# THE SKULL OF *ARSINOITHERIUM* (MAMMALIA, EMBRITHOPODA) AND THE HIGHER ORDER INTERRELATIONSHIPS OF UNGULATES

by

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# ABSTRACT

Detailed anatomical description of arsinoithere cranial remains from the Lower Oligocene, Fayum Depression, Egypt, provides the basic data for a systematic investigation. All cranial and some postcranial features are assessed from a phylogenetic standpoint. Several soft tissue characters are then added to a cladistic analysis based on 54 derived ungulate morphological characters. The resulting phylogenetic hypothesis implies that perissodactyls, sirenians, proboscideans and arsinoitheres constitute a monophyletic unit (5 synapomorphies). However, increasing the tree length by 3 steps reveals a closer association between hyraxes and perissodactyls. Nevertheless, 13 synapomorphies link proboscideans, sirenians and arsinoitheres to the exclusion of all other ungulates. Form of the sphenopalatine and ethmoid foramina, recurved posttympanic process, absence of a fenestra rotundum in the petrosal, vestigial paroccipital process of the exoccipital and the highly unusual absence of a hypoglossal foramen in the skull, imply a robust sister-group relationship between arsinoitheres and proboscideans. In this analysis artiodactyls share only one derived character with all other ungulates studied. Monophyly of Ungulata, including Artiodactyla, is therefore only weakly supported. It is argued that pedal anatomy of hyraxes is non-homologous with that of Tethytheria. *Arsinoitherium* should now be classified within Tethytheria, sharing a sister-group relationship with Proboscidea. Hyraxes are excluded, thus refuting the concept of Paenungulata. However, monophyly of the wider concept, Pantomesaxonia, containing hyraxes, perissodactyls, sirenians, proboscideans and now, arsinoitheres, is supported by this study.

# RESUME

La description anatomique détaillée de restes crâniens d'arsinoïthères de l'Oligocene inférieur de la dépression du Fayoum (Egypte) fournit des données essentielles pour une étude systématique. Tous les caractères crâniens et quelques traits postcrâniens sont évalués d'un point de vue phylogénétique. Plusieurs caractères non-ostéologiques sont ensuite ajoutés pour procéder à une analyse cladisdique basée sur 54 caractères morphologiques dérivés d'ongulés. L'hypothèse phylogénétique en resultant implique que les périssodactyles, les siréniens, les proboscidiens et les arsinoïthères constiutent une unité monophylétique (5 synapomorphies). Cependant, une augmentation de la longeur de l'arbre par l'addition de trois étapes évolutive aboutit a une association plus étroite entre les hyrax et les périssodactyles. Quoi qu'il en soit, 13 synapomorphies lient les proboscidiens, les siréniens et les arsinoïthères a l'exclusion de tous les autre ongulés. La position des foramens ethmoïdiens et sphéno-palatins, le processus post-tympanique dirigé vers l'avant, l'absence d'une fenêtre ronde dans le pétreux, le processus paroccipital vestigial de l'exoccipital et l'absence exceptionelle d'un foramen de l'hypoglosse dans le crâne, impliquent que les arsinoïthères et les proboscidiens sont très certainement deux groupes-frères. Les artiodactyles ne partagent qu'un seul caractère dérivé avec tous les autre ongulés étudiés. La monophylie des Ungulata, Artiodactyls compris, n'est donc que faiblement corroborée. La position phylogénétique des Hyracoidea est équivoque mais on peut dire que l'anatomie dérivée du carpe et du tarse a été independamment dérivées chez les téthythères et chez les hyracoïdes. *Arsinoitherium* doit donc être maintenant classé parmi les Tethytheria tout en étant le groupe-frère des Proboscidea. Les hyrax sont exclus des Tethytheria et donc le concept de Paenungulata est réfuté. Quoi qu'il en soit, la monophylie d'un concept plus large, celui des Pantomesaxonia, rassemblant les hyrax, les périssodactyles, les siréniens, les proboscidiens et maintenant les arsinoïthères, est renforcée par cette analyse.

# INTRODUCTION

Arsinoitheres were first discovered at the turn of this centuty by H.L. Beadnell (Beadnell, 1901) and remain to this day one of the least understood of the archaic Tertiary mammal groups. The genus *Arsinoitherium* BEADNELL 1902, is well known only from the Jebel Qatrani Formation of the Fayum Depression, Egypt. These rhinoceros-sized herbivores constitute a dominant component of the well known Fayum mammal fauna (Bown *et al.*, 1982). The Jebel Qatrani Formation comprises 340 meters of fluviatile sandstones, mudstones, silts and gravels, unconformably overlain by the Widan el Faras basalt. The base of this basalt has been K/Ar dated at 31.0 ± 1.0 million years (Fleagle *et al.*, 1986). Although originally believed to have been upper Eocene (Beadnell, 1905), the Jebel Qatrani Formation is now held to be largely lower Oligocene. However, there is still some debate as to whether the age of the basal part of the sequence is latest Eocene or earliest Oligocene (Bown & Kraus, 1978; Simons, 1990). The type species of *Arsinoitherium* is *A. zitteli* BEADNELL 1902, but a questionable second species, *A. andrewsii* LANKESTER 1903, may also be present in the formation.

The only substantive work concerning *Arsinoitherium* occurs as a chapter in the classic monograph on Fayum vertebrates by C.W. Andrews (1906). The bizarre nasal horn cores and highly derived bilophodonty of the cheek teeth led Andrews to consider this genus sufficiently distinct as to merit the erection of a new mammalian order, the Embrithopoda. More recently three new genera have been added to the Embrithopoda; *Phenacolophus* (McKenna & Manning, 1977) from Asia, *Crivadiatherium* (Radulesco *et al.*, 1976) from Romania and *Palaeoamasia* (Sen & Heintz, 1979) from Turkey. These are "tooth taxa" and unfortunately of little help in illuminating higher level relationships. Andrews briefly compared his material with various large herbivorous mammals but tentitively envisaged a closer association of Embrithopoda with the order Hyracoidea than with any other known eutherian group. This presumed relationship was based primarily on his derivation of an arsinoïthère dental morphology from the dilambdodont pattern seen in primitive hyracoids. A close association between hyracoids and embrithopods was supported by Gregory (1910) and is echoed in many texts on mammalian evolution. Although dental anatomy continues to be endowed with considerable weight in determining mammalian interrelationships, it has long been appreciated that dental morphology is a weaker guide to phylogeny when employed at higher taxonomic levels (Matthew, 1909).

This paper presents a broad-based analysis of all non-dental aspects of the arsinoithere skeletal system. A detailed description of the skull of *Arsinoitherium*, with an attempt to extract phylogenetically useful information, forms the basic data. Added to this are discussions about relevant postcranial features and a reveiw of soft tissue characters commonly considered of systematic importance in the living taxa under consideration. Finally, a data matrix comprising 54 derived anatomical features is analysed using the MacClade computer algorithm to generate a phylogenetic hypothesis for living orders plus Embrithopoda.

## TERMINOLOGY

Cranial nomenclatlure follows that of McDowell (1958) and Novacek (1986), Periotic terminology follows that of MacIntyre (1972) and Cifelli (1982).

## ABBREVIATIONS

### Elements

| | |
|---|---|
| AS | alisphenoid |
| BS | basisphenoid |
| B-OCC | basioccipital |
| coc. | cochlea |
| EX-OCC | exoccipital |
| FR | frontal |
| JU | jugal |
| LA | lacrimal |
| MX | maxilla |
| NA | nasal |
| OS | orbitosphenoid |
| PA | parietal |
| PL | palatine |
| PMX | premaxilla |
| PRS | presphenoid |
| PT | pterygoid |
| pr. | promontorium of periotic |
| S-OCC | supraoccipital |
| SQ | squamosal |
| VO | vomar |

### Foramina, Fossae, Sulci

| | |
|---|---|
| alis, ca | alisphenoid canal |
| aqcoc. | cochlear aqueduct |
| aqve | vestibular aqueduct |
| ant. pal. f. | anterior palatine foramen |
| ces | cerebral surface of periotic |
| epitym. rec. | epitympanic recess |
| eth. f. | ethmoid foramen |
| ex. aud. me. | external auditory meatus |
| fo. | fenestra ovalis |
| fmma. | fossa muscularis major |
| fmmi. | fossa muscularis minor |
| glen. foss. | glenoid fossa |
| iam. | internal auditory meatus |
| inc. f. | incisive foramen |
| infra. ca. | infraorbital canal |
| me. lac. f. | median lacerate foramen |
| opt. f. | optic foramen |
| opth. f. | opthalmic foramen |
| ot. vac. | otic vacuity |
| post. lac. f. | posterior lacerate foramen |
| post. pal. f. | postpalatine foramen |
| prl. | promontorial lip of periotic |
| rep. | epitympanic recess of the periotic |
| sfa. | facial sulcus |
| sph. f. | sphenopalatine foramen |
| sphenorb. fis. | sphenorbital fissure |
| squ. sin. ca. | squamosal sinus canal |
| styl. f. | stylomastoid foramen |
| tafc. | tympanic aperture of facial canal |
| temp. ca. | temporal canal |
| temp. foss. | temporal fossa |

### Processes, Tuberosities

| | |
|---|---|
| cr. orb. temp. | crista orbitotemporalis |
| ectg. | ectotympanic groove |
| fr.h. | frontal horn |
| ju. tub. | jugal tuberosity |
| lambd. cr. | lambdoid crest |
| mfl. | mastoid flange of periotic |
| occ. cond. | occipital condyle |
| parocc. pr. | paroccipital process |
| postglen. pr. | postglenoid process |
| posttym. pr. | posttympanic process |
| sqf. | squamosal facet of periotic |
| tgp. | tegmen process |
| tto. | origin of m. tegmen tympani |
| tty. | tegmen tympani |
| tub. mx. | tuber maxillare |

### Institutional Abbreviations

| | |
|---|---|
| AMNH | American Museum of Natural History |
| BMNH | British Museum, Natural History |
| YPM | Yale Peabody Museum |

# METHODOLOGICAL CONSIDERATIONS

Homology is the basis on which systematists determine relationships among organisms. The concept of homology, its various meanings and philosophical justifications, is a subject in itself (see Patterson, 1982, 1987; Tomlinson, 1984, for penetrating discussions). However, in an evolutionary sense, homology is the essential similarity between characteristics of different individual organisms due solely to inheritance from a common ancestor. Following Patterson (1982), homologous characters are here considered to define monophyletic groups. As such, homologues only have meaning with reference to specific hierarchical levels of correspondence. Owen (1843, 1848) first made the distiction between homologous characters (essential structural correspondence) and analogous characters (structural and functional similarities derived from disparate sources). In an evolutionary context, analogous characters result from parallel or convergent evolution and are termed homoplasic (Lankester, 1870). The first task in any investigation of phylogeny is to distinguish homologies from homoplasies. Patterson (1892) has suggested three tests of homology: similarity, congruence and conjunction. The first, shared similarity, is usually that which initially suggests the possibility of homology (Cracraft, 1981). The congruence test is based on the assumption that a true homology will not contradict the characterisation of a specific grouping based on numerous other homologies (synapomorphies). Finally, the conjunction test suggests that putative homologues are refuted if found to occur in the same individual organism. According to Patterson, potential homologies that fail only the congruence test are parallelisms and those that fail both the similarity and congruence tests but pass the test of conjunction are convergent characters.

In order to answer the question, to which order of mammals are the Embrithopoda most closely related ?, it is necessary to narrow the field somewhat. It is now widely accepted that the class Mammalia consists of three major groupings: Monotremata, Metatheria, and Eutheria (Novacek *et al.*, 1988). *Arsinoitherium* was undoubtedly a placental mammal although only the absence of epipubic bones, upper molar stylar shelf and separation of the optic foramen from the sphenorbital fissure remain from a list of twelve eutherian autapomorphies given by Novacek *et al.* (1988), the rest of which are soft tissue characters. Within Eutheria, the Embrithopoda are thought to belong to the supraordinal grouping known as Ungulata. Ungulates constitute a vast array of extinct groups (see Savage, 1987 and Carrol, 1988) in addition to five surviving orders already differentiated by the early Palaeogene. Ungulata has long been considered a coherent group of mammals (Gregory, 1910) although there are only a meagre number of characters that unite this super-clade (Novacek *et al.*, 1988). Nevertheless, Prothero *et al.* (1988) strongly support the monophyly of ungulates, citing six autapomorphies:

1. Astragalus with shorter more robust head.
2. Foramen for superior ramus of the stapedial artery shifted to petrosal or lost.
3. Auditory bulla composed of ectotympanic.
4. Mastoid foramen lost.

5. Lower molar trigonid shortened anteroposteriorly.
6. Large posteriorly projecting hypoconulid on $M_3$.

Since most extinct "ungulate" orders are too poorly known or studied to enable precise comparison, an attempt is made here to determine the phylogenetic position of Embrithopoda within living orders alone. This decision accords with Patterson and Rosen's (1977) assertion that, as recent organisms are accurately contemporaneous and far better known than fossils, they should be the starting point in any systematic investigation involving fossils.

Nevertheless, full use is made of fossil members of the groups in question; in order to test homologies seen in extant members.

Features of arsinoithere anatomy are compared with a wide range of mammals including condylarths, commonly considered to be the basal stock from which the more derived orders of ungulates arose. Condylarthra is no longer considered monophyletic (Prothero *et al.*, 1988) but retains some utility as an umbrella term for archaic ungulates. In comparisons with living orders, the earliest unequivocal member is usually taken to be morphotypic for the group in question. Generally speaking, characters occurring most widely are treated as plesiomorphic whilst those with restricted distributions are considered apomorphic. Direct comparisons were made where material was available while primary published accounts were utilised in the absence of actual specimens.

## SKULL

Whereas many large extinct mammals are known only from fragmentary and often deformed skull material, *Arsinoitherium* is represented by an extraordinary array of cranial material. The genus *Arsinoitherium* is known from three complete adult, four complete sub-adult and one complete juvenile skull in addition to numerous partial skulls and skull fragments. The bone is often exceedingly well preserved and has only very rarely suffered postmortem deformation. The following description is based on the study of all available material and is a composite of observations made from different individuals. Cranial sutures in large ungulates tend to fuse very early in development; the interrelationships of various cranial elements presented below are therefore based largely on sub-adult specimens.

The principal work on the arsinoithere skull is still Andrew's (1906) thorough osteological description. However, he omitted certain details that were either not present in his material or overlooked. Moreover, Andrews made little attempt at detailed comparison of arsinoithere skull features with other eutherian groups. Consequently the cranium of *Arsinoitherium* has remained largely unexploited from a phylogenetic point of view.

## GENERAL CONFIGURATION

The most striking feature of the arsinoithere skull is the development of a formidable cranial armoury. A massive pair of anterior horns project anterodorsally, rising from a common base across the entire transverse width of the skull. In cross-section they tend to be triangular, the dorsal surface being flat and the anterior surface forming the triangular apex. A pair of much smaller cranial appendages rise at the base of the great horns on either side of the rostrum above the orbit. In anterior view the snout tapers to a remarkably narrow termination. Above the snout the nasal opening is capacious and retracted to a level above the anterior part of the first molar. In older individuals an ossification in the mesethmoidal cartilage descends from the anterodorsal border of the nares to fuse with the premaxilla below. The skull is widest dorsally between the smaller frontal horn cores, behind which the braincase narrows to a minimum width above the posterior part of a deeply excavated temporal fossae. More posteriorly it flares into the occipital region above the squamosal root of the zygoma. Due to pronounced forward tilting, the occiput is broadly exposed in dorsal aspect. A strong lambdoid crest forms a tight anteriorly directed arc that flares laterally to form robust tuberosities above the occipital condyles. The occipital condyles are large, pedunculate, widely spaced and, in dorsal view, project strongly behind the occiput.

## NASAL

### Description

The nasal bones of *Arsinoitherium* form the major portion of the aforementioned great horn cores and in consequence are the most aberrant of any mammalian group. The naso-facial suture (C7805) runs transversely across the base of the nasal inflation and descends anteroventrally to join the maxilla just posterior to and level with the nasal incision in lateral aspect (plate 1). Extracranial and intracranial surfaces of the nasals have diverged such that the nasals are invested with an extensive system of sinuses. These are confluent with the frontal sinus system, thus rendering the horn cores essentially hollow. Indeed, although strengthened by an internal system of buttresses, laminar bone of the horns is in some places as thin as 5mm. The ventral surface of the nasal bones constitutes the dorsal roof of the external nasal opening and in life would have housed the mesethmoidal cartilage along a median groove. The prenasal ossification present in older individuals was said by Andrews (1906) to have borne depressions for the attachment of nasal muscles. This assertion was presumably based on M.8463, which bears a distinct pit on the anteroventral part of the nasal septum. Re-examination of this specimen revealed that the pit is in fact an artifact of breakage. Moreover, no other specimens with complete nasal bars exhibit a pit in this position; it therefore seems unlikely that this late ossifying element would have borne muscle fibres.

## Discussion

The primitive condition for nasal bones in eutherian mammals is exemplified in early insectivore-like mammals where they are narrow, elongate and forwardly projecting (*Ictops* in Butler, 1956). Some eutherian groups secondarily reduce and/or retract the nasals (eg. tapirs, seacows and elephants) in order to accommodate hypertrophied nasal musculature. Although this is an advanced condition, it has occurred several times during placental evolution in groups as diverse as the South American astrapotheres and pyrotheres and some cetaceans; it is therefore a poor indicator of affinity. The nasals of *Arsinoitherium*, inflated and drawn out to constitute the massive anterior horn cores, are certainly apomorphic; indeed they do not compare with cranial appendages in any other mammal groups and are therefore of little use in determining higher order relationships. Although the nasal bones are unlike those of other ungulates, the nasal incision (in lateral view) lies a considerable distance behind the snout and possibly indicates the presence of a small proboscis.

