Description of the Braincase of Two Early Cretaceous Pterosaurs (Pterodactyloidea) from Brazil

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ABSTRACT

The braincase of *Tapejara wellnhoferi* and *Anhanguera* sp., two pterodactyloid taxa from the Early Cretaceous Santana Formation (Romualdo Member) of the Araripe Basin, Brazil, are described and compared with other archosaurian braincases. The presence of the orbitosphenoid, previously found in dinosaurs but absent in other archosaurs, is reported in pterosaurs for the first time, suggesting that this bone is an ornithodiran synapomorphy. Contrary to other archosaurs, there is an ossification (the pseudomesethmoid) on the anteroventral portion of those pterosaur braincases. A horizontal section through *Anhanguera* sp. revealed the presence of an interlaminar pneumatic cavity with a complex system of trabeculae above the cranial cavity. Therefore, the actual braincase is placed deeper inside the skull than was previously supposed, raising questions about whether some pterosaur endocasts reported in the literature express the true internal surface of the braincase or just of the exocranial lamina. The braincase of *Anhanguera* sp. has some birdlike features (reduced olfactory bulbs and lateral placement of the optic lobes) but its size indicates that the pterosaur brain was more reptilian than was previously thought.

INTRODUCTION

The braincase of pterosaurs is very poorly known mainly for two reasons. First, because of their fragility, pterosaurian remains are often damaged during deposition and diagenesis. The skull, in particular, is vulnerable to crushing and flattening, severely limiting de-

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tailed anatomical studies of the posterior region. Second, specimens with three-dimensionally preserved bones are rare and valuable. Thus, detailed preparation of the braincase, which in many cases involves removing the posterior region of the skull or bones that are obstructing anatomical features, is often discouraged.

Very few studies of pterosaur braincases are reported in the literature. Seeley (1870, 1871, 1901) was among the first researchers to describe pterosaur cranial material in some detail. Most of the specimens he studied, however, were fragmentary, and therefore provided only limited information about the braincase. Newton (1888) described the skull of *Parapsicephalus purdoni* from the Alum Shale (Upper Lias), but focused primarily on the endocast. Edinger (1927, 1941) described specimens from Solnhofen and the Cambridge Greensand, but also centered her observations on endocasts. More recently, Wellnhofer (1985) and Campos and Kellner (1985) described three-dimensionally preserved pterosaurian skulls with preserved braincases from Brazil. Those specimens, however, were not fully prepared and their observation were limited to the dermal skull roof and the occipital region. Bennett (1991) described the braincase of *Pteranodon* in some detail, but the specimens are crushed, limiting some observations.

This paper describes two pterosaur braincases found in Cretaceous rocks of the Araripe Basin, Northeast Brazil, and compares them with braincases from other archosaurs. The material studied here comes from the Romualdo Member, upper stratigraphic unit of the Santana Formation (Beurlen, 1971). The Santana Formation is known worldwide for the quantity and exquisite preservation of fossil remains (see Maisey, 1991, for a review). The Romualdo Member essentially comprises shales of Albian age (Lima, 1978; Pons et al., 1990), which contain calcareous nodules. Fossils are found in the nodules and in the shales, but only the former are exceptionally well preserved.

The two pterosaur specimens described here belong to the Desiree Collection, which is housed permanently in the Paleontology Section of the Departamento Nacional da Produção Mineral (Museu de Ciências da Terra—DNPM) in Rio de Janeiro, Brazil. Both were encased in calcareous nodules and are preserved three dimensionally.

The most complete specimen (MCT 1500-R) is referred to the tapejarid *Tapejara wellnhoferi*. It comprises the skull and mandible that were broken off and glued together (using an epoxy compound) with the mandible and the anterior portion of the skull inverted. Unfortunately, this and other artificial restorations, is common practice among fossil collectors in the Araripe region. The second specimen (MCT 1501-R) is referred to the Anhangueridae and comprises only the dorsoposterior region of the skull. Both specimens were prepared in detail, revealing several features previously unknown for pterosaurs.

ABBREVIATIONS

bo	basioccipital
bs	basisphenoid
clr	columellar recess
dep	depression
eo	exoccipital
f	frontal
fm	foramen magnum
fo	foramen
gr	groove
ifl	intermediate frontal lamina
ios	interorbital septum
j	jugal
la	lacrimal
ls	laterosphenoid
n	nasal
oc	occipital condyle
op	opisthotic
os	orbitosphenoid
p	parietal
pcf	postcranial fenestra
pfo	pneumatic foramen
po	postorbital
pr	prootic
psm	pseudomesethmoid
ptf	posttemporal fenestra
q	quadrate
res	resin
sac	sagittal crest
scp	sclerotic plate
so	supraoccipital
sq	squamosal
utf	upper temporal fenestra

(l or r following abbreviations indicates left or right side; roman numerals indicate foramina for cranial nerves.)

MATERIALS AND METHODS

The pterosaur braincases studied here were prepared utilizing chemical techniques. Although the employment of acids in fossils is a very old method (see Kellner, 1995a, for a review), the refinement of this technique for vertebrate fossils was done only in the 1950s (Rixon, 1949; Toombs and Rixon, 1959).

The procedures adopted here were developed particularly for three-dimensional tetrapods preserved in limestone (Kellner, 1991, 1995a; Rutzky et al., 1994). This technique is carried out by immersing the specimen in varying concentrations of formic acid solutions, which are saturated with calcium phosphate to prevent bone deterioration. The specimen is subsequently neutralized in plain water and dried. The exposed parts of the bone are protected with different solutions of a methacrylate resin (Paraloid B-72; Acriloid B-67) and the specimen is further immersed in the acid solution. This procedure is repeated until the desired preparation stage is reached.

Due to the fragility of both specimens, a weak 3% formic acid solution was used. In some exceptionally delicate areas, a thin coat of cyanoacrylate adhesive (super glue) diluted in acetone was applied to provide greater stability during the preparation process.

Several bones were covered with a reddish layer rich in iron, which was formed secondarily during diagenesis. This layer was not dissolved by acid, but had to be removed mechanically.

The tapejarid specimen (MCT 1500-R) was submitted to CT-Scan during an intermediate preparation stage. The results, however, were limited, apparently due to the small density contrast between the bone and the calcareous matrix.

The anhanguerid braincase was divided during the fossilization processes on a horizontal plane passing through the posttemporal fenestrae. To prevent the separation of those parts during the preparation process, the specimen was embedded in polyester resin. All lateral resin walls were removed after the ventral and lateral portions were pre-pared, allowing a complete view of the specimen. Subsequently, a horizontal section was cut through the top of the skull (embedded in resin), allowing preparation of the pneumatic cavity (or interlaminar pneumatic cavity) present between the external (exocranial) and internal (endocranial) laminae of the skull.

Some material was removed mechanically from the interlaminar pneumatic cavity of the anhanguerid braincase and etched in a 3% formic acid solution. After drying, samples were mounted on a conductive material (carbon-based tape). Some were coated with a gold-palladium layer, while others were coated with a carbon layer. Both were examined by scanning electron microscope (SEM model: Zeiss DSM 950). The carbon-coated samples were submitted to energy dispersive spectroscopy for elemental characterization in order to establish the composition of several parts of the specimen (e.g., bone, matrix).

Comparisons were made with Recent specimens of crocodilians and birds to help identify the cranial foramina. Previous interpretations of other fossil archosaur braincases were also used, particularly the descriptions available for *Allosaurus* (Madsen, 1976), *Sinraptor* (Currie and Zhao, 1993a), *Troodon* (Currie, 1985; Currie and Zhao, 1993b), *Syntarsus* (Raath, 1985), *Sphenosuchus* (Walker, 1990), *Rhamphorhynchus* (Wellnhofer, 1975), *Anhanguera* (Wellnhofer, 1985; Campos and Kellner, 1985), and *Pteranodon* (Bennett, 1991). The anatomical terminology follows Baumel and Witmer (1993), using the English equivalents of the Latin terms.

SYSTEMATIC PALEONTOLOGY

To date, 17 different pterosaur species have been named from the Romualdo Member (for a review see Campos and Kellner, 1985; Kellner, 1990; Wellnhofer, 1991b; Dalla Vecchia, 1993; Kellner and Campos, 1994). This relatively high number of named taxa seems to be inflated, especially since the earlier described species are based on incomplete material. Notwithstanding this, additional specimens have recently been recovered from the same deposits, which potentially represent new taxa (Kellner, 1995b). Thus, the ptero-
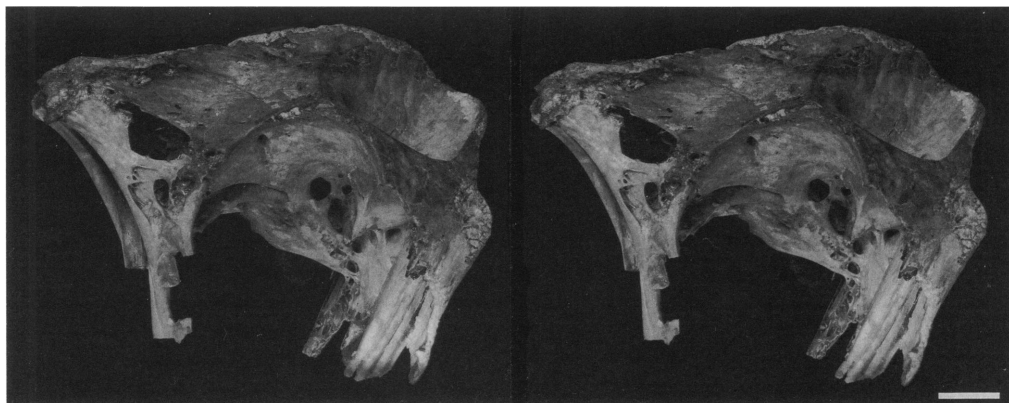
Fig. 1. *Tapejara wellnhoferi* (MCT 1500-R). Stereophotographs of the left lateral view of the skull. Scale = 10 mm.

saurian fauna was diverse in the Araripe region during the Albian.

The nasoantorbital fenestra of the specimen MCT 1500-R is extremely elongated with an extended premaxillary crest above, which are shared derived features of the Tapejaridae (Kellner, 1995b). The absence of a palatal ridge and the shape of the sagittal crest allows its identification as *Tapejara wellnhoferi*. So far, only two specimens of this species were known: the holotype, which consists of an incomplete skull (Kellner, 1989) housed in the DNPM (Rio de Janeiro), and a skull and mandible (AMNH 24440), housed in the American Museum of Natural History (Wellnhofer and Kellner, 1991). Specimen MCT 1500-R differs from both by being slightly larger and by greater fusion of the bones (e.g., lacrimal). These differences are here regarded as ontogenetic, with MCT 1500-R probably representing a comparatively older animal.

The systematic allocation of the second specimen (MCT 1501-R) is problematic, since it is formed only by the dorsoposterior region of the skull. Nevertheless its structure differs from that found in Tapejaridae, and therefore precludes membership in this group. MCT 1501-R differs from *Tropeognathus mesembrinus*, that has a larger and more robust parietal crest (Wellnhofer, 1987). The presence of a small and blunt sagittal crest, however, suggests affinities of MCT 1501-R with the Anhangueridae, a pterosaur clade also found

in the Romualdo Member (Campos and Kellner, 1985). The preserved portion of MCT 1501-R is virtually indistinguishable from *Anhanguera blittersdorffi*, described by Campos and Kellner (1985), and *Anhanguera santanae*, described by Wellnhofer (1985). The latter was originally named *Araripesaurus santanae*, but afterwards regarded as a species of *Anhanguera* (Kellner, 1990; Wellnhofer, 1991a). Comparisons with other described cranial materials from the Romualdo Member is not possible, since they lack the posterior region of the skull (see Wellnhofer, 1985; Leonardi and Borgomanero, 1985; Kellner, 1990; and Dalla Vecchia, 1993).

Considering the analysis above, the specimen MCT 1501-R is provisionally classified as *Anhanguera* sp.

DESCRIPTION AND COMPARISONS

The tapejarid specimen (MCT 1500-R: figs. 1–9) lacks the tip of the premaxillae, part of the middle portion of the skull, most of the sagittal crest, and the anterior and posterior ends of the mandible. The description presented here is limited to the parts that surround or are in direct contact with the braincase. A more detailed description of all other bones, including the mandible, is presented elsewhere.

Many sutures in the tapejarid specimen (MCT 1500-R) are not discernible as a result of fusion of the bones. Some bones, however,
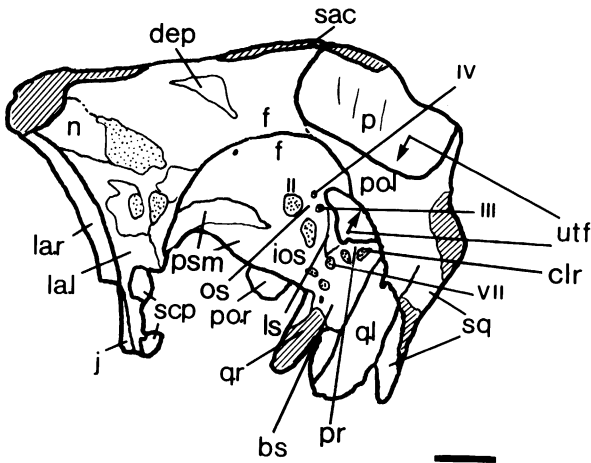
Fig. 2. *Tapejara wellnhoferi* (MCT 1500-R). Left lateral view of the skull. Scale = 10 mm.

are unfused or only partially connected to surrounding elements, allowing the determination of their shapes and limits. This combination of unfused, partially fused, and completely fused elements suggest that this specimen represents a young animal in the process of reaching the adult ontogenetic stage.

The specimen of *Anhanguera* sp. (MCT 1501-R: figs. 10–23) comprises only the dorsoposterior part of the skull and is fully described here. The estimated length of the skull is about 580 mm, which is based on the proportions of the posterior region of complete anhanguerid skulls (Campos and Kellner, 1985; Wellnhofer, 1991a).

