

RESTORATION OF THE SKULL OF *LEIDYOSUCHUS FORMIDABILIS*.

Drawing by Richard Mjos.

OSTEOLOGY OF THE  
EARLY EUSUCHIAN CROCODILE  
*LEIDYOSUCHUS FORMIDABILIS*, Sp. Nov.

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## INTRODUCTION

*Leidyosuchus* was apparently the best represented crocodile in the late Cretaceous and early Tertiary of western North America as indicated by the number of species that have been allocated to this taxon. The striking morphological diversity that occurs between species is not unlike the variability seen in *Crocodylus* yet it may be that further separations at the generic level will be called for ultimately; however, the present paper is not concerned with this problem. Its purpose is to present new evidence germane to our understanding of early eusuchian structures by way of the description of a new species. Conformance between this new form and the type species, *Leidyosuchus canadensis*, is not as good as it might idealistically be; however, lacking morphological evidence to the contrary, and considering the variability found in other genera, the prudent course would call for allocation of this new fossil to the genus

*Leidyosuchus*. Previous knowledge of early eusuchians is limited to relatively few specimens and, of the genus under consideration, to cranial materials largely. It is therefore especially significant that essentially the entire osteological character of this new form has been preserved and can be discussed in light of later eusuchians.

The material available for study is the result of the past five consecutive expeditions of the Paleontology Department of The Science Museum of Minnesota to western North Dakota, and work in its Wannagan Creek quarry. Specimens comprising this suite are intact, and partial, adult skulls, several of which have substantial portions of the postcranial skeleton. In addition, a fair amount of material pertaining to young specimens is available. Recent development of this assemblage now permits the following description and discussion.

## ACKNOWLEDGEMENTS

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The wealth of specimens available for this study was collected under the direction of chief preparator, Tom O'Brien, and myself, by: Bruce Chuchel, Charles Faraci, Peter Ganzel, Lee Halgren, Tim McCutcheon,

Ron Mjos, Mike O'Brien, Randy O'Brien, and Robert Spading, during the field seasons of 1970 through 1975.

Line drawings, Figures 8-11, 13, 15-21, 25, 28, 30 and 31 are the work of Ken B. Sander. Figures 4-7, 12, 14, 22-24, 26 and 27 were furnished by Richard Mjos. All photographs were done by Peter Ganzel.

I further wish to express appreciation to Nancy Petschauer for typing and editing this entire work, and to Marguerite Hawkinson for proofreading.

To Geneste M. Anderson, I wish to make grateful acknowledgement for her devoted interest and continuing support of this study, of which this paper is the third contribution.



## DESCRIPTION

FAMILY CROCODYLIDAE  
SUBFAMILY CROCODYLINAE  
GENUS LEIDYOSUCHUS

**Leidyosuchus formidabilis**, new species

*Type.* — SMM P71.16.28 Complete skull with lower jaw intact except for posterior part of left half.

*Horizon and Locality.* — SMM Wannagan Cr. quarry, lower level, Tongue River Formation, Paleocene, NW¼ Sec. 18, T. 141 N., R. 102W., Billings Co., North Dakota, U.S. National Grasslands.

*Referred Material.* — *Adult skulls:* P70.20.9, P72.34.87, P72.34.183, P74.24.6 with lower jaw, and P74.24.103. *Young skulls:* P70.20.407, P71.16.29, P72.34.202, P74.24.105, P75.22.6 yearling maxilla. *Mandibles:* P70.20.377, P70.20.388, P70.20.393, P70.20.412, P72.34.184. *Postcranial skeletons:* P74.24.6, P74.24.36. *Postcranial elements:* femur P70.20.171, ilium P70.20.404, cora-

coid P70.20.409, radius P70.16.3, scapula P71.16.10, ulna P71.16.17, ischium P70.16.21, proatlas P71.16.106, pubis P71.16.256, tarsus P72.34.95, branchial horn P72.34.126, humerus P72.34.203, juvenile vertebra P73.25.70, interclavicle P74.24.37, hatchling vertebra P74.24.185, young neurocentrum P74.24.186, and ribs P71.16.7, P71.16.24, P72.34.150, P72.34.185, P73.25.18.

*Diagnosis.* — A large, long-snouted eusuchian crocodile, agreeing in general habitus with other leidyosuchines. Distinguishable by its narrow, elongate premaxillary region, moderately long premaxillary-maxillary diastema, broad, short, rectangular cranial table, strongly curved retroarticular, unusually large supratemporal fenestrae, and long jaw symphysis that makes up nearly one-third the length of the dentary, and large, close-set third and fourth mandibular teeth of subequal size. Characteristics of the postcranial skeleton are its long forelimb and heavy coating of overlapping scutes.

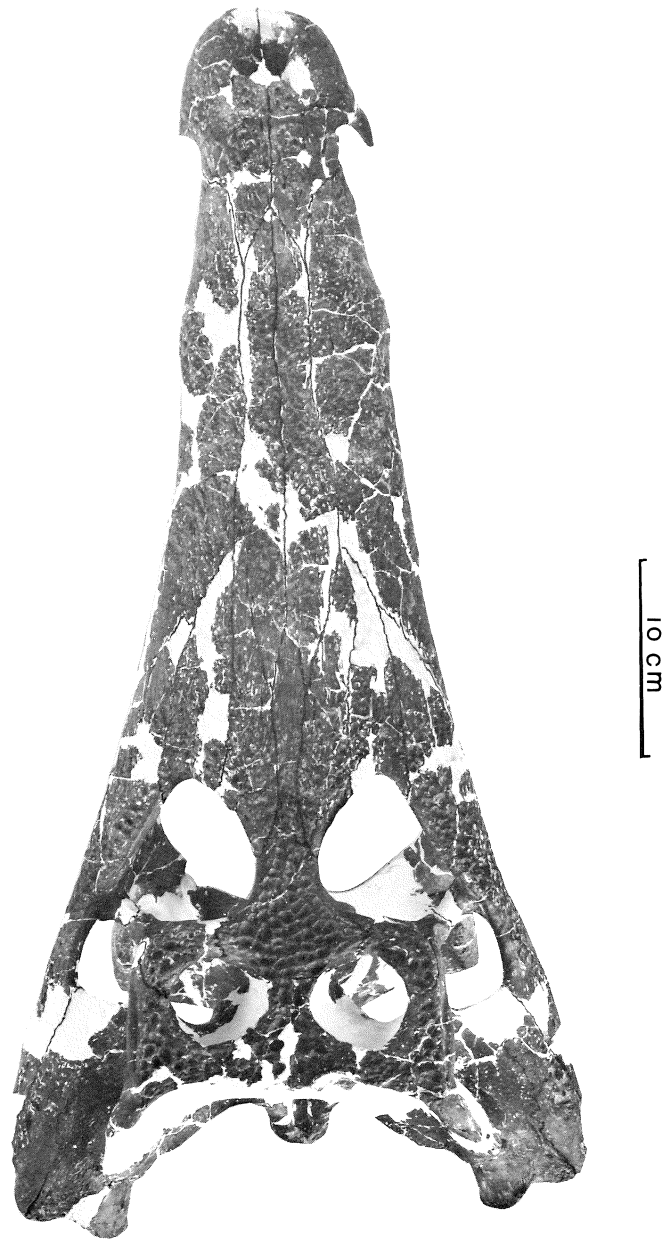


Fig. 1. *Leidyosuchus formidabilis*, type specimen SMM P71.16.28. dorsal view of skull.



Fig. 2. *Leidyosuchus formidabilis*, type specimen SMM P71.16.28. ventral view of skull.

## SKULL

Several skulls are selected as the type series for the present description. These are in various states of completeness, lacking only minor portions in most cases. All were somewhat crushed. Most of the individual cranial elements however are undistorted and an extraordinarily good skull habitus has resulted from the careful preparation of this material. The type specimen (Figs. 1 and 2) is especially useful in this description as it is nearly complete and may be regarded as an average-size adult. The skull meets the definition of *Leidyosuchus* (Mook, 1925), except it is a longer-snouted form than usual and is considerably larger than other species, and longer, with a length (supraoccipital to tip of rostrum) of 535 mm. Only *L. riggsi* with a length of 510 mm. (Schmidt, 1938) approaches it. The latter is of much lighter build, and morphological aspects setting the two apart are obvious. Aside from its much longer snout, the new fossil has good conformance to *L. acutidentatus*.

### Principal Cranial Openings

The *external nares* have a common sub-circular opening that is situated far forward. This positioning results in a low anterior rim. The opening is also relatively small, with its posterior edge at the level of the fourth premaxillary alveoli. It is partially divided at the rear by a bony bar created by extensions of the paired premaxillae. This is found in all of the present skulls, although not prominent in some, and to-

tally missing in the type specimen. The greatest length attained by this bar is 18 mm. and it is most frequently unequally divided between right and left sides.

Large *choanae* lie near center on the pterygoid plate, removed from the palatine sutures a considerable distance in the characteristic eusuchian fashion (Fig. 5). The opening shows an incipient median division from its anterior end; hence, it has a somewhat heart-shaped outline. It is usually irregular and anteroposteriorly elongated.

The region of the cranial table resembles *L. acutidentatus* most closely in shape and proportions. *Supratemporal fenestrae* are subcircular in both forms but oversized in the new fossil, actually to the point of nearly matching the size of the orbits in some of the adult specimens. Due to this unusual enlargement, the frontal has become incorporated to a considerable degree into formation of the anterior edge of the opening and the parietal is severely constricted. *Supratemporal fenestrae* are, as a rule, larger in long-snouted crocodiles. *L. riggsi* has a relatively longer, narrower rostrum, yet smaller openings compared to the present form, which has the greatest expression of this feature within the group, and, in this, most reminiscent of *Gavialis*. The *infratemporal fenestrae* are smaller than the superior temporal openings in spite of the postorbital bar's far-forward location at the expanded corner of the cranial table. A prominent *spina quadratojugalis* projects into the opening from the rear.

The *orbits* are slightly ovate but not much elongated, nor are they elevated at any part of their margins.

A well-developed *recessus oticus externus* occupies its normal place beneath a highly-expanded squamosal "overhang". The fact that this is so well developed indicates the presence of good audition with the advantage of a protective otic valve.

The *posttemporal fenestrae* are quite noticeably elongate slits in this crocodile, occupying a position just off the posterior rim of the cranial table, affecting parietals, squamosals, supraoccipital, and exoccipitals. They are quite widely separated compared to *Crocodylus*, for example (Fig. 6).

An *incisive foramen* exists as a conspicuous vacancy on the floor of the narial chamber. Its border is uneven and, in most of the specimens, its edge partially lost because of its thinness.

*Palatine vacuities* are large, extending from the level of the posterior edge of the orbits to the level of the twelfth maxillary alveoli. Elongation of the snout renders them narrow, yet the anterior border is not extremely pointed.

Pneumatization of the bones of the occipital region has been established to a considerable degree. A transverse canal connects the middle ear spaces, and a siphonium affording communication between the air spaces of the mandible and skull existed in life (Figs. 4, 6, 7 and 11). Ontogenetic progressional changes in some of the above cranial openings are illustrated in Figures 8 and 9.

### Cranial Bones

The rostrum of the new fossil is long, tapering from the outward edge of the jugal to the premaxillary-maxillary notch with modest irregularity. In lateral view, the dorsal line of the snout is quite straight with only slight upturning of the end. There

is no indication of preorbital crests, nor is there any preorbital bump which characterizes some later forms, e.g., *Crocodylus acutus*. There is heavy osteodermal sculpturing however. The labial line has pronounced undulation.

Lengthening of the *premaxillae*, wherein this portion of the snout has an overall length greater than its greatest overall breadth, accounts for its acutely rounded, only mildly bulbous shape — not so bold as in most species. In this respect it agrees most closely again with *L. riggsi*, as far as can be judged from the latter's incomplete nature. Dorsally, the premaxillary-maxillary sutures intertongue and send posterior prongs between the maxillae and nasals to the level of the third and fourth interalveolar area. Ventrally, there is a similar pattern developed but the sutures do not reach beyond the level of the first and second maxillary interalveolar space.

Each premaxilla contains five alveoli (Figs. 2 and 5). Only two complete, and two broken, teeth are held in the type. The fourth alveolus is largest, the third next in size, the first and fifth much smaller, and the second intermediate between the largest and smallest. Two large pits, inboard of interalveolar spaces between the first and second teeth, and the third and fourth, are present for the first and second mandibular teeth. The third mandibular tooth lodges just inside the wide premaxillary-maxillary notch that is located within a rather long diastema separating the fifth premaxillary and first maxillary alveoli. The notch is designed to accommodate the large fourth, as well as the only slightly smaller, third, caniniform mandibular teeth. The notch, further, has overall length appreciably less than *L. riggsi*, in which the same teeth were evidently involved, but greatly exceeds the span found in all remaining species as far as known.

The *maxillae* contribute only to the posterior portion of this notch. They are like those of *L. acutidentatus*, except much longer. The type specimen possesses 19 alveoli in each maxilla. From the first through the fifth, they increase in diameter rapidly. From here on, the characteristic pseudo-heterodont pattern continues.

Medial to the maxillae are contained the long *nasals*. Their greatest breadth is at the level of the eleventh alveoli. Anteriorly, they terminate at the level of the first alveoli. Posteriorly, the frontal wedges between them and there is considerable overlap, laterally as well as vertically.

*Prefrontals* and *lacrimals* are of somewhat the same size. The latter is a little broader and extends slightly more anteriorly. A wide lacrimal duct enters the orbital opening at its anterior edge. Both contribute about equally in formation of the rim of the orbit. "Prefrontal pillars" are present in most of the skulls available. These are considerably anteroposteriorly expanded, but show little lateral enlargement as many crocodylians do. The main superior passageway between the pair is quite circular, except for its flat roof. An inferior passageway is also formed by a medial constriction of the pair at one point. Ventrally, each half is suturally joined to palatines; and, as far as can be told, the pterygoids are involved as well. The prefrontal pillars are shown in Figures 10 and 11.

The *frontal* is a very heavy, deeply ornamented, and thickened element that reaches forward as far as the thirteenth or fourteenth maxillary alveoli. Its contact with the parietal is well into the level of the supratemporal fenestrae, hence is incorporated into its structure. It meets the *post-orbitals* about midway across the anterior rim of the supratemporal opening. The cranial table owes its rectangular shape, which seems to be a characteristic of only some

of the species of *Leidyosuchus*, to the laterally spread, and squared-off, postorbitals. Stout postorbital bars arise at the anterolateral corners and descend to join the jugal portion of the bar. Due to this expanded condition of the postorbitals, the postorbital bars are brought into an advanced position.

Posterior to the postorbitals, the *squamosals* are deeply incised by the supratemporal fenestrae. In filling out the cranial table posterolaterally, their lateral margins are projected outward to form the familiar "overhang" and the recessus oticus externus.

In juxtaposition, the solitary, medial *parietal* is bordered laterally by the squamosals. Their respective contacts are medial to the midway point around the posterior edge of the supratemporal openings. The openings for the canal of the temporo-orbital artery and the posttemporal passage can be observed in several specimens.

*Jugals*, *quadratojugals* and *quadrates* together produce the massive posterolateral portions of the skull. The ventral arch of the jugal is slight and the region of mandibular suspension is quite flat and directed more caudad than ventral. The jugal possesses a spacious cavity; and, just anterior to the process which forms the lower portion of the postorbital bar, it has a large medial opening. The quadratojugal is long and narrow, with some osteodermal sculpturing posteriorly, becoming very smooth toward the other end. A prominent spina quadratojugal is found at this end also. On the quadrate, the *foramen aëreum* is an obvious feature, as is the rather deep fissure of the cranio-quadrato passage. This fissure is emphasized by a prominent overlying flange that arises from the paroccipital process.

*Palatines* are narrow and moderately expanded forward at about mid-length. At their anteriormost extremity, however, they abruptly taper inward and meet at mid-line

to become a wedge between the maxillae. They do not have the squared shape indicated in some other species. Dorsally, a double trough is formed by the pair along their mid-line union.

The *pterygoids* are much expanded, with great lateral wings or flanges and enlarged posterior processes behind the choanae, whereby the blades are rather deeply incised. The pterygoid plate has sutural connection with the palatines at the rear margin of the palatine vacuity. The center wall of the palatine trough is carried into the choanal opening, and its termination gives the choanal opening its heart-shaped anterior half, as mentioned previously.

The *ectopterygoids* are very stout and join with the pterygoids for most of the length of the lateral wings.

Bones of the braincase are illustrated in mid-line section in Figure 11. A limited amount of pneumatization is present and a small transverse commissure connects the two middle ear cavities. Eustachian ramifications are well developed.

Most cranial nerves are in evidence in the composite materials at hand. A moderately large opening for cranial nerve V is situated laterally on the prootic-laterosphenoid suture. Associated with a prominent tympanic bulla are cranial nerves VIII and the fissure for numbers IX and X. Openings of number XII are located laterally on the exoccipital wall.

### Mandible

Figures 3 and 7 illustrate the remarkable form of the lower jaw, wherein the splenial shares in the formation of the symphysis. This condition appears in all but one species presently assigned to *Leidyosuchus*. The total symphyseal span in the new form is approximately one-third the length of the dentary and this proportion remains quite constant regardless of the

individual's age. It greatly exceeds that of other concerned species, with the possible exception of *L. riggsi*, in which the lower jaw is unknown. If *L. multidentatus*, with its long, slender jaw containing 28 alveoli, but an inordinately reduced symphyseal length, is indicative of the nature of the longer leidyosuchine mandible, the new fossil indeed represents a unique form. Furthermore, if the greater number of mandibular teeth, hence, a compatible number of maxillary teeth, is really indicative of the dental variation of the genus, then identifications based on tooth count have little value as well.

Of nine complete *dentaries* available, all but two specimens possess 22 alveoli. The two specimens contain only 21 discrete alveoli. Undulation or festooning of dentaries is well developed for such a long jaw. The dentary accounts for about two-thirds the total length of the mandible. A resemblance to *L. multidentatus* is the long gap that is found between the first and second alveoli. This gap is not as great in other known individuals, and can be attributed to their shorter jaw lengths. Another feature shared with the group, but excluding *L. multidentatus*, is the close proximity and similarity of size of the third and fourth alveoli. In these two traits the new jaw bears likeness to *Diplocynodon* (Mook, 1960). If not for the much greater symphyseal length of the former, which is only an adaptive accommodation of a large and long jaw, distinctions are not significant. The type specimen further demonstrates, by its undistorted condition, a good overall habitus of the mandible (Fig. 3 and frontispiece). The *articulars* are long and have a strong, dorsally curved retroarticular that stands in contrast to more brachyrostrate members of the genus, e.g. *L. sternbergi* and *L. acutidentatus*, in which it is directed more caudad in a plane near parallel to the slope

of the dorsal line of the head and does not follow the smooth curve of the angulars, as in the case of the present form. In this, it is like numerous other crocodiles. The dorsal direction of curvature, however, is not as much as that of *Crocodylus acutus*, where it may form a nearly right angle with the jaw line.

