

A NEW GENUS OF ICHTHYOSAUR FROM THE LOWER CRETACEOUS OF WESTERN CANADA

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Abstract: A new fauna of Lower Cretaceous (Albian) ichthyosaurs, which includes at least one new genus and species, was recovered from deposits of the Loon River Formation at Hay River, Northwest Territories, Canada. All Cretaceous ichthyosaurs have been referred to a single genus, *Platypterygius*. The Loon River Formation material, however, does not satisfy the diagnosis for *Platypterygius*, and it is distinctive enough to warrant the erection of a new genus and species of ichthyosaur. *Maiaspondylus lindoei* gen. et sp. nov. is distinguished from other ichthyosaurs by an extensive overlapping contact of the jugal and the maxilla; marginal teeth

with smooth crowns, fluted cementum, lingual curvature and implantation in a dental groove; and humerus with isomorphic proximal and distal ends, featuring three distal articular facets in which the medial articular facet is smaller than the lateral facets. The holotype and referred material is described here, and the relationship of *Maiaspondylus* to other ophthalmosaurs is discussed.

Key words: Ichthyosauria, Cretaceous, *Maiaspondylus*, Ophthalmosauria, Western Interior Seaway, Loon River Formation.

ICHTHYOSAURS were a highly successful group of diapsid reptiles that evolved an obligatorily aquatic mode of life. They are found in rocks dating from the Early Triassic (Spathian) to the Late Cretaceous (Cenomanian) (Sander 2000; Arkhangelsky 2001; McGowan and Motani 2003). All post-Triassic ichthyosaurs are presumed to be monophyletic because they share certain key features such as the pattern of rib articulation, a tailbend, aulacodont tooth implantation, and no space between the radius and the ulna (Sander 2000). All Cretaceous ichthyosaurs are referred to a single genus, *Platypterygius* Huene, 1922, which is diagnosed by the presence of four bones in the epipodial row of the forefin: the lageniform, the radius, the ulna and the pisiform (Wade 1984); the intermedium never contacts the humerus. The geological range of *Platypterygius* extends from the Valanginian to the Upper Cenomanian, a span of 50 million years (Arkhangelsky 2001). This genus also has a wide geographical distribution, with specimens known from Europe, Russia, Australia, and both North and South America (Arkhangelsky 2001).

All ichthyosaur material from the Cretaceous of North America has been referred to the species *Platypterygius americanus* (Nace 1939; McGowan 1972). Diagnostic Cretaceous ichthyosaur material from North America included the type material described by Nace (1939), a complete skull described by Romer (1968) and the fore-

fins associated with this skull, described by McGowan (1972). All of these specimens are from the Graneros Formation of Wyoming, which is Albian in age (McGowan 1972). Vertebral centra and other undiagnostic material has been found at numerous sites in western North America (Merriam and Gilmore 1928; Shimada 1996; H. Bryant, pers. comm. 2002; S. Cumbaa, pers. comm. 2004).

Several ichthyosaur specimens were recovered from a locality on the Hay River, Northwest Territories, Canada in 1971. They were found in rocks belonging to the Loon River Formation, which was deposited as part of the Western Interior Seaway during the Middle Albian (Singh 1971). This formation is exclusively marine and is composed of black marine shales and limestones at the locality (Forey 1975). Other vertebrates found in association with the ichthyosaurs include holostean, aspidorhynchiform, ananogmiid and clupeomorph fishes (Forey 1975). Whereas one of the Hay River specimens satisfies the diagnosis of *Platypterygius*, the others exhibit a different pattern of mesopodial organization and, in our opinion, this warrants the recognition of a new genus and species of Cretaceous ichthyosaur.

Institutional abbreviation. UALVP, University of Alberta Laboratory for Vertebrate Palaeontology, Edmonton, Alberta, Canada.

MATERIAL

UALVP 45635 and 45639–45643 are preserved in three dimensions, are heavily permineralized, and presumably weathered out of a poorly consolidated shale. No mechanical preparation was necessary, other than applying fixative to broken specimens, because the specimens were found as isolated elements washed free of the surrounding matrix. UALVP 45635 and 45639–45641 represent an ontogenetic series: UALVP 45635 is a juvenile, UALVP 45640 is a slightly larger juvenile, and UALVP 45639 and 45641 are adults. Two embryos are preserved in association with the vertebrae of UALVP 45639 (Maxwell and Caldwell 2003). Specimens were coated in ammonium chloride prior to being photographed.

SYSTEMATIC PALAEOLOGY

ICHTHYOSAURIA de Blainville, 1835

OPHTHALMOSAURIA Motani, 1999a

Genus MAIASPONDYLUS gen. nov.

Derivation of name. Greek, *maia* ('good mother'), in reference to associated embryonic material, and *spondylus* ('vertebra'), in reference to the location of the embryos on the vertebral centra.

Type species. *Maiaspondylus lindoei* gen. et sp. nov., from the Albian of the Northwest Territories, Canada.

Diagnosis. As for the type and only known species.

Maiaspondylus lindoei sp. nov.

