A COMPARISON OF THE MUSCULATURE INVOLVED IN THE RETRACTION OF THE HEAD AND NECK OF THE FAMILIES AND GENERA OF THE SIDE-NECKED TURTLES (TESTUDINES: PLEURODIRA: CHELIDAE AND PELOMEDUSIDAE)

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Susan Kaye Lucas

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Susan Kaye Lucas, daughter of Claude Durant and
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Susan Kaye Lucas

Master of Science, December 11, 1980 (B.S., Memphis State University, 1978)

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Directed by James Dobie

The plastra of six genera of pleurodires; Pelomedusa, Pelusios, Chelus, Hydromedusa, Phrynops and Platemys; was removed and the retractile neck musculature was identified after dissection. Origins, insertions and relations were noted throughout dissection.

The lateral flexors of the head and neck in the pleurodires examined have been identified as the Musculus retrahens capitis collique, Musculus scalenus, Musculus longus colli and Musculus coracohyoideus. In pleurodires, the retraction of the head and neck laterally beneath the carapace is accomplished by three movements involving the four muscle groups previously mentioned. The retractile mechanism in the Chelidae differs from that of the Pelomedusidae.

Upon investigating familial and generic relationships, the specifics of the musculature involved differentiates between the Chelidae and the Pelomedusidae. Pelomedusa and Pelusios were found to be closely related based on the musculature studied. Likewise, Chelus, Phrynops and Platemys appeared to be closely related based on the origins and insertions of the four muscle groups. The musculature of Hydromedusa was found to be different from the other South American chelids.

P. Bishop, Museum in Ropelulu, Hawail,

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Specimens used in this study were kindly furnished by Donald G. Broadley, National Museums and Monuments of Rhodesia; John C. Greig, Jonkershoek Nature Conservation Station in South Africa; The Pet Farm of Miami, Florida; Ernest E. Williams, Museum of Comparative Zoology at Harvard University; Ivanzir Vieira, Universidade Federal de Juiz de Fora in Brazil; and Alan Ziegler, Bernice P. Bishop, Museum in Honolulu, Hawaii.

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I. INTRODUCTION

The two suborders of turtles, Cryptodira and Pleuro-dira, differ primarily in the manner in which the head is withdrawn into the shell (Gaffney, 1971 and 1979). In the Cryptodira, the head is withdrawn by flexing the neck vertically to produce an S-shaped curvature, while in the Pleurodira, the neck is bent in either direction laterally and neck and head are pulled under the front edge of the carapace (Figures 1 and 2).

Cryptodira includes about 80% of all extant turtles, while Pleurodira consists of approximately 50 species separated into two families, the Pelomedusidae and the Chelidae. Pelomedusidae are found only in South America, Africa and Madagascar and Chelidae are located only in South America, Australia and parts of the New Guinea archipelago. Although both pleurodiran families presently are restricted to the southern hemisphere, fossil remains of pelomedusids are known from the northern hemisphere. No chelid fossil remains have been found in the northern hemisphere.

Various authors have proposed classification schemes for turtles, which have been based mainly on morphological attributes. Since so many cryptodiran specimens have been

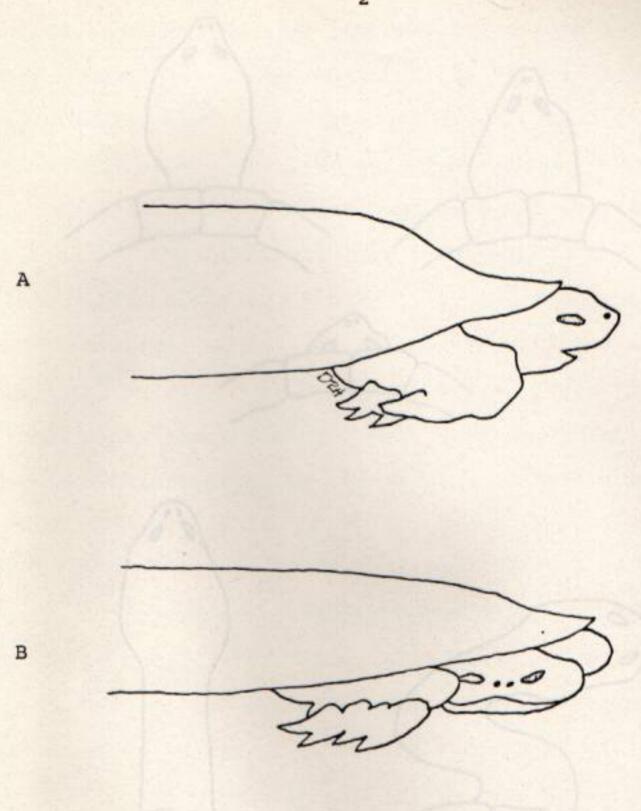


Figure 1. Lateral view of head and neck retraction.

