Hoplitomerycidae fam. nov. (Ruminantia, Mammalia) from Neogene fissure fillings in Gargano (Italy)

Part 1: The cranial osteology of *Hoplitomeryx* gen. nov. and a discussion on the classification of pecoran families

J. Leinders

Leinders, J. Hoplitomerycidae fam. nov. (Ruminantia, Mammalia) from Neogene fissure fillings in Gargano (Italy). Part 1: The cranial osteology of *Hoplitomeryx* gen. nov. and a discussion on the classification of pecoran families. — Scripta Geol., 70: 1-68, 4 figs., 10 pls, Leiden, April 1984.

It is concluded that the endemic Ruminantia from the Late Miocene island-fauna of Monte Gargano (Italy) originated from antlerless Cervidae. This in spite of the fact that these Ruminantia from Gargano evidently had horncore-like cranial appendages. The presence of horncores, in combination with the presence of characters diagnostic for the Cervidae, justifies the classification of the Gargano ruminants in a separate family: Hoplitomerycidae fam. nov. which family is included in the Cervoidea.
The classification of the pecoran families is discussed. The Giraffidae are more closely related to the Bovidae than to the Cervidae. It is proposed that the Giraffidae be transferred from the Cervoidea to the Bovoidea. *Palaeomeryx* is probably not closely related to the Giraffidae.

Joseph Leinders, Institute for Earth Sciences, P.O. Box 80.021. 3508 TA Utrecht, The Netherlands.

Introduction

The Neogene fissure fillings in the Mesozoic limestones of the Gargano Peninsula (Prov. Foggia, Italy) produce a remarkable vertebrate fauna. Freudenthal (1971) concluded from the unbalanced character of the fauna, the gigantism in rodents and insectivores and the presence of endemic species and genera, that the Gargano Peninsula must have been isolated from the mainland during the deposition of the fissure fillings.

This conclusion corroborates the data obtained from drilling in the Foggia graben, which separates Monte Gargano from the Italian mainland. According to Jacobacci (1962) these data show that the oldest, transgressive sediments on top of the Mesozoic limestones are of Langhian age, which demonstrates that the graben came into existence at the beginning of the Middle Miocene.

The fissured Mesozoic limestones of Monte Gargano are overlain by a calcarenite, which is considered te be of Late Miocene or Early Pliocene age (Freudenthal, 1971; D'Alessandro et al., 1979). Freudenthal (1976) demonstrated that the deposition of the red clays in the various fissures was not synchronous and he established a relative age sequence based on evolutionary trends in the endemic genus *Microtia* (Muridae, Rodentia). The studies of Ballmann (1973, 1976) on the fossil birds of Gargano support the conclusions of Freudenthal. According to Ballmann the avifauna is somewhat younger than the avifauna from La Grive in France (Late Aragonian, Mein zone 7/8). Freudenthal (1971) estimated the age of the fissure deposits to range from Late Vallesian to Early Turolian.

The following vertebrate taxa have been recognised in the fauna from the Gargano Promontory: Amphibia, Reptilia, Aves (Ballmann, 1973, 1976), Insectivora (Freudenthal, 1971, 1972; Butler, 1981), Rodentia (Freudenthal, 1971, 1976) Lagomorpha (Freudenthal, 1971), Carnivora, and Artiodactyla (Freudenthal, 1971). The Carnivora are only represented by relatively rare remains of an otter (Freudenthal, pers. comm.). The ruminants, which are the subject of the present paper, were the only ungulates inhabiting the former island. Leinders and Sondaar (1974) reported that the cannon bone of these ruminants is always fused with the navico-cuboid bone of the ankle joint, which they consider characteristic for endemic island ruminants (Fig. 1).

In this paper the cranial osteology of the ruminants from the Gargano Peninsula will be described and their classification within the suborder Ruminantia Scopoli, 1777 will be discussed. The differences in the cranial osteology can be divided into two groups: those observed between the various horncores and those between the skull fragments with the ear-region preserved. The different types observed in the former group will be referred to by the code: h.c. (= horncore) type I,II, etc., those of the latter group by the code: e.r. (= ear-region) type I, II, etc.. Only in one specimen (RGM 260 965) could both groups of characters be studied.

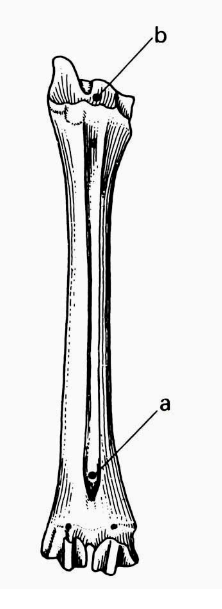

Fig. 1. Metatarsus III/IV sin. (RGM 261 101) from San Nazario 4 showing the distal closure of the gully (a) on the anterior side and the fused navico-cuboid (b).

Although it is very likely that the various skull fragments and horncores from Monte Gargano represent several different species, it is considered inopportune to introduce different formal species names on the basis of the cranial osteology. Such a classification is inadvisable due to the paucity of cranial fragments, and the difficulty in defining the differences in size of the various species from these skull fragments (size differences which are apparent from the dental elements). Furthermore, the differences in the morphology of the various horncores are difficult to evaluate (sexual dimorphism; juvenile or adult individuals); only one new species is formalized: *Hoplitomeryx matthei* gen. et spec. nov.; type-species of a new genus, which is the type-genus of a new family.

The dentition and the specific differences within the genus *Hoplitomeryx* gen. nov. will be subject of a separate publication.

Acknowledgements

My sincere thanks are extended to my supervisor P.Y. Sondaar for his continuous support and stimulating guidance. I am most grateful to M. Freudenthal (Leiden) for his permission to study the Gargano ruminants and for his guidance during fieldwork in Monte Gargano. I am greatly indebted to C.W. Drooger for his support and to C.W. Drooger, E. Heintz (Paris), A.J. van der Meulen, and P.Y. Sondaar for critical reading of the manuscript and constructive comments. I much appreciate stimulating discussions with P.Y. Sondaar, A.J. van der Meulen, J. de Vos (Leiden), E. Heintz, M. Freudenthal, A. van der Weerd (Calgary), E.P.J. Heizmann (Stuttgart), H. Thomas (Paris), L. Ginsburg (Paris), L.E.M. de Boer (Rotterdam), A.W. Gentry (London), C. Janis (Cambridge), A.A. Bosma, H.P. Brinkerink, H. de Bruijn, T. van Kolfschoten, and C.G. Rümke.

Collections were made available for study by: M. Freudenthal (Leiden), P.H.J. van Bree (Amsterdam), C. Smeenk (Leiden), E. Heintz (Paris), A.W. Gentry (London), and E.P.J. Heizmann (Stuttgart).

H.P. Brinkerink assisted in the field and prepared part of the fossils, for which I am grateful. I am much indebted to J. Luteijn who carefully made the plates and drew the reconstructions. S.A. McNab improved the English text.

I gratefully acknowledge the financial support of the Netherlands Organization for the Advancement of Pure Research (Z.W.O.).

Taxonomy

Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Infraorder Pecora Linnaeus, 1758
Superfamily Cervoidea Simpson, 1931

Family Hoplitomerycidae fam. nov.

Type genus — *Hoplitomeryx* gen. nov.

Diagnosis — Hoplitomerycidae are Ruminantia with unforked horncore-like cranial appendages. The skull roof is not pneumatized. The lacrimal duct opens into two orifices on the rim of the orbita. The gully on the anterior side of metatarsus III/IV closes above the distal end of the shaft (Fig. 1). Hoplitomerycidae have large, sabre-like upper canines and short premolar series from which P1 and P2 inf. are absent and P4 inf. is non-molarized. A large bicuspid third lobe is present on M3 inf.

Differential diagnosis — Hoplitomerycidae differ from:
A) Cervidae, Moschidae, Dremotheriidae, and Tragulidae by their non-deciduous, horncore-like cranial appendages.
B) Bovidae in having two lacrimal orifices on the rim of the orbita, by the presence of upper canines, and in the morphology of the gully on the anterior side of metatarsus III/IV; this gully closes above the distal end of the shaft.
C) Giraffidae by their non-pneumatized skull roof, in having two lacrimal orifices on the rim of the orbita, in the morphology of the gully on the anterior side of the metatarsus III/IV, in having a non-bilobed lower canine, in the presence of sabre-like upper canines, and in the larger angle between the basicranial and palatal planes.

Remarks on differences between the Hoplitomerycidae and the other pecoran families

A) Palaeomerycidae Lydekker, 1883. This family, which is generally included in the Giraffoidea, is poorly defined in the literature and the number of genera included has changed frequently. According to Thenius (1979) the family includes the following genera: *Palaeomeryx* von Meyer, 1834, *Triceromeryx* Villalta, Crusafont & Lavocat, 1946, *Propalaeomeryx* Lydekker, 1883, and *Climacoceras* MacInnes, 1936.
Palaeomeryx: Ginsburg and Heintz (1966) listed the following characteristics of this genus: absence of an ethmoidal opening, advanced molarisation of P4 inf., no diathrodial facet on the metatarsal III/IV, metatarsal III/IV and metacarpal III/IV equal in length, and presence of giraffoid ossicones on the skull. Hoplitomerycidae differ from *Palaeomeryx* by the absence of P2 inf., the less complex P4 inf., the absence of a 'pli- *Palaeomeryx*' in the lower molars, by the difference in length between metatarsals and metacarpals, and by the presence of horncore-like frontal appendages.
Triceromeryx: this poorly known genus from the Iberian Peninsula is reported to have a supra-occipital ossicone in addition to an ossicone above each orbita; this feature distinguishes the genus from all other Eurasian ruminants. According to Hamilton (1973) the lower dentition is very similar to that of *Palaeomeryx*.
Propalaeomeryx: is based on a single molar from the Siwaliks and is insufficiently known. The upper molar (M3 ?) figured by Lydekker (1883, fig. 2) differs from that of the Hoplitomerycidae by the less oblique position of paracone and metacone, the less pronounced mesostyle, and by the presence of an anterior cingulum.
Climacoceras: this African genus is characterized by the peculiar, non-deciduous, supra-orbital appendages. Two types of ossicones have been described. *C. africanus* has a straight beam with irregular-positioned short tines, projecting at right angles from the beam, whereas the second ossicone type described by Hamilton (1978) is very antler-like and resembles the antler of *Cervus elaphus*, but shows no sign of a basal burr. *Climacoceras* differs from Hoplitomerycidae by the morphology of the ossicones, the presence of P2 inf., and by the bilobed, giraffoid type, lower canine.
B) Dromomerycidae: according to Thenius (1969) this North American family results from a development parallel to the Old World Palaeomerycidae. The trend in Dromomerycidae towards supra-occipital ossicones (e.g. *Cranioceras*), the parallel basicranial and palatal planes, and the complex morphology of P4 inf. differentiate them from Hoplitomerycidae.

C) Protoceratidae: although the advanced genus *Synthetoceras* of this North American family also shows nasal appendages, large upper canines and a reduced premolar dentition, the family differs largely from the Hoplitomerycidae. The forked median appendages have a far more anterior position on the nasalia and the orbital appendages have a blunt distal end, which causes the appendages to resemble giraffoid ossicones rather than horncores. A caniniform P1 inf. is present and P4 inf. is less complex. The foot structure of the protoceratids has remained remarkably primitive with unfused metacarpals III and IV, strong lateral metacarpals and separate cuboid and navicular bones (Patton & Taylor, 1973).

D) Antilocapridae: this North American family has many features in common with the Cervidae. The presence of horncores in this cervoid family (Leinders, 1979; Leinders & Heintz, 1980) is considered to be a parallel development with the Hoplitomerycidae. Both families combine diagnostic characters of the Cervidae with the presence of horncores. The Antilocapridae are divided into two subfamilies: Antilocaprinae and Merycodontinae. Antilocaprinae differ from Hoplitomerycidae by the absence of upper canines, the presence of P2 inf., and by their high- crowned cheek teeth. The Merycodontinae, which is the ancestral group of the Antilocaprinae, differ from Hoplitomerycidae by the morphology of their cranial appendages. These forked, bony outgrowths from the skull resemble antlers but were probably non-deciduous, although they show a burr-like structure near the base.

Hoplitomeryx gen. nov.

Derivatio nominis — Combination of the Greek words hoplites (heavy-armed warrior) and merykazo (to ruminate).

Type species — *H. matthei* spec. nov.

Diagnosis — *Hoplitomeryx* has two horncores above each orbita and one horncore in the sagittal plane on the posterior part of the nasalia. The rest of the diagnosis corresponds to that of the family.

Differential diagnosis — At present *Hoplitomeryx* is the only genus in the new family.

Hoplitomeryx matthei spec. nov.

Derivatio nominis — The species is named after Dr Matthijs Freudenthal in appreciation of his work in Monte Gargano and the fact that he gave permission to study the ruminants.

Holotype — Cranium RGM 260 965 (Pls 1, 2)

Type locality — Fissure filling with the code Pirro 11a in the limestone quarry Pirro between Poggio Imperiale and Apricena (Prov. Foggia, Italy).

Age — Late Miocene: on the relative time scale of the various fissure deposits in the Mesozoic limestones of Gargano based on rodents (Freudenthal, 1976), as well as on the scale based on the avifaunas (Ballmann, 1976), Pirro 11a fits in with the youngest localities (Fig. 3).

Diagnosis — The skull size of *H. matthei* is about the same as that of the roe-deer (*Capreolus capreolus*). The rest of the diagnosis fits in with that of the genus.

Differential diagnosis — The different taxa within the genus will be defined by dental characteristics, which will be the subject of a separate publication.

Storage of the material — The material discussed is stored in the Rijksmuseum van Geologie en Mineralogie (RGM) in Leiden.

Description of the holotype cranium (RGM 260 965)

GENERAL REMARKS

The anterior part of the skull is poorly preserved. Premaxillae and most of the maxillae and nasalia are missing. Most of the palatum is present but in a poor, fragmented condition. The dentition is represented only by two worn premolars (P3 and P4 sup. sin.). Only the dorsal parts of the orbitas are preserved and the zygomatic arches are missing. The cranial appendages above the orbitas are incomplete but the proximal implantations of the two horncores above each orbita are present. The braincase, basicranium and ear region are well preserved.

The sutures between the various bones of the cranium are not traceable, which indicates, as do the worn premolars, that the skull is that of an elderly individual.

FACIAL REGION

The facial part of the skull is in a poor condition. The palatum is present from P3 sup. backwards, but the sutures between the palatine process of the maxillae and the palatine bones, as well as the palatine foramina are not visible. In the lateral direction the palatum is concave to the same degree as in *Hydropotes*. Both the palatine process and the right maxilla are missing. P3 and P4 on the left maxilla are present (Pl. 1, B, 1), but are very much abraded. The two premolars are small relative to the size of the skull, even if the advanced stage of wear is taken into consideration.

	L	W
P3 sup.	6.4 mm	7.5 mm
P4 sup.	5.8 mm	9.1 mm

The nasalia are missing so that the septum nasi (Pl. 1, 2) can be traced from the level of P3 sup. up to that of the anterior margin of the orbitas.

On the left side the dorsal part of the facial region is present, although in a poor condition. Since it is not possible to trace the sutures between the maxillae, and the nasal and lacrimal bones the extension and position of the lacrimal bone cannot be established. It is not possible to decide whether a lacrimal fossa and vacuity were present or not. On the right side of the skull the dorsal part of the rim of the orbita is still complete with part of the lacrimal bone, as indicated by the presence of two lacrimal orifices (Pl. 1, B, 3). In cervids the lacrimal fossa is situated just in front of the lacrimal orifices. Skull RGM 260 965 shows a small part of the lacrimal bone in front of the orifices, which has no inclination in the medial direction. This may indicate that no lacrimal fossa was present or that it was situated more dorsally than usual in cervids.

ORBITAL REGION

Only the upper parts of the orbital margins are preserved in the holotype. The rim of the right side orbita shows two lacrimal orifices (Pl. 1, B, C, 3). The upper orifice is situated slightly more on the internal side of the rim than the lower one. Between both orifices there is a prominent tubercle. Both orifices have a very high (dorsal) position on the margin of the orbita: just where the rim curves from horizontal at the top of the orbita to vertical at the front of the orbita. In all cervids observed the lacrimal orifices are halfway along the vertical part of the anterior rim (Leinders & Heintz, 1980). The dorsal margin of the orbita, behind the lacrimal orifices, is curved in medial direction (Pl. 1, C, 4).

The posterior part of the upper margin of each orbita supports the two horncores. On the right side of the skull the proximal part of each horncore is preserved. Both horncores have their insertion in common; from this insertion the smaller, most lateral horncore is directed outwards in a plane at right angles to the sagittal plane, pointing upwards at an angle of about 40° with the palatal plane. The second horncore, which has a larger diameter, points backwards and slightly outwards (Pl. 1, A, B, C, 5 and 6; Pl. 2, A, 5 and 6). On the left side orbita the lateral horncore is broken off at its insertion (Pl. 1, A, 7), whereas the medial one is more complete than the one on the right side. The surface of the upper half of this medial horncore is marked by numerous longitudinal grooves and small foramina, which are absent on the lowest 2 cm of the horncore. The transition between the grooved surface and the smooth basal part of the horncore is not marked by a constriction. The conical horncore is laterally compressed, which results in an oval cross section. On the rightside orbita the basal part of the lateral horncore is present. The diameter of its circular cross section is about half of the antero-posterior diameter of the medial horncore. The distal part of the fragment shows longitudinal grooves, whereas its base has a smooth surface. At the proximal end of the grooved surface a slight constriction is visible. The lateral horncore is inserted on the root of the supra-orbital process of the frontal bone. On the ventral surface of this part of the supra-orbital process a dome-like fossa is present underneath the insertion of the horncores (Pl. 2, A, B, 8).

The supra-orbital region is damaged, but one supra-orbital foramen is present. It is situated just antero-medially of the insertion of the medial horncore. The foramen opens ventrally in the depression underneath the horncores. The supra-orbital groove in front of the foramen is a broad, ovally shaped, depression with a rough surface (Pl. 1, C, 9).

The internal parts of the orbitas show no sutures between the various bones. The pterygoid crest (Pl. 1, B, 10) above the large foramen orbito-rotundum (Pl. 1, B, 33) is weakly developed and comparable with that of *Muntiacus muntjak*. The medium-sized optic foramen (Pl. 1, B, 34) is slightly elongated in the antero-posterior direction. The optic foramina of the left and right side orbitas are separated and not combined into one as in the Tragulidae and in *Muntiacus muntjak*. The perpendicular part of the palatine bone is slightly concave. On the right side of the skull the upper and medial wall of the infra-orbital foramen is preserved; from this it can inferred that this foramen had a large diameter (Pl. 1, B, 11; Pl. 2, B, 11).

ROOF OF THE CRANIUM

The sutures between the various bones of the skull roof are not visible, except for part of the contact between the parietal and squamosal. The roof is domed in antero-posterior direction as well as from side to side, the top of the dome being in the sagittal plane, slightly posterior of the line between the insertions of the horncores. The posterior part of the roof, towards the nuchal crest, flattens and becomes almost horizontal. The nuchal crest, the distal part of which is preserved (Pl. 1, A, 12; Pl. 2, A, 12), is very prominent. The dorsal limit of the origo region of the temporal muscle is marked by a low ridge, which runs from the back of the medial horncore to the nuchal crest at a point 1 cm lateral of the sagittal plane (Pl. 1, A, 13). The skull roof is perforated by three relatively large foramina: one in the sagittal plane (Pl. 1, C, 35), almost 2 cm in front of the nuchal crest, and two others, one on each side of the skull, just above the suture between the parietal and squamosal bones (Pl. 1, A, C, 36). The parieto-squamosal suture (Pl. 1, A, 14) is in between the lower and upper borders of the temporal fossa, as is normal in the Cervidae. In the Bovidae the suture is nearer the lower border of the temporal fossa (Brooke, 1878).

NUCHAL REGION

The occipital part of RGM 260 965 is large, especially the condyles, relative to the size of the skull. In side view (Pl. 1, A, B) the nuchal surface of the supra-occipital bone is concave. The dorsal part, with a prominent external occipital protuberance (Pl. 2, A, 15), is vertical, whereas the ventral part slopes backwards. Due to this curvature of the supra-occipital bone the condyles and the foramen magnum occupy a very posterior position. Even though the nuchal crest is very prominent, the ventral part of the occipital bone, which forms the dorsal margin of the foramen magnum, extends further backwards than the dorsal part of the nuchal crest. This configuration is also present, although to a lesser extent, in the fossil *Taurotragus arkelli* figured by Gentry (1978) and in *Gazella* (the occipital of which is not concave), but is very like the configuration observed on a skull of *Dicrocerus elegans* from Sansan (Sansan 3008, Mus. Natl. Hist. Nat., Paris). The side-to-side diameter of the large foramen magnum is larger than the dorso-ventral diameter and the dorsal parts of both condyles are set wide apart.