### PREMAXILLA

## Description

In lateral aspect (plate 1) the premaxilla-maxillary suture rises at the posterior border of the canine alveolus and trends steeply posterodorsally to contact the nasal at a horizontal suture that runs posteriorly from the nasal incision. Where this suture contacts the narial border a distinct bony swelling rises to provide a point of muscle attachment. In some individuals the dorsal moiety of the premaxilla actually makes a short contact with the frontal bone. Indeed, even in individuals where this contact is not present the premaxilla is excluded from the frontal by only a very short lateral suture between nasal and maxilla. The paired premaxillary bones converge dorsally below the nasal opening, where they fuse anteriorly but remain open more posteriorly, presumably to house the cartilaginous nasal septum (Andrews, 1906). In palatal aspect (plate 2) the premaxillary-palatine suture courses posteriorly from the canine alveolus and disappears abruptly as it rises into the incisive foramen. This foramen is a single deep, posterodorsally trending cavity. Palatal exposure of the premaxilla is short and houses the alveoli of an incisiform canine and three incisors that are therefore closely crowded. The alveolus of the first incisor is enlarged relative to succeeding incisors, contralateral teeth being separated by a short gap along the premaxillary mid-line suture.

## Discussion

The premaxilla in most mammals is a small element confined to the front of the snout. However, in arsinoitheres the premaxilla extends posterodorsally, approaching and sometimes contacting the frontal. This is a very rare condition in eutherian mammals and has been used to unite sirenians with proboscideans (Novacek, 1986; Novacek & Wyss, 1986, 1988). Tassy & Shoshani (1988), on the other hand, prefer to treat premaxillary-frontal contact as being independently attained in both sirenians and proboscideans. They base their assertion on the observation that this contact is not present in *Moeritherium* (Upper Eocene of Egypt) (Tassy, 1981). Although the premaxilla does not actually contact the frontal in *Moeritherium*, it does extend posterodorsally and is therefore excluded from that contact by only an exceedingly short nasomaxillary suture. A posterodorsally extensive premaxilla is therefore retained here as a derived character present in tethytheres and arsinoitheres (character 2 in table 1).

As glirids (Novacek, 1985) and plesiadapid primates (Gingerich, 1976) also possess a premaxillary-frontal contact it therefore seems likely that this condition could be correlated with either a retracted nares or enlargement of the upper incisors. It could also be argued that the somewhat retracted nares and massively expanded nasal horns in *Arsinoitherium* have led to the independent acquisition of this character. However, if an extended premaxilla were a prerequisite for retracted narial openings or the development of large nasal appendages, one would expect the living tapir and extinct titanotheres to possess this characteristic. In both animals, the premaxilla is small and confined to the anterior portion of the snout. Moreover, the premaxilla of living hyraxes with remarkably enlarged incisors does not approach the frontal bone.

The configuration of the incisive foramina varies within mammals, although most commonly they are rather small, paired openings at the anterior end of the palate. Rodents and lagomorphs exhibit a highly derived state in which the foramina are long, narrow openings set more posteriorly in the palate (Novacek, 1985). In arsinoitheres there is a single large foramen. Such confluence of the incisive foramina is a very restricted character within eutherians (character 3 in table 1). Amongst ungulates, perissodactyla and artiodactyls of primitive aspect possess paired anteriorly situated incisive foramina. Hyraxes also exhibit the more general state. The arsinoithere condition is shared with the early proboscideans, *Moeritherium* (Tassy, 1981) and *Numidotherium* (Mahboubi *et al.*, 1986) and with sirenians. Evidently the same condition was achieved secondarily in some perissodactyls including *Tapirus* and could be correlated with retraction of the narial opening. The incisive foramina are associated with Jacobson's organ, a chemosensory sac situated in the anterior nasal chamber. The derived state of the incisive foramen in tethytheres and arsinoitheres may well reflect a modification of this organ associated with hypertrophy of the upper lip.

## MAXILLA

### Description

As mentioned above, in lateral aspect the maxilla contacts the nasal for a short distance along a horizontal suture although in some specimens the premaxilla interposes sufficiently to preclude this contact (plate 1). Just posterior to the latter contact the maxilla descends posteroventrally to contact the lacrimal posterodorsally. Below this junction it forms a broad contact with the anterior process of the jugal behind. The infraorbital canal which transmits the infraorbital nerve (second branch of the trigeminal nerve), artery and vein, emerges just below and in front of the lacrimal (above posterior loph of first molar) and opens posteriorly into the anterior orbit. The infraorbital canal is completely enclosed by the maxilla; it is exceedingly short and of great diameter. The maxilla forms a dominant component of the orbit (plate 3) The maxillary dental capsule is greatly expanded (tuber maxillare) and constitutes the floor of the orbit. A dorsally trending flange of maxilla forms the anterolateral orbital wall, thus excluding the palatine from any possible contact with the lacrimal. In palatal view the maxilla is extensive (plate 2). A maxillary-palatine suture runs from the posterolateral margin of the palate forwards along the tooth row. Level with the middle of the second molar, the suture turns abruptly medially to join the mid-line suture at about ninety degrees. Anteriorly the maxilla forms the posterior border of the incisive foramen. The zygomatic process of the maxilla arises lateral to the last molar; it is very short and makes only a limited contribution to the zygomatic arch.

## Discussion

Contact between the maxilla and frontal in the lateral wall of the face in *Arsinoitherium* is very short due to appreciable retraction of the narial incision and expansion of the nasal bones. Maxillary-frontal contact is reduced in many disparate groups of eutherian mammals and in ungulates is largely a reflection of posterior expansion of the nasal bones. The wide distribution of this characteristic is taken to indicate its plesiomorphic nature. However, Prothero *et al.* (1988) have drawn attention to a potentially derived condition in perissodactyls where the pars facialis of the lacrimal excludes the frontal from the maxilla by contacting the nasal bone (character 11 in table 1). There is some variation in this trait within Perissodactyla although primitive members (*Hyracotherium, Palaeotherium*) show the derived condition and are therefore taken to be archetypal. Interestingly, this character is variably present in living hyraxes where the maxillary-frontal contact is always marginal. However, *Megalohyrax* (Oligocene, Egypt) has a more extensive lacrimal pars facialis (Gregory, 1920) which, nevertheless, does not contacts the nasal bone. This suggests that the derived state in some living hyraxes has no bearing on the perissodactyl condition. McKenna (pers. comm.) would consider this feature to be pleisiomorphic for mammals in general. Although a nasal-lacrimal contact is known in marsupials, since it is absent in the earliest eutherians (Kielan-Jaworowska, 1981, p. 30), and unknown in any other eutherian group, with the exception of perissodactyls, it is here maintained as derived for Perissodactyla.

The exceedingly large diameter and anteroposterior shortening of the infraorbital canal in *Arsinoitherium* (character 4 in table 1) is highly derived with respect to Muller's (1934) postulate of a long and narrow infraorbital foramen being primitive for mammals. Novacek & Wyss (1986) considered the very short infraorbital canal in sirenians and proboscideans to be synapomorphic whilst Tassy (1981) utilised its position (under the orbit) to unite the two. Tassy's character, however, appears to be more the result of anterior positioning of the orbit in *Moeritherium* and sirenians. Certainly, the remarkable shortening of the infraorbital canal of *Arsinoitherium* is a derived state which may prove to be synapomorphic (linking tethytheres and embrithopods), although the position of the orbit is not advanced as in tethytheres. The exceedingly broad calibre of the canal in arsinoitheres is matched only by the condition in sirenians and presumably reflects hypertrophy of the nerves and vessels supplying the upper lip. Although the infraorbital canal in more modern proboscideans is of large calibre, in Palaeogene genera (*Palaeomastodon, Barytherium, Numidotherium* and *Moeritherium*) this opening is actually quite small although sometimes very short. The infraorbital canal in remaining modern orders (hyraxes, perissodactyls and artiodactyls) is fairly long and narrow and presumably plesiomorphic. However, more specialised members of Perissodactyla secondarily shorten the canal.

The maxilla makes a variable contribution to the orbital mosaic of bones in eutherian mammals. Novacek (1980, 1985) has considered the transformation of orbital characters and generally concurs with Muller's (1934) scheme for primitive eutherians. In *Arsinoitherium* the maxilla makes an extensive contact with the frontal in the anterior orbital wall, thus confining and excluding the palatine from this region of the orbit (character 5 in table 1). Assertions that the primitive condition is one in which the maxilla is excluded from contact with the frontal in the anterior orbit by expansion of the palatine are based on the fact that this situation obtains in a wide variety of mammals (some marsupials, carnivores, tree shrews, artiodactyls and perissodactyls) and is characteristic of known Cretaceous therians (Kielan-Jaworowska, 1981). However, it has been argued that the expanded orbital process of the maxilla in archaic primates is primitive (Le Gros Clark, 1959; Cartmill, 1975) and that expansion of the palatine in the orbit of other primates is a neomorphic development. With respect to ungulates, proboscideans and to a lesser extent sirenians, exhibit an expansion of the maxilla within the orbit as do modern hyraxes. Perissodactyls and artiodactyls however, show the primitive arrangement. Unfortunately the functional significance of the various character states in this part of the skull are poorly understood. Novacek (1980) suggested that enlargement of the palatine reflected enlargement of the eye and that expansion of the maxilla within the orbit could be correlated with enlargement of the nasal chamber. However, tubulidentates with enlarged palatine and reduced maxillary contributions to the orbit possess reduced eyes and an enlarged nasal chamber (Thewissen, 1985). Although the classical assignment of polarity is accepted here (enlarged orbital process of the palatine being primitive); in agreement with Novacek (1985), more detailed ontogenetic studies within a variety of taxa are required before transformations in this anatomical region of the skull can be considered unequivocal.

## PALATINE

### Description

In ventral view the palatine is pierced by a pair of small oval foramina at a point level with the middle of the second molar and just posterior to the point at which the palatine-maxillary suture turns towards the midline (plate 2); the foramina open into faint anteriorly trending troughs. Posterior palatine canals, that in life would have transmitted the descending palatine veins, form large oval openings situated lateral to the posterolateral edge of the palate, behind the last molar. The palatine constitutes the medial border whilst a posteriorly directed process of the maxilla completes the lateral margin of the postpalatine canal. From this opening the palatine vein would have risen in a groove situated on the posteromedial side of the tuber maxillare that debouches into the posterior orbit. The posterior border of the palate rises to form the rounded lip of a rather weak post palatine torus curving in a gothic arch towards the mid-line. The mid-line apex of the postpalatine torus is level with the posterior loph of the last molar. A faint tubercle rises on either side of the postpalatine mid-line. More posteriorly the palatine wings thin to contact the pterygoid process of the alisphenoid on either side. In most mammals a lateral vertical process of the palatine is broadly exposed in the orbital fossa, whereas in *Arsinoitherium* this element is represented only by a remarkably small moiety (plate 3). It is confined anteriorly by the orbital process of the maxilla and ventrally by the expanded tuber maxillare. The sphenopalatine foramen (orbitonasal foramen of Andrews, 1906: Text-fig. 4), which in living mammals conveys the sphenopalatine nerve, artery and vein, pierces the palatine just posterior to the orbital flange of the maxilla and is closed ventrally by the expanded dental capsule of the maxilla. A thin process of the palatine projects more posteriorly and is underlain by an equally thin projection of the alisphenoid against which the palatine terminates. Located at this point is a smaller, slit-like foramen: the dorsal palatine foramen (for descending palatine artery and nerves). In younger specimens a sub-vertical suture occurs on the pterygoid flange which is here held to be the junction between the descending process of the palatine in front and a descending process of the alisphenoid behind.

## Discussion

In palatal view, the presence of a short elliptical postpalatine canal in *Arsinoitherium* is an unusual feature. This structure occurs in some lipotyphlan insectivores and tubulidentates. However, in these groups the canal is enclosed within the palatine whilst in arsinoitheres it is closed laterally by a process from the maxilla (as in some rodents). There is no development of a large postpalatine canal in any other group of ungulate and so its development in *Arsinoitherium* must be treated as either pleisiomorphic or autapomorphic.

As previously discussed, a large orbital process of the palatine contacting the lacrimal is primitively present in the anterior orbital wall of therian mammals. In arsinoitheres the palatine is confined to the anteroventral corner of the orbit by an orbital wing of the maxilla in front and by the frontal above. The palatine in hyraxes and sirenians is broadly exposed within the orbit but is precluded from contact with the lacrimal by the maxilla. There is no orbital exposure of the palatine in proboscideans (Tassy, 1981), which presumably reflects the ventral expansion of the frontal and dominance of the maxilla in the orbital floor. Perissodactyls exhibit the primitive condition, in which the palatine makes a broad contact with the lacrimal in the orbit. Russell *et al.* (1983) described an archaic artiodactyl (*Diacodexis pakistanensis*) in which the palatine is exposed in the orbit but precluded from contact with the lacrimal by a descending process of the frontal that contacts the ventrally confined maxilla. Their comparisons with a whole range of early artiodactyls revealed that the condition in *D. pakistanensis* was not typical and presumably represents a specialization in that genus. The typically primitive condition is present in most artiodactyls and is here considered archetypal for the order. Great reduction of the palatine in the orbit of *Arsinoitherium* is treated as a derivation (character 6 in table 1).

Two foramina typically pierce the orbital wing of the palatine and show some variation within eutherians. The sphenopalatine foramen and dorsal palatine foramen in lipotyphlan insectivores open into a common orbital recess that appears to be a eutherian specialization (Novacek, 1986). More commonly and presumably therefore more primitively, the sphenopalatine and dorsal palatine foramina are well separated and situated high in the orbit. In artiodactyls and perissodactyls the sphenopalatine foramen is a large circular opening within the body of the orbital wing of the palatine while the dorsal palatine foramen is either missing or merged with the sphenopalatine foramen. A more restricted condition is seen in proboscideans, where the sphenopalatine foramen is more anteriorly situated and notches the maxillary border within the floor of the orbit (character 8 in table 1). The sphenopalatine foramen in *Arsinoitherium* is also anteriorly situated and confined to the maxillary border. In common with proboscideans, the derived position of this foramen in arsinoitheres is undoubtedly correlated with reduction of the orbital wing of the palatine. Hyraxes appear to be independently specialised in this regard; the sphenopalatine foramen is situated posteriorly, medial to the tuber maxillare where it notches the anterior border of the alisphenoid.

## LACRIMAL

### Description

The lacrimal of *Arsinoitherium* is observed as a discrete ossification only in juvenile individuals where it occurs as a tiny trapezoidal bone bearing a faint tubercle in the superior border of the antorbital rim. It is confined dorsally and medially by the frontal and anteriorly by the maxilla. Ventrally it abuts the dorsally ascending ramus of the jugal. In none of the specimens studied was there a traceable lacrimal foramen.

### Discussion

Gregory (1920) presented a detailed appraisal of lacrimal morphology in mammals. He considered the confinement of the lacrimal to the antorbital rim as being the generalised and therefore primitive condition within mammals. The pars facialis of the lacrimal in artiodactyls is greatly enlarged, often housing a fossa or vacuity and is considered autapomorphic within ungulates (Prothero *et al.*, 1988). The lacrimal is also exposed on the face in perissodactyls and some hyraxes (see discussion of frontal), although not to the same extent as in artiodactyls and if derived, is probably independently so. Positionally the lacrimal in *Arsinoitherium* is typically primitive although the complete lack of a nasolacrimal foramen is surely derived. Blainville (1844) cited loss of the lacrimal foramen as one of a number of characters linking Proboscidea and Sirenia. There is no distinct lacrimal or lacrimal foramen in *Moeritherium* (Andrews, 1906; Tassy, 1981) and no lacrimal foramen has been described in *Numidotherium* although the bone is present (Mahboubi *et al.*, 1986). Moreover, the *Barytherium* skull from Dor el Talha (Libya) has no obvious lacrimal foramen (pers. obs.). However, early sirenians do possess a nasolacrimal foramen

(Savage, 1976), so that its loss in more modern sirenians must be considered as secondarily derived within the group. Due to the presence of a lacrimal foramen in such primitive elephantiforms as *Phiomia* and *Deinotherium*, its absence in *Moeritherium* has been considered autapomorphic for the genus (Tassy, 1981; Tassy & Shoshani, 1988). If reversal in elephantiform progenitors seems unlikely, the independent loss of the nasolacrimal foramen in Palaeogene proboscideans and arsinoitheres must be invoked.

## JUGAL

### Description

The jugal in arsinoitheres is a very long element constituting almost the whole of the zygomatic arch. In contrast to many mammals, the jugal exhibits very little lateral bowing. The anterior part of this element forms the aforementioned anterodorsally projecting ramus that terminates against the lacrimal, forming the external antorbital rim. It bears an extremely prominent laterally projecting bony process that emanates from almost the length of the orbital rim below the lacrimal and presumably anchored exceedingly powerful nasolabial muscles (plate 3b). The jugal-maxillary suture trends posteroventrally to terminate at a level just behind the last molar, at which point there occurs a prominent muscular groove. The jugal then rises posterodorsally forming the free zygoma, to contact the zygomatic process of the squamosal near the back of the orbit. The ventral border of the jugal progrades posteriorly to the anterior margin of the glenoid cavity where a robust process from the squamosal overrides it in a strong almost horizontal suture above the alisphenoid canal (plate 1). In ventral view (plate 2), at the posterior margin of this suture, the jugal is slightly expanded transversely and excavated, thus making an anterolateral contribution to the temporomandibular joint.

