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A Huge Thecodont Skull From The Triassic of Brazil

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SINOPSE

Este trabalho trata da descrição geral de um grande crânio do tecodonte *Prestosuchus chiniquensis*, coletado na Sanga Pascual, perto de Candelária, no Estado do Rio Grande do Sul, sul do Brasil.

As afinidades desta forma são discutidas, indicando sua posição intermediária entre *Luperosuchus* e *Saurosuchus*. Suas implicações bioestratigráficas e evolutivas são também comentadas, no contexto do Triássico da América do Sul.

ABSTRACT

This paper deals with the general description of a huge skull of the thecodont *Prestosuchus chiniquensis*, collected at Sanga Pascual, near Candelária, Rio Grande do Sul, in southern Brazil.

The affinities of this form are discussed, indicating that it occupies an intermediate position between *Luperosuchus* and *Saurosuchus*.

Biostratigraphical and evolutionary implications of the new find are also commented on.

INTRODUCTION

As it is well known, most of the information concerning the thecodont reptiles of the Santa Maria Beds (Middle to Upper Triassic) is restricted to Huene's descriptions (1935-1942) of the material gathered during his expedition of 1928 to southern Brazil.

It might be also noted that bad preservation and the fragmentary state of the material have not helped very much to establish securely the relationships of the genera *Rauisuchus*, *Prestosuchus*, *Rhadinosuchus*, *Hoplitosuchus* and *Procerosuchus*.

Starting in 1969, the Institute of Geociences has made several collecting trips to the Triassic of southern Brazil which have resulted in the finding of additional and better preserved thecodont remains. Outstanding among them is a huge skull, totally preserved, with the lower jaw attached. Several vertebrae are loosely associated

with the skull. No appendicular elements were found. This material, determined as *Prestosuchus chiniquensis*, was collected at Sanga Pascual, near Pinheiros, Candelária County, in 1972.

Only a brief and generalized description is provided in this paper, as a full account of the entire cranial and post-cranial osteology of this form is being prepared for future publication.

TAXONOMY AND MORPHOLOGY

CLASS REPTILIA
 SUB-CLASS ARCHOSAURIA
 ORDER THECODONTIA
 SUB-ORDER PROTEROSUCHIA
 FAMILY RAUISUCHIDAE

Genus *PRESTOSUCHUS* Huene 1942.

Type-species: two species, *P. chiniquensis* and *P. lorricatus*, were described by Huene in 1942, but no type-species was then designated. *Prestosuchus chiniquensis* is here proposed as such.

Horizon and Locality: Rosario do Sul-Santa Maria Beds, Therapsida Assemblage-zone, Chañarensis age; collected in Sangas of Candelária and São Pedro Counties, Rio Grande do Sul State, Brazil.

Partial generic diagnosis: thecodont with a large skull, reaching a length of 88.0 cm (including the associated lower jaw), strongly built, deep and narrow. External naris irregularly triangular. Premaxilla with a quadrangular main body and an ascending posterior process separating the maxilla from the border of external naris. Four premaxillary teeth in each ramus, exhibiting serrations on the anterior and posterior edges. Antorbital fenestra of moderate size, lying in the center of a basin-like area. No

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accessory antorbital fenestra. Orbits keyhole-shaped and posteriorly inclined, as in *Saurosuchus*. Concave posterior aspect of quadrate and posterior spur of squamosal delimiting an otic notch. Skull roof elevated in the region of nasals, as in *Luperosuchus*. No parietal foramen. Interparietal small and conical, with no dorsal expression. Pterygoids meeting in midline. No teeth on pterygoid flanges.

Prestosuchus chiniquensis Huene 1942

(Fig. 1)

Material: a complete skull, with attached lower jaw, plus several vertebrae, deposited at the Department of Paleontology and Stratigraphy, Institute of Geosciences, Federal University of Rio Grande do Sul, under catalogue number PV 0156 T(G).

Horizon and Locality: Rosario do Sul-Santa Maria beds, Therapsid Assemblage-zone, Chañarensis age, collected in Sanga Pascual, near Candelária City, Rio Grande do Sul State.

Diagnosis: *Prestosuchus chiniquensis* and *Prestosuchus loricatus* may in fact constitute a single species. Thus, the specific diagnosis will be postponed until more decisive evidences on this problem are available.

DESCRIPTION

The skull of *Prestosuchus chiniquensis* is strongly built, deep and narrow.