Iordansky (1973) notes, in many species, particularly in old specimens, the dorsal curvature is strong. The difference between young and old specimens in this respect cannot be determined at present, due to lack of complete mandibles of young animals.

By way of further description, there is a great broadening of the articular, just behind the concavities, for quadratic articulation. This is created by an unusual amount of medial projection, which, in turn, results in this portion of the bone having twice the breadth of the articulating surface immediately anterior to it. A most interesting aspect, however, is the presence of the foramen aëreum. Among ten articulars, painstakingly examined for this feature, only a single, very large individual (P74.24.6) was found to possess it. The opening is relatively small, as compared to alligatorines, but more typical of some other forms, such as *Crocodylus*, for example; yet it is unmistakably developed in both right and left jaw halves. It is located precisely as it is in several specimens of *Alligator mississippiensis* examined, just off the posterior margin of the smooth, dense articular surface, even to the small, sharp elevation behind it, that, by its nature, would afford protection to the siphonium. This elevation is lacking in specimens not having a detectable foramen.

*Surangulars* and *angulars* are about the same length and reach nearly to the tip of the retroarticular process. In this, the former differs from *L. sternbergi* and *L. acutidentatus* as well. It is about the only fea-

ture in which the new form bears closest resemblance to *L. multidentatus*. Their lateral surfaces exhibit the greatest osteodermal sculpturing. The surangular reaches forward to the area of the last dentary alveolus and the angular extends well beyond, to near the level of the eighteenth alveolus. With the dentary, they form a very large *external mandibular fenestra*.

The *coronoids* are small bones, having a typical form, and are rather sharply notched posteriorly. They contain several tiny foramina distributed on both of the broad sides.

The *splenials* are wide, solid plates, pierced by a main, single foramen, presumably the *intermandibularis oralis*, in the symphyseal zone.

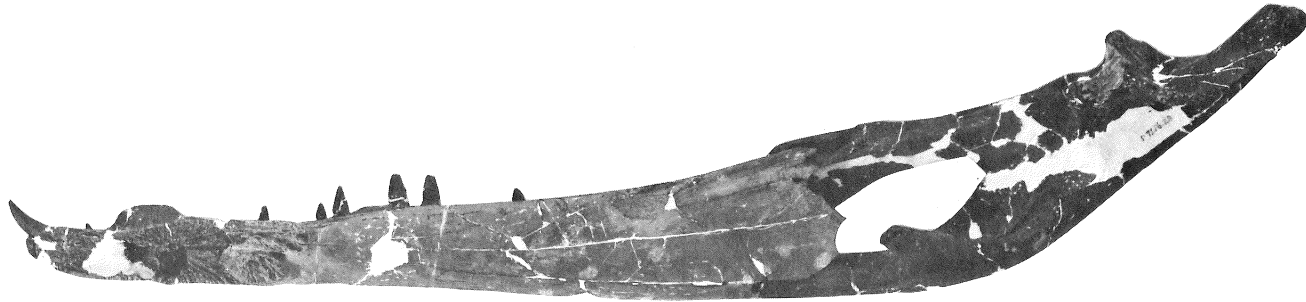
*Hyoid*. — All that remains of the hyoid apparatus is the branchial horn. The cornu branchiale I (Fig. 12), is very like that found in *Crocodylus porosus*, yet quite different from that found in *C. acutus*. As shown by Schumacher (1973), this structure is variable in shape depending on age. It is quite consistent in shape in the present material, although none regarded as yearling size or less are known. It is stout and durable as attested to by the large number found. It is a shaft that is flattened and bent towards its distal end. At this point it widens into a characteristic flange. The distal portion beyond is twisted out of the plane of the proximal portion and its terminus is sculptured for a cartilaginous epibranchial.

## Dentition

From the twenty skulls and mandibles examined during the course of the present study, the following dental formula for adult *L. formidabilis* is derived:

$$\text{pm } 5 \quad \frac{\text{m } 18-20}{\text{d } 21-22}$$





A

10 cm



B

Fig. 3. Right mandible of *Leidyosuchus formidabilis*, type specimen SMM P71.16.28. A, internal view with splenial in place; B, external view.

Tooth count among the crocodylians is regarded as having some importance in detailed systematics. In extant taxa, a tally can be made which takes into account the inconsistencies in number of teeth occurring in the mouth. The situation is not as easily demonstrated with regard to fossil species for the obvious reason of inadequacy of materials. Among the species of *Leidyosuchus*, for example, the number of maxillary teeth is reported at 19 for some, 20 for others. These numbers seem hardly adequate for taxonomic use as they are based, in most cases, on solitary, poorly preserved specimens. However, with a suite of specimens such as represents the present new form, a reasonable basis of the standard dental complex is possible. Its potential taxonomic application as regards leidyosuchines is yet uncertain.

The type specimen contains 19 maxillary alveoli; two other adult skulls, P72.34.87 and P74.24.6, each contain the same number. Still another adult skull, P74.24.103, contains only 18 discrete maxillary alveoli. A fifth very large specimen, P72.34.183, displays 20 alveolar cavities in its maxillary. Disparity between right and left elements is not unusual either, as demonstrated by the adult skull, P70.20.9. Nineteen are present in one side, and 20 in the other. In a small, young skull, P70.20.407 (Fig. 33), determination of the exact number is hampered by lack of differentiation of individual alveoli. Teeth, for most of the jaw's length, are contained in a common alveolar groove. Fortunately, 17 teeth are preserved; some remain only as broken bases, but situated much as they grew. Allowing for subsequent increase of jaw length and full development of alveoli, the final complement of maxillary teeth in this specimen would be 18 to 20.

The greatest number of alveoli occurring in the largest skull does not necessarily in-

dicade addition of an indefinite number of teeth as the skull length continues to increase with age. The "maximum" number of teeth, as noted, turns up in more average-size skulls also. However, the smallest specimen, believed to represent the first year of growth or less (Fig. 34), contains space for, at most, 16 teeth. In Figure 9, this stage would be represented by E. The posterior few alveoli are incipient as slight expansions within a shallow alveolar groove. It is also not determined at what stage of growth the precise number of alveoli for any particular, normally developing bone is achieved, but it is evidently a concomitance of the establishment of the posterior alveoli.

Tooth replacement in *Crocodylus* proceeds irregularly after adulthood, and replacement does continue throughout life (Edmund, 1969). An anomaly such as that found in P70.20.9, where there is disagreement between paired maxillae, is not unusual. Irregular positions of teeth are often found (Iordansky, 1973). It merely indicates a lag of one side in the production of additional teeth. It is seen in the present evidence that the standard number of maxillary teeth characterizing this form might vary from 18 to 20 in a normal individual depending somewhat on its relative age. Tooth replacement would appear to have proceeded irregularly during adulthood and throughout life as judged by germ teeth in the largest specimens. This follows the regime found in living crocodylians.

Iordansky (1973) has tabulated dental formulae for living crocodylians and shown the modest variability in tooth number of closely related taxa. The above formula shows, by standards of extant species, the present, rather long-snouted skull possessed a large number of teeth. As far as can be ascertained from the current study, the

formula may have certain potential application for generic significance if not for the inclusion of *L. multidentatus*, with its reported 28 mandibular teeth and an assumed compatible number of maxillary teeth. The inferred differences between this species

and others of the genus are similar, for example, to those existing between *Crocodylus* and *Tomistoma*. It may be that further knowledge of *L. multidentatus* will bring about its reassignment.

TABLE I.

Measurements of holotype skull SMM P71.16.28 in millimeters

Length of skull, posterior border of cranial table to tip of snout .....	540
Greatest length of skull along quadrate to tip of snout .....	620
Length, posterior border of cranial table to level of anterior edge of orbit .....	148
Length of cranial table, posterior border of squamosal to anterior border of postorbital along lateral rim of supratemporal fenestra .....	82
Length, posterior border of cranial table to level of maxillary-premaxillary notch .....	470
Length of orbits .....	67
Length of supratemporal fenestrae .....	46
Length of palatine vacuity .....	160
Greatest breadth of skull at quadratojugals .....	287
Breadth at level of snout base (15th maxillary alveoli) .....	152
Breadth at maxillary-premaxillary notch .....	69
Breadth at level of 5th premaxillary alveoli .....	91
Greatest breadth of cranial table across squamosals .....	159
Breadth of orbits .....	64
Breadth of supratemporal fenestrae .....	50
Narrowest breadth of interorbital plate .....	31
Narrowest width between supratemporal fenestrae .....	20
Narrowest breadth of palatines .....	25.6

Measurements of holotype mandible SMM P71.16.28

Greatest length of mandible, retroarticular to tip of jaw .....	697
Greatest length of dentary .....	485
Length of symphysis .....	158
Breadth of articulated mandibles at level of 6th and 7th interalveolar space .....	63
Greatest breadth of articulated mandibles at level of 4th mandibular alveoli .....	81.5
Greatest breadth of articulated mandibles at posterior end of splenials (est.) .....	246

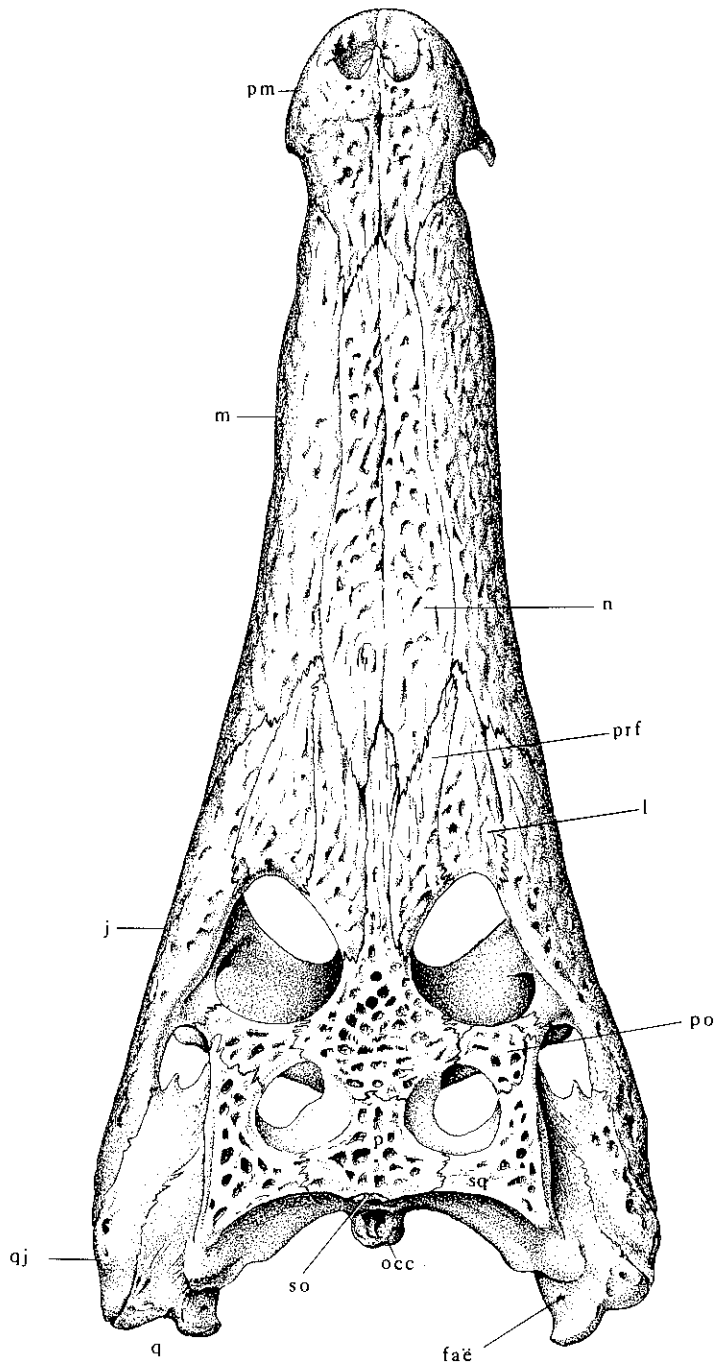


Fig. 4. Dorsal view of skull of *Leidyosuchus formidabilis*. f, frontal; faë, foramen aëreum; j, jugal; l, lacrima; m, maxilla; n, nasal; occ, occipital condyle; p, parietal; pm, premaxilla; po, postorbital; prf, prefrontal; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal.

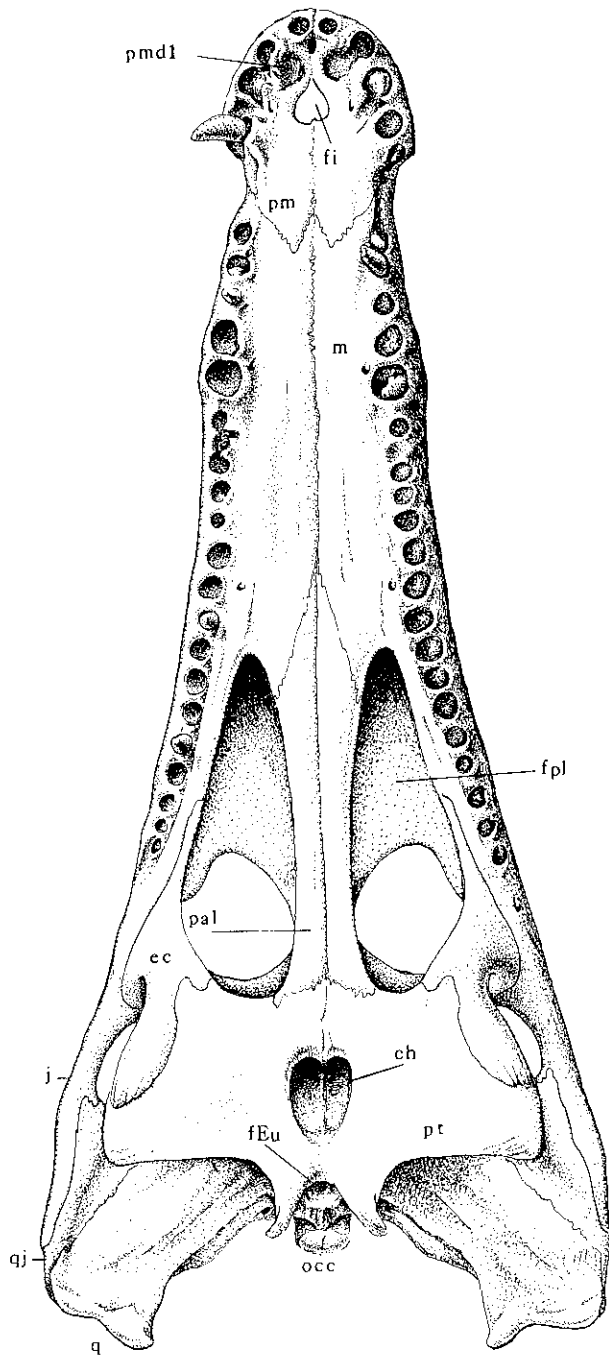


Fig. 5. Ventral view of skull of *Leidyosuchus formidabilis*. ch, choanae; ec, ectopterygoid; f.Eu, Eustachian foramen; fi, incisive foramen; fpl, palatal fenestra; j, jugal; m, maxilla; occ, occipital condyle; pal, palatine; pm, premaxilla; pmd 1, pit for first dentary tooth; pt, pterygoid; q, quadrate; qj, quadratojugal.

## ONTOGENETIC NOTES (SKULL)

From an ontogenetic approach, the smallest, essentially complete skull of the series, P70.20.407. (Fig. 33), which is probably a young adult stage, and several, somewhat larger, young adults, P71.16.29, P72.34.202, and P74.24.105, all represented in Figures 8 and 9, contribute rather extensively to our knowledge of the entire skull throughout its subadult-adult development.

The smallest skull lacks premaxillae, having lost them at the maxillary contacts, as well as the regions of the quadrates. Its estimated length (supraoccipital to tip of rostrum) is 270 mm., about half the length of an average adult skull. The skull of the very young individual is known from only a few minor fragments but these offer a glimpse of even the earliest pre-adult stages of development. A left maxilla, P75.22.6 (Fig. 34), belongs to a very small skull with an estimated total length of about 8 or 9 cm., hence, a total skeletal length of between 50 and 60 cm., as based on relative lengths of some extant forms. I would judge its age to have been not more than one year. Teeth are incipient and sculpturing of the exposed bone is delicate. Most of the thin palatal portion is lacking. At the level of the twelfth and thirteenth alveoli,

the border of the palatine vacuity is still detectable. Anteriorly, a slight swelling of the labial margin shows the area of the largest fourth and fifth teeth. Fifteen or sixteen teeth would have been the total complement in this young specimen when alive.

Ontogenetic changes and the rate of change pretty well follow established post-embryonal development of extant crocodylians (Iordansky, 1973). These are illustrated in Figures 8, 9 and 34. Regarding the general rostral form, it gradually increases its width and undulations once the juvenile stage is passed. The cranial table grows relatively slower than the rostrum. Orbits become more ovate, and become relatively less in dimension with age. Supratemporal fenestrae also become circular but increase their size appreciably. Choanae tend to migrate toward the back of the pterygoid plate. Osteodermal sculpturing intensifies greatly with age and individual teeth become modified, from long, thin, sharply-pointed cones to heavier structures with more bluntly terminated apices. Attainment of separate alveolar identity for each tooth is mentioned in the previous section.

## POSTCRANIAL SKELETON

Description of the postcranial skeleton rests with several partial skeletons, including several young skeletons. In addition,

many associated elements, representing the range of postembryonal stages, are used as supplemental material.

