorly, the neural spines are directed posterodorsally. Posteriorly, the neural spines become more erect and laterally compressed.

Dorsal vertebrae

The first dorsal vertebra is disarticulated, but lies close to the posterior end of the cervical series. It bears a keel-like tubercle on the ventral surface of its centrum that resembles that on the last (seventh) cervical vertebra of *Plioplatecarpus*. The dorsal vertebrae are characterized by ventral, elongate synapophyses that extend the full height of the centrum. In more posterior dorsal vertebrae, the less massive synapophyses bear smaller, vertically oval facets. The zygapophyses are well developed in the anterior vertebrae. In more posterior vertebrae, they become reduced in size, but remain functional throughout the preserved series. The neural spines are tall and anteroposteriorly broad, as in *Plioplatecarpus* and *Platecarpus*. The outline of the central condyles ranges from horizontally oval in the anterior dorsals, to "heart-shaped" in the mid-dorsals, to quasi-circular in the posteriormost dorsals.

Pygal vertebrae

A series of 10 pygal vertebrae are preserved in dorsal view. Their neural arches have been sheared off at their bases and displaced to the right, exposing their left sides. An additional isolated pygal vertebra was not included in the panel mount. A count of 11 pygal vertebrae falls within the range of 10 (Holmes 1996) and 12 (Holmes et al. 1999) reported for *Plioplatecarpus*, but much higher than the five pygal vertebrae reported in *Platecarpus* (Russell 1967). The roughly pear-shaped centrum condyles resemble those of *Plioplatecarpus primaevus* (Holmes 1996, fig. 12) in outline. The bases of the broad transverse processes span the entire length of the vertebral centrum. In all cases, the processes have been broken near their bases and lost, making it impossible to compare their orientation with that of other plioplatecarpines.

Caudal vertebrae

The caudal vertebrae are identified by the presence of haemapophyseal facets. Two disarticulated proximal caudal vertebrae are preserved immediately posterior to the pygal series. In both cases, the centrum condyles are slightly higher than wide, but otherwise resemble those of the pygal vertebrae in outline. An additional three caudal vertebrae that are not included in the panel mount are slightly smaller, but bear well-developed transverse processes, so must have originated from the proximal part of the tail.

Ribs

Approximately 16 broken, disarticulated ribs, only four of which bear holocephalous heads, are preserved (Figs. 2, 3). A sulcus is present on the medial surface of each rib directly beneath the head. Proximally, the ribs are circular in cross-section, but become mediolaterally flattened at their distal ends. This is in sharp contrast to the distally rounded or "inflated" condition seen in other North American *Plioplatecarpus* species (Burnham 1991; Holmes 1996) and the uniformly flattened condition seen in *Platecarpus*.

Appendicular skeleton

Pectoral girdle and forelimb

The scapula (Figs. 2, 3, 8) is similar to that of *Plioplatecarpus* in possessing a relatively narrow embayment on the ventral surface of the posterior blade, and an anterior blade margin that extends dorsally and near-perpendicular to the scapular neck, although it does not extend as far anteriorly as in *Plioplatecarpus primaevus*. However, as in *Platecarpus*, the scapular blade tapers dorsally at its posterior limit, and the overall sizes of the scapula and coracoid are approximately the same (Russell 1967, fig. 44). This is in contrast to the condition in *Plioplatecarpus*, in which the scapula is distinctly larger than the coracoid.

The fan-shaped coracoid differs little from that of *Platecarpus* or *Plioplatecarpus*. The emargination at the anteroventral edge of the fan is deeply excavated. The smooth scapular facet gives no evidence of an interdigitating sutural contact with the scapula.

The preserved elements of the pectoral limb (Figs. 2, 3, 9)