Almost all bones preserved in MCT 1501-R are unfused and thus sutures are easily distinguished. This suggests that the specimen represents a juvenile of younger ontogenetic stage compared to the tapejarid material (MCT 1500-R).

FRONTAL

The frontal of *Tapejara wellnhoferi* (figs. 1, 2) forms the skull roof above the orbit. It comprises two bony laminae (the medial is anteriorly very delicate and highly fenestrated) separated by bony struts (= trabeculae). Anteriorly, it overlies the nasal and contacts the lacrimal. A large piriform opening is present between the nasal, frontal, and lacrimal.

There is no evidence of a prefrontal or a postfrontal.

On the dorsal side, the frontals fuse at the midline, forming the base of a sagittal crest. They are overlain by the premaxillae (not preserved in this specimen, but see Wellnhofer and Kellner, 1991). The contact of the frontal with the parietal is marked by a well-developed ridge, which extends from the lateral margin above the orbit to the posterior portion of the sagittal crest. In the middle part near the base of this crest, there is a small depressed area ending laterally in a foramen. Inside the orbit, another foramen with a shallow groove leading to the pseudomesethmoid could be observed.

The anteromedial contact of the frontal and the pseudomesethmoid is marked by a deep furrow that turns smoother posteriorly.

The suture between the frontal and postorbital is sigmoidal and runs dorsoventrally inside the posterior margin of the orbit. The limits with the laterosphenoid cannot be determined, although it is possible that the latter also contacted the postorbital in this region.

On the specimen referred to *Anhanguera* sp. the frontals are not completely fused dorsally, and join at the midline in a straight suture. The anterior part of the frontal is not preserved in this specimen. Laterally, the frontal contacts the postorbital (also not preserved) and posteriorly it is fused with the
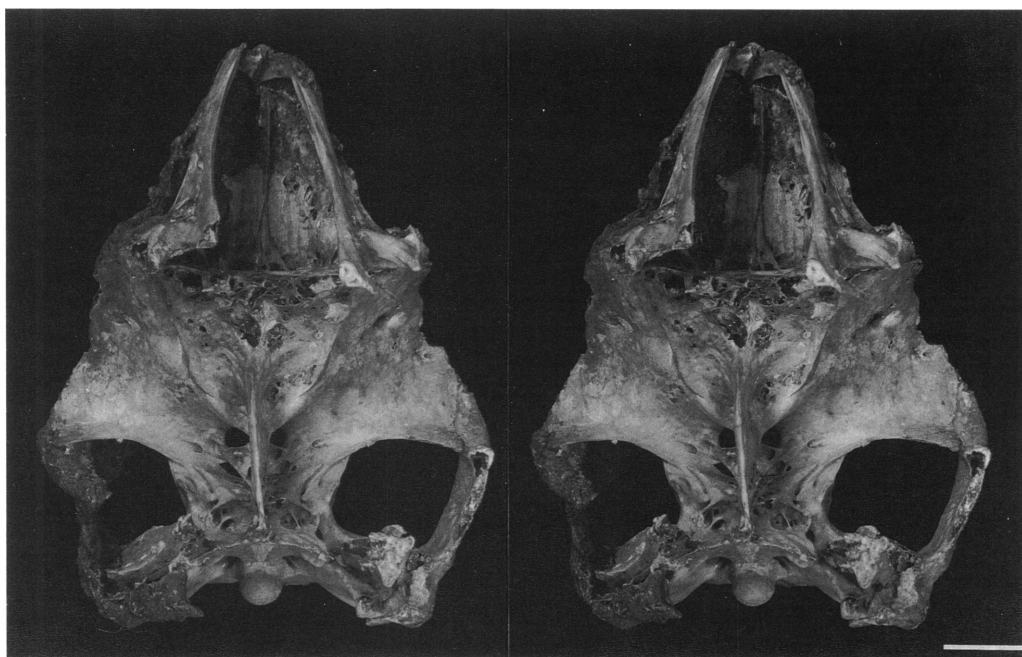
Fig. 3. *Tapejara wellnhoferi* (MCT 1500-R). Stereophotographs of the ventral view of the braincase. Scale = 10 mm.

parietal. The contact between frontal and parietal is marked by a well-developed ridge (similar to that of *T. wellnhoferi*), starting above the dorsoposterior margin of the orbit and extending backward to the midline of the skull. The frontal, therefore, forms the major portion of a blunt sagittal crest present at the posterior region of the skull (not figured here, but see Campos and Kellner, 1985). The limits with the laterosphenoid cannot be observed.

In most other pterosaurs, the frontals do not form a sagittal crest. The notable exception is *Pteranodon,* where the extended sagittal crest is mainly composed by those bones (Bennett, 1991). The frontal in *Dsungaripterus* forms the basis for the cranial crest, as in *Tapejara,* but differ by being more flat.

PARIETAL

The parietal in *Tapejara wellnhoferi* (figs. 1, 2) forms the anterior, medial, and posterior margins of the upper temporal fenestra. Anteriorly, the contact with the frontal is marked by a well-developed ridge, while the suture with the postorbital is almost straight, running dorsoventrally inside the upper temporal opening.

Near the dorsolateral contact with the frontal, the parietal displays a depressed area whose function is unknown. Dorsally, the parietals fuse and form the basal portion of a sagittal crest, and are overlain by the posterior extensions of the premaxillae (not preserved in this specimen, but see Wellnhofer and Kellner, 1991).

The suture between the parietal and squamosal runs vertically to the anterodorsal margin of the posttemporal fenestra; the contact of the parietal with other bones (e.g., supraoccipital, laterosphenoid, and prootic) cannot be established in this specimen. Two small foramina are present inside the upper temporal opening: one in the anteroventral and another in the posterior part, the latter well above the posttemporal fenestra. It is very likely that the laterosphenoid participates in the anteroventral one. These foramina possibly served as passageways for blood vessels.
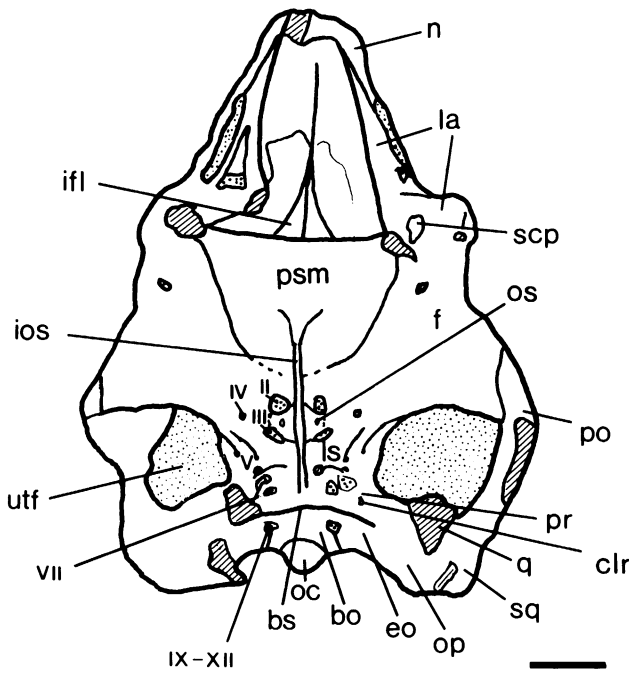
Fig. 4. *Tapejara wellnhoferi* (MCT 1500-R). Ventral view of the braincase. Scale = 10 mm.

In *Anhanguera* sp., the parietals are fused dorsally. Their border with the frontals is marked by a developed ridge (described above). The extent to which the parietals participate in the sagittal crest is unknown, but it is clearly not to the same degree as the frontals. Posterolaterally, the parietals join the frontals participating in the articular surface of the postorbital (not preserved). The limits with the supraoccipital cannot be established with confidence. Anteroventrally, the parietal is overlain by a thin plate extending from the laterosphenoid, marked by an irregular suture. Ventrally, the parietal has a notch to receive the prootic.

The parietal region shows some variation among pterosaurs (see Wellnhofer, 1978, for a general review). In most taxa, the parietals are comparatively small bones, confined to the posterior region of the skull, which do not form a cranial crest. *Tropeognathus* has a short and blunt parietal crest, that overhangs the posterior margin of the skull (Wellnhofer, 1987). *Gallodactylus* and *Dsungaripterus* have the parietals extending backward, forming a parietal crest (Fabre, 1976; Young, 1973). *Tapejara* differs by having a posterior exten-

sion of the premaxillae above the parietal crest (Wellnhofer and Kellner, 1991), which is lacking in *Gallodactylus* but could be present in *Dsungaripterus* (personal obs.). *Tupuxuara* follows the condition of *Tapejara* but has a much larger cranial crest extended posteriorly (Kellner and Campos, 1990, 1992).

The extension of the parietals in the occipital region can only be observed in a few pterosaur specimens. According to Wellnhofer (1975: fig. 4), the parietals in *Rhamphorhynchus* extend posteriorly and are expanded in the occipital region. Diverging from this condition, the parietal is excluded from the occipital region in many pterodactyloids like *Anhanguera* (Wellnhofer, 1985; and MCT 1501-R), *Tapejara* (Wellnhofer and Kellner, 1991; and MCT 1500-R), *Dsungaripterus* (personal obs.), and *Pteranodon* (Bennett, 1991). In early pterodactyloids like *Pterodactylus, Gnathosaurus,* and *Germanodactylus* (see Wellnhofer, 1970), the condition is not clear: although the parietals apparently participate in the occipital region, most of the specimens are too crushed for a positive identification.
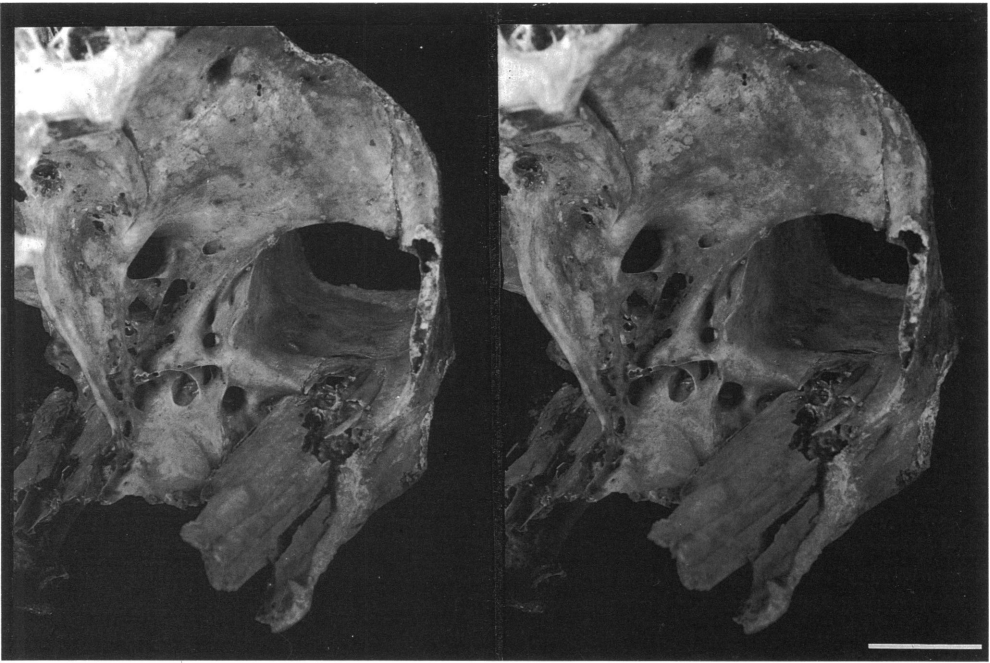
Fig. 5. *Tapejara wellnhoferi* (MCT 1500-R). Detail stereophotographs of the ventrolateral oblique view of the braincase, showing most cranial foramina. Scale = 10 mm.

In other archosaurs, the extension of the parietal varies. In recent crocodilians, the parietals are small bones that occupy a posterodorsal position in the skull but are excluded from the occipital region (see Iordansky, 1973). In primitive crocodilomorphs, however, the parietal reaches the occipital surface as in *Sphenosuchus* (Walker, 1990). In theropods, the parietal participates in the occipital region, although the extension varies among taxa (see Madsen, 1976; Raath, 1985; Currie and Zhao, 1993a, 1993b). Similarly, a large ventral parietal flange overlaps the posterodorsal edge of the supraoccipital of *Protoavis* (Chatterjee, 1991), which is absent in modern birds (Jollie, 1957; Chatterjee, 1991).

POSTORBITAL

Only the left postorbital of *Tapejara wellnhoferi* is complete in MCT 1500-R (figs. 1–6). It is a triangular bony plate that forms the posterior margin of the orbit, participates in the lateral margin of the upper temporal fe-

nestra, and the dorsal margin of the lower temporal fenestra. Anteriorly, this bone contacts the frontal and parietal, posteriorly the squamosal, and ventrally the jugal. On the lateral side of the skull, the suture between the postorbital and the squamosal runs in a ventral direction inside the upper temporal opening. On the medial side, this suture could not be observed, and therefore it is not clear to what extent the postorbital forms the lateral wall of the upper temporal opening. In this area, there is a well-developed concavity on the medial side of this bony wall.

The contact with the jugal cannot be determined in this specimen. Nevertheless, it seems that the ventral process of the postorbital is overlain laterally by the jugal, as observed in another specimen of this taxon (Wellnhofer and Kellner, 1991).

No postorbitals were preserved in the specimen of *Anhanguera* sp.

