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A new elasmosaurid from the early Maastrichtian of Angola and the implications of girdle morphology on swimming style in plesiosaurs

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Abstract

We report here a new elasmosaurid from the early Maastrichtian at Bentiaba, southern Angola. Phylogenetic analysis places the new taxon as the sister taxon to *Styxosaurus snowii*, and that clade as the sister of a clade composed of (*Hydrotherosaurus alexandrae* (*Libonectes morgani* + *Elasmosaurus platyurus*)). The new taxon has a reduced dorsal blade of the scapula, a feature unique amongst elasmosaurids, but convergent with cryptoclidid plesiosaurs, and indicates a longitudinal protraction-retraction limb cycle rowing style with simple pitch rotation at the glenohumeral articulation. Morphometric phylogenetic analysis of the coracoids of 40 eosauropterygian taxa suggests that there was a broad range of swimming styles within the clade.

Keywords: Plesiosauria, locomotion, pectoral girdle, Elasmosauridae, marine reptiles

Introduction

We report here a new elasmosaurid plesiosaur from the early Maastrichtian of Angola, and provide a description and a phylogenetic analysis. The new taxon possesses unusual features of the limb and pectoral girdle morphology that suggest a peculiar mode of locomotion; we therefore also explore the implications of girdle morphology on swimming style in a phylogenetic morphometrics framework.

Plesiosaurs are members of the Eosauropterygia (Rieppel, 1994), which include pachypleurosaurs, nothosaurs and pistosaurs best known from the Middle Triassic epicontinental shallow seas of Europe and China (Rieppel, 2000). Elasmosauridae are regarded as the sister group of Cryptocleididae within Plesiosauria (Ketchum & Benson, 2010; Benson & Druckenmiller, 2014). The origin of Elasmosauridae is unclear but its record extends from the mid-Hauterivian (Evans, 2012) to the end of the Maastrichtian (Vincent et al., 2011).

By the earliest Jurassic, plesiosaurs were fully adapted to a pelagic lifestyle and two major Bauplans (plesiosauromorph and pliosauromorph) had emerged in multiple phylogenetic lineages (O'Keefe, 2001; Benson et al., 2012). Plesiosauromorphs have long necks and relatively small, anteriorly abbreviated heads, whereas the pliosauromorph Bauplan includes forms with larger elongate heads and relatively short necks (O'Keefe & Carrano, 2005). However, all plesiosaurs share unique features of their limbs and girdles amongst secondarily adapted Mesozoic marine reptiles. Swimming style based on paraxial quadrupedal locomotion is largely accepted (e.g. Watson, 1924; Robinson, 1975), although details of limb motion are more contentious (e.g. Thewissen & Taylor, 2007; Lingham-Soliar, 2000).

The morphological transition between terrestrial forms, presumably in the early Triassic, to fully marine forms known from the Jurassic and Cretaceous involves profound reorganisation of the girdle elements along with elaboration of the limbs as paddles in a unique body plan without modern analogue. Plesiosaurs likely share a distant relationship with terrestrial sprawlers (Rieppel, 1997, 2000) and on entry to the marine realm employed paraxial rowing (Schmidt, 1984; Storrs, 1986; Lin & Rieppel, 1998; for a different opinion see Sues, 1987). Within Diapsida, there are two primary modes of aquatic locomotion: limb-based swimming (e.g. turtles, penguins) and trunk-and-tail-based lateral undulation (e.g. varanoids, iguanids, crocodyliforms). Among extant paraxial swimmers there are two main styles: rowing (e.g. trionychid turtles) and underwater flying (e.g. sea turtles). In underwater rowing the main locomotory vector components are protraction and retraction, whereas in underwater flying the main locomotory vector component is adduction and abduction (Carpenter et al., 2010). Within plesiosaurs, both rowing and underwater flying have been proposed (Watson, 1924; Robinson, 1975; Carpenter et al., 2010). Araújo & Correia (in press) provide a detailed analysis of the pectoral myology of plesiosaurs.

In this contribution, we first describe the osteology of the new taxon and perform a character-based parsimony analysis to determine its phylogenetic position. We then perform an additional analysis employing a continuously variable morphometric character, a quantification of coracoid shape, to develop a testable model of evolution for this bone in Eosauropterygia. We conclude with a brief discussion of the implications of girdle and limb morphology and musculature variation on swimming style in plesiosaurs.

Materials and methods

Institutional abbreviations

CMN – Canadian Museum of Nature, Ottawa, Canada; IVPP – Institute for Vertebrate Paleontology and Paleoanthropology, Beijing, China; KHM – Kaikoura Historical Museum, Kaikoura, New Zealand; MGUAN – Museu de Geologia da Universidade Agostinho Neto, Luanda, Angola; SMF – Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany; TMM – Texas Memorial Museum, Texas, USA; YPM – Yale Peabody Museum, New Haven, USA.

Materials

MGUAN PA103 (Figs 2 and 3), complete pectoral and pelvic girdle, cervical and dorsal vertebrae, partial forelimb (humerus, radius and ulna and isolated phalanges) and several dorsal ribs. MGUAN PA270 (Mateus et al., 2012, Figure 11), pubis, ischium, femur and completely articulated posterior limb.

Phylogeny

Phylogenetic analyses of the new taxon used the data matrix of 177 characters and 67 taxa modified from Ketchum & Benson (2010), with the nothosaurid *Cymatosaurus*, as the outgroup. Codings can be found in the Appendix. The analysis was run in TNT v1.1 (Goloboff et al., 2008) with 20 independent hits using the defaults of 'xmult' command and 10 cycles of tree drifting (Goloboff et al., 2008). Tree Fuse was run with 22 replicates and over 1 × 10^9 rearrangements. A single parsimonious tree was retrieved with a tree length of 1136.78. Resampling scores were calculated using 100 replications of symmetric resampling (Goloboff et al., 2003). Each data set was analysed with a single addition and the resulting tree collapsed with tree bisection reconnection (TBR) (Goloboff & Farris, 2001). Group supports were calculated by TBR-swapping the trees, and registering of the number of steps needed to unite a clade. Both absolute (Bremer, 1994) and relative Bremer supports are presented (Goloboff & Farris, 2001). Continuous characters (both meristic and non-meristic) were analysed as such (Goloboff et al., 2006), i.e. ranges and ratios were plotted in the matrix with the actual values, without the need to create arbitrary groupings. Vincent et al. (2011) matrix was also coded and is 67 characters × 22 taxa, focused particularly on elasmosaurid taxa (10 out of 23). The outgroup included the pachypleurosaur *Serpianosaurus* and the nothosaur *Simosaurus*.