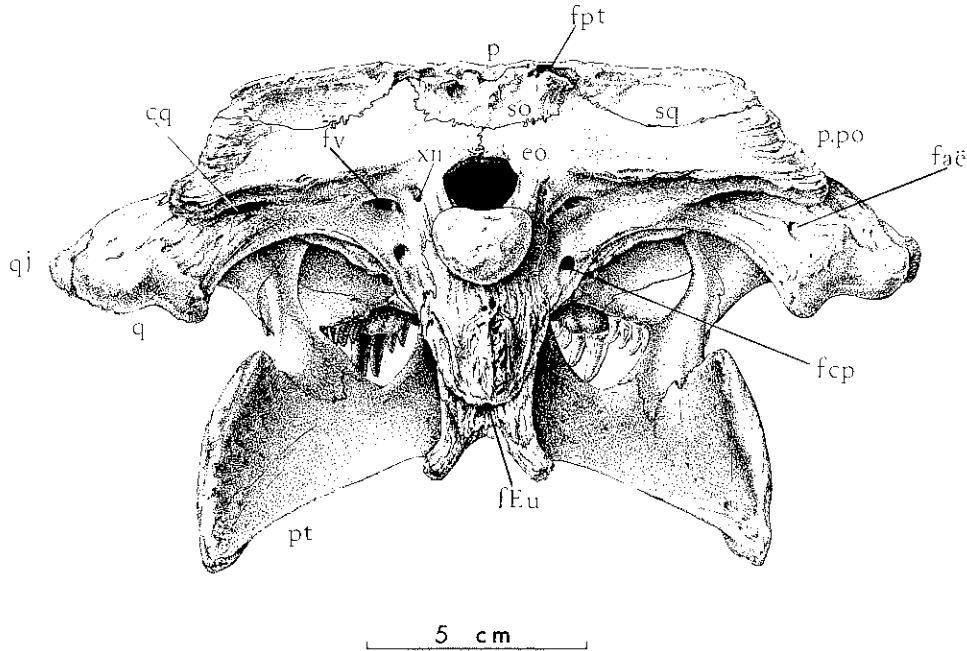


Fig. 6. *Leidyosuchus formidabilis*, SMM P71.16.29. posterior view of skull. cq, cranio-quadrate passage; eo, exoccipital; faë, foramen aëreum; fcp, carotid foramen; fEu, Eustachian foramen; fpt, posttemporal fenestra; fv, foramen vagi; p, parietal; p.po, paroccipital process; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; XII, corresponding cranial nerve canal.

### Vertebral Column

The column has no unusual characteristics that depart from the typical vertebral homogeneity of the group. Taken collectively, the vertebral column does possess aspects distinctive of the new taxon. The subregional vertebral complement comprises 9 cervicals, 15 dorsals, 2 sacrals, and about 35-40 caudals. The following descriptions and referred figures are based largely on skeletons P74.24.6 and P74.24.36.

**Cervical vertebrae** — The atlas has a free crescentric intercentrum, paired winglike neurocentra, and a large centrum (odontoid) fused to a very short, stout axis centrum, which all together form a rather standard crocodylian assemblage (Fig. 13). Location of the rib facets on the first intercentrum show the usual association of a flattened holocephalus rib. The atlantal centrum, as

well, exhibits a ventrolateral articular facet for a flat rib. This facet is well separated from the odontoid-axis suture, lying more centrally on the odontoid. The axis centrum is short, anteroposteriorly, by comparison with *L. multidentatus*. It is also different from this species in showing less development of the posterior condyle. The centrum has a prominent hypapophysis anteroventrally.

The axis neural arch is quite short anteroposteriorly, and the neural spine is unlike that found in the Crocodylinae. On the contrary, it has great height with a rather short caudad projection that thickens posteriorly and poses the likeness of an alligatorine spine. It differs from *L. multidentatus* in the same ways, as well as lacking the lateral lamina noted by Mook (1930) as being peculiar to his species.

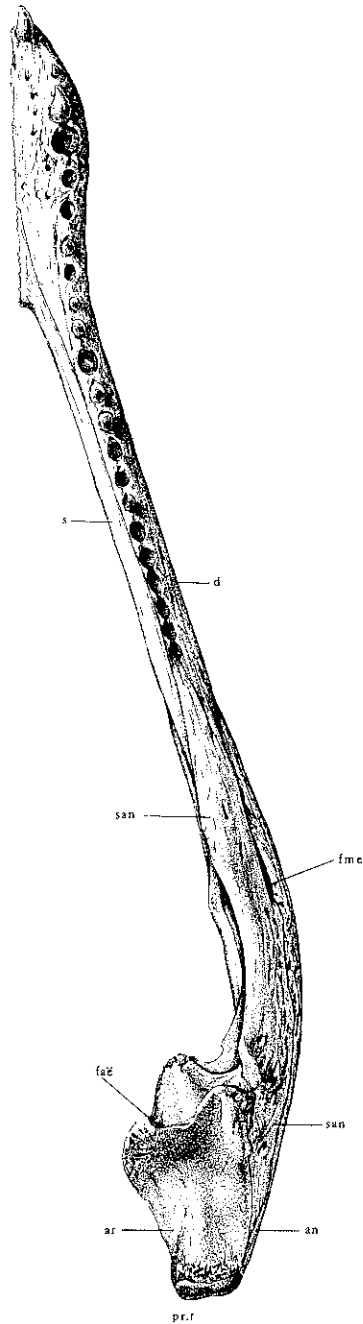


Fig. 7. Right lower mandible of *Leidyosuchus formidabilis* in occlusal view. an, angular; ar, articular; d, dentary; faë, foramen aëreum; fmc, external mandibular fenestra; pr.r, retroarticular process; san, surangular; s, splenial.



An interesting structure is the proatlas. Its two halves are fused dorsally to form one piece, which, when viewed from above, has a boomerang shape. Of the four available specimens, one is complete (Fig. 14). Dorsally, it has a sharp ridge along midline and it has a small, acutely pointed projection arising from an anterodorsal location. In lateral aspect, a deep emargination of the anterior edge and the inflation of the caudal extremities that overlie the intercentra characterize this element. It spanned an otherwise unprotected segment of the spinal cord between the skull and the vertebral column.

Cervicals three through nine — These vertebrae are strongly procoelous (Fig. 13). By way of comparison with *Crocodylus*, cervicals three, four, and five have somewhat broader neurocentra, with lower and wider neural spines in lateral view. The anteroventral hypapophyses on these are not salient features. Young specimens usually have no trace of this feature. Development of the hypapophysis is prominent on number six and grows progressively stronger through the ninth cervical vertebra. This structure is noted as taking a straight ventral orientation, with only slight anterior inclination showing in an occasional specimen. In fact, in numerous specimens examined, the inclination is caudad. From number six on, the neural spines narrow and increase steadily in height. The seventh, eighth, and ninth are swollen by heavy lateral ridges that run vertically. The last two are most expanded, much taller, and rugose at their summits. From the first through the last, the rib facets are normal in their respective locations. The parapophyses move from their inferior positions on number three to the neurocentral suture on number nine. In numbers eight and nine, the parapophyses are reduced and oriented

more vertically rather than horizontally, as in preceding elements. Their tubercular facets are enlarged as the diapophyses increase in length. As far as can be demonstrated with the incompleteness of the cervical series of *L. multidentatus*, vertebrae of the present form have more abbreviated length and less exaggeration of the cup-and-ball articulations.

Dorsal vertebrae — Assessment of the numerous dorsal vertebrae indicates that 15 elements completed the series. Here, again, the procoelous condition prevails. Dorsals are readily separated from cervicals in location of rib facets and elongation of diapophyses. Only the first two in the series have parapophysial facets situated on the centra. These are at the superior border, as in the last cervical; but here the likeness ends, as these increase appreciably in length and the lateral processes angle rearward. Anteroposterior width of the neural spines is also about twice that of the cervicals.

The third dorsal centrum is especially distinctive by want of a capitular facet, which has moved up onto the base of the transverse process, and the acuteness and cephalad inclination of its hypapophysis (Fig. 15).

The fourth dorsal is apparently without a hypapophysis, at least as is discernible from the materials available. All diapophyses angle posteriorly and upward. The dorsal angulation begins with the second element in the series and continues through the remaining free rib-bearing vertebrae. The neural spines are similar to those of *Crocodylus acutus*, only a bit stouter and shorter. Zygapophysial surfaces are very large and, as characteristic of dorsal vertebrae, extend below the level of the neural canal. A median dorsal vertebra is shown in Figure 16.

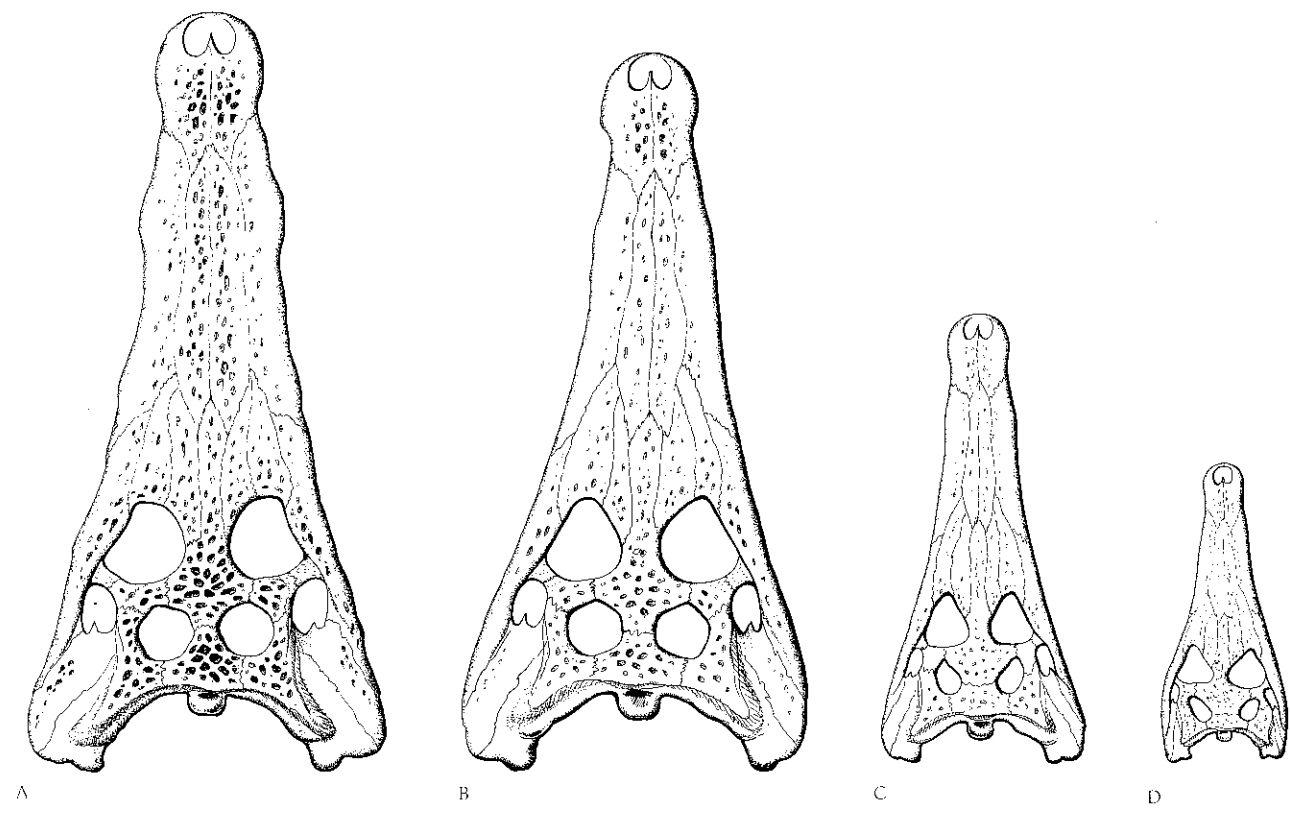


Fig. 8. Ontogenetic development of the skull of *Leidyosuchus formidabilis*, in dorsal aspect. A and B, large adults; C, small adult; D, sub adult.

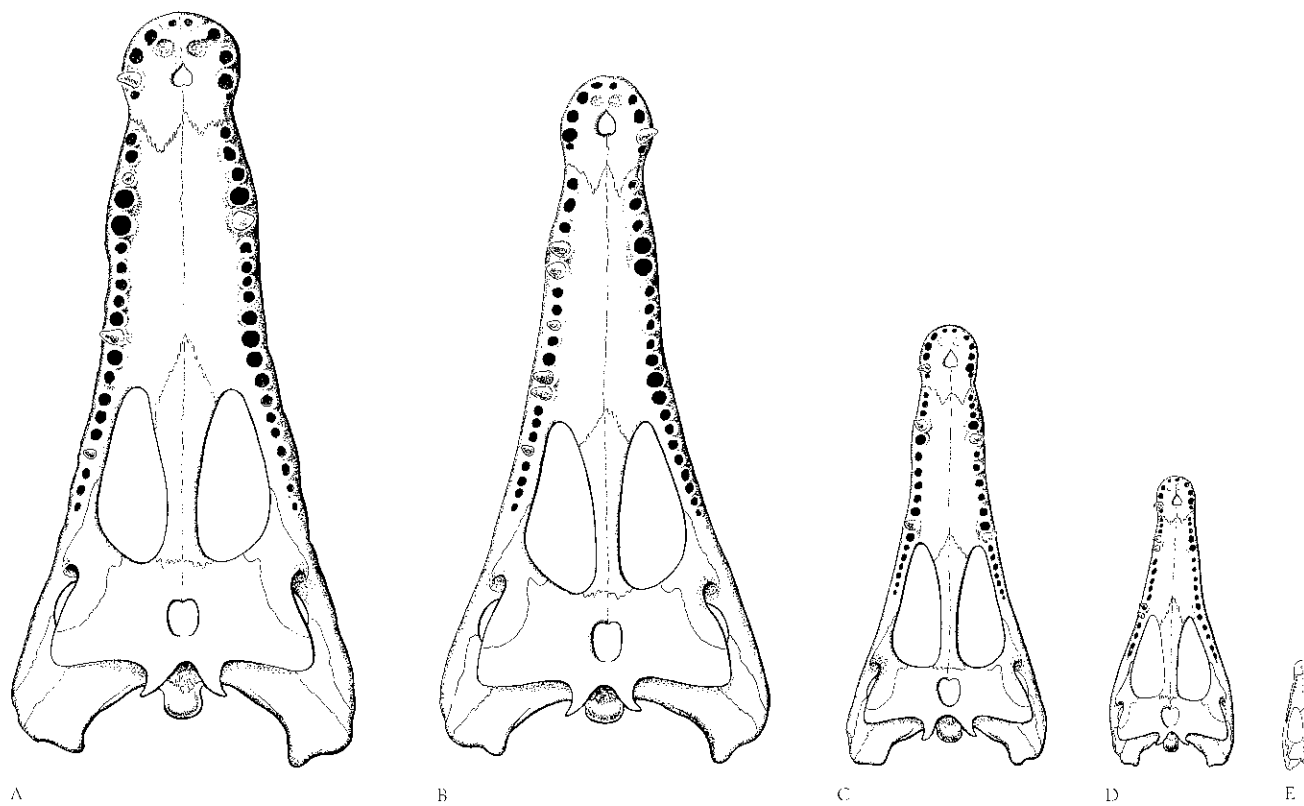


Fig. 9. Ontogenetic development of the skull of *Leidyosuchus formidabilis*, in ventral aspect. A and B, large adults; C, small adult; D, sub adult; E, less than one year of age.

The last dorsals, or lumbar, are at least three in number. Their form is consistent with the existing plan. Neural spines are low and the transverse processes stout, and directed essentially straight out (Fig. 17).

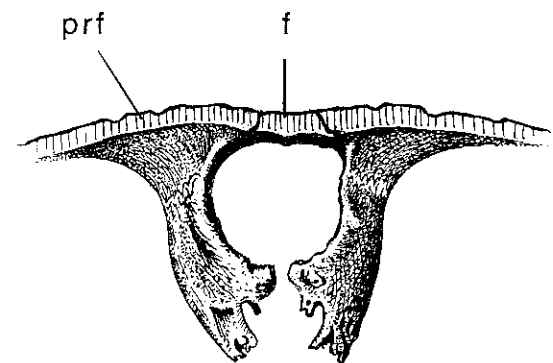


Fig. 10. Partial section of the skull of *Leidyosuchus formidabilis*, showing prefrontal pillars in anterior view; f, frontal; prf, prefrontal.

Sacrum — Two vertebrae make up the sacral series (Fig. 18). They are like those found in *C. acutus*, except in certain minor details. The centra are depressed and the anterior articular surface of the first centrum has unusual breadth. It is concave, as is the posterior surface of the second element. At their union, both centra are reduced in diameter and have flat contact faces. Each centrum supports massive transverse processes arising, on the first, from the front half of the centrum and extending beyond to overlap the first presacral centrum. On the second element, they begin along the posterior four-fifths of the length of the centrum and reach beyond to a point where they overlap the first caudal vertebra. These processes protrude boldly to join the ilia. Corresponding surfaces are irregular, yet a fairly well defined border can be observed. The distal ends of the second element's processes are not preserved, but contact areas on the ilia indi-

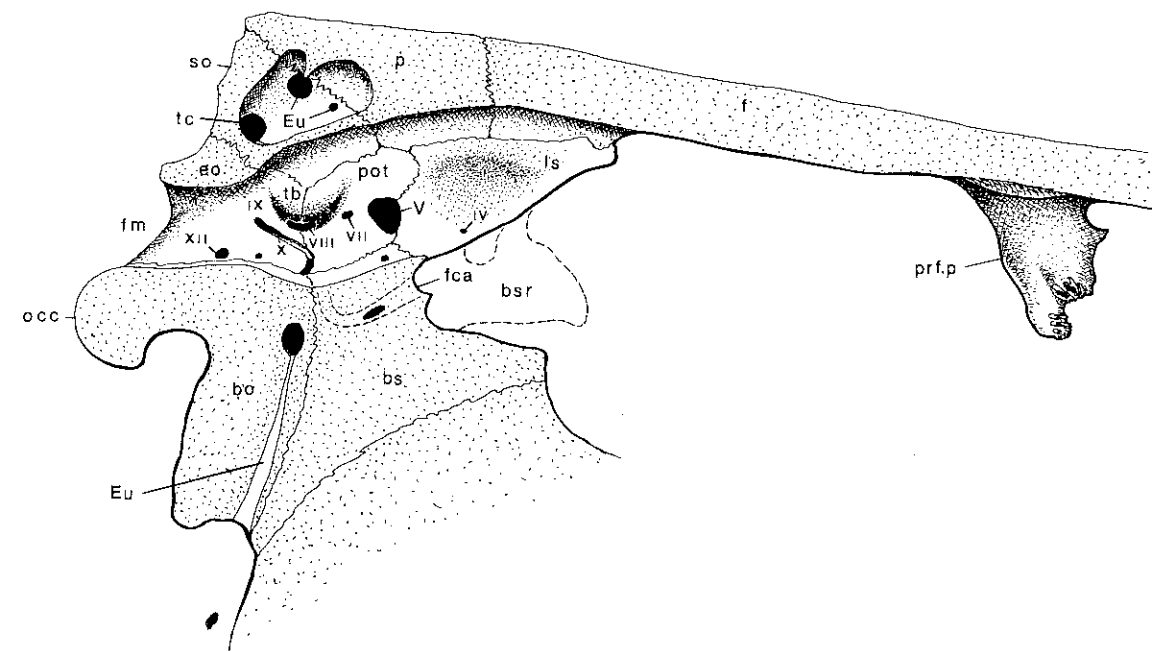


Fig. 11. Cranial bones and canals in sagittal view.