The postorbital is conservative in most pterosaur taxa, forming a lateral triangular plate that participates in the same cranial openings (i.e., orbit, upper and lower tem-
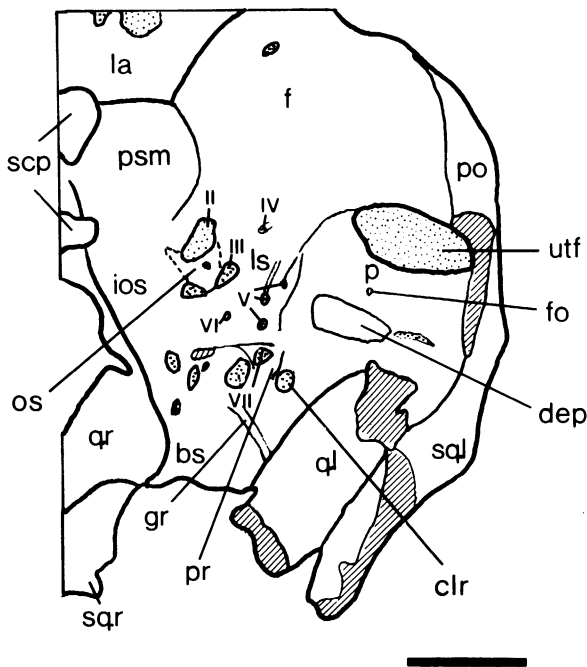
Fig. 6. *Tapejara wellnhoferi* (MCT 1500-R). Detail of the ventrolateral oblique view of the braincase, showing most cranial foramina. Scale = 10 mm.

poral openings), although the shape and the extension of the processes might vary (see Wellnhofer, 1978). According to Wellnhofer (1970), the postorbital in *Pterodactylus, Gnathosaurus,* and *Germanodactylus* is totally or partially excluded from the orbit by the presence of a postfrontal.

In Recent and most fossil crocodilians, the postorbitals are positioned dorsally and bear a descending process that contacts the ascending process of the jugals (Iordansky, 1973), differing from the condition in pterosaurs. In carnosaurs like *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie and Zhao, 1993a), the postorbital is a heavy element, that has a T-shaped lateral outline. In other theropods, this bone is always more robust in comparison with that of pterosaurs (e.g., Currie, 1985). In modern birds, the postorbital is absent.

SQUAMOSAL

The squamosal of *T. wellnhoferi* participates in the lateral margin of the upper tem-

poral fenestra, the posterodorsal margin of the lower temporal fenestra, and the anterolateral margin of the posttemporal fenestra (figs. 1–8). It contacts the postorbital anterolaterally along a vertical suture, and overlaps the ascending process of the quadrate laterally and posteriorly. In the posterior region, the squamosal bears a process directed anteroventrally. This bone also contacts the parietal and the supraoccipital (no suture is visible).

The contact of the squamosal with the opisthotic is complex (figs. 7, 8). Beginning at the middle part of the anteroventral margin of the posttemporal fenestra, the suture between these bones extends across this opening, terminating at its posterolateral margin. From this point it runs almost vertically for about 9 mm, abruptly changes direction to a 12 mm long diagonal line directed medially, and turns again horizontally ending at the lateral margin of the postcranial fenestra.

No squamosal is preserved in *Anhanguera* sp. In other anhanguerids, the squamosal forms the posterolateral region of the skull
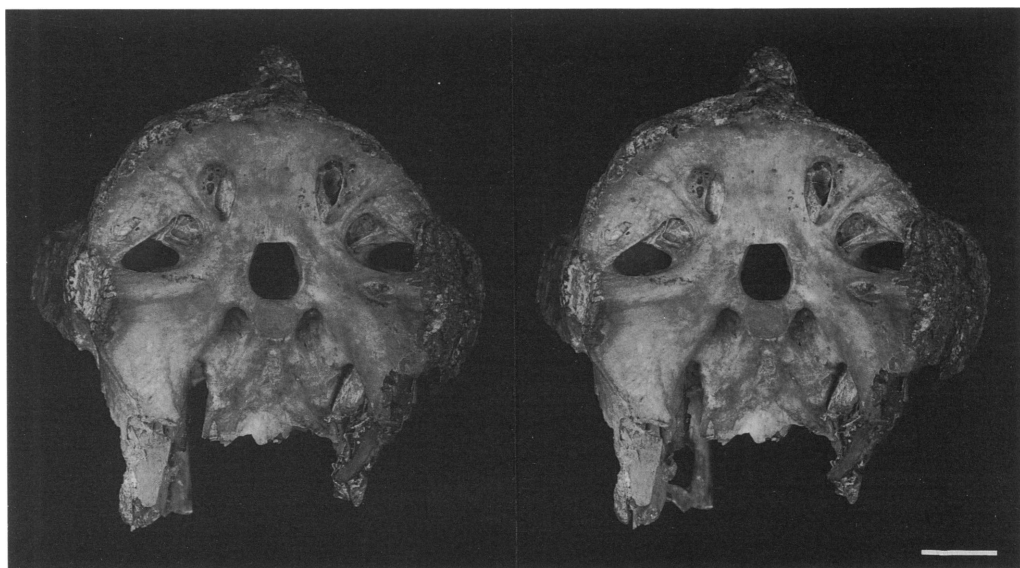
Fig. 7.   *Tapejara wellnhoferi* (MCT 1500-R). Stereophotographs of the occipital region. Scale = 10 mm.

and overlaps the ascending process of the quadrate (Wellnhofer, 1985; Campos and Kellner, 1985).

Among pterosaurs, the contact between the squamosal and quadrate varies. Contrary to that of most pterosaurs, the lateral quadrate-squamosal contact is very reduced in *Eudimorphodon, Dimorphodon,* and *Rhamphorhynchus* (Wild, 1978; Wellnhofer, 1978). According to Wellnhofer (1975), the squamosal in *Rhamphorhynchus* expands in the occipital region. This differs from the pterodactyloids where the occipital region can be observed as in anhanguerids (Wellnhofer, 1985; Campos and Kellner, 1985), tapejarids, *Pteranodon* (Bennett, 1991), and *Dsungaripterus* (personal obs.) where the squamosal is limited to the posterior borders of the skull.

In Recent and many fossil crocodilians, the squamosal is a wide, horizontal bone that expands laterally and posteriorly, forming the dorsolateral part of the occipital region (Iordansky, 1973). The same position of the squamosal is found in carnosaurs like *Allosaurus* (Madsen, 1976) and *Sinraptor* (Currie and Zhao, 1993a). This differs from the more lateral position that the squamosal occupies in the pterosaur skull.

The squamosal is also laterally placed in

some theropods, particularly those closely related to birds like troodontids (Currie, 1985; Currie and Zhao, 1993b), and in modern birds (Jollie, 1957). In those forms, the squamosal is expanded on the occipital region (see Chatterjee, 1991), similar to the condition reported in the pterosaur *Rhamphorhynchus* (Wellnhofer, 1975), but differing from the condition observed in pterodactyloids, as described above.

QUADRATE

In *Tapejara wellnhoferi,* the quadrate articulates with the exoccipital/opisthotic and the squamosal under the ventral margin of the posttemporal fenestra (figs. 5, 6). It is not clear in this specimen if the prootic also contacts the quadrate. On each side, the shaft of the quadrate is broken, preventing a detailed observation of this region.

No quadrate is preserved in the anhanguerid specimen (MCT 1501-R) examined here.

SUPRAOCCIPITAL

The upper portion of the occiput in *Tapejara wellnhoferi* consists of the supraoccipital (figs. 7,8), which extends dorsoposteriorly
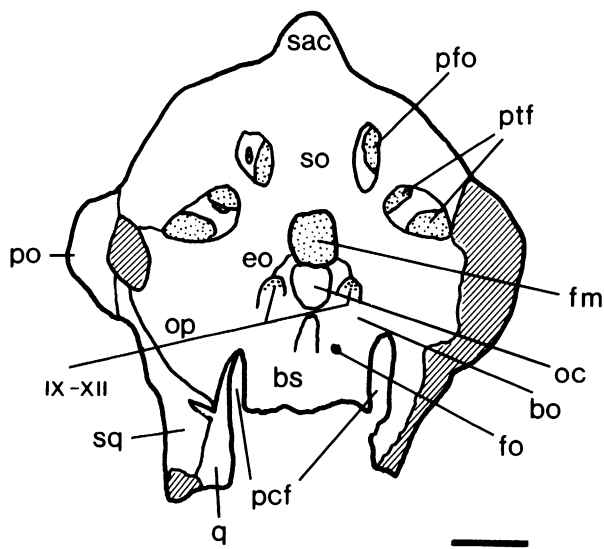
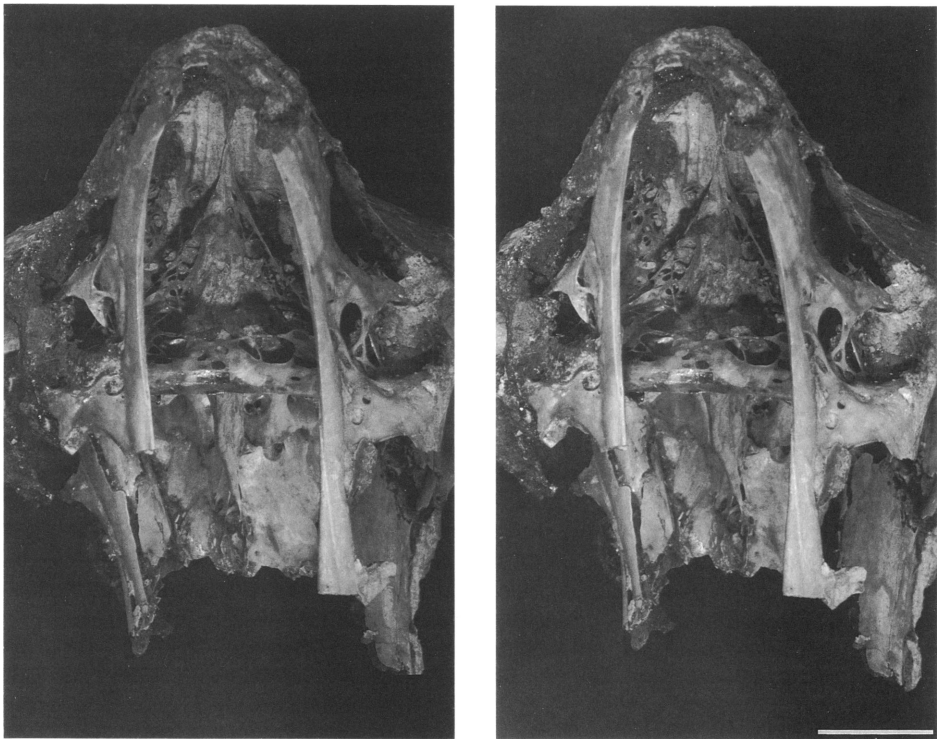Fig. 8.   *Tapejara wellnhoferi* (MCT 1500-R). Occipital region. Scale = 10 mm.

Fig. 9.   *Tapejara wellnhoferi* (MCT 1500-R). Stereophotographs of anterior view of skull, showing the intermediate frontal laminae. Scale = 10 mm.
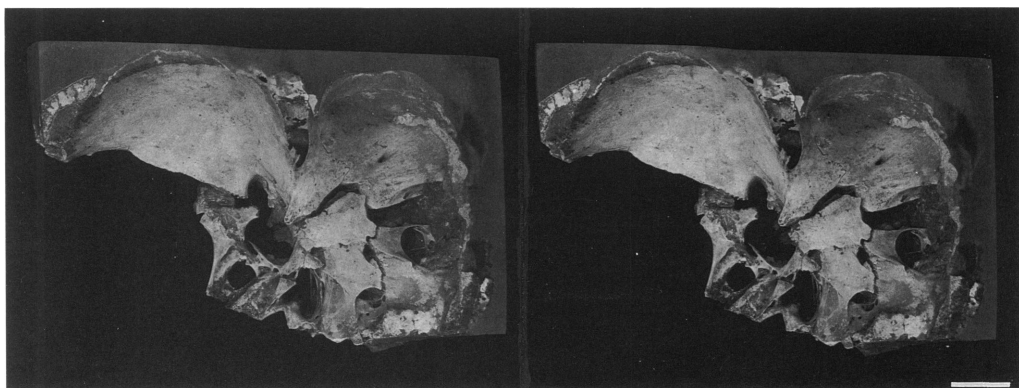
Fig. 10. *Anhanguera* sp. (MCT 1501-R). Stereophotographs of lateral view of skull. Scale = 10 mm.

and encloses the ventral part of the sagittal crest (not preserved in this specimen, but see Wellnhofer and Kellner, 1991). The supraoccipital also forms the dorsal margin of the foramen magnum and expands laterally to enclose the upper half of the posttemporal fenestra. The contacts with other bones (parietal, exoccipital, opisthotic, squamosal) are not clear.

On the upper part, the supraoccipital is pierced by two large pneumatic foramina, which are elongated in the dorsoventral direction. Another small pneumatic foramen is also preserved on the dorsal margin of the posttemporal fenestra.

In occipital view, the lateral sides of the supraoccipital are very rugose, particularly over the posttemporal fenestra. A small protuberance is present above the foramen magnum, lateral to which several rugosities can also be found. Those features are presumably for attachment of the neck musculature.

The supraoccipital in *Anhanguera* sp. also forms the upper portion of the occiput but since this taxa does not have a well-developed sagittal crest on the back of the skull, it does not extend as far posteriorly as it does in *Tapejara*. The supraoccipital bears a ridge on the midline above the foramen magnum that extends upward. A well-developed pneumatic foramen is developed lateroventrally on each side of this ridge.

In this specimen (MCT 1501-R), the supraoccipital is fused to most surrounding bones but not to the exoccipital and opisthotic, which have been slightly displaced from their natural position. Ventrally the supraoccipital contacts the exoccipital along an irregular horizontal surface that extends medially.

