Part II: The skull

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ABSTRACT

One of the earliest known complete dentitions and skulls of a metatherian mammal are represented by *Pucadelphys andinus* MARSHALL & MUIZON, (1988) from the early Paleocene age Santa Lucía Formation at Tiupampa (type locality of the Tiupampan Land Mammal Age) in southcentral Bolivia. A detailed analysis of the dentition, dentary and skull reveals that the vast majority of states in *Pucadelphys* can be regarded as mammalian and/or tribosphenid plesiomorphies, while metatherian synapomorphies include: cheek tooth formula of P3/3+ M4/4; prootic canal reduced in length and width, and does not open endocranially; prootic sinus continues onto squamosal side of petromastoid within a deep sulcus; presence of sphenoparietal emissary vein which occupies deep sulcus on squamosal side of petromastoid, is continuous with sulcus for prootic sinus, and exits skull through postglenoid foramen; length/width ratio of fenestra vestibuli 1.4; and absence of stapedial artery. *Pucadelphys* lacks an ossified alisphenoid bulla, but has what is interpreted to be a small anterior lamina of the petromastoid and a large foramen ovale (exit of V3) which opens between the anterior lamina and alisphenoid. The presence of an anterior lamina of the petromastoid fused to the pars petrosa associated to the presence of an anteroposteriorly expanded alisphenoid in *Pucadelphys* seems to contradict the hypothesis of PRESLEY & STEEL (1976) and PRESLEY (1981) on the evolution of the tribosphenid middle ear and lateral wall of the skull based on ontogenetic studies. This is the first record of an anterior lamina in a tribosphenid fossil mammal. The molar structure of *Pucadelphys* is indistinguishable from members of the family Didelphidae, and it is placed in this family, within the Order Didelphimorphia. *Pucadelphys* represents a classic example of mosaic evolution and illustrates that we have much to learn about early metatherian and tribosphenid evolution.

RÉSUMÉ

Deuxième partie : le crâne

Les crânes et dentitions de *Pucadelphys andinus* MARSHALL & MUIZON, (1988) décrits dans ce travail sont parmi les plus anciens connus chez les métathériens. Ils proviennent du Paléocène inférieur de la Formation Santa Lucía à Tiupampa (localité-type de l'âge de mammifères continentaux, Tiupampien) en Bolivie centrale. Une analyse détaillée de la dentition, du dentaire et du crâne révèle que la grande majorité des états de *Pucadelphys* peuvent être considérés comme des plésiomorphies au sein de mammifères et/ou des tribosphénides. Les synapomorphies de métathérien sont : dents jugales au nombre de P 3/3 et M 4/4; canal prootique réduit en longueur et en largeur, ne s'ouvrant pas à l'intérieur du crâne; sinus prootique se prolongeant sur la face squamosale du pétromastoïde dans un profond sillon; présence d'une veine émissaire sphénopariétale occupant un profond sillon sur la face squamosale du pétromastoïde, en continuité avec le sillon pour le sinus prootique et sortant du crâne à travers le foramen postglénoïde; rapport longueur/largeur de la fenêtre vestibulaire de 1,4; absence d'artère stapédiale. *Pucadelphys* ne possède pas de processus tympanique de l'alisphénoïde mais possède une petite lame antérieure du pétromastoïde et un grand foramen ovale (sortie du V3) qui s'ouvre entre la lame antérieure et l'alisphénoïde. La présence, chez *Pucadelphys*, d'une lame antérieure du pétromastoïde fusionnée à la pars petrosa et associée à la présence d'un alisphénoïde dilaté antéro-postérieurement, semble contredire l'hypothèse de PRESLEY & STEEL, (1981) et PRESLEY (1981) sur l'évolution de l'oreille moyenne et de la paroi crânienne des tribosphénides, fondée sur des études ontogénétiques. Il s'agit du premier signalement d'une lame antérieure du pétromastoïde chez un mammifère tribosphénide fossile. La structure des molaires de *Pucadelphys* est indifférenciable de celle des membres de la famille des Didelphidae et ce genre est rangé dans cette famille au sein de l'ordre des Didelphimorphia. *Pucadelphys* représente un exemple classique d'évolution en mosaïque et illustre bien que nous avons encore beaucoup à apprendre sur les débuts de l'évolution des métathériens et des tribosphénides.

RÉSUMÉ DÉVELOPPÉ

Les os crâniens et basicrâniens de mammifères sont des éléments très importants dans les reconstructions phylogénétiques. Toutefois, très peu de crânes de mammifères tribosphénides sont connus pour le mésozoïque et le Paléocène inférieur et aucun crâne de métathérien incontesté n'est connu au mésozoïque. Plusieurs squelettes et crânes d'un marsupial Didelphidae (*Pucadelphys andinus*) ont été découverts dans le Paléocène inférieur de la Formation Santa Lucía (Bolivie) et constituent, avec celui de *Mayulestes ferox* (un borhyaenoïde provenant du même gisement), les plus anciens crânes complets connus rattachés avec sécurité à ce groupe de mammifères.

Dans ce travail nous présentons une description détaillée des crânes de *Pucadelphys andinus* MARSHALL & MUIZON (1988), nous discutons ses principaux caractères crâniens et les analysons dans une optique orientée vers la compréhension de la phylogénie des tribosphénides (Marsupiaux et Placentaires). Sont décrits successivement les dents supérieures, les dents inférieures, le dentaire et le crâne.

Famille Didelphidae
Pucadelphys andinus MARSHALL & MUIZON, 1988

DESCRIPTION

La formule dentaire de *Pucadelphys andinus* est I 5/4, C1/1, P 3/3, M4/4. Les incisives supérieures sont disposées en série continue et sont jointives. Elles sont croissantes de I1 à I4 et I5 est réduite. Les prémolaires sont biradiculées et présentent une forte augmentation de taille de P1 à P3. Elles ont une couronne simple constituée d'une grande cuspide triangulaire et d'un minuscule talon postérieur. La P3 est haute et sa couronne descend nettement plus bas que le plan occlusal des molaires. Les molaires supérieures sont triangulaires et présentent un paracône plus petit que le métacône (pour M1-M3), une centrocrista en V et un protocône relativement gros avec un bord postérieur renflé. La métacrista est petite mais légèrement plus grande que la paracrista. La plateforme stylaire est développée et possède des styles bien marqués. Les incisives inférieures sont de taille croissante de i1 à i4 et sont jointives. Les prémolaires inférieures sont semblables aux supérieures. Les molaires inférieures possèdent un trigonide élevé plus large que long. Le protoconide est légèrement plus grand que le métaconide, lequel est nettement plus développé que

le paraconide. La protocristide, droite et tranchante, est orientée transversalement. Le talonide possède un bassin profond et des cuspides bien marquées, entoconide et hypoconulide étant distinctement accolés. Le dentaire présente une branche horizontale longue et gracile, une fosse massétérine peu profonde, un vaste processus coronoïde et un condyle situé au-dessus du plan occlusal. Le crâne possède un museau court et obtus. Les arcades zygomatiques sont grandes et montrent une orbite en communication avec la fosse temporale. Il possède une légère crête sagittale pariétale et une crête lambdoïde marquée. Les nasaux sont allongés et présentent un forte dilatation de leur extrémité postérieure. Les prémaxillaires sont graciles et sont perforés ventralement par des foramens incisifs allongés, lesquels affectent également les maxillaires. L'arc dentaire est presque semi-circulaire. Les maxillaires possèdent une ouverture du canal infraorbitaire située au-dessus de P3. Le palatin possède un fort torus postpalatin situé en arrière de M5. En vue ventrale, maxillaires et palatins ne présentent pas de foramens palatins. Le lacrimal forme le bord antérieur de l'orbite; il est grand et s'étend largement sur la face dorsale du rostre. Le jugal est un os gracile, sigmoïde qui participe à l'élaboration de la cavité glénoïde. Le frontal occupe environ le tiers du crâne en vue dorsale et latérale. Il porte parfois un petit processus supraorbitaire et participe à la formation du foramen ethmoïdien. Le pariétal est une vaste plaque osseuse qui constitue la majeure partie du toit et des parois de la cavité crânienne. L'orbitosphénoïde est un os petit qui possède un grand foramen sphénorbitaire situé à sa jonction avec le frontal et le palatin. L'alisphénoïde forme la région antérieure et latérale de la boîte crânienne. Cet os participe à la formation de trois foramens. Le foramen ovale est énorme et se situe entre le bord postérieur de l'alisphénoïde et le bord antérieur du pétromastoïde, médialement à la cavité glénoïde. Antéro-médialement, le foramen entocarotidien est bordé latéralement par l'alisphénoïde et médialement par le basisphénoïde. Un foramen rotundum bien marqué s'observe antérieurement. Il n'existe pas de processus tympanique de l'alisphénoïde. Le squamosal présente une cavité glénoïde profonde et allongée transversalement, munie d'un grand processus postglénoïde et d'un petit processus préglénoïde. Le squamosal possède quatre foramens sur sa face externe : 1) le foramen postzygomatique, sur le bord postérieur de la racine postérieure de l'arcade zygomatique, dorsalement à l'apex du processus postglénoïde, 2) le foramen subsquamosal qui s'ouvre dorsalement au méat auditif externe, 3) le foramen postglénoïde, le plus grand, dont l'ouverture est située sur le flanc postérieur de la racine postérieure de l'arcade zygomatique, 4) le foramen posttemporal qui s'ouvre entre le squamosal et la pars mastoidea du pétromastoïde. Ventralement, le squamosal participe à la formation du bord latéral du foramen ovale. Le pétromastoïde est un os complexe formé de la pars petrosa et la pars mastoidea. Cette dernière affleure largement sur la face postérieure du crâne entre l'exoccipital, le squamosal et le supraoccipital. Ventralement, la pars mastoidea participe à la formation de la moitié latérale du petit processus exoccipital et, latéralement, forme un processus mastoïde relativement grand. Le bord ventral de la pars mastoidea forme une lèvre dirigée antéro-ventralement qui constitue le processus tympanique caudal (*sensu* WIBLE, 1990). Il forme une partie du plancher du sinus mastoïde épitympanique. Une échancrure stylomastoïdienne bien marquée s'observe latéralement au processus mastoïde; elle donne passage au nerf facial et à la veine latérale de la tête. Le bord latéral du processus mastoïde s'étend antéro-dorsalement, séparant le bord latéral du sinus mastoïde épitympanique de la fossa incudis, située dans la région postérieure du récessus épitympanique. La pars petrosa présente un grand promontoire lisse et piriforme dont l'apex est dirigé antéro-médialement. Il est bordé antéro-médialement par un sinus marqué correspondant au passage de la carotide interne se dirigeant vers le foramen carotidien; latéralement au sinus carotidien se trouve la fosse du muscle tensor tympani. Le bord médial du promontoire présente un sillon interne marqué pour le passage du sinus pétreux inférieur. Sur la face latérale du promontoire, la fenêtre ovale se situe à la hauteur du bord postéro-dorsal du méat auditif externe; son rapport longueur/largeur est de 1,4. Antéro-latéralement à la fenêtre ovale, dans le sillon qui borde latéralement le promontoire, se trouve l'ouverture postérieure du canal facial secondaire. Latéralement à cette ouverture, se trouve un petit foramen, l'ouverture médiale du canal prootique. Le récessus épitympanique est une petite dépression allongée située latéralement au canal facial; son extrémité postérieure est la fossa incudis. Sur la face dorsale ou cérébelleuse du pétromastoïde s'observe une grande fossa subarcuata et le méat auditif interne. Quatre sillons entourent le corps du pétromastoïde sur sa face cérébellaire : 1) ventro-médialement, le sillon pour le sinus pétreux inférieur, 2) postéro-ventralement, un sillon vertical pour le sinus jugulaire, 3) postéro-dorsalement une petite poche représente le sillon pour le sinus sigmoïde, 4) le long du bord dorso-latéral se trouve un sillon allongé pour le sinus prootique. Antéro-latéralement à la crista petrosa, dans une aile osseuse se projetant antéro-dorsalement, se trouve une dépression pour le lobe temporal du cerveau et le ganglion trigéminé. Chez les autres Didelphidae le ganglion repose sur l'alisphénoïde et il n'existe pas de projection osseuse. Cette aile antéro-latérale du pétromastoïde contribue au plancher et au bord interne de la paroi crânienne. Elle représente apparemment une relique de la lame antérieure du pétreux (*sensu* CROMPTON & JENKINS, 1979). Sur la face ventrale du pétromastoïde, un contact irrégulier s'observe entre le bord antéro-latéral du promontoire et la plateforme osseuse qui constitue le bord postérieur du foramen ovale. Cette portion représente aussi probablement une partie de la lame antérieure du pétromastoïde. Sur la face latérale de l'os, on observe un sillon profond et large qui recevait le sinus prootique; à son extrémité ventrale, un petit foramen correspond au débouché latéral du canal prootique.

DISCUSSION

La comparaison des crânes de *Pucadelphys* est problématique du fait de l'absence de crânes de marsupiaux fossiles du Tertiaire ancien ou du Crétacé qui soient raisonnablement bien connus. *Asiatherium* du Crétacé supérieur de Mongolie (SZALAY, 1993) est probablement un marsupial mais sa description détaillée est en cours et, de surcroît, cette espèce est loin de faire l'unanimité quant à son attribution aux métathériens. *Mayulestes ferox* MUIZON (1994) du même âge et du même gisement que *Pucadelphys*, est connu par un crâne remarquablement complet mais sa description détaillée est en cours. En revanche il existe de nombreux restes dentaires de marsupiaux dans le Crétacé supérieur d'Amérique du Nord et dans le Paléocène d'Amérique du Sud. La discussion comprendra donc une première partie qui comparera les dents de *Pucadelphys* aux formes voisines d'Amériques du Nord et du Sud, et une seconde partie qui passera en revue les principaux caractères crâniens de *Pucadelphys* afin d'en déterminer la polarité et qui tentera d'analyser les modalités de l'évolution du crâne chez les Theria et plus précisément chez les Tribosphenida.

COMPARAISON DENTAIRE. — Parmi les Didelphidae fossiles d'Amérique du Sud, *Sternbergia itaboraiensis* du Paléocène "moyen" d'Itaboraí (Brésil) est l'espèce qui se rapproche le plus de *Pucadelphys andinus* par la taille et la structure de ses dents à tel point que la première constitue un ancêtre morphologique idéal pour la seconde. *Pucadelphys* et *Sternbergia*, en plus de leur structure dentaire presque identique, possèdent la même morphologie du protocône renflé postérieurement, et le même important développement des styles B et C. Les molaires de *Sternbergia* diffèrent toutefois de celles de *Pucadelphys* par leur bassin du trigone, moins profond, leur paracône, plus réduit, leur centrocrista formant un V plus marqué, leur plateforme stylaire, plus petite, leur talonide, plus large, leur trigonide, plus bas, leur hypoconulide et entoconide, plus grands et par la présence d'un cingulum labial.

Deux autres Didelphidae d'Itaboraí présentent d'importantes ressemblances structurales avec *Pucadelphys* ; ce sont : *Marmosopsis juradoi* et *Itaboraidelphys camposi*. Bien que dans ces cas la ressemblance ne soit pas aussi frappante que pour *Sternbergia*, *Pucadelphys* pourrait également représenter un bon ancêtre morphologique pour ces deux genres.

Pucadelphys montre également d'intéressantes ressemblances avec plusieurs espèces d'*Alphadon* et de *Protalphadon* d'Amérique du Nord, genres classés parmi les Peradectidae par MARSHALL *et al.* (1989). Les trois genres présentent des structures dentaires similaires mais *Pucadelphys* diffère des deux formes nord-américaines par la possession d'une centrocrista en V, d'un paracône plus petit que le métacône (ils sont sub-égaux chez *Alphadon* et *Protalphadon*) et d'un protocône à flanc postérieur renflé, trois caractères de Didelphidae. En fait, *Alphadon marshi* représente un bon ancêtre structural pour les Didelphidae (CLEMENS, 1966) et donc pour *Pucadelphys*. Cette interprétation confirme l'hypothèse de CLEMENS (1966) et de CROCHET (1980) qui pensent que les Didelphidae pourraient avoir leur origine parmi les Peradectidae nord-américains. Il est d'ailleurs intéressant de constater que certains spécimens d'*Alphadon marshi* ont une centrocrista en V et un paracône plus petit que le métacône (CIFELLI, 1990 : 315).

ANALYSE DE CARACTÈRES. — Sont passés en revue et discutés ci-dessous les états de caractères qui paraissent importants pour la compréhension de l'évolution des mammifères. Ils seront présentés dans l'ordre suivant : dentition, dentaire, os du crâne, foramens crâniens, et région auditive.

CARACTÈRES DENTAIRES

Nombre d'incisives. — *Pucadelphys* présente l'état plésiomorphe qui est la possession de 5/4 incisives.

Structure des incisives supérieures. — *Pucadelphys* est plésiomorphe par la morphologie conique de ses incisives qui sont d'une hauteur subégale.

Structure des incisives inférieures. — Tous les Didelphidae actuels ont une i3 dont la racine est décalée en quinconce vers l'arrière. Cette disposition est absente chez *Pucadelphys* qui retient donc l'état plésiomorphe pour ce caractère.

Nombre de molaires et prémolaires. — *Pucadelphys* présente P3/3 et M4/4, ce qui constitue l'état plésiomorphe de ce caractère au sein des marsupiaux.

Structure des molaires et prémolaires. — Avec une centrocrista en V, un paracône plus petit que le métacône et un protocône renflé postérieurement, *Pucadelphys* est en parfait accord avec la structure dentaire observée chez les Didelphidae.

DENTAIRE

Processus angulaire infléchi. — *Pucadelphys*, qui possède une telle structure, présente l'état plésiomorphe de ce caractère au sein des Tribosphenida.

Sillon mylohyoïdien. — La présence d'un sillon mylohyoïdien chez *Pucadelphys* est une plésiomorphie au sein des mammifères.

Foramen mandibulaire labial. — L'absence de ce type de foramen chez *Pucadelphys* représente l'état apomorphe de ce caractère puisqu'il existe chez la plupart des mammifères primitifs comme *Kielantherium*, *Prokennalestes*, *Oetlestes*, et *Zalambdalestes*. Sa présence chez *Microbiotherium gallegoense*, un Microbiotheriidae du Miocène inférieur d'Argentine, constitue probablement une réversion.

OS DU CRÂNE

Orbite grande et confluente avec la fosse temporale. — *Pucadelphys*, qui présente la condition observée sur tous les crânes de thériens du Crétacé, est plésiomorphe pour ce caractère.

Lacrimal. — Un lacrimal possédant une grande aile faciale est un état plésiomorphe présent chez *Pucadelphys*.

Contact nasal-lacrimal. — Un contact maxillaire-frontal est l'état plésiomorphe de ce caractère qui se rencontre chez les cynodontes, les tritylodontes, les multituberculés, *Morganucodon*, *Vincelestes*, et *Deltatheridium*. Il existe également chez les Borhyaenoidea (probablement un état plésiomorphe) et chez le vombatoïde *Wynyardia* (probablement une réversion). *Pucadelphys*, avec un net contact nasal-lacrimal, présente donc l'état dérivé de ce caractère.

Contact alisphénoïde-pariétal. — *Pucadelphys* présente un large contact entre l'alisphénoïde et le pariétal, ce qui constitue l'état plésiomorphe de ce caractère.

Fosses palatines. — L'absence de fosses palatines chez *Pucadelphys* est un état plésiomorphe qui existe également chez les cynodontes, les monotrèmes, les multituberculés, *Vincelestes*, *Deltatheridium*, et chez de nombreux métathériens.

Processus préglénoïde du frontal. — Cette plésiomorphie probable des Tribosphenida est présente chez *Pucadelphys*.

FORAMENS DU CRÂNE

Canal transverse. — Cette structure est absente chez *Morganucodon*, les monotrèmes, les multituberculés, les Deltatheroida, les Borhyaenoidea, certains Didelphidae, certains Dasyuridae et *Pucadelphys*, et constitue l'état plésiomorphe au sein des mammifères. Un canal transverse est présent chez tous les autres marsupiaux.

Foramen ovale. — Le terme de foramen ovale est ici utilisé pour désigner le passage de la branche mandibulaire du trijumeau (V3) indépendamment des os qu'il traverse. Le terme de foramen pseudovale utilisé par plusieurs auteurs (MacINTYRE, 1967; ARCHER, 1976a) est extrêmement confus car souvent utilisé avec des sens différents.

Foramen subsquamosal. — La présence de ce foramen chez *Pucadelphys* est un état plésiomorphe retrouvé chez tous les métathériens et chez les euthériens crétacés, *Asioryctes* et *Kennalestes*.

Foramen postzygomatique. — La présence de ce foramen chez *Pucadelphys* est une plésiomorphie qui se retrouve chez tous les marsupiaux.

RÉGION AUDITIVE

Bulle tympanique ossifiée. — *Pucadelphys* ne possède pas de processus tympanique de l'alisphénoïde. L'absence de bulle tympanique ossifiée représente apparemment l'état plésiomorphe chez les mammifères (NOVACEK, 1977). L'absence de processus tympanique de l'alisphénoïde est une plésiomorphie chez *Pucadelphys* (et non une réversion, comme cela fut supposé par MARSHALL & KIELAN-JAWOROWSKA, 1992) et l'étude du crâne de *Mayulestes*, qui ne possède pas non plus de processus tympanique de l'alisphénoïde, suggère que ce caractère est apparu plusieurs fois au cours de l'évolution des marsupiaux (MUIZON, 1994).

Orientation de l'ectotympanique et de la membrane tympanique. — Les avis divergent sur la position primitive de l'ectotympanique. Pour NOVACEK (1977), la position primitive est subhorizontale car cette disposition est présente chez les monotrèmes et chez *Lambdopsalis* et parce que l'ectotympnique est subhorizontal dans les stades précoces du développement ontogénique de tous les mammifères. Pour KIELAN-JAWOROWSKA (1981) l'ectotympanique est primitivement orienté à 45° car c'est la position de l'angulaire (= ectotympanique) chez les cynodontes et chez *Morganucodon*. De plus, l'ectotympanique des euthériens *Asioryctes* et *Kennalestes*, qui fut retrouvé *in situ* sur certains spécimens, présente une position à 45° de l'horizontale. Bien que l'ectotympanique de *Pucadelphys* soit inconnu, la position de la fenêtre ovale laisse supposer qu'il avait une position subverticale comme chez tous les autres marsupiaux. Quel que soit l'état plésiomorphe de ce caractère, la condition de *Pucadelphys* serait donc dérivée.

Sinus auditif. — L'absence de sinus auditifs chez *Pucadelphys*, qui sont en général abondants et vastes chez la plupart des autres marsupiaux, est un état plésiomorphe au sein du groupe.

Contribution de la pars mastoidea à l'occiput. — Cet état, présent chez *Pucadelphys* ainsi que chez de nombreux autres mammifères, est apparemment une plésiomorphie pour les Tribosphenida.

Mastoïde et processus paroccipital. — L'absence de processus paroccipital et la petite taille du processus mastoïde, comme cela se rencontre chez *Pucadelphys*, représentent apparemment un état primitif pour les mammifères.

Forme de la fenêtre ovale et de la base du stapes. — Avec un rapport longueur/largeur de la fenêtre ovale de 1,4, *Pucadelphys* est voisin de la condition plésiomorphe pour les marsupiaux.

Artère stapédiale. — L'artère stapédiale est présente chez les embryons de tous les mammifères actuels mais seulement chez les adultes d'*Ornithorhynchus* et d'euthériens. Son parcours, marqué par un profond sillon sur le promontoire, a été mis en évidence chez les multituberculés et chez de nombreux euthériens fossiles. L'artère stapédiale disparaît chez les marsupiaux adultes, lesquels ne présentent pas de sillon sur le promontoire et sont caractérisés par cette synapomorphie. La présence d'une artère stapédiale chez l'adulte est une plésiomorphie chez les mammifères et l'absence de sillon du promontoire (perte de l'artère stapédiale) chez *Pucadelphys* serait indicateur d'un état apomorphe au sein des mammifères mais plésiomorphe au sein des marsupiaux.

Cours de la carotide interne. — Le cours de ce vaisseau chez *Pucadelphys* est situé sur le bord médial du promontoire. Cette disposition est également présente chez tous les autres marsupiaux, chez les monotrèmes, chez les euthériens du Crétacé supérieur d'Asie et chez certains euthériens actuels (rongeurs, lagomorphes, ongulés) et constitue l'état plésiomorphe (PRESLEY, 1979). L'état apomorphe, où la carotide interne est latérale au promontoire, existe chez tous les autres euthériens et a dû apparaître plusieurs fois au cours de l'évolution. *Pucadelphys* retient donc l'état plésiomorphe pour ce caractère.

Sillon pour le nerf facial. — La présence d'un sillon pour le nerf facial, chez *Pucadelphys*, est une plésiomorphie au sein des mammifères.

Sinus et foramen pétreux inférieurs. — La présence de ces structures chez *Pucadelphys* constitue une plésiomorphie au sein des mammifères.

Lame antérieure. — Le pétromastoïde de *Pucadelphys* possède une lame antéro-latérale qui participe à la formation de la paroi interne de la boîte crânienne. À la hauteur de cette lame, la paroi externe du crâne est formée par l'alisphénoïde et le squamosal. Médialement cette lame possède une fosse qui recevait très probablement le ganglion trigéminé. Chez des mammifères primitifs comme *Morganucodon*, *Haldanodon*, les multituberculés, *Vincelestes* et les monotrèmes, le pétromastoïde présente une grande lame antérieure qui participe seule à la formation de la paroi latérale du crâne. Elle s'articule antérieurement avec le bord postérieur de l'alisphénoïde et sa face médiale présente une fosse qui recevait le ganglion trigéminé. Chez les marsupiaux et les placentaires actuels, il n'existe pas de lame antérieure du pétromastoïde et, seul, l'alisphénoïde participe à la construction de la paroi latérale du crâne. WIBLE (1990) a cependant noté qu'il existait parfois chez certains marsupiaux, une structure extrêmement réduite qui pourrait représenter une relique de la lame antérieure des mammifères primitifs. La structure laminaire observée chez *Pucadelphys*, laquelle possède sur sa face médiale la même fosse pour le ganglion trigéminé que celle observée chez les mammifères non-tribosphéniques cités plus haut et qui occupe la même position que chez ces formes, est ici considérée comme homologue de la lame antérieure. La présence chez *Pucadelphys* d'une lame antérieure encore bien développée, quoique nettement plus réduite que chez les mammifères non tribosphéniques, semble démontrer que la réduction et la disparition de la lame antérieure du pétromastoïde est une synapomorphie des Tribosphenida, comme l'avait mentionné WIBLE (1990). *Pucadelphys* représente une étape intermédiaire dans cette réduction: chez ce genre, la lame antérieure est expulsée de la face externe de la paroi latérale du crâne par l'apparition d'une articulation du squamosal avec l'alisphénoïde mais reste toujours présente, bien que réduite, sur la face interne de la paroi latérale du crâne. A ce stade, la paroi latérale du crâne, dans la région antérieure du pétromastoïde, est donc une double lame dont la portion latérale est formée par le squamosal et l'alisphénoïde et la portion médiale par la lame antérieure du pétromastoïde. Le stade suivant (marsupiaux et placentaires actuels) voit la disparition de la lame antérieure. *Pucadelphys* est donc la démonstration paléontologique de la polarité d'un caractère important de l'évolution de la paroi crânienne des mammifères et confirme les hypothèses de WIBLE (1990) et de HOPSON & ROUGIER (1993).

CONCLUSIONS

Le crâne de *Pucadelphys* représente un cas classique d'évolution en mosaïque. *Pucadelphys* possède de nombreux caractères plésiomorphes de marsupiaux, de Tribosphenida, de thériens et de Mammifères. Il possède néanmoins des caractères apomorphes qui tendent à le rapprocher de la famille des Didelphidae. La présence d'une lame antérieure du pétromastoïde est un caractère plésiomorphe pour un marsupial qui tendrait à en faire le groupe frère de tous les autres marsupiaux et donc à le placer dans un taxon nouveau; en fait *Pucadelphys* présente déjà l'apomorphie des Tribosphenida consistant en une réduction de la lame antérieure du pétromastoïde, une structure qui a pu disparaître plusieurs fois au cours de l'évolution de ce groupe. L'absence de processus tympanique de l'alisphénoïde (structure longtemps considérée comme une synapomorphie des marsupiaux) tendrait également à en faire le groupe frère plésiomorphe pour ce caractère de tous les autres marsupiaux ou à envisager une réversion. En fait, l'étude de *Mayulestes ferox*, un borhyaenoïde du même gisement que *Pucadelphys* et ne possédant pas de processus tympanique de l'alisphénoïde, a montré que cette structure était sans doute apparue plusieurs fois au cours de l'évolution des marsupiaux et ne constitue pas un obstacle à la classification de *Pucadelphys* parmi les Didelphidae.

Les seuls caractères dérivés, au sein des marsupiaux, que possède *Pucadelphys* sont ceux de la structure de ses molaires supérieures qui le rangent sans équivoque au sein des Didelphidae.

INTRODUCTION

Skulls and basicranial bones of mammals are very important in phylogenetic studies, yet these elements are extremely rare in rocks of Cretaceous and earliest Paleocene Age. Because of a dearth of such specimens, little is known of the early cranial evolution of Tribosphenida (metatherians, eutherians and their common ancestors with tribosphenic dentitions; *sensu* MCKENNA, 1975). In fact, the character states of skull features in the direct common ancestor of metatherians and eutherians are unknown, yet inferences about these states have been made based on study of a few late Cretaceous specimens and of Cenozoic and living taxa (KEMP, 1982; 1983).

To date, there are only two non-tribosphenid therians for which cranial material is known. One is a eupantothere from the late Jurassic of Portugal, *Henkelotherium guimarotae* which is represented by a very partial skull associated with a nearly complete skeleton (HENKEL & KREBS, 1977; KREBS, 1987; KREBS, 1991), and the other is the eupantothere *Vincelestes neuquenianus* from the early Cretaceous of Argentina, which is known from nearly complete skulls and skeletons which have not yet been fully described (BONAPARTE & ROUGIER, 1987; ROUGIER & BONAPARTE, 1988; ROUGIER *et al.*, 1992; HOPSON & ROUGIER, 1993).

