Buoyancy, Locomotion, Morphology of the Pelvic Girdle and Hindlimb, and Systematics of Cryptodiran Turtles

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INTRODUCTION

Bony armor appeared independently many times in reptilian evolution. The chelonian type of armor, however, appeared only once. Chelonian armor is basically a large dorsal shield of plates fused to the axial skeleton connected laterally between the forelimbs and hindlimbs to a large ventral shield of plates. Although all turtles share this basic armor arrangement, there has been some diversification within this unique pattern. Possession of a bony shell has limited the directions and manners of chelonian diversification; however, no other group of armored tetrapods has undergone such a wide adaptive radiation nor have any others demonstrated the temporal tenacity of turtles.

The most obvious limitation imposed by a shell would seem to be a restriction of limb movement. The shell has affected chelonian locomotion but not to the degree that might be expected. The typical reptilian limb position is a sprawled posture with the proximal segments of the paired appendages held perpendicular to the body axis. The presence of a shell has not altered this basic posture but has limited the extent of the arc through which the limbs can move. In contrast to other reptiles, the retraction of the forelimbs and the protraction of the hindlimbs in turtles are restricted by the bridge of the shell.

The chelonian's deviation from the typical reptilian locomotor pattern would be expected to have attracted some interest. Ironically only one author (Walker, 1962, 1963) has shown more than cursory interest in it. In fact, there has been a general lack of interest in any form of quadrupedal locomotion in reptiles. Only Schaeffer (1941) and Snyder (1952, 1954) have analyzed or described the patterns of quadrupedal locomotion in the American alligator and lizards, respectively. Both of these investigators attempted to relate the anatomy of the locomotor structures to locomotor behavior. Such an approach has been utilized here; however, the specific goal has been a taxonomic analysis of cryptodires. Basically, three character complexes, locomotion, myology, and osteology of pelvic girdle and hindlimb, are examined. These three character complexes have not been previously examined, either singly or as a group, to determine their value as indicators of phylogenetic relationships within the cryptodires. With these additional and new data, our present classification and its implicit relationships can be tested and possibly improved.

The order of presentation of the character complexes is locomotion, osteology, and myology. This arrangement is deliberate and not one of convenience or chance. The two morphological complexes form a single functional unit whose principal function is locomotion. To understand the variation within the functional unit, it is necessary first to determine the patterns of variation in the function. This approach permits the investigator

to better analyze the patterns of morphological variation and to delineate more accurately the evolutionary trends in the function and the functional unit.

ACKNOWLEDGMENTS

LOCOMOTION AND BUOYANCY

Vertebrate locomotion has two primary divisions, axial and appendicular. In axial locomotion, the propulsive force is produced by flexing the body and/or tail, whereas in appendicular locomotion propulsion is generated by the movements of fins or limbs. These two classes of locomotion are not mutually exclusive, for elements of both are seen in the progression of most vertebrates; however, one form is usually predominant over the other. Axial locomotion is the primitive condition for the Vertebrata and remains the dominant pattern in aquatic species. Few fish depend upon appendicular locomotion. The majority of tetrapods that have returned to an aquatic existence have likewise returned to axial locomotion. Two extant taxa of tetrapods, birds and turtles, are notable exceptions to the dependence of aquatic vertebrates on axial locomotion. Both of these groups have aquatic members that use appendicular locomotion exclusively. Their restriction to this form of locomotion is correlated with the rigidity of the trunk vertebrae.

In birds, the rigidity of the trunk vertebrae is one of the many anatomical adaptations associated with flight. Unlike birds, the rigidity of the

trunk vertebrae in turtles is a result not of a specialized locomotor pattern but of a specialized protective device. Although this adaptation for protection imposes some limitation on chelonian locomotion, the locomotor pattern of turtles is not strikingly different from that observed in other tetrapods. Romer (1966) has suggested that of the extant reptiles, turtles may possess a locomotor pattern closest to that of primitive reptiles, since the appearance of the shell may have fixed the original pattern of walking.

The present study is an attempt to describe the locomotor patterns in one extant group of turtles, cryptodires, and to relate it to their limb morphology. The basic assumption of this approach is that the cryptodires are a monophyletic group. Since there is no evidence to the contrary (Williams, 1950), several specific questions can be asked of the data: (1) What are the interrelationships of the cryptodiran taxa based on limb morphology and locomotion, and how do these relationships differ from those implied by our present classification? (2) Do cryptodires have more than one discrete pattern of locomotion? If so, how are the patterns correlated with our present phylogenetic interpretations? (3) What evolutionary trends are discernible in each character complex and in the character complexes as a single functional unit? Cryptodiran turtles were chosen for the study, since they are readily available. This is a fortunate circumstance, because cryptodires are very diverse in form and habits. Whereas the pleurodires are entirely aquatic, the cryptodires have members that span the entire continuum from completely terrestrial to nearly completely aquatic.

In the study of limb morphology, I have found it necessary to restrict my examination to one pair of limbs, in order to examine a larger systematic representation in detail. The hindlimbs were selected for two reasons: (1) The main propulsive appendages in quadrupedal locomotion of most tetrapods are the hindlimbs. (2) The emphasis on the hindlimbs for propulsion appears to be reflected in the diverse morphology of the pelvis. Only two groups of cryptodires, the sea turtles and carettochelyids have shifted the locomotor force from the hindlimbs to the forelimbs. Although this would be a logical reason for excluding them from the present study, the actual reason was the difficulty of obtaining detailed information on their locomotor habits.

Many aspects of locomotion can be examined. My emphasis is on determining the gait sequence and the specific movement of the hindlimb segments throughout the locomotor cycle. The investigations include the patterns observed in both aquatic and terrestrial locomotion. All turtles, no matter how aquatic, exhibit terrestrial locomotion, for they all must come ashore to deposit their eggs. No attempt is made to describe aquatic locomotion in terrestrial forms, as this is an unnatural situation and observations indicate abnormal limb movements of the terrestrial forms in water. In addition to the investigations of locomotor patterns, a brief study of buoyancy in turtles has been included.

LOCOMOTOR PATTERNS

MATERIALS AND METHODS.—Locomotor patterns were recorded on 16 mm film at 32 or 64 frames per second. The latter speed is ideal, since there is seldom any blurring of rapid limb movement. The locomotor patterns were recorded for two contrasting situations, terrestrial and aquatic. In the terrestrial setup, a lined (8 cm squares) platform (40 cm × 90 cm) was set on a table, and a forwardly inclined mirror was placed along the back edge of the lined platform. Photo floods were set at both ends of the platform to produce sufficient light for high speed cinematography. The camera was set perpendicular to the long axis of the platform, 8 to 10 feet away and level with the platform. This arrangement allows the viewer to see the movement of both left and right limbs. In addition, the camera was far enough from the platform so that the viewer was nearly perpendicular to the turtle at all times. To record limb movement from a posterior view, a mirror was set at a 45° angle on one end of the platform, and as the turtle walked away from the mirror the camera recorded the image in the mirror.

The cinematographic arrangement for recording aquatic locomotion was nearly identical to that for terrestrial locomotion. A lined (8 cm squares) platform was placed against the front plate of a 3-meter tank. A forwardly inclined mirror was placed along the back edge of the platform. The camera was set level with the platform, perpendicular to its long axis and approximately 6 feet from it. Lighting was provided by 3 or 4 photoflood lamps. Only lateral views were photographed since it was impossible to record posterior views with the present camera arrangement.

The films were analyzed on a Vanguard Motion Analyzer, which enables the viewer to examine the film frame by frame and keep an accurate count of the frames examined. Essentially, two types of data were taken from the films, gait sequences and descriptions of hindlimb movements. Gait sequences are discerned by the gait formula method of Hildebrand (1966). This method enables the observer to describe symmetrical gaits, i.e., footfalls of both pairs of feet, fore or hind, evenly spaced in time, by graphing two percentages, percent of stride that each foot is on the ground and percent of stride that fore footfall follows ipsilateral hind footfall. Hindlimb movements were recorded by a written description and the measurement of various limb angles.

TERRESTRIAL LOCOMOTION.—*Gait Sequences:* Until recently, the sequence of limb movements in terrestrial locomotion was described and illustrated by a single method, the footfall formulae of Muybridge (1899). Muybridge originally recognized seven footfall formulae. This number was increased slightly by Howell (1944). The footfall formulae do not show the relative duration of various support patterns, and their manner of presentation does not allow comparison of more than two or three formulae at a time. In 1965, Hildebrand introduced the gait formulae which greatly facilitate the comparison of gaits between different taxa or individuals.

The gait formula indicates the relative duration and sequence of various support patterns. It is the method employed herein. A modification of Hildebrand's method of gait analysis has been proposed recently by Dagg and de Vos (1968 a and b). They believe their method to be more discriminating than the gait formulae when closely related species are compared, but I have not had time to test it with my data.

Where possible, a gait formula for a single locomotor period was calculated by averaging several gait formulae from several consecutive strides. However, approximately a fifth of the following gait formulae were calculated from a single stride. Even though this may produce a slightly higher variation, their presentation is justifiable since they are similar to gait formulae based on several strides.

An inspection of the distribution of the gait formulae (Fig. 1) shows immediately that the speed of progression is slow. The graph also illustrates that in the majority of the gaits, an individual limb is in contact with the ground, thus supporting the body for more than 75 percent of a stride. In addition, it indicates that the body is being supported by three limbs for at least 60 percent of the stride interval. There are two brief periods, i.e., each 20 percent or less of the stride interval, when the body is supported by a forelimb and its diagonally opposite hindlimb. These unstable periods alternate with periods of tripodal and stable support. As the turtle's speed approaches a moderate walk, the length of the two periods of instability increases to approximately 60 percent of the stride. At this speed, the turtle actually appears to be running. The instability is obvious, for at the end of each period of diagonal support, the plastrom hits the ground before the turtle recovers its balance. Thus for a turtle to walk without losing its balance, each limb apparently must be in contact with the ground for a least 70 percent of the stride.

In no instance does a turtle or any other vertebrate (see overlay in Fig. 1) have each limb in contact for over 90 percent of the stride interval. This appears to be a physical limit imposed on locomotion, i.e., it is impossible to have a smooth, constant forward progression when contact is over 90 percent.

The series of terms on the abscissa of the graph (Fig. 1) describe the sequences of limb movement. Most of the gait formulae fall into two categories, the diagonal couplet of a lateral sequence and the trot. In the trot, a forelimb and its diagonally opposite hindlimb swing forward at the same time. Lateral sequence gaits are those in which the footfall of a hindfoot is followed by the footfall of the ipsilateral forefoot (in a diagonal sequence gait, the hind footfall is followed by the diagonally opposite fore footfall). The diagonal couplet indicates that successive footfalls, i.e., those closest in time, are of the diagonally opposite limbs. The singlefoot notation describes the situation when the footfall of each limb is evenly spaced in time.

There is little taxonomic correlation with kinds of gaits. Most of the gait formulae in the lateral sequence, singlefoot category, are from *Chelydra*
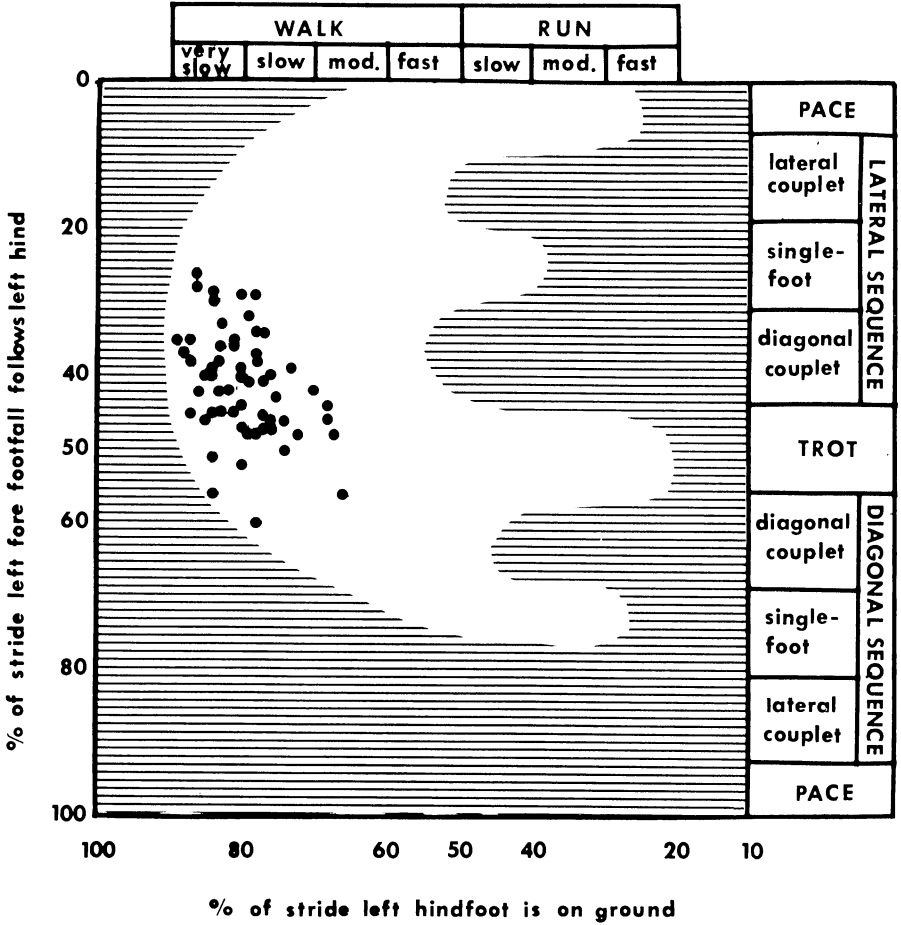
FIG. 1. The distribution of 66 gait formulae calculated for terrestrial locomotion in 19 species of cryptodires (Appendix I). The overlay shows the area in which the gait formulae of terrestrial vertebrate locomotion fall. The overlay and the terminology are those proposed by Hildebrand (1966).

serpentina; however, one *Chrysemys scripta* and one *Terrapene carolina* show this gait, and one of the *Chelydra* gaits is a lateral sequence, diagonal couplet gait. The lateral sequence, diagonal couplet gait and the trot are shown by testudinids, kinosternids, and trionychids. The terrestrial testudinids, *Terrapene carolina* and *Gopherus polyphemus,* have only lateral sequence gaits, and with only two exceptions, the gaits are diagonal couplets. The single, diagonal sequence gait is from a *Clemmys insculpta* and is based on a single stride.

It has been suggested that in a trot or lateral sequence gait there is danger of collision between ipsilateral limbs. The bridge of the shell precludes any collision in chelonian locomotion. In addition, the walking trot and

the lateral sequence, diagonal couplet gait provide the most stable support sequences, since these gaits maximize the period of tripodal support. As a whole, these are the gaits used by most small and/or slow moving vertebrates.

The previous discussion implies that the movement and timing of each limb during a single stride is symmetrical and without variation. In actuality limb movement is not symmetrical nor should it be expected to be, for no known biological system is truly symmetrical. Hildebrand (1966) points out that variation is greater in poor ambulators than in cursors, in young than in adults, and in small bodied taxa than in large bodied ones. Variations can be attributed to biological and abiological causes, e.g., the animal changes speed, pauses, or loses its balance, or the camera changes speed or frames are miscounted.

Table 1 illustrates the variation of foot contact observed in *Clemmys marmorata,* which is characteristic for the other species examined. For a gait to be truly symmetrical, pairs of limbs must be in contact for the same amount of time and evenly spaced in time. The forefoot contact divided

TABLE 1

VARIATION IN TIMING OF LIMB MOVEMENT DURING TERRESTRIAL LOCOMOTION OF
Clemmys marmorata

Specimen	Symmetry of anterior and posterior pairs		Symmetry of ipsilateral pairs		Variation of hindfoot contact		Variation of footfall lag	
	RF/LF	RH/LH	LF/LH	RF/RH	LH/S	RH/S	LH-F/S	RH-F/S
A ♂	103	99	98	101	83	82	42	41
B ♀	113	108	93	98	80	84	44	38
C ♀	102	101	93	94	83	83	45	43
D ♂	106	106	102	103	78	83	34	33
E ♀	101	101	100	100	73	87	39	38
F ♀	100	102	98	95	77	79	41	34
G ♀	104	101	95	98	78	79	38	38

The percentages are determined from the length of support of each limb and stride length in *Clemmys marmorata.* RF, right forefoot; LF, left forefoot; RH, right hindfoot; LH, left hindfoot; RH–F, lag between footfall of right hind and right forelimb; LH–F, lag between footfall of left hind and left forefoot; S, stride length.

by the hindfoot contact would be equal to 100 percent. Such an event was realized only once. Likewise variation between anterior and posterior pairs of limbs is present. In fact, the variation between these pairs is of the same magnitude as between ipsilateral pairs. As noted previously, the amount of variation is not unexpected, since turtles are small and walk slowly.

Hindlimb Movements: Limb movement is cyclic and usually divided into two phases, retraction and protraction. During retraction, the limb acts both to support the body and to propel it forward. Protraction is a recovery phase providing neither support nor propulsion. The retractive phase in terrestrial locomotion is usually delimited by the period of contact

with the substrate between the footfall and the liftoff, the protractive phase
by the period of no contact between the liftoff and the footfall. During
retraction the limb is essentially stationary, for the body pivots on the limb
and swings craniad. In protraction, the body is stationary relative to the
limb, which is moving craniad.

The following descriptions will be restricted mainly to the movements
circumscribed by the crus and pes, for the thigh or propodium is usually
hidden beneath the shell. The limb movements described will be those of a
slow walk. Also, rather than give a detailed description of the hindlimb
movements for all taxa, I will review in detail the movements in *Gopherus
polyphemus*. The other species will be compared with it. *G. polyphemus* is
a completely terrestrial turtle belonging to a sub-family which has been
terrestrial since the early Tertiary (Williams, 1950). It is assumed that its
gait reflects adaptations to terrestrial locomotion and not a compromise
pattern of an aquatic or semiaquatic turtle.

The retractive phase in *G. polyphemus* (Figs. 2 and 3) begins with a
nearly flat-footed footfall. The heel touches slightly before the toes. The toes
or claws are directed anteriorly, although the fourth toe has a distinct
anterolateral orientation. As retraction continues, the distal end of the foot
begins to rotate outward. At the termination of retraction, the toes are
pointed laterally and the fourth toe posterolaterally. Initially, the center
of the plantar surface of the foot appears to be the center of support. With
the rotation of the foot and the crus, the center of support shifts antero-
medially as the posterior edge and then the lateral edge of the foot lose
contact with the ground.

At footfall, the crus is perpendicular or inclined posteriorly to no more
than 100°. As the body passes anteriorly over the limb, the crus becomes
progressively more inclined anteriorly. At the stage prior to liftoff, the
anterior inclination is between 20° and 30°. Although the crus is not tilted
laterally or medially at footfall, it has a distinct lateral inclination of 60°
to 70° prior to liftoff. Throughout the retractive phase, the thigh retains a
nearly horizontal orientation, although during the latter part of retraction
its distal end slopes downward slightly.

During the initial stage of protraction the foot (Figs. 2 and 3), specifi-
cally the anteromedial edge, is dragged forward for an instant before liftoff
occurs. As the foot rises, the claw of the first toe is the last surface to leave
the substrate. Once the foot is lifted, it remains well above the substrate.
With the movement forward the crus and foot rotate anteriorly so that the
fourth toe twists from its posterolateral to an anterolateral position. This
rotation is completed by the time the foot reaches the vertical plane
through the acetabula.

Throughout the protractive phase, the thigh maintains a horizontal
orientation. The crus begins the phase with a strong anterior inclination.
The anterior inclination is retained throughout most of the protraction.
Only after the knee has reached the vertical plane through the acetabula
does the foot swing beneath the knee. The limb is perpendicular to the
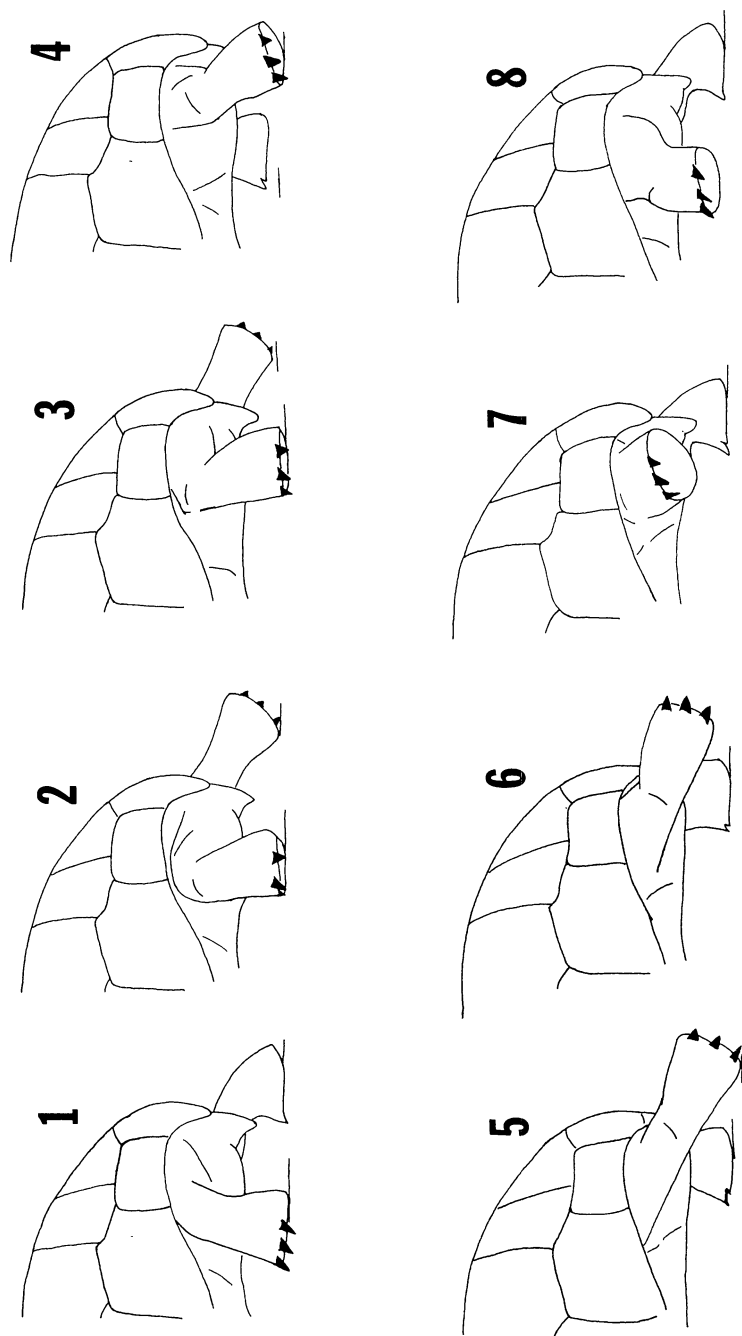
FIG. 2. Lateral view of the left hindlimb of *Gopherus polyphemus* during a single stride of terrestrial walking. 1-4, retractive or propulsive phase; 5-8, protractive or recovery phase; 1, footfall; 5, beginning of protraction.
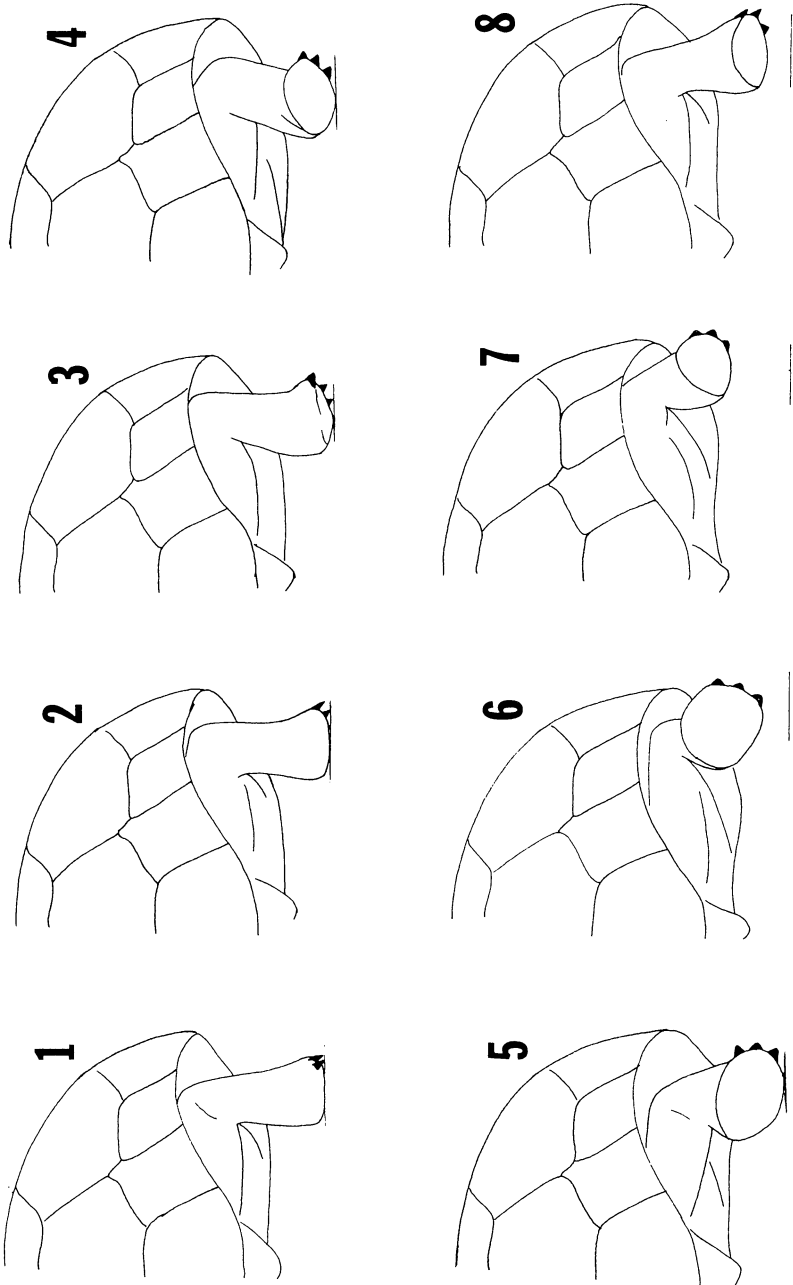
FIG. 3. Posterior view of the right hindlimb of *Gopherus polyphemus* during a single stride of terrestrial walking. The numbering is identical to that in Figure 2.

ground prior to footfall. The lateral inclination of the crus is lost early in protraction. There is no stage at which the crus is inclined medially, i.e., where the foot is swung outward beyond the margin of the shell.

During the entire cycle the body is held well above the substrate. There is no suitable quantitative means of describing the level of the body that is comparable from taxon to taxon, since any measurement of distance will be a stronger indicator of body size than of height above the ground. Thus, a qualitative description must suffice. In *G. polyphemus,* the opposite foot and ankle are visible from a lateral view. In addition, the body is relatively stable throughout the entire cycle with little perceptible rolling or pitching.

In all the turtles examined (Appendix I), the manner of foot contact is essentially flat-footed with the entire plantar surface and the tips of the claws striking the ground simultaneously. In some instances, the toes or heel strike a moment ahead of its opposite. Variation of this sort is not divided along taxonomic lines, nor is it associated with size or age, but is frequently observed in a series of adjacent strides of a single turtle. The foot always appears to be placed with its longitudinal axis parallel to the anteroposterior axis. As in *Gopherus,* all turtles initially have the center of support in the middle of the plantar surface. As the body passes forward, the limb develops a strong anterior inclination, the crus rotates, and the center of support shifts anteriorly then anteromedially.

At footfall, the crus forms two angles with the horizontal, an antero-posterior one and a mediolateral one (Table 2). In *Chrysemys* (Fig. 4), *Clemmys, Malaclemys, Kinosternon,* and *Sternothaerus,* the crus at footfall is usually perpendicular to the substrate; however, unlike the relatively stable crural orientation in *Gopherus,* these taxa show a wide range of variation from stride to stride or locomotor period to locomotor period. The three hinged taxa, *Cuora, Emydoidea,* and *Terrapene,* characteristically

TABLE 2

RANGE OF VARIATION IN ANGLES OF LIMB PLACEMENT AT BEGINNING AND END OF RETRACTION

| Genus	Footfall		Liftoff	
	antero-posterior angle	medio-lateral angle	antero-posterior angle	medio-posterior angle
Chelydra	120–140	50–60	30–40	50–60
Cuora	60–80	60–70	20–30	110–120
Chrysemys	50–120	30–60	10–30	110–140
Clemmys	70–110	45–60	5–30	100
Emydoidea	60–80	40–50	10–20	120–160
Malaclemys	70–110	50–60	15–20	110–120
Terrapene	40–60	40–50	5–20	130–140
Gopherus	90–100	80–90	20–30	120–130
Kinosternon	100–110	60	10–30	–
Sternothaerus	80–110	40–60	10–30	90–120
Trionyx	110–130	30–40	10–30	–
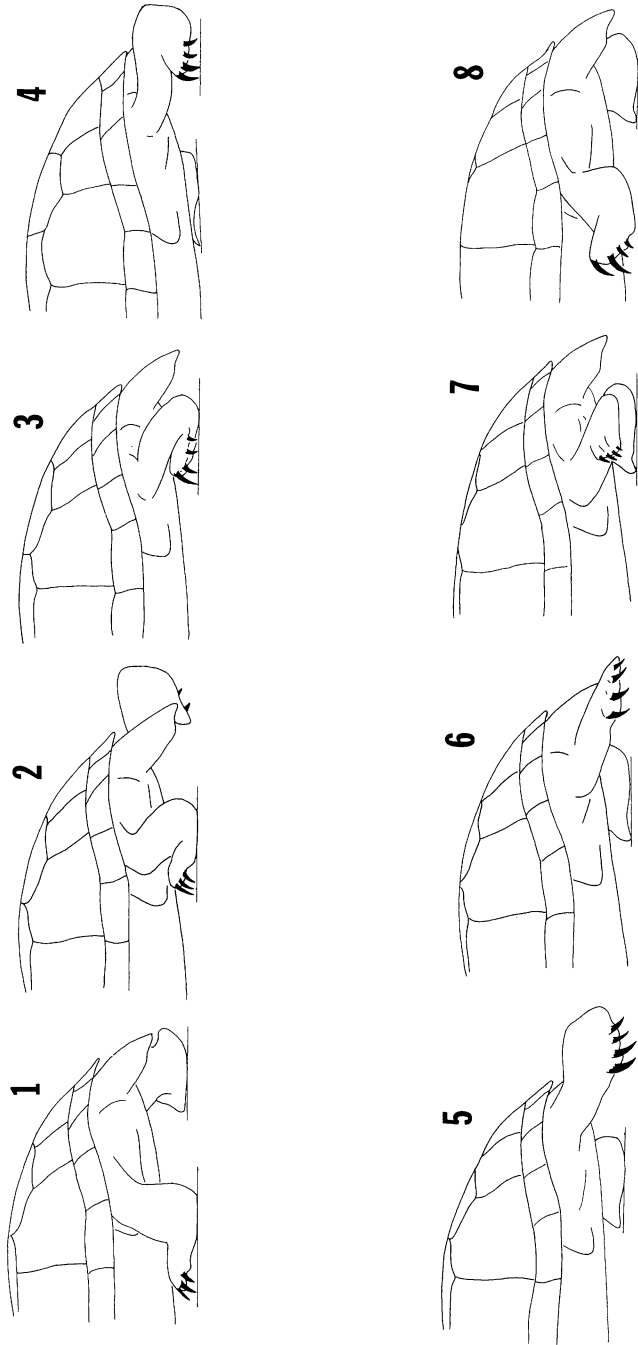
FIG. 4. Lateral view of the left hindlimb of *Chrysemys scripta* during a single stride of terrestrial walking. The numbering is identical to that in Figure 2.

fail to swing the foot anteriorly beneath the knee and thus the crus at foot-
fall has a distinct anterior inclination. Both *Chelydra* and *Trionyx* have a
pronounced forward footfall with the foot falling anterior to the knee.
This anterior placement increases the length of the step and the entire
stride. The anteroposterior crural inclination does not show any correlation
with taxonomic or ecological groups but with the size and extent of the
plastra. Those taxa with large, well-developed plastra tend to restrict the
anterior placement of the foot to the level of the knee. Reduction of the
plastron and narrowing of the bridge (see *Chelydra* and *Trionyx* in Table 2)
appears to enable those taxa to have a forward footfall. In the hinged taxa
(Terrapene and *Cuora),* the plastron is extremely large with a wide bridge
and a posterior footfall. The crus at footfall is inclined medially in all
the taxa except *Gopherus* (Fig. 3). The medial inclination of the crus
produces the typical sprawled posture of ectothermic tetrapods.

