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# STUDIES ON THE FOSSIL SNAKE *DINILYSIA PATAGONICA* WOODWARD: PART I. CRANIAL MORPHOLOGY

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## ABSTRACT

A snake fossil described in 1901 by Sir Arthur Smith Woodward and named *Dinilysia patagonica* is significant not only because of late Cretaceous age but because it is essentially a complete specimen. It was recovered from sandstone deposits near the Río Neuquén, Chubut Territory, Argentina. Relatively little notice has been accorded this significant fossil, primarily because it was incompletely prepared. Since many significant features of the specimen were thereby concealed, Woodward described *Dinilysia* as "a typical member of the Order Ophidia" and related it to the modern burrowing snake *Anilius* (= *Ilysia*). The present study indicates that he was mistaken in the first of these statements but at least partially correct in the second.

The following snakelike characters are present: (1) prokinetic skull, (2) loss of both temporal arches, (3) ventral enclosure of brain by frontal and parietal bones, (4) loose articulation of dentary with posterior mandibular bones. Other snake resemblances also occur, and the skull has a distinctly snakelike appearance.

The lizardlike (or primitive) characters are more numerous than those present in modern snakes. The most striking are (1) palatine bones that are deeply channeled for the internal choanae and that lack the an-

terior toothed projections of modern snakes, (2) presence of a jugal bone, (3) presence of both postfrontal and postorbital bones, the latter contacting the jugal as shown on the original cast of the specimen, but now broken on the fossil, (4) single trigeminal foramen, (5) pterygoid bones vertical posteriorly, (6) a single opening in the front of the braincase for olfactory tracts, (7) stapedial footplate not enclosed by a crista circumfenestralis, (8) large, laterally-projecting basipterygoid processes.

Unusual or unique features of *Dinilysia* are the robust nasal septum, the vomers underlain by palatines, the low position of the fenestra rotunda on the occiput, the peculiar shape of the jugals, the deeply-grooved transverse suture between parasphenoid and basioccipital, and both the size of the paroccipital process and the relatively large supratemporal bone. The peculiar oval jaw joint is unique and unlike both the strongly saddleshaped articulation of snakes and the similar but less extreme joint of lizards.

Characters in *Dinilysia* that show resemblance to the modern aniliid snakes are: (1) the large paroccipital processes, (2) the dorsal exposure of the prootic as a tiny sliver surrounded by parietal, supratemporal, supraoccipital, and exoccipital bones, (3) the shape of the supraoccipital, (4) the large stapes, (5) the broad attachment of the quadrate bone to the paroccipital process, (6) the wide, *Cylindrophis*-like cultriform process of the parasphenoid.

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The lizardlike characters do not relate *Dinilysia* to any particular group of lizards; indeed most of the characters are probably generalized lepidosaurian features. Some aspects of the occiput and the palate (especially the posterior palatine and pterygoid region) resemble those of the Recent platynotan *Lanthanotus*, but there are also non-platynotan resemblances, such as the depth of the choanal impressions on the palatines.

*Dinilysia* is a mosaic, but in spite of its lizardlike features it is clearly a snake and shows detailed resemblances to the modern Aniliidae that cannot be dismissed as convergent. These modern forms are probably the closest relatives of *Dinilysia* among living snakes, and the unique features do not seem fundamental enough to weaken this relationship. *Dinilysia* should be placed in a family separate from the Aniliidae, and probably belongs at the base of the superfamily Booidea.

## INTRODUCTION

Fossil snake remains tend to be both infrequent and fragmentary. The majority of snake fossils consist of vertebrae and ribs, parts that, although furnishing certain characters of interest to systematists, are quite strikingly similar from group to group. Few snake skulls have been preserved as fossils and, thus, this greatest potential source of information pertinent to the phylogeny of the Serpentes has been all but wanting.

It is thus remarkable that one of the very oldest known fossil snakes, *Dinilysia patagonica* Woodward (1901) from the Upper Cretaceous of South America, is excellently preserved and includes a nearly complete skull, mandibles, and many vertebrae. Such a specimen might be the focal point of all speculations on the origin and early evolution of the snakes, but, despite considerable interest in snake ancestry (see especially Bellairs and Underwood, 1951; McDowell and Bogert, 1954; Underwood, 1957), *Dini-*

*lysia* has received little more than mention. This is not altogether surprising; Woodward's original description of *Dinilysia* is brief and draws attention to few characters that are not present in many living snakes. Woodward underlined this rather unexciting portrayal of almost the oldest fossil snake with the statement that, on the basis of cranial structure, *Dinilysia* is "a typical member of the order Ophidia" (1901: 178).

We have had the opportunity to re-examine the skull of *Dinilysia*, and further preparation by one of us (RE) has exposed the palate for study. We are unanimous in our opinion that *Dinilysia* is *not* a "typical" snake, and that it possesses both specialized and primitive features so far unknown in other snakes. It is our aim, here, to re-describe what seems to us the most important fossil snake yet discovered and to note some of the ways in which *Dinilysia* resembles other members of the Squamata. We hope in this way to place *Dinilysia* in its proper context and to enable it to be discussed intelligently in relation to the origin and early evolution of snakes. We do not, however, propose such a discussion here. It is evident to us that further advances in the study of snake origins will require the study of primitive living snakes in more meticulous detail than is found in any work now available, and definitive conclusions may require the discovery of critical fossils still unknown.

## ACKNOWLEDGMENTS

We are most grateful to Dr. Rosendo Pascual (Museo de La Plata, La Plata, Argentina) for the loan of the type specimen of *Dinilysia patagonica*, and also to Dr. Mario E. Teruggi of the same institution, who brought the specimen to the United States for our use. We also thank Professor Bryan Patterson of the Museum of Comparative Zoology, whose constant harassment contributed materially to the speed of completion of this manuscript.

The manuscript has been read critically



by Dr. Samuel B. McDowell (Rutgers, The State University, Newark, New Jersey), Dr. Garth Underwood (Sir John Cass College, London) and Dr. Thomas Parsons (University of Toronto). We have found their suggestions very helpful although we alone accept responsibility for the accuracy of the interpretations offered herein.

Mr. Anthony Laska made excellent casts of the skull; these are the more remarkable when the soft and delicate condition of the fossil is considered. Figures 5–12 were prepared by Mr. László Meszoly, and the photographs were made by Mr. Fred Maynard of Boston University.

We are grateful to a number of sources for financial aid during the course of this project. An American Philosophical Society Grant No. 3665 to Estes made possible preparation and some of the illustrations, and his research time was supported in part by National Science Foundation grants GB-1683, GB-4303 and GB-7176. Travel and research time for Frazzetta was provided in part by his National Institutes of Health Postdoctoral Fellowship during 1964–65 and his N. S. F. grant GB-5831. The Milton Fund of Harvard University supported the preparation of some of the figures.

## THE GEOLOGICAL OCCURRENCE AND PRESERVATION OF THE SPECIMEN

The unique specimen of *Dinilysia patagonica* consists of an articulated skull, jaws, and most of a vertebral column. It is preserved in a reddish brown sandstone that contains a high percentage of clay-sized particles cementing the medium sand grains. It was recovered from the sandstone deposits near the Río Neuquén, Chubut Territory, Argentina (Feruglio, 1949). These widespread late Cretaceous sediments were laid down following a great marine transgression in southern South America and are bounded above and below by strata bearing plant and animal fossils of characteristic late Cretaceous aspect; the age of the specimen is thus unquestionable.

The deposits seem to have been formed on a flood plain; in this and their relationship to marine transgressions they resemble many North American late Cretaceous deposits formed under a similar regime.

The associated fauna includes giant horned turtles and large carnivorous dinosaurs.

The preservation of the bone is excellent; it is white when newly prepared and resembles Recent bone. Unfortunately, it is also chalky and brittle and does not absorb protective substances such as Alvar or Glyptal readily.

The skull and jaws are little eroded except at the terminal snout region. Some of the materials used in the past to protect the specimen have resulted in damage over the years: shellac has dried, shrunk and exfoliated some of the surfaces, and mastic, a soft waxy substance (in part beeswax) used to fill some crevices, has permeated the surrounding bone, making it cheesy in texture and difficult to preserve.

There is little, if any, distortion or crushing evident. The chief agent that has disturbed the specimen is weathering, most of which seems to have been post-depositional and subaerial. A large pre-depositional crack extends across the right temporal process and is the only instance of crushing significant enough to warrant comment. As a result, the process itself is depressed below the dorsal skull level and separated from the dorsal skull table by a broad, matrix-filled area. A fragment of bone, probably a part of the prootic in the region of the above-mentioned crack, lies on the right pterygoid. There is apparently no distortion of the individual bones; only a simple dislocation seems to have occurred.

As originally preserved (Plates 1 and 2) the jaws were agape, and the elements of the right mandible were almost separated and bent at an unnatural angle. This indicates that some maceration had probably occurred before burial, but not sufficient to disarticulate the specimen.



Unfortunately, the most serious damage to the specimen has been suffered since the entrance of *Dinilysia* into the literature. The most important such changes are the breakage and loss of parts of the maxillae, the postorbital bar, and the loss of the left dentary region. These are discussed in more detail under the sections on the respective bones. We regret to say that there has been additional damage to the specimen during this study as a result of the very brittle nature of the bone. The posterior end of the right dentary with the splenial is now missing. The right postdentary bones have lost some bone dorsally. The right maxilla has been badly cracked posteriorly and some bone lost on the dorsal surface. Preparation of the skull necessary to study important features has resulted in many minor breakages. The snout region was broken and repaired with minor loss of bone and slight dislocation of elements after the casting of the specimen. Fortunately almost all of the above damage has been suffered subsequent to photographing (except Plate 5 of the occiput), illustration and casting. Thus the figures represent the specimen at its best while available to us.

A cast of the specimen as it was during Woodward's description is in the British Museum (Natural History). Dr. Alan Charig has very kindly had this copied for our study and states that the copy faithfully reproduces the original *cast*. Two views of the copy are figured here as Plate 2. Unfortunately, the original cast does not give more than the gross shape of the specimen, but it does allow some questions about the original specimen to be discussed: the number of maxillary and dentary teeth, the original extent of the maxillae, and the extent of the postorbital bar. These will be discussed in the appropriate sections.

We repeat below Woodward's original description; his figures (1a, 1b, 1c of his plate XX) are reprinted here as Plate 1. We do this (1) because the views expressed by Woodward are of interest; (2) because

this is a report on the specimen before it suffered the damage that has resulted in its present diminished condition; and (3) because reproduction of Woodward's description in itself provides the reader with all previous substantive literature dealing with this fossil: other than the diagnosis of the family Dinilysiidae given by Romer (1956: 570), there have been no citations that are not mere mentions (or abstracts of this study; Estes, 1966; Estes et al., 1966).

"II. An Extinct Ophidian, *Dinilysia patagonica*, gen. et sp. nov. (Plate XX.)

"Mr. Roth's discovery of a fossil Ophidian in the red sandstone of Nequén, associated with typical Mesosuchian Crocodiles, has already been recorded,<sup>2</sup> but the unique specimen referred to has not hitherto been studied. It comprises the greater part of the skull and mandible, and fragmentary remains of the anterior half of the vertebral column; the cranium being in an especially good state of preservation.

"The skull (Plate XX, figs. 1, 1a) is long, narrow, and depressed, with the cranial region as long as the facial region. It seems to have been widest at the occiput, where the otic region is very massive; and the maximum compression is immediately in front of this, where the parietals rise into a prominent sagittal crest. The constitution of the hinder part of the skull is best seen on the left side of the fossil, where there is only one slight antero-posterior crack (x) in the bones. The right postero-lateral angle, on the other hand, is fractured and displaced downwards. The foramen magnum, which is filled with matrix, is completed above by the exoccipitals (*ex.occ.*), which meet in the middle line. They are directly continuous on each side with a great, expanded piece of bone (*op.*), which curves backwards as well as outwards and abuts upon the bone at the upper end of the quadrate. This expansion of the exoccipital is probably the opisthotic, which is similarly fused with the exoccipital in Lacertilia and the extinct Mosasaurs. Above the exoccipitals is the short but laterally-extended supraoccipital (*s.occ.*), which completes the sagittal crest behind. Its lateral extremity on the left is in contact with a small trace of bone (*o.*), which is exposed between the opisthotic, parietal, and the bone

<sup>2</sup> A. Smith Woodward, *Anales Mus. La Plata—Paleont. Argent.* no. iv (1896), p. 1.



at the upper end of the quadrate. The fragment is doubtless the highest point of the anterior otic bone, of which the upper part is otherwise completely buried by the surrounding elements. The parietals (*pa.*) occupy nearly half the entire length of the cranium, curve downwards to form the side walls, are much compressed in their anterior two-thirds, and rise into a conspicuous sagittal crest. They are flattened in the middle line at their anterior end, and are not pierced by a pineal foramen. Each of the frontals (*fr.*) is nearly three times as long as broad, and slightly widest at its truncated anterior end. There is no supra-orbital bone; but posteriorly and anteriorly the outer border of the frontal is slightly notched for the accommodation of the postfrontal and prefrontal respectively. The postfrontal (*pt.f.*) seems to have partly bounded the comparatively small orbit (*orb.*) behind; but this bar is broken away on both sides. The prefrontal (*pr.f.*), best preserved on the left (fig. 1a), is flattened and triangular in shape, almost equilateral; it is only slightly in contact with the postero-lateral angle of the nasal bone. The nasals (*na.*) are also flattened and triangular in shape, but antero-posteriorly elongated and with a somewhat concave outer side which bounds the relatively large narial opening (*nar.*). They are widest at their articulation with the frontals. They are incomplete in front, and the premaxillae are unfortunately not shown. The greater part of the palate is obscured by matrix or broken away, but some features at the postero-lateral angles of the cranium and in the facial region are well shown. As observed especially on the left side (fig. 1), a long and narrow plate of bone (*s.t.*) forms the postero-superior boundary of the parietal and otic region, and seems to constitute the articulation for the quadrate. This is doubtless the element commonly named supratemporal in Snakes, Lizards, and Mosasaurs. The quadrate (*qu.*) is evidently short and broad, but is only imperfectly shown in section on the left side. Its remains (Pl. XX, fig. 1c) are not readily interpreted; but the upper end of the bone seems to be displaced outwards and incomplete in the fossil, while the more expanded lower end shows the large notch which usually forms a loose articulation for the pterygoid in Snakes. At first sight, it might be supposed that the quadrate was of the same form as that of the Mosasaurs, with a deep posterior notch for the auditory meatus; but closer study seems to make this interpretation impossible. At the side of the cranium, below the supratemporal and parietal, the upper border of a large prootic (*pr.o.*) is

exposed; while between this bone and the orbit the downwardly curved portion of the parietal forms a sharp longitudinal lateral ridge (*r.*). There are no traces of temporal arcades. The short pterygoids (*pt.*) are partly exposed, and a portion of the palatine below the orbit on the left side bears traces of two comparatively minute teeth. There are distinct remains of an ectopterygoid or transverse bone (*ec.*) on each side between the pterygoid and maxilla; and a fragment on the left side seems to show that this element overlapped the maxilla to a considerable extent. The maxilla itself (*mx.*) is relatively large, and best preserved on the right side. It is stout and curves inwards in front. It articulates not only with the pterygoid behind by the intervention of the transverse bone, but also with the palatine by a broad articular palatal process which extends inwards from its middle. It likewise articulates directly with the prefrontal in an extensive suture. It shows 14 or 15 large shallow sockets for the implantation of teeth (fig. 1b); and one dental crown preserved at the hinder end of the left maxilla is very slender and recurved. The fragmentary remains of the mandible show it to have been of the usual slender ophidian type, with a very loose articulation between the dentary (*d.*) and articulo-angular region (*ag.*); and the dentary exhibits a series of large shallow tooth-sockets like those of the maxilla.

"Behind the skull there are remains of a long series of typical ophidian vertebrae, which do not present any features worthy of special note. The neural arches are shown to have borne delicate low spines, though nearly all of these have been broken away and are only represented by their bases in the fossil (Plate XX, fig. 2, *n.*). The ribs (*r.*) are very stout.

"From this description it is evident that the Patagonian fossil in question represents a typical member of the order Ophidia. As shown, however, by the conformation of the occiput and the relatively small size of the quadrate, it belongs to one of the more generalized types. Its closest allies may therefore be sought among the Boidae and Ilysiidae, which still constitute so large and characteristic a part of the Ophidian fauna of South America. The skull bears much general resemblance to that of a *Boa constrictor*, but is readily distinguished from the latter by its non-projecting supratemporal and relatively small quadrate. It is similarly distinguished from the skull of all the other Boidae.<sup>1</sup> In precisely this character,

<sup>1</sup> G. A. Boulenger, Catalogue of the Snakes in the British Museum (Natural History), vol. i (1893).



on the other hand, the fossil skull agrees with that of the existing Ilysiidae; and its occipital region is almost identical with that of the South American genus *Ilysia*.<sup>2</sup> The resemblance to the latter, indeed, is so close that, although the coronoid region of the mandible is not observable in the fossil, there need be little hesitation in referring the extinct type now described to the family Ilysiidae. It differs from the existing genera of the family in its more numerous marginal teeth and relatively smaller palatine teeth; in its elevated sagittal crest; and in the presence of well-developed neural spines on the vertebrae. It also differs from the South American *Ilysia*, though agreeing with the Javan *Cylindrophis*, in the possession of a small postfrontal bone. It may, in fact, be regarded as a comparatively gigantic forerunner of the Ilysiidae, analogous to *Glyptodon* among the Armadillos and *Phororhachos* among the Cariamias. Whereas the modern representatives of the family are small and degenerate burrowing snakes, the largest less than a metre in length, the extinct Patagonian snake, judging by the size of its vertebrae, must have attained a length of at least two metres. It had a relatively large head, and probably resembled the modern Boas in habit.

"This fossil evidently represents a hitherto unknown genus, which may be named *Dinilysia* and defined thus:- Marginal teeth of moderate size, about 14 or 15 in the maxillary series; palatine teeth relatively minute. Head rather large, the occipito-parietal region constituting half of the skull, with elevated sagittal crest; frontals longer than broad; small postfrontals present; prefrontals triangular, almost equilateral, only slightly in contact with nasals, which are long and narrow, tapering forwards. Vertebrae with low, delicate neural spines.

"The type species, of which remains are now described, may be named *D. patagonica*, and defined by the minor characters of the head-bones already noted."

Woodward's description of *Dinilysia patagonica* is not only short but unfortunately inadequate. Our major disappointment with Woodward's description is simple, though not trivial—Woodward stopped short of treating those characters that make *Dinilysia* both a unique animal and a significant discovery. This complaint applies to those parts that were exposed when Woodward

examined the specimen as well as to those portions that were hidden and for which, of course, Woodward could not be held accountable. Woodward's failure to recognize the distinctive nature of *Dinilysia* might well have stemmed from the paucity of comparative material available to him. He mentions specific comparisons of *Dinilysia* with *Ilysia* (= *Anilius*) and also with *Boa constrictor*, but lists no other boiform genera by name. Perhaps with a larger collection of cranial material to hand Woodward might have been more able—or more confident—to identify certain features that set *Dinilysia* sharply apart from all other snakes. We attempt below to correct the deficiencies of Woodward's description.

## A REDESCRIPTION OF THE CRANIAL REGION OF *DINILYSIA PATAGONICA*

### General Features of the Skull

In general aspect, the skull is flat and broad anteriorly with the orbits opening dorsally as well as laterally (Figs. 1a-b and 3). Behind the level of the frontals the braincase becomes narrower and gracefully lengthened. Caudally the posterior braincase swells smoothly transversely to produce a pair of strong, posterolateral projections. A more detailed account now follows in which each bone is treated individually.

### SNOUT COMPLEX

#### Premaxilla

Examination of the jagged cross section through the anterior ends of the nasals in *Dinilysia* reveals no indication of premaxillary structures. In addition, the copy of the original British Museum (NH) cast indicates that the maxillae extended close to the midline (see Plate 2). These facts might indicate that the premaxilla was of limited lateral and vertical extent were it not that, in many modern boids, the maxillae possess considerable freedom for transverse displacements. In some of these, the anterior

<sup>2</sup> G. A. Boulenger, *tom. cit.* (1893, p. 132, fig. 8.)