Phylogenetics morphometrics

In order to develop a testable model of morphological evolution of the coracoid, we also performed a phylogenetic morphometric analysis following the methods of Catalano et al. (2010) and Goloboff & Catalano (2011). Phylogenetic morphometrics employs Farris optimisation by applying parsimony analysis to 2D or 3D spatial continuum (Catalano et al., 2010) using homologous landmarks. A set of landmarks is regarded as a single character by the algorithm. In this case, one character with 14 landmarks was used, forming the character 'outline shape of the right coracoid in ventral view'. Forty pachypleurosaur, nothosaur, pistosaur and plesiosaur taxa were scored. For further information see Supplementary Material.

Systematic paleontology

SAUROPTERYGIA Owen, 1860
EOSAUROPTERYGIA Rieppel, 1994
PLESIOSAURIA de Blainville, 1835
ELASMOSAURIDAE Cope, 1869 *sensu* Ketchum & Benson, 2010
Cardiocorax mukulu gen. et sp. nov.

Holotype – MGUAN PA103, complete pectoral and pelvic girdle, cervical and dorsal vertebrae, partial forelimb (humerus, radius and ulna, and isolated phalanges) and several dorsal ribs.

Referred specimen – MGAUN PA270 is a more incomplete specimen preserving a pelvic girdle and a single hind limb in articulation. This specimen was found in the same horizon at about 7 m from the holotype.

Etymology – Genus name refers to the heart-shaped fenestra between the coracoids derived from the Latinised Greek *Kardia* and Latinised Greek *corax,* meaning raven or crow, which also gives rise to the name 'coracoid'. The species name *mukulu* means 'ancestor' in Angolan Bantu dialects.

Locality and horizon – Southern Angola, Namibe Province, Bentiaba, Bench 19 (Fig. 1), Mocuio Formation of the São Nicolau Group (Cooper, 2003), Namibe Basin (Jacobs et al., 2006). Strganac et al. (2014) reports the age of this interval (Bench 19) as early Maastrichtian (71.40–71.64 Ma).

Diagnosis – *Cardiocorax mukulu* is characterised by the following autapomorphies: coracoid, bilateral ventral buttress of the coracoid asymmetrical; scapula, highly reduced dorsal blade of the scapula, medial contact between scapulae and clavicles extending along all of their medial surface, scapular shaft with ellipsoid cross-section broadly splaying anteriorly; clavicle, clavicular ventral area nearly as broad as the scapular area, median contact between clavicles extend along all their medial length; cervical vertebrae, the posterior cervical neural spines have an angled apex, the posterior cervical neural spines nearly touch its adjacent neural spines, transversally broad neural spines: length of base of neural spines slightly smaller to centrum length.

Description

The holotype (MGUAN PA103) preserves five cervical and one dorsal vertebrae, proximal portions of dorsal ribs, the complete pectoral and pelvic girdles, and a partial forelimb (humerus, radius and ulna, and isolated phalanges). Preservation is generally good, with little or no plastic deformation, but exhibits some recent weathering. Referred specimen MGUAN PA270 is a more complete articulated limb and pelvic girdle, and augments the description of these elements.

Vertebrae and ribs

A continuous series of five complete cervical vertebrae and one anterior cervical lacking the neural spine and neural arch, and one dorsal centrum (Fig. 2) are preserved in MGUAN PA 103. The first isolated cervical preserved has a binocular-shaped articular facet. The vertebral centrum has a lateral longitudinal ridge and a ventral keel at mid-height and mid-width, respectively. The foramina subcentralia perforate from the ventral to the dorsal side of the vertebra and are surrounded by a broader ventral concavity. The neural arch arises slightly medial to the articular facet. The circular articular facets are visible in posterior cervicals. The lateral keel is visible in one posterior cervical that extends along the dorsal third of the centrum, being more