Plate 1; Text-figures 1–5, 6A

Derivation of name. Trivial name in honour of Al Lindoe, who collected the specimens.

Holotype. UALVP 45635, an incomplete, disarticulated individual preserved in three dimensions.

Paratypes. UALVP 45639, two embryos agglutinated to eight articulated vertebrae (adult); UALVP 45640, 14 articulated vertebrae (juvenile); UALVP 45641, 12 articulated vertebrae (adult); UALVP 45642, fragmentary snout including right and left maxil-

lae with teeth, partial premaxillae, right and left dentaries with teeth, possible left splenial; UALVP 45643, fragmentary snout including right maxilla, partial lacrimal, partial jugal, partial prefrontal.

Locality and horizon. A locality (60° 01' N, 116° 57' W) on the Hay River, Northwest Territories, Canada; Middle Albian (Singh 1971).

Diagnosis. Humerus equally expanded proximally and distally, bearing three distal articular facets; medial articular facet of the humerus smaller than lateral facets; teeth curving medially and firmly set in dental groove, crowns smooth, cementum bearing vertical striations, base quadrangular in cross-section; jugal extending over maxilla but not contacting premaxilla.

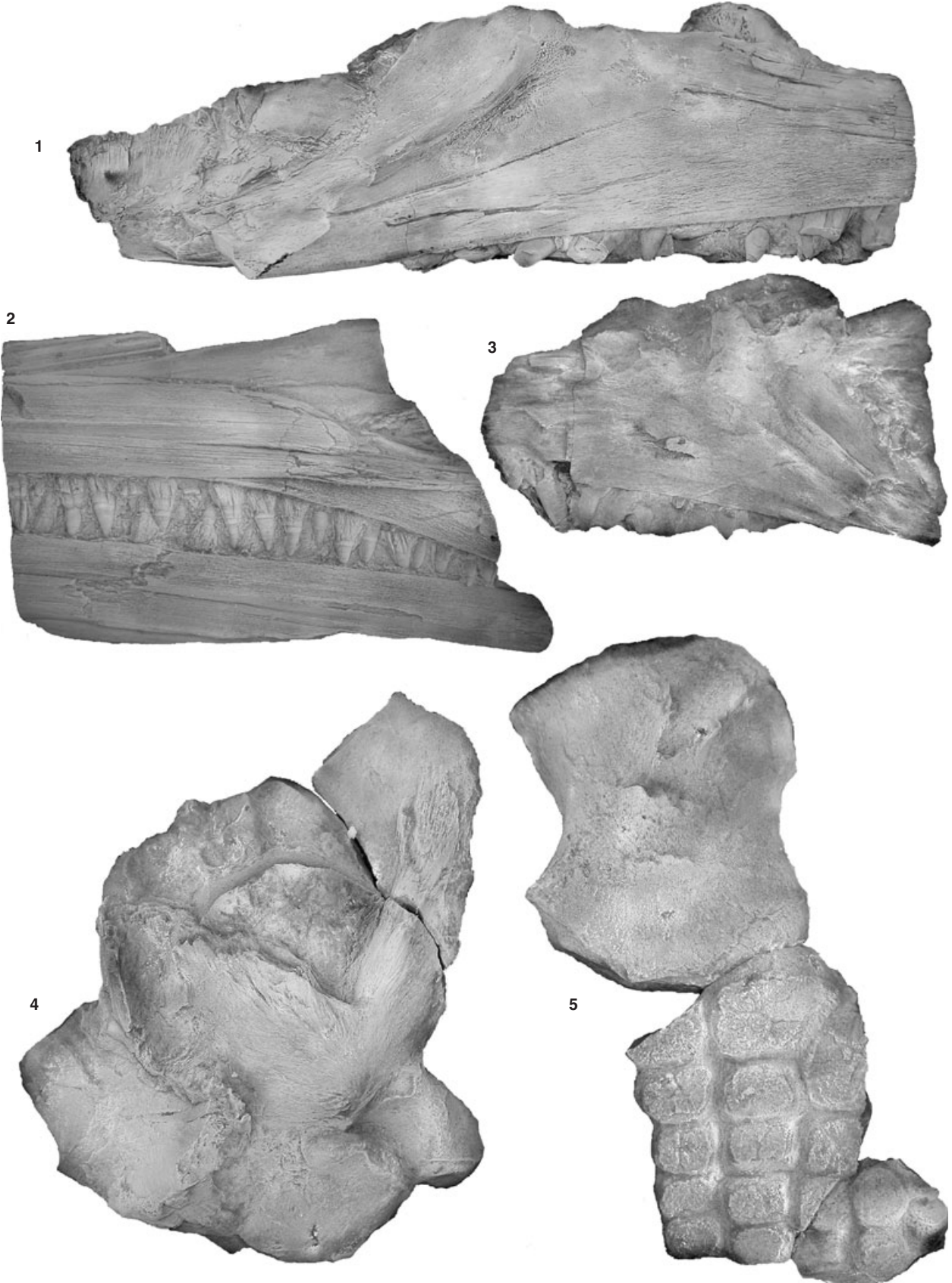
Description

Antorbital region. Overlying the entire preserved length of the premaxilla are the nasals, which are reduced anteriorly. Fragments of the nasals are preserved in UALVP 45643 (Pl. 1, fig. 1; Text-fig. 1C). They are plate-like bones that curve to form a semicircle when viewed in cross-section. Posteriorly, they widen and give rise to lateral processes that curve ventrally. The ventral surface is concave, but several long, thin bones with an anterior-posterior orientation have been preserved in this region, associated with a tooth. On the ventral surface of the projection of the right nasal is a triangular socket. This feature on the left nasal is obscured by broken bone, most likely a rib fragment, because the nasals have been compressed such that they overlap each other causing the left nasal to fracture (UALVP 45635).