Fig. 9. *Plioplatecarpus nichollsae* CMN 52261. Reconstructed paddles. (A) pectoral (B) pelvic. as, astragalus; cm, medial centrale; dc, distal carpal; dt, distal tarsal; f, femur; fi, fibula; h, humerus; i, intermedium; r, radius; ti, tibia; u, ulna.
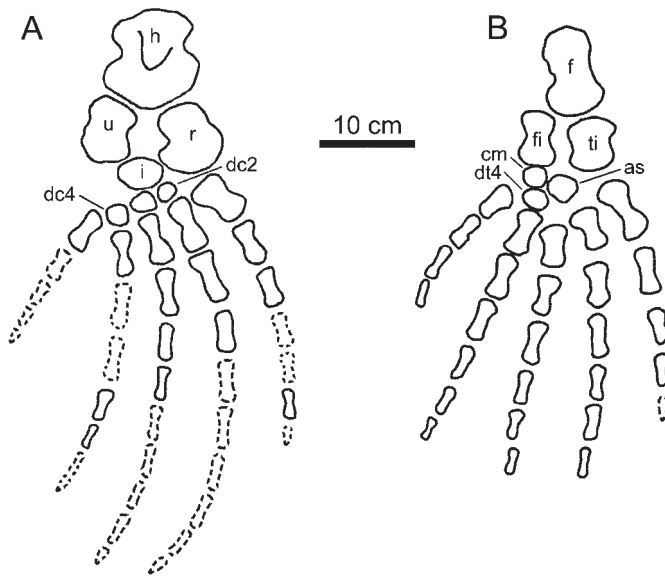
are closely comparable to those of *Plioplatecarpus* (Lingham-Soliar 1994; Burnham 1991; Tokaryk 1993; Holmes et al. 1999). The humerus is a stout and robust element with a broad, gently domed glenoid condyle, poorly defined post-glenoid process, and a massive ventral pectoral crest separate from the deltoid crest that is located on the anterior edge of the bone. In contrast with *Plioplatecarpus*, in which the width of the distal humeral expansion exceeds the length of the humerus, these two dimensions are equal. Although it bears a well-developed entepicondyle, a distinct ectepicondyle is lacking.

Russell (1967) described the overall morphology of the radius as identical in *Platecarpus* and *Plioplatecarpus*. However, the radius of *Plioplatecarpus primaevus* bears a distinct keel on its anterior surface that is not present in *Platecarpus*. Although gypsum infiltration and swelling has damaged the anterior border of the radius in CMN 52261, the overall morphology appears closer to that of *Plioplatecarpus primaevus*. In contrast with *P. primaevus*, in which the ulna is slightly longer than the radius, the ulna and radius of CMN 52261 are of equal length. Otherwise, the ulna is similar to that of *P. primaevus*.

Four carpals are preserved. Based on their size, shape, and positions (Figs. 2, 3, 9A), these probably represent the intermedium, second, third, and fourth distal carpals. The putative intermedium is slightly larger than the others. A fifth carpal, often seen in mature *Platecarpus* and *Plioplatecarpus* (Russell 1967; Caldwell 1996; Holmes et al. 1999), could not be identified.

The hourglass-shaped metacarpals and phalanges do not differ from those of other members of the Russellosaurina. The first metacarpal, although large, is not expanded as in mosasaurines (Bell 1997, fig. 8). Several isolated metapodials and (or) phalanges are stored separately from the panel mount, but no specific associations with the articulated portion of the forelimb could be established.

Pelvic girdle and hind limb

One ilium and one ischium are present (Figs. 2, 3). Preservation is too poor to determine whether they are from the left or right side, but their proximity to the proximal end of the left femur makes the former more likely. If this is correct, the iliac blade curves anterodorsally from the acetabulum, as in *Platecarpus*, but in contrast to *Plioplatecarpus primaevas*, in which it curves posterodorsally. Otherwise, it is quite comparable to that of *Plioplatecarpus*. The ischium resembles that of *Plioplatecarpus* in general outline, in particular the small size and proximal position of the crest-like tubercle.

The left rear paddle (Figs. 2, 3, 9B) is remarkably undisturbed considering the generally disarticulated condition of the skeleton. This indicates the possibility that the positions of at least some of the elements were adjusted during preparation and mounting of the specimen. Nevertheless, the positions of the elements are plausible, and there is no evidence that the limb is a composite.

The hourglass-shaped left femur is preserved in dorsal view. Proximally, the hemispherical head is horizontally oval as in *Platecarpus*, and unlike the circular outline in *Plioplatecarpus primaevus*. A prominent internal trochanter is present on the anteroventral surface of the proximal head. The fourth trochanter appears to be relatively smaller than that of *Plioplatecarpus*, possibly the result of postmortem damage or incomplete preservation. The distal end of the femur is expanded horizontally to articulate with the tibia and fibula. The articular facets are irregularly ridged and grooved. The horizontally oval distal articular surface, as in plioplatecarpines generally (Russell 1967; R.H., personal observation) exhibits no clear separation between the tibial and fibular facets.