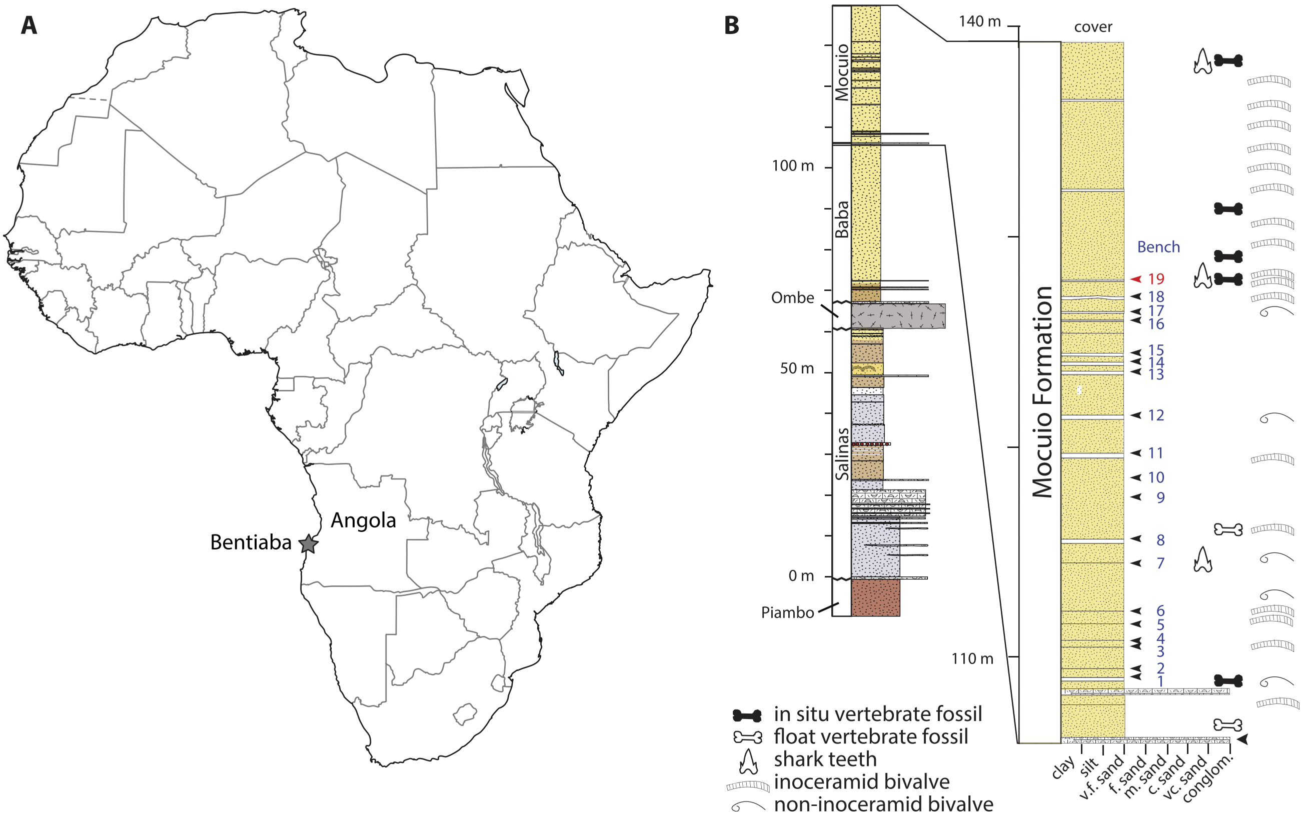

Fig. 1. A. Geographical location of the locality in Angola. B. Geological context and stratigraphic column with the position of Bench 19, the layer which produced the specimens described herein.

Fig. 2. MGUAN PA103 vertebral elements. A. Sequence of posterior cervical vertebrae and rib. B. Anterior cervical vertebra. C. Dorsal rib. D. Dorsal vertebra.

prominent on the posterior half of the centrum. The centra are slightly amphicoelus with a thickened rim surrounding the outer region of the articular facet. Because of poor preservation the ventral foramina subcentralia cannot be seen. Single-headed, transversally flattened ribs are attached on the centra ventrolaterally, tapering posteriorly and lacking anterior processes. The neural spines are blade-like, much narrower than the centra, but at the level of the neural arches they are only slightly narrower than the width of the centrum. Because of post-mortem crushing it is impossible to determine the shape of the neural canal. The neural spines are broad anteroposteriorly to the base and are completely fused to the centra, although fractured at the base of the neural spine. The dorsal border of the neural spine is remarkably angled dorsally. The dorsal portion of the neural spines is further elaborated with anterior and posterior projections at their mid-height. Thus, the neural spines touch those adjacent, forming a tear-shaped void (Fig. 2). The posterior cervical neural spines nearly touch adjacent neural spines, a condition readily distinguished from that of *Callawayasurus*, which despite a small posterior projection near the neural spine apex has a clear separation between cervicals. No dorsoventral bending occurs among cervicals such as seen in the posterior section of the cervical vertebrae in *Albertonectes* (Kubo et al., 2012). A posterior projection on the neural spine is also seen in *Callawayasaurus* (Welles, 1962), but the anterior projection is autapomorphic for this taxon (see Supplementary Material). Despite some breakage it is still possible to conclude that a posterior increase in height of the neural spines is not present. The zygapophyses are horizontal relative to the sagittal plane, unlike *Futabasaurus*, *Albertonectes* and *Terminonatator*. The postzygapophysis is flat and steeply inclined dorsolaterally in posterior view, fitting with the same angle on the prezygapophysis of the following vertebra. All centra are longer than they are high.

The dorsal centrum is acoelus, being wider compared to the length and height. In lateral view, the articulation for the neural arch is well marked. The articulation for the neural arch forms two broad ellipsoid surfaces in dorsal view. The ventral surface is perforated by two pairs of foramina subcentralia. The dorsal ribs have a small constriction around the head and taper ventrally. The single articular facet of the ribs is mediolaterally ellipsoidal.

Pectoral girdle

Pectoral girdle elements from a single individual (MGUAN PA103) were found mostly articulated except for the right scapula, which is displaced and overlaps the right coracoid (Fig. 3). The preglenoid portion of the pectoral girdle is subequal in size to the postglenoid portion of the pectoral girdle (Figs 3 and 4). The longitudinal pectoral bar is formed by the coracoid, scapula and clavicle, making a continuous slight prominence along the ventral surface, which is an unusual condition in elasmosaurids (e.g. *Callawayasaurus*, *Wapuskanectes, Hidrotherosaurus, Aphrosaurus*). The lateral scapula-coracoid contact (i.e. not the glenoid facet) has one distinct

