

TWO TOXOCHELYID SEA TURTLES

FROM THE LANDENIAN SANDS OF ERQUELINNES (HAINAUT), OF BELGIUM

BY

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Among the superb materials of fossil sea turtles preserved in the Institut royal des Sciences naturelles de Belgique in Brussels there are two forms, hitherto thought to be cheloniids, that definitely belong to the family Toxochelyidae. As such they are the first unquestionable representatives of this family recognized outside of North America ⁽²⁾. Both forms were found in a sand pit near Erquelinnes (Hainaut), along the Franco-Belgian border in sands of lower Landenian age (early Eocene). They are thus probably younger than the latest North American forms which occur in greensands of late Maestrichtian or Paleocene age of New Jersey. Both of the Belgian forms have close relatives in New Jersey.

I am very grateful to the Director of the Institut royal des Sciences naturelles de Belgique, Dr. A. CAPART, and Dr. E. CASIER, Directeur de Laboratoire honoraire, for their kind permission to study the outstanding fossil turtle materials in their care. My thanks are also due to Dr. TIBOR PERENYI, staff artist at Field Museum of Natural History, for his help with the illustrations. The work was made possible by a grant from the National Science Foundation, GB 6195.

1. DOLLOCHELYS CASIERI.

Order CHELONIA

Suborder CHELONOIDEA

FAMILY TOXOCHELYIDAE.

SUBFAMILY TOXOCHELYINAE ZANGERL, 1953.

DOLLOCHELYS n. gen. ⁽³⁾.

Characterization. — Toxochelyines with elongated carapace — carapace width being less than 90 % of the total length of the carapace — and with large lateral fontanelles.

⁽¹⁾ Field Museum of Natural History, Chicago, Illinois 60605.

⁽²⁾ The reference of *Toxochelys gigantea* OERTEL from the Lower Aptien of Karstendamm near Hannover, Germany, to the Toxochelyidae is uncertain (ZANGERL, 1953, p. 260).

⁽³⁾ In honor of LOUIS DOLLO who had a great interest in the adaptations of turtles to the marine environment.

Maximal width of carapace disc less than 60 % of total carapace length. Antero-lateral peripherals very narrow. Average width of pygal smaller than length.

Type species : *Dollochelys casieri* n. sp.

Dollochelys casieri n. sp. ⁽¹⁾.

H o l o t y p e . — I.R.Sc.N.B. No. 1631 : most of a carapace, lacking the anterior end, both hyoplastra, a fragment of a hypoplastron, both xiphiplastra, an incomplete proximal left humerus fragment, a fragment of a left scapula and the forward portion of the right ramus of the mandible.

L o c a l i t y . — Erquelinnes (Hainaut), Belgium.

H o r i z o n . — Lower Landenian, Early Eocene.

C h a r a c t e r i z a t i o n . — Carapace with narrow disc, measuring 63 % of the known carapace length. Plastron very narrow between axillary and inguinal notches, with a plastral index of about 34. Vertebral shields very wide : length of vertebral 3 only 65 % of width. Length of suprapygal 1 about 60 % its width. Mandible as in *Toxochelys*, but with greater posterior protrusion of chin shelf beyond border of masticatory surface.

The above mentioned specimen, currently on exhibit at the Institut royal des Sciences naturelles, was prepared free of matrix and mounted for display in 1888. It was identified as *Argillochelys antiqua* (KÖNIG) and referred to by DOLLO (1907) who mentions the remains of six individuals, one of them mounted. The latter is no doubt the present specimen (I.R.Sc.N.B. No. 1631). There seems little doubt that DOLLO identified the specimen; the type of *Argillochelys antiqua*, however, is a skull, figured in lateral and posterior views which renders detailed comparison with the mandibular fragment of the Erquelinnes specimen impossible. It seems probable that DOLLO considered the better known *Chelone breviceps* OWEN as synonymous with *Chelone antiqua* KÖNIG and identified the Belgian specimen on the basis of *Chelone breviceps*. The toxochelyid turtles were poorly known at the time and it is perfectly understandable that DOLLO did not recognize it as such.

A partial skull with a well preserved mandible (I.R.Sc.N.B. No. 1653), probably one of the six specimens mentioned by DOLLO (1907) appears to belong to a cheloniid turtle.

D e s c r i p t i o n . — The mandibular fragment of the type specimen consists of most of the right dentary, including the posterior two-thirds of the symphysis (Pl. I, A; Pl. II, 1, a). In the symphyseal region two shelves can be distinguished as, for example, in *Toxochelys* : a dorsal shelf that bore the horny beak, and a ventral shelf that extends backwards below the sulcus Meckelii. In this form the ventral shelf (chin shelf) at the symphysis had about the same width as the dorsal shelf, and is thus considerably wider than in *Toxochelys*. The cutting edge of the dentary is exceedingly sharp, and the horn-covered « triturating » surface, a little ways behind the symphysis, is steeply inclined inward; thus the mandible was clearly a cutting not a crushing device, and the inference is justified that the skull had a primary palate.

The carapace (Pl. I, B; Pl. II, 2; Pl. III, A) is oval in outline, provided with large fontanelles and relatively narrow « bridge » peripherals.

⁽¹⁾ In honor of EDGAR CASIER, former chef of the Laboratoire de Paléontologie at the Institut royal des Sciences naturelles, to whom I am personally indebted for his kind hospitality during my stay at Brussels.

Neurals 3 to 7 are of the usual hexagonal type with the antero-lateral sides being the shortest; neural 2 is subrectangular and neural 8 is divided into two short elements. None of the neurals is keeled. The proportion of width to length of the neurals is about 1 : 1.4.

There are two suprapyrgals, shaped as in *Toxochelys*, but the fontanelles have reduced their original areas to such an extent that the second element is no more than a narrow medial strip of bone, narrowest at its posterior end where it is suturally connected with the pygal. It borders the fontanelles medially. The pygal is, on the average, considerable longer than wide, though its posterior width equals that of its length at the midline.

All of the preserved costal plates except the sixth show the lateral margins, so that the width of the carapace disc can be accurately determined, but the width of the fontanelles depends on the correctness of the mounting of the peripheral rim of the shell, since the free rib ends are all missing. Assuming the present mount to be correct, costal ribs 3 and 4 are covered by plates to about 60 % of their length.

The peripherals 4 to 6 are « bridge » peripherals; they are narrow and approximately triangular in cross section with the inner face gently concave and provided with well defined rib pits. The antero-posterior extent of this « bridge » region is relatively very short and bears out the interpretation of the morphology of the plastron (see below). Behind the sixth, the peripherals increase rapidly in width to the 11th element which, near the pygal, is about twice as wide as the 7th peripheral is anteriorly. These posterior peripherals are flat plates and the dorsal and ventral surfaces approach the sharp outer edges in the manner of thin wedges.

The epidermal shield pattern of the carapace shows no unexpected features. The shield furrows are weakly imprinted on the bones (Pl. I, B), but there is no difficulty in determining the pattern (Pl. II, 2). The length-width ratio of the third vertebral shield is about 1 : 1.5 (index 65), that of the fourth is 1 : 1.

The plastron (Pl. III, A; Pl. III, B) of this specimen shows an interesting error in the mounting that must have escaped the scrutiny of Professor DOLLO. As mounted, it appears as if the right hyo- and hypoplastra were preserved in sutural union. But both bones are hyoplastra, joined along the hyo-hypoplastral suture. The posterior element is the right hyoplastron, the anterior bone the left hyoplastron. A small fragment of the left hypoplastron of the postero-medial expanse of the element may have been oriented as shown in plate III, B. Of the xiphoplastra the right element is virtually complete, but is mounted in reversed position. The element is fairly slender, widest at midlength and thickest at mid-width. Both the lateral and medial edges are sharp.

Although the lateral width of the hyoplastron cannot be determined directly, enough is preserved to permit a reasonable reconstruction (Pl. III, A). The preserved portion of the hyo-hypoplastral suture measures 47 mm, and the configuration of the remains of the plates suggests that it measured about 70 mm. The most striking and significant aspect of this plastron is the narrowness of the hyoplastra between the most posterior point of the axial notch and the hyo-hypoplastral suture; and it is reasonable to assume that the distance between the most anterior point of the inguinal notch and the mentioned suture on the hypoplastron was only a very little longer, as is true in all members of the genus *Toxochelys*. Thus the plastral index (ZANGERL, 1953) lies in the vicinity of 37 which is much lower than has been observed in any cheloniid sea turtle, and is as low as has been observed in the *Toxochelyidae* (ZANGERL, 1953, p. 161).

A low plastral index such as this is characteristic of the toxochelyine sea turtles and the preserved parts of this plastron agree very well in shape with this interpretation.

The scapular fragment (Pl. II, 1, *b*) shows no features of interest, and the proximal fragment of the left humerus (Pl. II, 1, *c, d, e*) shows the proximal position of the radial tuberosity which is typical in the toxochelyids. The placement of the fragment in relation to the bone as a whole is shown in figure (Pl. II, 1, *e*).

Comparisons. — Among the toxochelyine sea turtles *Dollochelys casieri* shows the greatest similarity to a specimen in the collection of Peabody Museum, Yale University which I recognized as a new species and tentatively referred to the genus *Toxochelys* (*T. atlantica*,

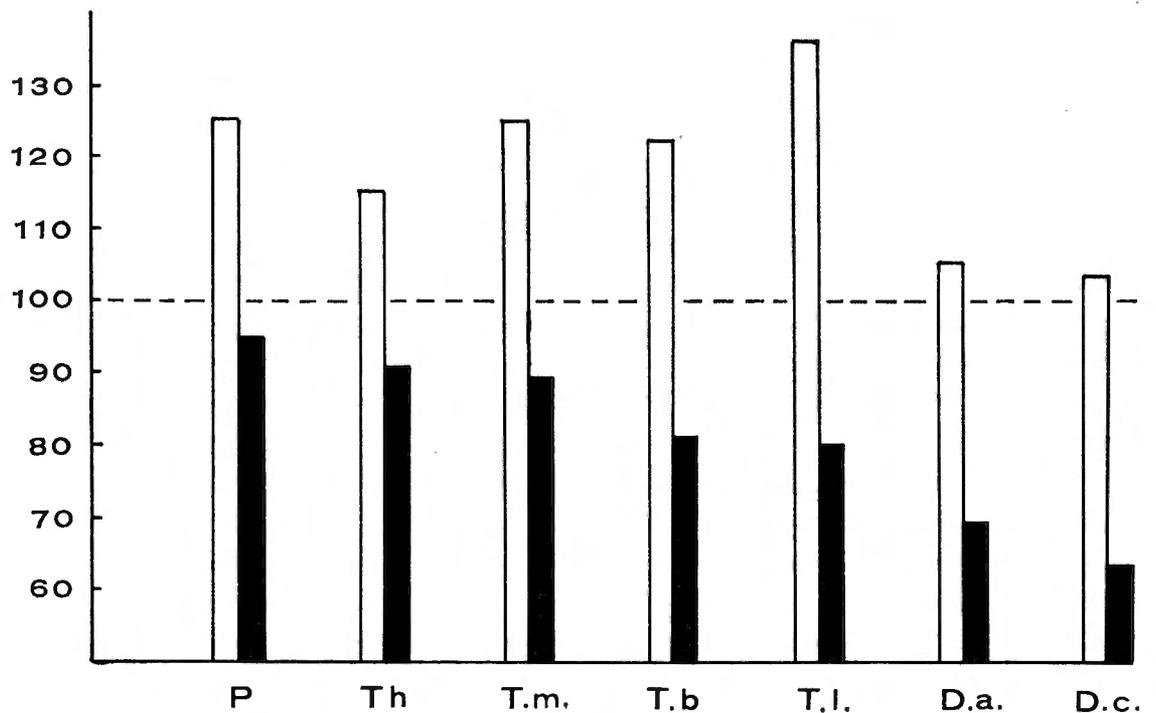


FIG. 1. — Relative width of the carapace (white bars) and carapacial disc (neural plus costals, black bars).

Length of carapace (anterior suture of C2 to posterior margin of pygal)=100.
 P=*Porthochelys*; Th=*Thinochelys*; T.m.=*Toxochelys moorevillensis*; T.b.=*Toxochelys barberi*; T.l.=*Toxochelys latiremis*; D.a.=*Dollochelys atlantica*; D.c.=*Dollochelys casieri*.

ZANGERL, 1953) even though the oval outline of its carapace differed from all other species of the genus. The similarity between these two species is in fact so great that the species *atlantica* should be transferred to the new genus *Dollochelys*. The two forms differ from the other members of the Toxochelyinae by the oval shape of the carapace and the more highly reduced carapacial disc (fig. 1). The differences between the two species are relatively minor, reflecting in *D. casieri* a more advanced condition of marine adaptation (greater fontanellization) and differences in proportion of the pygal plate and the vertebral shields.

***Dollochelys atlantica* ZANGERL.**

Synonymy :

- Toxochelys atlantica* (ZANGERL), Fieldiana Geology, 1953, Mem. 3 (4), p. 196, fig. 79.
Lytoloma wielandi HAY (in part), Carnegie Inst., 1908, Publ. 75, p. 157, text figs. 196, 197.
Lytoloma angusta WIELAND, not COPE (in part), Amer. J. Sci., 1904, 18, p. 187, fig. 3, pls. 6-8.

Holotype. — Y.P.M. 625, carapace, lacking anterior end, collected in 1869.

Locality. — West Jersey Marl Company pit, 1.5 miles east of Barnsboro, Gloucester County, New Jersey.

Horizon. — Hornerstown formation, probably latest Cretaceous (late Maestrichtian), or possibly Paleocene (see discussion in BAIRD, 1964, pp. 22-24).

Emended characterization. — Carapace disc measuring about 68 % of carapace length (anterior suture of costal 2 to posterior end of pygal). Length of vertebral 3 about 76 % of width. Length of suprapygal 1 at midline about 30 % of width.

2. REDESCRIPTION OF ERQUELINNESIA GOSSELETI DOLLO, 1886 ⁽¹⁾.

Introduction.

In 1881, L. DOLLO received from Professor J. GOSSELET of the Faculté des Sciences de Lille the first lots of bones pertaining to the species of sea turtle redescribed below. From that time on the Musée de Bruxelles received much additional material of this turtle, all from a sand pit near Erquelinnes (Hainaut) along the Franco-Belgian border. In 1886, DOLLO reported that bones belonging to at least 14 individuals were at hand. He determined the systematic position of this species by means of a number of « tables of comparison » which led to the conclusion that it is a sea turtle of the general group that includes the modern *Chelonia mydas*. DOLLO's comparisons further suggested that the fossil belongs to an as yet undescribed genus and species which he called *Pachyrhynchus* ⁽²⁾ *gosseleti*.

DOLLO's determination of the systematic affinity came as close to being correct as was possible at the time. Although some members of the family to which *Erquelinnesia* belongs were known, including the genus *Osteopygis* to which it is closely related, most of the material was very fragmentary and an understanding of the family characteristics of the cheloniid, toxochelyid and thalassemydid sea turtles was still far from satisfactory by 1908 when HAY revised the turtles of North America.

The situation changed little until the late forties when much new toxochelyid material was collected in the late Cretaceous Mooreville Chalk of Alabama, in the Niobrara Chalk of Kansas, and in the Pierre Shale of South Dakota. This new material permitted a revision of the family Toxochelyidae and its characterization and delimitation against the Cheloniidae and Thalassemydidae (ZANGERL, 1953).

⁽¹⁾ I am very grateful to Dr. E. CASIER who kindly provided me with his notes and drawings that were made under his direction in an effort to redescribe this material.

⁽²⁾ *Pachyrhynchus*, however, was preoccupied and DOLLO later (1887) substituted the name *Erquelinnesia*.

The toxochelyid turtles, although they resemble the cheloniids in many other respects, have a characteristically specialized plastron with a low plastral index. In this feature *Erquelinnesia* is an unmistakable toxochelyid. This family assignment is further strengthened by the presence of nasal bones, observed in *Toxochelys*, but absent in the Cheloniidae. In most respects, however, the Toxochelyidae and the Cheloniidae have evolved along parallel paths, for example, in the differentiation of the locomoter apparatus and the construction of the palate (primary and secondary palates in both families).

Three subfamilies of Toxochelyids can be distinguished :

1. Toxochelyinae, forms with primary palates and flat, more or less circular, unkeeled shells;
2. Osteopyginae with extensive secondary palates and moderately arched, oval, unkeeled shells;
3. Lophochelyinae with incipient secondary palates and moderately arched, cordiform carapaces that are provided with sagittal keels.

Erquelinnesia, with its enormously expanded secondary palate and oval unkeeled shell clearly belongs to the Osteopyginae.

At the time of the revision (ZANGERL, 1953) none of the European forms, as described, could be assigned with certainty to the family Toxochelyidae. Thus it was tentatively assumed that the group was restricted to North America and had died out at the close of the Cretaceous.

Order CHELONIA

Suborder CHELONOIDEA

FAMILY TOXOCHELYIDAE.

SUBFAMILY OSTEOPYGINAE.