The entire limb distal to the femur appears to have rotated 180° before burial (or possibly during the mounting process), exposing the epipodials, tarsals, metatarsals, and pes in ventral view. The tibia is 64% the length of the femur. It is an especially robust bone, only slightly longer than wide, and bears a distinct flange on one side of the shaft. This flange is also present in *Plioplatecarpus primaevus*, but is described as occupying the posterior margin of the shaft (Holmes 1996). However, the occurrence of a similar flange on the anterior side of the shaft in *Clidastes*, *Mosasaurus*, and *Tylosaurus* (Russell 1967) suggests that the tibia of *P. primaevus* was incorrectly oriented in the original description. Selenite encrustation has damaged the anterior surface of the tibia of CMN 52261 and leaves in question the shape of this flange. Only a slight mid-shaft constriction is present in our specimen, which is more similar to the condition in *P. primaevus*, and contrasts with the more deeply emarginated mid-shaft of *Platecarpus*. Both proximal and distal heads are expanded, with the femoral facet being slightly wider dorsoventrally than the distal end. Both articular facets are roughened.

The hourglass-shaped fibula is about the same length as the tibia. The crural foramen, bordered by the tibia and fibula, is lenticular in outline, as in most other mosasaurs.

Three tarsal bones, here identified as the astragalus, calcaneum, and fourth distal tarsal, are present. The astragalus, located immediately adjacent to the tibia–fibula articulation, is the largest of the three. It does not exhibit the large groove for the perforating artery seen in *Platecarpus*, although this

may have been obscured by selenite-induced swelling. The calcaneum lies proximal to the similarly sized fourth distal tarsal, and together they are positioned just lateral to the astragalus.

Compared to most other mosasaurs, the podials are relatively short and stout. This results in a short and broad hind paddle (Fig. 9B). The first metatarsal is 35% longer than the average length of the others. As in the fore paddle of *Plioplatecarpus* (Holmes et al. 1999), the fifth metatarsal is hooked, and the fifth digit is divaricate. All digits appear complete except for the first, which appears to be missing the terminal phalanx, giving a complete phalangeal formula of 4-5-5-5-3. This is the same count reported for *Platecarpus*, although the pes has been figured with a formula of 5-5-5-4-3 (Russell 1967, fig. 62).

Phylogenetic analysis

To assess the phylogenetic relationships of CMN 52261, we began with the most recent comprehensive phylogenetic analysis of the Mosasauroidea (Bell, 1997; Bell and Polcyn 2005). We scored CMN 52261 and *Plioplatecarpus primaevus* (see Appendix A), and included these taxa in Bell and Polcyn's data matrix of 144 characters and 41 taxa (for a total of 43 taxa). The matrix was entered into MacClade 4.06 (Maddison and Maddison 2003) and analyzed using PAUP 4.0b10 (Swofford 2002). As in the original analysis (Bell and Polcyn 2005), all characters were treated as unordered and unweighted, and the DELTRAN option was used. The analysis produced nine most parsimonious trees with a length of 425 steps, a consistency index (CI) of 0.417, a homoplasy index (HI) of 0.584, a retention index (RI) of 0.764, and a rescaled consistency index (RC) of 0.318. A strict consensus tree (Fig. 10) shows CMN 52261 as the sister taxon to *P. primaevus*, and this clade forms a polytomy with Bell and Polcyn's "*Plioplatecarpus* AMNH sp.," and "*Plioplatecarpus* RMM sp.." All nine equally most parsimonious trees showed the sister-group relationship between *P. primaevus* and CMN 52261, although the relationships of the other two *Plioplatecarpus* are not as robust. "*Plioplatecarpus* RMM sp." plots either as a sister taxon to "*Plioplatecarpus* AMNH sp." or to the monophyletic group formed by CMN 52261 and *P. primaevus*. Otherwise, the topology of our strict consensus tree (Fig. 10) is the same as Bell and Polcyn's tree (Bell and Polcyn 2005, fig. 7).

Discussion

Based on our current understanding of mosasauroid interrelationships, (Bell 1997; Bell and Polcyn 2005), CMN 52261 forms a sister-group relationship with *Plioplatecarpus primaevus*, and this clade in turn either forms a sister-group relationship with "*Plioplatecarpus* RMM sp." or the clade ("*Plioplatecarpus* RMM sp." + "*Plioplatecarpus* AMNH sp."). Consequently, we include CMN 52261 within the genus *Plioplatecarpus* as a new species, *Plioplatecarpus nichollsae*. This new species shows two unique features: a thickened ventral rim of the naris and a short supratemporal fenestra.

