COMPARATIVE MYOLOGY OF THE

CROCODYLIAN SHOULDER

AND FORELIMB

THESIS

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By

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To Grampa

To Tia Mimi and George

To Mando and Memo

ACKNOWLEDGEMENTS

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ABSTRACT

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The Crocodylia are the only extant reptilian member of the great Archosaurian lineage. As such, they represent the only living link between the extinct thecodonts, pterosaurs, dinosaurs and the extant birds. Much valuable work on crocodilian ecology, behavior, physiology and anatomy has been accomplished over the past century. Despite this attention there still remain many unanswered questions concerning the form and function of the locomotory systems and systematics within this historically diverse taxon. The pelvic and hind limb musculature and postcranial skeleton of crocodilians are well known, but the pectoral girdle and forelimb musculature has not been adequately studied. Presently the Eusuchia are divided into one or more families composed of different subfamilies depending on the author. The most current classification of the Order

Crocodylia places the extant members into three Families. The placement of *Tomistoma schlegelii* is a major point of contention between morphological and molecular data sets. My study consisted of a comparative dissection between *Tomistoma schlegelii, Gavialis gangeticus* and *Caiman crocodilus*. The shoulder and pectoral musculature was found to be conservative between the taxa. *Gavialis gangeticus* was unique among the others by having fused forearm flexors. This character further supports the morphological hypothesis for the placement of *G. gangeticus* as the sister group to the rest of the extant Crocodylia. In addition, the results may impact several fields of study ranging from crocodilian ecology to dinosaur reconstruction and locomotion.

INTRODUCTION

Evolution of the Crocodylia

The Crocodylia are the only extant reptilian member of the great Archosaurian lineage. Crocodilians embody the only living link between the extinct thecodonts, pterosaurs, dinosaurs and the extant birds (Tarsitano et al., 1989). Archosaurs are defined by the diapsid condition and a mandibular and antorbital fenestra (Romer, 1986). A divergence more than 200 MYA produced the Ornithosuchia, that eventually gave rise to birds, dinosaurs, pterosaurs and the Pseudosuchia. Despite the name "false crocodiles" the Pseudosuchia gave rise to modern crocodilians and their long line of extinct and diverse relatives. The first divergence within the Pseudosuchia resulted in the separation of the Parasuchia from the Suchia, the ancestral line of modern crocodilians. The Suchia is represented by Gracilisuchus, Aetosauria (armored forms), Rauisuchia and the group Crocodylomorpha. From the last group arose the terrestrial Sphenosuchians and the Crocodyloformes. The Crocodyloformes consisted of terrestrial and small agile Protosuchids and the Mesoeucrocodylia. The long-snouted marine Thallatosuchians and the Metasuchians arose from the Mesoeucrocodylia. The Metasuchia include many extinct forms including the Sebeosuchids and the Neosuchia or "new crocodiles" (Buffetaut, 1982). Several extinct forms are placed within the Neosuchia including the Eusuchia, which in turn contain *Leidyosuchus, Hylaeochampsa, Stomatosuchus* and the crown group Crocodylia (Steel, 1973; Brochu, 1992).
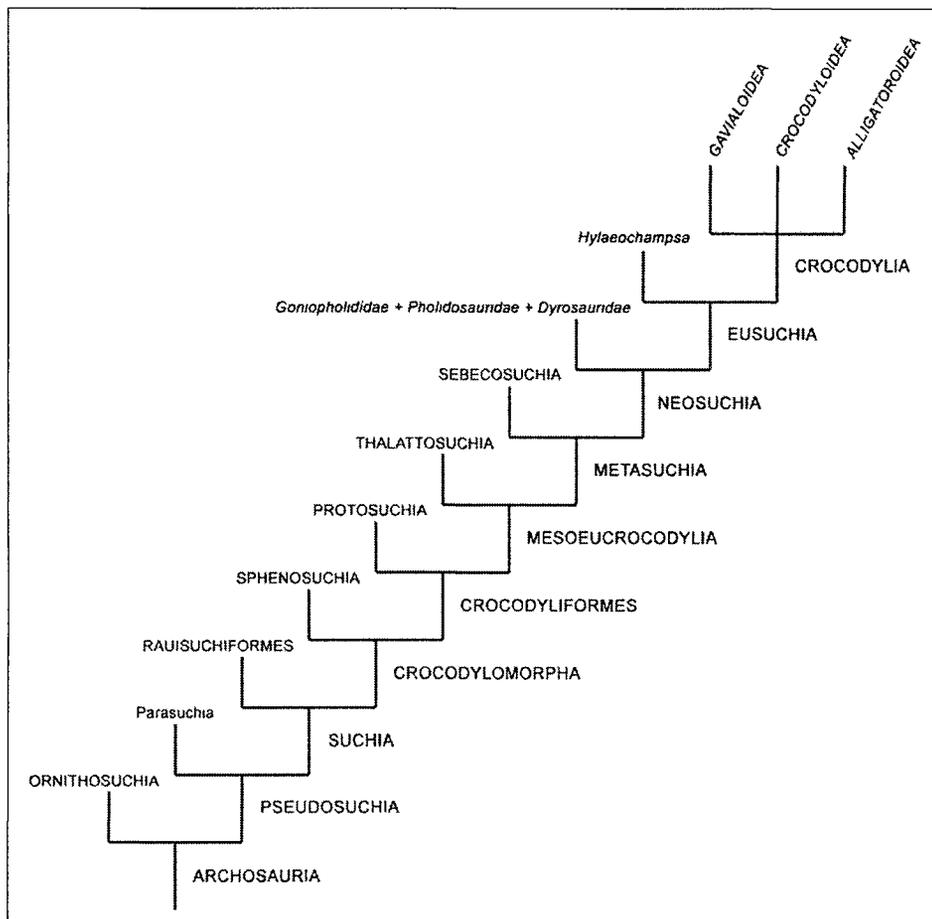
Fig. 1. A diagrammatic representation of crocodilian evolution.

The Systematic Problem

The most current classification of the Order Crocodylia places the extant members

into three Families. The Family Alligatoridae contains the genera *Alligator, Caiman,*

Melanosuchus and *Paleosuchus*. The Family Crocodylidae is divided into two sub-

families; Crocodylinae into which the genera *Crocodylus* and *Osteolaemus* are placed

and Tomistominae whose sole living representative is *Tomistoma schlegelii*. The Family

Gavialidae is also represented by one living member, *Gavialis gangeticus* (King &

Burke, 1997).

Classically and morphologically, Romer (1986) and Steel (1973) place all living crocodilians into the family Crocodylidae, subdividing this taxon into four subfamilies: the Alligatorinae which include the alligators and caimans; the Crocodylinae which include the crocodiles and *Osteolaemus*; the Tomistominae which includes the genus *Tomistoma*, and finally the Gavialinae which includes the genus *Gavialis*. Some workers have placed *Gavialis* into a separate family to suggest a different origin than the rest of the Eusuchia (Mook, 1934; Kalin, 1955; and Sill, 1968). Dowling and Duellman (1975) proposed a phylogeny with no inferred relationships between the genera (Densmore, 1983). Using molecular data *Tomistoma schlegelii* has been consistently aligned with *Gavialis gangeticus* (Densmore, 1983; Densmore and Dessaurer, 1984; Densmore and Owen, 1989; Densmore and White, 1991, Hass et al., 1992). These results conflict with morphological phylogenies by placing *Tomistoma* as the sister group to *Gavialis* This relationship essentially suggests that they share a recent common ancestor and that *Gavialis* is recently derived (Middle Tertiary). The extant taxa are grouped by molecular evidence (Densmore, 1983; Densmore and Dessaurer, 1984) as follows: (*Alligator* (*Crocodylus* (*Tomistoma* (*Gavialis*)))). Morphological data from the hind limb musculature, trunk musculature and braincase suggests a basal (Middle Cretaceous) divergence of the gharials from the rest of the Crocodylia (Tarsitano et al., 1989; Frey et al., 1989) (Figure, 2). It should be noted that alligatorid relationships have not been contested. *Crocodylus* and *Osteolamus* have been consistently grouped together, and *Gavialis* is always placed as the sister group to alligatorids+crocodylids. Therefore, the two competing theories produce highly congruent results when *Gavialis* is removed from analysis (Brochu, 1997; Poe, 1996).
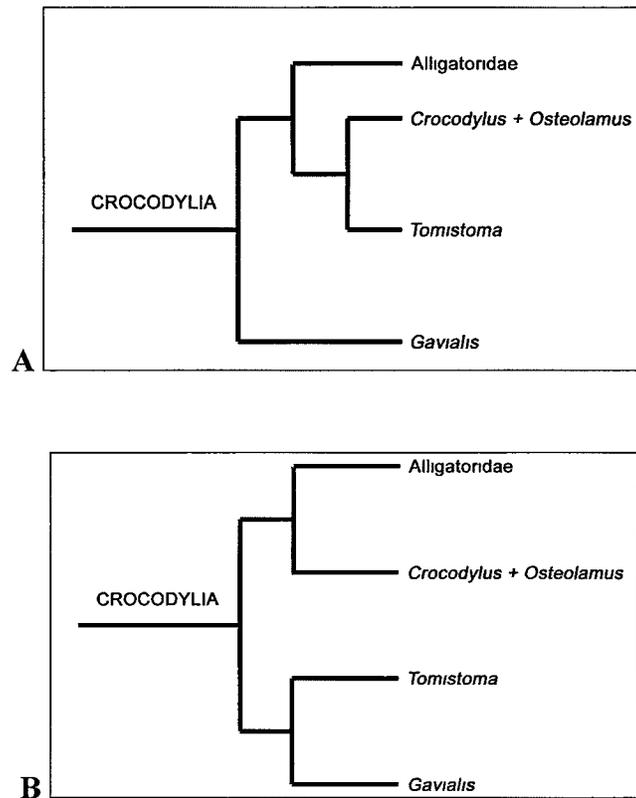
Fig. 2. Two competing hypothesis for relationships within the Crocodylia, modified from Densmore 1989, Brochu, 1997 and Frey, 1989.