E m e n d e d c h a r a c t e r i z a t i o n . — Toxochelyid turtles with relatively generalized shells and skulls provided with extensive secondary palates. Symphysis of mandible more than one-third the length of the ramus. Nasal bones present. Carapace moderately arched with or without lateral fontanelles. Neuralia unkeeled. Peripheral edge of carapace not, or only slightly, serrated. Plastron weakly connected to carapace by lateral prongs of hyo- and hypoplastra, or entirely membranous.

Erquelinnesia DOLLO, 1887.

S y n o n y m y :

Euclastes COPE, 1867 (preoccupied).

Lytoloma COPE, 1870 (nomen vanum-ZANGERL, 1953).

Pachyrhynchus DOLLO, 1886 (preoccupied).

E m e n d e d c h a r a c t e r i z a t i o n . — Skull with very extensive secondary palate; choana near posterior ends of pterygoids. Mandible with correspondingly large triturating surface. Carapace moderately arched, consisting of fairly thin bones. Continuous lateral fontanelles and post-nuchal fontanelles present. Nuchal plate more than three times as wide as long. Vertebral shields much wider than long. Connection of plastron to carapace by

membrane only. Hyo-, hypo- and xiphiplastra not suturally connected at midline. Plastral index 35 to 40 in presumed adult individuals, higher in immature specimens.

Type of genus : *Erquelinnesia gosseleti* DOLLO, 1886.

***Erquelinnesia gosseleti* DOLLO, 1886.**

Synonymy :

- Pachyrhynchus gosseleti* DOLLO, 1886, p. 138.
Euclastes gosseleti DOLLO, 1888, p. 115.
Erquelinnesia gosseleti DOLLO, 1907, p. 393.
Lytoloma gosseleti DOLLO, 1909, p. 108.
Erquelinnesia gosseleti HAY, 1908, p. 160.
Erquelinnesia gosseleti MOODY, 1968, p. 130.

Holotype. — I.R.Sc.N.B. No. 1563, a nearly complete carapace, partial plastron, good skull and mandible, part of the tail, part of pelvis. Presently on exhibit.

Locality and horizon. — Sand pit near Erquelinnes (Hainaut), Belgium. Lower Landenian (Early Eocene).

Referred specimens. — All from the same locality and horizon as the holotype.

- I.R.Sc.N.B. No. 1585, fragment of mandible; carapace lacking anterior end; left hyo- and hypoplastral fragments.
 I.R.Sc.N.B. No. 1628, skull and mandible; partial carapace; both hyo- and xiphiplastra; left humerus; metacarpal I; right ilium.
 I.R.Sc.N.B. No. 1629, incomplete, but good carapace and plastron.
 I.R.Sc.N.B. No. 1632, skull and mandible; partial carapace and plastron.
 I.R.Sc.N.B. No. 1633, partial skull; partial carapace; left xiphiplastron.
 I.R.Sc.N.B. No. 1634, partial carapace; plastral fragments; left humerus; ilium fragment, both pubes; right femur and tibia.
 I.R.Sc.N.B. No. 1635, skull; fragmentary shell.
 I.R.Sc.N.B. No. 1636, partial carapace.
 I.R.Sc.N.B. No. 1638, partial carapace; good plastron lacking epiplastra and right xiphiplastron.
 I.R.Sc.N.B. No. 1641, mandible.
 I.R.Sc.N.B. No. 1642, mandible.
 I.R.Sc.N.B. No. 1643, mandible; nuchal plate; suprapygals 1; three costals; fragment of right hyoplastron, left hypoplastron; some limb bones, but association with shell is in doubt.
 I.R.Sc.N.B. No. 1644, mandible.
 I.R.Sc.N.B. No. 1645, mandibular fragment.
 I.R.Sc.N.B. No. 1646, mandible.
 I.R.Sc.N.B. No. 1647, mandible.
 I.R.Sc.N.B. No. 1648, mandible.
 I.R.Sc.N.B. No. 1649, fragmentary skull.
 I.R.Sc.N.B. No. 1950, partial skull.
 I.R.Sc.N.B. No. 1651, snout fragment.
 I.R.Sc.N.B. No. 1652, mandible.
 I.R.Sc.N.B. No. 1683, large portion of a skeleton on a slab, somewhat crushed; shell; pelvis; hind limb and part of foot; articulated tail.
 I.R.Sc.N.B. No. 3669, mandibular fragment; part of carapace disc; fragment of coracoid.
 I.R.Sc.N.B. No. R2, mandible.
 I.R.Sc.N.B. No. R3, fragment of mandible.
 I.R.Sc.N.B. No. R7, fragment of mandible.
 I.R.Sc.N.B. No. R8, fragment of mandible.
 I.R.Sc.N.B. No. R10, partial skull.
 I.R.Sc.N.B. no number, mandible.
 Carnegie Museum No. 3462, partial skull; partial carapace.

C h a r a c t e r i z a t i o n . — Same as that for genus.

D e s c r i p t i o n . — In overall proportion *Erquelinnesia gosseleti* resembles very much the modern Alligator snapping turtle *Macrochelys temmincki*, since both have enormous skulls relative to the size of the shells (fig. 2). In large specimens of *Macrochelys* there appears to be a sexual difference in the general proportions of the skulls — the males having broader,

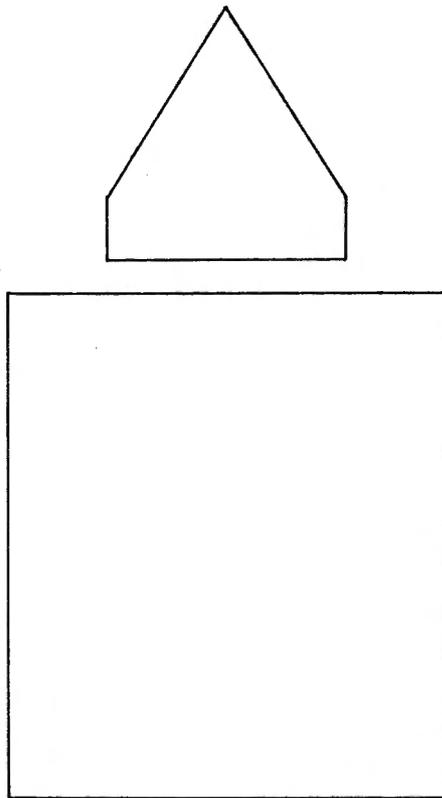


FIG. 2. — Skull and shell proportions of *Erquelinnesia gosseleti* based on dimensions of type specimen, I.R.Sc.N.B. No. 1563.

more massive and more blunt-snouted skulls, but this has not been adequately documented. The skulls and the mandibles of *Erquelinnesia* also show considerable differences in proportion, e.g. skulls Nos. 1563 and 1628, plate IV, but the triturating edges of the mandibles belonging to these skulls both form angles of 64° . If this angle is plotted against the symphyseal length of the 13 available mandibles (fig. 3) most specimens have angles between 60° and 70° in the symphyseal length range of 65 to 90 mm. Only two specimens have significantly wider angles. A sexual dimorphism can thus not be demonstrated at present.

Although close to 30 specimens are now available for study the material does not lend itself to satisfactory statistical treatment because most skeletons are notably fragmentary and the form and dimensions of many of the better shells, as mounted, reflect the judgement of the preparator.

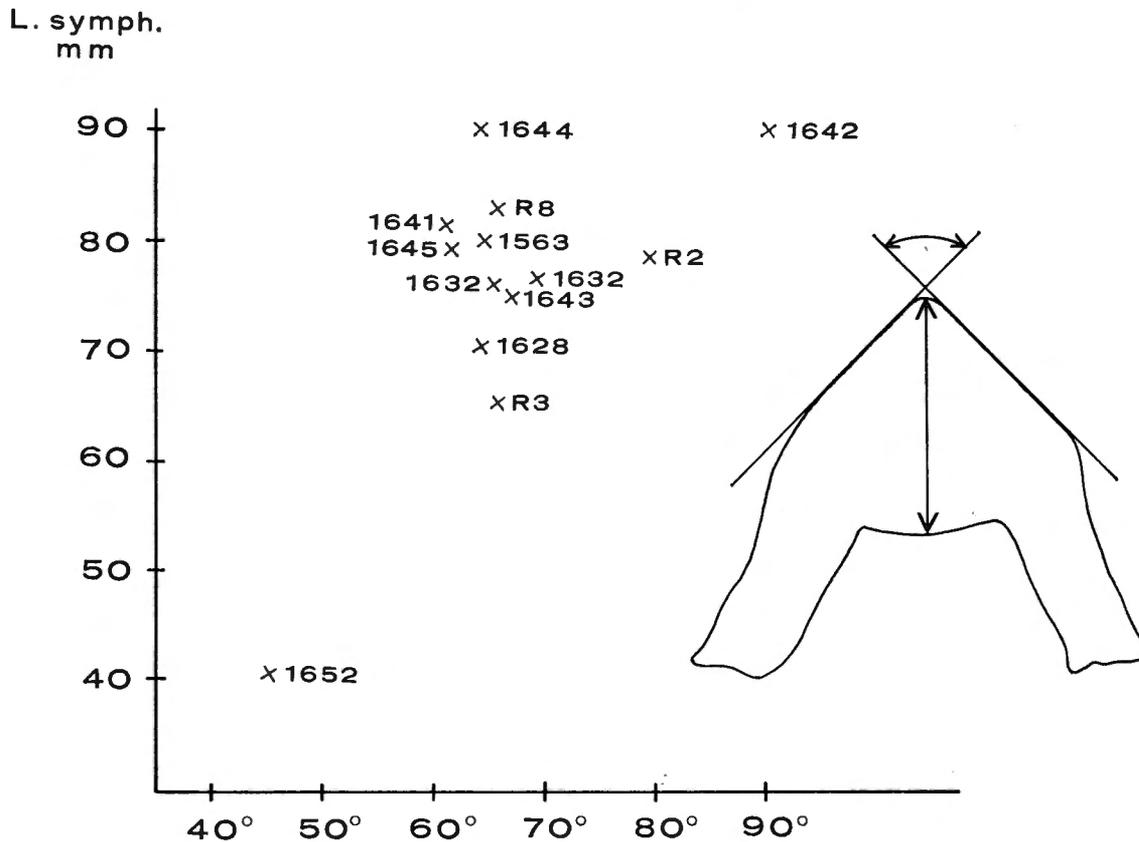
Mandible of *Erquelinnesia gosseleti*

FIG. 3. — Angle between the mandibular cutting edges plotted against length of symphysis, in *Erquelinnesia gosseleti*.

Skull.

The best skulls in the material from Erquelinnes are those of the type (1563) and 1628; less complete are 1632, 1650, 1659 and Carnegie Museum 3426. In addition there are several isolated mandibles.

The morphology of the skull is dominated by the extreme durophagous specialization of the masticatory apparatus. This consists of a very extensive, massive secondary palate; enormous quadrato-prootic bosses (Processus trochleares of SCHUMACHER, 1953-1954) which provide (in *Caretta*) pseudo-joint surfaces over which the tendons of the adductor mandibularis externus muscles slide; large, roofed-over temporal cavities for the adductor mandibularis externus masses, and a stout mandible with a very long symphysis and a broad triturating surface. Probably correlated with this extraordinary masticatory apparatus are the almost complete fusion of the bones of the cranial roof and the overall solid construction of the skull.

The skull (Pl. IV, 1; Pl. IV, 2; Pl. V; Pl. VI; fig. 4, 5) is widest at about the level of the tympanic funnel. From there it tapers forward to a fairly pointed snout and backwards to the tips of the squamosals. In side view the skull roof descends gently from the highest place on the supraoccipital process to a point above the anterior rims of the orbits. From there the profile, mostly controlled by the nasals and the lateral rims of the nostril, falls off steeply to the ventral edge of the external naris. The orbits face antero-laterad and slightly upward;

their antero-posterior diameter measures about $1/4$ the distance from the tip of the snout to the posterior end of the squamosals. The temporal region is roofed over to about the same extent as in *Chelonia mydas* and, as in this form, there seems to be some excavation of the lateral margin in the quadratojugal area.

The sutures between the roof bones of the skull are almost completely obliterated; only here and there, in specimen No. 1628, can a suture be followed for a short distance. The nasal bones, by contrast are separate and prominent (Pl. V; fig. 5).

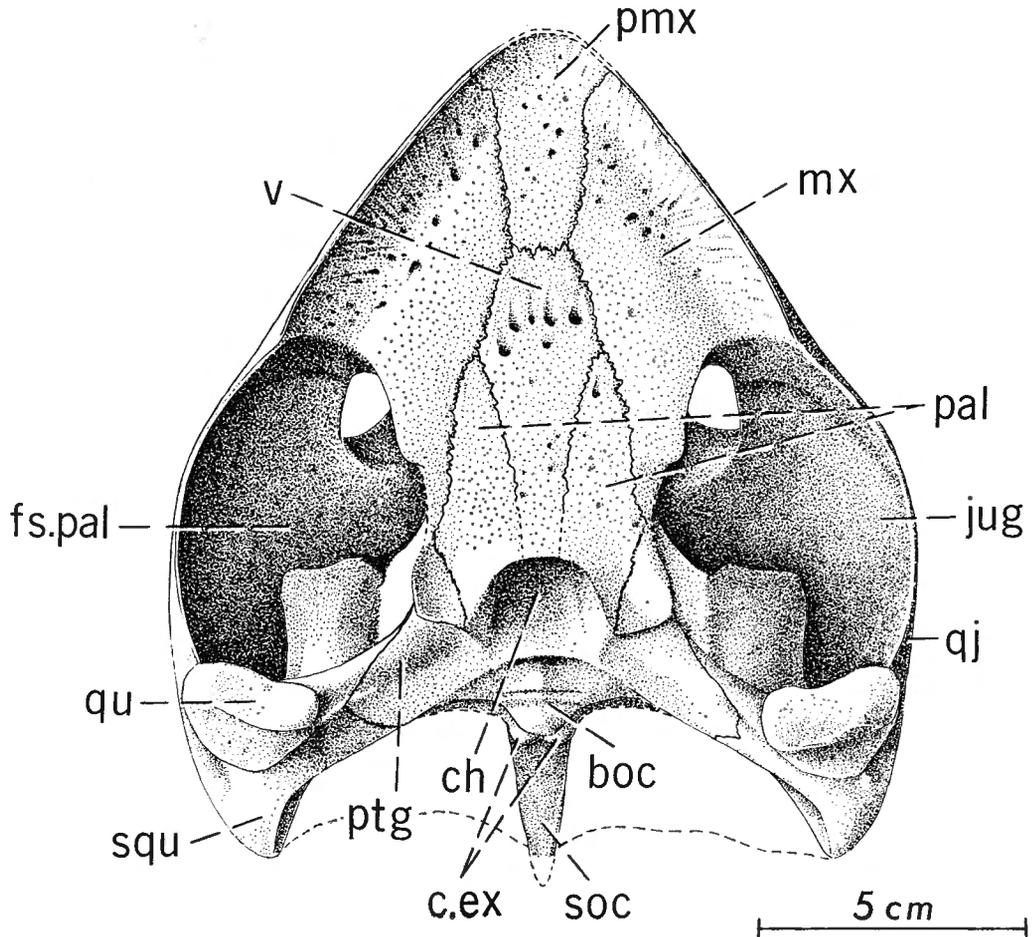


FIG. 4. — Ventral aspect of the cranium of *Erquelinnesia gosseleti*, I.R.Sc.N.B. No. 1563. pmx=premaxilla; mx=maxilla; v=vomer; pal=palatine; jug=jugular; qj=quadratojugal; qu=quadrate; squ=squamosal; ptg=pterygoid; boc=basioccipital; soc=supraoccipital; c.ex=exoccipital condyles; ch=choana; fs.pal=fenestra palatina of temporal fossa. Some details of the suture pattern were obtained from Carnegie Museum 3426.

The most interesting aspect of the skull is the palate. The nasal passages are under-shelved clear back to the posterior wings of the pterygoids. The palatines extend backward beneath the pterygoids as thin sheets of bone. They terminate by forming, along with the pterygoids, two spoon-shaped processes that flank the choanal opening (fig. 4). The slightly concave surfaces of these processes lie behind the triturating area and probably served as areas of origin for the ventral portion of the pterygoideus muscle. The triturating area has a rugose surface and is pierced by numerous, often large, nutritive foramina (Pl. IV, 2). None of the

specimens permit a detailed description of the extent to which the different bones participate in the formation of the nasal passages; the sagittal and transverse sections depicted in figures 6 and 7, accordingly, are somewhat digrammatic and constructed from information derived from several skulls.