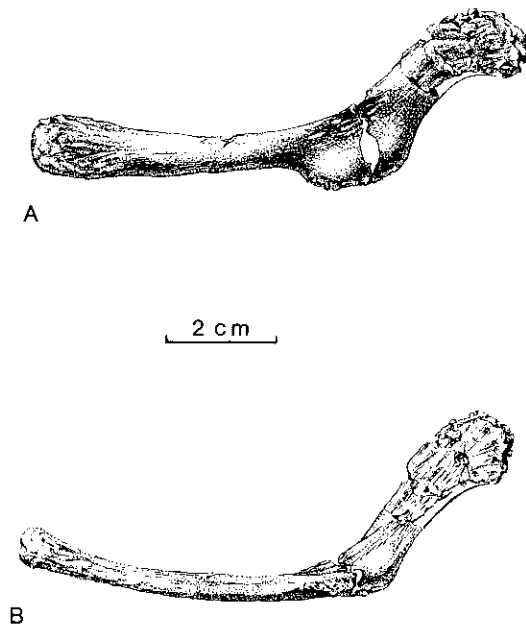


Fig. 12. Right branchial horn of hyoid apparatus (P72.34.126.) of *Leidyosuchus formidabilis*. A, internal view; B, ventral view.

cate that they were spread well up onto the posterior tip of the iliac blade, considerably more than those of the first set of processes.

Along the posterior edge of the first transverse process is a rather sharp keel. Its anterior edge is squared off. Prezygapophyses on the first element are large, those of the second only slightly smaller, and to some degree stronger, than those of *C. acutus*. Along with the position of the base of the transverse process, which helps cradle the first caudal centrum, this provides a strong connection between the sacrum and tail. This is not unlike the form of the second sacral of *Leidyosuchus canadensis* (Lambe, 1908). Zygapophysial development between the two sacrals is intermediate, as the incomplete remains would show. Neural spines are present for the most part and indicate a low form that was broad anteroposteriorly.

Mook's description of *L. multidentatus* (1930) was based on a number of postcrania, including the two sacrals, the second of which exhibits a peculiar feature. On the posterior surface of the centrum is a small ball superposed on the concave surface. This condition is in decided contrast with that of modern crocodiles as noted by Mook. It is also unlike anything found in the present suite of specimens. The present sacrum is further different from Mook's specimen in the nature of the transverse processes, wherein those of the present specimen are appreciably longer, and the base of the second extends posteriorly beyond the centrum.

Caudals — The complete number of caudal vertebrae is undetermined in spite of the goodly number on hand. All general sections of the tail are well represented and a reasonable estimate of the number of elements comprising a complete series would be somewhere from 35 to 40. The exact number, of course, could vary from one individual to another. The first in the series is typically biconvex, with greatest swelling on the posterior face (Fig. 19). All of the anterior centra, to at least midway along the series, have a pair of longitudinal ventral ridges. Anterior elements occasionally show lateral ridging as well. Transverse processes are present for most of this distance. These decrease, from rather elongate structures in the first few vertebrae, to a mere vestige at some point before the neural spines reach their maximum development and the tail has its greatest lateral compression. At this point, the new crocodile apparently had a slightly higher tail than *Crocodylus acutus*, as suggested by the length of neural spine, and the indicated presence of strong chevrons in this area. A median distal vertebra of the new crocodile, in the vicinity of the eighteenth, which is the vertebra that has the longest neural spine in *C. acutus*, (Mook, 1921),

has a proportionately longer spine as preserved; and yet it is estimated to be missing three to five mm. from its tip. A strong, powerful tail is indicated, undoubtedly most functional as a very effective propulsive organ in the water.

Zygapophyses and neural spines are developed from the first to the most distal caudals. The first few spines are fairly broad anteroposteriorly and gradually thin as they increase in length toward mid-length of the tail. From this point on, they gradually diminish, as do the zygapophyses, to the end. In Figure 19 is represented one of the last elements showing evidence of a neural spine and zygapophyses. The neural arch is still complete and a faint trace of the procoelous condition of the centrum persists. There were, perhaps, only four to six small bones beyond this point.

### Chevrons

Again, as with the caudal vertebrae, the total number is unknown. A selection of various examples (Fig. 20) has been made from the present material to give a general idea of their nature which is like that of *Crocodylus*. Their most noticeable form is their substantial length.

### Ribs

Cervical ribs — Ample material is preserved to show that on all cervical vertebrae were ribs of the characteristic crocodilian type. The first two, borne by the first intercentrum, and centrum, respectively, are flat and elongate. Number one is longer and holocephalous. Number two possesses a poorly formed tuberculum, which terminates in an irregular edge to support connective tissue. The next rib, articulating with the third vertebra, is similar to those carried by the fourth through the seventh vertebrae. They are stout and short with a

prominent capitulum and a very long tubercular section, arising at nearly right angles to a horizontally-oriented shaft. The anterior projection of this increases in length from the third to the sixth or seventh, wherein it about equals the posterior projection. The form of the eighth is an elongated shaft continuous with the capitular projection, forming a smooth curve directed posteroventrally. Both capitular and tubercular surfaces are considerably reduced in size. The latter is somewhat more massive. The anterior prong remains as a prominent crest on the shaft at the level of the tuberculum.

The ninth rib is much heavier and somewhat longer than the preceding rib. Articulating areas are about the same size in each and the crest on the shaft is very strong. Figure 21 affords a composite suite of the cervical rib series.

Dorsal ribs — Matching dorsal ribs with vertebrae is a bit unreliable, even from the large quantity of specimens found. This is not necessary, at any rate, to derive an appropriate reconstruction of the thoracic and lumbar subregions of the skeleton. As stated, there were very likely 15 dorsal vertebrae. Ribs borne by these may, in turn, be divided into: two (R10 and R11) anterior thoracic ribs, having capitular contact with parapophysial facets that are situated below the neurocentral suture on their respective vertebrae, and six or seven, possibly more, beginning with (R12), longer, mid-thoracic types, in which the tuberculum becomes the principal contact with the vertebra, and the capitular surface is diminished in accord with movement of the parapophysis to a more dorsad location above the neurocentral suture near the base of the transverse process. Finally, there are at least three (R22, R23, and R24) which are not free and are best regarded as lumbar processes. The three, or

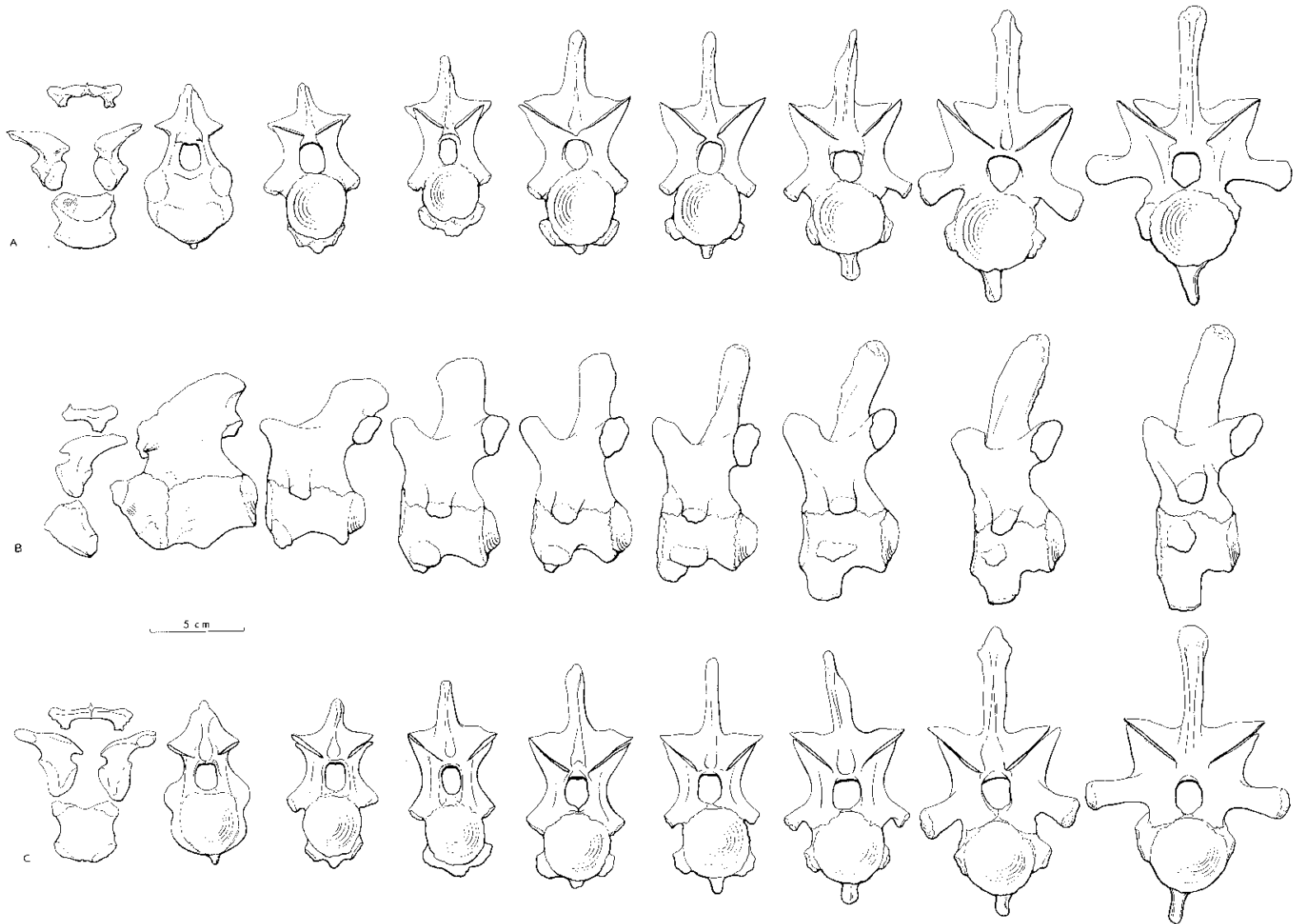


Fig. 13. Cervical vertebrae of *Leidyosuchus formidabilis*, with neurocentra splayed; A, anterior view; B, lateral view; C, posterior view.

so, intervening ribs between the last of the series (R12 to R18) and (R22) are somewhat conjectural, but probably were simple free structures not greatly unlike those found in *Crocodylus*.

It cannot be illustrated, with satisfaction, at what level the rib facets on the transverse processes finally merge to create a synapophysis; nor is it clear how many lumbar actually may be designated. The number and form of the anterior dorsal ribs suggests that the vertebrocostal canal was appreciably reduced at the level of the third (R12) dorsal rib, and the supposed arrangement of ribs seems most acceptable at present. Representatives of the ribs of various dorsal sections are illustrated in Figure 22.

Many pieces of wide, as well as narrow, rod-like elements, belonging to ventral ribs, are included in the material. Their associations with the major ribs are not obvious, but there is every indication of a belly region well fortified with ventral thoracic and abdominal ribs.

**Caudal ribs** — Transverse processes (pleuropophyses) are found on the largest caudal vertebrae. Evidence of these structures is lost near mid-length, as judged from both adult and subadult remains.

### Sternum

The interclavicle is a well ossified structure (Fig. 23). From six specimens available for comparison, several of which are nearly complete, its shape is that of an elongate double-edged blade with a somewhat variable outline. Constrictions, mostly along the anterior portion of the margin, offer solid attachments for the cartilaginous sternum. Greatest constriction occurs about one-third of the length back from the anterior tip. Posterior to this, the edge of the blade is a smooth, cartilaginous surface.

### Pectoral Girdle

Some 25 pectoral elements preserve an accurate knowledge of the primary girdle. The most remarkable aspect of the involved bones is their relative shortness as compared to limb bone length, and as a girdle unit to the lengths of the limbs themselves.

The scapula has more length than the coracoid. The blade of the former is broader and the shaft more anteroposteriorly compressed. Its superior border has a cartilaginous margin, swung in a wide arc, whereas the blade of the latter is abruptly truncated and rounded only at its posterior corner. Its distal edge has a strong area for attachment of sternal cartilage. The shaft is also rounded and thicker than that of the scapula. At the extremities of contact with each other, both bones are much thickened and their adjoining surfaces rugose. Both are drawn out and narrowed anteriorly along this surface. The glenoid is contributed to more or less equally by these elements.

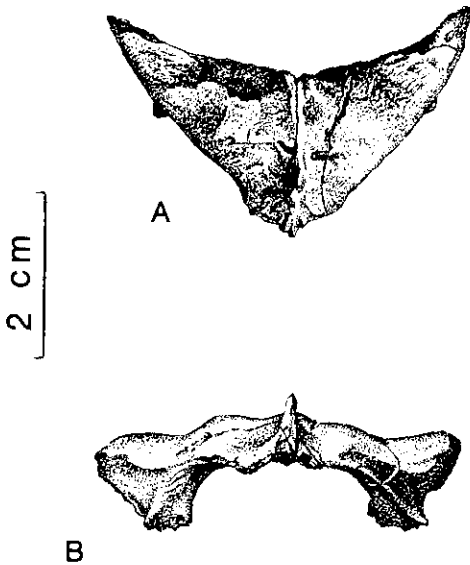


Fig. 14. Proatlas of *Leidyosuchus formidabilis*. SMM P71.16.106. A, dorsal view; B, anterior view.



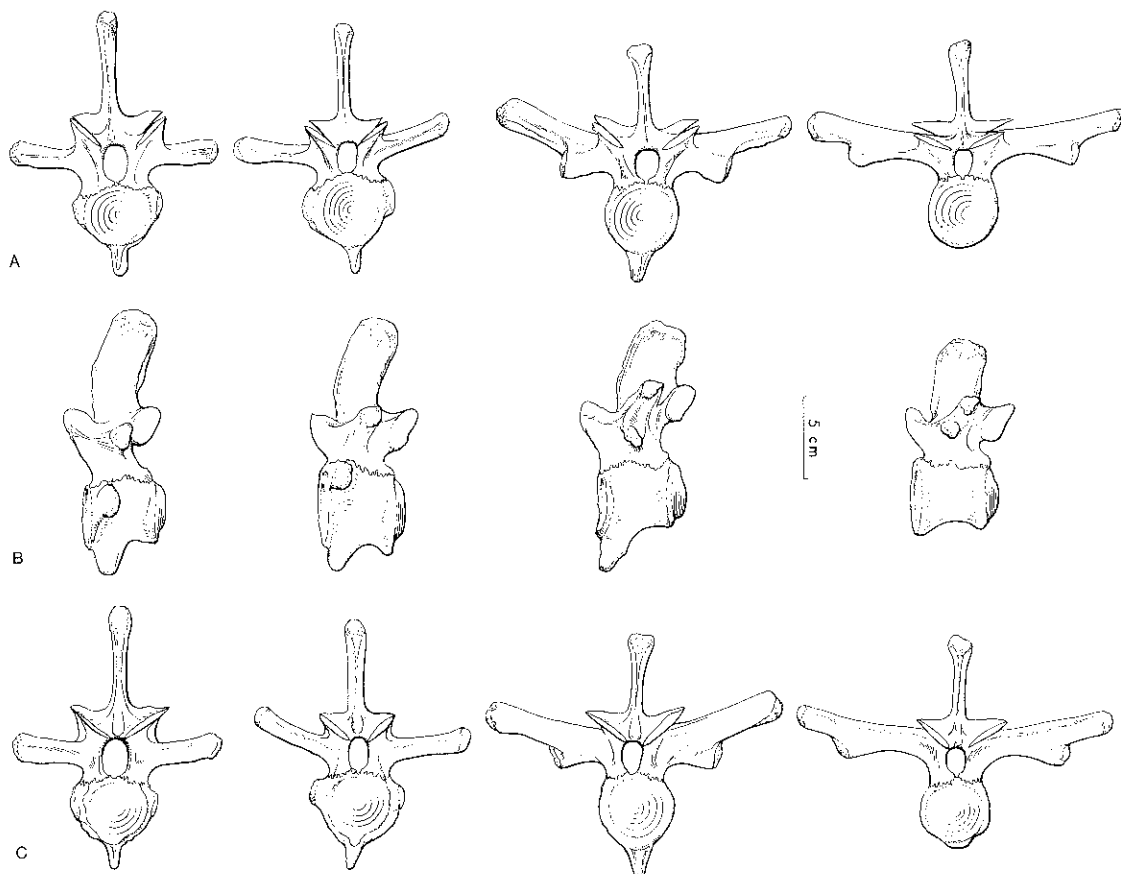


Fig. 15. First four dorsal vertebrae of *Leidyosuchus formidabilis*. A, anterior view, B, lateral view; C, posterior view.

In normal contact alignment, each extends obliquely backward, and an internal arc of about 89 degrees is inscribed between the two blades when viewed from directly in front or behind (Fig. 24). This is due chiefly to the bold, inward inclination of the pair. The acuteness of angulation is somewhat more than that seen in many other crocodylians. It precisely resembles some alligatorine specimens in this respect. Examination of scapulae and coracoids reveals a marked consistency of this relationship with one another. The result of

the relative shortness of the girdle elements themselves, and the more medial inclination of their respective blades, is a depressed shoulder region with a low silhouette.

Notable features of these bones are areas of roughness for muscle attachment above the glenoid cavity, and a heavy crest along the posterolateral portion of the same side of the scapula. On the coracoid, the glenoid is sharply set apart from the base of the bone, and a large foramen penetrates the widest portion of the base near its center.