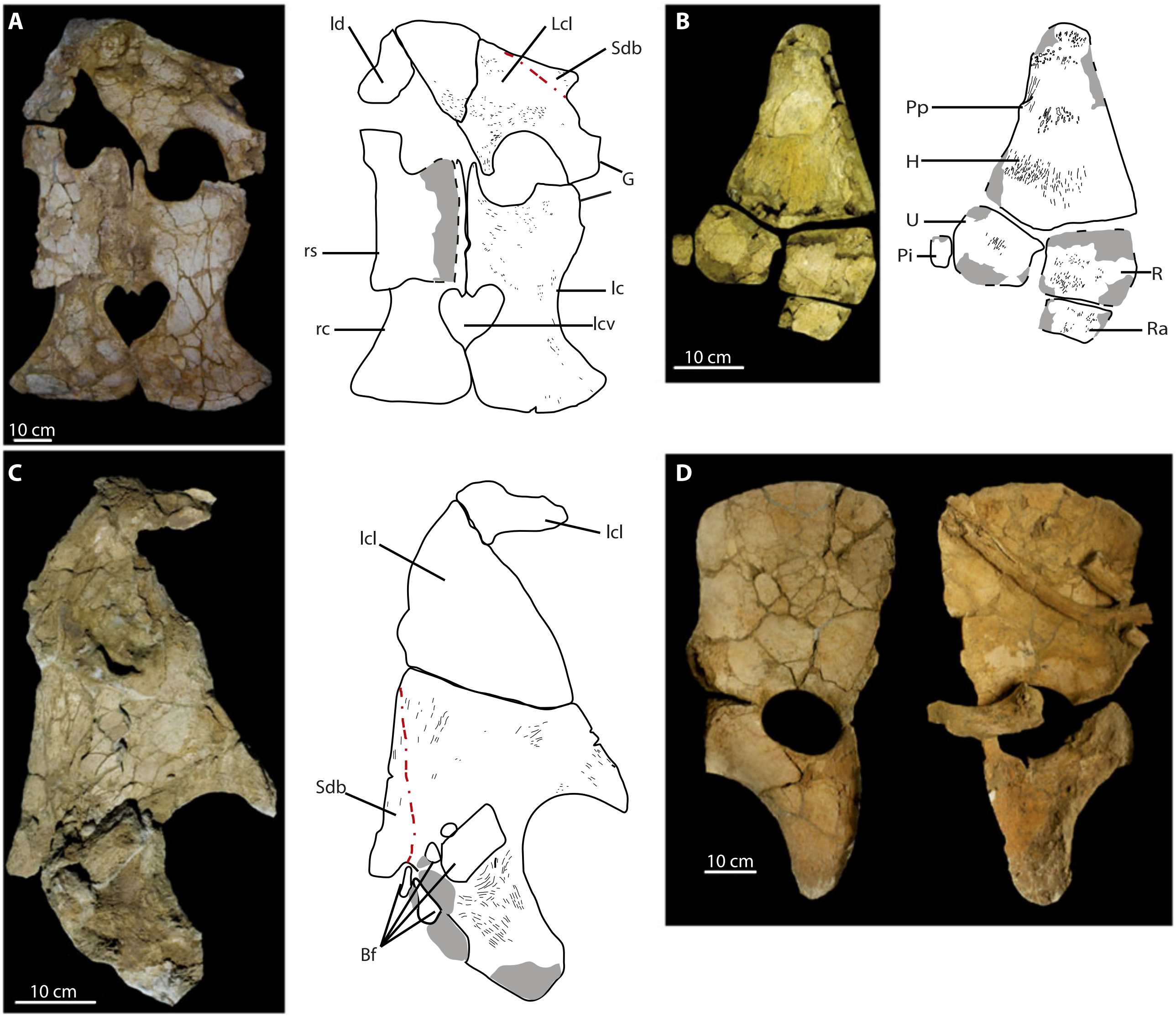

Fig. 3. MGUAN PA103 pectoral and limb elements. A. Pectoral girdle in ventral view. B. Forelimb elements as preserved. C. Left scapula in dorsal view. D. Left pelvic girdle in dorsal and ventral views. Bf, bone fragments; G, glenoid; H, humerus; Icl, interclavicle; Icv, intercoracoid vacuity; lc; left coracoid; Lcl, left clavicle; Pi, pisiform; Pp, postaxial process; R, radius; Ra, radiale; rc, right coracoid; Sdb, scapula dorsal blade; U, ulna; Icl, interclavicle; rs, right scapula; lcv, intercoracoid vacuity.

triangular facet for the articulation between the coracoid and scapula.

The coracoid is a flat bone and, as in other plesiosaurs, is thickest around the glenoid. Both preglenoid projections are complete and undistorted. The preglenoid projection of the coracoid is short and narrow, and although it clearly surpasses the anterior margin of the scapular facet, it diverges slightly laterally, but to a lesser extent than the condition in *Trinacromerum brownorum*, which is distinctly angled (Thurmond, 1968). The shape and proportions of the preglenoid projection resemble that of an unnamed elasmosaurid from the Lowest Maastrichtian CMN9454 from Canada (Sato & Wu, 2006), but is shorter than in the Albian elasmosaurid *Wapuskanectes* (Druckenmiller & Russell, 2006) from Canada. The *Aphrosaurus* preglenoid projection is very short (Welles, 1943) and it is nearly non-existent in an aristonectine elasmosaurid from Angola (Araújo et al., in press) or *Hydrotherosaurus* (Welles, 1943). There is an asymmetrical ventral buttress of the coracoids with the right coracoid overlapping the left with a lip of bone, unlike the symmetrical ventral buttress in *Wapuskanectes* or *Mauisaurus*. This is not a result of post-mortem distortion because, despite a small horizontal crack, even without repositioning there is clearly a lip of bone that overlaps dorsally. The medial posterior process tapers considerably and is much shorter than the anterior process of the coracoid. The coracoid possesses well-defined posterior cornua, giving a cordiform appearance to the intercoracoid foramen, also present in *Wapuskanectes* and *Styxosaurus*. The posterior intercoracoid symphysis forms a 10-cm long contact between the posteromedial processes, unlike most elasmosaurids. There are no median coracoid perforations, as seen in Leptocleidia (e.g. Benson & Druckenmiller, 2014). The postero-lateral coracoid wings, as seen in late Cretaceous polycotylids and to some extent in some elasmosaurids, such as cf. *Aristonectes* (TMM43445-1), are gentle projections formed by the lateral and posterior borders. The lateral border is concave posterior to the glenoid and the posterior convex as in *Plesiosaurus* (Owen, 1883; Storrs, 1997) and *Leptocleidus* (Andrews, 1922), and many elasmosaurids (e.g. *Hydrotherosaurus*, *Aphrosaurus*, *Albertonectes*). *Dolichorhynchops* possesses a concave lateral border and straight posterior border. The extremities of the bone exhibit a rugose pattern punctuated by several nutrient foramina.

Both scapulae are present in MGUAN PA103, although the left is slightly displaced and rotated, and the right significantly displaced and overlying the right coracoid. Although the scapula exhibits the typical triradiate shape (e.g. Andrews, 1910), the reduced dorsal blade of the scapula contrasts with its broad ventral area. This is an unusual feature for elasmosaurids (Figs 3 and 4, and a similar but more conservative condition in an unnamed elasmosaurid CM Zfr145; Hiller et al., 2005). The median contact between the scapulae extends along its entire anteroposterior length. The medial coracoscapular contact is reduced and only the tip of the posterior process of the scapula contacts the coracoid medially, enclosing a large coracoid 'foramen' (for homology see Araújo & Correia, in press). The scapular shaft is thick, ellipsoid in cross-section and splays anteriorly into a flat and thin plate of bone. The anterior edge of the scapula is concave and forms an acute angle laterally. The dorsal blade of the scapula arises laterally from the scapular shaft. The dorsal blade angles posteriorly, is 5–7 cm long and tapers to a blunt apex. The glenoid face and the medial coracoscapular contact are subtriangular and rugose.

The ventral area of the scapula nearly equals the area of the clavicle, a condition not yet observed in elasmosaurids and other plesiosaurians (e.g. *Thalassomedon*, *Morenosaurus*, *Albertonectes*, *Callawayasaurus*). The clavicle is a large, flat bone, subtriangular in shape and with a blunt anterior apex. The shape of the clavicle is unique among plesiosaurs (in contrast with, for example, *Futabasaurus*, *Albertonectes* and *Thalassomedon dentonensis*). It contacts its counterpart medially along its entire length. Ventrally, a small medial lip of bone projects posteriorly, partially enveloping the anterior border of the scapula. Anteriorly it contacts the interclavicle, which is poorly preserved.