In figure 8 I have attempted to compare, in semi-diagrammatic fashion, the palates of turtles with primary palates with forms in which there is a differing degree of undershelving of the nasal passages. In *Chelydra* and *Toxochelys* the choanal openings communicate directly

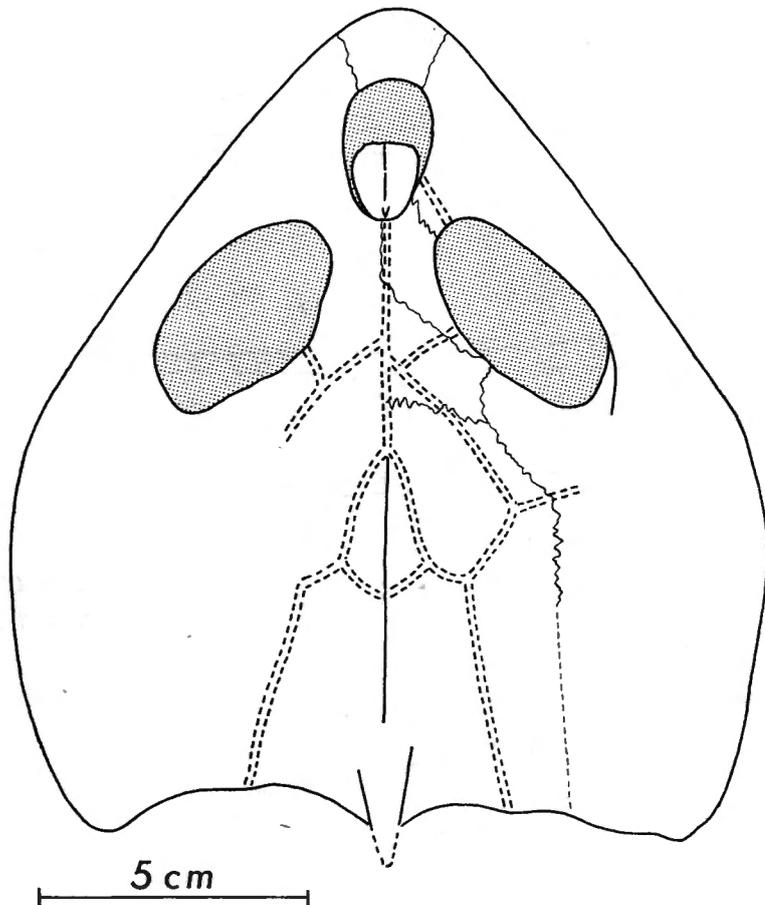


FIG. 5. — Dorsal view of the cranium of *Erquelinnesia gosseleti* showing part of the suture pattern and the epidermal shield furrows.

with the nasal chamber. This is also true in *Ctenochelys*, but here we see an incipient stage in the series leading to the secondary palate: the antero-lateral wings of the vomer are rugose and thick, the triturating surfaces are relatively broader due to medial extension of the maxillae, augmented by ventro-medial expansions of the palatines. The next stage is represented by *Eretmochelys* in which the vomer forms a short, sagittal pillar separating very short nasal passages between the nasal chamber and the choanal openings. In *Chelonia* the vomer pillar is considerably longer (as are the nasal passages) and it ends, as in *Eretmochelys* at the choanal openings. *Caretta* resembles *Chelonia*, but here the edge of the choana lies some distance behind the posterior termination of the vomer pillar. In *Erquelinnesia* the vomer pillar is much elongated and the undershelving of the nasal passages extends considerably beyond the posterior

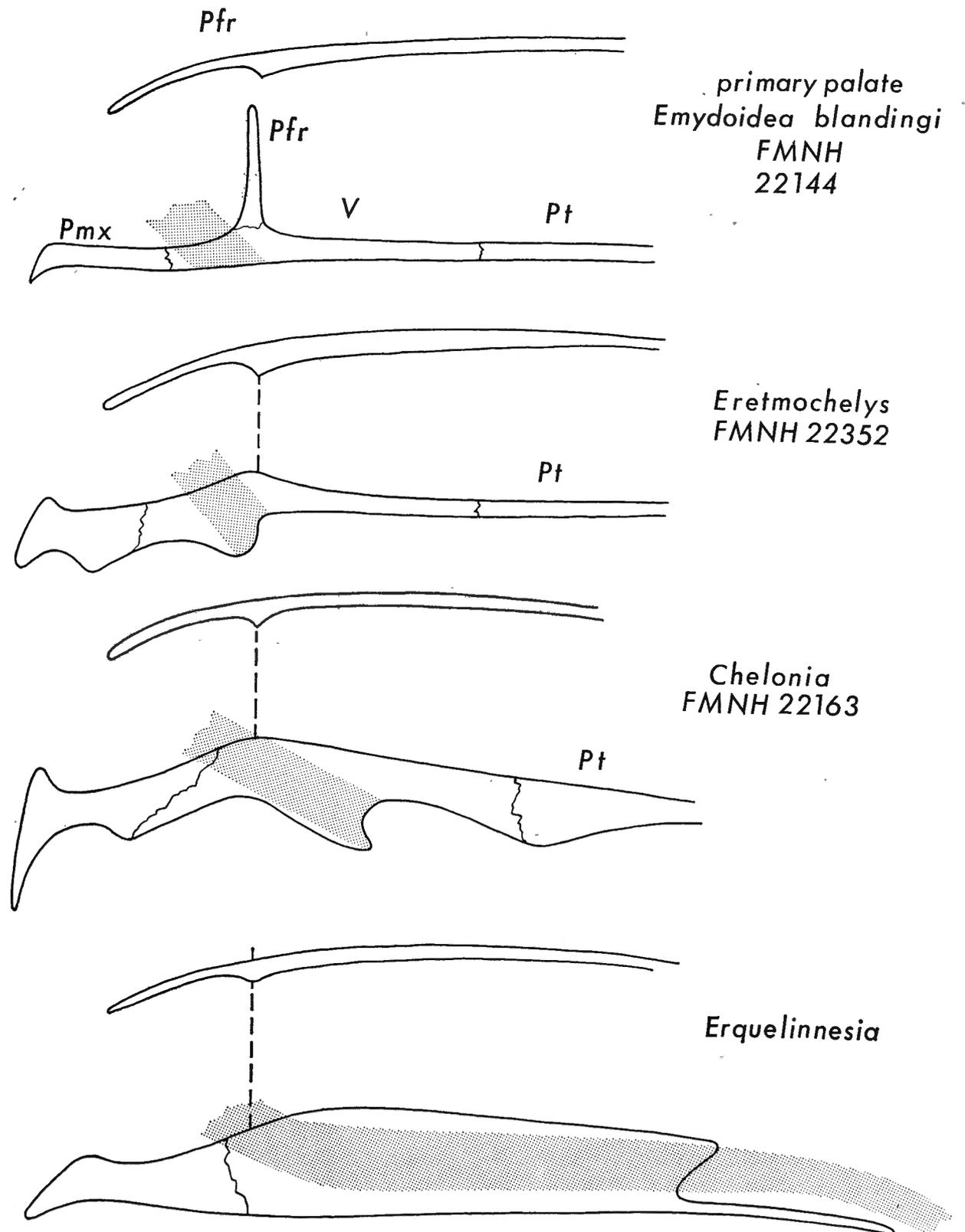


FIG. 6. — Diagrammatic sagittal sections through the skulls of turtles with primary and differing degrees of secondary palates. The course of the nasal passages — on either side of the sagittal plane — is indicated by shaded areas.

end of the pillar, back to the region of the basisphenoid. In the modern cheloniid genera illustrated in figure 8, although they have secondary palates, the position of the vomer and palatines with regard to the skull as a whole is much the same as in forms with primary palates. In *Erquelinnesia*, however, both bones are posteriorly displaced, and the premaxilla extends much farther backward than in the compared forms.

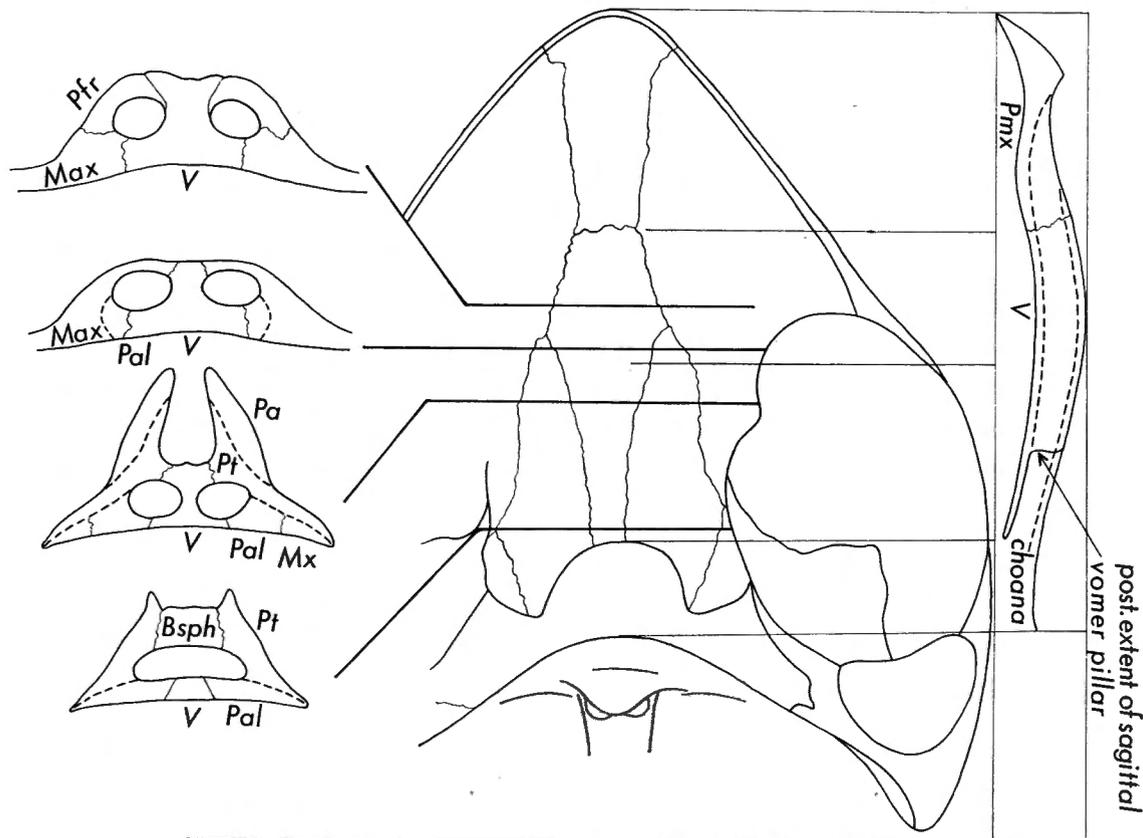


FIG. 7. — Sketch of the palatal aspect of the skull of *Erquelinnesia gosseleti* with semi-diagrammatic sagittal section and several cross sections through the palate. The information is derived from several specimens.

Pfr=prefrontal; Max=maxilla; Pal=palatine; V=vomer; Pa=parietal; Pt= pterygoid; Bsph=basisphenoid.

Of all of the toxochelyid turtles previously known, only *Osteopygis* has an extensive secondary palate. Unfortunately only a single anterior skull fragment has thus far become known (Y.P.M. 913a, WIELAND, 1904, fig. 2; HAY, 1908, pl. 28, figs. 7, 8, pl. 29, fig. 1; ZANGERL, 1953, fig. 61). In this form the secondary palate is approximately as extensive as in the modern *Caretta* (fig. 8e), but the vomerine pillar extends to the edge of the choana, and the palatines are posteriorly displaced as in *Erquelinnesia*. The fragment differs from *Erquelinnesia* not only in the extent to which the nasal passages are ventrally undershelfed, but also in that the premaxillae are not fused. In the shape of the triturating surface and the very low triturating edges, however, the two species are very closely comparable.

In terms of the differentiation of the secondary palate *Osteopygis* is thus somewhat advanced beyond the *Caretta* stage, in the direction toward the *Erquelinnesia* palate, but does

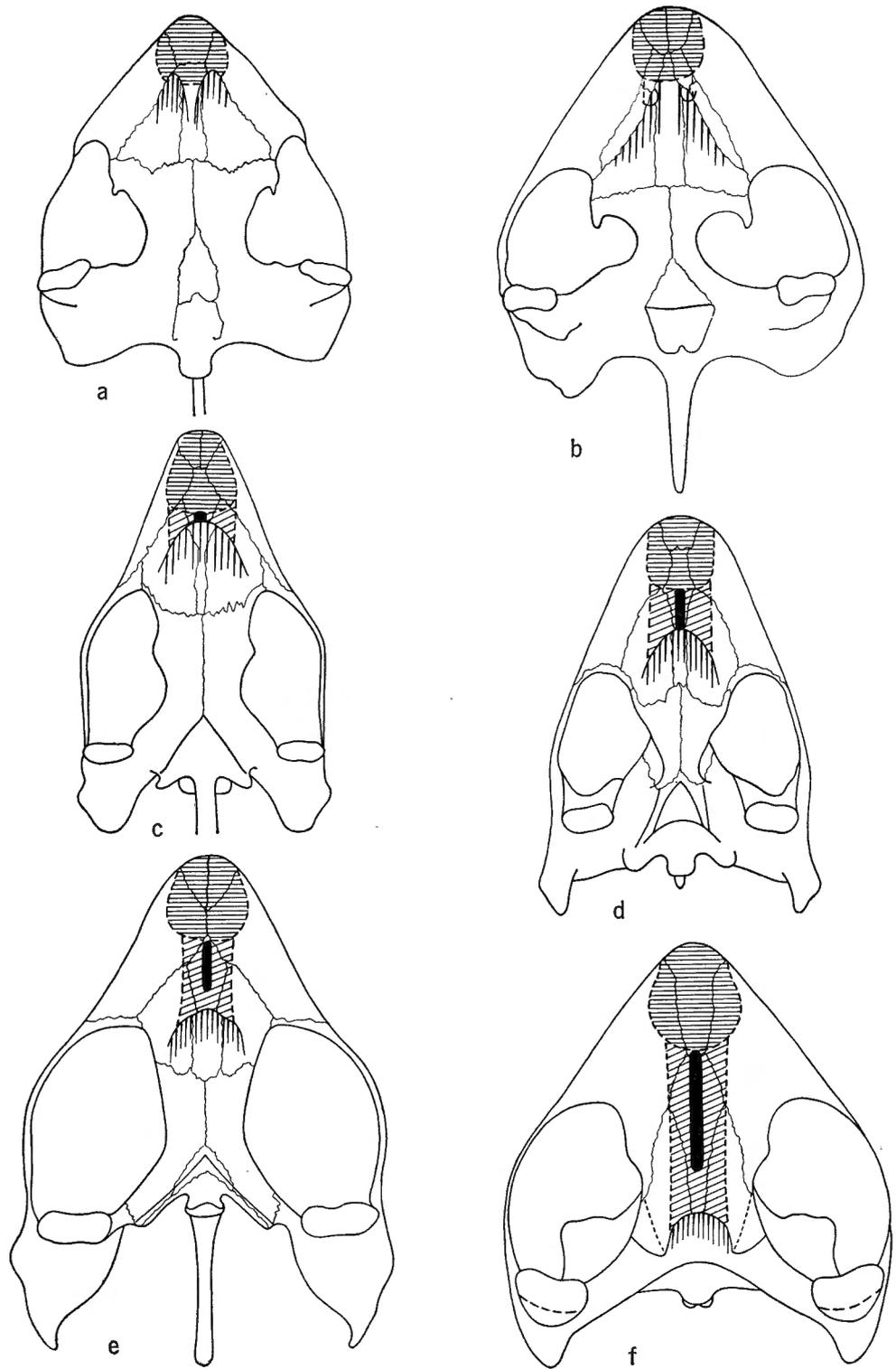


FIG. 8. — Comparison of the nasal cavity, nasal passages and position of the choanal opening(s) in turtles with primary and secondary palates.

a, *Chelydra serpentina*; b, *Ctenochelys procaz*; c, *Eretmochelys imbricata*; d, *Chelonia mydas*; e, *Caretta caretta*; f, *Erquelinnesia gosseleti*. Horizontal shading, nasal cavity; diagonal shading, nasal passages; vertical shading, choanal opening(s); black, vomer pillar.

not display the latter's extreme condition. The more posterior position of the palatines in *Osteopygis* and *Erquelinnesia*, as compared to *Caretta*, does not seem to be a necessary correlate of the formation of an extensive secondary palate, since it occurs neither in *Caretta* nor *Chelonia*, and probably represents a specialization in the evolutionary line to which both *Osteopygis* and *Erquelinnesia* belong.

The detailed comparison of the skulls of *Osteopygis* and *Erquelinnesia*, to the extent presently possible, reveals only slight proportional differences: in *Erquelinnesia* the snout appears slightly elongated perhaps thereby accounting for the relatively longer antero-posterior dimension of the palatal component of the premaxillae which in this genus have fused sagittally.

If there is great similarity between the skulls of these two genera, the correspondence between the mandibles is even more striking, and includes similar aspects of individual variation.

The mandible of *Erquelinnesia* (fig. 9) is stout and provided with a very large triturating surface. This is produced by the elongation of the mandibular rami along the symphysis which amounts to about 58 % of the total sagittal length of the mandible. The relative size of the triturating surface of *Erquelinnesia* compared to those of *Caretta* and *Osteopygis* is readily apparent if one connects the foramina mentalia by a transverse line (fig. 10). In *Caretta* this line runs behind the posterior edge of the triturating shelf; in *Osteopygis* it traverses it near its posterior margin; in *Erquelinnesia* the line intersects the symphysis at about mid-length.