### Discussion

A large jugal is generally accepted as primitive for eutherians (Novacek, 1986 and taxa cited therein; p. 39), being present in Cretaceous members of that subclass (Kielan-Jaworowska, 1981). Nevertheless, extension of the jugal to the posterior margin of the glenoid fossa has been treated as a synapomorphy linking Proboscidea, Sirenia and Hyracoidea (Novacek, 1982, 1986; Novacek & Wyss, 1986, 1988). The jugal in sirenians stretches further posteriorly than in most mammals although it in fact ends at the anterior border of the glenoid cavity as in arsinoitheres. Moreover, the posteriorly extended jugal in hyraxes forms a lateral facet that articulates with the mandibular condyle whereas in proboscideans there is no such articulation (Fischer, 1989). It therefore seems likely that extension of the jugal to the posterior border of the glenoid cavity in proboscideans and hyraxes evolved independently and that sirenians and arsinoitheres exhibit a more primitive state (Tassy, 1981; Tassy & Shoshani, 1988; Fischer, 1988). This assertion is strengthened by consideration of an additional jugal specialisation obtaining in proboscideans. In *Arsinoitherium* the jugal primitively forms the border of the orbital rim (Gregory, 1920) whereas the anterior part of the jugal in proboscideans is reduced such that the expanded maxilla constitutes the antorbital rim (character 13 in table 1). All other ungulates including sirenians and hyracoids exhibit the primitive condition of the anterior jugal.

## FRONTAL

### Description

The frontal occupies most of the skull roof in arsinoitheres. In dorsal view it forms an undulating almost transverse suture with the nasal bones at the base of the great anterior horn cores. On either side, dorsolaterally above the level of the last molar, the frontals are inflated to form a smaller pair of hollow horn cores. From a mid-point between the frontal horns the fronto-parietal suture trends posterolaterally on either side. This contact then progrades on to the lateral side of the skull, trending ventrally and slightly posteriorly to contact the ascending alisphenoid process and presumably the dorsal margin of the orbitosphenoid (plate 1). Due to lacrimal reduction, the frontal contacts the anterior ramus of the jugal at the superior corner of the antorbital rim. It also contacts the dorsal border of the orbital maxillary flange. More posteriorly it descends to contact the tiny orbital eminence of the palatine and the orbitosphenoid behind.

### Discussion

Ventral expansion of the frontal in arsinoitheres and proboscideans has already been mentioned (see discussion under palatine) and is considered to be an advance over the more generalised condition where, although still a dominant component of the orbit, there is no appreciable expansion ventrally.

In ungulates the frontal shows some interesting variation with regard to its configuration in relation to elements in the posterior part of the orbit. Primitively the frontal contacts the parietal and a dorsal process of the alisphenoid in the posterior orbital wall (ie. present in lipotyphlan insectivores, leptictids, rodents, tubulidentates, didelphid marsupials, sirenia and arsinoitheres). However, in artiodactyls the orbitosphenoid is expanded over the alisphenoid thus precluding a frontal alisphenoid contact (Prothero *et al.*, 1988). Some perissodactyls (*Pachynolophus*: Savage *et al.*, 1965) and hyraxes exhibit a similar configuration. The dorsal meoity of the alisphenoid in proboscideans is reduced and overlain by the orbitosphenoid, which nevertheless fails to contact the parietal above, thus allowing a short contact between the frontal and squamosal (Tassy, 1981). The proboscidean condition appears to be autapomorphic (character 16 in table 1) and although the configuration in hyraxes, some perissodactyls, and artiodactyls is undoubtedly apomorphic, it is unclear whether the preclusion of a contact between alisphenoid and frontal is synapomorphic or independently achieved in these groups.

## PARIETAL

### Description

Dorsally the parietal forms a major portion of the hinder part of the cranium in *Arsinoitherium.* It contacts the frontals anteriorly as previously described. Essentially, the parietal forms the flattened roof of the brain case, the posterior transverse narrowing of the latter reflects the small size of the cerebrum. The dorsolateral margin of the parietal forms the posterosuperior border of a deeply excavated temporal fossa. In lateral aspect just posterior to the point at which the alisphenoid is interposed between the frontal and squamosal, a suture between the parietal above and the squamosal below rises in a posterodorsal direction within the temporal fossa before trending horizontally around the lateral expansion of the lambdoid crest (plates 1 and 4b). Sutures between the parietal and supraoccipitals behind, are indistinguishable in all observed specimens although they probably occur in the region of the highly rugose lambdoid crest (plate 4a). An interesting feature occurs in the Cairo juvenile skull (C.7805) in the form of a small foramen situated in the centre of the parietal on the skull roof. This is interpreted as the foramen emissarium parietale, often present in sirenians. Presumably this opening functioned to drain the dorsal parietal sinus. It is thought to be a remnant structure of the interparietal bone that in most ungulates, if present at all, is only distinguishable in juvenile specimens. This structure has not been observed in any of the other cranial specimens and must therefore have disappeared early in development.

### Discussion

There seem to be few features of the parietal that vary systematically. However, Novacek & Wyss (1986) drew attention to the significance of the interparietal ossification in eutherian phylogeny. This element forms early in ontogeny and is often indistinguishable in adult skulls. The wide distribution of this feature amongst eutherian groups surely attests to its plesiomorphic nature. Its absence in pholidotans and edentates is considered synapomorphic (Novacek & Wyss, 1986), while lack of an interparietal in proboscideans is probably autapomorphic for the group. In all ungulate groups where the interparietal is present, with the exception of sirenians, it apparently fuses with the supraoccipital bones early in ontogeny. In contrast, the interparietal of sirenians fuses with the parietals often leaving a remnant foramen. This foramen, here termed the foramen emmissarium parietale, situated in the middle of the skull roof, is also present in a juvenile arsinoithere skull (C. 7805: see Andrews, 1906; Plate III, fig. 2). The presence of this structure is taken to indicate the early occurence of an interparietal ossification which then fused with the parietal bones rather than the supraoccipitals. Interparietal fusion with the parietals is treated as derived for ungulates (character 19 in table 1).

Prothero *et al.* (1988) used the position of the ethmoid foramen which usually pierces the frontal, as a character in their data matrix for ungulates. They considered an ethmoid foramen situated above the posterior palate to be derived within ungulates. However, no meaningful relationship between the posterior palate and ethmoid foramen could be discerned during this study. Nevertheless, retraction of the ethmoid foramen so that it emerges from below the crista orbitotemporalis does appear to be of restricted distribution. In fact, amongst ungulates this feature characterises arsinoitheres and proboscideans alone (character 17 in table 1). Sirenians are unique amongst ungulates in lacking an ethmoid foramen.

## PRESPHENOID

### Description

The presphenoid is indistinguishable in all individuals except in one extremely young individual (AMNH 13505) where the palate is completely missing thus exposing the unfused posterior roof of the external nares (plate 5). Posteriorly the presphenoid is indistinguishable from the saddle-like pterygoids but anteriorly it extends as a narrow splint of bone which penetrates the posterior bifid terminus of the vomer.

## ORBITOSPHENOID

### Description

The exact sutural outline of the orbitosphenoid is not discernible in any of the available skulls, although some vague lines of possible contact can be seen in AMNH. 13506. Nevertheless, several orbital features can be utilized as landmarks to give a general idea of this element's configuration. The crista orbitotemporalis generally marks the approximate contact between the alisphenoid and orbitosphenoid posteriorly and posterodorsally (plate 3a). A thin finger of bone interposed between the posterior process of the palatine and the tuber maxillare is here held to mark the anteroventral limit of the alisphenoid. It therefore follows that the orbitosphenoid contacts the palatine above this along the posterior border of the palatine. The optic foramen in therians is characteristically enclosed by the orbitosphenoid; it is a large circular foramen located under the orbitotemporal crest above and in front of the sphenorbital fissure (plate 3b). The course of the optic nerve is marked by a crest emerging from under the crista orbitotemporalis. The optic foramen probably approximates the posterior limit of the orbitosphenoid, as in most mammals it is located just anterior to the junction of that element with the alisphenoid. An ethmoid foramen is situated just above and slightly in advance of the optic foramen (on a level with the back of the tuber maxillare) and probably marks the dorsal extent of the orbitosphenoid. Slightly in front of and on a line with the ethmoid foramen, just underneath the anterior most extent of the crista orbitotemporalis, there is a much smaller foramen (indistinct in most specimens except M. 8463). It is here termed the ophthalmic foramen (possibly for the ophthalmic nasociliary nerve). If present, this opening usually pierces the frontal adjacent to its contact with the orbitosphenoid. There is some variation in eutherians as to whether the ethmoid and ophthalmic foramina are housed within the orbitosphenoid or frontal; nevertheless they are both usually situated around the juncture of these two elements and are therefore useful features for delimiting the former.

## Discussion

Variation of this element within ungulates has already been discussed in relation to the posterior orbit and the frontal (above). Position and form of the optic foramen has received some consideration from mammalian systematists. The optic foramen is separated from the sphenorbital fissure in *Asioryctes*, *Kennalestes* (Kielan-Jaworowska, 1981), all condylarthran grade ungulates, hyracoids, artiodactyls, sirenians, proboscideans and arsinoitheres and is considered to be the primitive eutherian condition. However, this foramen opens more anteriorly within the orbit in sirenians, proboscideans, perissodactyls, artiodactyls and arsinoitheres than in hyraxes and hippomorph perissodactyls in which it is retracted. Novacek (1986) treated the more posterior position of the optic foramen as being primitive for eutherians but due to the more anterior situation of this foramen in ungulates of primitive aspect (Russell, 1964; Gazin, 1965, 1968) retraction of the optic foramen might equally well be treated as derived within ungulates.

### ALISPHENOID

## Description

The alisphenoid in mammals is a complex element making a contribution to several regions of the skull. It is largely exposed in the posterior orbital wall. A strong dorsal apophysis contacts the frontal anteriorly, the parietal posterodorsally and the squamosal posteriorly (thereby excluding the frontal from the squamosal). A strongly expanded ventral process makes the greatest contribution to the pterygoid flange. In young individuals the pterygoid flange is breached anteriorly by a sub-vertically open suture that probably delimits the contact between the pterygoid process of the palatine and alisphenoid. In older individuals the pterygoid plate is completely fused as one element bearing a prominent tuberosity for attachment of the external pterygoid muscles. Several foramina pierce the orbitotemporal process of the alisphenoid and are shielded in lateral aspect by the anterodorsally trending flange of the crista orbitotemporalis. As stated above, the latter probably marks the contact between orbitosphenoid and alisphenoid (plate 3). Largest of these openings is the sphenorbital fissure (anterior lacerate foramen) which usually conveys the occulomotor (III), trochlear (IV) and abducens (VI) cranial nerves and the ophthalmic and maxillary divisions of the trigeminal (V) nerve. As there is no discrete foramen rotundum, it must be assumed that the remainder of the trigeminal and transverse vein also pass through the sphenorbital fissure. Situated below and slightly posterior to the sphenorbital fissure is the anterior opening of the alisphenoid canal for passage of the maxillary vein and artery (provided the inferior ramus of the stapedial artery is annexed by an anastomosis from the external carotid artery). The alisphenoid canal is unusually large, fairly short and bridged by a flat lamina of bone laterally. The alisphenoid curves onto the ventral surface of the cranium adjacent to the transversely expanded glenoid fossa in the squamosal (plate 6), with which it form a longitudinal suture. Lateral to the glenoid fossa the alisphenoid forms the anterior limit of the otic vacuity. The foramen ovale, which conveys the mandibular branch of the trigeminal nerve, is in most mammals completely enclosed by the alisphenoid. In *Arsinoitherium* however, the foramen ovale notches the posterior border of the alisphenoid and comes to be confluent with the anterior lacerate foramen (plate 6). In some specimens a short process of the squamosal, emanating from the medial edge of the glenoid cavity, projects medially across the alisphenoid notch, forming a partial bridge over the foramen ovale.

## Discussion

As mentioned above, the typical configuration of the mammalian alisphenoid includes development of a strong dorsal eminence contacting the parietals. This condition obtains in arsinoitheres.

Arsinoitheres possess a distinct ectopterygoid process of the alisphenoid (sutural junction visible in juvenile individuals) that provides an increased area of attachment for the external pterygoid muscle. This process is absent in all known ungulates and is rare within eutherians as a whole; it is here considered to be autapomorphic for arsinoitheres.

In primitive Cretaceous eutherians (Kielan-Jaworowska, 1981) the sphenorbital foramen and foramen rotundum are confluent. This condition is therefore considered primitive for eutherians (Muller, 1934; Novacek, 1980). Indeed, there is no separate foramen rotundum in lipotyphlan insectivores or tubulidentates (Thewissen, 1985). Novacek (1986) considered that among ungulates, neither hyracoids, artiodactyls, perissodactyls nor proboscideans possessed a distinct foramen rotundum (table 3; p. 85). This is patently false; all living ungulates bar sirenians possess a discrete foramen rotundum. Indeed, amongst archaic ungulates, *Arctocyon* (Russell, 1964), *Meniscotherium* (Gazin, 1965), *Phenacodus* (Simpson, 1933), *Diacodexis* (Russell *et al.*, 1983) and primitive members of modern ungulate orders, *Moeritherium* (Tassy, 1981) and *Hyracotherium* (Edinger, 1948) all possess a distinct foramen rotundum. *Hyopsodus* (Gazin, 1968), sirenians and arsinoitheres appear to lack a round foramen and retain the primitive condition. However, since development of a foramen rotundum is a widespread and early attained character in ungulates, it is possible that the three taxa above, secondarily lost this opening.

An alisphenoid canal for passage of the maxillary artery is commonly present in eutherians. Its absence in artiodactyls including *Diacodexis* (Russell *et al.*, 1983) and cetaceans (Kellogg, 1936) is surely derived, whereas loss of the alisphenoid canal in living sirenians is neomorphic as evidenced by its presence in *Prorastomus* (Savage, 1976). All other ungulates including arsinoitheres (except arctocyonids and *Hyopsodus*) exhibit the primitive possession of an alisphenoid canal. Novacek (1986), in contrast to previous statements (Novacek, 1980), treated the absence of an alisphenoid canal as primitive and fallaciously attributed this state to several ungulate groups (hyraxes, proboscideans and sirenians).

## BASISPHENOID

### Description

In ventral view the basisphenoid is fused with the presphenoid in front and the pterygoids laterally and is indistinguishable from those elements (plates 5 and 6).

Posteriorly the basisphenoid forms a thick, short rod that makes an obvious sutural contact with the slightly dorsiflexed basioccipital. This suture remains unfused even in fully mature individuals. The pterygoid flanges pass back to the level of the basisphenoid-basioccipital suture where a weak groove passes medial to it, presumably marking the course of the eustachian tube. Internally, the basisphenoid is pierced on either side by large oval conduits for passage of the optic nerve from the braincase.

## SQUAMOSAL

### Description

The squamosal is a large and important element forming the posterolateral wall of the braincase. In *Arsinoitherium* it joins the parietal in the temporal fossa along the previously mentioned suture and joins the alisphenoid anteriorly and ventrally. Within the temporal fossa the squamosal-parietal suture trends posterodorsally from its juncture with the alisphenoid to the anterolateral edge of the lambdoid crest. From this point it courses horizontally across the crest before descending abruptly in an almost vertical suture with the exoccipital bones. In ventral view the continuation of this suture trends posterolaterally around the posttympanic process of the squamosal before descending into the otic vacuity (plate 6). Slightly above and below the squamosal-parietal suture there are a variable number of small foramina opening into shallow surface grooves that pierce the braincase wall. These foramina, here termed squamosal sinus canals (plate 4b), converge on a deeply excavated sinus in the squamosal above and lateral to the periotic bones (epitympanic sinus). In turn, vessels that ramify in the epitympanic sinus seem to emanate from a wide, shallow groove notching the squamosal at the anterolateral border of the otic vacuity (plate 6). This groove progrades dorsally towards the epitympanic sinus along the internal surface of the squamosal, above the external auditory meatus (the significance of these structures is discussed later). Below the sinus canals, the squamosal is expanded transversely and raised laterally into a prominent crest that marks the dorsal edge of a rather short zygomatic root bounding the posteriolateral part of the temporal fossa. A tiny foramen sometimes pierces the squamosal below the crest, just above the level of the external auditory meatus and is confluent with the aforementioned groove leading to the epitympanic sinus. In ventral view the glenoid fossa is large and transversely extended; its medial edge forms a raised lip whilst more laterally it becomes concave, extending onto the backward prolongation of the jugal where the concavity is continued in an oval depression. A wide tongue-like process, the postglenoid process, curves posteriorly behind the glenoid cavity providing a strong posterior wall to the fossa. The external auditory meatus is extremely wide both transversely and anteroposteriorly. A large posttympanic process is strongly curved anteriorly. In most complete specimens it approaches or even contacts the recurved postglenoid process. The roof of the external auditory meatus is below the level of the epitympanic sinus as mentioned above.