A. Cryptodira

B. Pleurodira

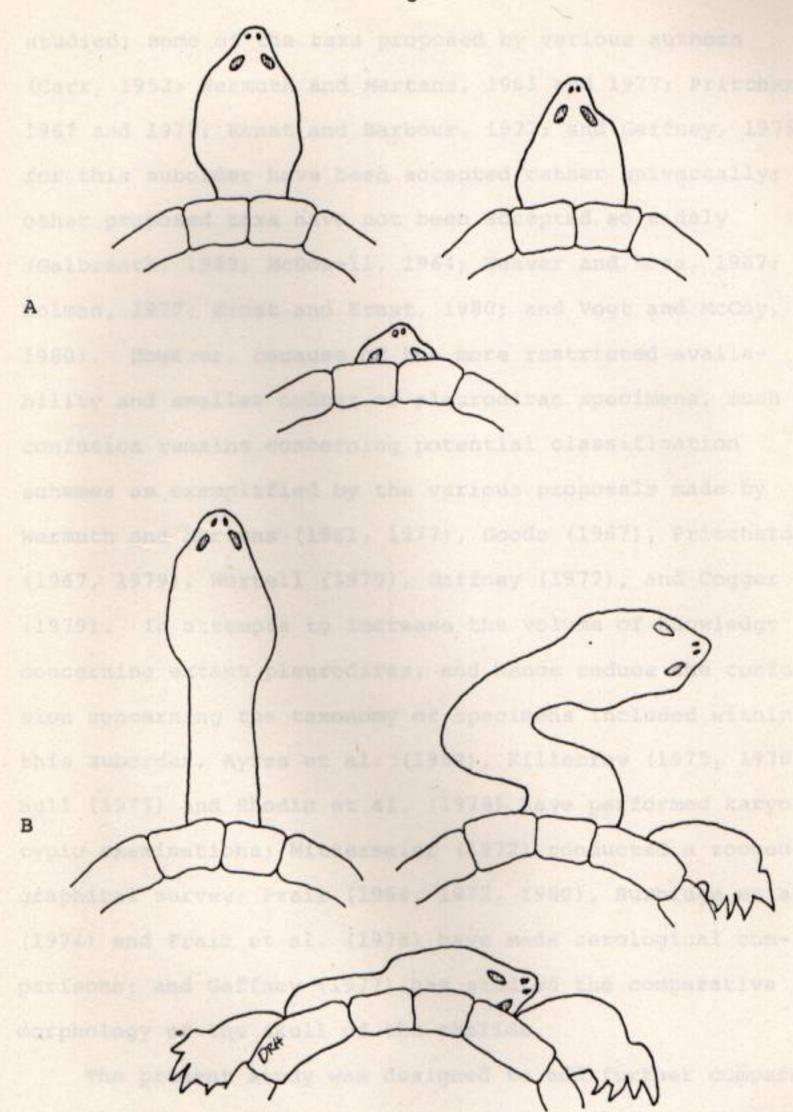


Figure 2. Dorsal view of head and neck retractions.
A. Cryptodira

B. Pleurodira

studied, some of the taxa proposed by various authors (Carr, 1952; Wermuth and Mertens, 1961 and 1977; Pritchard, 1967 and 1979; Ernst and Barbour, 1972; and Gaffney, 1975) for this suborder have been accepted rather universally; other proposed taxa have not been accepted so widely (Galbreath, 1948; McDowell, 1964; Weaver and Rose, 1967; Holman, 1977; Ernst and Ernst, 1980; and Vogt and McCoy, 1980). However, because of the more restricted availability and smaller number of pleurodiran specimens, much confusion remains concerning potential classification schemes as exemplified by the various proposals made by Wermuth and Mertens (1961, 1977), Goode (1967), Pritchard (1967, 1979), Worrell (1970), Gaffney (1977), and Cogger (1979). In attempts to increase the volume of knowledge concerning extant pleurodires, and hence reduce the confusion concerning the taxonomy of specimens included within this suborder, Ayres et al. (1969), Killebrew (1975, 1976), Bull (1977) and Rhodin et al. (1978) have performed karyotypic examinations; Mittermeier (1972) conducted a zoogeographical survey; Frair (1964, 1972, 1980), Burbidge et al. (1974) and Frair et al. (1978) have made serological comparisons; and Gaffney (1977) has studied the comparative morphology of the skull of the chelids.

The present study was designed to add further comparative morphological data to the pool of knowledge concerning pleurodires, specifically concerning the muscles responsible for head and neck retraction beneath the carapace. The only previous study concerning these muscles was reported by Shah (1963), who compared the neck musculature of a single cryptodiran specimen (Deirochelys reticularia) with that of a single pleurodiran specimen (Chelodina sp.). The study reported herein was initiated to identify and compare the muscles responsible for head and neck retraction among the genera of the pleurodires. Further, the general patterns of these muscles were compared between the Pelomedusidae and the Chelidae.

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muscled. After the skip was describe from the head and

neck; the paravertebral nuscles of the trunk were dissected

and themselfied. Desgine, insertions and relations were

nored throughout the dissections.

II. THE RETRACTILE NECK MUSCULATURE OF PLEURODIRES: FUNCTION AND PHYLOGENETIC SIGNIFICANCE

Description of the Rennactile Musculamina

Materials and Methods

All dissections were performed on specimens preserved by fixation with formaldehyde. Specimens of the Pelomedusidae included Pelomedusa subrufa (5 individuals); Pelusios sinuatus sinuatus (1); and Pelusios subniger (2). Specimens of the Chelidae included Chelus fimbriatus (1); Hydromedusa sp. (1); Phrynops sp. (1); and Platemys platycephala (1). Locality data, when available, and the museum from which the specimens were obtained are included within the appendix.

On each specimen the plastron was freed from the carapace by sawing through the bridge on each side with a Stryker bone saw. The plastron then was removed from the body of the turtle after the pelvic girdle attachment had been severed. The right forelimb was removed, as were most of the visceral organs, to facilitate access to the muscles. After the skin was removed from the head and neck, the paravertebral muscles of the trunk were dissected and identified. Origins, insertions and relations were noted throughout the dissections.

Results

Description of the Retractile Musculature

The principal lateral flexors of the head and neck in
the pleurodires examined have been identified as the

Musculus retrahens capitis collique, the Musculus scalenus,
the Musculus longus colli and the Musculus coracohyoideus
(Figure 3). The following is a general description of
these muscles.

Mm. Retrahens Capitis Collique

In all prior reports the Mm. retrahens capitis collique has been considered a single muscle in both cryptodires and pleurodires (Noble and Noble, 1940; Ashley, 1955; Shah, 1960, 1963; Bramble, 1974). However, in all of the pleurodires examined in this study, the Mm. retrahens capitis collique consists of three separate muscles (Figure 3), each with a unique origin and insertion. Dobie and Williams (personal communication), working with presumably homologous muscles in cryptodires, named these muscles based on their relative positions: the M. retrahens capitis collique wentralis; the M. retrahens capitis collique medialis; and the M. retrahens capitis collique dorsalis.

The M. retrahens capitis collique ventralis is the longest, and most massive, of the three muscles. In both families it arises from either the neural or the costal plates, depending on the species, and dorsal vertebrae

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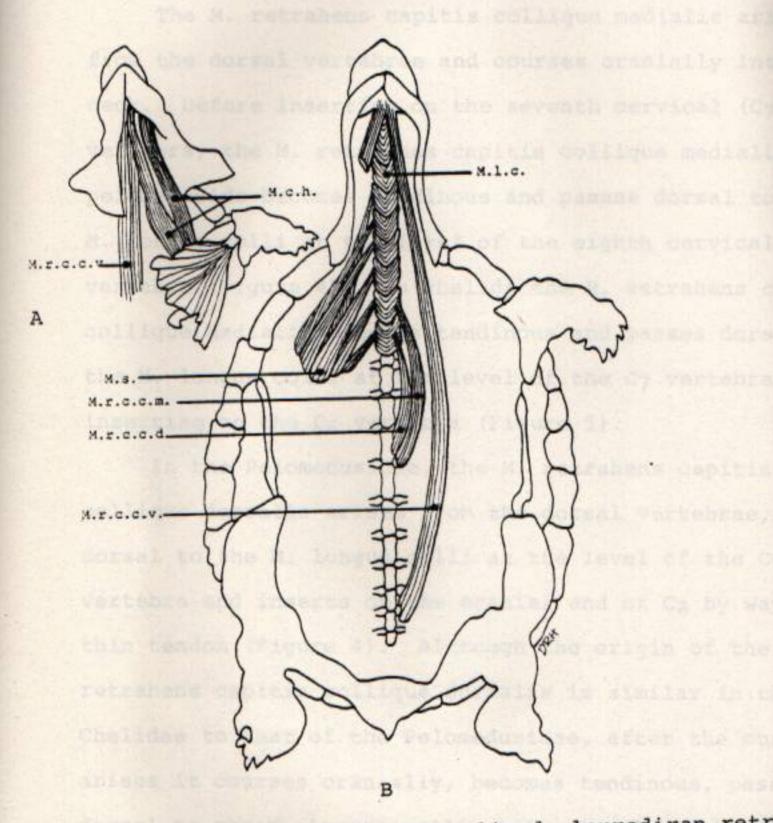