Comparative Anatomy of the Limb Musculature

The pelvic and hind limb musculature and postcranial skeleton of crocodilians are

well known (Gadow, 1882; Furbringer, 1876; Romer, 1923; Mook, 1921; Wettstein,

1937; Schaeffer, 1941; Cruickshank, 1979; Brinkman, 1981; Hecht and Tarsitano, 1983;

Parish, 1986). Crocodilians are unique among tetrapods by having elongated carpel

elements (Tarsitano, pers. comm.). Moreover, the pectoral girdle musculature has not

been adequately studied and there are few studies on the forelimb musculature of

crocodilians (Furbringer, 1876; Chaisson, 1962; Brochu, 1992). The purpose of this

study is to compare the pectoral musculature of representatives from each Family within the Order Crocodylia. The goals of my study are:

1. To describe the forelimb musculature of the living Crocodylia

2. To compare the shoulder and forelimb musculature among the crocodilian families

3. To evaluate the absence or presence of phylogenetic data from the musculature

The questions I hope to answer include the following: (1) how does the forelimb musculature differ among the living Crocodylia; (2) does the difference in pectoral musculature of three subfamilies of the Crocodylia shed light in the placement of *Tomistoma* in the Crocodylinae? The results of this investigation may impact other fields of study by answering the questions stated above. There may be phylogenetic data in the arrangement of the shoulder and forelimb musculature. The origin and insertion data may help in understanding dinosaur locomotion and its possible effects on their natural history. Finally, a better description of the crocodilian forelimb and shoulder musculature will be produced as a consequence of this study.

MATERIALS AND METHODS

Specimens

The three species used in this study include: *Tomistoma schlegelii* (Muller, 1838)

Museum of Natural History University of Kansas Nr. 157993, *Gavialis gangeticus*

(Gmelin, 1789) Nr. 229859 and *Caiman crocodilus* (Linnaeus, 1758) private property. A

fourth specimen, *Crocodylus acutus* (Cuvier, 1807), was dissected by Furbringer (1876).

Each was chosen as a representative from their respective Family. *Tomistoma schlegelii*

and *Crocodylus acutus* belong to the Family Crocodylidae, *Gavialis gangeticus* belongs

to the Family Gavialidae and *Caiman crocodilus* belongs to the Family Alligatoridae.

Tomistoma schlegelii (Figure 3) is the only extant member of the Subfamily

Tomistominae (Kalin, 1955), which ranges temporally from the Late Eocene to the

present day. *T. schlegelii* is a longirostrine crocodilian with a braincase and tail

musculature similar to other crocodilians (Tarsitano et al., 1989). Its 76-84 conical teeth

are arranged as follows: 4-6 premaxillay, 15-16 maxillary and 19-20 mandibular units.

The fourth tooth is also exposed and fits into an indentation of the upper jaw like other

crocodilians. Adult *T schlegelii* are relatively large when compared to the rest of the

extant Crocodylia. Mature males can attain a length of 5 meters, while breeding females

are usually always smaller in size. *Tomistoma* jaws have distinctive dark bands that may

fade when individuals reach maturity. Their spatial range is restricted to South East Asia,

specifically Malaysia, Borneo, Sumatra, Indonesia, and the southern tip of Thailand.

Their habitat consists of flowing bodies of fresh water and dense vegetation. *T. schlegelii* is listed as CITES Appendix I and is on the IUCN Red List (Endangered). There is insufficient population data, but surveys have found that the estimated wild population is under 2,500 individuals (Britton, 2002). Their numbers are most likely decreasing due to habitat loss, resource depletion, and human encroachment (Groombridge, 1987; Ross, 1998). These threats, compounded with hunting, have continued to deplete their numbers.

Present thought is that the Gavialinae most likely diverged from the rest of the Crocodylia in the late Cretaceous, and only one species remains today. *Gavialis gangeticus* (Figure 4) is another longirostrine eusuchian. Unlike *Tomistoma* where the snout tapers gradually the gavialoid elongated snout is distinctly demarcated from the braincase. *G gangeticus* also has a non-verticalized braincase and unique tail musculature in comparison to other extant crocodilians (Tarsitano et al., 1989; Frey et al., 1989). *G. gangeticus* has a total of 106-110 interlocking teeth of which 5 are premaxillary, 23-24 are maxillary and 25-26 are mandibular. It is also distinct from other extant eusuchians in that males grow a fleshy, bulbous narial excrescence (Maskey 1977). Gharials (presently the accepted common name) are relatively large compared to other extant eusuchian taxa. Lengths of 4-5 meters are easily attained and lengths up to 8 meters are possible (Tarsitano, pers. comm.). Their range lies along four major rivers in the northern regions of India and surrounding countries. They are located in the Ganges, Indus, Mahanadi and Brahmaputra rivers, where fast-flowing water is preferred. Their terrestrial abilities are severely limited, especially with age (Bustard & Singh, 1978). Their muscles can not support an erect stance used by other crocodilians when traversing

terrestrial environments. In addition their limbs are laterally compressed with fringes of scales on the posterior edge. Gharials are listed as CITES Appendix I and are on the IUCN Red List (Endangered). There are less than 2500 individuals belonging to a fragmented wild population. Gharial populations are threatened by human encroachment and hunting (Groombridge, 1987; Britton, 2002).

Caiman crocodilus (Figure 5) is a member of the Alligatoridae which diverged sometime during the Middle Cretaceous. They are represented by nine extant species divided into two subfamilies, the Alligatorinae and the Caiminae. *C. crocodilus* is moderate-sized and broad-snouted. It has distinct cranial ridges and grows up to a length 2.5 meters. *C. crocodilus* has a total of 72-78 teeth, of which 5 are premaxillary, 13-14 are maxillary and 18-20 are mandibular. The fourth tooth fits into a socket in the maxillary bone when the jaw is closed. Its geographic range extends from southern Mexico to Brazil. *C. crocodilus* is a generalist both in habitat and diet, but seems to prefer still or slow-moving waters. Large populations occur in the wild and they are not threatened or endangered. This is probably due to a lack of hunting which may be attributed to dermal osteoderms present in the ventral skin making their hides difficult to tan (Britton, 2002).
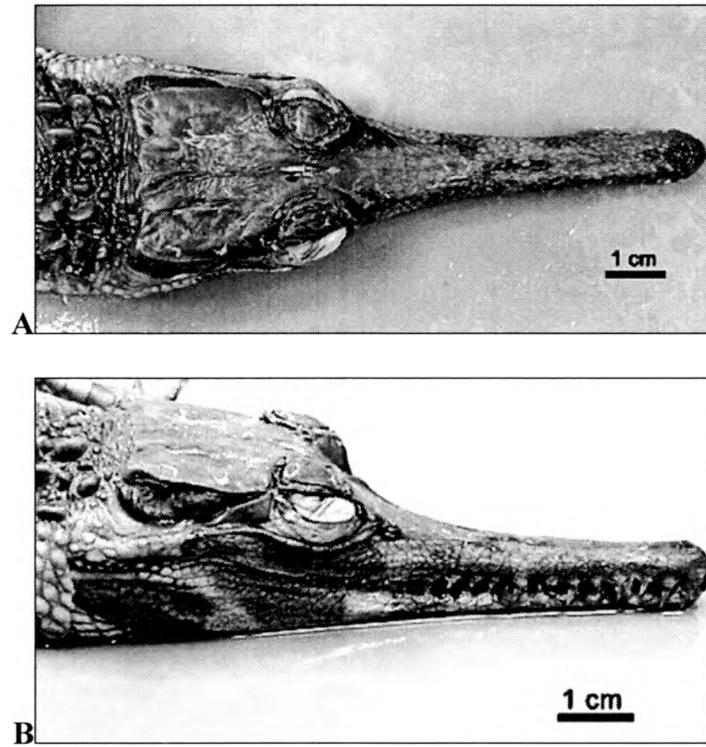
Fig. 3. A head study of the *Tomistoma schlegelii*
specimen. A= dorsal view, B = lateral view.
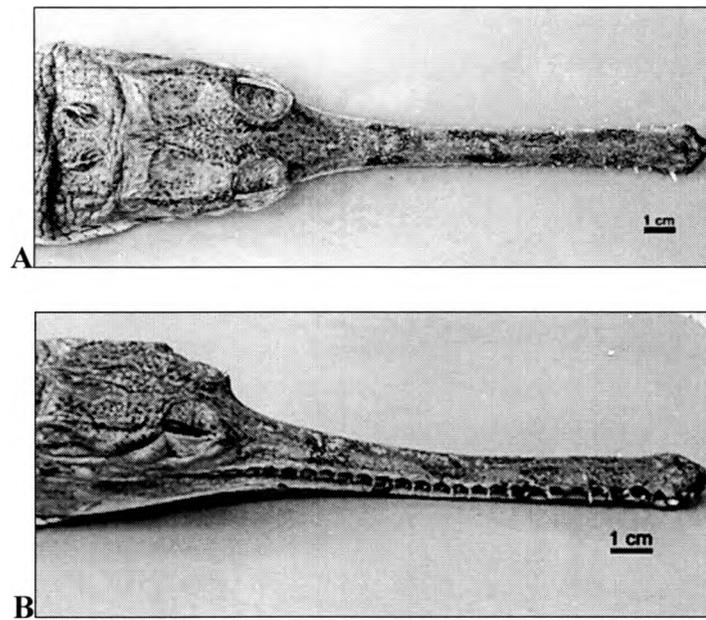
Fig. 4. A head study of the *Gavialis gangeticus*
specimen. A= dorsal view, B = lateral view.
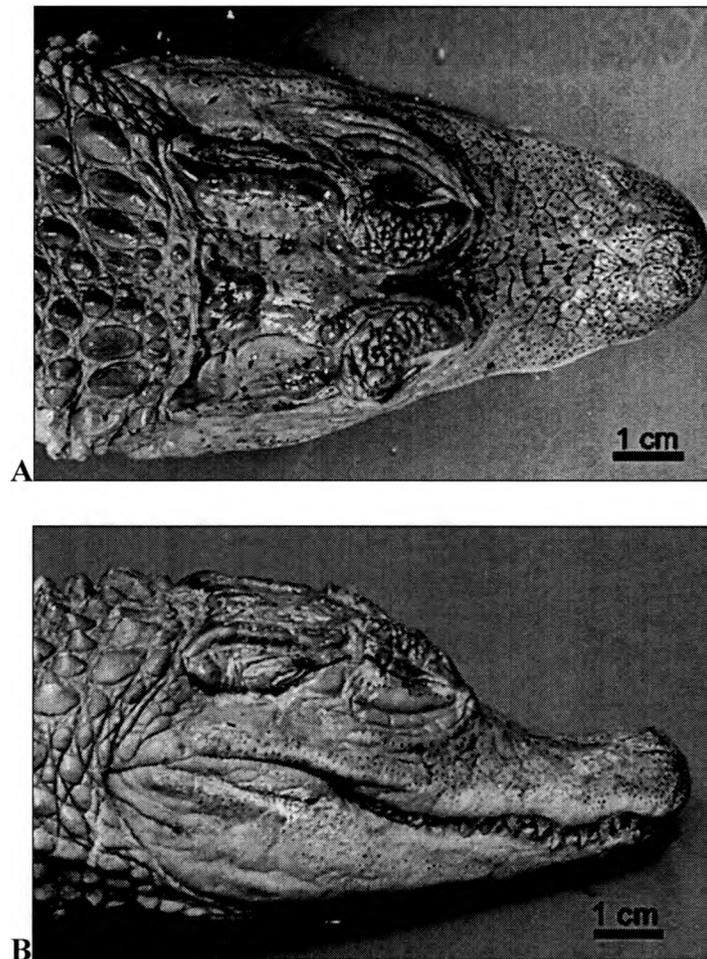
Fig. 5. A head study of the *Caiman crocodilus* specimen.
A= dorsal view, B = lateral view.