In more "primitive" pterosaurs like *Rhamphorhynchus* (Wellnhofer, 1975), the supraoccipital is comparatively small bone similar to that in other archosaurs (see Chatterjee, 1991). In the pterodactyloids where the occiput can be observed (e.g., anhanguerids, tapejarids, *Pteranodon,* and *Dsungaripterus*), the supraoccipital forms an expanded plate and occupies most of the upper portion of the occipital region, and is pierced by two well-developed pneumatic foramina (which are absent in *Rhamphorhynchus,* although it has several other foramina in this area—see Wellnhofer, 1975). Similar to that in most archosaurs (with the exception of some fossil and modern crocodilians—see Iordansky, 1973) this bone participates in the foramen magnum.

In all pterosaurs, the occiput has a posttemporal fenestra, which is a primitive feature for archosaurs, and becomes greatly reduced or lost in theropods (Chatterjee, 1991). According to Wellnhofer (1975), the supraoccipital in *Rhamphorhynchus* does not take part in the posttemporal fenestra, thus differing from the condition observed in *Anhanguera, Pteranodon, Dsungaripterus,* and tapejarids.
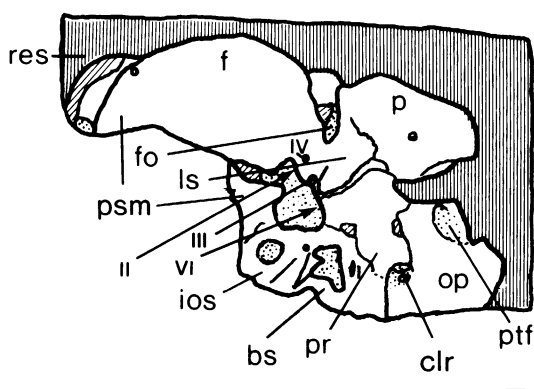
Fig. 11. *Anhanguera* sp. (MCT 1501-R). Left lateral view of skull. Scale = 10 mm.

EXOCCIPITAL AND OPISTHOTIC

The exoccipital in *Tapejara wellnhoferi* is fused to the opisthotic laterally, forming a compact unit which obscures the contacts between those bones (figs. 7, 8). Dorsally, the exoccipital-opisthotic plate is also fused to the supraoccipital and anteriorly it is fused to the prootic. Posterolaterally it contacts the squamosal and posteroventrally it contacts the basioccipital. Laterally, the opisthotic forms the paroccipital process, which is more massive than other cranial bones.

Anteriorly, near the medial margin of the posttemporal fenestra and inside the upper temporal opening, there is a depression between the exoccipital-opisthotic, parietal, and possible the prootic (figs. 5, 6). Above the anterior margin of this lateral depression, a weak diagonal ridge runs dorsoposteriorly, ending in a small foramen.

In occipital view, the exoccipital forms the lateral margin of the foramen magnum, joining the basioccipital ventrally, without participating in the occipital condyle. The paroccipital processes are developed laterally and expand gradually to the borders of the skull. Dorsally, the paroccipital process is very thick and displaced posteriorly with respect to the supraoccipital. It encloses the lower portion of the posttemporal fenestra and ventrally forms the dorsal margin of the postcranial fenestra. Lateroventrally the opisthotic forms an articulation surface that receives the pos-

teroventral process of the squamosal (figs. 7, 8). Ventrally, a bony flange from the base of the opisthotic is directed ventromedially and joins the basioccipital, forming the passages for the cranial nerves IX–XII.

The ventral surface inside the posttemporal fenestra is concave and possesses a few scattered foramina, the largest directed vertically near its lateral border (figs. 7, 8).

In *Anhanguera* sp., the exoccipital is also fused to the opisthotic. The contact between the opisthotic and the prootic, however, is well demarcated by an irregular suture which trends ventrally (figs. 10, 11, 14, 15). In this specimen, it can be seen that the opisthotic forms the ventrolateral margin of the columellar recess (see Cranial Nerves).

The exoccipital-opisthotic are comparatively small in *Rhamphorhynchus* (see Wellnhofer, 1975) but generally form a well-developed bony plate in pterodactyloids. The latter condition is also observed in Recent birds (e.g., Jollie, 1957; Chatterjee, 1991) and in *Troodon* (Currie, 1985). In modern crocodilians (Iordansky, 1973), carnosaurs (Madsen, 1976; Currie and Zhao, 1993a), and in some other theropods like *Syntarsus* (Raath, 1985), the lateral margin of the paroccipital processes is not as expanded.

BASIOCCIPITAL

The basioccipital in *Tapejara wellnhoferi* is situated below the foramen magnum and comprises the occipital condyle (figs. 7, 8). The suture between the basioccipital and exoccipital originates at the ventral margin of the foramen magnum and extends to the dorsal margin of the opening. This opening is further divided by a small splint of bone that is pierced by several foramina, which are apparently related to the passages of cranial nerves (see Cranial Nerves).

The occipital condyle is rounded, and its dorsal surface slightly flatter than the ventral surface. A medial vertically elongated rugose area is present below the occipital condyle. Laterally, there is another rugose area on each side of the condyle (slightly less developed). Ventrally, the basioccipital and the basisphenoid are fused, forming a laterally expanded plate.

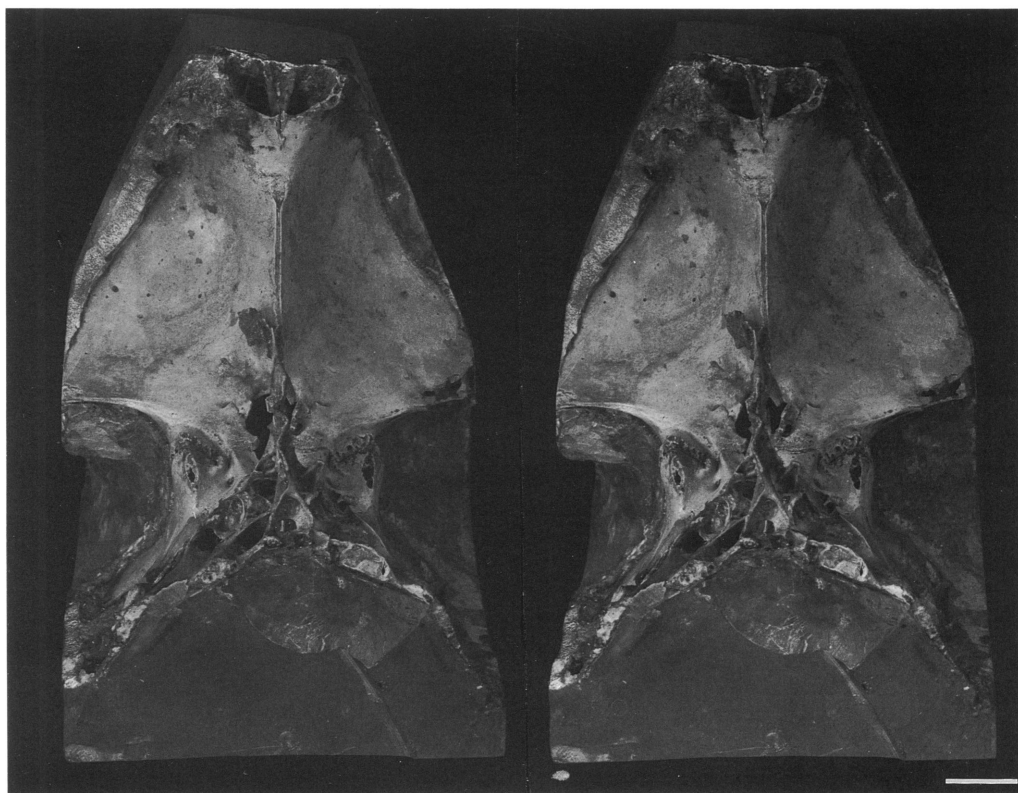The basioccipital of *Anhanguera* sp. is sim-

Fig. 12. *Anhanguera* sp. (MCT 1501-R). Stereophotographs of ventral view of braincase. Scale = 10 mm.

ilar to that of *T. wellnhoferi*. The occipital condyle, however, is not preserved in the anhanguerid specimen.

According to Bennett (1991), the lateral parts of the occipital condyle in *Pteranodon* are formed by the exoccipitals, differing from the condition in *Tapejara*. In *Anhanguera santanae*, the occipital condyle is apparently only formed by the basioccipital (Wellnhofer, 1985), while the condition in *Rhamphorhynchus* is not determined (Wellnhofer, 1975). In most archosaurs, the exoccipital participates in the occipital condyle, although the extent of this participation varies (e.g., see Chatterjee, 1991).

BASISPHENOID

The basisphenoid in *Tapejara wellnhoferi* is fused with the basioccipital (figs. 7, 8). Consequently, the suture lying between them has been obliterated. The upper part of the ba-

sisphenoid is expanded. Below, this bone is comparatively thin and forms the medial border of the postcranial fenestra, up to the point where it contacts the basipterygoid. Anteriorly, several bony struts connect the basisphenoid with the interorbital septum. This connection does not extend to the basal portion of the basisphenoid.

In the specimen of *Anhanguera* sp. studied here, only the upper portion of the basisphenoid (also fused with the basioccipital) is preserved, and thus provides no additional information (figs. 10, 11, 14, 15). There is, however, one anhanguerid skull housed at the Naturkunde Museum in Karlsruhe (Germany) where a thin, bony lamina originating from the basisphenoid (and possibly also part of the parasphenoid) joins the interorbital septum.

The basisphenoid is very poorly known in pterosaurs. Wellnhofer (1975: 11, fig. 4a) reconstructed this bone in *Rhamphorhynchus*
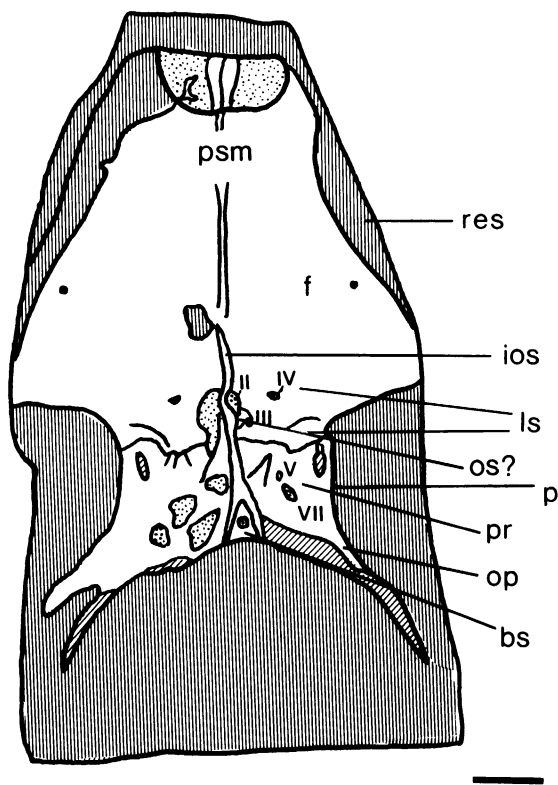
Fig. 13. *Anhanguera* sp. (MCT 1501-R). Ventral view of braincase. Scale = 10 mm.

as being essentially horizontal. In the rhamphorhynchoid specimens that I examined, however, the basisphenoid is elongated and anteroventrally directed, as seen in other pterosaurs (e.g., Wellnhofer, 1985; Campos and Kellner, 1985; Bennett, 1991).

In other archosaurs, the basisphenoid is not as elongated as in pterosaurs despite the fact that some have well-developed basipterygoid processes, as e.g., *Syntarsus* (Raath, 1985). In modern crocodilians, the main part of the basisphenoid is hidden by the quadrate and the pterygoids (Iordansky, 1973). In birds, the basipterygoid processes are reduced or lost (Chatterjee, 1991), contrasting to the well-developed basipterygoid processes in pterosaurs.

PSEUDOMESETHMOID

An ossified structure inserted between the medial part of the frontals was found in the

pterosaur braincases studied in this paper. This bone forms the anteromedial surface of the orbit and the interorbital septum (figs. 1–6), and is here called the pseudomesethmoid (see Discussion).

In *Tapejara wellnhoferi,* the pseudomesethmoid is expanded anteriorly and contacts the posteromedial portion of the lacrimal. On the left side, a tiny cylindrical ossified structure is preserved lying ventral to the anterior process of the pseudomesethmoid; its function is unknown. Toward the posterior end, the pseudomesethmoid forms a plate that gradually narrows and is enclosed by a posterior bony expansion, that is possibly formed by the frontals.

About 9 mm from its anterior margin, the pseudomesethmoid forms the interorbital septum, which is a bony plate directed ventrally. Posteriorly, the interorbital septum is connected with the basisphenoid by a series of bony struts. The anteroventral edge of the interorbital septum is very sharp but becomes more blunt toward the posterior region. The interorbital septum is connected with the orbitosphenoids and the laterosphenoids through bony processes.