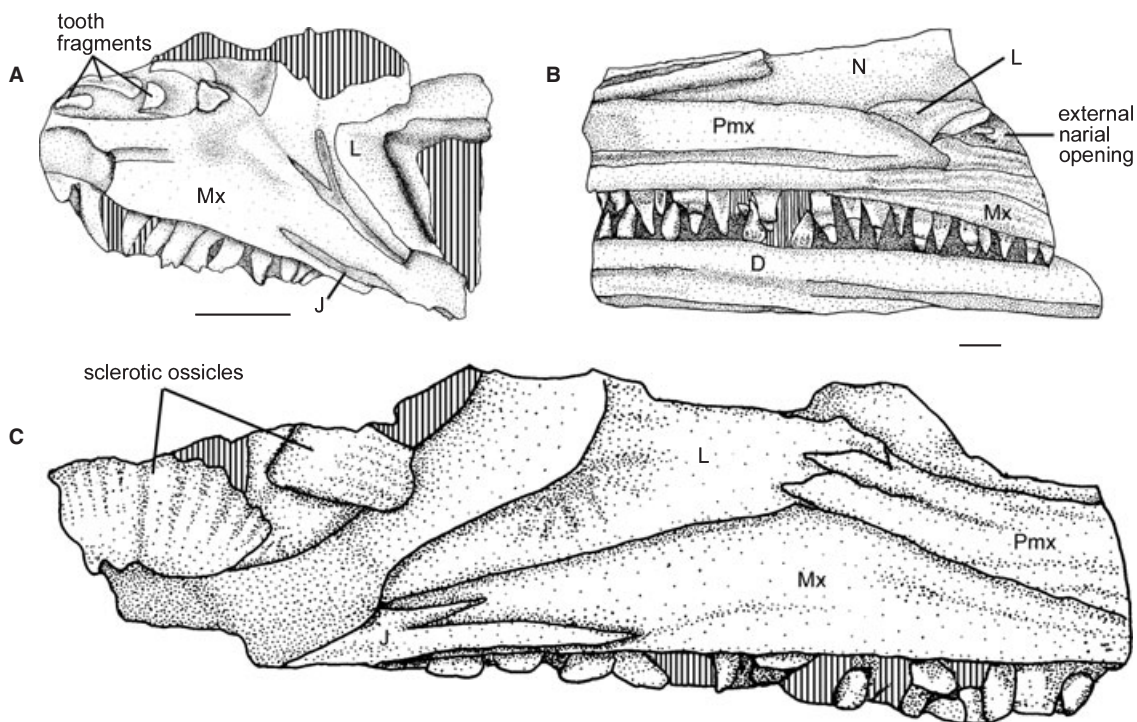
The premaxilla is wide and is grooved anteroposteriorly. Posteroventrally, it overlies the maxilla, excluding it from the lateral surface of the upper jaw. A wedge-shaped gap immediately posterior to the premaxilla and dorsal to the maxilla represents the external narial opening. The maxilla is a triangular, tooth-bearing element. It bears a dorsal projection, which is overlapped by the premaxilla-lacrimal contact in such a way as to be separated from the body of the maxilla in lateral view. The widest point of the maxilla lies slightly posterior and ventral to the premaxilla-lacrimal contact. The jugal is a thin sliver overlying the maxilla and extending anteriorly to tooth position 4 or 5 (Pl. 1, figs 1, 3; Text-fig. 1A, C). It curves ventral to the maxilla posteriorly, and makes contact with the lacrimal. The lacrimal forms a broad, concave plate posteriorly, and constitutes the anterior border of the orbit. A depression is located on its lower surface under the lip formed by the orbital margin. The lacrimal extends

EXPLANATION OF PLATE 1

Figs 1–5. *Maiaspondylus lindoei* gen. et sp. nov., Hay River, Northwest Territories, Canada; Loon River Formation. 1, UALVP 45643, right upper jaw fragment, lateral view; $\times 1$. 2, UALVP 45642, left upper jaw fragment, lateral view; $\times 0.75$. 3, UALVP 45635, left upper jaw fragment, lateral view; $\times 1.5$. 4, UALVP 45635, elements of the basicranium and the dorsal skull roof, dorsal view; $\times 1$. 5, UALVP 45635, left forefin, dorsal view; $\times 1$.