Eutherians are the best known of late Cretaceous tribosphenids, and complete or partial skulls of *Asioryctes*, *Barunlestes*, *Kennalestes* and *Zalambdalestes* have been described from the ?late Santonian and/or Campanian of Asia (KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980).

In sharp contrast, basicranial remains of metatherians from the late Cretaceous are extremely rare. Deltatheroida, the possible plesiomorphic sister-group of marsupials (KIELAN-JAWOROWSKA & NESSOV, 1990; MARSHALL & KIELAN-JAWOROWSKA, 1992) are known by several partial skulls and by one almost complete skull (e.g. ANONYMOUS, 1983), although the basicranial region has not been described. Specimens of metatherians which have been described include a right ventrolateral corner of a skull of *Eodelphis browni* (Stagodontidae) from the Belly River Formation of Alberta (MATTHEW, 1916); a left ventrolateral corner of a skull of *Didelphodon vorax* (Stagodontidae) from the Lance Formation of Wyoming (CLEMENS, 1966; a second ear region described by CLEMENS as *D. vorax* is a multituberculate; see WIBLE, 1990); a nearly complete left petromastoid from the Hell Creek Formation of Montana which ARCHIBALD (1979) described as either *Pediomys hatcheri*, *P. florencae* or *Alphadon rhaister* but which WIBLE (1990) calls Petrosal Type D (possibly *A. rhaister*); and ten petromastoids from the late Cretaceous of North America which WIBLE (1990) refers to as Petrosal Type A (one specimen, probably *Pediomys hatcheri* or *P. florencae*), B (one specimen, possibly *P. hatcheri* or *P. florencae*), and C (eight specimens, indeterminate). Recently TROFIMOV & SZALAY (1993) gave a short presentation of a new marsupial from the late Cretaceous of Mongolia. The specimen is an almost complete skeleton of a *Monodelphis scalops* -sized animal which has a marsupial dental formula and marsupial features in its dental morphology. In the early Paleocene of the Santa Lucía Formation (Bolivia) another specimen of early Metatheria is a partial skeleton of a new borhyaenoid, *Mayulestes ferox*, MUIZON, 1994, which includes a very complete skull. As mentioned in its preliminary description, the skull of *Mayulestes* bears several features that question the traditional definition of Metatherians.

In this part of the volume we describe nearly complete skulls of the metatherian *Pucadelphys andinus* MARSHALL & MUIZON (1988) from the early Paleocene age Santa Lucía Formation (*sensu* GAYET *et al.*, 1992) at Tiupampa in southcentral Bolivia (Fig. 1). With a nearly complete undescribed skull of a deltatheroid from the late Cretaceous of Asia (ANONYMOUS, 1983; KIELAN-JAWOROWSKA & NESSOV, 1990), the marsupial skeleton mentioned above (TROFIMOV & SZALAY, 1993), and the skeleton of *Mayulestes*, these are among the earliest complete skulls of metatherians (or possible metatherians) yet known. As shown below, these skulls reveal numerous character states which have important bearing on the phylogenetics of Metatheria, in particular, and on Tribosphenida, in general. The postcranial skeleton is described in the part III of this volume (MARSHALL & SIGOGNEAU-RUSSELL, 1995).

ABBREVIATIONS OF INSTITUTIONS. — MNHN, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris; YPFB Pal, paleontology collection of Yacimientos Petrolíferos Fiscales de Bolivia in the Centro de Tecnología Petrolera, Santa Cruz, Bolivia.

SYSTEMATIC PALEONTOLOGY

Serial designation for teeth follows LUCKETT (1992) contra ARCHER (1978), HERSHKOVITZ (1982), MARSHALL & MUIZON (1988) and MUIZON (1992) (i.e. premolars are P1, P2, P3; deciduous tooth is dP3; permanent molars are M1, M2, M3, M4); terminology for molar structure is shown in Figure 5; usage of Metatheria follows MARSHALL *et al.* (1989), [although we admit that the Deltatheroida could possibly be included in this taxon as recommended by KIELAN-JAWOROWSKA & NESSOV (1990) and MARSHALL & KIELAN-JAWOROWSKA (1992); usage of Theria follows KIELAN-JAWOROWSKA *et al.* (1987), and Tribosphenida follows McKENNA (1975); suprageneric ranks of Metatheria follows MARSHALL *et al.* (1989). All measurements are in millimeters (mm). Abbreviations of teeth are as follows: c, lower canine; C, upper canine; i, lower incisor; I, upper incisor; m, lower molar; M, upper molar; p, lower premolar; P, upper premolar.

Legion TRIBOSPHENIDA McKenna, 1975
Infraclass METATHERIA Huxley, 1880
Order DIDELPHIMORPHIA (Gill, 1872) Marshall *et al.*, 1989
Family DIDELPHIDAE Gray, 1821
Genus *PUCADELPHYS* Marshall & Muizon, 1988

TYPE-SPECIES. — *Pucadelphys andinus* MARSHALL & MUIZON, 1988
DIAGNOSIS. — Same as for type and only known species.

Pucadelphys andinus MARSHALL & MUIZON, 1988

HOLOTYPE. — YPFB Pal 6105, a nearly complete skull (missing part of left zygomatic arch) and associated dentaries with alveoli of I2-5, and I1 and C1-M4 present on right side; alveoli of I1 and I3-5, crowns of I2 and C1, roots of P1, P2 missing, posterior half of P3, and M1-4 present on left side; right dentary missing ventromedial edge of horizontal ramus with alveoli of i1 and i4, root of i2, complete i3, complete c1-m4 (p3 not fully erupted); posterior part of left dentary

RIGHT UPPER MOLAR

LEFT LOWER MOLAR
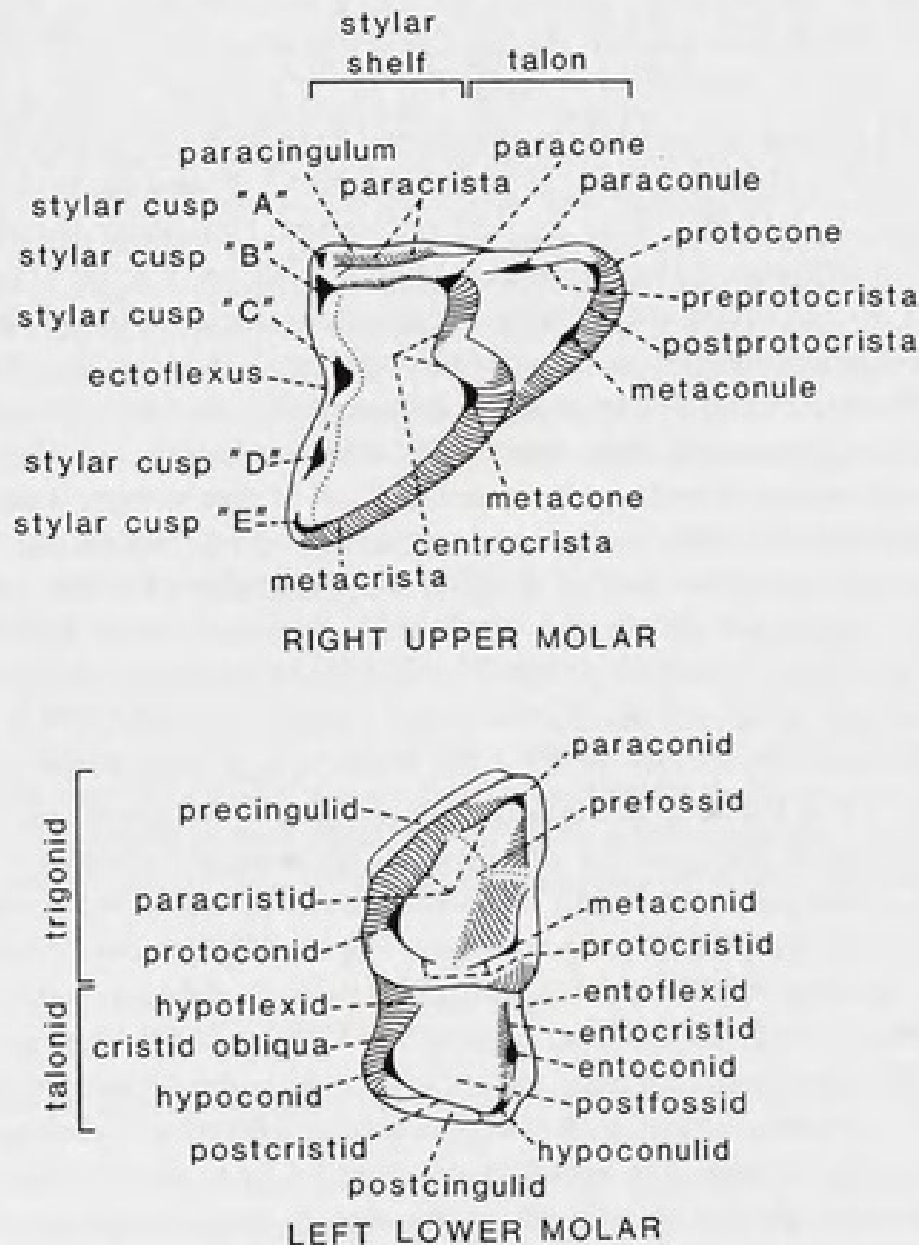
FIG. 5. — Terminology for molar structure of a generalized marsupial (after MARSHALL, 1987).

FIG. 5. — *Terminologie de la structure des molaires d'un marsupial primitif (d'après MARSHALL, 1987).*

with m1-4; and associated articulated partial skeleton of neck and thoracic regions (figured by MARSHALL & MUIZON, 1988, Figs 1, 3A).

HYPODIGM. — The holotype, YPFB Pal 6105; YPFB Pal 6107, greater part of skull and articulated dentaries with root of right C1 and complete right P1-M4 and p2- m4, complete left C1-M4 and c1-m4, and palatal and basicranial part of skull crushed slightly internally; YPFB Pal 6108, greater part of dorsoventrally crushed skull with associated dentaries, with complete C1-M4, alveoli of i1-4 and c1-m4 present (missing tips of p3 and m3 protoconid) on right side, and root of C1, complete P1-M4, root of c1, alveoli of p1, p2-3 present (missing all but bases of crowns) and m2-4 present (m2 missing tips of para-and metaconid, m4 missing tip of paraconid) on left side; YPFB Pal 6109, rostral part of skull with right C1-P3 and trigon of M2, left P1-M4 (figured by MARSHALL & MUIZON, 1988, fig. 3B), greater part of left dentary with bases of c1 and p1, and p2-m4 complete (figured by MARSHALL & MUIZON, 1988, fig. 3C); YPFB Pal 6110, greater part of skull and articulated dentaries with most of dentition (missing only I1-5, left P1 and tip of left p2) and part of articulated thoracic region of skeleton (figured by MARSHALL & MUIZON, 1988, fig. 2); YPFB Pal 6470, anterior part of skull (dorsoventrally crushed) with left I2 complete, alveoli of I1 and I3-5, complete C1-M4, right C1-M4 complete, basicranium with complete right petromastoid and four articulated vertebrae, anterior half of right dentary with c1 and p2-m2 complete, and alveoli of p1, and greater part of left dentary with i1 complete, alveoli of i2-4, c1 complete, roots of p1, and p2-m4 present (trigonid of m4 missing); YPFB Pal 6471, premaxilla with right C1-P1, fragment of left maxilla with M2-4 complete and attached zygomatic arch with glenoid fossa, exoccipital region of skull with three articulated vertebrae, anterior ends of left and right dentaries with c1-p1 in each, and posterior part of left dentary with m3-4; YPFB Pal 6472, right maxilla and premaxilla with complete C1-M4, complete right dentary with bases of i1-4, and complete c1-m4; YPFB Pal 6473, left maxilla with complete M1-4, greater part of left dentary with root of i1, base of i2, complete i3-4, c1 missing tip of crown, and virtually complete p1-m4; YPFB Pal 6474, greater part of left dentary of juvenile with three incisors and alveolus of a fourth, c1 erupting, p2 and m2 complete, and trigonid of erupting m3; YPFB Pal 6475, right maxilla with M1-4 (M2 missing anterolabial corner of crown); YPFB Pal 6476, right maxilla with M2-4; YPFB Pal 6477, right maxilla with M2-3 and parastyle of M4; YPFB Pal 6478, right maxilla with M2-3; YPFB Pal 6479, anterior part of right dentary with c1-p3 complete and broken base of m1; YPFB Pal 6480, fragment of a right dentary with posterior half of p3, complete m1, and trigonid of m2; YPFB Pal 6481, fragment of right dentary with m3-4 (trigonids broken on both); YPFB Pal 6482, fragment of right dentary with m1 missing trigonid and complete m2; YPFB Pal 6483 (=MNHN Vil 118), an isolated left m2 missing tip of paraconid (figured by MUIZON et al., 1984, fig. 8); YPFB Pal 6484 (=MNHN Vil 127), an isolated left m4 missing tip of metaconid and posterior edge of entoconid (figured by MUIZON et al., 1984, fig. 9); YPFB Pal 6485, fragment of left maxilla with broken roots of C1-P1 and complete P2-M4.

HORIZON AND LOCALITY. — The specimens of *Pucadelphys andinus* described here were recovered from the Santa Lucía Formation (*sensu* GAYET *et al.*, 1992) at Tiupampa, located about 95 km southeast of Cochabamba (see MARSHALL *et al.*, part I of this volume).

AGE. — Tiupampan Land Mammal Age (*sensu* ORTIZ JAUREGUIZAR & PASCUAL, 1989; MARSHALL, 1989), early Paleocene (VAN VALEN, 1988; GAYET *et al.*, 1992; BONAPARTE *et al.*, 1993; MUIZON & BRITO, 1993; MARSHALL *et al.*, part I of this volume).

DIAGNOSIS (skull morphology only). — I5/4 C1/1 P3/3 M4/4; I1-5 in continuous series (no diastem); i3 not staggered; cheek teeth structure as in Didelphidae: paracone smaller in size in occlusal view and distinctly lower in lateral view than metacone; centrocrista V-shaped with apex of V pointing labially toward stylar cusp C; stylar shelf well developed; stylar cusp B highest of stylar cusps; stylar cusps A, C and D subequal in size and only slightly smaller than stylar cusp B; parastyle spur-like, extends anteriorly and overhangs posterolabial edge of preceding tooth; remnant of mylohyoid groove; large medially inflected angular process; rostrum short; secondary palate solid (no evidence of vacuities) and extends posteriorly to point behind M4; nasals narrow anteriorly, much expanded posteriorly with W-shaped contact with frontals; small frontal-maxilla contact; lacrimal with large facial wing; lacrimal canal large, opens within orbit; orbit confluent with temporal fossa; jugal participates in formation of preglenoid process; glenoid fossa situated posteriorly opposite anterior half of promontorium; subsquamosal foramen present; tympanic area uncovered, no evidence of ossified auditory bulla or of ossified ectotympanic; tympanic membrane apparently oriented obliquely at 45° or more from horizontal; no auditory sinuses; promontorium large, teardrop-shaped, inflated ventrally; sulci for facial nerve, sigmoid sinus, inferior petrosal sinus, prootic sinus, and sphenoparietal emissary vein; internal carotid artery medial in position; no evidence of transverse canal; prootic canal for lateral head vein (vena capitis lateralis) present; petromastoid with anteroanterior laminar structure which is regarded here as homologous to the anterior lamina of the non-tribosphenid mammals; foramen ovale (exit for V3) located posteriorly opposite anterior part of glenoid fossa, rimmed anteriorly by alisphenoid and posteriorly by anterior lamina of petromastoid; external acoustic meatus very small.

DESCRIPTION

Anatomical features are described in the following order: upper dentition, lower dentition, dentary and skull .

I1-5 (Figs 10 and 12). — The right I1 is preserved in YPFB Pal 6105 and the left I2 in YPFB Pal 6470; both teeth have small rounded crowns. As shown by the alveoli of I1-5 preserved on the right and left side of YPFB Pal 6105 and left side of YPFB Pal 6470, a slight size increase occurs from I1 to I4 (I3 and I4 are subequal in size) and I5 is smaller than I4, being similar in size to I1. The edges of the alveoli of I1-4 are on the same level, while that of I5 is situated more dorsally in the anteriormost edge of a large fossa in the posterior part of the premaxilla which accomodates

the tip of c1. I1-5 occur in a continuous sequence with no spaces between them or between the left and right I1's. A distinct diastema (1.4 mm on left side of YPFB Pal 6105) separates I5 from C1.

C1 (Figs 10 and 12). —This tooth is large, pointed and arcs ventroposteriorly such that the tip of the crown is about ventral to the posterior edge of the crown base. In cross section C1 is ovoid, being longer than wide (2.2 mm x 1.2 mm at the base of right C1 in YPFB Pal 6105). C1 is consistently larger than c1 in specimens where both are preserved. C1 is either in direct contact with P1 or separated from it by a very small diastema.

P1-3 (Figs 6 and 7). — These three teeth are all double-rooted; an increase in crown length, width and height occurs from P1 to P3. P1 is considerably smaller than P2-3 (Table 1); in occlusal view it is ovoid, a low ill-defined heel occurs posterobasally, and the crown tip lies ventral to the posterior edge of the anterior root. P2 is slightly smaller than P3 (Table 1); the crown tip lies ventral to the anterior edge of the posterior root, at about the same height as the occlusal surfaces of M1-4. A distinct cusp occurs posterobasally and a very small cuspule occurs anterobasally. Weak basal cingula usually occur along labial and lingual edges of crown posteriorly, and there is a distinct posterolingual swelling of the crown. P3 is the largest of upper premolars; the crown tip lies medially below the center of the tooth and is considerably higher than the occlusal surfaces of M1-4. There is a distinct posterobasal cusp, an anterobasal cuspule (which is larger than that on P2), a distinct posterobasal cingulum labially, and a weaker basal cingulum lingually which extends from the anterobasal cuspule to the posterobasal cusp.

M1-4 (Figs 6 and 7). — In average length M1=M2>M3>M4 and in average width M1<M2<M3>M4 (Table 1). The protocone is large, broad anteroposteriorly, and inflated basally, particularly posterolingually. The preprotocrista is slightly shorter and more rectilinear than the postprotocrista which has a distinct posterolingual bow on M1-3. The trigon is distinctly basined on M1-3, less so on M4. The para- and metacone are well developed on M1-3. The paracone is slightly smaller in occlusal view and lower in lateral view than the larger and higher metacone on M1-3 (on M4 the paracone is very large and high and the metacone, very reduced to absent). The metaconule is slightly larger than the paraconule on M2-3, subequal on M1. The centrocrista is V-shaped (dilambdodont; sensu CROCHET, 1980) with apex of V pointing labially toward stylar cusp C. The para- and metacone are weakly V-shaped (not connate) with their apex pointing lingually toward the para- and metaconule, respectively. The paracone, the centrocrista and the metacone form a weak W-shaped structure in occlusal view. The paracrista is low, short, rectilinear, and unites the paracone with a large stylar cusp B on M1-4. The metacrista is low, slightly longer than the paracrista on M1-3 (particularly on M1-2) and with a posterior bow (on M2-M3). The stylar shelf is well developed on M1-3 with an anteroposteriorly elongate basin separating para- and metacone from the row of large stylar cups. The stylar cusp B is the largest of stylar cusps; the stylar cusps A, C and D are also well developed, subequal in size and only slightly smaller than the stylar cusp B on M1-2. On M3 the stylar cusp A is subequal to B, while C and D are more reduced; on M4 stylar cusps A and B are fused into a large parastyle (other stylar cusps are extremely reduced or absent). There is no distinct evidence of a stylar cusp E on M1-4. A prominent parastyle, formed by spur-like stylar cusps A and B, extends anteriorly and
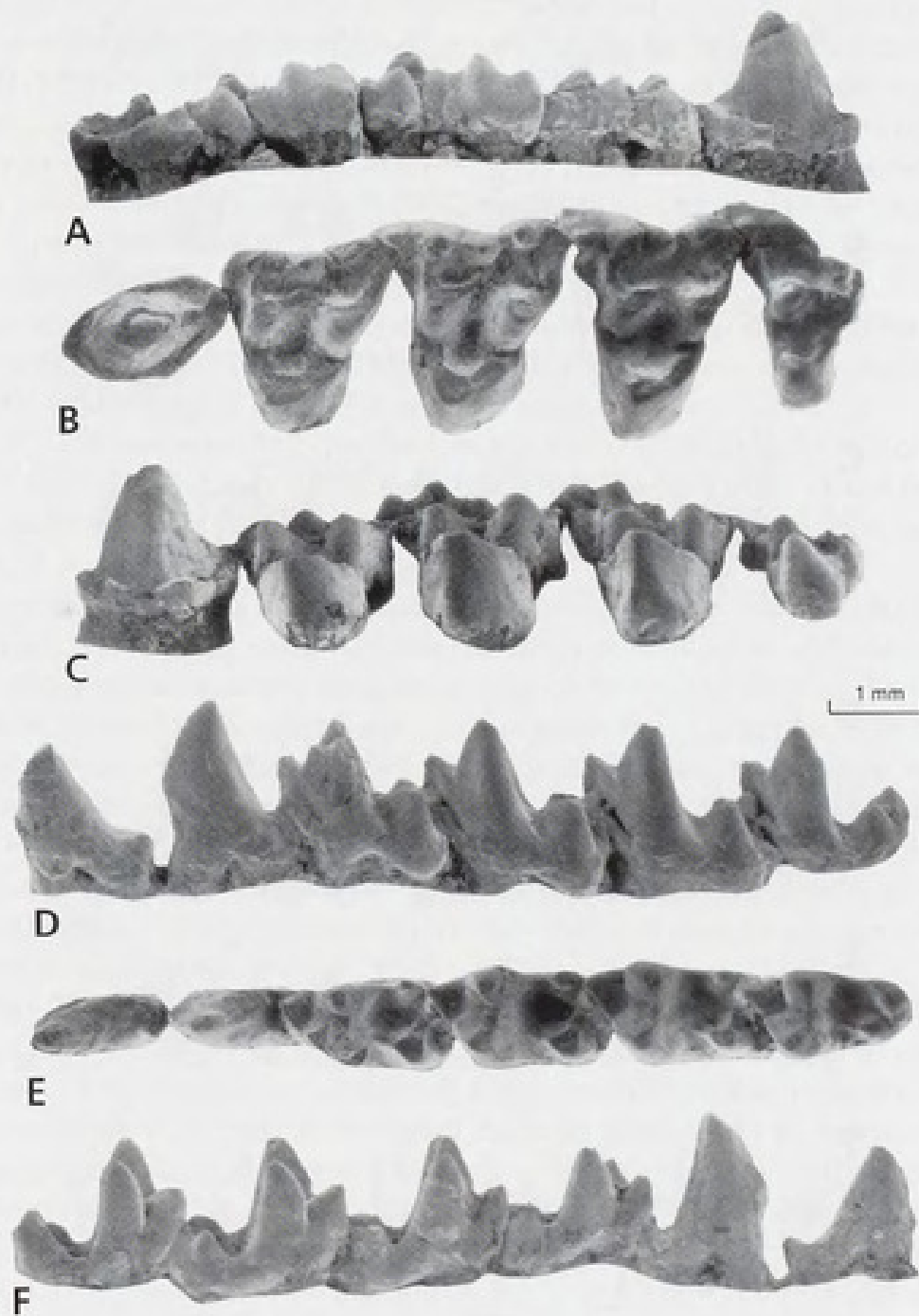
FIG. 6. — *Pucadelphys andinus*. SEM photos of left P3-M4 (A, labial; B, occlusal; C, lingual views) of YPFB Pal 6470; and left p2-m4 (D, labial; E, occlusal; F, lingual views) of YPFB Pal 6109. X 15.

FIG. 6. — Pucadelphys andinus. *Photos MEB de P3-M4 gauches (A, vue labiale; B, vue occlusale; C, vue linguale) d'YPFB Pal 6470; et p2-m4 gauches (D, vue labiale; E, vue occlusale; F, vue linguale) d'YPFB Pal 6109. X 15.*
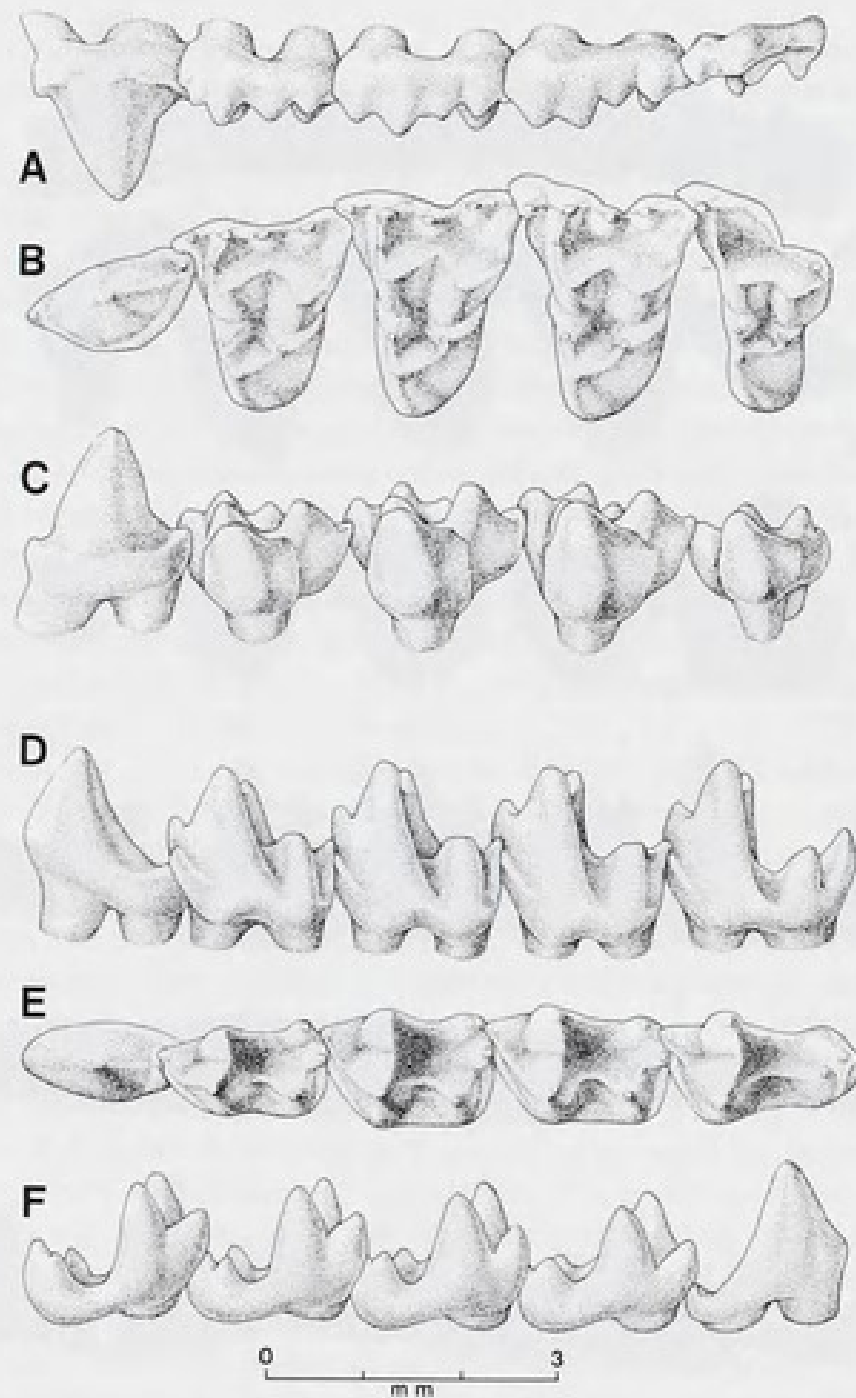
FIG. 7.—*Pucadelphys andinus.* A-C, left P3-M4 (A, labial; B, occlusal; C, lingual views), based on YPFB Pal 6109 and 6470; D-F, left p3-m4 (D, labial; E, occlusal; F, lingual views), based on YPFB Pal 6109 and 6473.