As the body swings cranially, the crus develops a strong anterior inclina-
tion and simultaneously begins to rotate. The rotation of the lower limb
begins early in retraction but is slight until the last third of the retractive
phase. Initially, the pivot of rotation is in the center of the plantar surface.
The pivot moves forward until it is centered on the first and second toes
prior to protraction. This manner of pivoting gives the impression that the
toes are swinging laterally. Although they are directed laterally at the
end of retraction, it has been the heel that has moved by an upward and
an inward rotation. The rotation of the heel changes the inclination of the
crus from an initial medial slant to a lateral one. The latter inclination is
difficult to measure accurately; nonetheless, the values in Table 2 suggest
that the lateral inclination is nearly equivalent to the medial one. The
anteroposterior inclination varies from approximately 5° to 40°. Even
though there is no correlation with taxonomic grouping, there appears to be
a direct correlation between the angle of inclination and the distance of the
body above the substrate. *Chelydra* and *Gopherus* hold their bodies high
above the substrate and in turn have smaller inclinations and also less
variation.

Protraction is initiated by the forward movement of the limb. During
this initial movement, the foot is not raised but is dragged over the sub-
strate. In *Chelydra, Cuora, Emydoidea, Kinosternon,* and *Sternothaerus,*
the foot is dragged only a short distance before it is lifted. The foot of
Terrapene is dragged only slightly or not at all, whereas the foot touches
the substrate for a proportionally long period in *Chrysemys, Clemmys,*
Malaclemys, and *Trionyx.* Once the limb is raised, it is raised to varying
heights which are probably in part, but not entirely, associated with the
height of the body above the substrate. In general, *Chelydra, Cuora, Emy-*
doidea, Terrapene, Kinosternon, and *Sternothaerus* lift their feet high, and
Chrysemys, Clemmys, Malaclemys, and *Trionyx* hold their feet barely
above the substrate. There are exceptions to this, particularly in the latter
category, since one *Trionyx spinifer,* a *Chrysemys picta,* many *Chrysemys*
scripta (Fig. 4), and a *Clemmys insculpta* kept the foot high during pro-

traction. In all taxa, the lateral rotation of the feet is corrected by the time the foot reaches the vertical plane through the acetabula. Likewise, the limb is never swung strongly outward in protraction. In *Gopherus* and *Chelydra,* the limb is brought nearly straight forward. In the other genera, the limb swings outward slightly, i.e., the distal half of the foot may be beyond the margin of the carapace.

The bodies of *Chelydra, Cuora, Terrapene, Kinosternon,* and *Sternothaerus* are also held well above the substrate in a slow walk. The body is sufficiently high that at least the distal quarter of the crus and the entire foot of one side are visible from the opposite side. In contrast, no more than the bottom half of a foot can be seen beneath the bodies of *Chrysemys, Clemmys, Emydoidea,* and *Malaclemys.* The body is seldom held at that level in *Chrysemys,* for it is usually impossible to see the opposite foot. In *Trionyx,* both extremes are observed. It is not clear how size and/or maturity affect the height, for large *Clemmys marmorata* hold their bodies lower than small *C. marmorata.* Yet in some of the *Chrysemys,* the smaller individuals did not hold the body any higher, and it may have been proportionately lower. There is little doubt that speed alters the height of the body since two *T. spinifer* of equal size traveling at different speeds show the opposite extremes, viz., very slow walk, body high; moderate walk, body skimming. Speed also affects the stability of the body but is definitely not the only factor involved. When body stability is checked at a very slow walk, *Chelydra, Cuora,* and *Terrapene* have very little body movement other than a slight downward pitch. *Sternothaerus* and *Kinosternon* have a larger pitch than the preceding genera but only slightly so. In the remaining taxa, there is a distinct up and down movement of the entire shell and frequently a yawing motion.

AQUATIC LOCOMOTION.—Most chelonian species are aquatic or semiaquatic; in point of fact, only the testudinids have members that are strictly terrestrial and seldom enter the water except by accident. The boundary between aquatic and terrestrial species is very broad and ill defined. Rather than quibble over a definition of semiaquatic, it is simpler and possibly wiser to lump all the species that enter the water voluntarily into a single class and then examine the locomotor patterns of this group as a whole. When this is done, two distinct locomotor patterns are evident in aquatic turtles. The first pattern is true swimming, for the body and limbs do not touch the bottom, and propulsion is produced by the displacement of water. In the other pattern, called bottom-walking, propulsion results from the feet pushing against the bottom. These two locomotor patterns are readily apparent from casual observations, yet they have received little more than cursory mention (Reed, 1957; Mertens, 1960).

Gait Sequences: The method of gait analysis used to describe aquatic locomotion is the same as that for terrestrial locomotion with one major modification: swimming animals do not have a footfall sequence or contact with the substrate. Retraction of the limb in aquatic locomotion is compar-

able to contact in terrestrial locomotion, as they are both the propulsive stages. Footfall or the beginning of retraction is defined as the first movement of the foot posteriorly. Retraction is finished when the foot starts to move anteriorly. Bottom-walking is analyzed in the same manner as swimming so that a discussion of the two aquatic gaits will have the same standards for comparison. Like the gait formulae for terrestrial locomotion, most formulae are calculated from several strides, although approximately one quarter of these are from a single stride.

The speed of aquatic locomotion can be determined from Figure 5. It is necessary to use the terrestrial gait terminology for two reasons. (1) There is no existing terminology which describes the sequence of limb movement in aquatic locomotion. (2) Although the gait terminology implies patterns of support which usually do not exist in aquatic locomotion, the terms also describe the sequence of limb movements thus aiding comparison.
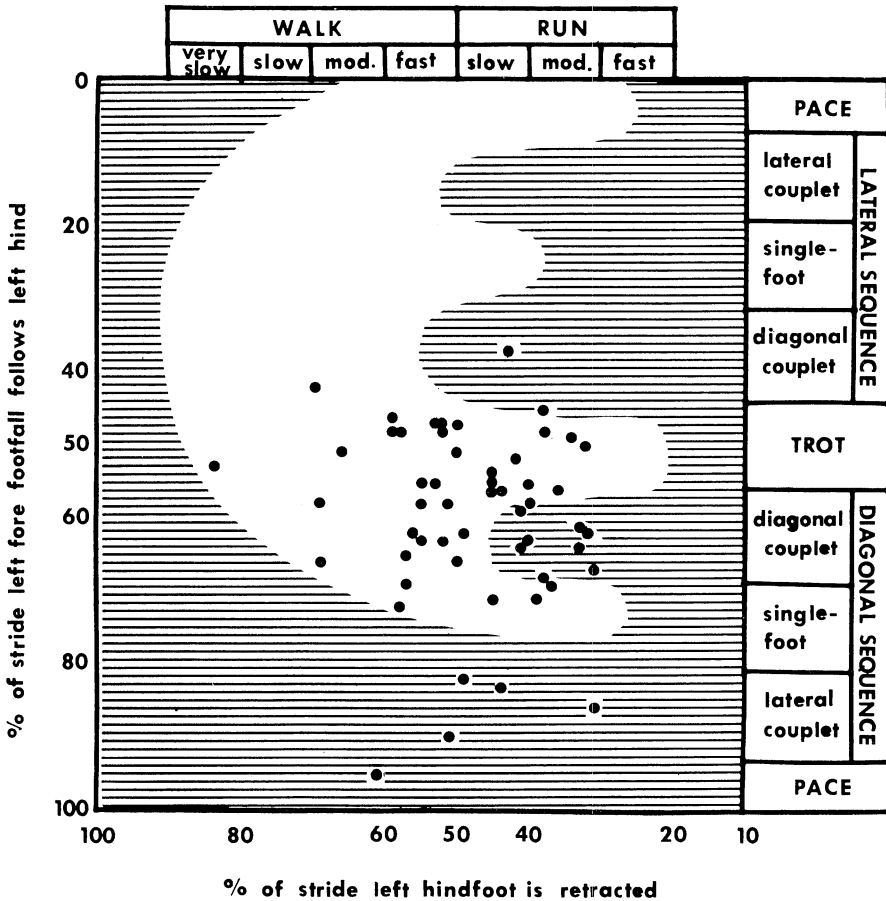
FIG. 5. The distribution of 56 gait formulae calculated for aquatic locomotion in 17 species of cryptodires (Appendix II). The overlay encloses the area in which gait formulae of terrestrial locomotion of vertebrates fall.

The speed ranges from a very slow walk to a moderate run with the majority of the gaits clustered within the limits of the fast walk and moderate run categories. This is the opposite of the distribution of terrestrial gaits, for there the maximum rate of progression is a moderate walk. At the latter speed, the turtle momentarily loses its balance twice during each stride, and the loss of support prevents turtles from progressing faster. In an aquatic environment, support is no problem. The buoyancy produced by the displacement of water reduces the weight to a negligible figure, and the limbs are used entirely for propulsion and steering in swimming taxa and only slightly for support in bottom-walkers. Since buoyancy reduces the need for support, the limbs move faster, and the turtles attain the speed of a moderate run. The importance of this buoyancy becomes more apparent when the support sequence of a moderate running trot is examined. At this speed and gait sequence, there are two periods of no support, each 15 percent of the stride, and two periods of diagonal limb support, each 35 percent of the stride. Such a support sequence is obviously far beyond the physical capabilities of turtles in a terrestrial situation.

We have seen in the terrestrial locomotion section the probable reasons that prevent turtles from progressing more slowly than a very slow walk. The question to be asked here is why turtles do not move faster than a moderate run in water. Perhaps my sample is too small to demonstrate a faster gait (see Appendix II). If this is true, there must be, nonetheless, some upper limit. In terrestrial locomotion, the upper limit appears to be imposed by the necessity of tripodal support for at least 40 percent of the stride. Support, however, is not required by a swimming turtle. The limiting factor may be the maximum speed of limb movement. There has to be a period of limb protraction and the maximum speed with which this can be accomplished will determine the maximum gait speed of chelonians. Perhaps, 30 per cent of a stride interval may be the minimum period of protraction for turtles.

If we turn our attention from gait speed to gait sequence (abscissa of Fig. 5), we find that as in terrestrial locomotion many of the gait formulae can be classified as trots; however, unlike terrestrial gaits, the majority of the remaining gaits are diagonal sequence gaits, viz., the fore footfall following that of a hindlimb is of the diagonally opposite forelimb. The shift to diagonal sequence gaits is associated with an increase in speed and appears to be associated with the spacing of the footfall to produce an evenly distributed support sequence throughout the stride in terrestrial locomotion. In turtles within an aquatic environment, support would not be a requirement as is illustrated by the number of diagonal sequence, diagonal couplet gait lying outside of the overlay (Fig. 5).

In aquatic locomotion, the reason for this shift might be related to steering. The trot and the diagonal sequence, diagonal couplet gait may be the sequence of limb movement which produces a minimum amount of yawing, i.e., side to side or lateral deviation, during forward progression. The five gait formulae below the overlay were calculated from single

strides and may represent limb movement during a steering movement or to correct yawing.

Neither gait sequence nor gait speed show any taxonomic correlations. Each of the four families examined is able to trot or progress by a diagonal sequence gait. The minimum speed is shown by a *Chrysemys picta,* maximum speed by a *Chrysemys scripta* and *Clemmys guttata.* None of the *Chelydra serpentina* moves faster than a fast walk. Nor is there any correlation between swimming or bottom-walking and gait sequence or gait speed.

The variation in the timing of limb movements is greater in aquatic locomotion (Table 3) than in terrestrial locomotion (Table 1). Although Table 3 expresses the variation in only *Sternothaerus minor,* it is representative of that observed in the other species. A value of 100 percent indicates symmetry in movement of a pair of limbs, and such a condition is observed only once. A comparison of the variation in three pairs of limbs, bilateral pairs, ipsilateral pairs, and diagonal pairs, demonstrates the lack of symmetry in all three combinations; however, the variation of diagonal pairs appears to be less than that for either bilateral or ipsilateral pairs. A possible explanation for this reduced variation is that to minimize yawing it is essential that the diagonally opposite propulsive elements operate for the same time at the same force. This also helps to explain the variation between right and left members in hindfoot retraction and footfall lag, because the timing of one member of a bilateral pair is not synchronized with the other member of a bilateral pair but rather to its diagonally opposite mate.

Hindlimb Movements: Since there are two distinct patterns of aquatic locomotion, it will first be necessary to describe and to discuss the variation in each pattern separately. It must be noted that an individual turtle is not limited to one pattern; however, when a turtle actively moves away from a frightening object or to a new food source, it characteristically uses the same pattern of locomotion. When data are available on both patterns in a single species, both will be discussed.

Of the two patterns of aquatic locomotion, swimming is the less similar to terrestrial walking. *Trionyx* is an excellent swimmer and provides an ideal example for chelonian swimming.

In *Trionyx* (Fig. 6), the retractive phase begins with the flexed limb lying in the inguinal pockets. As the limb begins to move posteriorly, it is extended simultaneously. It is fully extended at or slightly anterior to the vertical plane through the acetabula. The limb remains fully extended until it swings posteriorly and become nearly parallel to the longitudinal body axis. At this point, protraction begins with the knee and hip joints flexing. The limb swings anteriorly to the inguinal pocket. During this entire locomotor cycle, the thigh and crus move in a horizontal plane, with only a slight vertical deviation.

Although the foot swings through this horizontal plane, its axis changes in relation to the plane. As retraction begins, the transverse axis of the

TABLE 3

VARIATION IN TIMING OF LIMB MOVEMENT DURING AQUATIC LOCOMOTION OF *Sternothaerus minor*

Specimen	Symmetry of bilateral pairs		Symmetry of ipsilateral pairs		Symmetry of diagonal pairs		Variation of hindfoot retraction		Variation of fore footfall lag	
	RF/LF	RH/LH	LF/LH	RF/RH	LF/RH	RF/LH	LH/S	RH/S	LH-F/S	RH-F/S
A ♂	86	83	91	94	109	75	58	47	48	57
B ♂	100	111	112	104	104	110	53	55	47	49
C ♀	145	80	80	143	100	115	56	44	62	49
D ♀	122	93	85	107	96	98	58	44	72	53
E ♀	102	134	99	76	74	101	69	54	66	59
F ♀	108	101	94	112	95	101	53	53	55	46

The percentages are determined from the length of retraction of each limb and length of stride in *Sternothaerus minor*. Morphological abbreviations identical to those in Table 1.
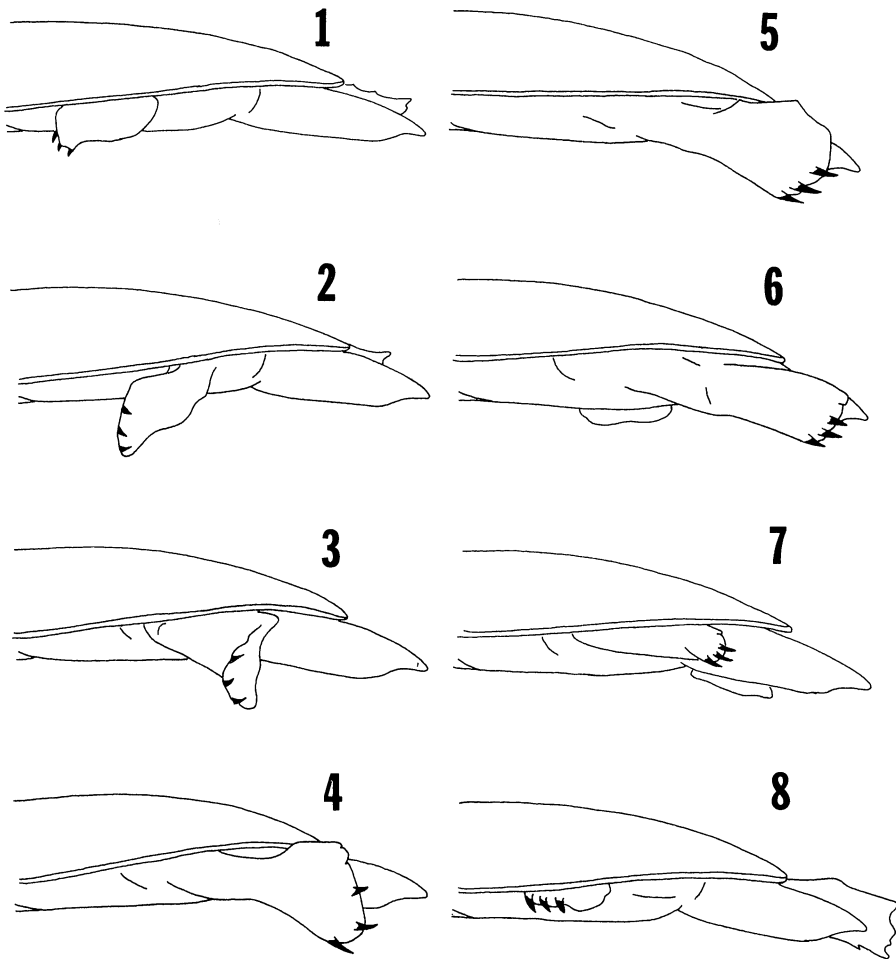
FIG. 6. Lateral view of left hindlimb of *Trionyx spinifer* during a single stride of swimming. 1–4, retractive phase; 5–8, protractive phase; 1, beginning of retraction; 5, beginning of protraction.

foot is horizontal. The anterior edge begins to rotate downward. At the acetabular level, the foot is extended entirely beyond the shell and its transverse axis is perpendicular to the horizontal. For the remainder of retraction, the foot remains perpendicular. The toes and webbing are fully spread, presenting a maximum surface area to the water. The spreading of the toes probably results as much or more from the physical pressure of the water as contraction of the short digital extensors. With the termination of retraction, the toes come together, and the foot remains vertical. As protraction begins, the anterior edge of the foot rotates upward rapidly and becomes horizontal before it passes beneath the shell. The foot is, therefore, feathered for most of the protractive phase. During protraction, the limb moves anteriorly directly beneath the carapace rather than swinging outward beyond the shell's margin.

Of the other turtles examined, none maintains its limbs in a horizontal plane throughout the retractive phase. *Chrysemys* and *Malaclemys* retract their limbs slightly ventrolaterally to the horizontal plane, whereas *Cuora, Emydoidea, Clemmys* and *Kinosternon* have a pronounced ventrolateral inclination during retraction. In all of these, the limb moves upward during the last quarter of retraction and completes retraction in a horizontal plane.

All turtles begin retraction with the thigh tucked in the inguinal pocket, but unlike *Trionyx* the entire limbs of the others are not strongly flexed and do not lie tightly in the pocket. This difference in limb posture at this stage may account for the initial lateral or anterolateral extension of the limb at the beginning of retraction, in contrast to the more posterolateral extension in *Trionyx*. This method of limb extension permits the foot to rotate to a vertical position at or slightly after the posterior swing begins, whereas in *Trionyx* the foot usually rotates during the initial part of the swing.

In turtles with well-developed webbing, viz., *Chrysemys, Malaclemys,* and *Kinosternon,* the toes are spread widely. The hind feet of *Clemmys, Cuora,* and *Emydoidea* do not appear to have the flexibility found in the former genera and are not spread as broadly. This feature is also evident during the initial stage of protraction, because the former genera have a distinct collapse or inward folding of the foot as in *Trionyx* and the latter genera have no noticeable change in foot shape.

Trionyx is able to retract its limb so that at the termination of retraction the entire limb axis is nearly parallel to the body axis. None of the other genera appears to have this ability, since their thighs never pass beyond a posterolateral inclination, although the crus and foot become parallel to the body axis. The posterior inclination of the thigh is greatest in *Chrysemys* and *Malaclemys* and least in *Cuora* and *Emydoidea.*

During the protractive phase, the limb is held horizontal in all taxa. Unlike *Trionyx,* other genera swing their limbs outward and forward rather than nearly directly forward as in *Trionyx.* The extent of the outward arc varies from cycle to cycle, but generally appears to be slightly less

in the web-footed taxa than in those with reduced webbing. All turtles consistently hold their feet horizontal on the forward swing. This feathering is not modified by the size of the arc.

As would be expected, the hindlimb movements in bottom-walking (Figs. 7 and 8) are similar to those encountered in terrestrial locomotion (Fig. 2). The most noticeable differences are the speed of limb movement and the ease with which the body is propelled forward. In addition, some features of swimming, e.g., extension of the foot webbing, are incorporated into bottom-walking. Of the four families photographed, the chelydrids and the kinosternids rarely exhibit any form of aquatic locomotion other than bottom-walking. Likewise, some semiaquatic testudinids frequently move by bottom-walking. The following detailed description is based on the limb movements of *Chelydra serpentina*.

In *Chelydra* (Fig. 7), the retractive phase begins with the thigh and crus tucked in the inguinal pocket. The plantar surface of the foot is parallel to the substrate and the longitudinal pedal axis extends anteroposteriorly. The initial limb extension is anteroventral, but before contact is made the limb begins to swing posteriorly. At footfall, the crus is nearly perpendicular (90°–100°). With a continuation of retraction, the body moves forward over the stationary limb. This results in an anterior inclination (15°–30°) of the crus. Preceding protraction, there is a light medial sweep of the limb, which is terminated by the anterior protraction. The limb moves forward in nearly a straight line. There is no exaggerated lateral swing.

As the foot moves ventrally with the initiation of retraction, the toes tend to tilt downward so that they are the first to touch the substrate. In many instances, the toes and extreme anterior part of the plantar surface are the only portions of the foot in contact with the substrate during the retractive phase. Once the crus passes the acetabular level, there is a pronounced medial rotation of the heel with the claws, particularly the first and second, acting as the pivot. With the final medial sweep, the foot lifts and the toes are oriented posteriorly. During protraction, the foot is held high and is accompanied by a slow rotation of the foot to re-establish the anteroposterior orientation. This rotation produces a planing or feathering movement thus presenting a minimal surface area to water resistance. During both the retractive and the protractive phase, the size of the foot remains essentially the same, because there is no spreading of the foot in retraction.

In the kinosternids, *Kinosternon* (Fig. 8) and *Sternothaerus,* the retractive phase also begins with the limb in a tucked position. The limb generally extends anteroventrally and at contact is inclined posteriorly (100°–130°). In one *S. carinatus,* the limb was inclined consistently at 70° to 80°. The inclination prior to protraction varies from 10° to 20°. There is usually a strong medial sweep that culminates with protraction. The limb appears to move directly forward during protraction. At footfall the foot is tilted so that only the first and second toes touch. The toes are spread
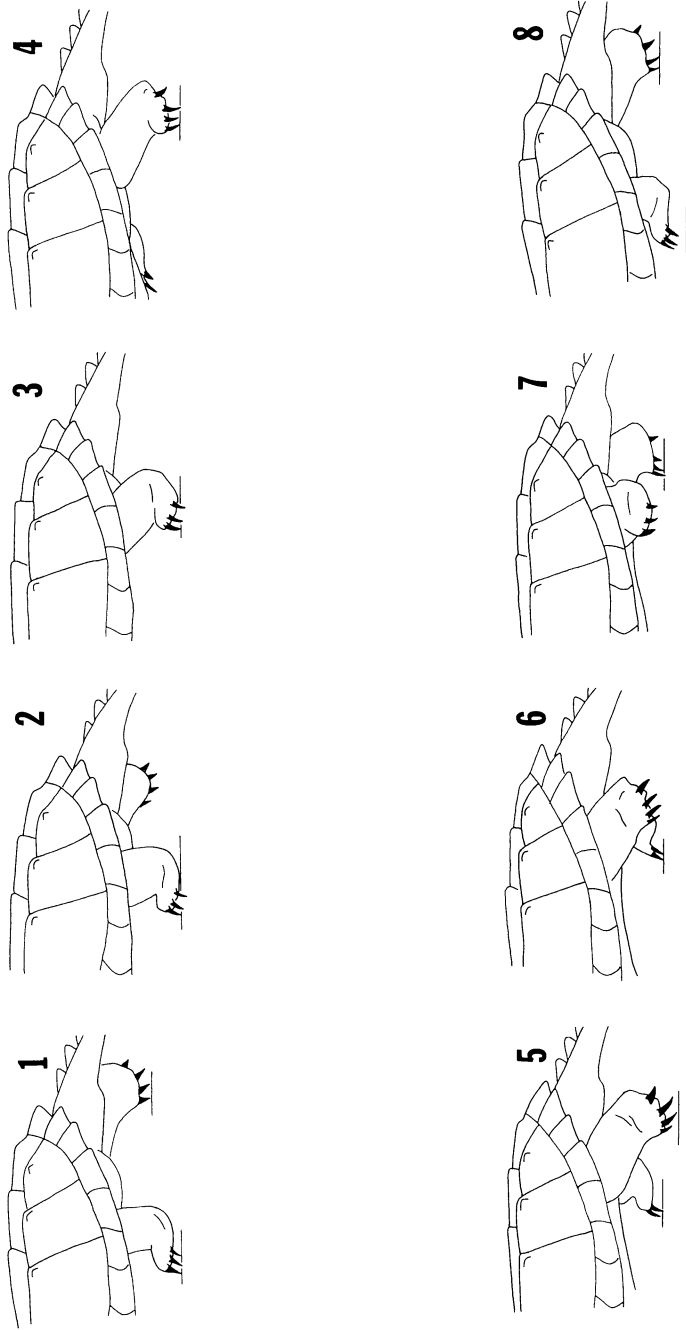
FIG. 7.   Lateral view of the left hindlimb of *Chelydra serpentina* during a single stride of bottom-walking. The numbering is identical to that in Figure 6.
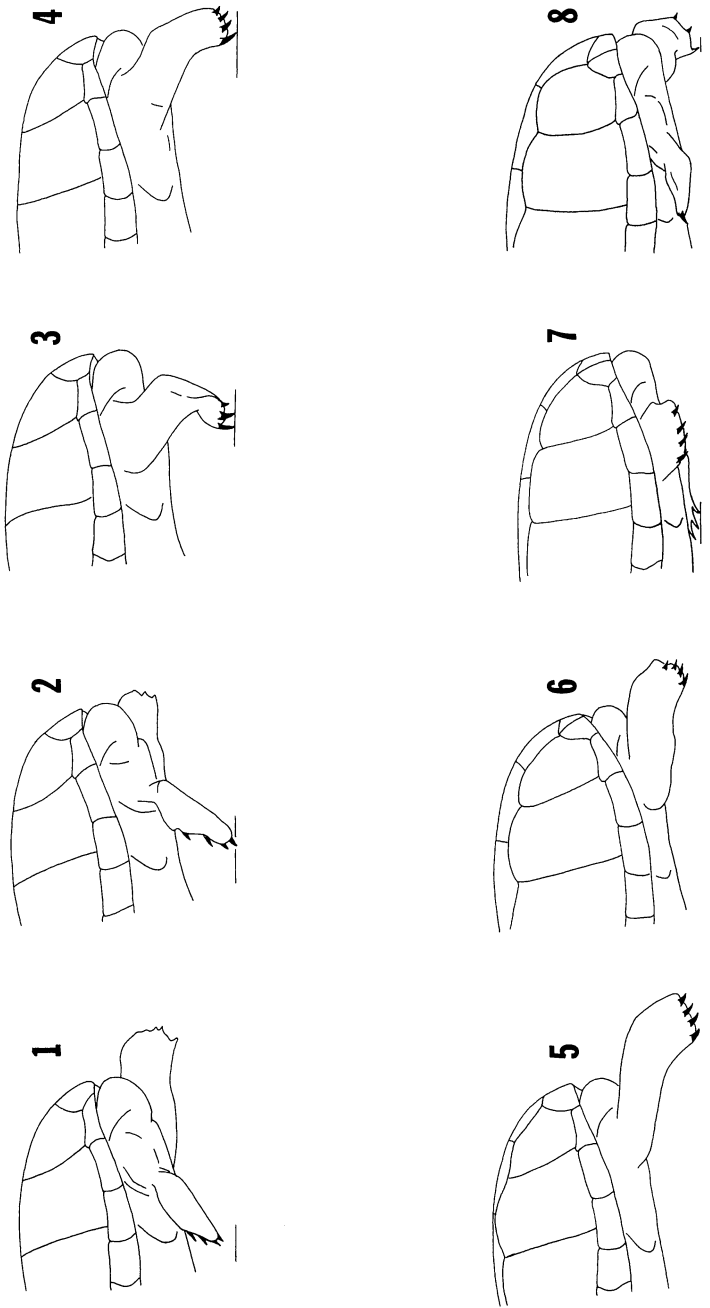
FIG. 8. Lateral view of the left hindlimb of *Kinosternon bauri* during a single stride of bottom-walking. The numbering is identical to that in Figure 6.

widely thus drawing the webbing taut. This foot posture and manner of contact is usually held throughout the retractive phase until the medial sweep begins. The entire plantar surface may establish contact, but usually this changes to the above foot posture as the foot develops a strong anterior inclination. The foot is held high and feathered during protraction.

The crus at footfall in the aquatic or semiaquatic testudinids, *Chrysemys, Clemmys, Cuora,* and *Emydoidea,* is inclined anteriorly (60°–80°), as it is at the end of retraction (10°–30°). Unlike *Chelydra* and the kinosternids, the crus is held in a ventrolateral plane rather than in a nearly perpendicular plane. The ventrolateral inclination appears to be greatest in *Chrysemys,* which may be associated with their being swimmers. Protraction usually begins before the limb has started the medial sweep which terminates retraction in chelydrids and kinosternids. The absence of this medial sweep causes the limb to arc outward during protraction. At footfall, the claws are usually the first to reach the bottom. The plantar surface also touches the substrate and remains in contact for most of the retractive phase. Steps with only the claws in contact are infrequent in the aquatic testudinids and have not been observed in *Chrysemys.* Preceding protraction, the foot swings upward and backwards. This movement appears to be the only time that propulsion is gained by pushing against the water. Although the foot may be spread during this latter thrust, it is distinctly seen only in *Chrysemys* and occasionally in *Clemmys.* During protraction the foot is held high in all genera except *Chrysemys.* In all of the aquatic testudinids, there is a distinct feathering in association with reorientation of the pedal axis.

PRÉCIS.—Turtles exhibit both terrestrial and aquatic locomotion. In both forms of locomotion, the propulsive force is supplied by the appendages.

Gait sequences, as determined by the gait formulae, show that in most instances turtles move in a trot or modified trot. In terrestrial locomotion, the speed of progression is a slow or very slow walk with a strong tendency towards lateral sequence gaits. The speed of progression in aquatic locomotion is usually at a fast walk or a slow run with a tendency for the gaits to be diagonal sequence ones. There is no obvious correlation between gait sequences or speed and taxonomic division.

The gaits analyzed herein are classified as symmetrical gaits. This implies that the time of retraction or protraction for a pair of limbs is the same and evenly spaced. Such symmetry is observed infrequently and is not to be expected in turtles. Variation or asymmetry is greater in aquatic locomotion than in terrestrial locomotion. Part of the asymmetry in aquatic locomotion appears to be associated with the necessity of synchrony in diagonally opposite limbs.

The movements of the hindlimbs in terrestrial locomotion do not demonstrate any strong taxonomic correlation, although some ecological or behavioral correlations are suggested. The anteroposterior inclination of

the crus has a distinct anterior inclination in the hinged taxa, *Cuora, Emydoidea,* and *Terrapene.* In *Chelydra* and *Trionyx* with reduced plastra it has a distinct posterior inclination, and for the remaining taxa it is almost perpendicular. The walkers, either aquatic or terrestrial, tend to hold the foot high during protraction.

In aquatic locomotion, two distinct patterns of progression are present and reflected in the movements of the hindlimb. Bottom-walkers propel themselves by pushing against both the bottom and the water; during the retractive phase their hindlimbs are vertical. Swimmers move their hindlimbs in a horizontal plane, and propulsion is obtained by pushing against the water. Although both patterns are used by a single turtle, a given taxon uses only a single pattern as its main mode of locomotion. The trionychids and the aquatic testudinids are swimmers. The chelydrids, kinosternids, and semiaquatic testudinids are bottom-walkers. There is an additional differentiation among the bottom-walkers. The chelydrids and testudinids usually hold their hindfeet horizontally in retraction. The kinosternids tilt their feet so that the webbing is expanded.

<div align="center">BUOYANCY</div>

Buoyancy usually is not a factor considered in a study of locomotion, even though locomotion may occur in an aquatic environment. With few exceptions, the analysis of aquatic locomotion has been restricted to fish. In general, teleosts are able to adjust their buoyancy and to remain stationary at any horizontal level in the water without an expenditure of muscular energy. They are able to adjust their specific gravity by regulating the flow of gases into and out of the swim bladder (Alexander, 1966). This ability allows a fish to use the majority of its locomotor effort for forward propulsion rather than dissipating a part of it on the maintenance of vertical stability.

The necessity for a study of buoyancy in turtles rests on the supposed inability of turtles to adjust their specific gravity. Because of this a swimming turtle is forced to devote a portion of its locomotor activity to the maintenance of a vertical stability. The only comparative data on chelonian buoyancy was presented by Williams and Han (1964). They determined the specific gravity of two *Terrapene carolina* and two *T. coahuila* and found that the semiaquatic *T. coahuila* is denser and is thus less buoyant than the terrestrial *T. carolina* (Table 4). In an abstract of a paper presented at a meeting, Schubert-Soldern (1966) recognized five groups of turtles based on their specific gravities and habits. Unfortunately no mensural data are provided to evaluate his conclusion. This section documents the buoyancy in a larger taxonomic and ecological sample of turtles and attempts to determine if there is any relationship between buoyancy and taxonomic, ecological, or locomotor groupings.