In *Anhanguera* sp., the limits of the pseudomesethmoid with the surrounding bones, especially with the frontal, cannot be established because of fusion (figs. 10–15). Anteriorly, the pseudomesethmoid plate is less expanded than in *Tapejara wellnhoferi.* The anterior extension of the interorbital septum is not fully preserved but its presence can be determined by a sulcus on the midline of the skull. Posteriorly, the interorbital septum is formed by a very thin sagittal bony lamina, that is pierced by several openings, differing from the more robust bony plate found in *Tapejara wellnhoferi.*

The anteroventral region of the braincase can only be observed in a few pterosaur specimens. In one skull of *Tapejara wellnhoferi,* Wellnhofer and Kellner (1991) identified a bony plate at the anterior part of the braincase (still unprepared) as a questionable laterosphenoid. In light of the new information provided by the specimens studied here, this bone can be reidentified as the pseudomesethmoid. While redescribing *Pteranodon,* Bennett (1991) attributed the anteroventral ossification of the braincase as part of the laterosphenoid. The laterosphenoids, how-
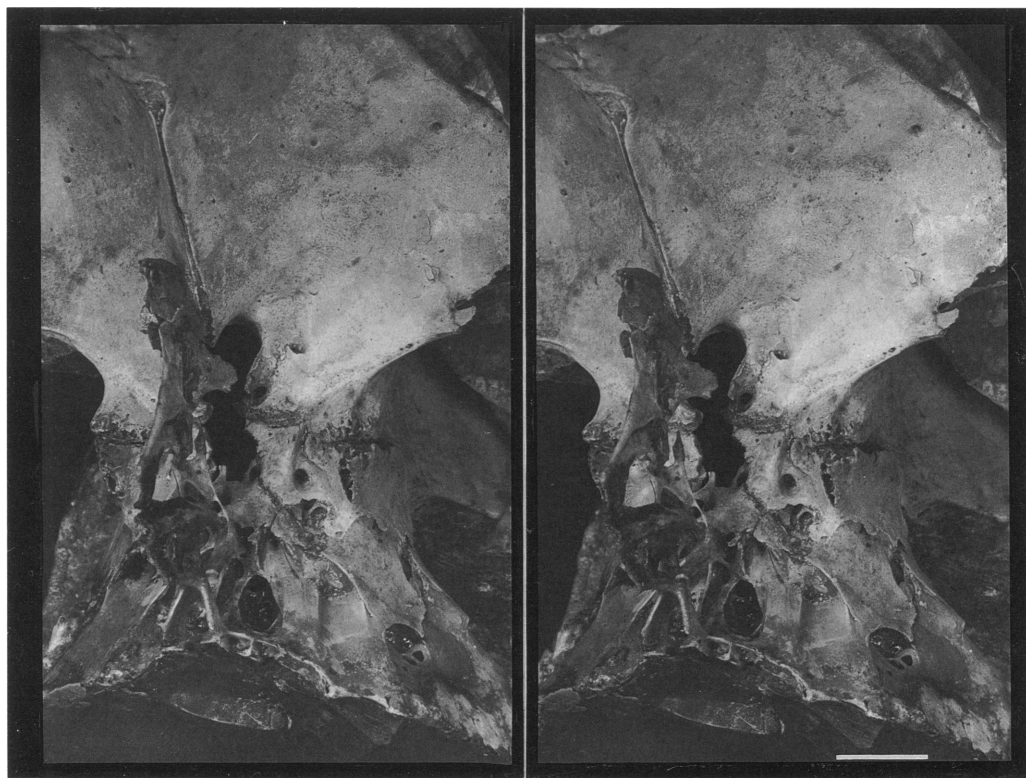
Fig. 14. *Anhanguera* sp. (MCT 1501-R). Detail of stereophotographs of ventrolateral oblique view of braincase, showing most cranial foramina. Scale = 10 mm.

ever, are paired elements anterior to the prootic but still confined to the posterior region of the orbit (e.g., Currie, 1985; Giffin et al., 1987; Chatterjee, 1991; Clark et al., 1993; Currie and Zhao, 1993a). Therefore, this anteroventral ossification of the braincase of *Pteranodon* might also be pseudomesethmoid.

LATEROSPHENOID

The laterosphenoid of *Tapejara wellnhoferi* contacts the frontal and the pseudomesethmoid anteriorly, the orbitosphenoid medially, and the parietal and the prootic posteriorly; the limits between those bones, however, are very difficult to establish in this specimen. A medially directed bony process connects the laterosphenoid with the interorbital septum. Posteriorly, this bone participates and is pierced by some openings for cranial nerves (see Cranial Nerves).

In *Anhanguera* sp. the contacts between the laterosphenoid and the frontals are not discernible, but posteriorly, a suture with the parietals can be partially observed. The laterosphenoid is expanded under the ventrolateral surface of the parietal and participates or encloses a foramen, situated inside the upper temporal opening. Compared to the same foramen in *Tapejara wellnhoferi,* the one in *Anhanguera* sp. is very large.

The laterosphenoid is not fused to the prootic, which lies posteroventrally. The suture between those bones is irregular; it starts medially between the openings for cranial nerves II and III, and runs posterolaterally until it reaches the laterosphenoid-parietal suture.

In most archosaurs, the laterosphenoid has a lateral process that joins the frontal and forms the articulation surface for the postorbital. Whether pterosaurs have the same lateral extension of the laterosphenoid can-
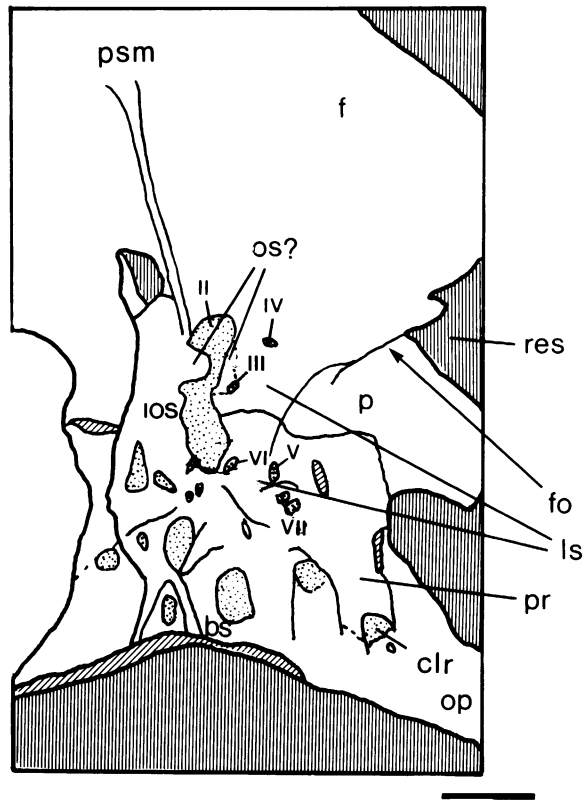
Fig. 15. *Anhanguera* sp. (MCT 1501-R). Detail of ventrolateral oblique view of braincase, showing most cranial foramina. Scale = 10 mm.

not be determined in the available specimens.

ORBITOSPHENOID

Two small and delicate ossifications lying within a large vacuity of the ventral portion of the cranial cavity and ventrally to the laterosphenoid are observed in the tapejarid braincase (MCT 1500-R). These paired bones fused at the midline, forming a rhomboid-shaped structure and are connected anteriorly with the interorbital septum, laterally and posteriorly with the laterosphenoid. Each of those bones, here interpreted as the orbitosphenoids, bears a small lateral foramen of unknown function. Posteriorly, they enclose a larger, medial, rounded foramen, which opens dorsally to the cranial cavity and ventrally to the interorbital fenestra, the latter connecting the orbits.

In the anhanguerid specimen, the orbitosphenoid is not fully preserved and was possibly destroyed before fossilization. Its presence, however, can be determined by the rugose medial margins of the laterosphenoid. Furthermore, there is a small, incomplete process on the anteromedial margin of the left laterosphenoid and another dorsal process of the interorbital septum; these are possibly part of the orbitosphenoid.

The orbitosphenoid is absent in crocodilians (Iordansky, 1973) and apparently also in several primitive archosauriforms (see Clark et al., 1993). The condition in birds is complex, with some authors (e.g., Jollie, 1957) regarding this area as composed of one bone (the orbitosphenoid), while others observed two distinct elements—a smaller medially placed orbitosphenoid and a larger laterally placed pleurosphenoid (e.g., Goodrich, 1930), the latter regarded as the laterosphenoid by

most workers on fossil archosauriforms (Clark et al., 1993). A distinct orbitosphenoid has been reported in several theropods (Madsen, 1976; Currie, 1985; Currie and Zhao, 1993a) and ornithischians (e.g., Giffin et al., 1987; Horner, 1992). Its presence in pterosaurs suggests that this bone has a wider distribution within archosaurs, and is present at least at the ornithodiran level.

PROOTIC

The prootic in *Tapejara wellnhoferi* is firmly fused with the neighboring bones, which obscure the contacts between them (figs. 3–6). Nevertheless, this bone has a very complex morphology and participates in several openings for cranial nerves.

In *Anhanguera* sp., the prootic lies between the laterosphenoid, parietal, and opisthotic (figs. 10–15). It forms the upper margin of the columellar recess and, as in *Tapejara wellnhoferi,* also participates in some foramina for the cranial nerves (see Cranial Nerves).

According to Chatterjee (1992), the prootic was articulated with the quadrate in another arhanguerid skull. This observation, however, could not be confirmed in MCT 1501-R, where the prootic slightly overlaps the opisthotic but not enough to meet the quadrate. In the tapejarid braincase, the lateral extension of the prootic cannot be determined. A prootic articulation is found in crocodylomorphs and ornithurine birds (Chatterjee, 1992) and is absent in theropods.

INTERMEDIATE FRONTAL LAMINAE

An extremely delicate structure was observed in a pneumatic space in front of the brain cavity of *Tapejara wellnhoferi,* posterior to the nasoantorbital fenestra (figs. 3, 4, 9). This structure is formed by two symmetrically displaced triangular bony plates (here called intermediate frontal laminae), which apparently are part of the frontal bone. They arise from the base of the medial portion of the frontals, and extend parallel to them. The intermediate frontal laminae are connected medially, but do not connect the frontal laterally, leaving a passage between them.

The intermediate frontal laminae are extremely thin and highly perforated, particularly in the center. Anteriorly, this structure is bordered on the ventral side by another equally delicate horizontal bony surface that is formed by the dorsolateral part of the pseudomesethmoid.

Toward the anterior region of the skull, each intermediate frontal lamina develops a shallow, but long process that runs through the ventral midline of the frontals. The contact between those processes is marked by a small groove, which is completely enclosed by them anteriorly.

Anhanguera sp. lacks the above-described structure. Instead, a septum formed by the frontals separates the two halves of the skull in front of the brain cavity. In the anterior region, this septum separates two oval channels (7 × 5 mm) that are bordered dorsally by the frontals and ventrally by the pseudomesethmoid. Those channels are connected with the nasoantorbital fenestra (figs. 12, 13). The interior of those channels is wrinkled, with several ridges on the lateroventral part (fig. 19). Those ridges run anteroposteriorly toward the septum and some are pierced by lateral openings.

The presence of the intermediate frontal laminae has never been recorded before in archosaurs (see Discussion).

SKULL CAVITY

The roof of the anhanguerid skull (MCT 1501-R) was removed, revealing the existence of a well-developed pneumatic space (interlaminar pneumatic cavity) between the external (exocranial) and internal (endocranial) lamina of the bones that form the skull roof (figs. 16, 17). After very delicate preparation, a complex system of trabeculae inside the interlaminar pneumatic cavity was exposed, which lies over the actual braincase (that contains the cranial cavity).

The trabecular system can be divided into two major areas. The anterior area is formed by a central bony plate, which extends vertically from the midline between the frontals and partially divides the anterior part of the interlaminar pneumatic cavity. On each side of this central plate, there are four more plates, which are displaced symmetrically with respect to the midline of the skull. All those plates end on the anterior margin of the braincase. Open spaces are found between them covered dorsally and ventrally by a meshwork of bony struts. Near the central

plate, two channels bordered by the frontals connect the interlaminar pneumatic cavity with the nasoantorbital fenestra.

The posterior area of the trabecular system is formed by a meshwork of bony struts, which, although more irregular, tend to be directed perpendicular to the sagittal plane of the skull.

Some parts of the trabeculae were removed and analyzed by Scanning Electron Microscopy (SEM). The cross section revealed that the trabeculae are formed by compact bone perforated by lacunae for osteocytes; the latter do not show any particular orientation (fig. 18).

Considering the topographic position of the bones forming the cranial cavity, the major part of the trabecular system is apparently formed by the frontal. Other bones that participate in the braincase, such as the parietal and the supraoccipital (perhaps also the exoccipital/opisthotic), appear to participate in the trabecular system as well, although the extent of this participation cannot be determined.

The braincase lies deep within the interlaminar pneumatic cavity. Its maximum length (parallel to the dorsal plane, excluding portion for the olfactory bulbs) is 29 mm; and its maximum width (between the lateral surface of the cerebral hemispheres) is 27 mm.

The most developed part of the braincase is formed by two comparatively large hemispheres, each lying lateral to the sagittal plane of the skull. Anteriorly, each bears a process, possibly for the olfactory bulbs. Posterodorsal to them, there is a small centrally positioned pealike structure. Lateroventral to this structure, the dorsal surface of the braincase expands until it joins the lateral sides of the interlaminar pneumatic cavity. Posteriorly, the braincase surface extends almost vertically, enclosing a relatively large channel.

Considering their positions and shapes, it is very likely that in life those structures surrounded the cerebral hemispheres dorsally, the cerebellum dorsoposteriorly, and the optic lobes laterally.

ADDITIONAL SKULL ELEMENT

On the left side of the anhanguerid specimen, above the columellar recess, a delicate, flat bone was found loosely embedded in the matrix (not illustrated). Because of its fragility, this bone was strengthened with layers of cyanoacrylate adhesive (super glue) diluted in acetone. This bone is incomplete and displays a very complex shape.

The unbroken end of this bone forms a flat surface, which is pierced on one side by two foramina. Toward the broken end, three processes are visible. The proximal one has a square outline; both remaining processes are rodlike and are separated by an angle of about 42°.

According to the position of this bone in the skull, it is probably part of the columella, including the stapes. If this interpretation is correct, it differs from the columella observed in Recent reptiles (Baird, 1970) and birds (Starck, 1995), by being more flattened and by having a more complex outline. Further preparation of this bone is necessary before a detailed description can be made.

FORAMINA FOR CRANIAL NERVES

The braincases described here are very pneumatic and exhibit several foramina. The interpretation of which foramen might be the passage for a particular cranial nerve is based on comparisons with Recent bird and crocodilian specimens, as well as with descriptions of other archosaur braincases.

There is no evidence of the pathway of the olfactory nerve (I) within the braincase of either specimen. This nerve possibly emerged through a large, medial opening positioned anterior to the laterosphenoid.