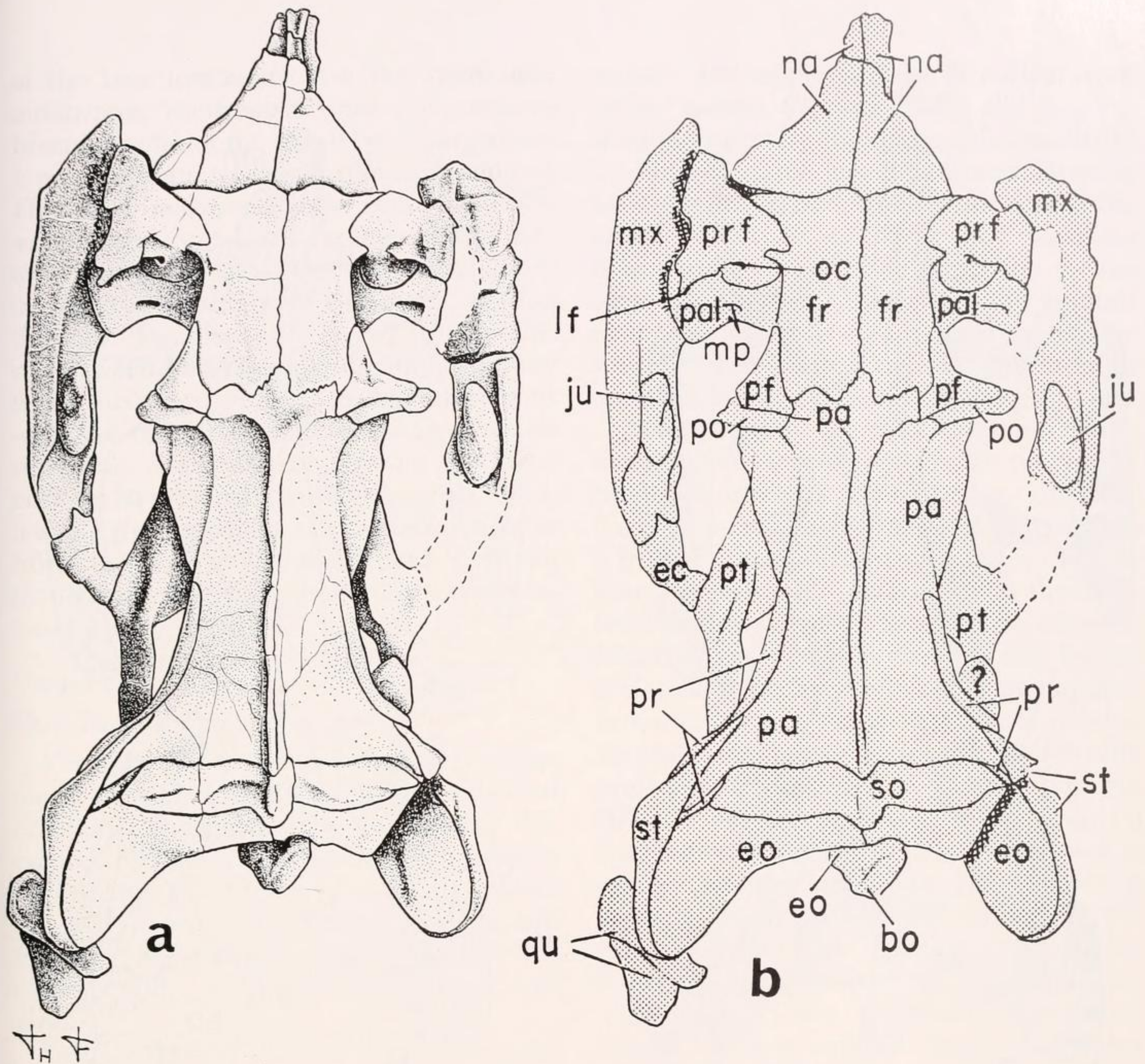


Figure 1. *Dinilysia patagonica*; dorsal view of skull. Abbreviations on p. 62.  $\times 1.5$ .

maxillary tips can be brought fairly close to the cranial midline following removal of the premaxilla. Moreover, in certain boids with wide premaxillae (e.g. *Boa*, *Eunectes*), the premaxillary transverse process lies just in front of the tips of the maxillae.

#### Nasal Figs. 1, 2a–b, 3, 7; na.

The paired nasals together form a nearly equilateral triangle in dorsal view whose anterior apex is displaced slightly to the right. The anteriormost portions of the nasals are badly eroded and incomplete. Originally, the posterolateral nasal corners extended to the lateralmost limits of the

anterodorsal edges of the frontals to produce a wide zone of contact between these elements at the nasofrontal articulation (Fig. 1). The nasofrontal articulation is described below in the section on the frontal.

In lateral view, the nasals are relatively thick. Anteriorly, their inferior surfaces slope gently ventromedial and form a thickened internasal partition.

#### Septomaxilla Figs. 2a–b, 3, 7; sm.

Although the snout region is broken, there is no real difficulty in interpretation



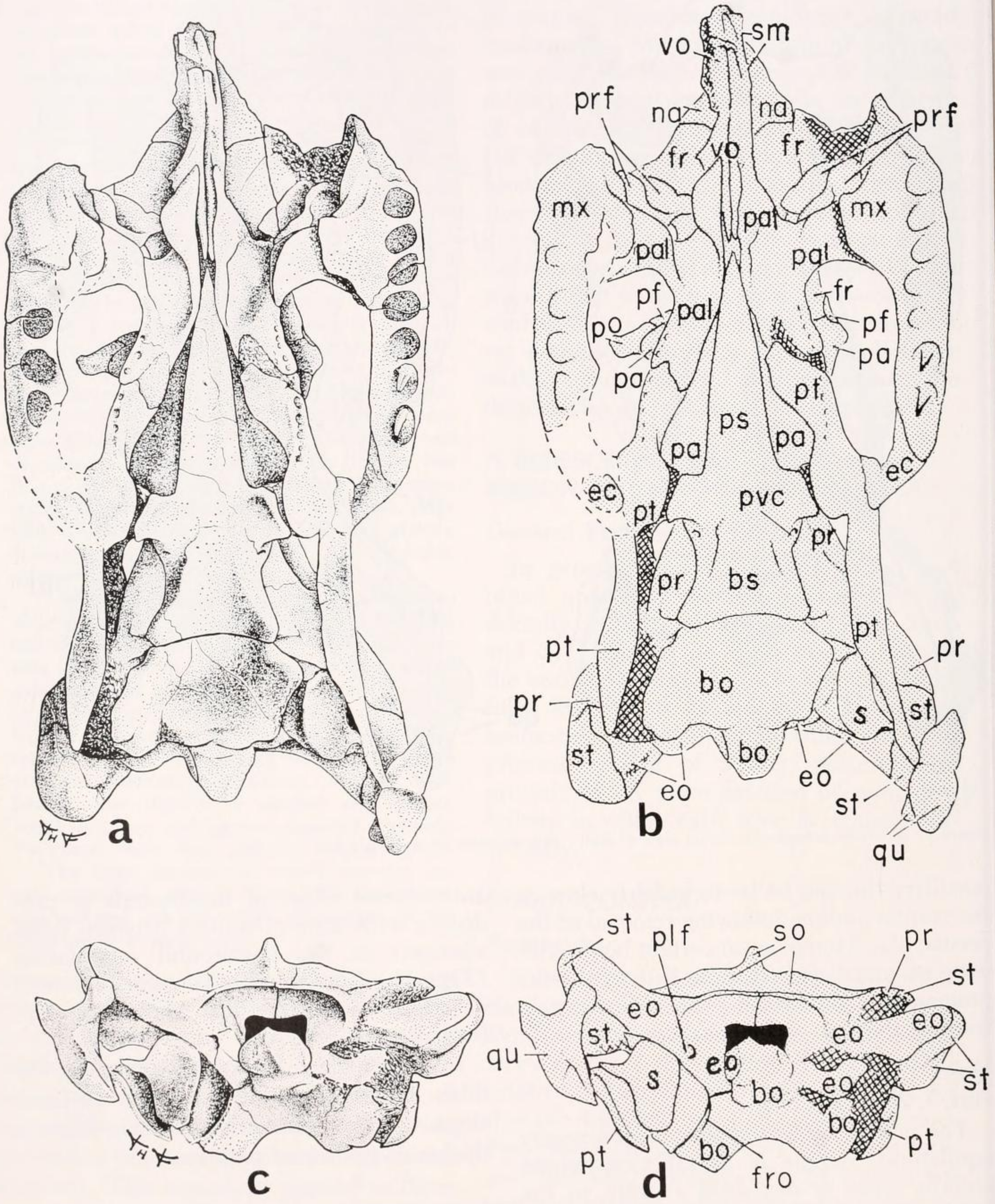


Figure 2. *Dinilysia patagonica*; ventral and occipital views of skull. Abbreviations on p. 62.  $\times 1.5$ .



of the bone remnants. On the right side, a thin bony shelf extends along the anteroventral border of the nasal, beginning about 4 mm anterior to the nasofrontal contact. This shelf makes a gentle curve ventrally as it extends anteriorly, and its dorsal surface is inclined lateroventrally throughout its length. Anteriorly, the cross section through the snout (Fig. 7a) shows this plate of bone to be applied closely to bony fragments that appear to be continuous with the vomers (see below). On the left side, only a tiny bar of bone in the same position represents the septomaxilla. Posteriorly this fragment slopes dorsally away from the vomer, leaving space between them that must have housed the vomeronasal organ.

#### Vomer

Figs. 2a–b, 3, 7; vo.

Ventrally and posteriorly, the vomer meets the palatine at a somewhat indistinct junction. The junction is more easily discerned on the right where the palatine appears to extend forward as a flat, pointed process ventral to the vomer. On the left, however, a line of demarcation between the corresponding palatine and vomer is not clear.

Just anterior to the vomer-palatine junction on the right, the vomer is slightly widened laterally; medially and more posteriorly, the vomers are visible between the palatines as a pair of slender, rodlike processes (Figs. 2a–b), each of which is the ventral edge of a vertically oriented plate. Anteriorly the vomers are separated from their posterior portions by a matrix-filled crack. Their anteriormost portions directly underlie the septomaxillae (Fig. 7b).

### BRAINCASE

#### Frontal

Figs. 1, 2a–b, 3; fr.

In dorsal view both frontals together are longer than wide and are separated by a longitudinal, very slightly irregular median

suture. The upper surface of each is very gently convex anteromedially and bears a shallow concavity that is bounded medially by the convexity just noted, and laterally by a slightly raised frontal rim above the orbit. About six or seven tiny foramina extend in a crooked line along the medial slope of this rim. Posteriorly the frontals meet the parietal in a jagged transverse suture, while posterolaterally the frontals are indented by portions of the postfrontals.

Anterolaterally the upper surfaces of the frontals are joined by dorsal tonguelike processes of the prefrontal bones. Dorsally, these elements each appear to extend into a frontal notch that accommodates them so that the prefrontal surfaces are at the same level as those of the frontals. The adjacent edges of the dorsal prefrontal and frontal surfaces lie against one another and appear to be tightly connected. Each prefrontal is very slightly notched to receive the laterally projecting frontal edge. The notch horizontally divides the prefrontal into the dorsal tonguelike process just described, and a smaller ventral tonguelike process that is pressed against the lower surface of the frontal and is visible ventrally and posterolaterally (Figs. 2a–b).

Anterior to the prefrontal the dorsal frontal surface widens suddenly, transversely increasing the anterior frontal border as it meets the nasals.

A comparison between dorsal and ventral lines of demarcation separating the nasals and frontals reveals that, although the upper line is relatively straight and transverse, the lower line is shallowly V-shaped and lies from one (medially, at the apex of the V) to nearly five millimeters (about 30% of the total nasal length) in advance of the dorsal juncture (compare Figs. 1a with 2a, 1b with 2b). Examination of the lateral edge of the right nasal shows that posteriorly the nasal suddenly becomes vertically thinner where it lies upon an anteriorly projecting frontal shelf that underlaps it; the rostral borders of the paired frontal



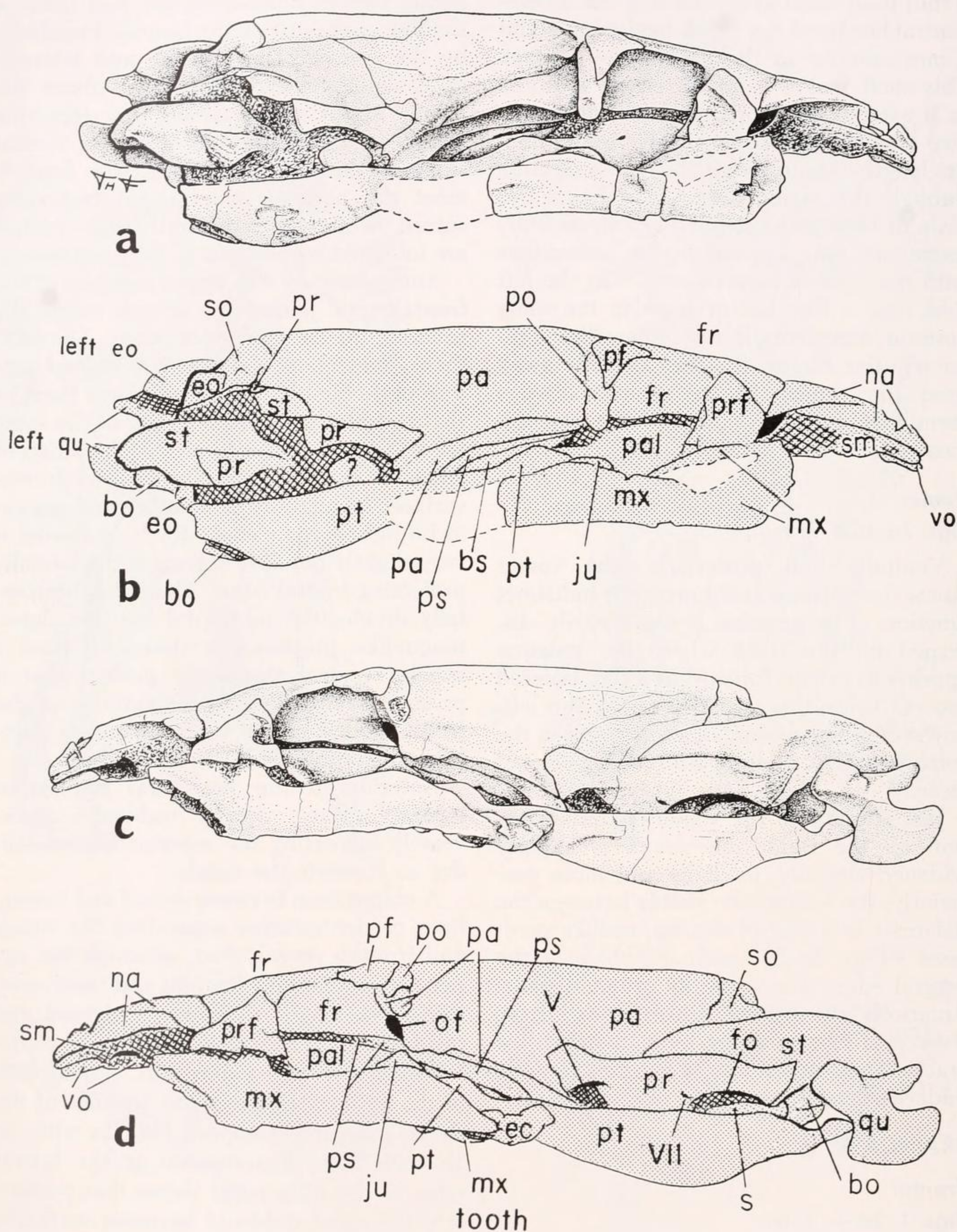


Figure 3. *Dinilysia patagonica*; lateral views of skull. Abbreviations on p. 62.  $\times 1.5$ .



shelves produce the V-shaped demarcation from the nasals that is seen in ventral view. The area of contact between nasals and frontals is thus extensive, both longitudinally and transversely.

The frontals possess lateral descending walls that meet anteriorly to enclose a single, median opening for the olfactory tracts. This opening is triangular in form with the base formed by the flattened inferior surfaces of the dorsal frontal table, and with the apex lying in the midline at a point that is posterior and ventral to the base. The base itself lies about five millimeters posterior to the level of the dorsal nasofrontal line of juncture. A suture between the two descending walls of the frontal continues caudad from the ventromedian apex of the opening and is shortly hidden from view as it passes dorsal to the vomers.

In the orbital region the descending walls of the frontals slope ventromedially at roughly 45 degrees, and are gently concave. The degree of concavity slightly increases posteriorly in the region of the optic foramen. The frontal forms the anterior border of the optic foramen. The anteroventral border is provided by a small, caudally-pointed frontal process that projects beneath the foramen and does not meet the parietal; instead, the posteroventral rim of the optic foramen is formed by the basi-parasphenoid, which is closely united to the frontals along the ventral midline. The dorsal and posterior walls of the foramen are formed by the parietal. The frontal meets the parietal above the foramen and bulges laterally just beneath the postfrontal.

#### Postfrontal

Figs. 1, 3; pf.

There are, on each side, two distinct elements in the postorbital region. The anteriormost pair of elements contact both frontal and parietal and seem to be homologous to the postfrontals of lizards. On the right side, the postfrontal bears a lateral

fingerlike portion (lacking on the left) and appears to be complete.

Each postfrontal has a horizontally flattened and tapered anterior process that lies snugly in a dorsal frontal recess along the posterolateral edge of the frontal. The lateral border of the anterior process blends smoothly with that of the frontal, but caudally it expands laterally and ventrally to lie upon the corresponding postorbital bone and adjacent parietal as the fingerlike process noted above. Neither the anterior nor the lateral process extends onto the orbital surface of the frontal.

Dorsomedially, and just posterior to the frontals, each postfrontal terminates in a short, longitudinal parietal-postfrontal suture.

#### Postorbital

Figs. 1, 3; po.

The second pair of elements in the postorbital region lies just beneath and slightly behind the postfrontals, and appears to represent the postorbital bones of lizards. No portion of the postorbital extends along the inferior surface of the frontal or parietal. Instead, each bone lies on the postorbital process of the parietal so that the bone is wedged between the postfrontal above and the parietal below. Posteriorly the bone is exposed beneath and behind the postfrontal, the transverse caudal border of its lateral extension paralleling that of the postfrontal. At the medial end of the short postfrontal-parietal suture, the parietal sends a short bony spur laterally that overlaps the postorbital medially (see Fig. 3). There is a small but distinct fossa ventral to each postorbital, floored and terminated medially by the parietal.

On the left side the lateral projection of the postorbital is missing, while on the right the postorbital curves ventrally as it extends laterally beyond the tip of the postfrontal. The lateral postorbital process is wider and less horizontally flattened than is the postfrontal.



The free lateral end of the right postorbital has a somewhat rough and uneven texture indicating that a still more latero-ventral extension of the bone has been broken away. The situation is confused by an inconsistency in Woodward's paper. His figure of the dorsal view of the skull (Fig. 1 in Plate 1) shows the left postorbital region much as it still appears in the specimen today. On the right, Woodward figures a postorbital bar that continues ventrolaterally from the fingerlike process of the postorbital bone as figured here to connect with a peculiar element (interpreted in the present paper as a jugal) lying on the surface of the maxilla. It is unfortunate that Woodward did not figure the right lateral view of the skull, for his written description seems to contradict his pictorial presentation. He surmised that the postorbitals (= postfrontals of Woodward) "partly bounded" the orbit posteriorly, but goes on to say that the postorbital "bar is broken away on both sides." Woodward's choice of the word "broken" to describe the lack of a postorbital connection to the jugal makes it unclear whether he intended to convey that the specimen was damaged after it was illustrated, or that such a connection was never present in his specimen (in which case his figure is in error). Although his figures are somewhat unclear in several respects, they appear to be quite accurately and carefully rendered, and, if the postorbital bar is shown incorrectly, it is the only major mistake we can find in Woodward's illustrations. Furthermore, it is significant that Woodward raised the issue at all, since he regarded *Dinilysia* as a relatively unmodified snake, readily comparable to *Boa constrictor*.

It is easily possible that the postorbital bar could have been damaged during Woodward's examination of the specimen. The fossil is very brittle and, even with careful handling, several areas have crumbled away and have required restoration so that the specimen as it appears at this

writing does not match our own figures as well as it first did. Unfortunately the presence or absence of a postorbital connection with the presumed jugal element influences our functional interpretation (to be presented in a future paper).

Evidence provided by the cast of the specimen in the British Museum (Natural History), and mentioned above in the section on preservation, indicates that the figure is correct, and that the postorbital bar was originally complete on the right side. The cast shows bone continuous from the skull roof to the maxilla. Woodward's statement that the postorbital bar was broken thus may have referred to breakage after the cast was made. We thus conclude, on the basis of available evidence, that when the specimen first came into Woodward's hands the postorbital met the jugal.

#### Parietal

Figs. 1, 3; pa.

Dorsally and anteriorly, the parietal begins between the postfrontals and postorbitals at the jagged frontoparietal suture. In this region the parietal is flattened with a slight medial concavity; this essentially flat portion quickly narrows posteriorly and continues caudally as the dorsal edge of the sagittal crest. On either side of the anterior extremity of the crest, the parietal is hollowed to form a concavity that becomes shallower posteriorly and extends anterolaterally to the level of the postfrontal-parietal suture. More laterally, the parietal contour drops sharply downward onto a prominent shelflike modification of the bone. This shelf juts laterally and somewhat ventrally so that its upper surface slopes at least 30 degrees below the horizontal; the inferior surface of the shelf is smoothly concave. Anteriorly the shelf curls upward to meet the postorbital process of the parietal. Posteriorly it extends ventrally to the anterior border of the trigeminal foramen.