Figure 3. Ventral view of generalized pleurodiran retractile musculature. A. View with limb attached.

B. View with limbs removed. M. coracohyoideus (M.c.h.); M. longus colli (M.l.c.); M. retrahens (capitis collique dorsalis (M.r.c.c.d.); M. retrahens capitis collique medialis (M.r.c.c.m.); trahens capitis collique ventralis (M.r.c.c.v.); M. scalenus (M.s.).

and courses cranially into the neck to insert on the basisphenoid bone of the skull by way of a thick tendon shared with its homolog (Figures 3, 4 and 5).

The M. retrahens capitis collique medialis arises from the dorsal vertebrae and courses cranially into the neck. Before inserting on the seventh cervical (C7) vertebra, the M. retrahens capitis collique medialis of pelomedusids becomes tendinous and passes dorsal to the M. longus colli at the level of the eighth cervical (C8) vertebra (Figure 4). In chelids the M. retrahens capitis collique medialis becomes tendinous and passes dorsal to the M. longus colli at the level of the C7 vertebra before inserting on the C6 vertebra (Figure 5).

In the Pelomedusidae, the M. retrahens capitis collique dorsalis arises from the dorsal vertebrae, passes dorsal to the M. longus colli at the level of the Cg vertebra and inserts on the cranial end of Cg by way of a thin tendon (Figure 4). Although the origin of the M. retrahens capitis collique dorsalis is similar in the Chelidae to that of the Pelomedusidae, after the muscle arises it courses cranially, becomes tendinous, passes dorsal to the M. longus colli at the level of the Cg vertebra and inserts on the C7 vertebra rather than on the Cg vertebra as in the Pelomedusidae (Figure 5).

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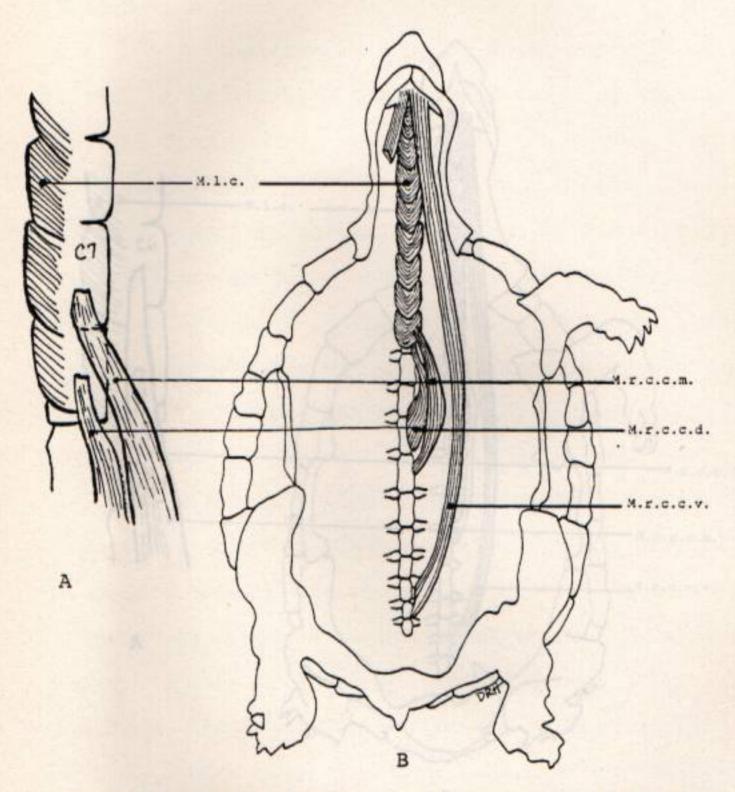


Figure 4. The M. longus colli and the Mm. retrahens capitis collique of the family Pelomedusidae. A. View of specific insertions. B. View of generalized origins and insertions. M. longus colli (M.l.c.); M. retrahens capitis collique dorsalis (M.r.c.c.d.); M. retrahens capitis collique medialis (M.r.c.c.m.); M. retrahens capitis collique ventralis (M.r.c.c.v.).

TROOF THE MOST M.r.c.c.v. A

Figure 5. The M. longus colli and the Mm. retrahens capitis collique of the family Chelidae. A. View of specific insertions. B. View of generalized origins and insertions. M. longus colli (M.l.c.); M. retrahens capitis collique dorsalis (M.r.c.c.d.); M. retrahens capitis collique medialis (M.r.c.c.m.); M. retrahens capitis collique ventralis (M.r.c.c.v.).

The precise origin and insertion for each of the Mm. retrahens capitis collique are listed in Table 1 for each genus.

M. Scalenus

The M. scalenus in Chelodina was reported by Shah (1963) to be a single muscle consisting of four fascicles arising from various positions on the scapula. Although the M. scalenus has been identified as a single muscle in the current study, it actually consists of six fascicles and arises from the first costal plate of the carapace in both families (Figure 3). The fascicles of the M. scalenus have been numbered 1 through 6, with fascicle 1 being the most medial in position. After a fascicle arises from the first costal it proceeds toward the lateral side of the neck. In the Pelomedusidae, fascicle 1 becomes tendinous, joins the lateral aspect of the portion of the M. longus colli which arose from the C7 vertebra and together they insert on the C6 vertebra. This pattern repeats cranially along the neck with every fascicle of the M. scalenus joining the lateral aspect of the respective M. longus colli and then inserting on the next vertebra cranial to the origin of that particular division of the M. longus colli (Figure 6). scalenus of chelids (Figure 7) exhibits an organization quite different from that found in the pelomedusids.