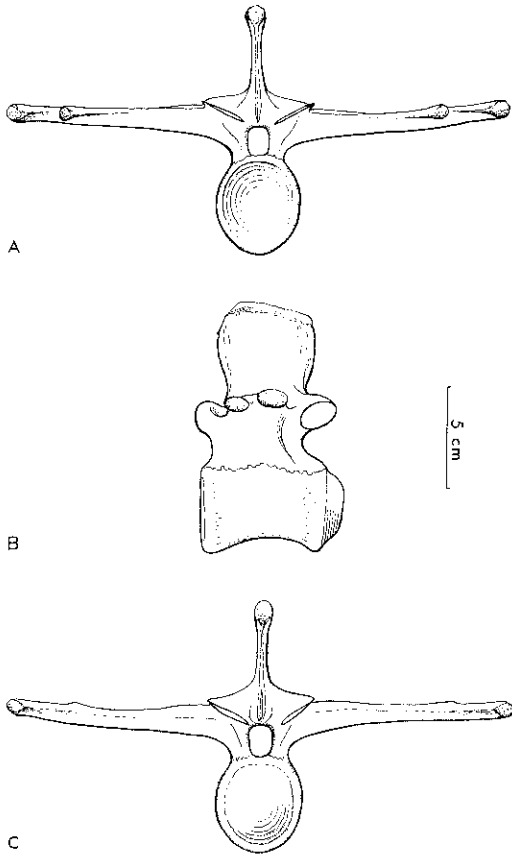


Fig. 16. Median dorsal vertebra of *Leidyosuchus formidabilis* (about number eight); A, anterior view; B, lateral view; C, posterior view.

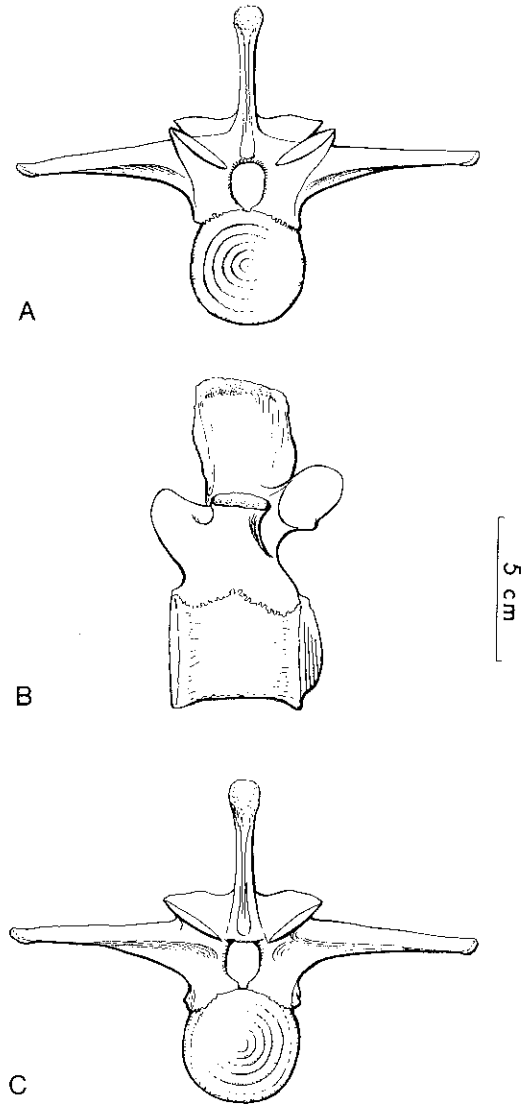


Fig. 17. Lumbar vertebra of *Leidyosuchus formidabilis*. A, anterior view; B, lateral view; C, posterior view.

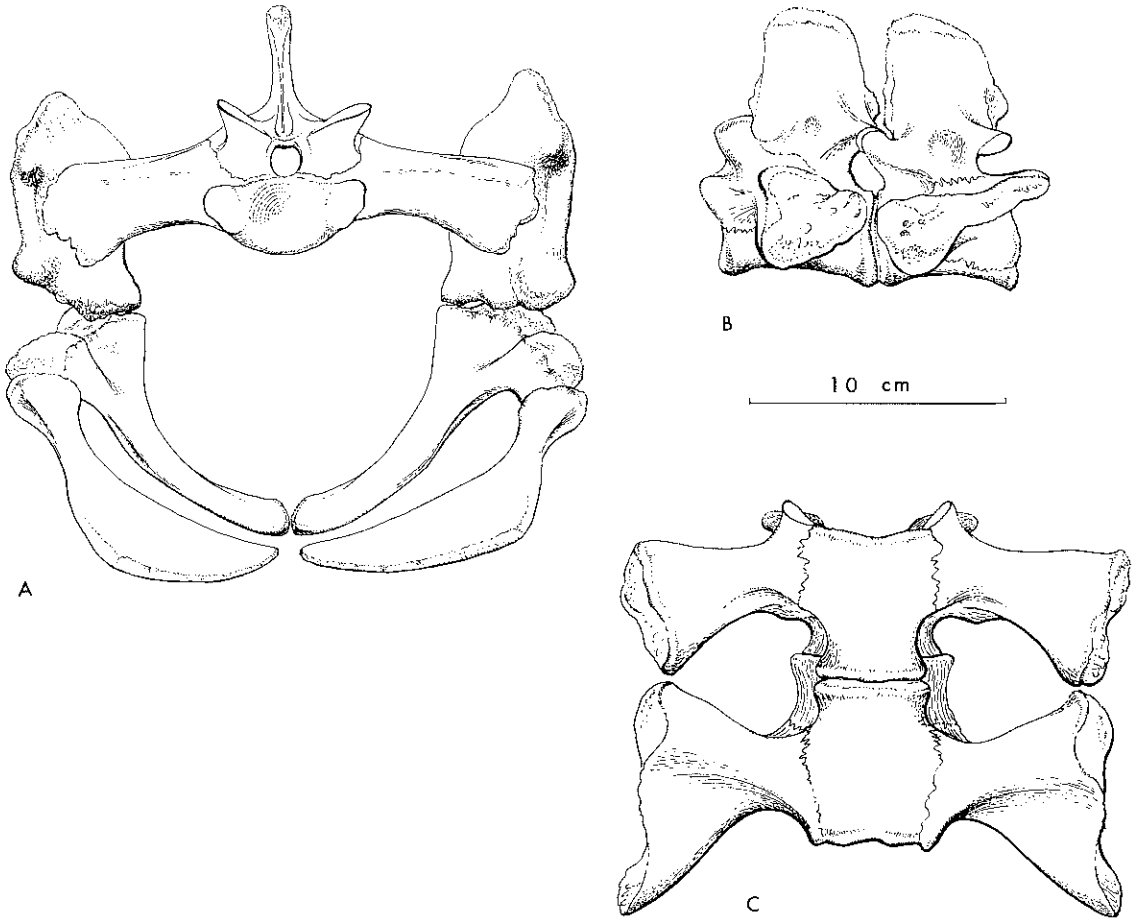


Fig. 18. Pelvic girdle of *Leidyosuchus formidabilis*. A, anterior aspect of fully articulated pelvis; B, lateral aspect of two sacral vertebrae with ribs; C, ventral aspect of sacrum with ribs.

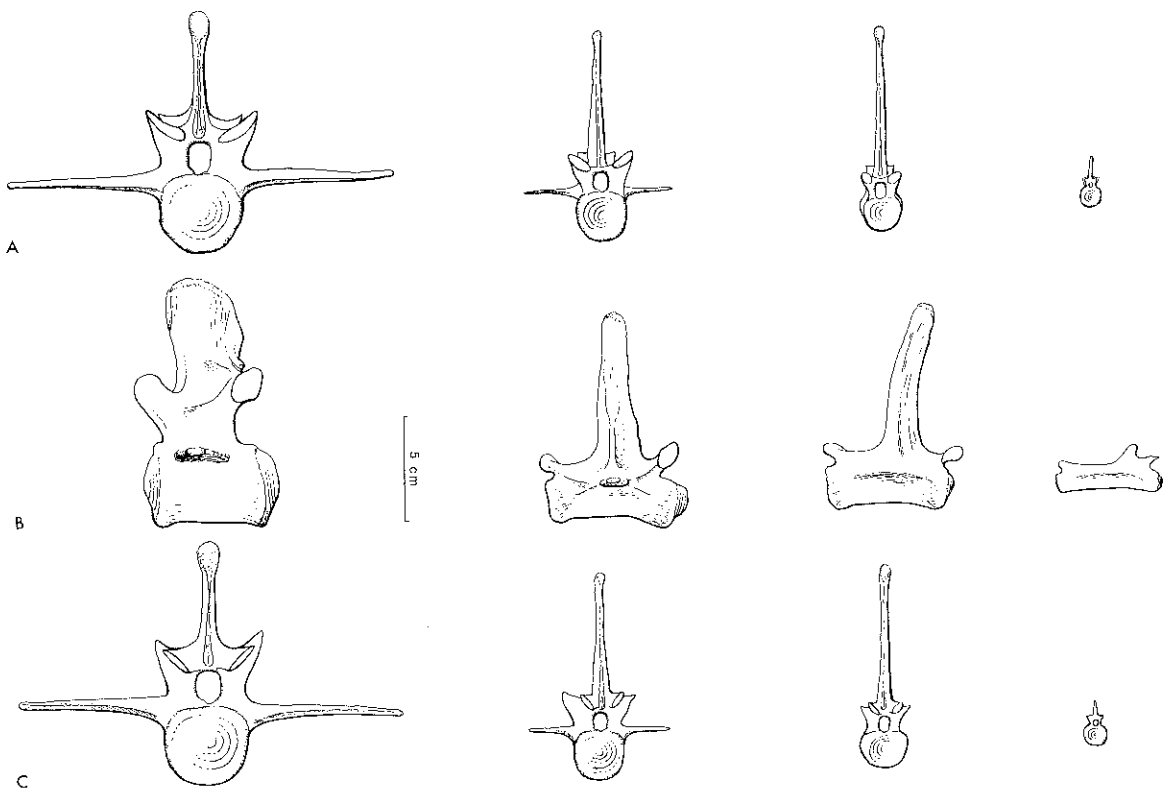


Fig. 19. Caudal vertebrae of *Leidyosuchus formidabilis*, representing (left to right) the first, approximately eighteenth, distal, and extreme distal sections of the tail. A, anterior view; B, lateral view; C, posterior view.

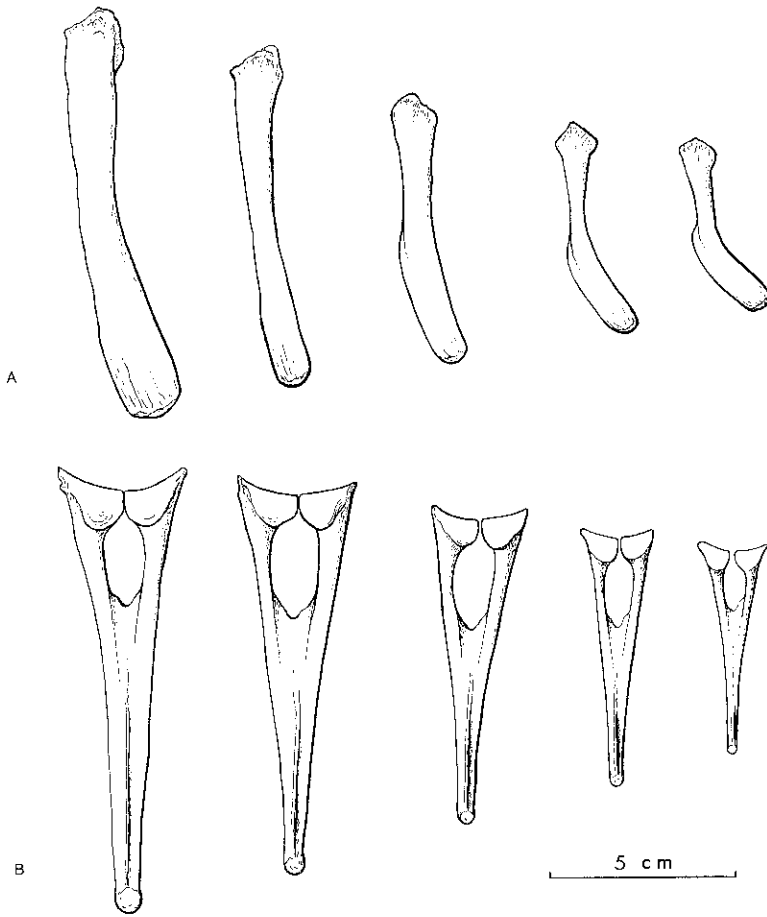


Fig. 20. Proximal, medial, and distal chevrons of *Leidyosuchus formidabilis*. A, lateral view; B, posterior view.

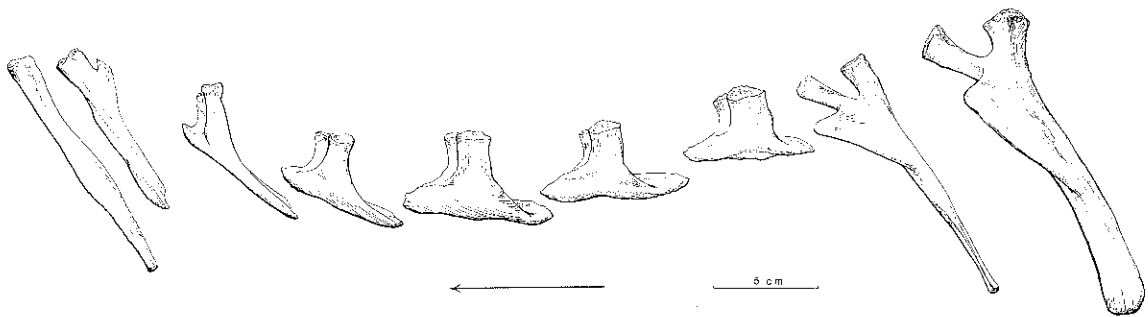


Fig. 21. Cervical rib series of *Leidyosuchus formidabilis*.

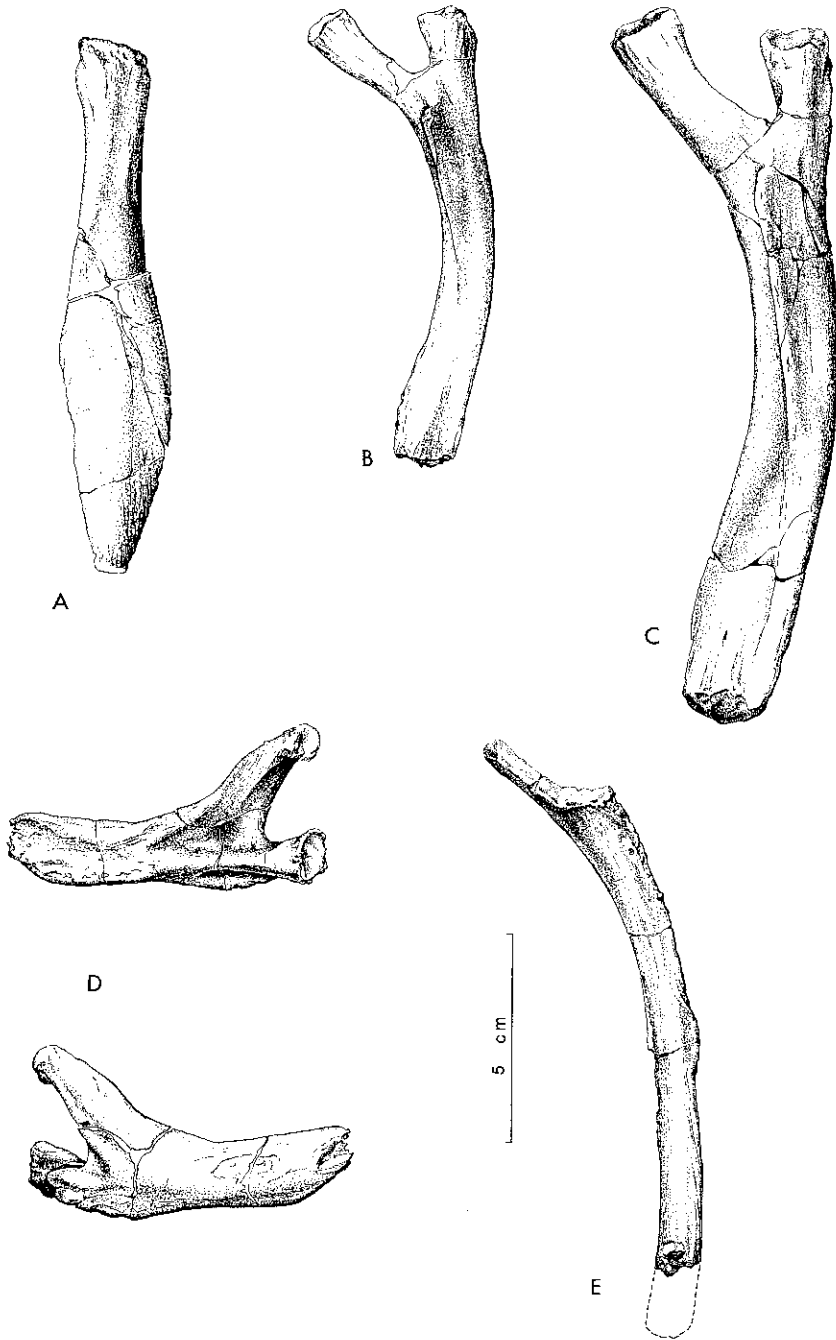


Fig. 22. Ribs representing various regions of the skeleton of *Leidyosuchus formidabilis*. A, first cervical rib SMM P73.25.18. B, anterior dorsal rib SMM P71.16.7. C, large median trunk rib SMM P72.34.185. D, third cervical rib SMM P71.16.24, in medial and lateral views. E, posterior dorsal rib SMM P72.34.150.