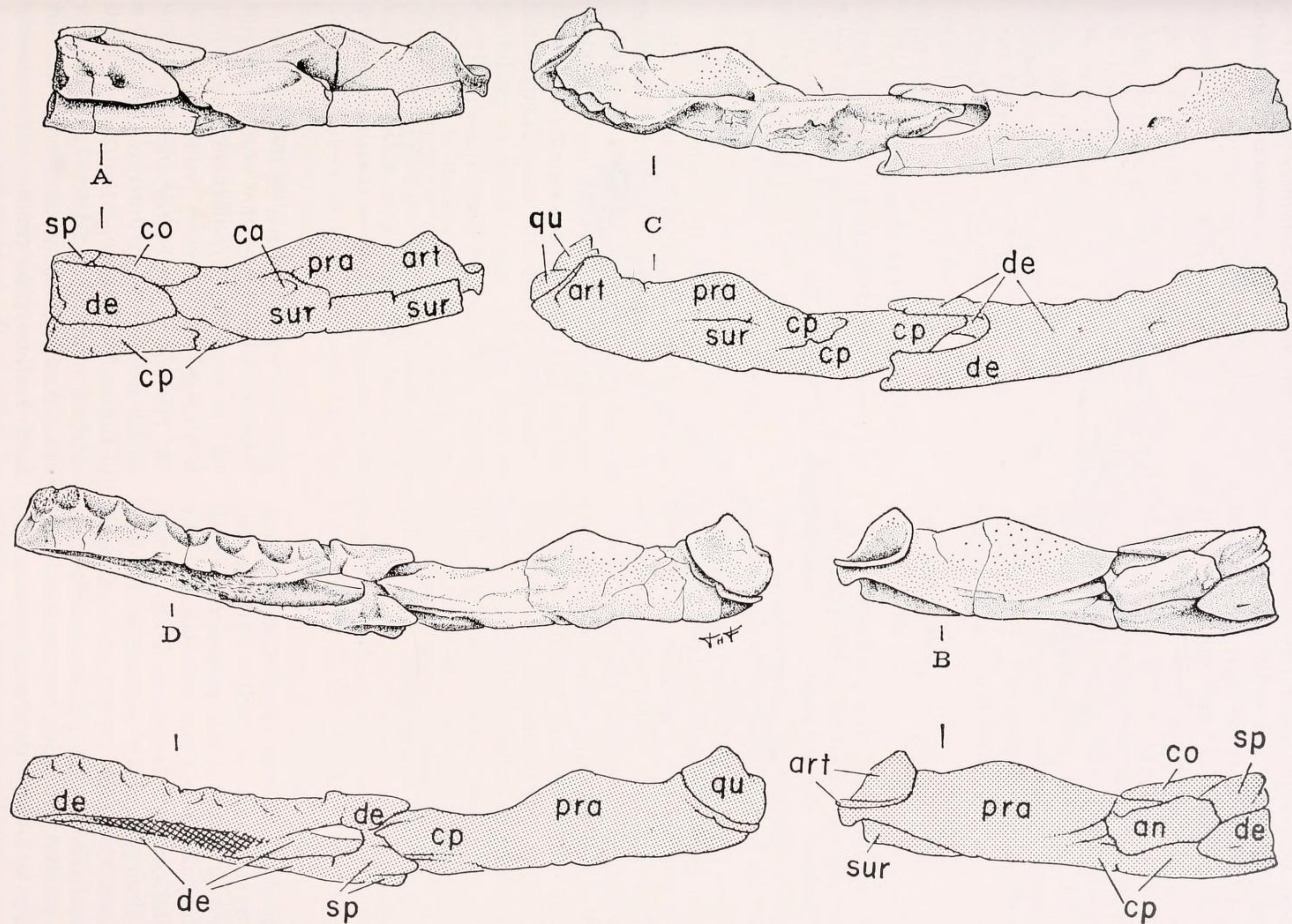


Figure 4. *Dinilysia patagonica*; A, labial, and B, lingual views of fragmentary left mandible; C, labial, and D, lingual views of right mandible in natural articulation. Abbreviations on p. 62.  $\times 1.5$ .



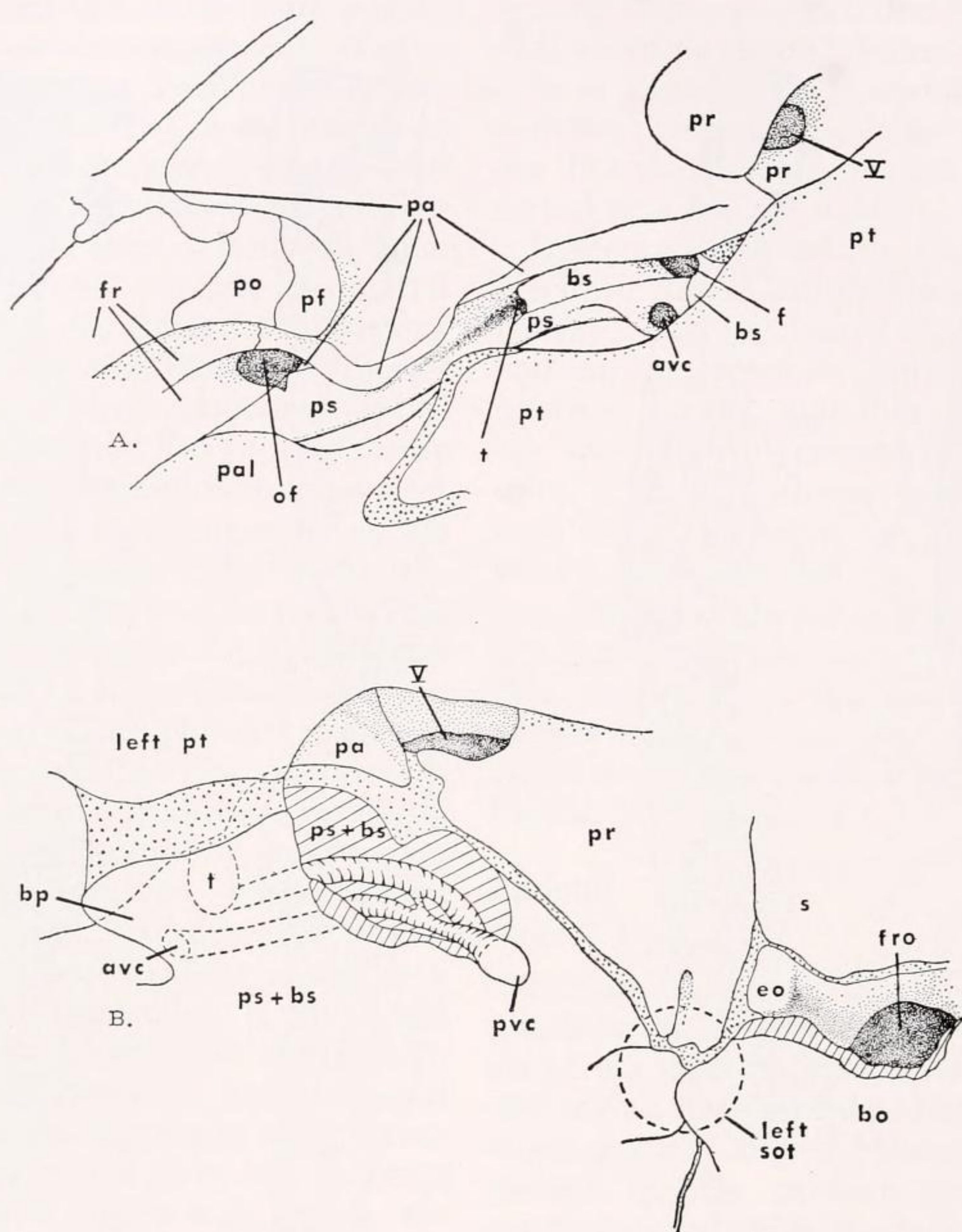


Figure 5. *Dinilysia patagonica*; A, oblique dorsolateral view of left basiparasphenoid and surrounding elements; note anterior separation of basisphenoid from parasphenoid. B, oblique ventrolateral view of area between basipterygoid process and fenestra rotunda, showing partial excavation of vidian canal and canal dorsal to it opening at f on Fig. 5a, and area between sphenopalatine tuber and stapes. Foramina in dark stipple, matrix in coarse stipple, excavated or broken areas in hatched line; abbreviations on p. 62; both  $\times 3$ . Diagrammatic.

The elongated major portion of the parietal shows a faint cerebellar swelling that widens gradually until, posteriorly, it expands smoothly but markedly laterad. The parietal contacts the prootic both laterally and dorsoposteriorly, extending narrowly between the supratemporal and a dorsally exposed sliver of the prootic (see below). The parietal joins the supraoccipital posteriorly in a long, transverse suture.

Anteroventrally the parietal forms the

posterior and dorsal rim of the optic foramen. In this region the ventral parietal surface joins the parasphenoid with which it is firmly sutured as far posteriorly as the anterior border of the trigeminal foramen. At the level of the basipterygoid processes of the basiparasphenoid, the parietal is developed ventrally and laterally to contribute a small, lateral portion to the base of each basipterygoid process. Immediately posterior to the level of the basipterygoid



process, the parietal is narrowly included in the anteroventral border of the single trigeminal foramen.

### Prootic

Figs. 1, 2, 3, 5; pr.

The prootics are relatively large. On the left, the bone is complete, while on the right it is divided by a wide vertical fracture, which has dislocated the entire supratemporal process ventrally. Much of the ventrolateral part of the right prootic is covered by matrix and by a small piece of bone that may be a dislocated piece of the right prootic.

The anterior border of the prootic begins dorsal to the basiptyergoid processes. The large, single trigeminal foramen lies in a notch on the anterior border and is almost entirely enclosed by the prootic except for a small contribution from the parietal anteroventrally. The tiny facial foramen lies on the anterior margin of the fenestra ovalis; the latter is partly excavated into the posterior border of the prootic.

Ventrally the prootic comes into broad contact anteriorly with the basiparasphe-noid and extends posteroventrally to the basioccipital, contributing to the basioccipital tubera as noted below. At the level of the basiparasphe-noid-basioccipital suture, the prootic is shallowly though sharply excavated to form a small, bony "step" (see Fig. 2a). This step anteriorly bounds a depression that is medially and posteriorly delimited by tuberos processes of the basisphenoid and basioccipital.

The prootic bulges laterally as it continues posteriorly onto the supratemporal process. This portion of the bone, just before reaching its caudal sutural limit with the supratemporal, is abruptly flattened in a parasagittal plane as is the adjacent supratemporal. At its posterior end, the prootic interdigitates strongly with the supratemporal and the prootic-supratemporal suture courses medially at this point on the ventral surface of the supratemporal process.

Dorsal to the supratemporal, and bounded by it, the parietal, and supra- and exoccipital elements, there is a separate, sliverlike bone, which represents an internal portion of the prootic that "breaks through" the braincase to be exposed dorsally, in isolation from the rest of the prootic. Examination of the large posterior fracture of the prootic on the right reveals that the break has cut this bony sliver, and that it is continuous with the prootic but separated externally by the long diagonal suture of supratemporal and parietal.

### Supratemporal

Figs. 1-3; st.

The supratemporals begin on the transversely-expanded posterior portion of the braincase as rather narrow wedges that each lie between the parietal above and the prootic below. At the level of the dorsal prootic sliver each strip becomes vertically deepened and continues caudal to and beyond the posterior tip of the lateral part of the prootic. Here the supratemporal expands ventrally to form a parasagittally-flattened plane that is continuous with the flattened posterior surface of the prootic. Caudally, the supratemporals extend well posterior to the level of the occipital condyle and cover the lateral, and part of the ventral, portions of the enlarged paroccipital processes of the exoccipital bones.

### Supraoccipital

Figs. 1, 2c-d, 3; so.

This element is a very wide, short, median bone sutured anteriorly to the parietal, laterally to the sliver-like process of the prootic, and caudally to the exoccipitals. The bone bears a median crest that is continuous with the sagittal crest of the parietal. On either side of the crest there is a ridge that begins at the parieto-supraoccipital border and extends posterolaterally to the posterior supraoccipital border, thickening progressively toward its posterolateral end. At the supraoccipital-exoccipi-



tal border, posterior and medial to the ridge, a prominent depression is present on each side.

### Exoccipital and Opisthotic

Figs. 1–3; eo.

Each exoccipital (including a fused opisthotic) dorsally makes contact with the supraoccipital, prootic, and supratemporal. Posterolaterally each is expanded laterally to form a large paroccipital process that continues caudally posterior to the occipital condyle and that possesses a wide, flat superior surface facing dorsomedially. Posteromedially, the exoccipitals overhang the foramen magnum to form an awninglike rim.

Much of the occiput is formed by the exoccipitals. Here they descend to form the lateral borders of the foramen magnum and, since they join and provide the dorsal and lateral portions of the condyle, they also form most of the ventral border. Lateral to the condyle, the exoccipitals extend transversely as a pair of wide, tongue-like processes (broken off on the left) that lie beneath the paroccipital processes and floor the posterior lacerate foramina ventrally, concealing them from view. On the right, the bony tongue is well preserved, and is sutured to the basioccipital ventrally. The fenestra ovalis and the fenestra rotunda are separated by another, more ventral process of the exoccipital; this process continues ventrally and projects to meet the prootic and the basioccipital below the fenestra ovalis, where it contributes to the posterior portion of the rather complex sphenoccipital tubercle (Fig. 5b).

### Basioccipital

Figs. 1–3; bo.

This unpaired ventral bone begins anteriorly at a broad, transverse suture with the basiparasphenoid. At the ends of this suture the basioccipital develops ventrally a pair of tuberos processes that lie adjacent to similar developments of the basi-

parasphenoid. Caudad to the level of these processes, the medial surface of the basioccipital bends dorsally, while the lateral surfaces continue posterolaterally from the tuberos processes as ventrally-developed walls enclosing a wide, short concavity. The left lateral surface is partially broken away to reveal the opening of the fenestra rotunda; on the right, the lateral wall extends toward the pterygoid.

Anterolaterally the basioccipital joins the prootics, while posterolaterally it meets the exoccipitals. Posteromedially the bone narrows and produces a transverse ridge at the base of the occipital condyle. The basioccipital forms the ventromedian part of the condyle. The basioccipital can be seen dorsally as a thin sliver separating the exoccipitals, and it contributes about one-half of the body of the condyle itself.

### Basiparasphenoid

Figs. 2, 3, 5; bps.

This ventral element begins posteriorly at its transverse suture with the basioccipital, where it is bounded laterally by the prootics. The posterolateral corners are strongly developed ventrally to form a pair of tuberos processes that lie in contact with similar developments of the basioccipital. Between these processes the ventral surface of the basiparasphenoid forms a wide trough that narrows anteriorly, where it is bounded by a pair of low but sharp ventral ridges that tend to converge toward one another anteriorly. These ridges originally bore laterally-developed crests, setting off groovelike pockets dorsally. Unfortunately these delicate crests have not survived this present study, but a small portion of the right one may be seen in Figure 2a and b. Lateral to these ridges and directly posterior to the basipterygoid processes are the paired posterior openings of the vidian canals.

The laterally-placed basipterygoid processes have convex articulating surfaces that face more laterally than ventrally; their axes are anteroposteriorly elongated, and



their ventromedial surfaces are gently concave. The ventral margin of each process is thickened and is separated slightly from the pterygoids. The joint between the processes and the pterygoids is straight and has a slight anteromedial-posterolateral orientation. The dorsal sides of the processes are partially covered by moderate ventral downgrowths of the parietals. The anterior vidian canals occur far laterally on the basi-ptyergoid processes.

The parasphenoid and basisphenoid are separate anterior to a foramen that opens dorsomedial to the anterior opening of the vidian canal (Fig. 5). The lateral and medial borders of this foramen are formed by the basisphenoid, its visible dorsal border formed by the parietal, and its ventral border by the parasphenoid. The basisphenoid extends anteriorly from this foramen about one-third of the distance to the optic foramen. At this point on both sides it stops abruptly at prominent, matrix-filled trabecular grooves (Fig. 5a), and the parasphenoid expands dorsally to meet the parietal, filling the gap in front of the basisphenoid. The trabecular grooves lie wholly in the cultriform process of the parasphenoid, although they approach the parietals closely.

The cultriform process of the parasphenoid is wide posteriorly near the basi-ptyergoid processes, but tapers anteriorly and is closely pressed to parietal, basisphenoid, and, presumably, frontals. The inferior surface of the bone, between the basi-ptyergoid processes and its meeting with the palatines, bears a distinct, elongated concavity.

The tapered anterior end of the parasphenoid extends between and slightly dorsal to the palatines; the tip stops short of the posterior extremities of the vomers.

## STAPES

Figs. 2, 3; s.

On the left side, posteroventral to the prootic, there is a stapes consisting of a

relatively large footplate and, as preserved, a delicate columellar process. Medially the bone is inserted into a fenestra ovalis, which is in turn set into a deep cleft in the posterior surface of the deeply emarginated prootic and the exoccipital. The fenestra ovalis is separated from the fenestra rotunda by an anteroventrally-projecting process of the exoccipital. The columellar process is broken, but extends toward the quadrate and approaches the posterior portion of the pterygoid. Whether or not it abutted against the quadrate is conjectural because of columellar breakage and quadrate dislocation.

## SUSPENSORIA OF THE PALATO-MAXILLARY ARCH; THE ARCH ITSELF

### Prefrontal

Figs. 1–3; prf.

The prefrontals are horizontally flattened so that their entire lateral surfaces could be equally well designated as dorsal. Since the prefrontal forms the anterior orbital wall, this flattening extends the orbit laterally so that it opens as much superiorly as laterally.

The external surface of each prefrontal (better preserved on the left than on the right) is roughly an equilateral triangle, with the lateral side lying upon a dorsal expansion of the maxilla, and the medial corner forming a dorsal tonguelike process that is inserted into the upper frontal surface. The anterior prefrontal margin extends from this dorsal corner and crosses the lateral corner of the nasal to terminate against the maxilla.

The ventral tonguelike process that lies against the lower frontal surface bears a pronounced transverse elevation that caudally delimits a deep prefrontal concavity that opens medioanteriorly. The ventral edge of this elevation is expanded anteriorly as a flattened, horizontal surface that comes into contact with the palatine and maxilla.

Posteriorly, in the anterior orbital region,



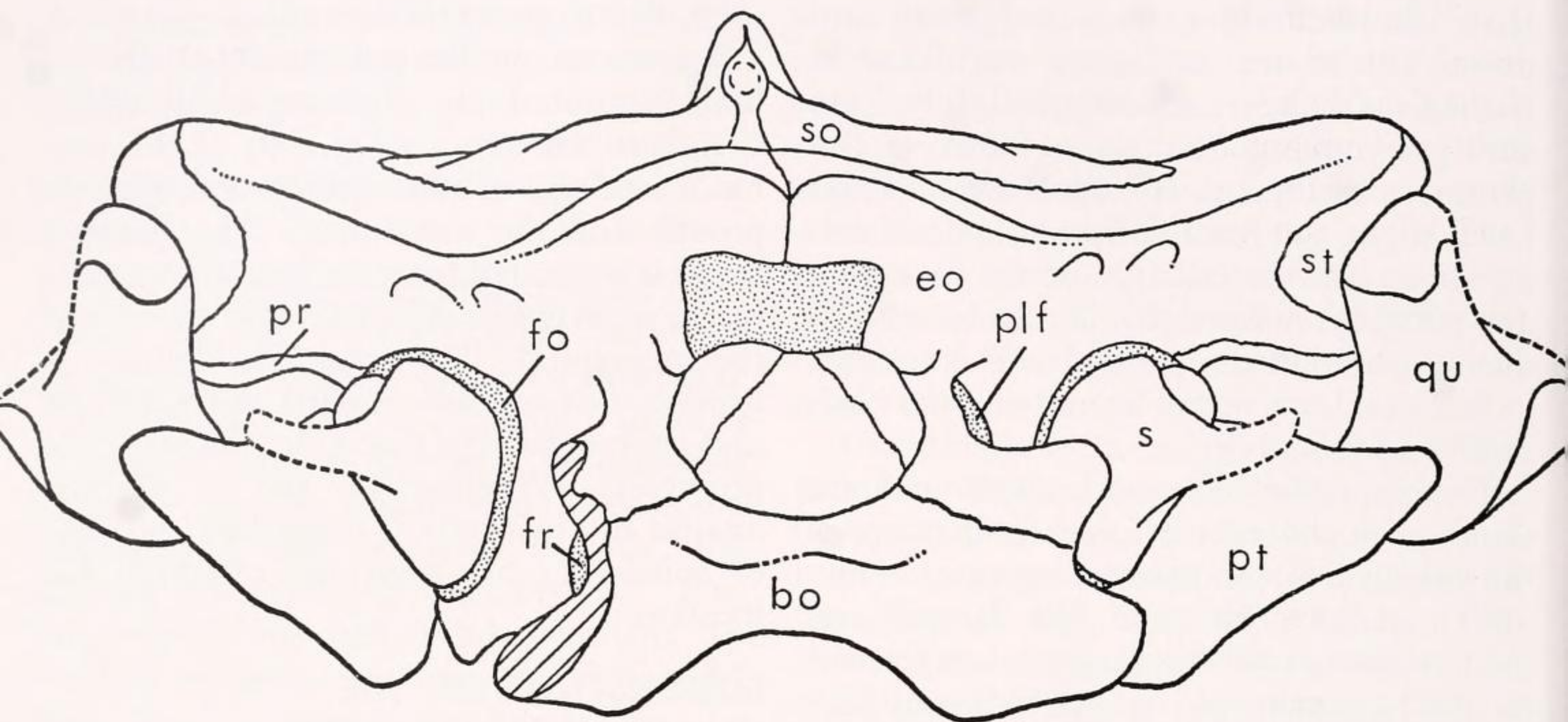


Figure 6. *Dinilysia patagonica*; reconstruction of occiput. Abbreviations on p. 62.  $\times 3.5$ . Dotted line = conjectural; structures missing on one side restored from the other; broken exoccipital-basioccipital hatched and not restored, in order to show fenestra rotunda. Diagrammatic.

each prefrontal descends and then flattens horizontally where it rests upon the upper surface of the lateral palatine process (see below). Here the prefrontal is perforated by the combined orbitonasal canal and lacrimal foramen, which on both sides is nearly closed ventrally by the prefrontal.

#### Palatine

Figs. 2a-b, 6; pal.