Shoulder Musculature

M. latissimus dorsi (ld) – (*dorso humeralis*) (Furbringer, 1876) originates from mid-

dorsal fascia of thoracic region and joins the tendon of the *M. teres major* that inserts into

the posterior side of the proximal end of the humerus (Chaisson, 1962). It is a sheet-like

triangular muscle that adducts and slightly rotates the humerus.

M. trapezius (trp) – (*cucullaris*) (Furbringer, 1876) originates from the mid-dorsal fascia

of the cervical and thoracic region and inserts on the middle anterior surface of the

scapula just above the insertion of the *M. deltoideus scapularis inferior*. It is also a triangular muscle that draws the scapula dorsally and anteriorly (Chaisson, 1962).

M. levator scapulae superficialis (lss) – (*collo-scapularis superficialis*) (Furbringer, 1876) originates from the first two cervical ribs along with the *M. sternomastoideus* and inserts on the anterior edge of the scapula just below the *M rhomboideus* and above the *M. strenomastoideus*. It is a triangular sheet of muscle that supports the cervical area and moves the neck laterally and draws the scapula anteriorly (Furbringer, 1876; Chaisson, 1962).

M. serratus superficialis (ss) – (*thoraci-scapularis superficialis*) (Furbringer, 1876); (*serratus posterior*) (Chaisson, 1962) originates from the first to fourth thoracic ribs near the costal cartilages and inserts into the posterior edge of the scapula. It is a triangular sheet of muscle that acts as the antagonist to the *M. levator scapulae superficialis* and draws the scapula posteriorly and ventrally (Furbringer, 1876; Chaisson, 1962).

M. rhomboideus (rh) – originates from the fascia of the *M longissimus* complex and inserts into the upper anterior corner of the medial surface of the scapula. It is a long band of muscle that draws the scapula medially and anteriorly (Furbringer, 1876; Chaisson, 1962).

M. deltoideus scapularis superior (dss) – (*dorsalis scapulae*) (Furbringer, 1876) originates from the anterior half of the upper lateral surface of the scapula and joins the

tendon of the *M teres major* that inserts into the tuberosity on the anterior lateral surface of the head of the humerus. It is a columnar shaped muscle that draws the humerus anteriorly (Chaisson, 1962). It is exposed in all the taxa.

M teres major (tmj) – originates from the posterior half the dorsolateral surface of the scapula and joins a tendon that it shares with the *M. latissimus dorsi* and inserts into the posterior side of the proximal end of the humerus. It is a columnar shaped muscle that draws the humerus posteriorly (Furbringer, 1876; Chaisson, 1962).

M deltoideus scapularis inferior (dsi) – originates from the anterior angled surface of the lower scapula and inserts into the internal tuberosity of the humerus (Furbringer, 1876; Brochu, 1992). It is a thick triangular muscle that wraps around the head of the humerus and draws the humerus forward (Chaisson, 1962).

M. supracoracoscapularis (sps) – originates from the anterior surface of the lower scapula and upper coracoid and inserts into the internal tuberosity of the humerus. Most of this fan-shaped muscle lies on a shallow depression on the scapula. It wraps over the area where the scapula and coracoid meet and draws the humerus forward and is deep to the *M. supracoracoideus* (Furbringer, 1876; Chaisson, 1962).

M scapulo-humeralis profundus (shpr) – originates from the posterior lower surface of scapula and inserts into the anterior dorsal edge of the humerus. This is a deep muscle

that stretches in a broad fan from origin to insertion. It draws the humerus dorsally (Furbringer, 1876).

Pectoral Musculature

M sternomastoideus – (stm) (*capiti-sternalis*) (Furbringer, 1876) the posterior portion of this muscle (*sterno-atlanticus*) (Furbringer, 1876; Reese, 1915) originates from the dorsal posterior surface of the interclavicle and inserts into the atlas and cervical ribs (Brochu, 1992). It is a thick band of muscle that aids in lateral movements of the neck, especially movements performed during feeding.

M. supracoracoideus (spc) – originates from the anterior medial surface of the coracoid and inserts into the internal tuberosity of the humerus (Furbringer, 1876; Chaisson, 1962). It is a triangular muscle that aids in forward and dorsal movement of the humerus.

M. pectoralis (p) – originates from the ventral side of the interclavicle and costal cartilages along with the *M sternomastoideus* and inserts into the internal tuberosity of the humerus. It is a large fan-shaped muscle that acts as the primary mover of humeral flexion (Furbringer, 1876; Chaisson, 1962; Brochu, 1992).

M. coraco-brachialis brevis (cbb) – originates from the ventral length of the coracoid blade and inserts just medial to the internal tuberosity of the humerus. It is a triangular sheet of muscle stretched out between the coracoid and the humerus that lies deep to the *M. pectoralis* and aids in drawing the humerus forward (Furbringer, 1876).

M. episterno-hyoideus (esthy) – originates from the posterior corners of the anterior expansion of the interclavicle and inserts into the hyoid bone. It is a long band of muscle that lies above the trachea and may help in swallowing (Furbringer, 1876; (sternohyoideus) Chaisson, 1962; Brochu, 1992).

M. coracohyoides (ch) – originates from the hyoid and inserts along with the M. supracoradoideus into the anterior border of the coracoid. This is usually a band like muscle that may assist in swallowing. It lies deep to the *M. episterno-hyoideus* and *M sternomastoideus*

Brachial Musculature

M. anconaeus scapularis lateralis externus (asl) – originates from the posterior lower lateral surface of the scapula just above the point of contact with the humerus and joins a broad, heavy tendon that inserts into the posterior border of the ulna. It is a long, heavy muscle on the posterior side of the humerus that extends the forearm (Furbringer, 1876; Chaisson, 1962).

M anconaeus humeralis lateralis (ahl) – originates from the entire medio-posterior surface of the humerus and joins a broad, heavy tendon that inserts into the posterior border of the ulna. It is a long, thick muscle on the lateral side of the humerus that extends the forearm (Furbringer, 1876; Chaisson, 1962).

M. humero-radialis (hr) – originates from the proximo-lateral surface on the shaft of the humerus just behind the insertion of *M. deltiodes scapularis inferior* and inserts into the proximal anterior-medial surface of the radius. Its originating fibers decussate with the inserting fibers of *M. deltoideus scapularis*. It is a long muscle that lies on the lateral surface of the humerus and flexes the forearm (Furbringer, 1876; Chaisson, 1962).

M. humero-antebrachialis inferior (hai) – (*brachialis inferior*) (Furbringer, 1876) originates from the proximal half of the anterior surface of the humerus and inserts into the proximal anterior-medial surface of the ulna and the proximal posterior-medial surface of the radius along with the *M brachialis*. It is a long thin muscle that lies on the anterior surface of the humerus that flexes the forearm (Furbringer, 1876; Chaisson, 1962).

M biceps (b) – (*coraco-antebrachialis*) (Furbringer, 1876) originates from a thin tendon on the anterior upper surface of the coracoid just anterior to the origin of *M croaco-brachialis brevis* and the coracoid foramen (Brochu, 1992). It inserts into the proximal anterior-medial surface of the ulna and the proximal posterior-medial surface of the radius along with the *M. humero-antebrachialis inferior* (Chaisson, 1962). It is a long, thin muscle that lies on the medial surface of the humerus and flexes the forearm.

M. anconaeus humeralis medialis (ahm) – a deep head of the anconaeus complex that originates from the entire medio-posterior surface of the humerus and joins a broad, heavy tendon that inserts into the posterior border of the ulna. It is a broad, oblong

muscle that lies deep on the medial side of the humerus that extends the forearm (Furbringer, 1876; Chaisson, 1962).

M. anconaeus coraco-scapularis (acs) – originates from the posterior curve on the upper half of the coracoid just below the glenoid fossa and joins a broad heavy tendon that inserts into the posterior border of the ulna. It is a long, thin muscle that lies on the posterior medial surface of the humerus (Furbringer, 1876; Brochu, 1992).

Forearm Musculature

Lateral

M humero-carpi ulnaris (hcu) - originates from the lateral condyle of the humerus and inserts into the entire border of the ulna and ulnare. It is the first muscle from the exposed ulna on the lateral side of the forearm. It flexes the forearm and extends the manus (Brochu, 1992; Chaisson, 1962).

