REDESCRIPTION OF *WOOLUNGASAURUS GLENDOWERENSIS* (PLESIOSAURIA: ELASMOSAURIDAE) FROM THE LOWER CRETACEOUS OF NORTHEAST QUEENSLAND

SVEN SACHS

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Woolungasaurus glendowerensis Persson, 1960, was based on an incomplete postcranial skeleton, comprising cervical, pectoral, dorsal and caudal vertebrae, an almost complete sacrum, as well as elements of the pectoral and pelvic girdles and of the fore and hind paddles. Following comparisons with specimens referable to all valid genera of the Elasmosauridae, this specimen and additional material is identified as belonging to *Styxosaurus*. It is the earliest record of this genus and the first in the Southern Hemisphere. ❑

Plesiosauria, Elasmosauridae, Woolungasaurus, Styxosaurus, *Lower Cretaceous, northeast Queensland.*

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The Elasmosauridae are a well-known family within the Plesiosauroidea. Most skeletal remains are known from the Northern Hemisphere (especially North America, Carpenter, 1999). In Australasia, only few localities have yielded their remains (Cruickshank et al., 1999). An almost complete, but badly crushed skull from the Aptian of northeast Queensland is a new species of *Tuarangisaurus*. In about the same region as the skull, Glendower Station near Prairie, postcranial skeletal remains were discovered by A.W. Fergusen at his landholdings in 1891 (QMF3567) and 1893 (QMF3568). This specimen was described by Persson (1960) as a new genus and species, *Woolungasaurus glendowerensis.* Persson not always adequately described the remains and also misidentified some elements. His diagnosis is based on weak characters of the vertebrae, the coracoid and the propodials. For these reasons Welles (1962) considered the genus a *nomen dubium*.

The purpose of this paper is to redescribe and classify the postcranial material referred to *Woolungasaurus glendowerensis*. The type material and other referred specimens are housed in the Queensland Museum (QM). Besides a postcranial skeleton is described, which is on display at the Richmond Marine Fossil Museum, Richmond. It is more complete than the type and can be referred to the same taxon, as all elements preserved in both specimens are identical (Tables 1, 2).

In the comparison, all elasmosaur genera (revised by Carpenter, 1999 and Storrs, 1999) have been considered, except for the doubtful taxa, *Fresnosaurus* Welles, 1943, *Moraenosaurus* Welles, 1943 and *Aphrosaurus* Welles, 1943.

INSTITUTIONAL ABBREVIATIONS. AMNH, American Museum of Natural History, New York, USA; ANSP, Academy of Natural Sciences, Philadelphia, USA; DMNH, Denver Museum of Natural Sciences, Denver, USA; QM, Queensland Museum, Brisbane, Australia; RMF, Richmond Marine Fossil Museum, Richmond, Australia; SDSM, South Dakota School of Mines, Rapid City, USA.

SYSTEMATIC PALAEONTOLOGY

SAUROPTERYGIA Owen, 1860
PLESIOSAURIA De Blainville, 1835
PLESIOSAUROIDEA Nopcsa, 1928
ELASMOSAURIDAE Cope, 1868
Styxosaurus Welles, 1943

TYPE SPECIES. *Styxosaurus* (*Cimoliosaurus*) *snowii* Williston, 1890.

DIAGNOSIS. See Carpenter (1999:158).

Styxosaurus glendowerensis comb. nov.

Woolungasaurus glendowerensis: Persson, 1960: 11-16.
Woolungasaurus glendowerensis: Welles, 1962: 47-48 (nomen dubium).
Woolungasaurus glendowerensis: Persson, 1963: 22.
Woolungasaurus glendowerensis: Persson, 1982: 649-650.
Woolungasaurus glendowerensis: Kear, 2003: 288-289 (nomen dubium, sensu Welles, 1962).

MATERIAL. Holotype: QMF3567. Incomplete skeleton (Fig. 1A) comprising 24 cervical vertebrae (including the

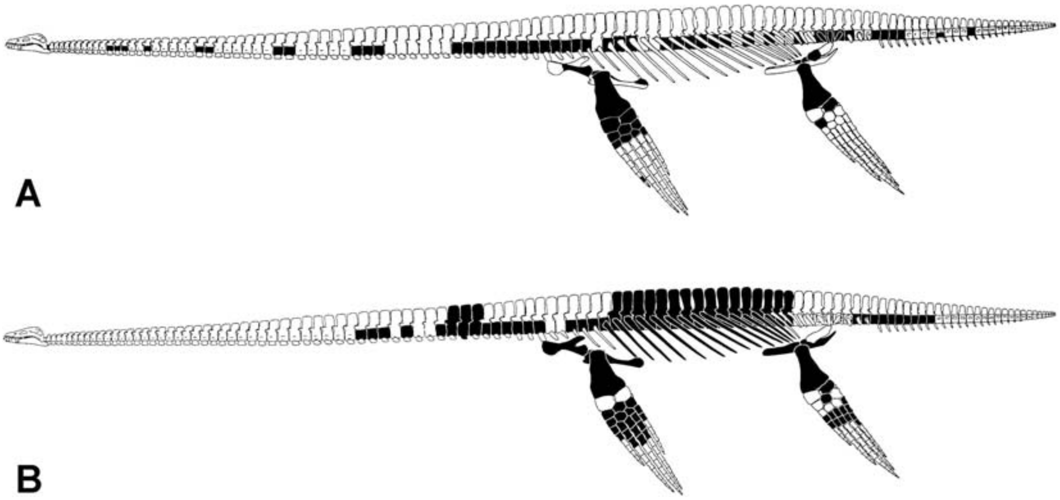

FIG. 1. Outline drawings of the skeletons of *Hydrotherosaurus* (after Welles, 1943), showing the elements present in QMF3567 (A) and RMF R271 (B). Rib-fragments are not included in (A) because of their unclear positions.

axis); 3 pectoral vertebrae; 9 dorsal vertebrae; 3 sacral vertebrae; 7 caudal vertebrae; 2 partial scapulae; partial coracoids; right humerus; 1 ulna; 1 radius; 9 carpals, including 1 intermedium; two phalanges; both femora; the left ?fibula; 1 tarsal; 2 ?metacarpals; 1 phalange; a partial ?pubis; a partial ?ilium; a partial ?ischium; and unidentifiable girdle elements. From Glendower Station, near Prairie, Flinders Shire, North Queensland. Horizon: Wallumbilla Formation, Doncaster Member (Late Aptian, Lower Cretaceous; Day, 1969) (Fig. 2).

REFERRED SPECIMENS. RMF R271, an incomplete skeleton (Fig. 1B) comprising 15 cervical vertebrae, 3 pectoral vertebrae, 17 dorsal vertebrae, 10 caudal vertebrae, both scapulae, coracoids, clavicles and humeri, 1 manual intermedium, 1 radiale, metacarpals I-III; both ischia, pubes, femora, 1 ?fibula, 1 tarsal ?intermedium and 26 phalanges. From Grampian Valley, Richmond Shire, North Queensland, Wallumbilla Formation, Doncaster Member, Late Aptian, Lower Cretaceous (Day, 1969) (Fig. 2).

QMF3568, incomplete left humerus. Locality: No locality data were associate with the specimen, but it most probably belongs to holotype.

QMF2634, anterior portions of both coracoids and two dorsal vertebrae. From Claypan Ridge near Rainscourt Station, Richmond Shire, Queensland. Horizon: Wallumbilla Formation, Doncaster Member (Late Aptian, Lower Cretaceous; Day, 1969) (Fig. 2).

DIAGNOSIS. Small elasmosaurid circa 5m long; axis centrum longer than wide or high; lateral longitudinal crest in cervical vertebrae absent from posterior of mid-cervical region; three pectoral vertebrae; sacral ribs I and II robust compared with sacral rib III; sacral rib I oriented posteriorly at an angle of about 35°, sacral rib II oriented posteriorly at an angle of about 30°; sacral rib III slender compared with sacral ribs I and II and straight; anterior portion of coracoid with prominent transverse keel medially on ventral side; intercoracoidal foramen prominent, heart-shaped; coracoid blade longer than anterior coracoid portion; scapula anteroposteriorly long and dorsoventrally slender; scapula shaft slightly concave medially; prominent ridge separating ventral shaft from dorsal process of scapula; dorsal process posteriorly directed at 60° to horizontal plane; clavicles slender, posteriorly curved at 45° to horizontal plane; clavicula suture straight, forming distinct sagittal vault ventrally; humerus more prominent than femur; ulna and radius almost quadratic; femora more slender than humeri; fibula pentagonal; foramen obturatum broad oval; pubic symphysis straight; posterior edge of pubis, forming border of foramen obturatum, wide and slightly concave; ischium slender in relation to pubis; anterior edge of ischium wide and slightly concave.

DESCRIPTION.

Vertebrae. QMF3567 includes 47 vertebrae, comprising 24 cervicals, 3 pectoral, 9 dorsals, 3 sacrals and 7 caudals (including a caudosacral vertebra) (Table 1). Only 9 are preserved in association with parts of the neural arches. There are a number of isolated neural arches and neural spines. Persson (1960: 12) stated that all neural

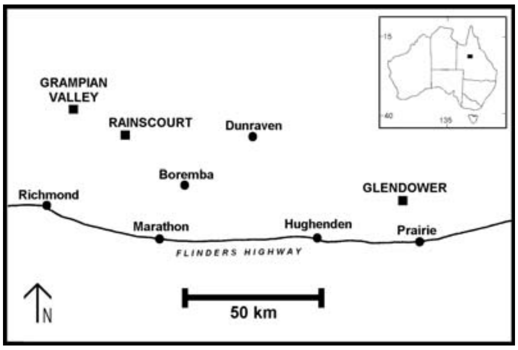

FIG. 2. Map of the Richmond – Hughenden area in north Queensland showing the localities of QMF3567 at Glendower, QMF2634 at Rainscourt and RMF R271 at Grampian.

arches are fused with the centrum without a visible suture; however, there are sutures visible on two of the dorsal vertebrae, which still bear parts of the neural arches. Also, in all cervical vertebrae, the neural arches are broken at the same level, suggesting that they were not fused with the centra. This, at least, suggests that QMF3567 represents a juvenile or sub-adult individual.