The foramen magnum and the occipital condyles project posteriorly, whereas in all other ruminants observed the foramen and condyles are more ventrally directed. In side view the blunt crest on the condyles, which divides the articulation surface into a dorsal and a ventral part, is at an angle of about 50° to the palatal plane (Pl. 1, B, 17). In most other ruminants this angle is larger. In *Hydropotes* for example it is about 80°. The position of the condyles in *Gazella* is intermediate, whereas in *Dicrocerus* the position of the condyles is comparable with that in RGM 260 965. The ventral surfaces of the condyles are almost in the same plane as the base-occipital (Pl. 2, B, 18 and 19). The incisura inter-condyloidea, which separates the ventral surfaces of the left and right side condyles (Pl. 2, B, 20), is relatively narrow and deep as in *Capreolus capreolus*. Only in *Moschus* is the incisura narrower and the condyles almost in contact with each other in the sagittal plane.

The large condyloid fossa (Pl. 2, B, 21) is moderately deep and almost circular. A large foramen condyloideum perforates (Pl. 1,B, 22) the postero-dorsal part of the fossa, and two smaller foramina for the nervi hypoglossi (Pl. 1, B, 23) are present in the ventral part of the fossa, situated slightly more anteriorly than the foramen condyloideum. The two ventral foramina are situated posteriorly of the entrance of a gully which passes through the antero-ventral border of the fossa and which continues anteriorly on the lateral side of the basi-occipital. The gully transmits the hypoglossal nerve.

BASICRANIAL REGION

The angle between the basicranial and palatal planes is c. 16°, which is comparable with that in *Capreolus* (14°) and *Tragulus* (15°). In *Hydropotes* both planes are almost parallel (4°).

The ventral articulation surfaces of the condyles are relatively flat and almost confluent with the basi-occipital (Pl. 2, B, 18 and 19), whereas in most Cervidae the anterior margin of the ventral articulation surface is bordered by a prominent transversal ridge. The basi-occipital is trapezoid in outline; its greatest width (near the anterior margin of the condyles) is twice as large as the smallest transversal diameter (near the articulation with the basi-sphenoid). A median crest, such as one finds in *Capra* and *Tragulus*, is absent.

The ventral surface of the basi-occipital is slightly concave, which is not the case in most cervids. The contact between the basi-occipital and basi-sphenoid is marked by two prominent basilar tubercules (Pl. 2, B, 24). The lateral borders of the anterior half of the basi-occipital and the posterior part of the basi-sphenoid are in contact with the medial wall of the left bulla tympanica (Pl. 2, B, 25), separating the foramen lacerum posterius (Pl. 2, B, 26) from the foramen lacerum anterius (Pl. 2, B, 27). The lateral border of the posterior part of the basi-occipital partly contacts the petrosal (Pl. 2, B, 28).

The ventral surface of the basi-sphenoid (Pl. 2, B, 29) is strongly convex from side to side. Its longitudinal axis is in line with that of the basi-occipital. In both features RGM 260 965 resembles *Capreolus*. The posterior part of the basi-sphenoid contacts the medial side of the bulla. The posterior side of the temporal wing of the basi-sphenoid borders the anterior side of the foramen lacerum anterius and shows two small, posteriorly projecting tubercules (Pl. 2, C, 30). The sulci formed by these tubercules transmit the carotid artery and the mandibular nerve, which emerge from the foramen lacerum anterius. The part of the basi-sphenoid in front of the foramen lacerum anterius and medial of the foramen ovale (Pl. 2, C, 31) is slightly grooved for the passage of the artery and nerve (Pl. 2, C, 32). In most ruminants these grooves are bordered by sharp crests. As in RGM 260 965, these sharp crests are also absent in *Tragulus*. At its lateral side the medium-sized foramen ovale is separated from the relatively deep infratemporal fossa by a sharp crest, which contacts the bulla posteriorly and, which is confluent with the medial part of the postglenoid process (Pl. 2, C, 37). This configuration fits in best with that of *Muntiacus* and *Elaphodus*. However, in these genera there is a crest at the medial side of the foramen ovale (which is absent in RGM 260 965), the crest at the lateral side of the foramen is less pronounced, the infratemporal fossa (Pl. 2, B, 38) is smaller and shallower, and the medial side of the postglenoid process is lower and not confluent with the antero-lateral border of the bulla.

The zygomatic arches are missing on both sides of the skull, but most of the articulation surfaces for the lower jaws are preserved. The infratemporal fossa forms a broad depression, the lateral margin of which, near the temporal condyle, is hardly visible, just as in *Tragulus, Hydropotes, Elaphodus*, and to a lesser degree also in *Muntiacus*. In most ruminants this border is marked by a more or less prominent ridge. The antero-posterior diameter of the infratemporal fossa is as large as in *Muntiacus*. Posteriorly the fossa leads into a small foramen (Pl. 2, C, 39), just medially of the postglenoid process. In contrast to *Muntiacus*, the ventral side of this foramen is completely enclosed in RGM 260 965.

The postglenoid process is a high, sharp-edged, and straight ridge with a small but sharp incurvation slightly medially of the middle (Pl. 2, C, 40). This incurvation is part of the entrance to the temporal canal, which is situated between the external acoustic meatus and the postglenoid process (Pl. 2, C, 41). The incurvation, which is narrower than in all other ruminants observed, divides the postglenoid process into a medial and a lateral part (Pl. 2, C, 42 and 43). Posteriorly the medial part contacts the proximal part of the external acoustic meatus (Pl. 2, C, 44) and the anterior side of the bulla. The hyoid bone articulates with the ventral surface of the external acoustic meatus just posteriorly of the medial part of the postglenoid process (Pl. 2, C, 49).

The posterior side of the lateral part of the postglenoid process is partly in contact with the meatus acousticus externus, which completes the enclosure of the entrance to the temporal canal: the posterior, medial, and lateral walls are formed by the external acoustic meatus, and the anterior wall by the postglenoid process. Normally in ruminants, except for the Tragulidae (which have no postglenoid process) and the Giraffidae (van Kampen, 1905), the external acoustic meatus is not in contact with the lateral part of the postglenoid precess, which leaves the lateral side of the entrance to the temporal canal open. On the anterior side of the lateral part of the postglenoid process a relatively deep glenoid cavity (Pl. 2, B, 45) is developed, for the articulation with the condyle of the lower jaw. The lateral part of the postglenoid process is generally more prominently developed in Cervidae than in Bovidae.

Just above the insertion of the zygomatic arch, the squamosal bone shows a deep, oval-shaped fossa (Pl. 1, A, 46). In Recent ruminants the morphology of this fossa is variable: it is absent in *Tragulus* and *Moschus*, shallow in *Muntiacus, Capreolus* and *Capra*, clearly present, although less deep than in RGM 260 965, in *Hydropotes* and *Gazella*. The fossa in the fossil cervid *Dicrocerus* bears the closest resemblance to that of the holotype of our species.

EAR REGION

The medium-sized, inflated bulla tympanica (Pl. 2, B, 25) has a smooth regular surface. The ventro-dorsal diameter of the ovoid shaped bulla is smaller in relation to its antero-posterior diameter than in *Hydropotes* and *Tragulus*, which also have inflated bullas. *Hoplitomeryx* differs from the other ruminants by the more anterior position of the bullas. Normally the bulla does not extend further forewards than the suture between basi-occipital and basi-sphenoid, whereas in RGM 260 965 the anterior one-third of the bulla is alongside the basi-sphenoid.

The posterior side of the bulla is bordered by the foramen lacerum posterius and by the root of the processus paroccipitalis (Pl. 2, C, 47). Although the processus paroccipitalis is broken off, the smooth rounded posterior surface of the bulla indicates that there has been no contact between the bulla and the processus. Normally in ruminants with an inflated bulla (e.g. most Bovidae and *Axis*) both elements are in contact; this results in a flattened and rough surface at the posterior side of the bulla. *Hydropotes* and *Tragulus* are the only exceptions observed. In both genera only the most dorsal part of the posterior side of the bulla contacts the root of the processus paroccipitalis, RGM 260 965 seems to have had a similar configuration. The medial side of the bulla contacts the bones of the basicranium as in most ruminants with an inflated bulla. Only in *Hydropotes* is the bulla widely separated from these bones, and through the gap the petrosum becomes visible, as is the case in ruminants with small, non-inflated bullas (e.g. most cervids). The antero-dorsal side of the bulla forms the ventral wall of the foramen lacerum anterius and eustachian tube. In most ruminants this part of the bulla is grooved for the reception of the eustachian tube (very clear in *Hydropotes*). In both RGM 260 965 and in *Tragules*, the eustachian tube passes dorsally of the bulla, leaving only a hardly visible depression.

On the anterior side of the bulla, ventrally of the foramen lacerum anterius, a small processus styliformis (or muscular process) is present (Pl. 2, C, 48). This process is the origo of the levator palati muscle, which raises the soft palate and thus closes the posterior nares (Sisson & Grossman, 1964). In RGM 260 965 the processus styliformis is reduced to a small, sharp-pointed tubercule, which corroborates the general rule that in ruminants with inflated, smooth-surfaced bullas, the muscular process is small (van Kampen, 1905). In *Tragules*, as an extreme example, no muscular process is developed. But also in ruminants with an inflated bulla, like *Gazella, Hydropotes* and *Axis*, the processus styliformis is dorsally extended into a low ridge, which forms the lateral wall of the eustachian tube. In RGM 260 965 there is no such extension of the muscular process.

The lateral side of the bulla of the type specimen is incompletely preserved, but from the fragments it can be inferred that the outline of the lateral side was convex, without a prominent vagina for the hyoid bone. The articulation for the hyoid bone is variable in the Ruminantia and consequently also the morphology of the vagina on the bulla, which receives the root of the hyoid bone. But whatever the shape and position of the insertion for the hyoid bone may be, an impression on the bulla for the hyoid bone is always visible in ruminants. The extreme lateral position of the insertion of the hyoid bone on the ventral side of the external acoustic meatus (Pl. 2, C, 49) caused the hyoid bone to pass laterally of the bulla without leaving an impression. Due to the anterior position of the bulla and external acoustic meatus the root of the hyoid bone inserts immediately behind the medial part of the postglenoid process (in *Anoa* and *Antilocapra* the insertion is also close to the postglenoid process). The absence of a vagina for the hyoid bone and the anterior position of its insertion are unique characters among the Ruminantia.

In *Hoplitomeryx* the bulla is hollow and not filled with cancellous tissue (Pl. 1, B, 50). An empty bulla is normal in all ruminants except Camelidae, Tragulidae, Tragelaphini, and Bovini; in these taxa the bulla is filled with cancellous tissue (van Kampen, 1905).

Due to the absence of the left bulla on RGM 260 965 the medial part of the external acoustic meatus and the annulus tympaticus (Pl. 2, C, 51), for the attachment of the membrana tympani, are visible. The outline of the annulus is of oval shape and comparable with that of *Capra*, which also has no bony laminae radiating from the annulus, as present in *Gazella*.

The long, cylindrical external acoustic meatus is closed all around. The lateral part of the tube is horizontal and points slightly backwards (Pl. 2, C, 44). The medial part of the tube bends dorsally into the bulla. On the ventral side of the tube, near the contact with the bulla, there is a relatively deep pit, in which the root of the hyoid bone articulates (Pl. 2, C, 49). This pit, which has a slit-like opening in its postero-lateral wall, is formed mainly by the external acoustic meatus, whereas in other ruminants the bulla largely participates in the enclosure of the articulation surface. The anterior side of the pit is only separated from the medial part of the postglenoid process by a thin wall formed by the external acoustic meatus.

The anterior side of the external acoustic meatus, antero-laterally of the pit for the hyoid bone, shows a relatively large, vertical groove, which opens into the temporal canal. The anterior side of this groove is covered by the postglenoid process, by which the oval-shaped passage to the temporal canal is completely enclosed (Pl. 2, C, 41). According to van Kampen (1905) the Giraffidae show the same configuration. Webb and Taylor (1980) report that also in the primitive *Hypertragulus* from the Upper Eocene of North America the lateral half of the postglenoid process is pressed against the external auditory meatus. Normally in ruminants there is no contact between the meatus acousticus and the lateral part of the postglenoid process, leaving the lateral side of the passage to the temporal canal open.

On the ventral side of the external acoustic meatus there is a longitudinal, low, broad crest (Pl. 1, A, 52), which bounds the lateral side of the pit for the hyoid bone. The morphology of this ridge is variable in the Ruminantia. For example in *Gazella* no ridge is present, whereas in *Capra* the ventro-medial extension of the prominent ridge partly covers the lateral side of the vagina for the hyoid bone on the bulla. The ridge on the tube of RGM 260 965 is comparable with that in *Hydropotes*, but in the latter genus the tube is directed strongly backwards and upwards, whereas in *Hoplitomeryx* the lateral part of the external acoustic meatus is horizontal. Moreover, in *Hydropotes* the dorso-posterior part of the tube is open as in most cervids and in the Giraffidae. In *Hoplitomeryx* the tube is closed all arround, which is the normal configuration in most, but not in all, bovids and in *Tragulus*. According to van Kampen (1905) a closed tube is correlated with the presence of an inflated bulla, except in the genus *Hydropotes* in which an open tube is combined with an inflated bulla. Van Kampen also reports a closed tube in *Axis*, the other cervid genus with inflated bullas. However, according to my observations on two skulls of *Axis porcinus* (ZMA 9639, Zool. Mus., Amsterdam and 1898-181 Mus. Natl. Hist. Nat., Paris) the external acoustic meatus is open at its dorso-posterior side. *Axis* differs also from *Hoplitomeryx* by the presence in the former genus of a more prominent longitudinal ridge on the ventral side of the acoustic tube and a deep vagina for the hyoid bone.

In side view (Pl. 1, A) the anterior side of the external acoustic meatus of RGM 260 965 is completely bordered by the prominently developed lateral part of the postglenoid process. The dorsal part of the acoustic tube is closely surrounded by the squamosum. The lateral half of the posterior side of the tube is uncovered, whereas its medial part contacts the mastoid (Pl. 2, C, 53). In *Antilocapra* too, the tube partly contacts the mastoid.

The external part of the large mastoid bone is almost triangular in outline and in dorsoantero-ventropostero direction strongly concave (Pl. 1, B, 53). The anterior margin of the mastoid, near the contact with the squamosum, is part of the temporal crest (Pl. 1, A, 54). These features fit in best with those present in *Damaliscus*.

The dorsal part of the mastoid shows a unique morphology, since only its most dorsal part contacts the occipital bone. From the level of the most dorsal margin of the condylus, and from this level downwards, the posterior margin of the mastoid is separated from the occipital bone by a slit-like opening (Pl. 1, A, 55), which opens dorsally into the foramen lacerum posterius. A slit-like opening between mastoid and occipital has not been observed in other Ruminantia (but is present in *Equus*).

The ventral side of the mastoid shows at its posterior side an almost triangular facet for the articulation with the root of the paroccipital process (Pl. 2, C, 47). This facet forms a large angle with the posterior margin of the mastoid (Pl. 2, B, 47). This character has also been noticed in *Moschus* and in cervids like: *Hydropotes, Axis, Muntiacus*, and *Capreolus*, whereas in *Tragulus* and in bovids such as *Gazella, Tetracerus, Tragelaphus*, and *Damaliscus* the suture between mastoid and paroccipital process is almost in line with the posterior side of the mastoid. In *Capra* the morphology is intermediate.

Although the paroccipital processes on both sides of the skull are broken off, it can be concluded from the facets that the root of the process was inserted only on the posterior part of the ventral side of the mastoid. In all Recent ruminants observed the root of the process contacts the whole ventral side of the mastoid, except in *Damaliscus* where only the posterior part of the ventral side contacts the process. However, in *Damaliscus* this is only part of the contact, since also half of the posterior side of the mastoid articulates with the paroccipital process.

On both sides of skull RGM 260 965 the surfaces of the contact facets are smooth and regular, which indicates that, although the skull is that of an eldery individual, the root of the paroccipital process had not grown together with the mastoid. Judging from the contact facets it appears that the paroccipital processes must have been relatively small and slender.

The small stylo-mastoid foramen (Pl. 2, C, 56) for the passage of the facial nerve has a relatively ventral position and is enclosed by the mastoid, bulla and external acoustic meatus.

Due to the absence of the left bulla, the ventral surface of the petrosum is exposed. The outline of this side of the petrosum is almost rectangular, with its longer axis directed antero-posteriorly. The postero-medial margin contacts the basi-occipital bone. Seen from the dorsal side (Pl. 2, C), the ventral surface dips gently in the lateral and anterior direction.

The relatively flat promontorium (Pl. 2, C, 57) is situated in the central part of the lateral half of the ventral surface. On the postero-lateral side of the promontorium the fenestra rotundum is present. Due to its vertical position the fenestra is difficult to observe on RGM 260 965. Anteriorly of the promontorium the lateral margin of the petrosum is curved inwards. This incurvation is part of the medial wall of the fossa tensoris tympani, into which the eustachian tube opens and in which the tensor tympani muscle arises. The tensor tympani inserts on the malleus, and by contracting it tenses the membrana tympani (Sisson & Grossmann, 1964). Normally in ruminants the petrosum has a more oblique position, the ventral surface dipping more steeply in the lateral direction, when one looks at the base of the skull (almost perpendicular in *Muntiacus*). Normally the fenestra rotundum is more posteriorly directed than in RGM 260 965 (e.g. in *Capreolus, Rangifer, Muntiacus, Hydropotes,* and *Tragulus*).

In *Capra* and *Gazella* the position of the fenestra resembles that of the type skull, whereas in *Antilocapra* it is intermediate. In the cervids mentioned above (except in *Capreolus*), as well as in *Antilocapra*, the fossa tensori tympani is larger, whereas in *Gazella* and *Tragulus* it is smaller and shallower. The fossa in *Capra* fits in best with that of RGM 260 965.

MEASUREMENTS

The diameters of the horncores are measured at right angles to their axis.

Right-side medial horncore:	
diam. ant.-post. near distal end of smooth surface	15.6 mm
diam. lat.-med. near distal end of smooth surface	10.2 mm
left-side medial horncore:	
diam. ant.-post near distal end of smooth surface	14.9 mm
diam. lat.-med. near distal end of smooth surface	10.5 mm
right-side lateral horncore:	
diam. ant.-post. near distal end of smooth surface	10.0 mm
diam. vent.-dors. near distal end of smooth surface	12.9 mm
distance between the distal end of the medial part of the smooth surfaces of the left- and right-side medial horncores (Pl. 2, A, 58)	61.5 mm
distance between the centres of the left- and right-side fossae underneath the horncores (Pl. 2, B, 8)	62.0 mm
maximum width of the roof of the cranium (Pl. 1, C, 59)	59.0 mm
side-to-side diam. of foramen magnum (Pl. 2, A, 60)	20.7 mm
diam. vent.-dors. of foramen magnum (Pl. 2, A, 61)	16.3 mm

maximum width of condyles (Pl. 2, A, 62)	40.9 mm
length of blunt crest on condyle (Pl. 7, D, 17)	23.0 mm
maximum width of basi-occipital (Pl. 2, C, 63)	26.7 mm
length of basi-occipital (Pl. 2, C, 64)	26.4 mm
length of bulla	21.2 mm
width of incisura inter-condyloidea (Pl. 2, B, 20)	2.4 mm

Remarks on the affinities of the holotype cranium

The morphology of the horncores and of the ear region of the type-skull will be referred to as h.c. type I and e.r. type I respectively.

The type-specimen of *Hoplitomeryx matthei* combines characteristics of various taxa within the Ruminantia. The bony outgrowths from the skull show the typical features of horncores: the conical outline, the surface showing longitudinal, irregular grooves and foramina for the passage and penetration of blood-vessels, and the smooth surface near the base, marking the proximal limit of the hornsheath.

Although the small lateral horncore partly inserts on the lateral side of the base of the medial horncore, the two appendages on each side of the skull are not considered as one forked horncore; this is because the lateral and medial horncores were covered by separate hornsheaths, since the boundaries between the grooved and the smooth surfaces are situated distally of the junction between the two horncores.

The lateral position of the cranial appendages on top of the orbitas is considered a primitive configuration in ruminants, because it is typical for the earliest Cervidae (Stehlin, 1937). The horncores in the Antilocapridae also have a lateral position on top of the orbitas and in several fossil representatives the orbital horncores are forked (Frick, 1937). In some of these forms, like *Stockoceros* and *Hayoceros* the cores start to diverge just above their common insertion. In these genera both cores on each orbit are situated in an almost parasagittal plane, whereas in *Hoplitomeryx* the lateral horncore is almost at right angles to the sagittal plane.