## Discussion

The squamosal sinus canals of *Arsinoitherium* are commonly present in eutherian mammals (rodents, lagomorphs, edentates, proboscideans, perissodactyls, carnivores etc.) and are presumably primitive. It has been suggested that these are venous channels draining blood from the external pinna of the ear (Tassy, 1981; Novacek, 1986; Sissons & Grossman, 1956). However, Wible (1986) contends that these foramina convey temporal rami from the posterior branch of the superior arm of the stapedial artery. Since the stapedial artery is reduced in all ungulates except some artiodactyls (in which squamosal sinus canals are absent) it seems unlikely that these foramina were arterial channels, at least in ungulates. Tassy (1981) noted that in *Moeritherium* the squamosal sinus canals passed ventrally on the inner surface of the squamosal to exit the cranium via a discrete foramen behind and medial to the glenoid fossa (orifice ventral du canalis temporalis: Plate VI, p. 146). He suggested that loss of the postglenoid foramen and development of this opening represented a proboscidean autapomorphy. However, in arsinoitheres a channel can be traced from the external openings of the squamosal sinus canals along the inner border of the squamosal to a shallow groove in the anterolateral edge of the otic vacuity which, although not completely enclosed by the squamosal, must correspond to the ventral opening described by Tassy. Moreover, the squamosal sinus canals in perissodactyls can be similarly traced to a ventral opening situated posteromedial to the glenoid fossa (temporal canal for the superficial temporal vein: Sissons & Grossman, 1956; p. 698). In light of the widespread occurrence of squamosal sinus canals it would seem at first sight that they represent a plesiomorphic condition within eutherians. However, development of a basicranial exit for the superficial temporal vein may well be derived for the aforementioned ungulates (character 24 in table 1). Certainly, loss of a postglenoid foramen in arsinoitheres and all modern ungulate groups except artiodactyls is an apomorphic state (Prothero *et al.*, 1988) as evidenced by the wide distribution of postglenoid foramina in non-ungulate groups.

The Glaserian fissure is a cleft medial to the postglenoid process that is generally present in eutherians. It usually conveys the inferior branch of the stapedial artery and chorda tympani from the tympanic cavity. Presence of a Glaserian fissure in marsupials and lipotyphlan insectivores (Novacek, 1986) probably indicates its primitive status with regard to mammals in general. With respect to modern ungulate orders, the Glaserian fissure is absent in all but primitive artiodactyls (Coombs & Coombs, 1982) and hyraxes where it is a fairly wide trough. *Arsinoitherium* lacks a Glaserian fissure and is therefore derived in this respect.

### PERIOTIC

(Plate 7)

The periotic bone (petrosal) of mammals is a complex ossification enclosing the spiral cochlea and semicircular canals. It also serves as a conduit for several important cranial nerves, arteries and veins. Being a complex structure somewhat functionally isolated from the rest of the skull, this element has yielded many characters deemed to be of phylogenetic significance. The petrosal was overlooked by Andrews (1906) and thus until recently had remained undescribed in arsinoitheres. This author (Court, 1990) has already provided a detailed description of two right periotic bones attributed to *Arsinoitherium.* Rather than repeating information already available, only a brief review of arsinoithere periotic features considered to be derived and therefore included in the ensuing character analysis, is presented here.

## Discussion

Absence of a subarcuate fossa on the cerebral surface of the petrosal is considered derived for eutherian mammals (Novacek & Wyss, 1986). It is well represented in *Protungulatum* (MacIntyre, 1972), the condylarth, *Hyopsodus* (Cifelli, 1982) and artiodactyls of primitive aspect (Court, 1990). Among extant ungulates only hyraxes possess a deep subarcuate fossa. The absence of this structure in arsinoitheres is therefore treated as derived.

In sirenians, proboscideans, and *Arsinoitherium,* the fenestra ovalis is distinctly round and large, obviously reflecting the shape of the stapedial footplate. Most commonly, the stapedial footplate in eutherian mammals tends to be oval and rather small. This is the condition seen in all ungulates with the exception of those already mentioned (character 28, table 1).

Court (1990) referred to the fenestra rotundum in arsinoitheres as showing an anomolous configuration; being vertically orientated and facing medially with respect to the fenestra ovalis. In tympanic view this opening is obscured by a ventroposteriorly directed lip of the promontorium. Novacek & Wyss (1986) used the position of the fenestra rotundum to support the monophyly of a clade including proboscideans, sirenians and hyracoids. Court (1990) however, while arguing for the homology of this structure in Sirenia and Proboscidea and arsinoitheres, considered the hyracoid condition to fail the criterion of similarity. The fenestra rotundum of hyraxes is greatly enlarged, subvertically orientated and faces posteriorly with respect to the fenestra ovalis. Moreover, there is no evident overgrowth of the promontorium and the outline of the opening is strangely irregular. Hyraxes therefore show an independently derived configuration of the fenestra rotundum.

Startling results recently published by Fischer (1990), have however, forced a reappraisal of certain features discussed by Court (1990). Court (1990) suggested that Embrithopoda and Proboscidea shared a unique loss of a discrete perilymphatic foramen in the petrosal. He therefore concluded that the cochlear aqueduct must have looped into the scala tympani via the fenestra rotundum. Based on morphogenetic studies, Fischer (1990) has now shown that the conspicuous opening traditionally referred to as the fenestra rotundum in both elephants and sea cows is, in fact, an enlarged perilymphatic foramen. Modern sea cows and elephants are shown to have failed to develop the typically therian fenestra rotundum. Since the bony morphology of the petrosal in both living elephants and *Arsinoitherium* is remarkably similar, it is here assumed that arsinoitheres also failed to develop a fenestra rotundum. However, as the Eocene sea cow *Prorastomus* exhibits the usual configuration (Court, 1990), loss of the fenestra rotundum in living forms is treated as a neomorphic state. Indeed, while Fischer (1990) regards, loss of the fenestra rotundum as a new synapomorphy for Sirenia and Proboscidea, it is here restricted to Proboscidea plus Embrithopoda (character 30 in table 1).

In arsinoitheres there is a very broad, open tympanic aperture for the facial nerve which descends from the internal auditory meatus well in advance of the fenestra ovalis. This condition obtains in *Arsinoitherium*, perissodactyls, proboscideans and in sirenians. However, in artiodactyls and hyracoids the facial nerve enters onto the tympanic surface of the petrosal laterad and only slightly anterior to the fenestra ovalis. The facial nerve branches at the geniculate ganglion within the body of the petrosal. The superficial petrosal nerve (anterior branch) is then conveyed anteriorly in the closed tube of the fallopian aqueduct to exit the petrosal terminally through the fallopian hiatus. Therefore, it is the posterior branch of the facial nerve that pierces the tympanic surface just anterolateral to the fenestra ovalis in artiodactyls and hyracoids. In sirenians, proboscideans and arsinoitheres, the geniculate ganglion would have been situated on the tympanic surface above the tympanic aperture of the facial nerve, the superficial petrosal nerve then diving directly into the median lacerate foramen. These three taxa therefore lack the fallopian aqueduct and hiatus typically found in eutherian mammals and must therefore be regarded as derived in this respect.

The stylomastoideum is the point at which the facial nerve exits the petrosal posteriorly. In hyracoids the tympanohyal and tympanic process join below the facial nerve as it exits the petrosal. However, since a tympanic process does not occur in the petrosal of perissodactyls, sirenians, proboscideans and embrithopods, the stylomastoid exit for the facial nerve is open. The presence of a petrosal tympanic process has a wide spread occurrence in mammals, its absence in the above mentioned taxa is therefore considered to be derived.

An expanded tegmen tympani enclosing the whole of the epitympanic recess occurs archetypally only in hyraxes and artiodactyls among ungulates (Court, 1990). Although Cifelli (1982) considered inflation of the tegmen tympani to be a derived feature at a high level within ungulates, only in the above mentioned groups was this found to be so. In all other taxa studied, the squamosal made a contribution to the lateral wall of the epitympanic recess, which, as the condition most commonly found in eutherians, was taken to be primitive (Court, 1990).

The absence of transpromontorial grooves in all ungulate taxa studied with the exception of artiodactyls (Coombs & Coombs, 1882), was taken to reflect the absence of the primitive eutherian condition (Wible, 1984, 1986).

Primitively, the mastoid eminence of the petrosal is broadly exposed on the basicranium and, in occipital view, projects between the squamosal and exoccipital bone. The absence of extracranial exposure of the petrosal mastoid region in arsinoitheres, proboscideans, sirenians (see Novacek & Wyss, 1987) and hyraxes is treated as derived in this analysis.

## OCCIPITALS

### Description

The supraoccipital occupies the whole of the occiput above the foramen magnum which is enclosed exclusively within the exoccipitals (plate 4a). A deep suture between the exoccipitals and supraoccipitals runs transversely across the back of the skull from the posterolateral extension of the lambdoid crest on one side to the other. In lateral view this suture crosses the lambdoid crest and descends in contact with the squamosal in front. At its most ventral extent, the exoccipital-squamosal suture turns medially around the base of the posttympanic process of the squamosal. In occipital view the exoccipital is raised into a very weak paraoccipital process situated low down on the posteromedial side of the posttympanic process. The plane of the occiput is inclined strongly forwards above the foramen magnum (faces dorsally and posteriorly) and is broadly visible in dorsal aspect. This part of the occiput is delimited by an extremely strong lambdoid crest that arcs forward. The lateral extremities of the lambdoid crest form great pointed tuberosities projecting posteriorly above the level of the occipital condyles. Within the wide fossa delimited by the lamdoid crest, the occipital surface is divided by a strong longitudinal crest that is pittted with muscle scars. The anterolateral edge of the lambdoid crest forms the posterior border of the temporal fossa. Below this the rugosity flares laterally to reach the middle of the external auditory meatus. The foramen magnum faces posteriorly; its dorsal border arcs towards the ventral limit of the nuchal crest above the level of the condyles and is set farther forward than the ventral border. The occipital condyles are widely spaced and pedunculate. In a dorsoventral plane they are highly convex, the curvature being more extensive dorsally than ventrally. Transversely the condyles are more gently convex although they both form segments of the same broad arc. In ventral view the sutures between the exoccipital and basioccipital are indistinguishable in all specimens studied. Anteriorly the basioccipital is a thick rod-like bone that joins the basisphenoid at a jagged suture close to the junction of the latter with the pterygoid flange. It is marked by a faint median ridge but in general the basilar muscle scars are poorly developed. Just posteromedial to the foramen ovale notch in the alisphenoid, there is a wide shallow groove in the lateral edge of the basioccipital corresponding to the median lacerate foramen. This emerges directly from the anterior border of the otic vacuity. This fossa, which houses the periotic, is extremely capacious and always found empty in the observed specimens. Presumably this testifies to the weak connection of the periotic to the surrounding basilar elements. More posteriorly the basioccipital flares laterally and presumably merges with the exoccipitals around the hinder border of the otic vacuity. At the posteriomedial border of the vacuity there is a deep notch corresponding to the posterior lacerate foramen. Since there is no discrete hypoglossal foramen detectable in any of the specimens studied, it must be assumed that the hypoglossal nerve exited the cranium via the posterior lacerate foramen along with the internal jugular vein. A less obvious groove notches the posterolateral border of the vacuity at the junction between exocciptal and squamosal bones. This represents the stylomastoidium; the point at which the facial nerve exits the tympanic cavity (plate 6b).

## Discussion

The derived amastoid condition in *Arsinoitherium* has already been discussed (under periotic).

The vestigial nature of the paroccipital process of the exoccipital in arsinoitheres is a rare condition in eutherian mammals. A well developed process occurs in creodonts, true carnivores, didelphid marsupials, most lipotyphlan insectivores, rodents, lagomorphs and amongst ungulates; artiodactyls, perissodactyls, hyracoids, and sirenians. The vestigial condition of this process in proboscideans and arsinoitheres is therefore considered to be derived.

All mammals with the exception of monotremes, proboscideans and *Arsinoitherium* possess an hypoglossal foramen in the basioccipital bones just anterior to the occipital condyles. This exceedingly rare condition must surely be derived within the taxa here under consideration.

Novacek (1989) used the presence of a weak lambdoid crest and expanded occiput to unite the sirenians, hyracoids and proboscideans. However, its has been pointed out (Fischer, 1989) that a number of fossil hyraxes have strong lambdoid crests, thus invalidating this synapomorphy.

In *Arsinoitherium* the foramen magnum is enclosed completely by the exoccipital bones. Shoshani (1986) suggested this as a paenungulate synapomorphy without appreciating that in hyraxes the supraoccipitals form the dorsal closure of the foramen magnum. Tassy & Shoshani (1988) have suggested that this character is variable in sirenians. Nevertheless, a foramen magnum enclosed solely by the exoccipitals occurs in *Prorastomus* and is therefore maintained as a useful derivation in this analysis.

# POSTCRANIAL CHARACTER DISCUSSION

## PEDAL ANATOMY

The configuration and interrelationships of the various elements that constitute the mammalian ankle and wrist joints have been, from a phylogenetic standpoint, the most debated aspects of mammalian postcranial anatomy (Szalay, 1977; Szalay & Drawhorn, 1980).

Among ungulate eutherians the debate has centred around the significance of an alternating (paraxonic or diplarthral) arrangement of carpal and tarsal elements versus a serial (mesaxonic or taxeopodal) arrangement. The early phenacodontid condylarth, *Phenacodus primaevus*, has the serial configuration, which led Cope (1897) to suggest this as being the primitive condition in ungulates. Based on the study of a wider range of condylarthran grade ungulates, Matthew (1897) noted that *Phenacodus* was in fact atypical of archaic ungulates, the majority exhibiting the alternating pattern which he then considered to be primitive for ungulates in general. This view was amplified by Matthew & Simpson (1937) and has since become the accepted dogma.

## THE UNGULATE CARPUS

A serial carpus in which there is no interlocking of the distal carpal row with the proximal row occurs in some fissiped carnivores, insectivores, rodents and amongst ungulates, in some phenacodontids, *Meniscotherium*, proboscideans, sirenians, hyraxes (Rasmussen *et al.*, 1990) and also in *Arsinoitherium*. The vast majority of other eutherians exhibit the alternating pattern, in which there is an interlocking between the lunar and unciform elements. It therefore seems reasonable to concur with the idea of a serial carpus being the derived condition amongst eutherians in general (character 44, table 1).

The serial pattern has been taken as one of the principal characters in support of a special relationship between sirenians, proboscideans and hyraxes (Shoshani, 1986; Novacek, 1982, 1986; Novacek & Wyss 1986; Novacek *et al.*, 1988). On this basis arsinoitheres should be included in a somewhat streamlined reformation of Simpson's (1945) paenungulate concept. Indeed, desmostylians cannot be excluded on the basis of their highly autapomorphous tarsal construction which Novacek & Wyss (1987) contend could easily have arisen from a serial arrangement. However, the homologous nature of the serial carpus in hyraxes and tethytheres has been strongly challenged (Fischer, 1986, 1989; Prothero *et al.*, 1988). Fischer (1986) determined, with the use of X-ray photographs, that the serial arrangement of carpal bones in modern hyracoid facilitated an ability to invert and evert the hand by rotation at the mid-carpal joint. Manual manipulation of dried hyracoid carpal bones by this author confirms Fischer's findings. The proximal carpal bones remain essentially fixed while the distal row are able to rotate about the long axis of the hand. The functional significance of a serial arrangement of carpals in elephants and arsinoitheres has already been explained (Court, 1989). Yalden (1971) interpreted the midcarpal joint in elephants as a deviational hinge adding to ulnar deviation during flexion. On the contrary, the mid-carpal joint in arsinoitheres and elephants acts as a rotary joint during weight bearing; the proximal row sliding across the distal row rather than twisting relative to it as in hyracoids. Fischer contends that the hyrax carpus is secondarily derived from a perissodactyl-type cursorially adaped carpus enabling hyraxes to climb. The arsinoithere-elephant type of carpus is developed in order to counter outward rotatory moments generated through the planted limb which would tend to dislocate the wrist (caused by the forward and medial stride of the contralateral limb in these wide bodied forms). In short, I concur with Fischer in considering the carpus of hyracoids and proboscideans to have been independently derived in response to disparate functional demands.