Axis. QMF3567. Most of the centrum of the axis except for its dorsal surface is preserved (Fig. 3A-C). It is anteroposteriorly elongated, clearly longer than wide or high giving it a rectangular outline in lateral view. The ventral surface is concave and bears a sharp sagittal crest that originates from the edge of the anterior articular facet and terminates at the edge of the posterior one. In the middle of the crest two barely visible nutritive foramina are present. On both sides of the sagittal crest the ventral surface is slightly despressed. The rib facets are prominent, broad oval in outline and are situated laterally in about the middle of the centrum. The anterior and posterior articular facets of the centrum are incomplete, in which the dorsal edges are missing. When complete they probably had a nearly circular outline. Both articular facets are weakly concave and surrounded by thickened edges, of which the ventral sides are bulged. The dorsal side of the centrum is planar, as the entire dorsal section of the vertebra is missing. In the centre of the dorsal side, two long-oval foramina are situated.

The size and the shape of this vertebra suggest that it represents the axis. Most described elasmosaurs with preserved anteriormost cervicals are adult individuals. In this stage the axis is coossified with the atlas and forms the atlas-axis complex (Carpenter, 1999). Only in juvenile individuals can the axis be found as an isolated element.

Remarks. Usually in elasmosaurs, as in *Occitanosaurus* (Bardet et al., 1999), *Muraenosaurus* (Andrews, 1910), *Brancasaurus* (Wegner, 1914), *Libonectes* (Welles, 1949), *Hydrotherosaurus* (Welles, 1943), *Aristonectes* (Gasparini et al., 2003) and *Tuarangisaurus* (Wiffen & Moisley, 1986) the axis is anteroposteriorly short and high. This feature is found in most plesiomorphic sauropterygians Only the advanced elasmosaurs *Styxosaurus* (Welles & Bump, 1949; Carpenter, 1999), *Hydralmosaurus (*Cope, 1877, Welles, 1952) and *Elasmosaurus* (Cope, 1869; Welles, 1952) have an axis that is long and low.

Cervical Vertebrae. QMF3567. The next anteriormost of the preserved cervical vertebrae (Fig. 3D-F) is clearly larger than the axis and may, after its size and proportion, have come from the middle of the anterior section of the neck (based on comparisons with the cervical vertebrae of *Styxosaurus snowii*, after Welles & Bump, 1949: table 2). The remaining anterior cervical vertebrae have a rectangular centrum that is longer than wide or high. In about the mid-section of the neck, the shape of the vertebrae becomes more quadratic in dorsal view, in which the centra are clearly wider than long.

All cervical centra bear a pair of long-oval nutritive foramina in the centre of their ventral surface. These foramina are separated by a ridge that is thinnest in the anterior vertebrae and becomes broader and flatter in the posterior cervicals. Lateral of the ridge, the ventral surface is longitudinally excavated. This depression is deepest in the anterior cervical vertebrae. The rib facets are very prominent. They are situated about in the middle of the lateroventral surface in the anterior vertebrae, where they are anteroposteriorly expanded. Beginning in about the mid-cervicals, the rib facets begin to shift dorsally so that by the most posterior cervicals they are situated in the centre of the lateral surface. Here, their articular facets have a high oval outline and are expanded laterally. Anteriorly and posteriorly of the articular facets the lateral surface is concave.

The centra of the anterior cervical vertebrae bear a sharp horizontal crest in the middle of the lateral surface. It was differently named (Brown, 1981: 330), and is here called 'lateral

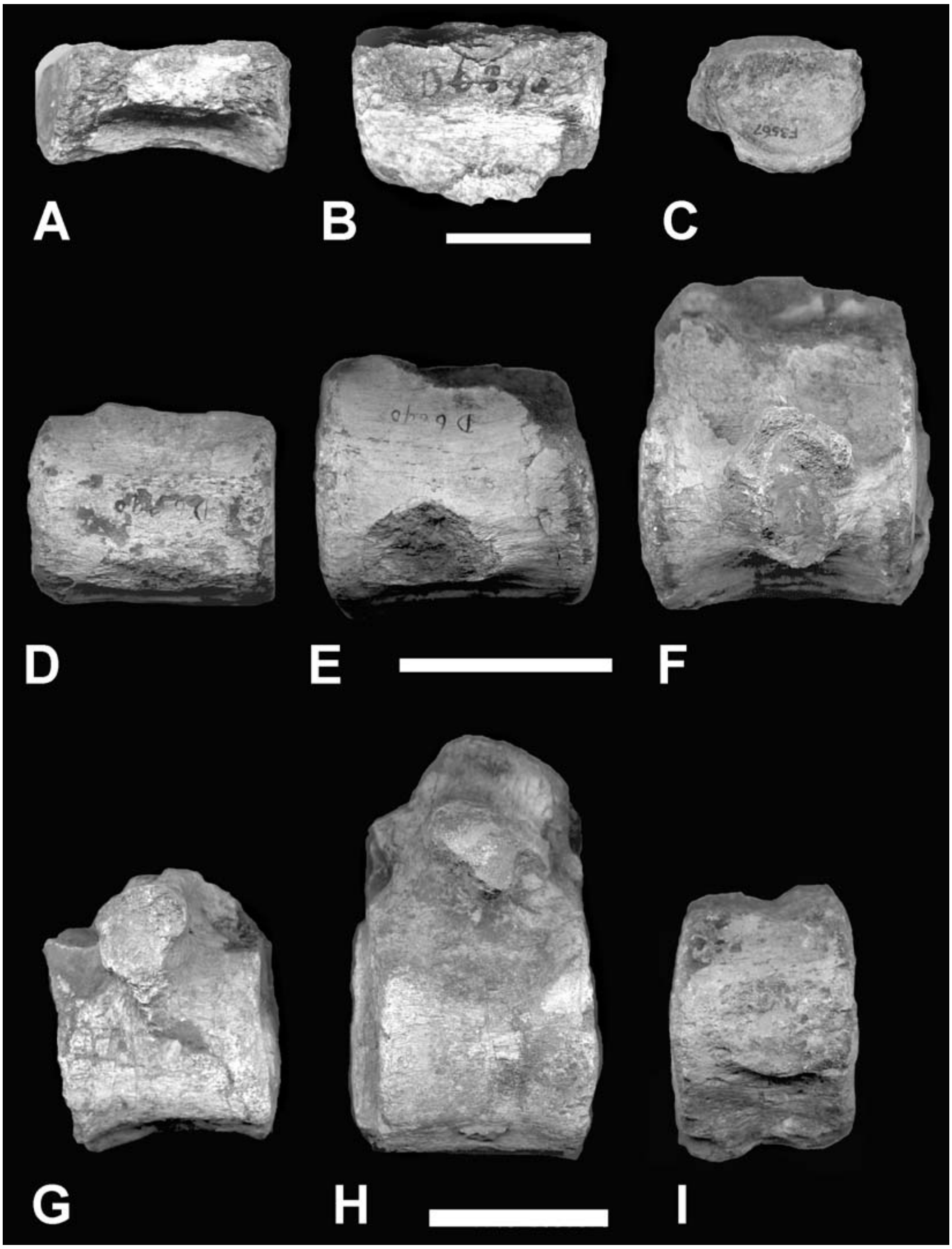

FIG. 3. A-C, QMF3567; axis centrum in lateral (A), ventral (B) and posterior (C) views. Scale = 2 cm. D-F, QMF3567; lateral views of an anterior (D), mid (E) and posterior (F) cervical vertebra. G, QMF3567; pectoral vertebra in lateral view. H, QMF3567; dorsal vertebra in lateral view. I, QMF3567; caudal vertebra in lateral view. Scales = 5cm.

longitudinal crest', following Welles (1943) and Persson (1963). Dorsal and ventral to the crest, the surface of the centrum is concave. The lateral longitudinal crest is absent after approximately the mid-cervical region. The anterior and posterior articular facets of the centra are broad oval in shape and weakly concave. Conspicuously these facets are wider in the anterior- and posteriormost vertebrae, while they are nearly circular in the mid-cervicals. The neural canal is moderately deepened, so that the dorsal surface of the anterior and posterior articular surfaces is just slightly concave. The edge of the articular facets is relatively thin; their ventral surface lacks a notch.

RMF R271. The 15 cervical vertebrae preserved in the Richmond specimen are from the mid- and posterior section of the neck (Table 1). They resemble in shape the cervical vertebrae of QMF3567 and shall therefore not be described.

Remarks. Most elasmosaurs possess a number of slightly variable synapomorphies in the cervical vertebrae. In general, at least in adult or subadult elasmosaurs, a pair of nutritive foramina is present in about the middle of the ventral surface, separated by a sagittal keel. Also a lateral longitudinal crest is developed in the anterior cervicals, mostly reaching back to the mid-cervical level, but sometimes also into the posterior region of the neck (e.g. in *Microcleidus* (Owen, 1865), *Thalassomedon* (Welles, 1943), *Hydralmosaurus* (Cope, 1877) or *Callawayasaurus* (Welles, 1962)). Brown (1981) discussed the significance of the lateral longitudinal crest and mentioned that it is sometimes missing in juveniles (e.g. in *Muraenosaurus*) and is only fully developed in adult elasmosaurs. Its position in the vertebrae (in the mid-, dorsal or ventral section of the lateral centrum) is highly variable and therefore of no phylogenetic relevance. However, the presence of a lateral longitudinal crest in QMF3567 indicates that already in some long-necked juveniles a well developed crest was present. Also the presence is not limited to the Elasmosauridae, as a similar crest has been found in the plesiosaurids *Plesiosaurus brachypterygius* and *P. guilelmiimperatoris* (Bardet et al, 1999; Fraas, 1910). The shape of the vertebrae, which is either quadratic or rectangular in lateral view can be considered as phylogenetically significant (Brown, 1981). The general shape of the cervicals is similar to that of *Microcleidus* (Owen, 1865, pl. 5), *Styxosaurus* (Welles & Bump, 1949: pl. 85) *Terminonatator* (Sato, 2003: fig. 9) and *Elasmosaurus* (Cope, 1869: pl. 2, fig. 5 & pl. 3).