In the Ruminantia the presence of unbranched cores covered by hornsheaths is the main characteristic of the Bovidae. O'Gara and Matson (1975), for example, concluded from the similarity in horn structure that the rank of the Antilocapridae should be lowered to that of a subfamily. They included the Antilocaprinae in the Bovidae. However, as shown by Leinders (1979) and Leinders & Heintz (1980), the Antilocapridae probably branched off from the Cervidae and for this reason these authors proposed to shift the Antilocapridae from the Bovoidea to the Cervoidea. This reconstruction of the antilocaprid phylogeny is based partly on the morphology of the orifices to the lacrimal duct. Leinders and Heintz (1980) demonstrated that the two- orifices-on-the-rim-of-the-orbit configuration is stable in the Cervidae. The one-orifice-inside-the-rim-of-the-orbit configuration in the Bovidae (as well as in the Moschidae) is constant, except in the Bovini and Tragelaphini in which taxa a variety of configurations have been observed, including the cervid and the bovid types.

Skull RGM 260 965 has two lacrimal orifices on the rim of the orbit (Pl. 1, B, 3), which is indicative for close affinities with the Cervidae. However, it can be argued, in view of the variation in the morphology of the orifices in the Tragelaphini and Bovini, that skull RGM 260 965 represents a 'cervid type' variant of these bovids. This hypothesis is contradicted by the presence of a hollow bulla tympanica on the holotype skull (Pl. 1, B, 50). According to van Kampen (1905) and my own observations, the bullas in the two mentioned bovid tribes are filled with cancellous tissue. However, skull 1144 (Mus. Nat. Hist. Nat., Paris) of *Taurotragus* has an empty bulla. This observation seems to contradict the suggestion made by van Kampen (1905) that cancellous tissue occurs not only in *Tragelaphus*, but also in other large antelopes. *Taurotragus* differs from *Hoplitomeryx* by the more oblique position of its bullae (only the anterior side of the bulla contacts the basi-occipital) and by the angle between basi-occipital and basi-sphenoid.

Features that can be used for classification on family level — other than cranial appendages and lacrimal orifices — are hard to find in the comparative osteology of pecoran skulls and none of them is conclusive.

Garrod (1877) and Brooke (1878) mentioned the position of the parieto-squamosal suture near the temporal fossa as a distinctive character between Bovidae and Cervidae. In Cervidae the suture is situated more dorsally than in bovids: in the latter group this suture is nearer the lower than the upper border of the temporal fossa (Brooke, 1878). Several exceptions to this general rule have been observed: the cervids *Hydropotes, Cervus elaphus, Cervus nippon,* and *Muntiacus reverii* have sutures less than half way up the temporal fossa, although these sutures are still situated higher than in most bovids. In the bovid genera *Alcelaphus, Boselaphus, Taurotragus,* and *Saiga* the suture is nearer the upper border of the fossa and is in the same position as in the Cervidae. The two Recent tragulid genera have opposite configurations: in *Tragulus* the position of the suture parallels that of the Cervidae, whereas in *Hyemoschus* the bovid configuration is present. In *Moschus* and *Okapia* the morphology of the orifices is like that present in the Bovidae. *Hoplitomeryx* (as well as *Dicrocerus elegans*) shows the cervid type of suture position.

Generally in Cervidae the lateral part of the post-glenoid process is more prominent than in Bovidae in which family the articulation of the lower jaw seems to take place more along the medial side of the process. However, within the Bovidae several exceptions have been noticed: a) in *Litocranius* no post-glenoid process is present at all (as in *Tragulus*); b) in *Damaliscus, Alcelaphus* and *Redunca* the medial part of the post-glenoid process is extended laterally; c) in *Cephalophus* and *Sylvicapra* a lateral part of the post-glenoid process is developed, but less prominently than in Cervidae; d) in *Taurotragus* the lateral part of the process is prominent and almost contacts the external acoustic meatus.

The morphology of the post-glenoid process of RGM 260 965 resembles that generally present in cervids, but *Taurotragus* and giraffids have similar configurations.

Sir Victor Brooke (1872) remarked about the morphology of the ear region:'....this part of the cranium, so widely removed from the modifying power of adaptation..' However, in view of the diversity in the morphology of this region within the ruminant families it seems probable that the structure of the ear is highly correlated with the way of life of the various ruminants.

An inflated, smooth-surfaced, bulla tympanica is common in bovids, whereas this type is exceptional in cervids. Van Kampen (1905) and van der Klaauw (1931) suggested that in cervids the large bulla is probably the original configuration from which the small type (the usual one in cervids) has been derived. This suggestion corroborates the presence of large bullas in *Hydropotes*, which is the most primitive representative of the Cervidae living today. However, in primitive Cervoidea like the Recent genus *Moschus* and the Upper Oligocene genus *Dremotherium* the bulla is relatively small (Sigogneau, 1968); it is also small in the Miocene cervid *Dicrocerus* (Ginsburg, pers. comm.).

	resembles Bovidae	resembles Cervidae	typical in RGM 260 965
2 lacrimal orifices		×	
horncores	×		
number and position of horncores			×
slit between mastoid and occipital			×
outline mastoid			(×)
position occipital condyles			(×)
outline basi-occipital		(×)	
basi-occipital and basi-sphenoid in same plane		(×)	
morphology post-glenoid process		(×)	
position parieto-squamosal suture		(×)	
combination of features in ear region			×
inflated bullae	(×)		
absence of vagina on bullae			×
morphology muscular process			×
anterior position of bullae			×
laterally directed external acoustic meatus		(×)	
posterior side of external acoustic meatus closed	(×)		
contact between post-glenoid process and ext. acoust. meat.			(×)

Fig. 2. Summary of the main characteristics and affinities of skull RGM 260 965. (×) = character is not conclusive.

The morphology of the bulla and the external acoustic meatus in ruminants is extremely variable and seems to be primarily adaptive. Although the morphology of the ear region of RGM 260 965 combines characteristics of Bovidae, Cervidae and Giraffidae, it also shows features not observed in other ruminants: the anterior position of the bullae, probably no contact between bulla and paroccipital process, absence of a vagina for the hyoid bone, and the slit-like opening between the ventral part of the mastoid and the occipital bone. The morphology of the ear region does not seem to reveal much information about the relationship of *Hoplitomeryx*, but instead it emphasizes its unique position within the Ruminantia.

The triangular outline of the basicranium, the orientation of the basi-occipital and basi-sphenoid in the same plane only differentiates *Hoplitomeryx* from some of the Bovidae, whereas the angle between the basi-occipital and palatine bones differentiates it from *Hydropotes* and the giraffoids (including the Miocene African genera *Canthumeryx* (=*Zarafa*) and *Prolibytherium*).

Due to the combination of diagnostic characteristics of different families RGM 260 965 does not fit in with the existing taxonomical framework. This fact in combination with the unique features of the skull (Fig. 2) means that the classification of the new genus in a new family is the most plausible solution, in spite of the fact that the number of taxa included in the Hoplitomerycidae will be limited and the geographical occurrence of the family is restricted to part of southeast Italy.

The classification of the Hoplitomerycidae on superfamily level will be discussed in the chapter on their classification and origin.

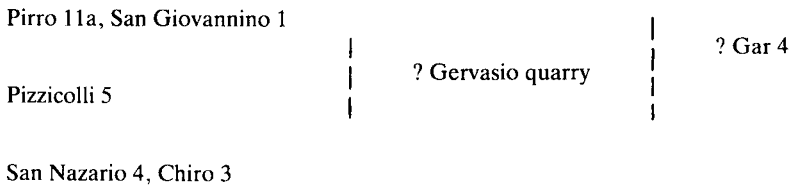

Fig. 3. Stratigraphical position of the localities mentioned in this paper as based on Freudenthal's (1976) and Ballmann's (1976) biozonations with rodents and birds respectively.
Due to the absence of rodent and bird material in the collection, the relative age of Mobilio 1 is unknown. The relative position of Gar 4 is unknown, but it is younger than San Nazario 4 and Chiro 3. Gervasio quarry has the same age as Pizzicoli 5 or is slightly younger.

Other skull fragments

RGM 260 944

Locality — A fissure filling with the code name San Giovannino 1 in abandoned limestone quarry near the farm of San Giovannino, south of the road between Apricena and Poggio Imperiale. San Giovannino 1 has been one of the most productive Neogene fissures in Monte Gargano and is the type locality of *Deinogalerix koenigswaldi* Freudenthal, 1972, *Microtia magna* Freudenthal, 1976, *Garganoaetus freudenthali* Ballmann, 1973, and *Tyto gigantea* Ballmann, 1973. San Giovannino 1 is the youngest locality on the relative time scale of Freudenthal (1976) and fits in with the youngest of the five biozones based on the avifauna (Ballmann, 1976) (Fig. 3).

Description — RGM 260 944 (Pl. 3) represents a skull roof with the medial horncores above the orbitas completely preserved. The lateral horncores above the orbitas are broken off near their insertions. Most of the nasalia is preserved and a large median horncore rises from the posterior part of the nasalia.

The part of the nasalia in front of the median horncore (Pl. 3, A, 66) is convex from side to side, although less convex than normaly in ruminants. In relation to the skull size this part of the nasalia has a large side-to-side diameter. Lateral of the insertion of the median horncore the nasal bone dips relatively steeply in the lateral direction. The suture between nasalia and frontal bones is not traceable.

The ventral sides of the nasalia show over their full length, in the sagittal plane, the root of the septum nasi (Pl. 3, C, 2), indicating the presence of a relatively thick septum the ossified part of which reached further forwards than in most other ruminants. In this respect the morpholoy of *Rangifer* resembles most that of RGM 260 944. On both sides the septum nasi is longitudinally bordered by the concave roof of the dorsal nasal meatus (Pl. 3, C, 67). In front of the insertion of the median horncore the dorsal nasal meatus widens laterally and the part of the nasalia forming the lateral wall of the meatus becomes very solid and thick. Underneath the anterior part of the insertion of the median horncore, the dorsal nasal meatus is laterally bordered by a large and almost semicircular fossa (Pl. 3, C, 68). Behind each fossa the bone of the nasalia is again very solid and thick. In this part of the bone a second, less deep and irregularly shaped fossa is present on both sides of the septum. Posteriorly the root of the septum nasi ends near the anterior margin of the cerebral cavity, which is marked by a sharp curvature of the frontal bone.

In dorsal view the roof of the braincase is very convex in the antero-posterior direction as well as from side to side (Pl. 3, A) and is comparable to that of the type-skull. In the supra-orbital groove (Pl. 3, A, 9) there is a supra-orbital foramen. The foramen is placed more anteriorly than on the type-skull and perforates the dorsal wall of the orbita (Pl. 3, C, 71), whereas in the type-skull it opens into the fossa underneath the orbital horncores (Pl. 2, B, 8). On the posterior part of RGM 260 944 the skull roof is not perforated by median or lateral foramina such as are found on the type-skull (Pl. 1, C, 35 and 36).

The median or nasal horncore curves backwards in the sagittal plane and in lateral view the posterior margin, which is less curved than the anterior margin, forms an angle of 45° with the dorsal surface of the nasalia (Pl. 3, B, 65). The horncore is compressed from side to side (Pl. 3, A), as a result of which its tip is elongated in the antero- posterior direction. The basal part of the horncore shows a smooth surface, which transforms, without a constriction, into an irregularly grooved surface distally. At the anterior side the grooved surface starts about 20 mm above the nasalia, whereas on the posterior side this distance is about 8 mm.

The position and orientation of the medial horncores on the posterior part of the orbitas (Pl. 3, B, 5), as well as the insertion of the lateral horncores (Pl. 3, B, 7) and the fossa underneath the orbital horncores (Pl. 3, C, 8), resemble the configuration of the type-skull. The morphology of the completely preserved medial horncores of RGM 260 944 is similar to that of the horncore on the nasal bones: no constriction between the smooth and the grooved surfaces, compressed from side to side and a flattened, antero-posteriorly elongated tip. In lateral view (Pl. 3, B) they show the same posteriorly directed curvature as the median horncore, but in posterior and in dorsal view (Pl. 3, A, D, 5) the medial horncores are oblique to the sagittal plane and show a distal divergence. This divergence fits in with the position of the partly preserved medial horncores of the type-specimen. The medial horncores on the orbitas of RGM 260 944, which have a larger diameter than those on the type-skull, are slightly smaller than the median horncore on the nasalia.

Measurements — The diameters of the horncores are measured at right angles to their axis.

median or nasal horncore:	
diam. ant.-post. near distal end of smooth surface	19.0 mm
diam. lat.-med. near distal end of smooth surface	15.1 mm
length of the grooved surface on the posterior side	67.6 mm
right-side medial horncore on orbita:	
diam. ant.-post. near distal end of smooth surface	17.3 mm
diam. lat.-med. near distal end of smooth surface	12.5 mm
length of the grooved surface on the posterior side	64.0 mm
left-side medial horncore on orbita:	
diam. ant.-post. near distal end of smooth surface	18.2 mm
diam. lat-med. near distal end of smooth surface	13.0 mm
length of the grooved surface on the posterior side	61.0 mm
insertion of the left side lateral horncore:	
diam. ant.-post.	10.9 mm
diam. vent.-dors.	13.0 mm
distance between the tips of left- and right-side medial horncores (Pl. 3, A, 69)	111.5 mm
distance between the distal ends of the medial part of the smooth surfaces of the left- and right-side medial horncores (Pl. 3, A, 58)	66.0 mm
distance between the centres of left- and right-side fossae underneath orbital horncores (Pl. 3, C, 70)	62.4 mm

Remarks on the affinities of RGM 260 944 — The skull roof from San Giovannino I closely resembles the type-specimen of *Hoplitomeryx matthei* (= h.c. type 1) in the convexity of the skull roof and in the position and orientation of the orbital horncores. The difference in the position of the supra-orbital foramen and the absence of foramina in the posterior part of the skull roof are considered to be of minor taxonomical significance since these features are variable in Recent ruminants.

Although RGM 260 944 is slightly larger than the type-skull, especially as far as the diameters of the medial horncores are concerned, the skull roof from San Giovannino 1 is assigned to *Hoplitomeryx matthei.* The anteriorly extended ossification of the septum nasi may function as a support for the nasal horncore. In the type-skull RGM 260 965 the septum has similar morphology (Pl. 1, C, 2), which suggests that a median horncore was present.

So far no ruminants are known with a single, large conical horncore in the sagittal plane on the nasalia. The pre-orbital appendages which are present in some other ruminants differ markedly from the median horncore present in *Hoplitomeryx*:

A) The short median ossicone in giraffids has a blunt distal end, and its surface shows no smooth surfaced proximal area. The median ossicone also has a more posterior position and inserts mainly on the frontalia above the very large frontal sinus (Ridewood, 1904). In the fossil form *Giraffokeryx* two nasal appendages are present, situated laterally of each other in a plane almost at right angles to the sagittal plane, just in front of the orbitas. Both appendages curve slightly backwards and in dorsal view they show a strong distal divergence. The tips of the ossicones are blunt.

B) The adult males of the bovid *Tetracerus* have four conical horns: two large ones on the posterior part of the skull and one pair of small horns medially on the frontalia at the level of the orbitas. *Tetracerus* is the only Recent ruminant with more than two cranial appendages covered by hornsheaths.

C) The nasal appendages occurring in the fossil Protoceratidae from North America have a more anterior position on the nasalia; they are forked and are more or less cylindrical with a blunt distal end.

The presence of a large median horncore confirms the unique position of the Hoplitomerycidae among the Ruminantia.

RGM 260 945

Locality — San Giovannino 1 (Fig. 3).

Description — RGM 260 945 (Pl. 4) represents a left-side cranial fragment with the dorso-posterior part of the orbita, the medial and lateral horncore and a small part of the skull roof.

In contrast to the specimen described above the medial horncore of RGM 260 945 is not curved in the posterior direction, but shows, in lateral view (Pl. 4, A), a slight anteriorly directed curvation. In anterior view (Pl. 4, B) the horncore is slightly curved inwards. The horncore is not compressed from side to side and its cross section is almost circular.

The lateral horncore inserts more ventrally on the postero-dorsal side of the supra-orbital process of the frontal bone (Pl. 4, C) than in the specimens described previously. The small outer horncore curves slightly upwards in a plane that is almost at right angles to the sagittal plane as well as to the palatal plane, and its axis is at an angle of about 45° to the plane of the medial horncore (Pl. 4, B). The lateral horncore is antero-dorsally slightly compressed.

RGM 260 945 also differs from the other described skull fragments by the more postero-medially situated place of insertion of both horncores. The fossa underneath the horncores is larger and more elongated in antero-posterior direction (Pl. 4, C, 8).

The supra-orbital fossa, the posterior part of which is preserved, is a broad and shallow depression in front of the medial horncore and is not sharply delimited. The supra-orbital foramen perforates horizontally the lateral wall of the fossa and opens into the orbita (Pl. 4, A). The part of the frontal bone medially of the horncores and orbita is less convex antero-posteriorly and from side to side than in the type-skull.

Measurements

medial horncore:	
diam. ant.-post. near distal end of smooth surface	15.9 mm
diam. lat.-med. near distal end of smooth surface	16.3 mm
length of grooved surface on the posterior side	60.1 mm
lateral horncore:	
diam. ant.-post. near distal end of smooth surface	10.6 mm
diam. vent.-dors. near distal end of smooth surface	12.9 mm
length of the grooved surface on the dorsal side	26.8 mm

Remarks on the affinities of RGM 260 945 — The skull fragment is approximately of the same size as *H. matthei*, but the shape and position of the horncores is different: the almost straight axis and circular cross-section of the medial horncore, its more postero-medially situated insertion, and the more ventral position of the insertion of the lateral horncore.

These differences seem to indicate that RGM 260 945 is not conspecific with *H. matthei* and that the specimen represents a second type: *Hoplitomeryx* horncore type II. In Ruminantia the variation in the morphology of the cranial appendages is generally relatively large and since the variation of the horncores from Gargano is insufficiently known, it does not seem opportune to establish a formal species on the morphology of RGM 260 945. It is not possible to group the various skull fragments in different size classes due to the paucity of cranial material and the absence of comparable measurements. The different size classes within the Hoplitomerycidae will be defined by means of the dental elements in a future publication.

Isolated median (nasal) horncores

RGM 260 902

Locality — San Giovannino 1 (Fig. 3).

Description — RGM 260 902 (Pl. 5, B) is a relatively robust median horncore, showing no curvature and its axis is at right angles to the nasalia. The cross-section of the horncore is almost circular. The part of the nasal bone present in front of the horncore is strongly convex from side to side and dips on each side steeply in the lateral direction.

On the left side RGM 260 902 is broken off along the suture between the nasal bone and maxillary and frontal bones, as a result of which the articulation surface is exposed (Pl. 5, B): at the middle of the ventral part the articulation surface for the maxilla and at the posterior part the one for the frontal bone. Both surfaces are large and suggest a firm connection between the various bones. The two articulation areas are not completely separated: the lowermost 2 mm of the bone in between both areas also has a rough surface. This part probably marks the contact between the maxilla and the frontal bone, which suggests that both bones were not separated by the ethmoidal vacuity which is normally found in Cervidae.

The ventral side of RGM 260 902 resembles the area underneath the median horncore of RGM 260 944. However, in the latter specimen the fossa underneath the nasal horncore is situated ventrally of the anterior part of the root of the horncore (Pl. 3, B, 68), whereas in RGM 260 902 the deep fossa is placed more posteriorly underneath the horncore.

Measurements

diam. ant.-post. near distal end of smooth surface	19.3 mm
diam. lat.-med. near distal end of smooth surface	16.5 mm
length of grooved surface on the posterior side	53.3 mm

Remarks on the affinities of RGM 260 902 — In *Hydropotes* the maxilla and the frontal bone are virtually in contact at the medial side of the ethmoidal vacuity. The existence of an ethmoidal vacuity does not seem to be diagnostic for Cervidae since the vacuity tends to be absent or to be reduced in the smaller cervids living on islands, e.g. in the Pleistocene deer from Crete and in several subspecies of *Cervus rusa* from islands in Southeast Asia (de Vos, pers. comm.).

RGM 260 902 differs from the previously described median horncore present on RGM 260 944 (Pl. 3, B, 65) by its straight axis, the almost circular cross-section, the steep lateral dip of the nasalia in front of the horncore, and by the more posterior position of the fossa underneath the horncore.