The palatines lack toothed anterior projections. Instead, the dentigerous portion does not extend anteriorly beyond the level of the lateral process of each palatine. A distinct, deeply impressed choanal channel is present, which is partially closed ventrally by sheetlike expansions from both lateral and medial edges of the palatine. Medial to the choanal channel, the sheetlike expansion is pressed against the lateral and inferior surfaces of the vomer as described above. The posterolateral dentigerous portion of each palatine is a thick, ribbonlike process facing ventromedially, and is rather smoothly continuous with the medial process. No teeth are preserved but small sockets for the subpleurodont teeth are per-

ceptible. If we may judge by the diameters of their sockets, the palatine teeth were relatively small. They extended forward in a single row from the palatopterygoid joint to the posterior level of the lateral palatine process. It is impossible to determine precisely their number; we estimate that each palatine bore about five or six teeth.

The lateral process of the palatine is formed by a sudden horizontal expansion and flattening of the lateral palatine edge, just anterior to the level of the first palatine tooth. This expansion provides a partial floor beneath the choanal passage in that region, but its major portion stretches laterally over the superior surface of the medial maxillary process and beneath the prefrontal. The lateral palatine process is very extensive in that it intervenes between prefrontal and maxilla in such a way as to all but prevent those elements from coming into contact, and it reaches transversely nearly to the ventrolateral edge of the prefrontal. Below the lacrimal foramen, the lateral palatine process is perforated by a transversely-widened maxillo-palatine foramen.



In dorsolateral view, just in advance of the dorsal lappet of the pterygoid, a tiny (venous?) foramen pierces the dorsal surface of the longitudinal portion of the palatine (Figs. 3, 8c).

Posteriorly the palatines join the pterygoids in a rather complex manner. Dorso-laterally the pterygoid sends forward a pointed projection that seems to lie in a correspondingly shaped shallow depression in the palatine surface. Ventrally (partially preserved on the left side) similar pointed processes are mostly broken away but presumably extended onto the undersurface of the palatine, as indicated by depressions in the bones. In effect, the palatine was clasped by these two projections (cf. Figs. 5a, 8c, 10a).

### Pterygoid

Figs. 1–3, 5–6; pt.

The anterior attachments of the pterygoids with the palatines have just been described. The pterygoid tooth row is continuous with that of the palatine. It appears, upon examination of the tooth sockets, that the approximately five pterygoid teeth were subequal to those on the palatine and that they diminished in size posteriorly. The last tooth socket lies just ahead of the level of the basipterygoid joint.

The internal process of the pterygoid is moderately developed, arises at the level of the basipterygoid, and meets the ventrolaterally facing basipterygoid surface.

At the level of the internal process, the lateral side of each pterygoid joins with an ectopterygoid. Again at the same transverse level, but dorsally, each pterygoid bears a sharp longitudinal ridge. Slightly posterior to this point the pterygoid becomes sharply compressed, the upper edge of the ridge continuing caudally as the dorsal margin of the compressed pterygoid portion. The posterior, compressed portion of the pterygoid is convex laterally and concave medially. Posteriorly the vertical dimension increases to the level of the basi-

cranial tubera and then decreases posteriorly; the dorsal border remains longitudinally straight. In ventral view, the posterior halves of the pterygoids are essentially straight. The posterior tips of the pterygoids (as seen on the left) are applied to the medial surface of the quadrate.

A small, pebblelike element (labelled “?” in the figures) lies upon the dorsal surface of the right pterygoid. This is probably a dislodged fragment of the nearby broken area of the prootic as noted above.

### Maxilla

Figs. 1, 2a–b, 3, 7; mx.

Woodward's figure shows the right maxilla as complete (Fig. 1 in Plate 1). It is sad to note that today neither maxilla is complete anteriorly. It is also regrettable that Woodward figured only the dorsal view of the right maxilla. On the original cast (Plate 2) the maxilla curves conspicuously downward anteriorly, is strongly excavated for the naris, and reaches almost to the midline.

At the present time, the maxilla on the left is somewhat better preserved than that on the right. In the region of the prefrontal, the lateral maxillary surface is flattened and turns upward to meet the lower margin of that element. The lateral maxillary surface is smooth and convex anteriorly; posteriorly it is somewhat dorsoventrally expanded and concave.

Dorsally, the superior maxillary surface receives the lateral palatine process that intervenes between prefrontal and maxilla. This process is very loosely articulated with the maxilla and is separated from it by a deep, matrix-filled groove. In this region the maxilla sends forth a flattened medial process that is seen in ventral view to extend mediad along the ventral surface of the palatine.

More posteriorly the maxilla bears a marked ridge running lengthwise on the dorsal aspect of the bone. This ridge sharply



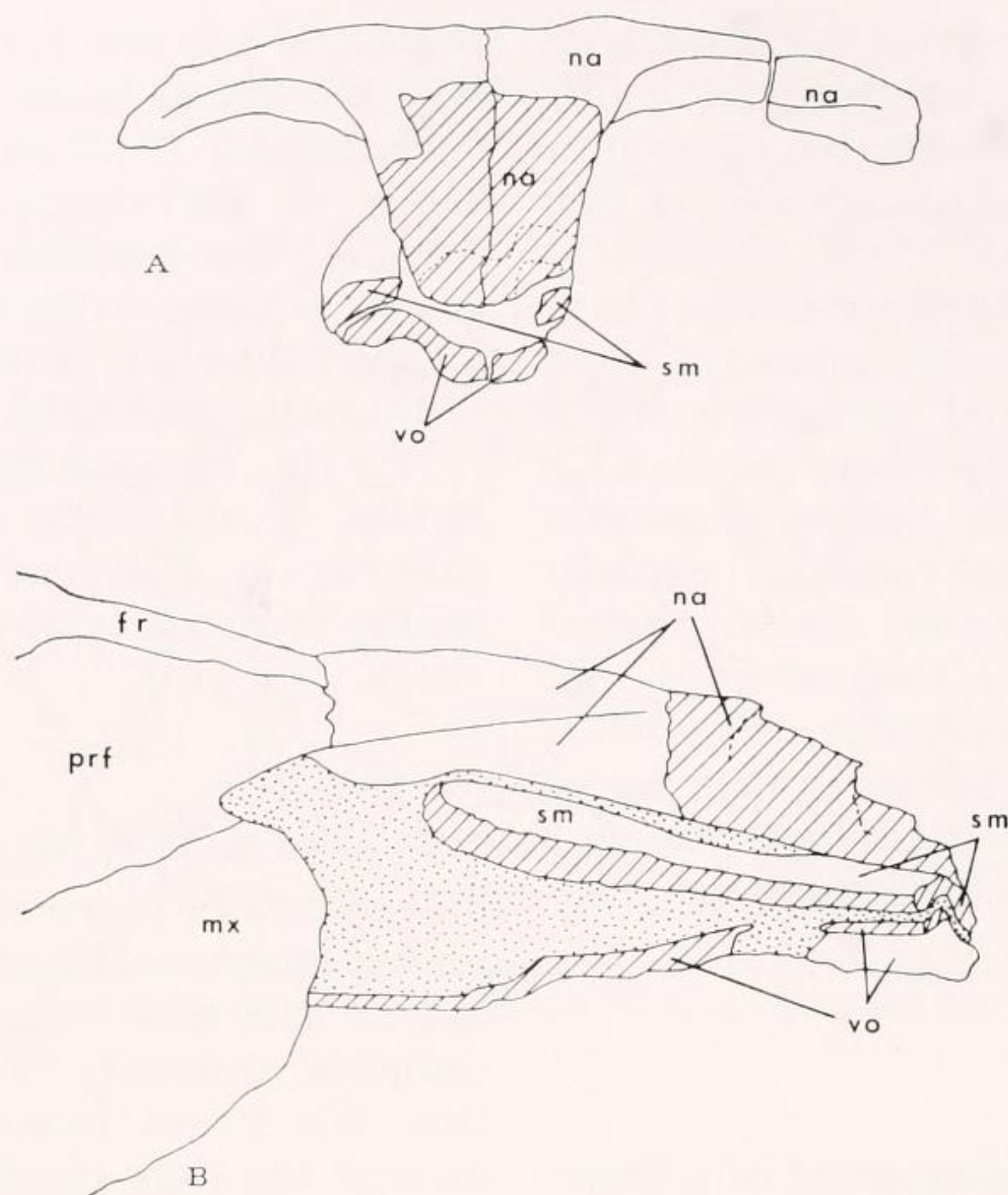


Figure 7. *Dinilysia patagonica*; A, anterior, and B, right lateral view of snout region; hatched line = broken surfaces. Abbreviations on p. 62.  $\times 3$ . Diagrammatic.

separates the lateral maxillary surface just described from the medial side of the maxilla. The surface of the medial side faces dorsomedially; caudally it becomes increasingly concave to form a rather deep, longitudinal channel that extends to the posterior limit of the bone. Lying in this channel, on each side, is a small fragmentary element interpreted here as the jugal (see below).

Ventrally each maxilla has a row of tooth sockets that follows the ventrolateral edge of the bone. Much of the ventral area is obscured on the right; on the left, there is evidence of seven maxillary teeth on the specimen today, but the cast indicates that at least thirteen maxillary teeth were originally present. There is no clear indication that the teeth decrease markedly in size posteriorly.

The posterior two sockets on the left contain remains of teeth. The anterior tooth is very fragmentary. The caudal surface of

the more posterior tooth is hidden by matrix, and its tip is broken away. However, its anterior and ventral surfaces are intact and visible; it arises from the maxilla as a thick, basal portion from which it curves very markedly caudad to give the appearance of a sharply bent cone. The backward sweep of this tooth does not quite lie in a parasagittal plane, but slants slightly inward at an angle of approximately 20 degrees to the longitudinal axis.

Posteriorly the maxillae are joined by the ectopterygoids (mostly absent on the right). Here the left maxilla bears, along its medial margin, a longitudinal groove (for the ectopterygoid) that extends forward to the level of the middle of the jugal.

### Ectopterygoid

Figs. 1, 2a-b, 3c-d; ec.

Unfortunately neither ectopterygoid is well preserved, and the right element is al-



most entirely lacking (though it was nearly complete in 1901). On the left, the ectopterygoid arises from the lateral edge of the pterygoid and, in the form of a small cylinder, passes forward and outward to the maxilla. It appears to abut against the caudal maxillary tip and to cover a very small portion of the upper maxillary surface, and a groove on the medial surface of the maxilla indicates that it once extended anteriorly to the level of the middle of the jugal.

### Jugal

Figs. 1, 2a–b, 3; ju.

A small bone lies in the longitudinal channel formed on each side of the dorso-medial maxillary surface. These elements are essentially symmetrical in position and in shape and are unlikely to be adhering fragments broken from some other portion of the skull. Each of these peculiar bones has the form of a flattened ellipsoid whose anterior end is turned upward toward the tip of the postorbital. They appear not to be portions of the ectopterygoids that have been accidentally isolated, since grooves for the anterior extensions of the latter occur on the medial sides of the maxillae. These bones are best interpreted as jugals.

In the natural condition, the dorsally turned anterior portion of the jugals must have made contact with the postorbitals as indicated on the original cast (see above, Postorbital).

### Quadrate

Figs. 1–3; qu.

Much of the left quadrate remains and is still attached to the skull. Its lateral surface is peculiarly flat, suggesting that a portion of this surface has been sheared off. The lower portion of the right quadrate is articulated with the right mandible; there is no remaining trace of the upper portion.

The quadrate was apparently a somewhat triradiate structure. The posterior arm

of the left element extends caudally behind the enlarged paroccipital process and the anterior portion is deflected laterally, indicating that the bone has slipped posteriorly. The normal position of the quadrate must have been more anterior, and the anterior quadrate arm must have come close to the caudally flattened part of the prootic.

The ventral arm of the essentially triradiate quadrate is somewhat flattened anteroposteriorly and expanded transversely. Its lower end curls posteriorly, presenting a smoothly convex hemispherical articulation surface ventrally.

The lateral side of the posterior end of the pterygoid articulates with the medial quadrate surface just dorsal to the level of the hemispherical expansion. The articulation surface was originally further anterior on the pterygoid before distortion of the quadrate.

### MANDIBLES

Fig. 4

Three mandibular fragments have been preserved. These consist of the posterior half of the left mandible, whose broken anterior end is neatly severed, and a nearly complete right dentary and a right "compound bone." The right elements can be fitted together, as shown in the figures, although they were originally distorted as shown in the original cast (Pl. 2) and in Woodward's figure (Pl. 1). The left dentary, present at the time of Woodward's study, has been lost.

### Compound Bone

Fig. 4; cp.

Different portions of the two compound bones possess badly eroded surfaces and parts. Examined together, however, the two bones provide a rather complete interpretation of the natural condition.

The articular area forms a shallow cup that opens dorsomedially to receive the hemispherical lower end of the quadrate



in a ball-and-socket joint. No retroarticular process of any sort is present, although the ventral surface of the mandible is broken posteriorly, and this region cannot be reconstructed with certainty.

The surangular process is represented only by a low, smooth, longitudinal ridge on the lateral surface of the compound bone. The prearticular ridge is well developed with a bluntly pointed dorsal contour. Between the surangular and prearticular processes the small mandibular fossa opens. Immediately anterior to this, the surangular bears a shallow longitudinal channel in its dorsal surface that extends alongside a narrower, rather inconspicuous channel on the anterolateral border of the prearticular lamella. The two channels together form an elongated concave area for coronoid articulation.

The right compound bone has lost the elements (coronoid, angular, splenial) that naturally adhere to it, and its anterior structure can be studied. The anterior end bears a short medial, and a larger lateral, projection. At the point where the two projections begin to diverge, a shallow groove runs posteriorly in which lay the coronoid. The ventral surface of the larger projection itself bears a groove (for the upper posterior end of the dentary) that ends abruptly near the base of the projection.

When articulated with the dentary, the larger lateral surangular projection fits in a notch between the dorsal and ventral caudal ends of the dentary; the shorter, medial projection makes contact with the splenial bar that connects the medial edges of the dorsal and ventral dentary ends.

### Dentary

Fig. 4; de.

Only the right dentary is preserved, although fragments of the posterior end of the left still remain attached to the posterior bones. The dentary curves mediad anteriorly, is slightly pointed and seems not

to have been firmly united with its fellow on the left.

Posteriorly the dentary forks into dorsal and ventral processes that are free laterally but are connected medially by the splenial. By comparison with the left mandible, the dorsal, tooth-bearing process on the right is seen to be incomplete at its lateral border, but the ventral process has only minor posterior breakage. The lateral notch between them communicates with Meckel's groove on the medial side. The lower, medial surface of the splenial bears a spleniodentary suture. A large, elongated alveolar foramen is formed between the splenial and the ventral surface of the tooth-bearing border of the dentary.

Anteriorly, on the medial side, Meckel's groove becomes narrower and approaches the ventral dentary margin where it terminates shortly behind the dentary tip.

Ten large tooth sockets are borne by the dentary as preserved, and also on the original cast of the left dentary. In addition to these, at least one smaller tooth socket may be present close to the anterior tip of the bone, but this is uncertain because of breakage. The size of the teeth appears to have diminished slightly caudad.

### Splenial

Figs. 4c-h; sp.

A portion of the splenial is preserved on the left in articulation with the posterior bones, and its articulation with the dentary is shown on the right.

On the left, a somewhat rectangular piece of bone is identifiable as the splenial by its position. It is bordered dorsally by the coronoid and upper dentary process, posteriorly by the angular, and ventrally by the lower dentary process.

### Coronoid

Figs. 4e-h; co.

The right coronoid is missing. A portion of the left coronoid lies in a shallow groove



medial to the dorsal tooth-bearing process of the dentary. Anteriorly it lies between the dentary on the dorsolateral side, and the splenial on the medial side. Posteriorly this fragment stops short of the prearticular lamella.

The coronoid must have extended posteriorly into the groove on the dorsal surface of the compound bone noted above; the latter bears striated attachment surfaces for its reception. The coronoid must have forked posteriorly, one part ascending the prearticular ridge medially as indicated by a roughened articulation surface, the other forming a coronoid process of unknown extent laterally on the surangular; the two processes thus complete the relatively narrow mandibular fossa anteriorly.

### Angular

Figs. 4g–h; an.

An angular appears only on the left mandible. It is short and thick as preserved, but can be seen to have extended posteriorly to the level of the mandibular fossa. It is traversed by a high ridge that extends the length of the preserved portion of the bone and probably did so throughout its original length, since a ridge is still present at the posterior end of the suture area.

The angular is positioned somewhat ventromedially and is slightly slanted upward anteriorly. Its anterolateral corner approaches, but no longer reaches, the coronoid; a groove presently exists between breakage surfaces of the two bones and it can only be surmised that the two bones met. The angular also makes extensive contact with the splenial anteriorly and touches the posterolateral edge of the lower caudal dentary process.

### Foramina of the Skull

Foramina are described briefly under the sections dealing with bones in which they occur; for convenience, a description of skull foramina in the context of their

surrounding bones is given here. Terminology follows that of Bahl (1937), although we do not necessarily agree to the appropriateness of the names applied.

The tiny lacrimal foramen (lf, Figs. 1, 8c) is completed dorsally by prefrontal and ventrally by palatine. Medially it seems to be confluent with the relatively large orbitonasal canal (oc, Figs. 1, 8c); the latter is floored ventrolaterally by the palatine.

The maxillo-palatine foramen (mp, Figs. 1, 8c) lies wholly within the lateral (maxillary) process of the palatine bone.

Dorsally, the anterior border of the optic fenestra (of, Figs. 3c–d, 5) is formed by the frontal, while posteriorly it is surrounded by the parietal. Its ventral border is completed by the parasphenoid.

Both anterior and posterior openings of the vidian canal (pvc, Figs. 2a–b, avc, Fig. 5) perforate the basipterygoid process of the basiparasphenoid. Both openings are about the same size. Mechanical excavation of the basipterygoid process shows that the vidian canal has a tiny, short anastomosis dorsally with a canal that appears to come from within the cranial cavity and leads anteriorly to an opening dorsal to the anterior opening of the vidian canal (Fig. 5). The dorsal canal is formed dorsally by the parietal, laterally by the basisphenoid, and ventrally by the parasphenoid. After leaving the anterior opening, the contents of the canal have left a channel on the basisphenoid.

The trigeminal foramen is single, and relatively large (V, Figs. 3c–d, 11a). It lies almost wholly within the prootic, but anteroventrally it receives a small contribution from the parietal.

The facial foramen (VII, Figs. 2c–d, 3c–d, 11a) opens through the prootic at the anterior margin of the fenestra ovalis.

The fenestra ovalis (Figs. 2c–d, 12a) is quite large, but it cannot be seen directly because of the massive, superimposed stapedial footplate. The foramen is formed by deep emarginations in the posterior part



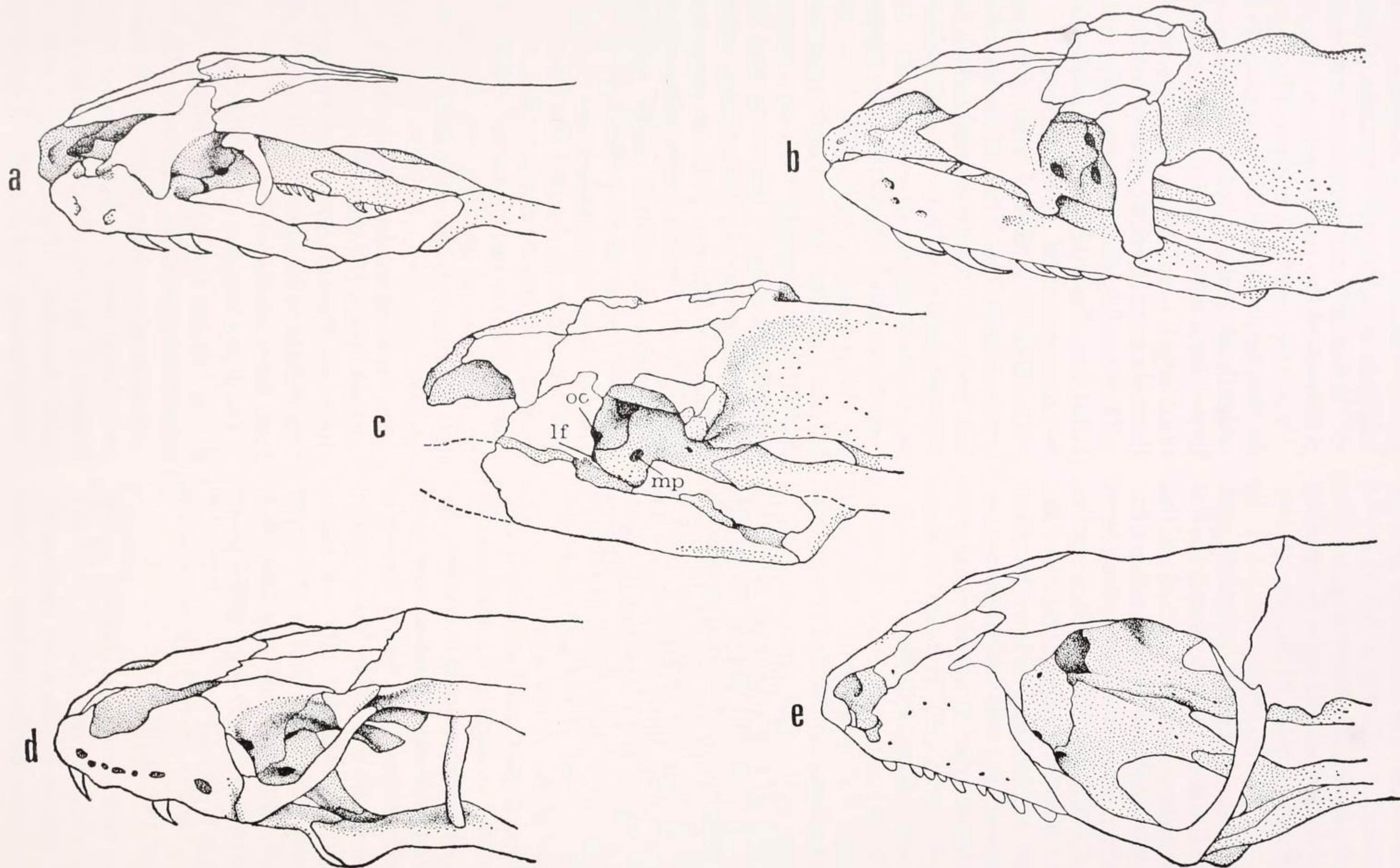


Figure 8. Oblique dorsolateral view of a, *Cylindrophis maculatus*, MCZ 34885,  $\times 4.5$ ; b, *Python molurus*, MCZ 4278,  $\times 1.5$ ; c, *Dinilysia patagonica*,  $\times 1.5$ ; d, *Lanthanotus borneensis*, MCZ 8305,  $\times 4.5$ ; e, *Tupinambis nigropunctatus*, MCZ 109890,  $\times$  about 2.5. Abbreviations on p. 62. Semidiagrammatic.



of the prootic and the anterior border of the exoccipital. The latter sends a lappet ventrally to the spheno-occipital tubercle; presumably this lappet represents a fused opisthotic.

