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AN ANCIENT EUSUCHIAN CROCODILE FROM PATAGONIA¹

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Much work has recently been done on South American Crocodilia, recent and fossil, and their relationships and history are proving to have unusual interest both in themselves and in relation to the general faunal history of South America. This is particularly striking as regards the Cretaceous and Tertiary forms (see, among others, the papers by Rusconi, by Patterson, and by me cited in the references at the end of this paper). In 1931, the First Scarritt Expedition collected an unusual specimen which was turned over to Dr. Mook for study some years ago. His other duties and researches have so far made it impossible for him to identify or publish this specimen. Since a record of the specimen is an immediate necessity for South American studies being carried on by several different students and since I have in hand work on related animals and general problems, Dr. Mook has kindly turned this specimen back to me for preliminary study. The present paper carries this study only as far as necessary for these general purposes and it is hoped that Dr. Mook will later be able to give a more detailed account of the whole skeleton.

TAXONOMY

ORDER CROCODILIA

SUBORDER EUSUCHIA

Family *Crocodylidae*

Subfamily *Leidyosuchinae*

NECROSUCHUS,² NEW GENUS

TYPE.—*Necrosuchus ionensis*, new species.

DISTRIBUTION.—Salamanca Formation, Patagonia.

DIAGNOSIS.—Vertebrae strongly procoelous and skeleton generally eusuchian in character. Jaw long brevirostral. Dentary slender, depth exceeding width posterior to the eighth tooth. Mandible pointed anteriorly, narrow across symphysis, and not noticeably expanded at fourth tooth. Symphysis of dentary ending opposite the posterior end of the fourth tooth. Splenial entering symphysis, reaching alveolar

¹ Publications of the Scarritt Expeditions, No. 30.

² *Nekrós*, dead, + *σούχος*, crocodile—a sufficiently appropriate name, suggested by the fact that when we were collecting it a well-meaning lady asked us if it were dead.



Fig. 1. *Necrosuchus ionensis*. Right dentary of type, Amer. Mus. No. 3219. Internal, superior, and external views. One-half natural size.

border at seventeenth tooth. Sculpture on dentary slight, pits sparse except in symphysial region. Eighteen teeth in dentary. First two teeth large and subequal, third smaller, and fourth larger. Fifth to tenth alveoli well differentiated as a series of small individual size. From the eleventh to thirteenth the alveoli increase regularly in size, the thirteenth being nearly as large as the fourth, then they decrease more slowly to the last, eighteenth. Crowns of fifth and fifteenth teeth, at least, acutely pointed, with numerous carinae radiating from the tip.

Necrosuchus ionensis,¹ new species

TYPE.—Amer. Mus. No. 3219, right dentary and most of postcranial skeleton. Found by Olegario García Fanjul, First Scarritt Expedition, April 3, 1931.

HORIZON AND LOCALITY.—Summit of the Salamanca Formation, Uppermost Cretaceous or Basal Tertiary, on the Estancia Las Violetas, near Malaspina, Chubut, Argentina.

DIAGNOSIS.—Sole known species of genus as defined above.

OCCURRENCE AND AGE

Necrosuchus occurs at a particularly crucial point in Patagonian stratigraphy. For this reason and because the origins of most South American fossil crocodiles have been very inadequately recorded, its provenience will be given in some detail.

The Estancia las Violetas of Alfonso Menéndez Behety is very near (southeast of) the intersection of the 45th parallel south and the 67th meridian west, about ten kilometers south-southeast of the small settlement of Malaspina and about thirty kilometers west-northwest of the port of Bustamante in Chubut Territory, central Patagonia, Argentina. It is in a cañadón on the east (Atlantic) slope of a high flat-topped ridge connecting the Pampa de Castillo with the Meseta de Montemayor, and is about twenty-two kilometers from the present shore in a straight line to its nearest point, to the southeast.

Immediately below, southeast of, the estancia buildings there begins a great east-facing barranca which hence extends southward for approximately two leagues. The type of *Necrosuchus ionensis* came from the base of this barranca at its northern end. The following section was measured at this point (oldest beds at bottom):

	FEET
a.—Patagonian marine, probably in place but perhaps somewhat slumped.....	(not measured)
b.—Outcrop covered.....	10
c.—Poorly exposed white tuff, clay, fine sand and fine conglomerate, often with a basal black clay.....	ca.40

¹ Latin, *ion* (in Pliny), violet, *-ensis*, from the locality, Las Violetas.

	FEET
<i>d.</i> —Very irregular platy tuff, white with red and yellow spots...	4
<i>e.</i> —White, soft tuff, the upper foot or so silicified and purplish...	6
<i>f.</i> —Hard tuff, brown and vesicular when weathered.....	6
<i>g.</i> —Soft ash-gray tuff.....	6
<i>h.</i> —Buff to reddish tuff, the upper part hard and weathering vesicular.....	7
<i>i.</i> —Yellowish or gray-green sand, probably volcanic, with some lava pebbles.....	ca.20
<i>j.</i> —Rather massive gray-green to brownish tuffs grading into volcanic sand with pebbles of pumice.....	ca.60
<i>k.</i> —A hard concretionary band weathering brown.....	1
<i>l.</i> —Pale gray tuff with concretions.....	15
<i>m.</i> —Fine sand and gray clay.....	10
<i>n.</i> —Thin-bedded platy gray sandstone.....	15 ±
<i>o.</i> —Fine and coarse sand and gravel with innumerable pieces of fossil wood: HORIZON OF <i>Necrosuchus ionensis</i>	15 ±
<i>p.</i> —Glauconitic bed with oyster shells.....	(base not exposed)

The upper part of the section includes the base of the marine Patagonian, Basal Miocene, and what is evidently a truncated Río Chico-Casamayor series with a possible facial equivalent of the so-called *argiles fissilaires*. A few scanty mammal bones, not exactly identifiable but surely early Tertiary, were found in bed *c*. No fossils were found in beds *d*–*n*. The upper beds are not pertinent here and need not be further discussed in this paper, although they are of unusual stratigraphic interest.