In dorsal view it has an elongated triangular shape, with a long preorbital region. The external naris are irregularly, triangular the apex pointing posteriorly. The antorbital fenestra is of moderate size. The orbits are typically keyhole-shaped, with the longer axis inclined. The supratemporal fenestrae are mainly dorsal, but partially visible in lateral view. Infratemporal fenestrae are large, with subtrapezoidal outlines. There is no accessory antorbital fenestra between premaxilla and maxilla.

The right half of the skull suffered compression and distortion, causing the displacement of the right suspensorium towards the sagittal plane and also the sliding of the right nasal component over the left one.

No unequivocal sculpturing was detected on the skull surface, but this may be due to conditions of fossilization.

The skull and associated lower jaw present the following maximum dimensions:

length - from anterior border of premaxilla to tip of retroarticular process of lower jaw 88.0 cm.

width - taken across the skull, at the ventrolateral border of quadratojugals, but certainly altered by compression 36.0 cm.

height - from parietal on elevated medial border of supratemporal fenestra to ventral border of lower jaw 42.0 cm.

The premaxilla has a quadrangular main body, from which two dorsal processes arise. As in other rauisuchids, the posterodorsal process precludes the entry of the maxilla into the nasal border. There are four premaxillary teeth in each ramus, the longest one (the 3rd of the left premaxilla) reaching 7.40 cm. Premaxillary teeth are less laterally compressed than the ones in the maxilla and exhibit serrations on the anterior and posterior borders.

The maxillary segment below the antorbital fenestra is deep and the bone shows a moderate bulge in the area immediately posterior to the suture with the premaxilla. In the laterodorsal expression, the maxilla slants posteriorad to meet the nasal, prefrontal and lacrimal above the antorbital fenestra.

This opening lies at the center of a subtriangular basin, whose outermost limit is a line which starts from below the orbit and follows the general contour of the fenestra, descending almost vertically on the lacrimal as a median ridge, to reach its starting point. Due to the existence of this basin, the lateral edge of the skull table projects as a ridge along the contact area of nasal, prefrontal and lacrimal bones.

The are 11-12 laterally compressed and posteriorly curved teeth in the maxilla. The third tooth on the left ramus at 10.0 cm is the longest. Serrations line two thirds of the anterior border, disappearing in the proximal third. Posterior serrations extend up to near the alveolar border, at least in some of the teeth.

Jugal and postorbital bones agree well with the general structure of these bones in the other rauisuchids.

At the posterodorsal angle of the skull, the lower edge of squamosal meets the upper end of the quadrate and sends a short spur backward. The quadrate is a tall column (22.0 cm), expanded at both ends and presents a concave posterior aspect. Its articular lower end, observed from the occiput, exhibits two condyles, the inner being the larger. Above its median constricted zone, it expands again to form a pterygoid wing medially and a lateral wing, which appears as an elevated area in the lateral expression of the bone, immediately posterior to the suture with the quadratojugal. The concave posterior surface of the quadrate and the squamosal spur define the otic notch. The quadratojugal does not contribute to the articular facet for the articular bone.

The nasal bones are very long (41.0 cm) and show narrow anterior ends (2.0 cm) by means of which they fit into the ascending anterior processes of the premaxillae. Nasals and frontals suture along a zig-zag line where the former reach their maximum width (8.0 cm).

As Romer (1971) has noticed for *Luperosuchus fractus*, the nasals of *Prestosuchus chiniquensis* also rise upward above the general line of the skull roof, but not so markedly as in the Argentinian form.

Both the frontals and the anterior extensions of the parietals have their median surfaces bounded on either side by elevated areas, which become conspicuous ridges at the anteromedial angle of the supratemporal fenestrae. No parietal foramen is found.

The occipital surface is almost perpendicular. The large occipital condyle is in great part formed by the basioccipital. It lies 15.0 cm ahead of the suspensorium region. The paroccipital processes are long and distally expanded in the vertical plane. They are closely bounded to the occipital expression of the parietals with no post-temporal fenestra visible along the contact area. The sutural limits of the exoccipitals can not be clearly observed. The supraoccipital is well developed and has a triangular outline. At the apex of the triangle, a small conical interparietal can be seen but this bone does not extend onto the dorsal surface of the skull.