The fenestra rotunda (fro, Figs. 2c-d, 12a) is large. Dorsally it is separated from the fenestra ovalis by the lappet of exoccipital described above, and ventrally it is completed by the basioccipital.

The foramen lacerum posterius (plf, Figs. 2c-d, 12a) opens through the posterior surface of the exoccipital, lateral to the foramen magnum. In occipital view, it is concealed behind a small tongue of the exoccipital. No separate hypoglossal foramina are associated with it on the occipital surface, nor does excavation show that such foramina appear within the mouth of the foramen.

The foramen magnum (Figs. 2d, 12a) is surrounded by the exoccipitals, except ventrally, where the latter are separated on the midline by a tiny wedge of basioccipital.

Comparisons dealing with the foramina appear within the context of the discussion below.

## DISCUSSION

Comparisons of *Dinilysia* with modern snakes indicate that it shows greatest similarity to the primitive snake families Boidae and Aniliidae (*sensu lato*), especially to the latter. However, the aniliid complex is itself in great need of study: no detailed osteological descriptions of *Loxocemus*, *Xenopeltis*, *Cylindrophis*, or *Anilius* exist. In addition, *Dinilysia* has some characters that appear unique and others that invite comparison with lizards rather than with snakes. A full scale comparison of *Dinilysia* with all the forms that should be utilized will be a lengthy task and one requiring an abundance of illustration. It is, in fact, still in the future.

We feel, however, the need to put *Dinilysia* in its approximate context at this time.

Without making every comparison or providing final judgment on its position in the phylogenetic sequence, we do wish to call attention to its most conspicuous characters indicate its position relative to other snakes and most obvious resemblances, and so and to lizards, as we now see it.

To do this as nearly as possible without bias, we have chosen as the specimens to be used for our first comparisons with *Dinilysia* a few primitive snakes, *Python sebae* and *Epicrates cenchris* (described by Frazzetta, 1959), and certain lizards, *Lanthanotus borneensis* (discussed by McDowell and Bogert, 1954), *Varanus monitor* (elaborately described by Bahl, 1937), *Tupinambis nigropunctatus* (taken as an example by Jollie, 1960), *Mabuya carinata* (described by Rao and Ramaswami, 1952) and *Ctenosaura pectinata* (discussed by Oelrich, 1956). We have added a few observations from skulls of *Cylindrophis* and *Anilius* at hand. By these admittedly very specific, but we hope judiciously distributed comparisons, we have tried to avoid the unjustified generality of statement that afflicts so many discussions of the characters and relationships of higher groups. We admit out of hand that comparisons so secured will not necessarily be the most relevant. However, until thoroughgoing investigation provides greater assurance, we can present only a very preliminary assessment of the position of *Dinilysia*. We do not pretend to attempt more. *When, therefore, in the comparison below we contrast lizards and snakes, we mean no more than that within our sample all the lizards and all the snakes were each congruent with the other examined members of their suborder.*

We shall score below (in italicized phrases) the ascertainable characters of *Dinilysia* as "snakelike," "lizardlike," "intermediate" or "unique." Here again the statements should be taken only in the context of the comparisons expressly made. Certain comparisons are omitted at this time, e.g.



comparisons with the as yet poorly understood typhlopids and leptotyphlopids.<sup>1</sup>

The skull of *Dinilysia* is incomplete, but its preserved parts will be discussed *seriatim*, following the sequence of the description.

No indication of premaxillae exists at present; however, the original cast of the specimen (Plate 2) shows the right maxilla extending close to the midline, appearing to imply that the premaxilla was originally of relatively small lateral extent. The smooth tip of the maxilla on the cast probably indicates a loose articulation with the premaxilla, as in extant snakes, instead of the sutural connection characteristic of lizards. *This feature therefore would be scored as a strong resemblance to snakes.*

The descending lamellae of the two nasals in *Dinilysia* are extremely thick and short and together form an extraordinarily robust septum almost one-third as wide as the widest part of the two horizontal nasal lamellae above (Fig. 7). In snakes there are thinner, deep, sharply defined descending nasal lamellae (Frazzetta, 1959). In lizards there is instead a cartilaginous nasal septum. *In having a bony rather than a cartilaginous nasal septum Dinilysia is snake-like. In the thickness of its septum it is unique.*

The vomers of *Dinilysia* are visible between the palatines ventrally as a pair of slender, rodlike processes with limited vertical or lateral extent (Figs. 2, 10), rather than the prominent vertical lamellae of the vomers in extant Boidae (Frazzetta, 1959: 457). In lizards the vomers may have considerable lateral expansion (e.g. *Lanthano-*

*tus* but not *Varanus*). *In neither snakes nor lizards are the vomers underlain by a portion of the palatines (see below) as they appear to be in Dinilysia. The vomers of Dinilysia are thus neither snakelike nor specifically lizardlike.*

In *Dinilysia* the frontals have lateral descending walls that meet to enclose a single median anterior opening. In boid snakes the frontals form a pair of openings by sending down not only lateral but median walls to surround the olfactory tracts. Lateral walls descend from the frontals in *Varanus* and *Lanthanotus* but not in *Ctenosaura*, *Tupinambis* or *Mabuya*. *The presence of lateral descending walls of the frontal in Dinilysia represents a step toward the snake condition and one that would be expected in an intermediate form.*

The nasofrontal articulation is extensive in *Dinilysia* and the frontals send elongated lappets anteriorly under the nasals. The overall extensiveness of the contact contrasts with the type of articulation between frontal and snout complex described in snakes (Frazzetta, 1959, 1966). Evidently snout mobility about the nasofrontal joint was less than, or at least differed from, that of boids. Discussion of the type of kinesis possible in *Dinilysia*, and the comparison of this with lizard and snake kinesis is, however, deferred to a future paper (Frazzetta, in preparation). *The difference from snakes in the extent or kind of mobility between nasals and frontals, and the relationship of nasals and frontals is lizardlike and primitive.* This difference is surprising only if it is accepted that one of the primary and defining adaptations of snakes is a prokinetic joint that permits rotational movements (see Albright and Nelson, 1959; Frazzetta, 1966).

The anteriormost element in the postorbital region is probably homologous to the postfrontal of lizards; the posterior probably is the postorbital. There has been some uncertainty regarding homology of the saurian postfrontals and postorbitals

<sup>1</sup> We have deliberately not included comparisons with the Scolecophidia (Typhlopidae and Leptotyphlopidae). We have felt (1) that the most evident resemblances were as much lizardlike (or primitive) as scolecophidianlike, (2) that the striking differences were specializations of the Scolecophidia irrelevant to the phyletic position of *Dinilysia*, and (3) that the Scolecophidia, like the Aniliidae, still need much careful study before much worthwhile can be said about them, although we have included statements about the latter group because of its clear relationship to *Dinilysia*.



with the ophidian elements in this region. The relationships of the two bones present in this region of *Dinilysia* have the same relationships to the frontal, parietal, and jugal as do the postfrontal and postorbital of *Tupinambis*. Neither bone extends medially along the descending frontal wall or contacts the prefrontal as does the pythonine supraorbital (Frazzetta, 1959: 461). We have thus no hesitation in homologizing these elements with the comparable ones of lizards. The supraorbital of pythons may be of heterotopic origin; a specimen of *Python molurus* examined by Frazzetta (FMNH 100419) has several such bones in the supraorbital area. On the other hand, it is equally possible that the pythonine supraorbital is the postfrontal of lizards, as suggested by McDowell and Bogert (1954). The presence in *Dinilysia* of twin bones having the saurian relationships to other skull bones gives the virtue of parsimony to the latter interpretation. For reasons noted in the description, we believe that a complete postorbital bar was present in *Dinilysia*, with the postorbital joining the jugal. A postorbital arch is present in boids but is joined to the palatamaxillary arch only by a ligament; the *Dinilysia* condition differs importantly in retention of the jugal—although a very peculiar jugal (see below). *The retention of both postfrontal and postorbital is a primitive squamate feature and might plausibly be expected in any very primitive snake.*

Dorsally the parietals of *Dinilysia* are applied to the occipital and otic bones, as in snakes; there is thus no posttemporal foramen like that of lizards. *In this feature Dinilysia is snakelike.*

The parietals in *Dinilysia* descend to provide a complete lateral covering to the brain, as in snakes. In none of the compared lizards is there any trace of a similar enclosure of the brain by the parietals. (In lizards there is also an epipterygoid in this region, which is absent in snakes and of which there is no evidence in *Dinilysia*.)

*The parietal downgrowths in Dinilysia are unequivocally snake characters.*

In *Dinilysia* the descending lamina of each parietal forms the anterior border of the trigeminal foramen as the similar lamina does for the anterior trigeminal foramen in *Epicrates*, *Anilius* and *Cylindrophis*, but not in *Python*. In the compared lizards, lack of the descending parietal lamina results in the trigeminal nerve taking its exit from a notch in the prootic rather than from a foramen. *The Dinilysia condition is again a snake character.*

The prootic is large in *Dinilysia*, larger than in the compared boids and lizards. In sharp contrast with the boids, there is only one trigeminal foramen bounded anteriorly by the parietal and hence anteriorly placed in a position, as before mentioned, comparable to the *incisura prooticum* of lizards and the anterior trigeminal foramen of *Epicrates*, *Anilius*, and *Cylindrophis*. *In this feature Dinilysia is lizardlike and more primitive than boid snakes but this feature is plausible in a very primitive snake.*

In *Dinilysia* the prootic is broadly notched posteriorly for the relatively enormous stapedial footplate, larger relatively than the very large footplates of *Anilius* and *Cylindrophis*. *Unlike these bones in snakes, the otic and occipital bones do not surround the footplate with a pericapsular chamber and the whole of the footplate is thus exposed as in lizards.* The exposed stapedial footplate is primitive and lizardlike, and, while not found in boids or advanced snakes, again might plausibly be expected to occur in a very primitive snake. The proportions of the stapes, with its large footplate and small, posterodorsally-directed columellar process, are as in *Anilius* and *Cylindrophis*, although even in the latter two forms the footplate is not relatively so large. The relative size of the stapes is unexpected and may be special to *Dinilysia*. *The stapes of Dinilysia has a generally lizardlike aspect, but in exposure of footplate, proportions of footplate to*



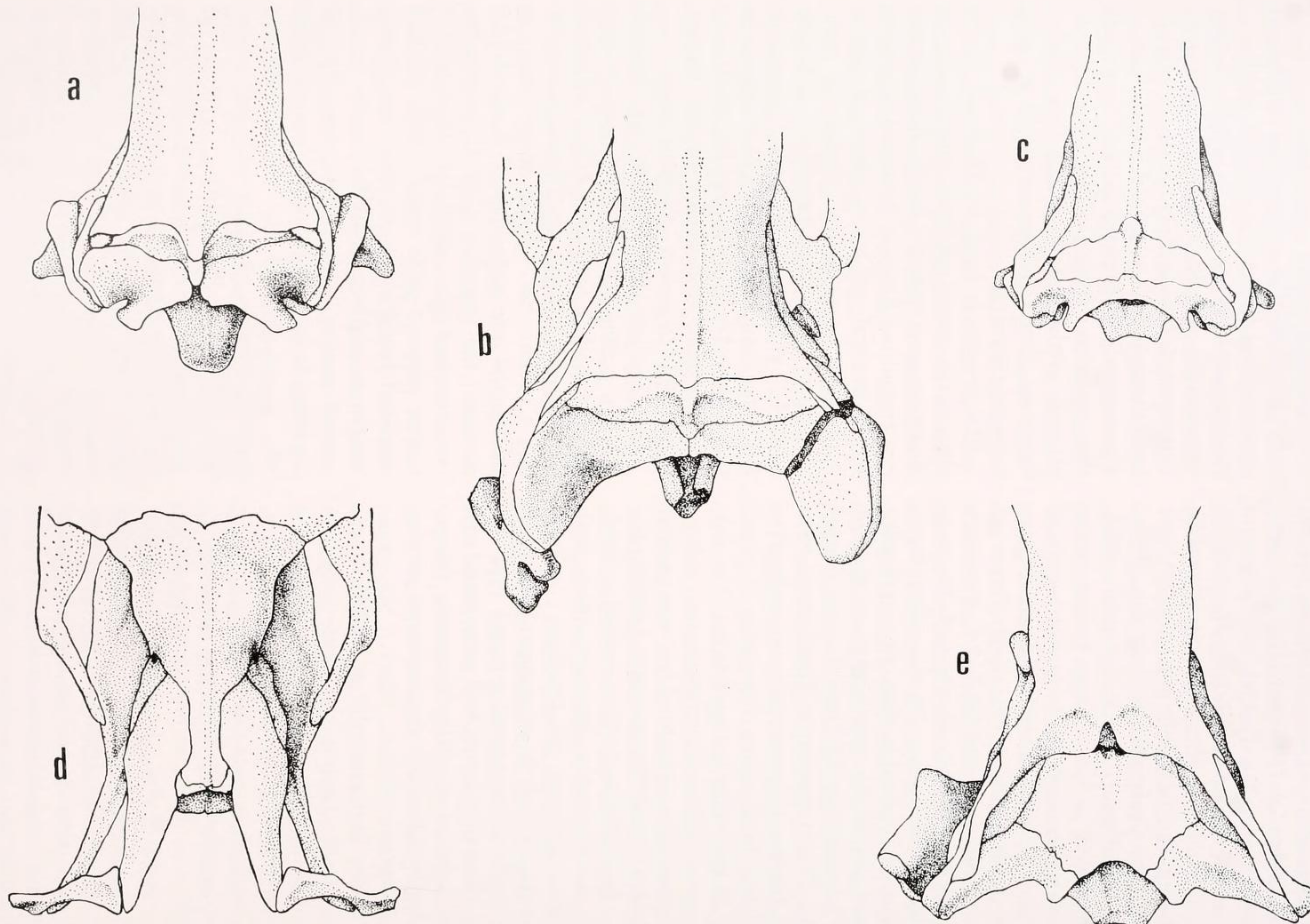


Figure 9. Dorsal view of posterior skull region of a, *Cylindrophis maculatus*, MCZ 34885,  $\times 4.5$ ; b, *Dinilyisia patagonica*,  $\times 1.5$ ; c, *Anilius scytale*, MCZ 857,  $\times 4.5$ ; d, *Python molurus*, MCZ 4278,  $\times 1.5$ ; e, *Lanthanotus borneensis*, MCZ 8305,  $\times 4.5$ . Right quadrates missing in b and e. Abbreviations on p. 62. Semidiagrammatic.



*columellar process, and connection of the latter to the footplate by a strong posterior crest (Fig. 6, etc.), it is specifically Anilius-like.*

The presence of a small dorsal exposure of the prootic, and its relation to surrounding bones, is exactly like the situation in *Anilius* and *Cylindrophis* (Fig. 9).

The massive supratemporals of *Dinilysia* are completely applied laterally to the paroccipital processes of the exoccipitals. They are like those of *Anilius* or *Cylindrophis* in being incorporated into the skull. They differ strikingly from the supratemporals of *Anilius* or *Cylindrophis* and resemble those of boids in being drawn out latero-posteriorly to a level *well behind* that of the occipital condyle, but are unlike those of boids in lacking a long *free* posterior projection: the paroccipital processes of *Dinilysia* are applied to the supratemporals all the way to their distal ends (Fig. 9).

The supratemporals of lizards are also very different: small, almost vestigial in *Ctenosaura* and *Mabuya*; relatively large in *Lanthanotus* and *Tupinambis*. In the latter two, however, most of the slender supratemporal lies alongside the posttemporal wing of the parietal; only a smaller posterior portion overlies the paroccipital process to make contact with the quadrate. In all compared lizards, posterior termination of the supratemporal lies only slightly behind the posterior level of the occipital condyle.

*The supratemporal of Dinilysia combines lizard and snake (in fact, boid) features in an unexpected way.* The strong association of supratemporal and paroccipital process is lacertilian, as we have stated, but the way in which the supratemporal is carried well behind the occipital condyle is like the situation in boids and suggests a way in which the slender exposed supratemporal of boids may have evolved: to obtain the snake condition from that characteristic of eosuchians and lizards we need only to have supratemporal and paroccipital proc-

ess extend well posteriorly with a posttemporal foramen present; next, as in *Dinilysia*, to close the foramen by secondary growth of supraoccipital and opisthotic; and then to achieve the more usual snake condition by secondarily reducing the paroccipital process to the anterior level from which it began. The incorporation of such an intermediate stage would not be obvious were it not in front of us. Interpretation of the sequence of functional adaptations that may have been involved in such an evolutionary series will necessarily require analysis of the mechanics of the entire skull and, if this evolutionary sequence is verified as occurring in the main line of snake origins, will have great importance for our understanding of the way of life of the first snakes.

The supraoccipital in *Dinilysia*, in its shape and relationships to surrounding bones, is closely comparable to this element in *Cylindrophis* and *Anilius* and is relatively much lower than the wedge-shaped element of *Python* or the vertical blade of *Epicrates*. In *Dinilysia*, as in the boids, *Anilius*, and *Cylindrophis*, a median knob on the supraoccipital continues the strong sagittal crest on the parietal. In contrast, lizards have either a median crest on the supraoccipital (*Ctenosaura*, *Tupinambis*; "processus ascendens" of Oelrich, 1956) rising to meet the parietal, the whole surface of which is at a distinctly higher level than that of the body of the supraoccipital, or (*Lanthanotus*, *Mabuya*) parietal and supraoccipital are at the same level at the point of contact but a small unossified prong ("processus ascendens tecti synotici" of most authors; "cartilaginous portion of the processus anterior" of Rao and Ramaswami, 1952) fits into a notch of the parietal. The difference in appearance of the two conditions in lizards *inter se* and as compared with conditions in *Dinilysia* and snakes is considerable. *In this regard, Dinilysia is clearly snake-like and specifically Cylindrophis-Anilius-like.*



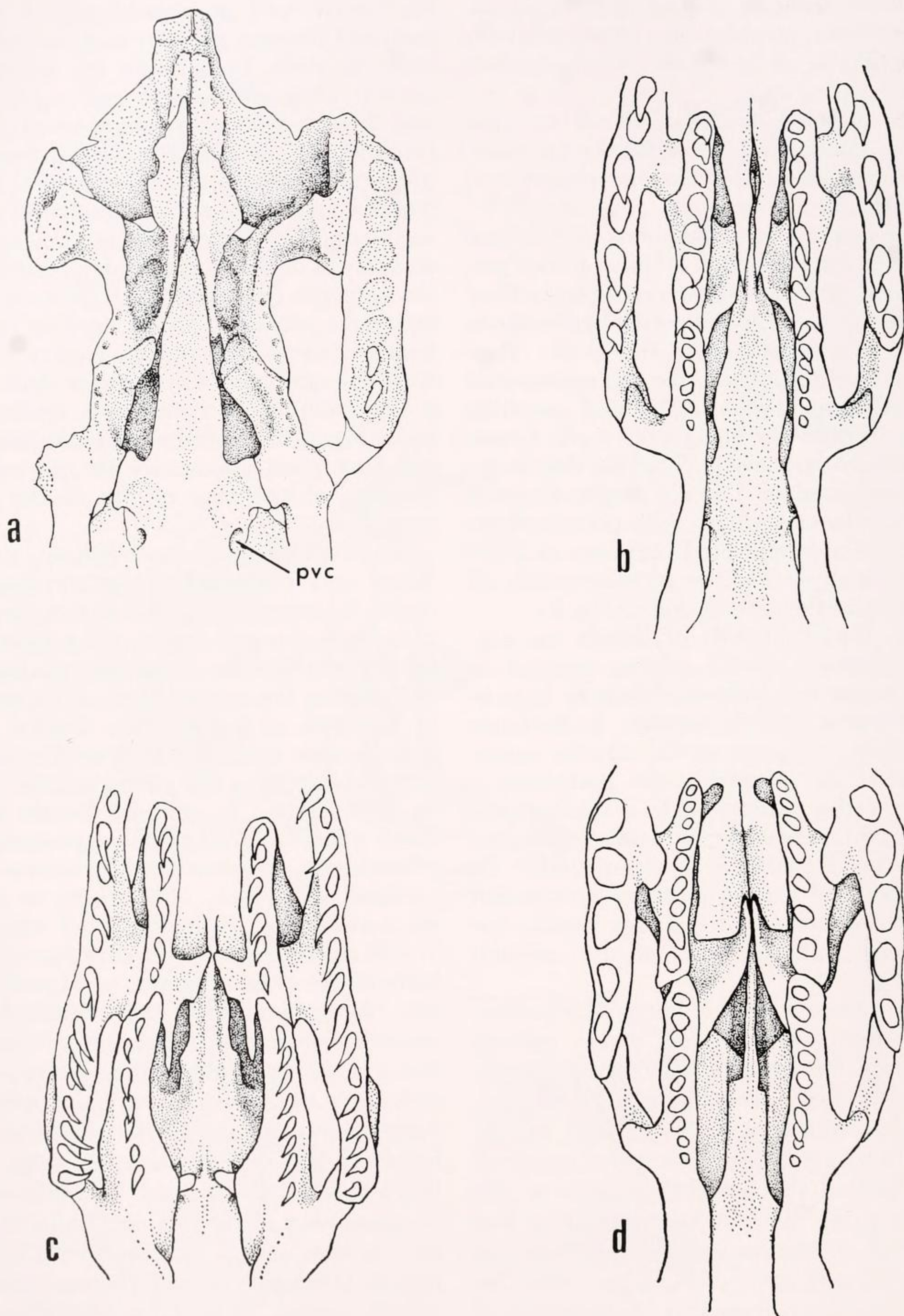


Figure 10. Palatal region of a, *Dinilysia patagonica*,  $\times 1.5$ , right maxilla and ectopterygoid removed; b, *Cylindrophis maculatus*, MCZ 34885,  $\times 4.5$ ; c, *Python molurus*, MCZ 4278,  $\times 1.5$ ; d, *Anilius scytale*, MCZ 17645,  $\times 4.5$ ; e, *Lanthanotus borne-*