From its stratigraphic position and from its character in exposures farther south, into which it can be traced almost continuously, the bed *m* of the above section is almost surely the guide horizon called “banco negro” or “banco negro inferior” in the vicinity of Pico Salamanca, although at the exact point where the present section was measured it is not black and is otherwise atypical. Similarly beds *n* and *o* are not green at this spot and are also atypical but seem to correspond with the “banco verde” of the coastal region farther south. The “banco negro” is commonly taken by convention as the base of the supra-Salamancan series. What this series should be called at any particular point is still very doubtful. It may be the base of the Río Chico or there may be, at least in some places, an intercalated series between the Salamanca and the Río Chico of distinct age or facies. The “banco negro” generally seems to be conformable or at most only locally disconformable on the Salamanca. In this section it is apparently conformable.

The "banco verde" is generally taken as the summit of the Salamanca and this seems to be the character of our bed *o* and perhaps also *n*. Bed *p* is certainly part of the true marine Salamanca and although *o* is of quite different facies, it is probably conformable on and part of the same series as *p*. From the general distribution of the Salamanca, this locality is not far from the western limit of that sea. Bed *p* was probably deposited in shallow epicontinental waters, despite the presence of glauconite. Bed *o* seems to represent a beach, lagoon, or estuarine deposit at, or very near, the shore of the Salamanca sea and formed here when the sea was retreating to the eastward, not to return until the much later Patagonian transgression. The abundant wood in this bed, although completely silicified, has in some places, including this locality, exactly the appearance of driftwood piled up under recent shore or estuarine conditions.

If this interpretation is correct, the bed *o*, where *Necrosuchus* was found, may be synchronous with a marine horizon in the Salamanca farther south along the present coast, where the Salamanca sea was deeper and of longer duration, and with terrestrial deposits farther inland, beyond the area of the Salamanca sea, probably included in the summit of the nominal Chubutiano although in this case surely somewhat and perhaps decidedly younger than typical Chubutiano.

Ameghino considered the Salamanca Formation to be of Cenomanian age. Most recent authors (e.g., Feruglio, 1929) call it Senonian. It is impossible to review all the very complex evidence here, but as far as I am able to judge, it appears to set the Senonian as the upper limit of possible age and does not appear to exclude the possibility or even the probability of a lesser age, perhaps Danian or Montian. I suspect that the Salamanca lies almost on the Cretaceous-Tertiary line, as this line is commonly drawn by vertebrate paleontologists (e.g., between Danian and Montian or between Hell Creek and Puerco equivalents). It may be terminal Cretaceous or it may well be early Paleocene. The condition is strikingly similar to that of the Cannonball in North America.

This tentative conclusion was reached before studying *Necrosuchus*. The evidence of this single form, of a conservative group, is of course not conclusive, but it is consistent with this conclusion as to age and it is probably more consistent with it than with any other opinion. *Necrosuchus* is surely a eusuchian and generally modern in type. Its closest ally is probably *Leidyosuchus* in North America, a genus known from Belly River to Torrejon, or roughly Upper Senonian to late Montian or early Thanetian. The known distribution of *Leidyosuchus* thus nearly

corresponds with the limits placed on the possible age of the Salamanca, at the summit of which occurs this close ally of *Leidyosuchus*. There is some reason to believe that *Necrosuchus* in Patagonia would be younger than the earlier appearances of *Leidyosuchus* in North America, a suggestion far from conclusive but carrying some weight in the absence of conflicting evidence.

DESCRIPTIVE NOTES

The skeleton consists of most of the trunk, with articulated vertebrae, ribs, scutes, and fore and hind limbs, with an associated dentary. The dentary is the most characteristic bone preserved and since it proves adequate for positive diagnosis and determination of affinities the present preliminary paper is based almost entirely on this bone. The postcranial elements, not yet completely prepared, have been examined sufficiently to show that they agree with the evidence of the dentary. Although less characteristic than cranial parts, these skeletal remains are nevertheless of much interest and will be described later. They are unusually well preserved; for instance, the partly cartilaginous sternum and sternal ribs are articulated and clearly shown.

The skeleton is that of a thoroughly modernized, eusuchian crocodile, differing in numerous details but in no fundamental features from other known members of this general group.

Most of the important characters of the dentary are given in the generic diagnosis. The splenial is missing, but the surface on the dentary to which it was applied is sharply defined and shows beyond doubt that the splenial did enter the symphysis. There is a foramen in the dentary on the lower rim of the alveolar canal, posterior to the symphysis, probably correlated with the presence of an aperture in the splenial at this point, as in *Leidyosuchus*. The alveolar border is moderately "festooned," falling somewhat between first and fourth teeth, more markedly between fourth and thirteenth, and thereafter straight. The alveoli are all complete, well separated, and about equally spaced throughout. The twelfth and thirteenth teeth are closer than the others, but even their alveoli are not in contact. The fourth alveolus is definitely spaced from either the third or fifth, despite its enlargement.

Although only the fifth and fifteenth teeth have the crowns preserved, analogy with related forms makes it probable that their similarity indicates essential lack of differentiation in form in the whole series. They are sharply pointed, subconical but with curved crowns, with the usual fore-and-aft crests barely indicated but with numerous well-defined,

subequal, radiating carinae. Although tooth form is generally of little value in identifying crocodiles, these do appear to be distinctive from most or all of the known possibly related genera.

TOOTH DIFFERENTIATION

The crocodiles are, in general, homodont animals. It is, however, well known that within this group there may be considerable difference in form between the various teeth of one individual and that even when all the teeth have approximately the same form they may differ markedly in size. Such tooth differentiation is particularly striking in various alligatorids, including the South American caiman-group, and it is also typical of *Leidyosuchus* and *Necrosuchus*. In attempting to classify *Necrosuchus ionensis* largely on the characters of its dentary,¹ it was necessary to analyze this differentiation and to estimate its significance. The methods and results are here given from the point of view of the study of the affinities of this single species, but these results suggest that tooth differentiation among crocodiles is more exactly measurable and more significant than has hitherto appeared and that it will be worth while to employ similar methods more widely in the study of this group.