In *Tapejara wellnhoferi,* the optic nerve (II) passes through a large, single medial opening, bordered by the frontals, laterosphenoids, and orbitosphenoids (figs. 3–6). The interorbital septum is positioned ventral to this foramen and does not divide it, which is the case in some birds (Baumel and Witmer, 1993). Posteroventrally there is a smaller opening enclosed anteriorly by the orbitosphenoid and laterally by the laterosphenoid, that might have served as the passage for the oculomotor nerve (III).

Anhanguera sp. (figs. 10–15) has a configuration for the passages of the optic (II) and oculomotor (III) nerves similar to that of *Tapejara wellnhoferi.* The major difference is the comparatively smaller size of the foramen for the oculomotor nerve (only preserved on
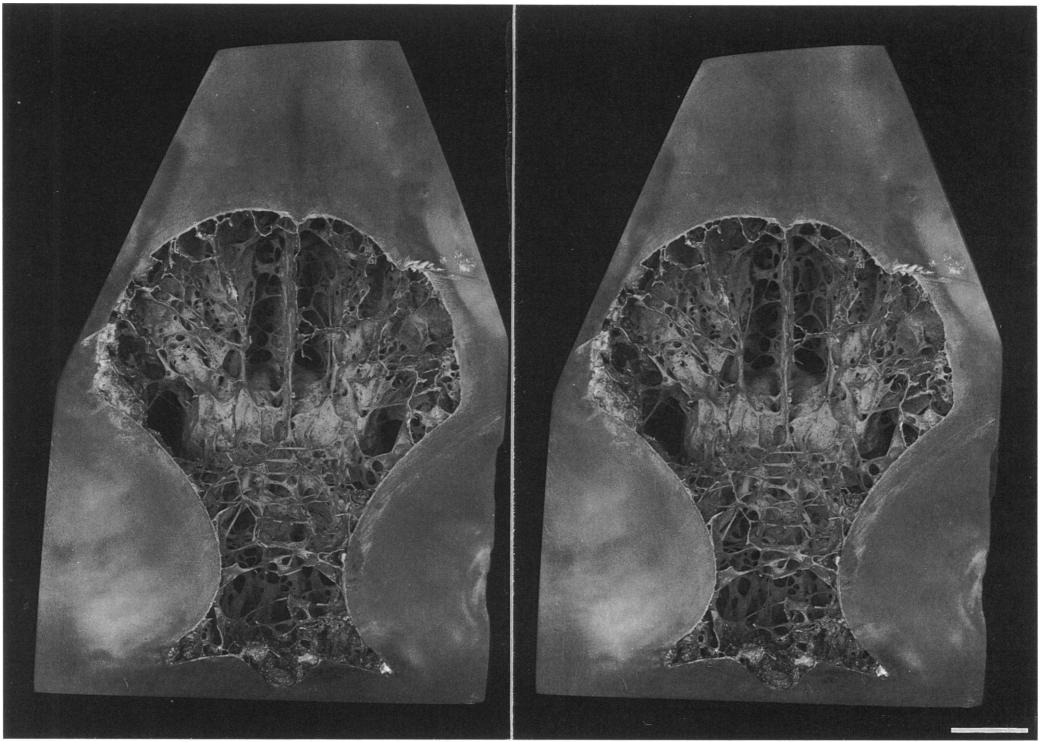
Fig. 16. *Anhanguera* sp. (MCT 1501-R). Stereophotographs of dorsal view, showing interlaminar pneumatic cavity after complete preparation. Scale = 10 mm.

the left side, where a process—possibly part of the orbitosphenoid—is connected with the laterosphenoid).

The foramen for the trochlear nerve (IV) in both braincases is much smaller than the previous ones and pierces the laterosphenoid. It is positioned anterolaterally to the foramen for the oculomotor nerve and lateral to the optic foramen (figs. 1–6, 10–15). In *Tapejara wellnhoferi* (figs. 1–6) the passage for the trochlear nerve is situated closer to the optic nerve than in *Anhanguera* sp. (figs. 10–15).

As in other archosaurs, the exit for the trigeminal nerves is positioned between the laterosphenoid and the prootic. The passages for the trigeminal nerve (V1, V2, V3) in *Tapejara wellnhoferi* are positioned inside a cavity bordered anteromedially by a curved, blunt ridge from the laterosphenoid which thickens medially; laterally, by a well-developed and sharp crest formed mainly by the prootic; and posteriorly by another crest formed by the laterosphenoid, that extends ventrally to a pointed process positioned lateral to the interorbital septum (figs. 5, 6). In this cavity, there are three foramina, which possibly represent independent passages for the ophthalmic, maxillary, and mandibular rami of the trigeminal. The smallest one is positioned anterolaterally with respect to the others. An elongated groove, directed toward the upper temporal opening, is present in front of the smaller foramen. Ventromedial to this foramen is another one, which is larger and has a similar but more marked groove. Both grooves are separated anteriorly by a pronounced ridge, which merges with the anteromedial margin of the upper temporal fenestra. The largest of all three foramina is positioned posteriorly and does not lead to any groove.

The configuration of the passages for the trigeminal nerve (V) in *Anhanguera* sp. differs from those described above. The cavity in which this cranial nerve is positioned is deeper and closer to the passages for the optic and oculomotor nerves. A single foramen for the trigeminal nerve is preserved. The lateral
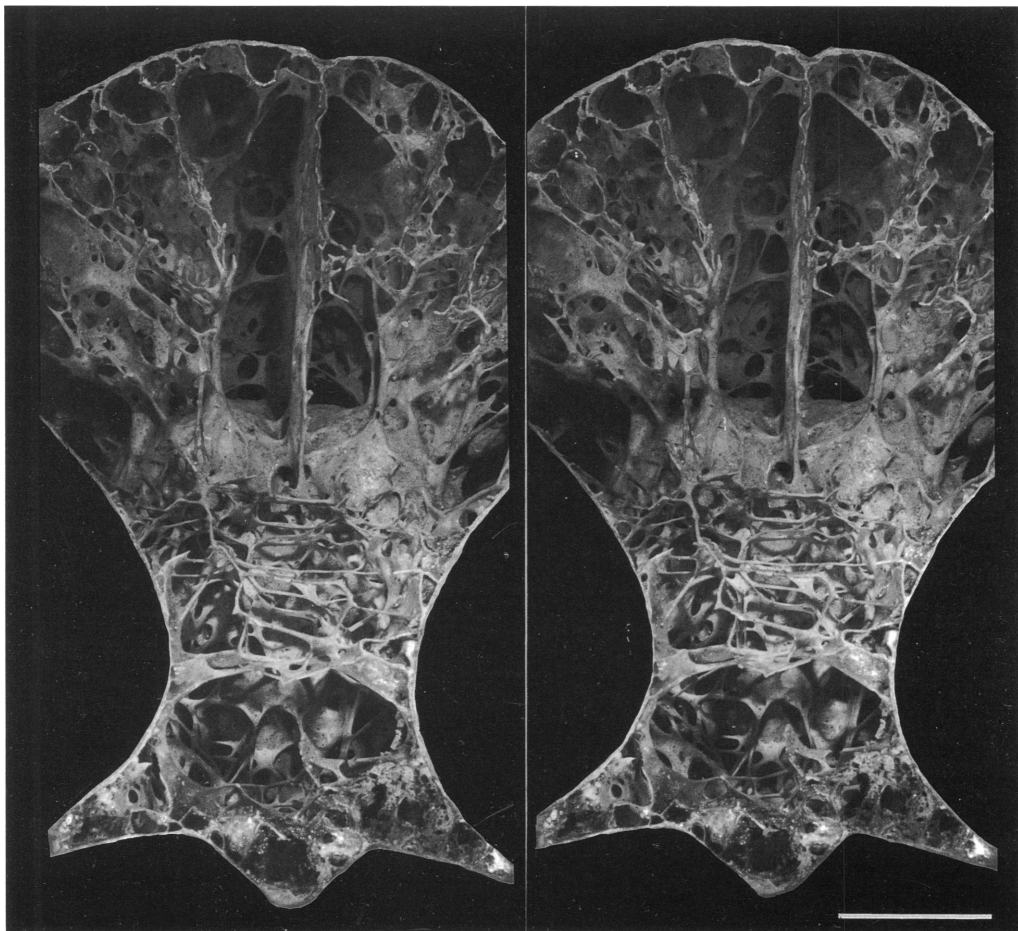
Fig. 17. *Anhanguera* sp. (MCT 1501-R). Enlarged stereophotographs of dorsal view, showing inter-laminar pneumatic cavity after complete preparation. Note position of braincase. Scale = 10 mm.

margin of the cavity containing the trigeminal nerve consists of two blunt processes, the anterior one formed by the laterosphenoid and the posterior one by the prootic.

The foramen for the abducens nerve (VI) in *Tapejara wellnhoferi* is present at the limits between the laterosphenoid and the basisphenoid (figs. 5, 6). A shallow, ventrally directed groove can be observed connected to this foramen on the left side.

In *Anhanguera* sp., the foramen for the abducens nerve (VI) is enclosed in a bony ring that is located at the medial margin of the laterosphenoid (figs. 14, 15).

The facial nerve (VII) in *Tapejara wellnhoferi* is located in a cavity posterior to the one that houses the trigeminal nerve, in the contact region of the opisthotic and the prootic (figs. 5, 6). There are at least three foramina, all leading into the braincase, which are possibly related to this nerve. This region in *Anhanguera* sp. is very similar, but the foramina are larger (figs. 14, 15).

The columellar recess of *Tapejara wellnhoferi* is rounded and has an external diameter of approximately 2 mm (figs. 5, 6). It forms a tube that is directed lateroventrally. The foramen ovale and the foramen for the acoustic nerve (VIII) cannot be observed in detail.

In *Anhanguera* sp., the columellar recess (figs. 14, 15), although not complete in this specimen, is not as well developed as in *T. wellnhoferi*.
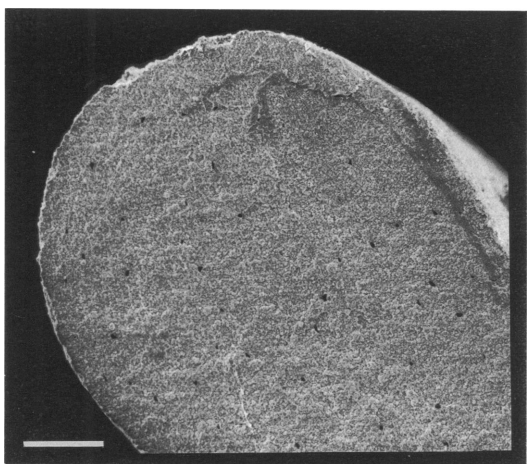
Fig. 18. Scanning electron micrograph of transverse section of a trabecula from *Anhanguera* sp. (MCT 1501-R). Scale = 50 μm.

In the occipital region of *Tapejara wellnhoferi,* lateral to the occipital condyle and bordered by the basioccipital and the exoccipital, a large opening encloses at least three foramina (four on the right side). Those foramina, which can also be seen from inside the foramen magnum, are very likely related to the passages for the hypoglossal (XII) nerve. Whether other cranial nerves [glossopharyngeal (IX), vagus (X), and accessorius (XI)] also pass through this opening cannot be determined (figs. 7, 8).

The same region in *Anhanguera* sp. is covered with polyester resin, which hinders a detailed examination.

The foramina for the cranial nerve could be observed in very few pterosaur braincases. Wellnhofer (1985) noticed a distinctive passage for the hypoglossal (XII) nerve above the occipital condyle, and interpreted the opening lateral to the occipital condyle as the passage for the cranial nerves IX, X, and XI. Such a position for the exit of XII has not been observed in the tapejarid braincase (MCT 1500-R). *Pteranodon* has a large foramen ventrolateral to the occipital condyle, which according to Bennett (1991) was the passage of cranial nerves IX to XII. Bennett (1991) also interpreted several other cranial foramina in *Pteranodon,* but which bones they relate to is not clear. The exit for the trigeminal (V) was described as positioned between the prootic and the supraoccipital (Bennett, 1991: 53). This is a very unusual position for the trigeminal, and, if correct, differs from usual position of this cranial nerve in other archosaurs and the pterosaur braincases described here.

SOFT TISSUE

During the preparation of the anhanguerid specimen (MCT 1501-R), some structures were found inside the brain cavity that were at least partially insoluble in the diluted formic acid solutions employed (figs. 20–23). Those structures consist of spongy layers that mimic the bone surface of the trabeculae and the braincase.

Examination of those structures by SEM shows that they present a different texture
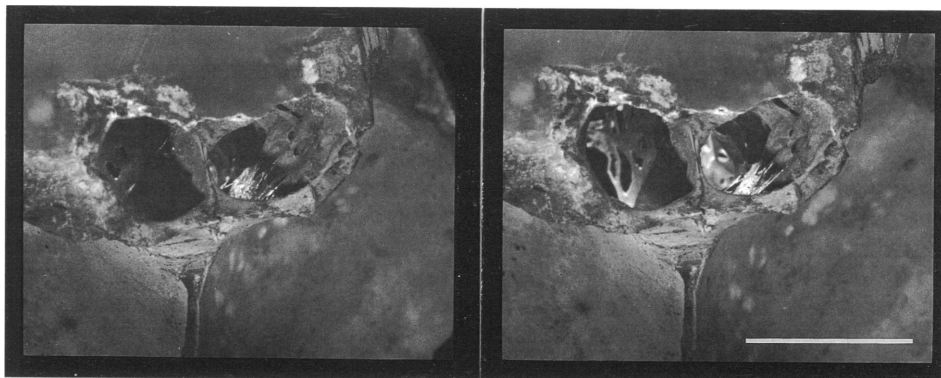

Fig. 19. *Anhanguera* sp. (MCT 1501-R). Stereophotographs of channels that connect interlaminar pneumatic cavity with nasoantorbital fenestra. Scale = 10 mm.