Plioplatecarpus nichollsae shares several derived features with other *Plioplatecarpus* species, including a uniquely robust humerus, at least 11 pygal vertebrae, a prominent swelling

Fig. 10. Strict consensus tree of nine most parsimonious trees. Each tree has a tree length of 425 steps, a consistency index (CI) of 0.417, a homoplasy index (HI) of 0.584, a retention index (RI) of 0.764, and a rescaled consistency index (RC) of 0.318. Based on the data matrix of Bell and Polcyn (2005), with *Plioplatecarpus nichollsae* and *P. primaevus* included (Appendix A).
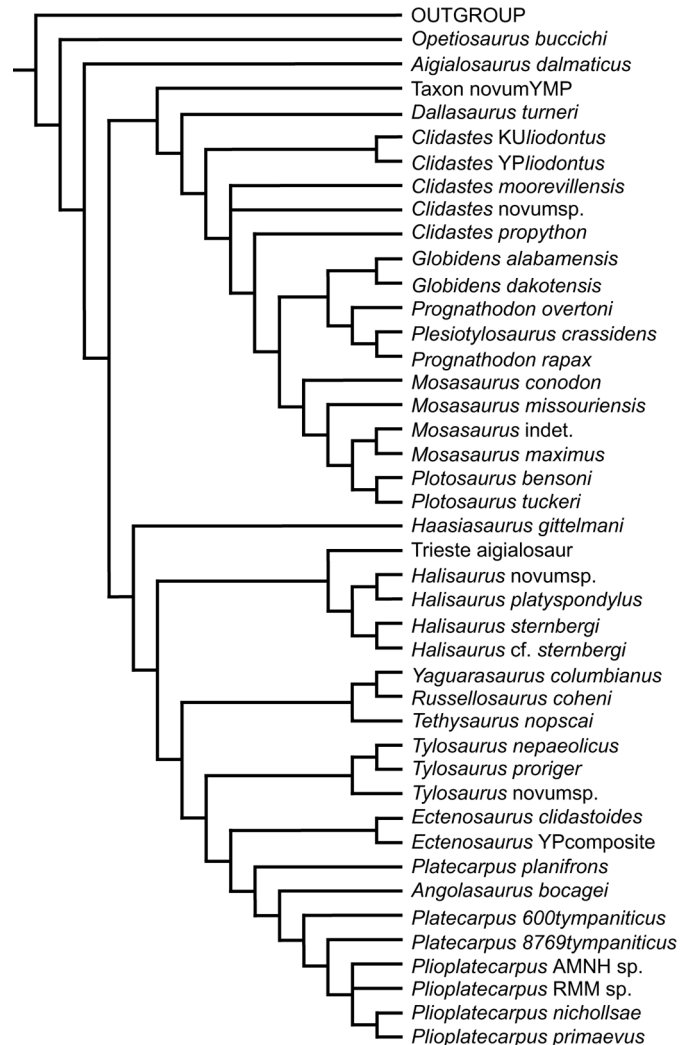
on the posterior surface of the quadrate shaft, a broad, rectangular frontal anterior to the orbits, a "peg and slot" articulation between the postorbitofrontal and jugal, a transversely oriented ectopterygoid process of the pterygoid, and an opening in the ventral surface of the basioccipital.

The presence of an opening, often of irregular shape and asymmetrical in position on the ventral surface of the basioccipital, has long been used to diagnose *Plioplatecarpus* (Dollo 1885). In all other mosasaurs including *Platecarpus*, the floor of the basioccipital between the basal tubera is completely ossified, and the median canal for the basilar artery is not exposed ventrally. Although these gaps have been referred to as "foramina" (e.g., Burnham 1991; Lingham-Soliar 1994), there is no evidence that they provided passage for blood vessels or nerves, and in particular should not be confused with the paired foramina in the basioccipital of *Plioplatecarpus houzeaui* (Lingham-Soliar 1994, fig. 21). The presence of a large opening has been reported in both *Plioplatecarpus*