Tooth differentiation in form is seen in its extreme among Crocodilia in *Allognathosuchus*, with fairly typical crocodilian teeth (but highly differentiated in size) in the front part of the jaw and depressed, crushing teeth (not much differentiated in size) in the posterior part. Although aberrantly strong in this genus, such qualitative differentiation is characteristic of the Alligatoridae and occurs in great or small degree in most genera of that family. It is nearly or quite absent in *Leidyosuchus*, *Necrosuchus*, and in the Crocodilidae generally.

On the other hand, *Leidyosuchus* and *Necrosuchus* have quantitative differentiation almost equal in degree to that of the jacaré-like alligatorids and similar, but not the same, in kind. This pattern of quantitative differentiation is clearly shown in the accompanying graphs (Figs. 2, 3), in which the serial numbers of the teeth are used as abscissas and the anteroposterior diameters of their alveolar mouths as ordinates,

¹ It has been implied that *Eocaiman* Simpson was based on inadequate material, although as a matter of fact it is the best known and most exactly identifiable of all South American Tertiary crocodilians and also by far the most precisely recorded as to horizon and locality. To anticipate the same reproach as to *Necrosuchus*: its dentary alone is a more adequate type than are the types of any South American Tertiary species except that of *Eocaiman cavernensis*; the comparative study here recorded showed that this dentary is very exactly identifiable (were this not true, it would not have been named); this is accompanied by an unusually well-preserved skeleton that supports and extends the evidence of the dentary although detailed study of it proved to be unnecessary for present purposes; and its origin is better known than is that of any other South American fossil crocodile except *Eocaiman*.

with a line joining the points so determined giving a pattern for each single specimen.

The first noteworthy fact is that these patterns are characteristic for the specimens here treated and may be inferred to be so for the species. Each has a distinctive pattern and the obvious resemblances and differences between these patterns correspond in an unexpectedly

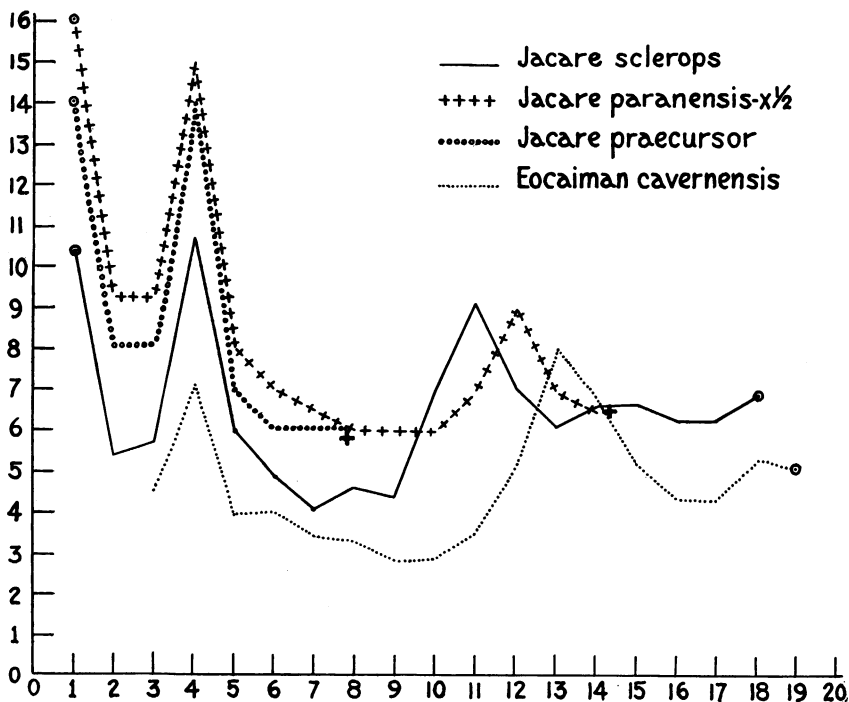


Fig. 2. Mandibular alveolar proportions in jacaré-like crocodilians. The vertical scale represents anteroposterior diameters of alveoli, the horizontal scale the serial numbers of the alveoli. Data for *Jacaré paranensis* and *praecursor* from Rusconi. The measurements for the large species *J. paranensis* have been divided by two to facilitate comparison of the dental pattern with the smaller species.

clear and exact way with the views as to classification and affinities based on other criteria. Thus specimens of the three species already referred to *Jacaré* (by Patterson, who calls the genus *Caiman*) on other grounds obviously give mere variants of the same pattern, which is hence (subject to more extended investigation) inferred to be generic. The type of *Eocaiman cavernensis* differs more from these three species than they do among themselves, but has some basic resemblance to them and

resembles them more than it does *Crocodylus americanus*, for instance, which is in agreement with the conclusion reached on other criteria that it belongs to a distinct genus of the *Jacaré*-group.

In the other series of graphs (Fig. 3), *Necrosuchus ionensis* is shown to give only a slight variant of the *Leidyosuchus sternbergii* pattern, and this sort of pattern is seen to be unlike that of the jacarés and also unlike that of a typical true crocodile, *Crocodylus americanus*.

The most striking mandibular tooth size characters of the *Jacaré*-group (including *Caiman*)¹ seem to be:

1.—First and fourth teeth subequal, larger than any others in the jaw with occasionally a single exception.

2.—Second and third teeth markedly smaller than first or fourth, usually subequal. (1 and 2 were also true of *Eocaiman cavernensis* although the first two alveoli do not permit exact measurement.)

3.—Fourth tooth followed by a series of six to eight smaller teeth, the smallest tooth in the jaw occurring in this series.

4.—A single tooth, eleventh to thirteenth in various cases, enlarged, nearly or quite as large as the fourth, with the series becoming abruptly smaller both anterior and posterior to it.

5.—Size differentiation as a whole strongly developed.

6.—Total number of teeth 18 to 22.

The characters of *Necrosuchus* and *Leidyosuchus* are:

1.—First tooth smaller than fourth; fourth the largest in the jaw but first equalled or exceeded by the thirteenth and sometimes by others.