Mm. Retrahens	Pelomedusa	Pelusios	Chelus	Phrynops	Platemys	Hydromedusa
Capitis Collique		No. of Contract of	THE STATE OF		SHIPS SALES	
M.r.c.c.v.						
Origin	Caudal 1/2		Caudal 1/2	Neural	Caudal 1	Caudal % of
W. N. S. S. S. S.	of neural	plate of	of neural	plate of	of costal	neural plate
	plate of	Doy and	plate of	DgV; Neural	plate of	of D8V;
	Day and	cranial	D ₉ V;	arch of	D9V;	Neural arch
	Neural arch	2 of D10V;	arch of	2100	arch of	Centrum of
	of D ₁₀ V		D10V		D10V	D10V
		D10V				
Insertion	Basis-	Same as	Same as	Same as	Same as	Same as in
	prenoid	in Pelo-	in Pelo-	in Pelo-	in Pelo-	Pelomedusa
		Medusa	Medusa	Medusa	mennsa	
M.r.c.c.m.						
Origin	Cranial k	Caudal 4	Cranial k		Same as	Cranial 5
	of DrV	trum of	arch of	Chelus	Chalus	arch of
	25.	DA and	DeV;			D7V; entire
		cranial 4	entire			length of
		of centrum	length of			centrum of
		of D ₅ V	centrum			Dev to Div
			of D5V to			
			.1.			
Insertion	Diapophy-	Same as in	Diapophy-		Same as	
	C ₇ V	retomedusa	C ₆ V	TIII CHETUS	TIII CIIETUS	CIIETUS
	,		,			

Table 1. Continued.

Phrynops Platemys Hydromedusa	s Neural arch of D6V; entire length of centrum of D5V to D1V	s Same as in Chelus
Platemy	Same as in Chelus	Same as in Chelus
Phrynops	Same as in Chelus i	Same as in Chelus
Chelus	Neural arch of D ₅ V; entire length of centrum of b ₄ V to b ₁ V	Diapophy- sis of C7V
Pelusios	Cranial y of centrum of D ₄ V; entire length of centrum of D ₃ V	Same as in Pelomedusa
Pelomedusa	Cranial 4 of centrum of D4V; entire length of centrum of D3V	Diapophysis of C8V
Mm. Retrahens Capitis Collique	M.r.c.p.d. Origin	Insertion

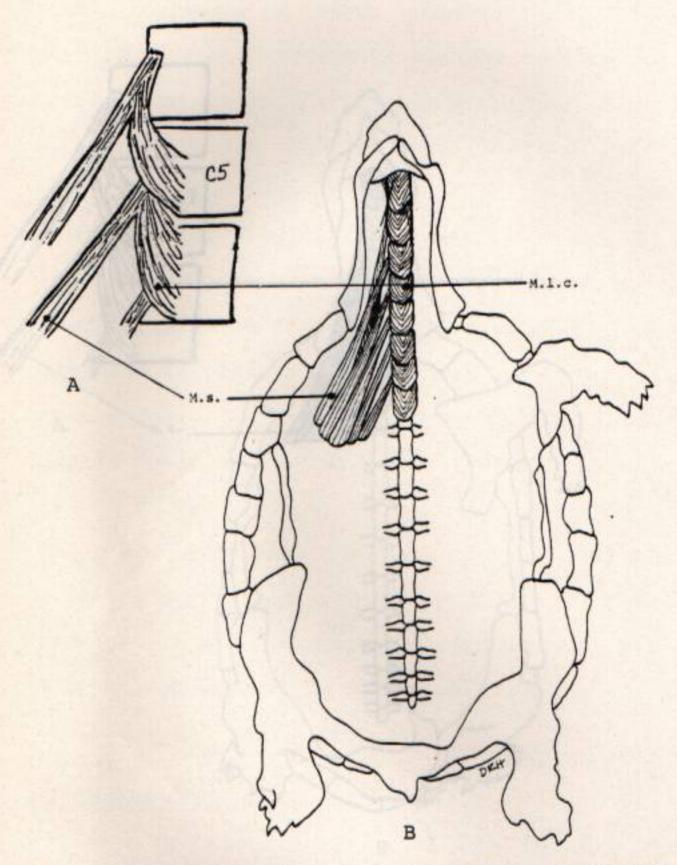


Figure 6. The M. longus colli and M. scalenus of the family Pelomedusidae. A. View of specific insertions. B. View of generalized origins and insertions. M. longus colli (M.l.c.);
M. scalenus (M.s.).

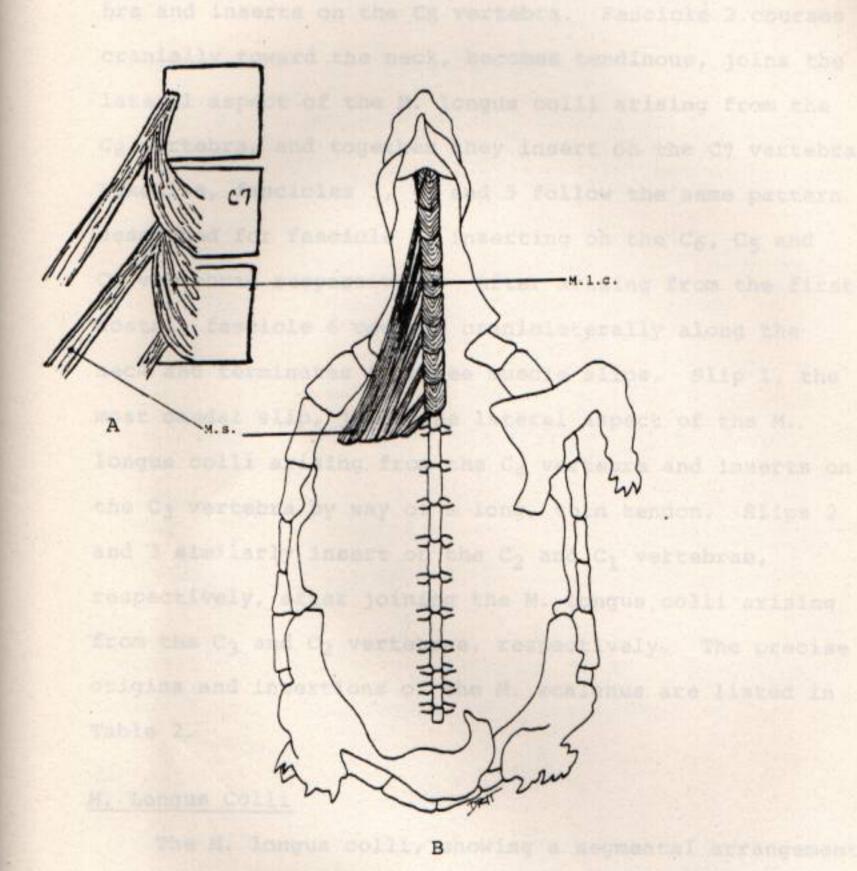


Figure 7. The M. longus colli and M. scalenus of the family Chelidae. A. View of the specific insertions. B. View of generalized origins and insertions. M. longus colli (M.l.c.);
M. scalenus (M.s.).