FIG. 7. —Pucadelphys andinus. A-C, P3-M4 gauches (A, vue labiale; B, vue occlusale; C, vue linguale), d'après YPFB Pal 6109 et 6470; D-F, p3-m4 gauches (D, vue labiale; E, vue occlusale; F, vue linguale), d'après YPFB Pal 6109 et 6473.

overlaps the posterolabial edge (i.e. metastylar region) of the preceding tooth. A distinct paracingulum extends along anterolabial edge of crown from stylar cusp A; it becomes very narrow below the tip of the paracone (it disappears on M4) and continues lingually to disappear below the paraconule. The ectoflexus is absent or very shallow on M1 and increases in depth from M1 to M3. M2 differs from M1 in being slightly wider, having a slightly deeper ectoflexus, and a longer paracrista relative to metacrista. M3 differs from M1-2 in having a distinct ectoflexus, an enormous spur-like parastyle on which stylar cusps A and B are large and subequal in size, smaller stylar cusps C and D, a metastyle area reduced in size relative to the more prominent parastyle area, para- and metacrista more subequal in length, and a crown less bulbous and narrower anteroposteriorly (i.e. more transversely elongate).

i1-4 (Fig. 8). — A left i1 is preserved in YPFB Pal 6470, a right i3 in YPFB Pal 6105, a right i4 in YPFB Pal 6472, and left i3-4 in YPFB Pal 6473. The i1-4 have simple ovoid crowns and increase slightly in size from i1 to i4; i4 is in direct contact with c1.

c1 (Fig. 8). — This tooth is large, pointed, arcs in anterodorsal direction. It is ovoid in cross-section, longer than wide (1.5 mm x 1.0 mm in right YPFB Pal 6105). The axis of the tooth is set at a slight oblique angle relative to the cheek tooth series (i.e. anterior edge labial, posterior edge more lingual). c1 is consistently smaller than C1.

p1-3 (Figs 6 and 7). — All three teeth are two-rooted. p1 is very small relative to p2-3, and is separated from c1 and p2 by small (0.5 mm) diastems. It is ovoid in occlusal view with the highest point of the crown set above the anterior edge of the anterior root. p2-3 are subequal in length and width (Table 1) although p2 tends to be slightly lower in height; both are distinctly premolariform with well developed posterobasal heels. The crown tips are about same level as protoconid tips of m1-4. The p2 differs from p3 in having the principal cusp narrower anteroposteriorly and inclined more anteriorly so that the tip occurs above the middle of the anterior root (on p3 the anteroposteriorly broader primary cusp is more dorsally directed so that tip occurs dorsal to posterior edge of anterior root); p2-3 occur in close succession without spaces separating them or p3 from m1.

m1-4 (Figs 6 and 7). — In average length m1<m2=m3>m4, in average width m1<m2=m3>m4 (Table 1). The labial side of teeth is higher than the lingual side, and the trigonid is well elevated above the talonid. The trigonid of m1 is relatively long (paraconid set anterolabially), while those of m2-4 are foreshortened anteroposteriorly and distinctly wider than long (paraconid set more lingually). The protoconid is the highest of the trigonid cusps and slightly higher than the metaconid. The paraconid is smaller than the metaconid and inclined anteriorly. Protoconid and metaconid are united by a straight trenchant protocristid. The talonid is broad and distinctly basined on m1-4, being wider than the trigonid on m1-3, and narrower on m4. The hypoconid is the dominant talonid cusp on m1-3; it is V-shaped in appearance, and considerably larger than entoconid and hypoconulid in occlusal view. In lateral view of m1-3 all three talonid cups are subequal in height. A short cristid obliqua contacts the trigonid at the posteromedial surface of the protoconid, labial to the protocristid notch. The hypoflexid is well developed on m1-4. Entoconid and hypoconid are subequal in size in occlusal view on m1-3, and the hypoconulid is "twinned" with the entoconid (i.e. set closer to entoconid than to hypoconulid). On m4 entoconid and
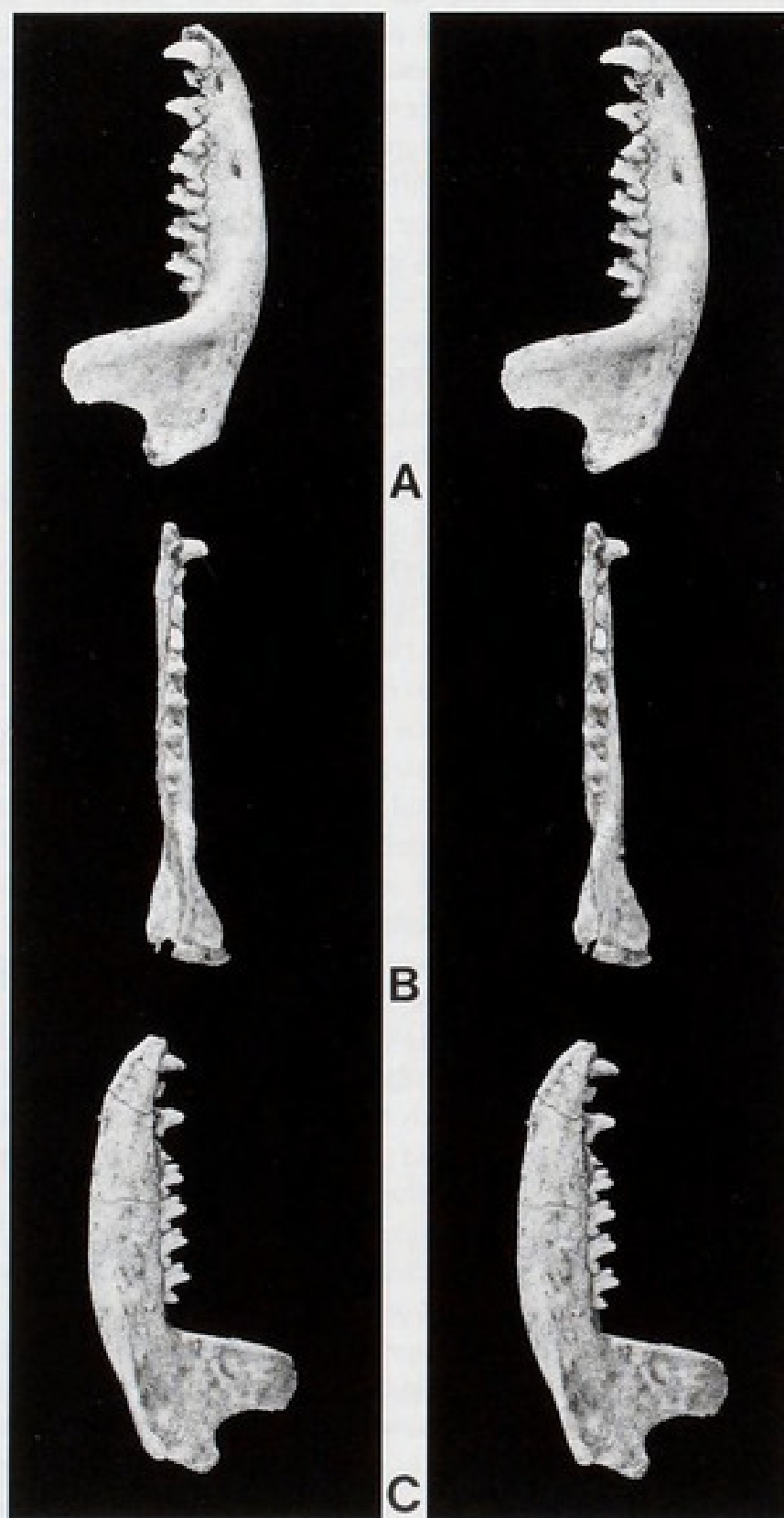
hypoconulid are fused basally, and the hypoconid is distinctly elevated above the much lower entoconid and hypoconid. A precingulid is well developed on m1-4; a postcingulid (i.e. shelf extending ventrolabially from tip of hypoconulid across posterior surface of hypoconid) is well developed on m1-3 but absent on m4.

DENTARY (Figs 8 and 9). — The horizontal ramus is long and slender. The ventral border of the bone is relatively flat between p1 and m3, bending dorsally anterior to p2 and posterior to m3. The deepest point occurs below m3-4, with a gentle decrease in depth from m3 to p1.

The articular surface of the symphysis is slightly rugose and covered by numerous vascular foramina; a well-developed symphyseal ligament was apparently present. The long axis of the symphyseal surface lies at an angle of about 40° to the horizontal axis of the dentary and extends posteriorly to below p2. There are typically two large mental foramina, one below p1 and another below m1. A groove on the medial surface of the dentary, about 1/3 of the way above the ventral edge, extends from the anterior edge of the angular process to below m1, becoming shallower anteriorly. This represents the mylohyoid groove (BENSLEY, 1902) and marks the course of a neurovascular bundle which probably included the mylohyoid artery and nerve. The angular process is very large and inflected medially; it is situated far posteriorly, more or less below the condyloid process. The mandibular foramen is situated dorsal to the anterior edge of the angular process and below the middle of the coronoid process. The masseteric fossa is shallow with a posteroventral border (between the condyloid process and the point directly ventral to the middle of the coronoid process) developed into a broad laterally directed shelf. In dorsal and ventral views, the posterior part of the dentary has a broad V-shape due to the large medially inflected angular process and the large laterally directed expansion of the posteroventral part of the masseteric border. The condyloid process is wide transversely; the portion projecting lateral to the vertical plane of the dentary is about three times longer (transversally) than that projecting medially. It occurs dorsal to the horizontal plane through m1-4, at about the same level as the tip of c1. Its articular surface is broadly convex dorsoposteriorly. The coronoid process of the ascending ramus is broad anteroposteriorly, thin transversely with the anteroposterior axis in the same vertical plane as the labial sides of m1-4. Its upper margin is rounded (convex dorsally) and its posterior border is markedly concave posteriorly.

GENERAL SKULL STRUCTURE (Figs 10 -14 and 16). — There are five partial or nearly complete skulls. The most complete and least distorted is the type YPFB Pal 6105 (Figs 10 and 18) which is the basis for the reconstructions in Figs 10, 15 and 17 along with details incorporated from other

FIG. 8. — *Pucadelphys andinus*. Right dentary of YPFB Pal 6108 (A, lateral; B, dorsal; C, medial views). Stereophotos X 2.5.

FIG. 8. — Pucadelphys andinus. Dentaire droit d'YPFB Pal 6108 (A, vue latérale; B, vue dorsale; C, vue médiale). Photos stéréoscopiques X 2.5.

specimens as indicated. In YPFB Pal 6105 the nasals and the left part of the rostrum anterior to the infraorbital canal are slightly crushed ventrally, but the remainder of the skull is virtually undistorted. Specimens YPFB Pal 6107 (Fig. 14) and 6110 (Fig. 13) are crushed slightly transversely, particularly in the basicranial and palatal areas. This crushing is most extreme in YPFB Pal 6110 where the basioccipital is missing, the exoccipitals are in near contact and the
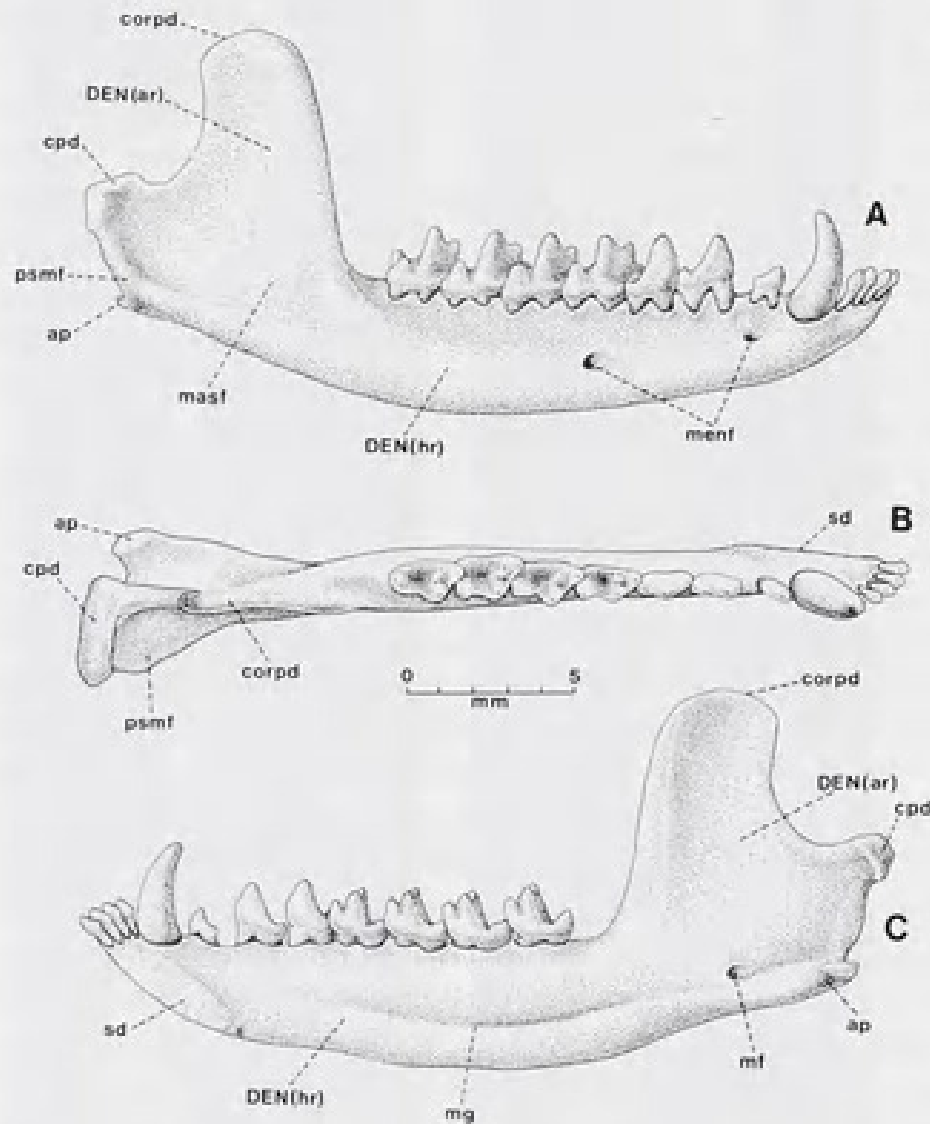

Fig. 9. — *Pucadelphys andinus.* Reconstruction of right dentary of YPFB Pal 6108 (A, lateral; B, dorsal; C, medial views). Abbreviations: **ap**, angular process of dentary; **corpd**, coronoid process of dentary; **cpd**, condyloid process of dentary; **DEN(ar)**, ascending ramus of dentary; **DEN(hr)**, horizontal ramus of dentary; **masf**, masseteric fossa; **menf**, mental foramen; **mf**, mandibular foramen (=inferior alveolar foramen); **mg**, mylohyoid groove (=meckelian groove); **psmf**, posterior shelf of masseteric fossa; **sd**, symphysis of dentary.

Fig. 9. — Pucadelphys andinus. *Reconstitution du dentaire droit d'YPFB Pal 6108 (A, vue latérale; B, vue dorsale; C, vue médiale). Abréviations: **ap**, procesus angulaire du dentaire; **corpd**, processus coronoïde du dentaire; **cpd**, condyle articulaire du dentaire; **DEN(ar)**, branche ascendante du dentaire; **DEN(hr)**, branche horizontale du dentaire; **masf**, fosse massétérine; **menf**, foramen mentonnier; **mf**, foramen mandibulaire (= foramen alvéolaire inférieur); **mg**, sillon mylohyoïdien (= sillon de Meckel); **psmf**, plateforme postérieure de la fosse massétérine; **sd**, symphyse du dentaire.*

anterior ends of the pars petrosa of the petromastoids are in direct contact. The fourth skull, YPFB Pal 6108 (Fig. 16), is crushed dorsoventrally and the dorsal surface is displaced to the left relative to the ventral surface. The rostral portion of the fifth specimen, YPFB Pal 6109 (Fig. 11), shows virtually no distortion on the right side, although the nasals are slightly depressed anteriorly and the posterior part of the left maxilla is separated from the rest of the skull.

In YPFB Pal 6105 the ratio of the condylar-premaxilla length (28.5 mm) and the breadth between the outer edges of the zygomatic arches (approx. 19.5 mm) is about 0.68. The ratio betweenthe condylar-canine length (25.0 mm) and the broadest point of the braincase measured between the outer edges of the mastoid processes (11.0 mm) is 0.44.

The most distinct aspect of the skull in dorsal view is the short rostrum and overall bilobed appearance, with a broad area between the lacrimals and another between the posterior bases of the large zygomatic arches (Fig. 12). The narrowest point of the skull, excluding the nasal region, is just anterior to the frontal-parietal suture, the site of the interorbital constriction. The orbit is broadly confluent with the temporal fossa.

A weak sagittal crest occurs in all specimens, but is best developed in YPFB Pal 6105 where it begins on the posterior part of the frontals; in the other specimens the sagittal crest occurs only on the parietals and begins at the frontal-parietal suture. In all specimens the sagittal crest becomes higher and more prominent posteriorly. A dorsoposteriorly directed lambdoidal crest of the postparietal is well developed in all specimens. In ventral view (Fig. 12) the palate, including the dentition, and the basicranium are similar in size and shape, being broadly triangular with their apices directed anteriorly.

In lateral view (Fig. 12) the recess for the external acoustic meatus is small, broadly U-shaped, and bounded posteriorly by a small posttympanic process of the squamosal; it is situated immediately ventral to the subsquamosal foramen and dorsoposteriorly to the postglenoid foramen. The glenoid fossa is situated far posteriorly, opposite the anterior extremity of the promontorium of the pars petrosa. The foramen ovale is also situated far posteriorly at the posteroventral corner of the alisphenoid opposite the anterior part of the glenoid fossa; it is rimmed anteriorly by the alisphenoid and posteriorly by the anterior lamina of the petromastoid; its lateral margin touches the squamosal suture. The occipital plate slopes upwards and slightly forwards from the occipital condyles.

Nasal (Figs 11 and 12). — Anteriorly the nasals are elongate and subequal in breadth. At a point approximately dorsal to P2 they flare sharply laterally and posteriorly toward the frontal-maxilla suture, where their sutures with the frontals abruptly bend medially and, before meeting, make a sharp bend anteriorly. The nasal-frontal suture thus has a distinct W-shape, with the base of the W pointing posteriorly and the top anteriorly. The anterior-most edges of the nasals are broken in all specimens, but as suggested in YPFB Pal 6105 (right side) and 6110 in which they are most complete, they extended somewhat beyond their point of contact with the premaxilla and were apparently slightly longer medially.

Premaxilla (Fig. 12). — In dorsal and lateral views the premaxilla is sharply V-shaped. The ascending process is directed posteriorly between the nasal and maxilla and its posterior extremity
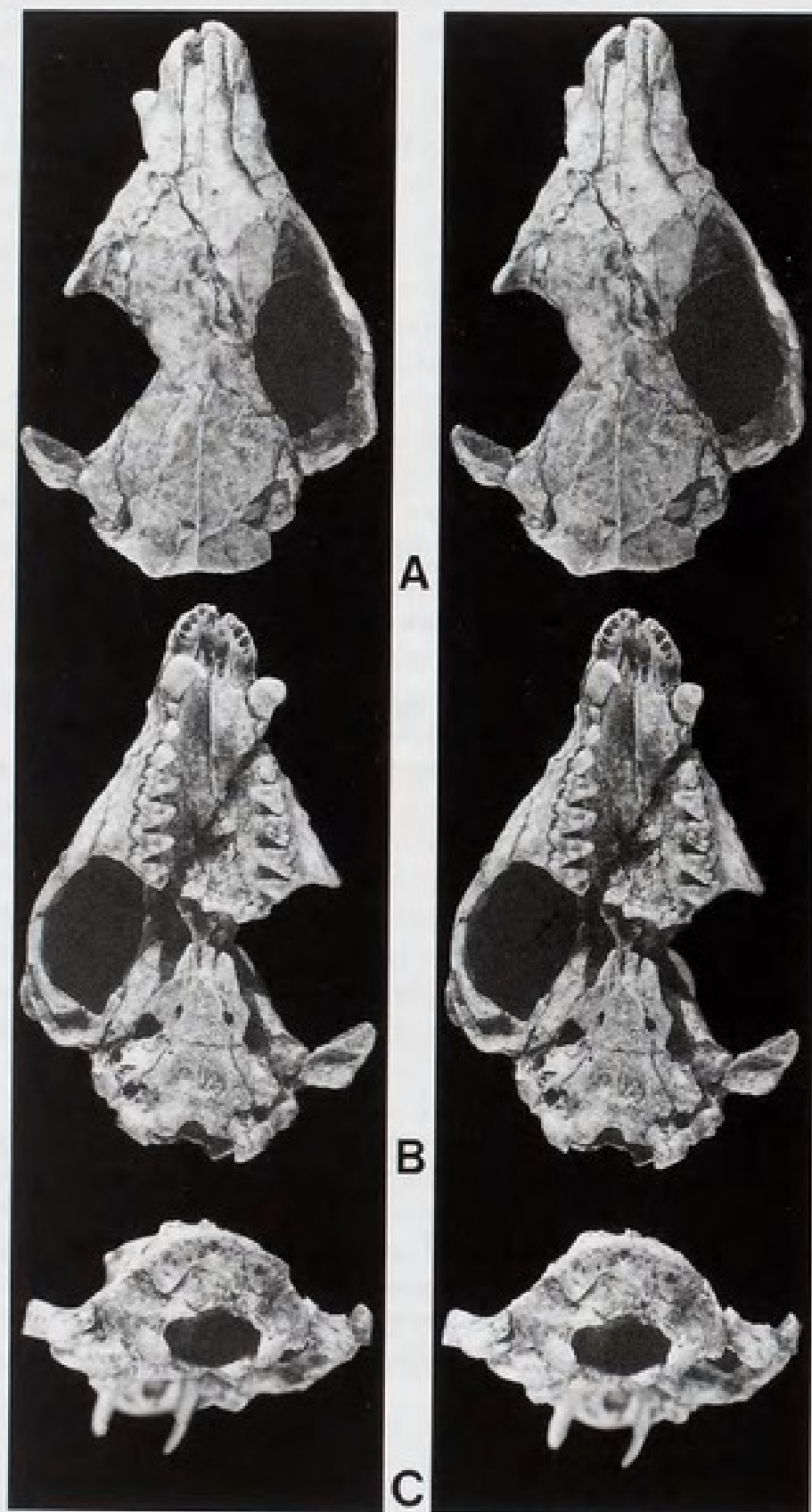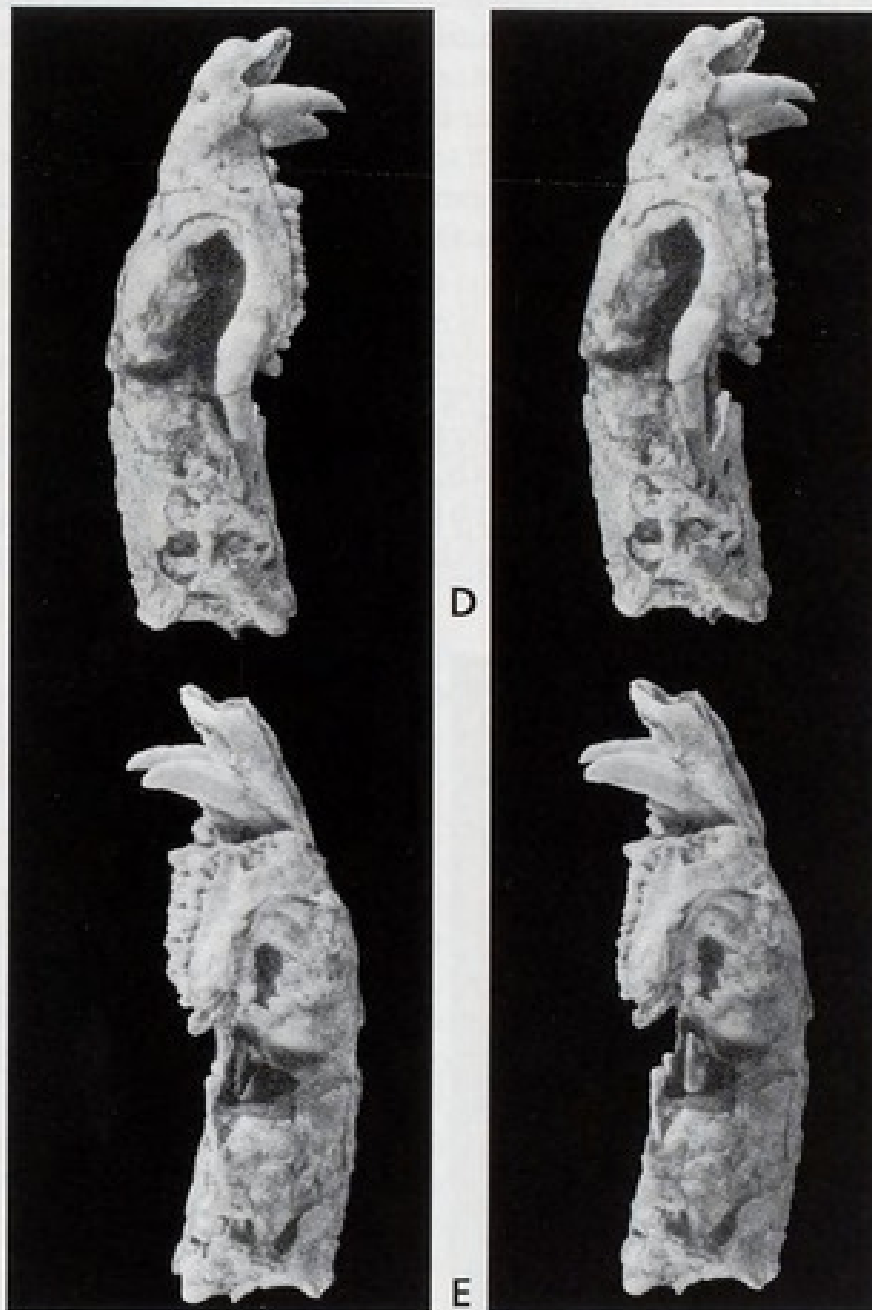
FIG. 10. —*Pucadelphys andinus.* Skull of YPFB Pal 6105 (holotype) (A, dorsal; B, ventral; C, occipital; D, right lateral; E, left lateral views). Stereophotos X 2.5.

FIG. 10. — Pucadelphys andinus. *Crâne d'YPFB Pal 6105 (holotype) (A, vue dorsale ; B, vue ventrale ; C, vue occipitale ; D, vue latérale droite ; E, vue latérale gauche). Photos stéréoscopiques X 2.5.*

is dorsal to the middle of C1. The ascending process of the premaxilla forms the dorsolateral edge of the nares and its lateral surface is slightly convex. The anterior edges of the two premaxillae have a distinctly rounded (sharply convex) shape when viewed dorsally. In ventral view the premaxilla-maxilla suture extends posteromedially from the anterior-most edge of the maxilla (lateral to I4), across the fossa which receives c1. Medially to the anterior mid-point of C1, the suture bends anteromedially and reaches the lateral edge of the incisive foramen in its posterior quarter. On the medial edge of the incisive foramen, the premaxilla-maxilla suture runs posteromedially from the posterior quarter of the foramen to the median plan of the skull. The paired incisive foramina are well developed and elongate anteroposteriorly, extending from a point medial to I3, anteriorly and to a point medial to the anterior edge of C1, posteriorly. The anterior 75% of the bar separating the incisive foramina medially is formed by the premaxilla; the posterior 25% is formed by the maxilla.

MAXILLA (Figs 12 and 15). — A small wing of the anterolateral edge of the maxilla overlaps the posterolateral edge of the premaxilla to a point labial to I5 and forms the lateral rim of the fossa between I5 and C1 (Fig. 12). Posterodorsally, the maxilla is wedged between the nasal and lacrimal, and has a small, but clear, contact with the frontal. From the posterior edge of the frontal-maxilla suture, the maxilla-lacrimal suture runs in an anterior direction, then anteroventrally along
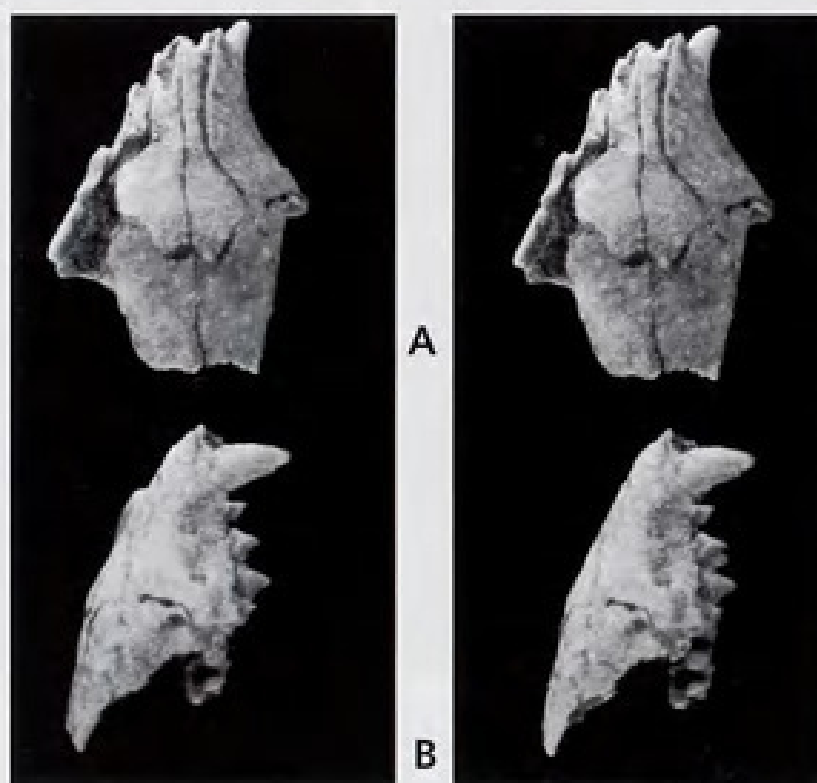

FIG. 11. —*Pucadelphys andinus*. Rostral part of skull of YPFB Pal 6109 (A, dorsal; B, right lateral views). Stereophotos X 2.5.

FIG. 11. — Pucadelphys andinus. *Portion rostrale du crâne d'YPFB Pal 6109 (A, vue dorsale; B, vue latérale droite). Photos stéréoscopiques X 2.5.*

the anterior rim of the orbit, contacting the jugal at the lower edge of the orbit dorsal to the posterior edge of M2. From that point, as seen in lateral and ventral views, the maxilla-jugal suture extends in a straight line posteroventrally.

The anterior (rostral) opening of the infraorbital canal is large, slightly elongate dorsoventrally (the ventral edge is slightly broader than the dorsal edge), and opens dorsal to P3. The posterior (orbital) opening is also large, slightly elongate transversely. The dorsal rim is formed by the lacrimal, the ventral and lateral rims by the maxilla, and the ventromedial rim by a sliver of the palatine which extends anteriorly between the lacrimal and maxilla into the infraorbital canal, as is clearly seen on left side of YPFB Pal 6105 (Fig. 15). The infraorbital canal transmits the infraorbital branch of V2, a branch of the infraorbital artery to the mesial side of maxilla and premaxilla, and a small vein in Recent metatherians (Archer, 1976a).

Within the orbit the maxilla forms the floor and, along its medial edge, has a broad contact with the palatine. The large postpalatine foramen is bordered by the maxilla laterally and by the palatine dorsally, medially and ventrally (Fig. 15).

In ventral view (Fig. 12), the posteromedial edge of the maxilla extends anteromedially from the lateral side of the postpalatine foramen, roughly parallel to the lingual edges of M3-4, and apparently has a broad transverse contact with the palatine medial to the embrasure between M2 and M3. This area of the palate is broken in all specimens and the suture itself is not visible; however, the relatively complete palate in YPFB Pal 6105 shows no vacuities in the palatal portion of the maxilla.

PALATINE (Figs 10 and 12). — The palatine contribution to the secondary palate is preserved only in YPFB Pal 6105 where it is nearly complete. The posterior edge of the palatine is a transversely thickened bar, the postpalatine torus, which extends below the level of the palate and which it encloses posteriorly. This torus lies posterior to the M4's and its maximum thickness is located laterally, posterior to the protocone's of the M4's. A large ovoid postpalatine foramen (which probably transmits the descending palatine vein, palatine artery and palatine branch of cranial nerve V) occurs at the posterolateral corner of the palatine (as seen only on the left side of YPFB Pal 6105). This foramen is clearly seen in anterior and posterior views, while in ventral view only the anteriormost edge is visible since the foramen is tucked above the postpalatine torus and opens vertically. The posterior surface of the postpalatine torus is ornamented by three spines: a lateral one on either side at the medial edge of the postpalatine foramen and a medial one at the contact of the two palatines. These spines give the ventral surface of the choanal orifice a broad m-shaped appearance. Immediately anterior to the torus and situated medially on each palatine is a pair of shallow parallel sulci (palatine sulci) which run anteriorly and probably extended to a middle palatine foramen as occurs in living *Didelphis*, although this foramen is not preserved in specimens of *Pucadelphys*. The anterior extent of the palatine is not fully preserved and the presence or absence of vacuities cannot be securely established, although if vacuities were present they were small. Given the relatively complete palate of YPFB Pal 6105, and the apparent absence of vacuities, the palate is shown as solid in the reconstruction (Fig. 12).