Pectoral and Dorsal Vertebra. QMF3567. Three pectoral vertebrae and 9 dorsal vertebrae are preserved (Fig. 3G-H). In the pectoral and anterior dorsal vertebrae, the centra are wider than long so that their articular facets have a broad oval outline. In the mid-dorsals the articular facets become more circular and the centra have a nearly quadratic outline in lateral view. The pectoral vertebrae bear prominent transversal processes with high oval rib facets as visible in lateral view. The latter are situated in the middle of the posterior section of the centrum. In the pectoral vertebrae the transverse processes come out of centrum, in the anterior dorsal vertebrae they are situated lateral to the neural arches. In these vertebrae the transversal processes are slightly oriented posterodorsally in lateral view, with the rib facets more triangular in cross-section. On one of the better preserved anterior dorsal vertebra, parts of the prezygapophyses as well as the ventral portion of the neural spine are preserved. The latter is also somewhat oriented posteriorly with an angle of about 20° to the vertical in lateral aspect. The anterior and posterior articular facets of this vertebra are nearly circular and weakly concave, with sharp borders. Ventrally, the nutritive foramina are situated in the middle of the centrum and are well separated by a broad, shallow, anteroposteriorly running ridge.

RMF R271. Three pectoral and 17 dorsal vertebrae are present in the Richmond specimen, representing the entire, or almost the entire, midsection of the skeleton (total number of pectorals/dorsals in *Styxosaurus snowii* 22, after Welles & Bump, 1949) (Table 1). Some dorsal vertebrae are complete and well preserved. The neural arches are short and robust; the neural spines are about 1.5 × as high as the centrum. In their general apperance the dorsal vertebrae of RMF R271 resemble those of QMF3567 and shall therefore not be described in more detail.

Remarks. According to Brown 1981 (sensu Seeley, 1874) pectoral vertebrae are transitional between cervicals and dorsals, in which the rib articulates with the centrum and the neural arch. Three pectoral vertebrae are present in *Occitanosaurus* (Bardet et al., 1999), *Muraenosaurus* (Andrews, 1910), *Brancasaurus* (Wegner, 1914), *Styxosaurus* (Welles & Bump, 1949), *Thalassomedon* (Welles, 1943) and *Hydralmosaurus* (Welles, 1952). In *Callawayasaurus* (Welles, 1962) and

Hydrotherosaurus (Welles, 1943) there are two. Wider than long centra are considered synapomorphies of the elasmosaurids. No other characteristic features could be taken from the pectoral and dorsal vertebrae.

Sacral Vertebrae. QMF3567. Three articulated sacral vertebrae are preserved (Fig. 4). On the right side (as well as on the left side in the first vertebra), the sacral ribs are connected with the centra. The centra are wider than long and high and somewhat higher than long. The articular facets of the centra have relatively sharp edges and are slightly concave. On the ventral surface of the centra nutritive foramina are absent. In the caudosacral vertebra three small foramina are present in the middle of the ventral surface. The neural spines are not preserved and the zygapophyses are only barely visible in the first and second vertebra, while they are missing in the third. The neural canal is filled with sediment in the first and second vertebra and is well exposed in the third sacral vertebra. Here it can be seen that the neural canal was very broad, occupying more than half of the dorsal surface of the centrum, whereas it seems to be smaller in the first sacral vertebra. The right sacral ribs are completely preserved as well as partially the left one of sacral vertebra I. All sacral ribs are about equal in length and connect the vertebrae in the dorsal half of their lateral midsection, but they also touch the ventral section of the neural arches. The first and the second rib widens laterally, while the third sacral rib is, compared to them, more slender. In dorsal view, the first sacral rib is posteriorly directed at about 35°, the second at about 30°. The third sacral rib is almost straight laterally oriented. In the caudosacral vertebra only the articular surface for the sacral ribs is preserved. These are situated dorsally in the lateral midsection, but reach not up to the neural arches.

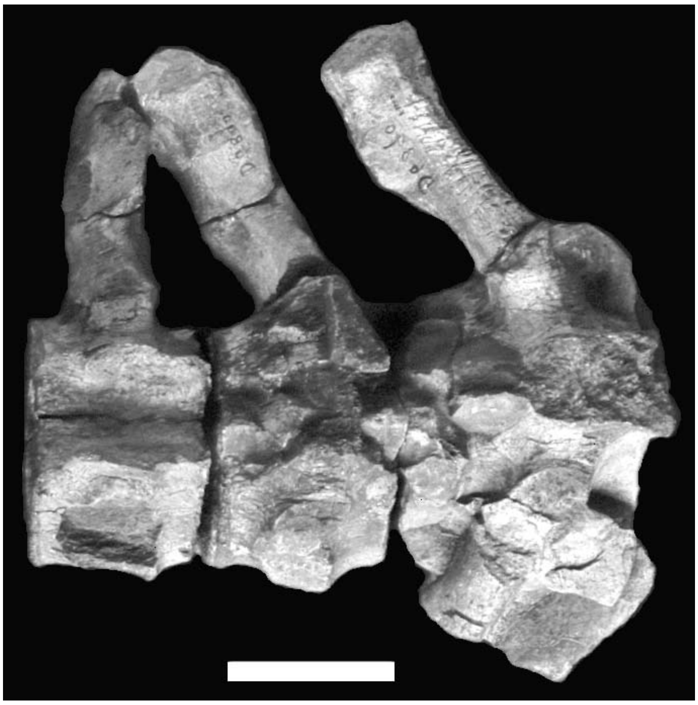
FIG. 4. Sacral vertebrae of QMF3567 in dorsal view. Scale = 5cm.

Remarks. It is unclear if the total number of sacral vertebrae is three or if the considered caudosacral vertebrae represents the fourth sacral vertebra. Usually four sacral vertebrae are present in elasmosaurids such as *Occitanosaurus* (Bardet et al., 1999), *Muraenosaurus* (Andrews, 1910), *Terminonatator* (Sato, 2003), *Styxosaurus* (Welles & Bump, 1949), Elasmosaurus (ANSP 10081, pers. obs. 2001) and Hydralmosaurus (Welles, 1952). The number is 3 in *Brancasaurus* (Wegner, 1914), *Thalassomedon* (Welles, 1943), and *Hydrotherosaurus* (Welles, 1943). A more detailed comparison was not possible, as only of *Muraenosaurus* (Andrews, 1910: fig. 56) and *Brancasaurus* (Wegner, 1914: figs 5, 6) good descriptions and figures of the sacral ribs have been published.

Caudal Vertebrae. QMF3567. Seven caudal vertebrae, including a caudosacral vertebra (see sacral vertebrae), are preserved (Fig. 3I). The centra are robust and wider than high and long and higher than long. The articular facets of the centra are slightly concave and surrounded by thickened edges. The surfaces for the articulation of the haemapophyses are situated in the ventral mid-section of the centrum and have a nearly triangular outline. A broad, shallow excavation separates the surfaces on each side. Between the anterior and posterior articular facet of the centrum there is a sharp crest. In the centre of the

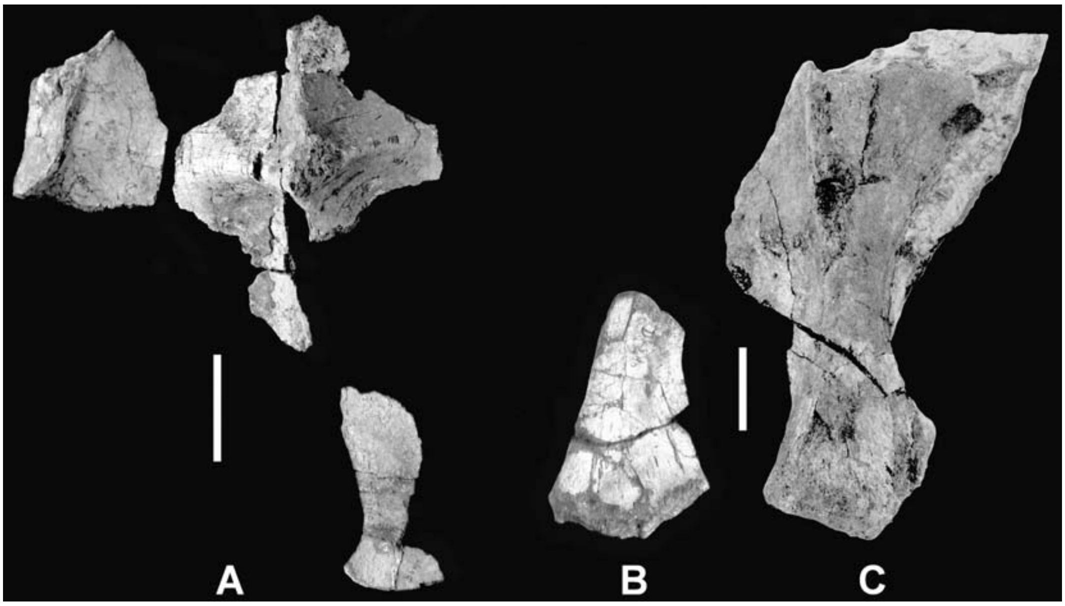

FIG. 5. A, QMF3567; coracoid fragments. Scale = 10cm. B, QMF3567; posterior section of the right scapula. C, RMF R271; right scapula. Scale = 5cm. All in ventral view.

ventral surface the nutritive foramina are present, which are relatively small and well separated. The rib facets are prominent, circular in outline and are situated in the middle of the lateral surface of the centrum. The shape of the vertebrae becomes more circular posteriorly, so that the proposed mid-caudal vertebra has a nearly circular articular facet in anterior view. In this specimen, the rib facets are very prominent and occupy almost the entire mid-lateral surface of the centrum.