The pterygoids meet in the midline, with no interpterygoid vacuity between them. Teeth are absent from the pterygoid flanges. More preparation is needed in the zone of the basispterygoid processes, but they do not seem to be fused to the pterygoids.

The lower jaw is firmly attached to the skull and this precluded total preparation of the palatal area. The symphyseal area is 15.0 cm long. The height of the jaw, taken at its posterior half, reaches a maximum of 14.5 cm. Clearly distinct sutures separate the dentary, angular and surangular bones. The mandibular fenestra is large.

DISCUSSION

As far as it can be judged from Huene's descriptions and materials, *Prestosuchus chiniquensis* and *P. loricatus* may in fact constitute only one species. The scarce and ill-preserved cranial type material of *Prestosuchus chiniquensis* does not allow a secure comparison with the above described specimen from Sanga Pascual at the specific level. Nevertheless, the lower jaw and particularly the premaxilla are very similar, in spite of the considerable difference in size.

Postcranials might have helped the accomplishment of better comparative results, but most of the critical elements are lacking. This is particularly true for the appendicular skeleton. All this facts considered, it appears as reasonable the determination of the present material as *P. chiniquensis*. We should not add any new taxon to the Brazilian thecodonts, until all the new materials can be studied and a review of the already gathered data is accomplished.

RELATIONSHIPS TO OTHER SOUTH AMERICAN RAUISUCHIDS

1) *Rauisuchus*, *Rhadinosuchus*, *Procerosuchus* and *Hoplitosuchus*

Among the *Rauisuchus* cranial pieces described by Huene, the premaxilla stands as the most useful for establishing differential criteria in reference to *Prestosuchus chiniquensis*.

This bone in *Rauisuchus* is sculptured and lightly built. An ascending posterior process is also present, but the main body has a rectangular shape, so that the lower narial border is nearer to the tooth line. On the contrary, the premaxilla of *Prestosuchus chiniquensis* has no visible sculpturing and its main body is quadrangular, causing the narial border to lie well above the tooth line. The post frontal of *Rauisuchus* has an elongated

rectangular outline when seen from above; in *P. chiniquensis* it is triangular in dorsal view. However, *Rauisuchus* has the same raised nasals, as found in *Prestosuchus* and *Luperosuchus*. This feature could be added to the ones listed by Sill (1974) as demanding the assignment of *Rauisuchus* to the same family of *Prestosuchus*.

In addition to the mentioned differences, the present stratigraphic evidence indicates that *Rauisuchus* belongs to an upper horizon (see below).

A very great size difference separates *Prestosuchus chiniquensis* from *Procerosuchus* and *Rhadinosuchus*. The latter genus was included by Romer (1972) in the Proterosuchidae. Hoffstetter (1955) had considered it as a senior synonym of *Cerritosaurus*, also from the upper levels of the Santa Maria beds. A more extended discussion on the subject is offered by Reig (1970). *Prestosuchus* and *Rhadinosuchus* are obviously unrelated forms, both in time and morphology. *Procerosuchus* belongs to the same assemblage-zone of *Prestosuchus*, but is very much smaller; the similarities pointed out by Huene do not seem sufficiently diagnostic.

Hoplitosuchus also exhibits large proportions but, as Bonaparte has suggested (1970), those could well be the result of post-mortem alteration and microscopic fragmentation. Again, a chronological difference occurs here, *Prestosuchus* being found in a lower stratigraphical level.

2) *Luperosuchus* and *Saurosuchus*

Luperosuchus fractus Romer 1971 and *Saurosuchus galilei* Reig 1959, respectively from the Chañares and Ischigualasto Formations in Argentina, are close relatives of *Prestosuchus chiniquensis*. The main observed differences and affinities between the three genera are plotted in Table 1. The below listed characteristics seem to indicate a placement of *Prestosuchus chiniquensis* as an intermediate form between *Luperosuchus* and *Saurosuchus*. Such position had already been pointed out by Sill (*op. cit.*) in his phylogenetic scheme (p. 353).

The similarities to *Luperosuchus* lie principally in the preorbital region, the nasals being raised in both forms. We could probably expect that, in case of better preservation, the *Luperosuchus* skull would have still more affinities to *Prestosuchus chiniquensis* in the preorbital region. For instance, the premaxillary segment below the

antorbital fenestra might present a wider area. In addition, both genera do not present any marked sculpturing on the skull surface.