A very interesting aspect is the similarity in the individual variation of the mandibles of *Osteopygis emarginatus* and *Erquelinnesia gosseleti*. In some individuals of both species the triturating surface is virtually flat or slightly concave. In others there is a slight rounded ridge along the symphysis, and in still others the triturating surface is notably convex.

Shell.

Even though none of the specimens of *Erquelinnesia gosseleti* have perfectly preserved shells, there is plenty of material to permit an adequate characterization and reconstruction of the shell (figs. 11, 12; Pl. VII).

The carapace is moderately arched and subquadrangular in peripheral outline. Its greatest width is at the level of the 8th pair of peripherals. The anterior margin is broadly concave. In the adult condition the carapace shows lateral and postnuchal fontanelles. The lateral fontanelles increase in width from the first of the 6th, then decrease to the 9th. In smaller specimens (e.g. Nos. 1585 and 1629; Pl. VII) the fontanelles are relatively wider which is the expected condition. The peripheral bones are narrowest at the junction between the second and third. From there their width increases fairly steadily to the 11th. The 11th peripheral, at the suture with the pygal, is nearly as wide as long in the type specimen (fig. 11). In the smaller shells mentioned above, the posterior peripherals are relatively narrower and the inner margins of these bones are strongly scalloped, a feature that is less pronounced in the larger specimens. All peripherals except the first two and the 10th are medially provided with pits for the reception of the free rib ends (Pl. VIII, 1). There are no pits along the inner faces of the bridge peripherals for the reception of any of the lateral prongs of the major plastral plates, as is the case in *Osteopygis* (ZANGERL, 1953, pp. 209-211). In peripherals 3 to 6 and in the anterior half of P7 the visceral surfaces are much expanded dorso-ventrally and these elements are thus to be considered as bridge peripherals, even though the functional bridge, to judge by the lateral spread of hyo- and hypoplastra is somewhat narrower. The nuchal is much wider than long. The pygal on the other hand is much longer than wide at its anterior end in large specimens, about as long as wide anteriorly in smaller individuals.

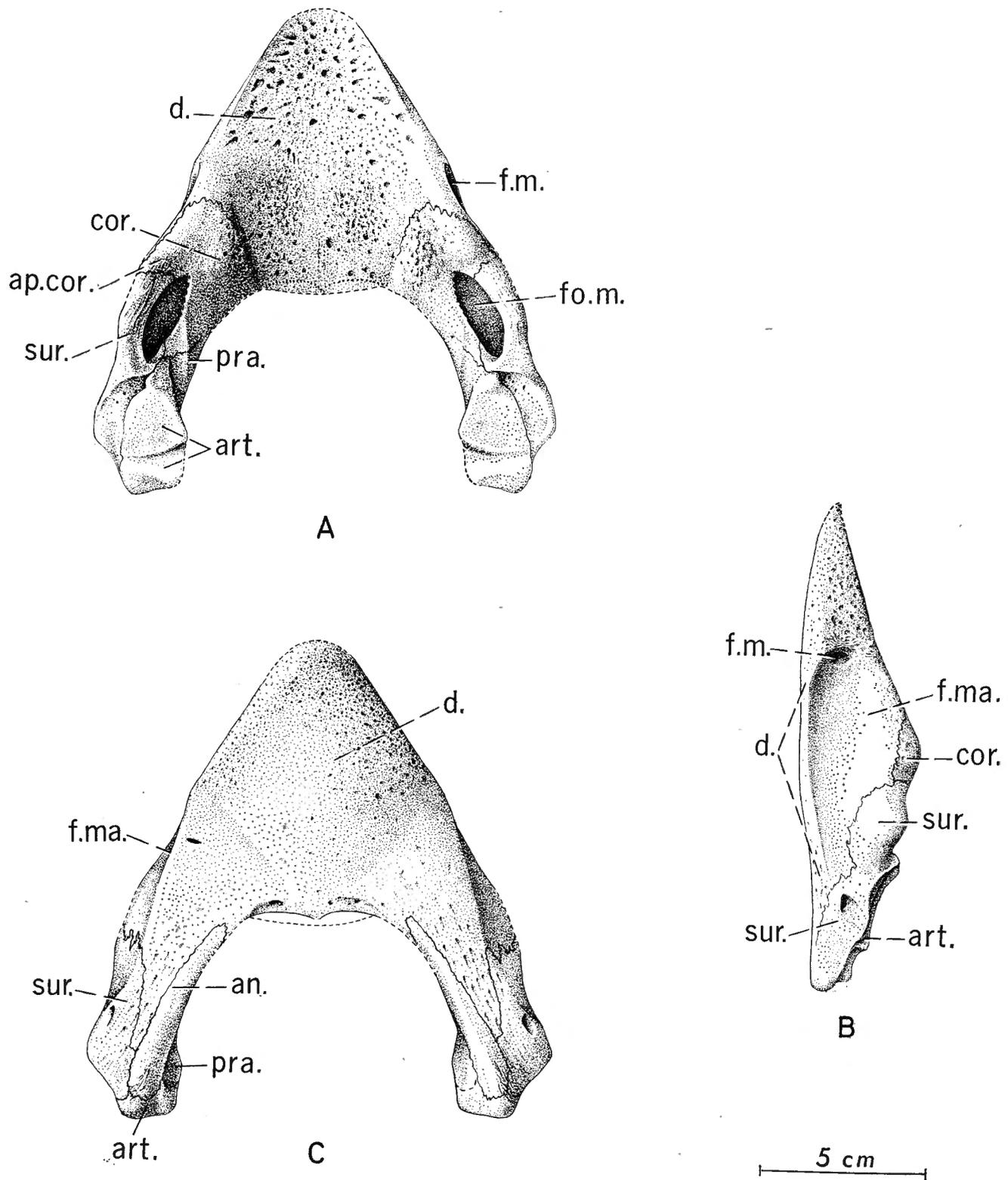


FIG. 9. — Mandible of *Erquelinnesia gosseleti*, I.R.Sc.N.B. No. 1563.
 A, in dorsal; B, in lateral and C, in ventral view. d.=dentary; cor.=coronoid; sur.=surrangular;
 pra.=preangular; art.=articular; an.=angular; ap.cor.=apex of the coronoid; f.m.=foramen
 mentale; fo.m.=fossa meckelii; f.ma.=fossa masseterica.

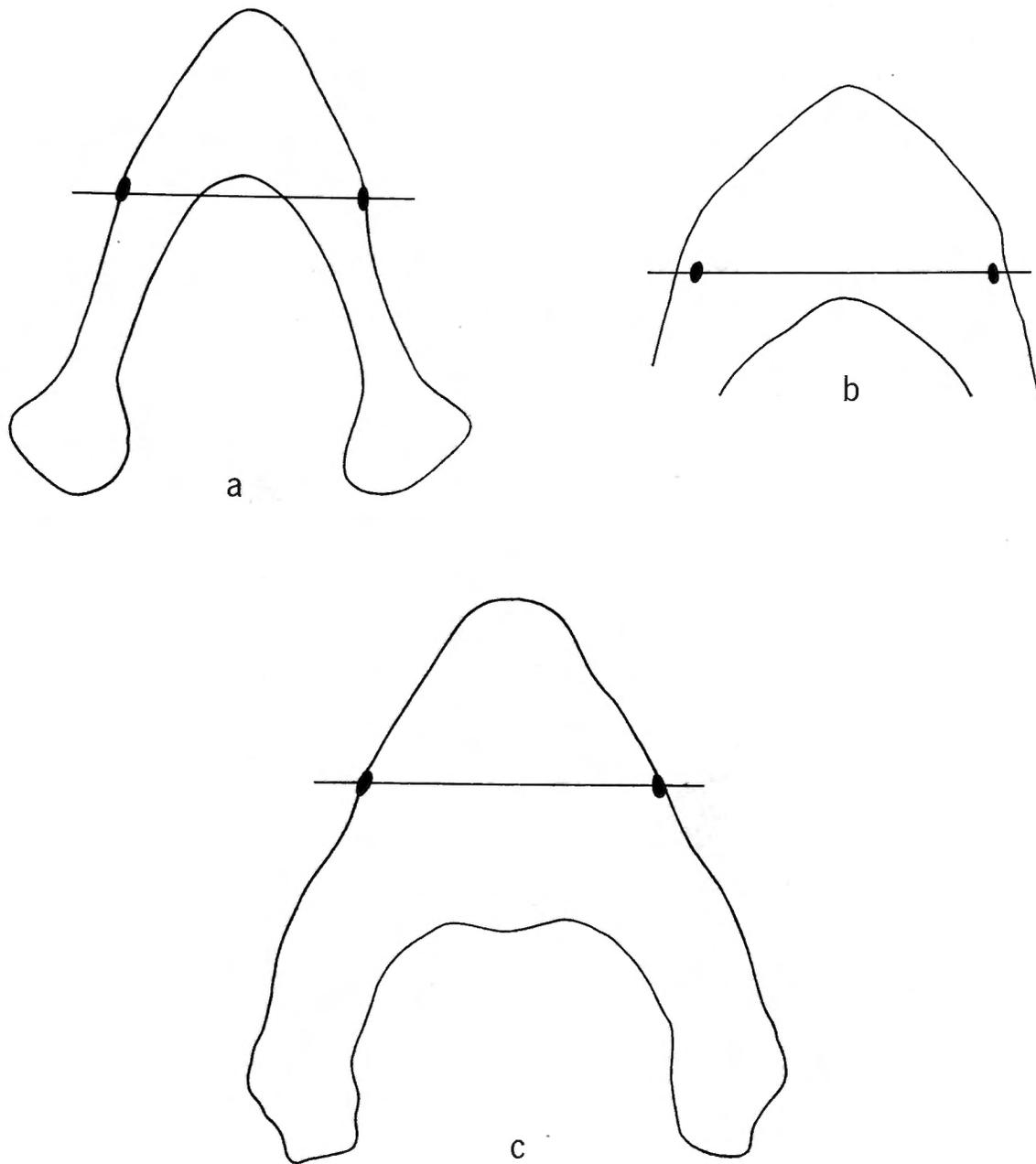


FIG. 10. — Proportional differences in the mandibles of a, *Caretta caretta*; b, *Osteopygis emarginatus*; c, *Erquelinnesia gosseleti*. Horizontal line connects foramina mentalia.

There are 8 neurals in the type specimen, but 9 in Nos. 1585 and 1629 and probably 3669. The first neural is antero-laterally excavated by the post-nuchal fontanelles, but it is essentially a four-sided rectangular element. Neurals 2 to 6 are six-sided with shorter antero-lateral than postero-lateral sides. In neurals 7 and 8 the lateral sides are of about equal length. The sacral region of the carapace shows notable individual variation and abnormal development of plates. In the type specimen the 8 neurals are followed by two suprapygals, the first being a narrow, v-shaped plate (fig. 11). In specimens Nos. 1585, 1629 (Pl. VII) and very probably in 3669

there are nine neurals while the first suprapygals is absent. But in both Nos. 1585 and 3669 there is an irregular ossicle along the left suture between the eighth costal and the second suprapygals (Pl. VIII, 1).

The epidermal shield mosaic is not strongly marked on the shell bones; the furrows are at best shallow and often not traceable. The pattern of the vertebral and pleural shields, however, can be made out satisfactorily in accord with that of other toxochelyid turtles and

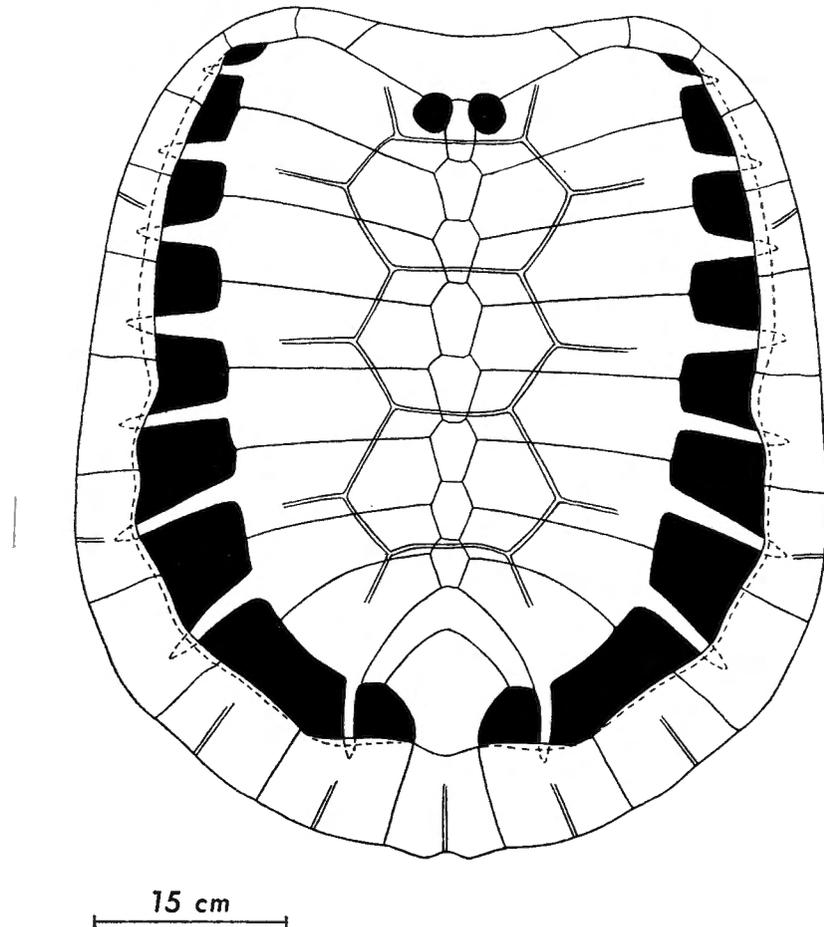


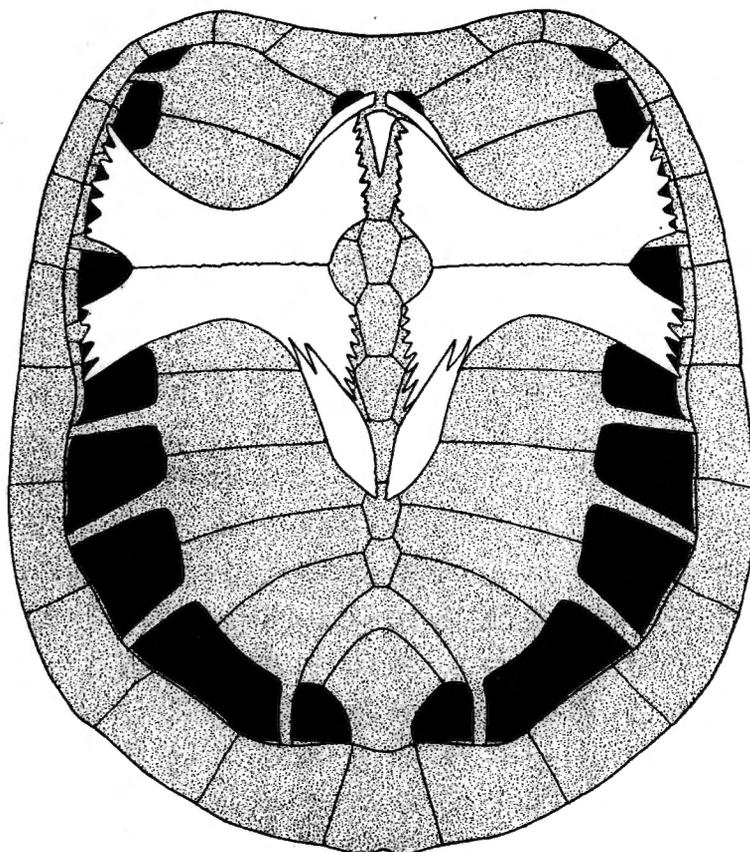
FIG. 11. — Reconstruction of carapace of *Erquelinnesia gossetti*, I.R.Sc.N.B. No. 1563.

in fact most turtle genera. The shape of the vertebral shields differs from that of *Osteopygis* by being considerably wider than long and resembles in this regard the vertebral shield proportions of *Toxochelys latiremis*.

The best preserved plastral bones are those of Nos. 1638 and 1629 (fig. 13). The plastron of the type specimen is very fragmentary and some pieces are incorrectly identified in the mount, but it does include a piece of the left epiplastron (fig. 12). In overall form the plastron of *Erquelinnesia* is typically toxochelyid with a very low plastral index (ZANGERL, 1953, 1958) ranging from about 35 in the (presumably mature) type specimen to 48 in No. 1629, to 59 in No. 1638. These figures span the range of values previously determined for all adequately known species of the family (ZANGERL, 1953, p. 161). If one ignores the higher values in

No. 1629 and especially 1638 which reflect an immature state of osteogenesis⁽¹⁾, it seems reasonable to suppose that the individual range of variation of the plastral index of *Erquelinnesia* lies between 35 and 40 in the adult condition.

The medial digitations of hyo- and hypoplastra indicate that there existed, along the median line, a continuous fontanelle from the entoplastron to the tips of the xiphiplastra. Medial and lateral fontanelles at either end of the hyo-hypoplastral suture were moderate in size, approximately as in *Toxochelys*.