¹ The nomenclature of recent crocodilians is in such a confused state that uniformity can probably never be achieved under the International Rules. It is an obvious case for consideration by the Commission, as has repeatedly been pointed out, but I am not aware that anything has been done about this. In general I have insisted, and still do insist, on strict adherence to the Rules, but the present situation, where their application is doubtful for part and absurd for the rest, is too much for even the most generous attitude toward Rules and Commission. I give below three sets of names applied by three authors to some of the genera and species involved in this paper. Werner attempts to follow the Rules strictly, but even here the use of *Jacaretinga* rather than *Caiman* for the genus usually called *Jacaré* is possibly incorrect under the Rules and he has fallen into at least one definite error. Separation of *Melanosuchus* as a genus is a matter of opinion. *Crocodylus niloticus* is worthy of note as a name applied in this system to a reptile not even belonging to the same family as the crocodile and not occurring within thousands of miles of the Nile. Schmidt follows his own interpretation of the Rules in the use of *Caiman* and common sense in rejecting *Crocodylus* (or *Crocodylus*) and *niloticus* as generic or specific names in the South American Alligatoridae. Mook's nomenclature follows almost universal usage, except that *Jacaretinga* has recently been often used for *Jacaré*.

Werner (1933)

Champse
C. acuta
Jacaretinga
J. crocodilus
Melanosuchus
M. niger
Crocodylus
C. niloticus

Schmidt (1928)

Crocodylus
C. acutus
Caiman
C. sclerops
= *Caiman*
C. niger
Paleosuchus
P. trigonatus

Mook (1921)

Crocodylus
C. americanus
Jacaré
J. sclerops
= *Jacaré*
J. niger
Caiman
C. trigonatus

I will not use Werner's arrangement, unless or until it is confirmed and made official by the Commission. Pending this, I see little reason to follow Schmidt. If one is going to disregard the Rules, it may as well be in favor of the most common and most generally understood usage. Mook's nomenclature represents this usage as well as does any one authoritative arrangement, and I shall follow it.

2.—Second and third teeth slightly unequal, one of them about equal in size to the first.

3.—A series of smaller teeth including among them the smallest in the jaw, following the fourth, as in the *Jacaré*-like genera.

4.—Thirteenth tooth (exact position perhaps variable with more material) enlarged and nearly equal to fourth, approximately as in the *Jacaré*-group, but transition to this tooth somewhat less abrupt anteriorly and markedly less so posteriorly, some of the more posterior teeth being nearly or quite equal to the thirteenth in size.

5.—Size differentiation well developed, but somewhat less than in the *Jacaré*-group.

6.—Total number of teeth in early species 18 or 19, within the *Jacaré*-group range (but number considerably greater in the Paleocene species of *Leidyosuchus*).

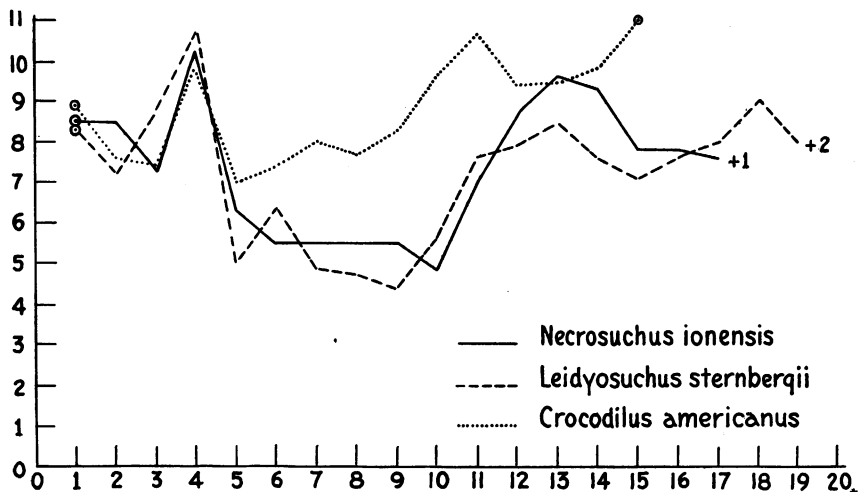


Fig. 3. Mandibular alveolar patterns in *Necrosuchus*, *Leidyosuchus*, and *Crocodilus*. The vertical scale represents anteroposterior diameters of alveoli, the horizontal scale serial numbers of the alveoli.

These differences from the jacarés are, on the whole, points of resemblance to *Crocodilus* and closely allied forms. The corresponding characters of *Crocodilus* appear to be as follows, subject to emendation since I have made no attempt to measure and plot a majority of the species of this protean genus:

1.—First tooth equal to or slightly smaller than fourth; the fourth usually equalled by two or several posterior teeth.

2.—Second and third teeth subequal, usually slightly smaller than first.

3.—Fifth tooth abruptly smaller than fourth and either the smallest in the jaw or about equal to the third; after the fifth the series increases steadily in size to about

the tenth or eleventh and there is no markedly differentiated small series as in the preceding two groups.

4.—Teeth from about the eleventh to the end of the series subequal and nearly or quite equal to the fourth; there is often a tendency for the eleventh tooth to be somewhat the largest.

5.—Size differentiation markedly less than in either of the preceding two groups.

6.—Total number of teeth usually 15.