MATERIALS AND METHODS.—The specific gravity or density of an object is found by dividing the weight of the object by its volume. Turtles were

TABLE 4

SPECIFIC GRAVITIES AND SINKING FACTORS OF SOME CRYPTODIRES

Species	N	Specific Gravity		
		Range	$\bar{x}$	S.F.
Chelydra serpentina	1		1.007	1007
Cuora amboinensis	1		1.020	1020
Notochelys platynota	1		1.053	1053
Chrysemys concinna	2	1.076–1.153	1.114	1114
Chrysemys floridana	3	1.032–1.159	1.110	1110
Chrysemys scripta	14	1.029–1.248	1.108	1108
Clemmys guttata	4	0.876–0.985	0.950	950
Clemmys insculpta	1		0.997	997
Emydoidea blandingi	2	0.974–0.981	0.978	978
Terrapene carolina	7	0.739–0.958	0.848	848
Kinosternon bauri	2	1.017–1.070	1.043	1043
Sternothaerus carinatus	7	1.006–1.221	1.082	1082
Sternothaerus minor	10	1.031–1.404	1.139	1139
Trionyx muticus	1		1.081	1081
Trionyx spinifer	1		1.076	1076
*Terrapene carolina	2	0.73 –0.80	0.76	760
*Terrapene coahuila	2	0.95 –0.96	0.96	960

N, number of specimens; $\bar{x}$, mean; S.F., sinking factor; *, data from Williams and Han (1964).

weighed on a triple beam metric balance, and the weights were recorded to the nearest gram. To determine their volume, turtles were placed in a container with an overflow spout. The displaced water was collected in a graduated cylinder, and the volume recorded to the nearest cubic centimeter. In volumetric determination, it is necessary to restrict the movements of the turtles, otherwise any disturbance of the water level usually produces a volume of overflow greater than that of the turtle. Initially, I used the balloon technique of Mosimann (1955) to restrict limb movement; however, I found that this method left small air pockets between the balloon and the body and occasionally smaller air pockets in the balloon. It was also impossible to obtain an accurate measurement of the balloon's volume because of its tendency to retain small bubbles of air. Since this technique produces an overestimate of the turtle's volume, the calculated specific gravity would be an underestimate. Adhesive tape was substituted. It effectively restricts limb movements, does not create air pockets, and its volume can be accurately measured.

The necessity of restricting limb movements in the above manner has a distinct disadvantage. Both the balloon technique and the adhesive tape method force the turtle to be as completely retracted into the shell as possible. This does not affect the turtle's weight but probably does reduce their volume. I am unable to state the amount of reduction, but a comparison (Table 4) of my densities and those of Williams and Han, who reduced limb movements by refrigeration, suggests that it is small. An advan-

tage of my method is that retraction of the limbs and neck forces air from the lungs. A similar situation is seen in diving turtles, for they usually exhale before or during the dive. Thus it seems likely that this technique gives an estimate of density close to that of a free swimming turtle.

Lowndes (1955) has introduced the use of the sinking factor (S.F.) into the study of animal densities. It is calculated by multiplying by 1000 the quotient obtained in dividing the density of an animal by that of its aquatic environment. Obviously, in fresh water the sinking factor is 1000 times the animal's density since the density of fresh water is one or nearly one. The reason for the use of the sinking factor here is to make my data more comparable to that in the fish literature and also when the densities of brackish or marine turtles are determined, the results will be directly comparable.

RESULTS AND DISCUSSION.—Turtles with sinking factors greater than 1000 will sink; those with less than 1000 will float. The distribution of turtles in the two categories is illustrated in Table 4. All of the sinking taxa are usually considered to be aquatic species. The floating taxa include one terrestrial species, *Terrapene carolina,* and three species, *Clemmys guttata, C. insculpta,* and *Emydoidea blandingi,* which are frequently regarded as semiaquatic.

The ability to sink has an obvious selective advantage for aquatic turtles. Since they cannot establish a hydrostatic equilibrium (Schubert-Soldern, 1966, said that *Chelodina longicollis* does), they must either float or sink. If they float, they would have difficulty in obtaining food or escaping from predators. It might be expected on the basis of the aquatic locomotor patterns that the bottom-walkers would tend to have higher sinking factors than the swimmers. This reasoning follows from the fact that since swimmers stay off the bottom, it would be to their advantage to be near hydrostatic equilibrium and not expend a large part of their locomotor effort to remain off the bottom; however, the reverse appears to be true (Table 4). One reason for this may be that bottom-walkers are typically poor swimmers. For them to surface and breathe, they must expend considerably more energy than swimmers. If they were denser than swimmers or had the average density of swimmers, they would be forced to expend even more energy to surface. Accordingly, there appears to have been a selective pressure on bottom-walkers to stay near hydrostatic equilibrium.

Although the adaptative significance of sinking in aquatic turtles seems clear, the significance of floating in terrestrial and semiaquatic turtles is obscure. The ability of the terrestrial *Terrapene carolina* to float when they fall in water certainly has survival value, but it is doubtful that this occurs frequently enough for it to have acted as a selective agent. The ability to float, or rather a larger volume-to-mass ratio, appears to be an adaptation for terrestrialism, since most terrestrial turtles have domed shells. Such a larger volume-to-mass ratio also occurs in the semiaquatic *Clemmys guttata, C. insculpta,* and *Emydoidea blandingi,* lending further

support to this hypothesis, because semiaquatic species would be expected
to sink and do in fact sink under natural conditions. However, the method
employed herein for determining their specific gravity does not reduce their
volume sufficiently for them to sink. This contrasting experimental and
field evidence suggests that lung volume and the associated enlargement
of the flanks determine whether a turtle will sink or float. The aquatic
species tend to have depressed shell profiles and the retraction of the head
and limbs compresses the viscera and probably collapses the lungs, whereas
the terrestrial and semiaquatic species tend to have higher shell profiles and
the retraction of the limbs and head does not appear to reduce lung volume
nor body volume as much. The supposed need for a larger volume-to-mass
ratio in a terrestrial situation and the necessity of sinking in an aquatic
one have led to what appears to be a compromise adaptation in the semi-
aquatic species. In the terrestrial *Terrapene carolina,* the sinking factor is
848, in the aquatic species 1007 to 1139. The semiaquatic species have
values of 950 to 997 which are very close to the boundary between floating
and sinking. This suggests that although they have a high volume-to-mass
ratio, it is sufficiently close to the boundary that further reduction of
body volume, probably through the expulsion of air, allows them to obtain
a sinking factor greater than 1000. An interesting test of this hypothesis is
to contrast the sinking factors of the terrestrial *Terrapene carolina* and its
semiaquatic derivative, *T. coahuila* (Table 4). The sinking factor of *T.
coahuila* is like that of other semiaquatic taxa and distinctly different from
its presumed ancestor, *T. carolina.*

It has been implied throughout this discussion that lung volume affects
the ability to sink or float by changing the volume of the body. Although
there are no numerical data on the volume of the body in relation to lung
size, there are a number of observations that support this supposition. In
order to breathe, aquatic turtles must surface periodically. Aquatic turtles
begin their ascent to the surface with a negative buoyancy. The locomotor
effort appears greater for this vertical ascent than during horizontal move-
ments. This is very obvious in bottom-walking taxa when placed in deep
water, as they literally struggle to reach the surface. When the snout extends
above the surface, locomotor effort stops, yet the turtle usually floats to the
surface. Likewise, a diving turtle often releases a bubble of air during the
initial stage of the dive. Both of these observations suggest that inhalation
has increased the body volume. It appears that the expansion of the body
volume results from the swelling of the inguinal pockets and cervicoaxil-
lary regions. When a turtle is floating at the surface, there is a distinct
bobbing of the shell and a simultaneous fluctuation of the inguinal pockets.
Mitchell and Morehouse (1863) and Gans and Hughes (1967) have shown
that there are cyclic contractions of the muscles of the inguinal pockets and
cervicoaxillary region which are associated with the inhalation-exhalation
phases of the ventilation cycle. It seems highly likely that as lung volume
increases the volume of the body also increases.

Even though no one has suggested a possible adaptive reason for the increase in body volume in terrestrial or partially terrestrial taxa, a larger body volume does exist as does also a greater lung volume. Agassiz (1857) has provided a series of lung volume and weight measurements which can be converted into lung volume to body mass ratios. *Terrapene carolina* has the highest value, 0.93; *Kinosternon subrubrum* and *Trionyx spinifer* the lowest, 0.06; *Chelydra serpentina* is also low, 0.11. In general, these ratios correspond well to the ability of a given species to float or sink, since the terrestrial species has nearly a 1:1 ratio, whereas the aquatic species have approximately a 1:10 ratio; however, the values for *Gopherus polyphemus* and *Chrysemys rubriventris* are 0.37 and 0.36, respectively. These values suggest that both the terrestrial *G. polyphemus* and the aquatic *C. rubriventris* would sink, and sinking would be expected only in the latter species. I have not determined the density for *G. polyphemus,* but I believe it would be similar to that of *T. carolina,* since *G. polyphemus* in water floats very high (Carr, 1952) like *T. carolina.* Perhaps the reason for the incongruity is that one of Agassiz's measurements is in error.

PRÉCIS.—Aquatic turtles have a sinking factor greater than 1000, terrestrial and semiaquatic turtles less than 1000. The former group sinks and the latter floats. The ability to sink is a distinct advantage to aquatic species. The ability to float has no obvious selective advantage in terrestrial or semiaquatic turtles.

The increase in body volume in relation to weight is thought to be, or associated with, an adaptation for terrestrialism. This appears to have led to a compromise situation in the semiaquatic species. Although body volume has increased, it is still possible for the semiaquatic species to reduce their volume to obtain negative buoyancy. Likewise, the volume of aquatic species has not decreased beyond a limit which would prevent them from obtaining a positive buoyancy.

Adjustment of body volume appear to be closely associated with regulation of lung volume. The inguinal pockets and cervicoaxillary region seem to be the regions that are protracted or retracted to adjust body volume.

MORPHOLOGY OF PELVIC GIRDLE AND HINDLIMB

There has been no lack of studies on chelonian appendicular morphology. Most of these studies appeared before or shortly after the beginning of the twentieth century. Owing to the type of anatomical investigations then in vogue, they are neither functional nor systematic in approach. The majority report on the anatomy of a single species of turtle and seldom with reference to other species or even to other reptiles. A few authors (e.g., Gadow, 1882; Hoffman, 1890; Sieglbauer, 1909) extended their investigations to more than one species of turtle and made comparison to turtles and other tetrapods. To my knowledge, only Baur (1891a) attempted to use

a part of the locomotor apparatus, the pelvis, to show the relationships of turtles. Boulenger (1889) used webbing, phalangeal formulae, and number of claws in his generic and familial definitions.

As previously mentioned, I have restricted my examination to the morphology of the pelvic girdle and hindlimb in order to increase the systematic coverage of the investigation. Within this section, the osteology and myology will be discussed separately to determine the systematic and functional trends demonstrated by the individual systems. Finally, I will endeavor to correlate the morphological architecture of posterior appendages with the locomotor patterns.

OSTEOLOGY

Osteology has had a long and important history in chelonian systematics. Our present classification (Williams, 1950; McDowell, 1961 and 1964) is based largely on osteological characters and almost exclusively so above the generic level. However, the use of the appendicular skeleton in classification has been slight. The reason for this is obscure. It may be attributed to the frequently held position that "adaptive characters are not good taxonomic characters." If this is the reason, it is hardly defensible, for there has been no attempt to prove or disprove the undesirability of the chelonian appendicular skeleton for taxonomic purposes. Only Zangerl (1953) has tried to illustrate how variation in the appendicular skeleton is correlated with habits of turtles, and then to use this information for the delineation of a group of extinct turtles. His work clearly shows that functional characteristics can be used in classification.

MATERIALS AND METHODS.—The specimens used in this study were from the University of Michigan Museum of Zoology herpetological skeletal collection. The entire collection was used for making comparisons and determining ranges of variation. Rather than list all the specimens examined, only the specimens from which osteological measurements were recorded are listed in Appendix III. Also to determine the position and number of elements in the pes, radiographs were made of approximately 30 alcoholic specimens, and these are likewise listed in Appendix III.

In order to supplement and confirm observational data, 20 measurements were taken; descriptions of these measurements are presented in Appendix IV. Because of the wide range in maximum adult size, it was deemed necessary to convert the measurements into ratios in order to have a standard of comparison among the different taxa. Engels (1940) has discussed the numerous pitfalls inherent in the comparison of ratios, particularly the problem of ratio being composed of two varying members. Since ratios are used to determine direction of change and amount of change, a ratio of measurements varying in the same direction will hide the direction or at least will underestimate the amount of change, whereas a ratio of measurements varying in opposite directions will overestimate the amount of change. In an attempt to avoid this pitfall, I have selected the length

of the eighth cervical centrum as a standard. Owing to its critical role in the articulation of the neck with dorsal vertebrae, it seems less likely to vary greatly among the different taxa. There are two methods for calculating ratios: (1) to total and average individual measurements and then to calculate a ratio for the average or (2) to calculate individual ratios for individuals and then to determine the average for the ratios. Engels (1940) has shown that the second method is probably more representative of the true values. I have used the second method. The osteological terminology in this section is that promulgated by Romer (1956).

PELVIC GIRDLE.—The cryptodiran pelvic girdle is composed of three pairs of bony elements, ilia, ischia, and pubes. The pubes and ischia form a horizontal, ventral plate, the puboischiadic plate. The pubes are fused medially along a pubic symphysis. The pubes form the anterior part of the bony plate, although they are preceded medially by a single, triangular, cartilaginous element, the epipubis. Posteriorly, the pubes are continuous with ischia laterally along the puboischial symphyses; medially, they are separated by a pair of puboischiadic foramina. The ischia are joined medially through an ischial symphysis. An ilium extends dorsally on each side from the puboischial symphysis to the carapace. Laterally on each side at the union of the three elements is a circular depression, the acetabulum, in which the femur articulates.

Contact with the axial skeleton is maintained by all pelvic elements; however, unlike the pleurodires there is no fusion of the girdle with the carapace and plastron. Dorsally, the ilium abuts against the carapace. In *Dermatemys,* kinosternids, chelydrids, and testudinids, the ilial articulation on the carapace is posterolateral to the union of the dorsal ribs on the ventral surface of the eighth pleural. In trionychids, the ilium does not articulate with a pleural, instead it abuts against the thick connective tissue portion of the carapace. The pleurals of a trionychid carapace are greatly reduced or lost. The point of articulation on the eighth pleural is variously modified. The area of articulation on the pleural in *Platysternon* and the chelydrids is not bordered anteromedially by a tuberosity, which is present in all of the other taxa. A rugosity on the eighth pleural of the former two taxa marks the articulation. The articulation in *Platysternon* is at the lateral extreme of the pleural, in the chelydrids on the middle of the pleural.

All testudinids examined except *Platysternon* had large tuberosities. The shape of the tuberosities is extremely variable, although the manner in which the ninth and tenth rib join it may be of some value in analyzing its form. The position of the tuberosity is usually on the proximal half of the pleurals; however, in *Cuora* and *Terrapene* it is displaced distally. This displacement suggests a terrestrial adaptation, but the terrestrial testudinines have a proximal tuberosity. Only in *Terrapene, Cuora,* and *Gopherus,* have I observed an erosion of carapace above the ilial articulation. The ilial tuberosities of kinosternids are small, and they are formed without any contribution from the ribs. In kinosternids, the ninth and tenth

dorsal vertebrae are free and lack ribs. *Dermatemys* also has a very small tuberosity, which is formed in part by the ninth dorsal rib; the tenth dorsal vertebra is free as in kinosternids.

The carapacial articulation is not the only dorsal articulation of the pelvis, for the distomedial surface of the ilium articulates with the two sacral ribs. On the basis of my observation this appears to be the condition for all cryptodires. The first sacral rib is almost always the larger, although in two specimens (a *Chelydra serpentina* and a *Clemmys insculpta*) the ribs were of the same size. The second sacral rib was never observed to be the larger. There is no fusion of the ribs with the ilium, but a thick collagenous plate lies between the two and forms a strong union.

Ventrally the pelvis rests on the plastron, anteriorly by means of the pectineal process (a lateral extension of the pubis) and posteriorly by the metischial process (a lateral extension of the ischium) and/or the postero-median edge of the ischium. I wish to note briefly the variation in ventral contact, but first I must emphasize that the contact I am reporting was obtained by setting the girdles on a plane surface. It must be realized that the dorsal surface of a plastron is not flat and thus these observations provide only an estimate of the actual condition. Nevertheless, the pubis and ischium do touch the plastron, for this was confirmed by dissections.

The only portion of the pubes in contact with the plastron is the distal edge of the pectineal process. Variation in contact results from the different shapes of this edge in the various taxa. Only the posterior part forms a contact in *Chelydra* and *Platysternon*. In the testudinids, the entire distal edge is in contact. *Kinixys* and *Terrapene* are exceptional with only the anterior edge in contact. This may be associated with a hinged shell, although *Cuora* does not show this condition and there is only a slight indication of it in *Emydoidea*. The kinosternids have only the posterior part touching. In *Trionyx* and *Lissemys,* the area of contact has shifted from the distal edge to the distoventral surface, creating a condition completely unlike that of any other cryptodiran taxa.

The posteroventral contact is of two types: (1) medially or paramedially along the posterior edge of the ischium or (2) distally on the tip of the metischial process. Although these two types of contact are not mutually exclusive, it is rare that both are observed in the same specimen. All cryptodires have medial or paramedial contact. Metischial contact is observed in a few *Chelydra, Chrysemys* and *Malaclemys*. In a few testudinines, *Terrapene,* and kinosternids, there is a tendency for the ischia to form a keel at the ischial symphysis. A single median ossicle frequently develops below the ischial keel in kinosternids and prevents the ischium from reaching the plastron. The ossicle appears to be a calcification of the hypogastroid cartilage (*sensu* Baur, 1891a).

The cryptodiran ilium presents a myriad of shapes in lateral aspect (Fig. 9). In contrast, when viewed from an anterior or posterior aspect, the ilium generally appears as a parallel-sided column with an enlarged base. Rather than attempt to describe the lateral aspect of many ilia, I wish only
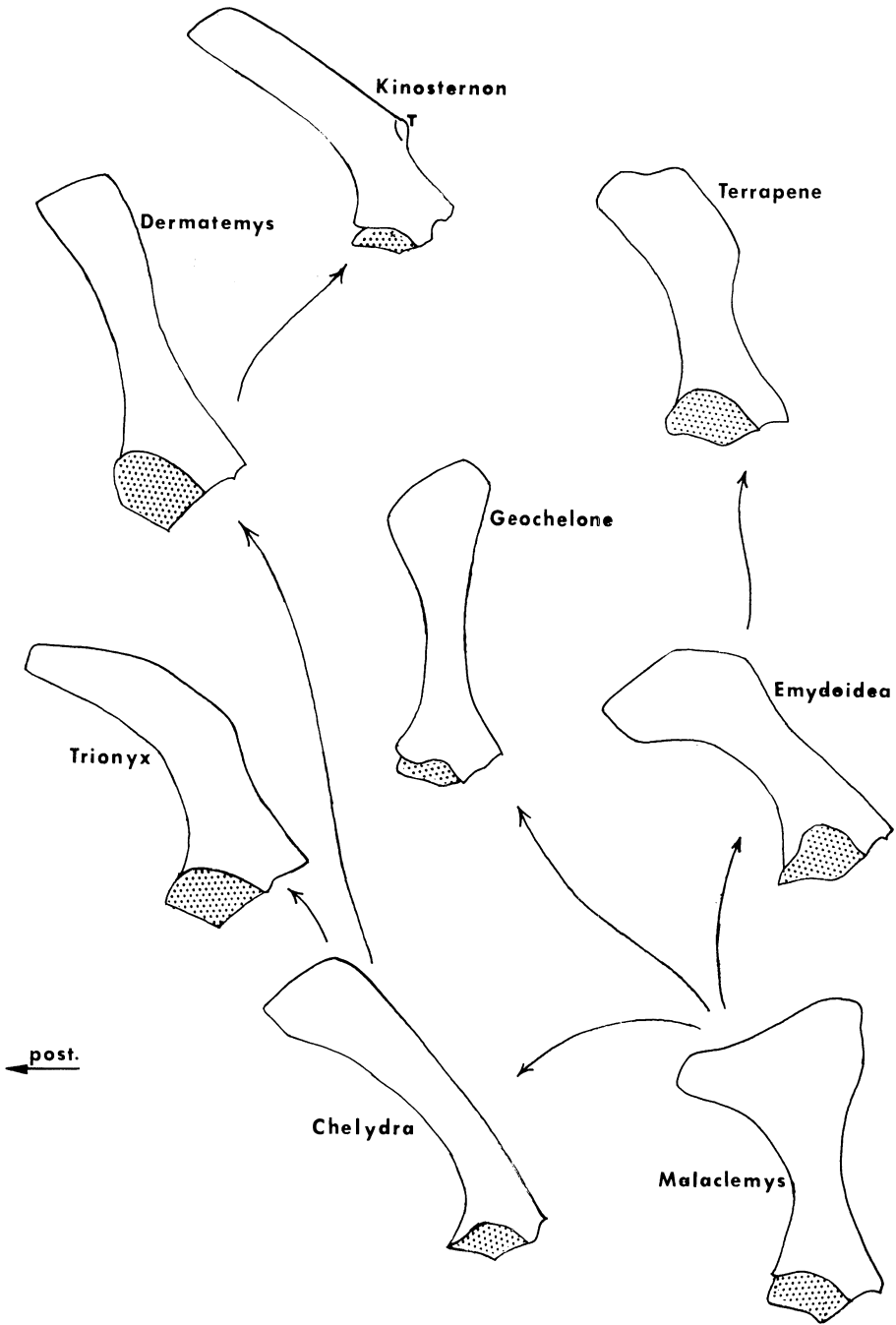
FIG. 9. The various forms of cryptodiran ilia, as seen in lateral aspect. The arrows indicate one possible direction of morphological modification. T., thelial process of kinosternids; stipple, acetabulum.

to discuss a few relevant features of ilial morphology. Although lateral ilial form is highly variable, it is possible to divide it into two distinct classes. In the testudinids and chelydrids, the ilium is spool-shaped with enlarged proximal and distal ends, whereas the ilia of *Dermatemys,* kinosternids, and trionychids have only the proximal end enlarged. The enlarged proximal end appears to be associated with establishment of a firm and broad articulation to the ischium and ilium. The enlarged distal end provides a larger surface area for attachment of muscles and for a wider articulation with the sacral ribs.

The anterior edge of the ilium is nearly straight in all families, except the trionychids. In the trionychids the ilium has developed a strong flexure, so that the distal half extends posteriorly. Only kinosternids have a projection, *thelial process,* on the anterior edge of the ilium (Fig. 9). The anterior edge is smooth in all other cryptodires. The thelial process projects from the second quarter of the ilium and provides an elevated area of attachment for the iliotibialis muscle. The lateral face of the ilium is smooth, but in the testudinids there is a tendency for the anterior and posterior edges to curve outward on the distal end to form a shallow fossa. Usually, this outward curvature is greater along the posterior edge. *Terrapene* shows the extreme condition with the formation of a horizontal ledge that nearly reaches the anterior edge. *Kinixys* and *Emydoidea* show less developed ridges. These ledges seem to be correlated in some way with a hinged shell. Medially, the enlarged distal end is rugose in chelydrids, trionychids, kinosternids, and *Dermatemys.* The testudinid ilium is also rugose in this region and in addition usually possesses a shallow fossa for the articulation of the sacral ribs.

The ilium possesses two axes of inclination, transverse and longitudinal. In the transverse plane, the ilium is usually perpendicular to the plastron or nearly so. Perpendicular ilia are absent only in chelydrids and kinosternids. In the chelydrids, the ilium is inclined outwardly at approximately 70°. The ilia of kinosternids are considered to be perpendicular, although the basal portion curves outward and the distal portion inward. The angle of inclination in the longitudinal plane (IA) ranges from 80° to 160°, i.e. from nearly perpendicular to strongly inclined posteriorly (Table 5). All testudinids examined, except *Emydoidea* and *Kinixys,* have nearly perpendicular ilia. Other testudinids for which only one or two specimens were available also have nearly perpendicular ilia. The ilia of *Chelydra, Emydoidea* and *Kinixys* are inclined at approximately 120°. The kinosternids have strongly inclined ilia of about 145°. The ilia of *Trionyx* are bent. The proximal half is nearly perpendicular and the distal half approximately 150°.

If my assumption of low variation of the eighth cervical vertebra is correct, the relative length of the ilium, IL/CCL, (Table 5) is the same among the different cryptodiran taxa. The ilium is from two to three times the length of the eighth cervical vertebra.

Although the puboischiadic plate (Fig. 10) is usually considered to be a flat surface parallel to the plane of the plastron, it is in actuality a curved

TABLE 5

MEASUREMENTS AND RATIOS OF THE ILIUM AND ACETABULUM

Species	IA				IL/CCL				AH/CCL			
	N	x̄	Range	s	N	x̄	Range	s	N	x̄	Range	s
Chelydra serpentina	7	122.4	113–134	6.5	7	2.1	2.0–2.2	0.1	7	1.0	0.7–1.1	0.10
Rhinoclemys rubida	1	85.0			1	2.2			1	1.2		
Chrysemys floridana	7	87.1	80–90	4.9	5	3.3	3.1–3.5	0.2	5	1.7	1.6–1.8	0.10
Chrysemys picta	22	99.0	85–110	8.9	21	3.1	2.5–3.7	0.3	21	1.5	1.2–1.9	0.16
Chrysemys scripta	10	86.5	80–90	4.1	8	3.0	2.7–3.3	0.2	7	1.5	1.3–1.6	0.10
Clemmys guttata	4	107.5	100–120	9.6	5	3.1	2.6–4.0	0.5	4	1.6	1.3–1.8	0.24
Clemmys insculpta	7	85.0	80–90	5.0	6	3.0	2.7–3.4	0.8	5	1.5	1.4–1.6	0.09
Clemmys marmorata	7	93.6	85–100	5.6	6	3.0	2.7–3.3	0.2	6	1.5	1.3–1.7	0.16
Emydoidea blandingi	10	22.5	115–130	4.9	9	1.9	1.7–2.0	0.1	9	1.0	0.9–1.1	0.06
Malaclemys geographica	5	81.0	80–85	2.2	2	3.2	3.2		2	1.4	1.4	
Malaclemys terrapin	3	100.0	100	0.0	3	2.8	2.6–2.9	0.2	3	1.5	1.5–1.6	0.04
Terrapene carolina	16	99.1	85–110	8.2	16	3.1	2.5–3.8	0.4	16	1.4	1.2–1.8	0.17
Terrapene ornata	9	92.8	90–100	4.4	9	3.0	2.7–3.3	0.2	9	1.6	1.3–1.6	0.13
Platysternon megacephalum	1	110.0			1	2.0			1	1.1		
Gopherus berlandieri	4	82.5	80–90	1.6	3	3.3	2.9–3.6	0.3	3	1.6	1.5–1.7	0.12
Gopherus polyphemus	4	93.7	85–105	8.5	4	2.2	1.7–2.4	0.3	4	1.1	1.0–1.2	0.12
Kinixys erosa	4	116.2	110–120	4.8	3	3.1	3.0–3.2	0.1	3	1.3	1.3–1.4	0.09
Claudius angustatus	2	145.0	140–150		2	2.6	2.6		2	0.9	0.9	
Kinosternon flavescens	12	145.4	135–155	7.2	11	3.1	2.8–3.3		11	0.9	0.7–1.0	0.09
Sternothaerus odoratus	19	142.6	130–150	2.9	18	3.0	2.7–3.4	0.2	17	0.9	0.7–1.1	0.10
Trionyx muticus (prox.)	2	110.0	100–120									
Trionyx muticus (dist.)	1	160.0										
Trionyx spinifer (prox.)	4	103.8	90–115	11.1	2	1.8	1.5–2.2		2	0.7	0.5–0.9	
Trionyx spinifer (dist.)	4	148.8	145–150	2.5	2	1.8	1.7–1.9		2	0.6	0.6–0.7	

Ilial angles (IA), ilium length to eighth cervical centrum length ratios (IL/CCL), and acetabular height to eighth cervical centrum length ratios (AH/CCL). N, number of specimens examined; x̄, mean; Range, range; range of variations; s, standard deviation. Morphological abbreviations and ratios described in Appendix IV.

surface. The pubis tends to be parallel to the plastron in most cryptodirans except in testudinines, but the ischium slopes posteriorly towards the plastron. The puboischiadic plate of trionychids is the closest approximation to a horizontal plane. None of the other cryptodires approaches the trionychid condition. The testudinids present a graded condition from a low slope of the ischium to a nearly vertical ischium. The lowest ischial slopes are seen in aquatic emydines such as *Graptemys* and *Chrysemys*. An almost vertical ischium is typical of testudinines; however, there does not appear to be a correlation between the slope and the degree of terrestrialism. The ischia of semiaquatic *Emydoidea* have a higher slope than those of *Terrapene,* and it is equal to or greater than that of *Gopherus.* The chelydrids have an intermediate condition, whereas the kinosternids possess a nearly vertical ischium.

The various inclinations of the ischium appear to have resulted in puboischiadic arches of different heights; however, a comparison of the heights of the acetabulum, AH/CCL, (Table 5) and the ischial inclination of different taxa does not support this conclusion. *Trionyx* has the lowest arch, kinosternids and *Chelydra* intermediate, and testudinids the highest. The ranges of variation of the families form a continuum. Apparently, the reduction in length of the puboischiadic plate gives the illusion of arches of different heights, because the relative length of the plate, LPP/CCL, (Table 6) shows that those turtles with the greatest ischial inclination have the shortest puboischiadic plate length.

The puboischiadic foramina (Fig. 10) lie in the middle of the puboischiadic plate between the ischia and pubes. In all cryptodires examined except the trionychids, the foramina are paired, i.e., separated on the midline of the pelvis by anterior extensions of the ischia and posterior extensions of the pubes. These extensions in the chelydrids are separated by a wide hiatus. In the testudinids, the extensions are in contact or separated by a narrow hiatus. The testudinines, *Clemmys, Emydoidea, Rhinoclemys, Terrapene,* and some *Chrysemys* show the former condition, *Chrysemys, Malaclemys, Platysternon,* and *Rhinoclemys* the latter. If the pubic and ischial extensions do not touch, the foramina are still separated by a cartilaginous strip on the midline. The pubic and ischial extensions of kinosternids do not meet, but the extensions are close and the hiatus is bridged by calcified cartilage. The staurotypines have very small extensions. The trionychids have proceeded one step further with complete loss of pubic and ischial extensions, although dissections reveal a median, ligamentous or cartilaginous band. The size of the foramina is subequal in the chelydrids, testudinids, and kinosternids. In the trionychids, they are half again as large as in the former families. This increase in size has resulted from an anterior expansion of the foramina, but it has not caused a proportionate increase in length of the puboischiadic plate, LLP/CCL, (Table 6). The shapes of the puboischiadic foramina vary from genus to genus (Fig. 10) with no discernible systematic pattern. Of all the turtles examined, only *Terrapene* shows a
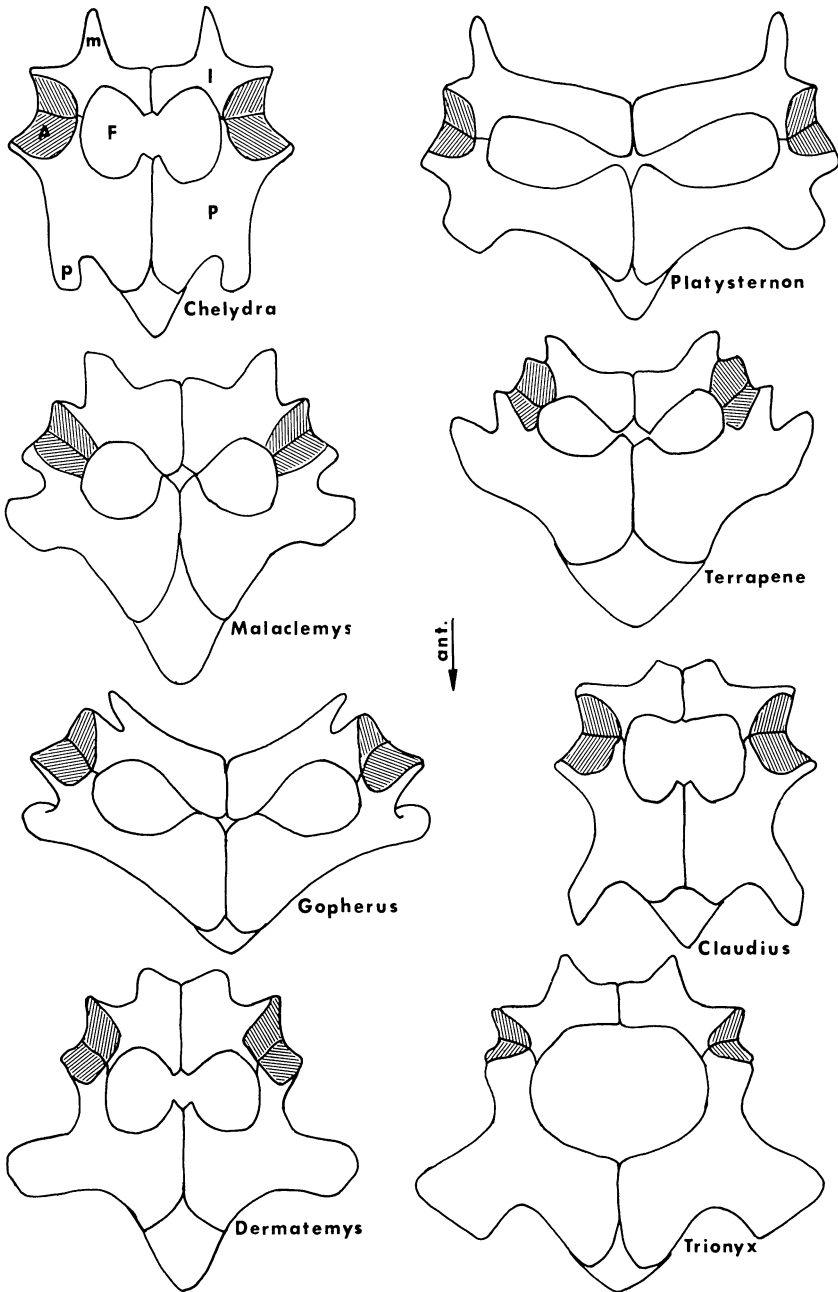
FIG. 10. Dorsal views of the puboischiadic plates of eight cryptodires, which illustrate the variation in form of the metischial processes (m), pectineal processes (p), and puboischiadic foramina (f). A, acetabulum; I, ischium; P, pubis.