RMF R271. Ten anterior caudals are present in the Richmond specimen (Table 1), which resemble in shape those of QMF3567 and shall therefore not be described.

Remarks. The general shape of the preserved caudal vertebrae corresponds well with that in *Styxosaurus snowii* (Welles & Bump, 1949: pl. 85), but the shape of the caudal vertebrae within the Elasmosauridae is not very informative taxonomically.

Ribs. QMF3567. Although numerous rib-fragments are presented in the holotype material, no complete ribs (except of the sacral ribs) could be assembled. In general, these fragments seem to belong to the dorsal ribs. They are single-headed and have a broad oval articulation surface that is slightly concave and somewhat oriented medially.

RMF R271. In the Richmond specimen a number of ribs and rib fragments are present. Among them there are some complete ribs, which show the for elasmosaurs typical appearance in having an oval cross section in the proximal shaft and a prominent caput that has a somewhat concave articulation surface with the rib facets of the dorsal vertebrae.

Coracoid. QMF3567, F2634. In the holotype material, most of the anterior section of both coracoids, as well as the anterolateral and posteromedial part of one coracoid, are preserved (Fig. 5A). Persson (1960) referred another fragmentary, but clearly larger pair of coracoids (QMF2634), consisting of the anteromedial parts, to the same taxon. The author agrees with Persson as the preserved section of the coracoids of QMF2634 are nearly identical with those of QMF3567. In ventral view, a blunt keel follows the coracoidal symphysis, as seen in QMF3567. A very prominent transverse keel is present in about the middle of the anterior section of each coracoid. It becomes larger medially towards the symphyseal surface and is very high and broad in the symphyseal margin, where the keels of both coracoids meet each other. Anteriorly and posteriorly of the keels, the ventral surface is deeply concave. The dorsal surface of the coracoids is slightly convex and only well rounded next to the medial keel. Another fragment belonging to QMF3567 represents the anterolateral articular part of one coracoid, but it cannot clearly be judged whether the right or left one. The scapular articular surface is relatively short compared with the glenoidal fossa. It has a triangular outline in lateral view and is somewhat oriented anteromedially at about 40° to the vertical plane. The glenoidal fossa is nearly twice as long as the scapular one and has a long oval outline in anterior view. Both facets bear barely preserved rugosities. Medial to the articular part, the bone becomes flattened dorsoventrally. This fragment corresponds well with the preserved anteromedial part. Another fragment of the holotype material represent the most posteromedial part of one coracoid, which is flattened dorsoventrally. The medial edge is straight in its anterior section and medially curved at the posterior end. The latter is slightly thickened and shows a convex curvature.

RMF R271. Both coracoids are almost completely preserved, as only the most posteromedial sections are missing. The coracoid fragments of QMF3567 and F2634 resemble them quite well. For this reason only the posterior part of the coracoid that is not preserved in the other specimens shall be described. The posterior portion of the coracoid forms a broad blade that flares out lateromedially in the most posterior section. Its edges are very thin. The lateral side of each coracoid, between the posterior edge of the glenoid fossa and the transitional from the lateral to the posterior edge is inwardly concave. In dorsal view the posterior edge of the coracoids is slightly curved sigmoidally. From lateral it runs slightly concave to a point at about its medial third and than well convex anteriorly. The medial edge of the posterior portion of the coracoid again is concave and anterolaterally oriented. The intercoracoidal foramen is prominent and about heart-shaped with an accordingly broader anterior portion. The posterior coracoid part is slightly longer than the anterior one.

Remarks. A characteristic feature of the three preserved coracoids is the presence of a prominent transverse keel in the anterior part. Similar keels are present in *Libonectes* (Welles, 1949: fig. 2), *Thalassomedon* (Riggs, 1939: fig. 111), *Hydralmosaurus* (Watson, 1924: fig. 9), *Callawayasaurus* (Welles, 1962: pl. 4), *Mauisaurus* (Welles & Gregg, 1971: fig. 8) and *Tuarangisaurus* (Wiffen & Moisley, 1986: figs 22, 23), but only in *Thalassomedon* and *Hydralmosaurus* are they as prominent as in QMF3567, QMF2634 and RMF R271. The posterior coracoid portions are connected by a large medial symphysis in the early elasmosaurid taxa *Microcleidus* (Watson, 1909: fig. 1), *Occitanosaurus* (Bardet et al., 1999: pl. 3) and *Muraenosaurus* (Andrews, 1910: fig. 62). In *Brancasaurus* this section is incomplete, but a long and rather narrow intercoracoidal foramen has been reconstructed (Wegner, 1914: pl. 9). A prominent intercoracoidal foramen is present in *Callawayasaurus* (Welles, 1962: fig. 6), *Thalassamedon* (Riggs, 1939: fig. 111), *Libonectes* (Welles, 1949: fig. 2), *Styxosaurus* (Welles & Bump, 1949: fig. 4), *Hydralmosaurus* (Welles, 1962: fig. 16) and *Hydrotherosaurus* (Welles, 1962: fig. 20). Of these taxa, the shape of the posterior coracoid portion and the relative proportions of the intercoracoidal foramen in *Thalassamedon*, *Styxosaurus* and *Hydralmosaurus* closely resemble those of Queensland specimens.

Scapula. QMF3567. Of both scapulae only the posterior portions of the glenoid fossa, coracoidal articular surface and the basal sections of the dorsal process are preserved (Fig. 5B). Both, the glenoid fossa and the coracoidal articular surface bear heavy rugosities and have a triangular outline in posterior view. The coracoidal articular surface is about 1.5 × as wide as the glenoid fossa. The latter is anteriorly oriented with an angle of about 60°. The basal section of the dorsal process is situated on the dorsomedial side of the fragment. Its surface as preserved has a slight medial orientation and its posterior edge is away from the lateral corner of the glenoid fossa, at a distance that is about equal with the length of the coracoidal facet. Towards the base of the dorsal process the upper surface of the scapula is dorsally convex. The lateral side of the scapula is flat and only at the level of the dorsal process somewhat concave. The medial side of the scapula bears a sharp edge that emerges posteriorly out of the surface of the coracoidal articular surface and forms the lateral edge of the scapular foramen. The ventral side of the scapula is flat and only somewhat curved posteriorly towards the articulation surfaces.

RMF R271. Both scapulae are almost completely preserved (Fig. 5C), in which in both only parts of the dorsal process are missing. The distal section resembles that of QMF3567 and shall therefore not be described. The medial side of the shaft is, in ventral view, slightly concave. Along the midline of the ventral side of each scapula a rather broad ridge is present, starting at the lateral

FIG. 6. QMF3567; ?interclavicle fragment in ventral view. Scale = 3cm.

edge of the glenoid fossa and running with a slight convex curvature to the middle of the anterior end of the scapula. Here the ridge separates the medial part of the anterior scapula and the dorsal process. The medial part of the anterior portion of the scapular is expanded medially. Its ventral surface is plain. The long axis of the dorsal process is oriented at an angle of about 120° to the medial shaft. Its lateral surface is clearly concave. The dorsal process is most complete in the left scapula. From the anteromedial corner the anterior edge of the dorsal process runs lateroventrally at an angle of about 60° to the horizontal. In anterior view both sections run lateromedially away from each other in a wide V. Dorsally, the surface medial to the dorsal process is clearly concave.

Remarks. It is synapomorphic among elasmosaurids that the coracoidal surface of the scapula is larger than the glenoid fossa (mostly by about 1.5 ×). The angle by which the surfaces stand to each other is variable between taxa. The shaft of the scapula, while proportionally long in RMF R271, is shorter in *Microcleidus* (Watson, 1909: fig. 1), *Occitanosaurus* (Bardet et al., 1999: pl. 3) and *Brancasaurus* (Wegner, 1914: pl. 9). In these taxa the dorsal process is also rather slender and posterodorsally expanded. The dorsal process is not as slender in *Muraenosaurus*, but still more elongate than in RMF R271 (Andrews, 1910: pl. 6). In *Callawayasaurus*, the dorsal process is also more elongate than in RMF R271 and so is the anteromedial section of the scapula (Welles, 1962: pl. 4). In *Libonectes* the shaft of the scapula is similar to those of the Queensland specimens, but is more robust and posteriorly curved in the anteromedial section (Welles, 1949: fig. 2). This is also the case in *Elasmosaurus* (Welles, 1943: fig. 4) and *Thalassamedon* (Welles, 1943: pl. 23). In the later, the dorsal process is also almost vertically directed. In *Hydrotherosaurus*, the scapula is more robust and medially oriented in the anterior sections and here also more medially expanded than in RMF R271 (Welles, 1943: fig. 8). Of *Hydralmosaurus* scapulae are present in AMNH 5835. They are similar to those of RMF R271, but more robust in the anteromedial sections (Welles, 1962: fig. 17). The scapulae of *Styxosaurus* (Welles & Bump, 1949: fig. 4) are very similar to those of the Richmond specimen, except that the shaft is somewhat shorter and the dorsal process is seemingly more expanded.

? Interclavicle. QMF3567. The present fragment is incompletely preserved (Fig. 6). The dorsal surface of the fragment is flat, while on the ventral surface the base of a sagittal keel is apparent. On both sides of the keel the surface is slightly concave. This fragment closely resembles a fragment of the holotype material of *Thalassomedon hanningtoni* (DMNH 1588), which Welles (1943: fig. 14) described as part of an interclavicle.