These graphs show the kind or pattern of size differentiation. It is more difficult to measure and to compare the degree of such differentiation in any adequate way. For this purpose a coefficient of differentiation is tentatively proposed that seems to fill the need for the particular groups here discussed. It is taken as one hundred times the mean deviation divided by the arithmetic mean of the anteroposterior diameters of the first fourteen mandibular alveoli for each individual.¹ The mean deviation for all the teeth is a measure of average size differences, hence of size differentiation, but is not comparable from one species or specimen to another because it depends also on absolute size and on the number of teeth, which are foreign to the character for which a measure is sought. These are eliminated by limiting the alveoli involved to the first fourteen and by dividing by the mean. In the groups of immediate interest here, the size differentiation is largely in the teeth anterior to the fifteenth. The number of rather uniform teeth posterior to the fourteenth varies from one in *Crocodylus* to fourteen in *Leidyosuchus multidentatus*. Obviously if all the teeth were included in the coefficient the figures for these two would not be comparable: that for *Crocodylus* (all species) would be relatively too high and for *Leidyosuchus multidentatus* (and to less extent other species of that genus) relatively too low. Basing the coefficient only on the anterior teeth, where the principal differentiation does occur, is a valid and simple way to avoid this difficulty, although not a perfect solution. Dividing by the mean makes the figure independent of the absolute size and permits valid comparison between individuals and species of different sizes. For instance, *Jacaré paranensis* is clearly a typical *Jacaré* as regards size differentiation, but the mean deviation for the first fourteen alveoli in an individual is 4.7 mm. as compared with only 1.6 mm. for an individual of *Jacaré sclerops*: the figures are not comparable because *J. paranensis* is much larger. Their coefficients are nearly the same.

¹ Calculated by adding the individual measurements, dividing by fourteen (giving the arithmetic mean), subtracting each measurement from this figure (giving the deviations), adding these deviations without regard to their signs, dividing by fourteen (giving mean deviation), dividing by the arithmetic mean, and multiplying by one hundred. This is a short series of easy arithmetical operations and is not as complicated in operation as it may sound in words. No simpler process seems to give a satisfactory result.

Coefficients thus calculated for individuals of some of the species here mentioned are:

<i>Jacaré paranensis</i>	27.7
<i>Jacaré sclerops</i>	24.6
<i>Leidyosuchus sternbergii</i>	22.3
<i>Necrosuchus ionensis</i>	21.5
<i>Crocodylus americanus</i>	11.9

COMPARISONS AND RELATIONSHIPS

Aside from some Jurassic fragments with no bearing on the present case, most of the known South American fossil crocodiles come from five different general regions. There are late Cretaceous and early Tertiary forms from Patagonia, late Cretaceous forms from Uruguay, Upper Cretaceous forms from Bahia and Pernambuco provinces in Brazil, late Miocene or early Pliocene forms from the Paraná, and Upper Tertiary forms from the Rio Purus in Brazil. The Paraná and Purus faunas, imperfectly known in both cases, include jacaré-like and gavial-like species all quite unlike *Necrosuchus*. The Uruguay and the Bahia-Pernambuco crocodiles, mentioned on a later page, are all mesosuchians, as far as known, and still more distant from *Necrosuchus*. In Patagonia *Notosuchus*, *Cynodontosuchus*, and *Microsuchus*, probably from the Cretaceous, are also mesosuchians.

Regarding another Patagonian crocodile, *Symptosuchus*, only the following brief diagnosis has been published (literal translation from Ameghino, 1899, pp. 9-10):

"In the family Goniophoridae there is to be added *Symptosuchus contortidens*, new genus and species, of much greater size than *Notosuchus*. Teeth conical-pointed, slender, somewhat curved, with longitudinal crests, prominent and slightly spiral, which converge toward the end of the crown but without reaching the apex; body armored, with dermal plates decorated with the same sculpture as in the caimans. Cretaceous of Patagonia (Guaranitic Formation)."

The type material evidently included only one or more loose teeth and one or more loose plates, and there is a decided possibility that the genus and species are not recognizable. As far as I know, this material has never been restudied, figured, or more fully described, and it is not at present available to me. The reference to the Goniophoridae (to which the notosuchids were then also referred) would exclude relationship to *Necrosuchus* if confirmed, but it was probably not based on any concrete evidence but only on the fact that only supposed goniophorids,

i.e., notosuchids, were then known from beds of comparable age in Patagonia.

The "longitudinal crests" of the teeth may have been like the carinae of *Necrosuchus*, but nothing is said as to their number and in *Necrosuchus* they are not spiral and do reach the apex. The two genera are probably distinct, as far as the data on *Symptosuchus* give any basis for decision, and everything known of the latter is so vague and uncharacteristic that in any case it is advisable to have a distinctive name for the fully characteristic and well known material of *Necrosuchus*. The age of *Symptosuchus* is unknown. Ameghino's "Guaranitic" included at least eight quite different formations ranging from Cretaceous to Oligocene in age.

Eocaiman (see Simpson, 1933), from the Casamayor, Eocene, was already definitely *Jacaré*-like and a member of this group of South American alligatorids. It differs from *Necrosuchus* in many ways: the tooth differentiation is characteristically different, its teeth do not have strong, subequal, multiple carinae, the posterior teeth have low and laterally compressed crowns,¹ the symphysis is markedly wider and slightly shallower, the splenial does not enter the symphysis, and the dentary as a whole is relatively shorter and stouter. It is unlikely that *Eocaiman* and *Necrosuchus* are closely related within the Eusuchia and almost impossible that *Necrosuchus* is ancestral to *Eocaiman*.

Kuhn (1933) has recently described a few fragments found by von Huene at Punta Peligro.² Although not found in place, these are recorded as from the "Schwarzen Leitschicht," that is, the "Banco Negro Inferior" of local geologists, which immediately overlies the probable equivalent of the bed in which *Necrosuchus* was found. Kuhn identified the specimens as cf. *Holops*, cf. *Bottosaurus*, cf. *Leidyosuchus*, gen. indet. non *Leidyosuchus*, and gen. indet. These rolled, broken, and uncharacteristic fragments, the largest 57 mm. in length, are not determinable beyond the fact that at least one procoelous, eusuchian crocodile is present. Probably some of these specimens belonged to *Necrosuchus*, but detailed comparison would have no particular interest or value. The comparisons with *Holops* and *Bottosaurus* are inconclusive and in part based on somewhat mistaken grounds. They do not need discussion, nor should these genera now be listed in the Patagonian

¹ Contrary to a criticism that has been made, this is a decided point of resemblance to, not of difference from, the genus *Jacaré*.

² This is essentially the type locality of the Salamanca Formation, as the formation is not exposed on Pico Salamanca and is well exposed at Punta Peligro, near the peak for which the formation is named.

fauna. Kuhn's paper was, however, important as giving the first certain record of pre-Casamayor eusuchians in South America.