15 cm

FIG. 12. — Reconstruction of plastron of *Erquelinnesia gosseleti* based on type specimen I.R.Sc.N.B. No. 1563 and other specimens.

Compared to the plastron of *Osteopygis*, that of *Erquelinnesia* is notably advanced in the direction of marine specialization as evidenced by the much looser connection (by dermal connective tissue only) with the peripherals, the greater degree of fontanellization and the relative thinness of the plates.

Very little need be said about the shield pattern of the plastron. In specimen No. 1638 there is a transversal imprint of a shield furrow on the hypoplastron, probably delimiting the

⁽¹⁾ A similar difference in the plastral indices was observed in specimens of different size (and thus age) of *Ctenochelys stenopora* (ZANGERL, 1953, p. 161).

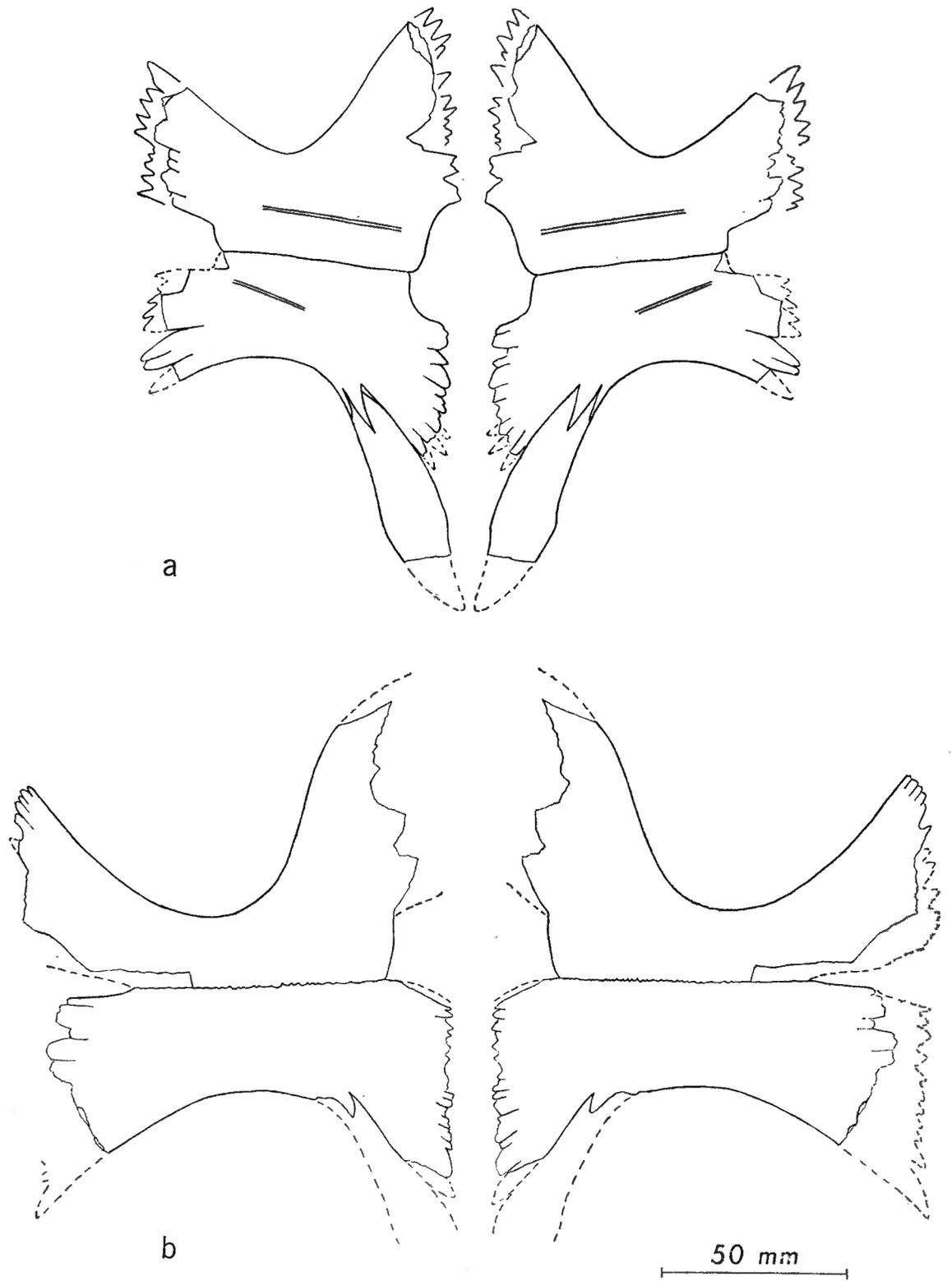


FIG. 13. — Plastra of half-grown specimens of *Erquelinnesia gosseleti*.
a, I.R.Sc.N.B. No. 1638; b, I.R.Sc.N.B. No. 1629.

abdominal shield anteriorly. A doubtful, weak imprint was noted on the hypoplastron (fig. 13). This does not correspond in its course with the posterior shield furrow of the abdominal shield as seen in *Osteopygis* and *Toxochelys weeksi*, the only toxochelyids in which the plastral shield pattern is fairly well known. The imprint in question thus may represent either the furrow of an abnormal scale, the anterior boundary of a much enlarged inguinal shield, or quite possibly not a shield furrow at all.

Shoulder girdle and forelimbs.

Of the shoulder girdle only the presumed left coracoid (I.R.Sc.N.B. No. 1638) and two humeri (I.R.Sc.N.B. Nos. 1634 and 1628) are preserved (Pl. VIII, 2). The coracoid is a relatively short, distally much expanded plate with a strong blunt ridge on the ventral face running from the humeral articular facette to the anterior edge of the bone, where it extends parallel to the margin (Pl. VIII, 2, c). On the dorsal side the coracoid is virtually flat. It is clearly toxochelyid rather than cheloniid in its shape.

The humerus is typically toxochelyid with a radial tuberosity very close to the caput humeri (Pl. VIII, 2, a, b; Pl. IX, 1, a, b). Both proximal and distal ends are strongly expanded and the shaft is slightly oval in cross section about mid-length. Angle α is about 150° , angle β about 34° . These compare very well to previously determined angles in toxochelyids ($\alpha=140^\circ$, $\beta=29^\circ$) and differ markedly from those in modern cheloniids ($\alpha=127^\circ$, $\beta=68^\circ$) (ZANGERL, 1953, p. 165).

Pelvis and hind limbs.

Specimen number 1683 consists of the posterior portion of the carapace, crushed flat. Attached to the inside of the shell is the pelvis, parts of both hindlimbs and a portion of the tail with the vertebrae in articulation (Pl. IX, 2). Unfortunately, all these bones are severely crushed against the visceral surface of the shell and this has resulted in considerable distortions, fracturing of elements and poor surface texture (Pl. IX, 2). In spite of these limitations it is possible to determine the principal features of the pelvis and portions of the rear extremities.

The pelvis, at first sight, seems to differ greatly from those of other toxochelyid turtles, because of the enormously expanded symphysis of the pubes (fig. 14), that extend considerably forward of a line connecting the tips of the antero-lateral processes. Furthermore the symphyseal contacts of the pubes and the ischia form a bridge lengthwise across the foramen obduratorum, dividing the opening into two smaller foramina. In this respect *Erquelinnesia* differs not only from the toxochelyids, but also from the cheloniids and the chelydrids, and resembles the testudinids. I have carefully examined this vast expansion of the pubes and ischia along the symphysis in order to determine to what extent, if any, calcifications of cartilage elements, (for example, prepubic cartilage) and cartilaginous fringes of the bones might be involved. The material in the most forward portion of the symphyseal region of the pubes has the same appearance as the capping substance at the ends of the antero-lateral pubic processes, which are cartilaginous in modern forms. It thus seems probable that the peculiar shape of this pelvis is due, in part, to cartilage calcifications. The state of preservation, however, does not permit a more detailed analysis of these relations.

The ischium is provided with a strong postero-lateral process as in all toxochelyids and in the chelydrids. The specific form of the ischium and its relative size within the pelvis are those typical of the toxochelyids.

Well preserved ilia (Pl. VIII, 2, d, e) are present in the type specimen, No. 1563 and No. 1634. The shape of these bones conforms well with that of other genera of toxochelyids,

in that the dorsal process that connects with the sacral ribs is long and sharply pointed posteriorly. The angle between this process and the axis of the shaft of the ilium, however, is somewhat larger ($=130^\circ$) than in *Toxochelys* and *Ctenochelys*, where it is about 110° .

A nearly complete, uncrushed femur and tibia are associated with No. 1634 (Pl. IX, 1). The femur is but slightly shorter than the humerus (measured between the proximal and distal joint surfaces). At mid-length the femur is nearly circular in section. The two trochanters are separated by a deep v-shaped incision as in *Toxochelys* and in the Chelydridae and other fresh-water turtles (Pl. IX, 1, *d*). The tibia is notably expanded proximally and slightly curved.

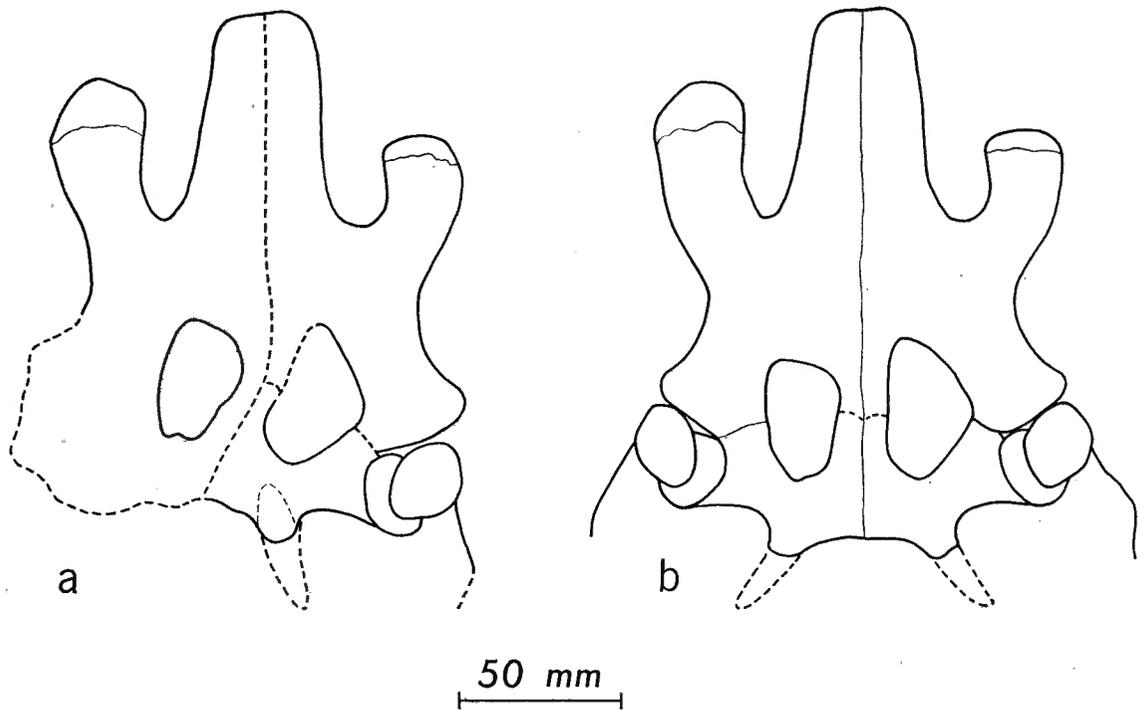


FIG. 14. — Pelvis of *Erquelinnesia gosseleti*, I.R.Sc.N.B. No. 1683.
a, tracing of slightly distorted bones; b, reconstruction.

The right zygapodium and part of the autopodium are preserved in articulation in number 1683; the femur is present, but mostly concealed from view (Pl. IX, 2). The structure of the autopodium of the hindlimb in toxochelyids was known only from very meagre remains (ZANGERL, 1953, fig. 70), but I suggested at that time that it was most likely chelydrid throughout. The present materials bear this out. The shapes of the tarsal bones and their arrangement (fig. 15), the relative stoutness of the metatarsal bones, especially the first, and the extensive joint facets on all of these bones clearly indicate that the foot was retractable and that it conforms quite closely with the condition observed in chelydrids.

A very slight trend toward the sea turtle condition is seen in the fact that the femur is somewhat shorter than the humerus and that the basipodium is relatively shorter than in *Chelydra* (fig. 16).

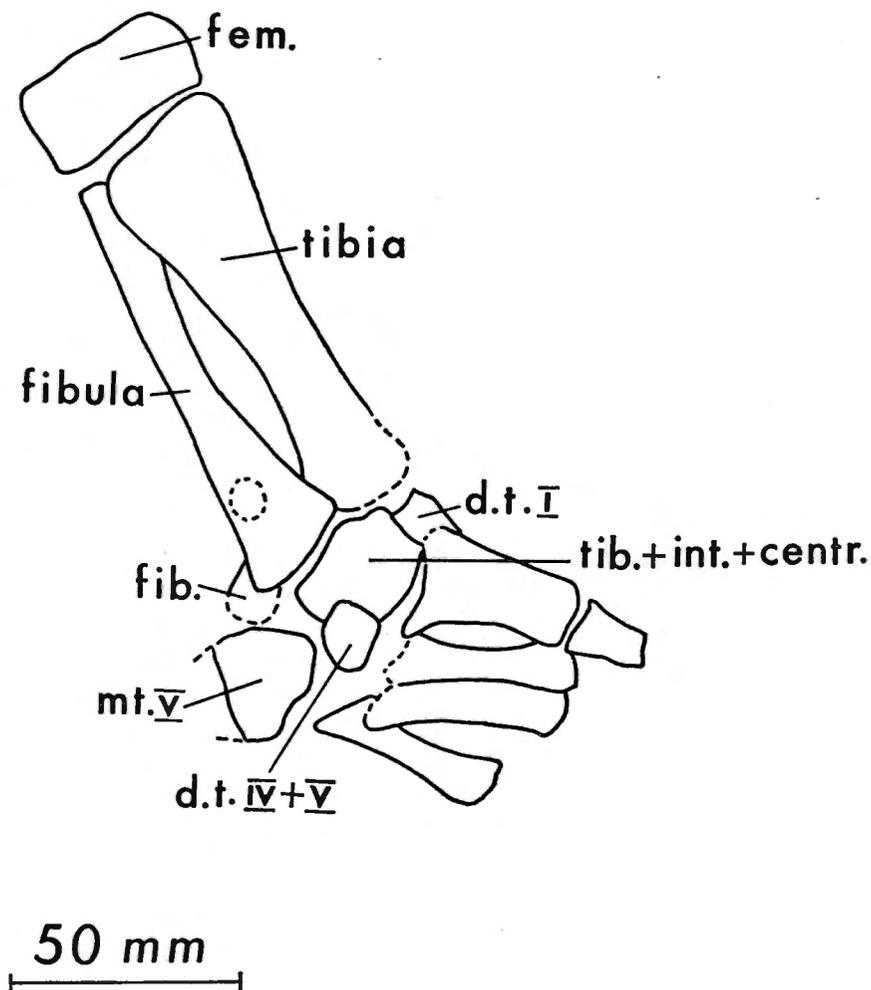


FIG. 15. — Hindlimb of *Erquelinnesia gosseleti*, I.R.Sc.N.B. No. 1683.
 fem.=end of femur; tib.+int.+centr.=fused tibiale, intermedium and centrale; fib.=fibulare; d.t.I=distal tarsal I; d.t. IV+V=distal tarsal IV+V; mt. V=metatarsal V.

Although the tarsal bones suffered considerable compression, the main elements are well enough preserved to show the remarkable similarities with the *Chelydra* tarsus. There is a large proximal element that articulates with both tibia and fibula, presumably the fused product of tibiale, intermedium and perhaps centrale. Lateral to this is a fibulare. Of the distal tarsals I and IV+V are in approximately correct position and a smaller element is lying displaced on the distal end of the fibula. Of the metatarsal bones the first is notably stouter than the others, the 5th is a flat plate (partly broken), functionally a part of the tarsus. Only the basal phalanx of the first digit is preserved, it is short and stout.