Forelimb

The humerus of MGUAN PA103 possesses a postaxial protuberance that is not present in the femora of other known plesiosaur taxa. The preaxial and postaxial borders of the humerus are nearly straight (Fig. 3). The postaxial border bears a protuberance at mid-shaft. The proximal is damaged but spherical in shape. The distal end bears two distinct epipodial facets. The preaxial border of the ulna is concave. A supernumerary element articulates on the distal lateral facet of the ulna. The radius is wider than long, rectangular and articulates with a very wide radiale anteriorly.

Pelvic girdle

A complete pelvic girdle and hindlimb (MGUAN PA270) referred here to *Cardiocorax mukulu* n. gen. et sp. was originally figured by Mateus et al. (2012, their Figure 11). The pubis and ischium are similar in morphology, proportions and size compared to the holotype specimen (MGUAN PA103), and only differs in having a more rounded anterior border and a more deeply concave lateral border of the pubis. These differences can be easily accounted for by intraspecific variation. The right ilium is missing, and all other elements are fractured but complete (Fig. 3). The median symphysis between left and right portions extends from the anterior edge of the pubis to the anteroposterior midpoint of the ischium and forms a median pelvic bar. In *Futabasaurus* an incipient median pelvic bar forms a diamond-shaped fenestra at the articulation of both halves of the girdle (Sato et al., 2006), but in MGUAN PA103 the median pelvic bar is completely connected, forming a straight structure, as in *Libonectes* and *Elasmosaurus*.

The pubis forms a sinuosity along the anterolateral border and the medial edge of the pubis is straight. The anterior surface of the pubis is not notched; rather it is gently angled in the median portion of the anterior surface. A flared lateral extension of the pubis as seen in *Mauisaurus haasti* (KHM N99-1079; Hiller et al., 2005) and *Terminonatator* (Sato, 2003), and a small well-defined notch on the lateral edge of the pubis (Bardet et al., 2008) is present in MGUAN PA103. The posterior surface of the pubis has well-defined flat facets for the femur, whereas the facet for the ischium is gently concave and an oval shape with the more acute curve on the lateral side.

Although an elliptical cross-section is discernible, it is not possible to determine the relative proportions of the distal and proximal facets of the ilium because the distal facet is not entirely preserved. The ilium is not twisted but curved (Storrs, 1997), but because of the symmetry of the element and the absence of facets it is impossible to discern the curvature direction. The ilium has a blunt and flattened proximal end, but again it is impossible to discern the flattening direction.

Hindlimb

In MGUAN PA270 (Mateus et al., 2012; their Figure 11), a nearly complete, semi-articulated hindlimb is present and articulated with the pelvis. The femur is proximally formed by a hemispherical capitulum separated by an isthmus sloping into a flat D-shaped tuberculum. The shaft of the femur is cylindrical with a ventral roughening at mid-shaft for muscle attachment. The shaft flares distally and forms three distinct facets. No supernumeraries were found in articulation with the posterior paddle, but there seems to be an articulation facet on the postaxial side of the femur. The flared distal portion of the femur has deep longitudinal striations for muscle attachment. The tibia is broader than long. The medial margins of the tibia and fibula are concave, whereas the distal and proximal margins are straight. The calcaneum and centrale are preserved and in situ but the astragalus is missing. Estimates are made difficult by the taphonomic displacement of some of the digits, but the minimum phalangeal formula is I-7, II-8, III-8, IV-8, V-7.

Results

Character-based parsimony analysis

Phylogenetic analysis produced a single parsimonious tree of 1136.78 steps (Fig. 4). The analysis recovered *Cardiocorax mukulu* as the sister taxon to *Styxosaurus snowii*, and that clade as the sister of a clade composed of (*Hydrotherosaurus alexandrae* (*Libonectes morgani* + *Elasmosaurus platyurus*)). These taxa collectively form the most derived elasmosaurid clade. Elasmosauridae is strongly supported by Bremer indices and GC values, and are united by short and distally wide femur (character 175), and the premaxilla completely splits the frontals and contacts the parietals (character 10 state 2).

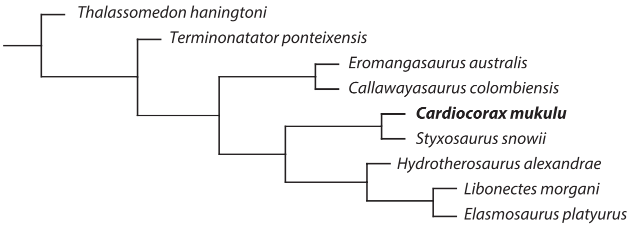

Fig. 4. Portion of recovered topology showing relationships of Cardiocorax mukulu. *See text and Supplementary Material Figures 1 and 2 for detailed results.*

Unequivocal characters supporting the position of *C. mukulu* include the ventrally notched anterior articular face of the cervical centra (Ketchum & Benson, 2010, 122:1) and the anteromedial margin of the coracoid contacts the scapula (Ketchum & Benson, 2010, 150: 1), despite convergency with non-elasmosaurid plesiosaurs such as *Plesiosaurus* or *Thalassiodracon*. The formation of the coracoid embayment is also another elasmosaurid apomorphy, present in *Cardiocorax* and noted in a previous phylogenetic analysis (e.g. Ketchum & Benson, 2010).

Morphometrics-based parsimony analysis

Our phylogenetics morphometrics analysis (see Catalano et al., 2010) of the coracoid shape recovered a topology consistent with the most generally recognised Eosauropterygia clades, and thus provides a possible evolutionary model for the coracoid (Fig. 5a). Within Plesiosauria, two clearly distinctive morphotypes emerged: the Elasmosauridae morphotype with the formation of an intercoracoid vacuity and the Polycotylidae-morphotype with a long preglenoid projection and posterior cornu.

Although resistant fit theta-rho analysis (RFTRA) as a re-aligning method provided a better tree score at the lowest level of search thoroughness (4.8), at higher levels the heuristic minimisation of differences method performed considerably better, with a tree score of 4.2 (Fig. 5d). At the levels of thoroughness 3 and 4, the tree score was similar to the re-aligning method by heuristic minimisation of differences. Yet, for individual landmark scores, the heuristic minimisation of differences method was less consistent relative to RFTRA (contrast Fig. 5b and c), which showed close individual landmark scores at all levels of thoroughness. The best tree score was achieved with heuristic minimisation of differences for the levels of thoroughness 3 (Fig. 5d) and 4. However, the tree that best mirrors generally accepted relationships in Eosauropterygia was calculated using heuristic minimisation of differences with the level of thoroughness 3. Additional trees are included in the Supplementary Material.