With the exception of the nearly contemporaneous and not exactly identified or named fragments described by Kuhn, *Necrosuchus* is thus quite unlike any previously known South American crocodilians. It is, however, closely similar to the North American genus *Leidyosuchus* Lambe, 1908, with its species *L. canadensis* Lambe, 1908, from the Belly River of Alberta, *L. sternbergii* Gilmore, 1910, from the Lance (*sensu stricto*) of Wyoming, *L. acutidentatus* Sternberg, 1932, from the Upper Ravenscrag of Alberta, and *L. multidentatus* Mook, 1930, from the Torrejon of New Mexico. It shows the following principal differences from these as a group:

1.—Teeth with many carinae; those of *Leidyosuchus* with only two and otherwise nearly smooth.

2.—First and second mandibular teeth subequal, third smaller; in *Leidyosuchus canadensis* (type of genus) and *L. sternbergii* the second is smaller than the first and the third larger than either, but in the aberrant *L. multidentatus* the proportions are more as in *Necrosuchus*, while in *L. acutidentatus* the third and fourth teeth are nearly equal.

3.—Number of mandibular teeth 18; 18, 21, 20, and 28, respectively, in the four species of *Leidyosuchus*.

4.—Symphysis more pointed, less expanded.

5.—Fourth tooth pointing more upward, outer contour of dentary not bulging outward here.

6.—Splénial reaching alveolar border somewhat more posteriorly (except *L. multidentatus*).

7.—Posterior part of dentary higher and more slender.

8.—Alveoli all discrete and well spaced; in *Leidyosuchus* the posterior alveoli and sometimes also the third and fourth tend to run together, but this is least noticeable in *L. multidentatus*.

There are also numerous distinctions from any one of the four North American species taken alone. For instance, *L. multidentatus*, although an exception to some of the above distinctions, is quite unlike *Necrosuchus* in the longer symphysis, the weakness of the splénial anteriorly, the very long, rod-like dentary, the remarkably large number of teeth, and other characters in which the genotype and *L. sternbergii* more nearly approach *Necrosuchus*.¹ The type of *L. acutidentatus* is remarkably well preserved, but the published data do not permit as complete comparison with *Necrosuchus ionensis* as for the other species. It seems, however, to differ from the latter at least as much as does *L.*

¹ *L. multidentatus* is so aberrant with respect to the other species that it may not properly belong in *Leidyosuchus*, although doubtless a close relative and to some extent united with them by *L. acutidentatus*.

sternbergii. Sternberg says that the mandible is intermediate between *L. sternbergii* and *L. multidentatus*. In *L. canadensis*, *sternbergii*, and *acutidentatus* the series of large posterior mandibular alveoli may be taken as beginning with the eleventh, in *L. multidentatus* with the twelfth or thirteenth, and in *Necrosuchus ionensis* also with the twelfth or thirteenth.¹

These various distinctions suffice to separate *Necrosuchus* generically either from typical *Leidyosuchus* or from *L. multidentatus*, but all are relatively minor and it seems certain that *Necrosuchus* is a close ally of *Leidyosuchus*. The skeletal characters support this conclusion, as far as they are known in *Leidyosuchus* (of which only a few scattered skeletal parts are known) and I have been able to compare them in *Necrosuchus*.

Leidyosuchus has been classified in the Crocodilidae as opposed to the Alligatoridae, and I tentatively retain this arrangement for *Leidyosuchus* and *Necrosuchus*. A revision or review of the general classification is beyond the scope of this paper, but it cannot but be noticed that this arrangement is not very satisfactory. *Leidyosuchus* and *Necrosuchus* differ from and resemble the Alligatoridae in different ways but about as much as they do the Crocodilidae. Moreover, when all forms are taken into account (note also, for instance, *Diplocynodon*), it seems doubtful whether crocodiles and alligators should really be separated as different families. In any case *Crocodylus* and its close allies, the *Alligator-Jacaré* complex, and *Leidyosuchus* and *Necrosuchus* (possibly also *Allodaposuchus*) evidently represent three different but similar groups of common origin in the Cretaceous. Perhaps it will eventually be most practical to place them as three subfamilies of Crocodilidae.²

CRETACEOUS AND EOCENE SOUTH AMERICAN CROCODYLIA

Modifying the usual classification somewhat to accommodate recently discovered forms, the following are the more important crocodylians now known from the late Mesozoic and early Tertiary of South America:

ORDER CROCODYLIA

SUBORDER SEBECOSUCHIA

Sebecidae

Sebecus Simpson. *S. icaeorhinus* Simpson, Casamayor Formation, Chubut.

¹ The series begins more abruptly in *L. multidentatus* than in the other species and the doubt is caused by the fact that the intermediate small series seems to have one more tooth on one side than on the other. In *Necrosuchus ionensis* it begins gradually and the doubt is caused by this fact.

² Without entirely endorsing it, attention may be called to Nopcsa's arrangement (1928) which places jacarés and alligators in the subfamily Crocodilinae and *Leidyosuchus* in a separate crocodylid subfamily Leidyosuchinae. The latter subfamily seems surely to be valid and I have adopted it in the taxonomy of the present form.

SUBORDER SUCHIA

INFRAORDER MESOSUCHIA

Goniopholidae

Goniopholis Owen. ? *G. hartti* (Marsh),¹ ? *G. derbianus* (Cope),²

Upper Cretaceous, near Bahia and Pernambuco, Brazil.

Notosuchidae

Notosuchus Smith Woodward. *N. terrestris* Smith Woodward, probably late Cretaceous, Neuquén.

Cynodontosuchus Smith Woodward.³ *C. rothi* Smith Woodward, same provenience as *Notosuchus*.

Brasileosaurus v. Huene. *B. pachecoi* v. Huene, Upper Cretaceous (Baurú Formation), Brazil.

Uruguaysuchus Rusconi.⁴ *U. aznarezi* Rusconi, *U. terrai*

Rusconi, Upper Cretaceous, Uruguay.

Mesosuchia incertae sedis:

Microsuchus Saez. *M. schilleri* Saez, Upper Cretaceous, Neuquén.