Clavicles. RMF R271. Both clavicles are present in the Richmond specimen. The left one is almost complete, while of the right only the most anterior section is preserved (Fig. 7). The clavicular symphysis is straight and only barely visible. Ventrally the surface on both edges of the symphyses is slightly thickened and convex, forming an anteroposteriorly running ridge that is better preserved in the anterior portion. Each clavicle wing is posteriorly oriented by an angle of about 115° of its long axis to the symphysis. Thus they are divided from each other by a wide angle, giving them a boomerang-like outline. The ventral surfaces of the bones are slightly convex and only the posterior edge is clearly inclined ventrally. The posterior part of the clavicles is preserved on the left one. It shows that the bone becomes narrower lateromedially towards its posterior end. The posteriormost preserved section is slightly convex in cross-section, and flattened dorsoventrally.

Remarks. Clavicles are only known in a few elasmosaur taxa. They have been described or figured for *Occitanosaurus* (Bardet et al., 1999, plate 3), *Microcleidus* (Watson, 1909: fig. 1), *Muraenosaurus* (Andrews, 1913: pl. 6), *Brancasaurus* (Wegner, 1914. pl. 9), *Thalassamedon* (Welles, 1943. pl. 23), *Callawayasaurus* (Welles, 1962: pl. 4), *Hydralmosaurus* (Welles, 1962: fig. 17) and *Libonectes* (Welles, 1949: fig. 2). In early taxa such as *Occitanosaurus*, *Muraenosaurus*, *Microcleidus* and *Brancasaurus*, the clavicles are rather short and not boomerang like shaped as in RMF R271. In *Libonectes* each clavicle wing is anteroposteriorly slender in its midsection and the anterior and posterior ends of the clavicular symphysis are separated. In *Hydralmosaurus* the clavicles are incomplete and in *Thalassamedon* they are less curved posteriorly and together form a rather straight posterior surface. In *Callawayasaurus* the clavicles are similar to RMF R271 in general shape, but they are clearly shorter lateromedially.

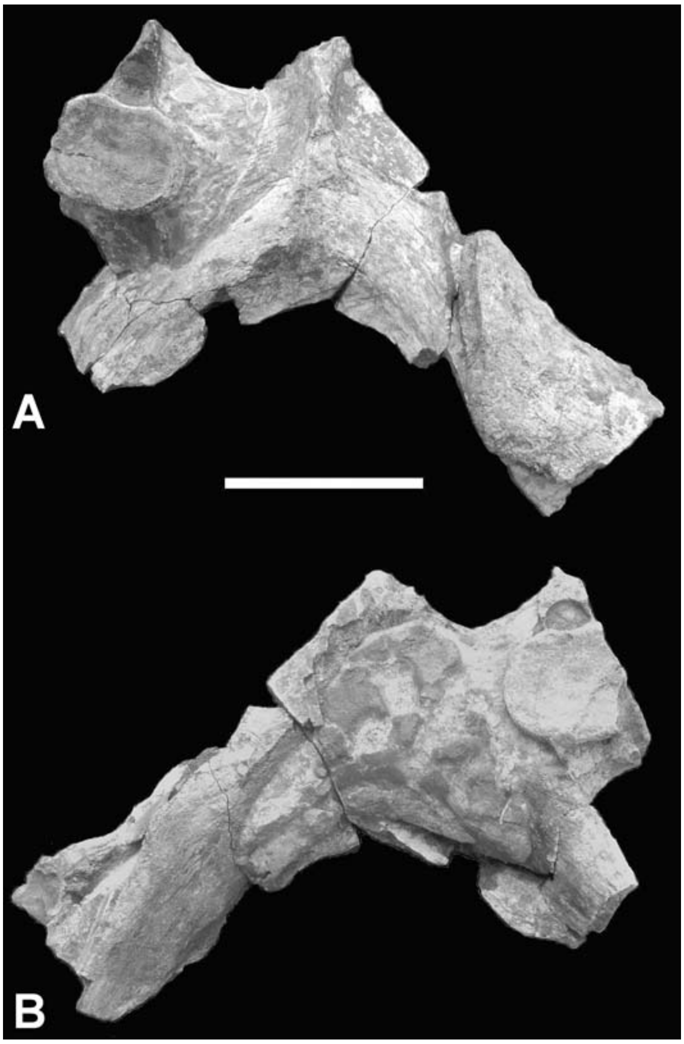

FIG. 7. RMF R271; clavicles in ventral (A) and dorsal (B) view. The flat element attached with the left clavicula arch might belong to a girdle element. Scale = 10cm.

Humerus. QMF3567, F3568. The holotype material includes the right humerus (Fig. 8A). This element is badly crushed and lacks the posterior mid-shaft section. Persson (1960) referred another, left, humerus (QMF3568) to the same individual, although its locality and the identity of the collector are unknown. As this specimen perfectly corresponds with the humerus of QMF3567, in shape and size, the author agrees with Persson's referral. This second specimen is less crushed than the preserved right humerus, but lacks the entire articular surface for the ulna. In general, the humeri are very stout and about one fifth longer than the femora. The capitulum is very prominent and occupies about two third of the proximal surface of the humerus. In proximal view, it has a broad oval outline, in anterior view it is very convex. The tuberosity is situated at a somewhat lower level than the capitulum, and proximally is separated from it by a shallow fossa. The tuberosity is also slightly displaced posteriorly. The entire proximal articulation surface is broader than the proximal shaft. The shaft is very short and robust and especially proximally broad oval in cross-section. Distally, it becomes gradually flattened lateromedially to a point in the lower third of the bone's length and then rapidly to the distal articulation surface. The

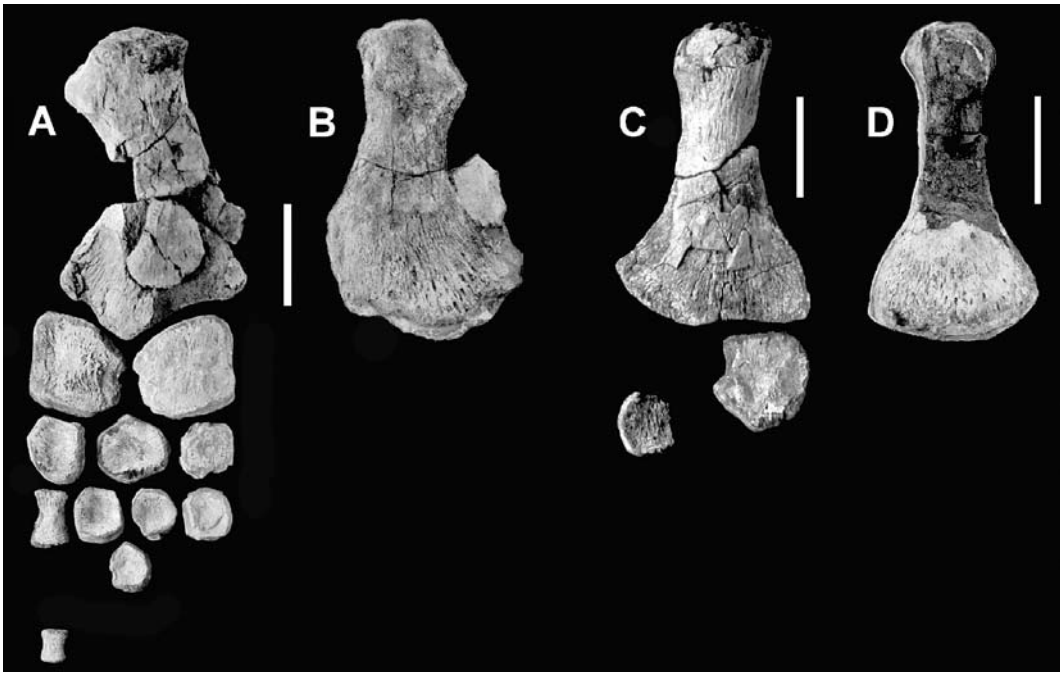

FIG. 8. A, Pectoral paddle. Humerus (QMF3568), radius, ulna, carpalia and metapodial elements (QMF3567). B, RMF R271, left humerus. C, QMF3567, pelvic paddle, showing the femur, fibula and ?metatarsal. D, RMF R271, right femur. Scales = 10cm.

distal portion of the bone widens anteroposteriorly. The radial articular surface is 1.5 × larger in area than the ulnar one. Both articular surfaces are slightly concave and mediodistally directed in lateral aspect. At the intersection of both articular surfaces there is a broad, blunt tip. The whole distal surface is inwardly concave. On the anterodistal side, a sharp ridge is present, extending onto the middle of the shaft. The posterodistal surface also bears a ridge along its edge about half as long as the anterior one.

RMF R271. Both humeri are preserved (Fig. 8B). Of these the right one is complete, while the left one is missing the distal articulation surfaces. Their shape resembles well that of the humeri of QMF3567 and F3568, except that the posterior edge of the shaft is more prominently convex.

Remarks.. In early elasmosaurs such as *Occitanosaurus* (Bardet et al., 1999: pl. 3), *Muraenosaurus* (Andrews, 1910: pl. 5), *Microcleidus* (Watson, 1911: fig. 2) and *Brancasaurus* (Wegner, 1914: pl. 9), the humeri and femora are not very distinct from each other in size and shape and can be described as rather long and gracile. The size difference of the femur and humerus of the Queensland specimen may relate to ontogenetic stage, so that this cannot be taken as a taxonomic feature. The general shape and proportions are very similar to those of the humeri of *Styxosaurus snowii* (Welles & Bump, 1949: fig. 5).