Fig. 11. Skull tables of selected mosasaurs, delineating the frontoparietal suture. (A) *Platecarpus ictericus* (redrawn from Russell 1967); (B) *Plioplatecarpus primaevus* (redrawn from Holmes 1996); (C) *Plioplatecarpus nichollsae*. Drawn to the same width.
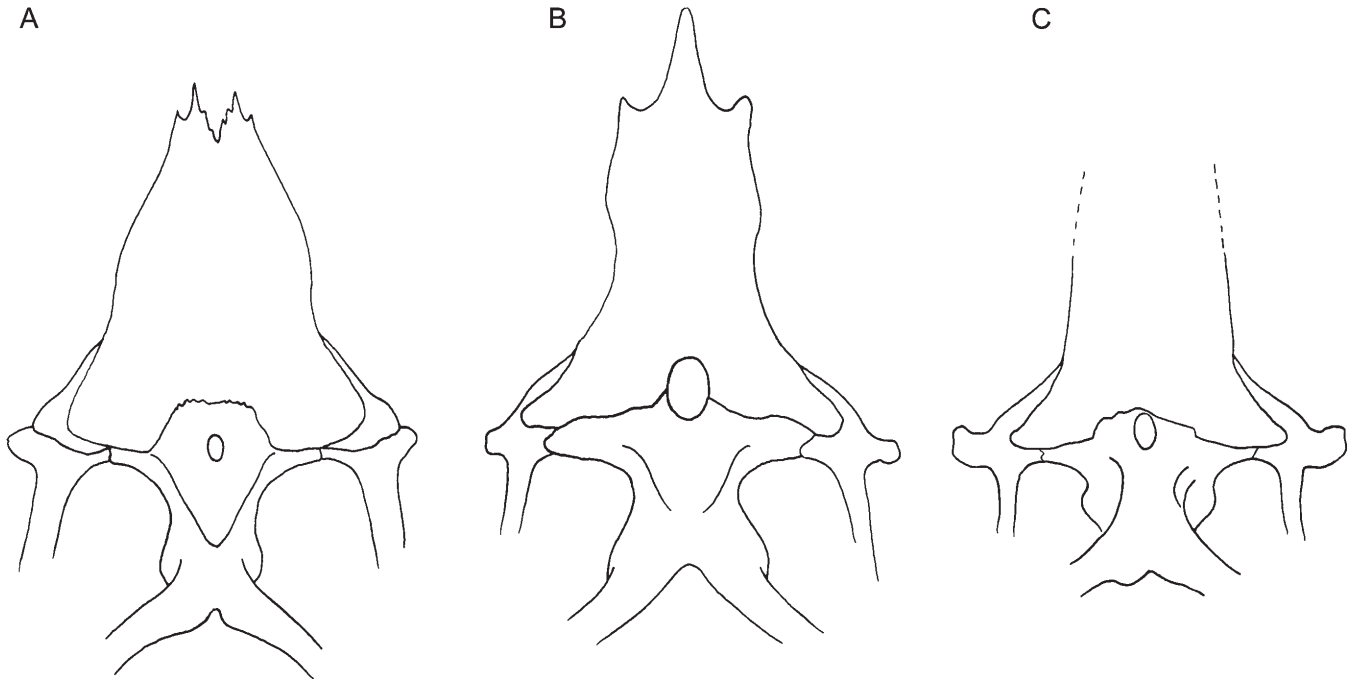
marshi (Dollo 1885) and *P. primaevus* (Holmes 1996). Smaller openings have been described in other specimens of *Plioplatecarpus*, UNO 8611-2 and a second unnumbered UNO specimen (Burnham 1991, fig. 13). *P. nichollsae* clearly shows a small opening comparable in size to that in the UNO specimens (Burnham 1991).

Plioplatecarpus nichollsae also shares a number of apparently primitive features with *Platecarpus*, including a frontal that forms almost all of the posterolateral portion of the skull table, a pointed rather than squared-off suprastapedial process, a long premaxillo-maxillary suture terminating dorsally immediately above the gap between the second and third maxillary teeth, a transversely oval ventral quadrate condyle, and probably an anterodorsally directed ilium.