MAXWELL and CALDWELL: *Maiaspondylus*



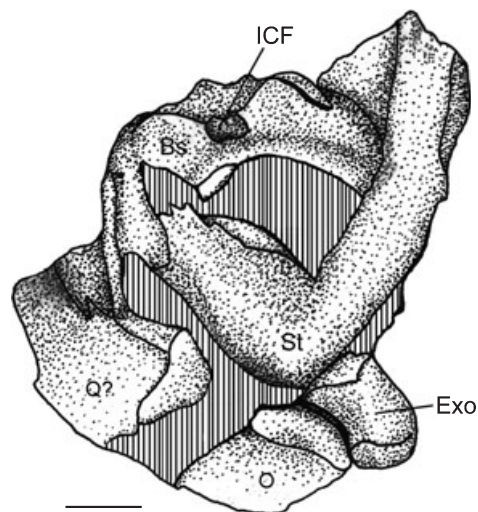
TEXT-FIG. 1. *Maiaspondylus lindoei* gen. et sp. nov., Hay River, Northwest Territories, Canada; Loon River Formation. Cranial fragments. A, UALVP 45635, upper jaw fragment. B, UALVP 45642, fragment of both upper and lower jaws. C, UALVP 45643, upper jaw fragment. Vertical lines represent damaged areas where bone structure is not visible. Abbreviations: D, dentary; J, jugal; L, lacrimal; Mx, maxilla; N, nasal; Pmx, premaxilla. Scale bars represent 10 mm.

anteriorly to the widest point of the maxilla, at which point it contacts the premaxilla (Pl. 1, fig. 1; Text-fig. 1C). The prefrontal underlies the lacrimal on the medial surface. Three sclerotic ossicles are preserved, but their morphology and relationships to each other are unclear because they are disarticulated and compressed.

Braincase and skull roof. Parts of the braincase and dorsal skull region are preserved in UALVP 45635 (Pl. 1, fig. 4; Text-fig. 2). The left supratemporal is partially preserved. It is convex in dorsal view and is V-shaped, with one side wider than the other. The exoccipitals are stout elements, curved medially, with triangular articulating facets at the exposed ends. The foramina are not visible, but there is some evidence that they are variable even within individuals (Maisch 1997). The opisthotic is incomplete; only the end bearing the squamosal facet is preserved.

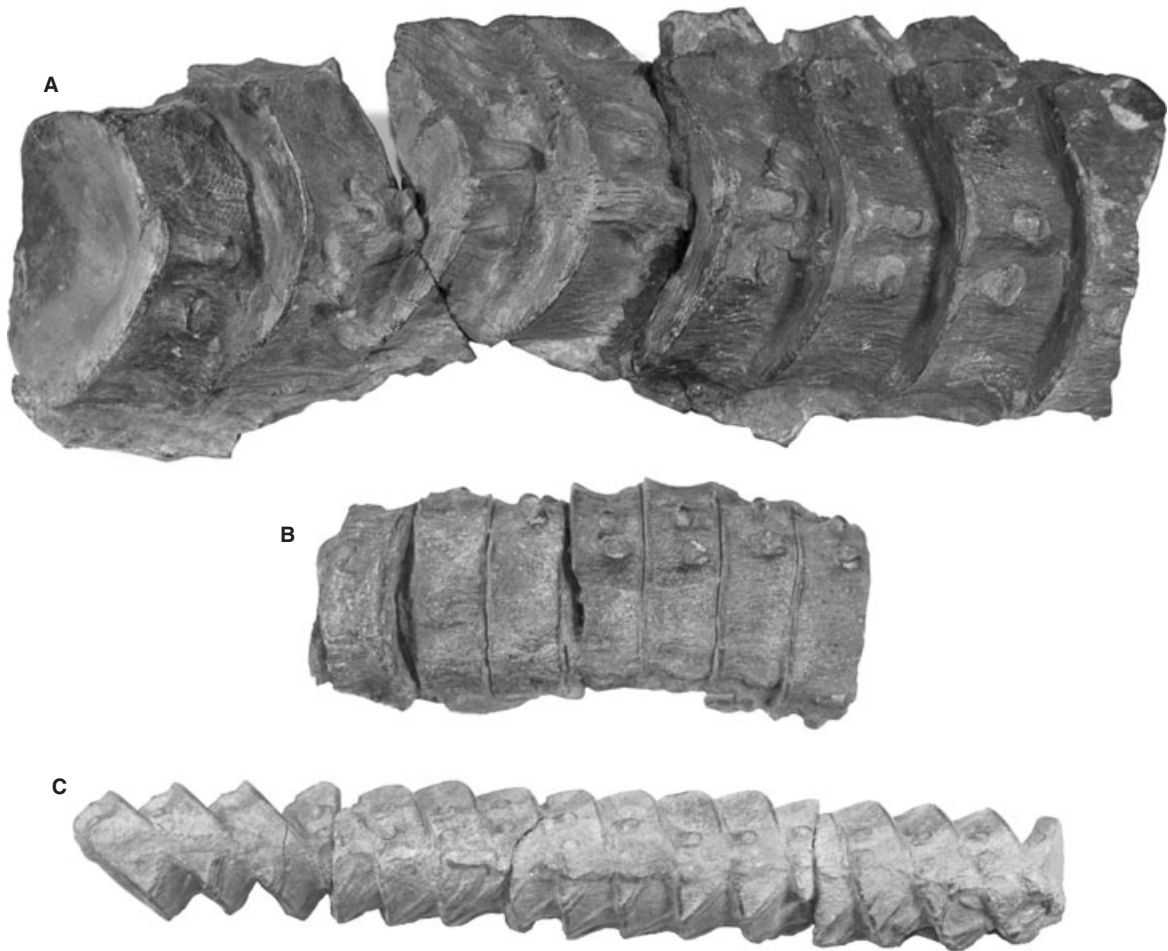
The basisphenoid has a flat ventral surface. It is oval in form, with the parasphenoid process forming a point anteriorly. The basiptyergoid processes extend laterally from the basisphenoid, and are above the dorsal surface. The internal carotid foramen is a round depression that is centred in the posterior half of the basisphenoid in ventral view. The area around the foramen on the dorsal surface is raised, and posterior to it the bone slopes upward almost vertically.