TABLE 6

MEASUREMENTS AND RATIOS OF THE PUBOISCHIADIC PLATE AND PECTINEAL PROCESS

Species	LPP/CCL				WA/CCL				BWPp/CCL			
	N	x̄	Range	s	N	x̄	Range	s	N	x̄	Range	s
Chelydra serpentina	7	2.1	1.9–2.3	0.1	7	2.2	2.0–2.3	0.1	7	0.4	0.3–0.4	0.04
Rhinoclemys rubida	1	2.6			1	4.1			1	0.5		
Chrysemys floridana	4	4.1	3.7–4.6	0.4	5	4.4	4.1–4.5	0.2	5	0.8	0.7–0.9	0.07
Chrysemys picta	21	3.5	3.2–4.6	0.4	21	4.1	3.5–5.0	0.3	21	0.8	0.6–1.2	0.12
Chrysemys scripta	7	3.8	3.4–4.0	0.3	8	4.0	3.5–4.2	0.2	8	0.8	0.6–0.9	0.10
Clemmys guttata	5	3.5	3.3–3.6	0.1	4	5.0	4.5–5.4	0.4	5	1.1	1.0–1.2	0.08
Clemmys insculpta	6	3.4	3.1–3.8	0.2	5	4.0	3.8–4.2	0.1	6	0.7	0.6–0.9	0.11
Clemmys marmorata	6	3.3	2.9–3.7	0.3	6	4.4	3.7–4.8	0.4	6	0.8	0.7–0.9	0.08
Emydoidea blandingi	7	2.1	2.0–2.3	0.1	9	2.7	2.6–2.9	0.1	9	0.6	0.5–0.7	0.06
Malaclemys geographica	2	4.0	4.0–4.1		2	4.5	4.5		2	0.8	0.8	
Malaclemys terrapin	3	3.7	3.3–4.1	0.4	3	3.7	3.7–3.8	0.1	3	0.7	0.6–0.7	0.04
Terrapene carolina	8	3.0	2.7–3.6	0.4	16	3.4	3.0–4.0	0.3	16	1.5	1.2–1.8	0.14
Terrapene ornata	8	3.8	2.9–4.8	0.6	9	4.0	3.5–4.6	0.3	8	1.3	1.2–1.4	0.07
Platysternon megacephalum	1	2.4			1	5.0			1	0.8		
Gopherus berlandieri	3	2.7	2.6–2.9	0.2	3	4.3	4.2–4.4	0.1	3	0.6	0.5–0.6	0.06
Gopherus polyphemus	4	2.2	2.0–2.5	0.2	4	3.1	2.8–3.6	0.3	4	0.4	0.3–0.4	0.03
Kinixys erosa	3	2.5	2.0–3.0	0.4	3	3.6	3.3–4.2	0.5	3	0.7	0.7–0.8	0.04
Claudius angustatus	2	2.4	2.3–2.5		2	2.0	1.8–2.1		2	0.3	0.3–0.4	
Kinosternon flavescens	11	2.0	1.9–2.2	0.1	11	3.3	3.0–3.4	0.1	11	0.7	0.6–0.9	0.08
Sternothaerus odoratus	18	2.1	1.7–2.3	0.2	17	2.3	2.1–2.5	0.1	18	0.6	0.5–0.7	0.07
Trionyx muticus	2	4.5	3.9–5.1		2	3.6	3.5–3.8		2	1.4	1.2–1.6	
Trionyx spinifer	2	3.2	3.2–3.3		2	2.6	2.6		2	1.0	1.0	

Length of puboischiadic plate to eighth cervical centrum length ratios (LPP/CCL), width of puboischiadic plate to eighth cervical centrum length ratios (WA/CCL), and pectineal process width to eighth cervical centrum ratios (BWPp/CCL). Statistical abbreviations explained in Table 5, morphological abbrebiations and ratios in Appendix IV.

tendency toward the reduction of the foramina, and this appears to be by calcification of the connective tissue sheaths in the foramina.

The width of the puboischiadic plate, WA/CCL, (Table 6) does not appear to be associated with foramina size but with length of the plate. The trend seems to be that as the plate becomes shorter or as the inclination of the ischium increases, the plate becomes narrower.

As previously mentioned, the pubis and the ischium bear lateral extensions. A pectineal process always projects from the body of the pubis, whereas the occurrence of a metischial process is sporadic (Fig. 10). Although the metischial process is present in all cryptodiran families examined, not all members of a single family have it. In the testudinids, the batagurines, emydines, and *Platysternon* have the process. In the testudinines, a process is present in *Gopherus* and absent in *Testudo* and *Kinixys*. The kinosternines have extremely small processes, the staurotypines none. The process is large in *Trionyx* but nonexistent in *Lissemys*. This sporadic distribution and the various forms and positions of the process suggest that the metischial process is a homoplastic structure at the familial level and cannot be validly compared among families.

In contrast, the stability of position of the pectineal process and its same relative shape in turtles are indicative of its homology within the suborder Testudinata. The shape of the process varies from fan-like in *Trionyx* to peg-like in *Kinixys*. Along with the variation in shape, there is comparable variation in size (Fig. 10). The BWPp/CCL ratio, relative width of pectineal process, in Table 6 gives an estimate of the size. *Trionyx* and *Terrapene* have the broadest processes.

Another distinct variable is the angle (PpA) at which the pectineal process projects from the pubic plate. The values in Table 7 give an approximation of this angle of projection. A value of 0° would indicate a process parallel with the longitudinal body axis, one of 90° a process perpendicular to the axis. Only chelydrids have the process extending anteriorly and parallel to the axis. In all other cryptodires, the process projects laterally. Terrestrial forms tend to have the process perpendicular to the body axis. It should be noted, however, that the manner of recording this angle (Appendix IV) yields only an approximation of the angle of the central axis of the process, and in some species the shape of the posterior edge of the process might provide a highly erroneous estimate.

The acetabulum is formed laterally at the junction of the ilium, ischium, and pubis, and the articular surface is composed of these three bones. The three elements generally contribute equally to it, although there is a tendency in the terrestrial taxa, *Rhinoclemys, Terrapene,* and the testudinids, for the ilial portion to be approximately two times as great as that of either of the other two elements. This tendency was also observed in the kinosternids, *Clemmys,* and *Emydoidea* but to a lesser extent. In association with this tendency, there is a reorientation of the articular face. Usually the articular face is directed laterally with a slight posterior slant, whereas in the aforementioned taxa the orientation is posterolateral. This reorien-

TABLE 7
MEASUREMENTS AND RATIOS OF THE PECTINEAL PROCESS AND FEMUR

Species	PpA				FL/CCL				FL/FH			
	N	$\overline{x}$	Range	s	N	$\overline{x}$	Range	s	N	$\overline{x}$	Range	s
Chelydra serpentina	7	6.0	2–13	5.9	8	3.1	2.7–3.8	0.3	8	10.1	7.1–13.4	2.1
Rhinoclemys rubida	1	70.0			1	3.9			1	7.1		
Chrysemys floridana	7	91.7	76–118	12.9	5	4.8	4.5–5.1	0.2	7	8.7	6.6–10.5	1.1
Chrysemys picta	22	57.4	33–73	10.7	22	4.5	3.6–5.5	0.4	23	7.9	5.9–10.1	1.2
Chrysemys scripta	10	52.6	32–83	15.0	8	4.5	4.3–4.7	0.1	10	8.1	7.3–8.8	0.5
Clemmys guttata	4	50.2	46–57	4.8	5	4.9	4.6–5.3	0.3	5	5.8	5.3–6.2	0.4
Clemmys insculpta	7	101.6	91–111	7.1	7	4.7	4.4–5.0	0.2	7	7.1	6.4–8.1	0.6
Clemmys marmorata	7	56.7	41–66	8.7	7	5.0	4.5–5.3	0.3	8	8.4	6.8–11.2	1.6
Emydoidea blandingi	10	55.0	49–64	6.1	10	3.4	3.3–3.5	0.1	11	7.0	6.0–8.2	0.7
Malaclemys geographica	5	69.6	59–81	10.1	2	5.6	5.5–5.7		4	10.1	8.6–12.3	1.5
Malaclemys terrapin	3	45.0	39–54	7.9	4	4.4	4.3–4.6	0.1	4	8.5	7.2–10.9	1.7
Terrapene carolina	16	98.8	79–117	11.1	15	4.3	3.7–5.1	0.4	16	6.4	5.2–8.2	0.7
Terrapene ornata	9	99.6	84–116	11.9	11	4.6	4.1–4.9	0.3	11	7.4	5.6–9.2	1.1
Platysternon megacephalum	1	34.0			1	4.1			1	9.7		
Gopherus berlandieri	4	103.2	87–117	13.1	3	3.9	3.8–4.1	0.2	5	7.8	5.7–9.1	1.3
Gopherus polyphemus	4	71.2	50–95	18.5	5	2.6	2.4–2.8	0.2	4	9.6	7.4–11.6	1.8
Kinixys erosa	4	90.2	75–99	10.6	3	4.5	4.4–4.7	0.2	4	6.6	6.0–7.6	0.7
Claudius angustatus	2	33.0	31–35		2	2.9	2.7–3.1		2	8.3	8.0–8.5	
Kinosternon flavescens	10	54.3	35–65	8.4	11	3.4	3.2–3.7	· 0.2	13	9.2	7.5–11.8	1.3
Sternothaerus odoratus	19	55.7	29–73	10.2	18	3.4	3.1–3.8	0.2	19	8.1	6.2–11.7	1.3
Trionyx muticus	2	58.5	57–60		2	3.8	3.4–4.1		2	9.0	8.1–9.9	
Trionyx spinifer	4	60.5	54–71	7.4	2	2.8	2.8		4	8.0	7.3–8.7	0.7

Pectineal process angles (PpA), femoral length to eighth cervical centrum length ratios (FL/CCL), and femoral length to femoral height ratios (FL/FH). Statistical abbreviations explained in Table 5, morphological abbreviations and ratios in Appendix IV.

tation is accomplished by the articular face of the ischium being parallel to the body axis and the face of the pubis approaching a perpendicular orientation. The ilial articular surface increases in area and develops a large overhang posteriorly. The edge of the acetabulum is notched at the three symphyses, puboilial, puboischial, and ischioilial. Elaboration of an ischioilial notch occurs in kinosternids and of a puboilial notch in testudinines.

Two other authors (Baur, 1891a; Ruckes, 1929) have examined the chelonian pelvis in a large number of taxa. Baur's study pertains entirely to the structure of the puboischiadic plate and especially to the medial puboischial symphysis and cartilaginous portion of the plate, the gastroids. My observations are in agreement with his except that I observed no medial puboischial contact in the kinosternines but a bridge of calcified cartilage. Nor can I concur with his statement that the epipubis does not ossify in the emydines, but instead is replaced by the pubis. The texture and appearance of the calcified epipubis in *Clemmys, Emydoidea,* and *Terrapene* are characteristic of calcified cartilage.

Ruckes analysed the structure of the chelonian pelvis as a secondary multiple truss or arch, and he attempted to correlate structural variation with mode of locomotion (terrestrial, palustral, aquatic). In his discussion of the inclination of the ilium, he suggested that a vertical ilium is associated with terrestrial habits, and a posteriorly inclined ilium with swimming habits. According to my observations, this is only partially correct, because all the testudinids tend to have a nearly vertical ilium, and at least half of these are true swimmers. In contrast, the chelydrids and kinosternids have inclined ilia, and although they are aquatic they are bottom-walkers. Another structural modification that Ruckes presumed to be associated with the principal locomotion environment was the height of the puboischiadic arch, high and narrow arches in terrestrial taxa and low and wide arches in aquatic taxa. As previously shown, the height of the arches is not significantly different in terrestrial and aquatic turtles, but the puboischiadic plate tends to be longer in aquatic taxa. Ruckes also suggested that in terrestrial testudinids the puboischiadic plate is bowed transversely. I observed no transverse arch, and the width of the plate, WA/CCL, (Table 6) offers no indication of such an arch in these turtles.

HINDLIMB.—The chelonian femur consists basically of a cylindrical shaft with an oval head arising dorsally from its proximal end. Proximally on either side of the head, the shaft forms large trochanters, an anterior trochanter minor and a posterior trochanter major. A large intertrochanteric fossa lies ventrally between the trochanters. Distally, the shaft is expanded into a posterior fibular condyle and an anterior tibial condyle. The femoral shaft is arched dorsally.

The length of the femur FL/CCL (Table 7) does not appear to be correlated with mode of locomotion or taxonomic groupings. There are, however, two general classes of femoral length, i.e., < 4.0 and > 4.0, in which little overlap exists. Both classes contain swimming and terrestrial

members, but class $<$ 4.0 contains all the bottom-walkers except *Platysternon,* which is close to the division line. This indicates that those taxa with mainly vertical rotation of the hindlimbs tend to have shorter propodia.

A comparison of the bowing of the femur, FL/FH (Table 7), presents a more obscure pattern than does femoral length. The range of variation is so great that any attempt to interpret the data seems futile. This extensive variation may be attributed, in part, to the mensural technique (Appendix IV).

The shape of the femoral head varies from circular through oval to spheroidal (Fig. 11). A circular, or at least a nonelongate, head is restricted to the kinosternids and chelydrids. The FHW/FHL, head width to length, value (Table 8) for a completely circular head is 1.0. The heads of the former two families approach this value as do those of a few testudinines. In the testudinids and trionychids, the femoral head is elongated in a proximodistal axis; however, the elongation does not occur through the longitudinal axis of the head but along a diagonal axis from proximoposterior to distoanterior corner. The circular head appears to be associated with walking, since the chelydrids and kinosternids are bottom-walkers, and the testudinines are terrestrial. The condition in *Terrapene* supports this association. Presumably, *Terrapene* is derived from an aquatic ancestor. Its femoral head is the least elongate of any emydines, although probably derived from an elongate condition as are those of the testudinines.

The head of the femur does not extend perpendicularly from the shaft but at a slight proximal inclination. I have not measured this angle since the curvature of the shaft prevented the establishment of a suitable base. The kinosternines and testudinines seem to approach a perpendicular condition, but this cannot be supported presently with measurements.

Generally, the femoral trochanters are not the same size (Fig. 11). In Table 8, the trochanter width ratio (WMi/WMa) falls into two classes $\geqq$ 1.1 or $\leqq$ 0.9. There is some overlap between the two classes, but it is slight. The class $\geqq$ 1.1 is characteristic of the testudinids and indicates that the trochanter minor is the larger. In the chelydrids, kinosternids, and trionychids, the ratio is less than 1 and the trochanter major is the larger. Another indication of trochanter size is the width of the proximal end of the femur, PW/CCL (Table 8). The range of variation of this ratio prevents a division into classes; however, low means are associated with walking taxa, either terrestrial or bottom-walkers, and high means with swimmers. In addition to indicating size, this ratio also expresses the degree of tro-chanteric flaring. In the testudinines, the trochanters are small and generally do not extend beyond the sides of the femoral head. The kinosternids and *Terrapene* have slightly larger trochanters with only a slight flare. Swimmers have the largest trochanters and the greatest flare, particularly the trionychids. This suggests that as the major limb movements become more horizontal, the trochanters become larger with a greater flare.

The intertrochanteric fossa lies ventrally between the trochanters. The extent of this fossa varies interfamilially. The LIF/LTM ratio, relative
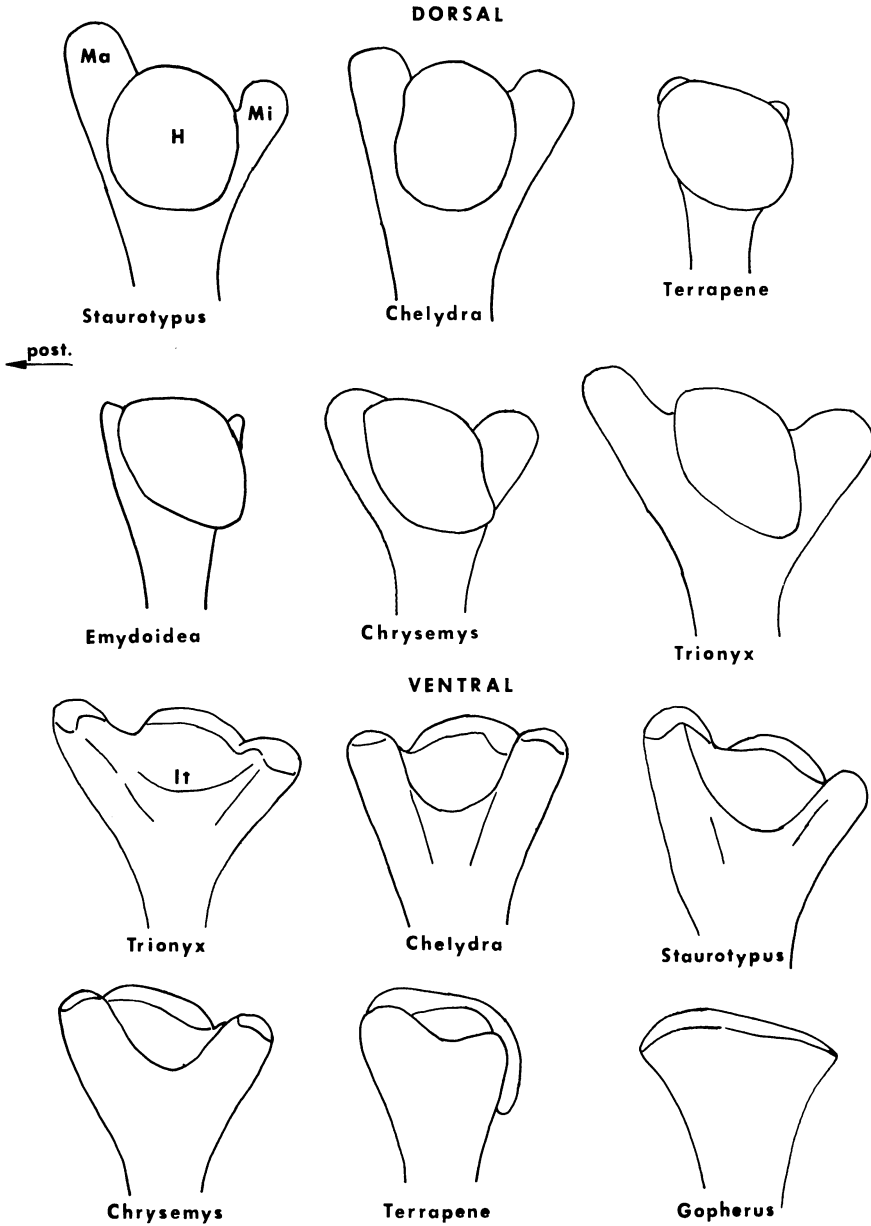
FIG. 11. The range of variation in the proximal end of the femur. The upper two rows are dorsal views, the bottom two rows, ventral views. H, femoral head; It, intertrochanteric fossa; Ma, trochanter major; Mi, trochanter minor; post, postaxial.

TABLE 8

MEASUREMENTS AND RATIOS OF THE FEMUR AND ITS HEAD

Species	FHW/FHL				WMi/WMa				PW/CCL			
	N	$\overline{x}$	Range	s	N	$\overline{x}$	Range	s	N	$\overline{x}$	Range	s
Chelydra serpentina	8	0.8	0.7–0.9	0.07	8	0.9	0.8–1.0	0.08	8	1.0	0.9–1.4	0.03
Rhinoclemys rubida	1	0.8			1	1.6			1	1.1		
Chrysemys floridana	7	0.6	0.6–0.7	0.04	7	1.5	1.3–1.7	0.13	5	1.5	1.4–1.6	0.09
Chrysemys picta	23	0.7	0.6–0.8	0.03	23	1.4	1.1–1.8	0.19	22	1.3	1.1–1.7	0.15
Chrysemys scripta	11	0.6	0.5–0.6	0.03	11	1.7	1.3–1.9	0.20	8	1.3	1.2–1.4	0.09
Clemmys guttata	5	0.7	0.7–0.8	0.01	5	1.3	1.1–1.4	0.14	5	1.3	1.2–1.4	0.09
Clemmys insculpta	8	0.7	0.6–0.7	0.03	8	1.6	1.2–1.9	0.23	7	1.2	1.2–1.3	0.05
Clemmys marmorata	8	0.7	0.6–0.7	0.04	8	1.3	1.2–1.5	0.13	7	1.3	1.1–1.5	0.12
Emydoidea blandingi	11	0.7	0.7–0.8	0.09	11	1.4	1.2–1.6	0.12	10	0.8	0.7–0.9	0.05
Malaclemys geographica	4	0.6	0.6	0.02	4	1.7	1.5–1.8	0.13	2	1.5	1.5–1.6	
Malaclemys terrapin	4	0.6	0.6–0.7	0.04	4	1.5	1.4–1.7	0.12	4	1.4	1.4	0.04
Terrapene carolina	16	0.7	0.7–0.8	0.05	16	1.5	1.2–2.0	0.21	16	1.1	0.8–1.3	0.12
Terrapene ornata	11	0.7	0.7–0.8	0.05	11	1.5	1.2–1.9	0.22	10	1.1	1.0–1.2	0.06
Platysternon megacephalum	1	0.7			1	1.3			1	1.2		
Gopherus berlandieri	5	0.8	0.7–0.8	0.04	5	1.5	1.2–2.1	0.33	3	1.2	1.1–1.2	0.02
Gopherus polyphemus	5	0.7	0.7–0.8	0.03	4	1.1	1.0–1.3	0.10	4	0.9	0.8–1.0	0.06
Kinixys erosa	4	0.7	0.6–0.8	0.06	4	1.1	0.8–1.5	0.30	3	1.1	1.0–1.1	0.06
Claudius angustatus	2	0.9	0.9–1.0		2	1.0	0.8–1.2		2	0.8	0.8	
Kinosternon flavescens	12	0.9	0.9–1.0	0.04	13	0.8	0.8–0.9	0.05	11	0.9	0.9–1.0	0.04
Sternothaerus odoratus	20	0.8	0.7–1.0	0.07	20	0.9	0.8–1.2	0.11	18	0.9	0.8–1.0	0.07
Trionyx muticus	2	0.6	0.6–0.7		2	0.9	0.9		2	1.4	1.2–1.6	
Trionyx spinifer	4	0.6	0.6–0.7	0.03	4	0.8	0.8–0.9	0.07	2	1.1	1.1	

Femoral head width to femoral head length ratios (FHW/FHL), trochanter minor width to trochanter major width ratios (WMi/WMa), and proximal width of femur to eighth cervical centrum length ratios (PW/CCL). Statistical abbreviation explained in Table 5, morphological abbreviations and ratios in Appendix IV.

length of fossa, yields an estimate of its size (Table 9). The trionychids have the largest fossa with a ratio range of 0.72 to 0.80, the chelydrids and kinosternids a range of 0.80 to 0.88, and the testudinids a range of 0.86 to 1.00. Terrestrial species usually have the fossa closed ventrally. The functional significance of fossa size is obscure. On the basis of the taxa examined, it would be possible to suggest the association of an enclosed fossa with terrestrial walking; however, Zangerl (1953) points out that sea turtles possess an enclosed fossa.

The distal end of the femoral shaft is slightly compressed and widened. Distally, the shaft is divided into an anterior tibial condyle and a posterior fibular condyle by a weak intercondylar fossa. This fossa is frequently absent. Aside from a shallow fossa for the flexor digitorum longus muscle ventrally on the fibular condyle, the condyles possess a smooth surface. The trochlear articular surface covers the entire distal end of the femur and extends onto the distoventral surface. The articular surface is smooth and convex in most turtles; however, in *Terrapene* and the kinosternids, the distoventral edge is elevated and cornice-like.

The epipodial elements of cryptodires are subequal in length (Fig. 20). In Table 9, the tibia to femur length ratio, TL/FL, provides a comparison for epipodial length among the taxa. No overall taxonomic or functional pattern is obvious. The aquatic testudinids tend to have shorter epipodial segments, terrestrial ones longer segments. On the other hand, the highly aquatic trionychids have the epipodium nearly as long as the terrestrial testudinids, and the bottom-walking chelydrids and kinosternids are intermediate between the aquatic testudinids and the trionychids.

The anterior element, the tibia, is a more robust bone than the fibula. The tibia is triangular in cross-section. The fibula is generally a flattened splint, but occasionally it is nearly cylindrical. The general form of the tibia is spool-shaped, although the distal enlargement is only half that of the proximal end. The tibia is relatively straight, albeit in a few specimens, there is an indication of a very weak dorsal curvature. A median longitudinal ridge, the cnemial crest, extends down the dorsum of the tibia, gradually flattening distally. The cnemial crest is sharpest in the trionychids and weakest in the testudinines. Proximally, the tibia articulates with the tibial and fibular condyles. The articular surface is triangular and weakly biconcave on the ventral half. The articular surfaces of the femur and tibia give the strong impression that the dorsal halves of the articular surface rarely come in contact. Distally, the tibia articulates with the astragulocalcaneum by means of a saddle-shaped joint. A projection extends from the tibia along the anterior face of the astragulocalcaneum. This projection is similar to the medial malleolus of mammals.

The fibula has the shape of a golf tee; the distal end is the larger. The fibula is relatively straight, and because of its flatness proximally, it has dorsal and ventral longitudinal ridges along the proximal half, particularly in the trionychids. Unlike the tibia, the proximal articulation abuts against only the posterior edge of the fibular condyle. Its articular

TABLE 9

MEASUREMENTS AND RATIOS OF THE TIBIA

Species	LIF/LTM				TL/FL				ML/TL			
	N	x̄	Range	s	N	x̄	Range	s	N	x̄	Range	s
Chelydra serpentina	8	0.84	0.81–0.87	0.02	8	0.76	0.74–0.79	0.02	8	0.30	0.25–0.32	0.02
Rhinoclemys rubida	1	0.92			1	0.77			1	0.30		
Chrysemys floridana	7	0.88	0.86–0.90	0.01	6	0.69	0.65–0.75	0.03	6	0.37	0.33–0.44	0.04
Chrysemys picta	23	0.89	0.86–0.92	0.01	23	0.68	0.64–0.73	0.02	23	0.35	0.30–0.40	0.03
Chrysemys scripta	10	0.89	0.87–0.91	0.01	9	0.70	0.66–0.73	0.02	10	0.37	0.35–0.38	0.01
Clemmys guttata	5	0.90	0.89–0.92	0.01	5	0.69	0.67–0.71	0.01	5	0.35	0.34–0.39	0.02
Clemmys insculpta	8	0.88	0.86–0.90	0.02	8	0.67	0.65–0.69	0.01	6	0.36	0.34–0.37	0.01
Clemmys marmorata	8	0.88	0.86–0.91	0.02	7	0.73	0.70–0.77	0.03	5	0.38	0.36–0.42	0.02
Emydoidea blandingi	11	0.90	0.88–0.92	0.01	11	0.68	0.60–0.72	0.03	10	0.32	0.30–0.35	0.02
Malaclemys geographica	4	0.88	0.87–0.90	0.02	4	0.71	0.69–0.73	0.02	4	0.37	0.37–0.38	0.01
Malaclemys terrapin	4	0.87	0.87–0.88	0.005	4	0.75	0.73–0.78	0.02	3	0.38	0.36–0.39	0.01
Terrapene carolina	16	0.92	0.90–0.94	0.01	12	0.77	0.73–0.81	0.06	14	0.32	0.28–0.40	0.03
Terrapene ornata	11	0.98	0.96–0.99	0.01	11	0.79	0.75–0.82	0.02	8	0.33	0.31–0.37	0.02
Platysternon megacephalum	1	0.88			1	0.70						
Gopherus berlandieri	5	0.99	0.98–1.00	0.01	5	0.79	0.78–0.83	0.02	4	0.15	0.13–0.19	0.05
Gopherus polyphemus	5	0.98	0.96–0.99	0.01	5	0.80	0.78–0.83	0.02	4	0.14	0.13–0.14	0.02
Kinixys erosa	4	0.97	0.96–0.97	0.002	4	0.87	0.84–0.90	0.02	3	0.17	0.16–0.19	0.04
Claudius angustatus	2	0.83	0.82–0.83		2	0.75	0.75–0.76		2	0.39	0.36–0.42	
Kinosternon flavescens	13	0.83	0.81–0.85	0.01	13	0.75	0.71–0.78	0.02	5	0.31	0.27–0.33	0.02
Sternothaerus odoratus	20	0.86	0.80–0.88	0.02	20	0.74	0.70–0.77	0.04	16	0.32	0.28–0.34	0.02
Trionyx muticus	2	0.78	0.77–0.78		2	0.79	0.78–0.81		2	0.42	0.39–0.46	
Trionyx spinifer	4	0.76	0.72–0.80	0.03	4	0.79	0.78–0.80	0.01	3	0.44	0.38–0.53	0.08

Relative length of intertrochanteric fossae (LIF/LTM), tibial length to femoral length ratios (TL/FL), and metatarsal length to tibial length ratios (ML/TL). Statistical abbreviations explained in Table 5, morphological abbreviations and ratios in Appendix IV.

surface is small, oval, and convex. The distal articular face is equal to that of the tibia; it is triangular and varies from flat to slightly convex. The tibia and fibula are in contact medially at both the proximal and distal joints. The complex articular surfaces of the fibula, tibia, and astragulocalcaneum suggest that the crurotarsal joint is not very flexible.

The chelonian tarsus may consist of seven elements, proximally the astragulus and the calcaneum, medially the centrale, and distally the four tarsalia or (distal tarsals). Four tarsalia were present in all cryptodires examined, and the pattern of the first three tarsalia sub-equal in size and distinctly smaller than the fourth is nearly invariable.

The condition of the astragulus, calcaneum, and centrale varies (Fig. 12). In the chelydrids, the three elements are usually separate and distinct, although in older individuals there appears to be fusion into a single element with the suture lines remaining distinct. Only two elements, the astragulus and the calcaneum, were observed in the testudinids, kinosternids, *Dermatemys,* and *Carettochelys.* In none of these taxa is there any indication of a centrale, nor evidence to support fusion as opposed to loss. The astragulus and calcaneum can be fused or separate in the above taxa. This condition varies intraspecifically and may be, in part, associated with age. In trionychids, a single element is present. This element is definitely the astragulus and does not appear to be a fused astragulocalcaneum complex. X-rays of young *Trionyx* do not show two proximal ossification centers, which suggests that the calcaneum is lost.

From the preceding discussion, it appears that the trend in the proximal tarsal elements has been one of reduction. The arrangement of tarsal elements (Fig. 12) and the lack of suture planes in hatchlings suggest that reduction is occurring by loss and not by fusion. This supposition must be confirmed by embryological studies. The presence of three proximal tarsal elements in some pleurodires, *Batrachemys, Chelys, Pelusios,* and *Phrynops,* strongly indicates that this is the primitive condition and supports Schaeffer's (1941) interpretation. It seems likely that the reduction of a proximal tarsal element would be in some way associated with locomotion; however, this correlation cannot be made presently. In Figure 12, a taxonomic distribution of tarsal arrangements is presented: chelydrids, kinosternids, and some testudinids are bottom walkers; trionychids, *Carettochelys,* and most aquatic testudinids are swimmers.

Although there is no exact functional correlation with the reduction of proximal tarsal elements, it is probably associated with the improvement of the mesotarsal joint in the pes. Schaeffer (1941) discussed the shift from a crurotarsal to a mesotarsal joint in the chelonian pes. The extensive articular surface on the distal end of the proximal tarsal elements attests to the importance of the mesotarsal joint. This is not, however, the only pedal joint. The surfaces of the tarsalia seem to be almost completely articular. X-rays of preserved specimens indicate a strong flexure between the tarsalia and metatarsals, especially for the anterior three tarsalia and meta-
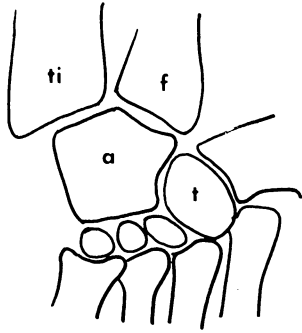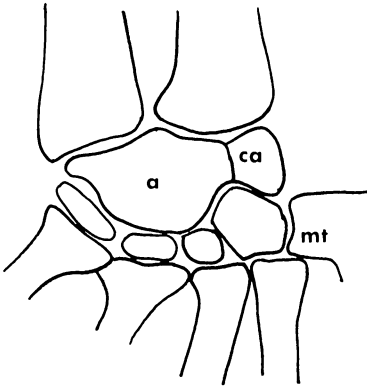
FIG. 12. The three patterns of tarsal arrangements in cryptodires, exclusive of sea turtles. a, astragulus; ca, calcaneum; ce, centrale; f, fibula; mt, metatarsal; pre, preaxial; t, tarsale; ti, tibia.

tarsals. Thus, both a mesotarsal and a tarsometatarsal joint appear to be functional in the cryptodiran pes.