Fig. 20. *Anhanguera* sp. (MCT 1501-R). Polished ventral section of skull roof above braincase. Note trabeculae (dark), some of which are surrounded by a lighter material (preserved soft tissue?). Scale = 10 mm.

not natural) produced during acid preparation. Alternatively, they could represent mineralization of the soft tissue that was originally connected to the trabeculae. Neither these nor similar structures were found during acid preparation of other pterosaur material (personal obs.), including different parts of this same specimen (e.g., inside the orbital cavities). To my knowledge, none was reported in any other fossil vertebrate. Furthermore, the preservation of very delicate parts of soft tissues has been reported in several fossils from the Romualdo Member (the same unit where MCT 1501-R was found), which includes fishes (Martill, 1988), other pterosaurs (Martill and Unwin, 1989; Kellner, 1994b), dinosaurs (Kellner, 1996), and crocodilians (Kellner, 1994a).

Although the observations above are not conclusive, it seems very likely that the structures preserved in the anhanguerid specimen represent part of the soft tissue that covered the trabeculae inside the cranial cavity of this pterosaur.

DISCUSSION

The three-dimensionally preserved braincases from the Romualdo Member described here present new information that bears on different aspects of pterosaur paleobiology and anatomy. For clarity, each one will be treated separately.

HOMOLOGY OF THE PSEUDOMESETHMOID

The pseudomesethmoid, as defined here, is an ossified structure that forms the anteromedial surface of the orbit and the interorbital septum. Extant crocodilians have a cartilaginous interorbital septum that extends forward and forms the cartilaginous internasal septum. This cartilaginous structure further divides the nasal passages above the secondary palate (Iordansky, 1973), thus differing from the bony structure observed in the pterosaur braincases described in this paper. In no other archosaur has an ossified element closing the anteromedial surface of the orbit been reported, except in birds, where this bone is called the mesethmoid and forms an interorbital septum. This raises the possibility that the structure found in pterosaurs and in birds is homologous.
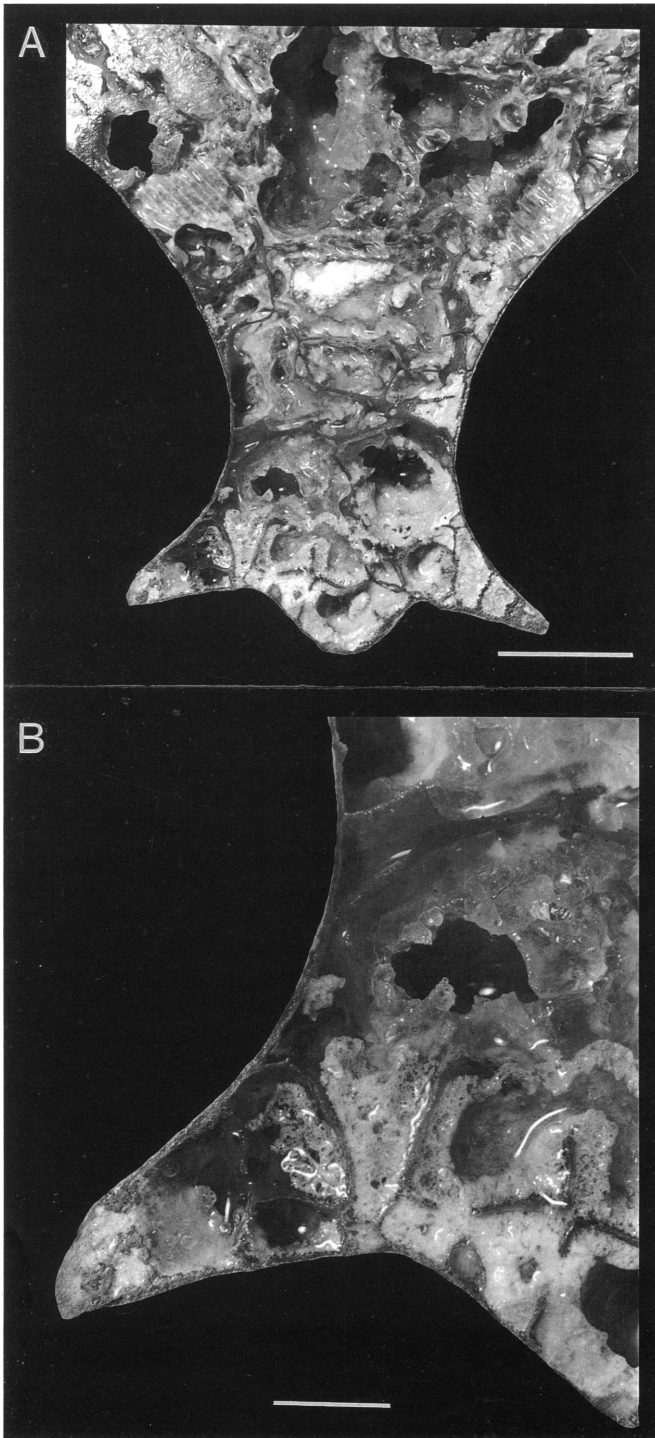
from the calcareous matrix (fig. 22A), and are directly associated with the trabeculae (figs. 20–22). They form concentric layers around cavities (figs. 22B, 23) which are interconnected, forming a complex network of openings inside the brain cavity. None of those (or similar structures) have been found inside the actual braincase.

Energy dispersive spectroscopy of carbon-coated samples from those structures shows that they are essentially formed by calcite. Phosphate is occasionally present, but in much lower quantities than in the bone.

There are two possible interpretations of those structures. They could be artifacts (i.e.,

Fig. 21. *Anhanguera* sp. (MCT 1501-R). **A,** Dorsal view showing interlaminar pneumatic cavity before complete preparation (2 hours in 3% diluted formic acid), scale = 10 mm; **B,** detail showing trabeculae with soft tissue, scale = 3 mm.
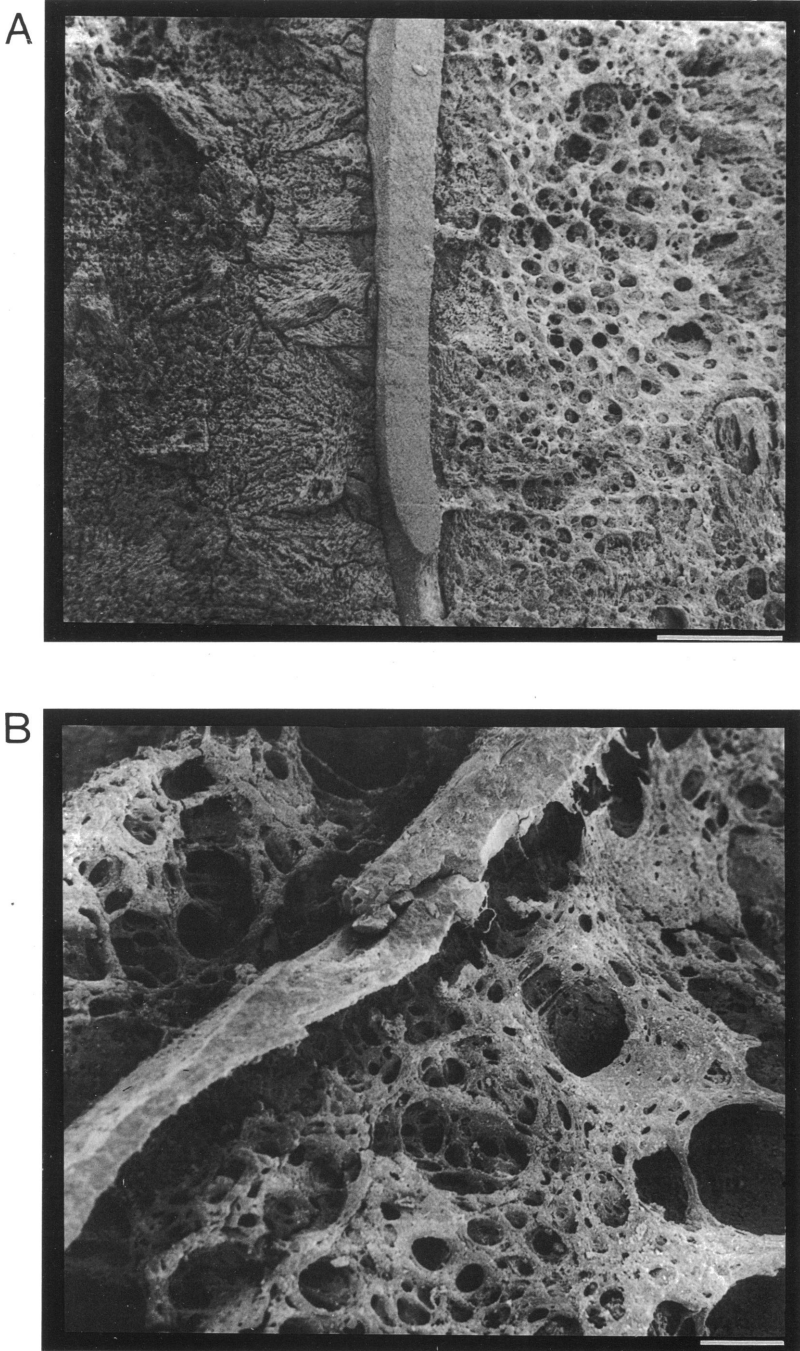
Fig. 22. Scanning electron micrograph of sample removed from cranial cavity of *Anhanguera* sp. (MCT 1501-R). **A,** Note calcareous matrix (left), trabecula (center), and soft tissue (right); **B,** another section, showing connection between soft tissue and trabecula. Scale = 200 μm.

As pointed out several times in the literature, homology is a fundamental concept of comparative biology (Bock, 1974) and central to any discussion about phylogeny (Patterson, 1982). Among the tests proposed by Patterson (1982) for homology is similarity
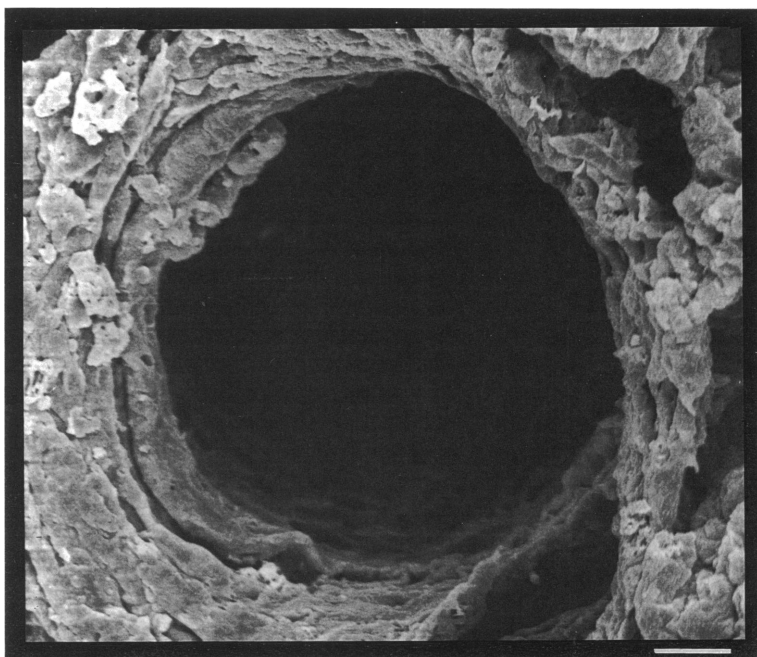
Fig. 23. Scanning electron micrograph of sample removed from *Anhanguera* sp. (MCT 1501-R). Detail of soft tissue. Scale = 10 μm.

(in fossils essentially restricted to the topography of the bones or elements and their relation to other structures), and congruence, i.e., agreement of a particular homology with other homologies. Some regard the latter as the only test in "the strict sense" (Pinna, 1991).

The avian mesethmoid tends to be very thick anteriorly, where it forms a triangular anterior bony plate, unlike the more delicate structure found in pterosaurs. Furthermore, it is exposed on the dorsal surface of the skull between the nasal processes of the premaxillae and frontals, and contacts the nasals ventrally (Jollie, 1957). The structure found in the pterosaur braincase does not contact the nasals or premaxillae, and is not exposed on the skull roof. Therefore, although it resembles the avian mesethmoid in its location and by forming an ossified interorbital septum, the structure observed in pterosaurs presents different relationships with other cranial bones, thus at least partly "failing" the test of similarity (sensu Patterson, 1982).

According to the current archosaurian phylogenetic hypothesis, pterosaurs are regarded as closely related to dinosaurs (Padian, 1984), being included in the Ornithodira (Gauthier, 1986), but excluded from Dinosauromorpha (Sereno, 1991). As pointed out before, no ossification of the anteromedial surface of the orbit has been observed in a dinosaur or in any other archosaur. Therefore, the ossified structure on this portion of the avian and pterosaur braincases very likely evolved independently. Otherwise, this structure would be regarded as a synapomorphy uniting pterosaurs and birds. Even in this case, because there are several synapomorphies arguing against a sister-group relationship between pterosaurs and birds, the avian mesethmoid fails the test of congruence (homology) with the pterosaurian structure (sensu Patterson, 1982).

Since osteological terminology should, whenever possible reflect homology (e.g., Clark et al., 1993), and in order to avoid any implication of homology with the avian mesethmoid, a new term (pseudomesethmoid) is here adopted for the pterosaurian structure.

PTEROSAURIAN ENDOCASTS

The braincase of pterosaurs is generally believed to enclose the brain very tightly, similar to the condition observed in mammals and in birds, but unlike the condition present in Recent reptiles (Hopson, 1979). Therefore, it has been assumed that an endocast of the braincase reflects the actual shape and structure of the brain (e.g., Seeley, 1871, 1901; Edinger, 1927, 1941; Jerison, 1973; Hopson, 1979; Langston, 1981; Wellnhofer, 1991b). Edinger (1941) also pointed out that the outside surface of the pterosaur skull could in many cases indicate the actual shape of the brain. The three-dimensional pterosaur braincases described in this paper provide a few caveats for those assumptions.