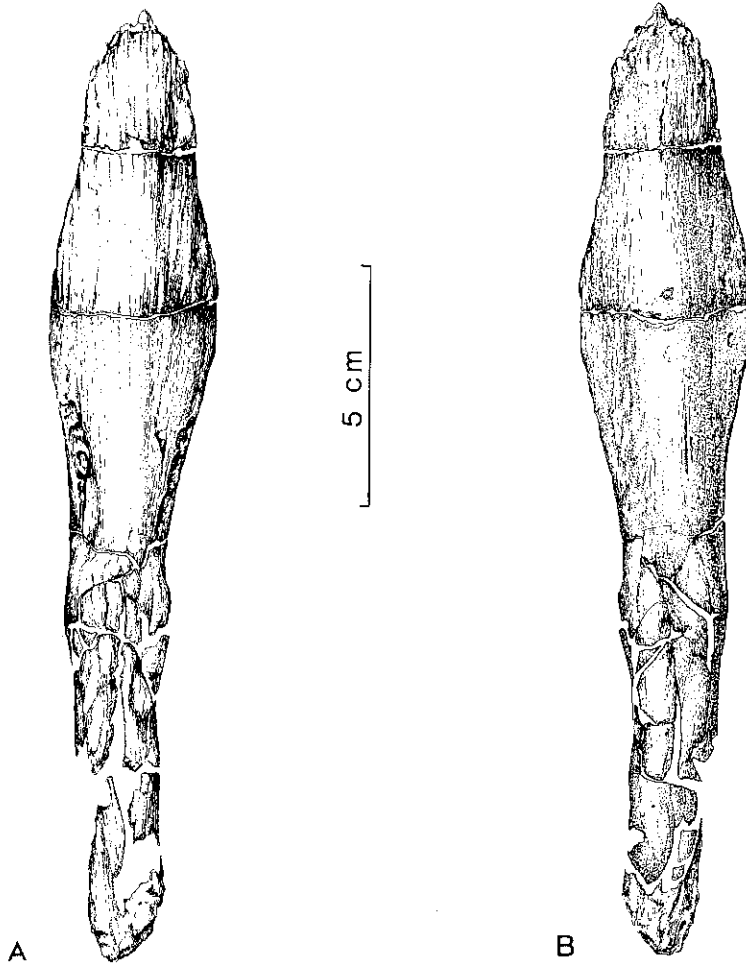


Fig. 23. Interclavicle of *Leidyosuchus formidabilis*, SMM P74.24.37. A, ventral view; B, dorsal view.

### Forelimb

Humerus — For a crocodile, the humerus is unusually long, having a length only slightly less than that of the femur (Table II). Otherwise, the humerus is characteristically crocodyloid. The shaft curvature is gentle. Extremities of the bone have moderate expansion, to more or less the same extent. The head is strongly turned medially, and the proximal articular surface is well defined over the entire end. The posterior part is most expanded. The distal

end of the bone is curved laterally, and its articular areas separated on a large capitellum and a smaller ulnar condyle by a deep trochlear groove. Within the proximal one-quarter length of the bone is located a small internal tuberosity, and opposite, on the anterior surface, a prominent deltopectoral crest. This feature is conspicuous, and situated relatively high upon the shaft by comparison with *Crocodylus*, due to the marked proportional differences in bone lengths between the two — the fossil being unusually long. The prominence of the crest

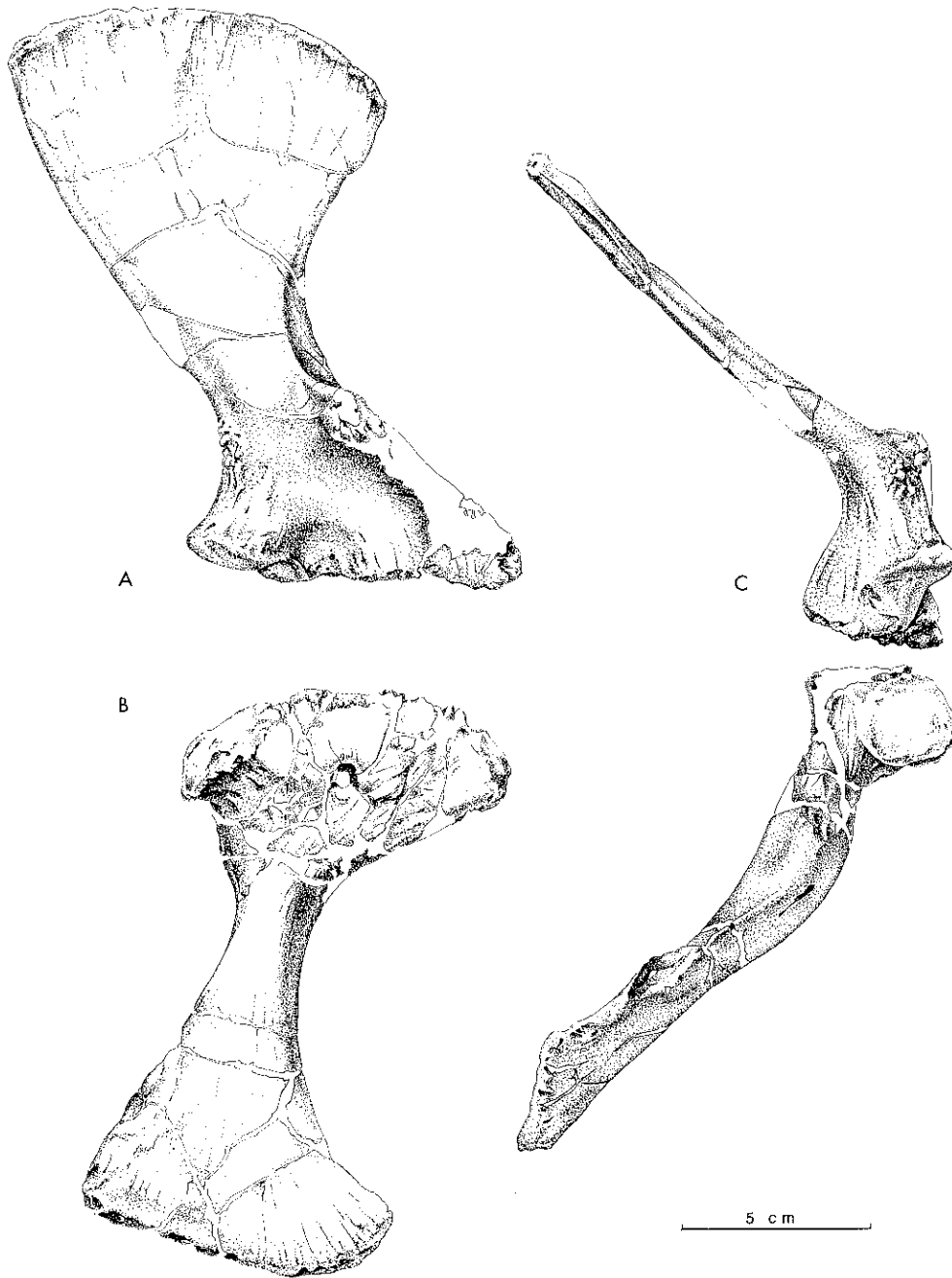


Fig. 24. Endochondral elements of pectoral girdle of *Leidyosuchus formidabilis*. A, SMM P71.16.10. right scapula; B, SMM P70.20.409. right coracoid; both in full lateral view; C, same, nearly articulated in posterior view.



is connected to the base of the head of the humerus by a very sharp, thin-walled ridge which in the best preserved specimens has no curvature. Distally it thickens and gradually coalesces with the shaft (Fig. 25).

Radius-ulna — The radius and ulna are also relatively long — the latter having greatest length (Fig. 26). Their lengths more closely approach that of the humerus than they do in the other crocodylians compared herein. Unlike *Crocodylus*, the ulnar length exceeds that of the scapula and coracoid, measured across the greatest length of both. Unfortunately, the ulna of *C. clavii* is unknown; however, its radius would indicate the relative proportions of the antebrachium were more or less like those of *C. acutus*. The radius and scapula of the new form are of subequal length. The radius is, further, a simple bone, swollen and flattened across its proximal end, and anteroposteriorly widened at the distal end. Well developed articular facets are present at both extremities. As in *Crocodylus*, this is the shortest of all the limb bones.

The ulnar shaft is somewhat flattened and it has pronounced curvature. The head is enlarged, the distal end considerably less so, and is otherwise of typical form.

Carpus — In being consistent with the propodial and epipodial regions of the limb, the carpals are quite elongate. The radial is much developed for association with the radius; and, laterally, a large area is provided for contact with the ulna. Narrowing of its shaft is amplified by its elongated shape. The same is true of the much smaller ulnare. Distally, these elements are expanded mildly, and a bit concave, centrally. The pisiform is an inconspicuous, irregular part. It is uncertain what the nature of any particular distal carpal might have been. Of these, all are of a generalized subrounded form.

Manus — The forefoot is of typical construction, having all five digits represented. The phalangeal formula is not apparent, but various proportional aspects of the rest of the foot, and the number and variety of individual phalangeal forms represented, suggest that something akin to the typical crocodylian count, with a large ungual on each digit, was the case. No evidence of what the nature of any modifications to claws of IV and V might have been was found. Various elements of the feet are shown in Figure 32.

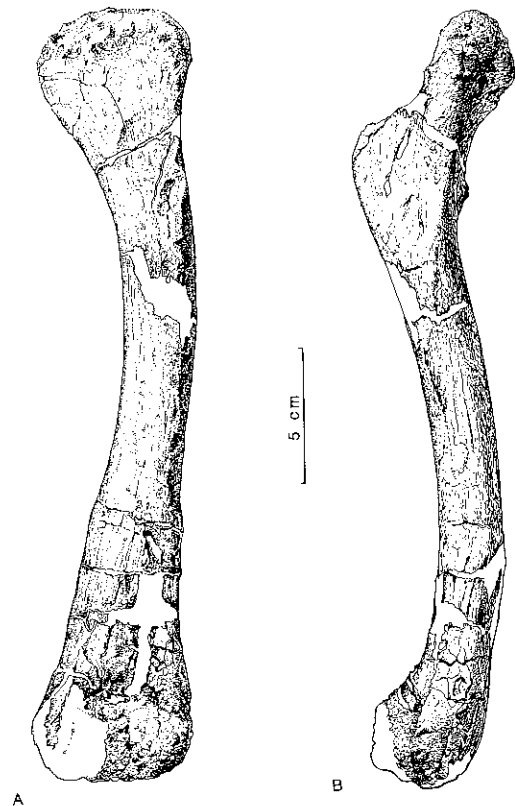


Fig. 25. Left humerus of *Leidyosuchus formidabilis*, SMM P72.34.203. A, ventral view; B, lateral view.

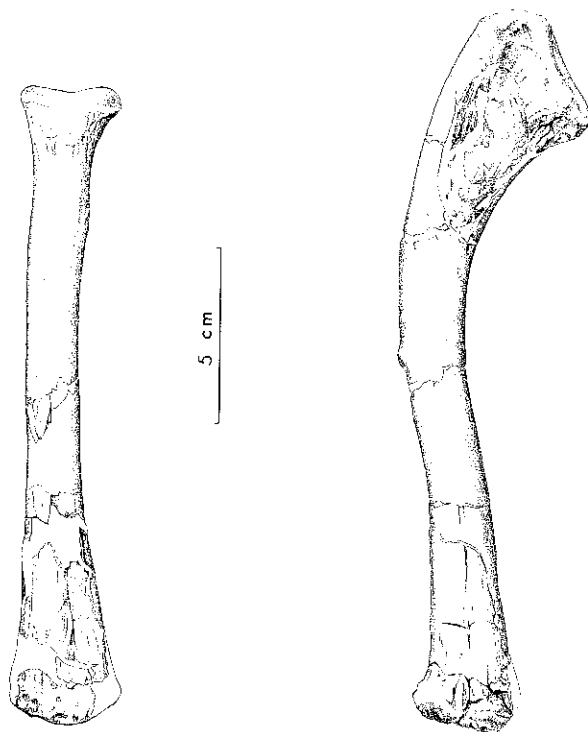


Fig. 26. *Leidyosuchus formidabilis*, A, right radius SMM P71.16.3. anterior view; B, left ulna SMM P71.16.17. medial view.

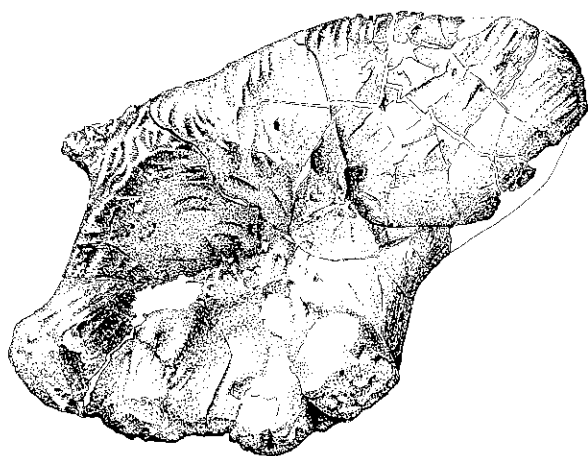
### Pelvic Girdle

Three elements making up the pelvic girdle show little that might be considered peculiar to the present taxon. Among the number of ilia looked at for structure and the variations that might exist, are convenient examples of individuals that give a good ontogenetic view of their form. The ilium is a heavy bone with a characteristic posterior extension of its blade, proportions of which are relatively constant, in spite of relative age. Superiorly, the border is highly rugose, and, anterodorsally, there is situated a prominent projection. An obvi-

ous feature is the sharp definition of the very large acetabulum.

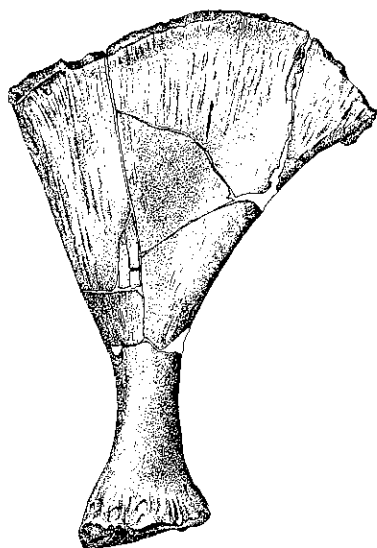
The pubis has the normal eusuchian form and relationship to other girdle parts, being appreciably smaller and of lighter construction. Other than its articulation with the anterior process of the ischium, its connections were by fibrous tissues only.

The ischium is stout and its iliac articular processes are strong. When connected with the ilium, a fairly large perforation is created within the acetabulum somewhat below its center. The articulated pelvic girdle is illustrated in Figure 18, and its various component elements in Figure 27.

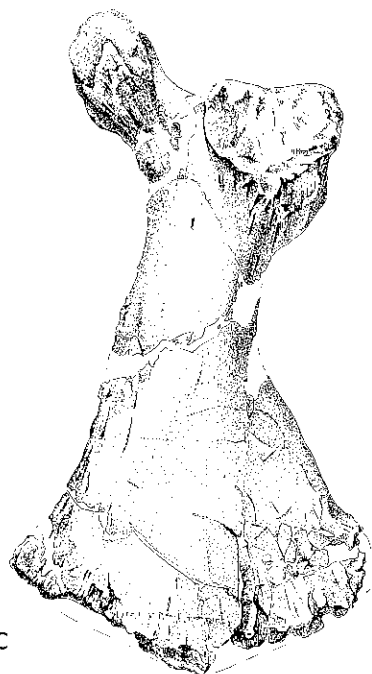


A

5 cm



B



C

Fig. 27. *Leidyosuchus formidabilis*, A, left ilium SMM P70.20.404. acetabular view; B, left pubis SMM P71.16.256. medial view; C, right ischium SMM P71.16.21. medial view.

### Hind Limb

Femur — This bone is long, but only slightly more so (< 10 percent) than the humerus, whereas, in other crocodiles, ac-

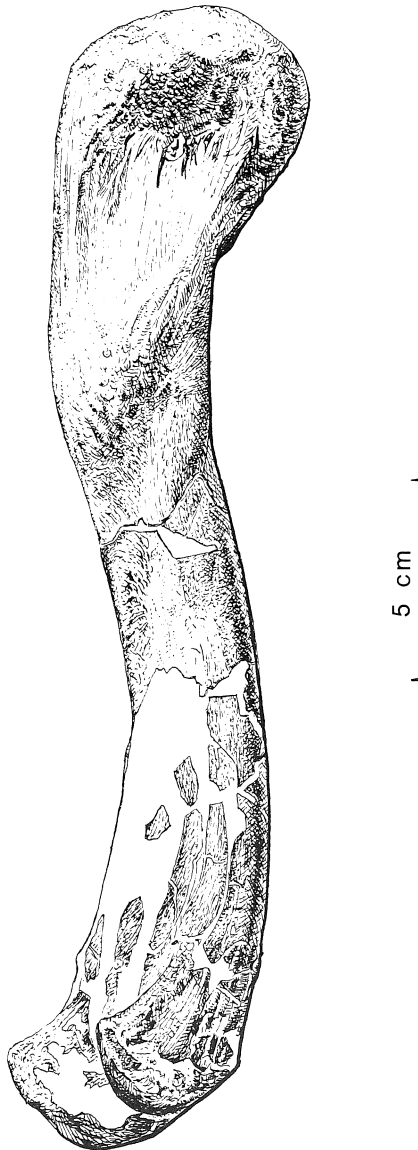


Fig. 28. Left femur of *Leidyosuchus formidabilis*, SMM P70.20.171. in dorsal view; B, left crus and tarsus of SMM P74.24.6. and SMM P72.34.95. in anterior view.

ording to Romer (1956), it is usually on the order of 20-25 percent greater. Humero-femoral ratios (Table II) of three eusuchians — two fossils, one extant — are here compared for illustrative purposes. Two specimens of the new form are included, one juvenile and one adult.

Proximal and distal expansions of the femur are modest. The upper end is a bit more enlarged and in a different plane because of mild twisting of the shaft. Condyles for epipodials are very strong and would allow a considerable degree of travel. A heavy, rugose fourth trochanter is located about one-third of the bone's length down from the proximal end. Deep striae characterize both ends above the articular areas.

Tibia-fibula — Of the available associated epipodial materials, only one set, representing the right tibia and fibula of SMM P74.24.6, is suitable to yield accurate measurements of the complete crus. These are shown in Figure 29, B.

The tibia is much more robust than the fibula. Proximally, it is much expanded, with a broad articular surface that is concave at its center. Striations on the shaft are mild and largely restricted to its ends. The remainder is rather smooth, with no salient muscle scars. Some slight, longitudinal ridges interrupt the smooth surface of the shaft, and these vary in pattern from one specimen to the next. Expansion is also pronounced distally and a well developed surface for intimate union with the astragalus is indicated, in which there would be no appreciable movement.

The fibula conforms well to characteristic crocodylian design. Most striking is its considerable length. The upper end is flattened, resulting in a narrow, lateral strip of articular surface. Distally, a good astragalar facet is found, lateral to the distal surface, for the calcaneum association. A fair amount of heavy striae occurs toward the extremities of the shaft.