M. humero-dorsalis (hd) – originates from the lateral condyle of the humerus and inserts into tendons that branch to the proximal phalange of each digit except the last. It is the second muscle from the exposed ulna on the lateral side of the forearm. It lies superficial to the *M humero-radialis brevis* and extends the digits (Brochu, 1992; Chaisson, 1962).

M extensor-carpi radialis (ecr) – originates from the lateral condyle of the humerus and inserts into the radiale. It is the third muscle from the exposed ulna on the lateral side of the forearm. The primary action of this muscle is to extend the manus (Brochu, 1992;

Chaisson, 1962). Chaisson (1962) notes that the belly of this muscle is fused with the *M. humero-dorsalis*.

M humero-radialis longus (hrl) – originates from a tendinous loop which covers the inserting tendon of the *M humero-radialis* and inserts into the anterior border of the radius. It is the fourth muscle from the exposed ulna on the lateral side of the forearm, and its primary action is to flex the forearm (Chaisson, 1962).

M humero-radialis brevis (hrb) – originates from the lateral condyle of the humerus and inserts into the proximo-lateral half of the radius. It is oriented at an angle from the ulna and is used to help flex and rotate the forearm (Chaisson, 1962). It lies deep to the *M humero-dorsalis* and the *M extensor carpi radialis*.

M extensor carpi radialis profundus (ecrp) – originates from the distal lateral half of the radius and inserts into the radiale. This muscle lies deep to the *M humero-dorsalis* and *M. extensor-carpi radialis* and it aids in extending the manus (Chaisson, 1962).

Medial

M Pronator teres (pt) – originates from the proximal medial surface of the ulna and inserts into the medial surface of the middle third of the radius. This muscle saddles the ulna and is the first superficial medial muscle from the ulna. Most of the body lies deep to the *M humero radialis internus* and the *M flexor digitorum communis profundus* (humeral head) (Chaisson, 1962).

M flexor-carpi ulnaris (fcu) – originates from the posterior medial condyle of the
humerus and inserts into the ulnare. This muscle is the second superficial muscle from
the ulna and it flexes the manus (Chaisson, 1962).

M flexor digitorum communis profundus (humeral head) (fdcp (h)) – originates from the
posterior edge of the medial condyle of the humerus and inserts into the palmar
aponeurosis along with the ulnar head of the same muscle. This muscle lies superficial to
the *M pronator teres* and *M flexor digitorum communis profundis* (ulnar head). It is the
third superficial muscle from the ulna (Chaisson, 1962).

M humero radialis internus (hri) – originates from the medial condyle of the humerus
and inserts into the entire medial edge of the radius. This muscle aids in flexing the
forearm and is the fourth superficial muscle from the ulna (Chaisson, 1962).

M humero anteradialis (har) – originates from the anterior portion of the medial condyle
and inserts into the distal anterior edge of the radius. This muscle flexes the forearm and
is the fifth superficial muscle from the ulna.

M flexor digitorum communis profundis (ulnar head) (fdcp (u)) – originates from the
distal two thirds of the ulna and inserts into the palmar aponeurosies. This muscle lies
deep to the *M humero radialis internus* and the humeral head of the same muscle. It aids
in flexing the digits (Chaisson, 1962).

Dissections

Systematic dissections modeled after Furbringer (1876) were performed on the three representative specimens. First an incision was made ventrally from a point between the angulars down the midline of the body to about two thirds of the way to the hindlimb. Then another incision was made from the first point down the edge of the angular and around the jaw to the nuchal plates. The incision was continued around the nuchal plates then finished at the vertebral column. Another incision was made from the midline just above the pectoral region to and around the arm. The incision was continued at a 90° angle to the vertebral column. This exposed the superficial neck and shoulder muscles of the specimen when the skin was folded back over the vertebral column. Care was taken when separating the *M. trapezius* from the skin to avoid tearing. A decussate incision was made from the most caudal point of the midline incision to the vertebral column. The superficial pectoral and shoulder muscles were exposed when the skin was folded back over the vertebral column. This was done carefully to prevent tearing of the *M. latissimus dorsi*.

An incision was made down the length of the arm to the wrist where another incision circumvents the wrist. The skin was removed exposing the forelimb musculature. To expose the deep muscles of the shoulder the *M latissimus dorsi* and the *M trapezius* were cut and reflected. Then the *M anconaeus scapularis lateralis, M deltoideus scapularis inferior, M teres major* and *M. deltoideus scapularis superior* were cut and reflected to expose the *M. coraco-brachialis brevis, M scapulo-humeralis profundus* and *M. supracoraco scapularis*. To expose the deep muscles of the pectoral and neck region

the *M episternal hyoides*, *M pectoralis* and *M sternomastoideus* were cut and reflected.

To expose the deep muscles of the lateral forearm the *M. humero dorsalis* and

M extensor carpi radialis were cut and reflected. Also, the *M flexor carpi ulnaris*,

M flexor digitorum communis profundus (h), *M humero radialis internus* and *M humero*

anteradialis were cut and reflected to expose the deep muscles of the medial forearm.

RESULTS

In comparing the shoulder musculature of the three species only minor differences were found. In *T. schlegelii* the *M. latissimus dorsi* was reduced and exposed the *M. teres major*. The *M. trapezius* and *M. latissimus dorsi* are very large in *G gangeticus*, they completely cover the *M. levator scapulae superficialis and M serratus superficialis* respectively. The *M. deltoideus scapularis superficialis* lies mostly deep unlike the other taxa where it was exposed (Figure 6). *C. crocodilus* had a comparatively larger *M deltoideus scapularis inferior*, most likely due to its increased adaptation to terrestrial environments (Figure 7). The *M coracohyoides* had a triangular cross-section in *G. gangeticus*, whereas in *C. crocodilus* and *T. schlegelii* it was flat and band-like. The differences seen in the shoulder musculature may be reflected in the osteology, as the gharial scapula was much more flared than *Caiman*, *Tomistoma* or *Alligator mississippiensis* (Brochu, 1992).

A comparison of the brachial musculature and the pectoral musculature also showed no significant differences other than size due to environmental adaptation. Overall, the muscles were similar in arrangement, showing the conservative anatomy of the four genera with differing levels of terrestrial capabilities. The musculature of the medial forearm did show significant differences in that only *G. gangeticus* had fused flexors. The *M. humero radialis internus* and *M humero anteradialus* formed a single unit unlike the other species studied (Figure 15). Figure 17 shows a summary of origin and insertion areas on the crocodilian forelimb and pectoral girdle.