RGM 260 944 (Pl. 3) is the only specimen known from Gargano in which the nasal and orbital horncores are associated. This specimen demonstrates that in *Hoplitomeryx matthei* the medial horncores above the orbita and the nasal horncore are very similar: same backward curvature, ovally shaped cross-section, and with roughly the same dimensions (the medial horncores on the orbitas are slightly smaller than the nasal horncore).

The median horncore present on RGM 260 945 (Pl. 4) resembles RGM 260 902: almost straight axis, circular cross-section and slightly less robust, which may indicate that the nasal horncore represents the same, second type of the Hoplitomerycidae as does RGM 260 945 (*Hoplitomeryx* h.c. type II).

RGM 260 898

Locality — San Giovannino 1 (Fig. 3).

Description and remarks — RGM 260 898 (Pl. 5, A) is a short, conical median horncore with an almost straight axis (slightly curved anteriorly), circular cross-section, and the fossa at its ventral side is situated just in the middle underneath the root of the horncore. Apart from the difference in dimensions, it closely resembles RGM 260 902 and could represent a juvenile individual of *Hoplitomeryx* h.c. type II. However, the possibility cannot be excluded that RGM 260 898 represents a female or a third species.

Measurements

diam. ant.-post. near distal end of smooth surface	12.2 mm
diam. lat.-med. near distal end of smooth surface	13.6 mm
length of grooved surface on the posterior side	34.0 mm

RGM 260 922 AND RGM 260 923

Locality — San Giovannino 1 (Fig. 3).

Description and remarks — The median horncores RGM 260 922 (Pl. 5, C) and RGM 260 923 (Pl. 5, D) are both curved backwards, compressed from side to side and resemble the nasal horncore of *H. matthei* (Pl. 3, 65).

Although the distal part of RGM 260 922 (Pl. 5, C) is missing the horncore seems to have been slightly longer than in RGM 260 944 (Pl. 3) and RGM 260 923 (Pl. 5, D). Attached to the ventral part of RGM 260 922 there is a fragment of the septum nasi, bordered on both sides by the dorsal nasal meatus. The left side fossa underneath the horncore (Pl. 5, C, 68) is situated under the anterior part of the insertion as in *H. matthei*, but in the present specimen the fossa is deeper (larger ventro-dorsal diameter). Also a smaller fossa is present posteriorly of the main fossa. On the right side, the anterior fossa is smaller, whereas the posterior one is larger than the one on the left side, resulting in two fossae which are almost indentical.

The ventral side of RGM 260 923 (Pl. 5, D) reveals fewer morphological features, but the most dorsal parts of the main fossae underneath the horncore are visible, indicating an anterior position, and a smaller ventro-dorsal diameter than in RGM 260 922.

The grooved surface on the left side of RGM 260 923 shows a relatively deep, longitudinal gully (Pl. 5, D). The medial wall of the gully is perforated by several large, ventro-dorsally elongated pores. The gully probably received a blood vessel, from which side branches penetrated into the bone.

The most distal part of the tip is broken off.

Measurements of RGM 260 922

diam. ant.-post. near distal end of smooth surface	19.2 mm
diam. lat.-med. near distal end of smooth surface	15.0 mm
length of grooved surface on the posterior side (specimen incomplete)	49 mm

Measurements of RGM 260 923

diam. ant.-post. near distal end of smooth surface	19.7 mm
diam. lat.-med. near distal end of smooth surface	15.8 mm
length of grooved surface on the posterior side (specimen incomplete)	61 mm

RGM 261 098

Locality — A fissure with the code Mobilio 1 in limestone quarry Mobilio between Poggio Imperiale and Apricena. Due to the absence of rodent and bird material in the collection from this locality the position of the fauna on the relative time scale is unknown.

Description and remarks — Nasal horncore RGM 261 098 (Pl. 5, E) curves backwards and is almost as long as the nasal horncores described for *H. matthei*. However, the horncore from Mobilio 1 is much more slender and its ventral half is less compressed from side to side.

RGM 261 098 also differs from RGM 260 902 (*Hoplitomeryx* h.c. type II) by its less circular cross-section, its antero-posteriorly elongated tip, its backward curvature and its less robust morphology. RGM 261 098 probably represents a third type (*Hoplitomeryx* h.c. type III).

Measurements

diam. ant.-post. near distal end of smooth surface	13.9 mm
diam. lat.-med. near distal end of smooth surface	12.1 mm
length of grooved surface on the posterior side	55.6 mm

Isolated orbital horncores

RGM 261 097

Locality — A fissure filling with the code name San Nazario 4 exposed in a road cutting on the north side of the road between Rodi Garganico and Lesina, at the junction with the road to Apricena.

On the basis of the avifauna, Ballmann (1976) recognizes five biozones in the various fissure deposits of Monte Gargano. San Nazario 4 fits in with the third one, which is characterised by the first occurrence of *Tyto robusta* (still relatively small in this zone) and by the absence of *Garganoaetus*; the latter genus is characteristic for the two younger biozones. The position of San Nazario 4 in the middle of the stratigraphical range of the various fissure fillings is also demonstrated by the relative age sequence based on rodents (*Microtia* lineage 2 and the cricetid lineage; Freudenthal, 1976) (Fig. 3).

Description and remarks — RGM 261 097 (Pl. 5, F) represents a right-side pair of orbital horncores. The medial horncore is slender and is curved in the postero-medial direction. Instead of a distal divergence as shown by the right- and left-side medial horncores of *H. matthei*, RGM 261 097 indicates a distal convergence of the medial horncores. The cross section is almost circular, except for the antero-medial side, which is slightly flattened over the full length of the horncore. This flattened part is relatively smooth and less grooved than the other parts of the core, where the proximal end of the grooved surface is marked by a very slight constriction.

In contrast to the medial horncore, the lateral horncore is relatively small and squat. The straight axis of this horncore is almost at right angles to the sagittal plane and the cross-section is circular. The transition between the grooved and the smooth-surfaced parts of the core is marked by a very clear constriction of the latter part.

RGM 261 097 differs from *Hoplitomeryx matthei* by the smaller, more slender, and less laterally compressed medial horncore, which also shows a different curvation. It differs also from *Hoplitomeryx* h.c. type II (RGM 260 945, Pl. 4) by the more slender and more backwards inclined medial horncore, as well as by the relatively smaller lateral horncore, which shows no dorsal curvation.

RGM 261 097 may represent the same type as the nasal horncore RGM 261 098 (*Hoplitomeryx* h.c. type III): both are slender horncores with their distal halves more laterally compressed than the proximal parts and the nasal horncore being slightly larger than the medial orbital horncores.

Measurements

Medial horncore:

diam. ant.-post. near distal end of smooth surface	13.8 mm
diam. lat -med. near distal end of smooth surface	15.1 mm
length of grooved surface on the posterior side	47.0 mm

Lateral horncore:

diam. ant.-post. near distal end of smooth surface	9.9 mm
diam. vent.-dors. near distal end of smooth surface	11.3 mm
length of grooved surface on the dorsal side	21.4 mm

RGM 261 099

Locality — A fissure filling with the code Pizzicoli 5 in the limestone quarry Pizzicoli between Poggio Imperiale and Apricena.

On the relative time scale based on rodents, fissure Pizzicoli 5 fits in with the interval between San Giovannino 1 and San Nazario 4 where *Microtia* lineage 3 (*Microtia magna*) is present together with the final and largest forms of the cricetid lineage (Freudenthal, 1976, fig. 4) (Fig. 3).

Description and remarks — RGM 261 099 (Pl. 5, G) represents the proximal part of a medial horncore and a complete lateral horncore from the right side.

The proximal part of the medial horncore is compressed from side to side, which results in an ovally shaped cross-section as in *H. matthei*, but the diameter of the basal part of the horncore is slightly larger. In side view the anterior and posterior margins of the core fragment show less divergence than the corresponding part of the medial horncore of *H. matthei*, indicating that the complete core of RGM 261 099 was probably longer than the horncores of *H. matthei*.

The lateral horncore is relatively short and squat. Its straight axis, without the dorsal curvature found in *Hoplitomeryx* h.c. type II (Pl. 4), is oblique to the sagittal plane. The lateral horncore is compressed antero-posteriorly and there is no constriction near the transition between the grooved and smooth surfaces. The type-skull of *H. matthei* shows only the proximal part of the lateral horncore (Pl. 1, C, 6), which differs from RGM 261 099 by its smaller diameter and its circular cross section.

The fossa underneath the horncores (Pl. 5, G) is much larger and deeper than in *H. matthei* (Pl. 2, A, 8) or *Hoplitomeryx* h.c. type II (Pl. 4, C; 8). This may indicate that RGM 261 099, which will be referred to as *Hoplitomeryx* h.c. type IV, represents a larger animal than one would expect on the basis of the diameters of the horncores alone.

Measurements

Medial horncore:

diam. ant.-post. near distal end of smooth surface	16.7 mm
diam. lat.-med. near distal end of smooth surface	14.0 mm

Lateral horncore:

diam. ant.-post. near distal end of smooth surface	9.9 mm
diam. vent.-dors. near distal end of smooth surface	14.0 mm
length of grooved surface on the dorsal side	27.1 mm

The condyle of RGM 261 092 has almost the same dimensions as the corresponding one on the type-skull of *H. matthei*, but the dorsal articulation surface has a smaller latero-medial diameter and the condyloid fossa (Pl. 6, A, 21) is smaller and less deep. The foramen condyloideum (Pl. 6, A, 22) is also smaller and has a slightly more anterior position. Due to the extreme dorsal position of the condyle the two foramina nervi hypoglossi (Pl. 6, A, 23) have a more postero-dorsal position and the gully, which transmits the hypoglossal nerve from the foramina in anterior direction (Pl. 6, A, 73), is posteriorly extended and has a more oblique position to the palatal plane.

As in type-skull RGM 260 965 only the dorsal part of the mastoid is in contact with the occipital bone (Pl. 1, A, 55), but in RGM 261 092 the slit-like opening between the ventral half of the occipital and mastoid bones is wider (Pl. 6, A, 55).

The rough, laterally exposed surface of the mastoid bone (Pl. 6, A, 53) is less concave than in the type-skull (Pl. 1, B, 53). The articulation area for the paroccipital process on the postero-ventral side of the mastoid is a conical depression (Pl. 6, A, C, 47), which is different from the flat contact facet on the type-skull (Pl. 2, C, 47).

In the same way as in the type-skull the stylo-mastoid foramen (Pl. 6, A, 56) is enclosed by the mastoid, the external acoustic meatus, and the bulla, but it is larger in the skull fragment from San Nazario 4.

The long external acoustic meatus (Pl. 6, A, C, 44) is laterally directed. The lateral part of the tube is horizontal, whereas its medial part bends ventrally into the bulla (Pl. 6, C, 50). On the medial end of the ventral side of the tube, just near the junction with the bulla, there is a depression which receives the root of the hyoid bone (Pl. 6, C, 49). The insertion of the hyoid bone resembles that of the type-skull (Pl. 2, C, 49) but is slightly larger. The external acoustic meatus differs from that of the type-skull (Pl. 1, A, 52) by the absence of a longitudinal ridge on the ventral side of the tube (Pl. 6, A, 44).

The postglenoid process (Pl. 6, C, 42, 43) resembles that of the type-skull. However, in RGM 261 092 the postglenoid process is not in contact with the anterior side of the external acoustic meatus, but in contrast to the type-skull, both structures are (Pl. 2, C, 41) widely separated, as a result of which the entrance to the temporal canal (Pl. 6, A, C, 41) is not enclosed laterally.

The dorsal part of the bulla present on RGM 261 092 shows that the cavity (Pl. 6, C, 50) was not filled with cancellous tissue. The position, outline, and internal structure of the bulla are comparable with those of the type-skull.

The latero-ventral surface of the petrosum (Pl. 6, C, 74) is less elongated antero-posteriorly than in the type-skull of *H. matthei* (Pl. 2, C). The details of the morphology of the dorsal side of this surface are not visible.

The medial (endocranial) surface of the petrosal (Pl. 6, E) has a relatively large anterodorsal-posteroventral diameter. In the centre there is an anterodorsal-posteroventral elongated, deep internal acoustic meatus (Pl. 6, E, 75). The bottom of the meatus is divided, by an antero-posterior ridge, into a dorsal and a ventral part. In each part two foramina, penetrating into the petrosal, are present. The acoustic and the facial nerve enter the petrosal through the internal acoustic meatus.

Dorsally of the meatus a prominent petrosal crest (Pl. 6, E, 76) is present, which separates the flat dosral surface from the medial (endocranial) surface.

In front of the internal acoustic meatus a broad gully runs anteriorly (Pl. 6, E, 77)

The postero-dorsal part of the medial side is dominated by a broad and relatively deep depression: the floccular fossa (Pl. 6, E, 78).

The medial surface of the petrosal bears some resemblance to that of *Gazella*, especially as far as the prominent petrosal crest and the well developed gully anteriorly of the meatus acousticus are concerned. However, the meatus is less deep in *Gazella* and the fossa subarcuata is very weakly developed. The petrosal of *Muntiacus* is more elongated antero-posteriorly; the petrosal crest, although very sharp, is less prominent, and the gully in front of the meatus is very shallow and narrow. *Muntiacus* resembles RGM 261 092 by the presence of a deep floccular fossa.

Remarks on the affinities of RGM 261 092 — Many of the peculiar characteristics observed on the type-skull of *Hoplitomeryx matthei* are also present in RGM 261 092: dorsal position of the condyles and foramen magnum, large lateral exposure of the mastoid bone, slit-like opening between mastoid and occipital bones, inflated bulla, very lateral position of the insertion of the hyoid bone, and the orientation of the external acoustic meatus.

Although these resemblances demonstrate that RGM 261 092 represents a hoplitomerycid, it does differ from the type-skull in the following way: extreme dorsal position of the condyles, the different morphology of the facet for the articulation with the paroccipital process, and the widely separated postglenoid process and external acoustic meatus. These differences make it likely that the specimen from San Nazario 4 is not conspecific with *H. matthei.*

The extreme dorsal position of the condyles seems to indicate that RGM 261 092 represents a more specialized hoplitomerycid than *H. matthei.* Since San Nazario 4 is older than type-locality Pirro 11a of *H. matthei,* this would demonstrate the presence of at least two lineages within the Hoplitomerycidae.

The reverse argument — that the ancestral form had dorsally orientated condyles which evolved on the Gargano island into a more ventral position — is very improbable, because no ruminant, living or fossil, has been observed which such extreme dorsal condyles as are present in RGM 261 092.

The hoplitomerycid type as represented by RGM 261 092 will be referred to as: *Hoplitomeryx* e.r. (ear region) type II.

RGM 178 286

Locality — Fissure filling with the code name Chiro 3 in the limestone quarry Chiro between Poggio Imperiale and Apricena.

The rodents from Chiro 3 are comparable to those from San Nazario 4 (Freudenthal, 1976) (Fig. 3).

Description and remarks — RGM 178 286 (Pl. 5, H) represents a left-side pair of horncores. The relatively small and slender medial horncore has a straight axis and its cross-section is circular.

On the lateral side, near the insertion of the medial horncore, a laterally protruding, small tubercle is present which is the equivalent of the lateral horncore (Pl. 5, H). The tubercle does not have a grooved surface and was probably not covered with keratine.

RGM 178 286 could represent a juvenile, showing the initial stage of development of the lateral horncore. However, this would suggest that the development of the lateral and medial horncores was not synchronous, since the latter core is more advanced. On the other hand, RGM 178 286 could also be interpreted as part of a hoplitomerycid without functional lateral horns.

Measurements

Medial horncore:	
diam. ant.-post. near distal end of smooth surface	11.4 mm
diam. lat.-med. near distal end of smooth surface	10.3 mm

RGM 260 926

Locality — San Giovannino 1 (Fig. 3).

Description and remarks — RGM 260 926 (Pl. 5, I) represents the proximal half of a medial horncore and a complete lateral horncore.

The proximal fragment of the small medial horncore is compressed laterally (ovally shaped cross-section) and curves backwards. It resembles the medial horncore of *H. matthei* but is smaller.

The relatively large lateral horncore has a circular cross-section and shows a slight, anteriorly directed, curvature. Although a complete lateral horncore of *H. matthei* is not known, RGM 260 926 seems to differ from this species, not only by its size, but also by the more ventrally placed insertion of the lateral horncore.

RGM 260 926 probably represents yet another type of orbital horncore from a hoplitomerycid smaller than *H. matthei* (= h.c. type I) and will be referred to as h.c. type V.

Measurements

Medial horncore:	
diam. ant.-post. near distal end of smooth surface	12.5 mm
diam. lat.-med. near distal end of smooth surface	9.2 mm
length of grooved surface on the posterior side (specimen is not complete)	15 mm
Lateral horncore:	
diam. ant.-post. near distal end of smooth surface	7.8 mm
diam. vent.-dors. near distal end of smooth surface	7.5 mm
length of grooved surface on the dorsal side	17.7 mm

Isolated fragments of the ear region

RGM 261 092

Locality — San Nazario 4.

Description — RGM 261 092 (Pl. 6, A, C, E) is a fragment of the right side of a cranium with the condyle and the ear region preserved.

Normally in Ruminantia the articulation surfaces of the occipital condyles are divided by a blunt crest into a dorsal and a ventral part and both parts are nearly at right angles to each other. The dorsal articulation surface is more or less perpendicular to the palatal plane and the ventral one parallel to the basicranium.

Both articulation surfaces on the condyle of RGM 261 092 have a completely different orientation: the dorsal surface (Pl. 6, A, 72) is not vertical but horizontal (parallel to the palatal plane) and the ventral one (Pl. 6, A, 18) faces laterally and not ventrally as it normally does. When compared to the usual configuration in ruminants the condyle of RGM 261 092 is twisted dorsally over an angle of about 90°, leaving the opening of the foramen magnum situated completely on the posterior side of the skull. The orientation of the condyles of the type-skull of *H. matthei* (Pl. 1, B, 17) and of *Dicrocerus elegans* is intermediate between that of RGM 261 092 and the more ventral orientation in most other Ruminantia.

RGM 261 093

Locality — San Nazario 4 (Fig. 3).

Description — RGM 261 093 (Pl. 6, B, D, F) represents a left-side skull fragment showing the petrosal, external acoustic meatus and the lateral part of the postglenoid process.

The long external acoustic meatus (Pl. 6, B, 44) resembles closely that of *Hoplitomeryx* e.r. type II (RGM 261 092). The articulation surface for the hyoid bone on the ventral side of the tube (Pl. 6, D, 49) has a more postero-lateral location, through which the stylo-mastoid foramen is reduced to a slit-like opening (Pl. 6, D, 56).

The main difference between RGM 261 093 and RGM 261 092 (*H.* e.r. type II) is the smaller gap between the postglenoid process (Pl. 6, D, 43) and the external acoustic meatus in the former specimen. Although the postglenoid process is not pressed against the external acoustic meatus as in the type-skull of *H. matthei* (Pl. 2, C, 43, 44) the entrance to the temporal canal (Pl. 6, D, 41) is laterally enclosed by a bone bar, which connects the lateral part of the postglenoid process with the anterior side of the external acoustic meatus (Pl. 6, D, 43, 44).

The petrosal (Pl. 6, F) is similar to that of RGM 261 092 (Pl. 6, E).

Remarks on the affinities of RGM 261 093 — Apart from the difference in distance between the postglenoid process and the external acoustic meatus, RGM 261 093 closely resembles RGM 261 092 (*Hoplitomeryx* e.r. type II).

Both fragments were found not far from each other in the fissure together with several fragmentary skull parts, all of which could belong to one, crushed skull. If RGM 261 093 and RGM 261 092 are the left- and the right-side ear regions of the same individual, this indicates that the distance between the postglenoid process and the external acoustic meatus is extremely variable, or that the right-side fragment (RGM 261 092) has developed anomalously. The latter explanation is the more likely one.

RGM 260 933

Locality — San Giovannino 1 (Fig. 3).

Description — RGM 260 933 (Pl. 6, G, J) represents a right- side petrosal with most of the mastoid and part of the squamosal present. The bulla and the external acoustic meatus are missing.

The present fragment is much larger than the corresponding part of *H. matthei* (skull RGM 260 965) or *Hoplitomeryx* e.r. type II (Pl. 6, A-F).