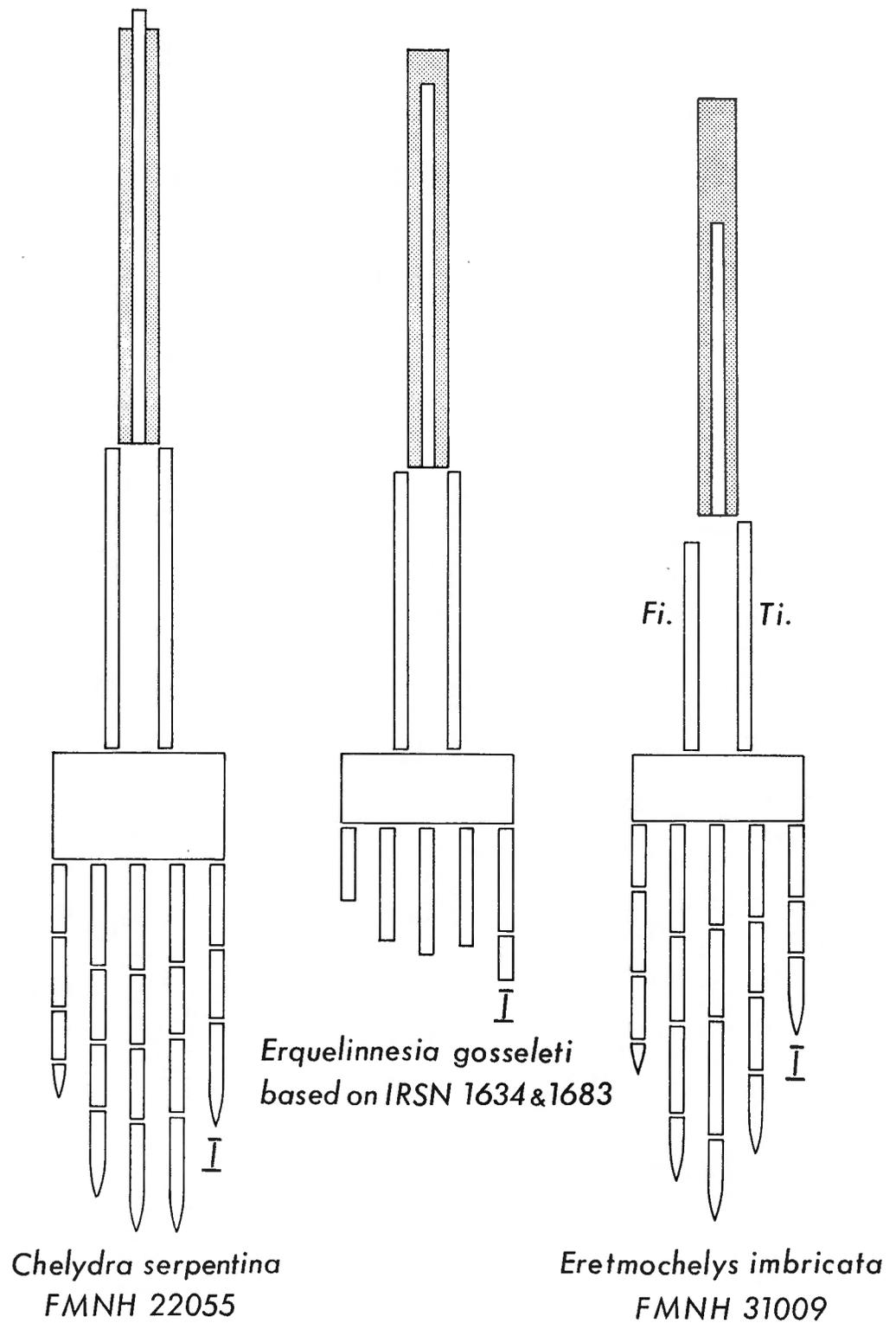


FIG. 16. — Comparison of the proportions of the hindlimb of *Erquellinnesia gosseleti* with those of a freshwater turtle, and a modern sea turtle. The shaded element represents the relative length of the humerus.

3. GLOSSOCHELYS PLANIMENTA (OWEN)
FROM THE LONDON CLAY OF HARWICH, ESSEX.

S y n o n y m y :

- Chelone planimentum* OWEN, 1841, 1842.
Chelone crassicosata OWEN and BELL, 1849 (in part ?).
Thalassochelys planimentum COPE, 1870.
Puppigerus crassicosatus COPE, 1870 (in part ?).
Glossochelys harvicensis ⁽¹⁾ SEELEY, 1871.
Pachyrhynchus planimentum DOLLO, 1886.
Lytoloma planimentum LYDEKKER, 1889*b*.
Lytoloma crassicosatum LYDEKKER, 1889*b* (in part ?).

Among the sea turtle materials from the London Clay described by OWEN and BELL (1849) two skulls (*loc. cit.*, pls. 9 and 11) resemble the cranium of *Erquelinnesia gosseleti* so closely that the conclusion seems justified that they belong to toxochelyid, rather than cheloniid turtles, and more precisely, to members of the subfamily Osteopyginae. The shell, figured by OWEN and BELL (*loc. cit.*, pl. 10) and stated to have originally been part of the same individual as the skull (*loc. cit.*, pl. 9), on the other hand, differs notably from the carapace of *Erquelinnesia gosseleti* (and, for that matter, any other toxochelyid with unkeeled shell). The same is true of another carapace (*loc. cit.*, pl. 10 A), while the carapace (type specimen) of *Chelone crassicosata* (*loc. cit.*, pl. 12) should be difficult to distinguish from the smaller shells of *Erquelinnesia gosseleti*. LYDEKKER (1889*a*) claims to have seen an individual of *Chelone crassicosata* with skull and carapace associated that he said proved the correctness of OWEN's contention that the type specimen carapace (OWEN and BELL, 1849, pl. 12) and the skull (*loc. cit.*, pl. 11) belong to members of the same species. This would suggest that the type material (skull and shell) is toxochelyid. MOODY (1968) however identified and described a partial skeleton (lacking the skull) as *Chelone crassicosata* and placed it into his cheloniid genus *Eochelys*. All this clearly reveals the virtually insurmountable difficulties inherent in the identification of incompletely preserved remains of different ontogenetic age in primitive cheloniid and moderately specialized toxochelyid sea turtles. Anatomic features such as robustness of costal plates, relative distinctness of ribs beneath the costals, circular versus flattened distal rib cross sections and many other features of the carapace are subject to individual and age variation both in the cheloniid and toxochelyid turtles and have led to much confusion.

The carapace (type specimen) of *Chelone crassicosata* shows no features that identify it as either toxochelyid or cheloniid. The carapace of *Chelone planimentum* [which is not beyond all doubt the same individual as the (type) skull] likewise could belong to a toxochelyid or a cheloniid; however, neural plates in which the antero-lateral and postero-lateral sides are of about equal length occur in toxochelyids only in forms with keeled shells (Lophochelyinae), and none of the London Clay sea turtles are known to have pronounced carapacial keels. On the other hand, unquestionable cheloniids such as the form illustrated by OWEN and BELL, 1849, plate 2, as *Chelone breviceps*, show the described shape of the neural plates.

In contrast there is no such uncertainty about the skulls of the *planimentum-crassicosata* material illustrated by OWEN and BELL, which clearly belong to osteopygine toxochelyids.

The problems stated above obviously cannot be resolved without access to the collections; in order to avoid the possibility of further complicating the already confused taxonomic situa-

⁽¹⁾ *Chelone harvicensis* GRAY, 1831 has not been properly described and is not adequately preserved to permit a convincing demonstration that it is, or is not conspecific with the type specimen of *Chelone planimentum*. It seems thus best to consider *C. harvicensis* a nomen nudum.

tion I shall not attempt to characterize the London Clay osteopygine sea turtle except for a justification to retain the generic name *Glossochelys* proposed by SEELEY (1871).

At the time of OWEN and BELL's study of the material neither of the skulls in question had been prepared from beneath. The « crassicostata » specimen (OWEN and BELL, 1841, pl. 11) was later prepared from the underside and LYDEKKER (1889b) gives a description and good illustration. This clearly shows that the choanal opening lies behind a line connecting the anterior rims of the palatal apertures of the temporal fossae. As such it is probably slightly farther posterior than in *Osteopygis*, but not nearly as far back as in *Erquelinnesia*, and in fact represents an intermediate condition. Unfortunately, we still do not have a complete skull of *Osteopygis* and this hampers the comparison of the two forms, but in the position of the choanal opening the London Clay skull resembles *Osteopygis* more closely than *Erquelinnesia*. Since it is not now possible to make a convincing case that the London Clay form is a species of *Osteopygis* or *Erquelinnesia*, it seems most judicious to accept, tentatively, SEELEY's proposal retaining the species in the genus *Glossochelys*, and to postpone its characterization pending restudy of the materials.

4. SPECIMENS OF DOUBTFUL TOXOCHELYID AFFINITY.

In the collections of Field Museum of Natural History in Chicago and the Institut royal des Sciences naturelles de Belgique there are some fragmentary turtle remains, including mandibles from an Albian sand of Texas and a lower Senonian glauconite in Belgium respectively. The mandibles are indistinguishable from each other and resemble the mandible of *Osteopygis* so closely that one is tempted to conclude that they belong to turtles of the subfamily Osteopyginae.

Although such an assignment remains a possibility, there is sufficient circumstantial evidence to suggest caution. The material from the Paluxi Sand of Texas consists of about a dozen lots of turtle fragments, all collected at the surface, clearly belonging to at least three different species. Even though the lots represent pieces that were found close together, there is no certainty that the fragments of each lot belonged to one individual. In several lots there is unmistakable evidence of a mixture of fragments of different species. Among these specimens there are three partial mandibles of unmistakably osteopygine character. The only difference between them and the lower jaw of *Osteopygis* is the slightly shorter symphyseal dimension of the triturating shelf.

The same applies to a mandibular fragment from a glauconite of lower Senonian age from Loncée, Belgium, to which DOLLO (1909) tentatively assigned the name *Glaucochelone lonzeensis* (nom. nud.). This specimen is currently on exhibit at the Institut royal des Sciences naturelles; also on exhibit, and in storage there are additional turtle fragments from Loncée which clearly belong to different taxa of turtles.

Aside from the flat-shelved mandibles none of the fragments of the Texas, or the Loncée material could be recognized as belonging to a toxochelyid; in fact some characteristic shell plates in the lots from Texas, such as nuchal plates, mandibles and plastral bones are quite distinctly non-toxochelyid. This also is the case of the mandible referred to as *Tomochelone lonzeensis* (nom. nud.) by DOLLO (1909).

In view of these uncertainties, and the fact that broad mandibular triturating surfaces have evolved repeatedly and independently (in different families) a number of times, I believe caution is very much in order in the assignment of the mandibles in question. The matter cannot be settled until associated specimens of the Texas, or the Loncée species are recovered.

5. THE PHYLOGENETIC
AND ZOOGEOGRAPHIC SIGNIFICANCE
OF *DOLLOCHELYS CASIERI*, *ERQUELINNESIA GOSSELETI*
AND *GLOSSOCHELYS PLANIMENTA*.

The recognition of three unquestionable toxochelyid sea turtles among the fossil sea turtle materials of Europe is of both phylogenetic and zoogeographic interest. The morphology of these species permits the conclusion that they are not merely close relatives, but very probably descendants of two North American forms; the three species are more highly specialized in the direction of marine adaptation than the North American relatives; they occur later in time than the North American relatives which are among the geologically youngest toxochelyids on the North American continent, and occur along the Atlantic seaboard in New Jersey. None of the Cretaceous sea turtles of Europe can be definitely identified as toxochelyid.

This would suggest that the Toxochelyidae originated in North America, perhaps along the Gulf Coast from where they spread both north into the Niobrara Sea and east to the Atlantic coast. This is suggested by the occurrence of similar genera and species in the Niobrara Chalk of Kansas and the Mooreville Chalk of Alabama (and elsewhere in the Gulf coastal chalk deposits), yet the similar pairs of forms show somewhat different specializations.

Of the forms of the Niobrara Sea all apparently died out except *Toxochelys latiremis* whose descendant in the Pierre Sea was *Toxochelys browni* (fig. 17). Similarly, of the Gulf Coast species only *Toxochelys* and *Prionocheles* persisted into the Marlbrook Marl (approximately a time equivalent of the Pierre Shale) and one species of *Toxochelys* extends into basal Maestrichtian sediments (Coon Creek Tongue of the Ripley Formation); the remainder appear to have died out in this area. The latest toxochelyids occur in the greensand deposits of New Jersey where they have persisted into the time of deposition of the basal Hornertown sediments (see BAIRD, 1964, for a discussion of the age of these deposits). All three subfamilies are represented: the Toxochelyinae by *Dollochelys atlantica*, the Lophochelyinae by *Peritresius ornatus* and the Osteopyginae by *Osteopygis emarginatus*. There is no evidence of toxochelyids in any Cenozoic deposit of the Atlantic coastal plain. Evidently the last toxochelyids of North America died out at the very end of the Cretaceous period.

About this time the toxochelyids extended their range northeastward across the Atlantic to western Europe. According to VAN HILTON (1962) the distance across the Atlantic was considerably shorter than at present (fig. 18).

The first records of toxochelyids in Europe occur in the Sables d'Erquelinnes (Landenian): *Dollochelys casieri* and *Erquelinnesia gosseleti*. Virtually beyond doubt they are descendants of *Dollochelys atlantica* and *Osteopygis emarginatus* respectively. *Dollochelys casieri* has not been recognized among the classical remains of sea turtles of the London Clay, but a close relative of *Erquelinnesia gosseleti*, *Glossochelys planimenta* is thus the last survivor of the family which appears to have vanished during Eocene time (fig. 17).

Toxochelyids, in contrast to cheloniid sea turtles, never had a cosmopolitan distribution. None of them became fully pelagic forms; their distribution was restricted either to epicontinental seas, or the continental shelf of southern and eastern North America and Western Europe. Areas of chalk deposition seem to have been their favored habitat.

The pattern of extinction of this family — from west to east — was clearly accompanied by a gradual range displacement east and north-eastward.

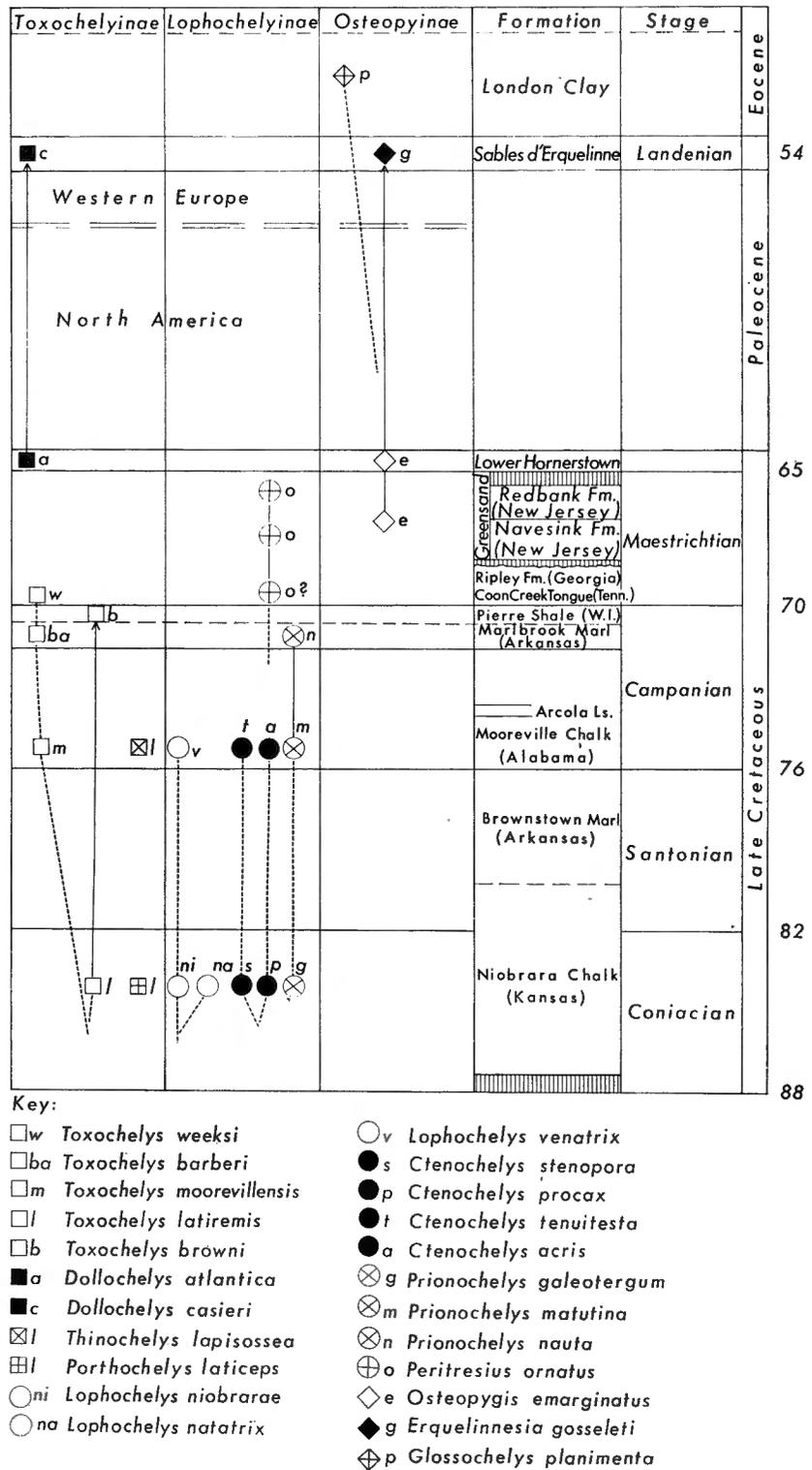


FIG. 17. — Phylogenetic and temporal relationships between the known genera and species of sea turtles of the family Toxochelyidae.