Fascicle 1 becomes tendinous soon after its origin, passes dorsal to the M. longus colli arising from the Cg vertebra and inserts on the C8 vertebra. Fascicle 2 courses cranially toward the neck, becomes tendinous, joins the lateral aspect of the M. longus colli arising from the Cg vertebra, and together they insert on the C7 vertebra. Likewise, fascicles 3, 4, and 5 follow the same pattern described for fascicle 2, inserting on the C6, C5 and C4 vertebrae respectively. After arising from the first costal, fascicle 6 courses craniolaterally along the neck and terminates in three muscle slips. Slip 1, the most caudal slip, joins the lateral aspect of the M. longus colli arising from the C4 vertebra and inserts on the C3 vertebra by way of a long, thin tendon. Slips 2 and 3 similarly insert on the C2 and C1 vertebrae, respectively, after joining the M. longus colli arising from the C3 and C2 vertebrae, respectively. The precise origins and insertions of the M. scalenus are listed in Table 2.

M. Longus Colli

The M. longus colli, showing a segmental arrangement in most turtles (Noble and Noble, 1940; Ashley, 1955; Shah, 1963), forms the ventralmost layer of muscles in the neck region. In pleurodires, the M. longus colli adjacent to the C₈ vertebra arises from the midventral line of the centrum of the same vertebra and inserts on

Table 2. Origins and Insertions of the M. Scalenus

M. Scalenus	Pelomedusa and Pelusios	Chelus, Phrynops, Platemys and Hydromedusa
Fascicle 1		
Origin	Costal 1 Plate	Same as in Pelomedusa
Insertion	Diapophysis of C6V	Diapophysis of CgV
Fascicle 2		
Origin	Costal 1 Plate	Same as in Pelomedusa
Insertion	Diapophysis of C5V	Diapophysis of C7V
Fascicle 3		
Origin	Costal 1 Plate	Same as in Pelomedusa
Insertion	Diapophysis of C4V	Diapophysis of C6V
Fascicle 4		
Origin	Costal 1 Plate	Same as in Pelomedusa
Insertion	Diapophysis of C3V	Diapophysis of C5V
Fascicle 5		
Origin	Costal 1 Plate	Same as in Pelomedusa
Insertion	Diapophysis of C2V	Diapophysis of C4V
ascicle 6		
Origin	Costal 1 Plate	
Insertion	Diapophysis of C ₁ V	
lip 1 ·		
Origin		Costal 1 Plate
Insertion		Diapophysis of C3V

Table 2. Continued.

M. Scalenus	Pelomedusa and Pelusios	Chelus, Phrynops, Platemys and Hydromedusa
Slip 2 Origin	OF SHE SALES SA	Costal 1 Plate
Insertion		Diapophysis of C2V
Slip 3 Origin	oreneses-res or	Costal 1 Plate
Insertion		Diapophysis of C ₁ V

bree joing farming I through to respectively, of the W.

rectus carvings described and named by theb [1963] . The

scalenus before innertion (Figure 7).

scalenes (Figure 5) before the liberation while the H. Longos

the diapophysis of the C7 vertebra (Figure 3). Likewise, the portions of the M. longus colli lying adjacent to the C7, C6, C5, C4, C3 and C2 vertebrae arise from the midventral line of the centrum of the same vertebra and insert on the diapophyses of the C6, C5, C4, C3, C2 and C1 vertebrae, respectively. The M. longus colli adjacent to the C1 vertebra inserts on the basioccipital and the pterygoid after arising from the midventral line of the same vertebra. Part of the insertion of the M. longus colli adjacent to the Cl vertebra is by means of a tendinous connection from a craniolateral slip to the pterygoid. In the Pelomedusidae, the M. longus colli of the C7, C6, C5, C4, C3 and C2 vertebrae joins fascicle 1 through 6, respectively, of the M. scalenus (Figure 5) before its insertion while the M. longus colli of the C8, C7, C6, C5, C4, C3 and C2 vertebrae in the Chelidae joins the respective fascicle or slip of the M. scalenus before insertion (Figure 7).

M. Coracohyoideus

Schumacher (1973) identified the muscle arising from the coracoid and inserting on the hyoid apparatus as the M. coracohyoideus (Figure 3), which resembles the Musculus rectus cervicus described and named by Shah (1963). The M. coracohyoideus of pleurodires arises from the dorso-lateral surface of the coracoid and courses cranially toward the hyoid apparatus. As described by Schumacher (1973), a bundle is formed by the collection of the most

dorsally located fibers inserting on the apex of the cornu branchiale I by way of a tendon. The majority of the fibers run beyond the cornu branchiale I and insert on the posterior lateral process of the corpis hyoidis (Figure 3). No variation was found in the origin or insertion of the M. coracohyoideus among any of the pleurodires examined.

Familial and Generic Comparisons Mm. Retrahens Capitis Collique

The origins and insertions of two of the three muscles included in the Mm. retrahens capitis collique can be used to differentiate between the two families of pleurodires (Table 1). The M. retrahens capitis collique medialis of the pelomedusids arises from the fourth dorsal (D4) and fifth dorsal (D5) vertebrae and inserts on the C7 vertebra; on the other hand, in the chelids it arises from the D1-D7 vertebrae and inserts on the C6 vertebra. Likewise, the two families differ in the nature of the M. retrahens capitis collique dorsalis. In Pelomedusidae, it arises from the D3 and D4 vertebrae and inserts on the Cg vertebra. By contrast, the M. retrahens capitis collique dorsalis of the Chelidae arises from the D4, D5 and D6 vertebrae, with muscular connections along the entire length of the dorsal vertebrae cranial to these, and inserts on the C7 vertebra.

Within the Pelomedusidae, the two genera examined (Pelomedusa and Pelusios) are distinguishable by slight differences in the origins of all three muscles of the Mm. retrahens capitis collique (Table 1).