Part of the orbital or laterovertical process of the palatine is preserved in YPFB Pal 6105 (left side), 6108 (left side) and 6110 (right side) (Fig. 15). A large elliptical sphenopalatine foramen, which transmits the sphenopalatine artery and nerve into the naso-pharyngeal space above the
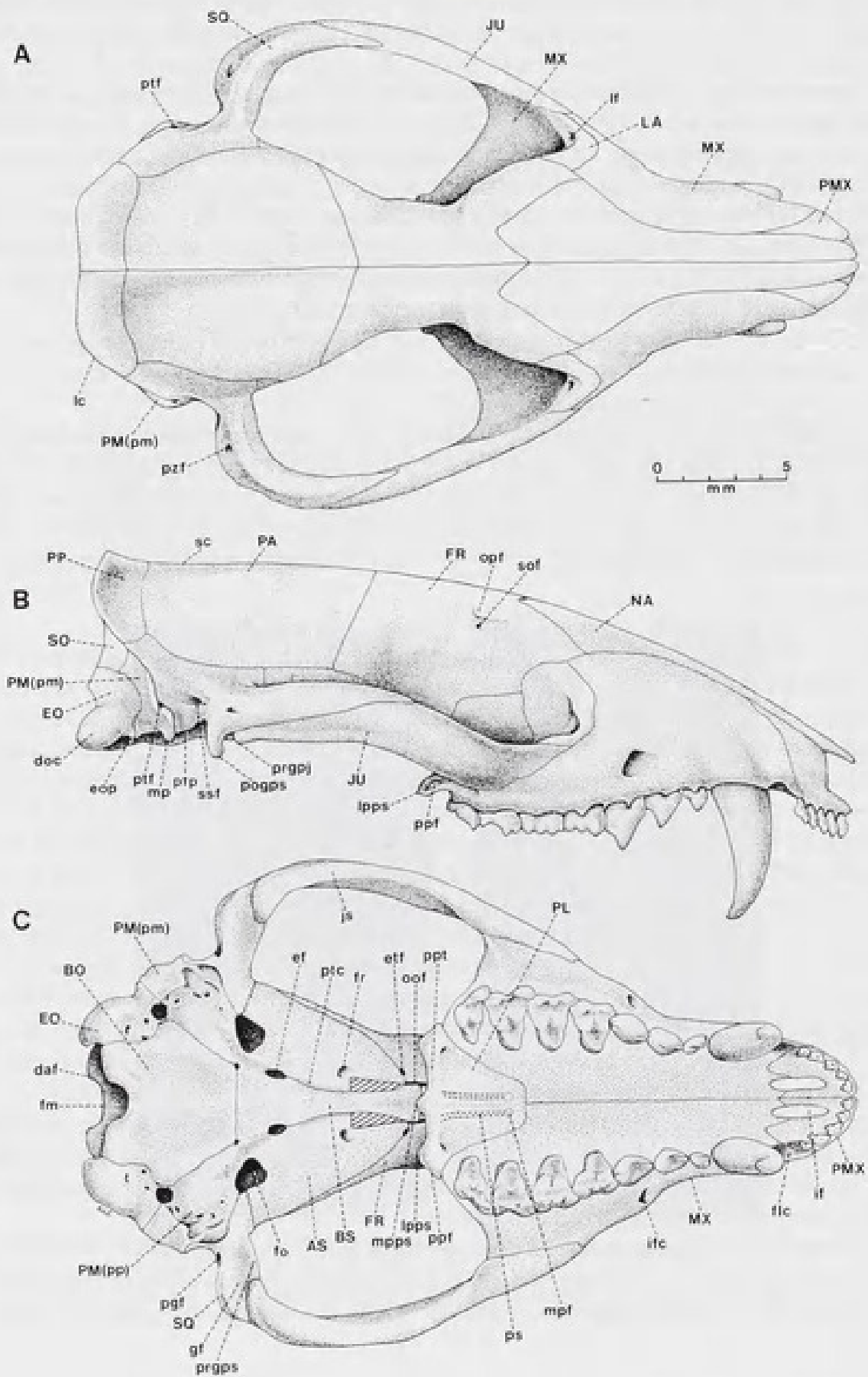
palate, has a posteriorly directed opening within the vertical surface of the palatine at the posteromedial edge of the orbit just dorsomedial to the postpalatine foramen.

The palatine makes a small contribution to the medial edge of the orbital floor, extending medially in sutural contact with the maxilla from the lateral side of the postpalatine foramen, then almost directly anteriorly into the ventromedial corner of the infraorbital canal (Fig. 15). Its contact with the lacrimal is a broad suture extending ventrally from the anterior point of contact with the frontal to the lower edge of the infraorbital canal, where it turns sharply anterodorsally into that canal. Dorsally the palatine has a broad and nearly horizontal contact with the frontal; this suture extends posteriorly to a point above the sphenopalatine foramen where it bends ventroposteriorly to a point just posterodorsal to that foramen, then extends posteriorly along the ventrolateral edge of the orbitosphenoid, and has a small contact posteriorly with the anterior edge of the basisphenoid (as seen in YPFB Pal 6105, left side) (Fig. 15).

LACRIMAL (Figs 12 and 15). — This bone forms the anterior rim of the orbit. In dorsolateral view, the large facial wing of the lacrimal has a distinct quarter-moon shape. Viewed posterolaterally (Fig. 15), the lacrimal has a rectangular shape (long axis is dorsoventral) and contacts the maxilla anterodorsally, anteriorly and ventrolaterally, the jugal anteroventrally, the frontal dorsoposteriorly, and the palatine ventroposteriorly and ventromedially. The large elliptical shaped lacrimal

FIG. 12. — *Pucadelphys andinus.* Reconstruction of the skull (A, dorsal; B, right lateral; C, ventral views) based primarily on YPFB Pal 6105 (holotype). Abbreviations: **AS**, alisphenoid; **BO**, basioccipital; **BS**, basisphenoid; **daf**, dorsal atlantal facet; **doc**, dorsal occipital condyle; **ef**, entocarotid foramen (=anterior carotid foramen, carotid canal); **EO**, exoccipital; **eop**, exoccipital process; **etf**, ethmoid foramen; **flc**, fossa for lower canine; **fm**, foramen magnum; **fo**, foramen ovale; **FR**, frontal; **fr**, foramen rotundum; **gf**, glenoid fossa; **if**, incisive foramen; **ife**, infraorbital canal; **JU**, jugal; **js**, jugular sulcus; **LA**, lacrimal; **lc**, lambdoidal crest (=nuchal crest); **lf**, lacrimal foramen; **lpps**, lateral postpalatine spine; **mp**, mastoid process; **mpf**, middle palatine foramen; **mpps**, medial postpalatine spine; **MX**, maxilla; **NA**, nasal; **oof**, optic-orbital foramen; **opf**, supraorbital process of frontal; **PA**, parietal; **pgf**, postglenoid foramen; **PL**, palatine; **PM(pm)**, pars mastoidea of petromastoid (=mastoid s.s.); **PM(pp)**, pars petrosa of petromastoid (=petrosal s.s.); **PMX**, premaxilla; **pogps**, postglenoid process of squamosal; **PP**, postparietal; **ppf**, postpalatine foramen; **ppt**, postpalatine torus; **prgpj**, preglenoid process of jugal; **prgps**, preglenoid process of squamosal; **ps**, palatine sulcus; **ptc**, pterygoid canal; **ptf**, posttemporal foramen; **ptp**, posttympanic process; **pzf**, postzygomatic foramen; **sc**, sagittal crest; **SO**, supraoccipital; **sof**, supraorbital foramen; **SQ**, squamosal; **ssf**, subsquamosal foramen (=suprameatal, postsquamosal).

FIG. 12. — Pucadelphys andinus. *Reconstitution du crâne (A, vue dorsale; B, vue latérale droite; C, vue ventrale) principalement d'après YPFB Pal 6105 (holotype). Abréviations: **AS**, alisphénoïde; **BO**, basioccipital; **BS**, basisphénoïde; **daf**, facette atlantale dorsale; **doc**, condyle occipital dorsal; **ef**, foramen entocarotidien (=foramen carotidien antérieur, canal carotidien); **EO**, exoccipital; **eop**, processus exoccipital ; **etf**, foramen ethmoïdien; **flc**, fosse pour la canine inférieure; **fm**, foramen magnum; **fo**, foramen ovale; **FR**, frontal; **fr**, foramen rotundum; **gf**, fosse glénoïde; **if**, foramen incisif; **ife**, canal infraorbitaire; **JU**, jugal; **js**, sillon jugulaire; **LA**, lacrimal; **lc**, crête lambdoïde (=crête nuchale); **lf**, foramen lacrimal; **lpps**, épine postpalatine latérale; **mp**, processus mastoïde; **mpf**, foramen palatin moyen; **mpps**, épine postpalatine médiale; **MX**, maxillaire; **NA**, nasal; **oof**, foramen optico-orbitaire; **opf**, processus supra-orbitaire du frontal; **PA**, pariétal; **pgf**, foramen postglénoïde ; **PL**, palatin; **PM(pm)**, pars mastoidea du pétreux (=mastoïde s.s.); **PM(pp)**, pars petrosa du pétromastoïde (=pétreux s.s.); **PMX**, prémaxillaire; **pogps**, processus postglénoïde du squamosal; **PP**, postpariétal; **ppf**, foramen postpalatin; **ppt**, torus postpalatin; **prgpj**, processus préglénoïde du jugal; **prgps**, processus préglénoïde du squamosal; **ps**, sillon palatin; **ptc**, canal ptérygoïde; **ptf**, foramen posttemporal; **ptp**, processus posttympanique; **pzf**, foramen postzygomatique; **sc**, crête sagittale; **SO**, supraoccipital; **sof**, foramen supraorbitaire; **SQ**, squamosal; **ssf**, foramen subsquamosal (=suprameatal, postsquamosal).*
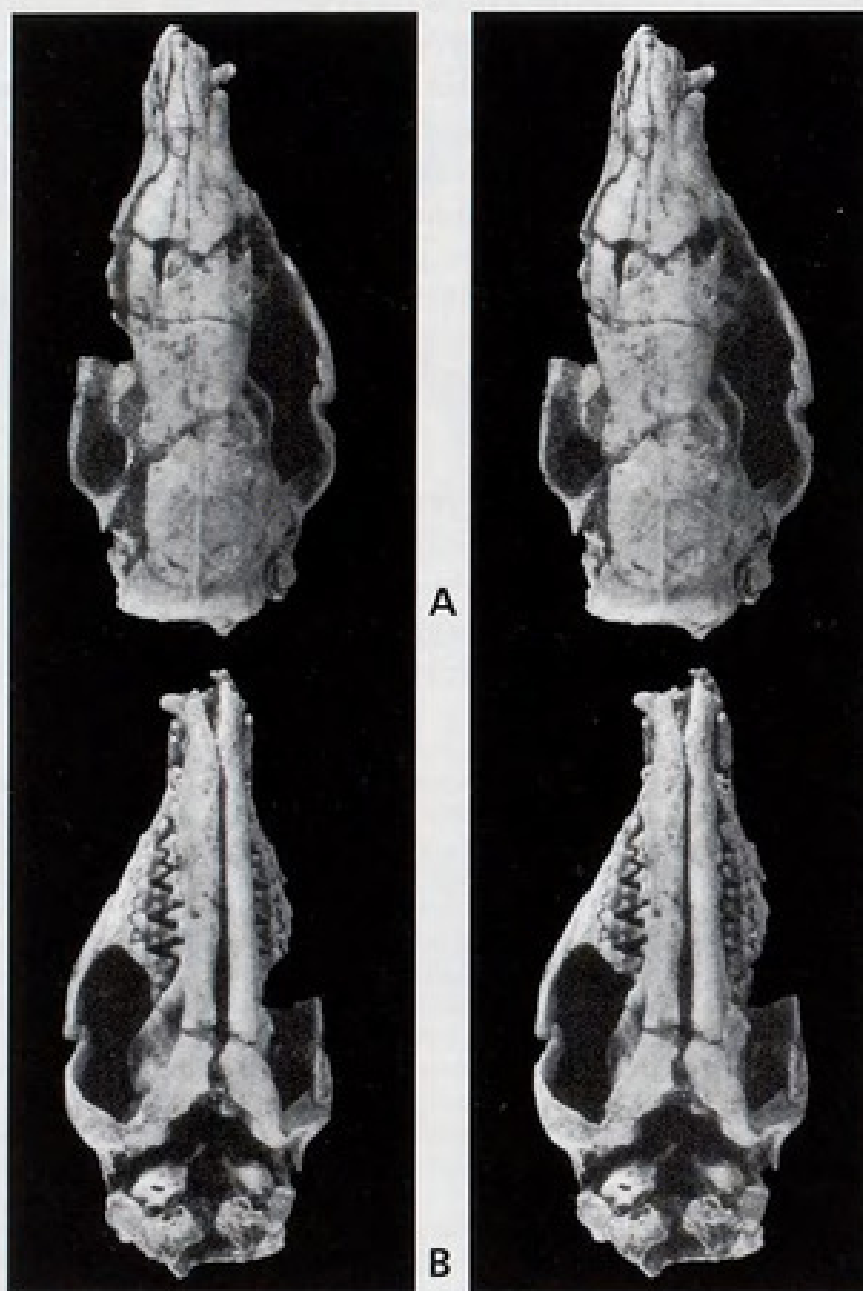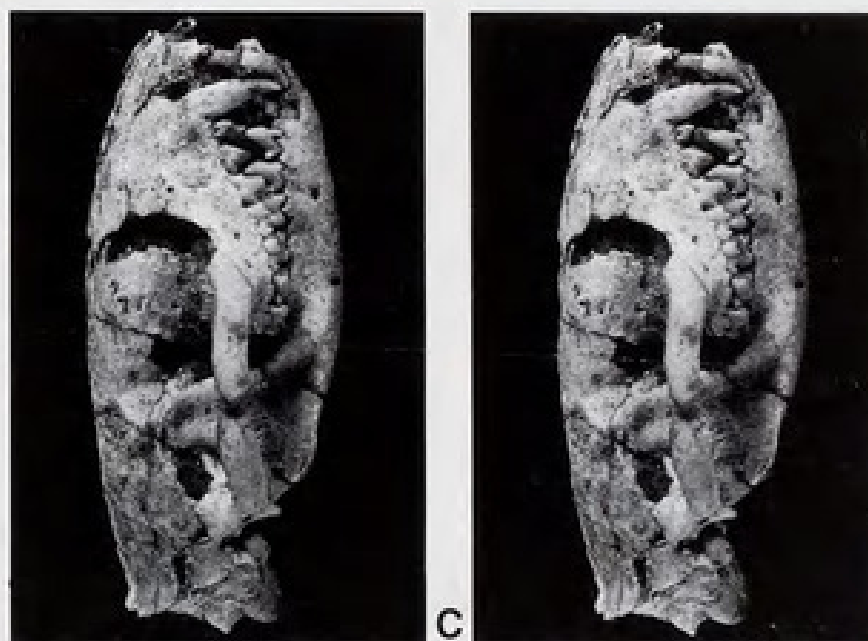
FIG. 13. — *Pucadelphys andinus*. A-C, skull with attached mandible of YPFB Pal 6110 (A, dorsal; B, ventral; C, right lateral views). Stereophotos X 2.5.
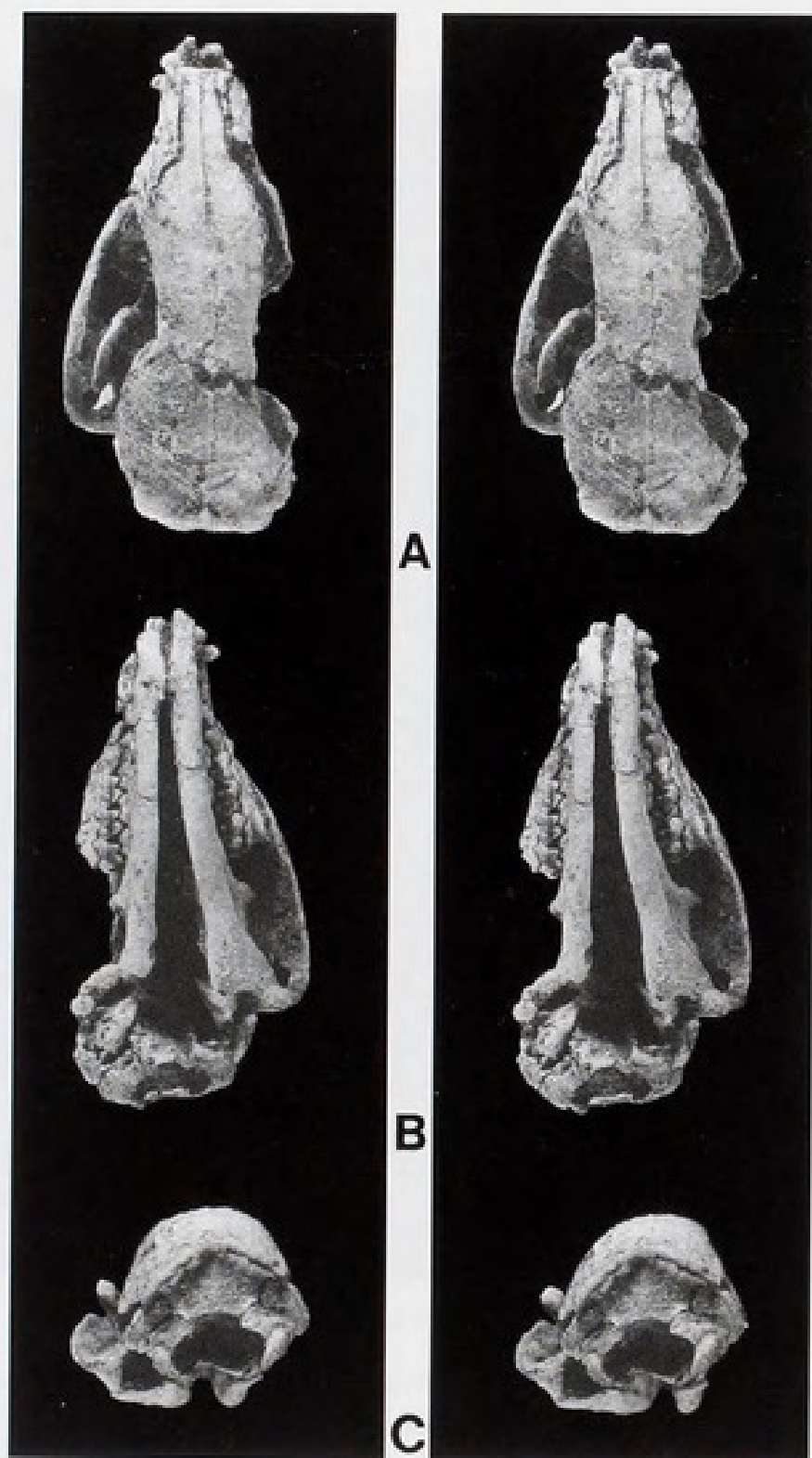
FIG. 13. — Pucadelphys andinus. A-C, crâne et mandibule en connexion d'YPPFB Pal 6110 (A, vue dorsale; B, vue ventrale; C, vue latérale droite). Photos stéréoscopiques X 2.5.

C

foramen, which transmits the naso-lacrimal duct, opens within the orbit and has two distinct canals of subequal size situated one above the other along a dorsomedial-ventrolateral axis (Fig. 15).

JUGAL (Fig. 12). — Complete jugals are preserved in YPFB Pal 6105 (right side) and 6471 (left side). This is a large bone which contributes to the formation of about 60% of the zygomatic arch. Anteriorly it has a broad diagonal contact with the maxilla, a small contact with the lacrimal anterodorsally-anteromedially, and it forms the ventral edge of the orbital rim. From its contact with the maxilla it arcs in a posterolaterodorsal direction, being dorsoventrally deep and transversely narrow. At its dorsal and lateral greatest extent, which is approximately lateral to the interorbital constriction, the jugal makes contact with the zygomatic process of the squamosal dorsally and continues ventrally along it to the anterolateral edge of the glenoid fossa where it forms a large preglenoid process. In lateral view, the ventroposterior spine of the jugal and dorsal zygomatic process of the squamosal have an elongate diagonal contact (Fig. 12). A shallow sulcus occurs along the ventrolateral edge of the jugal contribution to the zygomatic arch marking the point of insertion of the masseter muscle (Fig. 12). The greater part of the zygomatic arch, including the jugal and squamosal contributions, is subequal in breadth and depth.

FRONTAL (Figs 12 and 15). — This bone covers all of the medial 30% of the dorsal area and most of the medial 30% of the lateral area of the cranium. Anteriorly it has a distinct W-shaped contact with the nasals (Fig. 12), and lateral to this is a small distinct contact with the maxilla. The lacrimal contact is broad and nearly horizontal dorsally, and broad but nearly vertical laterally. There is a broad nearly horizontal contact with the dorsal edge of the orbital part of the palatine, and a small wedge of the frontal extends ventrally and separates the palatine and orbitosphenoid
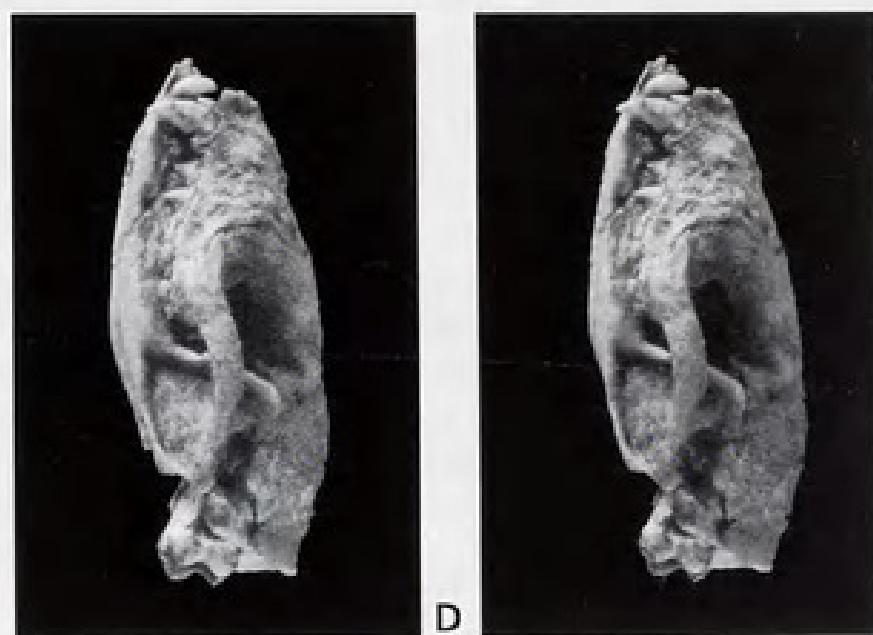
(Fig. 15). The frontal contacts the small orbital contribution of the orbitosphenoid along its anterior and dorsal edges. More posteriorly, the frontal has a broad arcuate contact with the alisphenoid, ventral to the interorbital constriction on the anterior surface of the cranium. The contact with the parietal extends from the lateral surface of the anterior part of the cranium in an almost straight line dorso-dorsoanteriorly, just posterior to the interorbital constriction. A weak supraorbital process is sometimes present (as in YPFB Pal 6105 and 6108) on the anterolateral surface of the frontal, and a small anteriorly opening supraorbital foramen consistently occurs just ventral to this process within the dorsal edge of the orbit. A well developed oval-shaped ethmoid foramen opens anteriorly at the frontal-alisphenoid-orbitosphenoid contact. The anteromedial and dorsal wall of this foramen are formed by the frontal, the posterolateral wall by the alisphenoid, the anteroventral wall by the orbitosphenoid, and the posteroventral wall by the basisphenoid as seen in YPFB Pal 6105 (right side) and 6108 (left side).

PARIETAL (Fig. 12). — The large plate-like parietals cover the greater part of the dorsal and dorsolateral surfaces of the cranium. They have a broad ventroposteriorly directed contact with the frontal, a broad continuous contact with the dorsal parts of the alisphenoid and squamosal ventrally, and a broad convex contact with the postparietal posteriorly. The outer walls of the parietals are distinctly convex, reflecting the presence of well developed cerebral hemispheres, and are ornamented dorsomedially by irregular scars for attachment of the temporalis muscle.

These scars are seen to some degree in all specimens, but are most prominent in YPFB Pal 6105 in which a distinct scar-region on the left parietal extends from the frontal-parietal suture directed toward, but not reaching, the postparietal-squamosal suture. On the right parietal of YPFB Pal 6105 and in all other specimens these scars are less distinct and are concentrated on the dorsomedial area of this bone.

POSTPARIETAL (Figs 12 and 17). — This bone is tightly fused with the parietal and the suture is often difficult to identify. Nevertheless, careful study shows that the contact with the parietal is broadly concave and extends ventrally where it meets the dorsoposterior end of the squamosal, then turns sharply posteriorly having a nearly horizontal suture with the squamosal. A distinct suture separates the postparietal from the underlying supraoccipital (Fig. 17). The postparietal overhangs the entire dorsal edge of the supraoccipital so that the lambdoidal crest is formed entirely by the posterior edge of the postparietal. Viewed posteriorly the postparietal also overlaps the dorsolateral edge of the pars mastoidea of the petromastoids (Fig. 17).

ORBITOSPHENOID (Fig. 15). — Parts of this bone are preserved only in YPFB Pal 6105 and 6108. Viewed laterally this bone makes a small contribution to the posteroventral base of the orbital region. It contacts the frontal anteriorly and dorsally, the palatine anteroventrally and the basisphenoid posteroventrally. In ventral view it forms the posteromedial roof of the choanal orifice, the posterolateral parts of the roof are formed by small wings of the palatine. Within the orbit (Fig. 15) a large ovoid, anteriorly opening optic-orbital foramen (which transmits cranial nerves II, III, IV, V1, VI, the ophthalmic artery, and a vein which drains the eye to the cavernous sinus) has the entire medial wall formed by the orbitosphenoid, the anteroventral edges by the palatine, the anterior and dorsal edges by the frontal, and apparently the alisphenoid posterolaterally although the alisphenoid is broken in this area in all specimens. The posterior side of the orbitosphenoid has a distinct convex saddle-shaped surface marking the confluence of the left and right optic-orbital foramina; the posterodorsal part has the form of laterally projecting horns which separate the upper edge of the optic-orbital foramen from the lower edge of the more dorsally situated ethmoid foramen.

ALISPHENOID (Figs 12, 15, and 19). — This bone forms most of the anterior ventrolateral parts of the ventral surface of the cranium. Anterodorsally it has a broad horizontal contact with the frontal (Fig. 15); posterodorsally a broad horizontal contact with the parietal; posteriorly a broad convex contact with the squamosal, which continues ventrally toward the base of the zygomatic process, passes anteriorly around it, continues on the ventral surface of the skull and reaches the posterolateral corner of the foramen ovale (which transmits V3, and possibly the major transverse sinus of the external jugular vein; see below) (Figs 12 and 19). The alisphenoid forms the anterior rim of the foramen ovale and, at its contact with the petromastoid, lateral to the position of the small medial lacerate foramen (which is located at the junction of the basisphenoid-basioccipital-petromastoid-alisphenoid; *sensu* MacIntyre, 1967) it extends anteriorly in tight sutural contact with the basisphenoid, bisects the entocarotid foramen (alisphenoid forms lateral rim, basisphenoid

medial rim), which transmits the internal carotid artery and a small vein from the inferior petrosal sinus, and continues anteriorly to the anterior edge of the basisphenoid. The anteroventral extent of the alisphenoid is not preserved in any specimen, but it probably formed the posterolateral rim of the optic-orbital foramen as in *Didelphis*, and based on the size and breakage surface anteroventrally there was clearly a wing-like structure which extended anterolaterally toward the lateral edge of the choanal orifice (Fig. 15). On the anteroventral surface, immediately lateral and parallel to the basisphenoid contact, is a sulcus marking the position of the pterygoid canal (for the pterygoid or vidian nerve; see JOLLIE, 1962: 44) or sutural contact with the pterygoid (seen in YPFB Pal 6105). This bone is not well preserved in any specimen. The pterygoid canal can be followed posteriorly to the anterolateral edge of the entocarotid foramen. Immediately lateral and slightly dorsal to this canal is a large ovoid, anteriorly opening foramen rotundum (seen only in YPFB Pal 6108) which transmitted the maxillary branch of the trigeminal nerve, V2 (JOLLIE, 1962: 44) (Figs 12 and 15).
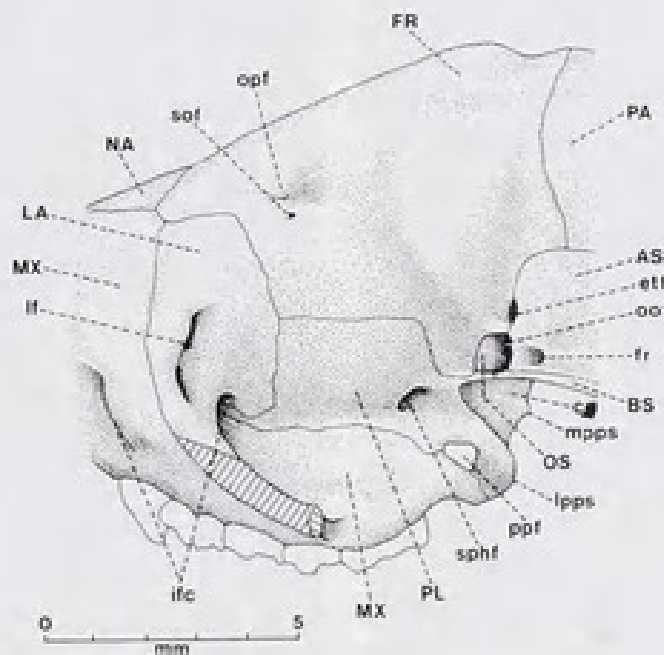

FIG. 15. — *Pucadelphys andinus*. Detail of left orbital region based primarily on YPFB Pal 6105 (holotype). Abbreviations: **AS**, alisphenoid; **BS**, basisphenoid; **co**, choanal orifice; **etf**, ethmoid foramen; **fr**, foramen rotundum; **FR**, frontal; **ifc**, infraorbital canal; **LA**, lacrimal; **lf**, lacrimal foramen; **mpps**, medial postpalatine spine; **MX**, maxilla; **NA**, nasal; **oof**, optic-orbital foramen; **opf**, supraorbital process of frontal; **OS**, orbitosphenoid; **PA**, parietal; **PL**, palatine; **ppf**, postpalatine foramen; **sof**, supraorbital foramen; **sphf**, sphenopalatine foramen.