All cryptodires possess five metatarsal elements. The first four metatarsals are typical digital elements, being cylindrical with slightly expa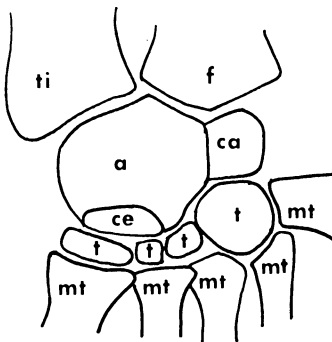nded proximal and distal ends. In contrast, the fifth metatarsal is depressed dorsoventrally and is rectangular in outline. The lengths of the metatarsals are not equal: *Chelydra*, 2=3=4>1=5; *Damonia*, 2=3=4>1>5; *Rhinoclemys*, 2=3≤4>1=5; *Chrysemys*, 2=3=4>1>5; *Clemmys*, 2=3>4>1>5; *Emydoidea*, 2=3>4≤1>5; *Malaclemys*, 2=3=4>5>1; *Terrapene*, 2=3>1>4≤5; *Platysternon*, 2=3=4>1≤5; *Gopherus*, 2=3=4>1≤5; *Kinixys*, 3>2>1=4=5; *Dermatemys*, 1=2=3=4>5; *Claudius*, 2=3=4>1=5; *Kinosternon*, 2=3=4>1≤5; *Staurotypus*, 2>3>4>1≤5; *Sternothaerus*, 2=3=4>1≤5; *Carettochelys*, 2=3=4 >1>5; *Lissemys*, 4>3>2>1>5; *Trionyx*, 4>3>2>1>5. Although these metatarsal formulae are not based on mensural data, the formulae illustrate variation within and between individuals. It should also be noted that the most common formula, 2=3=4>1≤5, occurs equally in terrestrial and in aquatic taxa and that only *Kinixys* and the trionychids have a very different pattern. The constancy of the formula prevents any taxonomic or functional interpretation.

Unlike the metatarsal formulae, ·a comparison of the lengths of the second metatarsals by the metatarsal length to tibia length ratio, ML/TL, (Table 9) demonstrates a functional and taxonomic correlation. The testudinines have the lowest ML/TL ratios, 0.13–0.19, which indicate a reduction in metatarsal length with adaptation to terrestrial locomotion. The next cluster of ratios, around 0.31, are of bottom-walking, semiaquatic, and terrestrial species; the terrestrial species are *Terrapene*. In comparison to the testudinines, *Terrapene* is thought to be a relatively recent terrestrial group. A cluster of ratios around 0.36 is formed by aquatic and semiaquatic testudinids. In the trionychids, the ML/TL ratio has its highest mean value, 0.44. The trend is for the metatarsals to increase in length with the shift from terrestrial walking to swimming.

As stated previously, there appears to be a tarsometatarsal joint in addition to the mesotarsal joint. Generally, the articulation between the tarsale and metatarsal is of the following pattern. Metatarsal I articulates with tarsale I, metatarsal II with tarsalia II and III, metatarsal III with tarsalia III and IV, metatarsal IV with tarsale IV and proximoanterior edge of metatarsal V, and metatarsal V with posterior edge of tarsale IV. This pattern is typical of all families examined. Even though the above pattern is common to all taxonomic and locomotor divisions, there is a tendency for the proximal bases of the metatarsal to develop an anteroposterior overlap with increasing aquatic habitats. The terrestrial testudinines have very little or no overlap, the bottom-walking chelydrids and kinosternids weak overlap, and the aquatic emydines and especially the trionychids strong overlap.

The primitive phalangeal formula of cryptodires (Table 10) appears to be 2, 3, 3, 3, 3. This formula is possessed by members of the chelydrids, testu-

TABLE 10
PHALANGEAL FORMULAE OF THE PES

Taxon					
Chelydridae					
Chelydra	2,	3,	3,	3,	3
Macroclemys	2,	3,	3,	3,	3
Testudinidae					
Batagurinae					
Damonia	2,	3,	3,	3,	3
Mauremys	2,	3,	3,	3,	3
Rhinoclemys	2,	3,	3,	3,	2
Emydinae					
Chrysemys	2,	3,	3,	3,	3 or 4
Clemmys	2,	3,	3,	3,	3
Deirochelys	2,	3,	3,	3,	3
Emydoidea	2,	3,	3,	3,	2
Malaclemys	2,	3,	3,	3,	4
Terrapene	2,	3,	3,	2 or 3,	1 or 2
Platysterninae					
Platysternon	2,	3,	3,	3,	2
Testudininae					
Geochelone	2,	2,	2,	2,	1
Gopherus	2,	2,	2,	2,	0 or 1
Kinixys	2,	2,	2,	2,	1
Dermatemydidae					
Dermatemys	2,	3,	3,	3,	4
Kinosternidae					
Kinosterninae					
Kinosternon	2,	3,	3,	3,	3
Sternothaerus	2,	3,	3,	3,	3
Staurotypinae					
Claudius	2,	3,	3,	3,	2 or 3
Staurotypus	2,	3,	3,	3,	3
Carettochelydidae					
Carettochelys	2,	3,	3,	3,	3
Trionychidae					
Trionychinae					
Pelochelys	2,	3,	3,	4,	3
Trionyx	2,	3,	3,	4,	3
Lissemyinae					
Lissemys	2,	3,	3,	4,	3

Italicized numbers indicate the presence of a keratinous claw cone on the ultimate phalanx.

dinids, kinosternids, and carettochelydids. Two morphological trends are evident. A reductional trend occurs in the testudinids in association with terrestrial locomotion. Commonly, the tortoises or testudinines have a formula of 2,2,2,2,1. In *Gopherus,* all the phalanges of the fifth toe may be lost. In *Terrapene,* a terrestrial emydine, there is a reduction of the phalanges in the fourth and fifth toes. *Emydoidea, Platysternon,* and *Rhino-*

clemys have lost a phalanx of the fifth toe; these genera are either semiaquatic or bottom-walkers. Two distinct multiplication trends are evident and are associated with swimming taxa. The trionychids have added a phalanx to the fourth toe, and *Chrysemys, Malaclemys,* and *Dermatemys* have added a phalanx to the fifth toe.

In Table 11, the PhL/CCL ratio provides a comparison for the variation in phalangeal length from taxon to taxon. If we consider the means, it is possible to erect three classes, >0.77, <0.69–>0.40, and <0.30. All members of the first class except *Claudius* are swimmers and showed hyperphalangy. The middle class contains swimmers, bottom-walkers, and terrestrial forms. Their phalangeal formula is usually 2, 3, 3, 3, 3 to 1. Only *Gopherus polyphemus* illustrates a length reduction. A similar reduction would be expected in other tortoises, since they all have elephantine hindlimbs.

The PhL/ML ratio (Table 11) records the proportional length of the proximal phalanx and the metatarsal. In the testudinines, kinosternids, and trionychids, the metatarsal and proximal phalanx are nearly equal in length. In the remaining taxa, the proximal phalanx is approximately half as long as the metatarsal. This distribution cannot be logically explained on a taxonomic or a functional basis.

The general form of the phalanges is like that of the metatarsals, i.e., cylindrical with expanded ends. Only the ultimate phalanges vary from this basic shape, and they are conic. The conic shape is associated with their role as claw cores. The chelydrids, testudinids, *Dermatemys,* and kinosternids possess four claws, the trionychids three, and *Carettochelys* two. The fifth toe always lacks a claw. As claw loss occurs, it proceeds anteriorad. Another feature of phalangeal morphology that is usually restricted to the proximal phalanges is the development of proximoventral shelves (phalangeal condyles of Boulenger?) extending under the distal ends of the metatarsals. The presence of these shelves varies intraspecifically, and thus does not permit a functional or taxonomic interpretation.

Since Zangerl (1953) showed proportional differences in the length of fore- and hindlimbs between fresh-water and sea turtles, an attempt was made to determine if the length of hindlimb was associated with locomotor habits of cryptodires. The relative length of hindlimbs, FL+TL+ML+PhL/CCL, (Table 11) was determined. The intraspecific range of variation for this ratio is so large that it is impossible to draw any definite conclusions.

Historical Résumé: To the best of my knowledge, there are no published studies of comparative hindlimb osteology of cryptodires. This is especially true for the propodial and epipodial elements. Zangerl (1953) is the only author who has presented any comparative data for these elements, and unfortunately he examined few taxa and usually only one specimen of each. I have found no exceptions to his observations on the propodial and epipodial elements of the hindlimb, and frequently I have obtained mensural support for his observations.

TABLE 11

MEASUREMENTS AND RATIOS OF THE PHALANGES AND LIMBS

Species	PhL/CCL				PhL/ML				FL+TL+ML+PhL/CCL			
	N	x̄	Range	s	N	x̄	Range	s	N	x̄	Range	s
Chelydra serpentina	7	0.51	0.41–0.69	0.09	7	0.74	0.66–0.87	0.07	7	6.5	5.8–8.3	0.8
Rhinoclemys rubida	1	0.42			1	0.47			1	8.2		
Chrysemys floridana	3	0.96	0.79–1.16	0.19	5	0.79	0.68–0.91	0.09	3	10.5	10.0–10.8	0.4
Chrysemys picta	20	0.78	0.59–0.94	0.08	22	0.73	0.62–0.81	0.04	20	9.4	7.8–11.5	0.9
Chrysemys scripta	7	0.79	0.71–0.92	0.07	8	0.68	0.65–0.77	0.04	6	9.6	9.1–10.1	0.4
Clemmys guttata	5	0.67	0.60–0.84	0.10	5	0.56	0.51–0.64	0.06	5	10.1	9.6–10.7	0.5
Clemmys insculpta	3	0.68	0.53–0.77	0.10	4	0.59	0.54–0.65	0.05	3	9.6	8.8–10.2	0.8
Clemmys marmorata	4	0.90	0.85–1.00	0.07	5	0.63	0.60–0.68	0.04	4	10.9	10.2–11.4	0.6
Emydoidea blandingi	9	0.46	0.42–0.51	0.09	10	0.61	0.54–0.71	0.05	9	7.0	6.7–7.3	0.2
Malaclemys geographica	2	1.07	0.97–1.17		4	0.73	0.66–0.78	0.05	2	12.3	12.0–12.6	
Malaclemys terrapin	2	0.86	0.85–0.86		2	0.68	0.63–0.72		2	10.0	9.8–10.3	
Terrapene carolina	13	0.64	0.51–0.75	0.08	13	0.58	0.52–0.63	0.04	13	9.6	8.6–11.6	0.9
Terrapene ornata	8	0.66	0.50–0.77	0.08	8	0.55	0.49–0.62	0.04	8	10.1	8.8–11.1	0.7
Platysternon megacephalum												
Gopherus berlandieri	3	0.51	0.46–0.56	0.04	4	1.09	0.98–1.17	0.08	3	8.0	7.7–8.5	0.4
Gopherus polyphemus	4	0.26	0.24–0.28	0.02	4	0.94	0.90–1.00	0.04	4	5.1	4.8–5.3	0.2
Kinixys erosa	2	0.61	0.55–0.67		3	0.87	0.85–0.89	0.02	2	9.7	9.4–9.9	
Claudius angustatus	2	0.78	0.68–0.87		2	0.90	0.87–0.93		2	6.8	6.2–7.4	
Kinosternon flavescens	5	0.52	0.47–0.61	0.06	5	0.66	0.59–0.70	0.04	5	7.3	6.8–7.9	0.4
Sternothaerus odoratus	13	0.65	0.58–0.74	0.06	14	0.82	0.76–0.90	0.05	13	7.2	5.8–8.1	0.7
Trionyx muticus	2	1.09	1.03–1.15		2	0.87	0.86–0.88		2	9.1	8.3–9.9	
Trionyx spinifer	2	0.88	0.86–0.89		3	0.94	0.84–1.02	0.08	2	6.8	6.7–7.0	

Phalangeal length to eighth cervical centrum length ratios (PhL/CCL), phalangeal length to metatarsal length ratios (PhL/ML), and limb length to eighth cervical centrum length ratios (FL + TL + ML + PhL/CCL). Statistical abbreviations explained in Table 5, morphological abbreviations and ratios in Appendix IV.

Although the osteology of the pes has attracted more attention, the scope of such studies is frequently limited to observations on a few crypto-dires and a comparison to other reptiles. The morphology of the chelonian tarsus was discussed by Baur (1885), Hoffman (1890), and Schaeffer (1941). Hoffman described the ontogeny of the tarsus in approximately 10 genera, in which he followed a terminology he had published earlier. This terminology was in error as demonstrated by Baur (1885). In Schaeffer's (1941) classic study of the evolution of the tetrapod tarsus, he appears to have restricted his observations on the chelonian tarsus to two cryptodiran genera. He demonstrated the presence of a mesotarsal joint but did not mention a tarsometatarsal joint which I have described above. None of the three authors attempted to draw a taxonomic conclusion from their observations on turtles.

Baur (1887), Boulenger (1889), Hoffman (1890), and Zangerl (1953) discuss the phalangeal formulae of various cryptodires. Baur gave a formula 2, 3, 3, 4–5, 4 for trionychids. Boulenger showed that this formula is common only for the forelimb. Hoffman gave 2, 3, 3, 4, 2 for trionychids and 2, 3, 3, 3, 1 for emydines. His low numbers for the fifth toe probably resulted from the small terminal phalanges having been lost during the skeletal preparation. Zangerl reported four instead of three phalanges on the fifth toe of *Chelydra*. Although I never observed more than three, the variation in this toe in other genera may account for the additional phalanx, but 2, 3, 3, 3, 3 is typical for *Chelydra*. Zangerl also stated that fresh-water turtles bear claws on the first three toes. This is true only for the trionychids, but most other turtles have claws on the first four toes.

PRÉCIS.—The ilium of trionychids does not articulate dorsally with the pleurals as in other cryptodires. The articulation on the pleural is usually bordered anteromedially by a tuberosity. Medially, the ilium articulates with the two sacral ribs. Ventrally, the pelvis rests on the plastron along the posterior edge of the ischium and the pectineal processes.

The shape of the ilium in lateral aspect falls into two classes. The chelydrids and testudinids have spool-shaped ilia; the kinosternids, *Dermatemys,* and trionychids have inverted tee-shaped ilia. The anterior edge of the ilium bears a thelial process in the kinosternids; all other taxa lack this process.

The longitudinal inclination of the ilium ranges from 80° to 160°. In most testudinids, the ilium is nearly perpendicular. *Chelydra, Emydoidea,* and *Kinixys* possess an ilial inclination of approximately 120°. The kinosternids and trionychids have a strongly inclined ilium of about 150°. The length of the ilium is proportionately similar in all cryptodires.

Differences in the height of puboischiadic arches are more apparent than real. The appearance results from a shortening of the entire pubo-ischiadic plate in association with development of a vertical ischium.

In trionychids, there are no medial pubic or ischial extensions which create paired puboischiadic foramina. The staurotypines have very small

extensions. The chelydrids and kinosternines have larger extensions, but these are not in contact. In the testudinids, large pubic and ischial extensions are in contact or separated by a narrow hiatus.

The metischial process may not be a homologous structure at the familial level. The pectineal process is present in all cryptodires and there is a tendency in terrestrial species for it to be perpendicular to the body axis.

There is an indication that walking taxa tend to have proportionately shorter femora. The femoral head is least elongated in the chelydrids and kinosternids. In general, the swimming taxa tend to have the greatest elongation of the head. Testudinids have the trochanter minor larger than the major; the major is the larger in the chelydrids, kinosternids, and trionychids. Trochanters are largest in the swimming taxa. Of the cryptodires examined, the terrestrial testudinids have the greatest reduction of the intertrochanteric fossa. The tibia and fibula are subequal in length.

The proximal tarsal elements show three patterns. Chelydrids have three distinct elements, astragulus, calcaneum and centrale. Two elements, astragulus and calcaneum, are observed in the testudinids, kinosternids, *Dermatemys,* and *Carettochelys.* These elements may be fused or separate. In the trionychids, the proximal tarsal element appears to be composed of only the astragulus. The main pedal joint is the mesotarsal joint; however, a tarsometatarsal joint also appears to be functional.

All cryptodires have five metatarsals. The lengths of the metatarsals in most species follow this formula, $2=3=4>1\lesssim5$. There is a tendency for the metatarsals to become proportionately larger with the shift from terrestrial locomotion to swimming.

The primitive phalangeal formula in cryptodires is probably 2, 3, 3, 3, 3. Terrestrial taxa tend to reduce the number of phalanges and swimming taxa to increase the number. Swimming taxa usually have the longest phalanges.

A Prim Network, a type of phenogram, (Fig. 13) was generated by using the values in Tables 5 to 11 (for the concept of the Prim Network, see Prim, 1957;the computer program used to generate the networks herein was developed by James S. Farris, State University of New York, Stony Brook.) On the basis of these limited osteological data, an interesting phenetic clustering was obtained. The testudinids, kinosternids, and trionychids were each linked as a natural group. The terrestrial members of the testudinids are clustered with the exception of *Gopherus polyphemus.* *Chelydra* is more similar to *Platysternon* than to any other taxon. The trionychids are linked to the kinosternids.

MYOLOGY

The numerous studies on the myology of the limbs and girdle have led to a plethora of names and a corresponding absence of any synthesis of knowledge. Recently, this has been remedied by Walker (in press) who described in detail the myology of the forelimbs and hindlimbs of *Chrysemys*
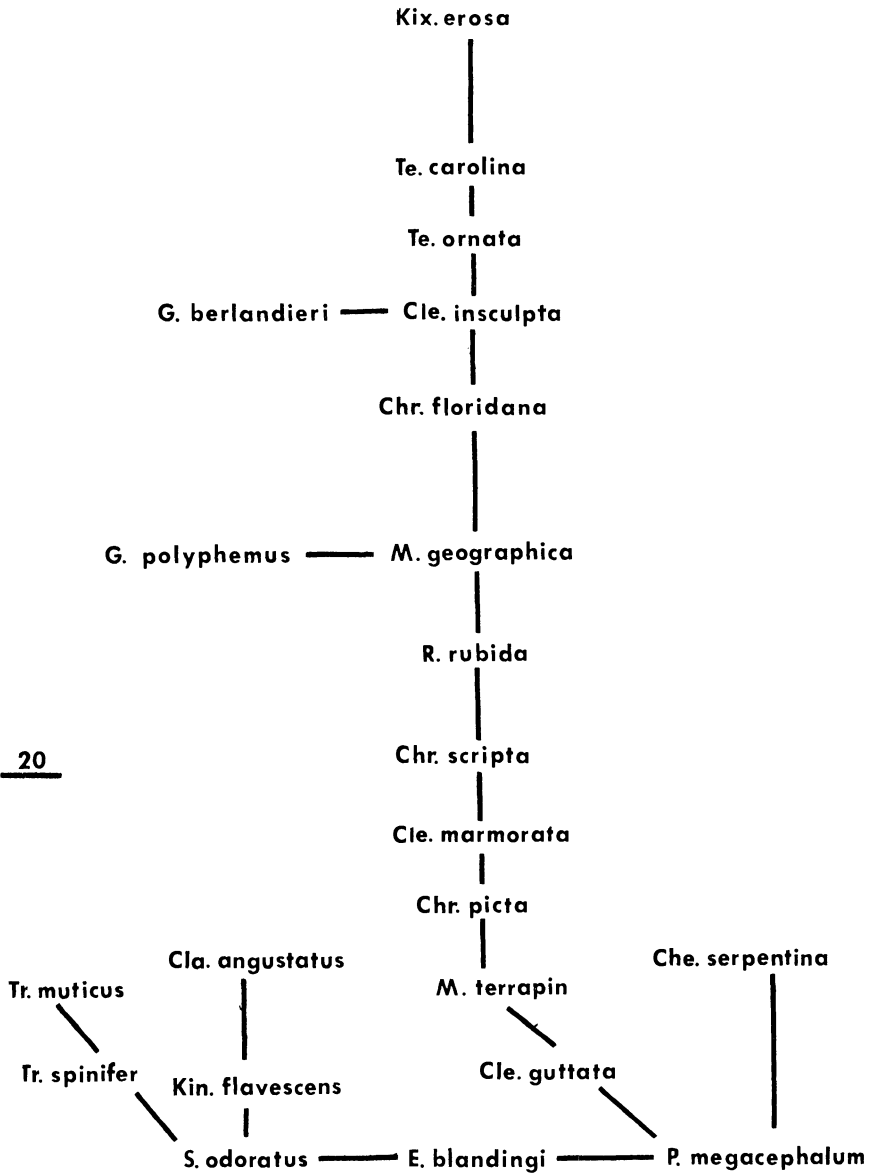
FIG. 13. A Prim Network for 22 cryptodiran species generated on the basis of 24 osteological characters. The species and characters are those in Tables 5 through 11. The length of the connecting lines indicates the relative degree of similarity; the bar insert represents 20 units of difference.

scripta and contrasted the myology of other chelonian species to that form. In so doing, he has synthesized all previous terminologies. His terminology reflects the relationship of chelonian myology to that of other reptilian groups, particularly lizards. This alone is reason for it to become a standard and I have used it here.

Since Walker made an extensive review of the literature in compilations of his synonymy, I will mention only the more pertinent literature. Gadow (1882) examined three genera, *Emys, Clemmys,* and *Testudo,* and appears to have been the first to report the existence of different myological patterns in turtles. The main emphasis of Gadow's study was a comparison of hindlimb myology of all extant orders of reptiles. Both Hoffman (1890) and Sieglbauer (1909) examined and described the myology in a wide variety of species. Axt (1917), in addition to describing the myology of the hindlimb and girdle of *Emydoidea blandingi,* demonstrated the variable nature of the branches of the lumbosacral nerve plexus. More recently, George and Shah (1958) have published on the myology of the hindlimbs of *Lissemys punctata.* Unfortunately, they have misidentified some muscles by what appears to be a failure to examine the older literature on chelonian myology. In a study of pelvic and hindlimb musculature of quadrupedal reptiles, Kriegler (1961) examined three species of turtles, *Testudo graeca, Trionyx sinensis,* and *Eretmochelys imbricata;* however, his main interest was the musculature of lizards.

MATERIALS AND METHODS.—This study was initially restricted to an investigation of cryptodiran turtles exclusive of the sea turtles. To this end, I have tried to examine a representative of every family and subfamily of cryptodiran turtles. I have been fairly successful in my coverage and lack data only on the family Carettochelyidae. However, the list of the specimens dissected (Appendix V) shows the unequal treatment given to the various taxa. The bias reflects the availability of specimens, for I have used those taxa which were readily obtainable, i.e., Nearctic species.

As a consequence of the difficulties imposed on dissection by the presence of a shell, I believe it is of value to describe briefly the method employed to remove it. The carapace is sawed transversely on a line that passes through the middle of the eighth marginal and third costal scutes and along the suture between the third and fourth vertebral scutes. A second transverse cut passes through the middle of the femoral scutes of the plastron. With the completion of these cuts, the posterior third of the body can be separated by cutting through the viscera and inguinal skin and muscle. The third cut is parasagittal on the carapace, just lateral to the dorsal vertebrae. This cut must be made with care, for if the saw passes too deeply, muscles will be destroyed. After these three saw cuts are made, the plastron is removed by freeing it from the skin and sliding a knife between the rectus abdominis and the plastron. The next step is to remove the skin from the leg, and finally the carapace half is removed by cutting the testoiliacus around the distal end of the ilium.

The following four parameters were recorded during the dissections: (1) areas of attachment, (2) fascicular arrangement, (3) types of attachments, and (4) shape. Of the four, I considered the areas of attachment to convey the most information, since I was searching for gross morphological differences that might reflect phylogenetic relationships and functional adaptations. With a knowledge of areas of attachment, the course and hence the leverage of a muscle can be reconstructed, and an inference to its role in locomotion can be made. Any shift of the attachment will affect the lever arm of the muscle and its function, thus several questions may be asked. Are the shifts in attachment reflected in the locomotor habits of the turtles and if so, how? What functional relationships are suggested by the myological patterns and locomotor habits of a species? Do the functional relationships reflect phylogenetic association or mechanical convergence? The area of attachment was recorded by a verbal description and by plotting the attachment on an outline of the bony elements.

The other three parameters were recorded also by verbal description. The terminology of Matulionis (1966) is used to delineate the fascicular arrangement. Types of attachment are recorded as tendinous or fleshy, and the shape of the muscle is described briefly. Frequently, the shape of a muscle is disclosed by the fascicular arrangement. In addition, fascicular arrangement can provide an estimate of the strength of a muscle.

Many other parameters, e.g., volume, weight, length, could have been recorded, but since my primary interest was gross morphological change, I deemed it unnecessary to record them. In addition, the amount of variation that results from mensural techniques, state of preservation, and manner of removal and cleaning the muscle seem to outweigh the usefulness of these data. It has also been demonstrated (Gans and Bock, 1965) that this type of mensural data yields little functional information when not accompanied by experimental data.

COMPARISON.—The standard procedure for comparing the musculature of different species is to describe the musculature of one species in detail and then to enumerate the deviations of other species from that of the first. The disadvantage of this method is that both the reader and the author frequently become swamped in a quagmire of descriptive detail, and the goal of discovering the systematic and functional significance of the data is lost. To avoid this predicament, the details of the origin and insertion of each muscle in each genus are presented in Appendix VI. A series of illustrations (Figs. 14–16) will enable the reader to familiarize himself with the chelonian pelvic and hindlimb musculature. To supplement the Appendix, a series of origin and insertion maps (Figs. 17–20) is presented with the discussion of the corresponding muscle groups. This enables me to discuss the muscles simply with the intent of determining the systematic and functional implications of the various muscle arrangements. The terminology used is presented in Table 12.