INFRAORDER EUSUCHIA

Crocodilidae

Necrosuchus Simpson. *N. ionensis* Simpson, Salamanca Formation, Chubut.

Alligatoridae

Eocaiman Simpsn. *E. cavernensis* Simpson, Casamayor Formation, Chubut.

Crocodilia incertae sedis:

Thoracosaurus bahiensis Marsh, cf. *Holops* (fide Kuhn), cf. *Bottosaurus* (fide Kuhn), crocodile "gen. ind. non *Leidyosuchus*" (fide Kuhn), *Symptosuchus contortidens* Ameghino, etc.

The peculiar and specialized nature of *Sebecus* implies a long history and probably relatives will eventually be found elsewhere, but at present it seems to be only very distantly related to any other known reptiles. The Brazilian forms referred doubtfully to *Goniopholis* are not very adequately known, but it is evident that members of this general group are present. This sort of crocodile is widespread in marine and semi-marine Cretaceous beds in the northern hemisphere and it is interesting but not surprising to learn that they also reached South America.

Cynodontosuchus, *Microsuchus*, and *Brasileosaurus* can be set aside as inadequately known or studied and probably related to better known notosuchids. *Notosuchus* and *Uruguaysuchus* are relatively well known

¹ Described by Marsh under *Crocodylus* from teeth and uncharacteristic fragments. Woodward (in Mawson and Woodward, 1907) referred a symphysis and other fragments to this species, on rather insecure grounds, and placed it in *Goniopholis*.

² Described by Cope (1885) as *Hyposaurus derbianus*, based on relatively good material, a lower jaw, and other parts, not figured. *Hyposaurus* is provisionally made a synonym of *Goniopholis* by Mook (1925). The Cretaceous Brazilian forms need revision.

³ It is not quite certain that this poorly known form belongs in this family.

⁴ Probably a synonym of *Brasileosaurus*.

and are evidently allied but well distinguished genera, representing a very peculiar, archaic side branch of the Mesosuchia. They cannot be closely allied to *Goniopholis*, as was at first supposed, and surely they are not ancestral or at all closely related to any of the latter forms known from South America (or elsewhere).¹ These notosuchids have been compared with various other small, brevirostral forms but no intimate relationship has been established. Thus Mook (1934) refers *Libycosuchus* definitely and *Hoplosuchus* doubtfully to the Notosuchidae. Stromer (1914) concluded that the resemblance of *Libycosuchus* to *Notosuchus* is superficial and that the two are not really closely related, and in this I concur, as far as I can judge from the literature. In any case the relationship cannot be close enough to have any decisive bearing on paleogeography or correlation. Among many other facts, it is noteworthy that *Libycosuchus* is at least as old as *Notosuchus* and probably older, yet is distinctly more specialized in numerous characters.

Hoplosuchus was originally described as an aëtosaur (Gilmore, 1926), but von Huene (1933) has given good reasons for considering it a crocodile, parallel or more or less distantly allied to the Atoposauridae. It does suggest a form such as could well have given rise to the Notosuchidae, but this remains only a possibility as long as the detailed structure of *Hoplosuchus* is unknown.

Eocaiman is surely related to *Jacaré*, *Caiman*, and allied late Tertiary and Recent South American forms, carrying the history of this distinctively Neotropical group back into the Eocene in the same region. It is, of course, unlikely that a single Patagonian specimen and species should represent the actual ancestry of the later forms, but this genus does so structurally and no definite character excludes it from the actual ancestry. The only known fact opposing this is that one Paraná species of *Jacaré*, *J. praecursor*, is said by Rusconi (1933) to have the splenial entering the symphysis. Since, however, the splenial very closely approaches the symphysis in the type of *Eocaiman cavernensis*, it is entirely possible that it entered it in other species of the genus, or even in other individuals of the species. The close resemblance of *Eocaiman* to *Allognathosuchus* shows approach to the common stock of the alligators (s. s.) and the jacarés (s. l.). The tooth differentiation is of quite the same sort in *Allognathosuchus* and in the jacaré-group, only in

¹ In his very admirable summary of the fossil Crocodilia, von Huene (1933) denies special relationship between *Notosuchus* and *Uruguaysuchus* and seeks to derive the alligatorids from *Uruguaysuchus*. This is not the place to discuss the question fully, but I have studied it at great length and am convinced that in this one point v. Huene is mistaken. It seems extremely probable that Rusconi was correct in placing *Uruguaysuchus* in the Notosuchidae, and it seems impossible that it should be ancestral to *Eocaiman* or other Tertiary alligatorids.

Allognathosuchus it has gone to an extreme that removes that group from the *Alligator* main-line, but not far.

The different position of the posterior apex of the alveolar diameter graph in *Eocaiman* and in species of *Jacaré* (Fig. 2) is not opposed to close relationship. In *Eocaiman cavernensis*, Eocene, it is on the thirteenth tooth, in *Jacaré praecursor*, Miocene-Pliocene, on the twelfth, and in *J. sclerops*, Recent, on the eleventh in the specimens illustrated. It is, however, both individually and specifically variable even in contemporaneous forms and is often on the twelfth in the recent species. It is easy to frame a reasonable hypothesis adequate to explain this variation and to explain a possible tendency for the apex to shift forward with the passage of time. In the first place, reduction would be most likely to occur in the smallest teeth, which are between this apex and the fourth tooth, and such loss would shift the apex forward. From a broader point of view, there is considerable evidence that a size pattern in a dentition is inherited as a whole and not by the inheritance of an individual size factor for each separate tooth, and this would perhaps be particularly true in a dentition with numerous teeth all of about the same form. In such a case, individual homologies in the teeth would be more or less incidental or nominal and the important character would be the whole pattern as a unit. Slight shifting, compression, or expansion of the pattern with respect to the concrete series of individual teeth might readily occur and would have little bearing on affinities or descent.

The relationship of *Eocaiman* to *Allognathosuchus* is one of many facts tending to indicate common origin of North and South American faunas in the Cretaceous. *Necrosuchus*, with its close approach to *Leidyosuchus*, is an even more striking example of the same sort.