## THE UNGULATE TARSUS

Ungulate tarsal elements have similarly been categorized as either alternating (cuboid articulation with the astragalar head) or serial (cuboid articulates solely with the distal face of the calcaneum). Again a simplistic polarizing of ungulate tarsal structure into a primitively alternating and derived serial pattern has been perpetuated in the literature. However, detailed study of ungulate tarsi from a functional perspective reveals a number of specializations within the two broad categories. For instance, the

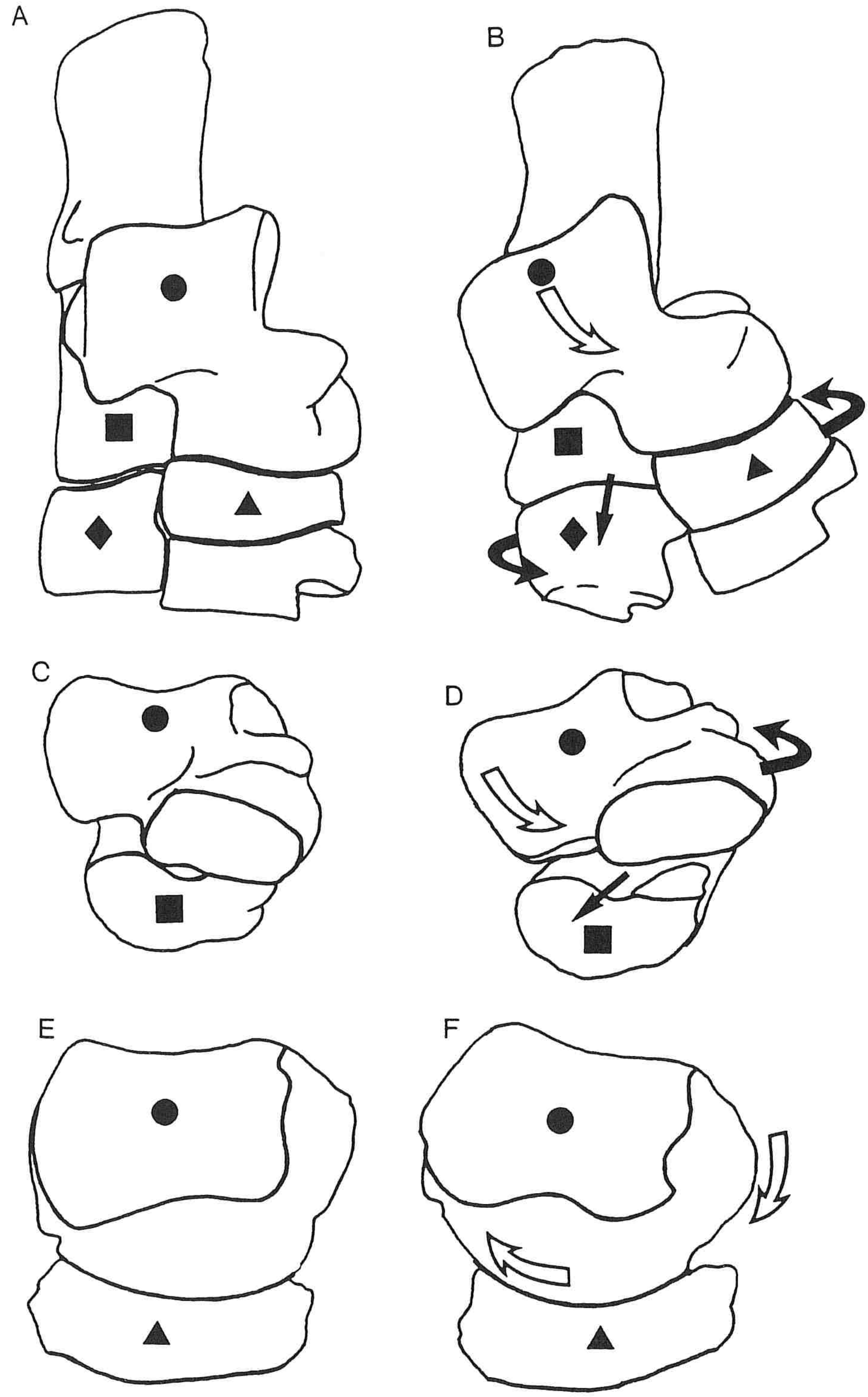

Fig. 1.— **A**: hyrax tarsus anterior view close packed; **B**: hyrax tarsus anterior view tarsal in rotation; **C**: hyrax astragalus and calcaneum distal view close packed; **D**: hyrax astragalus and calcaneum tarsals in rotation. **E**: *Elephas* astragalus and navicular anterior view close packed; **F**: *Elephas* astragalus and navicular in rotation. Circle = astragalus; square = calcaneum; triangle = navicular; diamond = cuboid.

double pulley developed in the artiodactyl tarsus (Schaeffer, 1947), although alternating, is clearly a specialisation over the arctocyonid condition (Szalay, 1977).

Apart from Schaeffer (1947) there have been few attempts at a functional understanding of ungulate tarsal specialisations. Osborn suggested that the alternating pattern reflected a need for increased support as ungulates became more digitigrade. However, this was based on the erroneous assumption that a serial plantigrade stance was the primitive condition. Indeed the serial tarsus of elephants has already been interpreted as a response to mechanical demand for a more vertically orientated foot (Court, 1989).

The tarsus of hyracoids and proboscideans has been used as a synapomorphy linking these two taxa. Detailed scrutiny however, reveals a number of striking differences. Firstly, the astragalus and calcaneum in hyracoids are able to slide anteroposteriorly relative to one another. Secondly, the cuboid is carried on the distal face of the calcaneum, which, itself, is set off to the lateral side of the tarsus (fig. 1). In proboscideans the astragalus is able to rotate on the calcaneum about the long axis of the limb. Moreover, the cuboid is carried on the distal face of the calcaneum, situated behind and directly below the astragalus. Also, the cuboid in proboscideans underlies and buttresses the navicular laterally, whereas in hyracoids it lies adjacent to the navicular. These differences are simply explained in functional terms. As the calcaneum slides forward relative to the astragalus in hyraxes it moves anteromedially (fig. 1). At the end of its translation, the distal face of the calcaneum has moved from its lateral position level with the astragalar head to a point in advance of the astragalar navicular facet and directly underlying it. The result is that the cuboid must move ventrally and medially with respect to the navicular, causing an inversion of the tarsus as a whole. This ability of hyraxes to invert the foot is borne out in X-ray photographs presented by Fischer (1986; p. 26). A requirement to shift the cuboid relative to the navicular precludes the alternating pattern, in which the cuboid is carried, at least partly, on the distal head of the astragalus. As previously explained, the serial pattern of elephants is a response to quite different functional demands (repositioning of tarsal element to cope with realignment of principal force vectors in a mechanically more advantageous sub-vertically aligned foot). These two contrasting arrangements cannot be considered homologous.

The tarsus of *Arsinoitherium* shares a number of features in common with that of proboscideans: i.e. a dorsoventrally compressed astragalus bearing a large tuberculum mediale and a curved translatory facet on the calcaneum for the fibula. Moreover, the tarsus seems to have functioned in a similar manner to the tarsus of elephants. However, strictly speaking the tarsus is alternating, the cuboid articulating with the astragalar head (contra Cifelli, 1983). The alternating tarsus of *Arsinoitherium* has already been explained functionally as an effect of its more plantigrade stance (Court, 1989). Since the carpus shares the derived serial pattern with tethytheres, the question remains as to whether the alternating tarsus of arsinoitheres is primary or secondarily derived from the proboscidean-type (reversal). Comparison with a typical early pentadactyl ungulate-like mammal exhibiting an alternating tarsus, is instructive. The Eocene pantodont *Coryphodon* is a heavily built ungulate-like mammal with a primitive alternating tarsus that exhibits a number of interesting differences in comparison with arsinoitheres.

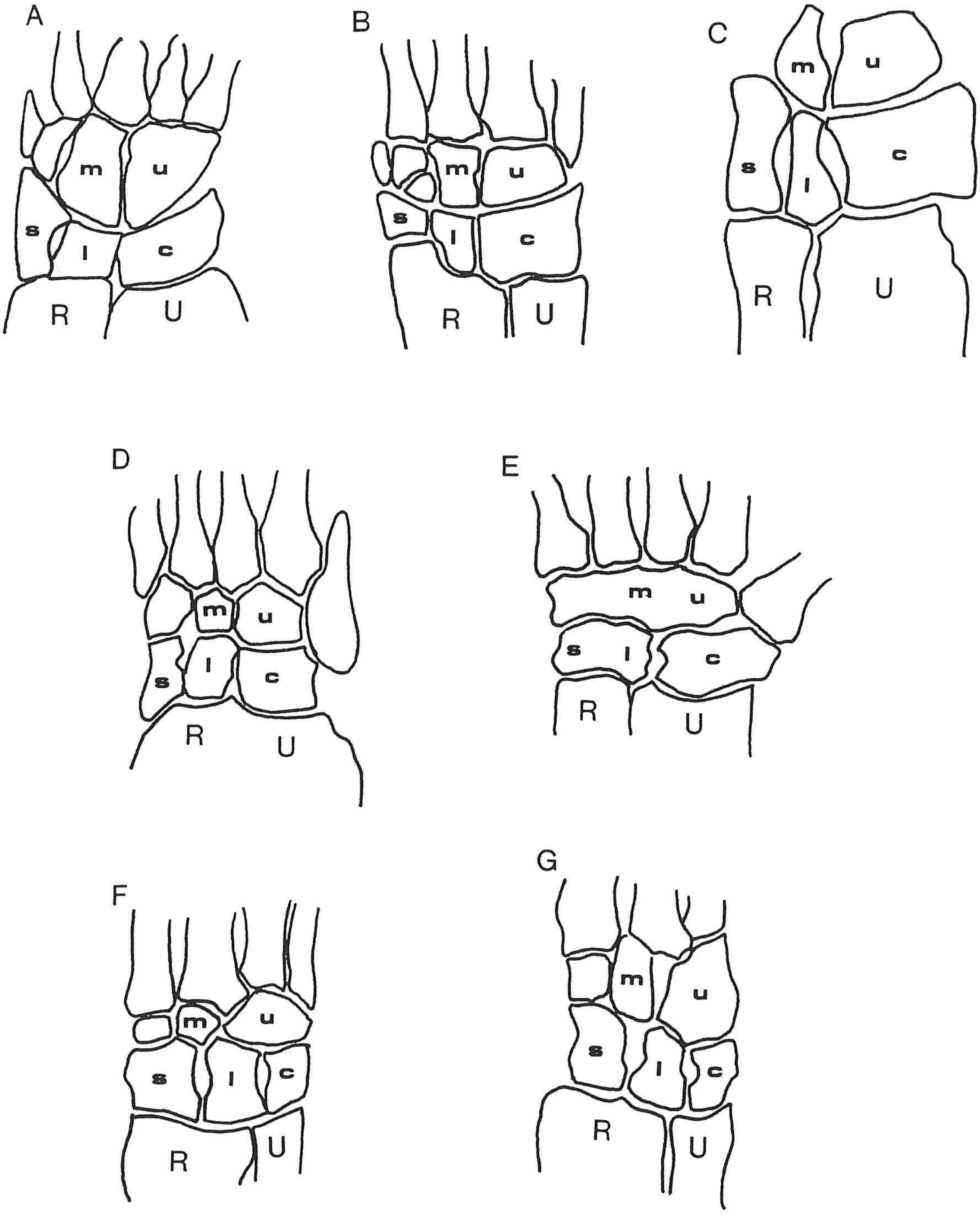

Fig. 2.— Diagramatic representation of the carpus in **A**: *Loxodonta*; **B**: *Procavia*; **C**: *Arsinoitherium*; **D**: *Trichechus*; **E**: *Dugong*; **F**: *Hyrachyus*; **G**: *Rhinoceros*. C = cuneiform; l = lunar; m = magnum; R = radius; s = scaphoid; U = ulna; u = unciform. Modified from Yalden (1971).

Firstly, the distal face of the calcaneum projects laterally around the astragalar head and bears a fairly large facet for the cuboid. Secondly, the cuboid articulatory facet on the astragalar head forms almost a right angle with the navicular facet. Thus the cuboid is orientated almost laterally and is buttressed behind by the posterolaterally extended calcaneum. Furthermore, in barylambdid pantodonts there is no calcaneal articulation with the fibula (Simons, 1960). In complete contrast, the cuboid articulation of the calcaneum in *Arsinoitherium* is very small and situated underneath and behind the astragalar head. Moreover, the cuboid articulation on the astragalar head shows no angular discontinuity with that of the navicular. Therefore the arsinoithere tarsus does not appear to be comparable with the typically primitive condition.

McKenna & Manning (1977) attributed *Phenacolophus fallax* (MATTHEW & GRANGER 1925), from the Palaeocene of Mongolia, to the Embrithopoda. They describe a poorly preserved astragalus and calcaneum. Although they were unable to determine whether the astragalus articulated with the cuboid, they suggest, on the basis of the calcaneum, that it probably did. On the contrary, my own examination of the calcaneum revealed an exceedingly large facet for the cuboid on its distal face; it therefore seems highly unlikely that the astragalus would have borne any part of the cuboid. Modification of the arsinoithere tarsus over the primitive alternating form and the likely serial pattern of tarsals in *Phenacolophus* certainly add to the possibility of a reversal in the foot structure of *Arsinoitherium.*

## PROXIMAL CARPAL JOINT

The relative contributions of the distal radius and ulna to the proximal carpal joint exhibit an interesting distribution within ungulates (fig. 2). Enlargement of the ulna relative to the radius and the consequent enlargement of the cuneiform in the proximal carpal row is a characteristic that has been used to define the Proboscidea above the level of *Moeritherium* (Domning *et al.*, 1986; Mahboubi *et al.*, 1986; Tassy & Shoshani, 1988). This condition is even more marked in *Arsinoitherium.* The apomorphic state of this character seems unequivocal (character 43, table 1). In all known condylarths the radius is dominant in the antebrachium as it is in perissodactyls, artiodactyls and hyraxes. It is possible that enlargement of the ulna is correlated with large body size although presence of the primitive state in *Uintatherium*, the elephantine dinoceratan, the largest of American titanotheres (Osborn, 1927), metamynodon-like rhinoceritiods, and the largest of all land mammals, *Paraceratherium*, indicates that this is not necessarily the case. Moreover, the derived state in *Numidotherium* (Mahboubi *et al.*, 1986), which is a small proboscidean genus of Eocene age, and in modern sirenians, indicates that this feature is not merely a response to the carriage of large body masses on land.

## REDUCTION OF THE CLAVICLE

Presence of a clavicle is widespread within nearly all groups of mammals except ungulates. Within ungulate groups only periptychids, hyopsodontids and primitive artiodactyls possess a clavicle; in all more derived forms it is lost. Early loss of the clavicle in ungulates is treated as a derived character for all ungulates except Artiodactyla (character 48, table 1).

## REDUCTION OF THE SCAPULAR ACROMION PROCESS

Reduction of the scapular acromion process was used as a derived character for ungulates by Prothero *et al.* (1988), a paenungulate synapomorphy (Shoshani, 1986) and a hyracoid, perissodactyl synapomorphy (Fischer, 1986) whilst Tassy & Shoshani (1988, p. 307) suggested it as a potential synapomorphy uniting tethytheres, hyracoids, perissodactyls and embrithopods. Presence of a strong acromion process in *Arsinoitherium* either invalidates the later suggestion or implies that the character has reverted to the primitive state in arsinoitheres.

## THORACIC VERTEBRAL NUMBER

Prothero *et al.* (1988) considered that the number of thoracic vertebrae vary systematically within mammals. Primitively, eutherian mammals possess 12-15 thoracic vertebrae, whereas all higher ungulates except artiodactyls have increased the number (19-21). Prothero *et al.* (1988) considered this to be a derived character for arsinoitheres. There is no complete vertebral series known for *Arsinoitherium*; however, within vertebral collections studied, thoracic vertebrae are numerically dominant which may indicate an increased number. Nevertheless, this character must remain equivocal until a complete series is known.

## OTHER POSTCRANIAL CHARACTERS

Few other postcranial characteristics appear to be phylogenetically useful within ungulates. Although loss of the entepiconylar foramen may well define ungulates at a high level (but retained in *Numidotherium*; Mahboubi *et al.*, 1986), several postcranial feature used by Prothero *et al.* (1988; table 8.1; p. 206) appear either to vary allometrically or to be primitive for ungulates in general. The humerus is either straight or cranially bowed in more derived ungulates, which does seem to contrast with the caudally bowed humerus in most mammals including those of condylarthran grade. However, this feature is probably correlated with size. Such disparate groups as the pantodonts, *Coryphodon*, *Titanoides*, the South American homalodotheres, pyrotheres and astrapotheres and the giant wombat-like marsupial, *Diprotodon*, all have straight or cranialy bowed ulnae. The presence of a large third trochanter is generally present in all archaic ungulate-like groups and shifts more ventrally in larger forms as the superficial gluteal muscle becomes adapted more for power than speed (Gregory, 1912; Smith & Savage, 1957). In contrast to Prothero *et al.*'s assertion of the derived nature of this character, the converse appears more likely: absence of a large third trochanter is probably the derived state within ungulates. However, absence of a third trochanter in arsinoitheres (contra Prothero *et al.*, 1988) is a feature prone to homoplasy for it reflects hypertrophy of the m. gluteus medialis at the expense of the m. gluteus superficialis in graviportally adapted mammals (Gregory, 1912; Gambaryan, 1974). This also appears to be the case in uintatheres and pyrotheres.

## SOFT TISSUE CHARACTERS

In addition to the "hard" anatomical characters discussed in the preceding sections, several features of ungulate "soft" anatomy have been mentioned in the literature as being of phylogenetic importance. Although it is obviously impossible to assess these character states in extinct forms, they must be included in a phylogenetic hypothesis involving extant groups. Indeed, computer algorithms for tree generation will adjust for missing data (MacClade and PAUP). Relevant characters are reviewed below.

### PLACENTA

Novacek & Wyss (1986) recently reasserted Wislocki & Westhuysen's (1940) observation that a zonary placenta associated with a free reduced yolk sac and enlarged sacculated allontoic vesicle, represents a feature uniting hyraxes, proboscideans and sirenians. Certainly the presence of a zonary placenta seems to support this clade but its occurrence also in tubulidentates and carnivores (Luckett, 1977) indicates the possibility of independent acquisition.

### EUSTACHIAN DIVERTICULUM

Horses, tapirs and hyraxes share the presence of a sac-like inflation of the membranous part of the eustachian tube. Although this feature was mentioned by Van der Klaauw (1937), Fischer (1986, 1989) more recently emphasised the phylogenetic implications. So far as is known, presence of a eustachian diverticulum is a unique derivation uniting hyraxes and perissodactyls.