The ventral side (Pl. 6, G) shows, in the squamosal part, a large circular foramen postglenoideum (Pl. 6, G, 41) in front of a broad transversal gully, which receives the external acoustic meatus (Pl. 6, G, 79). The lateral part of the mastoid (Pl. 6, G, 53) has a rough surface and is slightly convex, but less so than in the type-skull. Mastoid and squamosal are not fully fused and the suture between both bones is clearly visible (Pl. 6, G, 80). Near the medial side of the mastoid the lateral wall of the stylo-mastoid foramen is present (Pl. 6, G, 56) (the medial part of the foramen is normally enclosed by the bulla, which is missing on RGM 260 933). Through the stylo-mastoid foramen the facial nerve enters into the middle-ear region where it is transmitted towards the petrosal by a groove: the sulcus facialis (Pl. 6, G, 81). The nerve enters the petrosal through the apertura tympanica canalis facialis (Pl. 6, G, 82), which is located just laterally of the fossa tensoris tympani (Pl. 6, G, 83). This fossa is the origo of the tensor tympani muscle, which is inserted on the malleus and tenses the membrana tympanica.

The stapedius muscle, which is inserted on the stapes and functions as tensor of the annular ligament by which the stapes is fixed in the fenestra vestibuli, arises from a slightly elongated fossa in the posterior part of the middle-ear region: the fossa stapedius (Pl. 6, G, 48).

The lateral part of the promontorium (Pl. 6, G, 57) with the fenestra vestibuli and the fenestra cochlea is broken off. Except for the promontorium, which is smooth-surfaced, the latero-ventral side of the petrosal shows a rough and irregular surface.

In addition to the difference in size, the endocranial side of RGM 260 933 (Pl. 6, J) differs from the petrosal of RGM 261 092 (Pl. 6, E) in several morphological respects. Antero-ventrally the internal acoustic meatus (Pl. 6, J, 75) is not sharply limited as in RGM 261 092 but the antero-ventral part of the petrosal slopes more gradually into the meatus. The gully anteriorly of the meatus (Pl. 6, J, 77) is less broad and the petrosal crest (Pl. 6, J, 76) is more extended anteriorly. The floccular fossa on the posterior part of the petrosal (Pl. 6, J, 78) is very shallow and comparable with that in *Gazella.*

Remarks on the affinities of RGM 260 933 — The foramen postglenoideum (Pl. 6, G, 41) has the same location as on RGM 261 092 (Pl. 6, A, 41): anteriorly of the external acoustic meatus (Pl. 6, G, 79). The foramen also occupies an anterior position in *Tragulus, Muntiacus* and *Cervus.* In *Hydropotes, Moschus* and *Gazella* the foramen is located dorsally of the external acoustic meatus.

The mastoid is not fully fused with the squamosal bone, which is the normal condition in Recent ruminants, even in aged individuals. However, in the Hoplitomerycidae the fusion between both bones, as well as between the other elements of the skull, seems to have been completed at a much earlier stage of the ontogeny since in other specimens the suture cannot be traced. This may indicate that RGM 260 933 represents a relatively young individual. Nevertheless RGM 260 933 is much larger than the ear region of the type-skull (*H. matthei*; Pl. 2, C) and RGM 261 092 (*Hoplitomeryx* e.r. type II; Pl. 6, A, C, E). The hoplitomerycid represented by RGM 260 933 will be referred to as *Hoplitomeryx* e.r. type III.

RGM 261 100

Locality — A fissure filling with the code Gar 4 in the limestone quarry Chirro between Poggio Imperiale and Apricena.

In locality Gar 4, *Microtia magna* is present, which indicates that the fissure fits in with the younger part of the stratigraphical range (Freudenthal, 1976, fig. 4, *Microtia* lineage 3) (Fig. 3).

Description and remarks — RGM 261 100 (Pl. 6, H, K) is almost the same part of the skull as RGM 260 933.

The ventro-lateral side (Pl. 6, H) resembles closely the specimen described previously (Pl. 6, G), but it is smaller and the mastoid is fully fused with the squamosal. The petrosal is slightly more elongated antero-medially and in contrast to RGM 260 933 the lateral part of the promontorium with the two fenestra is preserved. The large fenestra cochlea (= fen. rotunda) (Pl. 6, H, 85) opens in the postero-lateral direction and, in front of this, the smaller fenestra vestibuli (= fen. ovalis) (Pl. 6, H, 86) opens in ventro-lateral direction.

The orientation of both fenestrae resembles that of *Capreolus*. However, in this genus, as well as in *Hydropotes, Muntiacus* and *Cervus*, the fossa tensoris tympani (Pl. 6, H, 83) is much wider. In *Gazella* the fossa is narrow and trench-like as in RGM 261 100, but it is less deep. Also the fenestra vestibuli is different in *Gazella*: it is more medially located and its diameter, in relation to that of the fenestra cochlea, is larger.

RGM 261 100 is about the same size as RGM 261 093 (*Hoplitomeryx* e.r. type II) (Pl. 6, B, D, F). However, the endocranial side of this specimen shows a floccular fossa and a gully in front of the internal acoustic meatus, which are more pronounced than in the specimen from Gar 4. Because the natural variation of these characters is not known it is difficult to decide whether RGM 261 100 fits in with *Hoplitomeryx* e.r. type II, or whether it represents a different type.

RGM 261 096

Locality — San Nazario 4 (Fig. 3).

Description and remarks — RGM 261 096 (Pl. 6, I, L) is a left-side petrosal which is slightly smaller than that of RGM 261 093 (Pl. 6, B, D, F) (*Hoplitomeryx* e.r. type II).

The endocranial side of RGM 261 096 (Pl. 6, L) differs from that of *Hoplitomeryx* e.r. type II (Pl. 6, F) by the less deep internal acoustic meatus (Pl. 6, L, 75), the shallow fossa subarcuata (Pl. 6, L, 78) and by the shorter petrosal crest (Pl. 6, L, 76).

The orientation of the fenestra cochlea on the ventro-lateral side (Pl. 6, I, 85) resembles that of *Hoplitomeryx* e.r. type II.

On the type-skull of *H. matthei* only the ventro-lateral side of the petrosal is visible (Pl. 2, B, C, 28). This surface of RGM 261 096 is less elongated antero-posteriorly and the fenestra cochlea (Pl. 6, I, 85) is more posteriorly directed than in the type-skull.

RGM 261 096 seems to represent another different type of petrosal *Hoplitomeryx* e.r. type IV).

RGM 261 102

Locality — Gervasio quarry between Poggio Imperiale and Apricena. The material labelled with the code Gervasio quarry was collected by employees of the quarry and offered to Dr Freudenthal. The location of the fissure in the quarry from which the material came is not known.

In this collection *Tyto robusta* and *Tyto gigantea* are present. *T. gigantea* is of the same size as *T. gigantea* from San Giovannino. Both species are present in the three youngest biozones of the zonation of Ballmann (1976). However, *T. robusta* is reported to be extremely rare ('kaum oder überhaupt nicht vorhanden') in the youngest biozone (biozone 1). In the oldest of the three youngest biozones (biozone 3) *Tyto gigantea* is significantly smaller than the representatives of the species from the biozones 2 and 1.

Gervasio quarry should therefore be placed in biozone 1 or 2. Because of the presence of *T. robusta* in Gervasio quarry and the rarity of this species in biozone 1, the locality is tentatively placed in biozone 2 and is probably of the same age as Pizzicoli 5 or slightly younger (Fig. 3).

Description — RGM 261 102 (Pl. 7) represents a left-side ear region with part of the basicranium, the foramen magnum and both condyles preserved.

In side view, the ventral part of the nuchal surface of the supra-occipital bone (Pl. 7, C, 87) slopes backwards forming an angle of about 55° with the basicranium, which is comparable with the morphology present in *H. matthei* (RGM 260 965) (Pl. 1, A). The foramen magnum and the occipital condyles (Pl. 7, C, 16, 18) project posteriorly, although slightly less than in the type-skull of *H. matthei* and much less extremely than in RGM 261 092 (e.r. type II) (Pl. 6, A). The foramen and the condyles are smaller than those of the type-skull. The foramen magnum is circular (Pl. 7, B, 16) in contrast to the ovally shaped foramen in RGM 260 965 (Pl. 2, A, 16).

The incisura intercondyloidea (Pl. 7, A, 20) is similar to that of the type-skull (Pl. 2, B, 20) but in RGM 261 102 the limit between the ventral articulation surface of the condyles (Pl. 7, A, 18) and the basi-occipital bone (Pl. 7, A, 19) is marked by a more prominent ridge (Pl. 7, A, 88) than in the type-skull. The condyloid fossa (Pl. 7, D, 21) is comparable with that of the type-skull (Pl. 2, B, 21) and thus deeper than in RGM 261 092 (e.r. type II) (Pl. 6, A, 21).

The trapezoid-shaped basi-occipital (Pl. 7, A, 19) is slightly concave in the same way as on the type-skull, whereas the basilar tubercules of RGM 261 102 (Pl. 7, A, 24) are less prominent.

Laterally the basi-occipital and the posterior part of the basi-sphenoid (Pl. 7, A, 29) are bordered by the bulla tympanica (Pl. 7, A, 25). The ventral surface of the basi-sphenoid is convex from side to side. The part medially of the foramen ovale (Pl. 7, A, 31) and in front of the foramen lacerum anterius is more deeply grooved (Pl. 7, A, 32) than in the type-skull (Pl. 7, C, 32). The cerebral side of the basi-sphenoid shows, antero-medially of the internal opening of the foramen ovale, an oval-shaped depression (hypophyseal fossa) (Pl. 7, D, 90) for the housing of the hypophysis.

The infratemporal fossa of RGM 261 102 (Pl. 7, A, 38) is smaller and less deep than in the type-specimen (Pl. 7, B, 38) and resembles that of *Muntiacus*.

The glenoid cavity (Pl. 7, A, 45) and the postglenoid process resemble closely the morphology of the type-skull. The lateral part of the postglenoid process (Pl. 7, A, 43) is well developed as it normally is in Cervidae. As in *Hoplitomeryx matthei* and in contrast to RGM 261 092 (Pl. 6, A, 41), the entrance to the temporal canal (Pl. 7, A, 41) is completely enclosed by the postglenoid process and the external acoustic meatus (Pl. 7, A, 44). Also the fossa above the root of the zygomatic arch (Pl. 7, C, 46) resembles that of RGM 260 965 (Pl. 1, A, 46).

The anterior half of the very large, inflated and smooth-surfaced bulla tympanica (Pl. 7, 25) is preserved. Although RGM 261 102 represents a smaller hoplitomerycid than *H. matthei*, its bulla is larger, especially the ventro-dorsal diameter, and protrudes even further ventrally than the paroccipital process (Pl. 7, D, 89). In Cervidae like *Hydropotes* and *Axis kuhlii*, which have large inflated bullae, the paroccipital process reaches further ventrally than the bulla. *Tragulus* shows a bulla which is relatively as deep as the bulla of RGM 261 102 and protrudes also ventrally of the paroccipital process. Whereas the bulla of *Tragulus* is filled with cancellous tissue, the bulla of RGM 261 102 is hollow (Pl. 7, B, 50) as is the bulla of the type-skull (Pl. 1, B, 50) and of RGM 261 092 (Pl. 6, C, 50).

On the anterior side of the bulla a small processus styliformis is present (Pl. 7, A, 48); it is less sharply pointed than the processus of the type-skull (Pl. 2, C, 48). From the processus a low ridge runs dorsally (Pl. 7, D, 48) to the lateral side of the passage for the eustachian tube. In RGM 261 102, and similarly in the type-skull, the eustachian tube passes antero-dorsally of the bulla towards the middle-ear region. There is no gully present on this part of the bulla for the reception of the eustachian tube, whereas there is such a gully in the bulla of *Hydropotes*.

The pit in which the hyoid bone inserts (Pl. 7, A, 49) is in the same position on the external acoustic meatus as in RGM 260 965 (Pl. 2, C, 49) and RGM 261 102 (Pl. 6, C, 49). However, in the specimen from Gervasio quarry the pit is deeper and has a larger diameter. The longitudinal ridge on the ventral side of the external acoustic meatus (Pl. 7, A, C, 52), which encloses the lateral side of the pit for the insertion of the hyoid bone, is more prominent than in the other two skull fragments mentioned. A further difference between RGM 261 102 and the type-skull is the larger distance between the pit and the medial part of the postglenoid process (Pl. 7, A, 42).

The lateral side of the bulla of RGM 261 102 shows a vagina for the reception of the hyoid bone (Pl. 7, A, C, 91), whereas the bulla of the type-skull (Pl. 2, B, 25) does not. In the description of the type-skull it is mentioned that the absence of a vagina on the bulla is a typical feature of skull RGM 260 965 (Fig. 2). Apparently this absence is not typical for all hoplitomerycids. However, in ruminants with bullae as large as those in RGM 261 102 the vagina is much deeper, except in the case of *Tragulus*. In this genus, with very large bullae and a shallow vagina, the hyoid bone inserts more posteriorly than is normal in other ruminants: near the posterior margin of the bulla, just in front of the root of the paroccipital process. In the more advanced ruminants the hyoid bone inserts in the middle of the lateral side of the bulla, dorsally of a deep vagina on the bulla.

In ruminants with an inflated bulla, except for *Tragulus* and *Hydropotes*, most of the posterior side of the bulla articulates with the paroccipital process. Although the paroccipital process of the type-skull is broken off it was concluded from the round and smooth posterior surface of the bulla that there was virtually no contact between the bulla and paroccipital process.

In RGM 261 102 the paroccipital process is preserved (Pl. 7, C, 89), but here the posterior part of the bulla is missing. In side view (Pl. 7, C) the dorsal part of the anterior margin of the paroccipital process is less oblique to the basicranium than the ventral part and the dorsal part probably articulated with a small surface on the postero-dorsal side of the bulla. In the latter respect RGM 261 102 differs from the type-skull. In *Tragulus* and *Hydropotes* the contact between the bulla and the paroccipital process resembles the morphology of RGM 261 102.

In both Recent genera, however, the paroccipital process is slender and runs ventrally, almost at right angles to the palatal plane, whereas in RGM 261 102 the process is relatively short and broad and runs more posteriorly, oblique to the palatal plane. The outline of the paroccipital process resembles that of *Axis kuhlii*, but in this cervid too the short process has a ventral position.

The paroccipital process of RGM 261 102 articulates with a large surface on the postero-ventral side of the mastoid. The suture between both elements (Pl. 7, C, 92) is oblique to the basicranial plane. Although the paroccipital process of the type-skull is not preserved, it can be inferred from the contact facet on the mastoid that the paroccipital process was different from that of RGM 261 102. This contact facet on the mastoid of RGM 260 965 (type-skull) (Pl. 2, C, 47) is small and almost parallel with the basicranial plane for which reason the paroccipital process of *H. matthei* is reconstructed (Pl. 8) as being somewhat similar to that of *Hydropotes*: slender, with the axis of the process almost at right angles to the basicranial plane. The largely exposed mastoid (Pl. 7, C, 53) with an irregular surface as well as the long, transversely directed and circular enclosed external acoustic meatus (Pl. 7, C, 44) have almost the same morphology as the type-skull.

The endocranial surface of the petrosal bone of RGM 261 102 (Pl. 7, D) differs from that of RGM 261 092 (e.r. type II) from San Nazario (Pl. 6, E, F) by the smaller and less deep internal acoustic meatus (Pl. 7, D, 75), by its shallower floccular fossa (Pl. 7, D, 78) and by its slightly shorter petrosal crest (Pl. 7, D, 76). RGM 260 933 (e.r. type III) (Pl. 6, J) is larger than the petrosal of the skull fragment from Gervasio quarry (RGM 261 102) and its petrosal crest protrudes more anteriorly (Pl. 6, J, 76). RGM 261 100 from Gar 4 (Pl. 6, K) is slightly smaller, especially the antero-postero diameter, the gully anterior of the internal acoustic meatus is less deep (Pl. 6, K, 77) and its petrosal crest is less pronounced (Pl. 6, K, 76). RGM 261 096 (e.r. type IV) (Pl. 6, L) is much smaller and especially its petrosal crest (Pl. 6, L, 76) is very short compared to that of RGM 261 102 (Pl. 7, D, 76).

Measurements

side-to-side diam. of foramen magnum (Pl. 2, A, 60)	15.9 mm
diam. vent.-dors. of foramen magnum (Pl. 2, A, 61)	14.8 mm
max. width of condyles (Pl. 2, A, 62)	32.7 mm
length of blunt crest on condyle (Pl. 7, D, 17)	20.0 mm
max. width of basioccipital (Pl. 2, C, 63)	19.0 mm
width of incisura intercondyloidea (Pl. 7, A, 20)	2.3 mm

Remarks on the affinities of RGM 261 102 — RGM 261 102 is smaller in size than and differs from the type skull (= e.r. type I) by the circular foramen magnum, the slightly more ventral orientation of the foramen magnum and condyles, the larger bullae, the presence of a (shallow) vagina on the bulla for the insertion of the hyoid bone; the contact between the paroccipital process and the bulla, the larger pit for the insertion of the hyoid bone, the more pronounced longitudinal ridge on the ventral side of the external acoustic meatus, and by the different articulation between mastoid and paroccipital process.

Judging from the condyles, RGM 261 092 (Pl. 6, A, C, E) (e.r. type II) represents a hoplitomerycid of about the same size as RGM 261 102. However, there are considerable differences in the morphology of both specimens: the very different orientation of the condyles, the deeper condyloid fossa of RGM 261 102, the larger insertion of the hyoid bone, different articulation between paroccipital process and mastoid, and the different morphology of the endocranial surface of the petrosal bone.

In RGM 261 092 the lateral part of the postglenoid process is widely separated from the anterior side of the external acoustic meatus (Pl. 6, C, 43, 44). This in contrast to the configuration in RGM 261 102 (Pl. 6, A, 43, 44). The significance of this difference is not clear. RGM 261 093 (Pl. 6, D, 43, 44), which is very probably the left side ear region of the same individual as RGM 261 092, shows in this respect a morphology that is similar to that of the type-skull and of RGM 261 102.

Because none of the different morphologies of the endocranial surfaces of the isolated petrosals (Pl. 6, G-L) seems to fit in with the morphology of RGM 261 102, this specimen from Gervasio quarry is considered to represent yet another type of hoplitomerycid: *Hoplitomeryx* e.r. type V.

Recapitulation of the differences in skull morphology

Five different types of horncores have been recognized, assuming that the nasal horncore RGM 260 902 and the orbital horncore RGM 260 945 from San Giovannino 1 both belong to the same type (h.c. type II), and also that the nasal horncore RGM 261 098 from Mobilio 1 represents the same type (h.c. type III) as the orbital horncores RGM 261 097 from San Nazario 4.

Pirro 11a	h.c. type I (= *H. matthei*) (Pls. 1, 2)
San Giovannino 1	h.c. type I (Pl. 3)
	h.c. type II (Pl. 4)
	h.c. type II (Pl. 5, B)
	h.c. type V (Pl. 5, I)
Pizzicoli 5	h.c. type IV (Pl. 5, G)
San Nazario 4	h.c. type III (Pl. 5, F)
Mobilio 1	h.c. type III (Pl. 5, E)

The material is insufficient to demonstrate the presence of sexual dimorphism or to separate juvenile individuals from adult ones. RGM 260 898 (Pl. 5, A) could represent a juvenile or female variant of RGM 260 902 (Pl. 5, B) (h.c. type II). The same could be argued for RGM 261 098 (Pl. 5, E) in relation to RGM 260 923 (Pl. 5, D) (*H. matthei* = h.c. type I) which has, in addition to its slenderness, an almost circular cross-section at its proximal part. The nasal horncores of *H. matthei* are compressed from side to side over their full length. RGM 261 098 is thought to represent the same type as RGM 261 097 (Pl. 5, F) (h.c. type III).

The differences in the size of the various types of horncores are not as large as the size differences in the dental and postcranial elements, which seems to indicate that larger hoplitomerycidae had relatively small horns.

For the reasons mentioned above it is considered inopportune to base formal species on the various types of horncores.

Five different types of ear region morphologies have been recognized:

Pirro 11a	e.r. type I (*H. matthei*) (Pls 1, 2)
San Giovannino 1	e.r. type III (Pl. 6, G, J)
Gervasio quarry	e.r. type V (Pl. 7, A-D)
San Nazario 4	e.r. type II (Pl. 6, A-F)
	e.r. type IV (Pl. 6, L)

The differences in the morphology of the petrosals are difficult to evaluate since the natural variation in morphology is insufficiently known. Like the horncores, the petrosals show less variation in size than one would expect from dentition and postcranials. However, RGM 260 933 (Pl. 6, G, J) (e.r. type III) is much larger than the other petrosals and represents a large hoplitomerycid.

The skull fragments RGM 261 092 from San Nazario 4 (Pl. 6, A, C, E) and RGM 261 102 from Gervasio quarry (Pl. 7, A-D) do not fit in with *H. matthei* either, although there are no extremely large size differences. RGM 261 092 seems to be more specialized than *H. matthei* (= e.r. type I) and *Hoplitomeryx* e.r. type V (RGM 261 102), although San Nazario 4 is older than Pirro 11a and the Gervasio quarry.