The recent discovery of *Eocaiman* and *Necrosuchus* shows how great is the chance that apparent faunal differences are due in part to lack of discovery.¹ Nevertheless there is little probability that the two faunas will ever be found to be essentially the same. Many North American animals seem never to have reached South America, and similarly there are groups in South America even at the beginning of the Tertiary for which close Holarctic allies or parallels are not known. The suggestion is that a connection existed but that it was to some degree selective, a differential migration route along which passed numerous animals but not integral faunas, and further that the whole South American fauna probably did not enter by this one route and at this one time. This is a

¹ Doubtless true of the North American fauna as well as the South American, despite the fact that much more work has been done in North America.

very broad problem which I hope to discuss at more length elsewhere. At present it suffices to show the tendency of the growing body of evidence derived from the Crocodilia.

REFERENCES

- GILMORE, C. W. 1910. '*Leidyosuchus sternbergii*, a new species of crocodile from the *Ceratops* beds of Wyoming.' Proc. U. S. Nat. Mus., XXXVIII, pp. 408-502.
1926. 'A new aëtosaurian reptile from the Morrison Formation of Utah.' Ann. Carnegie Mus., XVI, pp. 325-348. [*Hoplosuchus kayi*.]
- VON HUENE, F. 1931. 'Verschiedene mesozoische Wirbeltierreste aus Sudamerika.' Neues Jahrb. Min. etc., Beil.-Bd. LXVI, Abt. B, pp. 181-198. [*Brasileosaurus pachecoi*, described as a coelurosaur but later (v. Huene, 1933), said to be a crocodile possibly of the same genus as *Uruguaysuchus aznarezi*; other crocodiles are mentioned but they are not identifiable and are not specially noticed in the present paper.]
1933. 'Ein Versuch zur Stammesgeschichte der Krokodile.' Centralbl. Min. etc., Jahrg. 1933, Abt. B, No. 11, pp. 577-585.
- KUHN, O. 1933. 'Über Reste procoeler Crocodilier aus der obersten Kreide von Patagonien.' Pal. Zeits., XV, pp. 81-92.
- LAMBE, L. M. 1908. 'On a new crocodilian genus and species from the Judith River Formation of Alberta.' Trans Roy. Soc. Canada, Ser. 3, I, pp. 219-244. [*Leidyosuchus canadensis*.]
- MOOK, C. C. 1921. 'Skull characters of recent Crocodilia with notes on the affinities of the recent genera.' Bull. Amer. Mus. Nat. Hist., XLIV, pp. 123-268.
1925. 'A revision of the Mesozoic Crocodilia of North America.' Bull. Amer. Mus. Nat. Hist., LI, pp. 319-432.
1930. 'A new species of crocodilian from the Torrejon beds.' Amer. Mus. Novitates, No. 447, pp. 1-11. [*Leidyosuchus multidentatus*.]
1934. 'The evolution and classification of the Crocodilia.' Journ. Geol., XLII, pp. 295-304.
- NOPCSA, F. 1928. 'Palaeontological notes on reptiles. VII. On the classification of the Crocodilia.' Geol. Hungarica, ser. Pal., I, Fasc. 1, pp. 75-84.
- PATTERSON, B. 1936. '*Caiman latirostris* from the Pleistocene of Argentina, and a summary of South American Cenozoic Crocodilia.' Herpetologica, I, pp. 43-54.
- RUSCONI, C. 1933a.¹ 'Sobre reptiles cretáceos del Uruguay (*Uruguaysuchus aznarezi*, n.g. n.sp.) y sus relaciones con los notosúquidos de Patagonia.' Inst. Geol. Montevideo, Bol. No. 19, pp. 1-64. [Also *U. terrai*.]
- 1933b. 'Observaciones críticas sobre reptiles terciarios de Paraná (familia

¹ Copies bear the printed date 1933 and separates were distributed in 1934. Rusconi (pers. com.) states that the paper was issued in September, 1932. No question of priority is involved and I cite by the printed date to facilitate finding the paper.

- Alligatoridae).' Rev. Univ. Nac. Córdoba, XX, pp. 1-52. [This and the preceding paper cited from separates.]
- DE SAEZ, M. D. 1928. 'Un nuevo goniofórido argentino.' An. Soc. Ci. Argentina, CVI, pp. 287-290. [*Microsuchus schilleri*.]
- SCHMIDT, K. P. 1928. 'Notes on South American caimans.' Field Mus. Nat. Hist., Pub. 252; Zool. Ser., XII, No. 17, pp. 205-231.
- SIMPSON, G. G. 1933. 'A new crocodilian from the *Notostylops* beds of Patagonia.' Amer. Mus. Novitates, No. 623, pp. 1-9. [*Eocaiman cavernensis*.]
1937. 'New reptiles from the Eocene of South America.' Amer. Mus. Novitates, No. 927, pp. 1-3. [*Sebecus icaeorhinus*.]
- STERNBERG, C. M. 1932a. 'A new fossil crocodile from Saskatchewan.' Canadian Field Nat., XLVI, pp. 128-133. [*Leidyosuchus acutidentatus*.]
- 1932b. 'The skull of *Leidyosuchus canadensis* Lambe.' Amer. Midland Nat., XIII, pp. 157-169.
- STROMER, E. 1914. 'Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltier - Reste der Baharije - Stufe (unterstes Cenoman). 1. Einleitung und 2. *Libycosuchus*.' Abh. K. Bayer. Akad. Wiss., Math.-phys. Klasse, XXVII Bd., 3 Abh., pp. 1-16.
- WERNER, F. 1933. 'Reptilia Loricata.' Das Tierreich, Preus. Akad. Wiss. Berlin, 62 Lief., pp. i-xiv, 1-40.
- WOODWARD, A. S. 1896. 'On two Mesozoic crocodilians, *Notosuchus* (genus novum) and *Cynodontosuchus* (genus novum), from the red sandstones of the Territory of Neuquen (Argentine Republic). An. Mus. La Plata, Pal. Argentina, IV, pp. 1-20.