Ulna. QMF3567. Only one ulna is preserved (Fig. 8A). It is almost quadratic in outline in lateral view. The proximal margin is the longest side of the bone. Its medial margin is oriented anterodistally at an angle of about 45° to the horizontal. The anterior side of the ulna is the shortest. It bears a notch in its mid-surface that is deeper medially than laterally. The distal surface of the ulna is slightly shorter than the proximal one. At its most anterior section, where it connects to the intermedium, the distal margin is oblique proximally at an angle of about 40° to the horizontal. The distal and the proximal surfaces are long oval in outline in distal and proximal aspect. The posterior margin of the ulna is straight and almost as long as the proximal one. It is lateromedially flattened, and bears a blunt crest.

Remarks. The shape of the ulna varies within the genera of the Elasmosauridae. In early elasmosaurids, such as *Occitanosaurus* (Bardet et al., 1999: pl. 3) and *Microcleidus* (Watson, 1911: fig. 2) the ulna is a semi-circular element, while in *Muraenosaurus* (Andrews, 1910: pl. 4) and *Hydrotherosaurus* (Welles, 1943: pl. 19) its outline is more rectangular in lateral view. The rather quadratic shape of QMF3567 is also found in *Styxosaurus* (Welles & Bump, 1949: fig. 5), *Thalassomedon* (Riggs, 1939: fig. 111), *Terminonatator* (Sato, 2003: fig. 13), *Callawayasaurus* (Welles, 1962) and *Mauisaurus* (Welles & Gregg, 1971: fig. 9).

Radius. QMF3567. The radius is broader and more robust than the ulna, but has a similar size and is almost quadratic in outline (Fig. 8A). The distal surface is long oval in outline and relatively broad in distal view. The posterior side is the shortest, and bears a broad notch in its mid-section that is deeper medially than laterally. The proximal and distal surfaces are equally shaped, but the proximal surface is oriented posterodistally at an angle of about 30° to the horizontal. The anterior surface is somewhat longer than the distal one and rather straight. Its edge bears a blunt crest that is relatively smaller than that of the ulna. In contrast to the ulna, a clearly deeper depression is developed at the medial surface of the bone.

Remarks.. Mostly the radius is clearly larger than the ulna as in *Muraenosaurus* (Andrews, 1910: fig. 63), *Terminonatator* (Sato, 2003: fig. 13) or *Thalassomedon* (Riggs, 1939: fig. 111 – here the radius was determined as ulna). In *Styxosaurus*, however, the radius and ulna are about the same size as each other. In most elasmosaurids, the shape of the ulna is roughly rectangular. This condition is seen in *Occitanosaurus* (Bardet et al., 1999: pl. 3), *Microcleidus* (Watson, 1911: fig. 2), *Hydralmosaurus* (Watson, 1909: fig. 9), *Hydrotherosaurus* (Welles, 1943: pl. 13), *Mauisaurus* (Welles & Gregg, 1971: fig. 7) and *Thalassomedon.* A similar, more quadratic radius is present in *Muraenosaurus* (Andrews, 1910: fig. 63), *Libonectes* (Welles, 1949: fig. 3), *Callawayasaurus* (Welles, 1962: pl. 4) and *Styxosaurus* (Welles & Bump, 1949: fig. 5).

Carpalia. QMF3567. There are 9 carpals represented in the holotype material (Fig. 8A). Because of the bad preservation only the intermedium clearly could be identified. In relation to the tarsal and the fibula, the carpalia are clearly more thickened and more robust, so probably belong into the fore-paddle. One element is somewhat larger and of about quadratic shape and is interpreted as either the radiale or the ulnare. The intermedium is roughly hexagonal in outline, with all its sides approximately the same length. It also is relatively robust and clearly broader than the fibula. Therefore it might represent the intermedium of the fore-paddle.

RMF R271. An in situ block contains in original arrangement the radiale and intermedium. Only the anteroventral surface of the radiale is preserved, while the intermedium is complete and resembles in shape that of QMF3567.

Metapodials/Phalanges. QMF3567. Two ?metacarpals and one phalange are included in the holotype material (Fig. 8A). The ?metacarpals, of which one is completely preserved, while the other is only represented by its proximal section, are very robust and are interpreted as belonging to the fore-paddle. They are elongate dorsoventrally, constricted on the anterior and posterior sides and have a broadened proximal end that is broad-oval in proximal view. The preserved phalange is only about half as large as the ?metacarpal. It is stout and not much higher than it’s wide. It is therefore interpreted as belonging to the distal portion of the paddle.

RMF R271. The metacarpal I-III, as well as seven phalanges are preserved, which because of their size, can clearly be determined as belonging to the pectoral paddle. The metacarpals are of circular shape and are somewhat shorter than the proximal phalanges. In addition, 19 phalanges are present. It cannot be determined whether these elements belong to the pectoral or pelvic paddle.

Femur. QMF3567. Both femora are presented in the material of QMF3567 (Fig. 8C). The right femur is completely preserved, while the left is missing its antero- and posterodistal surfaces. The femora are relatively stout and robust, but clearly more slender than the humeri. Their proximal articular surface bears a prominent capitulum that is nearly circular in outline in proximal view. In anterior view it can be seen that the capitulum clearly slopes down, at an angle of about 45° to the horizontal. The trochanter is situated medially; it is separated from the capitulum by a shallow dorsoventral depression in the posterior surface. The entire proximal surface of the trochanter is distally oriented and eroded in both specimens. It also is weakly constricted from the proximal portion of the shaft. The shaft is relatively short and has equally slightly curved anterior and posterior edges. In cross-section it is nearly circular proximally, becoming flattened anteroposteriorly in about its distal fourth. A crest like structure is present at the junction of the anterior and posterior edges. Of these the posterior one is very prominent and reaches to the proximal end of the lower third of the bone. The anterior crest is somewhat shorter than the posterior one and terminates in the proximal end of the lower fourth of the bone-length. The articulation facets for the tibia and fibula are well preserved in the right femur. The fibular facet is about 1.5 × larger than the tibial one. Its surface is nearly straight in lateral view, while the tibial facet is clearly proximally curved and therefore slightly convex. At the intersection of both facets a broad, very shallow tip is developed. In distal view, the distal end of the femur has an elliptical outline and is somewhat inwardly concave.

RMF R271. The general shape of the femur resembles that of the femora of QMF3567. Only the distal surface is differently shaped (Fig. 8D), in which no lip-projections are present on the anterior and posterior side and the articular surfaces are not as well developed as in QMF3567. The latter might partially be due to erosion.

Remarks. As with the humeri, the size of the femora can vary during ontogeny. The only femora of similar shape to that of QMF3567 and RMF R271 are those of *Styxosaurus* (Welles & Bump, 1949: fig. 5), *Hydralmosaurus* (Welles, 1962: fig. 16), *Terminonatator* (Sato, 2003: fig. 13) and *Callawayasaurus* (Welles, 1962: pl. 4). In QMF3567, *Styxosaurus*, *Callawayasaurus* and *Terminonatator*, the anterior and posterior sides of the shaft are about equally slightly concave, but in *Hydralmosaurus* the anterior side is rather straight and the posterior one strongly concave

Fibula. QMF3567. In the material of QMF3567, there is an eroded, somewhat pentagonal shaped bone that is interpreted as the left fibula (Fig. 8C). It is clearly smaller and more slender in lateromedial diameter than the radius and ulna. The proximal side is nearly straight and moderately thickened lateromedially. The posterior side of the element is slightly convex. The articular facets for the fibulare and intermedium are about equal in lengths and are anterodistally directed at an angle of about 45° to the horizontal. The fibulare facet is somewhat more thickened lateromedially. Of both facets the intermedium one is the largest. The anterior side of the fibula is the smallest side of the bone. Its entire surface is concave.

RMF R271. One ?fibula is present in the Richmond material. It resembles the shape of that present in QMF3567 and shall therefore not be described.

Remarks. The fibula is mostly more rectangular in shape as it can be found in *Occitanosaurus* (Bardet et al., 1999: pl. 4), *Thalassomedon* (Welles, 1943: pl. 24), *Hydrotherosaurus* (Welles, 1962: fig. 16), *Muraenosaurus* (Andrews, 1910: pl. 4) and *Mauisaurus* (Welles & Gregg, 1971: fig. 4, here wrongly determined as a tibia). In *Styxosaurus* (Welles & Bump, 1949: fig. 5), *Terminonatator* (Sato, 2003: fig. 13) and *Hydralmosaurus* (Welles, 1962: fig. 16) the shape of the fibula is more quadratic in outline. Distally, the articular facets are usually oriented at a lower angle to each other than in the fibula of QMF3567. In addition, the fibulare facet is mostly somewhat larger than the intermedium one (e.g. in *Occitanosaurus*, Bardet et al., 1999, *Thalassamedon*, Welles, 1943 and *Hydralmosaurus*, Welles, 1962). The fibula is similar in size and shape to that of *Callawayasaurus* (Welles, 1962: fig. 5).

Tarsalia. QMF3567. Only a single element could be identified as tarsal (Fig. 8C). It is more flattened than the other mesopodials of similar size and has a rectangular outline. At one side, the edge is crest-like and is slightly concave. The sides opposite of the latter, as well as the proximal and distal surfaces are broader. In comparison, it is very similar with the first tarsal of *Styxosaurus*, shown by Welles & Bump (1949: fig. 5), but somewhat more dorsoventrally elongate in shape.

Pubis. RMF R271. The pubes are incompletely preserved and represented by both symphysial sections, as well as the articular facets for the ischium and acetabulum on the right pubis. The symphysis that is completely preserved on the right pubis is almost straight. The medial part of the pubis is thickened dorsoventrally. In about the middle of the symphysial surface a broad, low ridge is visible dorsally. The medial surface also bears slight rugosities. At the most anterior section the symphysial surface becomes somewhat lower dorsoventrally and is slightly anterolaterally directed. The posterior edge of the pubis that formed the anterior frame of the foramen obturatum is very thin and, as preserved, slightly inwardly concave. The articulation section is massively developed. Both articulation facets stand to each other by an angle of about 110°. The acetabular surface is about 1.5 × the size of the ischial one and is somewhat depressed. In posterior view the acetabular surface has a broad-oval outline. The ischial surface is triangular in shape; the facet surface is plain and bears rugosities.