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A

B

C
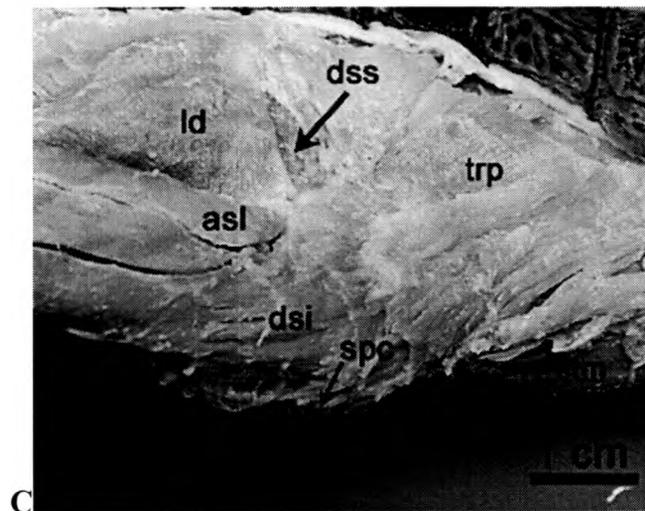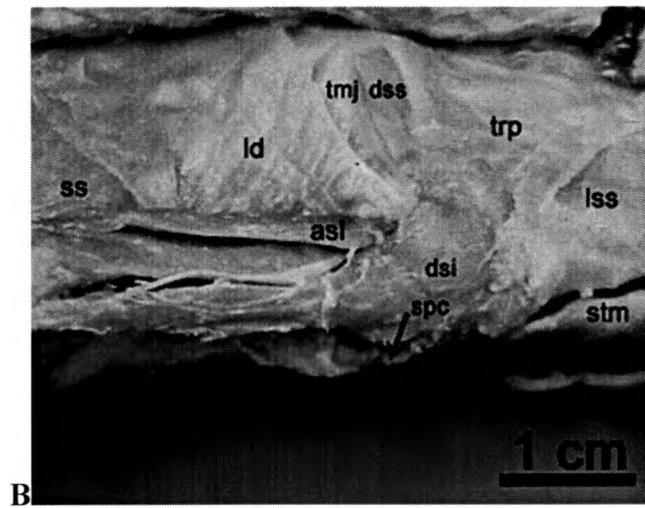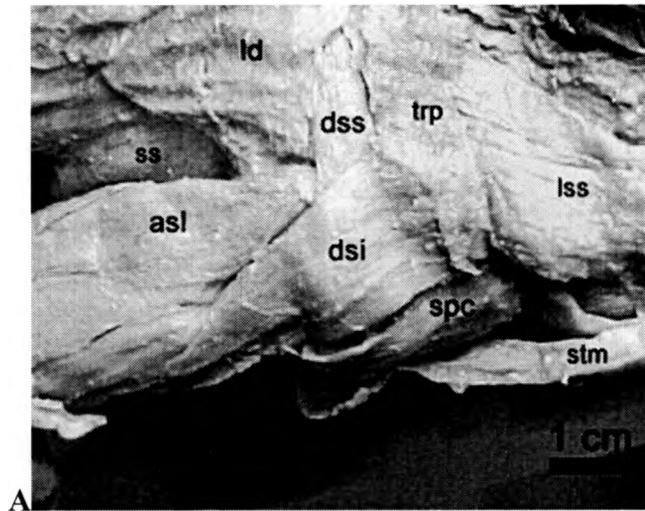
Fig. 6. The superficial musculature of the shoulder. A = *C. crocodilus (trp* cut*)*, B = *T. schlegelii*, and A= *G. gangeticus.*
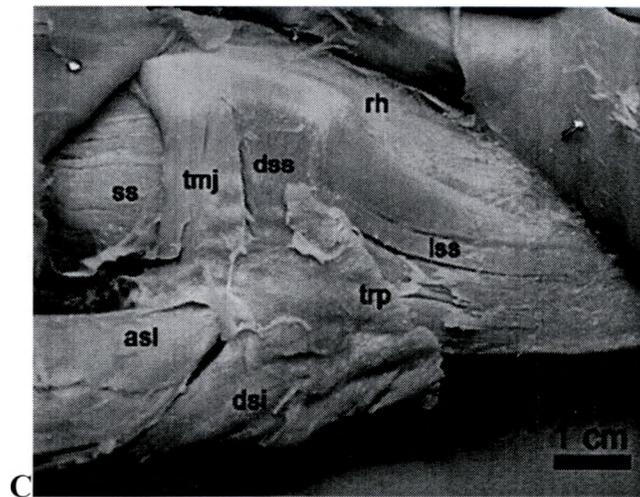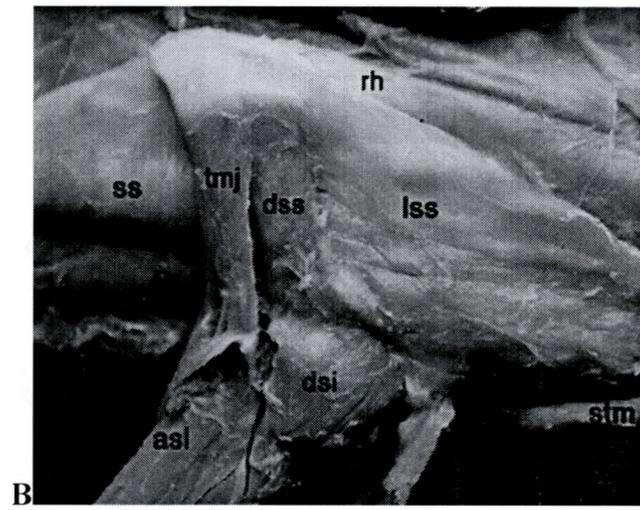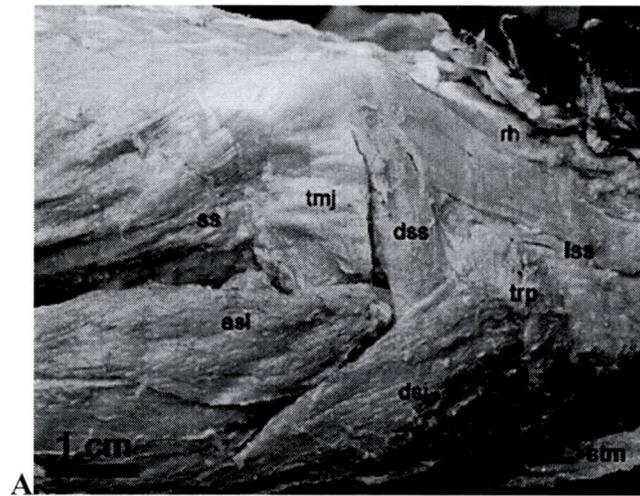
Fig. 7. The first deep layer of shoulder muscles. A = *C. crocodilus*, B = *T. schlegelii*, and A= *G. gangeticus*.
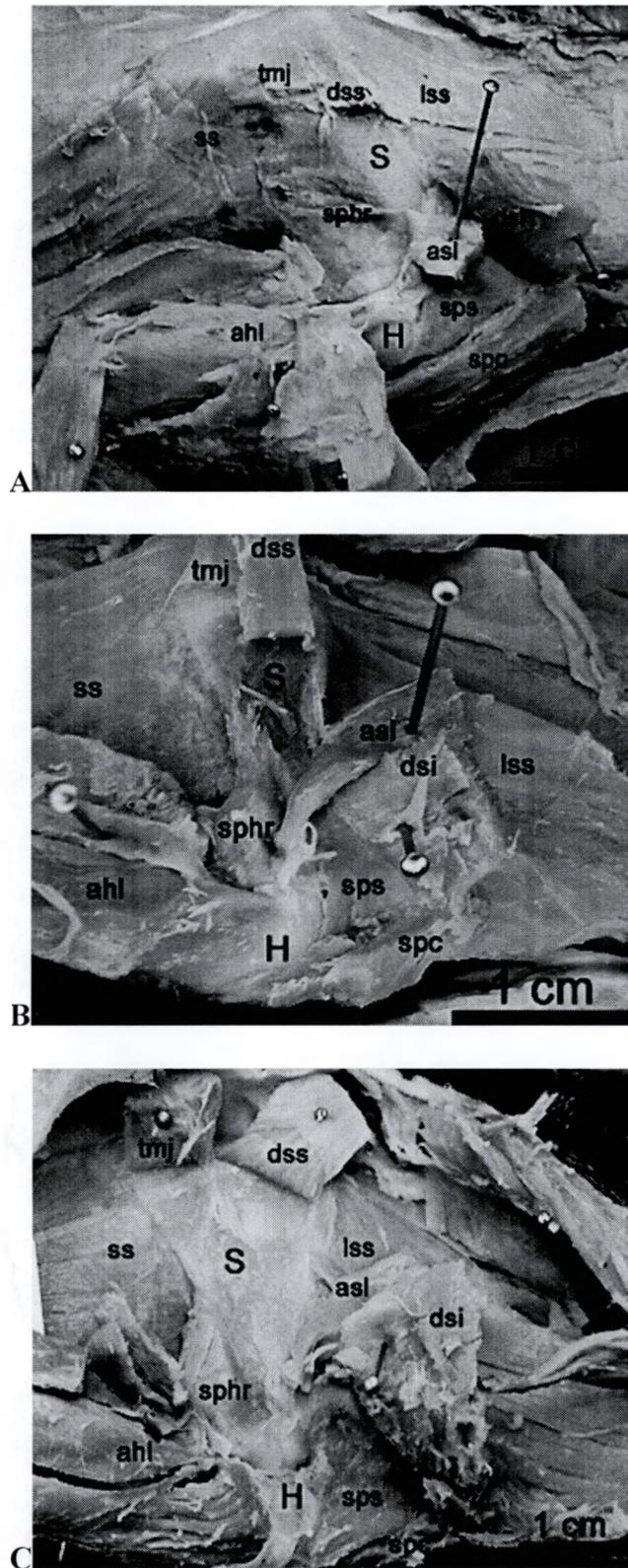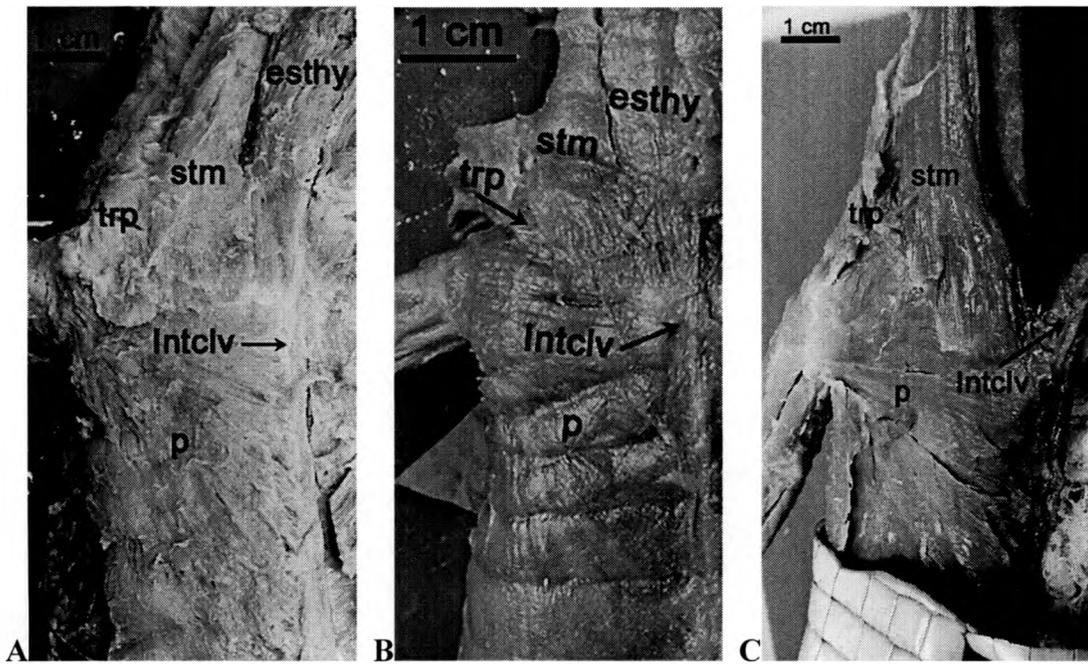
Fig. 9. The superficial pectoral musculature. A = *C. crocodilus*, B = *T. schlegelii*, and A= *G. gangeticus*.