Discussion of the classification of pecoran families

It is not difficult to group the Recent pecorans into the various families on the basis of their frontal appendages. The Bovidae are characterized by the horncores covered with a keratine sheath, the Cervidae by antlers, the Antilocapridae by the annual shedding of the forked hornsheaths and the Giraffidae by skin-covered ossicones. Ruminants without cranial appendages can be classified by means of cranial and postcranial osteological characteristics: *Tragulus* and *Hyemoschus* both in one separate family: the Tragulidae; *Hydropotes* in the Cervidae; and *Moschus*, the most puzzling genus of the Recent pecorans, in its own separate family: the Moschidae.

However, the phylogenetical relationships of these Recent families, as expressed in the classification on suprafamily level, is much more open to controversy:

Simpson (1945):	Suborder	Ruminantia
	Infraorder	Tragulina
	Superfamily	Traguloidea
	Family	Tragulidae
	Infraorder	Pecora
	Superfamily	Cervoidea
	Family	Cervidae
		Giraffidae
	Superfamily	Bovoidea
	Family	Antilocapridae
		Bovidae
Romer (1966):	Suborde	Ruminantia
	Infraorder	Pecora
	Superfamily	Traguloidea
	Family	Tragulidae
	Superfamily	Cervoidea
	Family	Cervidae
		Giraffidae
	Superfamily	Bovoidea
	Family	Antilocapridae
		Bovidae
Thenius (1969):	Suborder	Ruminantia
	Infraorder	Tragulina
	Superfamily	Traguloidea
	Family	Tragulidae
	Infraorder	Pecora
	Superfamily	Cervoidea
	Family	Moschidae
		Cervidae
	Superfamily	Giraffoidea
	Family	Giraffidae
	Superfamily	Antilocaproidea
	Family	Antilocapridae
	Superfamily	Bovoidea
	Family	Bovidae

Frechkop (1955) included the Giraffidae in the Bovoidea.

O'Gara and Matson (1975) lowered the rank of the Antilocapridae to a subfamily of the Bovidae.

Leinders (1979) and Leinders & Heintz (1980) proposed to transfer the Antilocapridae from the Bovoidea to the Cervoidea.

ANTILOCAPRIDAE

One of the problems discussed recently concerns the origin of the Antilocapridae. Leinders (1979) and Leinders & Heintz (1980) concluded that the pronghorn and its relatives arose from North American antlerless cervoids rather than from Eurasian bovids and it was therefore proposed to transfer the Antilocapridae from the Bovoidea to the Cervoidea. If this tranfer is correct it implies that the development of cranial appendages covered with keratine is not exclusively a feature of the Bovidae and that this feature developed at least once independently from the Old World bovids.

GIRAFFIDAE

The phylogeny and hence the classification of the Giraffidae is still the subject of controversy too. Generally the Giraffidae and the Cervidae are considered to have a common ancestry, which finds its expression in the classification of both families in one superfamily (e.g. Romer, 1966; Thenius, 1979).

On the other hand, Frechkop (1955) emphasized the similar ontogeny of giraffid ossicones and bovid horncores. Both types of appendages are not outgrowths from the frontal bones, as are the antlers of cervids, but develop from ossifications in the skin and fuse in a later stage with the cranial bones. Frechkop concludes: 'En realité un ossicone n'est pas autre chose que l'os cornu, ...', and consequently he includes the Giraffidae in the Bovoidea.

Hamilton (1978b) expresssed the same idea: 'This interpretation [of the cranial appendages in ruminants, J.L.] indicates that the Giraffoidea and Bovoidea are sister-groups; the Cervoidea is possibly the sister-group of the bovoid-giraffoid stem'. (Due to the grouping of the giraffids in a separate superfamily the suggested affinity between the giraffids and the bovids is not expressed in the classification).

However, the similarity in the ontogeny of the cranial appendages does not necessarily demonstrate close affinities between bovids and giraffids because the bovid-type ontogeny of ossicones merely excludes the antlered cervids from the ancestry of the giraffids. Dermal ossification and outgrowth from the cranial bones seems to be the only two possibilities which can cause the growth of bony, cranial appendages. A third group of the Ruminantia (e.g. de giraffids) developing such structures independently is bound to parallel the ontogeny of either the bovids or the cervids. Even if the Giraffidae arose from antlerless cervoids, the bovid-type ontogeny could have been selected.

I define the giraffoid ossicone as an 'os cornu' covered with skin and the bovoid horncore as an 'os cornu' covered with a keratine sheath.

The classification proposed by Frechkop is supported by the biochemical studies of Gaastra (1975), who reports: 'The percentage of differences between the amino-acid sequences of the ribonucleases from the giraffe and the bovids (Bovidae) is remarkably less than between the ribonucleases from the deer (Cervidae) species and the bovids, although the giraffoids are positioned as an early branch of the line to the deer in the phylogenetic tree of the ruminants'.

The oldest giraffoids are known from the lower Miocene (Aragonian, Mein zone 4, Daams & Freudenthal, 1981 discussed in detail the biostratigraphy of this part of the Miocene) of Gebel Zelten in North Africa. In this locality two genera, each representing a different lineage, have been indentified: *Prolibytherium* and *Canthumeryx* (= *Zarafa*) (Arambourg, 1961; Hamilton, 1973, 1978; Churcher, 1978).

According to my observations on the skull material in the British Museum (N.H.) both genera had one lacrimal orifice inside the rim of the orbita (Hamilton, 1973 however reports the presence of two orifices). The one-orifice-inside-the-orbita configuration represents the original pecoran morphology, still present in the Recent tragulids and most bovids (Leinders & Heintz, 1980).

Cervoids are characterised by two orifices on the rim of the orbita (Leinders & Heintz, 1980) and by the closed distal part of the gully on the anterior side of the metatarsal (Fig. 1) (Heintz, 1963; Leinders, 1979). However, *Moschus* combines a single lacrimal orifice inside the orbita with a closed distal part of the gully on the metatarsus, from which it can be inferred that in the cervoid phylogeny the closed gully preceded the two-orifices-on-the-rim morphology.

The one-orifice-inside-the-rim morphology of *Canthumeryx* (= *Zarafa*) and *Prolibytherium* is not conclusive for a non-cervoid ancestry of the giraffids for it could be that the giraffids branched off from a *Moschus* stage of evolution on the cervoid line. In that case, however, the gully on the metatarsal should already show the typical cervoid morphology. Hamilton (1973) remarked about the metatarsal of *Canthumeryx* (= *Zarafa*): 'a deep channel runs down the anterior face of the bone; this channel is open for its whole length as in *Okapia, Giraffa* and the bovids whereas in cervids the channel is roofed over the distal region'. In the Recent genera *Giraffa* and *Okapia* on the other hand, the gully is much reduced and no longer typically bovid-like. Hamilton also reports an open gully on the metatarsal of *Prolibytherium.* The metatarsal of the giraffid *Palaeotragus primaevus* from the middle Miocene of Fort Ternan (Kenya) (cast of KNM.FT 3106 in the Brit. Mus. Nat. Hist.) also shows the typical bovoid morphology of the gully, and Hamilton (1978a) reports that the distal part of the metatarsal of *Climacoceras* from Maboko (? Middle Miocene, Kenya) closely resembles that of *Palaeotragus primaevus*, except for the dimensions.

Especially the morphology of the gully on the metatarsus seems to exclude a cervoid ancestry for the giraffids — and hence their classification in the Cervoidea — since the closed, cervid-type gully is present at a very early stage of the cervoid phylogeny as represented by *Moschus.* At the stratigraphic level of Gebel Zelten (Aragonian; Mein zone 4; 'Burdigalian') the bovids and the cervids (e.g. *Eotragus* and *Procervulus*) already show the typical difference in the morphology of the gully on the metatarsus. Elsewhere cervoids (Giraffidae excluded) are absent in the African fossil record (except for the Plio-Pleistocene of North Africa).

Two other possibilities for the ancestry of the giraffids need to be considered: A) they arose independently from the ancestral ruminant stock, in which case they could be classified in a separate superfamily (Giraffoidea) besides the Traguloidea, Bovoidea and Cervoidea, or B) their ancestry is closely related to the bovoids, which could mean that the Giraffidae should be classified in the Bovoidea.

The bovoid morphology of the gully and the relative resemblance of the chemical structure of the ribonuclease seem to indicate a close relation between the Giraffidae and the Bovidae, in which case the resemblance in the ontogeny of ossicones and horncores is probably not due to parallel evolution but results from a common origin (as advocated by Frechkop, 1955). It is probable that the skin-covered os cornu is the less specialised morphology and preceded the horn-covered os cornu.

PALAEOMERYX

A major problem in this reconstruction of the giraffid phylogeny is the classification of *Palaeomeryx*, present in the Aragonian of Europe, since this genus shows giraffid as well as cervid characters which might indicate a cervoid ancestry for the Giraffidae. Simpson

(1945) classified *Palaeomeryx* in a subfamily (Palaeomerycinae) of the Cervidae. Romer (1966) preferred the original classification with *Palaeomeryx* as the type genus of a separate family of the Cervoidea (besides the Cervidae and the Giraffidae), which he considered ancestral to the Giraffidae. Kretzoi (1974) suggested that *Palaeomeryx* is not related to the giraffids but represents a parallel development.

Ginsburg and Heintz (1966) concluded that *Palaeomeryx* represents a giraffoid and suggested that the genus probably should be included in the Giraffidae. One argument for indentifying *Palaeomeryx* as a giraffoid is the presence of two isolated giraffoid ossicones in the Paris collection from Artenay ('Burdigalian'; Mein zone 4), which are supposed to belong to *Palaeomeryx*.

About the presence of ossicones Hamilton (1978a) remarks: 'The mere presence of ossicones is here identified as a plesiomorphic feature, as skin covered frontal appendages must have been present in the ancestors of the higher ruminants (Coope, 1968, p. 216). If this is so then the conclusion that *Palaeomeryx* must be a giraffid as it possesses ossicones (Ginsburg & Heintz, 1966) is invalid'.

According to Hamilton (1978a) the only (apomorphic) character by which an animal can be identified as a giraffoid is the presence of a bilobed lower canine. However, when the lower canine of an animal is not known (e.g. in the case of *Palaeomeryx*) '...., the relation of a species to the giraffoids may sometimes be established by using apomorphic features of the lower premolars. This cannot be done with species in which the lower premolars are close to the plesiomorphic pecoran pattern and for this reason I have excluded *Palaeomeryx, Propalaeomeryx* and *Prolibytherium* from the Giraffoidea'.

The argument that the presence of ossicones is a plesiomorphic feature and therefore cannot be used as a giraffoid characteristic is doubtful: A) the plesiomorphic condition in the ancestors of the higher ruminants is not the presence of skin-covered appendages but the absence of frontal appendages; B) even if the skin-covered ossicones of the giraffes indicate a retention of a primitive condition, ossicones, as such identified, can be used as an indication for giraffoid affinities as from the moment when the Bovidae and the Cervidae, with their different type appendages, came into existence (probably during the Early Aragonian).

The fact that the pattern of the lower premolars of *Palaeomeryx* resembles more the basic pecoran pattern than the pattern of the giraffoids, as such identified by Hamilton, does not rule out the possibility that *Palaeomeryx* represents a giraffid. As reported by Ginsburg & Heintz (1966) the pattern of the lower premolars of the more advanced representatives of *Palaeomeryx*, as present in Sansan ('Middle Helvetian', Mein zone 6), is more complex ('une molarisation avancée') than the 'plesiomorphic pecoran pattern' (Hamilton, 1978b). In fact the intermediate morphology of the lower premolars of the 'Helvetian-type' *Palaeomeryx* corroborates a cervoid ancestry for the Giraffidae. Although I do not agree with the arguments used by Hamilton, I agree with the conclusion that *Palaeomeryx* probably does not represent a giraffoid.

According to Ginsburg & Heintz (1966) *Palaeomeryx* from the 'Burdigalian' (Mein zone 4, e.g. Artenay) shows fewer giraffoid characteristics than the *Palaeomeryx* representatives from the 'Middle Helvetian' (Mein zone 6, e.g. Sansan) ('La forme du Burdigalien partage avec les Cervidés un certain nombre de charactères qui deviennent giraffoides sur la forme helvetienne'). The mentioned characters of *Palaeomeryx* which evolved during the Middle Aragonian from 'cervoid-type' to 'giraffoid-type' are: morphology of P4 inf., distal articulation surface of the humerus, the grooved surface on the anterior side of the distal part of the radius, and the posterior surface of the metapodials.

The change in the morphology of the last character (from a hollow cervid-type to a flat giraffid-type, posterior surface of the metapodials) is not convincing, because the metatarsus KNM.FT 3106 of the giraffid *Palaeotragus primaevus* from Fort Ternan (cast in the Brit. Mus. Nat. Hist.) shows a very concave (cervid-type) posterior surface.

The transition from cervid to giraffid characteristics in *Palaeomeryx* (especially the molarisation of P4 inf.) must have resulted from parallel evolution since in the 'Burdigalian' of Gebel Zelten the giraffoids are already represented, even by two different lineages.

Other giraffoid characters of *Palaeomeryx* mentioned by Ginsburg & Heintz are:

A) On the upper molars of *Palaeomeryx* the posterior wing of the protocone is not bifurcated, a feature which resembles the Giraffidae and the Bovidae. According to Ginsburg & Heintz the bifurcation is present in all cervids from deposits younger than the 'Lower Helvetian', but since *Palaeomeryx* is already present in the 'Burdigalian' the absence of this bifurcation can be explained as the retention of a primitive character in this genus. However, the use of this character for classification can be doubted since Crusafont (1961) reports the presence of a bifurcation in the probably closely related genus *Triceromeryx* from the 'Burdigalian-Vindobonian' of Spain, and Kretzoi (1974, pl. 1, fig. 3) figured an M3 sup. of *Palaeomeryx eminens* from 'helveto-tortonische' deposits near Hasznos (Hungary), which shows a bifurcated posterior wing of the protocone.

B) The importance of the reported absence of an ethmoidal vacuity is difficult to evaluate due to the paucity of cranial material of early cervids. Closure of the ethmodial vacuity, however, sometimes also occurs in Cervidae, e.g. in several subspecies of *Cervus rusa* from Southeast Asia and in the Pleistocene cervids from Crete (de Vos, pers. comm.).

C) The position of the ridge which separates the two articulation surfaces on the proximal part of the metacarpus. Heintz (1970) demonstrated that this ridge in bovids (and in giraffids) passes laterally of the central depression on the proximal surface of the metacarpal. This distinctive character is relatively constant, but nevertheless cervids sometimes show the bovid morphology, e.g. the Pleistocene cervids from Karpathos (Greece) (Sondaar, pers. comm.).

D) According to Ginsburg & Heintz the absence of a diathrodial facet on the proximal end of the metatarsal (Heintz, 1963) means that *Palaeomeryx* cannot be closely related to the Cervidae because this facet is present in all Miocene bovids and cervids. However, the facet is absent in all post-Miocene cervids (Heintz, 1970) and its absence in *Palaeomeryx* might be a progressive feature.

E) The equal length of metatarsals and metacarpals does not seem to be a useful diagnostic character for classification, since the differences in the ratio of length of frontlimbs to hindlimbs is probably highly adaptive (Oboussier & Ernst, 1977).

Ginsburg and Heintz demonstrated that the presence of *Palaeomeryx* is limited to Europe where it is represented by three species, which are part of one lineage: *P. kaupi* in the 'Burdigalian', *P. magnus* in the 'Helvetian', and *P. eminens* in the 'Tortonian' (they mentioned the possibility that *P. magnus* and *P. eminens* represent the same species). The evolutionary trends in this lineage are: increase in size and the transformation of certain cervid characteristics into giraffid characteristics.

Besides the cervid characteristics present in the 'Burdigalian' representatives of the genus, the anterior side of the metatarsus of *Palaeomeryx* shows the cervid-type (distally closed) gully (e.g. the metatarsus of *P. eminens* from Steinheim stored in the Staatl. Mus. Naturkunde in Stuttgart), which conclusively differentiates *Palaeomeryx* from the giraffids and the bovids.

During the Aragonian giraffids were not present in Europe and *Palaeomeryx* probably represented the ecological equivalent of the Giraffidae of Africa and resulted from parallel evolution from a cervoid ancestry.

The morphology of the orifices to the lacrimal duct of *Palaeomeryx* is not known. It is possible that *Palaeomeryx* evolved from the '*Moschus* stage' of evolution in the cervoid phylogeny (Fig. 4) in which case *Palaeomeryx* is expected to have one orifice inside the orbita. If *Palaeomeryx* has two orifices on the rim of the orbita (which is the more likely configuration) two possibilities should be considered: A) the genus evolved from the '*Hydropotes* stage' of the cervoid evolution (Fig. 4), in which case the ossicones are also due to parallel evolution with the giraffids; or B) they branched off from the 'pre-antler stage' (Fig. 4) in which case the 'ossicones' from Artenay represent the initial stage of antler development in the Cervidae: the skin-covered outgrowths from the frontalia, which are essentially different from the os cornu of Bovidae and Giraffidae and hence should not be labelled as ossicones.

The poorly known genus *Triceromeryx* from the Early Miocene of Spain shows an advanced stage of molarisation of the P4 inf., ossicone-like appendages above the orbitas and a bifurcated appendage on the supra-occipital bone. The lower dentition resembles closely that of *Palaeomeryx* (Hamilton, 1973) and *Triceromeryx* is probably part of the same adaptive radiation from a cervoid stock, paralleling the giraffids of Africa.

Crusafont (1961) considers *Triceromeryx* to be a parallel development with the Dromomerycidae from North America ('.., une réplique européenne des Dromomerycidae,..'). The same idea is expressed by Thenius (1979): 'Die Dromomeryciden gelten als neuweltliches Gegenstück zu den altweltlichen Palaeomeryciden'.

Judging from photographs (Janis, pers. comm.) the dromomerycid *Aletomeryx* from the Early Hemingfordian (Early Miocene) of Nebraska shows a cervid-type gully on the metatarsus and two orifices on the rim of the orbita, which indicates a cervoid ancestry (separate from the bovid-giraffid stock). This conclusion corroborates the suggestion of Crusafont (1961) that the dromomerycids could be an offshoot from the blastomerycids of North America.

It could be that *Palaeomeryx* and *Triceromeryx* represent an offshoot from North American dromomerycids who entered Eurasia together with *Anchitherium*, in which case *Palaeomeryx* and *Triceromeryx* could be included in the Dromomerycidae and diagnosed as follows: cervoids with ossicone-like cranial appendages, complex P4 inf., sabre-like upper canines, 'pli-*Palaeomeryx*' generally present on the lower molars, distal part of the gully on the metatarsus closed, and two lacrimal orifices on the rim of the orbita present.

Remarks on the frontal appendages in the Pecora

A wide variety of cranial appendages is found in different groups of ruminants. These appendages have complex functions related to habitat- adapted behaviour (Geist, 1974; Geist & Bromley, 1978; Janis, 1982). Such highly adaptive structures can only be used with great caution for classification on the family level.

In the diagnosis of the Hoplitomerycidae I have described their appendages as 'Horncore-like cranial appendages', and not as horncores, although they show typical features of horncores as present in the Bovidae and they almost certainly once were covered by a keratine sheath. This paraphrase was used because the formal use of the word horncore (= os cornu covered with a keratine sheath, as defined earlier in this paper) implies a similar ontogeny of the appendages as in bovids and in giraffids (ossifications in the skin). The appendages of *Hoplitomeryx* developed independently from the horncores of the Bovidae and although their morphology is similar, there is no apparent reason why such structures could not result from outgrowths from the cranial bones.

The presence of deciduous antlers identifies an animal as belonging to the Cervidae, since this curious type of appendage, as far as known, developed only once in the ruminant phylogeny. But on the other hand not all Cervidae have deciduous antlers: those representing the *Hydropotes* stage (Fig. 4) (e.g. *Hydropotes* and *Blastomeryx*) and the pre-antler stage (e.g. *Lagomeryx* and *Procervulus*) of the cervid phylogeny.

All the other cranial appendages occurring in the Ruminantia are skin-covered (the horn-covered appendages are considered to be a specialised form of the skin-covered type) allowing continuous growth throughout life. Phylogenetically the horn-covered appendages probably developed from skin-covered appendages (sensu stricto) by gradually increased keratinization of the skin, a process which took place at least three times in the ruminant history: in the Bovidae, Antilocapridae and in the Hoplitomerycidae.