### INTERNAL CAROTID ARTERY

The course of this vessel was previously discussed (petrosal characters) in order to emphasize the primitive nature of the osteologically reflected transpromontorial course of the internal carotid artery (Cifelli, 1982 and Wible, 1986). The perbullar course of the internal carotid seems to be a eutherian specialization which differs from the derived, extrabullar course in hyraxes and perissodactyls (Wible, 1986). It is therefore assumed that lack of promontory grooves in the petrosal of extinct forms represents either the perbullar or extrabullar course of the internal carotid artery. Fischer (1989) notes that in manatees the artery, "... runs within a reduplication of the tympanic sac through the tympanic cavity to the foramen lacerum medium. Since sirenians lack a tympanic bulla,

1. Nasals inflated to form massive, hollow horn cores.
2. Premaxilla posterodorsally extensive; contacting or approaching the frontals.
3. Incisive foramen single.
4. Extreme shortening and enlarged calibre of the infraorbital canal.
5. (a) Orbital flange of maxilla precludes palatine from anterior orbit.
   (b) Orbital exposure of the palatine greately reduced.
   (c) Palatine excluded from the orbital mosaic by maxilla.
6. Sphenopalatine foramen anteroventrally situated, notching the maxilla.
7. Lacrimal vestigial.
8. Pars facialis of lacrimal greately expanded often housing an antorbital fossa.
9. Pars facialis of lacrimal contacts nasal.
10. Zygomatic process of squamosal expanded dorsally and laterally.
11. Jugal reduced anteriorly. Maxilla forms antorbital rim.
12. Jugal extends to posterior border of glenoid articulation (non-homologous in hyracoids; see text).
13. Frontal alisphenoid contact precluded by expansion of the orbitosphenoid.
14. Frontal contacts squamosal.
15. Ethmoid foramen exits from underneath the crista orbitotemporalis.
16. Ethmoid foramen absent.
17. Interparietal absent or fuses with parietals.
18. Ectopterygoid process of the alisphenoid present.
19. Absence of the foramen rotundum.
20. Absence of the alisphenoid canal.
21. Absence of a postglenoid foramen.
22. Presence of a basicranial exit for the superficial temporal vein.
23. Posttympanic process recurved, approaches or contacts postglenoid process.
24. Absence of a Glaserian fissure.
25. Absence of a subarcuate fossa.
26. Large round fenestra ovalis.
27. Fenestra rotundum vertically orientated and facing medially with respect to fenestra ovalis.
28. Enlarged perilymphatic foramen of the periotic; fenestra rotundum fails to develop.
29. Tympanic aperture for the facial nerve situated well in advance of the fenestra ovalis.
30. Loss or reduction of the petrosal tympanic process such that the stylomastodium is unbridged.
31. Epitympanic recess housed entirely within the tegmen tympani.
32. Absence of promontory canals for the internal carotid artery.
33. (a) Extrabullar course of internal carotid artery.
    (b) Perbullar course of internal carotid artery.
34. Loss of stem of ramus superior of stapedial artery.
35. Loss of the proximal stapedial artery.
36. Amastoidy.
37. Paroccipital processes vestigial or absent.
38. Hypoglossal foramen absent.
39. Foramen magnum enclosed by exoccipitals.
40. Ulna enlarged relative to the radius in the proximal carpal joint.
41. Serial arrangement of carpal bones (non-homologous in hyracoids).
42. Astragalus dorsoventrally compressed and bearing a prominent tuberculum mediale.
43. Translatory facet for the fibula on the calcaneum.
44. Tarsus serially arranged (non-homologous in hyracoids- see text).
45. Reduction of the clavicle.
46. Reduction of the scapula acromion process.
47. Pachyostosis.
48. Zonary placenta and free reduced yolk sac.
49. Presence of a eustachian diverticulum.
50. M. styloglossus bifurcate.
51. M. sternoscapularis originates from sternum and inserts on the superior angle of scapula.
52. Paired pectoral mammae
53. Bifid apex of heart.
54. Fossa glandis at tip of penis.

Table 1.— Derived morphological characters for ungulate interordinal groupings.

passage of the internal carotid through the membranous floor of the tympanic chamber could well be considered homologous with the perbullar state in proboscideans.

## STAPEDIAL ARTERY

Wible (1987) presented a rigorous study of the stapedial artery in eutherians. In this, he highlighted several derivations within Ungulata. All modern ungulate orders are characterized by loss of the stem of the superior ramus and associated foramen passing between the tegmen tympani and squamosal (N.B. Wible includes Tubulidentata, which still possess this feature, within the ungulates. I follow Thewissen [1985] in considering tubulidentates to have arisen from outside Ungulata). The proximal stapedial artery is also lost from all modern orders with the exception of Artiodactyla (Coombs & Coombs, 1982).

## M. STERNOSCAPULARIS

Fischer (1986, 1989) asserts that in hyraxes and perissodactyls alone, the m. sternoscapularis originates from the anterior end of the sternum and after passing over the shoulder joint, inserts on the superior angle of the scapula.

## M. STYLOGLOSSUS

A bifurcation of the M. styloglossus before its insertion has been noted as a similarity between proboscideans, sirenians and hyraxes (Windle & Parsons, 1903). However, Fischer (1983) refutes the use of this character as it also occurs in some artiodactyls. Amongst living ungulates this feature does not occur only in perissodactyls. If the condition is reversed in perissodactyls, it is then possible that a bifurcate M. styloglossus represents an ungulate autapomorphy.

## PAIRED PECTORAL MAMMAE

Used as a tethytherian synapomorphy (Blainville, 1844; Tassy & Shoshani, 1988).

| | |
|---|---|
| HYPO. ANCESTOR | 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 0000 |
| ARTIODACTYLA | 00000 00100 00100 00001 00000 00000 10010 00000 00000 00001 0000 |
| HYRACOIDEA | 00001 00000 00100 00000 10000 00000 11211 10000 00001 10111 1001 |
| PERISSODACTYLA | 00000 00010 00000 00000 11011 00011 01211 00000 00001 10010 1001 |
| SIRENIA | 01111 00001 00000 11010 11011 11011 01111 10011 1??1 11101 0111 |
| EMBRITHOPODA | 11112 11000 00001 01110 11111 10111 01??? 11111 11101 00??? ???? |
| PROBOSCIDEA | 01113 10001 11011 01000 11111 10111 01111 11111 11111 10101 0111 |

Fig. 3.— Data matrix. 0 = primitive; 1, 2, 3 = derived states; ? = unknown. Multistate characters are unordered.

### BIFID APEX OF THE HEART

This feature was utilised by Tassy & Shoshani (1988) to support Tethytheria. However, they note that the ventricles in some cetaceans are also divergent at the tips.

### PENIS MORPHOLOGY

Presence of a fossa glandis at the tip of the penis was suggested by Fischer (1986) and taken up by Tassy & Shoshani (1988), as a synapomorphy uniting hyraxes, perissodactyls, sirenians and proboscideans.

## PHYLOGENY DISCUSSION

Gregory (1910) followed Andrews (1906) in placing the Embrithopoda closest to Hyracoidea while Simpson (1945) included arsinoitheres within his superorder Paenungulata (Proboscidea, Sirenia, Hyracoidea, and the extinct Pantodonta, Dinocerata, Pyrotheria and Desmostylia). McKenna (1975) cleaved the original paenungulate concept creating several new mirorders. He retained the paenungulate core of sirenians and proboscideans which he then allied with the extinct group Desmostylia to form the mirorder Tethytheria. Hyracoids were placed close to the Perissodactyla in the mirorder Phenacodonta (a relationship originating with Owen, 1848 and more recently, strongly supported by Fischer, 1986). Embrithopods were consigned by McKenna to the Eparctocyonia, a strange assemblage including artiodactyls and dinoceratans. Unfortunately, McKenna provided no explicit character evidence to support these higher level groupings. McKenna & Manning (1977) erroneously considered the dental morphology of *Phenacolophus* to be morphotypic for the Embrithopoda and placed them in a sister-group relationship to the living ungulate orders (apart from Artiodactyla) plus the extinct dinoceratans. Prothero *et al.* (1988) produced the same weak dental evidence to imply a sister-group relationship between embrithopods and their Pantomesaxonia (tethytheres, perissodactyls and hyracoids).

Table 1 summarizes character information deemed to be derived within the ungulate orders studied. Figure 4 depicts the first ungulate phylogenetic hypothesis including *Arsinoitherium*, that utilizes all non-dental aspects of embrithopodan anatomy. The most parsimonious trees constructed from the character information given in table 1 shows that, in agreement with Prothero *et al.* (1988), artiodactyls appear to be generally primitive with respect to other ungulate orders. Although easily characterized by at least five autapomorphies, the evidence linking Artiodactyla with all other ungulates is extremely meagre. Amongst the characters used by Prothero *et al.* (1988) to unite Ungulata, only the loss or shifting of the superior ramus of the stapedial artery to the petrosal (Wible, 1986), is considered a good non-dental character for Ungulata, although a bifurcation of the m. styloglossus may be a second if a reversal to the primitive state is allowed for Perissodactyla. Mindful of Butler's (1981) warning of the likely prevalence of parallelism and convergence in mammalian dental morphology, it

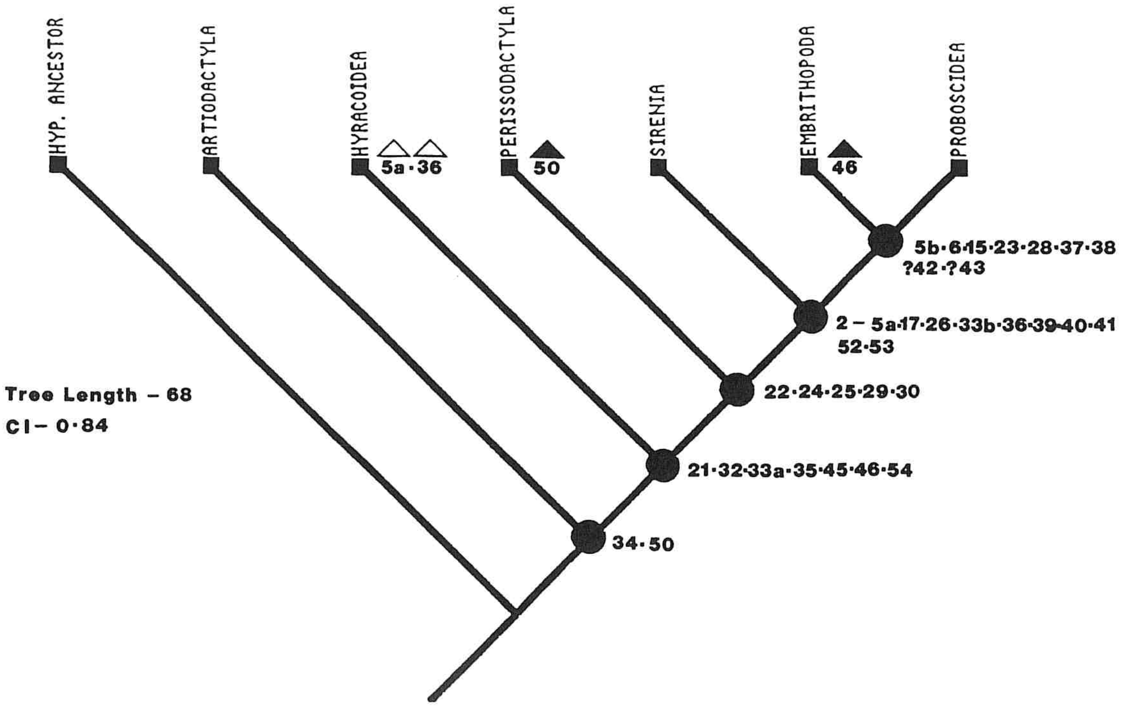

Fig. 4.— Most parsimonious phylogentic hypothesis. Numbers at nodes correspond to character in table 1. Only synapomorphous characters are depicted; character states for terminal taxa can be gleaned from figure 3.

seems unreasonable to utilize height of the molar trigonid, rounded cusps and presence of an $M_3$ hypoconulid (Prothero *et al.*, 1988) as unifying characters for such a huge and diverse supergrouping of eutherians. The remaining orders above Artiodactyla are characterized by at least six autapomorphies; seven if a redevelopment (reversal) of the scapula acromion process in embrithopods is allowed. This grouping is equivalent to Prothero *et al.*'s (1988) Pantomesaxonia but with the addition of Embrithopoda.

The essentiel instability in the cladogram concerns the relative positions of Hyracoidea and Perissodactyla within the above mentioned grouping. It costs only three more evolutionary step for hyraxes and perissodactyls to form a discrete clade from the arrangement in the figured tree. Either characters 49, and 51 are parallelled in both groups or they constitute synapomorphies. Character 33, concerning the course of the internal carotid artery was coded as a multistate, unordered character. Interestingly, in the most parsimonious tree the extra bullar course of the internal carotid artery characterises the common ancestor of all groups except artiodactyls (33a), undergoing a transformation to the perbullar course in the common ancestor of Sirenia, Embrithopoda and Proboscidea (33b). Thus, the transformation of this multistate character has been polarized by congruence. Nevertheless, if the less parsimonious arrangement of linking hyracoids with perissodactyls is preferred, then character 33a becomes a synapomorphy of that group while 33b characterises the group, sirenians, embrithopods and proboscideans. Thus, the two derived states of character 33 behave as separate derivations from the primitive transpromontorial course of the internal carotid artery. Whatever, there is no strong evidence to unite hyracoids with tethytheres or embrithopods. Parsimony dictates that amastoidy (36) occurred independently in hyracoids while pedal anatomy and the state of the jugal (Novacek & Wyss, 1986; Novacek *et al.*, 1988) fail the similarity test of homology (Patterson, 1982) as Fischer (1986) asserts. The sister-group relationship between Sirenia and Proboscidea (McKenna, 1975) has recently been challenged by Domning *et al.* (1986) who, based on dental evidence, suggested that desmostylians were more closely related to proboscideans than were sirenians. Although there is insufficient evidence to include desmostylians in this analysis, Novacek & Wyss (1987) have countered Tassy's (1981) suggestion that Desmostylia lack certain features characteristic of the group Sirenia plus Proboscidea, and it now seems likely that Desmostylia do form a natural group along with sirenians and proboscideans. Nevertheless, detailed evidence from all aspects of desmostylian anatomy is required before their exact position can be determined.

This analysis strongly suggests an expansion of Tethytheria to include the Embrithopoda. Some thirteen characters support the above clade while an additional seven imply a closer association between Proboscidea and Embrithopoda than with any other of the groups under consideration. Character 5 concerning orbital expansion of the maxilla and reduction of the palatine was coded as a multistate unordered character. The most parsimonious solution dictated that the three states be polarised in a transformation series leading from exclusion of the palatine from the anterior orbit (5a) in the common ancestor of thethytheres, to the extreme orbital reduction of the palatine in the common ancestor of embrithopods and proboscideans. In proboscideans the final step of complete elimination of the palatine from the orbit is autapomorphically attained (5c).

## CONCLUSIONS

The foregoing cladistinc analysis of anatomical characteristics drawn from all non-dental aspects of ungulate anatomy implies that the Embrithopoda occupy a position phylogenetically closest to Proboscidea. The long held association of hyraxes with arsinoitheres (Andrews, 1906; Gregory, 1910) or indeed, with proboscideans and sirenians together (Novacek & Wyss, 1986; Novacek *et al.*, 1988; Shoshani *et al.*, 1979; Simpson, 1945), is unsupported by available morphological evidence. Fischer's (1986) proffered sister-group relationship between perissodactyls and hyracoids is found to be less parimonious than an alliance of Perissodactyla with tethytheres to the exclusion of hyraxes.

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# PLATES

PLATE 1

A: lateral view of young skull CGM 7805.

B: explanatory diagram of (A).