On the other hand, the orbital and postorbital architecture of the skulls of *P. chiniquensis* and *Saurosuchus galilei* are closely similar. Both have an inclined, keyhole-shaped orbit and a subtrapezoidal infratemporal fenestra. The Brazilian form presents a small interparietal, a feature perhaps true for *Saurosuchus* and *Luperosuchus*, although this area is not preserved in the Argentinian genera.

Taking into consideration the sum of its morphological characteristics, *Prestosuchus chiniquensis* should be taken as more advanced, though not very markedly, than *Luperosuchus fractus*. The advanced characteristics are to be seen particularly in the orbital and postorbital regions.

Its relationships to *Saurosuchus* are very close. The only major structural difference between the two forms seems to be the complete joining of the pterygoids in *Prestosuchus*. Sill (*op. cit.*) considered the only apparent difference to be the more heavily constructed and less gracile femur of *Prestosuchus*. This same difference in bulk can now be demonstrated when the respective skulls are compared. In *Saurosuchus* all the skull openings are larger, producing a lighter architecture, whereas the larger and more massive *Prestosuchus* skull has proportionately smaller openings.

For the present, the general morphological characteristics of *Saurosuchus*, as far as the skull is concerned, point towards a more advanced evolutionary position for the Argentinian form over *Prestosuchus*.

This seems to be confirmed by their relative stratigraphic position as well.

BIOSTRATIGRAPHY AND GEOLOGICAL AGE

Present knowledge concerning the Triassic continental sediments of Rio Grande do Sul State presents several as yet unresolved problems. Among these are the relationships of the Santa Maria Formation, as formally proposed by Bortoluzzi (1974), to other Triassic sediments designated as Rosario do Sul Formation by Gamermann (1973).

According to Bortoluzzi, the Santa Maria beds are an independent geologic unit whereas Gamermann considers them as a lacustrine facies of his inclusive Rosario do Sul Formation. This formation

TABLE I

Main comparative cranial features of *Luperosuchus*, *Prestosuchus* and *Saurosuchus*

	<i>Luperosuchus fractus</i>	<i>Prestosuchus chiniquensis</i> (lower jaw included)	<i>Saurosuchus galilei</i>
Total length of the skull	60cm	88cm	67cm
Shape of external naris	irregularly triangular	the same	the same
Accessory antorbital fenestra	present	absent	present
Main body of the premaxilla	rectangular?	quadrangular	tending to quadrangular
Size of antorbital opening	large	moderate	large
Maxillary expression below antorbital opening	narrow?	wide	narrow
Nasals	rised upward the general line of the skull roof	moderately raised	not raised
Orbits	irregularly elliptic, main axis perpendicular	keyhole-shaped, main axis inclined	as in <i>Prestosuchus</i>
Shape of infra-temporal fenestra	sub-rectangular	subtrapezoidal	subtrapezoidal?
Posterior border of the infratemporal fenestra	nearly straight	curved, tending to a V-shaped contour	not preserved
Otic notch	shallow	more incised	not preserved
Parietal foramen	absent	absent	absent?
Interparietal	area of occurrence not preserved	present	area of occurrence not preserved
Sculpturing	absent	absent	present

would thus comprise two facies, one lacustrine, mainly formed by compact, richly fossiliferous mudstones (Santa Maria facies) and another made up of fluvial red sandstones, locally associated with mudstones. Only fossil woods have been found in the fluvial facies.

Further field work will probably substantiate one of the two interpretations. For the time being, it seems best for avoiding ambiguity to use the composite name, Rosario do Sul-Santa Maria Beds to indicate the totality of the Triassic sediments in southern Brazil.

In a previous paper (Barberena, 1977), the present author proposed a biostratigraphical zonation for the tetrapod-bearing sediments, in which three assemblage-zones are recognized, from top to bottom, as shown below.

1) *Rhynchocephalia Assemblage-zone*: identified at the type-area of the Santa Maria Formation (sensu Bortoluzzi) in Santa Maria City and in other sites elsewhere. The fossil content is overwhelmingly composed of rhynchosaurs (*Scaphonyx fischeri*). Therapsids are extremely rare. *Gomphodontosuchus brasiliensis* and *Therioherpeton cagnini* are the only representatives of the group. Dicynodonts are totally absent. Archosaurs are represented by the thecodonts *Cerritosaurus binsfeldi*, *Hoplitosuchus rauti*, *Rauisuchus tiradentes*, *Rhadinosuchus gracilis* and by the saurischian *Staurikosaurus pricei*. This association is typical for the Santa Maria City area. Other sites within this zone have yielded rhynchosaurs and cynodonts, but no archosaurs have been found so far.