FIG. 15. — Pucadelphys andinus. *Détail de la région orbitaire gauche principalement d'après YPFB Pal 6105 (holotype). Abréviations:* **AS**, *alisphénoïde;* **BS**, *basisphénoïde;* **co**, *orifice de la choane;* **etf**, *foramen ethmoïde;* **fr**, *foramen rotundum;* **FR**, *frontal;* **ifc**, *canal infraorbitaire;* **LA**, *lacrimal;* **lf**, *foramen lacrimal;* **mpps**, *épine postpalatine médiale;* **MX**, *maxillaire;* **NA**, *nasal;* **oof**, *foramen optico-orbitaire;* **opf**, *processus supraorbitaire du frontal;* **OS**, *orbitosphénoïde;* **PA**, *pariétal;* **PL**, *palatin;* **ppf**, *foramen postpalatin;* **sof**, *foramen supraorbitaire;* **sphf**, *foramen sphénopalatin.*

BASISPHENOID (Figs 12 and 15). — As seen in YPFB Pal 6105 and 6108, this is an anteroposteriorly elongate bone which is broadest posteriorly along its contact with the basioccipital and narrows anteriorly to its contact with the orbitosphenoid; sutures with the basioccipital and orbitosphenoid are distinct. Laterally it has broad contacts with the alisphenoid; these bones are tightly fused and the suture is, in places, difficult to identify. The posterior surface of the basisphenoid is convex ventrally, while anterior to the entocarotid foramen it is flat. The anterior end of this bone in YPFB Pal 6105 is broken transversely, a feature which appears to represent natural breakage but which may mark sutural contact between the basisphenoid (s.s.) and a smaller presphenoid. However, this bone is quite similar to that in *Didelphis* and appears to be the basisphenoid which is simply lacking its anterior end.

SQUAMOSAL (Figs 12, 17 and 19). — This bone has a broad concave contact with the alisphenoid anteriorly; a broad and nearly horizontal contact with the parietal dorsoanteriorly and dorsomedially, and with the postparietal dorsoposteriorly; an irregular vertical contact with the lateral surface of the pars mastoidea of the petromastoid posteriorly; and ventrally its contact with the petromastoid extends anteromedially from the lateral base of the mastoid process, passes along the lateral edge of the fossa incudis and epitympanic recess, and joins the short transversely oriented squamosal suture at the posterolateral corner of the foramen ovale.

In ventral view the glenoid fossa is deep and transversely elongate; a large postglenoid process of the squamosal occurs along its posterior edge and attains its greatest ventral extension medially; a much lower, but still distinct, preglenoid process of the squamosal occurs along the anteromedial edge of the fossa and a large preglenoid process of the posterior edge of the jugal borders the fossa anterolaterally.

Three foramina perforate the squamosal externally. The first and smallest is a postzygomatic foramen on the posterobasal surface of the zygomatic arch dorsal to the deepest point of the postglenoid process (Fig. 17). This foramen apparently transmits a vein from the squamosal root of the zygomatic arch to the sphenoparietal emissary vein (ARCHER, 1976a). It is usually single, transversely elongate, and opens laterally; however, it is sometimes double (as in left side of YPFB Pal 6105) with a second smaller opening set dorsomedially to the primary one.

The second foramen is the subsquamosal which is large, oval, and opens posteroventrally at the base of the zygomatic arch just dorsal to the external acoustic meatus (Fig. 12). It is most clearly seen in posterolateral view, while in dorsal view it is obscured by a posterior swelling of the squamosal along its upper edge and a similar but smaller swelling occurs along its lower edge. Thus, this foramen opens into a shallow postzygomatic depression in the squamosal. Externally the foramen opens within the squamosal, while internally (as seen in right side of YPFB Pal 6110) the medial side of the canal that it transmits is formed by the petromastoid and the lateral side by the squamosal (Fig. 19). This foramen transmits an artery from the postglenoid foramen onto the parietal area of the cranium which supplies the temporalis muscle, and a vein from the parietal area to the sphenoparietal emissary vein, which exits through the postglenoid foramen (ARCHER, 1976a; WIBLE, 1990).

The third and largest is the postglenoid foramen which is ovoid in shape and opens ventrolaterally along the posteromedial edge of the postglenoid process (Figs 12 and19). The course of the vessels this foramen transmits continues as a groove beyond the opening toward the ventromedial edge of the postglenoid process. The external opening occurs solely within the squamosal, while internally (as seen on the right side of YPFB Pal 6110; Fig. 19) at a level corresponding to the dorsal rim of the external acoustic meatus, the medial side of this canal is formed by the petromastoid and the lateral side by the squamosal. This foramen transmits the
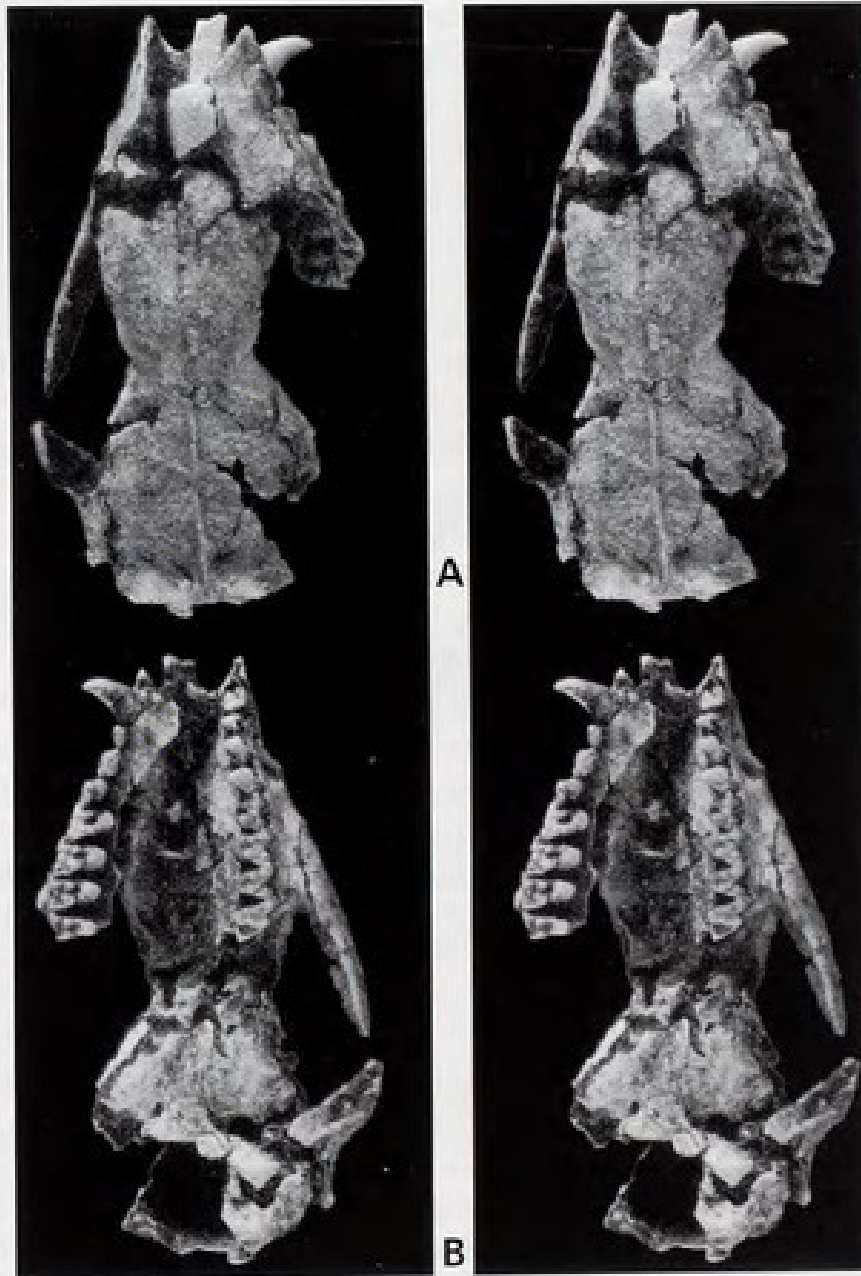

FIG. 16. — *Pucadelphys andinus.* Skull of YPFB Pal 6108 (A, dorsal; B, ventral views). Stereophotos, X 2.5.

FIG. 16. — Pucadelphys andinus. *Crâne d'YPFB Pal 6108 (A, vue dorsale; B, vue ventrale). Photos stéréoscopiques, X 2.5.*

sphenoparietal emissary (which externally becomes the postglenoid) vein from the prootic sinus (WIBLE, 1990), and the postglenoid artery (ARCHER, 1976a; WIBLE, 1990).

A fourth but smaller foramen, the posttemporal, opens between the squamosal and pars mastoidea of the petromastoid directly posterior to the subsquamosal foramen and dorsal to the mastoid process. This foramen transmits the arteria diploetica magna and vena diploetica magna (WIBLE, 1990) which pass through a canal bordered by the petromastoid medially and squamosal laterally (Fig. 21).

BASIOCCIPITAL (Figs 12, 17, 19 and 21). — As seen in YPFB Pal 6105, 6107 and 6470, this bone has the shape of an arrow-head base and the sutures with adjacent elements are well defined. The basioccipital has a broad transverse linear contact with the basisphenoid anteriorly between the left and right medial lacerate foramina. From these foramina it extends posterolaterally in contact with the medial surface of the pars petrosa of the petromastoid to the anteromedial corner of the posterior lacerate foramen, where it bends sharply medially forming a small but distinct convex rim over the inferior petrosal foramen (basioccipital forms ventral and medial rims, exoccipital forms ventromedial rim, and pars petrosa of petromastoid forms lateral rim) which transmits the inferior petrosal sinus. On the medial side of the foramen for the inferior petrosal sinus the basioccipital contacts the exoccipital and the suture arcs posteromedially to a point on the lateral side of the ventral occipital condyle. The posterior edge of the basioccipital forms the ventral rim of the foramen magnum where a pair of well developed ventral occipital condyles are separated by a distinct U-shaped intercondylar fossa. The foramen magnum transmits most of the sigmoid sinus of the transverse venous system and the spinal root of nerve XI out of cranium (DOM et al., 1970; WIBLE, 1990) and the vertebral arteries into cranium (ARCHER, 1976a).

The ventral surface of the basioccipital has a low medial keel extending anteriorly from the middle of the intercondylar fossa to the basisphenoid suture; the lateral edges of the basioccipital are elevated surfaces extending parallel to the petromastoid suture and they mark the floor of the inferior petrosal sinus; between each of these lateral elevations and the medial keel is a broad fossa for the rectus capitis muscle; the posterolateral edge of the basioccipital, between the elevated ventral occipital condyles and the ventral rim of the inferior petrosal foramen, is distinctly convex dorsally.

EXOCCIPITAL (Figs 12, 17, 19 and 21). — Viewed ventrally this bone contacts the basioccipital medially; it forms the posterodorsal rim of the inferior petrosal foramen anteromedially; and the medial and posterior rim of the posterior lacerate foramen (which transmits nerves IX, X, XI and probably a small branch of the sigmoid sinus to the internal jugular vein) anteriorly; it also makes a small contact with the pars petrosa of the petromastoid via a septum between the inferior petrosal and posterior lacerate foramina; and laterally it contacts the pars mastoidea of the petromastoid.

Ventrally, in the large fossa just anterior to the elevated prominence of the lower rim of the dorsal occipital condyle, are typically three small subequal-sized condyloid foramina (Fig. 19) which apparently transmit branches of cranial nerve XII as occurs in some specimens of *Didelphis*

(JOLLIE, 1962: 55) but may also transmit branches of the sigmoid sinus to the internal jugular vein (ARCHER, 1976a, fig. 2B). Of these three foramina the posterior-most passes under the medial part of the dorsal occipital condyle; a second occurs anterolaterally between the first and posterior lacerate foramen; and the third occurs anterior to the first and opens either totally within the exoccipital just lateral to the basioccipital suture or within the suture itself.

Viewed posteriorly (Fig. 17) the exoccipital has a broad arcuate (convex) contact with the pars mastoidea of the petromastoid which extends from the center of the exoccipital process ventrally to the junction with the supraoccipital dorsally, where it bends sharply medially having a slight arcuate (convex) contact with the supraoccipital to the dorsal edge of the dorsal atlantal facet; medially, it forms the lateral rim of the posteriorly facing and transversely ovoid foramen magnum. On its posterior dorsomedial surface, the exoccipital has a prominent dorsal atlantal facet at the point of contact with the supraoccipital and a large ovoid dorsal occipital condyle occurs ventromedially. The exoccipital contributes to the formation of the medial half of the very small exoccipital process ventrolaterally. The exoccipital process is delimited medially by a trough in the exoccipital separating it from the dorsal occipital condyle, and another trough laterally in the petromastoid separating it from the larger mastoid process.
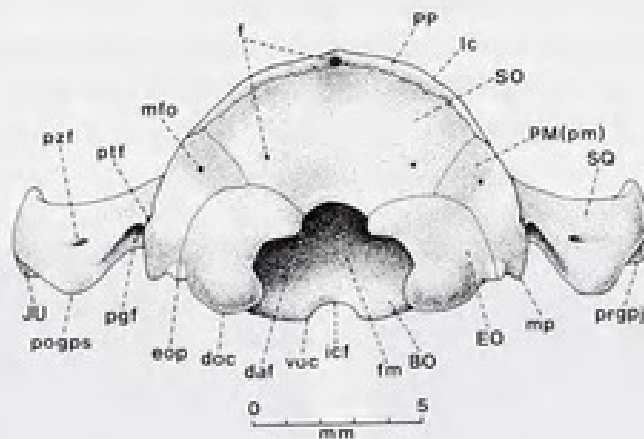

FIG. 17. — *Pucadelphys andinus*. Reconstruction of the posterior view of the skull and zygomatic arches, based primarily on YPFB Pal 6105 (holotype). Abbreviations: **BO**, basioccipital; **daf**, dorsal atlantal facet; **doc**, dorsal occipital condyle; **EO**, exoccipital; **eop**, exoccipital process; **f**, foramen; **fm**, foramen magnum; **icf**, intercondylar fossa; **JU**, jugal; **lc**, lambdoidal crest (=nuchal crest); **mfo**, mastoid foramen; **mp**, mastoid process; **pgf**, postglenoid foramen; **PM(pm)**, pars mastoidea of petromastoid (=mastoid s.s.); **pogps**, postglenoid process of squamosal; **PP**, postparietal; **prgpj** preglenoid process of jugal; **ptf**, posttemporal foramen; **pzf**, postzygomatic foramen; **SO**, supraoccipital; **SQ**, squamosal; **voc**, ventral occipital condyle.

FIG. 17. — Pucadelphys andinus. *Reconstitution de la vue postérieure du crâne et des arcades zygomatiques principalement d'après YPFB Pal 6105 (holotype). Abréviations: BO, basioccipital; daf, facette atlantale dorsale; doc, condyle occipital dorsal; EO, exoccipital; eop, processus exoccipital; f, foramen; fm, foramen magnum; icf, fosse intercondylienne; JU, jugal; lc, crête lambdoïde (=crête nuchale); mfo, foramen mastoïde; mp, processus mastoïde; pgf, processus postglénoïde; PM(pm), pars mastoidea du pétromastoïde (=mastoïde s.s.); pogps, processus postglénoïde du squamosal; PP, postpariétal; prgpj processus préglénoïde du jugal; ptf, foramen posttemporal; pzf, foramen postzygomatique; SO, supraoccipital; SQ, squamosal; voc, condyle occipital ventral.*

In YPFB Pal 6105 the distance between the outer edges of the dorsal occipital condyles is 8.0 mm and 4.5 mm between the inner edges; the maximum breadth of the foramen magnum, dorsal to the dorsal occipital condyles, is 5.0 mm and the maximum depth is 3.0 mm.

SUPRAOCCIPITAL (Figs 12 and 17). — This bone occupies most of the dorsal surface of the occipital plate and forms the dorsomedial rim of the foramen magnum. It has a broad contact with the exoccipital ventrolaterally, a broad contact with the pars mastoidea of the petromastoid laterally, and a broad arcuate contact with the postparietal dorsally. As noted above, the contact with the latter occurs ventral to the lambdoidal crest which is formed entirely by the postparietal. The occipital area is hidden in dorsal view by the postparietal extension of the lambdoidal crest. There is no distinct vertical medial crest, but in YPFB Pal 6105 the posterior surface is ornamented with small ridges, scars and shallow pits marking areas of insertion of the nuchal muscle (these features are not seen in other specimens). There are only three small foramina in the supraoccipital: one (left and right) dorsomedial to the point of contact of the petromastoid and exoccipital; and a single foramen dorsomedially, between the supraoccipital and postparietal below the lambdoidal crest at its point of contact with the sagittal crest.

PETROMASTOID (Figs 12, 17, 19 and 21). — This is the most complex bone of the skull. For purposes of description it can be divided into two principal components: the pars mastoidea which contributes to the formation of the lateral part of the occipital region and houses the subarcuate fossa on the cerebellar side; and the pars petrosa which houses the inner ear in a teardrop shaped promontorium on the ventral side between the basioccipital and squamosal, and the internal acoustic meatus on the cerebellar side (MacINTYRE, 1972).
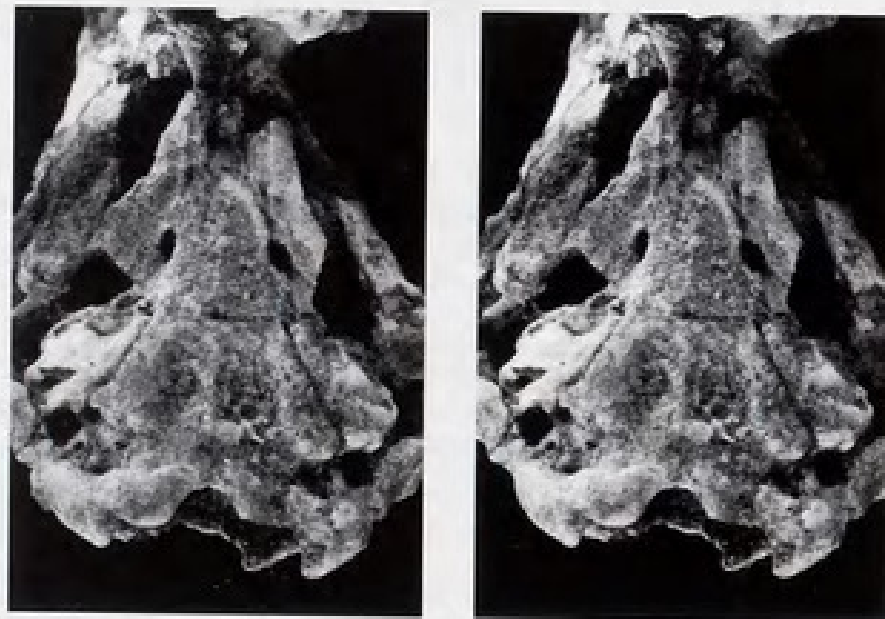

FIG. 18. — *Pucadelphys andinus.* Ventral view of basicranium of YPFB 6105 (holotype). Stereophotos, X 5.

FIG. 18. — Pucadelphys andinus. *Vue ventrale de la base du crâne d'YPFB 6105 (holotype). Photos stéréoscopiques, X 5.*

The pars mastoidea is best seen in posterior view (Fig. 19) where it occupies the lateral area of the occipital region and contacts the exoccipital ventromedially, the supraoccipital dorsomedially, the ventrolateral edge of the postparietal dorsally, and the squamosal along most of its lateral surface. A tiny mastoid foramen typically occurs on the posterior surface of the pars mastoidea just lateral to the supraoccipital-exoccipital-petromastoid juncture (Fig. 17), and internally opens along the posterior side of the sigmoid sinus (Fig. 21). A small posttemporal foramen (*sensu* WIBLE, 1990) occurs on the lateral surface of the occiput between the squamosal and the pars mastoidea (Figs 12 and 21; see below). A large ovoid surface facing ventrolaterally is ornamented with muscle scars, and was probably the major area for insertion of muscles which move the head and neck (Figs 12 and 17).

Viewed ventrally (Fig. 19) the pars mastoidea contributes posteromedially to the formation of the lateral half of the very small exoccipital process and it forms all of the larger mastoid process laterally. The anteroventral rim at its medial-most edge is united with the pars petrosa by a narrow bridge of bone on the lateral side of the posterior lacerate foramen. Lateral to this bridge, the anteroventral rim of the pars mastoidea forms an anteriorly directed lip which represents the caudal tympanic process of the petromastoid (*sensu* WIBLE, 1990). It underhangs a fossa located between it and the posterior end of the promontorium of the pars petrosa which is called the mastoid epitympanic sinus (*sensu* ARCHER, 1976a: 314). Lateral to the caudal tympanic process of the petromastoid, is the well developed mastoid process, and along its lateral and medial surfaces anteriorly is the stylomastoid notch, through which the facial nerve and lateral head vein leave the middle ear (WIBLE, 1990). The lateral extremity of the anteroventral rim of the pars mastoidea extends anterodorsally, up to the medial border of the fossa incudis at the posteromedial extremity of the epitympanic recess, lateral to the fenestra vestibuli.

The pars petrosa, viewed ventrally, is dominated by a large teardrop-shaped promontorium (=pars cochlearis) which is broadest posteriorly and tapers anteromedially to a point at the junction of the alisphenoid-basisphenoid-basioccipital. In lateral view the ventral border of the promontorium is at a level slightly dorsal to the ventral edge of the dorsal occipital condyles. The ventral surface of the promontorium is nearly smooth and the minor topographic variations largely reflect turns of the cochlear duct.

Anteriorly, a broad shallow depression is located between the promontorium and the large foramen ovale; it begins at the anteromedial edge of the large ovoid bulge of the promontorium, extends anterior and parallel to the basioccipital suture, crosses onto the alisphenoid just lateral to the medial lacerate foramen, and passes on the alisphenoid, to the posterior edge of the entocarotid foramen. This depression marks the route of passage of the internal carotid artery (i.e. sulcus for internal carotid artery) on its way to the entocarotid foramen; the passage of the internal carotid artery is thus situated medially (*sensu* PRESLEY, 1979). The large fossa lateral to this depression on the anterolateral surface of the promontorium is for insertion of the tensor tympani muscle. The medial edge of the promontorium parallel and adjacent to the basioccipital suture is elevated and rounded, a feature produced by the internal sulcus for the inferior petrosal sinus which exits the basicranium through the inferior petrosal foramen at the posteromedial edge of the promontorium.
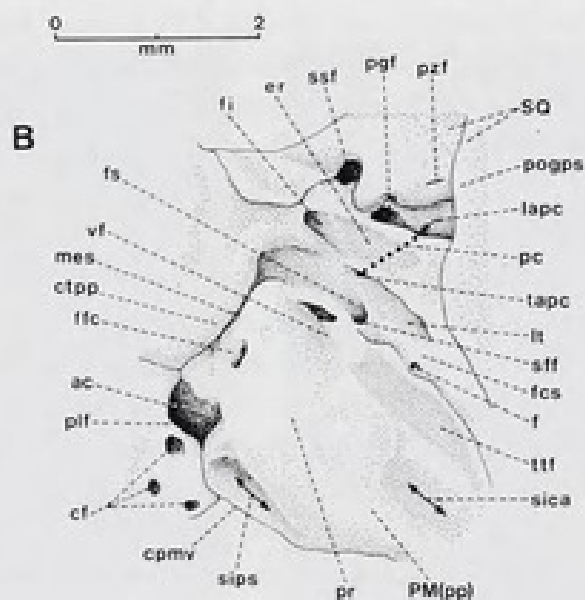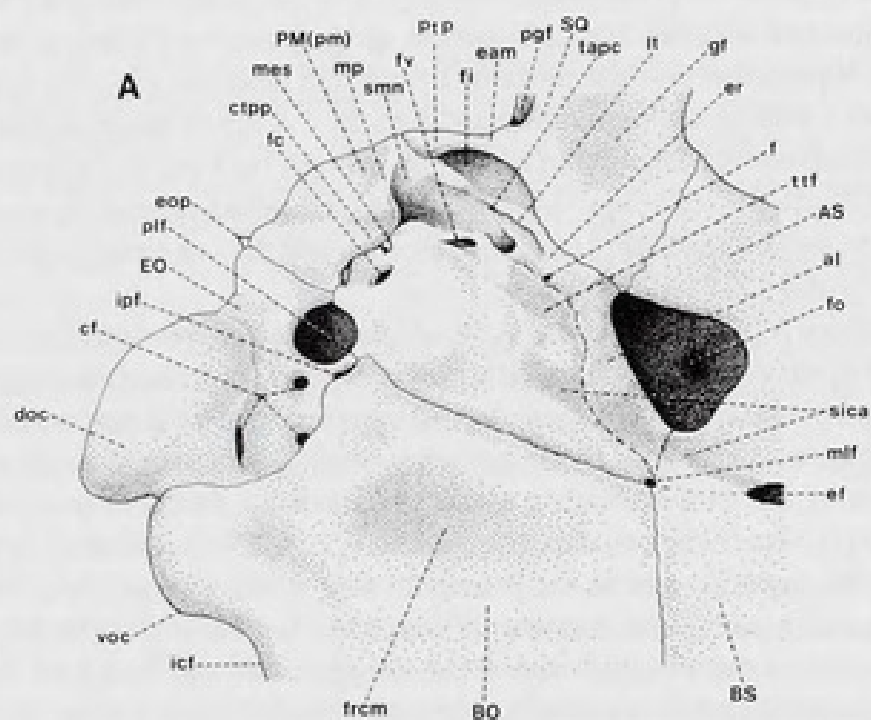
Two openings occur on the posterior surface of the promontorium. The first and smallest is the fenestra cochleae which is situated on the posterolateral surface of the promontory anterolateral to the lateral edge of the posterior lacerate foramen and opens laterally; it occurs at the ventral edge of a shallow depression, the fossula fenestra cochleae. Viewed posteriorly, this fenestra occurs immediately anterior to the small exoccipital process at the exoccipital-pars mastoidea suture, and its ventral opening is at about the same level as the medial part of the ventral rim of the pars mastoidea (i.e. the lowest point of the trough separating the exoccipital and mastoid processes). The second and larger opening is the fenestra vestibuli which accommodates the footplate of the stapes and annular ligament; it has an ovoid (anteroposteriorly elongate) shape, a length/width ratio of 1.4 based on two specimens, and occurs dorsally on the lateral surface of the promontorium within a shallow depression, the vestibular fossula. In lateral view, this fenestra is seen at the posterodorsal edge of the external acoustic meatus. It thus lies anterolateral and a little dorsal to the fenestra cochleae, and the two fenestra are separated by a broadly rounded and vertically oriented swelling of the posterolateral corner of the promontorium.

Fig. 19. — *Pucadelphys andinus*. A, reconstruction of the right side of the basicranium in ventral view, based on YPFB Pal 6105 (holotype) and 6110; B, right ear region in ventral view (YPFB Pal 6110). The foramen ovale is restored. Abbreviations: **ac**, aquaeductus cochleae; **al**, anterior lamina; **AS**, alisphenoid; **BO**, basioccipital; **BS**, basisphenoid; **cf**, condyloid foramen; **cpmv**, crista promontorii medioventralis; **ctpp**, caudal tympanic process of pars mastoidea of petromastoid; **doc**, dorsal occipital condyle; **eam**, external acoustic meatus; **ef**, entocarotid foramen (=anterior carotid foramen, carotid canal); **EO**, exoccipital; **eop**, exoccipital process; **er**, epitympanic recess; **f**, foramen; **fc**, fenestra cochleae (=rotunda); **fcs**, floor of cavum supracochleare; **ffc**, fossula fenestra cochleae; **fi**, fossa incudis; **fo**, foramen ovale; **frcm**, fossa for rectus capitis muscle; **fs**, facial sulcus; **fstm**, fossa for stapedial muscle; **fv**, fenestra vestibuli (=ovalis); **gf**, glenoid fossa; **icf**, intercondylar fossa; **ipf**, inferior petrosal foramen (=internal jugular foramen); **lape**, lateral aperture of prootic canal; **lt**, lateral trough; **mes**, mastoid epitympanic sinus of epitympanic recess; **mlf**, median lacerate foramen; **mp**, mastoid process; **pc**, prootic canal; **pgf**, postglenoid foramen; **plf**, posterior lacerate foramen (=jugular foramen); **PM(pm)**, pars mastoidea of petromastoid (=mastoid s.s.); **PM(pp)**, pars petrosa of petromastoid (=petrosal s.s.); **pogps**, postglenoid process of squamosal; **pr**, promontorium of pars petrosa of petromastoid; **ptp**, posttympanic process; **pzf**, postzygomatic foramen; **sff**, secondary facial foramen; **sica**, sulcus for internal carotid artery; **sips**, sulcus for inferior petrosal sinus; **smn**, stylomastoid notch; **SQ**, squamosal; **ssf**, subsquamosal foramen (=suprameatal, postsquamosal); **tapc**, tympanic aperture of prootic canal; **ttf**, tensor tympani fossa; **vf**, vestibular fossula; **voc**, ventral occipital condyle.