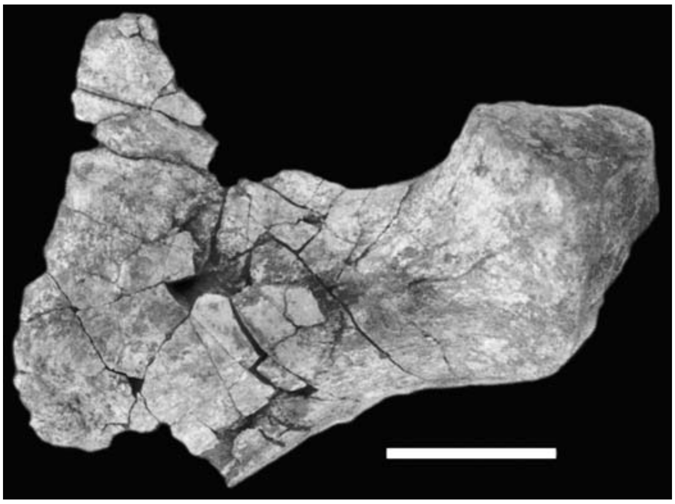

FIG. 9. RMF R271; right ischium in dorsal view. Scale = 5cm.

? Pubis. QMF3567. Only two fragments have been identified as belonging to the pubes. One represents the posteromedial articulation section. It comprises two facets, a small facet to the ischium and a large facet that forms the anterior section of the acetabulum. The facet to the ischium is triangular in outline and has a nearly straight articular surface that bears rugosities. The acetabular section is about twice as long as the ischial one and projects anterolaterally at an angle of about 45° to the horizontal. At the anterior side of the acetabular facet a thin edge is developed, running anteriorly. While the dorsal side of the fragment is strongly convex, the ventral surface is rather straight. In the holotype material, there is another fragment that clearly belongs to a girdle-element. After a detailed comparison, this fragment seems to appear in the medial part of the pubis. Its dorsal surface is shallowly concave, while the ventral surface is convex on one (probably the medial) side, where an articulation surface is developed. This surface probably represents the interpubic symphysis. It is relatively straight and bears some rugosities.

Remarks. In *Microcleidus* and *Occitanosaurus* the anterior section of the interpubic symphysis is strongly oriented anterolaterally and also the ischial and acetabular surfaces in these taxa stand to each other in a wider angle than in RMF R271 (Watson, 1909: fig. 11; Bardet et al., 1999: pl. 4). This is the case in *Muraenosaurus* too, where the acetabular surface is also clearly more prominent than in RMF R271 (Andrews, 1910: fig. 65). In *Brancasaurus* the anterior section of the medial symphysis is strongly oblique anterolaterally, the acetabular facet is about twice as large as the ischial one and the edge of the foramen obturatum is narrower and more concave than in the Richmond specimen (Wegner, 1914: pl. 9). *Hydralmosaurus* has a shorter medial symphysis and the edge for the foramen obturatum is more concave and narrower than in RMF R271. Also the most anteromedial section is clearly oblique laterally (Welles, 1962: fig. 16). In *Thalassamedon* a shorter interpubic symphysis is developed that shows no vault in the midsection and the edge of the foramen obturatum is wider than that in RMF R271 (Welles, 1943, pl. 23). In *Hydrotherosaurus* a very prominent acetabular articulation surface is present, which is clearly more prominent than the ischial one. The edge for the foramen obturatum is narrower and more concave than in RMF R271 and the interpubic symphysis is strongly curved laterally in the anterior half (Welles, 1943, fig. 9). *Elasmosaurus* has a narrower and more concave edge of the foramen obturatum, the anterior section of the pubis is well oblique anterolaterally and the acetabular articulation surface is about twice as long as the ischial one (Welles, 1963, fig. 14). The pubis of *Mauisaurus* is rather similar to RMF R271, only the interpubic symphysis is straight for its entire length (Welles & Gregg, 1971: fig. 4). In *Callawayasaurus* the edge of the foramen obturatum is narrower, but similarly slightly concave than in RMF R271 (Welles, 1962, plate 4). The pubis of *Styxosaurus* resembles in its general shape that of RMF R271 (Welles & Bump, 1949, fig. 4).

?Ilium. QMF3567. A fragment in the holotype material is interpreted as to be the ventral part of an ilium. The ventral section, that bears the articulation surface, is somewhat thickened.

TABLE 1. Measurements (in cm) of the vertebrae of QMF3567 and RMF R271. CV = Cervical vertebrae; PV = pectoral vertebrae; DV = dorsal vertebrae; SV = sacral vertebrae; CAV = caudal vertebrae; ic = incomplete; nm = not measurable.

QMF3567				RMF R271			
	Length	Width	Height		Length	Width	Height
Axis	3.5	ca. 2.5	ca. 2.5				
CV 1	5	4.6	3.2	CV 1	6	6	4.8
CV 2	5	4.8	3.2	CV 2	6.5	7	5.2
CV 3	5.4	5	3.6	CV 3	6.9	7 i.c.	5.5
CV 4	5 ic	4.3 ic	3.3 ic	CV 4	7	7.5 i.c.	5.5
CV 5	6.3	5.1 ic	4.6	CV 5	6.9	6	nm
CV 6	6.3	5.8	4.3	CV 6	6.5	8	6
CV 7	6.6	6.1	4.6	CV 7	6.8	7.5	5.5
CV 8	6.7	6.2	4.8	CV 8	6.3	6 i.c.	4.7
CV 9	7.3	7.6	5.4	CV 9	6.2	8 i.c.	6
CV 10	7.4	7.2 ic	5.5	CV 10	6.8	7.8	5.8
CV 11	7.9 ic	6.4 ic	5.6	CV 11	6.5	8	6 i.c.
CV 12	7.8	8	6.1	CV 12	6.5	8	6
CV 13	7.6	8 ic	6.2	CV 13	6.2	8.5 i.c.	5.8
CV 14	7.2	8.5 ic	6.4	CV 14	6.8	8.5 i.c.	6.5
CV 15	7.1	8 ic	6.4	CV 15	6.3	8.7	6
CV 16	7.6	8.5	6.3				
CV 17	7.6	8.3 ic	6.3				
CV 18	7.2	9.2	6.4				
CV 19	7.4	9.1	6.4				
CV 20	7.1	8.5 ic	6.4				
CV 21	7.2	9 ic	6.4				
CV 22	6.8	9.4 ic	6.7				
CV 23	6.8	9.8	6.8				
CV 24	7.1	9.7	6.8				
PV 1	7	9.5	7.2	PV 1	6.4	9.3	6.2
PV 2	7	9.3 ic	6.8	PV 2	6.3	nm	6
PV 3	7	9.7	6.5	PV 3	6.5	9.4	6.3
DV 1	7.2	8.5	7.4	DV 1	6.2	9.3	6.4
DV 2	7	8.5 ic	7.2	DV 2	6	8.8	6.2
DV 3	6.9	8.5	7.5	DV 3	6.4	8.8	6.8
DV 4	6.8	8.3	7.5	DV 4	6.4	9	6.4
DV 5	6.8	8.1	7.3	DV 5	6.2	nm	6.5
DV 6	6.8	8	7.9	DV 6	-	6.5	5
DV 7	6.7	7.8	7	DV 7	nm	7.2	nm
DV 8	6.4	7.7	7	DV 8	6	nm	nm
DV 9	5.2	7.2	5.8	DV 9	nm	6.5	6.5
				DV 10	nm	7.5	6.8
				DV 11	nm	8	7.6
				DV 12	nm	7.8	6.9
				DV 13	5.9	7.4	6.9
				DV 14	5.4	7.7	6
				DV 15	5	7.7	5.6
				DV 16	6.2	7.8	nm
				DV 17	5	7.2	5.7
CAV 1	4.8	7.7	5.5	CAV 1	4.3	7	5.5
CAV 2	4.7	7.3	5.7	CAV 2	4	7.3	6
CAV 3	4.2	8	5.6	CAV 3	4.3	nm	5.3
CAV 4	4.5	7.6	4.7 ic	CAV 4	3.8	6.8	5.4
CAV 5	4.8	4	5.7	CAV 5	4.1	6.9	5.7
CAV 6	4.2	6.6	5.4	CAV 6	3.9	6.7	5.4
CAV 7	4.5	nm	nm	CAV 7	3.6	6.3	5.3
SV 1	5.3	7.4	5.8	CAV 8	3.2	5.8	4.9
SV 2	5	7.1	5.5	CAV 9	3.8	6.2	5.5
SV 3	4.6	7.6	5.3	CAV 10	3.4	nm	nm

Above the articulation surface, the bone is more or less quadratic in cross-section. The anterior and proposed medial side of the fragment are about equal in length and have a nearly flat surface. The proposed lateral side, as well as the posterior one are strongly outwardly curved. The posterior side is shorter than the others. The dorsal end of the fragment is vertically oval in cross-section.

Ischium. RMF R271. Both ischia are present. The right one is almost complete, while of the left only the medial section is preserved (Fig. 9). The interischial symphysis is rather straight and only in its posterior third slightly posterolaterally curved. The symphyseal surface thins out dorsoventrally in about the posterior third, towards the posterior end. The anterior surface of the ischium is very thin and inwardly curved, forming the posterior frame of the foramen obturatum that is wide and well concave. The posterior side of the ischium is posteromedially curved, from the posterior border of the acetabular surface to the posterior end of the symphysis. In medial view the symphysis is very slightly sigmoidally curved. The laterally situated articulation facets are very massive. The pubic surface has a triangular outline in anterior view and bears some weak rugosities. The acetabular surface has about 1.5 × the size of the pubic one and is somewhat triangular in outline. It is more expanded posteriorly and its posterodorsal surface slightly oriented ventrally. In general the ventral surface of the ischium is slightly convex, the dorsal one slightly concavely formed.