2) *Dicroidium Assemblage-zone*: proposed for beds 30 meters thick, lying directly underneath the first zone and producing the well known *Dicroidium* paleoflora.

3) *Therapsida Assemblage-zone*: identified in outcrops in Candelaria and Chiniquá, as well as at other places in Rio Grande do Sul. Therapsids, represented by dicynodonts and gomphodont and carnivorous cynodonts, are predominant and associated with the thecodonts *Prestosuchus chiniquensis*, *Prestosuchus loricatus* and *Procerosuchus celer*.

To this zone also belongs the cotylosaur *Candelaria barbouri* and the problematic saurischian *Spondylosoma absconditum*. No rhynchosaurs have been found in it.

The fossil content of the two tetrapod zones is clearly distinct. Price (1946) had already noticed this feature, when generally commenting on the

faunal differences between the sites of Santa Maria, Candelaria and Chiniquá. The two latter sites showed pronounced faunal similarity and contrasted the Santa Maria area in having abundant therapsids and no rhynchosaurs. He suggested that this might reflect stratigraphic rather than ecologic separation. This possibility seems to be supported by the field work undertaken during the last few years. It has been shown (Barberena, *op. cit.*) that the dicynodont-producing outcrops alternate with the rhynchosaur-producing ones more or less along the E-SW belt of Triassic sediments in Rio Grande do Sul.

Geographic distances between these outcrops are small. It is worth mentioning here that one of the outcrops with rhynchosaurs is only 15 km from Chiniquá where dicynodonts are well represented. Ecological incompatibility is of course unlikely to be explanatory for this close proximity and exclusive occurrence. Stratigraphic separation stands as a much more plausible explanation. Geological mapping has shown that many of the rhynchosaur-bearing outcrops lie at higher levels than the ones with dicynodonts. This would account for the established higher altitudinal occurrence of the *Rhynchocephalia* Assemblage-zone. However, there are no known places where an actual contact between the two tetrapod zones can be found (assuming that the *Dicroidium* Assemblage-zone could have only local expression, as seems to be the case). This might lead to the assumption that the obtained higher position for the outcrops with rhynchosaurs could be due to faulting activity, known to have existed within the area.

Nevertheless, a closer consideration of the faunal associations in each of the two tetrapod zones, utilizing comparisons with the Argentinian Triassic faunas, permits finer resolution regarding their geological ages and stratigraphic relationships of their outcrops.

The overall aspect of the Therapsida Assemblage-zone fauna shows many affinities to the Chañares fauna, as follows:

- a) absence of rhynchosaurs;
- b) predominance of therapsids, with common genera such as *Dinodontosaurus* and *Massetognathus*;
- c) presence of *Prestosuchus*, a form not much advanced over *Luperosuchus*;
- d) presence of still undescribed thecodont re-

mains, quite similar to *Gualosuchus* and *Chañaresuchus*.

It should be stressed, however, the presence of forms more advanced in the Therapsida Assemblage-zone, as compared to the Chañares representatives. As it was pointed out in this paper, *Prestosuchus* is intermediate between *Luperosuchus* and *Saurosuchus*. Moreover, *Exaeretodon*, represented by *E. major* (Huene), makes its first appearance in the South American Triassic in the lower zone of the Rosario-Santa Maria beds. This seems to indicate that the age of the therapsid zone should not be considered as older than Middle to Upper Chañarensis.

The Rhynchocephalia Assemblage-zone, as defined in this paper, poses a different but correlated problem. Its faunal assemblage already exhibits the main components of the typical Ischigualastense rhynchosaur-cynodont-archosaurian association, but some Argentinian advanced members are lacking, such as the aetosaurian and ornithischian representatives. This perhaps would justify the inclusion of the whole Rosario-Santa Maria beds in the Chañarensis, with the rhynchosaur zone at the very top limit of this provincial age.