The musculature of the pelvic girdle is derived from two embryological
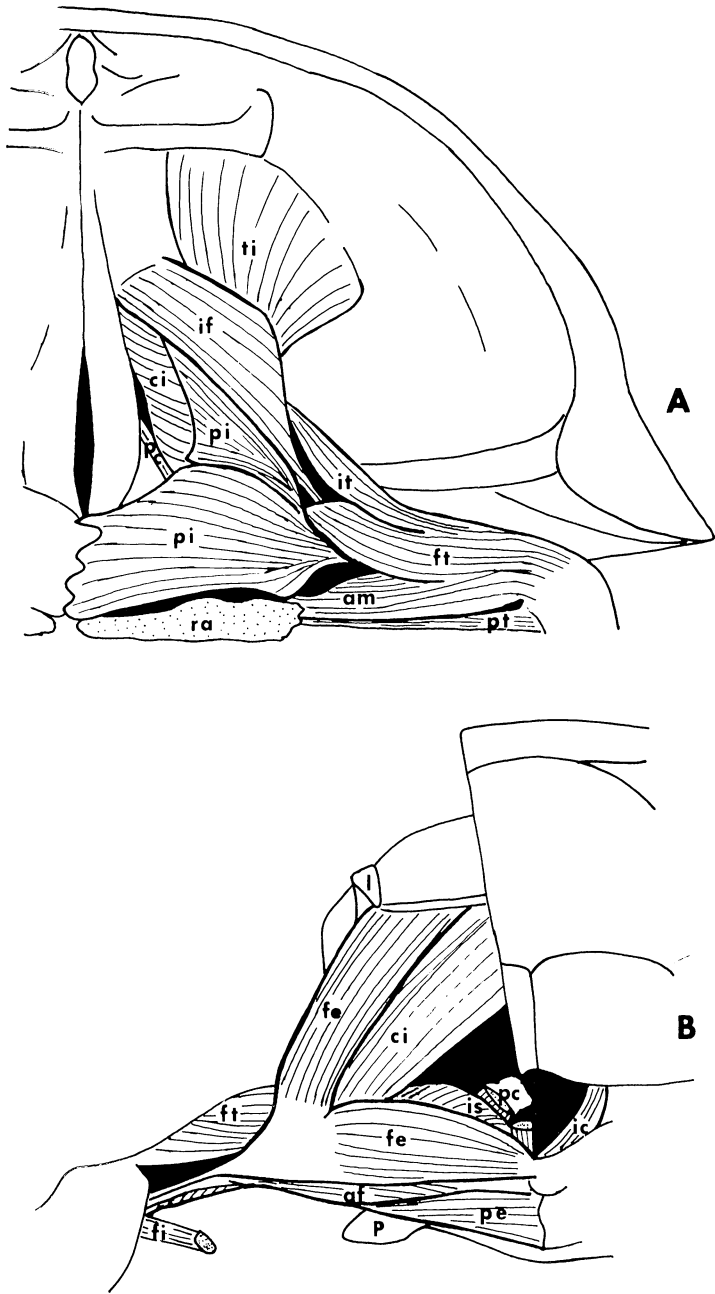
FIG. 14. The posterior appendicular musculature of *Emydoidea blandingi*. A. Anterior view of the pelvic and femoral region. B. Posterior view of the pelvic and femoral region; the proximal portion of the flexor tibialis internus has been removed. af, adductor femoris; am, ambiens; ci, caudi-iliofemoralis; fe, flexor tibialis externus; fi, flexor tibialis internus; ft, femorotibialis; I, ilium; ic, ischiococcygeus; if, iliofemoralis; is, ischiotrochantericus; it, iliotibialis; P, pubis; pc, pubococcygeus; pe, puboischiofemoralis externus; pi, puboischiofemoralis internus; pt, pubotibialis; ra, rectus abdominis; ti, testoiliacus.
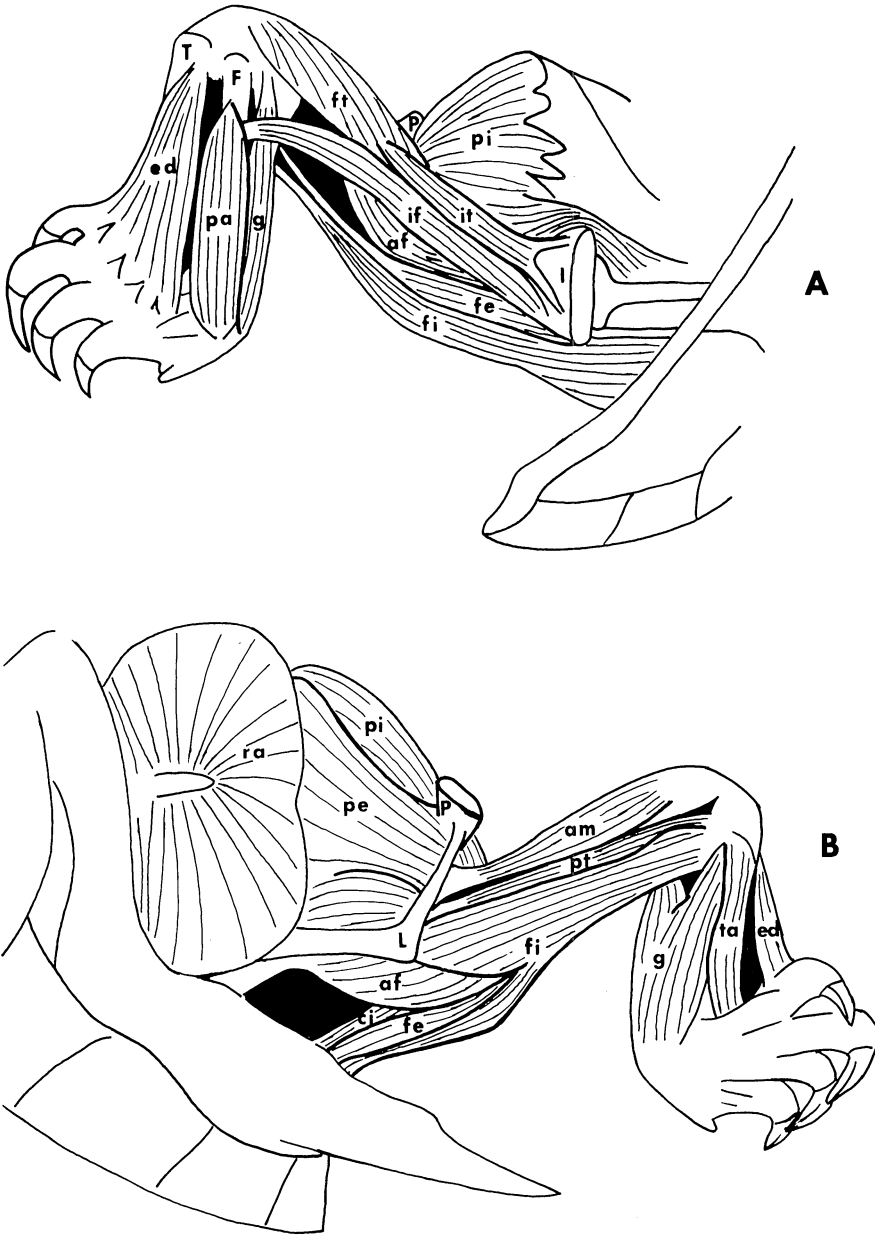
FIG. 15. The posterior appendicular musculature of *Emydoidea blandingi*. A. Dorsal view of girdle and limb; the left half of the carapace and the testoiliacus have been removed. B. Ventral view of girdle and limb; the left rectus abdominis has been removed. ed, extensor digitorum communis; F, fibula; g, gastrocnemius; L, puboischiadic ligament; pa, peroneus anterior; T, tibia; ta, tibialis anterior. Other abbreviations as in Fig. 14.
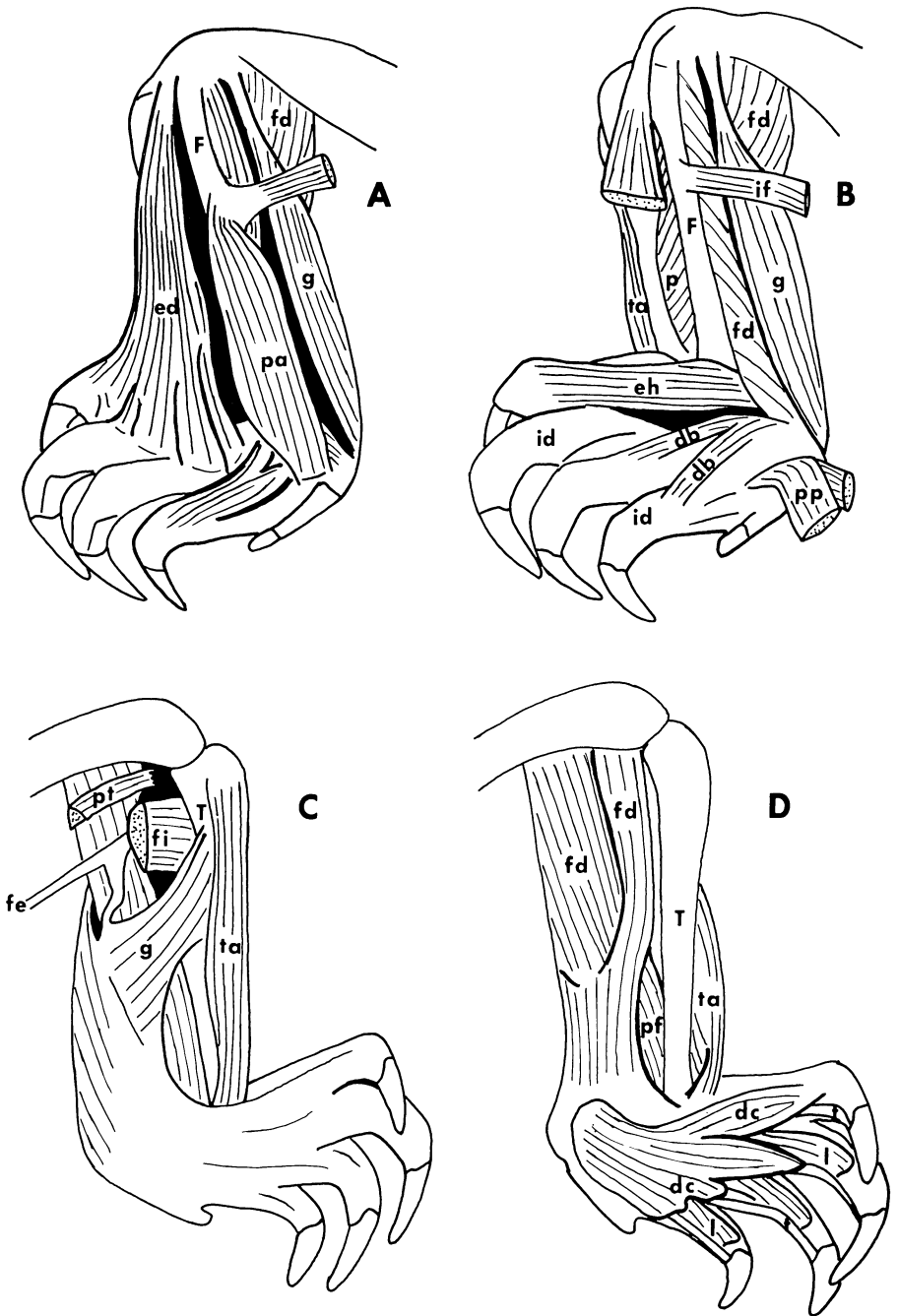
FIG. 16. The crural and pedal musculature of *Emydoidea blandingi*. A. Postero-dorsal view of the lower limb. B. Posterodorsal view of the lower limb with the extensor digitorum communis, peroneus anterior and peroneus posterior cut and laid aside. C. Anteroventral view of the lower limb. D. Anteroventral view of the lower limb; the gastro-cnemius and its aponeurosis have been removed and the tibialis anterior pulled aside. db, extensores digitorum breves; dc, flexor digitorum communis sublimis; eh, extensor hallucis proprius; fd, flexor digitorum longus; id, interossei dorsales; l, lumbricales; p, popliteus; pf, pronator profundus; pp, peroneus posterior; t, tendon of flexor digitorum longus flexor plate. Other abbreviations as in Figs. 14 and 15.
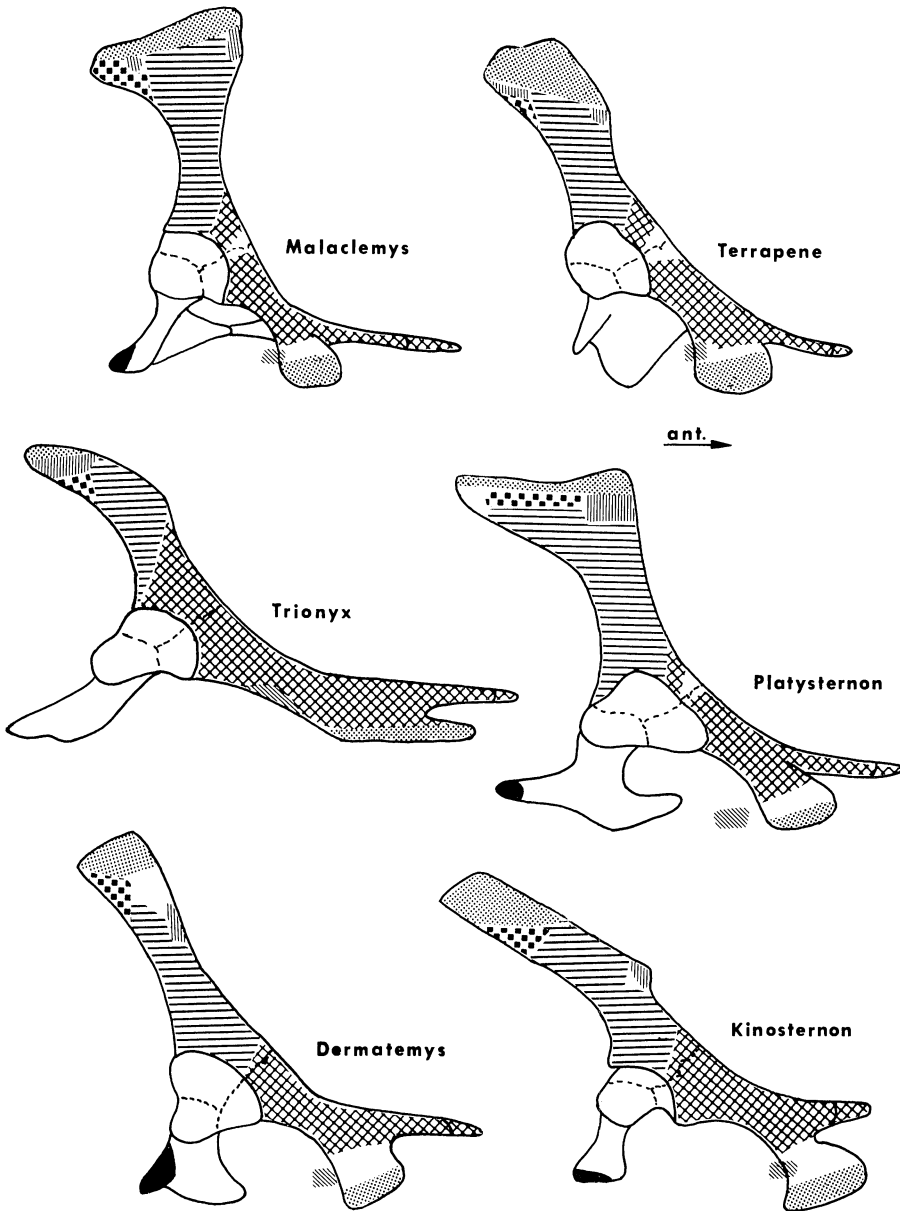
FIG. 17. Muscle attachments on the lateral surface of the ilia of *Malaclemys terrapin*, *Terrapene ornata*, *Trionyx ferox*, *Platysternon megacephalum*, *Dermatemys mawi*, and *Kinosternon integrum*. Stippled, axial musculature, testoiliacus and rectus abdominis; vertical lines, iliotibialis; horizontal lines, iliofemoralis; diagonal lines, ambiens; diagonal grid, puboischiofemoralis internus; checkerboard, iliofibularis; solid black, adductor femoris; unmarked region on ischia, puboischiofemoralis externus.
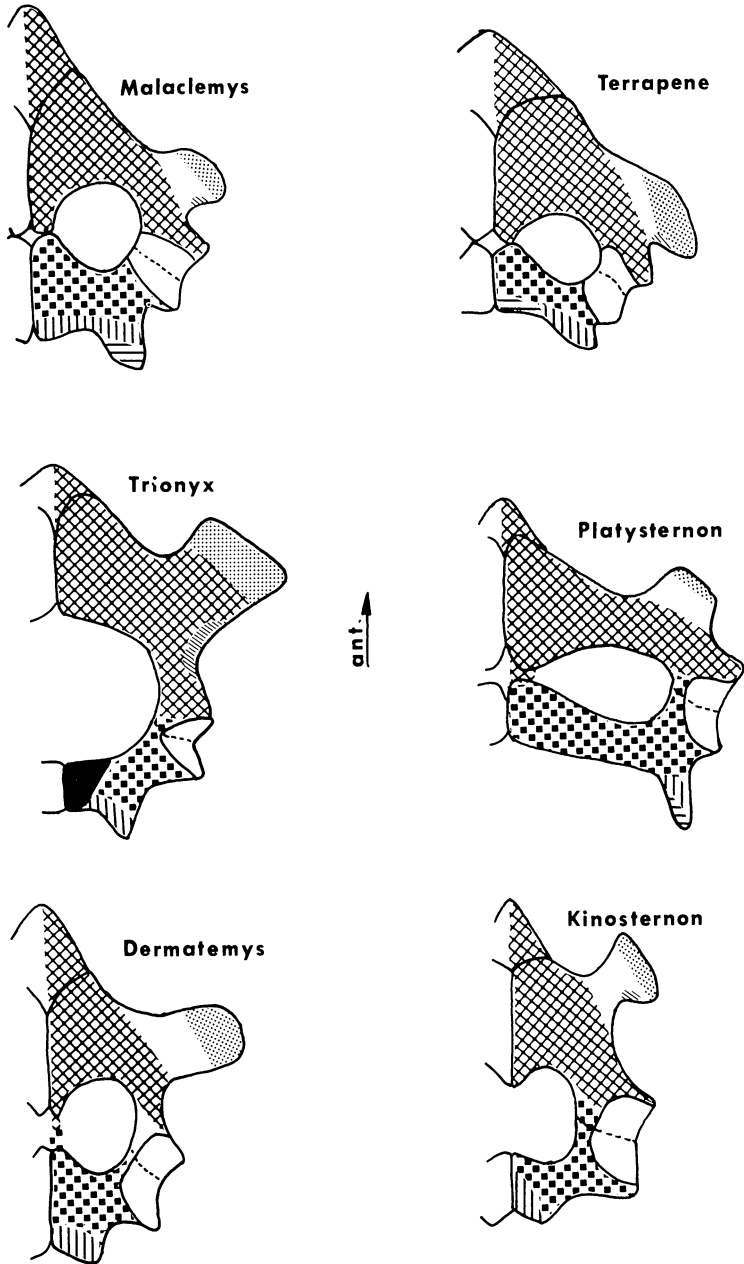
FIG. 18. Muscle attachments on the dorsal surface of the puboischiadic plates of cryptodiran turtles; the ilia have been removed. The species are the same as those in Figure 17. Stippled, rectus abdominis; vertical lines, flexor tibialis externus; horizontal lines, flexor tibialis internus; diagonal lines, ambiens; diagonal grid, puboischiofemoralis internus; checkerboard, ischiotrochantericus; solid black, femorotibialis.
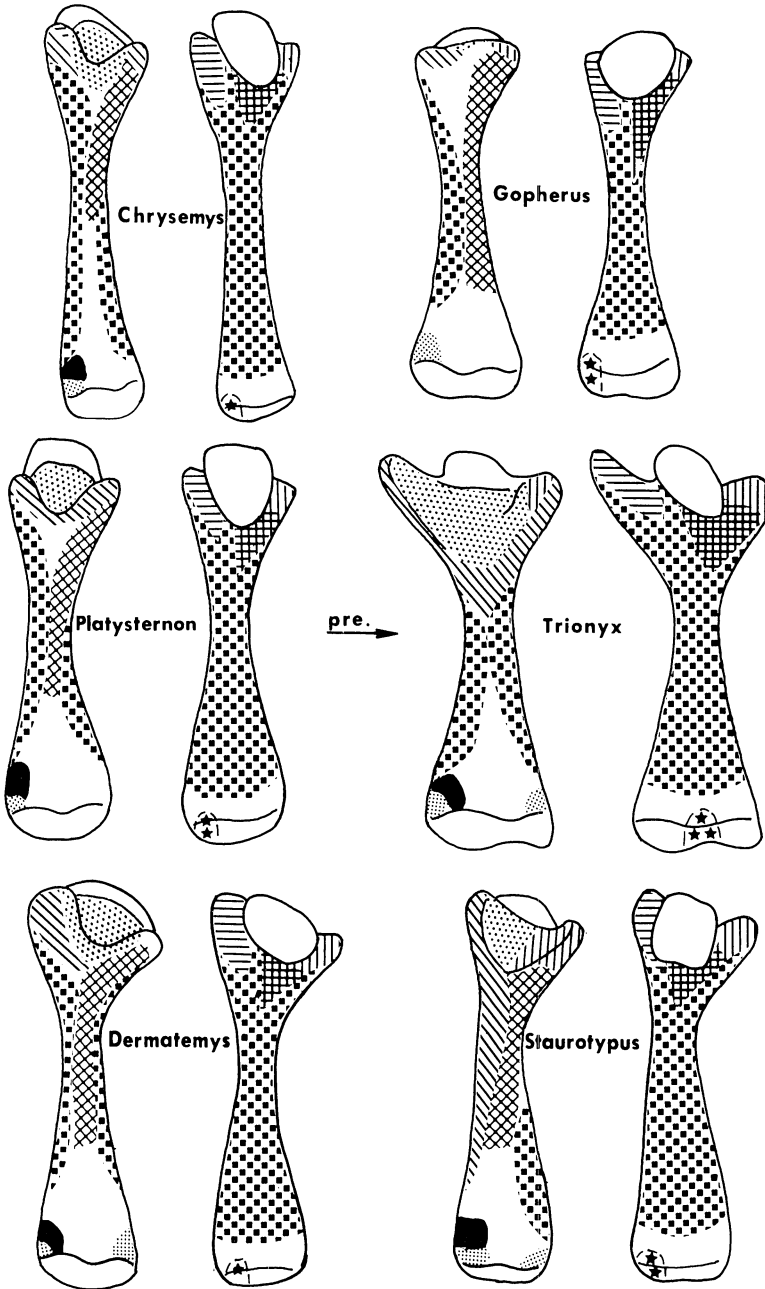
FIG. 19. Muscle attachments on the dorsal (right) and ventral (left) surfaces of femora of *Chrysemys picta, Gopherus polyphemus, Platysternon megacephalum, Trionyx ferox, Dermatemys mawi,* and *Staurotypus triporcatus.* Fine stipple, gastrocnemius; coarse stipple, ischiotrochantericus; vertical lines, puboischiofemoralis externus; horizontal lines, iliofemoralis; diagonal lines, caudi-iliofemoralis; perpendicular grid, puboischiofemoralis internus; diagonal grid, adductor femoris; checkerboard, femorotibialis; stars, extensor digitorum communis; black, flexor digitorum longus. pre., preaxial.
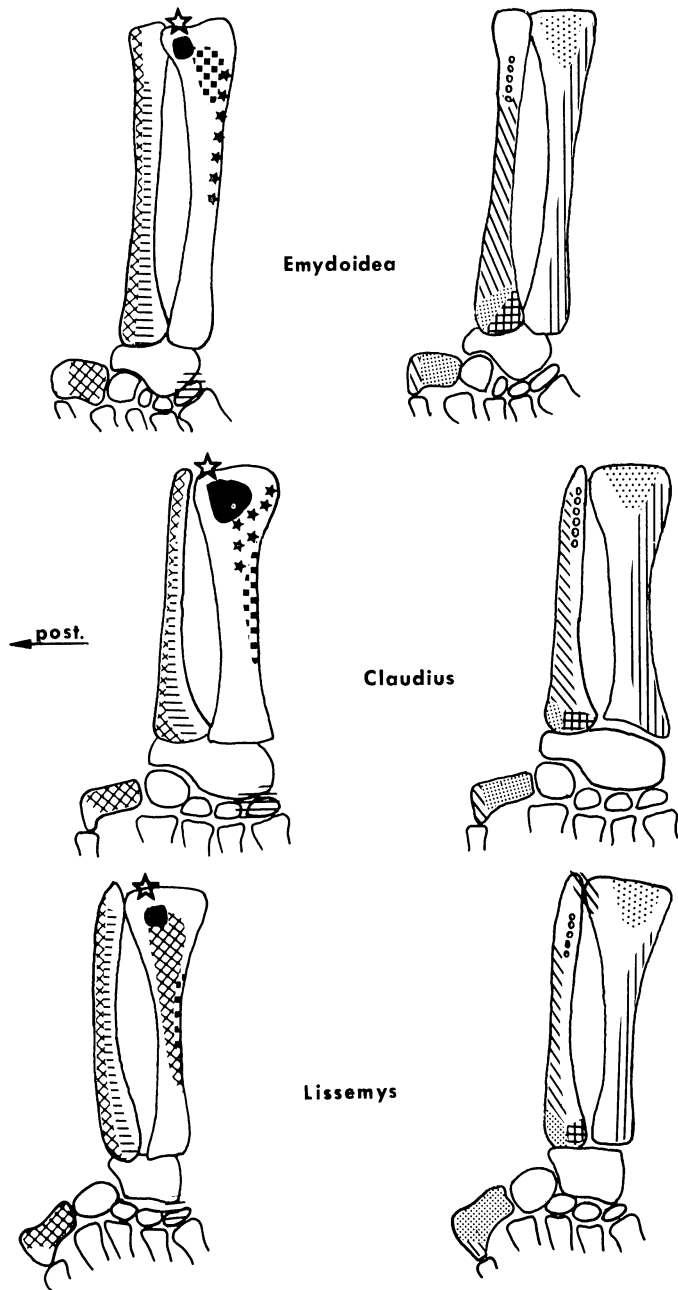
FIG. 20. Muscle attachments on the dorsal (right) and ventral (left) surfaces of the crura of *Emydoidea blandingi, Claudius angustatus,* and *Lissemys punctata.* Fine stipple, peroneus posterior; coarse stipple, triceps femoris; vertical lines, tibialis anterior; horizontal lines, pronator profundus; diagonal lines, peroneus anterior; diagonal grid, flexor digitorum longus; perpendicular grid, extensor hallucis proprius; checkerboard, flexor tibialis internus; large open star, pubotibialis; small solid star, gastrocnemius; open circle, iliofibularis; black, flexor tibialis externus. post., postaxial.

TABLE 12

MUSCULATURE OF THE PELVIC GIRDLE AND HINDLIMB

Axial	Appendicular			
	Dorsal		Ventral	
	Pelvic & Femoral	Crural & Pedal	Pelvic & Femoral	Crural & Pedal
Testoiliacus	Puboischiofemoralis Internus	Extensor Digitorum Communis	Puboischiofemoralis Externus	Gastrocnemius
Rectus Abdominis	Iliofemoralis	Peroneus Anterior	Caudi-iliofemoralis	Flexor Digitorum Longus
Ischiococcygeus	Iliofibularis	Peroneus Posterior	Ischiotrochantericus	Pronator Profundus
Pubococcygeus	Iliotibialis 1	Tibialis Anterior	Adductor Femoris	Popliteus
	Ambiens 1	Extensor Hallucis Proprius	Flexor Tibialis Internus 3	Flexor Digitorum Communis Sublimis
	Femorotibialis 1	Abductor Hallucis 2	Flexor Tibialis Externus 3	Lumbricales
		Extensor Digitorum Breves	Puboischiotibialis 3, 4	Interossei Plantares
		Interossei Dorsales	Pubotibialis 3	
			Caudifibularis 5	

Terminology after W. F. Walker, Jr. (In press).

1. These three muscles are frequently combined under the name Triceps Femoris.
2. I considered this muscle to be the anterior member of the Interossei Dorsales complex.
3. When discussed as a single functional unit, these four muscles are called the Flexor Cruris.
4. None of the cryptodires examined possessed this muscles.
5. This is an addition to Walkers terminology.

divisions, axial and appendicular. Of the axial division, only the testoilia-
cus and the rectus abdominis appear to be associated with limb movement.
The ischiococcygeus and pubococcygeus attach to the dorsal surface of the
pelvis and move the tail. The flattened, cone-shaped testoiliacus anchors
the ilium to the carapace. Outside of its double origin in *Lissemys,* varia-
tion is restricted to changes in relative size of the muscle and thus size of
attachment. The origin is stable. With enlargement, the testoiliacus en-
croaches more anteriorly onto the sixth pleural and further laterally on the
seventh and eighth pleurals. Enlargement of the insertion occurs by the
muscle extending further ventrad on the distal end of the ilium. The lar-
gest insertions are found in *Emydoidea, Terrapene,* testudinids, and kino-
sternids. This condition suggests a correlation between walking, either ter-
restrial or bottom-walking, and a sturdily anchored ilium.

The chelonian rectus abdominis has been considered as two separate
muscles, attrahens pelvium and retrahens pelvium, because it frequently
has two distinct fiber tracts, an anterior and a posterior one. They are
fiber tracts and not separate muscles, for as they approach the origin on the
pectineal process they are inseparable. In addition, the degree of separate-
ness of the tracts varies among the taxa. The aquatic testudinids usually
have a semicircular rectus abdominis with the fibers radiating outward as
vanes in a fan. In the chelydrids and terrestrial testudinids, a division into
two fiber tracts makes its appearance, though the muscle remains un-
divided. The two fiber tracts are subequal in size. The fiber tracts are
separated into two heads in *Dermatemys,* kinosternids, and trionychids. In
Dermatemys and kinosternids, the anterior head tends to be strap-like and
the posterior head fan-shaped. This arrangement is reversed in the triony-
chids.

The size of the origin is proportional to the size of the posterior
lobe of the plastron, i.e., taxa with reduced plastrons have smaller areas
of attachments. Likewise the size of the insertion is directly related to the
size of the pectineal process; however, the area of attachment also varies
interspecifically. *Clemmys, Malaclemys, Terrapene,* and *Trionyx,* one
species of each of these genera, has the rectus abdominis attached only to
the distal end, whereas in the other it covers nearly the entire pectineal
process.

Apparently the function of the rectus abdominis is to anchor the
pelvis to the plastron, thereby reducing movement of the girdle during
locomotion. This function is only a supposition as will be any comments
I make on the function of muscles. To date, we have little accurate knowl-
edge of muscle action during locomotion in vertebrates. The recent at-
tempts of human anatomists to study muscle action by simultaneous cine-
matographic and electromyographic records are producing a clearer under-
standing of the synergistic action of muscles during locomotion. Hopefully
this technique will be taken up by comparative vertebrate anatomists.

The appendicular muscles of the hindlimb and pelvic girdle are
divided into two basic functional groups, the dorsal or extensor muscles and

the ventral or flexor muscles. Each of these divisions can be further sub-divided into pelvic-femoral and crural-pedal units (Table 12). In the fol-lowing discussion, the muscles will be treated as members of these divisions with no attempt to contrast the antagonistic action of opposite dorsal and ventral muscles owing to the lack of direct information on muscle action.

The puboischiofemoralis internus has two distinct arrangements. In the chelydrids, kinosternids, and *Dermatemys,* it has a single site of origin dorsally on the pubis. In the testudinids and trionychids, it has a double origin, a head on the pubis and one on the distal end of the ilium and adjacent vertebrae. Its insertion is always dorsally on the neck of the femur and the base of the trochanter minor. The encroachment on the trochanter seems to be greatest in terrestrial testudinids and the trionychids, but occurs to a lesser degree in all other species examined. Since the position of the in-sertion does not change, a double-headed muscle will function differently than a single muscle. In both cases, the heavy triangular portion from the pubis will protract the limb and rotate its dorsal surface anteriorly. The dorsal head will lift the limb. These two patterns of limb movement appear to relate to the two aquatic modes of locomotion, bottom-walking to the single muscle and swimming to the double-headed muscle. It can be argued that terrestrial testudinids never swim voluntarily, but they are thought to be derived from aquatic ancestors, and the double head may have been retained.

The usual origin of the iliofemoralis is laterally and anteromedially on the ilium and ventrally on the last dorsal and first sacral vertebrae. Only in the trionychids is this origin divided into two heads. The insertion is always on the trochanter major and occasionally overlaps ventrally onto its edge. Whether single or double-headed, the function of the iliofemoralis is probably to lift the limb off the ground during protraction.

The sites of origin and insertion of the iliofibularis are invariable in the species examined. Some variation was observed in the size of the origin, but there is no obvious functional or taxonomic pattern. Its large origin and the narrow ilium in the Staurotypinae cause the origin to be continuous across the entire lateral face of the ilium. Contraction of the iliofibularis abducts the limb. Although it is a member of the extensor musculature and attaches dorsally on the fibula, its course indicates that it flexes and rotates the crus posteriorly.

The remaining three muscles, ambiens, femorotibialis, and iliotibialis, of the pelvic-femoral extensor division act as a single functional unit to extend the crus and in part to abduct the limb, since they have a common insertion on the proximal end of the tibia. The ambiens and the iliotibialis are two-joint muscles, for they extend across the hip and knee joint. The femorotibialis extends across only the knee joint.

The origin of the iliotibialis shows four different patterns of attach-ment. If the origin of testudinids, exclusive of *Platysternon,* is used as an end point, a morphological series can be constructed. I wish to emphasize that this is not necessarily the primitive arrangement, but it may be. In the

testudinids, the origin of the iliotibialis is by a bifurcated tendon attaching to the distoanterior and the distoposterior corners of the ilium. The origin of the trionychids is single and on the distoposterior corner. In *Platysternon* and the chelydrids, the origin is single and on the distoanterior corner. In *Dermatemys*, the single anterior origin has moved onto the anterior edge of the ilium and slightly proximally. Kinosternids are similar to *Dermatemys* with a single origin on the anterior edge, but the origin is restricted to the thelial process and is in a more proximal position. The different origins will produce different limb movements. With the double origin, the limb probably abducts directly upward when both parts contract, posterodorsally with contraction of the posterior part, and anterodorsally with that of the anterior part. The different origins suggest the following relationships, *Dermatemys* to the kinosternids and *Platysternon* to chelydrids. Anterior origins are associated with bottom-walking taxa and generally the double and posterior origins with aquatic forms or derivatives thereof.

The origin of the ambiens shows three general arrangements. An origin on the anterior portion of the puboischiadic ligament is found in *Chelydra, Chrysemys, Clemmys, Emydoidea, Malaclemys, Platysternon, Dermatemys* and *Claudius*. In *Rhinoclemys, Terrapene, Geochelone, Gopherus, Kinosternon, Sternothaerus,* and *Staurotypus,* the origin is on the pectineal process adjacent to the attachment of the puboischiadic ligament. The origin in trionychids has moved onto the pubic plate or muscle originating thereon. The latter two origins are associated with walking and swimming, respectively. The shift of the origin from the ligament to the plate barely changes the lever arm, elevating it only slightly.

Both the ambiens and iliotibialis join the femorotibialis. The type of union between the former two and the latter was either a firm union or a loose contact. In both types, the ambiens and iliotibialis share a common tendon that fuses distally with the tendon of the femorotibialis. Since the leverage arm is modified by the type of contact, limb movement will also be modified. However, the question remains as to whether these union types are real or an artifact of preservation.

The femorotibialis arises from nearly the entire dorsal surface of the femur and usually overlaps ventrally along the anterior and posterior borders. This overlap varies from a slight encroachment on the ventral surface in chelydrids to a complete enclosure of the ventral surface in trionychids. The proximal end is shallowly trifurcate, and each branch has been named. These names, vastus internus, vastus medialis, and vastus externus, suggest that the femorotibialis is composed of three distinct heads. This is erroneous, for the proximal end is simply irregular with no cleavage into separate muscle bundles. All the cryptodires have the massive origin on the femoral shaft. Only the trionychids have a distinct head, caput ischiadicum, arising dorsally on the ischium and can abduct the limb in addition to extending the crus.

The anteriormost member of the pelvic flexor musculature is the pubo-

ischiofemoralis externus. The sites of origin and insertion are relatively constant throughout the cryptodires examined. With the exception of *Platysternon* and *Chrysemys picta,* the muscle is usually divided into a pubic and an ischial muscle bundle. A third bundle is present in *Chelydra, Kinosternon,* and *Lissemys* arising in proximity to the pectineal process. The insertion for most species is dorsally on the trochanter minor and its ventral edge. The insertion of kinosternids and trionychids occupies in addition the anterior third of the intertrochanteric fossa. The function seems to be limb protraction and counter-clockwise rotation of the femur. Because of its intertrochanteric insertion in kinosternids and trionychids, rotation may be reduced.

The sites of origin and insertion of the caudi-iliofemoralis are nearly invariable. The origin is always centered over the second sacral vertebra and can extend anteriorly to the ninth dorsal vertebra or posteriorly to the second caudal vertebra. The insertion is on the ischiotrochantericus with the exception of *Trionyx,* where it has moved distally onto the ventral edges of the trochanters and shaft. The function is to retract and abduct the limb and rotate it counter-clockwise.

The ischiotrochantericus is similar to the previous two muscles, since it possesses the same origins and insertions in all the taxa examined. It acts to retract and rotate the limb.

The adductor femoris is also an invariable muscle. Its origin and insertion are constant in chelydrids, testudinids, dermatemydids, and kinosternids. As its name implies, it adducts the limb. In the trionychids, the adductor femoris is absent, and its role appears to be, at least partially, performed by the ischiotrochantericus, which extends distally onto the femoral shaft.

The remaining ventral pelvic muscles are often classified as a single functional unit, the flexor cruris. All members of the flexor cruris extend from the pelvis and/or adjacent vertebrae to the proximoventral surface of the crus. In general, their role would be to flex the crus and abduct the limb. They probably contract during the retraction phase of the locomotor cycle.

The pubotibialis is the anteriormost member of the flexor cruris. Unlike the other members, the pubotibialis has essentially the same origin and insertion in all cryptodires examined. A puboischiotibialis is supposed to border it posteriorly (Walker, in press); however, the only posteriorly adjacent muscle that I could find was the ventral head of the flexor tibialis internus.

The cryptodiran flexor tibialis internus shows three patterns of attachment, (1) a double origin and a double insertion, (2) a double origin and a single insertion, or (3) a single origin and a single insertion. Likewise, the flexor tibialis externus exhibits three patterns, (1) a double origin and a double insertion, (2) a single origin and a double insertion, or (3) a single origin and a single insertion. In both the internus and the externus, the ventral origin on the puboischiadic ligament and the insertion on the tibia are the attachments that are always present. The taxonomic distributions

of the various patterns are presented in Table 13. The proximity of the dorsal heads of the two muscles and their frequent interchange of fiber bundles must be stressed. In addition, *Dermatemys*, kinosternids, and triony-chids have a caudifibularis. This muscle appears to be derived from the anterior edge of the flexor tibialis internus. As far as I can determine, it has been recognized as a distinct muscle only by George and Shah (1958) in *Lissemys*. They labeled it flexor tibialis genicularis and reported its fusion distally to the flexor tibialis internus. My observations indicate that proximally it may interchange fiber bundles with internus, but distally it attaches to a fascia sheet over the crus and not to the internus.

The architecture of the flexor tibialis complex suggests that chelydrids and testudinids form a single natural phylogenetic group. The kinosternids, *Dermatemys* and trionychids are related, although *Dermatemys* and kinosternids are more similar to one another than either is to the trionychids. The evidence for the above statements is found in Table 13.