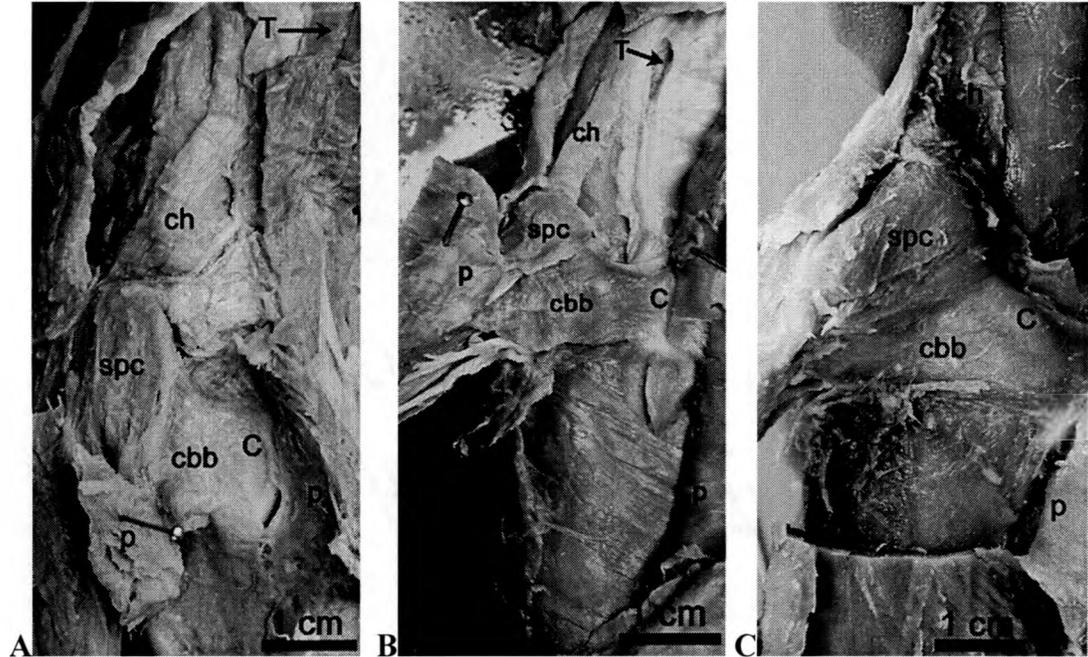
Fig. 10. The deep pectoral musculature. A = *C. crocodilus*, B = *T. schlegelii*, and A= *G. gangeticus*.
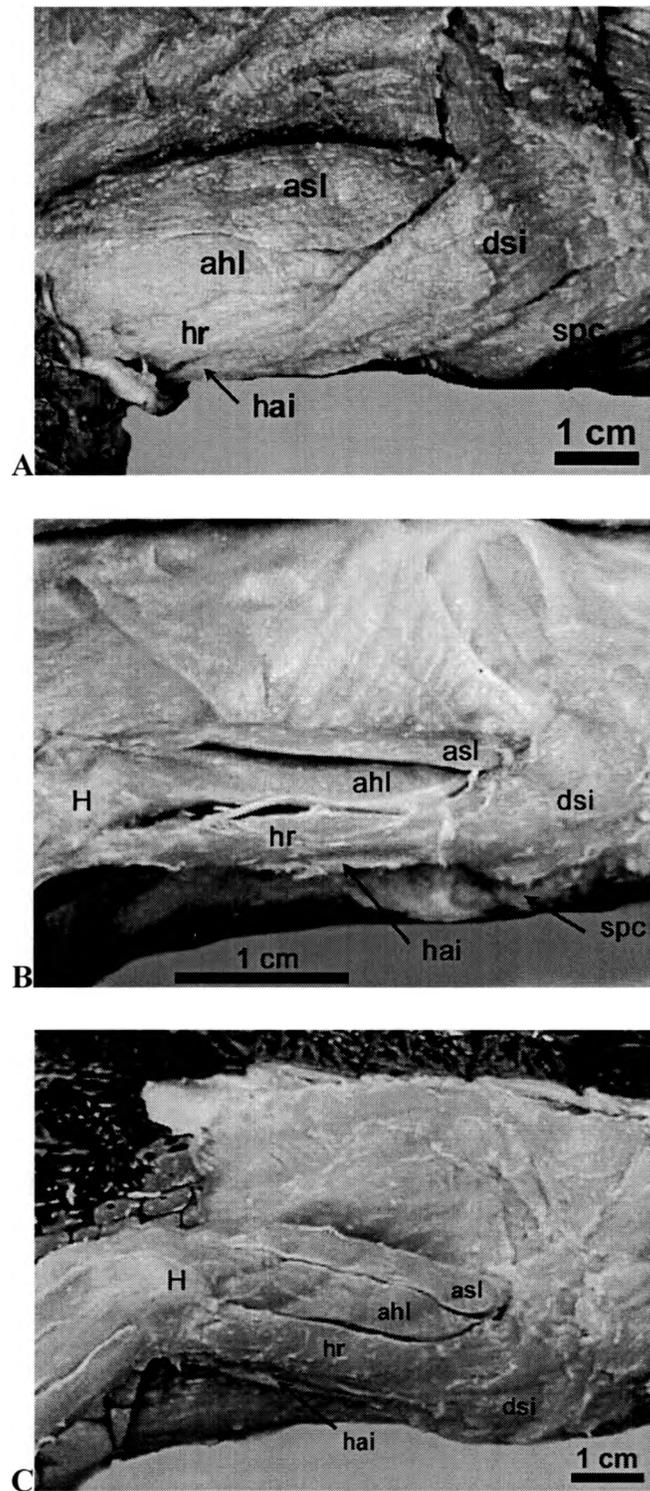
Fig. 11. The brachial musculature on the lateral side of the humerus. A = *C. crocodilus*, B = *T. schlegelii*, and A= *G. gangeticus*.
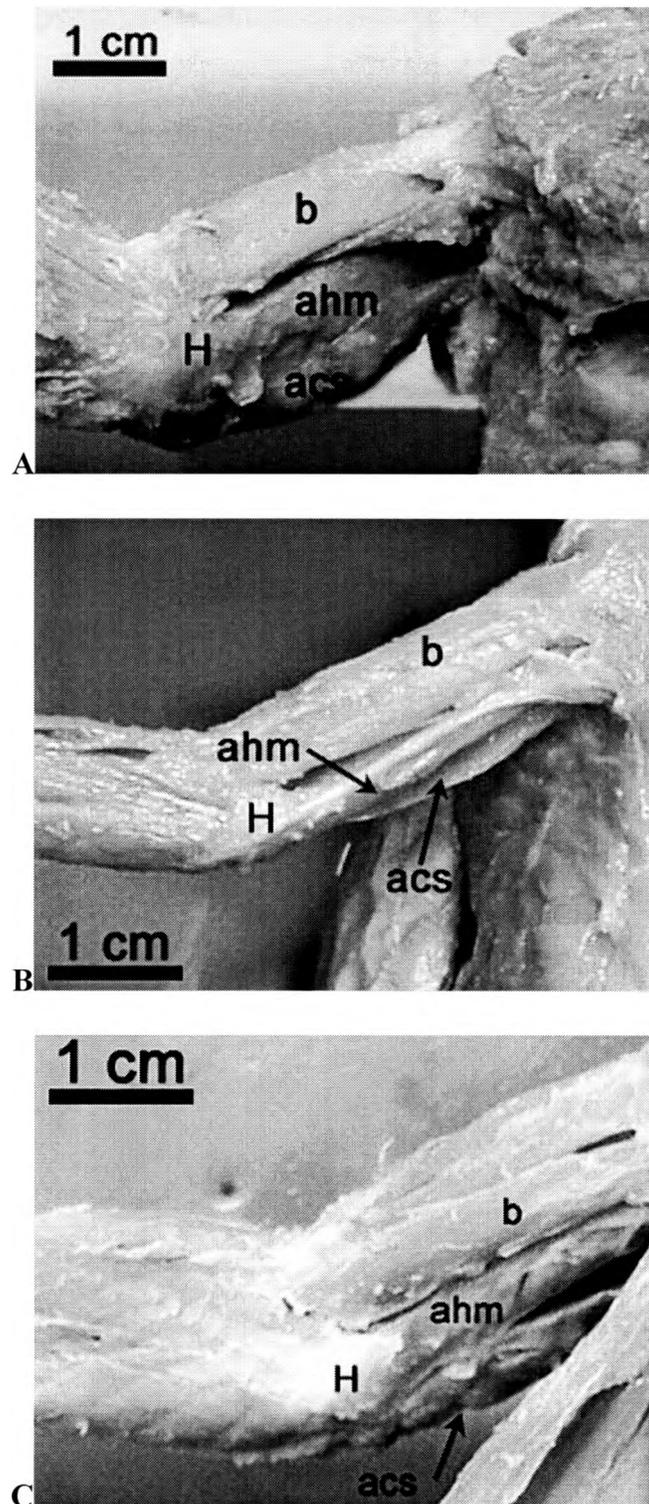
Fig. 12. The brachial musculature on the medial side of the humerus. A = *C. crocodilus*, B = *T. schlegelii*, and A= *G. gangeticus*.
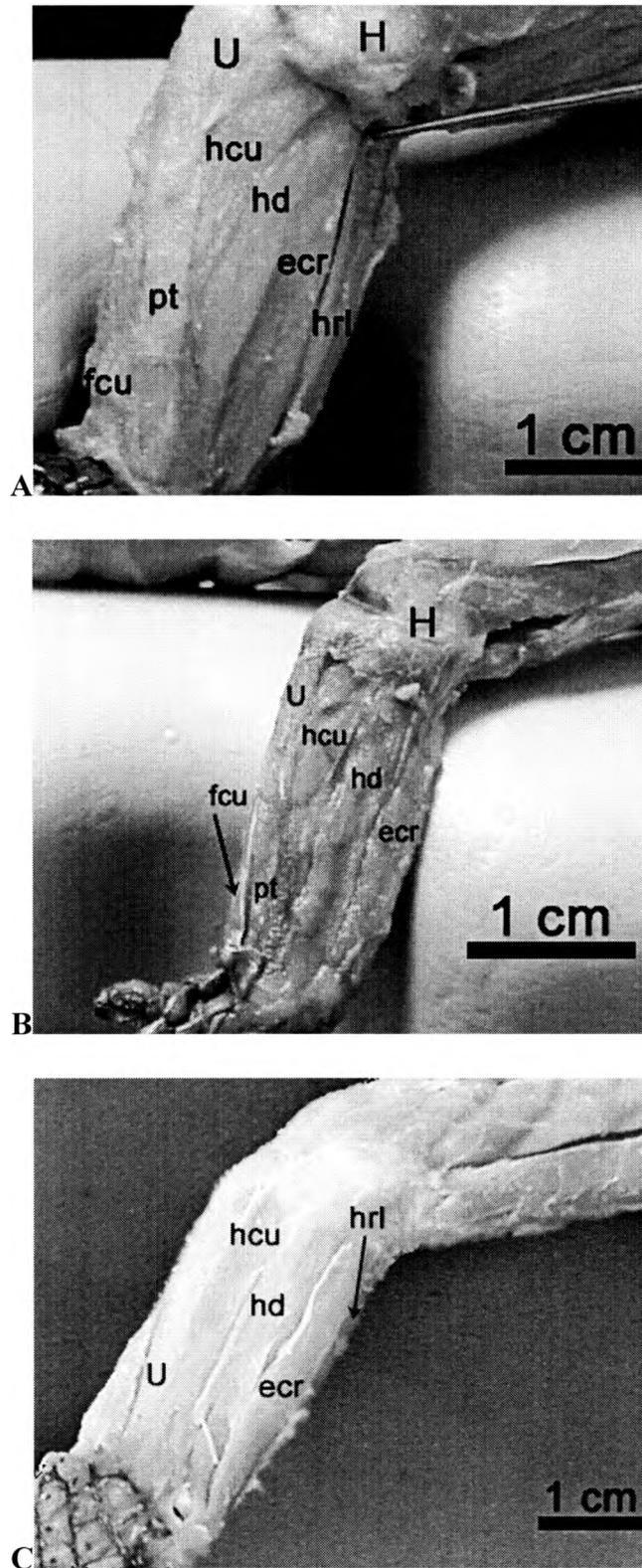
Fig. 13. The superficial forearm musculature on the
lateral side of the radius and ulna. A = *C. crocodilus*,
B = *T. schlegelii*, and A= *G. gangeticus*.
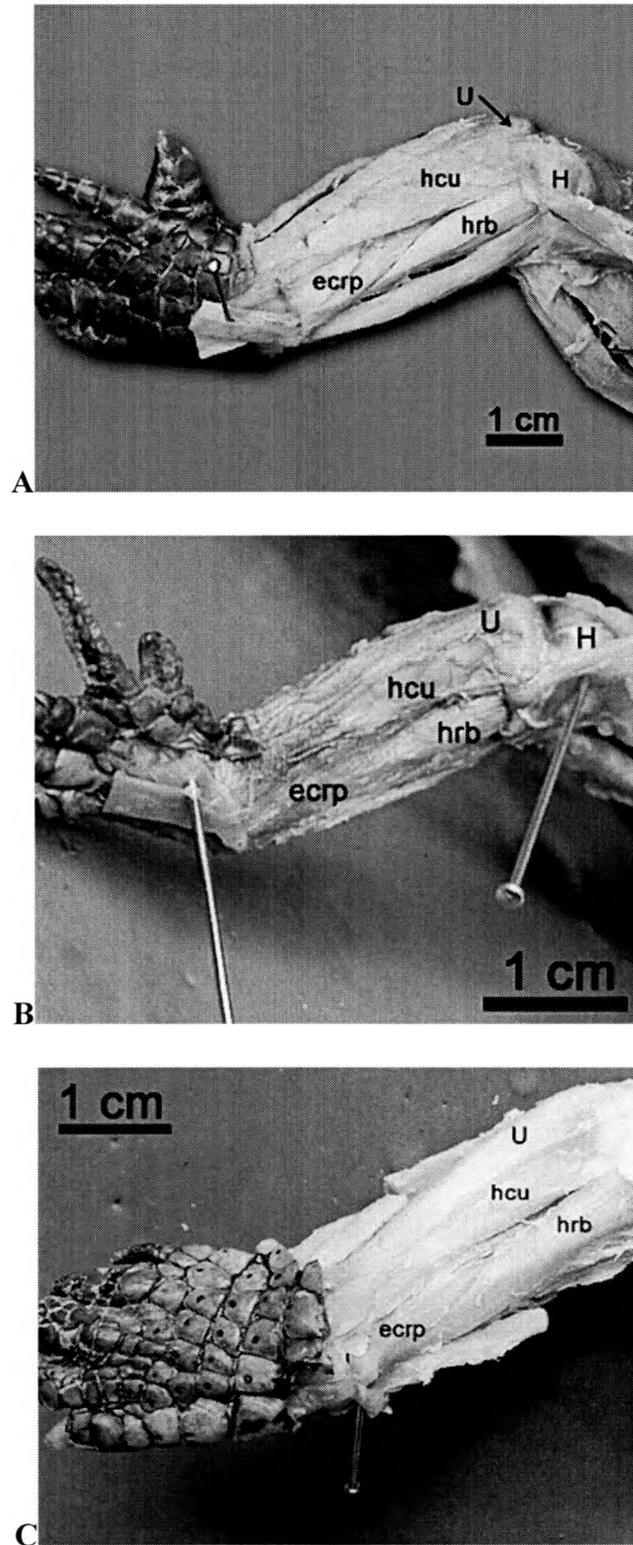