The dentary is grooved, and bears well-developed teeth, as in most other ichthyosaurs (Pl. 1, fig. 2; Text-fig. 1B). The teeth are conical in shape, have quadrangular bases and their tips curve medially. A cingulum, immediately distal to the juncture



TEXT-FIG. 2. UALVP 45635, elements of the basicranium and the skull roof in dorsal view. Vertical lines represent damaged areas where bone structure is not visible. Abbreviations: Bs, basisphenoid; Exo, exoccipital; ICF, internal carotid foramen; O, opisthotic; Q, quadrate; St, supratemporal. Scale bar represents 10 mm.

of the cementum and the enamel, is present on the teeth of UALVP 45642. The teeth of UALVP 45635 lack cingula (Pl. 1, fig. 3; Text-fig. 1A). Although the cementum bears vertical stria-



TEXT-FIG. 3. *Maiaspondylus lindoei* gen. et sp. nov., Hay River, Northwest Territories, Canada; Loon River Formation. Size comparison among thoracic vertebrae of different specimens, lateral view; $\times 0.65$. A, UALVP 45639, an adult. B, UALVP 45640, a juvenile. C, UALVP 45635, a juvenile.

tions, they are absent from the enamel (Pl. 1, figs 1–2; Text-fig. 1B–C).

Postcranial axial skeleton. Vertebrae from all regions of the vertebral column are present in the collection. It is also abundantly clear that these elements are from a large number of individuals; we base this conclusion on the varied size classes preserved (Text-fig. 3).

The anteriormost (cervical) vertebrae have tall, slender neural spines. The centra are rounded ventrally but are flattened on the dorsal surface, making the area under the neural arches very square. The vertebrae become larger caudally and bear a single rib articulation point on the dorsal surface as was argued by Maisch and Matzke (2000) as being typical of ichthyosaurian cervical vertebrae. The ribs have a shallow groove down the centre (UALVP 45635).

The thoracic vertebrae (Text-figs 3–4, 5A) are narrow, biconcave discs, almost all of which have suffered post-mortem deformation. The vertebrae of anterior thoracic origin have diapophyses still partially connected to the neural arch, and

parapophyses near the dorsal surface of the centra (Text-fig. 4A). The centra are round, and the articulation points for the neural arches are rectangular. The ribs are less robust than cervical ribs (Text-fig. 3C, UALVP 45635). UALVP 45639 (Text-figs 3A, 5) can be placed in the mid-thoracic region, because the diapophyses and the parapophyses are located low on the centrum (Maisch and Matzke 2000). These dia- and parapophyses are irregularly oval in form. The articular facets for the neural spines are oblong in shape. The remains of two embryos are associated with the centra (Maxwell and Caldwell 2003), and on the dorsal surface of one of the vertebrae is a regular diamond pattern that may represent embryonic ribs, based on the presence of a groove running parallel to the long axis of the structure (Text-fig. 5B). It is also possible that this pattern represents structures of the adult integument, although it does not resemble anything that has been described (Lingham-Soliar 1999, 2001). Vertebrae are also known from the posterior thoracic-anterior caudal region, based on the ventral migration of the diapophyses and the parapophyses and their eventual fusion into a single oval articulation point towards the posterior end of the string (Text-



TEXT-FIG. 4. *Maiaspondylus lindoei* gen. et sp. nov., Hay River, Northwest Territories, Canada; Loon River Formation. UALVP 45635, strings of subequal thoracic vertebrae; $\times 0.8$. A, anterior thoracic vertebrae in dorsal view. The neural spines have been flattened so that they are lying perpendicular to their correct orientation. The diapophyses are partially confluent with the neural arch, indicating the anterior origin of this series. B, mid-thoracic vertebrae in dorsolateral view. The diapophyses and parapophyses have shifted ventrally relative to their position in the anterior thoracic series.

fig. 4B; Maisch and Matzke 2000). The articulation points for the neural spines are hourglass-shaped in this region (UALVP 45635).