TABLE 13
TAXONOMIC DISTRIBUTION OF THE MUSCULAR CHARACTERS

Genus	Pif. Int.	Iliotib. Origin	Iliotib. Position	Ambiens	Ad. Fem.	Fl. F. Int. Origin	Fl. F. Int. Insert.	Fl. F. Ext. Origin	Fl. F. Ext. Insert.	Ext. D. Com. Position	Ext. D. Com. Division	Peroneus	Tib. Ant.	Gastroc.	Caudif.
Chelydra	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0
Rhinoclemys	1	1	.5	1	1	1	0	1	1	0	0	0	1	0	0
Chrysemys	1	1	.5	0	1	1	0	1	1	0	0	0	1	0	0
Clemmys	1	1	0	0	1	1	0	1	1	0	0	0	1	0	0
Emydoidea	1	1	.5	0	1	1	0	1	1	0	0	0	1	0	0
Malaclemys	1	1	.5	0	1	1	0	1	1	0	0	0	1	0	0
Terrapene	1	1	.5	1	1	1	0	0	1	0	0	0	1	0	0
Platysternon	1	0	0	0	1	1	0	0	1	0	0	0	1	0	0
Geochelone	1	1	.5	1	1	0	0	1	1	0	1	0	0	0	0
Gopherus	1	1	.5	1	1	0	0	1	1	0	1	0	0	0	0
Dermatemys	0	0	0	0	1	1	1	0	1	0	0	0	1	1	1
Kinosternon	0	0	0	1	1	1	1	0	1	0	0	0	1	0	1
Sternothaerus	0	0	0	0	1	1	1	0	1	0	0	0	1	0	1
Claudius	0	0	0	0	1	1	0	0	1	0	0	0	1	0	1
Staurotypus	0	0	0	1	1	1	0	0	1	0	0	0	1	0	1
Lissemys	1	0	1	2	0	1	1	0	0	1	0	1	1	0	1
Trionyx	1	0	1	2	0	1	1	0	0	1	0	1	1	0	1

These characters were used to construct the Prim Network (Fig. 21). Pif. Int., puboischiofemoralis internus; origin single 0, double 1. Iliotib., iliotibialis; origin single 0, double 1; position anterior 0, posterior 1, both .5. Ambiens, origin on ligament 0, on pectineal process 1, and on pubic plate 2. Ad. Fem., adductor femoris; absent 0, present 1. Fl. T. Int., flexor tibialis internus; origin single 0, double 1; insertion single 0, double 1. Fl. T. Ext., flexor tibialis externus; characterization same as internus. Ext. D. Com., extensor digitorum communis; origin on condyle 0, between condyles 1. Peroneus, origin on femur 0, not on femur 1. Tib. ant., tibialis anterior; absent 0, present 1. Gastroc., gastrocnemius; anterior head on femur 0, not on femur 1. Caudif., caudifibularis; absent 0, present 1.

Lying superficially on the dorsal surface of the crus, the extensor digitorum communis extends from the fibular condyle of the femur to the first four toes. The aforementioned attachments are common to all cryptodires except *Platysternon, Lissemys,* and *Trionyx.* The slip to the first toe is absent in *Platysternon.* In the trionychids, the origin has moved anteriorly to an intercondylar position. For most cryptodires, the muscle extends the crus and tends to supinate the pes, although the anterior origin in trionychids probably reduces the supinator action.

A number of authors (see synonymy in Walker, in press) have reported an extensor hallucis longus in trionychids. It has a common origin with extensor digitorum communis and inserts on the first toe, whereas the latter muscle inserts on the second, third, and fourth toes. My observations fail to support the recognition of the extensor hallucis longus as a muscle separate from the communis, for the anterior slip of the extensor digitorum communis is no less distinct in other cryptodires than in trionychids.

The peroneus complex covers the posterodorsal margin of the crus. Its course and sites of attachment indicate that it extends the pes, but probably more important, it draws the fifth toe posteriorly thereby spreading the toes. In all genera except *Terrapene, Gopherus, Kinosternon,* and *Sternothaerus,* two distinct muscles, peroneus anterior and peroneus posterior, are found. The two muscles frequently cohere to one another and the single peroneus may reflect a greater than usual cohesion of the two. Aside from the occurrence of two heads in the trionychid peroneus anterior, the form and attachments of this complex are stable.

The anterior margin of the crus is covered by the tibialis anterior. Like the peroneus complex, this muscle tends to be relatively consistent in form and attachment throughout the cryptodires. *Lissemys* shows one variation with an extension of origin onto the femur. The testudinines lack this muscle. Its anterior position suggests that it and the peroneus complex may be the main muscles involved in opening or spreading the plantar surface. The latter function is important for aquatic turtles with webbed feet.

The extensor hallucis proprius is almost invariable in the species examined. The slight variation in insertion is one of degree which probably does not change the action of the muscle in extending the first toe and supinating the pes.

Of the short digital extensors, the extensor digitorum breves present the most variation. The only variation in the interossei dorsales is five muscles instead of four in *Lissemys.* The extensores digitorum breves have no muscle to the first toe in *Rhinoclemys, Platysternon,* kinosternids, and trionychids. The functional and taxonomic significance of this variation is unclear.

In the testudinids, musculature of the pes is embedded in numerous thick layers of connective tissue. This has hampered dissection, and the determination of sites of attachment is difficult. The uncertainty of the origins and insertion of the short digital extensors and flexors was sufficiently great that they are not discussed or listed in the appendix.

The gastrocnemius with its two heads appears to be the major flexor for the entire pes. The anterior and posterior positions of the heads will permit clockwise or counter-clockwise pronation, depending upon which head contracts. The sites of attachment are relatively consistent; however, in *Dermatemys, Claudius, Staurotypus, Lissemys* and *Trionyx,* the anterior head has expanded and arises from the femur in addition to its usual origin on the tibia. The extension of the anterior origin probably does not affect the pattern of limb movement.

The sites of origin of the flexor digitorum longus are invariable. Aside from five flexor tendons in *Staurotypus,* a flexor tendon to each of the first four toes is invariable. The action of this muscle is to flex the anterior four toes, those which are usually clawed. Therefore, it is important in anchoring the pes during limb retraction.

The deep crural muscles, pronator profundus and popliteus, also present similar origins and insertions in the species examined. As its name suggests, the pronator profundus pronates the pes. Lying between the epipodial elements, the popliteus seems to be mainly an antitorque device.

The flexor digitorum communis sublimis and the lumbricales muscle groups arise from the flexor plate of the flexor digitorum longus and insert on the toes. Their manner of origin suggests that they help the flexor digitorum longus flex the toes. Since they are a series of separate muscles, they provide the finer movement of the individual toes. Both muscle groups usually possess four members. The lumbricales have a muscle to each of the last four toes. Only *Terrapene* deviates with a muscle to each of the middle three toes. The loss of the muscle to the fifth toe may be associated with the latter's reduction. If this assumption is true, the muscle may also be absent in the testudinines. *Dermatemys,* kinosternids, and trionychids have only a three-membered flexor digitorum communis sublimis. Since these three taxa encompass the complete range of aquatic locomotion, this grouping may represent a phylogenetic relationship.

Like their antagonist, the interossei plantares are nearly invariable. *Lissemys* has five muscles. All other species examined have four.

Muscles always attach to bone through a tendinous connection. The muscle fibers or fasciculi never attach directly to bone, nonetheless muscular attachments are usually classified as either tendinous or fleshy. The difference between the two means of attachment is that the tendon or connective tissue link between the muscle and the bone's periosteum is extremely short in the fleshy attachment. Generally, fleshy attachments are much larger than tendinous attachments.

In Table 14, the types of attachments have been summarized for the muscles examined. Since the most common condition is listed, I shall mention only the variation from this list. In *Platysternon* and the trionychids, the insertion of the testoiliacus has become partly tendinous; there is also a corresponding division of fiber bundles in these taxa. When the origin of the iliotibialis is double, the attachment is tendinous. With a single origin, the attachment is mainly fleshy. The heads of the flexor tibialis complex

TABLE 14

FASCICULAR ARRANGEMENT AND ATTACHMENT OF PELVIC AND HINDLIMB MUSCULATURE

Muscle		Fascicular Arrangement	Type of Attachment	
			Origin	Insertion
Testoiliacus		fan-shape	fleshy	fleshy
Rectus Abdominis		fan-shape	fleshy	fleshy
Puboischiofem. Int.	D.	parallel	fleshy	fleshy
	V.	fan-shape	fleshy	
Iliofemoralis		parallel	fleshy	fleshy
Iliofibularis		parallel	fleshy	tendon
Ambiens		parallel	tendon	tendon
Iliotibialis		parallel	tendon	tendon
Femorotibialis		parallel	fleshy	tendon
Puboischiofem. Ext.		fan-shape	fleshy	fleshy
Caudi-iliofemoralis		parallel	fleshy	fleshy
Ischiotrochantericus		parallel	fleshy	fleshy
Adductor Femoris		parallel	fleshy	fleshy
Flex. Tibialis Int.	D.	parallel	fleshy	fleshy
	V.	parallel	tendon	
Flex. Tibialis Ext.	D.	parallel	fleshy	tendon
	V.	parallel	fleshy	tendon
Pubotibialis		parallel	tendon	fleshy
Extens. Digit. Com.		fan-shape	tendon	tendon
Peroneus Anterior		parallel	fleshy	tendon
Peroneus Posterior		parallel	fleshy	fleshy
Tibialis Anterior		parallel	fleshy	tendon
Extens. Hall. Prop.		parallel	fleshy	tendon
Extens. Digit. Brev.		parallel	fleshy	tendon
Interossei Dorsales		parallel	fleshy	fleshy
Gastrocnemius	P.	parallel	fleshy	tendon
	A.	parallel	fleshy	
Flex. Digit. Longus	S.	parallel	tendon	tendon
	P.	parallel	fleshy	
Pronator Profundus		parallel	fleshy	tendon
Popliteus		parallel	fleshy	fleshy
Flex. Dig. Com. Sub.		parallel	fleshy	tendon
Lumbricales		parallel	fleshy	fleshy
Interossei Plantares		parallel	fleshy	fleshy

arising from the puboischiadic ligament are always partially tendinous, particularly the flexor tibialis internus. The insertion of the flexor tibialis internus on the tibia tends to be fleshy in the semiaquatic and aquatic testudinids and tendinous or partly tendinous in the other taxa. Usually the insertion of the pubotibialis is both tendinous and fleshy. The posterior head of the gastrocnemius is occasionally tendinous.

The fascicular arrangements (Table 14) of cryptodire musculature are of two types, parallel and radiate pinnate or fan-shape. The arrangements showed little to no variation among the taxa.

PRÉCIS.—The iliofibularis, iliofemoralis, femorotibialis, extensor hallucis proprius, interossei dorsales, puboischiofemoralis externus, ischiotrochantericus, flexor digitorum longus, pronator profundus, popliteus, lumbricales, and interossei plantares are essentially invariable in the species examined.

The insertion of the testoiliacus seems to be larger in those cryptodires whose main mode of locomotion is walking, either terrestrial or bottom-walking. The rectus abdominis grades from a single fan-shaped muscle to a double-headed muscle. There is no division of fiber bundles in aquatic testudinids, a slight division in chelydrids and terrestrial testudinids, and a complete separation in Dermatemys, kinosternids, and trionychids. The shape of the two heads in the latter three taxa differ. In trionychids, the anterior head is fan-shaped, posterior head strap-like. The converse situation is seen in Dermatemys and kinosternids. The puboischiofemoralis internus is single in the chelydrids, kinosternids, and Dermatemys. It has a double origin in the testudinids and trionychids.

Although the iliofibularis is a member of the dorsal extensor group, part of its action appears to be to flex the crus. The iliotibialis has a double tendon origin in the testudinines, emydines, and batagurines. All the remaining taxa have an iliotibialis with a single origin. The origin is on the distoposterior corner of the ilium in trionychids and on the distoanterior corner in Platysternon and the chelydrids. In the kinosternids, the origin is on the middle of the anterior edge of the ilium, for Dermatemys the origin is intermediate between that of kinosternids and chelydrids. The tendinous origin of the ambiens shifts from the puboischiadic ligament to the pectineal process to the pubic plate. The last two origin sites can be associated with walking and swimming habits, respectively.

In trionychids, the origin of the extensor digitorum communis has migrated from the usual fibular condyle to an intercondylar position. Also the peroneus anterior of trionychids has developed a new head on the femur. The testudinines lack the tibialis anterior. The anterior member of the extensores digitorum breves is absent in Rhinoclemys, Platysternon, kinosternids, and trionychids. The adductor femoris is absent in the trionychids.

In most cryptodires, the flexor tibialis internus has a double origin, but that of the testudinines has a single ventral origin. The insertion of this muscle is single in all cryptodires, except Dermatemys, kinosternines, and trionychids. The flexor tibialis externus has a double origin in batagurines, most emydines, and the testudinines. All other taxa have a single ventral origin. All but the trionychids have the flexor tibialis externus insertion on the tibia and the plantar aponeurosis of the gastrocnemius. A new muscle, caudifibularis, is found in Dermatemys, kinosternids, and trionychids. It appears to be derived from the flexor tibialis internus. The anterior head of the gastrocnemius has extended onto the tibial condyle of the femur in Dermatemys, kinosternids, and trionychids. The other taxa have the anterior origin restricted to the tibia.

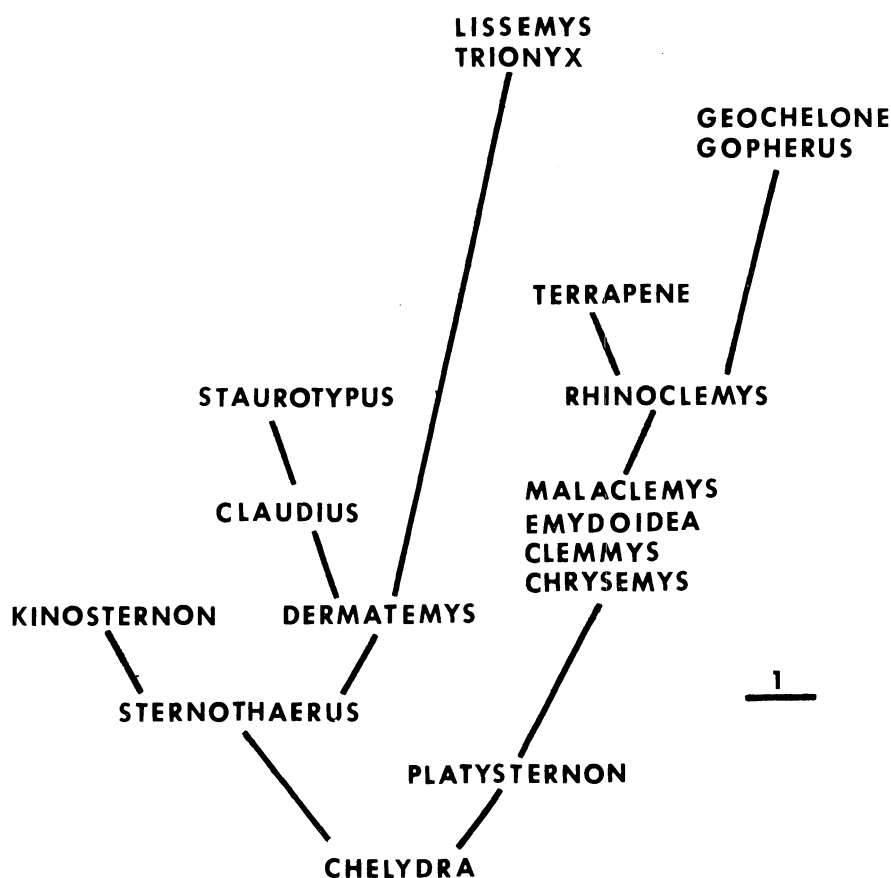A Prim Network (Fig. 21) has been generated on the basis of 15 muscu-

FIG. 21. A Prim Network for 17 genera of cryptodires formed on the basis of 15 musculature characters (listed in Table 13). The length of lines indicate the relative degree of similarity; the bar insert equals one unit of difference. The basal position of *Chelydra* is simply an attempt to make the network symmetrical.

lature characters (Table 13). Although the network is simply an expression of overall phenetic similarity, its groupings express the present taxonomic rankings. Three points are noteworthy: (1) *Chelydra* and *Platysternon* are closely linked; (2) *Dermatemys* and the kinosternids are equally linked to one another; (3) the trionychids are linked to the *Dermatemys*-kinosternid complex.

DISCUSSION AND CONCLUSIONS

Gait sequences of either terrestrial or aquatic locomotion do not reveal any taxonomic differentiation of cryptodires. There is, however, a differentiation of gait sequences between terrestrial and aquatic locomotion. In the former, the relative speed of limb movement is slower and the gaits tend to be lateral sequence gaits, whereas in the latter the gaits are diagonal

sequence gaits and the relative speed is faster. These differences do not appear to be correlated with adaptative differences between turtles but rather with the physical properties of the two environments. On land, the limb postures and sequence of limb movements must be so organized that they counteract the force of gravity and provide support throughout 70 percent of the stride, which enables a turtle to maintain its balance as it walks. Such a requirement forces the turtle to move slowly (a very slow or slow walk) and to maintain a support sequence (lateral gait sequence), which provides maximum balance. Lateral sequence gaits are the typical gaits of slow-moving quadrupedal vertebrates. The buoyancy provided by an aquatic medium greatly reduces the need for support, and the maintenance of balance is less difficult. Turtles can move from a fast walk to a moderate run and shift their gait or support sequence to the slightly less stable diagonal sequence gaits.

It must be noted that although the gaits of turtles are considered to be symmetrical gaits, the timing of movements between contrasting pairs of limbs is variable. This variation is greater in aquatic locomotion. Synchrony of movements is not between the members of ipsilateral pairs or left and right pairs as in terrestrial locomotion but between diagonally opposite limbs. It is suggested that the latter synchrony is obtained from the need to reduce yawing movements.

Although there are no distinct classes of locomotor patterns demonstrated by gait sequences, the locomotor behavior during aquatic locomotion reveals two distinct patterns, bottom-walking and swimming. These two patterns are reflected in the movements of the hindlimbs during aquatic locomotion and to a lesser degree during terrestrial locomotion. Members of the Chelydridae, Kinosternidae, and a few aquatic Testudinidae (*Cuora* and *Emydoidea*) are bottom-walkers. They travel along and remain in contact with the bottom. The swimmers, most aquatic Testudinidae and the Trionychidae, usually remain well above the bottom and, unlike the bottom-walkers, produce their entire propulsive force by pushing against the water.

During terrestrial locomotion, the hindlimb movements and associated body position of the bottom-walkers are more similar to those of the terrestrial *Gopherus* and *Terrapene* than they are to those of the swimmers, even though they share a common habitat with the latter. The bottom-walkers, *Chelydra, Cuora, Emydoidea, Kinosternon,* and *Sternothaerus,* barely drag their feet at the beginning of protraction, hold the limb high during protraction, and hold their body relatively stable during locomotion like the terrestrial taxa, distinctly unlike the swimmers, *Chrysemys, Clemmys, Malaclemys,* and *Trionyx*. In general, all the turtles except the hinged taxa, *Cuora, Emydoidea,* and *Terrapene,* place their limb perpendicular or anteroventrally at footfall. The large plastron of the hinged taxa appears to force them to extend their limb in a posteroventral direction.

The hindlimb movements in aquatic locomotion clearly reflect the two locomotor patterns. The swimmers move their limbs in a horizontal

plane throughout the entire locomotor cycle. In bottom-walkers, the limb passes through a vertical or strongly inclined plane during retraction and a horizontal plane with protraction. During protraction, the bottom-walkers tend to hold the limb close to the body, swimmers swing the limb outward.

Structurally, the aquatic testudinids and trionychids are quite dissimilar yet their swimming patterns are not very different. Are such differences as initial direction of extension and posterior extent of retraction sufficient justification to say that these taxa developed their pattern of swimming independently? The differences may suggest such an origin, but they hardly seem enough for a firm conviction.

On the other hand, bottom-walking appears to have two separate pathways of origin. The bottom-walking testudinids and chelydrids probably had semiaquatic or terrestrial ancestors. Upon their return to a more aquatic existence, they developed the bottom-walking behavior. Their terrestrial and aquatic locomotor patterns are nearly identical, and the slight differences can be accounted for by the density of water. However, I believe, the structure of the foot and its manner of use in retraction are the critical points. In these bottom-walkers, the webbing between the toes is relatively well-developed, yet the foot seems to lack the flexibility seen in swimmers and kinosternids. But more specifically, the webbing is barely spread during retraction, and even if it were, it would be nonfunctional during most of the retractive stroke since the foot is held flat against the substrate.

The kinosternids have well-developed webbing, and the foot is flexible. It is spread greatly during retraction and collapses or folds upon itself with protraction. At footfall, the foot of kinosternids is tilted laterally so that only the first and second toes touch the bottom. The toes spread widely and draw the webbing taut. Thus, the propulsive stroke is both against the water and the bottom. This suggests that the kinosternid mode of bottom-walking is derived directly from a swimming pattern and that it has not gone through a terrestrial or semiaquatic stage. This origin is not unrealistic as dermatemydids are possibly the ancestors of kinosternids (Zug, 1966), and the former are considered to be swimmers. Likewise, the suggested origin of bottom-walking in chelydrids and the aquatic testudinids is reasonable, as *Cuora* and *Emydoidea* are both semiaquatic taxa. *Chelydra* has a well-developed terrestrial locomotor pattern and is able to make extensive overland migrations (Cagle, 1944). In addition, it is likely that *Platysternon* is closely related to the chelydrids (McDowell, 1964; see Figs. 13 and 21). *Platysternon* is well-known for its ability to clamber over rough terrain and occasionally to climb trees (de Koningh, 1968) which suggests that the ancestors of the chelydrids were semiaquatic if not terrestrial.

It is impossible to divide all cryptodires into a series of categories based on specialized locomotor patterns, because the locomotor pattern of the strictly terrestrial taxa is one extreme of a continuum. All turtles are forced to maintain some level of competence for terrestrial locomotion so that they may come ashore and lay their eggs. To divide cryptodires into locomotor

categories, the first division is by necessity an ecological one, terrestrial and
aquatic. The terrestrial category would contain only those taxa which seldom
enter water voluntarily, and when in deep water, their limb movements
are not co-ordinated for efficient propulsion. The aquatic taxa, in contrast,
can propel themselves efficiently in water and are also able to progress effi-
ciently on land. There are no subdivisions of the terrestrial categories,
whereas the aquatic category can be subdivided into those taxa with fore-
limbs modified to form flippers and those with the forelimb not so modified.
The implication of this division is that one set of limbs provides the major
propulsive force, whereas the other sets act in steering. Unfortunately, there
is no direct quantitative evidence to support this implication. However,
Zangerl (1953) has shown that the forelimb and humerus are longer than the
hindlimb and femur in the anterior appendicular propulsion group and the
converse for the posterior appendicular propulsion group. Moreover, the
webbing of hindfeet is more extensive than that of the forefeet in the taxa
of the latter group. The posterior appendicular propulsion group is com-
posed of the bottom-walkers and swimmers which have been discussed
previously. The distribution of the cryptodiran taxa within these locomo-
tor categories is summarized in Table 15. The only category occupied by
a single, closely related group is terrestrial locomotion, and only testudinids
have successfully invaded this habitat.

It is probable that posterior propulsion is the primitive aquatic loco-
motor pattern. The taxa with anterior appendicular propulsion (Table 15)
are able to swim faster and also to swim continually for longer periods of
time. This ability suggests that the ancestors of these taxa were under a
strong selective pressure to develop a more efficient propulsive mechanism.
Initially, this pressure may have dominated the evolution of their hind-
limbs, as their feet are large and extensively webbed. However, at some
point the pressure to modify the hindlimbs shifted to the forelimbs, and they
were modified into flipper-like appendages. The hindfeet retained the form
observed in most swimming turtles. This shift to the forelimbs may have
occurred by the interaction of two selective pressures on the hindlimbs.
One continually selected for a good propulsive element and the other for a
good nest-digging tool. No matter how efficient a foot was as a propulsive
element, if it were sufficiently modified to prevent nest-digging or to reduce
the quality of nest construction that individual did not reproduce success-
fully, and the highly efficient propulsive element would be lost. Accordingly,
the selection for nest construction prevented the hindfoot from being modi-
fied beyond a certain structural level, and there was an increase in the
selection for the modification of the forelimbs as the main propulsive agents.

There are few morphological differences that can be attributed specifi-
cally to adaptation for terrestrialism. In the pelvis, the presence of a pubo-
ilial notch and a perpendicularly projecting pectineal process are character-
istic of terrestrial species. The functional significance of these is not clear.
The dorsal head of the puboischiofemoralis internus extends across the
notch, so that it may aid the dorsal abduction of the limb. The perpendic-

TABLE 15

TAXONOMIC DISTRIBUTION OF SIX LOCOMOTOR PATTERNS IN CRYPTODIRES

Taxon	Terrestrial	Aquatic	Bottom-Walking	Swimming	Appendicular Propulsion Anterior	Appendicular Propulsion Posterior
Chelydridae		+	+			+
Testudinidae	+	+	+	+		+
Batagurinae	+	+	+	+		+
Emydinae	+	+	+	+		+
Platysterninae		+	+			+
Testudininae	+					
Dermatemydidae		+		+		+
Kinosternidae		+	+			+
Kinosterninae		+	+			+
Staurotypinae		+	+			+
Trionychidae		+		+		+
Lissemyinae		+		+		+
Trionychinae		+		+		+
Carettochelyidae		+		+	+	
Cheloniidae		+		+	+	
Dermochelyidae		+		+	+	

The six divisions are explained in the text. + indicates that a member of the taxon exhibits the locomotor pattern.

ular position of the pectineal process suggests that it may act as a strut. The process of one side braces or resists the torque caused by the retraction of the opposite limb. The femur of a terrestrial taxon has a ventrally enclosed intertrochanteric fossa, and the trochanters are proportionately smaller with little flaring. In association with modification of the proximal end of the femur, the muscles (puboischiofemoralis internus and externus, and ischiotrochantericus), which insert in this region, have smaller areas of attachment. The positions of attachments are not changed in relation to one another, and the usual testudinid pattern is exhibited. Perhaps these reduced attachments result in less rotation of the limb when the muscles contract. The foot of the testudinines is elephantine. The joint is a mesotarsal joint, but unlike all other turtles it appears to be permanently flexed. The terrestrial *Terrapene* has an emydine-like foot with a beginning of toe fusion, and the mesotarsal joint is movable. In the testudinines, the tibialis anterior is absent. Its absence appears to be associated with the loss of flexibility or rotation of the foot. The lengths of the metatarsals and phalanges are proportionately shorter in the testudinines but not in *Terrapene*. A phalanx has been lost in the second, third, and fourth toe and two or three phalanges from the fifth toe in testudinines. In *Terrapene*, only the fourth and fifth toes show a reduction in phalanges.

If swimming taxa are contrasted to walking taxa, there are several structural modifications that appear to be functionally related to locomotor patterns. The length of the femur tends to be shorter in walkers. The head of the femur is circular in walkers and elongate in swimmers. Walkers tend to have shorter metatarsals and phalanges than do swimmers. In some swimmers, an extra phalanx has been added to the fourth or fifth toe. There are no myological modifications that reflect a swimming adaptation in contrast to a walking adaptation. Indeed, there is only a single myological difference that can be correlated directly with bottom-walking and that is the absence of the dorsal head of the puboischiofemoralis internus in chelydrids and kinosternids.

In extant cryptodires, there appear to be four distinct lineages (Zug, 1966), Dermatemydidae and Kinosternidae, Carettochelyidae and Trionychidae, Chelydridae and Testudinidae, and Cheloniidae and Dermochelyidae. The last lineage and Carettochelyidae are not examined in this study so they will go without comment. Two Prim Networks (Figs. 13 and 21) have been generated, and although they are phenetic constructs, they also support the existence of these lineages.

The first lineage contains a swimming family, Dermatemydidae, and a bottom-walking family, Kinosternidae. At first, this may suggest that they are unrelated, but the number of shared morphological attributes implies the converse and also indicates that dermatemydids are the ancestral group. In all cryptodires except this lineage, the last two dorsal vertebrae are fused to the carapace. *Dermatemys* has the tenth one free, kinosternids the ninth and tenth free (this condition recorded first by Siebenrock, 1907). All swimming cryptodires except *Dermatemys* have a dorsal head to the puboischiofemoralis internus; the bottom-walking kinosternids lack this head. Both taxa have a single-headed iliotibialis arising on the anterior edge of the ilium unlike any of the other lineages; however, in *Dermatemys* the origin is distal and in kinosternids in the middle on a thelial process. The dermatemydid condition appears to be intermediate between a single-headed origin on the distoanterior corner of the ilium and the kinosternid condition. These features, with several other shared characteristics, substantiate the closeness of dermatemydids and kinosternids and indicate that the latter were derived from the former.

Usually, the kinosternids are divided into two subfamilies, Staurotypinae and Kinosterninae. This division is evident in the morphology of the girdle and limbs. The kinosternines generally possess a metischial process and an extension from the pubis and ischium between the puboischiadic foramina; these are reduced or absent in the staurotypines. The anterior head of the gastrocnemius attaches on the tibia and femur in staurotypines, only on the tibia in kinosternines. The flexor tibialis internus has a double insertion in kinosternines, single in staurotypines.

The trionychids are a very distinct family of turtles. This is strongly reflected both in the osteological and myological architecture of their pelvic girdle and hindlimbs and has been repeatedly pointed out in the preceding

text. In 1966, I suggested that the carettochelydid-trionychid lineage might be a derivative of the dermatemydid-kinosternid lineage or at least the two lineages may have had a common ancestor. At that time, I was unaware that Baur (1891b) had intimated the same relationship. This supposition is supported by the present study in that these two lineages share a number of attributes that are found nowhere else in the cryptodires. Both have tee-shaped ilia strongly inclined posteriorly. Both have a distinct muscle, the caudifibularis, derived from the flexor tibialis internus. Similar architecture of the flexor tibialis complex and the gastrocnemius is shared by members of the two lineages. In other characters, the trionychids are closer to the dermatemydid-kinosternid lineage than any other group (see Prim Networks, Figs. 13 and 21).

The chelydrid-testudinid lineage is composed of terrestrial, bottom-walking, and swimming taxa. Even though this lineage shows the complete range of locomotor adaptation, all of its members share several morphological characteristics that substantiate its monophyly. All ten dorsal vertebrae are fused to the carapace. The ilium is spool-shaped and not greatly inclined. The puboischiadic foramina are distinctly separated. The metischial processes are similar in form and position. The structure of the flexor tibialis internus is identical in the two families, and they lack the caudifibularis.

In both the Prim Networks (Figs. 13 and 21), *Chelydra* is closer to *Platysternon* than to any of the other genera, and it is always linked to the testudinids through *Platysternon*. This implied relationship has been recently alluded to by McDowell (1964) and is certainly strengthened by this study. The two genera possess a common habitus unlike that of any other extant cryptodire. They have depressed carapaces, reduced plastra, enlarged heads, and long tails. In fact, the tails of *Chelydra* and *Platysternon* have more than 30 caudal vertebrae, whereas other testudinids, kinosternids, and trionychids have less than 20 caudal vertebrae. The osteology of their pelvic girdle and hindlimbs is similar. Both have a single-headed iliotibialis on the distoanterior corner of the ilium. Their ambiens arise on the puboischiadic ligament. The architecture of the flexor tibialis externus is the same in the two. Both chelydrids and *Platysternon* are bottom-walkers, and this may account for their similar morphology. However, other bottom-walkers do not share the above characteristics, which suggests that they are bottom-walkers because they had a common bottom-walking or nonswimming ancestor.

Kinosternids show several morphological similarities with chelydrids (specifically, see the myological Prim Network, Fig. 21). They are also both bottom-walking taxa. Their common locomotor pattern is sufficiently different to suggest that it is convergent rather than inherent. However, kinosternids have been considered as a subfamily of chelydrids (Williams, 1950) on the basis of other morphological features; therefore it should not be suggested that all of the similarities of systems presently being studied represent convergence to a similar locomotor pattern. A discussion of which simi-

larities are attributed to similar functional adaptations or which are a result of inheritance from a common ancestor would be completely speculative at this stage.

The incongruities between the chelonian fossil record (Holman, 1967) and our present interpretation of cryptodiran relationships make the presentation of a phylogeny of cryptodires hazardous. The trionychids are the only cryptodires to appear in the Jurassic. Structurally, they are a specialized group at their first appearance. A possible ancestral group, the dermatemydids, does not appear in the fossil record until the Upper Cretaceous contemporaneously, with some testudinids. In the Eocene, the carettochelyids appear, and in many ways they seem to be primitive and ancestral to the trionychids. It is not until the Miocene that unquestionable chelydrids appear and not until the middle Pliocene that kinosternids are found. It seems unlikely that the kinosternids could have undergone their great speciation in such a short time. More fossil material is urgently needed if we are to correct these incongruities.

SUMMARY

Cryptodires cannot be taxonomically subdivided by the present method of gait analysis. On land, turtles proceed at a very slow or slow walk and generally with a lateral sequence gait. In water, they move at speeds ranging from a fast walk to a moderate run with a diagonal sequence gait.