Fig. 19. — Pucadelphys andinus. A, *Reconstitution du côté droit de la base du crâne en vue ventrale d'après YPFB Pal 6105 (holotype) et 6110; B, vue ventrale de la région auditive droite (YPFB Pal 6110). Le foramen ovale est reconstitué. Abréviations: **ac**, aqueduc cochléaire; **al**, lame antérieure; **AS**, alisphénoïde; **BO**, basioccipital; **BS**, basisphénoïde; **cf**, foramen condylien; **cpmv**, crista promontorii medioventralis; **ctpp**, processus tympanique caudal de la pars mastoidea du pétromastoïde; **doc**, condyle occipital dorsal; **eam**, méat acoustique externe; **ef**, foramen entocarotidien (=foramen carotidien antérieur, canal carotidien); **EO**, exoccipital; **eop**, processus exoccipital; **er**, recessus épitympanique; **f**, foramen; **fc**, fenestra cochleae (=rotunda); **fcs**, plancher du cavum supracochleare; **ffc**, fossula fenestra cochleae; **fi**, fossa incudis; **fo**, foramen ovale; **frcm**, fosse pour le muscle rectus capitis; **fs**, sillon facial; **fstm**, fosse pour le muscle stapédial; **fv**, fenestra vestibuli (=ovalis); **gf**, fosse glénoïde; **icf**, fosse intercondylienne; **ipf**, foramen pétreux inférieur (=foramen jugulaire interne); **lape**, ouverture latérale du canal prootique; **lt**, dépression latérale; **mes**, sinus épitympanique mastoïde du recessus épitympanique; **mlf**, trou déchiré moyen; **mp**, processus mastoïde; **pc**, canal prootique; **pgf**, foramen postglénoïde; **plf**, trou déchiré postérieur (=foramen jugulaire); **PM(pm)**, pars mastoidea du pétromastoïde (=mastoïde s.s.); **PM(pp)**, pars petrosa du pétromastoïde (=pétreux s.s.); **pogps**, processus postglénoïde du squamosal; **pr**, promontoire de la pars petrosa du pétromastoïde; **ptp**, processus posttympanique; **pzf**, foramen postzygomatique; **sff**, foramen facial secondaire; **sica**, sillon pour la carotide interne; **sips**, sillon pour le sinus pétreux inférieur; **smn**, échancrure stylomastoïdienne; **SQ**, squamosal; **ssf**, foramen subsquamosal (=suprameatal, postsquamosal); **tapc**, ouverture tympanique du canal prootique; **ttf**, fosse pour le muscle tensor tympani; **vf**, fossette vestibulaire; **voc**, condyle occipital ventral.*

A large ovoid secondary facial foramen, which is the opening of the facial nerve (VII) canal into the middle ear, occurs just anterior to the dorsal edge of the fenestra vestibuli. The secondary facial foramen opens posteriorly and a sulcus for the facial nerve (sulcus facialis) occurs immediately posterior to this foramen and separates the fenestra vestibuli from the epitympanic recess and the lateral trough (see below); these features are clearly seen in YPFB Pal 6110 (Fig. 19).

The epitypanic recess is "the extension of the middle ear cavity that lies dorsal to the tympanic membrane and contains the mallear-incudal articulation" (WIBLE, 1990: 188), (see also VAN DER KLAAUW, 1931: 73; and ARCHER, 1976a: 226). It is also called the fossa capitis mallei. The posterior extremity of the epitympanic recess is a deep and narrow pit where the ligament of the crus breve of the incus attaches: it is the fossa incudis or fossa crus breve incudis. In *Pucadelphys*, the epitympanic recess is an oblique, slightly concave depression in the roof of the tympanic cavity, approximately three times longer than wide, and bordered laterally and medially by thin bony rims. It is limited anteriorly by the squamosal at the anterior edge of the postglenoid foramen. The lateral rim of the epitympanic recess forms the medial wall of the postglenoid foramen (this is clearly seen on the right side of YPFB Pal 6110).The fossa incudis is a small pit located at the posteromedial extremity of the epitypanic recess.

The lateral trough is a well developed anteroposteriorly elongate slit that opens medially just lateral to the secondary facial foramen. It is formed by a depression in the petromastoid overhanging the medial rim of the epitympanic recess as clearly seen on the right side of YPFB Pal 6110 (Fig. 19). In the posterior end of the lateral trough is a small foramen which represents the tympanic aperture of the prootic canal which connects the lateral head vein (vena capitis lateralis; ARCHER, 1976a: 302; WIBLE, 1990) to the prootic sinus (Fig. 19). The prootic canal has a lateral opening within the petromastoid (lateral aperture of prootic canal) into the postglenoid canal (as seen on left side of YPFB Pal 6110) where the lateral head vein joins with the prootic sinus at its juncture with the sphenoparietal emissary vein (Fig. 21).

A small fossa for the origin of the stapedius muscle (fossa stapedius or fossa muscularis minor) occurs on the medial side of the lateral part of the stylomastoid notch and dorsal to it, just posterolateral to the fenestra vestibuli, posterior to the sulcus for the facial nerve. The fossa is shallow, dorsoventrally elongated, and faces medially. It is backed on to the fossa incudis (Fig. 19).

A tiny anteriorly directed opening foramen occurs on the lateral side of the fossa for the tensor tympani muscle, adjacent to the promontorium between the secondary facial foramen and the foramen ovale (Fig. 19). This foramen leads into a passage which joins with the posterior end of the facial canal within the petromastoid.

Two tiny openings occur in the posteromedial wall of the petromastoid, within the posterior lacerate foramen, which connect with the vestibular cavity (Figs 19, 21). The first is the aquaeductus cochleae which transmits the perilymphatic duct and a vein; it is situated in a vertical sulcus just dorsal to the outer opening of the posterior lacerate foramen within the jugular sulcus, on the medial side of the bridge joining the pars mastoidea and pars petrosa. Viewed posteriorly this opening is at about the same level as the dorsal rim of the fenestra cochleae. The second

opening is the aquaeductus vestibuli which transmits a vein and the endolymphatic duct. It is a small vertical slit deep within the posterior lacerate foramen, dorsal to the aquaeductus cochleae, on the anterior side of the jugular sulcus at a level corresponding to the lower edge of the subarcuate fossa posterior to the crus commune (Fig. 21); it opens posteriorly on the back surface of the broad crista separating the subarcuate fossa and jugular sulcus.

The cerebellar surface of the petromastoid consists principally of a large broadly ovoid central body oriented dorsolaterally-ventromedially, with two large openings (Fig. 21). The first opening, the subarcuate fossa, is the more dorsoposterior of the two and is a deep spheroidal pocket which opens medially; it houses the paraflocculus of the cerebellum. The second opening, the internal acoustic meatus, is more ventromedially located and is separated from the subarcuate fossa by a broad horizontally oriented septum of which the posteromedial part is the crus commune. The internal acoustic meatus is a broad shallow opening containing two deeper pits separated by a low transverse septum. The larger of these pits is the foramen acusticum inferius which is set posteromedial to the other and serves for transmitting two branches of the vestibulocochlear nerve (VIII); it has a fusiform shape and opens dorsomedially. The smaller of the pits is the foramen acusticum superius which is set anterolateral to the first and is a vertical slit which opens posteromedially and a little ventrally; it transmits the facial (VII) and branches of the vestibulocochlear (VIII) nerves. The ventral rim of the internal acoustic meatus opens onto a large anteromedially projecting platform, which is rounded and thickened anteriorly to form a divide which separates, on the one hand a broad medially directed sulcus leading from the foramen acusticum inferius on its posterior side, and on the other hand a smaller more anteriorly directed and dorsally situated sulcus running from the foramen acusticum superius on its anterior side.

FIG. 20. — *Pucadelphys andinus*. View of the cerebellar (dorsomedial) surface of petromastoid of YPFB Pal 6470. Stereophotos. X 5.

FIG. 20. — Pucadelphys andinus. *Vue de la surface cérébellaire (dorso-médiale) du pétromastoïde de YPFB Pal 6470. Photos stéréoscopiques. X 5.*

Four principal sulci surround the central body of the petromastoid on its cerebellar surface (Fig. 21): 1) Along the ventromedial edge is an elongate sulcus for the inferior petrosal sinus which is bordered dorsally by the crista promontorii medioventralis. This sinus connects "the venous sinus (sinus cavernosus) encasing the pituitary gland and optic chiasma with the internal jugular vein just before it emerges from the inferior petrosal foramen" (MACINTYRE, 1972: 291). 2) Posteroventrally, is a shallow and nearly vertical sulcus for the jugular sinus. 3) Posterodorsally is a small pocket representing the sulcus for the sigmoid sinus. A tiny medially opening foramen in the deepest part of this sinus extends laterally and apparently connects with the canal from the small foramen in the dorsoposterior end of the sulcus for the prootic sinus (see below). There is also the cerebellar opening of the mastoid foramen for the occipital emissary vein. 4) Along the dorsolateral edge is an elongate sulcus for the prootic sinus, a primary tributary of the lateral head vein, which is walled by the squamosal laterally and by a crest of the petromastoid medially.

Anterolaterally to the crista petrosa is a large depression in an anterdorsally projecting wing of the petromastoid for part of the temporal lobe of the cerebrum and the trigeminal (=gasserian or semilunar) ganglion of the trigeminal nerve (V). In other didelphids the trigeminal ganglion lays on the alisphenoid and no anterodorsally projecting wing is observed. At the anteromedial edge of this depression along the lateral surface of the crista petrosa is a small foramen which opens anteromedially into a groove (seen clearly in YPFB Pal 6107 and 6470); this is the hiatus Fallopii which transmits the greater petrosal nerve, a branch of the facial nerve (VII). The anterolateral wing makes an extensive contribution to the floor of the middle cranial fossa (Fig. 21) and the internal side of the lateral wall of the braincase (the lateral side is formed by the squamosal and the alisphenoid; it apparently represents the relic of a reduced anterior lamina of the petrosal (*sensu* CROMPTON & JENKINS, 1979: 71, figs 3-5B, C) (see below for justification and discussion). In ventral view, an irregular contact is clearly seen between the anterolateral border of the promontorium and the flat shelf which forms the posterior edge of the foramen ovale in YPFB Pal 6105 (Fig. 19). This portion probably represents part of the anterior lamina. The anterior lamina is covered laterally by the squamosal and the alisphenoid. Its uncovered portion, visible in ventral view of the skull, lies medial to the squamosal. It forms the posterior rim of the foramen ovale, extending from the squamosal suture laterally across the anterior surface of the promontorium as a broad uneven ledge to the alisphenoid contact lateral to the medial lacerate foramen.

On the lateral (squamosal) side of the petromastoid (Fig. 21) is a broad shallow anteroventrally directed sulcus which transmitted the prootic sinus along its greater length and the sphenoparietal emissary vein ventrally. The lateral aperture of the prootic canal occurs at the anteroventral end of this sulcus and this aperture approximates the boundary between the prootic sinus (dorsally) and sphenoparietal emissary vein (ventrally). A small anteriorly directed opening foramen occurs dorsally on the petromastoid, just posterior to the sulcus for the prootic sinus. This foramen transmits a branch of the prootic sinus posteriorly within the pars mastoidea, and the canal apparently unites medially with the small foramen in the dorsal end of the sigmoid sinus (Fig. 21). A small shallow sulcus unites this foramen with the dorsoposterior edge of the sulcus for the prootic sinus (Fig. 21).
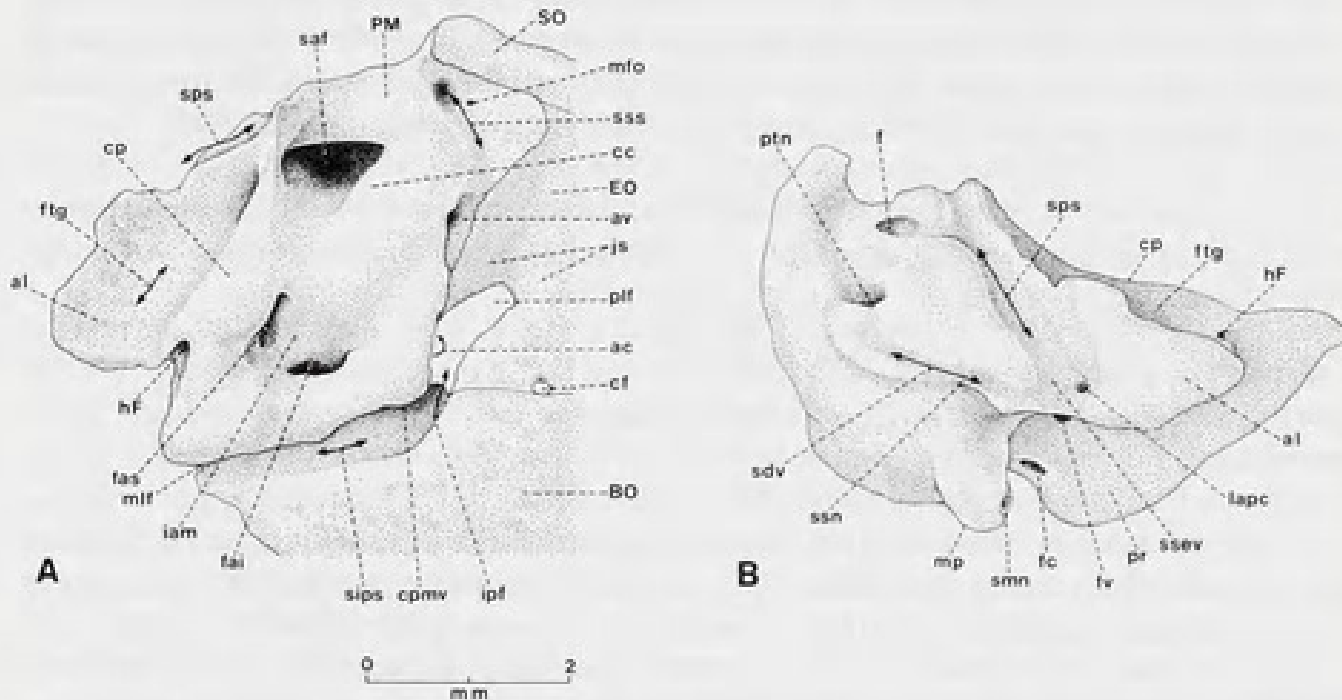
Fig. 21. — *Pucadelphys andinus*. Details of petromastoid (A, cerebellar or dorsomedial surface; B, squamosal or lateral surface), based on YPFB Pal 6470. Abbreviations: **ac**, aquaeductus cochleae; **al**, anterior lamina; **av**, aquaeductus vestibuli (=endolymphatic foramen); **BO**, basioccipital; **cc**, crus commune; **cf**, condyloid foramen; **cp**, crista petrosa; **cpmv**, crista promontorii medioventralis; **EO**, exoccipital; **f**, foramen; **fai**, foramen acusticum inferius (=area cochleae); **fas**, foramen acusticum superius (=area facialis); **fc**, fenestra cochleae (=rotunda); **ftg**, fossa for trigeminal ganglion; **fv**, fenestra vestibuli (=ovalis); **hF**, hiatus Fallopii; **iam**, internal acoustic meatus; **ipf**, inferior petrosal foramen (=internal jugular foramen); **js**, jugular sulcus; **lapc**, lateral aperture of prootic canal; **mfo**, mastoid foramen; **mlf**, median lacerate foramen; **mp**, mastoid process; **plf**, posterior lacerate foramen (=jugular foramen); **PM**, petromastoid; **pr**, promontorium of pars petrosa of petromastoid; **ptn**, posttemporal notch; **saf**, subarcuate fossa (=floccular, paraflocular fossa); **sdv**, sulcus for diploetic vessels; **sips**, sulcus for inferior petrosal sinus; **smn**, stylomastoid notch; **SO**, supraoccipital; **sps**, sulcus for prootic sinus; **SQ**, squamosal; **ssev**, sulcus for sphenoparietal emissary vein; **ssn**, subsquamosal notch; **sss**, sulcus for sigmoid sinus; **tapc**, tympanic aperture of prootic canal; **ttf**, tensor tympani fossa.

Fig. 21. — Pucadelphys andinus. *Détails du pétromastoïde (A, face cérébellaire ou dorso-médiale; B, face squamosale ou latérale), d'après YPFB Pal 6470. Abréviations:* **ac**, *aquaeductus cochleae;* **al**, *lame antérieure;* **av**, *aquaeductus vestibuli (=foramen endolymphatique);* **BO**, *basioccipital;* **cc**, *crus commune;* **cf**, *foramen condylien;* **cp**, *crista petrosa;* **cpmv**, *crista promontorii medioventralis;* **EO**, *exoccipital;* **f**, *foramen;* **fai**, *foramen acusticum inferius (=area cochleae);* **fas**, *foramen acusticum superius (=area facialis);* **fc**, *fenestra cochleae (=rotunda);* **ftg**, *fosse pour le ganglion trigeminal;* **fv**, *fenestra vestibuli (=ovalis);* **hF**, *hiatus Fallopii;* **iam**, *méat auditif interne;* **ipf**, *foramen pétreux inférieur (=foramen jugulaire interne);* **js**, *sillon jugulaire;* **lapc**, *ouverture latérale du canal prootique;* **mfo**, *foramen mastoïde;* **mlf**, *trou déchiré moyen;* **mp**, *processus mastoïde;* **plf**, *trou déchiré postérieur (=foramen jugulaire);* **PM**, *pétromastoïde;* **pr**, *promontoire de la pars petrosa du pétromastoïde;* **ptn**, *échancrure posttemporale;* **saf**, *fossa subarcuata (= fosse flocculaire ou paraflocculaire);* **sdv**, *sillon pour les vaisseaux diploetiques;* **sips**, *sillon pour le sinus pétreux inférieur;* **smn**, *échancrure stylomastoïdienne;* **SO**, *supraoccipital;* **sps**, *sillon pour le sinus prootique;* **SQ**, *squamosal;* **ssev**, *sillon pour la veine émissaire sphénopariétale;* **ssn**, *échancrure subsquamosale;* **sss**, *sillon pour le sinus sigmoïde;* **tapc**, *ouverture tympanique du canal prootique;* **ttf**, *fosse pour le muscle tensor tympani.*

A less well defined sulcus extends posteriorly from the sulcus for the sphenoparietal emissary vein along the ventral edge of the pars mastoidea, then bends dorsoposteriorly. This sulcus apparently transmitted the arteria diploetica magna and vena diploetica magna (*sensu*

WIBLE, 1990) which passed through the posttemporal foramen at the posttemporal notch. The vena diploetica magna united with the sphenoparietal emissary vein at a point level with the lateral aperture of the prootic canal. The sphenoparietal emissary vein and arteria diploetica magna passed ventrally and exited the skull through the postglenoid foramen (WIBLE, 1990).

ECTOTYMPANIC. — There is no evidence of an ossified ectotympanic (the bone which supports the tympanic membrane) nor are there facets in the ear region which marked the site of attachment of this bone.

DISCUSSION

The comparison of the skulls of *Pucadelphys andinus* is difficult in spite of the good preservation of the remains. As a matter of fact, there is no described skull of fossil marsupials from the Cretaceous, and the skull of Ma*yulestes ferox* from the early Paleocene of Tiupampa, with which *P. andinus* could reasonably be compared, is only known by a preliminary description (MUIZON, 1994) and its thorough study is under progress by one of us (C. M.). However, two undescribed probable metatherian skulls from the late Cretaceous of Mongolia have been mentioned in the litterature. KIELAN-JAWOROWSKA & NESSOV (1990) referred to the Metatheria a complete deltatheroidan skull well known as the Gurlin Tsav Skull and TROFIMOV & SZALAY (1993) mentioned the skeleton of a *Monodelphis scalops*-sized Asiadelphia from the Barun Goyot Formation of Mongolia. Another specimen, known from the middle Paleocene of São José de Itaboraí (Brazil), belongs to a polydolopid and consequently cannot be used for a comparison with a didelphid; furthermore, its very poor state of preservation does not permit reasonable comparisons. However, several well preserved skulls (or partial skulls) of primitive mammals are known from the Jurassic and the Cretaceous. The most important are: morganucodontids [*Morganucodon*, (KERMACK, 1963; and KERMACK *et al.*,1981)], *Gobiconodon* (JENKINS & SCHAFF, 1988), *Sinoconodon* (CROMPTON & LUO, 1993), docodonts [*Haldanodon* (LILLEGRAVEN & KRUSAT, 1991)], several multituberculates, [among others: *Kamptobaatar* and *Sloanbaatar* (KIELAN-JAWOROWSKA, 1971), *Catopsbaatar* and *Chulsanbaatar* (KIELAN-JAWOROWSKA, 1974), *Catopsalis* (KIELAN-JAWOROWSKA & SLOAN, 1974), *Kryptobaatar* and *Tugrigbaatar* (KIELAN-JAWOROWSKA & DASHZEVEG, 1978), *Nemegtbaatar*, (KIELAN-JAWOROWSKA *et al.*, 1986)], eupantotheres [*Vincelestes* (BONAPARTE & ROUGIER, 1987; ROUGIER & BONAPARTE, 1988; ROUGIER *et al.*, 1992; and HOPSON & ROUGIER, 1993)], deltatheroidans [*Deltatheridium* (KIELAN-JAWOROWSKA, 1975; a partial skull only) and the Gurlin Tsav skull, (KIELAN-JAWOROWSKA & NESSOV, 1990)], and eutherians [*Asioryctes*, *Barunlestes*, *Kennalestes* and *Zalambdalestes* (KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980)]. Although not directly related to *Pucadelphys* they are extremely useful for determining the primitive features of the genus. The skulls of Tiupampa (*Pucadelphys* and *Mayulestes*) are the oldest known undoubted marsupial skulls and, in the future, they will represent the best sample for the study of primitive marsupials. *Pucadelphys* is also one of the oldest known didelphids and its teeth can be compared with the abundant dental remains from the "middle"

Paleocene of Itaboraí which were revised by MARSHALL (1987). Consequently, the discussion will be divided into two sections. The first section will compare the teeth of *Pucadelphys* to those of the Paleocene didelphids of Itaboraí and of the late Cretaceous marsupial dental remains of North America related to the *Alphadon* group. The second section will consider the major cranial characters of *Pucadelphys* and, by comparing them to the available skulls of Mesozoic mammals, we will try to determine their phylogenetic state and polarity.

DENTAL COMPARISON. — Among all the fossil didelphids known in the lower Tertiary of South America, *Sternbergia itaboraiensis* from the middle Paleocene (Itaboraian) of São José de Itaboraí (Brazil) is the closest to *P. andinus* with respect to size as well as to tooth structure. Both species possess, among other features, the same didelphid characters, which are the paracone smaller than the metacone and the V-shaped centrocrista. The affinities of the two forms were noted since the first discoveries at Tiupampa by MUIZON *et al.* (1984) who described a tooth that they related to a "*Sternbergia*-like" marsupial and that must now be referred to *P. andinus*. *Sternbergia itaboraiensis* was described by PAULA COUTO (1970) on the basis of a mandible fragment with m4 and the talonid of m3. A revision of *S. itaboraiensis* was provided by MARSHALL (1987) who included in the hypodigm of the species several other specimens of the lower and upper dentition. With the exception of their dental structure, which is almost identical, *P. andinus* and *S. itaboraiensis* share the same morphology of the protocone, which is long anteroposteriorly, triangular-shaped, and inflated posteriorly, and the important development of the styles B and C. However, the two species clearly differ in the different development of several of their elements. The upper molars of *Sternbergia* differ from those of *Pucadelphys* in their shallower trigon basin, in their more reduced paracone, in their more deeply V-shaped centrocrista, in their smaller conules, in their smaller stylar shelf with a shallower basin, in the reduction of the style A which does not form a parastyle as large as in *Pucadelphys*, in their very reduced style D (while it is often the same size as style C or larger in *Pucadelphys*), in the reduction of the metacone of their M4 which is fused to the posterolabial angle of the tooth, in the loss of the posterior part of the stylar shelf basin of M4 and in the great anterolabial projection of the parastylar region of the stylar shelf of M4 with a larger paracrista. The lower molars of *Sternbergia* differ from those of *Pucadelphys* in that the talonids of m3 and m4 are always wider than the trigonids (in *Pucadelphys* the talonid of these teeth is sometimes as wide as the trigonid but is often narrower), in the anteroposteriorly longer trigonid, in the lower and stouter trigonid cusps, in that the metaconid and paraconid are more separated one from the other, a condition which more widely opens the trigonid basin lingually, in the hypoconid which has a better marked V-shaped morphology, in the larger hypoconulid and entoconid and in the presence of well developed anterior and labial cingula (they are absent in *Pucadelphys*). Most of the dental characters of *Pucadelphys* are more primitive than those of *Sternbergia* and, as already expressed by MARSHALL & MUIZON (1988) and MUIZON (1992), the former represents a good morphological ancestor for the latter, as far as the teeth are concerned.

Two other marsupials from Itaboraí share structural similarities with *Pucadelphys andinus*; they are *Marmosopsis juradoi* PAULA COUTO (1962) and *Itaboraidelphys camposi* MARSHALL & MUIZON (1984).

M. juradoi is known by several upper and lower jaws and its hypodigm has been revised by MARSHALL (1987). It differs from *P. andinus* in its smaller size, its upper molars proportionally slightly narrower and longer and its molar cusps sharper and less bulky. In comparison to those of *Pucadelphys*, the upper molars of *Marmosopsis* differ in having a higher metacone relative to the paracone, a smaller protocone, a shorter and straight preprotocrista, smaller conules, a shallower stylar shelf basin, a much higher metacrista which is straight in occlusal and anterior views (it is concave in *Pucadelphys*), a slightly shorter paracrista, reduced styles C, D, and E. The lower molars of *Marmosopsis* have a higher trigonid (relatively to the talonid) with a smaller and lower paraconid, a shorter talonid with a smaller and shallower basin, a crest-like entoconid which links the hypoconulid to the posterior edge of the metaconid (in *Pucadephys* and *Sternbergia* a distinct entoconid is present) and the loss of a distinct hypoconid on m4. *Marmosopsis* differs from *Sternbergia* and resembles *Pucadelphys* in having a relatively little marked V-shaped centrocrista (a primitive feature); however, it differs from both genera in having a very large and straight metacrista, in the crest-like entoconid, and in the reduction of the talonid of the m4 which has no hypoconid. MARSHALL & MUIZON (1988) and MUIZON (1992) have suggested that *Mizquedelphys* from the early Paleocene of Tiupampa could represent a possible morphological ancestor for *Marmosopsis*, as far as the teeth are concerned.

The molars of *Itaboraidelphys camposi* are also structurally similar to those of *Pucadelphys andinus* but differ from them in their size, approximately 50% larger, in their more robust morphology and in their lower and stouter cusps. The upper molars of *Itaboraidelphys* differ from those of *Pucadelphys* in being transversally narrower, in the more pronounced V-shaped centrocrista, in the larger conules, in the smaller style C which is clearly closer in size to style B than D and is sometimes twinned, and in the larger and straighter metacrista in occlusal view. The lower molars of *Itaboraidelphys* differ from those of *Pucadelphys* in their higher trigonid (relative to the talonid) which is more open lingually, in the shallower trigonid and talonid basins, in the stronger anterocingulid, in the shorter talonid and in the smaller hypoconulid. MARSHALL & MUIZON (1988) and MUIZON (1992) have stated that *Andinodelphys* from the early Paleocene of Tiupampa could represent a possible morphological ancestor for *Itaboraidelphys*, although MARSHALL *et al.* (1989) regard it as a plesion of indeterminate familial attribution which could be related to the origin of the Australian marsupials.

It is true that *Marmosopsis* and *Itaboraidelphys* differ more from *Pucadelphys* than does *Sternbergia*, which is the reason why we have suggested a closer relationship between the latter two (MARSHALL & MUIZON, 1988; MUIZON, 1992). However, there is apparently no feature that could exclude *Pucadelphys* from being a possible ancestor of *Marmosopsis* and *Itaboraidelphys*, as the principal derived features of *Pucadelphys* are the V-shaped centrocrista and the larger and higher metacone relatively to the paracone, two didelphid characters.

Pucadelphys also shows dental similarities with the various species of *Alphadon* and *Protalphadon* of the late Cretaceous of North America, which were classified in the family Peradectidae by MARSHALL *et al.* (1989). The three genera present a similar dental structure with large styles A to D, but *Pucadelphys* differs from the other two genera in possessing a V-shaped centrocrista (straight in *Alphadon* and *Protalphadon*), a paracone smaller than the metacone (they

are subequal in size in *Alphadon* and *Protalphadon*) and an inflated posterior base of the protocone, which are didelphid characters. CLEMENS (1966) has suggested that the Tertiary didelphids were structurally similar to species like *Alphadon lulli* and *Alphadon marshi*. As a matter of fact, *Alphadon marshi* represents a good structural ancestor for the dental morphology of *Pucadelphys andinus*, an observation which confirms the hypothesis of CLEMENS (1966), CROCHET (1980) and REIG *et al.* (1987) which states that the Didelphidae may have originated from the North American Peradectidae. It is noteworthy that some specimens of *Alphadon marshi* (from the Maastrichtian of the Scollard Formation, Alberta, Canada) have a slightly V-shaped centrocrista and a paracone smaller than the metacone (CIFELLI, 1990: 315); the same has been observed by SAHNI (1972: 383 and fig. 14p) in a molar referred to *Alphadon* cf. *rhaister* from the Campanian of Judith River Formation (Montana). However, when present, these features are generally less developed than in the Didelphidae.

CHARACTER ANALYSIS. — In this section we analyze character states in *Pucadelphys* which are of potential importance in phylogenetic inference. This analysis is made in order to determine which states are plesiomorphic or apomorphic for Metatheria in particular and Tribosphenida in general. The relevance of these states for the phylogenetic relationships of *Pucadelphys* are summarized in the conclusions below. The character states are discussed in the following order: dentition, dentary, skull bones, skull foramina, and ear region (petromastoid).

DENTITION

Number of incisors. — HERSHKOVITZ (1982) has shown that the ancestral metatherian (and probably eutherian) primitively had five upper and lower incisors, although the highest number known is 5/4 which resulted from the loss of i1. Therefore, so far, the plesiomorphic number of incisors for Tribosphenida and Metatheria is 5/4 (I1, I2, I3, I 4, I5/i2, i3, i4, i5) (MARSHALL, 1979; HERSHKOVITZ, 1982; CLEMENS & LILLEGRAVEN, 1986: 71). *Pucadelphys* thus retains the plesiomorphic state for Tribosphenida and Metatheria.