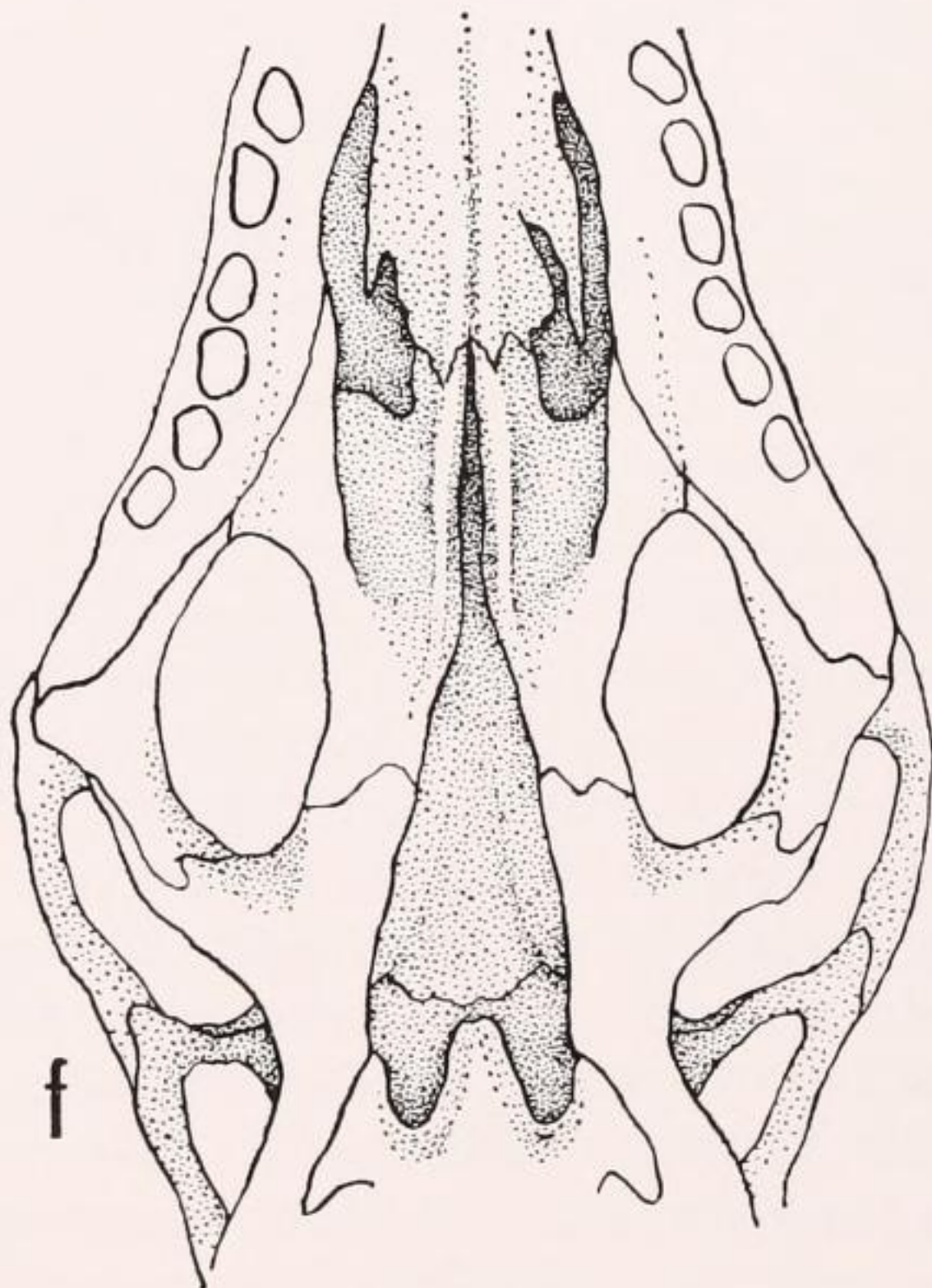
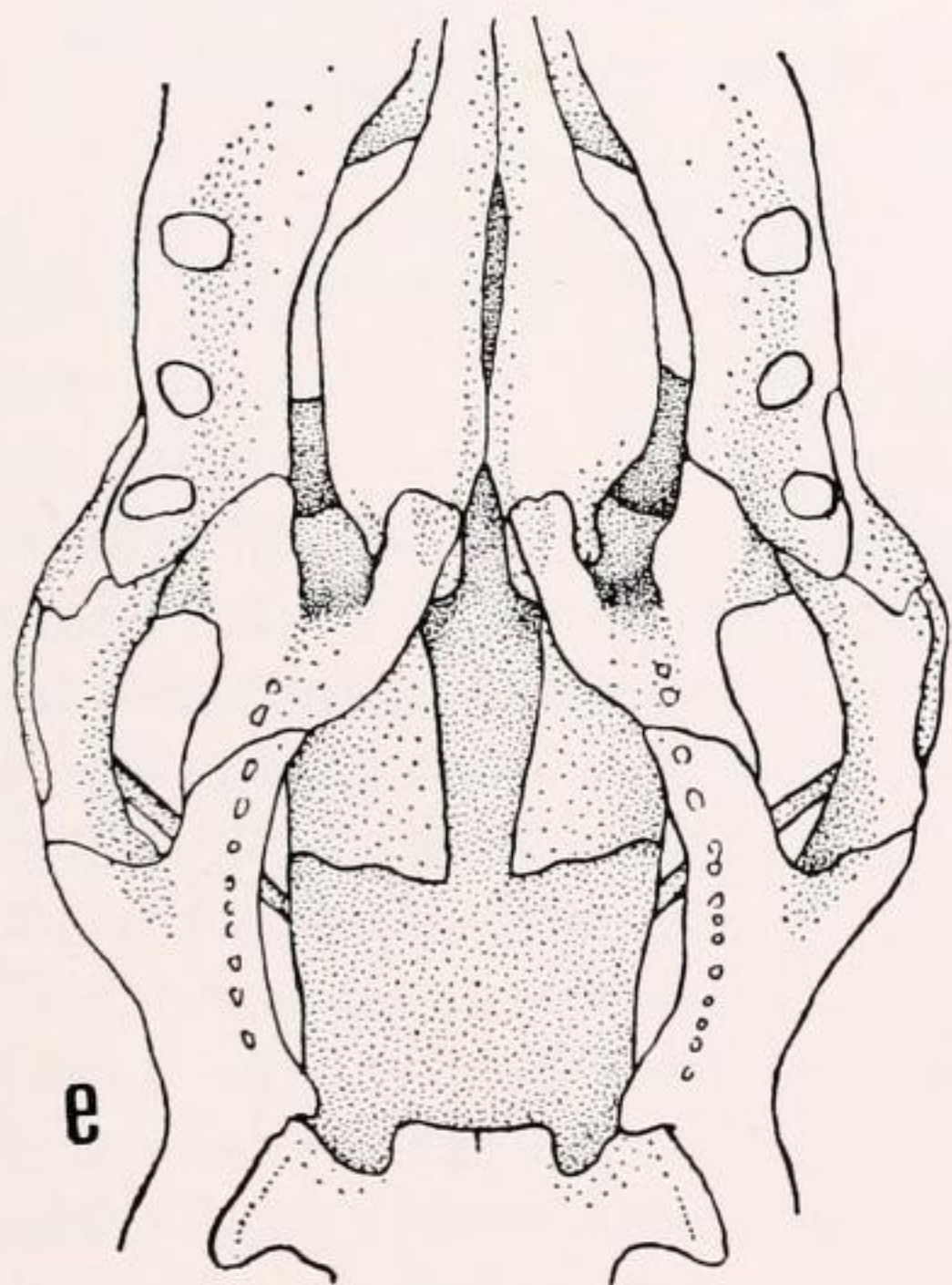
The exoccipitals of *Dinilysia* are in one regard strikingly snakelike: they meet on the midline and exclude the supraoccipital from the edge of the foramen magnum. The flat broad shelf that the exoccipitals form above the occipital condyle is, however, continued smoothly into the strong paroccipital process, which is carried backward with the supratemporal behind the occipital condyle, as noted above. This is in contrast to the condition in boids, in which the median exoccipital shelf ends abruptly in a notch separating the shelf from a rudimentary paroccipital process that at its extreme lateral projection does not extend further posteriorly than the extreme posterior level of the shelf and the condyle below it (*Python*), or does not extend further posteriorly than the level of the lateral margins of the foramen magnum (*Epicrates*).

In lizards the exoccipitals are always well lateral. They do not exclude the supraoccipital from the foramen magnum and may provide a very rudimentary lateral

shelf over the foramen magnum (*Ctenosaura*, *Mabuya*, *Lanthanotus*) or none at all (*Tupinambis*). In lizards the paroccipital process is more robust than in snakes but in no case does it project strongly backward carrying the supratemporal with it behind the level of the occipital condyle, as in *Dinilysia*.

As in both lizards and snakes, each exoccipital in *Dinilysia* forms a lateral third of the occipital condyle. As in *Python* and *Epicrates*, a lappet of exoccipital extends posteriorly underneath the moderate-sized posterior lacerate foramen, which faces directly posteriorly. In *Anilius* and *Cylindrophis* the posterior lacerate foramen faces more laterally than posteriorly and the bony process underneath is likewise posterolateral. Of the lizards compared, only *Lanthanotus* has a ledge beneath the posterior lacerate foramen and this forms a shallow trough leading posterolaterally (Fig. 12).

The exoccipital in *Dinilysia* participates in the dorsal margin of a large, widely-open fenestra rotunda that is directed ventro-



ensis, MCZ 8305,  $\times$  4.5; f, *Tupinambis nigropunctatus*, MCZ 109890,  $\times$  about 2.5. Abbreviations on p. 62. Semidiagrammatic.



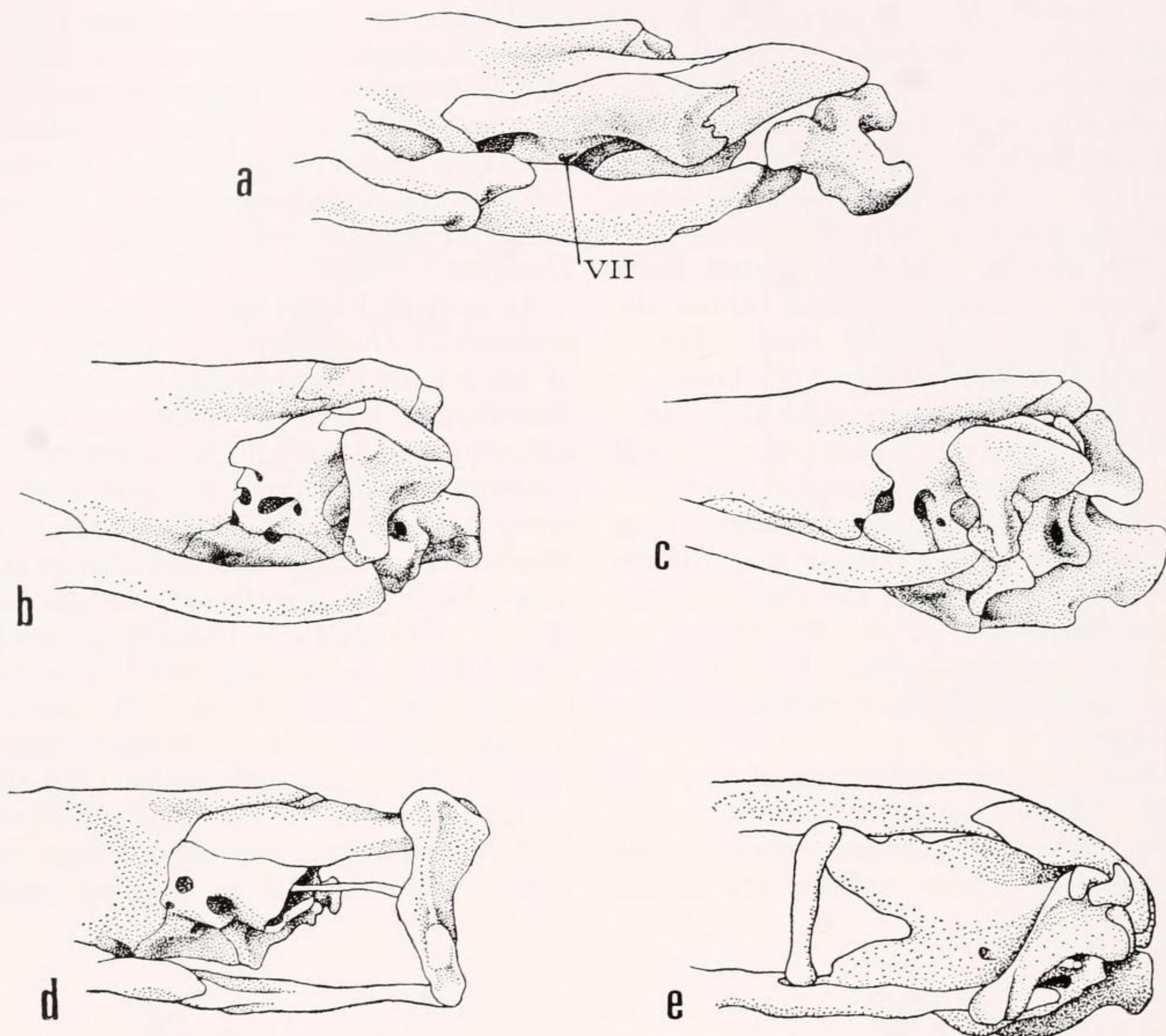


Figure 11. Lateral view of posterior skull region of a, *Dinilysia patagonica*,  $\times 1.5$ ; b, *Anilius scytale*, MCZ 17645,  $\times 4.5$ ; c, *Cylindrophis maculatus*, MCZ 34885,  $\times 4.5$ ; d, *Python molurus*, MCZ 4278,  $\times 1.5$ ; e, *Lanthanotus borneensis*, MCZ 8305,  $\times 4.5$ . Abbreviations on p. 62. Semidiagrammatic.

laterally. In snakes (*cf.* Baird, 1960), the fenestra ovalis (partly) and fenestra rotunda (wholly) are enclosed and almost walled off from view by a *crista circumfenestralis*, except in *Anilius* and *Cylindrophis*, in which the crista is not prominent and the stapedial footplate relatively large.

The crista circumfenestralis of snakes appears to correspond to the crista tuberalis of lizards (Säve-Söderbergh, 1947: 512; see also Oelrich, 1956: 1–17). The latter crista begins at the root of the paroccipital process and extends ventrally to the sphenoccipital tubercle (Oelrich), forming a posterior wall for the fenestra rotunda. The

snake condition can be derived from that of lizards by the growth forward and upward of the crista tuberalis until the fenestra rotunda is deeply concealed at the base of the crista, which then partly occludes the fenestra ovalis and encloses the stapedial footplate. The crista tuberalis in *Dinilysia* does not fully enclose the stapedial footplate and the fenestra rotunda is thus widely open as in *Anilius*, *Cylindrophis*, and lizards, but the fenestra rotunda is strikingly low on the occiput (below, instead of on the level of the condyle), a condition not found in the lizards and *a fortiori* not in snakes (Fig. 12).



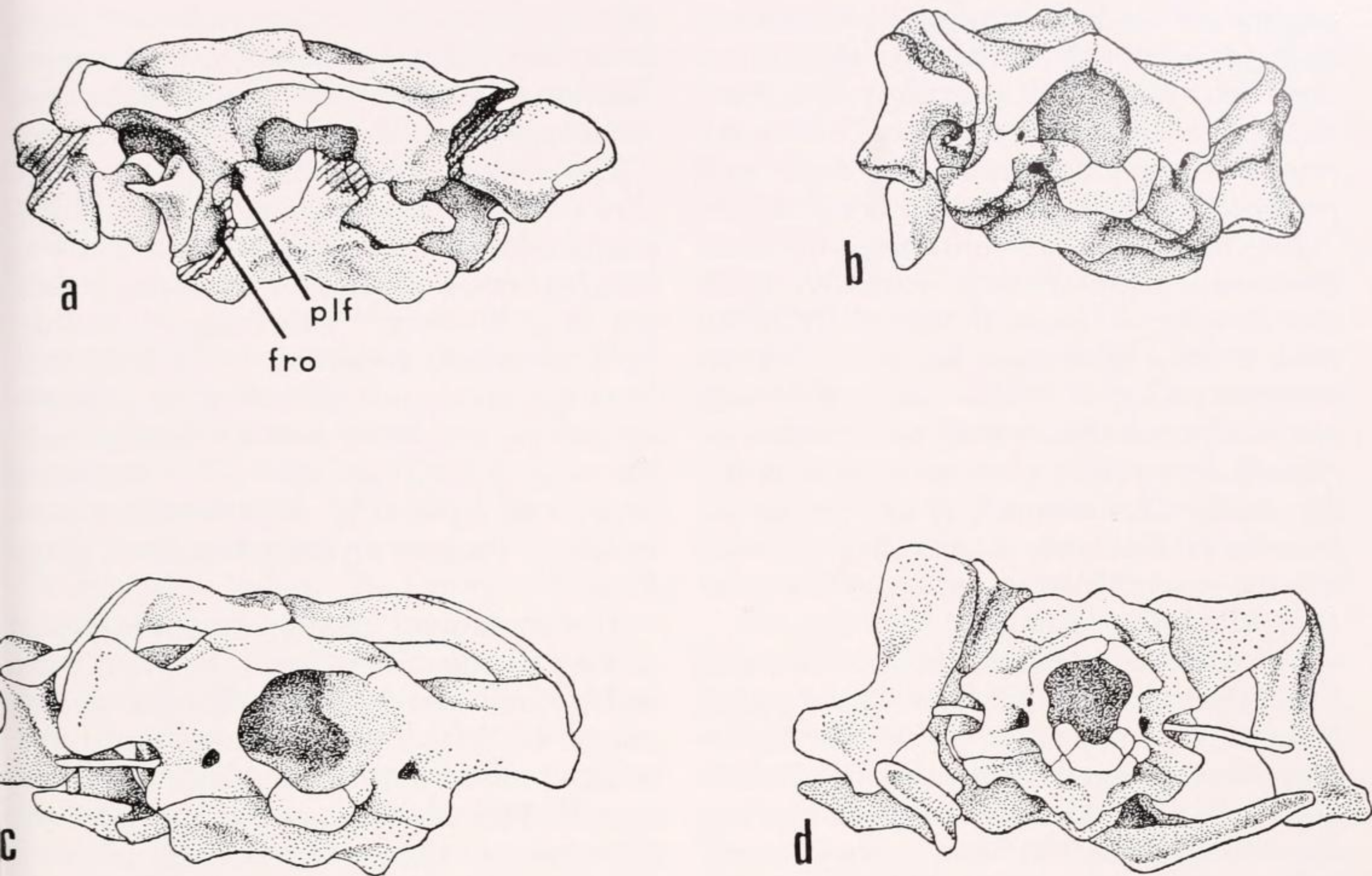


Figure 12. Oblique posterior view of occiput of a, *Dinilysia patagonica*,  $\times 1.5$ , hatched lines = breakage; b, *Anilius scytale*, MCZ 17645,  $\times 4.5$ ; c, *Lanthanotus borneensis*, MCZ 8305,  $\times 4.5$ ; d, *Python molurus*, MCZ 4278,  $\times 1.5$ . Right quadrates missing in a and c. Abbreviations on p. 62. Semidiagrammatic.

The absence of a *crista circumfenestralis* in *Dinilysia* is presumably a primitive condition and thus again is very plausible in a primitive snake. The low position of the fenestra rotunda, on the other hand, is clearly associated with the relatively enormous size of the stapedial footplate and may, like the latter, be special to *Dinilysia*.