The Mm. retrahens capitis collique of the chelids shows both differences and similarities. Chelus fimbriatus and Platemys platycephala, which have similar origins (similar due to the absence of neurals in the latter) and insertions for all of the muscles of the Mm. retrahens capitis collique, can be distinguished from Phrynops sp. by the origin of the M. retrahens capitis collique ventralis (Table 1) and from Hydromedusa sp. by the origin of all three muscles of the Mm. retrahens capitis collique (Table 1). The M. retrahens capitis collique ventralis of Hydromedusa sp. arises from the midventral line of the centrum of the D10 vertebra (Figure 8), where it joins its homolog before continuing to arise from the D9 vertebra and the neural plate which covers the Dg vertebra. The joining of the two M. retrahens capitis collique ventralis at their origin has not been observed in any other pleurodires examined.

M. Scalenus

The M. scalenus, which is highly developed in pleurodires, shows differences in the insertions of its six fascicles between the pelomedusids and the chelids. Pelomedusids have six fascicles of the M. scalenus which

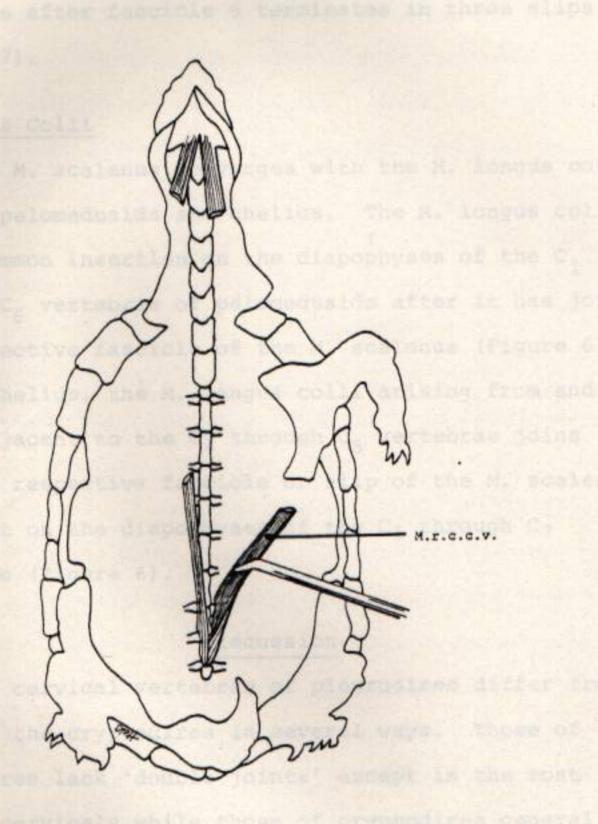


Figure 8. Ventral view of the origin of the M. retrahens capitis collique ventralis (M.r.c.c.v.) of Hydromedusa sp.

insert on the diapophyses of the C₁ through C₆ vertebrae (Figure 6). The M. scalenus of chelids has six fascicles but they insert on the diapophyses of all eight cervical vertebrae after fascicle 6 terminates in three slips (Figure 7).

M. Longus Colli

The M. scalenus converges with the M. longus colli in both pelomedusids and chelids. The M. longus colli has a common insertion on the diapophyses of the C₁ through C₆ vertebrae of pelomedusids after it has joined the respective fascicle of the M. scalenus (Figure 6). In the chelids, the M. longus colli arising from and lying adjacent to the C₂ through C₈ vertebrae joins with the respective fascicle or slip of the M. scalenus to insert on the diapophyses of the C₁ through C₇ vertebrae (Figure 6).

Discussion

The cervical vertebrae of pleurodires differ from those of the cryptodires in several ways. Those of pleurodires lack 'double joints' except in the most cranial cervicals while those of cryptodires generally have such 'double jointed' centra (Romer, 1956). In pleurodires the biconvex cervical centrum in the pelomedusids is the second while the fifth and eighth are biconvex in the chelids (Williams, 1950). However, in the

cryptodires the position of the biconvex centrum varies with respect to the individual group. Indeed, one group, the trioncychids, lacks a biconvex centrum (Romer, 1956). The zygapophyses of pleurodires are close together but are more distant from each other in cryptodires (Romer, 1956). In spite of these cervical vertebral differences, no pattern of vertebral morphological features seem to necessitate that the neck bending in pleurodires would have to be lateral in direction versus vertical in direction in cryptodires. Nevertheless the retractile neck musculature in pleurodires must act differently from that of cryptodires to produce the different neck movements observed in the two suborders when the head and neck are withdrawn under the carapace. The strap muscles in cryptodires should act simultaneously bilaterally, resulting in a vertical sigmoid curve when the neck is being retracted, whereas those of pleurodires would have to act mainly unilaterally, to produce the lateral deviation of the head and neck to either the left or right side.

In pleurodires, the retraction of the head and neck laterally beneath the carapace is accomplished by three movements. Initially, the head is drawn somewhat ventrally. Secondly, the most caudal two or three cervical vertebrae are moved to the side contralateral to that of the final head position. Thus if the head achieves

a final position beneath the right side of the carapace, the caudal cervical segments are drawn to the left. In the third movement, the head and remaining cranial cervical vertebrae are drawn ipsilaterally and caudally to a final resting position immediately under the cranial edge of the carapace.

Based on the origins and insertions of the four groups of muscles described in the present study, the head and neck movements presumably are accomplished as follows in pelomedusids. The first movement, ventral deviation of the head, would be accomplished by simultaneous contraction of the Mm. retrahens capitis collique ventralis and coracohyoideus bilaterally (Figure 9). In the second pelomedusid movement, deviation of the C7 and C8 vertebrae to the contralateral side would occur as a result of contraction of the contralateral Mm. retrahens capitis collique medialis and dorsalis, respectively (Figure 10A). Presumably contraction of the ipsilateral M. longus colli attaching to C7 - C8 vertebrae would assist in producing this phase of the second movement. Finally, contraction of the ipsilateral M. scalenus, the remaining ipsilateral M. longus colli and continued contraction of the ipsilateral Mm. retrahens capitis collique ventralis and coracohyoideus would complete the pelomedusid movement by drawing the rest of the neck and the head beneath the carapace (Figure 10B).