Only in aquatic locomotion are two distinct patterns evident, i.e., bottom-walking and swimming. The former is characterized by vertical limb movements, the latter by horizontal limb movements. Most aquatic testudinids and all trionychids are swimmers. Chelydrids, kinosternids, and some aquatic testudinids are bottom-walkers. It is suggested that bottom-walking has had two different origins, the kinosternid mode from a swimming ancestor, the chelydrid-testudinid mode from a terrestrial or semi-aquatic ancestor.

The dermatemydid-kinosternid and the chelydrid-testudinid lineages appear to form two natural, monophyletic groups. Further evidence is presented to show that the trionychids are related to the dermatemydid-kinosternid lineage. It is suggested that the chelydrids and platysternines are closely related, thereby providing an additional tie between the chelydrids and testudinids.

APPENDIX I

The gait formulae in Figure 1 were determined for the following species during terrestrial locomotion. The first number in the parentheses indicates the number of formulae calculated for that species; the second is the number of individuals used. The descriptions of hindlimb movement were also recorded for these species.

Family Chelydridae
    Chelydra serpentina (5, 2)
Family Testudinidae
    Cuora amboinensis (1, 1)
    Chrysemys concinna (4, 2)
    Chrysemys floridana (2, 1)
    Chrysemys picta (4, 1)
    Chrysemys scripta (2, 2)
    Clemmys guttata (1, 1)
    Clemmys insculpta (1, 1)
    Clemmys marmorata (7, 4)
    Emydoidea blandingi (2, 1)
    Malaclemys terrapin (4, 1)
    Terrapene carolina (9, 5)
    Gopherus polyphemus (5, 2)

Family Kinosternidae
    Kinosternon bauri (1, 1)
    Sternothaerus carinatus (5, 4)
    Sternothaerus minor (3, 3)
    Sternothaerus odoratus (2, 2)
Family Trionychidae
    Trionyx ferox (1, 1)
    Trionyx spinifer (7, 3)

APPENDIX II

The gait formulae in Figure 5 were determined for the following species during aquatic locomotion. The first number in the parentheses indicates the number of formulae calculated for that species, the second the number of individuals used. ,

Family Chelydridae
    Chelydra serpentina (4, 2)
Family Testudinidae
    Cuora amboinensis (4, 1)
    Notochelys platynota (1, 1)
    Chrysemys concinna (1, 1)
    Chrysemys picta (2, 1)
    Chrysemys scripta (9, 6)
    Clemmys guttata (4, 2)
    Clemmys insculpta (1, 1)
    Clemmys marmorata (5, 4)
    Emydoidea blandingi (5, 1)
    Malaclemys geographica (1, 1)
    Malaclemys terrapin (3, 1)

Family Kinosternidae
    Kinosternon bauri (5, 3)
    Sternothaerus carinatus (1, 1)
    Sternothaerus minor (6, 4)
    Sternothaerus odoratus (1, 1)
Family Trionychidae
    Trionyx spinifer (3, 2)

APPENDIX III

Osteological measurements or radiographs were made on the following turtles. Unless designated otherwise the specimens are from the University of Michigan Museum of Zoology herpetological collection. KKA, Kraig Adler collection and GZ, George Zug collection.

CHELYDRIDAE.—*Chelydra serpentina,* S58, S830–31, S1286, S2042, S2984, 99250, 127056; *Macroclemys temmincki,* 72528–29.

TESTUDINIDAE.—*Batagurinae: Mauremys caspica,* GZ90; *Rhinoclemys annulata,* 127064; *Rhinoclemys pulcherrima,* S2566; *Rhinoclemys rubida,* S2146. *Emydinae: Chrysemys concinna,* S789, 127058; *Chrysemys floridana,* S69, S459, S784–7, 128082; *Chrysemys nelsoni,* 127–59–60; *Chrysemys ornata,* S1757, S1839; *Chrysemys picta,* S76–82, S87, S94, S96, S100–1, S104–5, S108–9, S185, S260, S2373, S2994, S2996, S2998, 127057; *Chrysemys scripta,* S68, S75,

S116–7, S667, S1182–3, S2700, S2787, 128084; *Clemmys guttata*, S14–7, S1133; *Clemmys insculpta*, S7–13, S427, GZ25; *Clemmys marmorata*, S1–6, S258–9; *Deirochelys reticularia*, GZ50; *Emydoidea blandingi*, S18–21, S23–7, S406, S2538; *Malaclemys geographica*, S64, S70, S118, 127062–3; *Malaclemys terrapin*, S221, S2698, S2791, S2824; *Terrapene carolina*, S28–33, S40, S47, S435, S1169, S1214, S2985–7, 128085; *Terrapene coahuila*, 126148–49; *Terrapene ornata*, S34–9, S432–4, S1213, S2988. Platysterninae: *Platysternon megacephalum*, S3000, 112313, KKA213. Testudininae: *Gopherus berlandieri*, S2871, S2914–5, S2974–5; *Gopherus polyphemus*, S73, S184, 127307, GZ12, GZ34; *Kinixys erosa*, S182–3, S2567, 128090.

DERMATEMYDIDAE.—*Dermatemys mawi*, 75286, 79126, 119137.

KINOSTERNIDAE.—*Kinosterninae: Kinosternon bauri*, S2976–7, GZ16; *Kinosternon integrum*, S2147, S2699; *Kinosternon flavescens*, S54, S1211–2, S2954, 127065–6, 127242–3, 127246–7, 127250, 127254, 127259; *Sternothaerus odoratus*, S42, S44, S46–9, S110–2, S386, S392–5, S2978–83. Staurotypinae: *Claudius angustatus*, S1802, S2298, 72528, 117207, 117212, 117214, 117217–20, 117222; *Staurotypus salvini*, S1758, 87737, 87741–2, 87744.

CARETTOCHELYIDAE.—*Carettochelys insculpta*, 123941.

TRIONYCHIDAE.—*Lissemyinae: Lissemys punctata*, 121944, 123458, AMNH 90082; Trionychinae: *Pelochelys bibroni*, 68808; *Trionyx ferox*, 104024, 128087; *Trionyx muticus*, S222, 128086; *Trionyx spinifer*, S61, S2830–1, 74518, 74670, 88950(2), 89923, 112252, 116718, 123584, 126234, 128088.

APPENDIX IV

A series of measurements was taken from the bony elements of the pelvic girdle and hindlimb of cryptodires. Most of the measurements were converted into ratios to permit a comparison of different-sized taxa. The descriptions of the measurements and the ratios are arranged alphabetically according to the abbreviations used in the text.
Measurements.

AH.   Acetabular height; the perpendicular distance from the ventral plane of girdle contact to the center of the acetabulum.

BWPp.   Basal width of pectineal process; the distance across the proximal end of the process measured perpendicular to the longitudinal axis of the process.

CCL.   Eighth cervical vertebra length; the anteroposterior length through the centrum of the eighth cervical vertebra.

FH.   Femoral arch height; the perpendicular distance from a plane formed by the highest point on the ventral surface of the femoral shaft.

FHL.   Femoral head length; the maximum distance across the center of the femoral head.

FHW.   Femoral head width; the minimum distance across the center of the femoral head.

FL.   Femoral length; the distance from notch formed between head and trochanter major and the distal surface of condyles.

IA.   Ilial angle; the angle formed by the anterior edge of ilium and the ventral plane of pelvic contact. In some cryptodires the ilium possesses a sharp flexure, thus a proximal and distal angle were recorded. Angles greater than 90° indicate that the ilium is inclined posteriorly.

IL.   Ilial length; the distance from the proximoanterior to the distoanterior corner of the ilium.

LIF.   Length to intertrochanteric fossa; the distance between the bottom of fossa and the intercondylar concavity.

LPP.   Length of puboischiadic plate; the maximum anteroposterior distance across the pubis and ischium.

LTM.   Length to trochanter major; the distance from the center of the femoral condyles to the distal edge of trochanter major.

ML.   Metatarsal length; the longitudinal length of the metatarsal of the second toe.

PhL.   Phalangeal length; the longitudinal length of the proximal phalanx of the second toe.

PpA.   Pectineal process angle; the angle formed by the posterior edge of the pectineal process and pubic symphysis. An angle greater than 90° indicates a posteriorly directed process.

PW.   Proximal width of femur; the maximum distance across the flare of the trochanters and perpendicular to the longitudinal axis of the shaft.

TL.   Tibial length; the longitudinal length of tibia between proximal and distal articular surfaces.

WA.   Width between acetabula; the transverse distance across the puboischiadic plate from the center of one acetabulum to that of the other.

WMa.   Width of trochanter major; distance between ventral edge of trochanter major and junction of trochanter and femoral head.

WMi.   Width of trochanter minor; distance between ventral edge of trochanter minor and junction of trochanter and femoral head.

Ratios.

AH/CCL.	A relative measure of the longitudinal arching of the puboischiadic plate.
BWP_p/CCL.	An estimate of the size of the pectineal process.
FHW/FHL.	An indication of the shape of femoral head; a value of 1.0 denotes a circular head.
FL/CCL.	A relative measure of femoral length.
FL/FH.	A relative measure of the curvature of the femur.
FL+TL+ML+PhL/CCL.	A relative measure of hindlimb length.
IL/CCL.	A relative measure of ilial length.
LIF/LTM.	An estimate of the extent of the intertrochanteric fossa. A value of 1.0 denotes a ventrally closed fossa.
LLP/CCL.	A relative measure of the length of the puboischiadic plate.
ML/TL.	A relative measure of metatarsal length.
PhL/ML.	A comparison between metatarsal and phalangeal length.
PW/CCL.	An approximation to the amount of trochanteric flare.
TL/FL.	A relative measure of tibial length.
WA/CCL.	A relative measure of the width of the puboischiadic plate.
WMi/WMa.	A comparison of trochanter size. Values less than 1.0 indicate that trochanter major is the larger, 1.0 trochanters equal in size, and greater than 1.0, trochanter minor the larger.

APPENDIX V

The musculature of the pelvic girdle and hindlimb was dissected in representatives of all families and subfamilies of cryptodiran turtles except Carettochelyidae, Cheloniidae, and Dermochelyidae. The following species were dissected; the number in parentheses is the number of individuals examined.

CHELYDRIDAE
        Chelydra serpentina (2)

TESTUDINIDAE
    Batagurinae
        Rhinoclemys punctularia (1)
    Emydinae
        Chrysemys floridana (1)
        Chrysemys picta (1)
        Chrysemys scripta (1)
        Clemmys guttata (1)

        Clemmys insculpta (1)

        Emydoidea blandingi (2)

        Malaclemys geographica (1)

        Malaclemys terrapin (1)

        Terrapene carolina (1)

        Terrapene ornata (1)

    Platysterninae

        Platysternon megacephalum (2)

    Testudininae

        Geochelone carbonaria (1)

        Gopherus berlandieri (1)

        Gopherus polyphemus (1)

DERMATEMYDIDAE

        Dermatemys mawi (1)

KINOSTERNIDAE

    Kinosterninae

        Kinosternon integrum (1)

        Sternothaerus carinatus (1)

    Staurotypinae

        Claudius angustatus (1)

        Staurotypus triporcatus (1)

TRIONYCHIDAE

    Lissemyinae

        Lissemys punctata (2)

    Trionychinae

        Trionyx ferox (1)

        Trionyx spinifer (1)

APPENDIX VI

    The muscle attachments have been summarized and discussed in the text. The descriptions of the attachment sites are presented here to provide future dissectors with some additional details of my observations. The descriptions are greatly condensed and presented in a telegraphic style. Although this manner of presentation has caused a loss of some information, it enhances the retrieval of the more critical data.

    The format is the presentation of the most common origin and insertion. These common attachments are followed by the variant condition and the taxa in which they occur. The taxa possessing the most common attachment are not listed and are all those specimens examined (Appendix V) other than the variants. Since the short digital extensor and flexor muscles are composed of several individual muscles, the descriptions of these compound muscles present only the condition common to all members of the muscle group. Only the area of attachment is described, not the manner of attachment. My observations of the digital muscles (extensor digitorum breves, interossei dorsales, flexor digitorum communis sublimis, lumbricales, interossei plantares) of *Geochelone* and *Gopherus* have not been included.

TESTOILIACUS

Single Origin.—(all except *Lissemys*). Ventrally on posterior half of 6th pleural, entire 7th pleural, and anterior half of 8th pleural. *Chelydra*, also on 8th and 9th dorsal ribs and entire 8th pleural; *Clemmys, Geochelone,* not on 6th pleural but on entire 8th pleural; *Platysternon, Emydoidea, Gopherus, Claudius,* also on entire 8th pleural; *Dermatemys,* also ventrolaterally on 9th and 10th dorsal vertebrae; *Kinosternon,* also on entire 5th, 6th, and 8th pleurals and ventrolaterally on 8th and 9th dorsal vertebrae; *Sternothaerus,* also

on entire 6th pleural but not on 8th pleural; *Staurotypus,* also on entire 6th and 8th pleurals and ventrolaterally on posterior end of 7th, entire 8th, 9th, and anterior end of 10th dorsal vertebrae; *Trionyx,* also on 9th and 10th dorsal vertebrae and ribs but not on 6th pleural.

Double Origin.—*(Lissemys).* Anterior head: Ventrally on distal ends of 6th and 7th pleurals. Posterior head: Ventrally on 8th pleural.

Single Insertion.—(all except *Lissemys).* Laterally and anteriorly on distal end of ilium. Kinosternids, restricted to laterally on distal one-third of ilium.

Double Insertion.—*(Lissemys).* Superficial head: By tendon to distolateral edge of ilium and laterally on 1st few caudal vertebrae. Profound head: Laterally at two points on distal end of ilium.

RECTUS ABDOMINIS

Origin.—Dorsally on xiphiplastron and posterior half of hypoplastron. *Terrapene, Dermatemys, Kinosternon,* most of hypoplastron; *Lissemys,* also on posterior part of hypoplastron; *Trionyx,* entire hypoplastron.

Insertion.—Dorsally on distal one-half to one-third of pectineal process of pubis. *Clemmys guttata,* covers nearly entire process; *Clemmys insculpta,* only on distal tip of process; *Terrapene,* only on anterior edge of process but onto anterolateral edge of pubis; *Geochelone, Staurotypus,* trionychids, on entire process; *Gopherus,* only on anterolateral edge of process but anteriorly on ventral surface of puboischiadic ligament; *Dermatemys,* barely extends onto dorsal surface of process.

PUBOISCHIOFEMORALIS INTERNUS

Single Origin.—*(Chelydra, Dermatemys,* kinosternids). Dorsally on epipubis and pubis and anteriorly on base of ilium. *Chelydra,* also on ischium along midline and medially on base of ilium.

Double Origin.—(testudinids, trionychids). Dorsal head: Anteriorly and medially on distal end of ilium and ventrally on 1st sacral vertebra. *Rhinoclemys,* also on 2nd sacral rib; *Chrysemys,* also on last 2 dorsal vertebrae; *Clemmys,* also on last dorsal vertebra; *Emydoidea,* proximal end of ilium instead of distal; *Malaclemys,* proximal half of ilium instead of distal; *Geochelone,* also anteriorly on proximal end of ilium and 2nd sacral vertebra; *Lissemys,* not on vertebrae and extending medially along entire length of ilium; *Trionyx,* not on ilium. Ventral head: Dorsally on epipubis and pubis excluding most of pectineal process. *Clemmys,* also on anteromedial base of ilium; *Platysternon,* also on anterior edge of ischium; *Trionyx,* also anteriorly on base of ilium.

Insertion.—Dorsally on neck of femur and base of trochanter minor. *Dermatemys,* kinosternids, extension onto trochanter less.

ILIOFEMORALIS

Single Origin.—(all except trionychids). Laterally on proximal two-thirds more or less, of ilium, medially on distoanterior corner of ilium, and ventrally on 1st sacral rib. *Chelydra, Chrysemys, Terrapene,* also distoposterior corner of ilium; *Emydoidea,* not on 1st sacral but on 9th and 10th dorsal vertebrae and ribs; *Malaclemys, Geochelone, Gopherus,* same as *Emydoidea* and also on distoposterior corner of ilium; *Platysternon,* also on 10th dorsal and 1st sacral vertebrae; *Dermatemys, Kinosternon, Sternothaerus, Claudius, Staurotypus,* not on rib nor distoanterior corner of ilium but medially on anterior border of ilium.

Double Origin.—(trionychids). Medial head: Ventrally on 9th and 10th dorsal vertebrae and ribs. Lateral head: Laterally on middle half of ilium.

Insertion.—Dorsally on trochanter major. *Terrapene, Platysternon, Geochelone,* also onto its ventral edge.

ILIOFIBULARIS

Origin.—Laterally on distoposterior corner of ilium. *Malaclemys,* also on medial surface of same area, *M. terrapin* has additional head arising on ischiotrochantericus; *Sternothaerus, Claudius, Staurotypus,* origin restricted laterally to middle of ilium.

Insertion.—Dorsally on proximal end of fibula. *Emydoidea, Platysternon, Geochelone, Gopherus, Dermatemys, Lissemys,* dorsally on proximal second quarter of fibula.

ILIOTIBIALIS

Single Origin.—(*Chelydra, Platysternon,* kinosternids, trionychids). *Chelydra, Platysternon,* laterally on distoanterior corner of ilium; kinosternids, from thelial process of ilium; trionychids, laterally on distal end of ilium.

Double Origin.—(*Rhinoclemys,* emydines, *Geochelone*). By bifurcated tendon, one laterally on distoanterior corner of ilium, other laterally on distoposterior corner.

Triple Origin.—(*Gopherus*). Two laterally on distoanterior corner of ilium, one laterally on distoposterior corner.

Insertion.—Posterodorsally on distal end of femorotibialis. *Lissemys,* also proximally on fascia sheet over crus.

AMBIENS

Origin.—Laterally on anterior end of puboischiadic ligament. *Rhinoclemys,* only on posterior edge of proximal end of pectineal process of pubis; *Emydoidea,* only on middle of ligament; *Malaclemys,* also dorsally on process adjacent to ligament; *Terrapene, Sternothaerus,* barely on ligament but dorsally on distoposterior edge of process; *Geochelone, Kinosternon, Staurotypus,* only on proximoposterior edge of process; *Lissemys,* only ventrally on puboischiofemoralis internus near latter's insertion; *Trionyx,* only on edge of pubis posteriorad of process.

Insertion.—Anterodorsally on distal end of femorotibialis.

FEMOROTIBIALIS

Single Origin.—(*Chelydra,* testudinids, *Dermatemys,* kinosternids). Dorsally on femoral shaft extending slightly onto trochanters and overlapping ventrally along anterior, posterior, or both edges of shaft.

Double Origin.—(trionychids). Ischial head: Dorsomedially on ischium. Femoral head: Same as in single origin, except ventral surface more extensively covered in *Lissemys.*

Insertion.—Dorsally on proximal end of tibia in association with iliotibialis and ambiens.

PUBOISCHIOFEMORALIS EXTERNUS

Origin.—Ventrally from entire puboischiadic plate, usually by two fiber bundles, ischial and pubic. *Chelydra,* additional bundle from pectineal process; *Chrysemys picta, Platysternon,* no clear division into separate bundles; *Kinosternon,* additional separation on pubis; *Lissemys,* also distinct head dorsally on posterior one-third of puboischiadic ligament.

Insertion.—Dorsally on trochanter minor and ventrally along its edge. *Malaclemys, Terrapene, Geochelone, Gopherus, Kinosternon, Sternothaerus, Staurotypus,* trionychids, extending into intertrochanteric fossa to varying degrees, particularly prominent in kinosternids and trionychids.

CAUDI-ILIOFEMORALIS

Origin.—Medially on distal end of ilium and ventrally along vertebral column from 9th dorsal to 1st caudal vertebra. *Chelydra,* absent from ilium and dorsal vertebrae; *Rhinoclemys, Staurotypus,* not on ilium; *Terrapene, Geochelone, Gopherus, Sternothaerus, Claudius,* not on dorsal vertebrae; *Platysternon, Trionyx,* not on dorsal or caudal vertebrae; *Dermatemys, Kinosternon,* not on caudal vertebrae.

Insertion.—On ischiotrochantericus at its insertion and ventrally on edge of trochanter

major; *Rhinoclemys,* not on trochanters; *Terrapene,* not on trochanter major; *Geochelone,* not on trochanters but on iliofemoralis at its insertion; *Dermatemys,* only on trochanter major; kinosternids, *Trionyx,* on femur but not on ischiotrochantericus.

ISCHIOTROCHANTERICUS

Origin.—Dorsally on most of ischium, posterior border of pubis, and posteromedial on base of ilium. *Chelydra, Platysternon,* trionychids, not on pubis; *Rhinoclemys,* not on ilium; *Dermatemys,* kinosternids, restricted to ischium.

Insertion.—In intertrochanteric fossa, commonly confined to posterior one-half or two-thirds of fossa.

ADDUCTOR FEMORIS

This muscle is absent in trionychids.

Origin.—Dorsally on posterior one-half of puboischiadic ligament and edge of metischial process or ischium in absence of process. *Rhinoclemys, Gopherus,* not on ischium; *Terrapene,* only on middle of ligament; *Claudius,* only on ischium.

Insertion.—Ventrally on femoral shaft and occasionally in part from one or both trochanters.

FLEXOR TIBIALIS INTERNUS

Single Origin.—*(Geochelone, Gopherus).* Laterally on posterior one-third of puboischiadic ligament and metischial process. *Gopherus,* lacks attachment on ligament.

Double Origin.—(all except testudinines). Dorsal head: Medially on distoposterior corner of ilium, ventrally on 2nd sacral rib and vertebrae and first 2–3 caudal vertebrae. *Chrysemys, Clemmys, Emydoidea, Malaclemys, Dermatemys, Kinosternon, Trionyx,* not on ilium; *Claudius,* not on sacral vertebra or rib; *Lissemys,* not on ilium or sacral vertebra or rib. Ventral head: Laterally on at least posterior half of puboischiadic ligament and dorsally on distal end of metischial process or ischium. *Kinosternon, Trionyx,* not from ischium or its process; *Lissemys,* not from ligament.

Single Insertion.—*(Chelydra,* testudinids, *Claudius, Staurotypus).* Ventrally on proximo-anterior area of tibia.

Double Insertion.—*(Dermatemys, Kinosternon, Sternothaerus,* trionychids). Tibial slip: Ventrally on middle or proximal second quarter of tibia. Plantar slip: Anteriorly to proximal edge of plantar aponeurosis. Trionychids, posteriorly to fascia sheet over crus.

FLEXOR TIBIALIS EXTERNUS

Single Origin.—*(Chelydra, Terrapene, Platysternon, Dermatemys,* kinosternids, *Trionyx).* Dorsally on metischial process. Kinosternids, dorsally on distomedial area of ischium; *Trionyx,* also on extreme posterior end of puboischiadic ligament and posterior border of ischium.

Double Origin.—(testudinids except *Terrapene).* Dorsal head: Very variable. *Rhinoclemys,* distinct distally but arises as part of flexor tibialis internus; *Chrysemys,* medially on distoposterior edge of ilium, not distinctly separate from flexor tibialis internus; *Clemmys,* ventrolaterally on first two caudal vertebrae; *Emydoidea, Malaclemys,* posteromedially on distal end of ilium and ventrally on distal half of 2nd sacral rib; *Gopherus,* ventrally on 3rd to 5th caudal vertebrae; *Geochelone,* ventrally on 2nd sacral rib and vertebra and first two caudal vertebrae.

Single Insertion.—*(Trionyx).* Ventrally on proximoposterior corner of tibia.

Double Insertion.—*(Chelydra,* testudinids, *Dermatemys,* kinosternids). Tibial head: Ventrally on proximoposterior corner of tibia. Plantar head: Medially to proximal edge of plantar aponeurosis of gastrocnemius.

Two Separate Muscles.—*(Lissemys).* (1) Origin: Ventrolaterally on first three caudal vertebrae. Insertion: Dorsally on distal end of flexor tibialis internus. (2) Origin: Dorsally on posteromedial surface of ischium. Insertion: Ventrally on proximoposterior corner of tibia.

CAUDIFIBULARIS

This muscle occurs only in *Dermatemys*, kinosternids, and trionychids.

Origin.—Laterally on 1st or 1st and 2nd caudal vertebrae.

Insertion.—Posterolaterally to fascia sheet on crus over posterior head of gastrocnemius.

PUBOTIBIALIS

Origin.—Laterally on middle of puboischiadic ligament. *Rhinoclemys, Geochelone,* anteriorly on proximal aponeurosis of flexor tibialis internus; *Terrapene,* laterally on anterior end of ligament; *Lissemys,* laterally on posterior half of ligament.

Insertion.—Ventrally on proximoposterior corner of tibia and/or adjacent joint fascia.

EXTENSOR DIGITORUM COMMUNIS

Origin.—Dorsally on distal corner of fibular condyle of femur. Trionychids dorsally on distomedial surface of femur.

Insertion.—The insertion is very variable and is divided into four slips, one to each of the first four toes except for three to middle toes in *Platysternon. Chelydra, Kinosternon, Staurotypus, Lissemys,* on posterodorsal edge of proximal phalanx and distal end of metatarsal; *Rhinoclemys, Terrapene,* dorsally on short digital extensors; *Chrysemys, Sternothaerus, Claudius, Trionyx,* dorsally on distal end of metatarsal; *Clemmys,* dorsally on short digital extensor and occasionally to proximala nd penultimate phalanges; *Emydoidea, Malaclemys, Dermatemys, Platysternon,* dorsally on short digital extensors and to distal end of metatarsals; *Gopherus, Geochelone,* not divided into slips, on short digital extensors and associated fascia.

PERONEUS

This is a single muscle only in *Terrapene, Gopherus, Kinosternon,* and *Sternothaerus.* The other genera possess both a peroneus anterior and peroneus posterior.

Origin.—Posterodorsally on fibula. *Gopherus,* only on distal half.

Insertion.—Dorsally on metatarsal V and proximal end of proximal phalanx V. *Gopherus, Kinosternon,* only on metatarsal.

PERONEUS ANTERIOR

Single Origin.—(*Chelydra,* testudinids, *Dermatemys,* kinosternids). Posterodorsally on approximately distal two-thirds of fibula.

Double Origin.—(trionychids). Superficial head: Dorsally on fibular condyle of femur, proximoposterior corner of tibia, and proximoanterior corner of fibula. Profound head: Dorsally on distoposterior edge of fibula.

Insertion.—Dorsally on distal end of metatarsal V onto posterior edge of proximal phalanx V. *Chrysemys,* also joins plantar aponeurosis posteriorly; *Lissemys,* also on middle of metatarsal IV and to posterior edge of plantar aponeurosis.

PERONEUS POSTERIOR

Origin.—Dorally on distoposterior corner of fibula.

Insertion.—Dorsally on metatarsal V. *Chrysemys, Emydoidea, Staurotypus,* also on proximoposterior part of metatarsal IV.

TIBIALIS ANTERIOR

This muscle does not occur in *Geochelone* and *Gopherus.*

Single Origin.—(all except *Lissemys*). Dorsally along anterior edge of tibia.

Double Origin.—(*Lissemys*). Superficial head: Anteriorly on edge of tibial condyle of femur. Profound head: Same as in single origin.

Insertion.—Dorsally on proximoanterior edge of metatarsal and tarsale I and ventrally to

anterior edge of plantar aponeurosis. *Rhinoclemys, Chrysemys, Malaclemys, Dermatemys, Staurotypus,* not on tarsale I; *Terrapene,* not to aponeurosis; *Platysternon, Sternothaerus,* trionychids, only to metatarsal.

EXTENSOR HALLUCIS PROPRIUS

Origin.—Dorsally on distoanterior corner of fibula.

Insertion.—Dorsally on short digital extensors, particularly interossei dorsales, of first toe. *Chelydra, Chrysemys, Clemmys, Emydoidea, Gopherus, Kinosternon, Claudius,* trionychids, also to bones of first toe.

EXTENSOR DIGITORUM BREVES

Three separate muscles, one to each of middle three toes *(Rhinoclemys, Chrysemys, Platysternon, Sternothaerus,* trionychids); or four separate muscles, one to each of first four toes *(Chelydra, Clemmys, Emydoidea, Malaclemys, Terrapene, Dermatemys, Kinosternon, Staurotypus, Claudius).*

Origin.—Dorsally from fascia sheet over tarsale, usually radiate outward from common origin over tarsalia III and IV. *Chelydra,* also from metatarsals.

Insertion.—Very variable. *Chelydra,* dorsally to proximal end of ultimate phalanx of first toe or proximal end of penultimate phalanx of 2nd, 3rd, and 4th toes; *Rhinoclemys, Chrysemys, Platysternon,* dorsally on interossei dorsales and penultimate and ultimate phalanges; *Clemmys, Staurotypus,* dorsally on interossei dorsales; *Emydoidea,* dorsally on proximal end of metatarsal; *Malaclemys,* dorsally to interossei dorsales and penultimate phalanx; *Terrapene,* dorsally on interossei dorsales and proximal end of ultimate phalanx; *Dermatemys,* dorsally on distal end of proximal phalanx and penultimate phalanx; *Kinosternon,* trionychids, dorsally on proximomedial edge of penultimate phalanx; *Sternothaerus, Claudius,* dorsally on distal end of proximal phalanx.

INTEROSSEI DORSALES

All have four separate muscles, one to each of the first four toes, except *Lissemys,* which has five.

Origin.—Dorsally from metatarsal. *Sternothaerus, Claudius,* also on tarsale.

Insertion.—Dorsally on proximal phalanx. *Clemmys, Emydoidea, Malaclemys, Terrapene, Kinosternon,* also to proximal end of penultimate phalanx.

GASTROCNEMIUS

Double Origin.—Anterior head: Ventrally on proximoanterior area of tibia. *Malaclemys, Terrapene, Kinosternon, Sternothaerus,* cleft proximally by insertion of flexor tibialis internus; *Geochelone, Gopherus,* also extends onto anterior border of tibia; *Dermatemys, Claudius, Staurotypus, Lissemys,* cleft proximally by insertion of flex. tib. int. and also ventrally on tibial condyle of femur; *Trionyx,* also ventrally from anterior border of tibial condyle. Posterior head: Ventrally on distoposterior edge of fibular condyle of femur. *Malaclemys,* also slightly from adjacent edge of fibula.

Insertion.—Ventrally to distal end of flexor plate and adjacent short digital flexors and to posterior edge of metatarsal and proximal phalanx V. *Chelydra, Geochelone,* not on digital elements; *Chrysemys, Emydoidea, Terrapene, Platysternon, Gopherus, Staurotypus, Lissemys,* not on proximal phalanx. In some of specimens dissected this muscle also appeared to have four small tendinous slips inserting, one each, to flexor tendons.

FLEXOR DIGITORUM LONGUS

Single Origin.—*(Gopherus).* Ventrally on fibula.

Double Origin.—(all except *Gopherus).* Superficial head: Ventrally on distoposterior corner of fibular condyle of femur. Profound head: Ventrally on posterior edge of fibula. *Rhinoclemys, Chrysemys, Terrapene,* also extending ventrally onto proximal part of metatarsal

V. *Trionyx* has an anterior head arising ventrally from anterior border of tibia and a posterior head combining double origin mentioned above.

Insertion.—Distally in plantar region, muscle forms a thick, tendinous flexor plate, which divides at base of digits into four flexor tendons, one to each of first four toes; each flexor tendon inserts ventrally on proximal end of ultimate phalanx. *Geochelone,* flexor plate present but tendons not distinct; *Staurotypus,* five flexor tendons.

PRONATOR PROFUNDUS

Origin.—Ventrally on fibula, usually restricted to anterior half. *Platysternon, Trionyx,* also extending onto distoposterior corner of tibia.

Insertion.—Ventrally on tarsal fascia sheet centered over tarsale I.

POPLITEUS

Origin.—On anterior surface of fibula.

Insertion.—On posterior surface of tibia.

FLEXOR DIGITORUM COMMUNIS SUBLIMIS

Three separate muscles, one to each of middle three toes (*Dermatemys, Kinosternon, Claudius, Staurotypus,* trionychids); four separate muscles, one to each of first four toes (*Chelydra,* testudinids, *Sternothaerus*).

Origin.—Ventrally on distal end of flexor plate.

Insertion.—Ventrally on flexor tendon sheath near base of toe. *Chelydra, Dermatemys, Claudius,* also extending onto ventral edge of proximal phalanx.

LUMBRICALES

Four separate muscles, one to each of last four toes, in all except *Terrapene* which lacks muscle to fifth toe.

Origin.—Dorsally on distal end of flexor plate.

Insertion.—Ventrally on anterior edge of penultimate phalanx. *Chelydra, Terrapene, Platysternon,* also proximally on ultimate phalanx; *Clemmys,* only to distal end of metatarsal and proximal end of proximal phalanx; *Kinosternon, Sternothaerus,* only on proximal phalanx; *Dermatemys,* mainly to interossei plantares.

INTEROSSEI PLANTARES

Four separate muscles, one to each of first four toes, in all except *Lissemys* which also has one on fifth toe.

Origin.—Ventrally on metatarsal. *Chelydra, Clemmys, Malaclemys, Terrapene, Dermatemys, Sternothaerus,* also on adjacent tarsale; *Trionyx,* also on anterior edge of posteriorly adjacent metatarsal; *Lissemys,* for fifth toe, on proximal phalanx.

Insertion.—Ventrally on proximal end of proximal phalanx. *Lissemys,* for fifth toe, on proximal end of penultimate phalanx.

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