The basioccipital in *Dinilysia*, as is usual in lizards and snakes, provides a median third of the occipital condyle. As in lizards, there are large, projecting sphenoccipital tubera forming between them a concave channel on the ventral surface of the basioccipital. The very large extent to which the basioccipital participates in the posterior as well as ventral wall of the fenestra rotunda is unusual. In snakes the crista circumfenestralis, which is wholly of exoccipital origin, widely separates the basioccipital from the fenestra rotunda. In

*Lanthanotus* the basioccipital forms only a small part of the lower edge of the fenestra, and this narrow participation seems the usual lizard condition. The extensive participation of the basioccipital in the wall of the fenestra rotunda in *Dinilysia* is closer to the lizard than the snake condition.

The laterally-placed basipterygoid processes of the basiparasphenoid have convex articulating surfaces that face more laterally than ventrally, and the axis of the processes is anteroposteriorly elongated. This situation is in contrast to the closely spaced, ventrally-facing, lateromedially-elongated structures seen in boids, and more closely resembles the lizard configuration. On the other hand, the processes in lizards have a narrower stem and an expanded distal articulation in contrast to the broad, even width of the processes in *Dinilysia*. In *Anilius* and *Cylindrophis* the basipterygoid articulations



are lateral and anteroposteriorly elongated, as in *Dinilysia*, but the articulations in these two snakes are scarcely raised from the body of the basiparasphenoid. *Here the resemblances are partly to lizards and partly to the Anilius-Cylindrophis complex.*

The wide bladelike cultriform process of *Dinilysia*, gently concave ventrally, bears a striking resemblance to that of *Cylindrophis*. Even *Anilius* has a narrower, if stout, cultriform process, while those of lizards are feeble and thin as well as narrow, frequently distorted and curved upward in the dry skull. *The strength of the cultriform process in Dinilysia is snakelike but the specific resemblance is, as stated, to that of Cylindrophis (Fig. 10).*

The prefrontals in *Dinilysia* have a wide, firm, interlocking contact with both frontals and maxillae, much as in *Anilius* and *Cylindrophis*. In contrast *Epicrates* and *Python* have only a loose contact between prefrontals and maxillae. In lizards there are, of course, firm sutures with both bones but the prefrontal has little lateral exposure, being covered by the ascending process of the maxillae. In *Dinilysia*, as in *Lanthanotus*, *Varanus* and snakes, the prefrontals intervene between the maxillae and nasals. *The resemblance again is snakelike but specifically to Cylindrophis and Anilius rather than boids (Fig. 8).*

The palatines of *Dinilysia* are strikingly un snakelike in the absence of anterior toothed projections. In this respect they are like the palatines of lizards. Like lizards they have strong, wide medial processes to the vomers. Unlike *Lanthanotus*, *Varanus*, or *Ctenosaura* but like *Tupinambis*, these medial processes are deeply excavated for the choanal passages. Rather similar medial processes of the palatines occur in *Anilius* and *Cylindrophis*, but, as in *Tupinambis*, these processes at their medial terminations lie between or dorsal to the posterior ends of the vomers; they do not broadly underlie them as in *Dinilysia* (Fig. 10). *Here Dinilysia resembles some*

*lizards and seems more primitive than boids, but shows both some special resemblances to Cylindrophis and Anilius and some unique features as well.*

The dorsal surface of the palatine encloses the posterior opening of the maxillopalatine foramen in *Dinilysia*, as in *Python*, *Lanthanotus*, *Cylindrophis*, and *Varanus* but not as in *Mabuya*, *Tupinambis* or *Anilius*. In *Ctenosaura*, according to Oelrich, this foramen may be wholly within the palatine or may be completed laterally by the maxilla or the jugal or both. *This character appears to have little value for the placement of Dinilysia or any other form (Fig. 8).*

The tooth row on the posterior prong of the palatine of *Dinilysia* is gently curved and is continued by a row likewise gently curved on the pterygoid. This is unlike the straight rows (and much larger teeth) of snakes. The curvature is like that of *Lanthanotus*, but the pterygoid teeth are very much smaller in the latter. Other lizards are even more dissimilar. It is important that on the pterygoid and palatine in *Dinilysia* teeth appear to be enlarging and approaching the snake condition, but clearly in both size and in the curvature of the row they are some steps behind the snake condition. The implication would appear to be, as with the absence of the anterior toothed prong of the palatine, that in *Dinilysia* the characteristic method of snake feeding was not yet perfected.

The posterior quadrate process of the pterygoid of *Dinilysia* is a vertical plate with a sharp ventral edge as in lizards and *Cylindrophis*, not as in boids and *Anilius*, which have the ventral edge rotated medially so that the process is no longer a vertical plate. *It is interesting here that there is a resemblance to Cylindrophis as well as to lizards.*

The maxilla of *Dinilysia* is snakelike in its long, gently tapering anterior end and slight ascending process meeting the prefrontal; its general shape is specifically like



that of *Cylindrophis*. The two teeth that are preserved are comparable to those of snakes in their sigmoid conical form and in their implantation. *The snake resemblance is clear, and within snakes the resemblance is to Cylindrophis.*

The ectopterygoid in *Dinilysia* is a short and simple bone joining the lateral process of the pterygoid and the maxilla. If any slender process extended along the medial surface of the maxilla to provide much of the dorsolateral rim of the suborbital fenestra, as in boids, especially *Python*, it has not been preserved. There may have been a short anteromedial process, as in *Cylindrophis* and *Anilius*. In *Tupinambis* such a process excludes the maxilla from the margin of the suborbital fenestra. In *Varanus* and *Lanthanotus* the maxilla is similarly excluded from the suborbital fenestra, but this seems to be a result of the shortening of the maxilla (see McDowell and Bogert, 1954) rather than of any long anterior prong of the ectopterygoid. In other lizards a short anteromedial process is present: this is presumably a primitive character. *The Dinilysia ectopterygoid seems unspecialized and, if taxonomically important, is so only in its differences from certain forms, not in its resemblances.*

The element we interpret as a jugal is absent in snakes and is quite unlike any lizard jugal in form and position. Its rounded shape, and its occurrence in a trough on the dorsal surface of the maxilla, are unique. In lizards the jugal is characteristically larger and has more extensive contacts, not only with the maxilla as in *Dinilysia*, but with the ectopterygoid (all examined cases) and with the postfrontal or postorbital and sometimes (*Ctenosaura*, *Mabuya*) the squamosal. According to Jollie (1960), reduction or loss of the jugal accompanies loss of orbital and temporal arches as in burrowing forms or geckos. In snakes, both arches are gone but, if our interpretation of *Dinilysia* (as influenced by the original British Museum cast) is

correct, the jugal did in this form make contact with the postorbital and completed the orbital arch. It is thus peculiar, primarily in its shortened and compact form, lack of contact with the ectopterygoid, and insertion in a groove of the maxilla. The presence of a jugal in *Dinilysia* is a primitive character and is thus expected in a very primitive snake. Its special features are, however, wholly surprising and require special functional study. At the moment, it would seem more probable that these special conditions are peculiar to a specialized side branch and are not part of the main line transition in the shift from lizard to snake adaptive zones.

The extensive attachment of quadrate to paroccipital process is unlike that of any boid. *Anilius* and *Cylindrophis* approach *Dinilysia* in degree of expansion of the head of the quadrate, and in the short and dorso-ventrally-compressed shape of the bone. The strongly curved tympanic process of the quadrate is unlike that of any other squamate, but is approached in *Anilius* and *Cylindrophis*. *The oval distal quadrate articulation of Dinilysia is a unique feature and does not resemble the irregular articulation surface of lizards, or the related, more saddle-shaped snake condition* (see below, articular, and Frazzetta, 1959, figs. 1, 2). Again functional considerations and interpretations are important, but there now seems to be no reason to postulate the transformation of the lizard joint into the *Dinilysia* condition, and then to return to the saddle-shaped joint of snakes as part of the lizard-snake transition; this condition seems again to emphasize that *Dinilysia* is a specialized side branch of the early booid radiation.

The dentary is like that of snakes in having a strong reentrant notch posteriorly for the surangular. *No specific resemblances to lizards occur, and the general aspect is more as in boids than as in Anilius or Cylindrophis. In this feature Dinilysia resembles the snakes.*



The splenial is small and meets the angular in a vertical suture. *The resemblance here is to snakes, although the vertical splenial-angular suture occurs also in Lanthanotus.*

*The angular, in its shape, position, and articulation with the splenial is like that of snakes.*

The compound bone is complex and its resemblances less clear-cut than those of the dentary. It resembles that of snakes in having a narrow surangular projection fitting loosely into the dentary notch, and in lacking (apparently) a retroarticular process. It is unique in having a small mandibular fossa that is dorsal and dorsolateral in orientation, cut off from medial exposure by a strong ridge on the prearticular area, and exposed laterally by the absence of such a ridge on the surangular region. The prearticular ridge occurs in snakes, but it is relatively larger in *Dinilysia* and more acutely angled. The lack of a strong surangular ridge for the coronoid differs from the condition in any snake or lizard. *In Dinilysia, while the relations with the dentary and the apparent absence of a retroarticular process constitute a general approach to snake conditions, the mandibular fossa and articular joint form one of the most peculiar and unique features of this animal.*

The coronoid is in great part missing, but it has left articulation surfaces on the compound bone that allow some interpretation of its extent. In its relationship to the mandibular fossa, it shares some of the unique features of the latter. Two distinct articular surfaces occur at the anterior end of the fossa, one on the medial (prearticular) ridge, the other a deep notch immediately lateral to the fossa. This suggests that the coronoid forked narrowly around the anterior border of the fossa. *While the forking is a lizard feature, the close apposition of the two parts of the fork is unique to Dinilysia.* The main body of the coronoid projected vertically, forming a coronoid

process of unknown extent, and then culminated anteriorly in a strong, flat ventromedial strap of bone that is all that remains today of the coronoid bone itself. *This preserved part of the coronoid is as in snakes and lizards generally, except in Anilius, in which the coronoid is almost vestigial.*

## SUMMARY

*Dinilysia* is conspicuously a mosaic of primitive and specialized characters. It has lizardlike features and also some startling and unique peculiarities, but it is also clearly a snake and it has some detailed resemblances to the modern primitive snakes *Anilius* and *Cylindrophis* that seem difficult to dismiss as convergent.

The snakelike features—in fact booid snakelike—are as follows: (1) absence of temporal arches; (2) probable loose connection of premaxilla and maxilla; (3) presence of a bony nasal septum; (4) ventral enclosure of the brain by both frontal and parietal downgrowths; (5) absence of a posttemporal foramen; (6) parietals level with oto-occipital complex; (7) descending process of parietal completing trigeminal foramen anteriorly; (8) supraoccipital participation in sagittal crest; (9) exoccipitals excluding supraoccipital from foramen magnum; (10) lappet of bone present behind posterior lacerate foramen; (11) prefrontals intervening between maxillae and nasals; (12) reduced ascending process of maxilla; (13) strong, movable reentrant articulation of dentary and surangular on lateral side of mandible.

Characters more specifically similar to the *Anilius-Cylindrophis* complex are: (1) relatively large size of stapes, especially the footplate; (2) the peculiar dorsal exposure of the prootic; (3) wide-bladed *Cylindrophis*-like cultriform process of the parasphenoid; (4) prefrontal having a firm union with maxilla and frontals; (5) posterior (quadrate) process of pterygoid a vertical plate as in *Cylindrophis*; (6) quad-



rate a dorsoventrally compressed bone with an expanded head.

These resemblances to booid snakes are numerous, clear, and detailed; we believe that they require *Dinilysia* to be placed in the booid complex close to *Anilius* and *Cylindrophis*.

Nevertheless, there are also a number of very primitive features, quite in keeping with the Cretaceous age of the fossil, that make *Dinilysia* more lizardlike than any other known snake. Generalized lizard features are: (1) frontal lappets under nasals, limiting nasofrontal mobility; (2) postfrontal and postorbital both present; (3) trigeminal foramen single; (4) exposure of the stapedial footplate (= absence of a crista circumfenestralis); (5) large, laterally-projecting convex basipterygoid processes; (6) palatines with deep choanal grooves and without anterior toothed projections; (7) posterior processes of pterygoids vertical plates, concave medially; (8) jugal present (but see below); (9) a single opening in the anterior braincase for olfactory tracts.

These primitive lizardlike features are again numerous enough and impressive enough that, if *Dinilysia* is related to boids and aniliids, it must belong rather far down in the ancestry of the booid complex.

In its lizardlike aspects, it must be emphasized, *Dinilysia* does not show special affinity to any group of lizards. The lizard characters cited above are generalized and are primitive for squamates; the more detailed resemblances seem casual and random, inviting the suspicion that they are merely convergent. There are some specific resemblances to *Lanthanotus* or *Varanus*: (1) a somewhat *Lanthanotus*-like crista tuberalis behind the posterior lacerate foramen; (2) a *Lanthanotus*-like curvature of the anterior (palatine) processes of the pterygoids; (3) prefrontals that intervene between maxillae and nasals. But these are balanced by the ways in which *Dinilysia* appears to be more primitive than *Lantha-*

*notus* or *Varanus*; e.g. the deep choanal impressions on the palatines and participation of the maxilla in the suborbital fenestra (ways in which primitive snakes generally seem more primitive than *Lanthanotus*). There is neither special confirmation nor denial in our study for an anguimorph origin of snakes (cf. McDowell and Bogert, 1954). However, it is very possible that the expectation that *Dinilysia* will shed much light on snake origins is erroneous. It is perhaps already too close to extant groups of snakes to be helpful.

Yet, snake though it is and close though it seems to *Anilius* and *Cylindrophis*, there are aspects in which *Dinilysia* has provided wholly astonishing features. The strongly posterolaterally-produced paroccipital and supratemporal processes have been interpreted as an intermediate between lizard and snake conditions. If it is really an intermediate, it is one quite outside expectation. Beyond this, however, there are other aspects of *Dinilysia* that are special and unique: (1) the vomers *underlain* by anterior portions of the palatines; (2) the extraordinarily robust nasal septum; (3) the low position of the fenestra rotunda on the occiput; (4) the peculiar shape of the quadrate, as well as the oval quadrate-articular joint; (5) the almost incredible element that we call the jugal, and (6) the large supratemporal applied closely to the skull. These are so special, and are so far from being in any simple sense intermediate between lizard and snake, that *Dinilysia* seems likely to be off on its own side branch and away from the main line of the ancestry of modernized snakes. Related to booids it seems to be, and among these is closest to *Anilius* and *Cylindrophis*, yet it appears also to have been a very early and eccentrically divergent offshoot of this stock. Taxonomic expression of these conclusions need involve no change from that already given by Romer (1956: 570), who raised *Dinilysia* to family status and placed it at the base of the superfamily Booidea.



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## ABBREVIATIONS

- an = angular  
 art = articular  
 avc = anterior opening of vidian canal  
 bo = basioccipital  
 bp = basipterygoid process  
 bs = basisphenoid  
 ca = coronoid articulation surface  
 co = coronoid  
 cp = compound bone  
 de = dentary  
 ec = ectopterygoid  
 eo = exoccipital  
 f = unknown foramen  
 fo = fenestra ovalis  
 fp = foramen for palatine artery  
 fr = frontal  
 fro = fenestra rotunda  
 ju = jugal  
 lf = lacrimal foramen  
 mp = maxillopalatine foramen  
 mx = maxilla  
 na = nasal  
 oc = orbitonasal canal  
 of = optic fenestra  
 pa = parietal  
 pal = palatine  
 pf = postfrontal  
 plf = posterior lacerate foramen  
 po = postorbital  
 pr = prootic  
 pra = prearticular  
 prf = prefrontal  
 ps = parasphenoid  
 pt = pterygoid  
 pvc = posterior opening of vidian canal  
 qu = quadrate  
 s = stapes  
 sm = septomaxilla  
 so = supraoccipital  
 sot = spheno-occipital tuber  
 sp = splenial  
 st = supratemporal  
 sur = surangular  
 t = trabecular pit and groove  
 vo = vomer  
 V = trigeminal foramen  
 VII = facial foramen



Plate 1. *Dinilysia patagonica*; original plate from Woodward (1901); 1, dorsal and left lateral views of skull; 1b, ventral view of left maxilla showing tooth sockets; 1c, lateral view of left quadrate; 2, a portion of the vertebral column, dorsal view; all  $\times 1$ . Abbreviations used on this original plate may not coincide with those on p. 62.