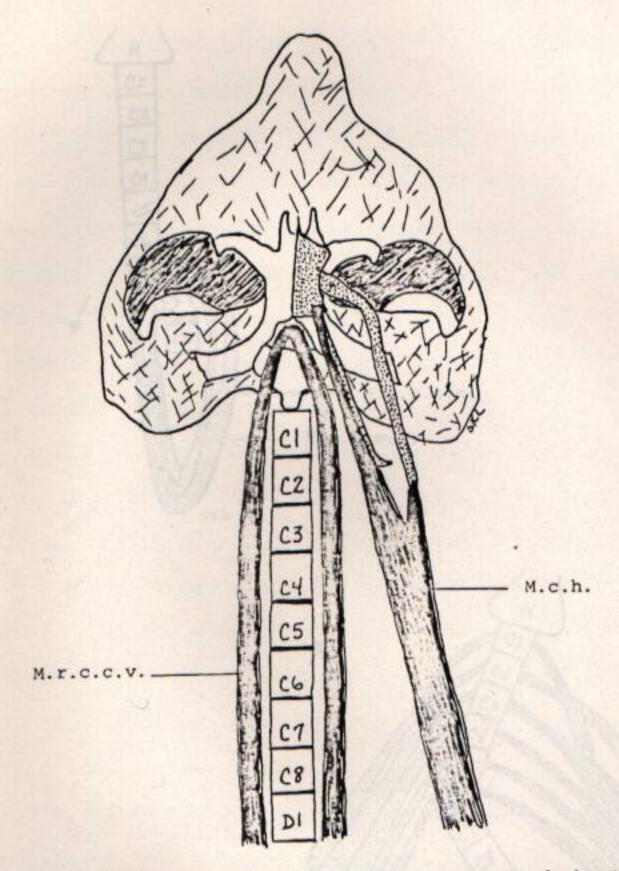
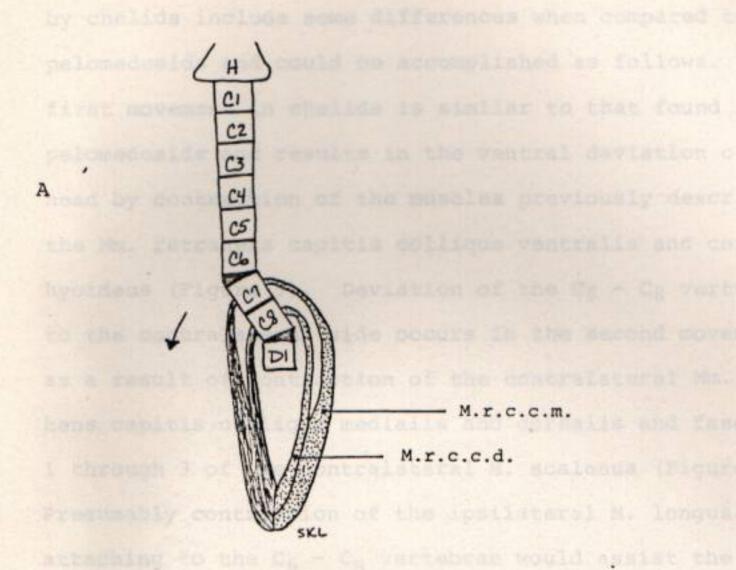


Figure 9. Muscles responsible for movement 1 in the Pelomedusidae and the Chelidae. M. coracohyoideus (M.c.h.); M. retrahens capitis collique ventralis (M.r.c.c.v.). M.c.h. and the hyoid apparatus are depicted unilaterally only but the Mm.c.h. on each side would have to contract simultaneously to assist in producing movement 1, i.e. head depression.



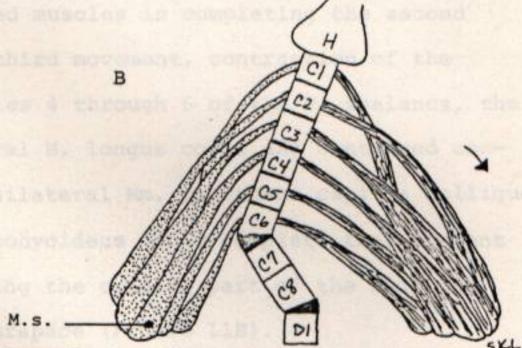
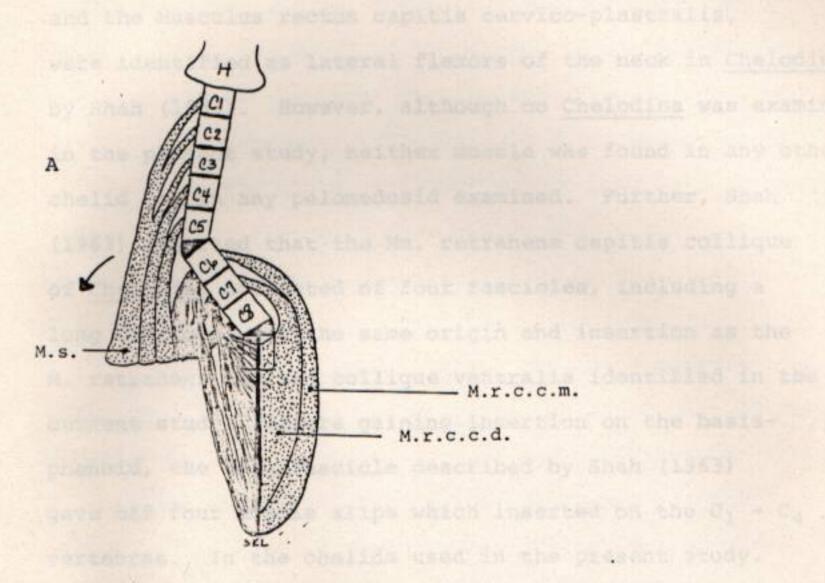


Figure 10. Dorsal view of: A. Movement 2; B. Movement 3 in the Pelomedusidae. M. retrahens capitis collique dorsalis (M.r.c.c.d.); M. retrahens capitis collique medialis (M.r.c.c.m.); M. retrahens capitis collique ventralis (M.r.c.c.v.); M. scalenus (M.s.).

Arrows indicate direction of movement.

The movements involved in neck retraction exhibited by chelids include some differences when compared to pelomedusids and could be accomplished as follows. The first movement in chelids is similar to that found in pelomedusids and results in the ventral deviation of the head by contraction of the muscles previously described, the Mm. retrahens capitis collique ventralis and coracohyoideus (Figure 9). Deviation of the C6 - C8 vertebrae to the contralateral side occurs in the second movement as a result of contraction of the contralateral Mm. retrahens capitis collique medialis and dorsalis and fascicles 1 through 3 of the contralateral M. scalenus (Figure 11A). Presumably contraction of the ipsilateral M. longus colli attaching to the C6 - C8 vertebrae would assist the previously described muscles in completing the second movement. In the third movement, contraction of the ipsilateral fascicles 4 through 6 of the M. scalenus, the remaining ipsilateral M. longus colli and continued contraction of the ipsilateral Mm. retrahens capitis collique ventralis and coracohyoideus would complete the movement in chelids by drawing the cranial part of the neck and head beneath the carapace (Figure 11B).