Furthermore it is quite possible that in fossil ruminants with skin- covered (sensu stricto) appendages (e.g. giraffids) the stratum corneum was thicker than normally in skin. The presence of a thin horn layer is difficult to prove from the morphology of the appendages. Even the horncore of an adult male of *Antilocapra* (rec. 422, Institute for Earth Sciences, Utrecht) shows only a very slightly grooved surface and a hardly visible constriction near the base.

In fact it would be surprising if there was not some kind of a horny protection covering the skin of, for example, the non-deciduous 'pre-antlers' of *Lagomeryx* and *Procervulus*, or the large and protruding cranial appendages occurring in fossil giraffids (e.g. *Injanatherium*, Heintz et al., 1981). Without a more than normal keratinized epidermis these structures would not only have been useless in intraspecific combat (other than pure display) but would also have been very vulnerable in everyday situations.

Classification and origin of the Hoplitomerycidae

The unique position of the Hoplitomerycidae among the other Pecora has been discussed earlier in this paper and seems to justify their grouping as a separate family.

In trying to classify the Hoplitomerycidae one encounters the same principal problem as with the Antilocapridae: both groups combine the presence of keratine-covered cranial appendages, which is a bovid characteristic, with morphological features strongly indicating a cervid ancestry.

It can be concluded that the presence of horncore-like structures alone does not a priori indicate a close relationship between the Hoplitomerycidae and the Bovidae, whereas the presence of two lacrimal orifices on the rim of the orbita, the closed distal part of the gully on the metatarsus and the presence of large upper canines in combination with the Late Miocene age of the hoplitomerycids (the giraffoids and the bovids lost their canines before Mein zone 4 of the Early Miocene) seem to provide solid evidence to suggest that the Hoplitomerycidae arose from cervoid ancestors. This should find its expression in the taxonomy by including the Hoplitomerycidae in the Cervoidea. The closed distal part of the gully on the metatarsus discloses the cervoid affinities of the hoplitomerycid ancestors, whereas the two-orifices-on-the-rim morphology excludes the Moschidae and restricts the affinities of the ancestors to the Cervidae (Fig. 4).

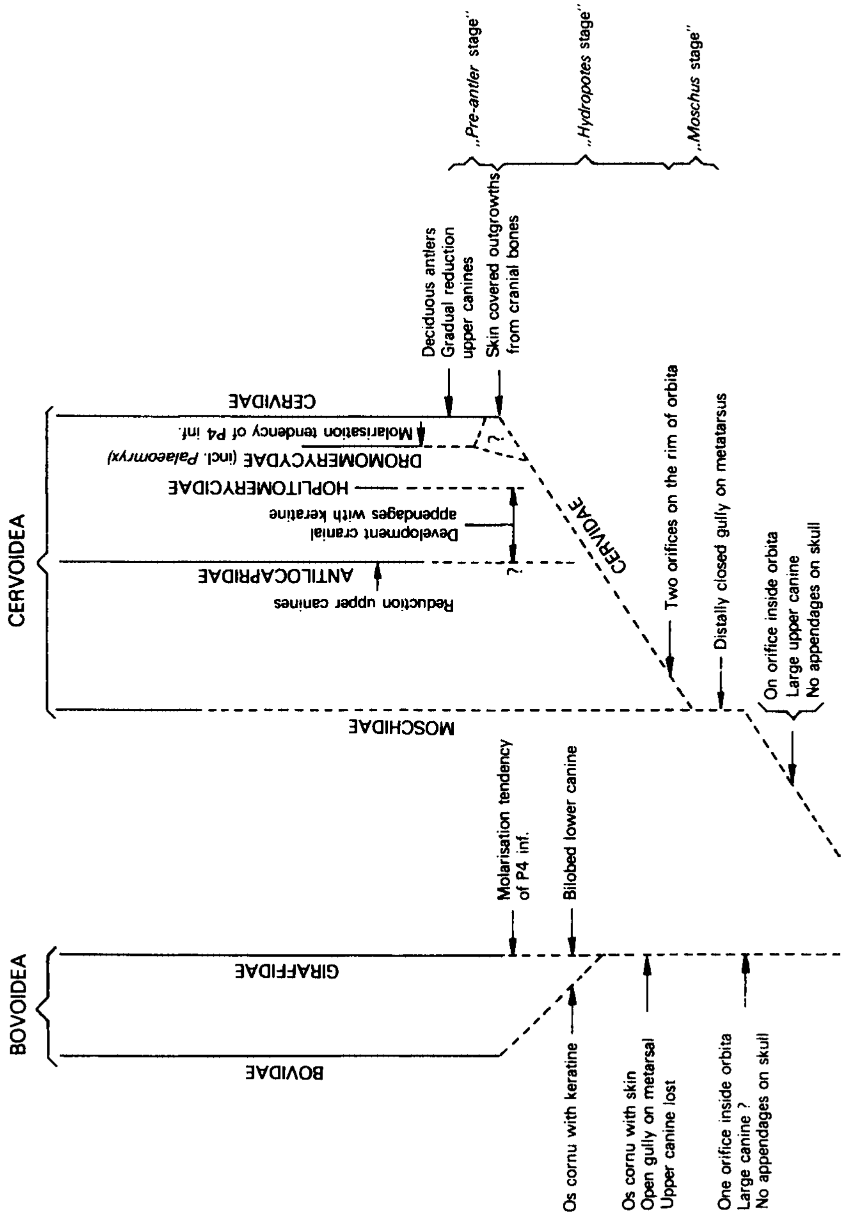

Fig. 4. Proposed classification, phylogeny and the successive acquisition of the main characteristics used for the classification of the pecoran families.

I have not found features which conclusively indicate whether the hoplitomerycids branched off from the *Hydropotes* stage, the pre-antler stage, or from the antlered Cervidae. However, the presence of non-deciduous, horn-covered appendages probably excludes the antlered Cervidae, since antlers represent a more advanced stage of evolution in the cervid phylogeny.

On the basis of the presence of horncore-like structures alone it cannot be ruled out that the Hoplitomerycidae branched off from the pre-antler stage (Fig. 4), because it is possible to derive a horn-like structure from the non-deciduous, skin-covered cranial appendages, present in this stage of the cervid evolution (as discussed earlier the 'pre-antlers' even may have been covered by thin hornsheaths).

On the other hand, the number and the configuration of the horncores are so different (presence of a nasal horncore and a second, laterally protruding horncore on the orbitas) from what is known and from what one would expect to be present in the ancestral group of the antlered Cervidae, it seems more plausible to consider the horncores of the Hoplitomerycidae as an independent attainment, which has no relation with the development of cranial appendages in other ruminants.

The idea that the hoplitomerycids arose from Cervidae without cranial appendages (*Hydropotes* stage) is supported by the presence of large canines in *Hoplitomeryx* (Pls 8,9). In antlerless cervids (e.g. *Hydropotes, Blastomeryx, Micromeryx*) long, slender, dagger-like upper canines are present. In the cervid phylogeny the gradual reduction of these canines is correlated with the development of antlers.

Primitive antlered cervids (e.g. *Muntiacus, Dicroceros*) still have large upper canines but these are relatively smaller and less slender than those present in antlerless cervids and in the Hoplitomerycidae. It is remarkable that in spite of the development of powerful cranial appendages in the hoplitomerycids the canines are still very large.

Hydropotes is the most primitive Cervidae living today and shows primitive features such as: no cranial appendages, large and slender upper canines, basicranial and palatal planes almost parallel, and a marginal position of the insertion of the hyoid bone on the postero-lateral side of the bulla. However, besides these primitive characters *Hydropotes* shows a P4 inf. of which the valley between paraconid and metaconid (vallee 2, Heintz, 1970, fig. 21) is lingually closed. Also *Micromeryx*, the European representative of the *Hydropotes* stage from the Aragonian (e.g. Steinheim, Sansan), has a molarized P4 inf. According to Frick (1937), *Micromeryx* is possibly related to the North American genus *Blastomeryx*. Judging from the dentitions figured by Frick the molarisation of P4 inf. of the Blastomerycinae is somewhat variable but is less advanced (e.g. in *Parablastomeryx*, Frick, 1937, fig. 22) than in *Hydropotes* or *Micromeryx*.

The advanced morphology of P4 inf. excludes *Micromeryx* from the ancestry of the Hoplitomerycidae which have non-molarized last lower premolars.

Dr Heizmann kindly allowed me to compare a recently discovered skull of a young individual of the poorly known genus *Amphimoschus* from Langenau (Mein zone 4), stored in the Staat. Mus. Naturkunde in Stuttgart (no. 40 693).

Because the configuration of the lacrimal orifices cannot be inferred from the specimen and the morphology of the metatarsal of *Amphimoschus* is not known to me, it is difficult to decide whether the genus, which has no cranial appendages, represents the *Moschus* or the *Hydropotes* stage of the cervoid phylogeny.

The crushed skull from Langenau shows some typical features in which it resembles *Hoplitomeryx*: large inflated, smooth surfaced bullae with a relatively anterior position, probable contact between the bullae and the basi-occipital, laterally directed external acoustic meatus, which is closed all around, and the lateral part of the postglenoid process is virtually in contact with the external acoustic meatus.

P4 inf. of *Amphimoschus* as observed in the Paris collection (Mus. Natl. Hist. Nat.) from Pontlevoy (Mein zone 5) is not molarized and the lower molars resemble those of *Hoplitomeryx* by the absence of a 'pli-*Palaeomeryx*' and by the typical morphology of the relatively large, bi-cusped, third lobe on M3 inf. of which the median valley between both cusps is posteriorly open (the posterior parts of both cusps are not connected as they are normally in ruminants). The dentition of *Amphimoschus* differs from that of *Hoplitomeryx* by: the bifurcation of the posterior wing of the protocone ('pli-protoconal'), the strongly developed entostyles and ectostylids and by the presence of P2 inf.

The distal articulation surface of a metacarpal of *Amphimoschus* present in the Stuttgart collection from Langenau shows on the anterior side a very short proximal extension, and the sagittal ridges on the anterior side of the articulation surfaces are less protruding than those in *Hoplitomeryx*, which indicates that the 'pogostick-locomotion' was even less developed in *Amphimoschus* than in *Hoplitomeryx*.

The 'pogostick-locomotion' is less developed in endemic island ruminants than in ruminants from balanced mainland faunas (Leinders, 1979). Because selective pressure on islands favours 'low-gear' locomotion (Leinders & Sondaar, 1974; Sondaar, 1977; Moyá-Solá, 1979; Leinders, 1979) the possibility that the more 'pogostick-like' morphology present in *Hoplitomeryx* was derived from 'low-gear-like' morphology present in *Amphimoschus* from Langenau seems improbable. However, it may be that in more recent representatives of *Amphimoschus*, e.g. those from Pontlevoy (Mein zone 5), the 'pogostick-locomotion' was more developed than in *Amphimoschus* from Langenau (Mein zone 4).

Whether *Amphimoschus* is the direct ancestor of the Hoplitomerycidae or not, the morphology of the cranium and the dentition of the original ruminant invader of the Gargano island probably closely resembled that of *Amphimoschus*.

Concluding remarks

The Ruminantia from Gargano are of great interest because A) they make it possible to study adaptive radiation and speciation of Miocene ruminants (most other fossil island faunas known are of Pleistocene age), and B) their peculiar anatomy and combination of taxinomical characteristics provokes a reconsideration of the taxonomical criteria used for the classification of the various families of the Pecora, as discussed in the previous chapters.

Information on the adaptive radiation and speciation of the Gargano ruminants can best be obtained from the dental and postcranial elements, since the cranial osteology reveals little about these evolutionary processes. However, from the differences in cranial morphology it can be concluded that radiation occurred in the Gargano ruminants. Since it is improbable that the peculiar arrangement of the horncores developed several times independently in different lineages it is assumed that the five horns developed early after the founder's population invaded the Gargano island.

The main peculiarities of the hoplitomerycid skull are: the number and position of the horncores, the strongly developed nuchal part of the skull, the posteriorly directed foramen magnum and occipital condyles, and the large inflated bullae.

It is remarkable that the development of cranial appendages in the hoplitomerycids was not coherent with a reduction in size of the large upper canines as is the case in the other Pecora. In antlerless cervoids the large upper canines are used in intraspecific combat as reported from the Recent genera *Hydropotes* and *Moschus*. According to Grzimek (1968) these genera have a very damaging combat behaviour. The canines inflict deep wounds on the combatants and most males show the scars of such wounds.

Antlers probably developed as defensive weapons against the canines of the opponent, as can be inferred from the combat behaviour of *Muntiacus* (Grzimek, 1968).

'A possible first stage in the evolution of antlers could be a defensive shielding against tusk blows. The larger the "protoantlers", the more effective the shield and at some point in their evolution the effectiveness of antlers made tusks obsolete' (McFarland et al., 1979). This hypothesis supports the idea that the first cranial appendages occurring in the cervid phylogeny (the non-deciduous 'pre-antlers' or 'proto-antlers') were probably not only covered by skin but also had some kind of a horny protection, since it is unlikely that without it the 'pre-antlers' could have functioned in the abovementioned way.

As a result of the further development of antlers the intraspecific combat became more 'ritualized' and less damaging (antler-wrestling).

According to Geist (1974) a high density and diversity of predators causes ungulates to select a non-damaging intraspecific combat behaviour (e.g. African bovids) ('The individual less likely to become prey is the one using "ritualized" combat and dominance displays'). In regions with low predation pressures 'such as in north-temperate environments, we can expect a relatively greater frequency of death and wounding through intraspecific combat. This appears to be so' (Geist, 1974).

In accordance with this statement the virtual absence of Carnivora on the former Gargano island may have resulted in an aggressive and damaging intraspecific combat behaviour of the hoplitomerycids, which could have caused the development of horns in addition to the canines.

However, it seems unlikely that the hoplitomerycid armament was used in an aggressive type of intraspecific combat, because this would probably cause an extremely high mortality rate. The morphology of the skull seems not to corroborate an extremely violent behaviour: firstly the skull roof is not strengthened with pneumatized bone tissue, such as is frequently found in bovids, secondly the orbital horncores are relatively weakly anchored to be skull, due to their lateral position on the orbitas. Especially the lateral orbital horncore, which is mainly supported by the postorbital bar, must have been very vulnerable because of its laterally protruding position (Pl. 9). Thirdly the posteriorly directed foramen magnum and condyles indicate that *Hoplitomeryx* carried its head much higher and that the ventral flexibility of the head was more restricted than is normal in ruminants. The posteriorly directed main horncores of *H. matthei* can only have been effective against conspecific opponents with the head in an extremely ventrally flexed position.

The absence of Carnivora on the Gargano island does not a priori mean that the Hoplitomerycidae were not up against predation pressures, since it is likely that large birds of prey partly filled the ecological niche of the Carnivora, a situation which is not uncommon in unbalanced faunas.

Ballmann (1973, 1976) reports a very high dominance (relative and absolute) of birds of prey in the avifauna from Gargano. The most common birds of prey are owls of the genus *Tyto* the largest species of which (*T. gigantea*), from the younger part of the Gargano faunal complex, is even larger than the Recent eagle owl (*Bubo bubo*). The owls were probably the main predators on the rodents on the island and according to Ballmann they could be responsible for the accumulation of rodent remains in the fissures.

In addition to the owls Ballmann reports the presence of diurnal birds of prey. The endemic eagle *Garganoaetus*, which shows morphological resemblances with the booted eagle, but is much larger, is known from the younger localities. The largest species (*Garganoaetus freudenthali*) reaches the size of the golden eagle. In view of their size it is possible that these eagles (partly) preyed upon the hoplitomerycids, since the golden eagle can attack successfyIly medium-sized pecorans like *Capreolus* (Grzimek, 1968).

The smaller pecorans (e.g. *Cephalophus*) seek protection from predators (which include birds of prey) by hiding in dense vegetation. Medium-sized pecorans may defend themselves, and their breed, actively against large birds of prey (e.g. *Capra ibex*, which uses its horns as a shield).

According to Ballmann the avifauna indicates that the landscape of the former island resembled a karst scenery: dry, open country with low, shrub-like vegetation and very limited tree growth. In such circumstances it is conceivable that the hoplitomerycids developed an active defensive behaviour against the birds of prey in which the horns played an important role: the nasal (median) horn and medial orbital horns shielded the head and the nuchal area of the animals, whereas the lateral orbital horns protected the eyes.

A number of cranial specialisations of the Hoplitomerycidae fit in with this hypothesis: the prominent nuchal crest and the large insertion area of the complexus muscle (the rough area between the nuchal crest and the external occipital protuberance, Pl. 2, A, 12 and 15) indicate that this muscle, which is the chief extensor of the head, was much more strongly developed than normal in ruminants of this size. The more erect position of the head and consequently, the greater backward flexibility, in combination with the strong neck muscle, indicates that *Hoplitomeryx* was capable of making powerful, backwardly directed blows with the horns in an area above the neck and shoulders.

The auditory sensitivity seems to have been well developed in the hoplitomerycids. This was probably not needed for the purpose of intraspecific acoustic communication such as occurs in animals which are living in areas with a very low population density (e.g. deserts), or for the purpose of avoiding predation by Carnivora because the only representatives of this order present on the island were relatively rare otters. It is possible that the large inflated bullae functioned as a warning system against birds of prey. Large inflated bullae are 'especially adapted to enhance the transmission of low frequency, low amplitude sounds [such as those produced by flying birds J.L.] from the tympanum to the inner ear' (McFarland et al., 1979).

However, there is a problem about the hypothesis that predation by the large, endemic diurnal birds of prey caused the selective pressure for the development of the typical hoplitomerycid morphology, since it was concluded earlier in this paper that the development of the five horns probably took place before the radiation of the founder's population, which does nor corroborate the fact that these birds are only known from the three youngest biozones (Ballmann, 1976).

A possible explanation, although speculative, could be found in the fact that the antlerless ancestors of the hoplitomerycids were probably small sized, since all known cervoids without cranial appendages, the living as well as the fossil ones, are all very small. These ruminants are vulnerable in sparsely vegetated environments and since it is conceivable that the founder population of the Gargano island was preyed upon by mainland birds of prey, the 'pre-hoplitomerycids', with their sabre-like upper canines and their probably aggressive type of intraspecific combat behaviour (pre-adaptations?), may have developed an active defensive behaviour because they had no other option than to stand and fight the birds of prey. These combats may have caused the selective pressure for the development of additional defensive structures on the cranium. The efficiency of the active defensive behaviour of the ruminants may have forced the mainland diurnal birds of prey to specialise in predation on hoplitomerycids, resulting in the endemic genus *Garganoaetus*.

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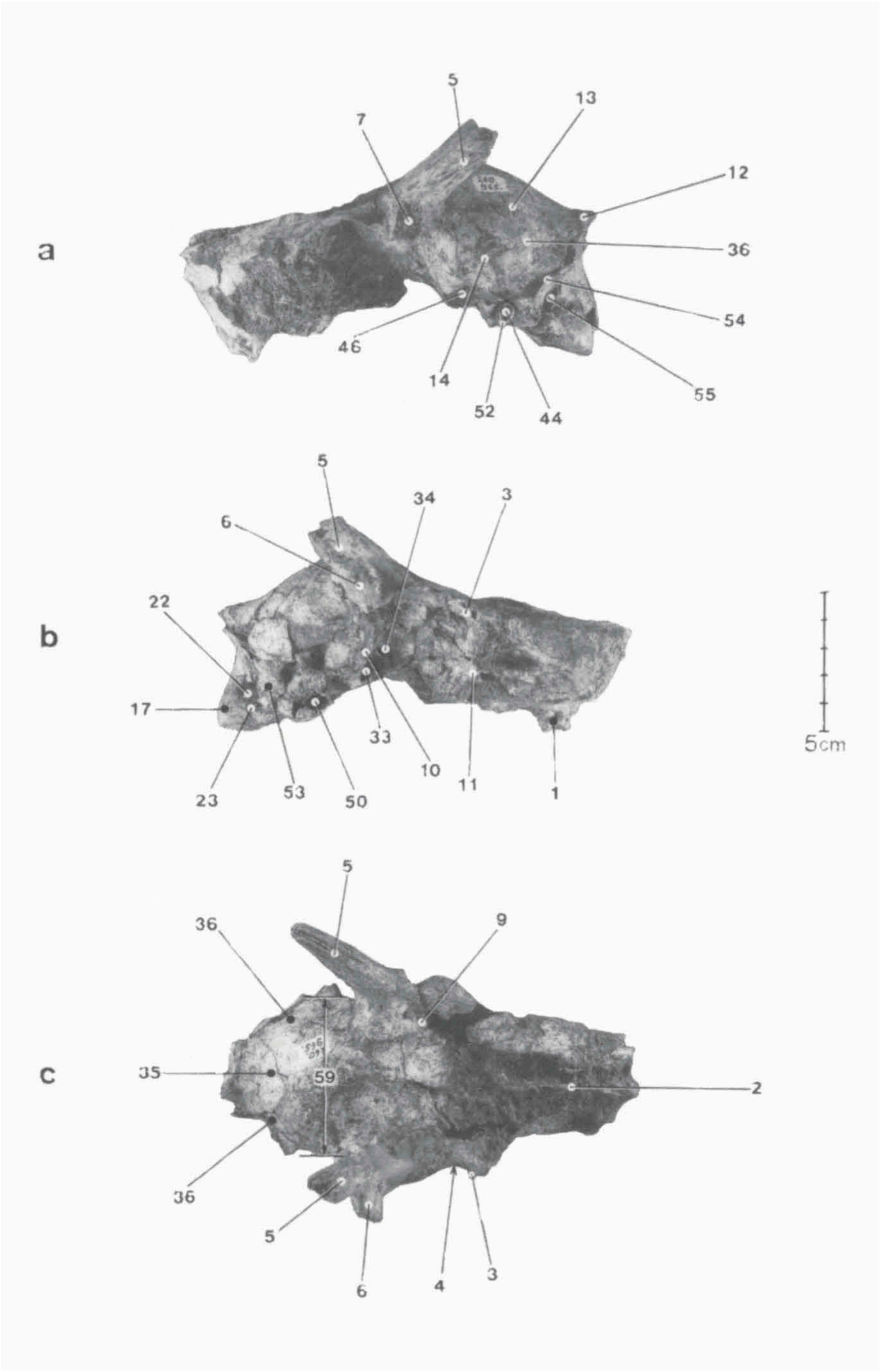
Manuscript received 12 January 1983.