Fig. 14. The deep forearm musculature on the lateral side of the radius and ulna. A = *C. crocodilus*, B = *T. schlegelii*, and A= *G. gangeticus*.
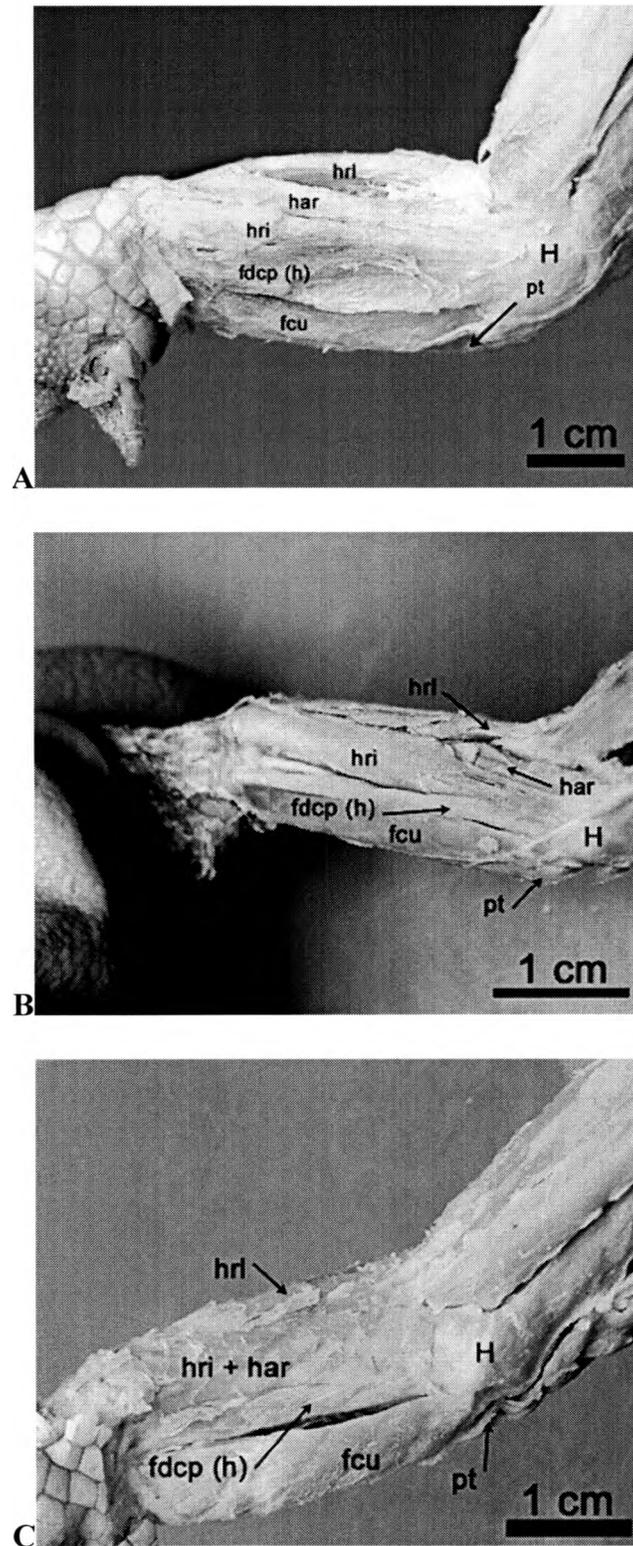
Fig. 15. The superficial forearm musculature on the
medial side of the radius and ulna. A = *C. crocodilus*,
B = *T. schlegelii*, and A= *G. gangeticus*.
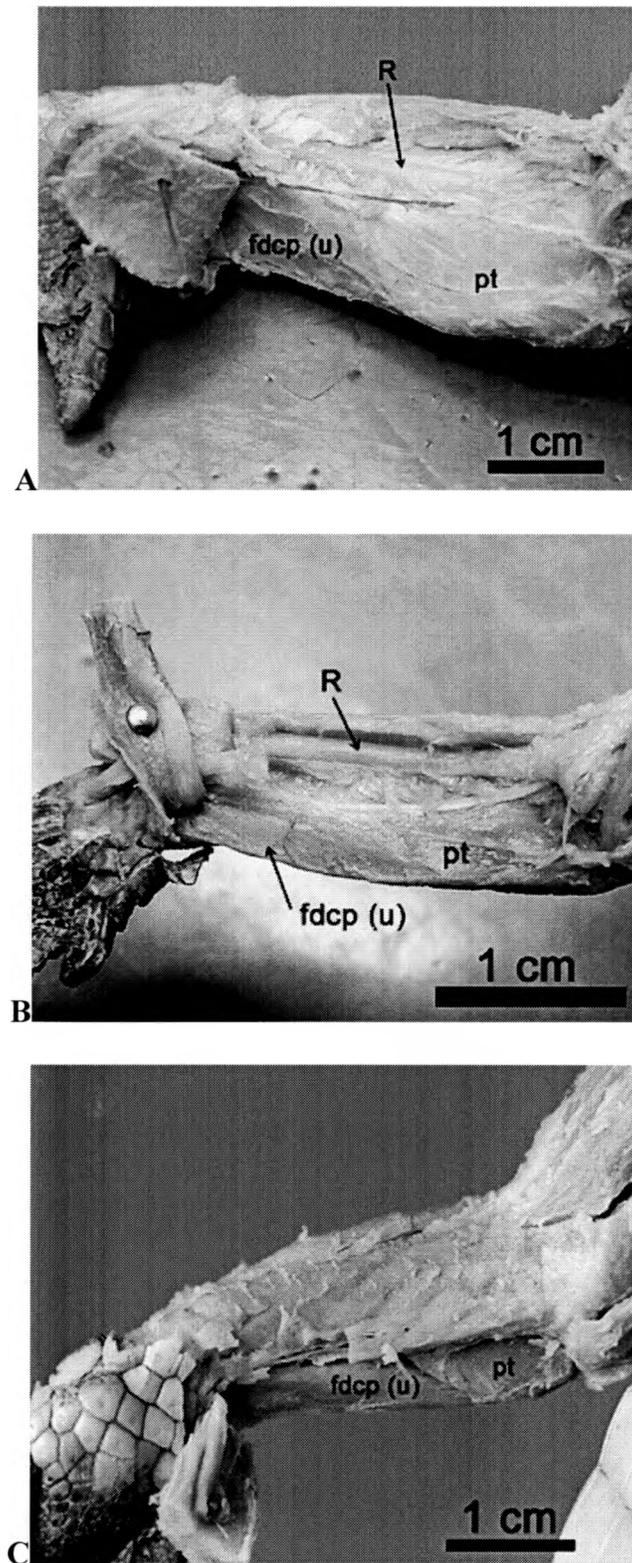
Fig. 16. The deep forearm musculature on the medial side of the radius and ulna. A = *C. crocodilus*, B = *T. schlegelii*, and A= *G. gangeticus*.
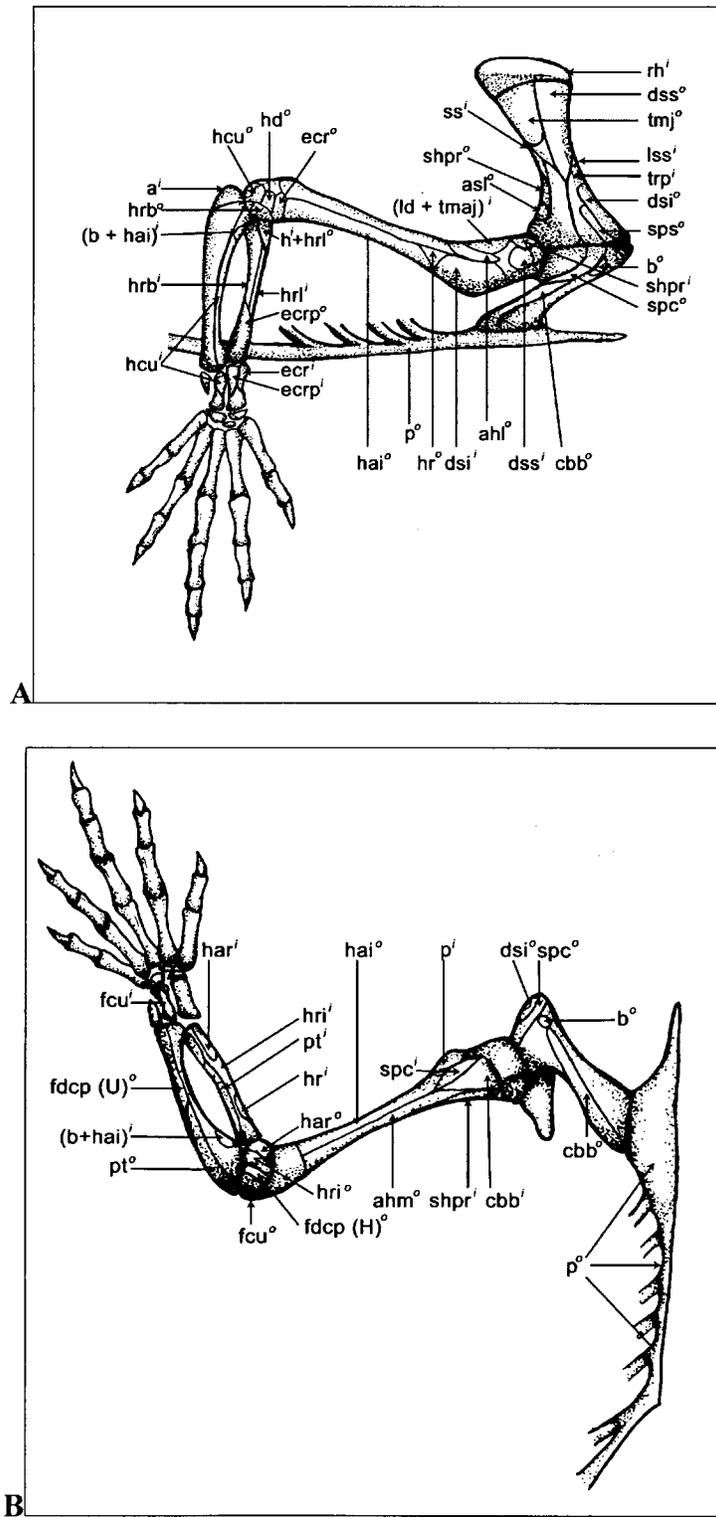
Fig. 17. Insertion and origin areas on the crocodilian pectoral girdle and forelimb, based on Furbringer (1876). A = lateral view, B = ventral view.