Caudal vertebrae possess a single, ventral, rounded rib articulation and the centra are round (Text-fig. 5C). The vertebrae slowly decrease in diameter posterior to the pelvic girdle (not preserved, but identified based on the presence of phalangeal elements of the hindlimb agglutinated to the centra). The posterior-most vertebrae are smooth and round, and the decreasing diameter between the anterior and posterior vertebrae in this string of six centra is pronounced in UALVP 45635.

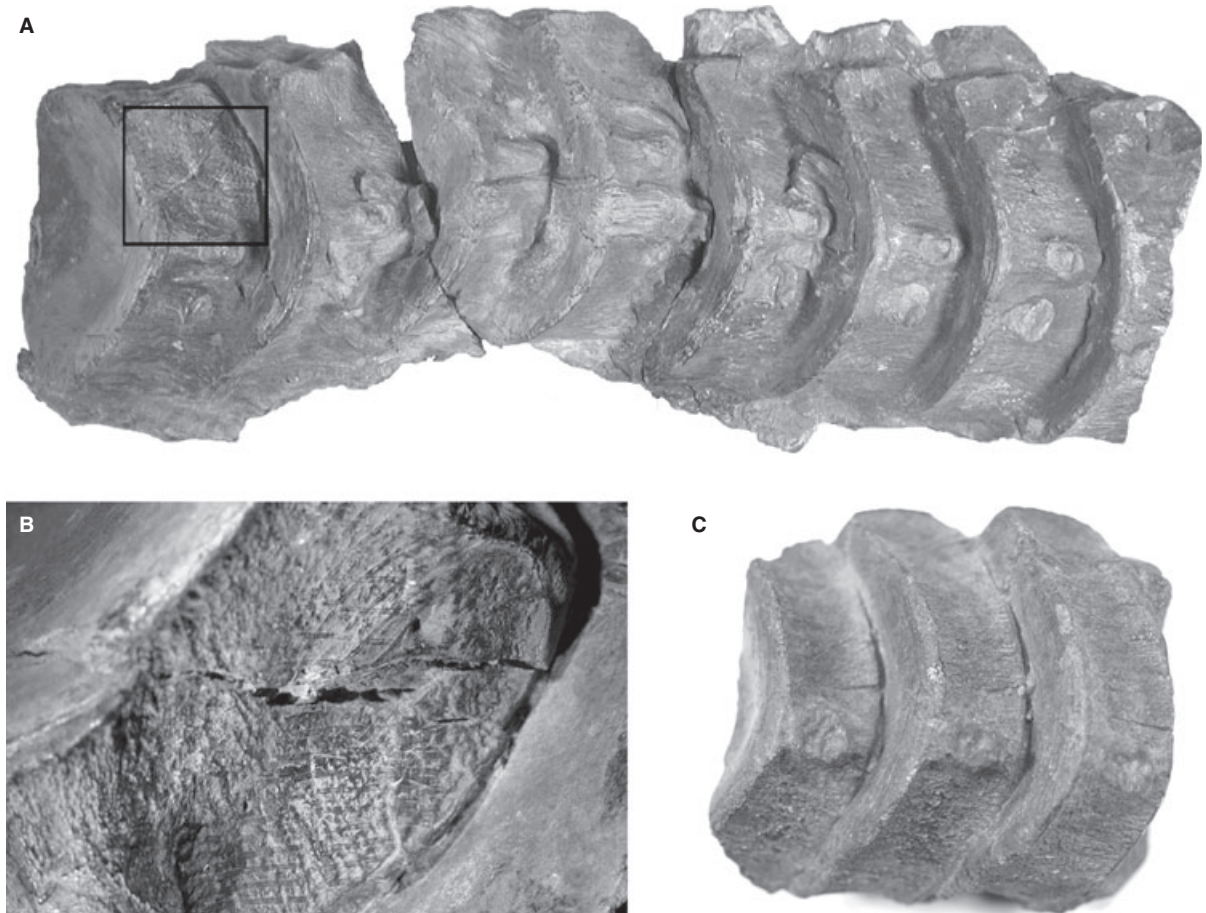
Forefin. The humerus is stout, flat, and equally expanded at its proximal and distal ends. In the juvenile UALVP 45635 (Pl. 1, fig. 5; Text-fig. 6A), it is 4.23 cm long, and the proximal and distal ends are both 3.23 cm wide. No forefins are known from any of the adult specimens. The dorsal trochanter of the humerus is large, and has an anterodistal orientation. The anterior flange is present only as a small ridge. There are three clear facets for the articulation of the epipodial elements: two lateral facets of equal size for the radius and the ulna, and a smaller medial one for the intermedium.

The ulna is large compared with the other elements in the forelimb, and is almost rectangular. Articulating with the posterodistal edge is the pisiform, a large, rounded element, only half of which is preserved. The intermedium does not extend distal to the ulna. The ulnare is directly distal to the ulna. The proximal digital elements are rectangular, and they decrease in length and become isodiametric as one progresses distally down each digit. The postaxial elements are almost rounded at the distal margin of the fin.