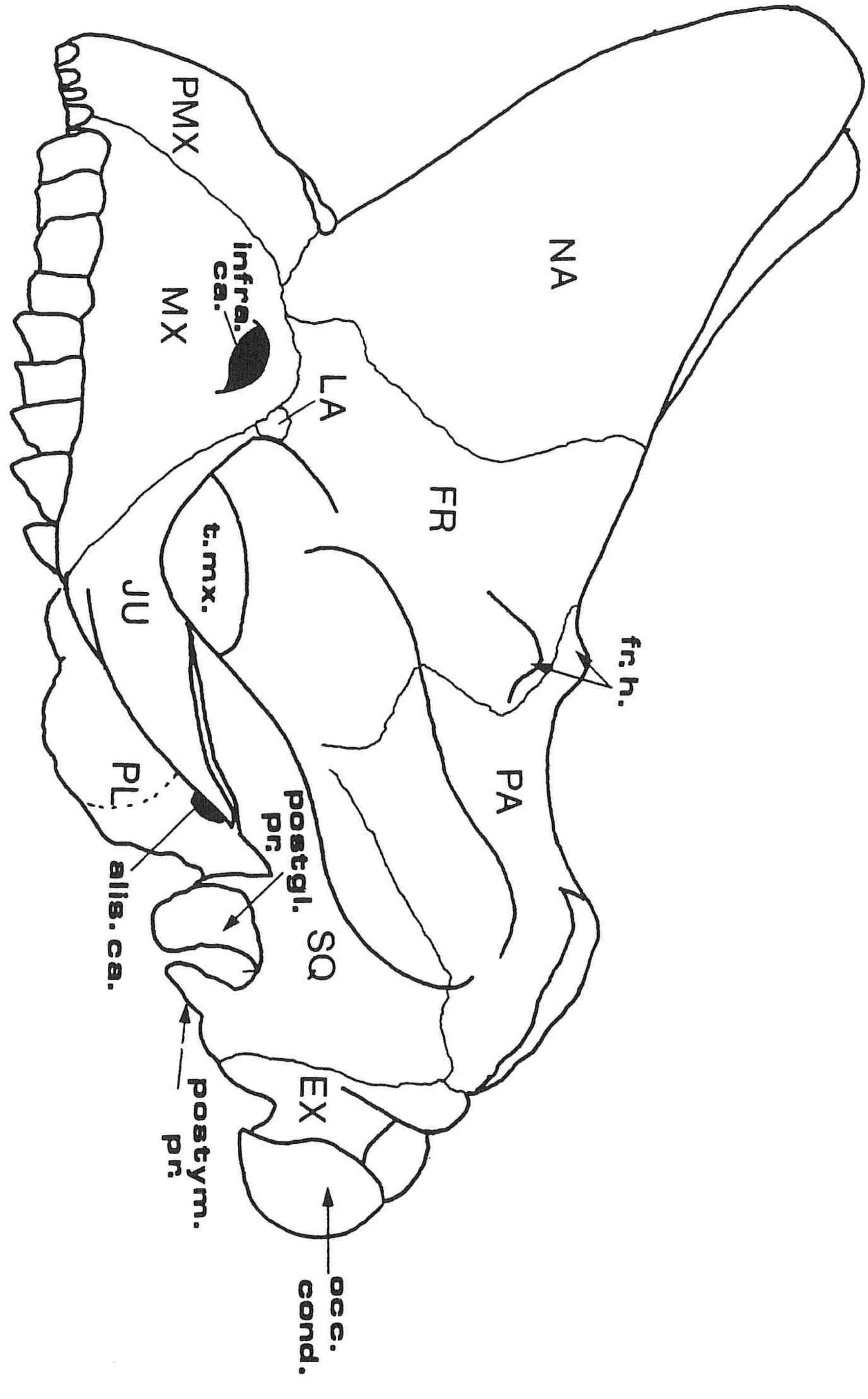


PLATE 1

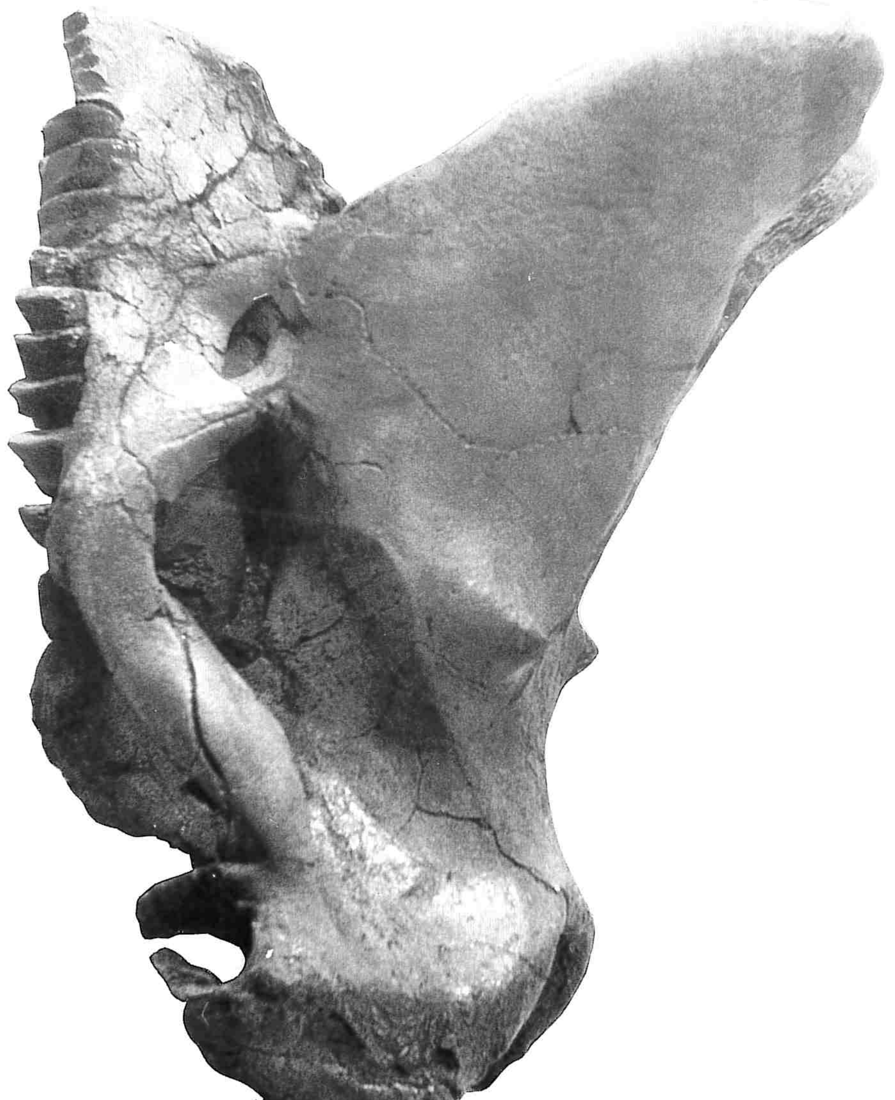


PLATE 2

Palatal view of *A. zitteli* BMNH 8463. White circles = reconstructed teeth.

PLATE 2

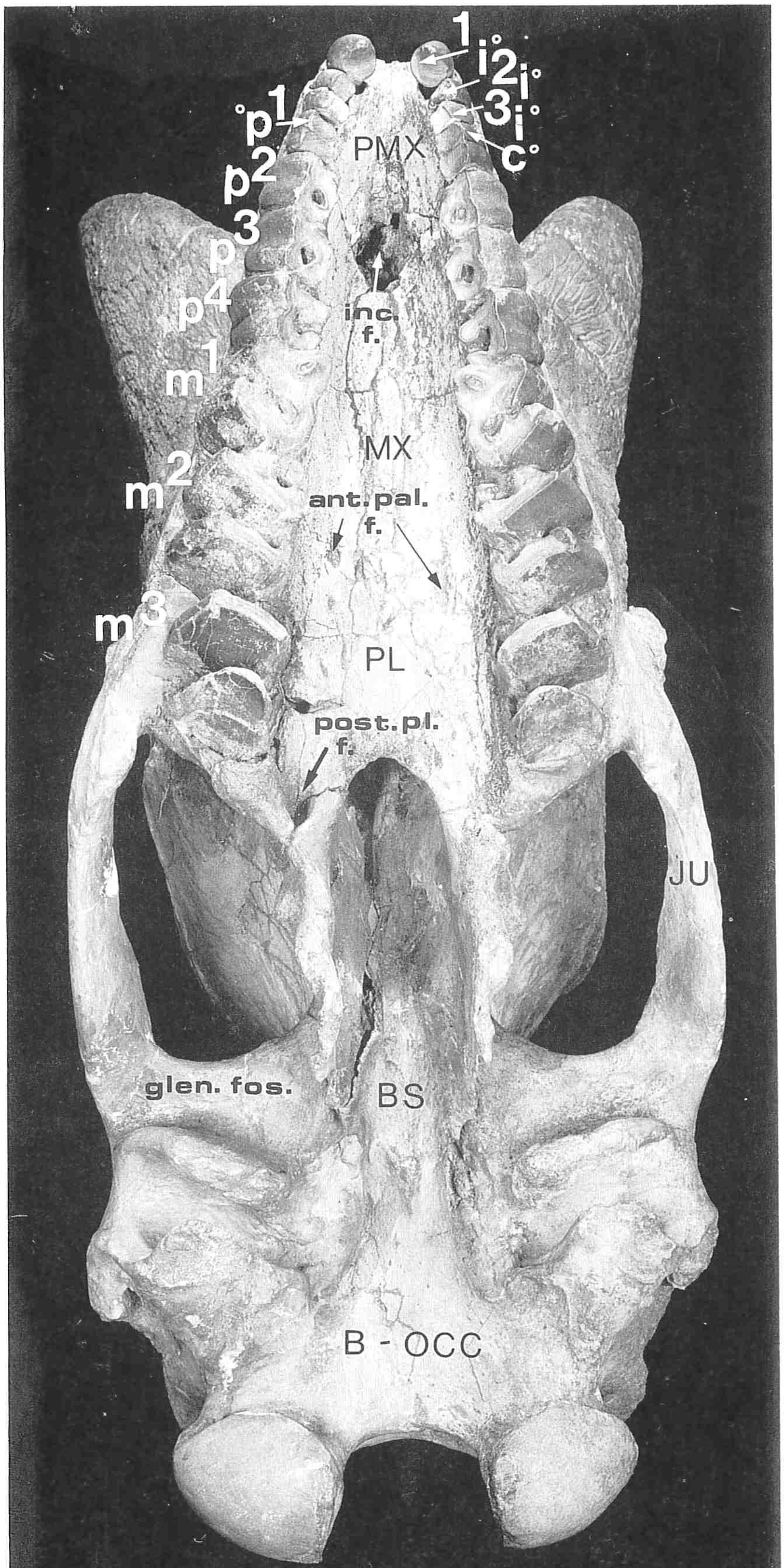

1
i°
2
i°
3
i°
c°
°p1
p2
p3
p4
m1
m2
m3
PMX
inc. f.
MX
ant. pal. f.
PL
post. pl. f.
JU
glen. fos.
BS
B - OCC
1(cm)2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38

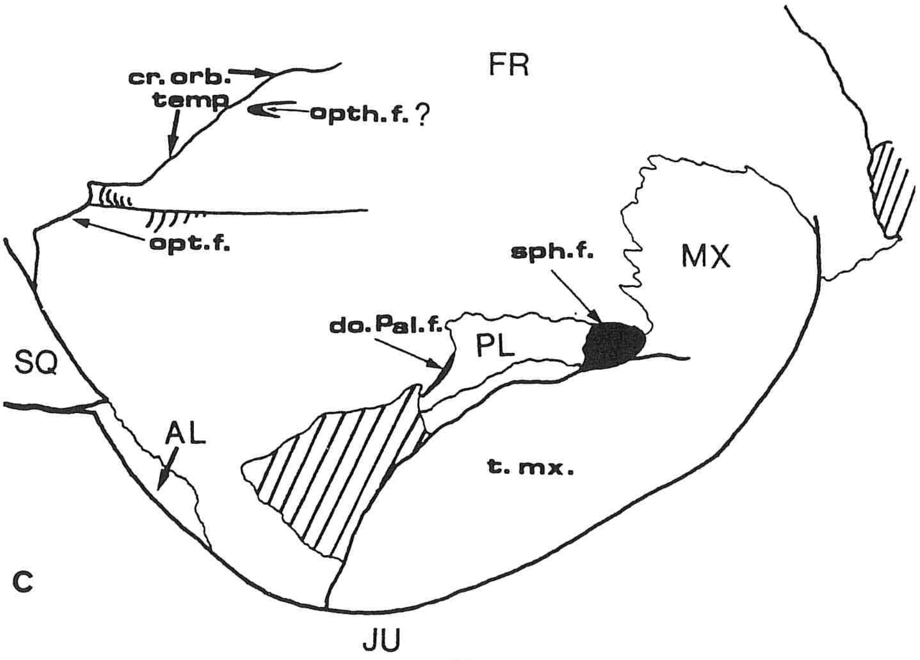
PLATE 3

a: lateral view of the right orbital mosaic, BMNH 8463.

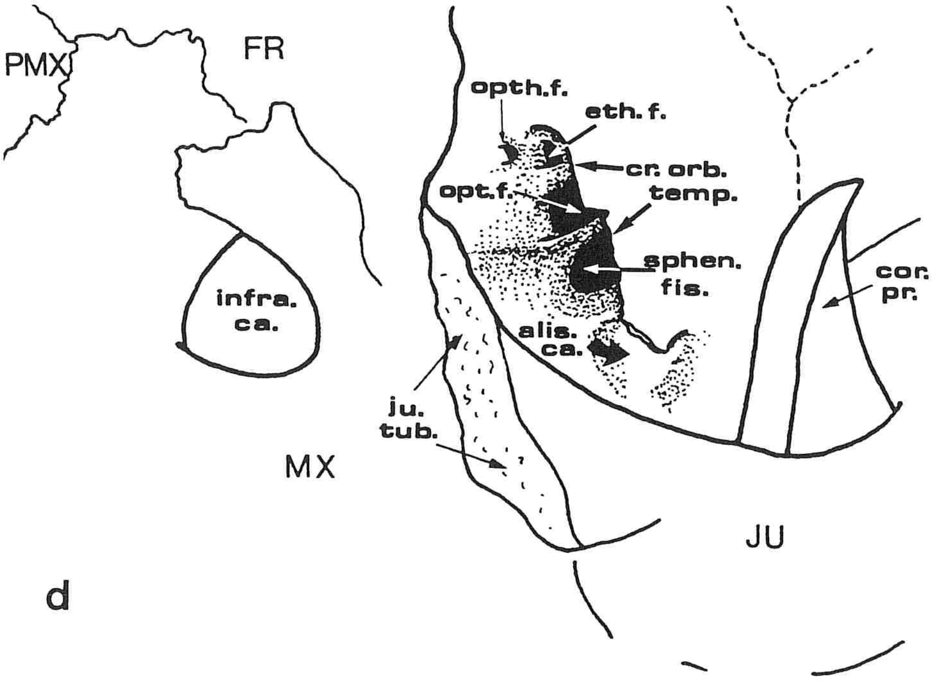
b: anterolateral view of left orbital region depicting skull foramina BMNH 8463.

c: explanitory diagram of (a).

d: explanitory diagram of (b).



c



d

PLATE 3

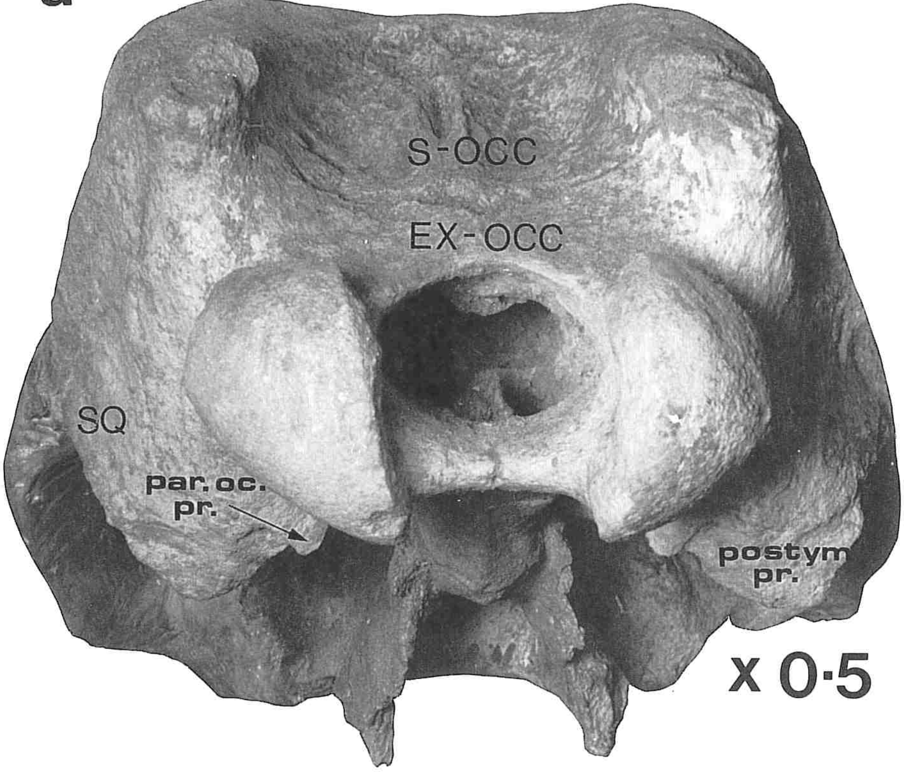
PLATE 4

a: occipital view of partial skull BMNH 8800.