Structure of upper incisors. — The relative size and structure of metatherian upper incisors are discussed by TAKAHASHI (1974), ARCHER (1976b), and REIG *et al.* (1987). Metatheria were apparently plesiomorphic in having I1-5 conical in shape, while the spatulate shape as occurs in Microbiotheriidae and Australian taxa is the derived state (ARCHER, 1976b; REIG *et al.*, 1987). Many Didelphidae (TAKAHASHI, 1974) and Dasyuridae (ARCHER, 1976b) have the I1 hypsodont and semiprocumbent relative to I2, and a small space (diastema) separated I1 and I2. Archer (1976b) regarded both states as plesiomorphic for Metatheria, and HERSHKOVITZ (1982) suggested that these states evolved subsequent to loss of the i1 and are associated with grooming. Although both states occur in many generalized metatherians, some taxa have one state but not the other. In addition, *Dromiciops* has I1-5 equally spaced and I1 is not hypsodont (see REIG *et al.*, 1987, fig. 49) as also occurs in some Dasyuridae (ARCHER, 1976b, Table 1). The states in *Pucadelphys* in which I1-5 are conical, subequal in height and equally spaced (no diastema) are apparently

plesiomorphic for metatherians because it is possible to derive all the variations seen in Didelphidae, Dasyuridae, Microbiotheriidae and other groups from a *Pucadelphys*-like ancestor. The states in *Pucadelphys* probably also occurred in the ancestral tribosphenid.

Structure of lower incisors. — HERSHKOVITZ (1982) illustrated that all fossil metatherians except Microbiotheriidae have what he termed a staggered i3 (i.e. the second incisor of the four occurring in generalized metatherians) which has "a bony alveolar buttress on labial surface, greater root exposure on lingual surface and medially staggered position of root and alveolus" (p. 191). In addition, the staggered i3 is larger than the i2, i4 or i5. Given the nearly universal occurrence of this staggered i3 in metatherians, HERSHKOVITZ concluded that this state was plesiomorphic for this group. He also demonstrated that this state occurs in an edentulous dentary from the Albian of Texas (see his fig. 5) which places a minimum age for the metatherian-eutherian dichotomy. However, the lower incisors in *Pucadelphys* (YPFB Pal 6107), Microbiotheriidae (MARSHALL, 1982) and generalized eutherians (HERSHKOVITZ, 1982) are arranged in a linear series and have no staggered i3. This state was thus probably plesiomorphic for Tribosphenida and was retained in eutherians and in a few metatherians (*Pucadelphys*, Microbiotheriidae). The staggered i3 is here regarded as a derived state which appears to be synapomorphic for metatherians except *Pucadelphys* and Microbiotheriidae.

Number of premolars and molars. — The plesiomorphic number of permanent premolars and molars in Tribosphenida was probably P5/5 and M4/4, while loss of one molar would account for the plesiomorphic state in eutherians of P5/5 and M3/3 and loss of two premolars for the plesiomorphic state in metatherians of P3/3 and M4/4 (DASHZEVEG & KIELAN-JAWOROWSKA, 1984, pp. 225-226). The loss of deciduous incisors, canines and premolars (only the P3/3 has a predecessor, the HDP 3/3) is also a derived state for metatherians (ARCHER *et al.*, 1985). *Pucadelphys* thus retains the plesiomorphic metatherian dental formula of P3/3 and M4/4.

Structure of premolars and molars. — The structure of the cheek teeth in generalized metatherians is discussed by ARCHER (1976b), REIG *et al.* (1987), MARSHALL (1987) and MARSHALL *et al.* (1989). Based on these studies, *Pucadelphys* has a cheek tooth structure which agrees perfectly with members of the family Didelphidae (i.e. paracone smaller and lower than metacone; V-shaped (dilambdodont) centrocrista; well developed stylar shelf with large stylar cusps A, B, C and D; posteriorly expanded protoconal base; trigonid shorter than talonid; cristid obliqua contacts posterior wall of trigonid labial to protocristid notch; entoconid tall and spire-like; hypoconulid lower than entoconid; well developed pre- and postcingulids). The cheek tooth character states of Didelphidae relative to other metatherians are listed in MARSHALL *et al.* (1989, figs 1, 2).

DENTARY

Inflected angular process. — The angular process of the dentary is strongly inflected medially in all metatherians except the living *Tarsipes* where it is absent, and in *Phascolarctos* and *Myrmecobius* where it is weakly developed. The angular process is inflected medially in most late Cretaceous eutherians from Asia (i.e. *Kennalestes*, *Asioryctes* and *Barunlestes*; KIELAN-

JAWOROWSKA, 1981, 1984; KIELAN-JAWOROWSKA *et al.*, 1979) and in some species of *Gypsonictops* and *Cimolestes* from North America, in Didymoconidae from the late Eocene-middle Oligocene of Asia, and in various groups of living and fossil rodents (MARSHALL, 1979 and references therein). One is also present in the early Cretaceous age pantothere *Vincelestes* from South America (BONAPARTE & ROUGIER, 1987) and in some triconodonts, symmetrodonts, and Multituberculata (MIAO, 1988: 878). The distribution of an inflected angular process suggests that it is a plesiomorphic state for Tribosphenida. *Pucadelphys* is thus plesiomorphous in this feature.

Mylohyoid groove. — The mylohyoid groove marks the course of a neurovascular bundle which includes the mylohyoid artery and nerve, and presumably in early taxa the persistent Meckel's cartilage (KREBS, 1971). It is present in Jurassic dryolestids (KREBS, 1971); in docodonts, triconodonts and eupantotheres (KIELAN-JAWOROWSKA, 1981: 61); in the early Cretaceous triconodont *Gobiconodon ostromi* (JENKINS & SCHAFF, 1988: 5); in the early therian *Kielantherium* (DASHZEVEG & KIELAN-JAWOROWSKA, 1984: 221); in the Cretaceous eutherians *Prokennalestes* and *Kennalestes* (KIELAN-JAWOROWSKA, 1981: 61 and KIELAN-JAWOROWSKA & DASHZEVEG, 1989); in some living adult eutherians [insectivorans, edentates, cetaceans; (BENSLEY, 1902)]; and in embryos of monotremes (WATSON, 1916). It is absent in multituberculates, some dryolestids (i.e. *Crusafontia*; KREBS, 1971), paurodontids (*Amphitherium*, *Peramus*); and some early eutherians (*Asioryctes*; KIELAN-JAWOROWSKA, 1981: 61). It is absent in the Deltatheroida (KIELAN-JAWOROWSKA & NESSOV, 1990), but present in *Pucadelphys*, embryos of some living marsupial taxa and, sporadically, in some adult specimens of *Didelphis*, *Trichosurus*, *Phalanger*, *Perameles* and *Petauroides* (BENSLEY, 1902). The presence of a mylohyoid groove is thus the plesiomorphic state for Mammalia, and *Pucadelphys* retains the primitive condition. The presence or absence of a mylohyoid groove appears (*contra* ARCHER *et al.*, 1985, fig. 3, point 14) to be of dubious value in phylogenetic inference.

Labial mandibular foramen. — KIELAN-JAWOROWSKA & DASHZEVEG (1989) named labial mandibular formen a small foramen on labial side of the dentary at the base of the coronoid process present in many primitive mammals. This small foramen occurs in *Kielantherium* (aegialodontid) from the early Cretaceous of Asia, in *Prokennalestes* (otlestid) from the Aptian-Albian of Asia, in *Otlestes* (otlestid) from the late Cenomanian of Uzbekistan and in *Zalambdalestes* (zalambdalestid) from the Campanian of Mongolia (DASHZEVEG & KIELAN-JAWOROWSKA, 1984; and KIELAN-JAWOROWSKA & DASHZEVEG, 1989), and in the microbiothere metatherian *Microbiotherium gallegosense* from the early Miocene of Argentina (MARSHALL, 1982). DASHZEVEG & KIELAN-JAWOROWSKA (1984) and KIELAN-JAWOROWSKA & DASHZEVEG (1989) regard the presence of this foramen as a therian plesiomorphy. There is no trace of this foramen in *Pucadelphys*.

BONES OF SKULL

There are numerous states in *Pucadelphys* which, as shown by previous workers, apparently represent Tribosphenida plesiomorphies. These include: nasals flared posteriorly (GREGORY, 1920: 139); alisphenoid and squamosal have major component in lateral wall of braincase (KERMACK *et al.*, 1981: 135; KEMP, 1982: 305, 1983: 372); glenoid fossa set posteriorly

opposite anterior half of promontorium (KIELAN-JAWOROWSKA, 1981: 65); occipital plate slopes upwards and slightly forwards from condyles (KIELAN-JAWOROWSKA, 1981: 65); and lambdoidal crest sharp, sagittal crest weak or absent (KIELAN-JAWOROWSKA *et al.*, 1979: 227).

Orbit large, confluent with temporal fossa. — This state occurs in *Vincelestes* (BONAPARTE & ROUGIER, 1987), Deltatheroida (KIELAN-JAWOROWSKA, 1975), *Zalambdalestes* (KIELAN -JAWOROWSKA, 1984: 113), *Asioryctes* and *Kennalestes* (KIELAN-JAWOROWSKA, 1981: 56), *Pucadelphys*, and in generalized Cenozoic and living metatherians and eutherians. This is apparently the plesiomorphic state for Theria.

Lacrimal. — The lacrimal has a large facial wing in cynodonts, *Morganucodon* (KERMACK *et al.*, 1981), *Vincelestes* (BONAPARTE & ROUGIER, 1987), *Deltatheridium* (KIELAN-JAWOROWSKA, 1975), *Pucadelphys* and in generalized living and fossil metatherians (GREGORY, 1920). In *Vincelestes, Deltatheridium, Pucadelphys* and in generalized living and fossil metatherians the lacrimal forms a prominent antorbital rim and the lacrimal foramen occurs within the orbital rim. The structure of the lacrimal and position of the lacrimal foramen in *Pucadelphys* apparently represents the plesiomorphic state for Tribosphenida.

Nasal-lacrimal contact.— A broad nasal-lacrimal contact occurs in cynodonts, tritylodontids, multituberculates, *Morganucodon* (KERMACK *et al.*, 1981), *Vincelestes* (BONAPARTE & ROUGIER, 1987, fig. 2A), *Deltatheridium* (Kielan-Jaworowska, 1975: 122, fig. 3A), and among metatherians only in South American Borhyaenoidea (MARSHALL, 1978; MARSHALL *et al.*, 1989) and in the Australian *Wynyardia* (GREGORY, 1920). A broad nasal-lacrimal contact is the plesiomorphic state for mammals (GREGORY, 1920). Living and other fossil metatherians (including *Pucadelphys*) are derived in having no nasal-lacrimal suture but a clear frontal-maxilla contact (GREGORY, 1920; MARSHALL & KIELAN-JAWOROWSKA, 1992). An intermediate condition within metatherians occurs in some Didelphidae (*Didelphis, Chironectes*) which have only a narrow and variable frontal-maxilla contact (GREGORY, 1920: 139). Most eutherians are also derived in having a broad frontal-maxilla contact (NOVACEK, 1986: 27).

Contact of alisphenoid and parietal. — A broad contact between the alisphenoid and parietal on the outside of the skull occurs in the early eutherians *Asioryctes* and *Kennalestes* (KIELAN-JAWOROWSKA, 1981), in *Pucadelphys*, and in many Cenozoic and living metatherians (i.e. all Didelphidae, Myrmecobiidae, most Dasyuridae, some Borhyaenoidea; ARCHER, 1976a: 309). There is no contact in Thylacinidae, Peramelidae, Vombatidae, some Phascolarctidae, some Borhyaenoidea, and some Dasyuridae (ARCHER, 1976a: 309). A broad alisphenoid-parietal contact is regarded as the plesiomorphic state in Tribosphenida.

Palate. — The bony palate is solid (without vacuities) in cynodonts, monotremes, some multituberculates (*Kamptobaatar*), the eupantothere *Vincelestes* (BONAPARTE & ROUGIER, 1987), the late Cretaceous eutherians *Zalambdalestes* (KIELAN-JAWOROWSKA, 1984: 108), most living and Cenozoic eutherians, the deltatheroidan *Deltatheridium* (KIELAN-JAWOROWSKA, 1975: 122), and many metatherians (Borhyaenoidea, *Sparassocynus, Caluromys, Dasycercus, Dasyuroides,* species groups of *Antechinus* and *Sminthopsis, Myrmecobius, Dactylopsila, Petaurus* and *Dactylonax*) (MARSHALL, 1979 and references therein). In contrast, the palate is perforated by large vacuities, often two pairs, in some multituberculates (i.e. *Sloanbaatar, Nemegtbaatar,*

Bulganbaatar and *Ptilodus*), some eutherians (rabbits, some rodents, macroscelidids, hedgehogs, *Carpolestes*), some Deltatheroida (KIELAN-JAWOROWSKA & NESSOV, 1990), and many living and fossil metatherians (MARSHALL, 1979; REIG *et al.*, 1987). Because of the wide occurrence of palatal vacuities among metatherians, their presence has generally been regarded as plesiomorphic for this group. However, when vacuities are present they are generally quite variable within families and even within species. Ontogenetic studies of metatherian embryos have shown that the palatal plates of the maxilla and palatine bones are at first solid and develop vacuities by gradual resorption of bone. These and other observations favor the view that a solid palate was the plesiomorphic state for mammals (MARSHALL, 1979 and references therein). *Pucadelphys* is thus plesiomorphic for this state.

Preglenoid process of jugal. — The jugal is deep, long and extends posteriorly to form a preglenoid process along the anterolateral edge of the glenoid fossa in the late Cretaceous metatherian *Didelphodon vorax* (CLEMENS, 1966: 72), in Cenozoic and living metatherians, in Deltatheroida (KIELAN-JAWOROWSKA & NESSOV, 1990), in the early Cretaceous eupantothere *Vincelestes* (BONAPARTE & ROUGIER, 1987), and in some living eutherians (elephants, some hyraxes, some rodents; MARSHALL, 1979). In some late Cretaceous eutherians from Asia (*Asioryctes*, *Kennalestes*, *Barunlestes*) the jugal is long, extends to the anterior edge of the glenoid fossa, but does not form a preglenoid process (KIELAN-JAWOROWSKA, 1981; 1984). The presence of a preglenoid process of the jugal is clearly a plesiomorphic state for metatherians, and the presence of this state in *Vincelestes* and some eutherians suggests that it is plesiomorphic for Theria as well. *Pucadelphys* thus retains the plesiomorphic metatherian (and therian) state.

FORAMINA OF SKULL

Pucadelphys retains two states which are regarded by some workers as plesiomorphic for Tribosphenida: V2 exits skull through foramen rotundum in alisphenoid (KERMACK *et al.*, 1981: 135), and presence of a foramen lacerum medium (MACINTYRE, 1967; ARCHER, 1976a). However, a foramen rotundum does not occur in *Kennalestes* or *Asioryctes*, and KIELAN-JAWOROWSKA (1981: 65) regarded a "foramen rotundum confluent with sphenorbital fissure" as the plesiomorphic therian state. The earliest known foramen rotundum in a eutherian occurs in the ?middle Campanian age *Barunlestes* (KIELAN-JAWOROWSKA & TROFIMOV, 1980).

Transverse canal. — There is no transverse canal in *Morganucodon* (KERMACK *et al.*, 1981), monotremes (WATSON, 1916), multituberculates (KIELAN-JAWOROWSKA *et al.*, 1986), Deltatheroida (KIELAN-JAWOROWSKA & NESSOV, 1990), Borhyaenoidea (except for a possible vestige in *Lycopsis*; MARSHALL, 1977: 415), *Pucadelphys*, some didelphids (i.e. *Caluromys*) and some dasyurids (some *Planigale*) (ARCHER, 1976a) or in late Cretaceous eutherians from Asia (*Asioryctes*, *Barunlestes*, *Kennalestes*, *Zalambdalestes*; KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980). Among metatherians a transverse canal occurs in thylacinids, myrmecobiids, peramelids, most didelphids and most dasyurids (ARCHER, 1976a).

ARCHER (1976a) regarded a transverse canal as a plesiomorphic state for metatherians, yet the distribution of this feature suggests that its absence was the plesiomorphic state for mammals. If this polarity is true, then a transverse canal evolved multiple times within metatherians, a

position supported by data in ARCHER (1976a: 307). For example, when present, the transerse canal, which transmits a major venous sinus that drains the base of the brain around the pituitary, varies considerably in size and morphology; "in dasyurids, thylacinids, some didelphids (e.g. *Marmosa* and *Monodelphis*) the canal passes not only into endocranium but also transversely through the basisphenoid", sometimes "via more than one canal". In these taxa the transverse venous sinus "may enter the endocranium via the sulci for the entocarotid canals", while in other taxa (e.g. peramelids and other didelphids) "both ends of this canal lead anteriorly for a considerable distance before communicating transversely through the basisphenoid".

ARCHER (1976a: 307) stressed that taxa which lack this canal have a venous drainage pattern considerably different from those taxa in which it is present. In some species of *Planigale*, for example, the "venous sinus passes transversely via the anterior edges of the enormous foramina pseudovale [*sic*, see below] which are so large that they incise the alisphenoid in the normal position of the transverse canal". Given the arrangement in some species of *Planigale*, we speculate that in metatherians like *Pucadelphys* which lack this canal, part of the venous drainage around the pituitary may leave the skull through the large foramen ovale. *Pucadelphys*, which lacks a transverse canal, retains the plesiomorphic metatherian (and mammalian) state.

Foramen ovale. — This term is used (*sensu* KIELAN-JAWOROWSKA *et al.*, 1986: 584) to designate the foramen which transmits the mandibular branch of the trigeminal nerve (V3). Within this definition is included the foramen "pseudovale" of earlier workers, a term which KIELAN-JAWOROWSKA *et al.* (1986: 584) "rejected as prejudicial to possible homology of anterior lamina of petrosal with part of mammalian alisphenoid (PRESLEY, 1981; KEMP, 1983)". This move took into consideration the fact that the shape of this foramen and detailed relations with surrounding bones vary within mammals, and that MACINTYRE's (1967) use of "pseudovale" is not consistent regarding these relationships since the foramen may either be totally surrounded by the anterior lamina or be in the junction between two or more bony elements. Because of this, "pseudovale" was regarded as not being a clear-cut alternative to ovale and its use implies a false impression of precision of definition (PRESLEY, personal communication, 1989). Thus, the term ovale is used in preference for homology regarding transmittal of the V3 and gives no weight to the bones surrounding the V3 in different mammal groups.

A great deal of confusion regarding the term ovale and "pseudovale"has resulted from the studies of MACINTYRE (1967) and ARCHER (1976a). MACINTYRE, for example, recognized a "pseudovale" in some living eutherians (i.e. some perissodactyls, artiodactyls, rodents) which formed as a result of the disappearance of a true foramen ovale (which was surrounded entirely by the alisphenoid) by its union with the foramen lacerum medium, which primitively in mammals is located at the junction of the alisphenoid-basisphenoid-basioccipital-petrosal (MACINTYRE, 1967: 834). In this sense, MACINTYRE's "pseudovale" is derived from an ancestral (plesiomorphic) state in which a true foramen ovale was surrounded by the alisphenoid which in turn is derived from yet another ancestral state in which a "pseudovale" was located between the anterior lamina of the petrosal and the alisphenoid. MACINTYRE's "pseudovale" is thus used in two significantly different non homologous contexts: true "pseudovale" (as in cynodonts, tritylodonts, monotremes) - true ovale (a derived state in generalized tribosphenids) - and "pseudovale" (=true ovale + foramen lacerum medium), (another derived state, in some living eutherians).

ARCHER (1976a) recognized a foramen ovale and "pseudovale" in the taxa he studied, and in some cases identified both on the same side of the same specimen (i.e. most Didelphidae: 307). He defined (p. 219) his "pseudovale" as: "Transmits cranial nerves. Sometimes carries very small arterial or venous anastomoses linking internal cranial and external cranial vessels and sometimes near its posterior edge, carries small branch of internal carotid artery into eustachian canal". In his Plate 1 where he labels this foramen on specimens, what he calls the "pseudovale" is in reality the medial lacerate foramen as evidenced by its position at the alisphenoid-basioccipital- basisphenoid-petrosal junction (MACINTYRE, 1967: 834). In other instances, ARCHER uses "pseudovale" *sensu* MACINTYRE (1967) in part, meaning the foramen formed by union of the medial lacerate foramen and ovale. ARCHER thus uses "pseudovale" in reference to two different nonhomologous foramina. However, ARCHER's use of foramen ovale appears to be correct (i.e. foramen in alisphenoid which transmits V3) and it is interesting that he regards (p. 307) its absence as a dasyurid plesiomorphy. Because ARCHER used the presence, absence and structural variation of his "pseudovale" and ovale in phylogenetic inference, his conclusions based on these features need reconsideration.

Subsquamosal foramen. — This foramen occurs in *Pucadelphys*, in all metatherian groups studied by ARCHER (1976a: 314) and in the late Cretaceous eutherians *Asioryctes* and *Kennalestes* (KIELAN-JAWOROWSKA,1981: 61). ARCHER (1976a) noted that this foramen is variably developed: in some specimens it occurs on one side of the skull but not the other, while in other specimens it lies adjacent to the postglenoid foramen and is separated from it by only a splint of bone. The presence of this foramen represents a plesiomorphic state within Theria (KIELAN-JAWOROWSKA, 1981: 65).

Postzygomatic foramen. — This foramen occurs in *Pucadelphys* and in all metatherian groups studied by ARCHER (1976a: 314). It is a plesiomorphic feature within Metatheria.

EAR REGION

Pucadelphys retains the following states which are plesiomorphic for Tribosphenida: a triossicular middle ear mechanism (MIAO & LILLEGRAVEN, 1986; KEMP, 1983); an inflated promontorium to house the spiral cochlea (MACINTYRE, 1972; PROTHERO, 1983: 1044); a fully coiled cochlea (380°) (MIAO & LILLEGRAVEN, 1986; WIBLE, 1990); a fossa incudis with prominent lateral wall formed by the squamosal (WIBLE, 1990); a true aqueductus cochleae (KERMACK *et al.*, 1981: 137; WIBLE, 1990); the internal acoustic meatus is a broad shallow pit with foramina which transmit a branch of the facial nerve (VII) and two branches of the acoustic nerve (VIII) (PROTHERO, 1983: 1041); the presence of a posttemporal foramen (WIBLE, 1990); and the presence of a lateral head vein (absence of this vein is a eutherian synapomorphy; MARSHALL, 1979; WIBLE, 1990). It also has three states which are metatherian synapomorphies: the prootic canal is reduced in length and width, and does not open endocranially (absence of this canal is a eutherian synapomorphy; WIBLE, 1990); the prootic sinus continues onto the squamosal side of the petromastoid within a deep sulcus (WIBLE, 1990); and the presence, on the squamosal side of the petromastoid, of a sphenoparietal emissary vein which occupies a deep sulcus continuous with the sulcus for the prootic sinus, and exits skull through the postglenoid foramen (WIBLE, 1990).

Ossified auditory bulla. — In *Pucadelphys* there is no evidence of an ossified auditory bulla. This same state occurs in monotremes, soricids, some talpids, and some fossil eutherians (i.e. *Asioryctes*, *Kennalestes*, *Palaeoryctes*) and apparently represents the plesiomorphic mammalian state (NOVACEK, 1977: 141). "A condition similar to that in the monotreme *Tachyglossus*, where the tympanic cavity was bordered ventrally by a thin connective tissue (dense fibrous and/or areolar) membrane located between the ventromedial surface of the nearly horizontal tympanic ring and the ventral surface of the petrosal, was the most primitive condition in monotremes, marsupials, and placentals" (NOVACEK, 1977: 144) (however, see below for discussion on the orientation of the typmanic ring).

Based on an authoritative study of fossil and living metatherians, ARCHER (1976a: 310) concluded that, among living taxa, didelphids were most plesiomorphic in aspects of their bullar morphology. REIG *et al.* (1987: 22) suggested that, among living didelphids, *Metachirus* and *Philander* were the most generalized. In these taxa the ossified bulla is incomplete: a small tympanic process of the alisphenoid occurs anteriorly, a small tympanic process of the pars petrosa of the petromastoid occurs posteriorly, and much of the middle ear in macerated skulls is open ventrally. This same architecture was regarded as the plesiomorphic metatherian bullar state by NOVACEK (1977) and apparently occurred in the late Cretaceous stagodontid *Didelphodon vorax* (CLEMENS, 1966: 55). There are thus two features (both absent in *Pucadelphys*) which warrant special consideration in the evolution of the metatherian bulla: the ossified tympanic process of the alisphenoid and the tympanic process of the pars petrosa.

An ossified tympanic process of the alisphenoid occurs in the vast major of metatherians and is generally regarded as a synapomorphy of that group (KIELAN-JAWOROWSKA & NESSOV, 1990), although its phylogenentic value has been recently questioned by MUIZON (1994). This feature is, however, absent in borhyaenoids [with the exception of *Cladosictis* and *Sipalocyon* (MUIZON, 1994)], in vombatids (PATTERSON, 1965), and in what appears to be a late Cretaceous metatherian that was figured but not discussed by MACINTYRE (1967, fig. 3). KIELAN-JAWOROWSKA (1981: 61) suggested that "the marsupial alisphenoid bulla originated from the enlarged quadrate ramus of the alisphenoid of early therians" and that in late Cretaceous eutherians (*Asioryctes* and probably *Kennalestes*) "a strongly inflated quadrate ramus of the alisphenoid occupies the same position as the alisphenoid bulla in marsupials and is probably homologous to it". However, in eutherians the alisphenoid rarely contributes to the formation of the ossified bulla and in those taxa where it is developed (i.e. macroscelidids, some insectivores; NOVACEK, 1977; SEGALL, 1970) it has a different shape and occurs in a different location than in metatherians (KIELAN-JAWOROWSKA, 1981: 61-62). Furthermore, in insectivores "the tympanic process of the basisphenoid takes the place of the tympanic process of the alisphenoid of marsupials" (SEGALL, 1970: 169). These observations clearly suggest that the ossified tympanic wing of the alisphenoid in metatherians and eutherians are nonhomologous and evolved independently in each group. This view is supported by the fact that an ossified alisphenoid bulla is absent in monotremes (WATSON, 1916), in the early Cretaceous eupantothere *Vincelestes* (BONAPARTE & ROUGIER, 1987; ROUGIER & BONAPARTE, 1988), in *Pucadelphys*, in *Mayulestes* (MUIZON, 1994) and in some late Cretaceous eutherians (KIELAN-JAWOROWSKA, 1981; 1984). Furthermore, MUIZON (1994) has shown that the absence of tympanic

process of the alisphenoid in *Mayulestes* and in most other borhyaenoids is a symplesiomorphy within the superfamily [not a reversal as stated by others (MARSHALL & KIELAN-JAWOROWSKA, 1992)] and that its presence in *Cladosictis* and *Sipalocyon* is a synapomorphy of this clade. The absence of a tympanic process of the alisphenoid in the didelphid *Pucadelphys* reinforces MUIZON's statement that this structure must have appeared several times during marsupial evolution and should not be used to diagnose this group of mammals.

The tympanic process of the pars petrosa (*sensu* REIG *et al.*, 1987; =rostral tympanic process of the petrosal, WIBLE, 1990; ectotympanic process of the periotic, ARCHER, 1976a: 230) is "intimately related" to the posteroventral end of the ossified ectotympanic; these bones are typically in contact but never fused (ARCHER, 1976a: 230). A tympanic process of the pars petrosa is absent and the promontorium is smooth in *Sinoconodon*, morganucodontids, triconodontids, *Vincelestes*, many metatherians (Deltatheroida, *Pucadelphys*, most Borhyaenoidea; living Phalangeridae, Vombatidae, and possibly Phascolarctidae), and many eutherians (late Cretaceous taxa from Asia, many Cenozoic and living goups) (WIBLE, 1990). A low ridge which may represent an incipient state of this structure occurs in the metatherian *Didelphodon vorax* and in Petrosal Types A-D of Wible (1990). This feature is well developed in living metatherians (except those mentioned above), in some eutherians (euprimates, erinaceomorphs), possibly in some multituberculates, and monotremes (although in this group it is not clearly homologous with that in metatherians and eutherians; WIBLE, 1990). The distribution of this structure among various groups thus suggests that mammals primitively had a smooth promontorium and lacked a tympanic process of the pars petrosa. WIBLE (1990) concluded that the absence of this feature was a plesiomorphic state for Eutheria, but was uncommital about the plesiomorphic state in Metatheria, suggesting only "that ridges and processes have been added to and lost from the promontorium a number of times in marsupials". We believe that metatherians (as in *Pucadelphys*) primitively lacked this structure and that it evolved independently in various lineages, possibly in association with the development and enlargement of an ossified auditory bulla.

Orientation of ectotympanic and tympanic membrane. — In living metatherians and eutherians (except soricids and some talpids) the ossified ectotympanic and tympanic membrane are oriented in a nearly vertical plane, and this state has been regarded as a therian synapomorphy (KEMP, 1983: 375). However, this view is not corroborated by fossil or ontogenetic evidence which suggests two other possibilities. First, NOVACEK (1977) suggested that the ectotympanic was primitively subhorizontal in position. This possibility is supported by the horizontal position of the ectotympanic in the living monotreme *Tachyglossus* (NOVACEK, 1977: 144, Fig. 6), in the late Paleocene multituberculate *Lambdopsalis* (MIAO & LILLEGRAVEN, 1986), and the knowledge that the ectotympanic is oriented horizontally in the early ontogeny in all mammals and remains in this position in monotremes but rotates to an inclined position in most therians (DE BEER, 1937) which thus represents a derived state (ROWE, 1988). Second, KIELAN-JAWOROWSKA (1981) suggested that the ectotympanic was primitively inclined at an angle of 45° from horizontal. This possibility is based on the observations that in cynodonts and some early mammals with a double jaw joint (i.e. *Morganucodon*) the angular (=ectotympanic) is sharply inclined (KIELAN-JAWOROWSKA, 1981: 38). Support for this possibility came with the discovery of the late Cretaceous eutherians

Asioryctes and *Kennalestes* in which the *in situ* ectotympanic was released from the lower jaw but still retains its primitive anterior position opposite the posterior part of the dentary and is roughly parallel to it at 45° from horizontal. If this does indeed represent the primitive therian state, then both the subhorizontal state in *Tachyglossus* and the near vertical state in some living metatherians and eutherians are derived conditions.