DISCUSSION

UALVP 45635, 45642 and 45643 form an ontogenetic series, with the holotype, 45635, representing a juvenile and the others being adults of varying sizes (Text-fig. 3). They can be grouped together as members of the same species by similarities of the upper jaw, namely the placement and orientation of the jugal, as well as the structure of the lacrimal and the maxilla (Text-fig. 1A–C). These characters vary extensively even within closely related groups (Maisch and Matzke 2000). Although UALVP 45642 possesses cingula on the teeth, the much smaller UALVP 45635 does not. This does not suggest that they are separate species, rather cingula are presumably an ontogenetic feature, as in *Brachypterygius* Huene, 1922, where they only appear on the teeth of fully grown individuals (Efimov 1998). Very few ichthyosaurs possess teeth that lack vertical striations: in post-Triassic ichthyosaurs, these are absent only from *Leptonectes* McGowan, 1996 and *Eurhinosaurus* Abel, 1909 from the Lower Jurassic, *Aegirosaurus leptospondylus* (Wagner, 1853) from the Upper Jurassic (Maisch and Matzke 2000) and *Maiaspondylus* from the Lower Cretaceous.

The teeth of *Maiaspondylus* are well developed, a character that is shared among *Brachypterygius*, *Aegirosaurus* and *Platypterygius* (Maisch and Matzke 2000). The teeth of *Brachypterygius* and *Platypterygius*, as well as *Maiaspondylus*, all possess quadrangular bases and crowns that



TEXT-FIG. 5. *Maiaspondylus lindoei* gen. et sp. nov., Hay River, Northwest Territories, Canada; Loon River Formation. Vertebrae. A, UALVP 45639, eight mid-thoracic vertebrae in lateral view; $\times 0.75$. Note the location of the diapophyses and the parapophyses on the lateral surface of the centra, supporting a thoracic position for this series of vertebrae. These vertebrae come from a sexually mature adult, as is evidenced by the presence of embryonic remains on the ventral surface. B, inset in A, showing spatial extent of rhomboidal pattern of criss-crossing fibres, possibly collagen fibres in the dermis; $\times 3.25$. C, UALVP 45635, caudal vertebrae; $\times 1.25$. Note the single parapophysis, located on the ventrolateral surface of the centrum.

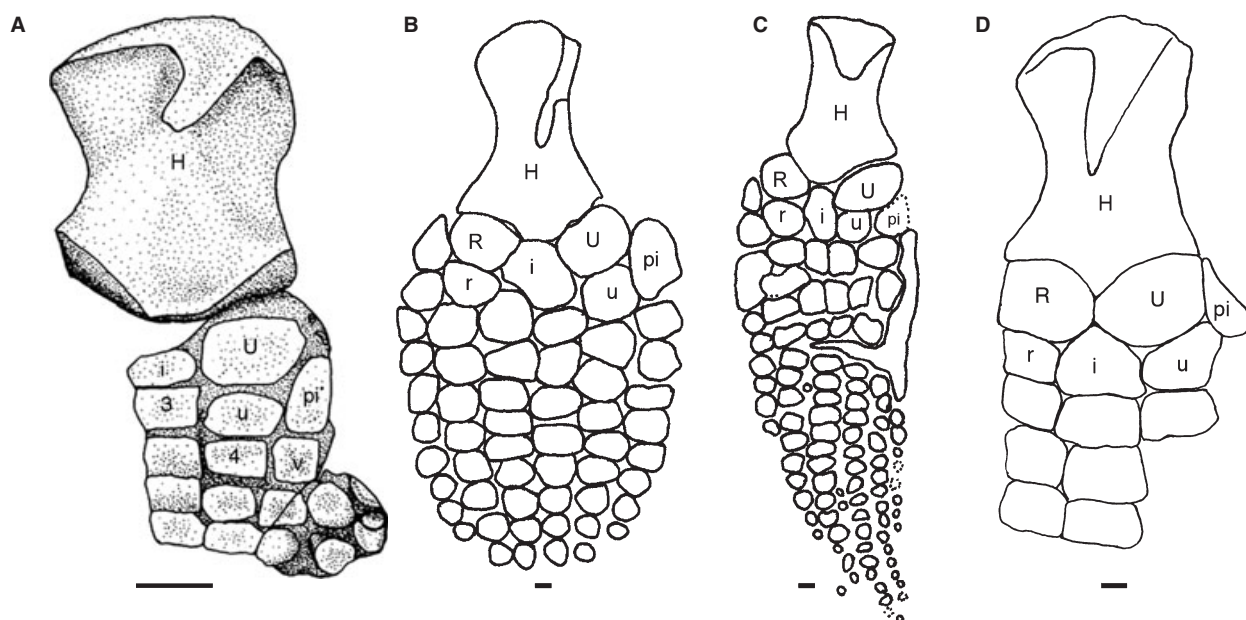
are circular in cross-section; the character state in *Aegirosaurus* is unknown (Bardet 1990; Efimov 1998; Arkhangel'sky 2001).