Discussion

In Fig. 6 we present a model of pectoral girdle evolution in Eosauropterygia. In basal forms we see major reduction of the

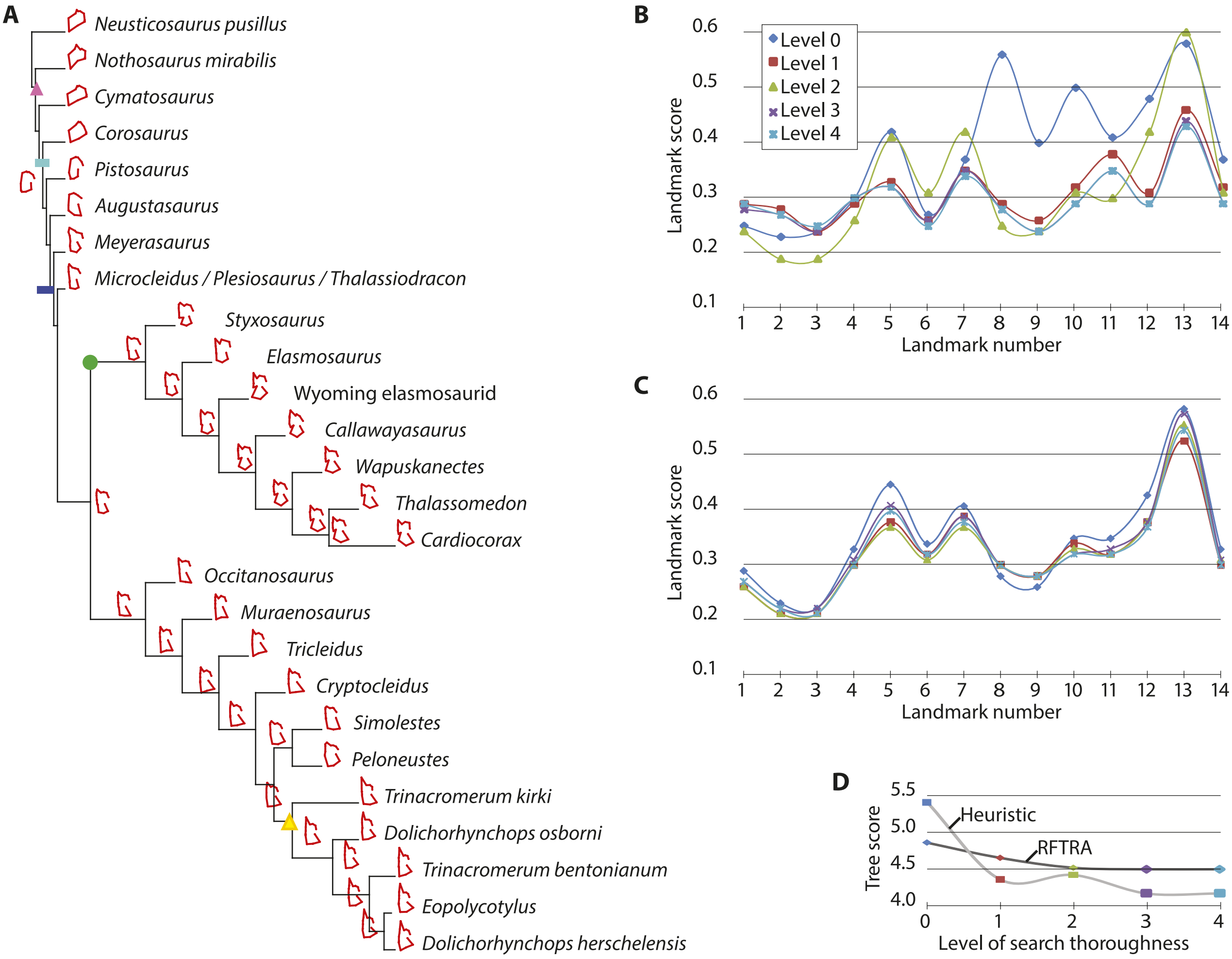

Fig. 5. Results of phylogenetic morphometric analysis. A. Preferred tree. Landmark scores for each landmark using (B) heuristic and (C) RFTRA search methods. D. Comparison of the overall tree score between the heuristic and RFTRA method. See Supplementary Material Figures 4–13 for all recovered trees.

clavicle, reduction of the coracoid buttresses, reduction of the dorsal blade and general ventralisation of the scapula, horizontal orientation of the coracoid, and formation of the clavicular-scapular arch. At the level of Pistosauria, we see high morphological disparity of the coracoid. After the Late Triassic morphological gap, we see formation of a large coracoid foramen, medial migration of the medial coracoid-scapula contact, expansion of the postglenoid projection, and a weakening of the scapular-clavicular articulation. Within pliosaurids, we see retention of a relatively conservative pectoral girdle with broad medial contact of the coracoids. In polycotylids there is a novel development of the posterior coracoid wings, but the scapula remains moderately expanded ventrally. Within elasmosaurids, we see the formation of the intercoracoid vacuity and in late elasmosaurs, extreme ventral development of the scapula and clavicle, formation of an extensive longitudinal pectoral bar and nearly complete elimination of the dorsal process of the scapula.

These evolutionary novelties are broadly correlated with optimisation of aquatic locomotion from terrestrial basal neodiapsid ancestors. However, notwithstanding the general model developed by Carpenter et al. (2010), significant differences in girdle and limb morphology in Plesiosauria suggest that different clades may have employed variations of rowing and underwater flying. The area of muscle attachments on the girdle elements reflects both the dominant direction and magnitude of forces that are applied to the limbs. The glenoid architecture should reflect motion to the extent the glenoid must resist forces applied to the limb and thus should also reflect the dominant motion vectors (i.e. protraction and retraction vectors). This is contrary to the reasoning of Carpenter et al. (2010), who suggested limb motion was greatest in the vectors defined by least restriction in the glenoid (i.e. adduction and abduction). Thus, an understanding of the myology, proportions of the limb and the glenoid architecture across the broader clade is critical to infer swimming styles and variation in stroke geometry.