P. Z. S. 1901, vol. I, Pl. XX

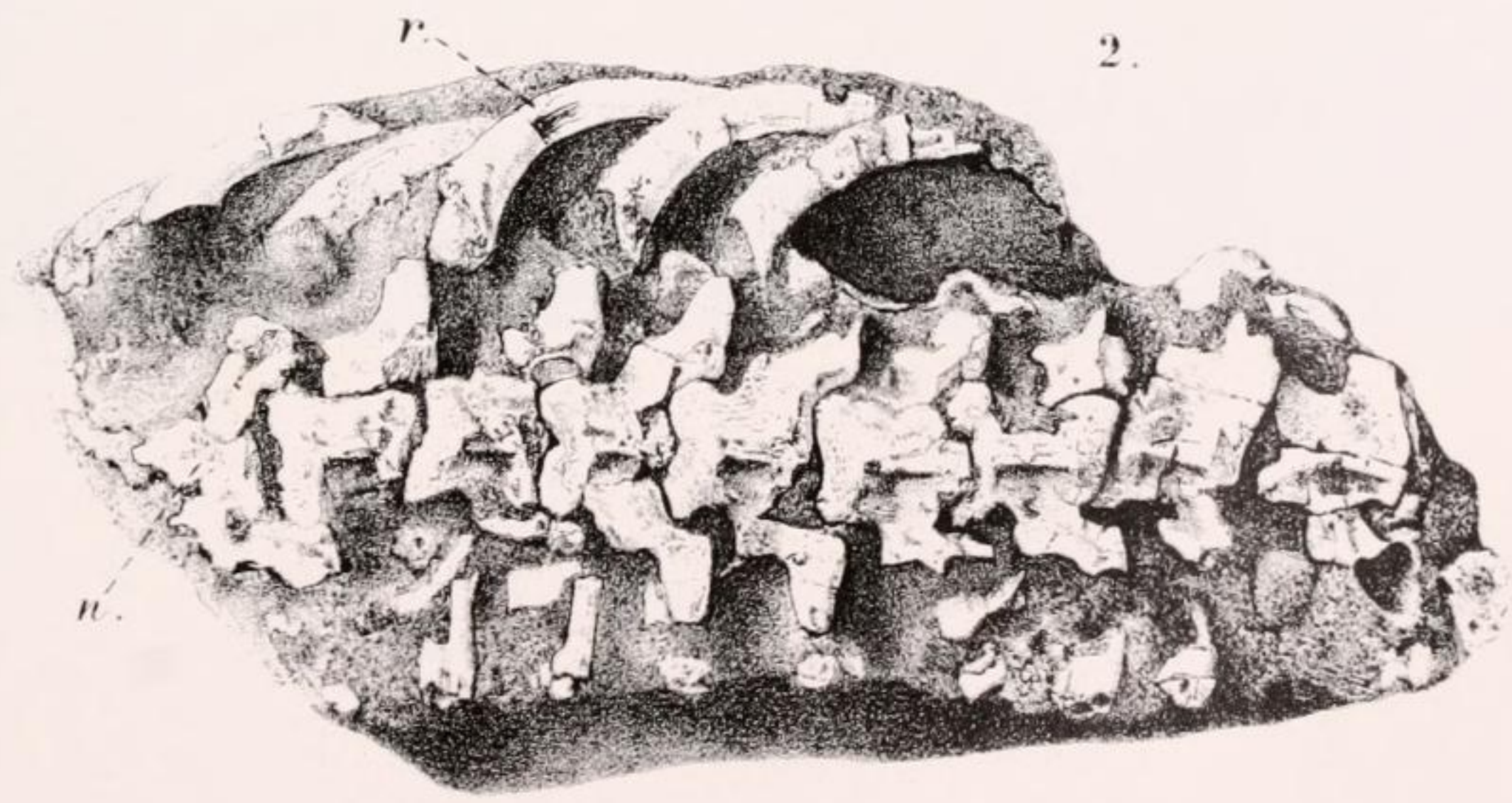
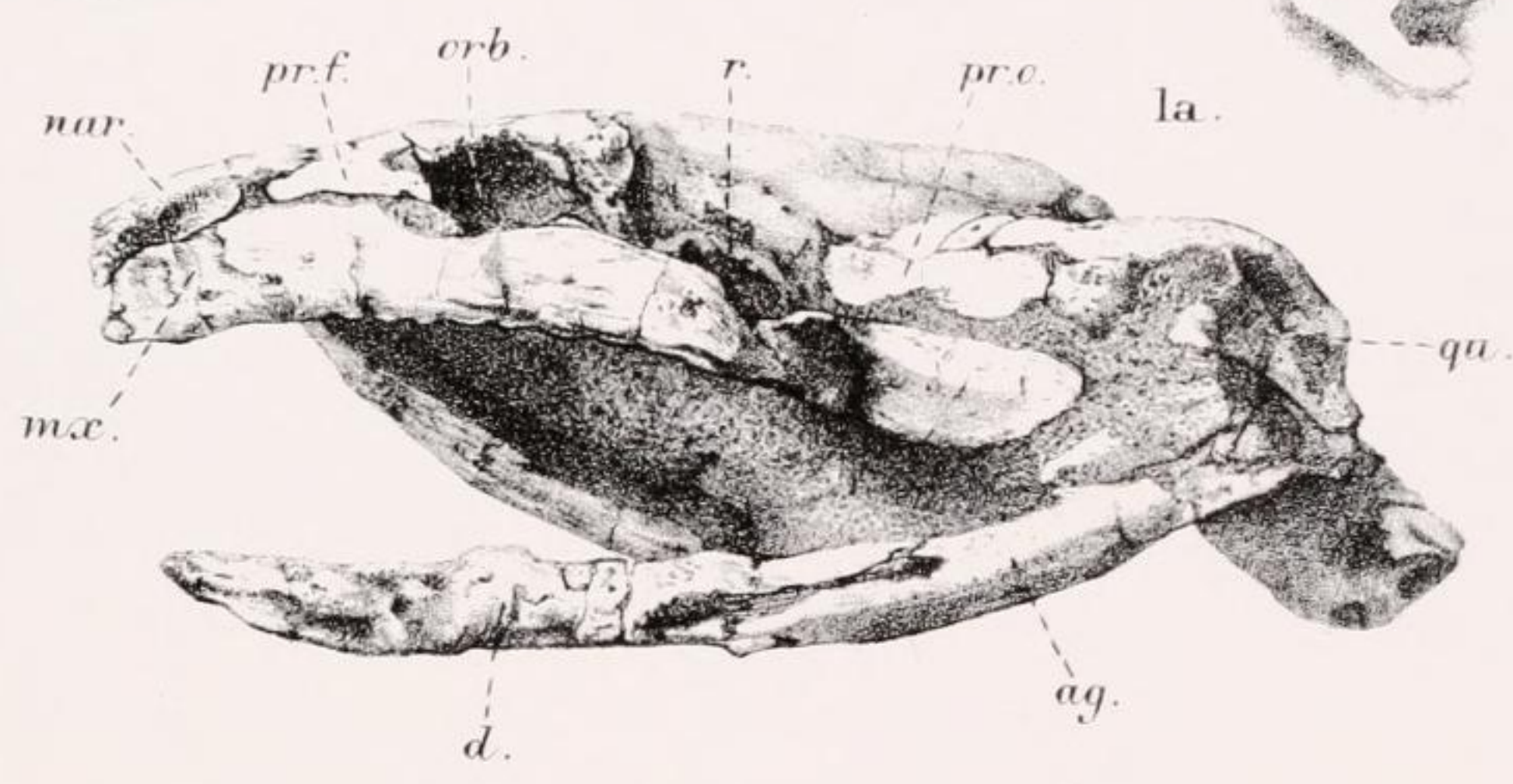
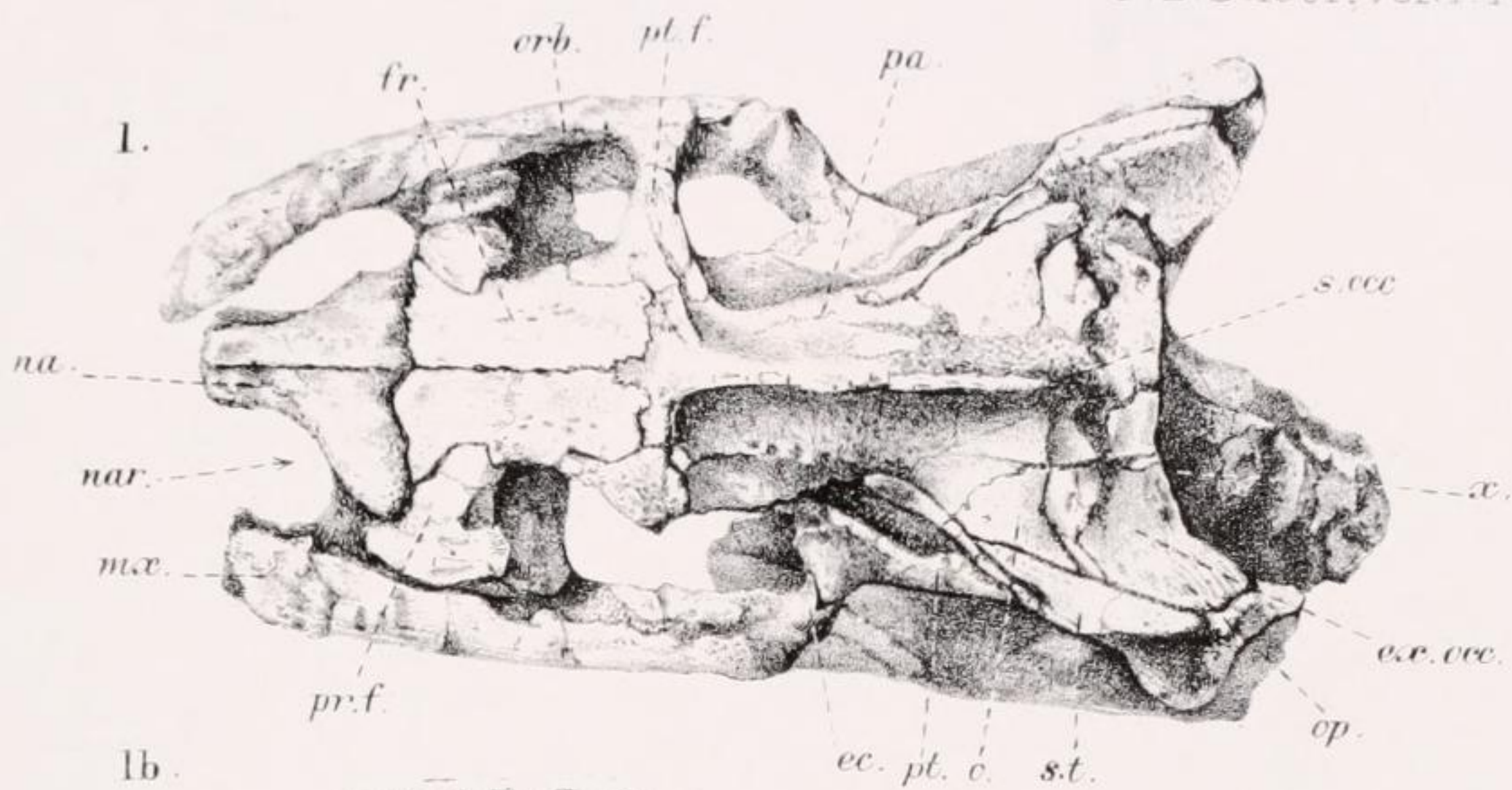




Plate 2. *Dinilysia patagonica*; right lateral and ventral views of copy of British Museum (Natural History) cast of original specimen of *Dinilysia*. Note complete postorbital arch and complete maxilla.  $\times 1.5$ .



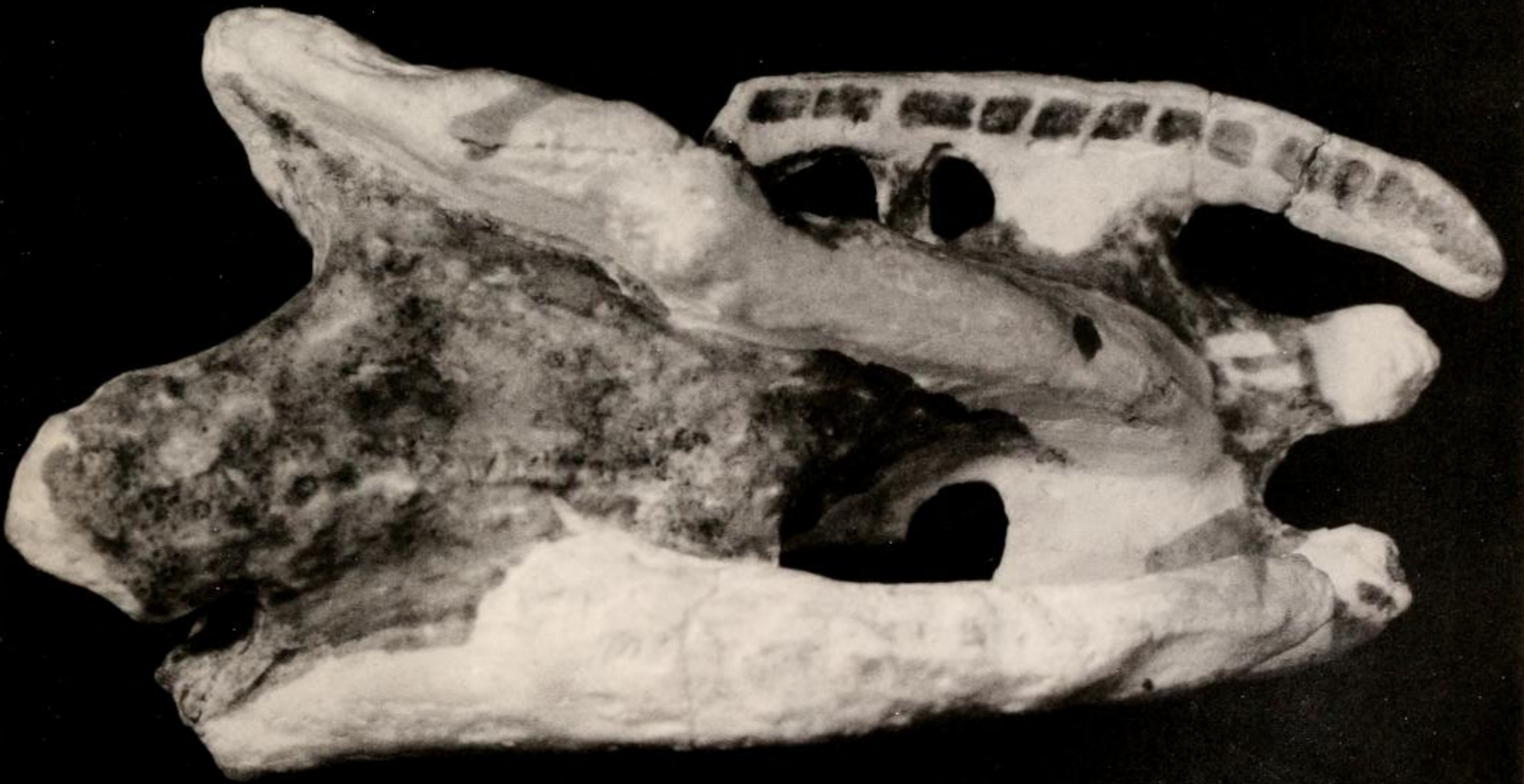




Plate 3. *Dinilysia patagonica*; dorsal view of skull.



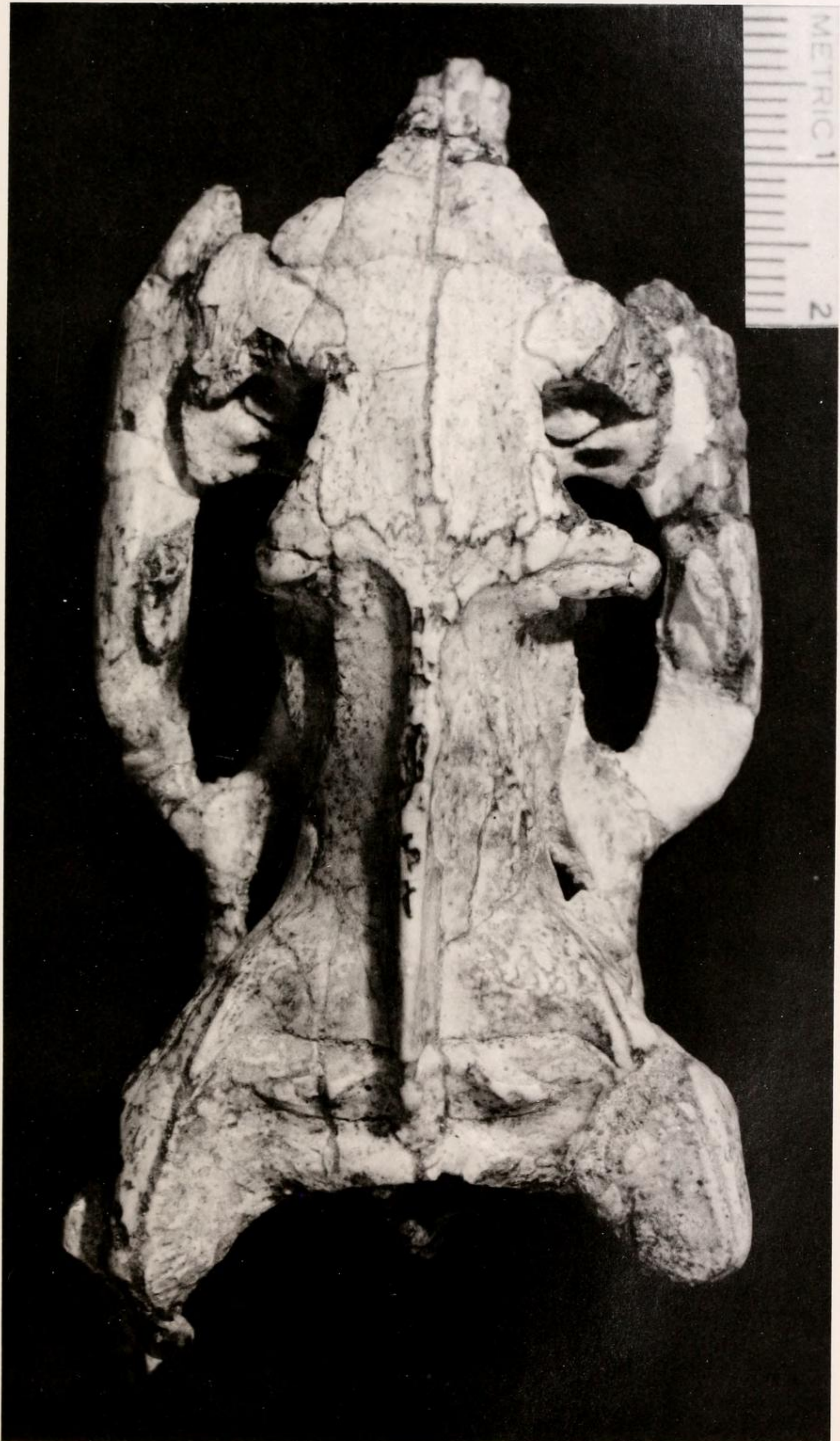
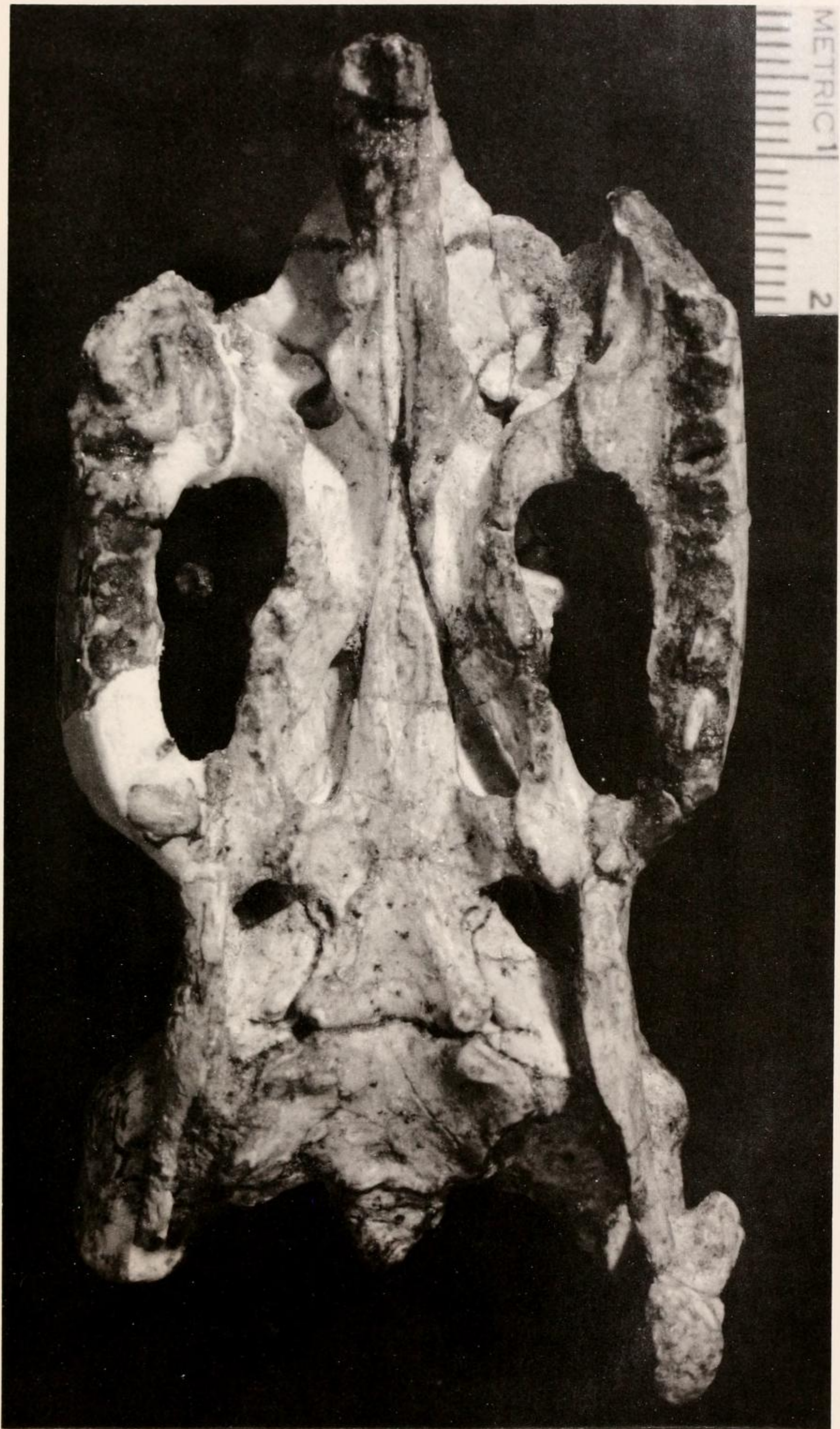




Plate 4. *Dinilysia patagonica*; ventral view of skull.







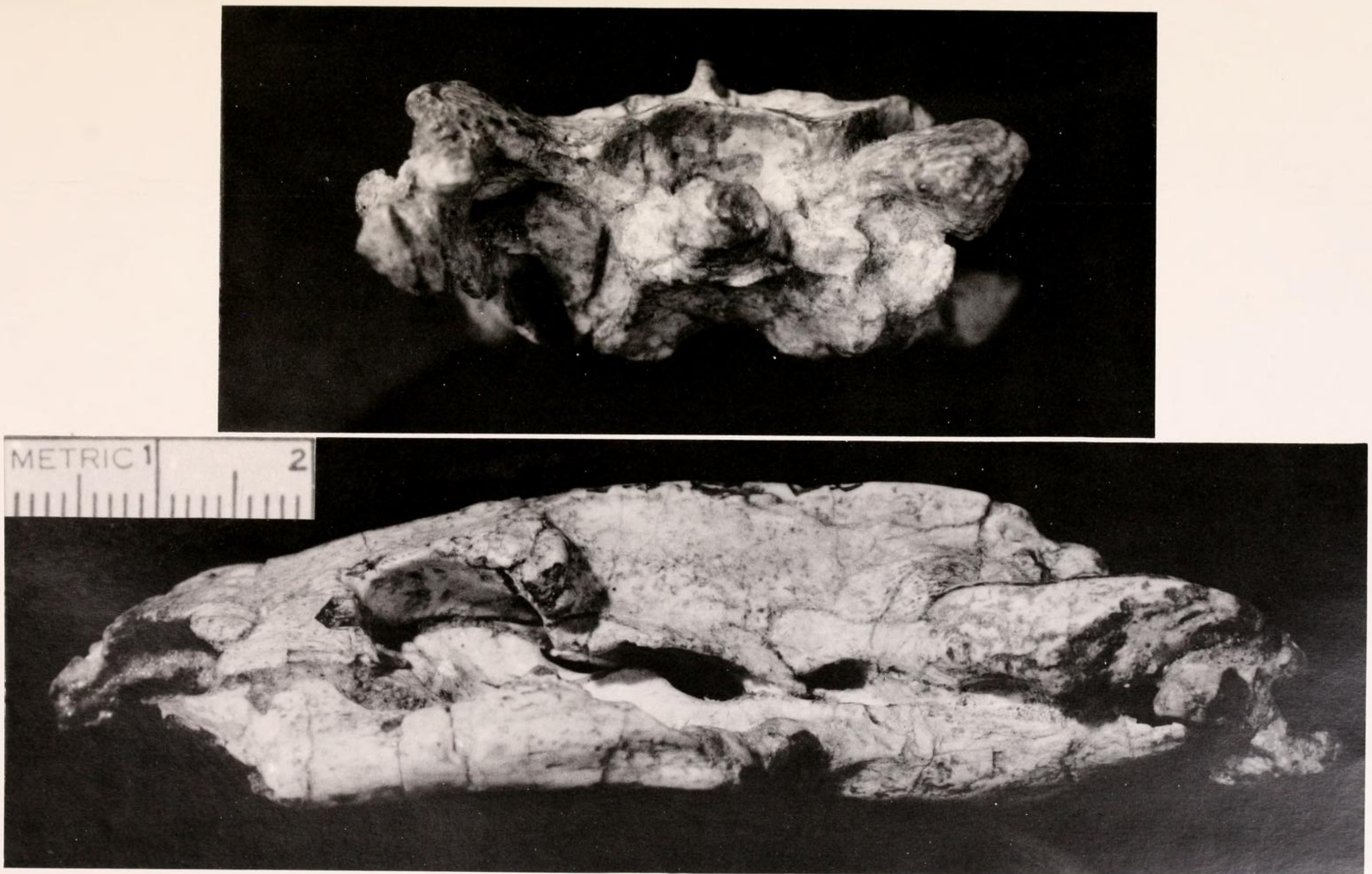


Plate 5. *Dinilysia patagonica*; left lateral and occipital views of skull.