Tarsus — The astragalus and calcaneum are of similar size and operate together in precisely the same manner as in later crocodiles, by sharing a ball-and-socket joint that provides the major movement between crus and foot. These elements are sturdy, and most numerous of the preserved mesopodials. They are both characterized by numerous, conspicuous, small foramina on all non-articulating surfaces. Both also have well developed facets for distal tarsal contacts, and, in the case of the astragalus, with metatarsal number I. The calcaneum bears a heavy, prominent, posterior tuber. Elements of the hind limb are shown in Figures 28 and 29.

A number of small bones that are regarded as distal tarsals are preserved. Most are fairly regular in form and do not differ in any uniform way from one another. Thus, their exact relationships within the foot are not certain; nor is it clear how many may have been contained in any single foot.

Pes — Except for digit V, the rest are extremely long and apparently bore claws. An attempted reconstruction, based on the many available metapodials, infers that number I is stoutest, number III, the longest, and number IV, thinnest of the lot. Number V is a mere nub. Little else can be stated definitely about its form and digital formula.



Fig. 29. A, left femur of *Leidyosuchus formidabilis*, SMM P70.20.171. in dorsal view; B, left crus and tarsus of SMM P74.24.6. and SMM P72.34.95. in anterior view.

TABLE II.

Comparison of three eusuchians — two fossil, one extant.  
 Figures for *Crocodylus clavis* and *C. acutus*, from Gilmore (1946).  
 Measurements in millimeters.

	<i>Crocodylus clavis</i> (Eocene) USNM 12719	<i>C. acutus</i> (Recent) AMNH 7139	<i>Leidyosuchus</i> <i>formidabilis</i> (Paleocene) SMM P74.24.36 (juv.)	<i>L. formidabilis</i> (Paleocene) SMM P74.24.6
Length of humerus	180	268	152	276
Length of femur	223	325	161	298 (est.)
Length of radius	107	149	—	—
Length of tibia	159	227	—	225
Humero-femoral ratio	.81	.83	.94	.93

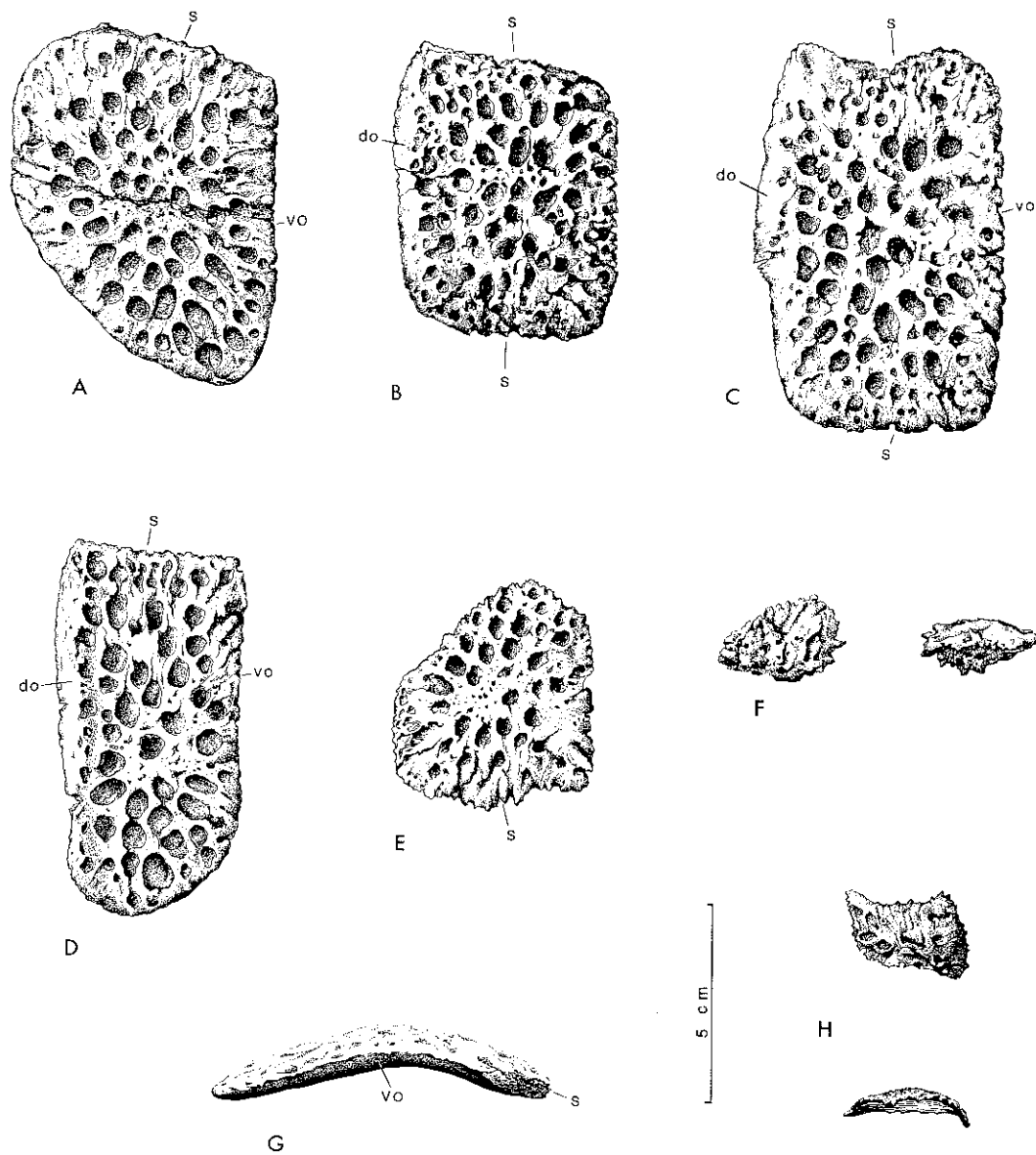


Fig. 30. Osteoderms of *Leidyosuchus formidabilis* in dorsal views. A, median nuchal; B, and C, anterior median dorsal scute, and posterior dorsal scute, respectively, with two sutural borders; D, lateral dorsal scute with one sutural border; E, distal lateral scute; F, marginal osteoderm with no contact surfaces; G, transverse aspect of lateral dorsal scute; H, palpebral (supraorbital) in dorsal and lateral (below) views; s, sutural border; do, area of dorsal overlap; vo, area of ventral overlap.

## OSTEODERMS

Postcranial dermal ossification is highly developed (Figs. 30 and 31). The nature of normal scutes of this crocodile is especially interesting, and probably as diagnostically significant for taxonomic purposes as scutellation is among extant taxa (Brazaitis, 1973). Scutellation appears primitive in two ways: (1) the absence of a distinct dorsal keel on individual scutes anywhere on the body, and (2) the overlapping arrangement of the major scutes. Unfortunately, a complete mosaic of their natural dispersal is not preserved; yet, fair amounts of the dermal armor have been found associated with individual skeletons in relatively undisturbed positions. In addition, a wealth of associated groups of a half-dozen, or so, and individual elements, are on hand to give us a good idea about these ossifications. Assuming the possession of a discrete group immediately behind the head, we may define the *postoccipitals*, *nuchals*, for those of the cervical region, and for those comprising the vast majority on the trunk — the *dorsals*. The postoccipitals are evidently irregular in shape and more or less flat. On the other hand, nuchals are quite distinctive in their triangular shapes. They are most often strongly arched for body contour. The principal nuchals are large and possess thin outer margins which possibly had minor overlap in some cases with associated scutes. A single nuchal has only one sutural contact, by which it joined its fellow at mid-line, and a slight median dorsal ridge. All together, there appear to have been at least four principal nuchals, grouped in a quadrate, and flanked on the sides by smaller, unridged ossifications. The

nuchal group seems to have been separated from the first dorsals, i.e., the neck had adequate protective covering, yet was independent in movement from the anterior trunk covering.

Individual scutes of the trunk (dorsals) are large, broad, and flat, without a central ridge. They are relatively thin for their size. Most are sculptured or pitted profusely on the upper side and smooth beneath. Some, among the largest, however, show broad areas devoid of any pitting. They were arranged in several rows covering the entire length of the body as well as a considerable portion of the tail. Most are somewhat arched and the outer ones are much extended laterally. On both upper and lower faces they are relieved along the anterior and posterior margins to accommodate the corresponding, overlapping margins of adjoining transverse rows of scutes, thus achieving a continuous, yet flexible, plating.

The area of overlap on the largest scutes may be as much as 10 mm. On smaller elements it is less, or totally absent in those of smallest size, and of more irregular shape. Those forming the central row down the back were laterally paired. This row and the associated first outboard row on either side were probably all overlapping types. Scutes comprising these principal median rows were sutured laterally with the exception of the outermost edges of the lateral ones, which were rounded (Figs. 30 and 31). The nature of additional rows is uncertain.

Many irregular, individual ossifications exist. The majority are flat — a number



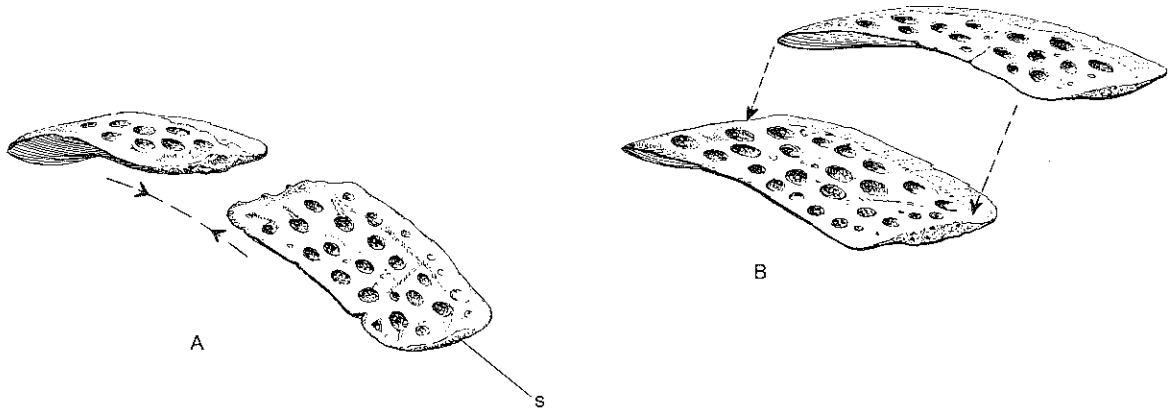


Fig. 31. Diagrammatic interpretation of major osteodermal associations in *Leidyosuchus formidabilis*. A, pair of median dorsal scutes in juxtaposition showing transverse sutural contact along mid-line. Note sutural surface as well on lateral border (s); B, tandem arrangement of overlapping median and lateral scutes from same side of animal.

are as high as they are broad and long, but without keels. It is usually these irregular ossifications that show the greatest "cross hatching" texture of the ventral surface.

Paratype material of *L. canadensis* (Lambe, 1908) includes numerous scutes which are not especially remarkable and have similarity with some belonging to *L. formidabilis*. Those having curvature also have a definite low, longitudinal keel on a central raised area developed on the upper side. Lambe, (ibid.), suggests that the scutes without such dorsal elevations are from the ventral surface. In comparing some several hundred scutes belonging to the new form, it becomes apparent that ridging of any sort is very minor and can hardly be referred to as "keeling." Relatively few of only the smaller scutes have such minor elevation. It is indicative, however, that they are of the shapes (mostly subangular) which would likely occur as nuchals or caudals (Fig. 36). The "keeling" of these scutes, in both taxa, may define the presence of crest whorls in the skin like those of later crocodylians. A marginal tract on the front edge of some scutes is also mentioned (Lambe, ibid.) as a possible overlap area. This is consistent with the present interpretation.

It is difficult to assess the number of scute rows, much less, the number of individual scutes that may have been present, not knowing the amount of gap between those of the cervical and trunk regions nor the extent of coverage. A conservative estimate, however, based on composite configurations would attribute something upwards of 150 individual and paired major scutes, and perhaps as many secondary ossifications, to a large adult animal. At least four longitudinal rows, incorporating one medial paired row, and one lateral to it on either side, covered the back and at least a portion of the tail. Shorter, additional rows were likely present as well. In any case, scutellation of *L. formidabilis* is extraordinary by modern design, wherein thick non-overlapping elements with prominent dorsal keels, characterize the dermal armor. In life, the Paleocene eusuchian would readily contrast with extant taxa.

Osteoderms, because of their occurrence on the back, along the flanks, and on parts of the legs and tail, afford physical protection. By functioning in this manner, of course, they invariably suffer damage which is often permanently imprinted as punctures or lesions of one kind or another. A large number of pathomorphic osteoderms

are included in the materials. These are largely principal dorsals. By their numbers and their much lower susceptibility to injury in comparison with those of the caudal region, the actual amount of damaged material must have been very substantial. According to Cott (1961), the tail can be expected to receive some seventy percent, and the body a mere four or five percent, of the total injury to a given individual. Aside from those scutes exhibiting conditions arising from traumatic experiences, are those resulting from disease. Both types frequently show unusual amounts of bone accretion and not uncommonly these elements are several times their normal thickness.

The presence of palpebrae is suspected; however, none were detected in direct contact with any of the skulls under discussion. Among the associated materials several curiously-shaped elements which might qualify are noted. Figure 30, H, illustrates one example. Its form is such that it seems unlikely that it would occur at any other place on the body or legs. The three specimens in hand are coarse on the convex (outer) surface and very smooth on the concave (inner) surface. Since bony eyelids are as likely to occur as not, these structures should be noted, and re-evaluated as such, in the light of future evidence. No indication of any structures which might be interpreted as sclerotic plates has been encountered.

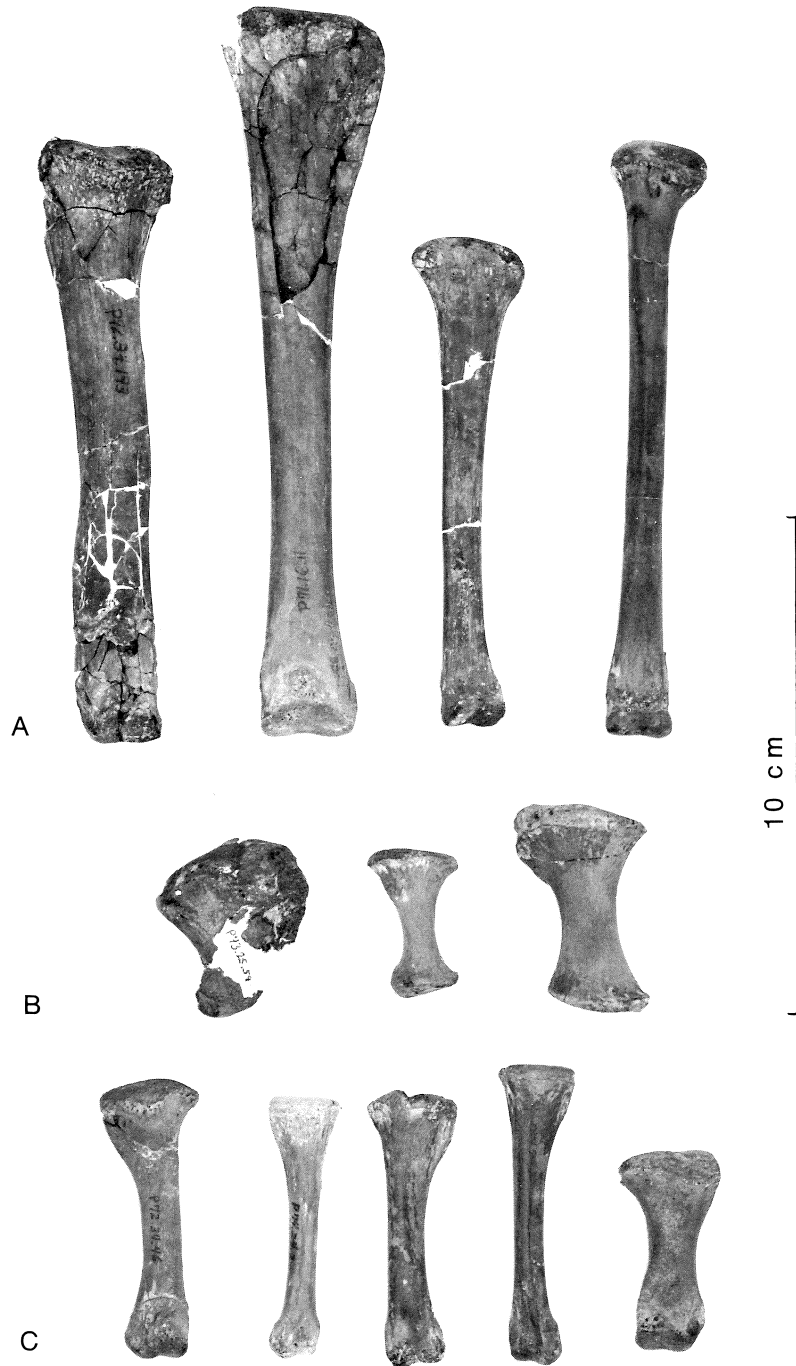


Fig. 32. Metapodials and mesopodials of *Leidyosuchus formidabilis*, from various sized individuals, from left to right. A, metatarsals I, II, III, and IV; B, metatarsal V, ulnar and radiale; C, metacarpal I, 3 intermediates and V.

## YOUNG POSTCRANIALS

The juvenile skull has been mentioned under a separate heading. The young postcranial skeleton is known from miscellaneous elements. Larger, subadult, forms are represented by many elements, including some articulated material. Agreement with general adult morphology is good in all and, as far as can be shown, proportional relationships are within what would be expected as the limits of variability. Young bones, especially those regarded as "yearling" size or less (estimated total body length of 600 mm. or less) are keener in detail and appreciably less swollen at the extremities.

Several postembryonal bones have been recovered by refined methods of treating the microscopic segment of the present material employing a wet-sieve technique. To illustrate a bit of early postembryonal development, two anterior cervical vertebral centra, P73.25.70 and P74.24.185, from two different individuals are available. The first (Fig. 35, A and B) belongs to an animal not more than several months of age. Strong parapophyses are present on a rather well formed procoelous centrum. The neural arch pedicels are established but are still quite smooth, although the usual "notch" is in evidence. Constriction of the neural canal had not yet begun and the paired foramina still are relatively large and ovoid in shape.