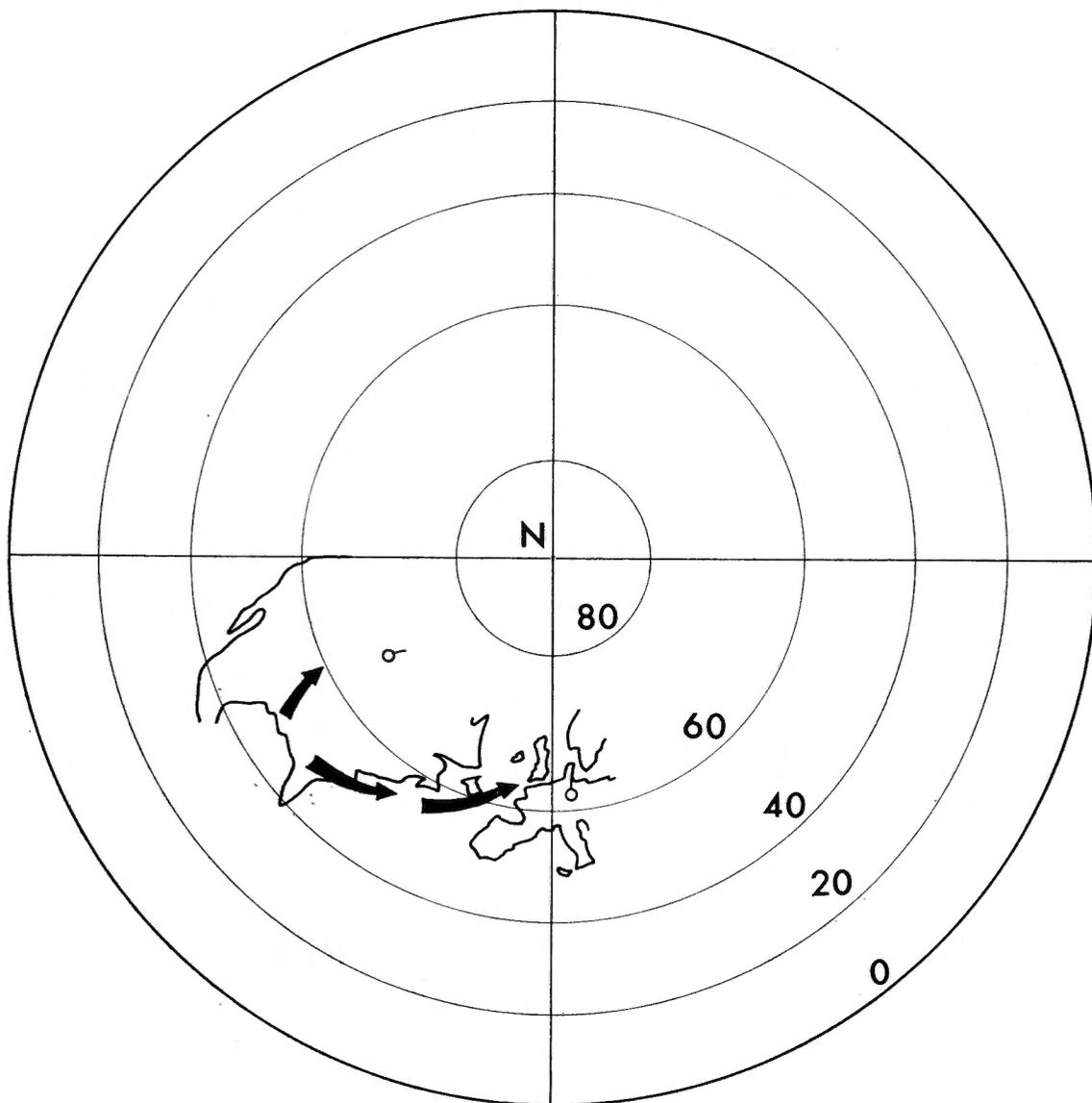


FIG. 18. — Relative position of the North American and European continents at the end of Cretaceous time (after VAN HILTON, 1962, fig. 7c). Arrows indicate presumed distribution routes of the toxochelyid sea turtles.

The reasons for this pattern of extinction were thus probably of a relatively local nature in contrast to the global factors that brought about the world-wide extinction of such organisms as ammonites or mosasaurs. The disappearance of toxochelyids in the interior of North America at the end of Campanian time, and from the Gulf Coast province in early Maestrichtian time immediately precedes the peak of Laramide orogenic activity. It would seem reasonable to assume that this could have had a profound effect upon the habitats of the western and southern populations, but would hardly have had any direct influence along the Atlantic seaboard. The extinction of the populations along the eastern fringes of North America at the very end of Cretaceous time might be related to drastic changes in ocean circulation in connection with the widening of the North Atlantic at that time (VAN HILTON, 1962).

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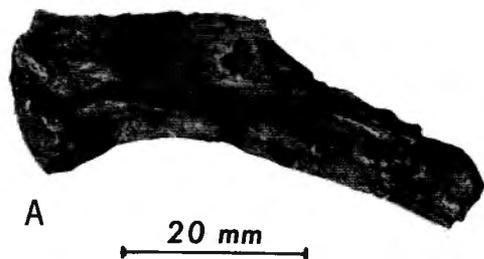
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PLATE I

EXPLANATION OF PLATE I.

FIG. A. — Mandibular fragment of *Dollochelys casieri*, I.R.Sc.N.B. No. 1631, internal view.

FIG. B. — Carapace of *Dollochelys casieri*, I.R.Sc.N.B. No. 1631, as presently mounted.



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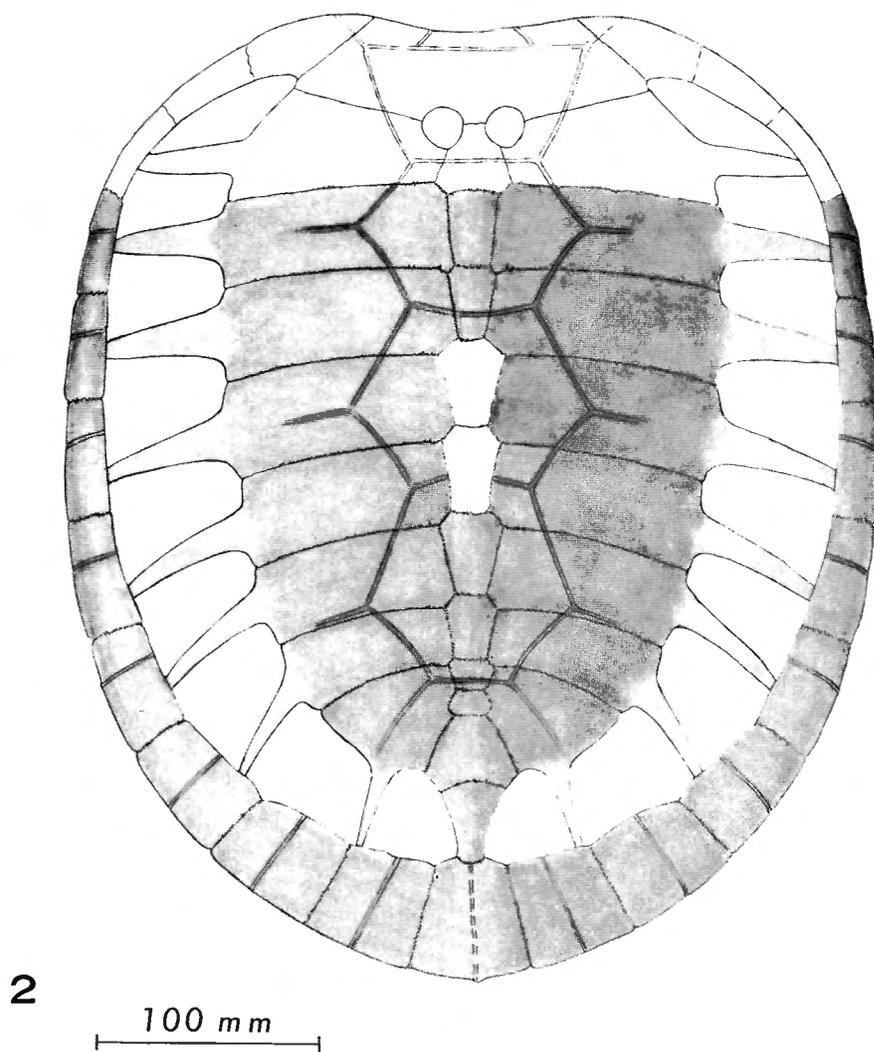
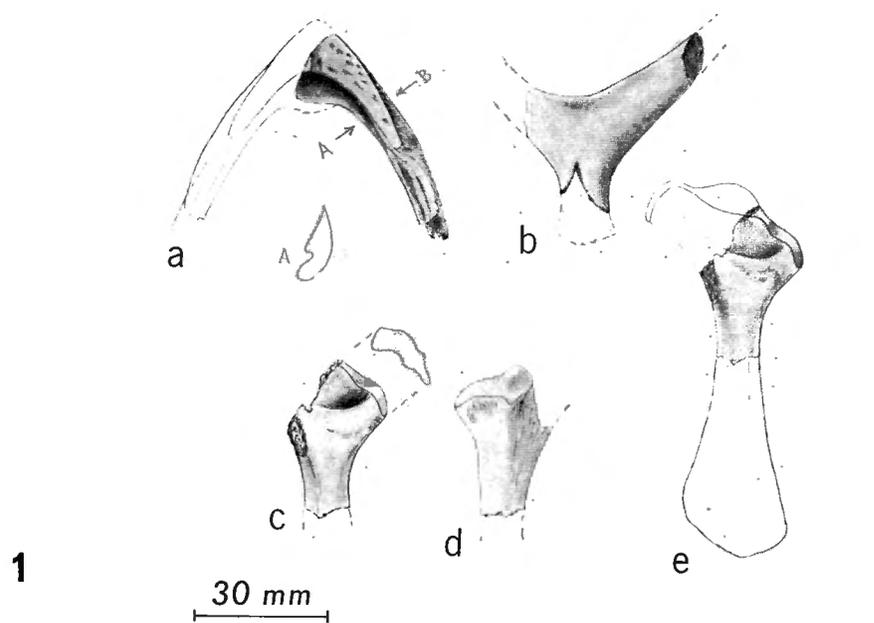


PLATE II

EXPLANATION OF PLATE II.

FIG. 1. — *Dollochelys casieri*, I.R.Sc.N.B. No. 1631. *a*, mandibular fragment, seen from dorsal aspect with a cross section A-B; *b*, fragment of the left scapula; *c* and *d*, opposite views of the proximal fragment of the left humerus; *e*, humerus fragment in relation to entire bone.

FIG. 2. — Semi-diagrammatic reconstruction of carapace of *Dollochelys casieri*, based on I.R.Sc.N.B. No. 1631.



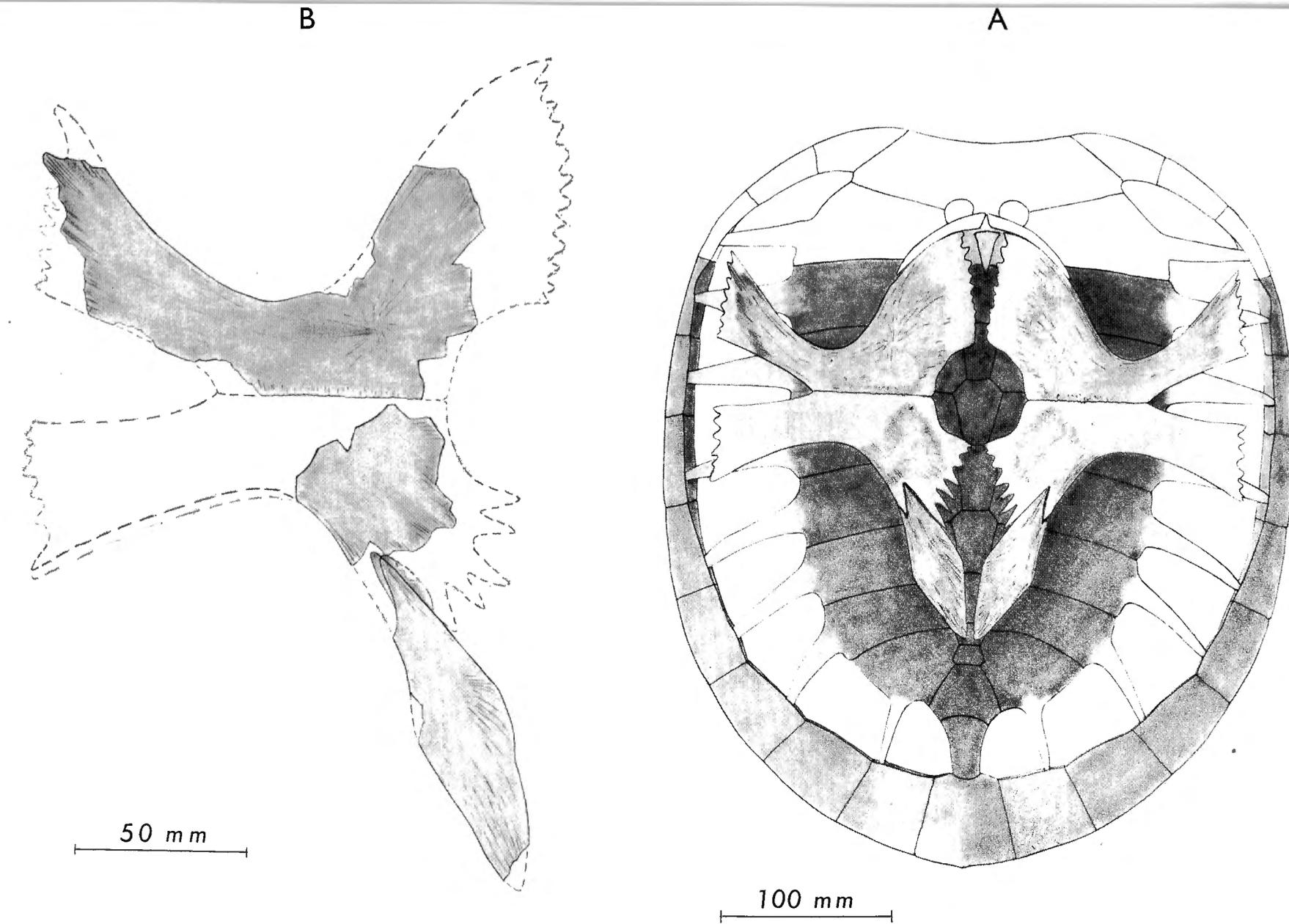
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PLATE III

EXPLANATION OF PLATE III.

FIG. A. — Semi-diagrammatic reconstruction of the shell of *Dollochelys casieri* as seen from the ventral aspect. Based on I.R.Sc.N.B. No. 1631.

FIG. B. — Preserved parts of plastron of *Dollochelys casieri*, I.R.Sc.N.B. No. 1631.



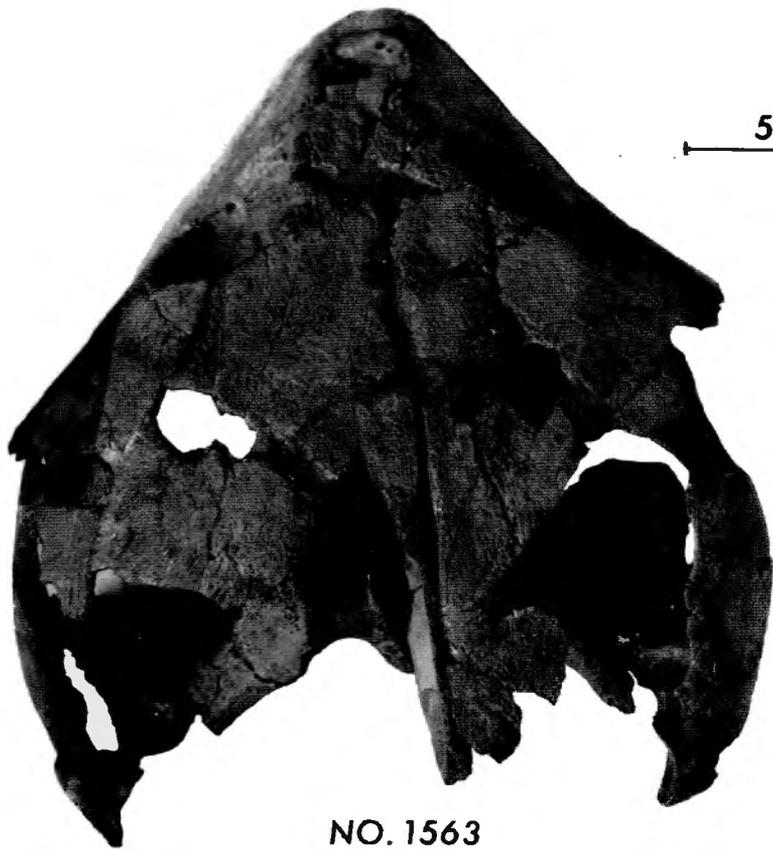
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PLATE IV

EXPLANATION OF PLATE IV.