The anhanguerid specimen (MCT 1501-R) clearly shows that the actual cranial cavity, that comprises the brain, is positioned much deeper inside the skull than was previously supposed. The skull roof in this taxon is very pneumatic, with the external (exocranial) lamina separated from the internal (endocranial) lamina by a well-developed interlaminar pneumatic cavity. Although it is very likely that the bones surrounding the cranial cavity of this pterosaur might in fact enclose the brain very tightly, any endocast based on the inner surface of the exocranial lamina of the skull roof will not reflect the correct shape and proportions of the brain of this taxon.

The pterosaur endocasts studied so far are based on specimens that have been found isolated (Seeley, 1870; Lewy et al., 1992), unveiled by the removal of the external cranial bones (Newton, 1888), or artificially constructed by casting the inner side of the skull roof, formed by the exocranial lamina (Edinger, 1927). If the condition observed in the anhanguerid specimen is a general feature for pterosaurs, questions arise regarding whether the natural endocasts found so far reflect the internal morphology of the cranial cavity or just the morphology of the interlaminar pneumatic cavity positioned *above* the cranial cavity. It is also not clear if endocasts made directly from or associated with the exocranial lamina of the skull roof will reflect the inner surface of the braincase in the detail that has been claimed.

SHAPE AND PROPORTIONS OF THE BRAIN

Based on the assumption that pterosaur endocasts replicate the shape and proportions of the actual brain, most authors regarded the pterosaurian brain as birdlike (Seeley, 1870, 1871, 1901; Newton, 1888; Edinger, 1927, 1941; Langston, 1981; Wellnhofer, 1991b). Opposing views that considered pterosaur brains to be more reptilian, are essentially based on estimations of brain/body size relationships (Jerison, 1973), although they admit the birdlike specialization of parts of the pterosaurian central nervous system (Hopson, 1979).

The anhanguerid specimen described here clearly shows that the size of the actual cranial cavity is much smaller than the cavity enclosed by the exocranial lamina of the skull roof and the floor of the braincase. In other words, the pterosaur brain in this taxon was proportionally smaller than expected, occupying maximally (if it completely filled the cranial cavity) less than one-third of the volume inside the space between the exocranial laminae and the floor of the braincase. As a comparison, the endocast recovered from *Parapsicephalus purdoni* (Upper Lias, Jurassic, England), that has been used as a general model for pterosaur brains (Hopson, 1979; Wellnhofer, 1991b), occupies almost the entire space between the exocranial laminae and the floor of the braincase (Newton, 1888; Edinger, 1927; Hopson, 1979).

Despite the fact that the estimated dimensions of the anhanguerid cranial cavity are larger than the endocast of *Parapsicephalus* (which, according to Hopson, 1979, has the following dimensions: length 25 mm; width 17 mm; estimated total length of skull about 190 mm), the relative size of the cranial cavity is proportionally smaller in the Brazilian specimen since the skull is about three times longer. Although any generalization based on the estimated measurements above might be premature, it seems that either pterosaur cranial cavities tended not to grow very much during their evolution, or that the endocast preserved in *Parapsicephalus* that was exposed by the removal of external cranial bones (Newton, 1888) might not represent the correct dimensions of the actual cranial cavity.

A summary of the current knowledge regarding the shape, size, and relations between the different parts of the pterosaurian brain was provided by Hopson (1979), based essentially on the endocast preserved in *Parapsicephalus*. The olfactory bulbs are short, closely appressed, and not well developed, which has also been observed in many Recent birds (Bang and Cobb, 1968). The cerebral hemispheres are large, slightly longer than wide. The optic tectum is the widest part of the endocast and lies posterolateral to the cerebral hemispheres. It is overlain by a developed cerebellum which has large, posteriorly oriented floccular lobes. Edinger (1927) pointed out that those are much larger than lobes in similar-sized birds.

The shape of the braincase (formed by the endocranial lamina of the skull roof) in the anhanguerid specimen shows some features that are distinct from this general pattern of the pterosaur brain. Anterior to the cerebral hemispheres, there is a bony projection located above an empty space on the basal portion of the skull (figs. 16, 17). This projection might have concealed the olfactory bulbs. If this interpretation is correct, then the olfactory bulbs were comparatively small and positioned very deep in the braincase, similar, but longer than those observed in an endocast from the Cambridge Greensand (Cenomanian, England) described by Edinger (1927: 108). The cerebral hemispheres are well developed, divided along the sagittal plane, and longer anteroposteriorly than mediolaterally. The optic lobes are positioned posterolateral to the cerebral hemispheres. The cerebellum is small, rounded, and positioned on the posterior region of the cerebral hemispheres on the sagittal plane of the skull. The floccular lobes must have been positioned posteroventral to the cerebellum, and were not as expanded as had been pointed out before.

Considering the interpretations above, the position of the optic lobes and the reduced olfactory bulbs in the anhanguerid specimen are a condition paralleled in modern birds, conforming to previous models of pterosaur brain structure (e.g., Edinger, 1927; Hopson, 1979). The relative size, however, suggests that the pterosaur brain (at least in this taxon) was more reptilelike, even more so than was previously reported by Jerison (1973) and Hopson (1979).

INTERMEDIATE FRONTAL LAMINAE

The intermediate frontal laminae are placed anterior to the actual brain cavity in *Tapejara wellnhoferi*. They appear to have been developed in response to the rearrangement of the cranial bones that resulted from the expansion of the nasoantorbital fenestra in this taxon. Similar development of the nasoantorbital fenestra is present in all other members of the Tapejaridae and in *Quetzalcoatlus*, the only member of the Azhdarchidae in which the posterior part of the skull is known (Kellner and Langston, 1994). Although more evidence is needed, the presence of those structures might be a further shared-derived feature uniting tapejarids and azhdarchids, in which the dorsal margin of the nasoantorbital fenestra is higher than the dorsal margin of the orbit (Kellner, 1995b).

In *Anhanguera* sp., the intermediate frontal laminae are not observed. Instead, the area anterior to the brain cavity has two channels, divided by a septum, that extend inside the cranial cavity. Although tentative, those channels in the anhanguerid specimen might correspond to the lateral channels of the intermediate frontal laminae in *T. wellnhoferi*.

The function of the intermediate frontal laminae is unknown. It does not seem to be a supporting structure providing more strength to the skull, since such structures never occur alone (e.g., Wellnhofer, 1985, and personal obs.) and tend to be formed by struts of bones oriented along lines of forces. The intermediate frontal laminae differ from supporting struts in being more delicate and dissimilar in arrangement.

According to the position of the intermediate frontal laminae, they resemble the cribriform plate of mammals, which is functionally associated with nasal turbinals. The intermediate frontal laminae differ from the mammalian structure by being more delicate and not completely occupying the passage between the braincase (frontals and nasals) and the nasal cavity (confluent with the antorbital fenestra in derived pterosaurs).

CRANIAL TRABECULAE

The interlaminar pneumatic cavity with an associated system of trabeculae present inside the skull of the anhanguerid specimen has never been described before in a pterosaur.

The simplest and most compelling interpretation for this trabecular system in *Anhanguera* sp. is that it provides support for the cranial bones without adding much weight. Analogous structures are present in birds, where they are called sandwich structures (Bühler, 1972). Although widespread among birds, sandwich structures are not found in all taxa (Winkler, 1979) and can vary during ontogeny (Warncke and Stork, 1977). These structures range from one-storied (e.g., domestic pigeon) to multi-storied (owls), comprising concentric perforated layers of bone separated from each other by small trabeculae (Bühler, 1972, 1986). The trabecular system in the anhanguerid specimen (MCT 1501-R) differs by not being oriented horizontally, and by displaying several symmetrical vertical plates.

Other functions for sandwich structures include thermal protection. This was demonstrated in greenfinches, where the air present in the bone lamellae in conjunction with the skull feathers prevents heat loss (Warncke and Stork, 1977). To what extent a thermoregulatory function of the trabeculae structure might have been possible for *Anhanguera* sp. remains unknown.

Since this trabecular system is directly linked with the nasoantorbital fenestra, arguments might arise that it also related to the respiratory system. The connection between the cranial cavity and the nasoantorbital fenestra is made by two well-developed channels that follow the midline of the skull. The surface inside those channels is wrinkled, particularly near the lateroventral sides (fig. 19). They are further separated from each other by a sagittal bony wall that also has a wrinkled surface, and which extends posteriorly inside the interlaminar pneumatic cavity (fig. 17). Some of the structures inside the channels are reminiscent of avian nasal turbinates (Bang and Wenzel, 1985), which are indicative of endothermy (Ruben, 1995). The

major caveat for this interpretation is related to the position of those structures (directly in front of the braincase, posterior to the nasal bones) and the absence of information on whether structures inside the channels are also present in the medioventral surface of the nasals.

Due to the lack of investigations of braincases and the associated pneumatic system in other pterosaurs, there is no assurance that a developed trabecular system associated with the interlaminar pneumatic cavity of the skull roof is a common feature in this group. There is, however, some indirect evidence of its presence in other pterosaurs. Although no section through the braincase of the tapejarid specimen was made, it is clear from observations through some cranial foramina that the cranial cavity was housed deep within the skull in this taxon, and was very likely separated from the exocranial laminae of the skull roof by a system of trabeculae. Newton (1888: 510–511), while describing the endocast of *Parapsicephalus,* mentioned that the brain cavity in another pterosaur skull (not figured or further identified), that was sectioned longitudinally through the midline, was positioned "under a considerable thickness of open cancellous bone." Seeley (1901: 54–55) mentioned that he removed "the thick covering of the cellular bone which originally extended" above the pterosaur endocast from the Cambridge Greensand (Cenomanian) he described (but did not figure before preparation was concluded). More recently, Bennett (1991: 30) noted that the posterodorsal region of the skull in *Pteranodon* (Late Cretaceous) was "underlain by sinuses above and around the orbit and the braincase."

Based on the observations above, it is very likely that the presence of pneumatic spaces including a trabecular system above the actual braincase is a widespread feature among pterosaurs and not unique to anhanguerids. The presence of a pneumatic foramen piercing the supraoccipital, that is found in *Pteranodon,* anhanguerids, *Dsungaripterus,* and tapejarids (and also possibly present in other pterodactyloids like azhdarchids), could be indicative of such a pneumatic space inside the skull roof.

It also seems likely that all pterosaur groups

might not have developed such a pneumatic system above the cranial cavity, and that the trabecular system might vary as the sandwich structures vary in Recent birds. More detailed studies of pterosaur braincases, including sagittal sections through the skull, are needed to further understand the distribution of those features within pterosaurs.

FEATURES OF THE
PTEROSAUR BRAINCASES

The classification of pterosaurs within Archosauria presented by Romer (1956) is accepted by most authors, although different proposals of pterosaurian relationships have been suggested (see Wild, 1978, 1983). Despite discussion on which taxa should be included in Archosauria (see Gauthier, 1986; Benton and Clark, 1988), there is at least one feature listed by Benton and Clark (1988) as an autapomorphy of archosaurs that can be observed in the pterosaur braincase: the presence of an ossified laterosphenoid.

Although most researchers regard pterosaurs as ornithodirans (Gauthier, 1986; Sereno, 1991), no features of the braincase have been found to support this hypothesis. The pterosaur braincases studied here, however, show the presence of two fragile bones that are interpreted as the orbitosphenoids. Those bones have been reported in several dinosaur braincases and are absent in crocodilians and apparently also in more primitive archosaurs (= archosauriforms, see Clark et al., 1993). Although more detailed comparisons of archosaur braincases are needed, it is possible that the presence of ossified orbitosphenoids might be an autapomorphic character of the Ornithodira.

One of the most distinguishing features of pterosaur braincases is the fragility of the bones, which is paralleled only in birds. Most elements are very thin and exhibit a smooth surface, contrasting to several bones found in other archosaurs like dinosaurs and crocodilians.

Among the similar features shared by the pterosaur braincases studied here, the most outstanding is the presence of anteroventral ossification, that is here called the pseudomesethmoid. An ossification in this region of the skull is absent in dinosaurs, crocodilians, and other primitive archosaurs (or archosauriforms); it is found only in modern birds, where it is called the mesethmoid. As discussed previously, it is unlikely that the avian mesethmoid is homologous to the pterosaurian pseudomesethmoid.

Another common feature of pterosaur braincases is the elongated and anteroventrally directed basisphenoid, that bears well-developed basipterygoid processes. In most other archosaurs, including modern birds, the basisphenoid is more horizontal and proportionally shorter (see Chatterjee, 1991).

The supraoccipital in the pterodactyloid pterosaurs (when observed) are expanded, forming most of the upper part of the occiput. This differs from most archosaurs but also from more "primitive" pterosaurs, as *Rhamphorhynchus* (based on the reconstruction presented by Wellnhofer, 1975).

Although both braincases studied here show a similar arrangement of skull elements, there are several differences between them. The most significant is in the region between the cranial cavity and the nasoantorbital fenestra. This area is expanded in tapejarids, probably in conjunction with the expansion of the nasoantorbital fenestra and the development of a sagittal crest on the posterior region of the skull. In anhanguerids, the posterior sagittal crest is very low and blunt.

Another difference lies in the configuration of the pseudomesethmoid. In *Tapejara wellnhoferi,* the anterior part of this bone is more expanded laterally than in *Anhanguera* sp. The interorbital septum (formed by the pseudomesethmoid) in *Tapejara wellnhoferi* is more massive. In the anhanguerid specimen, it is more delicate and perforated by more and comparatively larger openings that connect the orbits.

The positions of the foramina for cranial nerves are very similar in both pterosaur braincases, except for the trochlear nerve (IV), which is more close to the optic nerve (II) in the anhanguerid specimen, and the trigeminal nerve (V), which has distinct passages in the tapejarid specimen.

ACKNOWLEDGMENTS

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