Although the M. scalenus is present in cryptodires (Shah, 1963 and personal observations of a few cryptodires in the current study), it presumably contributes only slightly, if at all, to neck retraction.



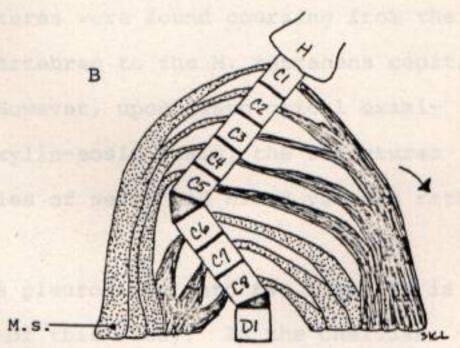


Figure 11. Dorsal view of: A. Movement 2; B. Movement 3 in the Chelidae. M. retrahens capitis collique dorsalis (M.r.c.c.d.); M. retrahens capitis collique medialis (M.r.c.c.m.); M. scalenus (M.s.).

= contracted = not contracted Arrows indicate direction of movement.

Two additional muscles, the Musculus testocapitis and the Musculus rectus capitis cervico-plastralis, were identified as lateral flexors of the neck in Chelodina by Shah (1963). However, although no Chelodina was examined in the present study, neither muscle was found in any other chelid nor in any pelomedusid examined. Further, Shah (1963) reported that the Mm. retrahens capitis collique of Chelodina consisted of four fascicles, including a long fascicle with the same origin and insertion as the M. retrahens capitis collique ventralis identified in the current study. Before gaining insertion on the basisphenoid, the long fascicle described by Shah (1963) gave off four muscle slips which inserted on the C1 - C4 vertebrae. In the chelids used in the present study, four fiber-like structures were found coursing from the first four cervical vertebrae to the M. retrahens capitis collique ventralis. However, upon histological examination using a hematoxylin-eosin stain, the structures were found to be bundles of nerve and blood vessels rather than muscular slips.

Separation of the pleurodires into two families is supported by the data of this study. In the Chelidae, both the Mm. retrahens capitis collique medialis and dorsalis arose from a position more caudally than in the Pelomedusidae and inserted one vertebra more cranially than in the Pelomedusidae (Table 1). Moreover, the

M. scalenus of the Chelidae inserted on all eight cervical vertebrae, with all but fascicle 1 joining with the respective M. longus colli. However, in the Pelomedusidae the M. scalenus-M. longus colli system inserted only on the C₁ - C₆ vertebrae (Table 2). This increased length of insertion for the M. scalenus should provide a stronger lateral flexor system in the chelids than in the pelomedusids; the former are characterized by their extremely long necks.

In the Pelomedusidae, the Mm. retrahens capitis

collique of Pelomedusa and Pelusios exhibited only slight

differences in origin; the origins and insertions of the

M. scalenus were identical in the two genera (Tables 1

and 2). This finding supports the suggestions of other

authors that these genera appear to be closely related.

A diploid number of 34 was reported for both Pelusios and

Pelomedusa (Killebrew, 1975), while Ayres et al. (1969)

reported either 26 or 28 chromosomes for Podocnemis,

depending on the species. Agglutination and precipitation

tests (Frair, 1980) likewise separate the pelomedusids into

the subfamilies Podocneminae, incorporating Podocnemis,

Erymnochelys and Peltocephalus; and Pelomedusinae, with

Pelomedusa and Pelusios.

The musculature pattern of the chelids examined lends support to the taxonomic groupings suggested by Frair (1980). The retractile muscles of the head and neck in

Chelus, Phrynops and Platemys have similar origins and insertions (Table 1) and thus would appear to be closely related as Frair (1980) indicated based on serum protein analyses. Likewise, on the basis of comparative morphology, these three genera, plus Chelodina and Hydromedusa, were included in the infrafamily Chelodd by Gaffney (1977). However, Gaffney (1977) included Phrynops, Chelus, Chelodina and Hydromedusa in the tribe Chelini on the basis of skull morphology, excluding Platemys. In the current study the common midline origin for both the left and right M. retrahens capitis collique ventralis was found only in Hydromedusa. Hydromedusa appeared to have the fewest serum proteins in common with other South American chelids (Frair, 1980) and has been suggested to share close relationships with various Australian chelids (Gaffney, 1977; Frair, 1980). The current study partially supports this hypothesis in that the origins and insertions for retractile neck musculature in Hydromedusa was found to be different from the other South American chelids. However, since no Australian chelids were available for dissection, examination for similar relationships between the retractile neck muscles of Hydromedusa and Australian chelids could not be conducted.

Acknowledgments

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I thank Rhea Humphries for the illustrations and Robert Mount for allowing me to observe a live Chelodina.

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APPENDIX

and Monuments of Rhodesia (UM); Jonkstander Rature
Consequence of Rhodesia of Comparative Rederal
Activated University (MES); and Universitative Rederal da
Juit do Pora in Static (UVJF); The natures used in the
present study include:

Pelumeduse Subrufa; five speciment (UM 1; JMCS-1; FF 1;

2. 1) from Africa. JMCS-1 is from Scherison, Cape
province, South Africa.

Pelumine simuatus simuatus; one speciment (UM 30636)

Trans Research Garcia, Monambique.

Pelumine Subriavis; one speciment (UM 9720) from Case Cus
Zimbares Rhodesia and ONL 1366) from Einzinhar.

Chalus finhriavis; one specimen (UFJF 1) from South
America.

Parymons sp. 1 one specimen (UFJF 2) from South
America.

Phrymons sp. 1 one specimen (UFJF 2) from South
America.

APPENDIX

Specimens were obtained from the National Museums and Monuments of Rhodesia (UM); Jonkershoek Nature Conservation Station in South Africa (JNCS); The Pet Farm of Miami, FL (PF); Museum of Comparative Zoology at Harvard University (MCZ); and Universidade Federal de Juiz de Fora in Brazil (UFJF). The turtles used in the present study include:

- Pelomedusa subrufa; five specimens (UM 1; JNCS 1; PF 1, 2, 3) from Africa. JNCS 1 is from Robertson, Cape Province, South Africa.
- Pelusios sinuatus sinuatus; one specimen (UM 30436) from Ressano Garcia, Mozambique.
- Pelusios subniger; two specimens: (UM 9720) from Que Que, Zimbabwe Rhodesia and (MCZ 3466) from Zanzibar.
- Chelus fimbriatus; one specimen (PF 4) from South America.
- Hydromedusa sp.; one specimen (UFJF 1) from South America.
- Phrynops sp.; one specimen (UFJF 2) from South America.
- Platemys platycephala; one specimen (PF 5) from South America.