Yet, the same data base has been interpreted by some workers to support both possibilities (i.e. subhorizontal is primitive and inclined at 45° is primitive), suggesting that differences between the two are relative and in part semantic. The best example is NOVACEK's (1977: 145) paper in which he argues that "the last common ancestor of marsupials and placentals... and the most primitive members of each group... had a simple tympanic ring only slightly inclined to the horizontal plane of the skull" which resembled the monotreme-like state. In his fig. 7a he illustrates this plesiomorphic state with the ectotympanic inclined at 35° from horizontal, while on p. 141 he notes that "the simple ring-shaped ectotympanic lies at a low angle (less than 50°) to the horizontal plane of the skull", a state seen in monotremes, soricids, some talpids, and possibly in *Asioryctes* and *Palaeoryctes*.

In *Pucadelphys* there is no evidence of an ossified ectotympanic, nor are there facts to demonstrate that one was present. Its absence is attributed to destruction during fossilization. The tympanic membrane was apparently subvertical or slightly obliquely oriented at an angle much larger than 45° from horizontal, because this is the general orientation of the fenestra vestibuli (see YPFB Pal 6110) and the ectotympanic parallels it in Recent mammals (J. WIBLE, written communication, 1990). Therefore, whatever the primitive condition is (either sub horizontal or at 45°) the inferred subvertical position of the ectotympanic of *Pucadelphys* would represent a derived condition.

Auditory sinuses. — "Auditory sinuses... are cavities within or between bones in the auditory region of the skull (other than the epitympanic recess) which communicate directly with the epitympanic recess" (ARCHER, 1976a: 226). Such sinuses are absent in *Morganucodon* (KERMACK *et al.*, 1981), monotremes (WATSON, 1916), *Vincelestes* (BONAPARTE & ROUGIER, 1987), late Cretaceous eutherians (*Asioryctes*, *Barunlestes*, *Kennalestes*, *Zalambdalestes*; KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980), and generalized living eutherians (VAN KAMPEN, 1905; NOVACEK, 1977). Among Cenozoic and living metatherians, auditory sinuses are primitively absent, although a small alisphenoid hypotympanic sinus appears in all groups studied by ARCHER (1976a) except some borhyaenoids. The absence of auditory sinuses in *Pucadelphys* thus represents the plesiomorphic state for mammals.

Pars mastoidea contribution to occiput. — The pars mastoidea has an extensive exposure on the occiput in monotremes (*Tachyglossus*), in late Cretaceous eutherians (*Asioryctes*, *Kennalestes*; KIELAN-JAWOROWSKA, 1981, fig. 2), and among metatherians in *Didelphodon vorax*, *Eodelphis browni*, Petrosal Types A and B from the late Cretaceous (WIBLE, 1990), in *Mayulestes* (MUIZON, 1994) and in many taxa studied by ARCHER (1976a). An extensive contribution of the pars mastoidea to the occiput also occurs in *Pucadelphys*, and this apparently represents the plesiomorphic state for Tribosphenida.

Mastoid and paroccipital processes. — These processes are either absent or only incipiently developed in *Morganucodon*, monotremes, *Vincelestes* (BONAPARTE & ROUGIER, 1987), in late Cretaceous Asiatic eutherians (*Asioryctes*, *Barunlestes*, *Kennalestes*, *Zalambdalestes*; KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980), and in most gener- alized metatherians (*Mayulestes*; Myrmecobiidae; most Dasyuridae; Caenolestidae; Microbiotheriidae; some Didelphidae, *Lestodelphys*, *Monodelphys*) (ARCHER, 1976a; REIG *et al.*, 1987). A well developed mastoid and/or paroccipital process does occur in various late Cretaceous (WIBLE, 1990), Cenozoic and Recent metatherian groups (ARCHER, 1976a; REIG *et al.*, 1987), where they are derived and apparently evolved independently in various lineages (ARCHER, 1976a). The absence of a paroccipital process and small size of mastoid process as occur in *Pucadelphys*, apparently represent or approximate the plesiomorphic state for mammals.

Shape of fenestra vestibuli and stapedial footplate. — The ratio of length to width of the fenestra vestibuli approximates or represents that of the stapedial footplate. In the monotreme *Tachyglossus* this ratio is 1.0 (SEGALL, 1970: 203, fig. 26); in *Morganucodon* 1.1, triconodontids and Bug Creek multituberculates 1.3, *Vincelestes* 1.0 (WIBLE, 1990); and the late Paleocene multituberculate *Lambdopsalis* bulla 1.0 (MIAO & LILLEGRAVEN, 1986). Among metatherians, living Didelphidae have ratios ranging from 1.3 - 1.5 (SEGALL, 1970), *Didelphodon vorax* 1.4 (ARCHIBALD, 1979), late Cretaceous taxa studied by WIBLE (1990) range from 1.3 - 1.6, while living *Dromiciops* and *Macropus* have 2.1 (SEGALL, 1970). Bug Creek eutherians range from 2.0 - 2.4 (ARCHIBALD, 1979) and living eutherians 1.8 - 2.9 (SEGALL, 1970). These data suggest that: a circular fenestra vestibuli with a ratio of 1.0 is plesiomorphic for Mammalia (ARCHIBALD, 1979; SEGALL, 1970; PROTHERO, 1983; MIAO & LILLEGRAVEN, 1986; WIBLE, 1990); a slightly ovoid fenestra with a ratio of 1.3 is a synapomorphy of metatherians and possibly Tribosphenida; *Pucadelphys* with a ratio of 1.4 approximates the plesiomorphic state for metatherians; and an elliptical fenestra with a ratio of 1.8 is a synapomorphy of eutherians (WIBLE, 1990).

Stapedial artery. — The stapedial artery, a branch of the internal carotid artery, occurs in embryos of living monotremes, metatherians and eutherians, but only in adults of *Ornithorhynchus* and some eutherians (PRESLEY, 1979). As evidenced by a groove which marks the course of this artery on the pars petrosa of monotremes and some eutherians, it is believed to have been present in multituberculates (KIELAN-JAWOROWSKA *et al.*, 1986), late Cretaceous eutherians from Asia (*Barunlestes*, *Zalambdalestes*; KIELAN-JAWOROWSKA, 1984: 108) and North America (WIBLE, 1990) and various Cenozoic eutherians (PRESLEY, 1979). In metatherians, a stapedial artery is absent in adults of all living taxa (TANDLER, 1899; PRESLEY, 1979) and the groove is absent in fossil taxa (ARCHER, 1976a; ARCHIBALD, 1979; CLEMENS, 1966; WIBLE, 1990). The presence of a stapedial artery in adults is thus a plesiomorphic state for mammals (PRESLEY, 1979: 241, fig. 3), while the absence of this artery in adult metatherians represents a synapomorphy of that group (WIBLE, 1990). *Pucadelphys*, which lacks a groove for this artery, has the plesiomorphic state for metatherians.

Course of internal carotid artery. — The course of the internal carotid artery, which is derived from the embryonic dorsal aorta, has two basic states in mammals which "arise by a process of differential growth affecting the relative positions of the dorsal aorta and cochlear promontory" (PRESLEY, 1979: 238). WIBLE (1986) cautions that the position of the internal carotid

artery with regard to the cochlear promontory cannot be inferred from the location of the entocarotid foramen alone. The probable plesiomorphic state for mammals (ARCHIBALD, 1979; PRESLEY, 1979) is called the medial internal carotid artery (MICA) where the vessel passes medial to the cochlear promontory on its way to the entocarotid foramen and leaves little or no trace on the bone. This state occurs in monotremes, all metatherians (MACINTYRE, 1972: 291), in late Cretaceous Asian eutherians (KIELAN-JAWOROWSKA, 1981: 58-59; 1984: 115; KIELAN-JAWOROWSKA & TROFIMOV, 1980), and in some living eutherians [e.g. rodents, rabbits, ungulates (PRESLEY, 1979; KIELAN-JAWOROWSKA, 1981: 57)]. The apomorphic state is called the promontory internal carotid artery (PICA) where the vessel passes upon or lateral to the cochlear promontory, often in a sulcus. This state occurs in some primates, insectivores and some carnivorans, and may have evolved multiple times (PRESLEY, 1979). *Pucadelphys* thus retains the plesiomorphic MICA state, where the course of the internal carotid is marked by a shallow sulcus.

In addition, the presence of a large entocarotid foramen between the alisphenoid and basisphenoid which transmits the internal carotid as in *Pucadelphys* appears to be the plesiomorphic state in metatherians (ARCHER, 1976a), eutherians (KIELAN-JAWOROWSKA, 1981), and their tribosphenid ancestor.

Sulcus for facial nerve. — A sulcus for the facial nerve on the petromastoid has been regarded as a synapomorphy of metatherians and eutherians (i.e. MACINTYRE, 1972); yet, this feature also occurs in morganucodontids, triconodontids, multituberculates, monotremes and the eupantothere *Vincelestes*; it is therefore a plesiomorphy for mammals (WIBLE, 1990). *Pucadelphys* retains the plesiomorphic state.

Inferior petrosal sinus and foramen. — The inferior petrosal sinus joins posteriorly with the internal jugular vein and exits the skull through the inferior petrosal (=internal jugular) foramen (ARCHIBALD, 1979). The term internal jugular foramen (=canal) was proposed by ARCHER (1976a) to replace the posterior carotid foramen of GREGORY (1910: 233) and PATTERSON (1965: 2) which they erroneously believed transmitted a branch of the internal carotid artery; this error was perpetuated by CLEMENS (1966: 73) and MARSHALL (1977, 1978).

A sulcus for the inferior petrosal sinus occurs in *Morganucodon*, monotremes, and in many metatherians and eutherians, and apparently represents a plesiomorphy (*nec* therian synapomorphy of MACINTYRE, 1972) within mammals. An inferior petrosal foramen occurs nearly universally in metatherians (ARCHER, 1976a: 309) but is apparently absent in some (microbiotheres, *Acrobates*, possibly *Phascolarctos*; PATTERSON, 1965: 6), and is widely distributed among fossil and living eutherians (PATTERSON, 1965). Its presence apparently represents the plesiomorphic state for Tribosphenida. *Pucadelphys* retains both an inferior petrosal sinus and foramen.

Anterior lamina. — The anterior lamina is a bony blade located at the anterodorsal border of the petrosal in several primitive mammals: *Adelobasileus, Haldanodon, Megazostrodon, Morganucodon, Sinoconodon, Trioracodon*, multituberculates, *Vincelestes*, and monotremes (see WIBLE & HOPSON, 1993 for original references). The anterior lamina is perforated by a foramen (foramen ovale) for the V3 (mandibular branch of the trigeminal nerve), in *Morganucodon, Sinoconodon, Adelobasileus*, most multituberculates, *Vincelestes*, and *Ornithorhynchus*. However, there is a single trigeminal foramen between the anterior lamina and alisphenoid in *Megazostrodon*

and *Haldanodon* (WIBLE & HOPSON, 1993). The V2 (maxillary branch of the trigeminal nerve) is also enclosed in the anterior lamina in *Morganucodon, Sinoconodon, Adelobasileus,* and *Vincelestes.*

In the non-tribosphenic taxa mentioned above "the anterior lamina contributes to the lateral wall of the cavum epiptericum, the extradural space within which the trigeminal ganglion lies" (WIBLE & HOPSON, 1993: 47). KERMACK *et al.* (1981: 119), in their authoritative study of the skull anatomy of *Morganucodon*, state that the trigeminal ganglion (= semilunar ganglion) lies in a deep pocket of the medial side of the anterior lamina, lateral to the medial opening of the aqueductus Fallopii for the facial (VII) cranial nerve. A similar condition is observed in *Trioracodon* (KERMACK, 1963: 87), in multituberculates (KIELAN-JAWOROWSKA *et al.*, 1986), in *Haldanodon* (LILLEGRAVEN & KRUSAT, 1991: 97) and in *Ornithorhynchus* (ZELLER, 1989a, b). The medial aspect of the anterior lamina of *Vincelestes* has not been described. In the recent didelphid *Monodelphis domestica*, the trigeminal ganglion lies anterolateral to the hiatus Fallopii in a shallow fossa of the alisphenoid and the anterior border of the petrosal (MAIER, 1987; HOPSON & ROUGIER, 1993). In *Pucadelphys*, the fossa observed on the medial side of the lamina of the pars petrosa anterolateral to the hiatus Fallopii, is interpreted here as the Gasserian fossa or fossa for the trigeminal ganglion. Since this ganglion is located in the anterior lamina of the petrosal in *Morganucodon, Trioracodon, Haldanodon*, multituberculates, and *Ornithorhynchus*, the anterior wing of the pars petrosa of *Pucadelphys* is interpreted here as a structure homologous to the anterior lamina of these early mammals. Furthermore, the anterior lamina of *Pucadelphys* occupies the same position as the anterior lamina in early cynodonts (KEMP, 1983: 375), morganucodonts (KERMACK *et al.*, 1981), triconodonts (KERMACK, 1963; CROMPTON & JENKINS, 1979, fig. 3-5 A-C), and *Vincelestes* (HOPSON & ROUGIER, 1993). The anterior lamina of *Pucadelphys* is greatly reduced when compared to that of *Morganucodon, Sinoconodon*, multituberculates and *Vincelestes* but it is larger than in any other marsupials. However, this feature does not constitute a true novelty for the group since WIBLE (1990: 200) and WIBLE & HOPSON (1993: 60), stated that the great reduction or absence of the anterior lamina of the petrosal is a synapomorphy of the marsupials and eutherians, therefore implicitly accepting the presence of a reduced anterior lamina in some Tribosphenida.

The presence of an anterior lamina in *Pucadelphys* confirms WIBLE's assertion that "the anterior lamina...may not be entirely absent in marsupials" (WIBLE, 1990: 200). As explained by this author, "the prootic canal runs through the anterior lamina of the petrosal in *Sinoconodon*, morganucodontids, triconodontids, multituberculates, and *Vincelestes*". The occurrence of a prootic canal in some marsupials seems to confirm that the structure it passes through may represent a reduced anterior lamina (in peramelids, dasyurids and some didelphids). However, WIBLE & HOPSON (1994) have recently shown that the prootic canal of marsupials is probably not homologous to that in morganucodonts, triconodonts, multituberculates, and *Vincelestes*. If they are correct, therefore, the prootic canal should not be used for homologies of the anterior lamina.

The anterior lamina of *Pucadelphys* differs from that of the non-tribosphenic mammals mentioned above, because it does not participate in the closure of the lateral wall of the skull; it is covered laterally by the squamosal and the alisphenoid which articulate together and replace the

anterior lamina in that function. At the level of the anterior lamina of *Pucadelphys*, the lateral wall of the skull is thus duplicated; it is formed by the alisphenoid and the squamosal laterally and by the petrosal (anterior lamina) medially. This condition demonstrates that the anterior lamina was expelled from the lateral wall of the skull before it totally regressed. As a consequence of the reduction of the anterior lamina, in marsupials, the mandibular branch of the trigeminal nerve (V3) exits the skull (via the foramen ovale) between the alisphenoid and the anterior border of the petrosal (this condition is very clear in the early diverging borhyaenoid marsupial *Mayulestes*). In *Pucadelphys*, however, the anterolateral border of the petrosal (the posterior edge of the foramen ovale) probably retains part of the anterior lamina; therefore, the foramen ovale of *Pucadelphys* is located between the alisphenoid and the anterior lamina of the petrosal. In eutherians the foramen ovale is located in the alisphenoid.

In morganucodonts, triconodonts, *Sinoconodon* and *Adelobasileus* the anterior lamina is large and the alisphenoid is relatively short anteroposteriorly but tall dorsoventrally (KERMACK, 1963; and KERMACK *et al.*, 1981; LUCAS & LUO, 1993; CROMPTON & LUO, 1993). Monotremes have a large anterior lamina posterodorsal to a reduced (anteroposteriorly and dorsoventrally) alisphenoid and posteroventral to the orbitosphenoid. In most multituberculates the anterior lamina is large, posterodorsal (or posterior) to a large orbitosphenoid and posterodorsal to the alisphenoid (KIELAN-JAWOROWSKA, 1971; 1974; KEMP, 1988). The alisphenoid of multituberculates is generally small (KIELAN-JAWOROWSKA, 1971; KEMP, 1982), but in the multituberculate *Lambdopsalis* it is large, totally separates the anterior lamina from the orbitosphenoid, and has tribosphenid proportions (MIAO, 1988). Large anterior lamina and alisphenoid also occur in *Vincelestes* (ROUGIER & BONAPARTE, 1988; HOPSON & ROUGIER, 1993).

The homologies of the anterior lamina and alisphenoid in monotremes and in the other non-tribosphenic mammals mentioned above have been discussed by PRESLEY & STEEL (1976), PRESLEY (1980; 1981), and HOPSON & ROUGIER (1993). The status of the anterior lamina of monotremes has been abundantly studied in order to elucidate whether or not it is homologous to the anterior lamina of the other non-tribosphenic taxa mentioned above. The anterior lamina in living monotremes is an intramembranous ossification called the "lamina obturans" which fuses secondarily to the pars petrosa (VANDEBROEK, 1964; WIBLE, 1990). PRESLEY (1981) has confirmed that the "lamina obturans", in living monotremes, is an independent center of intramembranous ossification within the sphenobturator membrane. This author also states that "there seem to be no fundamental difference between therians and monotremes in the early development of this bone. Difference arise only when it fuses with its neighbours. ... Cynodonts may have had an anterior part contributing to the broad blade of the epipterygoid and a posterior forming the smaller anterior process of the petrosal". The proportions of these two parts of the lamina obturans may have varied since in triconodonts (KERMACK, 1964) and morganucodonts (KERMACK *et al.*, 1981) the anterior lamina of the petrosal is large and the epipterygoid blade small. In multituberculates, given the extreme reduction of the alisphenoid (epipterygoid) the lamina obturans may have contributed extensively to the petrosal, approaching the monotreme condition (PRESLEY, 1981). These studies suggest that the anterior lamina fused to the pars petrosa as in early cynodonts, morganucodonts and triconodonts is derived from the posterior part of the "lamina obturans",

which apparently was an ossification independent from the pars petrosa; while the anterior lamina in monotremes, multituberculates represents some combination of posterior and anterior part of the "lamina obturans". MIAO (1988) has suggested that the "lamina obturans" has an apparent plasticity for alliance within itself and with adjacent bones, and this could explain the within group variability of the anterior lamina in multituberculates. Considering that the blade of the alisphenoid and the anterior lamina of the petrosal are probably equivalent, PRESLEY (1981) concluded that a simple change in the fusion of these elements during development could produce a therian pattern of the lateral wall of the braincase. This was ratified by KEMP (1983: 374), who noted: "the sidewall of the non-therian braincase is apparently homologous [s.l.] with the sidewall of the modern therian braincase, and the two groups differ only in the relatively trivial matter of which bone the anterior lamina [s.l.] finally fuses with towards the end of ontogeny".

Recently, HOPSON & ROUGIER (1993) have questioned the interpretation of PRESLEY & STEEL (1976), PRESLEY (1981), and KEMP (1983). PRESLEY (1981) and ZELLER (1989 a, b) have demonstrated that in *Ornithorhynchus* the lamina obturans (anterior lamina) ossifies within the spheno-obturator membrane, entirely separate from the otic capsule and only in later development becomes synostosed to it (HOPSON & ROUGIER, 1993: 278). The lamina obturans of *Ornithorhynchus* begins to ossify in the dorsal part of the spheno-obturator membrane, quite distant from the ala temporalis (the endochondral portion of the alisphenoid) and only late in ontogeny it expands anteroventrally to contact the small alisphenoid (HOPSON & ROUGIER, 1993: 282). MAIER (1987) described the development of the alisphenoid of *Monodelphis domestica.* He demonstrated that the intramembranous portion of this bone is initiated adjacent to the ala temporalis and only at a fairly late ontogenetic stage expands posteriorly to contact the otic capsule. HOPSON & ROUGIER (1993: 283-284) therefore conclude that: "even though both elements form in the spheno-obturator membrane, the developmental evidence indicates that they are distinct, therefore non-homologous, ossifications". The monotreme lamina obturans is presumably homologous with the anterior lamina (HOPSON & ROUGIER, 1993: 284) and therefore, contrary to PRESLEY & STEEL (1976) and PRESLEY (1981), the anterior lamina is not homologous with the intramembranous portion (formed within the spheno-obturator membrane) of the alisphenoid. Furthermore, the alisphenoid of *Vincelestes* is similar to that of modern therians in its great anteroposterior expansion and its position relative to the otic capsule. It is noteworthy that in *Ornithorhynchus* the trigeminal ganglion lies in a fossa of the medial side of the lamina obturans (ZELLER, 1989b). Therefore, the homology of the monotreme lamina obturans with the anterior lamina (which we accept here) reinforces the interpretation of the anterior lamina of *Pucadelphys,* since the trigeminal ganglion appears to lie constantly in the same structure, the small fossa on the medial side of the anterior lamina lateral to the hiatus Fallopii.

The occurrence of a reduced anterior lamina in a marsupial is by no mean a surprise since the evolution of the therian (*Vincelestes* + marsupials + placentals) lateral wall of the braincase is characterized by the development of an anteroposteriorly elongated alisphenoid (observed in all therians) and the reduction and loss of the anterior lamina of the petrosal in the Tribosphenida. The presence, in *Pucadelphys,* of an anterior lamina, large for a marsupial but reduced when compared to that of *Vincelestes* (the sister group of the Tribosphenida), demonstrates that the

morphology of the lateral wall of the braincase of *Pucadelphys* is intermediate between that of *Vincelestes* and that observed in the other marsupials. Therefore, it may approximate the condition of the ancestral Tribosphenida. The morphology of the lateral wall of the braincase of *Pucadelphys* corroborates WIBLE (1990) and WIBLE & HOPSON (1993) synapomorphy of the Tribosphenida (marsupials + placentals): reduction or absence (interpreted here as loss) of the anterior lamina of the petrosal. It is also in agreement with the interpretation of *Vincelestes* as the sister group of marsupials + placentals (Tribosphenida) (Row, 1993; and WIBLE & HOPSON, 1993). Furthermore, it corroborates the interpretation of HOPSON & ROUGIER (1993) who have refuted the hypotheses of PRESLEY & STEEL (1976) and PRESLEY (1981) on the homologies of the elements of the lateral wall of the mammalian braincase.

CONCLUSIONS

The skull of *Pucadelphys* represents a classic example of mosaic evolution. It has a commonly observed combination of plesiomorphic and apomorphic states which, collectively, complicates its placement in recent phylogenies (i.e. MARSHALL *et al.*, 1989; MARSHALL & KIELAN-JAWOROWSKA, 1992) although recent discoveries have shed some light to its interpretation (MUIZON, 1994). However that may be, it illustrates that we still have much to learn about early metatherian and tribosphenid evolution.

The vast majority of structures in the skull and dentary of *Pucadelphys* represents plesiomorphic states for Tribosphenida and/or Mammalia. A few features represent metatherian synapomorphies (i.e. cheek tooth formula P3/3 and M4/4; prootic canal reduced in length and width, and does not open endocranially; prootic sinus continues onto squamosal side of petromastoid within a deep sulcus; presence of sphenoparietal emissary vein which occupies a deep sulcus on squamosal side of petromastoid, is continuous with sulcus for prootic sinus, and exits skull through postglenoid foramen; length/width ratio of fenestra vestibuli; absence of stapedial artery) which securely demonstrate that *Pucadelphys* is a member of this group, as presently defined.

The remaining structures suggest contradictory affinities within Metatheria. The derived molar features agree perfectly with members of the Didelphidae (*sensu* MARSHALL *et al.*, 1989) and for this reason *Pucadelphys* has been assigned to this family (MARSHALL & MUIZON, 1988). However, *Pucadelphys* retains the plesiomorphic state of a non-staggered i3, while all other metatherians (except Microbiotheriidae) have the derived state of a staggered i3. It is also plesiomorphic in having I1-5 conical, equally spaced and I1 not hypsodont, while most other metatherians are derived in either having spatulate I1-5 (a synapomorphy of Australidelphia; MARSHALL *et al.*, 1989) or I1 hypsodont and separated from I2 (many Didelphidae and Dasyuridae).

The plesiomorphic mammal state of a clear nasal-lacrimal contact occurs among metatherians only in Borhyaenoidea, Deltatheroida (if they actually are metatherians) and the Australian *Wynyardia*, while all other known taxa (including *Pucadelphys*) have the derived state of a frontal-maxilla contact.

Pucadelphys lacks an ossified alisphenoid bulla, a feature present and traditionally regarded as a synapomorphy (KIELAN-JAWOROWSKA & NEŠSOV, 1990) in all other metatherians. The Deltatheroida, which apparently possess a tympanic process of the alisphenoid, are classified by KIELAN-JAWOROWSKA & NESSOV (1990) within the metatherians. The absence of a tympanic process of the alisphenoid in some Borhyaenoidea has been interpreted as representing a derived state from an ancestor which had an alisphenoid bulla (ARCHER, 1976a; MARSHALL & KIELAN-JAWOROWSKA, 1992). However, the morphology of the skull of *Mayulestes ferox*, a borhyaenoid from the early Paleocene of Tiupampa indicates that the lack of a tympanic process of the alisphenoid is the plesiomorph condition for the borhyaenoids (MUIZON, 1994). Furthermore, the absence of a tympanic process of the alisphenoid in *Pucadelphys*, an early Paleocene didelphoid may indicate its independent acquisition in the other members of the superfamily. It is noteworthy that a tympanic process is probably present in the late Cretaceous stagodontid, *Didelphodon* (CLEMENS, 1966) and in a probable marsupial (Asiadelphia) from the Barun Goyot Formation (middle Campanian) of Mongolia (TROFIMOV & SZALAY, 1993). This reinforces the idea that the tympanic process of the alisphenoid appeared several times independently within marsupials (MUIZON, 1994) and should not be used to diagnose this group, which, therefore, partially questions the inclusion of the Deltatheroida within the Metatheria (KIELAN-JAWOROWSKA & NESSOV, 1990).

The presence of an anterior lamina fused to the petromastoid, and a foramen ovale (exit of V3) which opens between the anterior lamina and alisphenoid represent the most peculiar structures in the skull of *Pucadelphys*. These features have not been reported as such in other tribosphenids, although their presence has been predicted in the tribosphenid ancestor because these states occur in non-tribosphenid mammals. Comparisons of *Pucadelphys* with *Vincelestes* (the sister group of the Tribosphenida) and with the other marsupials indicates that it represents a morphological stage of the structure of the lateral wall of the braincase, intermediate between the primitive (*Vincelestes*) and modern (tribosphenid) therians and therefore allows a better understanding of character states and evolution. It is probable that *Pucadelphys* represents or approximates the plesiomorphic state in the morphology of the lateral wall of the braincase of early Tribosphenida.

Pucadelphys thus appears to represent the paleontological confirmation of the hypothesis of HOPSON & ROUGIER (1994) who have refuted that of PRESLEY & STEEL (1976) and PRESLEY (1981) for the evolution of the tribosphenid ear region. If the skull of *Pucadelphys* was of early-late Cretaceous age and had a generalized tribosphenid molar structure, then it would probably be celebrated as the long sought "missing-link" and be readily accommodated and accepted into the current scheme of early tribosphenid evolution. However, *Pucadelphys* is a metatherian, has a derived didelphid molar structure, and is early Paleocene in age. Thus the predicted anterior lamina and foramen ovale bordered by it and the alisphenoid occur in a dentally derived and geologically recent metatherian.

Considering the major differences existing between *Pucadelphys* and the other didelphids (especially concerning the ear region and the lateral wall of the braincase), one could be tempted to classify it in a new family. However, as mentioned above, all the cranial features of *Pucadelphys* are plesiomorphic for marsupials and the only clearly derived features within marsupials concern

the dental morphology and relate *Pucadelphys* to the Didelphidae. We regard *Pucadelphys* as a primitive Didelphidae, member of the order Didelphimorphia (*sensu* MARSHALL *et al.*, 1989) because its molar structure (which is currently the foundation of metatherian systematics) is indistinguishable from that family. We thus give preference to molar structure in classifying *Pucadelphys* within Metatheria.

ACKNOWLEDGEMENTS

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TABLE 1.— Measurements (mm) of check teeth of *Pucadelphys andinus*.

Abbreviations: CV, coefficient of variation; N, number of specimen; OR, observed range of variation; SD, standard deviation; X̄, mean.

TABLEAU 1.— Mesures (mm) des dents jugales de Pucadelphys andinus.

Abréviations : CV, coefficient de variation ; N, nombre des spécimens ; OR, valeurs extrêmes observées ; SD, écart-type ; X̄, moyenne.

	P1 L	P1 W	P2 L	P2 W	P3 L	P3 W	M1 L	M1 W	M2 L	M2 W	M3 L	M3 W	M4 L	M4 W	M1-3 / M1-4 L	P1-M3 / P1-M4 L
Upper Check Teeth																
N	8	8	6	6	7	7	8	8	12	12	12	12	10	10	13	10
OR	0.8-1.0	0.4-0.6	1.5-1.6	0.8-0.9	1.6-1.9	0.8-1.0	1.7-2.0	1.8-2.0	1.7-2.1	2.2-2.4	1.7-2.0	2.3-2.6	1.0-1.2	2.2-2.3	4.8-5.4	8.5-9.3
X̄	0.90	0.49	1.53	0.85	1.77	0.94	1.86	1.89	1.92	2.29	1.86	2.44	1.08	2.28	5.08	8.88
SD	0.07	0.06	0.05	0.05	0.10	0.07	0.10	0.08	0.09	0.09	0.09	0.10	0.09	0.04	0.16	0.28
CV	7.78	12.24	3.27	5.88	5.65	7.45	5.38	4.23	4.69	3.93	4.84	4.10	8.33	1.75	3.15	3.15
Lower Check Teeth																
N	7	7	9	9	9	9	11	11	9	9	10	10	9	9	10	7
OR	0.8-1.0	0.4-0.6	1.3-1.5	0.7-0.9	1.3-1.6	0.7-0.9	1.7-1.9	1.0-1.2	1.8-2.0	1.2-1.3	1.8-2.0	1.2-1.4	1.7-2.0	1.0-1.2	6.8-7.7	11.0-12.1
X̄	0.87	0.51	1.42	0.77	1.47	0.80	1.80	1.09	1.89	1.24	1.90	1.28	1.83	1.13	7.07	11.30
SD	0.07	0.06	0.08	0.07	0.09	0.05	0.07	0.08	0.09	0.05	0.07	0.07	0.08	0.08	0.25	0.25
CV	8.05	11.76	5.63	9.09	6.12	6.25	3.89	7.34	4.76	4.03	4.21	5.47	4.37	7.08	3.54	3.10