The osteological correlates of muscles attachment sites define area and at times direction (Araújo & Correia, in press) and thus reflect to some degree the magnitude and vector of muscle forces. When examined within a system like the forelimb and pectoral girdle, the interaction of these forces and vectors

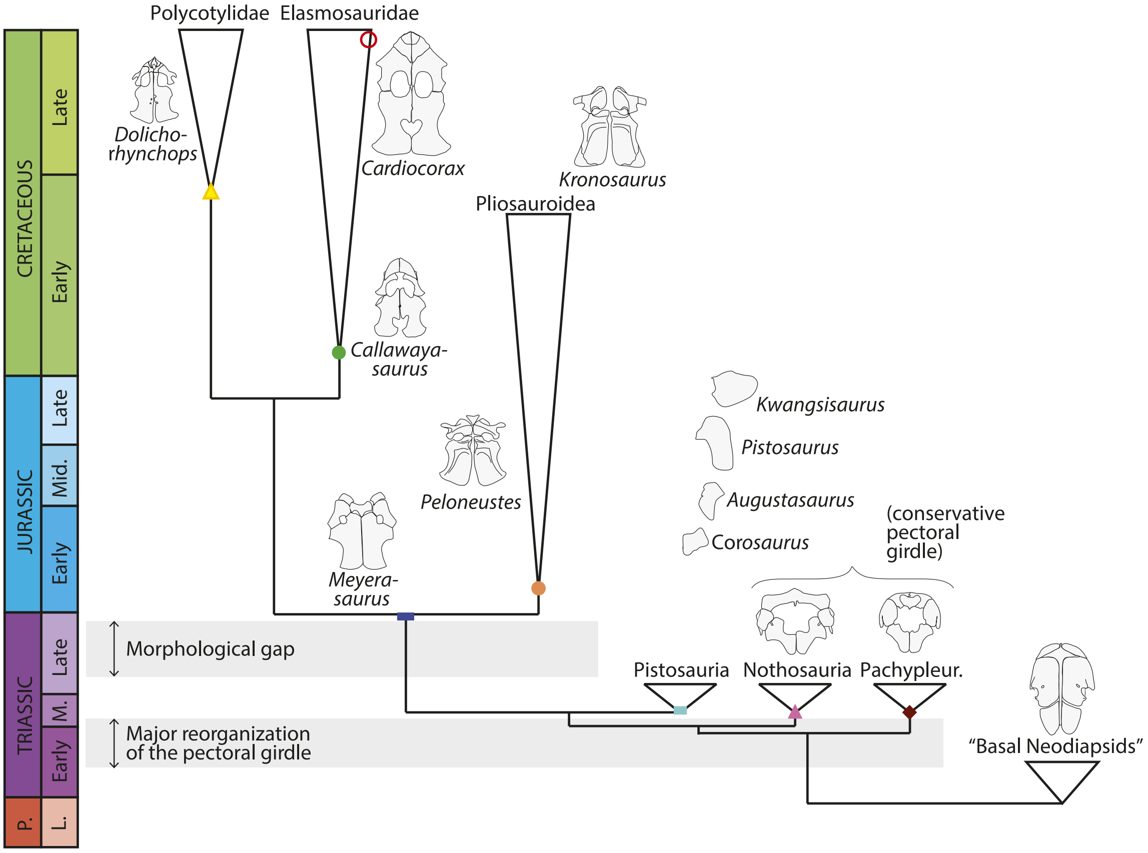

Fig. 6. Patterns of pectoral girdle evolution in Eosauropterygia. See text and Supplementary Material for discussion.

yields clues to the kinematics of that system. In basal neodiapsids, the levator scapulae, the serratus and the scapulodeltoideus originate on the dorsal blade of the scapula (Holmes, 1977). The areas of attachment of these muscles are reduced in Eosauropterygia because the lifestyle in a buoyant aquatic medium does not require, to the same extent, limb support musculature (Lin & Rieppel, 1998). Other secondarily-adapted paraxial swimmers, such as penguins (Schreiweis, 1982) and pinnipeds (Murie, 1871), also show selective limb muscle reduction and expansion. However, *Cardiocorax* demonstrates an extreme case of reduction of the levator scapulae, scapulodeltoideus and serratus in which the ventral area of attachment in the scapula is 14 times greater than the area of attachment on the dorsal blade.

The ratio of the coracoid area versus the total length of the individuals and the ratio of coracoid area versus the ventral area of the scapula is clearly contrasted in Cretaceous plesiosaurs, with policotylids and elasmosaurids being separated (Fig. 7a and b). This is indicative of the different swimming styles between these two clades, namely the use of the coracobrachialis and clavodeltoideus muscle (Araújo & Correia, in press). The average ratio between the dorsal blade area and the ventral surface in the sampled Eosauropterygia is 3.3 and in Elasmosauridae is 3.6 (Fig. 7c). The variation of almost an order of magnitude within the same family reflects the particular locomotory patterns of *Cardiocorax*. Typically for diapsids the levator scapulae and the scapulohumeralis insert directly on the dorsal portion of the scapula (Russell & Bauer, 2008). Basal cryptoclidids (sensu Ketchum & Benson, 2010) also have high ratios of the dorsal blade area and the ventral surface of the scapula (average 7.6), and *Cryptocleidus eurymerus* has a ratio of 10 (Fig. 7c). By this measure, the scapular muscles in basal cryptoclidids and *Cardiocorax* are comparable. *Cardiocorax* has a highly proximodistally reduced and distally expanded humerus (Fig. 3), rivaled only by *Cryptocleidus* (ratio is 0.3) among Eosauropterygia (Fig. 7d). However, the shortening of the humerus is a common trend among marine mammals (Fish, 1996) and marine turtles (Renous et al., 2008). The members of the Elasmosauridae possess the most derived condition of this aquatic adaptation (Fig. 7d) in having the lowest humeral ratio values (average is 1.4) among Eosauropterygia (average is 2.0). Along those lines, the radius ratio also tends to diminish along the evolution of the clade (Fig. 7e).