DISCUSSION

The musculature seen in these three specimens was concordant with the dissection done by Furbringer (1876). Functionally, fusing of the flexors in gharials may be due to lateral compression of the forearm. *Gavialis* is the most aquatic of all the extant Crocodylia and modifications for their environment seem plausible. This result agrees with previous morphological studies of the braincase, tail musculature and epaxial musculature, which place *Gavialis* as a sister group to all the other modern taxa (gharials (alligatorids + crocodylids)). In future studies more taxa should be dissected in order to determine if fused flexors are autapomorphies of *Gavialis*. There is a lack of post cranial morphological characters used in phylogenetic analysis of extant taxa, therefore the results of this study will add to the current literature (Brochu, 1992). Dinosaur reconstructions are based on muscle and tendon attachment scars left on fossilized bones. The information garnered from these residual attachments along with comparative studies like this one can be used to infer anatomical and biomechanical aspects of long extinct forms.

Other interesting aspects of *Gavialis* are the embryological differences in snout length between *G gangeticus* and *T schlegelii*. This implies that the *Gavialis* and *Tomistoma* elongate the snout in different ways. Elongation of the snout in *C catatphractus* and *C. johnstoni* is concordant with that of *Tomistoma* (Tarsitano, pers. comm.). In addition, a small capsule of tissue (most likely a salt regulation device) found

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in the eye socket of *Gavialis* may suggest a different origin from that of Tomistomidae

(Tarsitano et al., 1989; Frey et al., 1989). Investigations into these antorbital structures

are necessary to understand if gharials have a different salt regulation mechanism than

other crocodilians.

The dilemma with crocodilian systematics is that the group is morphologically

conservative and their extant diversity is nominal compared to other groups like

lepidosaurs. Contributing to this quandary is the lack of a close out-group, given that

their nearest living relatives are highly derived birds. Gavialoid fossils from the Late

Cretaceous and tomistomine fossils from the Eocene may support the morphological

phylogeny. Divergence times deduced from molecular data suggest a much later

divergence, but are contradicted by the fossil evidence. Of the extant Crocodylia,

Gavialis appears to be the most interesting form having a number of peculiar differences

from the other crocodilians.

Although Westphal (1962) pointed out that the longirostrine condition of *Gavialis*

and Thalattosuchians were the result of homoplasy, the differences in morphology of

gharials from the rest of the Eusuchia give the appearance at least that gharials are either

surviving mesosuchians or have branched off from the Eusuchia very early in their

evolution (Tarsitano et al., 1989). Every eusuchian verticalizes the braincase so that the

basisphenoid is nearly covered over by the basioccipital and pterygoid. In gharials the

basisphenoid is elongated and exposed. Moreover, the braincase is box-like with

enlarged supratemporal fenestra and elongated retroarticular processes (Kalin, 1955).

Given that gharials may have a unique salt regulation process and unique morphology

points to a hypothesis that at the very least they have a different origin than the

Tomistomindae.

APPENDIX 1. A table of muscle abbreviations and a brief description of differences between the taxa.

ABR	MUSCLE	*C. crocodilus*	*T. schlegelii*	*G. gangeticus*
	Shoulder Musculature			
ld	*M latissimus dorsi*			larger than others
trp	*M trapezius*			larger than others
lss	*M levator scapulae superficialis*			
ss	*M serratus superficialis*			
rh	*M rhomboideus*			
dss	*M deltoideus scapularis superior*			
tmj	*M teres major*			
dsi	*M deltoideus scapularis inferior*	larger than others		
sps	*M supracoracoscapularis*			
shpr	*M scapulo-humeralis profundus*			
	Pectoral Musculature			
stm	*M sternomastoideus*			
spc	*M supracoracoideus*			
p	*M pectoralis*			
cbb	*M coraco-brachialis brevis*			
esthy	*M episterno-hyoideus*			
ch	*M coracohyoides*			larger than others
	Brachial Musculature			
asl	*M anconaeus scapularis lateralis externus*		-	
ahl	*M anconaeus humeralis lateralis*			
hr	*M humero-radialis*			
hai	*M humero-antebrachialis inferior*			
b	*M biceps*			
ahm	*M anconaeus humeralis medialis*			
acs	*M anconaeus coraco-scapularis*			
	Forarm Musculature			
	Lateral			
hcu	*M humero-carpi ulnaris*			
hd	*M humero-dorsalis*			
ecr	*M extensor-carpi radialis*			
hrl	*M humero-radialis longus*			
hrb	*M humero-radialis brevis*			
ecrp	*M extensor carpi radialis profundus*			
	Medial			
pt	*M pronator teres*			
fcu	*M flexor-carpi ulnaris*			partially fused
fdcp (h)	*M flexor digitorum communis profundus* (humeral head)			
hri	*M humero radialis internus*			fused
har	*M humero anteradialis*			fused
fdcp (u)	*M flexor digitorum communis profundus* (ulnar head)			

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