However, the actual interpretation may be in fact more complicated. Recently found out-

croppings have yielded more advanced Santa Maria components, such as *Proterochampsia* and *Ischignathus* (?), yet undescribed, and the dicynodont *Jachaleria candelariensis* (Araújo & Gonzaga, in press), being this genus listed (Bonaparte, *op. cit.*) for the Coloradense of Argentina. Rhynchosauroids keep appearing in those new outcroppings, what renders the overall similarity to the Ischigualastense fauna even closer. Thus, on the grounds of present evidence, it is reasonable to admit the upper levels of the Rosario-Santa Maria beds as entering the Ischigualastense age. It is also sound to expect the finding of new forms to corroborate this assumption. Field work in progress will also provide additional stratigraphic and biostratigraphic data.

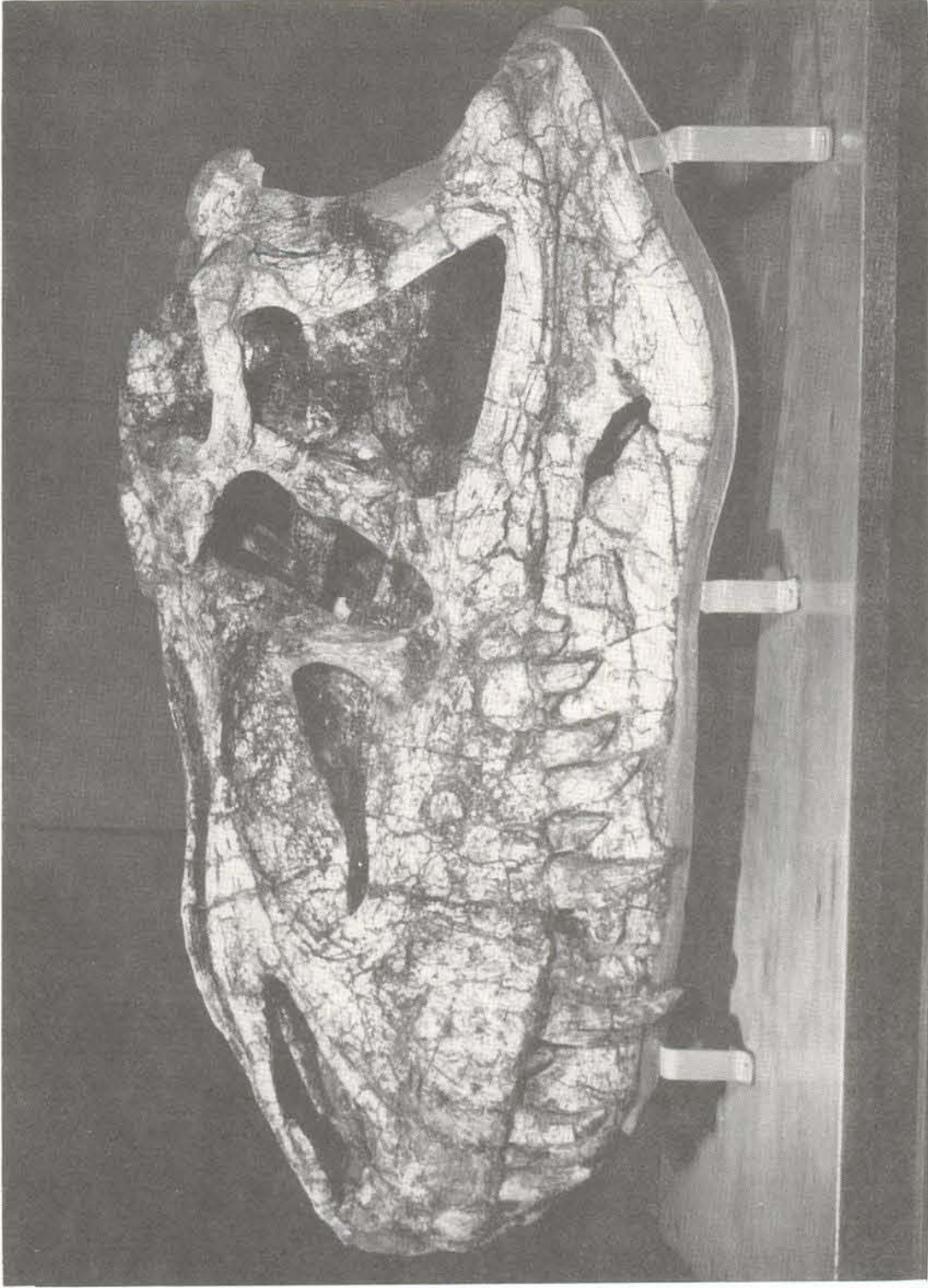
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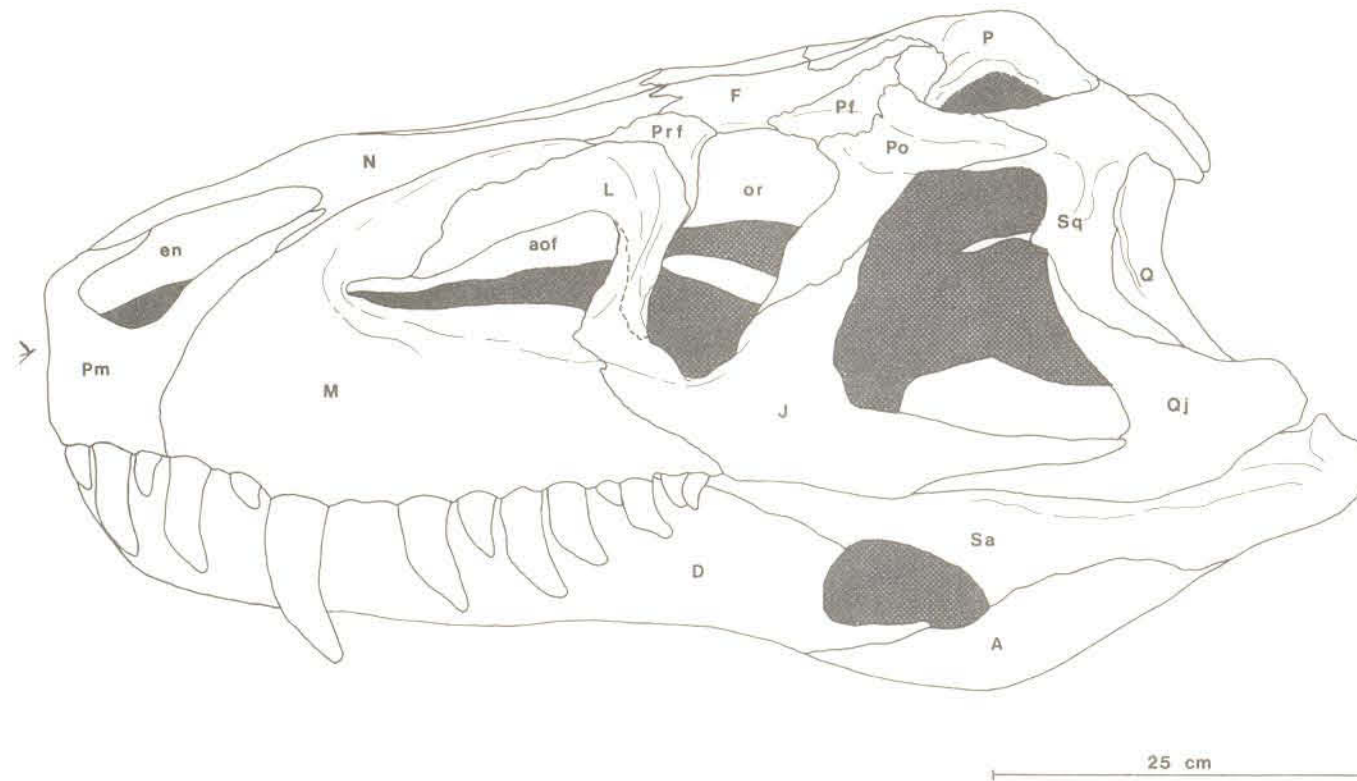
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Photograph 1 — *Prestosuchus chiniquensis*, Rosário-Santa Maria beds, Triassic, Candelaria County, Rio Grande do Sul State, Brazil.



List of abbreviations

- A. — angular
- aof. — antorbital fenestra
- D. — dentary
- en. — external naris
- F. — frontal
- J. — jugal
- L. — lacrimal
- M. — maxilla
- N. — nasal
- or. — orbit
- P. — parietal
- Pf. — postfrontal
- Pm. — premaxilla
- Po. — postorbital
- Prf. — prefrontal
- Q. — quadrate
- Qj. — quadratojugal
- Sa. — surangular
- Sq. — squamosal

Fig. — Skull of *Prestosuchus chiniquensis*. Lateral view. Rosário-Santa Maria beds, Triassic of Brazil, Candelaria County, R.G.S.