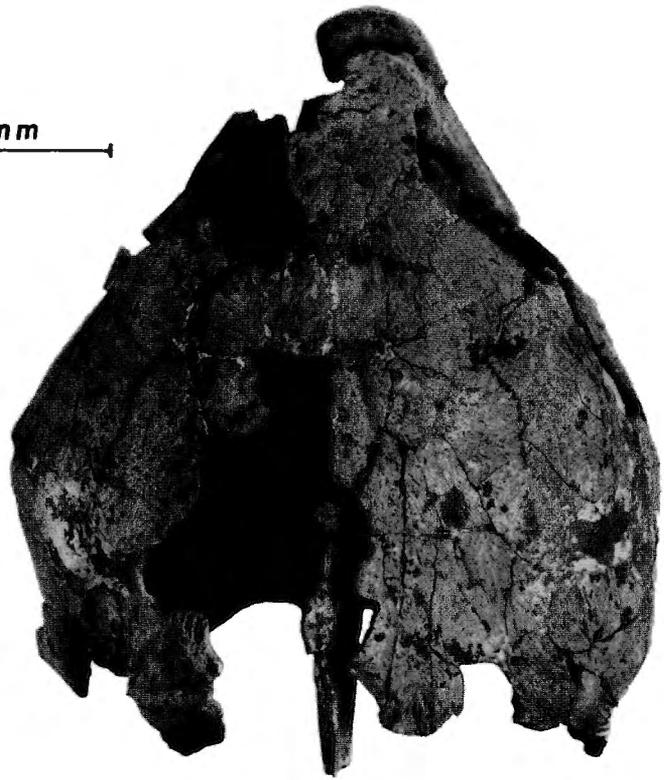
FIG. 1. — Skulls of *Erquelinnesia gosseleti*, I.R.Sc.N.B. Nos. 1563 and 1628. Note difference in width and general massiveness between these skulls.

FIG. 2. — Skulls of *Erquelinnesia gosseleti*, I.R.Sc.N.B. Nos. 1563 and 1628. Ventral views.

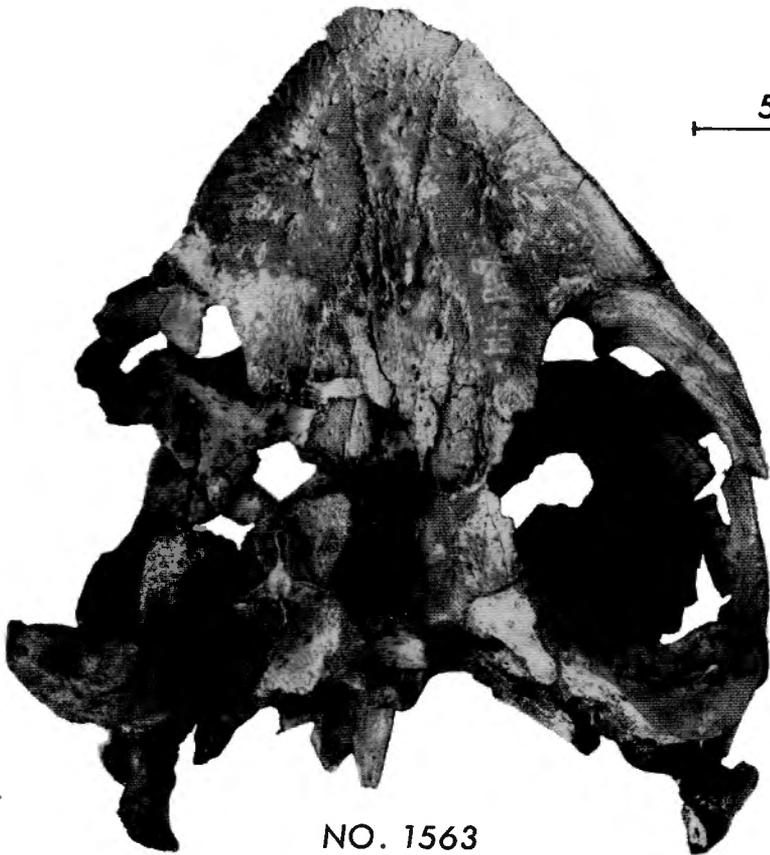


NO. 1563

50 mm

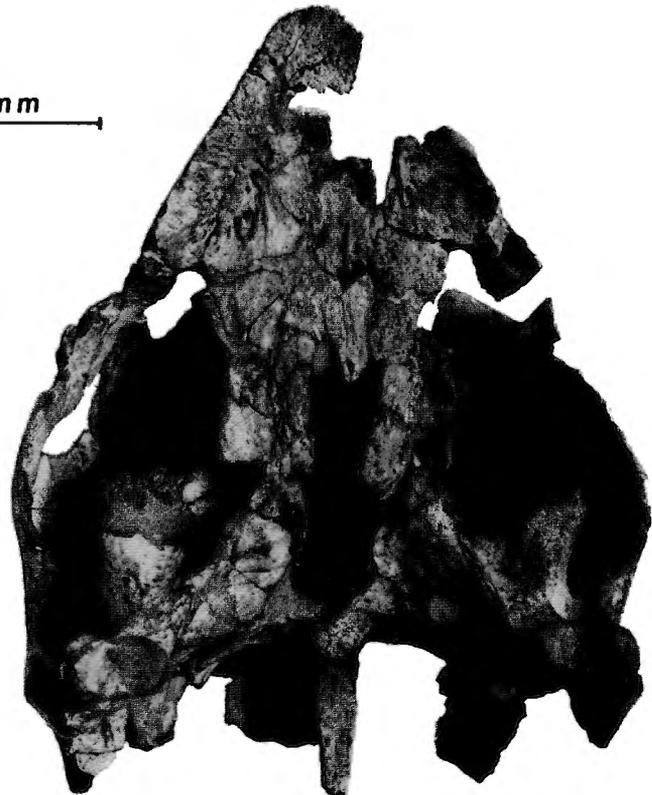


NO. 1628



NO. 1563

50 mm



NO. 1628

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PLATE V

EXPLANATION OF PLATE V.

Lateral view of the skulls of *Erquelinnesia gosseleti*, I.R.Sc.N.B. Nos. 1563 and 1628, and antero-dorsal view of 1563 to show the nasal bones.

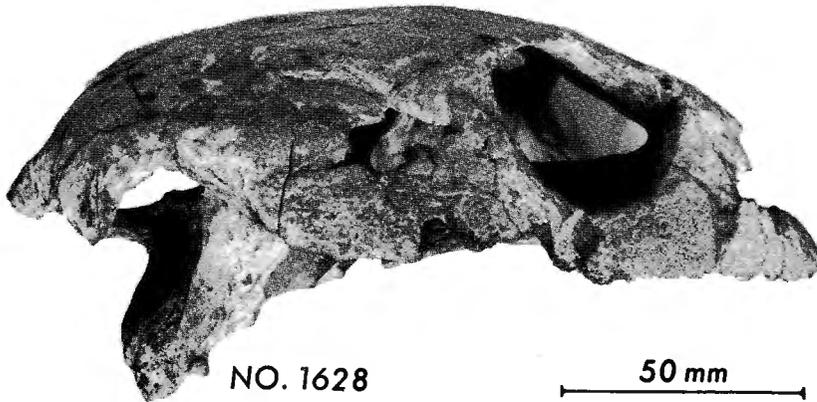


NO. 1563



NO. 1563

50 mm



NO. 1628

50 mm

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PLATE VI

EXPLANATION OF PLATE VI.

Posterior view of the skull of *Erquelinnesia gosseleti*, I.R.Sc.N.B. No. 1628 and dorsal, ventral and side views of the mandible of I.R.Sc.N.B. No. 1563.

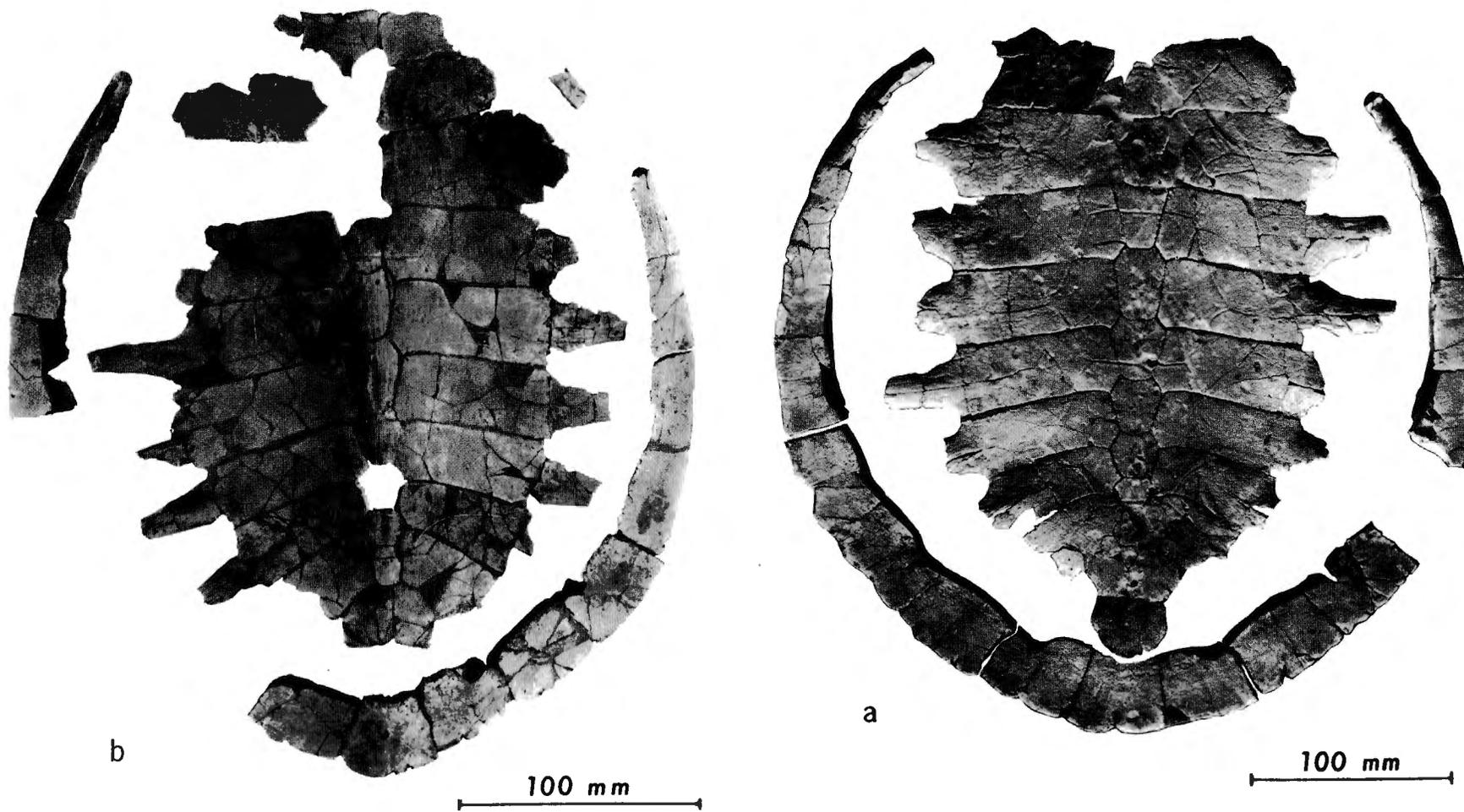


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PLATE VII

EXPLANATION OF PLATE VII.

Half-grown specimens of *Erquelinnesia gosseleti*. *a*, I.R.Sc.N.B. No. 1585, *b*, I.R.Sc.N.B. No. 1629.

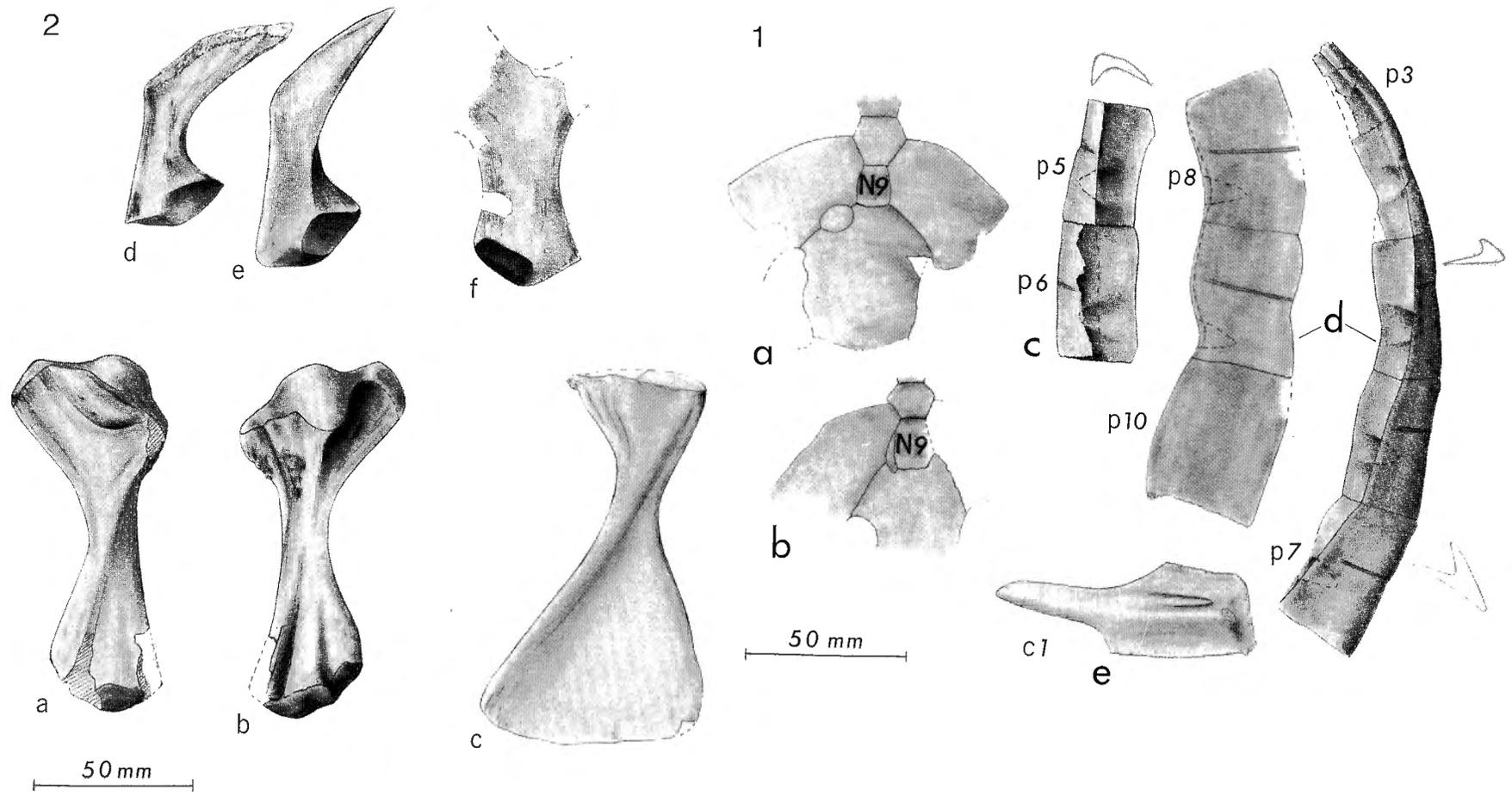


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PLATE VIII

EXPLANATION OF PLATE VIII.

- FIG. 1. — Details of shell morphology in *Erquelinnesia gosseleti*. *a*, sacral regions of shells I.R.Sc.N.B. No. 3669 and *b*, I.R.Sc.N.B. No. 1585 to show presence of asymmetrical shell plates next to neural 9. The first suprapygal is absent in both specimens. *c*, right bridge peripherals 5 and 6 in ventral view, I.R.Sc.N.B. No. 1629. *d*, left peripherals 3 to 10 in ventral view, I.R.Sc.N.B. No. 1585. The dotted line in p 8 and 9 is the dorsal edge of the plates; the medial face of p 10 is narrow and nearly flat. *e*, visceral view of *c* 1 to show the scar for the attachment of the first carapace rib, I.R.Sc.N.B. No. 1638.
- FIG. 2. — *Erquelinnesia gosseleti*. *a* and *b*, left humerus, I.R.Sc.N.B. No. 1628; *c*, left (?) coracoid, ventral view, I.R.Sc.N.B. No. 1683; *d*, ilium, I.R.Sc.N.B. No. 1634; *e*, ilium and *f*, pubis fragment of I.R.Sc.N.B. No. 1563.
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PLATE IX

EXPLANATION OF PLATE IX.

- FIG. 1. — *Erquelinnesia gosseleti*. *a* and *b*, humerus; *c* and *d*, femur; *e* and *f*, tibia of I.R.Sc.N.B. No. 1634.
- FIG. 2. — *Erquelinnesia gosseleti*, I.R.Sc.N.B. No. 1683, part of the posterior half of the shell, seen from the visceral surface. Specimen shows pelvis, part of the right hind limb and left femur as well as an articulated section of the tail.
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