The extreme distal expansion of the *Cardiocorax* with a doubly faceted distal border provides a broad articulation for interlocking zeugopodials (Fig. 3), a feature shared with *Cryptocleidus*. Similarly, *Cardiocorax* has a shortened radius (0.77 ratio) comparable only to other Late Cretaceous polycotylids such as *Dolichorhynchops* and *Edgarosaurus* (Fig. 7d and e). *Cardiocorax'* shortened propodials and zeugopodials would have

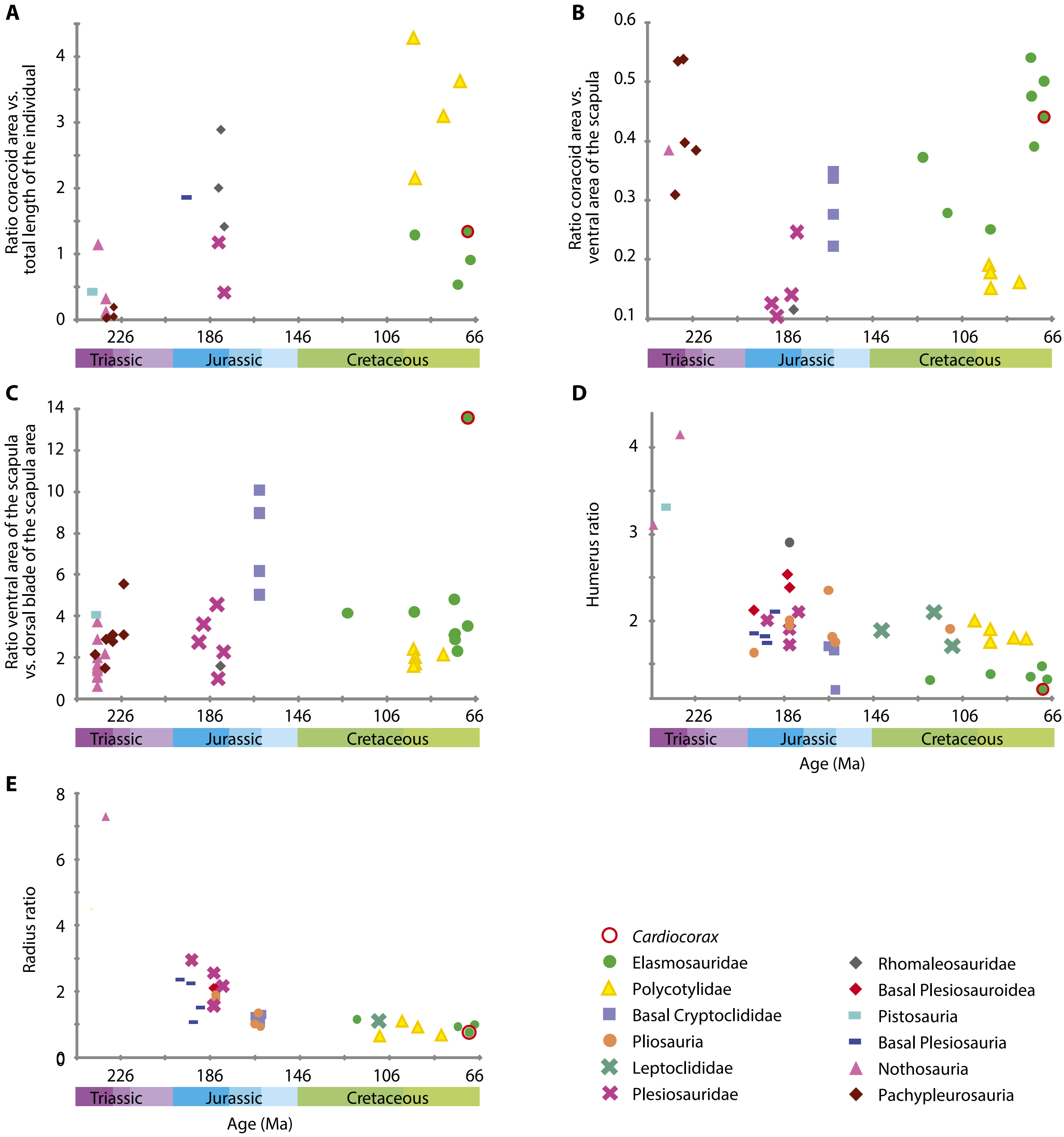

Fig. 7. Morphometric pectoral girdle variables against time. A. Ratio of the coracoid area versus the total length of the individual. Note the constrasting values between polycotylids and elasmosaurids, convergent with the ratios on pachypleurosaurids. B. Ratio of the coracoid area versus the ventral area of the scapula. Note the similar ratios for elasmosaurids and cryptocleidids. C. Ratio of the ventral area of the scapula versus the dorsal blade of the scapula area. Note the outlier position of Cardiocorax*, only comparable with that of cryptocleidids. D. Humerus ratio, length versus distal width. Note the tendency in Eosauropterygia for increasing massiveness of the propodials, a trend convergent with various secondarily-adapted organisms; E. Radius ratio, length versus distal width. As for the propodials the epipodials also tend to increase in massiveness to increase the mechanical advantage of locomotor muscles and paddle stabilisers. See Supplementary Material Tables 1–3.*

increased mechanical advantage of the extrinsic musculature inserting on the girdle for increased leverage (Araújo & Correia, in press). To cope with the force imparted by the muscles, the coracoids meet extensively posteriorly and there is a broad median contact between the scapulae and clavicles. Additionally, the contact between the clavicle and scapula is broad. The pectoral girdle is strengthened by the left–right asymmetric ventral buttress of the coracoid. Plesiosaurs have a thickened glenoidal portion of the coracoid, but a marked ventral buttress is most evident in Elasmosauridae and facilitates bending resistance between the two sides of the pectoral girdle. *Cardiocorax* pectoral and pelvic girdles present a structural extreme for quadrupedal subaqueous locomotion. The reduction of the attachment area of the dorsal blade of the scapula versus the expansion of the attachment area of the ventral area in *Cardiocorax* indicates atrophy of muscle groups that were primitively involved in terrestrial locomotion and, on the other hand, expansion of other muscle groups involved in quadrupedal subaquatic locomotion. Thus, the peculiar *Cardiocorax* pectoral girdle architecture has functional implications. The subequal coracoid ventral area and the clavicle and scapula ventral area, plus the reduced dorsal blade of the scapula, seem to be more compatible with a protraction-retraction limb cycle with change of the flipper pitch than with a figure eight limb cycle previously proposed for plesiosaurs (Robinson, 1975).

Supplementary Material

Supplementary material for this paper available on: http://dx.doi.org/S0016774614000444

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Appendix

Codings for Ketchum & Benson (2010)

Cardiocorax mukulu ? 1 1 1 1 2 1 2 0 2 ? 1 1 1 ? 0 ? ? 1 2 ? ? 1 0 1 0 1 1 0 1 1 1 1 0 0 ? 1.3 ? 1 0 1 1 1 ? 0.77 1 1 ? ? 1 0 0 1 1 1 1.27 0 ? ? ? ?

Codings for Vincent et al. (2011)

Cardiocorax mukulu ? 0 ? 1 1 1 0 1 1 1 1 ? 1 1 1 1 1 0 0 0 0 2 ? ?