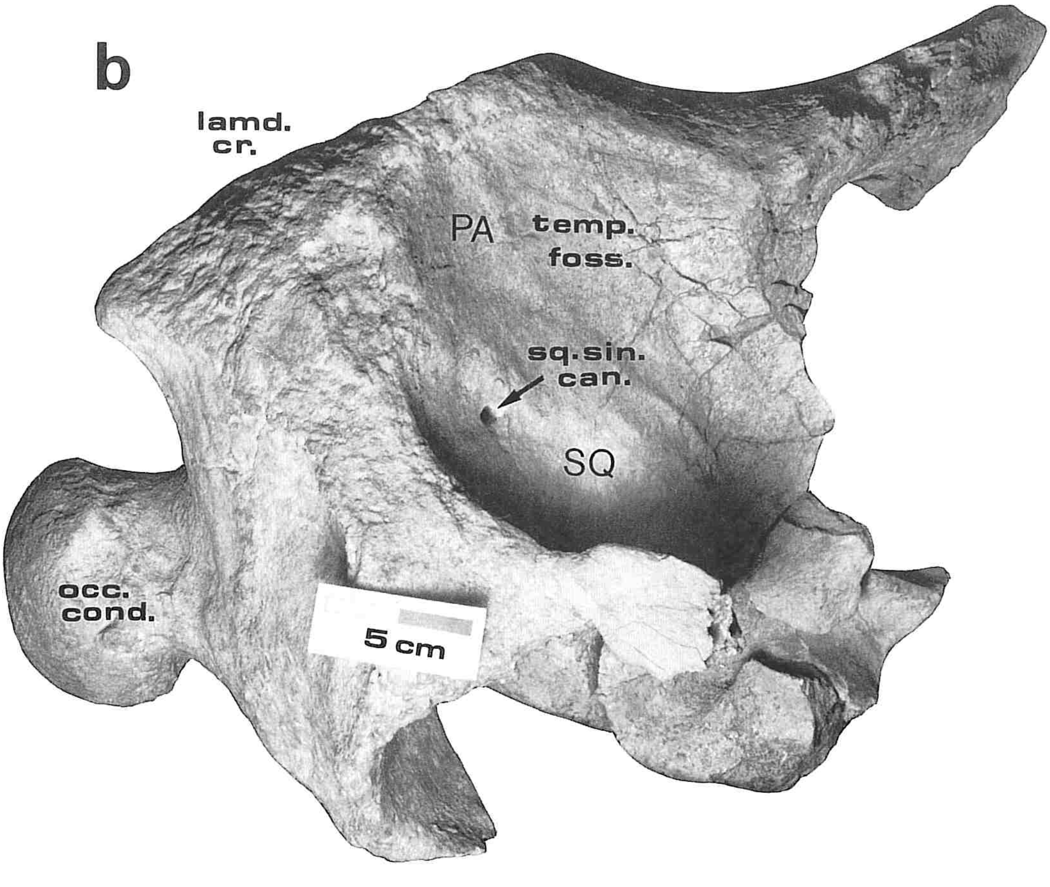
b: lateral view of right temporal portion of cranium, BMNH 8462.

PLATE 4

**a**


S-OCC
EX-OCC
SQ
par.oc.
pr.
postym
pr.
x 0·5

**b**

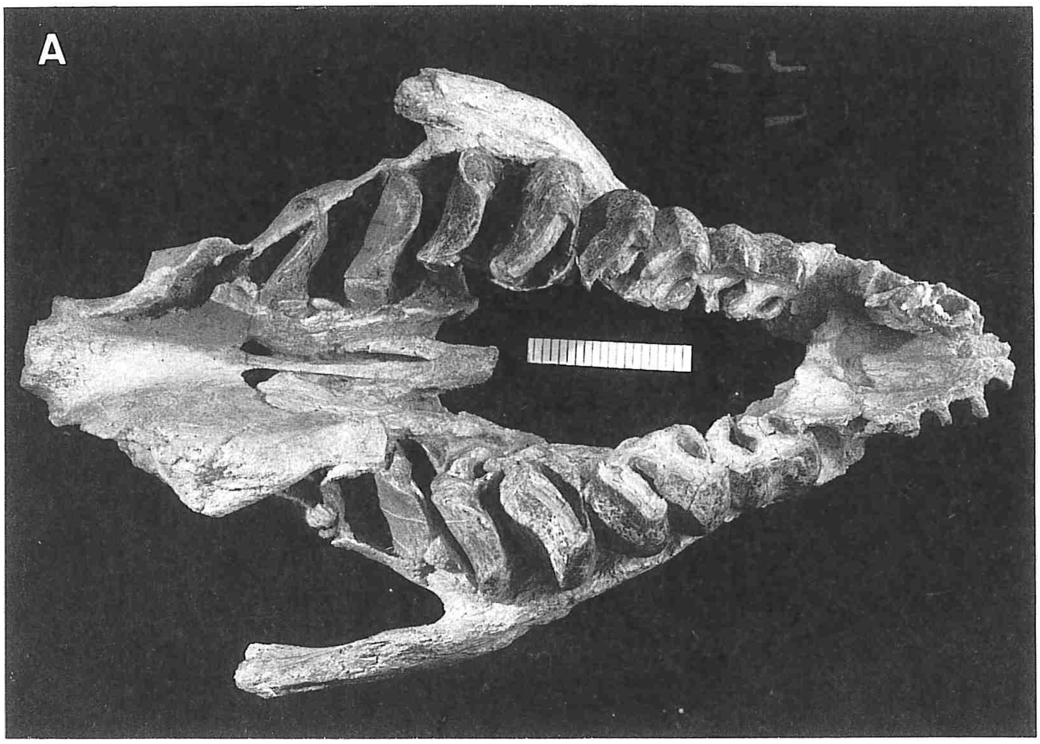

lamd.
cr.
PA
temp.
foss.
sq.sin.
can.
SQ
occ.
cond.
5 cm

## PLATE 5

A: palatal view of juvenile skull showing deciduous dentition, AMNH 13505.

B: explanitory diagram of (A).

PLATE 5



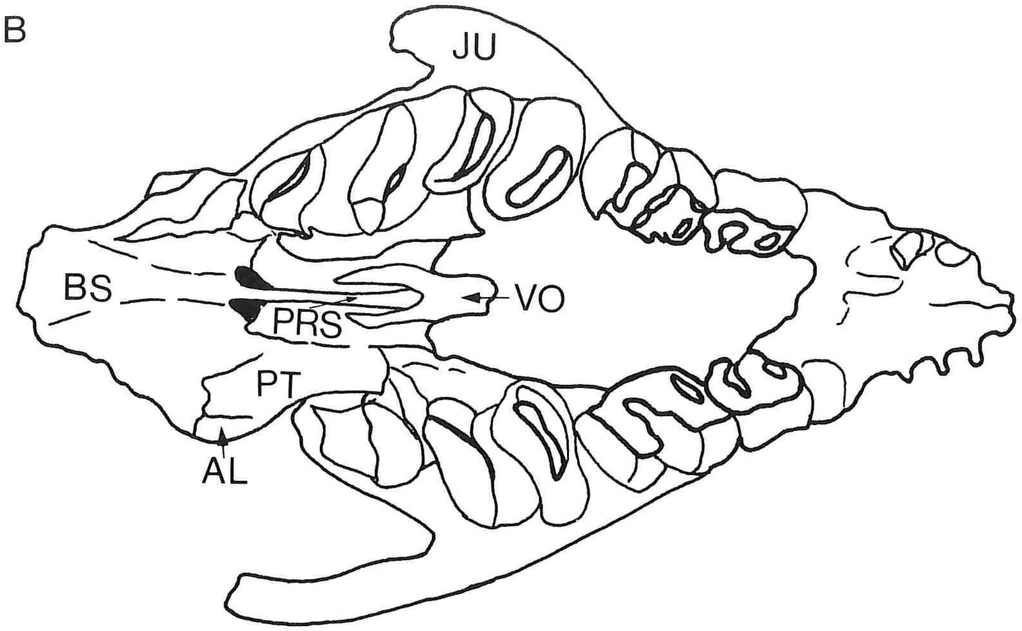


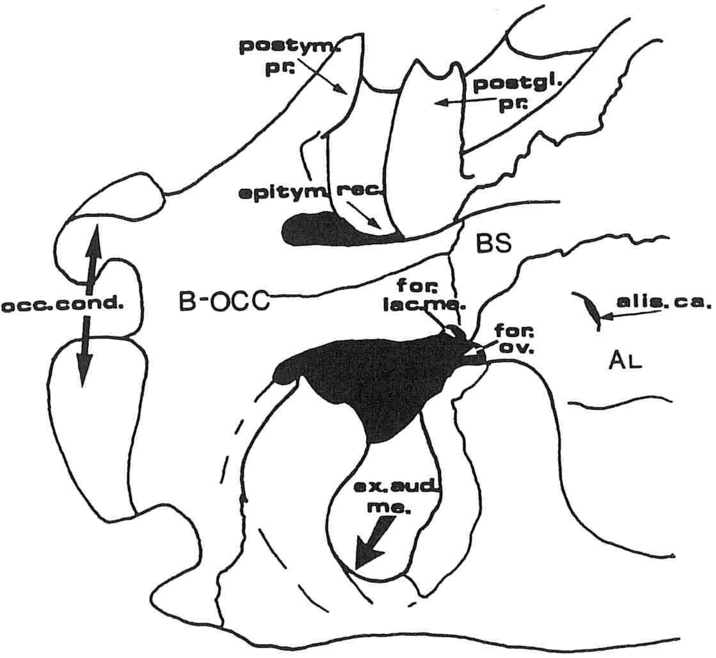
PLATE 6

a: ventrolateral view of left basicranium, BMNH 8000.

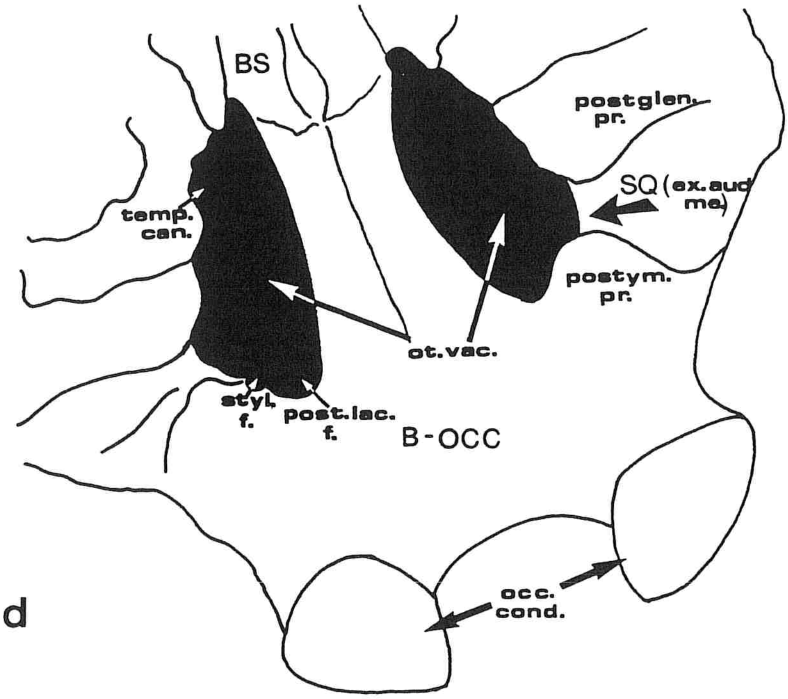
b: ventral view of basicranium, BMNH 8000.

c: explanitory diagram of (c).

d: explanitory diagram of (b).

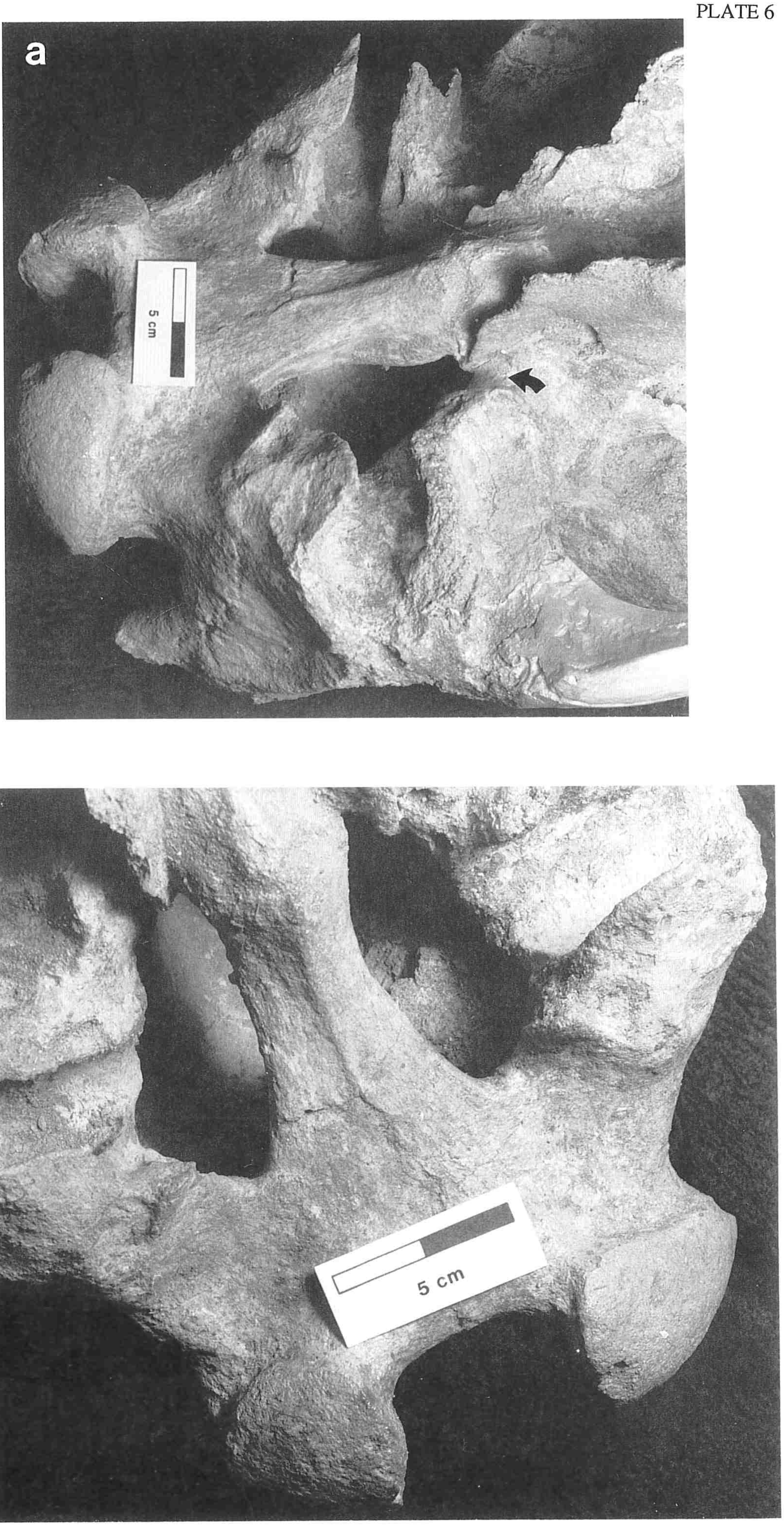


c



d

PLATE 6



# PLATE 7

Right periotic bone, BMNH 8000.

A: medial view with explaitory diagram.
C: ventral view with explanitory diagram.
E: dorsal view with explanitory diagram.

Right periotic bone, YPM 29982.

B: medial view with explanitory diagram.
D: ventral view with explanitory diagram.
F: dorsal view with explanitory diagram.

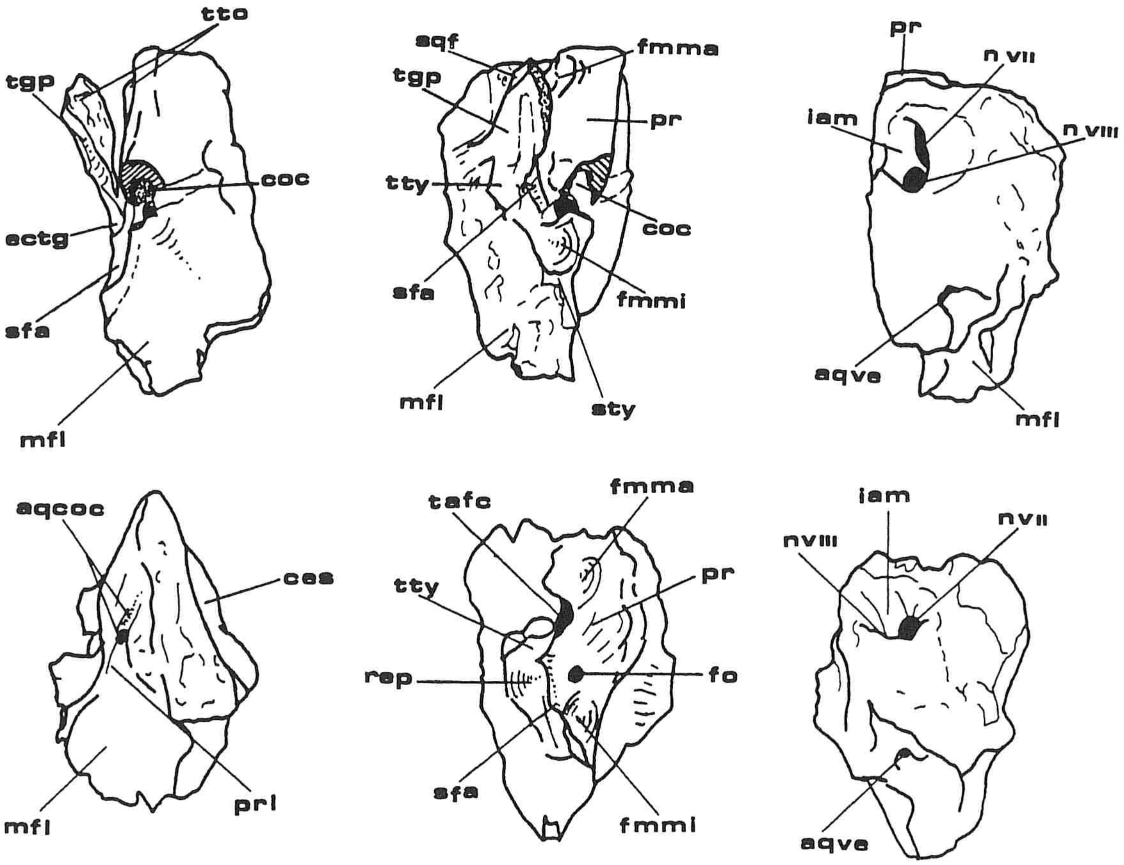


PLATE 7