The humerus of *Maiaspondylus* has three articular facets, the smallest one being located medially for articulation with the intermedium. This condition separates *Maiaspondylus* from the only previously recognized genus of Cretaceous ichthyosaur, *Platypterygius*, in which the intermedium does not contact the humerus; in *Platypterygius* the two largest articular facets are located beside each other (Text-fig. 6D; Wade 1990).

The humerus-intermedium contact does support an affinity with *Brachypterygius* and *Aegirosaurus*. In these two genera, however, the intermedium is elongate, spanning the epipodium and mesopodium, whereas in *Maiaspondylus* it is epipodial only and does not extend distal to the ulna (Text-fig. 6A–C; Motani 1999b; Fernández 2001). Another possible interpretation of the forelimb

structure of *Maiaspondylus* is that the medial facet represents a reduction of the radius, and the anterior facet belongs to an enlarged anterior extrazeugopodial element. This is unlikely because no ophthalmosaurs exist for which the two largest articular facets do not belong to the radius and the ulna, even when these two elements are not equivalent in size. There is also evidence for a progressively greater inclusion of the intermedium within the zeugopodium, as is evidenced by a comparison between the distal extent and shape of the intermedium in *Brachypterygius*, as compared with *Aegirosaurus* (Text-fig. 6B–C).

Even though there are similarities in the forelimb structure of *Maiaspondylus*, *Aegirosaurus* and *Brachypterygius*, *Maiaspondylus* is clearly distinct from these genera based on other features, one of which is humeral structure. The humeri of *Aegirosaurus* and of *Platypterygius* are widest at the distal end, and the humerus of *Brachypterygius* is



TEXT-FIG. 6. Left forefins of select ophthalmosaurs in dorsal view. A, *Maiaspondylus lindoei* (UALVP 45635). B, *Brachypterygius extremus* (modified from Motani 1999a). C, *Aegirosaurus leptospondylus* (modified from Bardet and Fernández 2000). D, *Platypterygius americanus* (modified from McGowan 1972). Abbreviations: H, humerus; i, intermedium; pi, pisiform; R, radius; r, radiale; U, ulna; u, ulnare; 3, 4, distal carpals; v, metacarpal 5. Scale bars represent 10 mm.

slightly wider at the proximal end (McGowan 1972; Efimov 1998; Arkhangel'sky 2000; Bardet and Fernández 2000). The structure of the humerus of *Maiaspondylus* differs from that of those genera by being equally expanded proximally and distally, and by being much less elongate.

In the upper jaw of *Maiaspondylus*, the jugal is forked and extends anteriorly to the widest part of the maxilla, and wraps around its posteroventral surface. This is inconsistent with the jugal of *Brachypterygius*, which extends far anteriorly and contacts the premaxilla (Kirton 1983). It does, however, roughly conform to that of many other ichthyosaurs, including *Aegirosaurus leptospondylus* and *Platypterygius longmani* (Wade 1984; Bardet and Fernández 2000).

There are biogeographical inconsistencies between *Maiaspondylus* and other ichthyosaurs sharing a similar zeugopodial structure. These differences are inconsequential on their own, because large ichthyosaurs were highly mobile and presumably could disperse widely, but they are significant when paired with the morphological changes that have occurred between *Maiaspondylus* and Jurassic genera. Temporal inconsistencies are also present: *Brachypterygius* is from the Upper Jurassic of England and Russia, with material also having been discovered in Madagascar (Fernández 1997; Efimov 1998; Arkhangel'sky 2001). *Aegirosaurus* is from the Upper Jurassic of Bavaria (Bardet and Fernández 2000).

Maiaspondylus is from the Lower Cretaceous (Albian), resulting in a gap of 20 million years between occurrences, with none of the Jurassic material having come from North America.

CONCLUSIONS

The unique combination of morphological features found in *Maiaspondylus lindoei* supports the erection of a new genus. Although it is probably nested within the Ophthalmosauria, based on the evidence for three elements in the zeugopodial row, its inclusion cannot be confirmed as defined by Motani (1999a) because of the incomplete nature of the specimen. The material that is present reveals that *Maiaspondylus* is unlike any known genus, either within or outside of the Ophthalmosauria. Although it is found in the same deposits as *Platypterygius* (Maxwell and Caldwell 2004), the structures of the zeugopodial row and tooth morphology clearly distinguish and thus separate the two genera. The unstriated tooth morphology links *Maiaspondylus* with *Aegirosaurus*, yet the shape of the humerus and the distal extent of the intermedium are inconsistent with this diagnosis. Differences in the humerus, the shape and alignment of the paddle elements, the unstriated tooth morphology and the abbreviated jugal distinguish *Maiaspondylus* from *Brachypterygius*.

All previously reported Cretaceous ichthyosaurs, both in North America and around the world, were assigned to the genus *Platypterygius*. This most recent find demonstrates that ichthyosaur diversity is greater than was previously acknowledged, in both the Cretaceous and in the Western Interior Seaway of North America.

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