QMF3567. One fragment represents the most posteromedial part of an ischium. Its medial surface is thickened dorsoventrally, but corroded. The preserved lateral edge is thin, but not sharp. It is strongly curved posterolaterally.

Remarks. In *Occitanosaurus*, *Brancasaurus* and *Muraenosaurus* the ischia are more expanded mediolaterally, the edges of the foramina obturata are deeply concave and the acetabular facet is larger compared with the ischial one, than in RMF R271 (Bardet et al., 1999; Wegner, 1914; Andrews, 1910). In *Microcleidus* the ischia are more expanded anteroposteriorly and the edge of the foramen

TABLE 2. Measurements (in cm) of QMF3567 and RMF R271.

QMF3567		RMF R271	
Scapula (left)		Scapula (left)	
Anteroposterior length	16.6 ic	Anteroposterior length	32
Diameter of distal articulation surface	11.7	Width of distal articulation surface	12.5
Diameter of glenoidal surface	5.3	Diameter of glenoidal surface	6.5
Diameter of coracoidal surface	5.5	Diameter of coracoidal surface	6.5
Length of glenoidal surface	5.8	Length of glenoidal surface	7
Length of coracoidal surface	7	Length of coracoidal surface	9.3
		Width of the anterior end	13
		Length anteropost. of dorsal process	24
		Dorsal process, greatest preserved expansion	10
Scapula (right)		Scapula (right)	
Anteroposterior length	19.5 ic	Anteroposterior length	29
Diameter of distal articulation surface	12.5	Width of distal articulation surface	12.5
Diameter of glenoidal surface	4.5 ic	Diameter of glenoidal surface	7
Diameter of coracoidal surface	4.8 ic	Diameter of coracoidal surface	6.5
Length of glenoidal surface	5.8	Length of glenoidal surface	7
Length of coracoidal surface	7.4	Length of coracoidal surface	7
		Width of the anterior end	12
		Length anteropost. of dorsal process	21
		Dorsal process, greatest preserved expansion	6
Coracoid (left)		Coracoid (left)	
Anteroposterior length	18 ic	Anteroposterior length	44 ic
Length of glenoidal surface	9.5	Length of glenoidal surface	9
Length of scapular surface	7.5	Length of scapular surface	7
Transverse expansion of medial vault	11	Transverse expansion of medial vault	7.5
		Width of posterior blade	26
		Length of anterior symphysis	20 ic
Coracoid (right)		Coracoid (right)	
Anteroposterior length	24 ic	Anteroposterior length	48 ic
Width of posterior blade			25.5
Length of glenoidal surface	nm	Length of glenoidal surface	11
Length of scapular surface	nm	Length of scapular surface	8
Length of anterior symphysis			23.5
Transverse expansion of medial vault	nm	Transverse expansion of medial vault	7.5
?Interclavicle		Clavicles	
Length anteroposteriorly	6 ic	Length anteroposteriorly, left	24.5 ic
Height dorsoventrally	2.3	Length anteroposteriorly, right	15 ic
		Length of symphysis	11.5
Humerus (left; QMF3568)		Humerus (left)	
Total length	31.5	Total length	32
Width distal	20	Width distal	18 ic
Lateromedial diameter of capitulum	3.5	Lateromedial diameter of capitulum	6.5
Lateromedial diameter of tuberosity	7.5	Lateromedial diameter of tuberosity	2.8
Anteroposterior diameter of capitulum	10.2	Anteroposterior diameter of capitulum	9
Anteroposterior diameter of tuberosity	10.7	Anteroposterior diameter of tuberosity	8.2
Humerus (right)		Humerus (right)	
Total length	31.5	Total length	26 ic
Width distal	nm	Width distal	nm
Lateromedial diameter of capitulum	7.4	Lateromedial diameter of capitulum	nm
Lateromedial diameter of tuberosity	3.9	Lateromedial diameter of tuberosity	nm
Anteroposterior diameter of capitulum	9.8	Anteroposterior diameter of capitulum	nm
Anteroposterior diameter of tuberosity	10.6	Anteroposterior diameter of tuberosity	nm

TABLE 2 (*Cont.*)

Ulna		Intermedium manus	
Anteroposterior length	10.5	Lateromedial width	7
Dorsoventral height	10.3	Dorsoventral height	8
Lateromedial diameter	4.2	Radiale manus	
Radius		Width	7.2
Anteroposterior length	11.4	MC I	
Dorsoventral height	10.5	Lateromedial width	6.5
Lateromedial diameter	5.4	Dorsoventral height	5.5
Intermedium manus		MC II - Lateromedial width	6
Lateromedially diameter	7	Dorsoventral height	5.2
Dorsoventral height	8	MC III – Lateromedial width	6.5
		Dorsoventral height	6.2
Femur (left)		Femur (left)	
Total length	27.5	Total length	nm
Width distal	18	Width distal	14
Lateromedial diameter of trochanter	4.3	Lateromedial diameter of trochanter	2
Lateromedial diameter of capitulum	6.5	Lateromedial diameter of capitulum	10
Anteroposterior diameter of trochanter	7.2	Anteroposterior diameter of trochanter	5.2
Anteroposterior diameter of capitulum	8.8	Anteroposterior diameter of capitulum	7.6
Femur (right)		Femur (right)	
Total length	26.5 ic	Total length	31
Width distal	nm	Width distal	16
Lateromedial diameter of trochanter	3.8	Lateromedial diameter of trochanter	nm
Lateromedial diameter of capitulum	7	Lateromedial diameter of capitulum	8
Anteroposterior diameter of trochanter	7.2	Anteroposterior diameter of trochanter	nm
Anteroposterior diameter of capitulum	9	Anteroposterior diameter of capitulum	9.2
Fibula		Pubis (left)	
Anteroposterior diameter	8.5	Length along symphysis	24.2
Lateromedial diameter	2.5	Length acetabular surface	nm
Dorsoventral height	9	Length ischial surface	nm
?Metatarsal I		Pubis (right)	
Anteroposterior diameter	5	Length along symphysis	17 ic
Lateromedial diameter	2.1	Length acetabular surface	7
Dorsoventral height	6	Length ischial surface	6
?Ilium		Ischium (left)	
Anteroposterior diameter	7	Width lateromedially	nm
Lateromedial diameter	6	Length along symphysis	20
Dorsoventral height	7.6	Length pubic articular surface	nm
		Length acetabular surface	nm
		Ischium (right)	
		Width lateromedially	21.5
		Length along symphysis	16.5 ic
		Length pubic articular surface	5.2
		Length acetabular surface	10

obturatum is more oriented posteromedially than in RMF R271 (Watson, 1909: fig. 11). In *Mauisaurus* the acetabular surface is larger and the posterior edge more concave than in RMF R271 (Welles & Gregg, 1971: fig. 8). In *Callawayasaurus* the ischium is generally more slender and posteromedially expanded, the edge for the foramen obturatum is posteromedially oriented and the acetabular surface is more prominent in relation to the pubic one as in RMF R271 (Welles, 1962: fig. 6). This is also the case in *Hydrotherosaurus*, except that the edge for the foramen obturatum is not as strongly oriented posteromedially (Welles, 1962: fig. 20). In *Hydralmosaurus* the edge for the foramen obturatum is less anteriorly curved in the medial section, the ischia are more robust and seem to be more expanded posteriorly than in RMF R271. Also the acetabular facet is more prominent in relation to the pubic one than in the Richmond specimen (Welles, 1962: fig. 16). In *Thalassamedon* the edge of the foramen obturatum is wider, the interischial symphysis is straighter and the ischia seem to be more expanded anteroposteriorly than in RMF R271. Also in *Elasmosaurus* the ischia are more elongate anteroposteriorly, the posterior edge is clearly posteriorly curved, the acetabular surface is more prominent and the edge of the foramen obturatum is narrower but more concave than in RMF R271 (Welles, 1962: fig. 14). In *Styxosaurus* the general shape resembles well that of the ischia of the Richmond specimen, only the posterior edge is more posteriorly oriented (Welles & Bump, 1949: fig. 4).

Unidentified Girdle Elements. There are numerous indeterminable, flat fragments preserved, which seem to belong to parts of the pectoral or pelvic girdle.

CONCLUSIONS

From the above comparisons it is evident that specimens QMF3567, QMF3568, QMF2634 (described as *Woolungasaurus glendowerensis* by Persson; 1960), and RMF R271 are most similar to material referred to *Styxosaurus*. *Styxosaurus* is known by one valid species, *S. snowii*, from the western interior of North America. All specimens so far have been found in sediments of Campanian age (Carpenter, 1999: 158-160), so that the Queensland *Styxosaurus* from the Aptian is the earliest record of this taxon and the first in the Southern Hemisphere.

The main osteological differences between *Styxosaurus snowii* and the Queensland specimens are the absence of a prominent transverse keel on the anterior portion of the coracoid, a more slender scapula, a relatively more slender femur and a fibula with pentagonal outline. All other elements described are almost identical or very similar to those of *Styxosaurus snowii*.

Facts that lead to the conclusion that *Woolungasaurus glendowerensis* is referable to *Styxosaurus* but distinct from *S. snowii* are the smaller size (it probably measured about 5m when fully grown, while the mounted skeleton of *Styxosaurus snowii* SDSM451 measures approximately 11m), its occurrence in the Southern Hemisphere and its older age. On the other hand, in the author's opinion, the differences are sufficient to confirm that *Woolungasaurus* is a junior synonym of *Styxosaurus*.

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