The second centrum (Fig. 35, a and b) belongs to a hatchling-size individual in which the procoelous condition is apparent. Because of its early age, this element lacks good ossification and is highly porous on its surfaces. No neural arch pedicels are yet

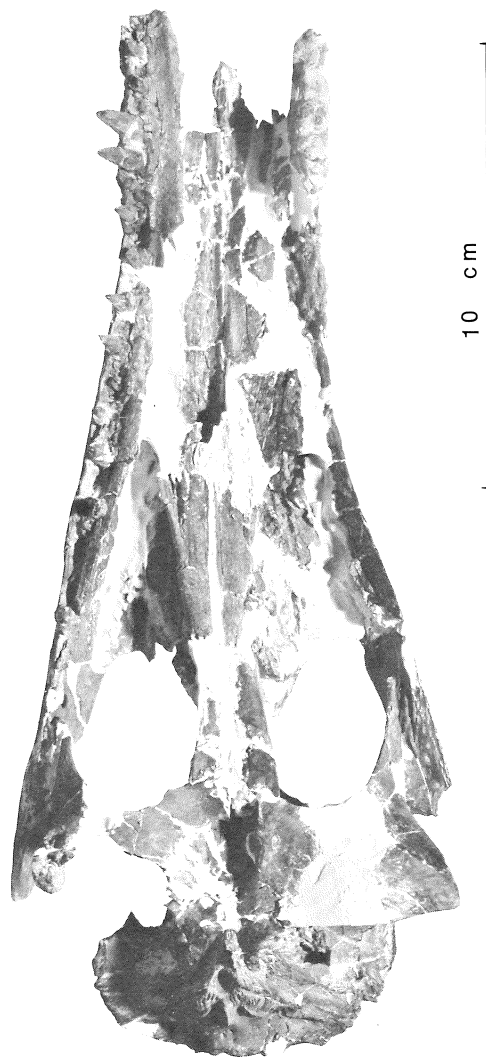


Fig. 33. Young adult skull of *Leidyosuchus formidabilis*, P70.20.407. in palatal view.

formed — hence, no evidence of a neural canal as such. Parapophyses are indicated and a prominent hypapophysis is located between them on the ventral surface. Paired dorsal foramina are exceedingly large and more circular than in the older specimen.

Another cervical element, P74.24.186 (Fig. 35, C), preserves in nearly complete detail the right atlas neurocentrum. Its relative size, compared to the centra of the two young animals described above, indicates

that it belonged to one similar in size to the larger of the two.

Most of the materials retrieved by the wet-sieve method are incomplete but nevertheless warrant notice here, not only from an ontogenetic standpoint, but, equally important, for the support they offer to my contention that the site of discovery was a nesting area for the new crocodile. This will be commented upon briefly below, and again in much greater length in subsequent reports on the site.

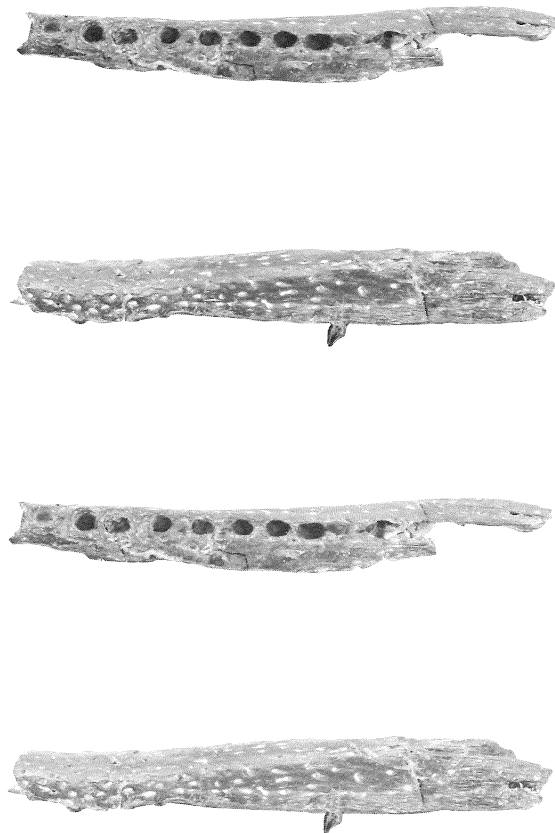


Fig. 34. Stereoscopic pairs of left maxilla of young animal, P75.22.6. exhibiting little festooning or osteodermal sculpturing.

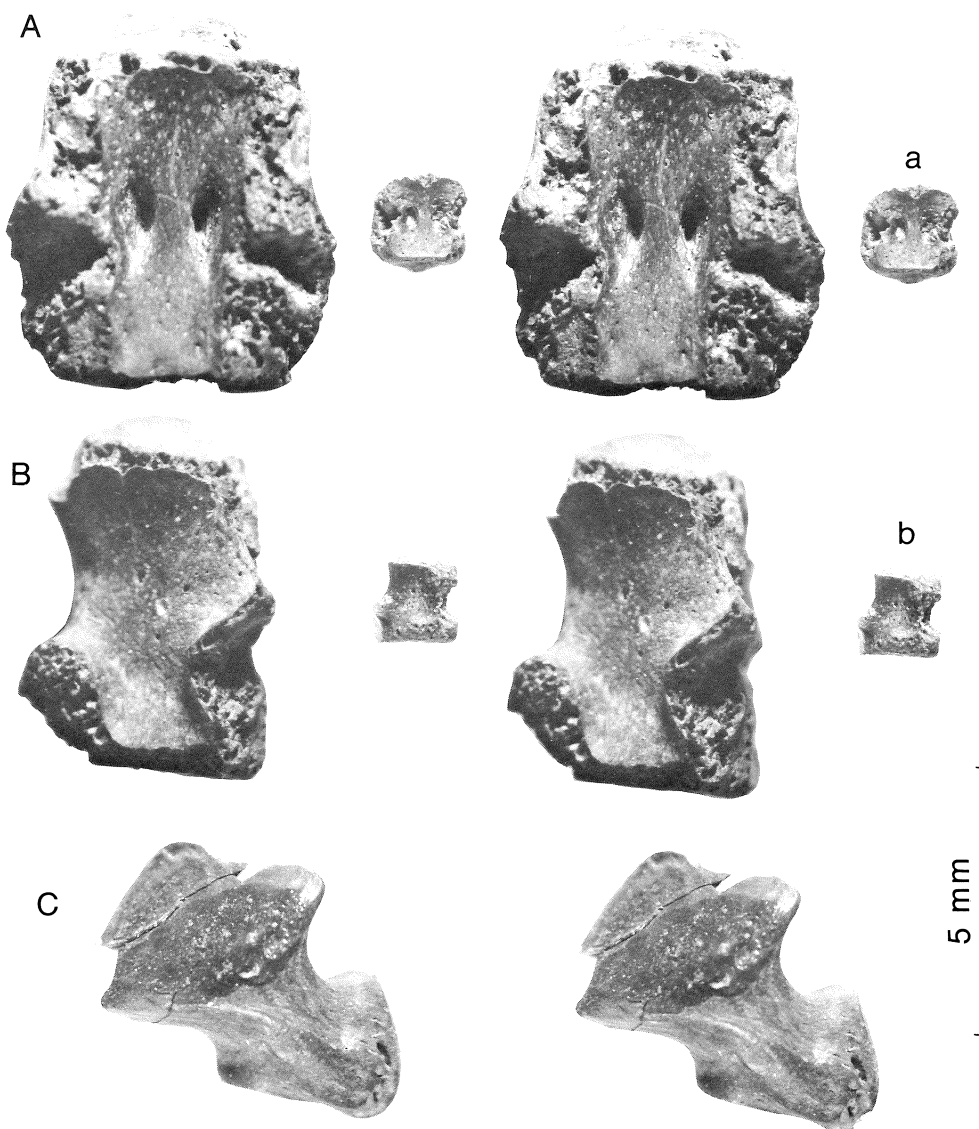


Fig. 35. Stereoscopic pairs of immature specimens of *Leidyosuchus formidabilis*. A, cervical centra of few month old individual and a, hatchling in dorsal view; B, b, same in lateral view; C, neurocentra of few month old individual in lateral view. P73.25.70. P74.24.185. and P74.24.186. respectively.

## NOTES ON FUNCTIONAL MORPHOLOGY

General habitus of the new form is typical of later crocodylians, even though modifications have been incurred along the way as adaptive specializations. It is especially interesting that the new fossil, by its splendid representation of skulls, and essentially the entire postcranial skeleton, can offer the opportunity to discuss points of functional morphology.

Cranial openings related to sensory functions indicate the advancements of later eusuchians were present. The structures of respiratory functions such as openings and passages, suggest the likelihood of narial valves and a gular flap. Large, dorsally situated, orbital openings, with possibly associated bony eyelids, indicate familiar functions of the employment of aerial vision. Also the absence of a sclerotic ring would suggest that nocturnal behavior had been established at this stage of eusuchian evolution. Pneumatization of bones of the occipital region, and a canal system, in addition to squamosal "overhang" and a deep recessus oticus externus, also implies good audition, probably with the protection of an otic valve.

Appreciable jaw length, large supratemporal openings, and a wide cranial table further characterize the skull. The elongation of the snout and the development of supratemporal fenestrae, which not only suggest a rather primitive condition, but also a high degree of development of the *M. adductor mandibulae*, bespeak a specialization for ichthyophagy. It furthermore exhibits considerable pseudoheterodonty in accord with corresponding festooning of the jaws, thus permitting greater capabilities

of holding large prey of a variety of body shapes. According to Iordansky (1973), the osteonal systems of the skull resist "masticatory pressure" and the preorbital crests of osteodermic relief strengthen the skull in omnivorous predators; and further, the absence of these features is an indication of ichthyophagous habits. The new form possesses neither preorbital bump nor other osteodermic relief; however, enough other morphological evidence, as indicated, would argue in favor of a more varied diet of vertebrates. It is reasonable to assume that it took prey regularly, at the shore line — lying in wait with its eyes and nose protruding above the water's surface, much as is the practice today of forms with comparable cranial design.

Concerning the mandible and its design, its unusually long symphyseal region certainly characterizes this new species, but not the genus. On the contrary, it is the only member wherein the jaw symphysis has such expression. The symphysis incorporates the splenial to a considerable degree, which is not unexpected in such a long-snouted form; yet, in the longest snout, *L. multidentatus*, it is stated to comprise no essential part of the symphysis (Mook, 1930). Langston (1973) notes that inclusion of the splenial strengthens the jaw as an adaptive feature of feeding specialization. It is herein considered just that — a reflection of the feeding behavior of this large crocodile, which, in turn, would have presumably departed somewhat from that of its shorter-snouted kin.

In some respects, a noticeable resemblance to alligatorines is unavoidable, viz.: in the



detailed form of the cervical vertebrae, especially the neurocentra, rib and shoulder conformations, and in the humerofemoral length ratio. Such similarity is likely only one of similar adaptation rather than of any other relationship. The elongate forelimb, in particular the propodial portion, must have had a special functional significance, perhaps in some combined amphibious-ambulatory behavior, or simply an

adaptation for increasing the animal's stride on land. Furthermore, it is of note that a rather substantial amount of osteodermal accretion exists — a condition that is expected in more terrestrial forms. These features suggest that well established terrestrial habits were combined with the more obvious amphibious behavior that is in evidence.

## ECOLOGICAL NOTES

The combination of natural environmental conditions that preserved the herein described specimens existed in a floodplain-backswamp, having meandering streams with levees and crevasse splays of load sand. Remarkable preservation of body fossils, as well as features of the environment, afford an unusual paleoecological view of this area. As this general topic is beyond the intent of the present paper, only minor commentary on this subject will be made wherever necessary to enhance the description of the new crocodile.

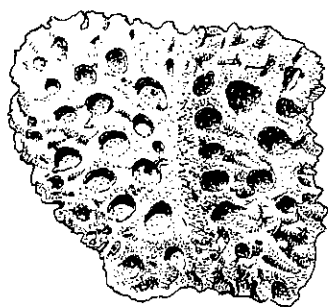


Fig. 36. Typical nuchal scute of *Leidyosuchus formidabilis* showing maximum development of a low central ridge.

Preservation of the specimens involved little replacement of the original bony structures, but did contribute some amount of post-mortem reorientation of the remains due to such factors as paleocurrents. Because of water movements, which were prevalent but not severe at all, skeletons have been, in all cases, somewhat disturbed.

Some of the best articulations occur in the sand (beach) facies of this backswamp; however, the bone itself is often eroded and shows "beach wear." It is not then always possible to associate postcranials with one another, nor with appropriate skulls. This fortunately accounts for only a small part of the complete assemblage of specimens. The heavy concentration of many individuals, often numerous bones on top of one another, especially in other areas of this deposit, did, however, yield ample material in association to allow reconstruction of the entire skeleton. Individual skulls show greatest damage to the anterior palatal region, mid-line sections of the premaxillae, and the pterygoids, wherever found in the site. Teeth are, as often as not, undisturbed, indicating little to no post-mortem transport. Skulls, being the heaviest parts, have been disturbed least by currents and wave action. In many instances, skulls with articulated mandibles have been completely undisturbed after initial deposition. Skulls are usually intact but always partially flattened, with occasional oblique distortions along the main longitudinal axis, due to compaction and settling into what was a very dense, mobile, muddy bottom layer of considerable thickness. This condition was the result of moderately rapid sedimentation that incorporated a quantity of plant debris. Large parts of tree "logs" are occasionally encountered at the bottom most often associated with skeletal remains. Skulls are nearly always oriented ventral side up, because of their "top-heavy" weight distribution; only in the few instances where

they have been found in immediate association with "logs," have they been otherwise situated. This is attributed to the flow of mud and water and the restrictions imposed by these "obstacles." Also, an occasional skull on the "beach" is right side up.

There is a certain degree of stratification throughout the one meter or less thickness of lignite, mud, silt, and sand containing the bones. Numerous elements were recovered from the sand facies which is beach remnant, as noted. Horizontal stratification within the shallow-water silt facies, and the deeper shale and mud facies is sharp. Here, materials occur in two levels (upper and lower, respectively) with the greatest accumulation of skulls and other large elements, as well as logs and great plant debris accumulation, within the lower level.

Preservation is fine here as the intimate contact with a thick carbonaceous layer provided a non-oxidizing situation. Immediately above, (upper level), the density of bones lessens upwards where, at about 70-80 cm. above the lignite layer, bones become quite scarce. It has not been determined as yet just what amount of time was required for these deposits to build.

The large sample of individuals herein referred to as "hatchling to adult stages" occur intermixed throughout most of the deposit and comprise the most conspicuous autochthonous segment of the fauna. This assemblage of individuals puts one in mind of the concentration of alligators sometimes found in "gator-holes," to elude the vicissitudes incurred by a falling water table. However, the presence of large fishes, and a well-developed wave cusp pattern on the beach line, plus the thick carbonaceous "bottom" layer, show that a condition much more stable than a temporary retreat existed. In fact, as with certain living crocodilians, the conditions governing the location of their nesting sites (Cott, 1961) are determined by several circumstances: (1)

a place with sufficient depth of soil to provide a suitable pit for deposition of eggs, (2) nearby shade for the mother to retire during the heat of the day, and (3) access to permanent water not too far away. All were present. The available evidence offers nothing that would detract from the site being a suitable nesting area. Moreover, the presence of numerous young, some of hatchling size, affirm this idea. The population was stable in the sense that it inhabited the area for a fair period of time, and was gregarious in makeup. The occurrence of sub-adults of two-to-four-foot lengths, with estimated ages between one and four years, might be interpreted as an expression of a behavior whereby individuals within this age range were not by choice isolated from the general population. The converse of this has been documented (Cott, *ibid.*) for *Crocodylus niloticus*, as a possible defensive behavior against cannibalism.

A variety of forms, which would readily qualify as potential predators of young crocodiles, are also in abundance. These include several species of chelonids, ganoid fishes, and possible large individuals of *Leidyosuchus*. *Champsosaurus* is also a conspicuous member of the fauna, although not especially numerous. With its mouth equipped with small, sharp, delicate teeth, it was proficient, no doubt, at capturing small fast-moving fishes — filling a gavial or garfish role. It too was perhaps prone to take other small forms such as young crocodiles as it is almost a certainty that the smaller champsosaur would occasionally fall prey, itself, to the crocodile — perhaps in greater numbers than we can guess. Their remains are not in abundance.

Several associated avian elements, namely, those of wading forms, provide allochthonous predators as well. Feeding as they do today on crocodile eggs, and the newly hatched, a considerable toll might have been taken.

It has been pointed out that very young individuals comprise a small segment of the material. Of this, posteranials of such a range in size document the presence of hatchlings to subadults. If not because of

losses sustained as prey, their remains would surely be found in even greater quantity. Possibly the paleoecological work currently in progress will have more to offer on all of the above topics.

## SUMMARY

The new, long-snouted crocodile is demonstrated to be distinct from other taxa. At present, in view of current taxonomy regarding the genus *Leidyosuchus*, it does not warrant separation beyond the specific level. Of the presently recognized species making up this diverse genus, affinities appear to be close to *L. riggsi* and *L. acutidentatus*, as with the type species *L. canadensis*, if the longer rostrum is considered an adaptation accompanying increased size and modification of feeding habits.

The general osteological character of the new form is typically that of later eusuchians. Bony structures and cranial openings also indicate that sensory functions were advanced and resembled those found in later forms.

Postcranials, as completely as they are known for the new form, lack adequate comparable materials among other leidyosuchines; therefore, it would seem that the postcranial skeleton herein described will serve as an early eusuchian model. Characteristics of the new skeleton are its large size, elongate foreleg, and heavy scutella-

tion. Potential terrestrial traits as these contrast to other morphological features, as well as the ecological evidence which favors a more aquatic behavior.

Ample accumulation and intermixing of bones and skeletons clearly show the gregariousness of this animal; and the considerable wealth of very young material, including hatchling-size individuals, confirms the notion that they shared the immediate habitat of the adult. As yet, no "nesting" evidence, as such, has been located, nor is it assumed what form a "nest" would have. The evidence is clear, however, that the site inhabited was probably a nesting area.

The circumstances of occurrence with many associated vertebrates, and the rather unique osteological character of this form, lead to the conclusion that the new crocodile was admirably suited as the principal predator of the backswamp, having good capabilities on land as well as in the water. In carrying out its daily functions, its role must have been not unlike that of larger species of *Crocodylus* today.

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