Plioplatecarpus nichollsae also shows a number of characters that are, to a greater or lesser degree, intermediate in their development between *Platecarpus* and *Plioplatecarpus* as previously diagnosed (Holmes 1996). These include the shape and relative size of the scapula (Fig. 8), rib shafts that are proximally circular in cross section, and a relatively large parietal foramen that approaches, but does not actually excavate the frontal. The size of the parietal foramen and its relation to the frontoparietal suture has long been used to distinguish *Platecarpus* and *Plioplatecarpus* (Russell 1967). As in most mosasaurs, *Platecarpus* (Fig. 11A) possesses a modest sized foramen that is completely enclosed within the parietal (e.g., Russell 1967, fig. 83; Bell 1997, fig. 6B), although in a few skulls referred to *Platecarpus somenensis* (e.g., Nicholls 1988) and *P.* "*coryphaeus*" (Baur 1892), the foramen approaches, and may touch, the suture (Bell 1997). *Plioplatecarpus* (Fig. 11B) is derived in possessing a much larger parietal foramen, the anterior half of which is bordered by the frontal (Lingham-Soliar 1994; Holmes 1996). This difference does not reflect a change in position of the suture, as the posterior

rim of the foramen exhibits the same positional relationship to the posterolateral corners of the skull table and anterior rim of the supratemporal fenestra in both taxa (Fig. 11). Rather, the increased size of the foramen in *Plioplatecarpus* is the result of forward migration of its anterior border into the frontal.

The recognition of *Plioplatecarpus nichollsae* and the suite of characters that diagnoses it raise questions regarding the diagnoses of both *Plioplatecarpus* and *Platecarpus*. The unusually large parietal foramen (anteroposterior length equal to about one-half of the interorbial width), generally considered to be diagnostic of the former genus, is lacking, as is the presence of a scapula that is distinctly larger than the coracoid. In addition, the presence of a distinctive frontoparietal suture, shared with *Platecarpus*, suggests that the internal structure of this suture (Bell 1997, character 19) may be more primitive than other *Plioplatecarpus* species. The significance of this last feature is unclear. Bell and Polcyn (2005) score all of the *Platecarpus* and *Plioplatecarpus* in their analysis "0" for this character. Yet *Plioplatecarpus primaevus* does not appear to conform to any of the states described (see Bell 1997), and it has been recognized recently that *Platecarpus planifrons* scores "1" for this character (T. Konishi, personal communication, 2006). Although clarification of these issues will ultimately be necessary before the various species of *Platecarpus* and *Plioplatecarpus* can be accurately diagnosed, these present inconsistencies with regards to the structure of the frontoparietal suture do not appear to impinge on their phylogenetic relationships. We recoded the affected taxa to reflect their morphology with respect to this character, but this had no effect on the topology of the resulting tree. Emendation of the diagnosis of the genus *Plioplatecarpus* addresses the immediate issues related to the phylogenetic placement of *P. nichollsae*. Nevertheless,

the presence of several anatomical features that are apparently intermediate between *Platecarpus* and *Plioplatecarpus* as traditionally diagnosed indicates that more work needs to be done before the phylogenetic significance of these features can be fully assessed. We believe that one important factor contributing to the current uncertainty is the apparent paraphyly/polyphyly of *Platecarpus* (Bell and Polcyn 2005, fig. 7; Fig. 10 of this paper). A revision of the genus *Platecarpus* by T. Konishi (personal communication 2006) promises to clarify the issue. Another complicating factor is the uncertain significance of the remarkable morphological variability exhibited by the mosasaurs that have been collected from the Pierre Shale in the region surrounding Morden, Manitoba (Cuthbertson 2004). Further study of this material will be necessary to resolve these problems.

Acknowledgments

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Appendix A

Table A1. Character coding for *Plioplatecarpus nichollsae* and *P. primaevus* based on character analysis of Bell and Polcyn 2005.

	1	11	21	31
Plioplatecarpus nichollsae	0?1000?100	?11???1???	1111?110??	?0??50????
Plioplatecarpus primaevus	0?1000?100	?110111???	1113011001	0010500110
	41	51	61	71
Plioplatecarpus nichollsae	?002110?12	00100?0101	111????51?	2??0???0??
Plioplatecarpus primaevus	?002100112	0010?00101	111100351?	2210100000
	81	91	101	111
Plioplatecarpus nichollsae	0???00020?	??0?000001	1000?????0	??02111100
Plioplatecarpus primaevus	0100000201	000?000000	100001???0	??01111100
	121	131	141	
Plioplatecarpus nichollsae	20011?0121	?110010?11	11?0	
Plioplatecarpus primaevus	3001100121	?11001011?	1?30	