EXPLANATION OF THE NUMBERS ON THE PLATES

1 = P3 sup. sin. and P4 sup. sin.
2 = septum nasi
3 = lacrimal orifices
4 = curvature of orbital rim
5 = medial horncore
6 = lateral horncore
7 = insertion lateral horncore
8 = fossa underneath orbital horncores
9 = supra-orbital groove
10 = pterygoid crest
11 = infra-orbital foramen
12 = nuchal crest
13 = limit origo of the temporal muscle
14 = parieto-squamosal suture
15 = external occipital protuberance
16 = foramen magnum
17 = blunt crest on occipital condyles
18 = ventral surface of condyle
19 = basi-occipital bone
20 = incisura inter-condyloidea
21 = condyloid fossa
22 = foramen condyloideum
23 = foramina nervi hypoglossi
24 = basilar tubercules
25 = bulla tympanica
26 = foramen lacerum posterius
27 = foramen lacerum anterius
28 = petrosal
29 = basi-sphenoid
30 = tubercles on the temporal wing of basi-sphenoid
31 = foramen ovale

32 = grooved lateral surface of the basi-sphenoid
33 = foramen orbito-rotundum
34 = optic foramen
35 = median foramen in skull roof
36 = lateral foramen in skull roof
37 = crest on the lateral side of the foramen ovale
38 = infratemporal fossa
39 = foramen medial of the postglenoid process
40 = incurvation in the postglenoid process
41 = entrance to the temporal canal (foramen postglenoideum)
42 = medial part of the postglenoid process
43 = lateral part of the postglenoid process
44 = external acoustic meatus
45 = glenoid cavity
46 = fossa above the insertion of the zygomatic arch
47 = contact facet for the paroccipital process
48 = processus styliformis (muscular process)
49 = pit for the insertion of the hyoid bone
50 = cavity of the bulla tympanica
51 = annulus tympanicus
52 = longitudinal ridge underneath ext. acoust. meat.
53 = mastoid bone
54 = temporal crest
55 = opening between mastoid and occipital bones
56 = stylo-mastoid foramen
57 = promontorium on the petrosal
58 = distance between the distal ends of the medial part of the smooth surfaces of the left- and right-side medial horncores
59 = maximum width of the roof of the cranium
60 = side to side diam. of foramen magnum
61 = diam. vent.-dors. of foramen magnum
62 = maximum width of condyles
63 = maximum width of basi-occipital
64 = length of basi-occipital
65 = median or nasal horncore
66 = nasalia
67 = dorsal nasal meatus
68 = fossa underneath nasal horncore
69 = distance between tips of left and right side medial horncores
70 = distance between the centres of left and right side fossae underneath orbital horncores
71 = foramen supraorbitale
72 = dorsal articulation surface of the condyle
73 = gully which transmits the hypoglossal nerve
74 = latero-ventral surface of the petrosal
75 = internal acoustic meatus
76 = petrosal crest
77 = gully anterior of internal acoustic meatus
78 = floccular fossa
79 = gully for the external acoustic meatus
80 = suture between mastoid and squamosal
81 = sulcus facialis
82 = apertura tympanica canalis facialis
83 = fossa tensoris tympani
84 = fossa stapideus
85 = fenestra cochlea (= fen. rotunda)
86 = fenestra vestibuli (= fen. ovalis)
87 = supra-occipital bone
88 = limit of the ventral articulation surface
89 = paroccipital process
90 = hypophyseal fossa
91 = vagina for the hyoid bone
92 = suture between paroccipital process and mastoid bone

Plate 1



Hoplitomeryx matthei gen. et sp. nov., RGM 260 965, type specimen, from Pirro 11a.
A: left side; B: right side; C: dorsal side.

Plate 1

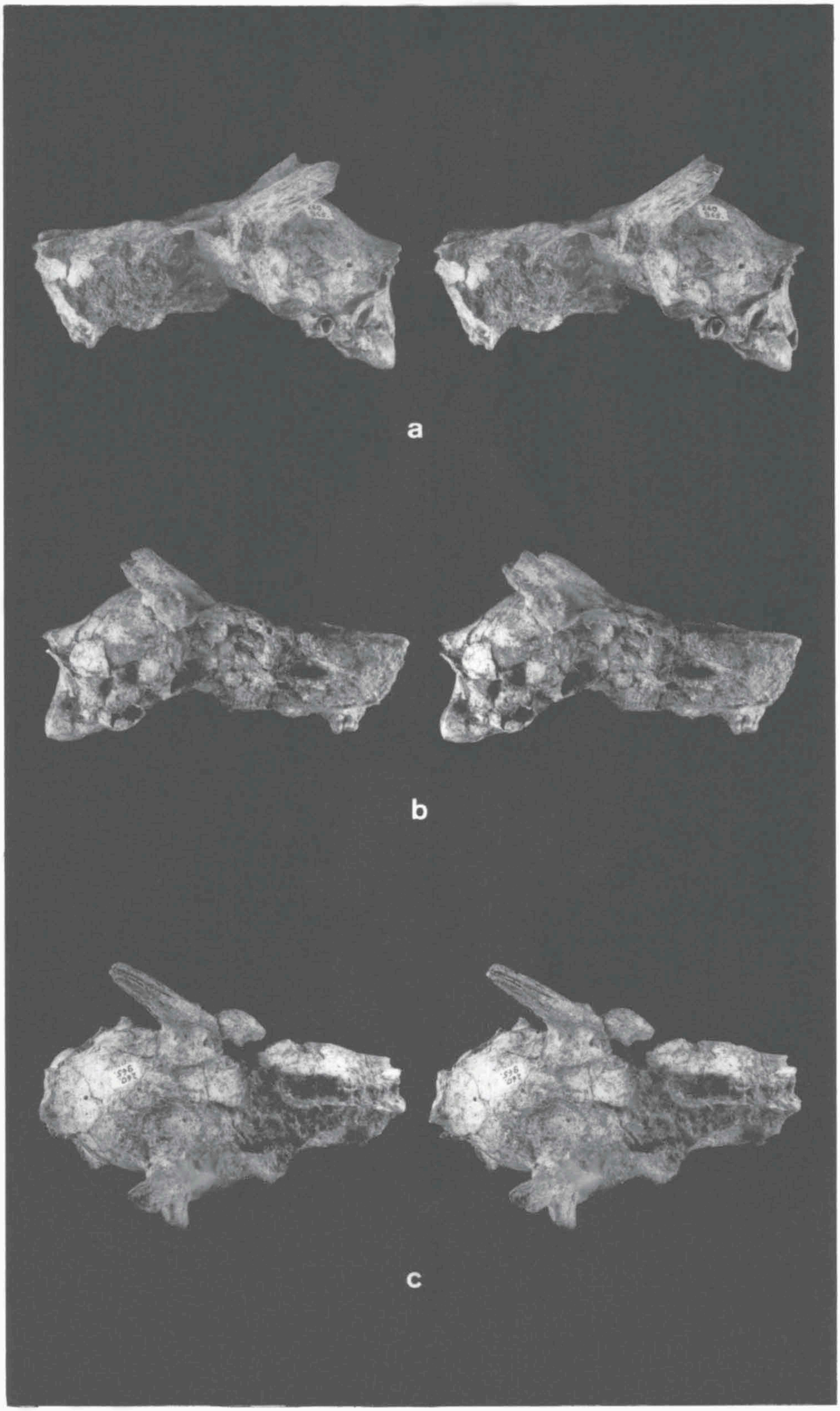
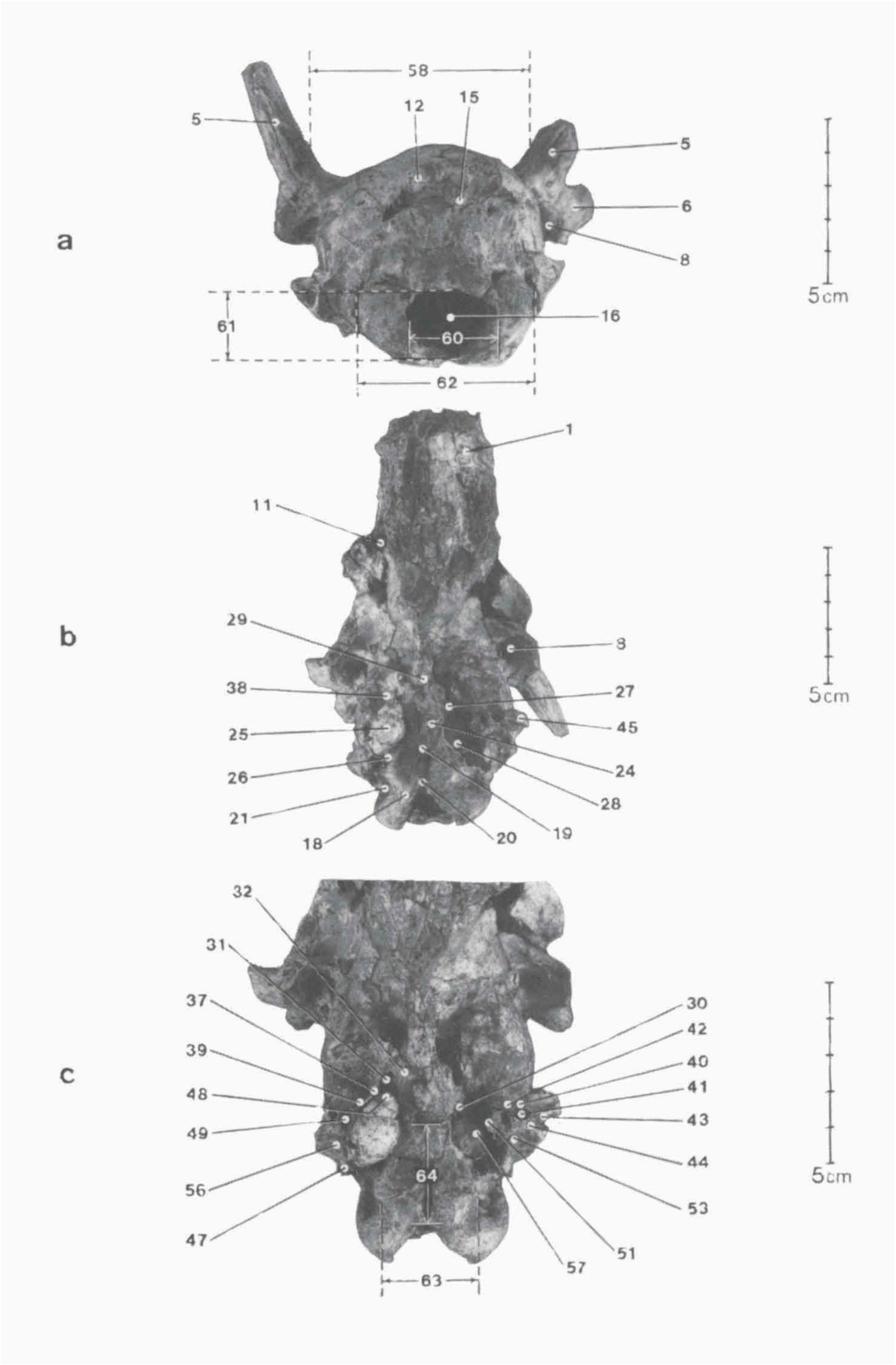


Plate 2



Hoplitomeryx matthei gen. et sp. nov., RGM 260 965, type specimen, from Pirro 11a.
A: nuchal side, B: ventral side; C: basicranium.

Plate 2

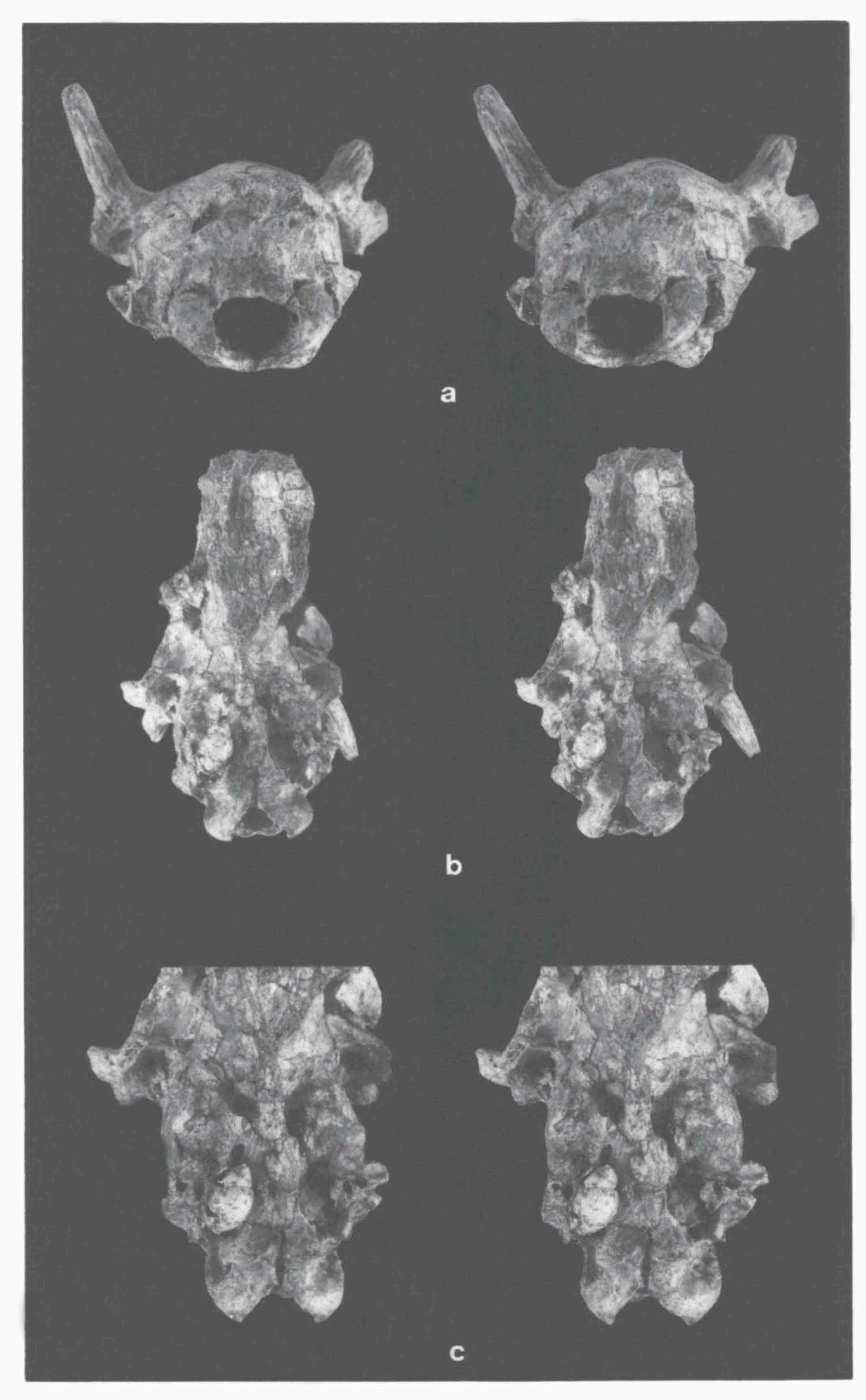
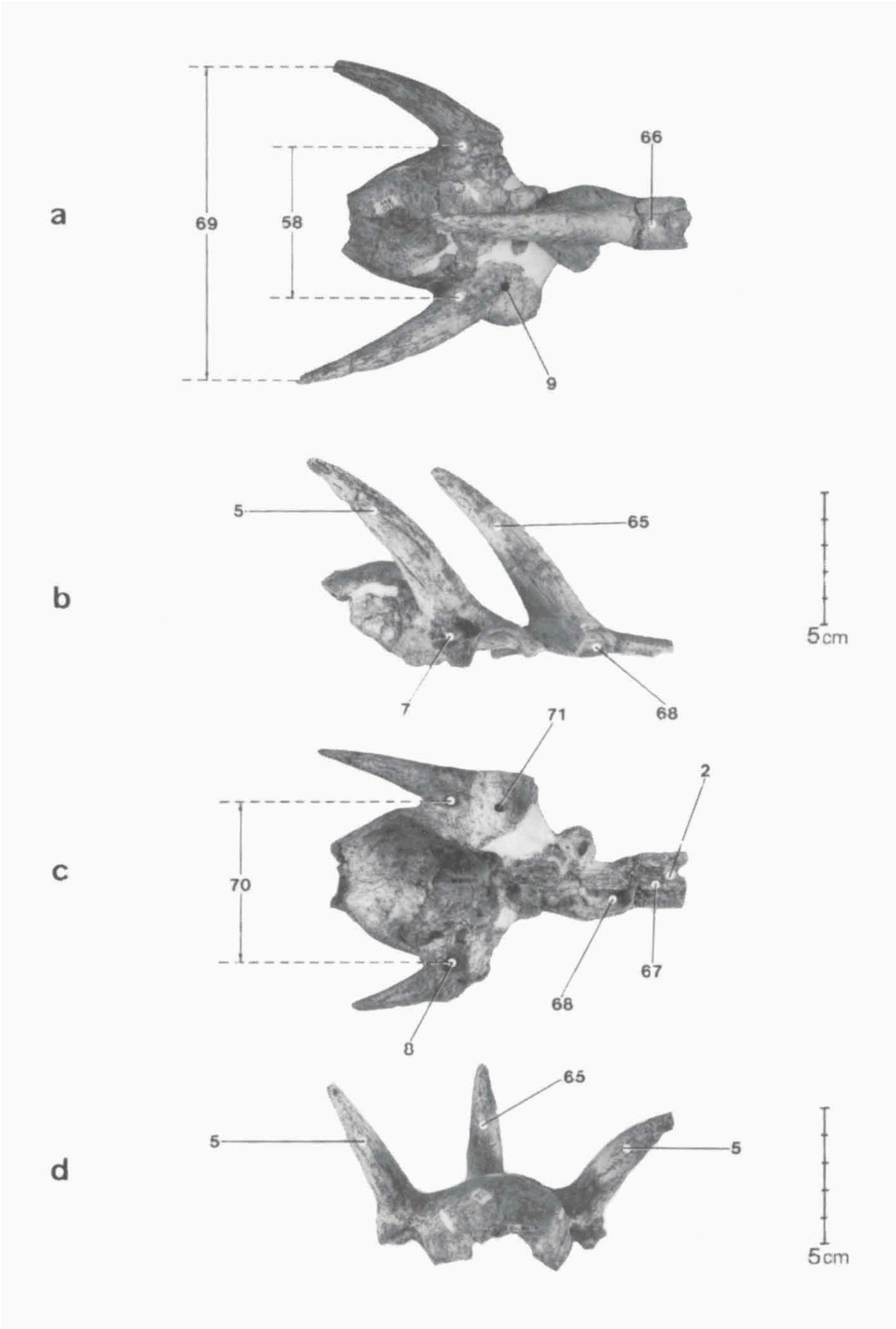


Plate 3



Hoplitomeryx matthei gen. et sp. nov., RGM 260 944, skull roof and nasalia, from San Giovannino 1.
A: dorsal side; B: right side; C: ventral side; D: nuchal side.

Plate 3

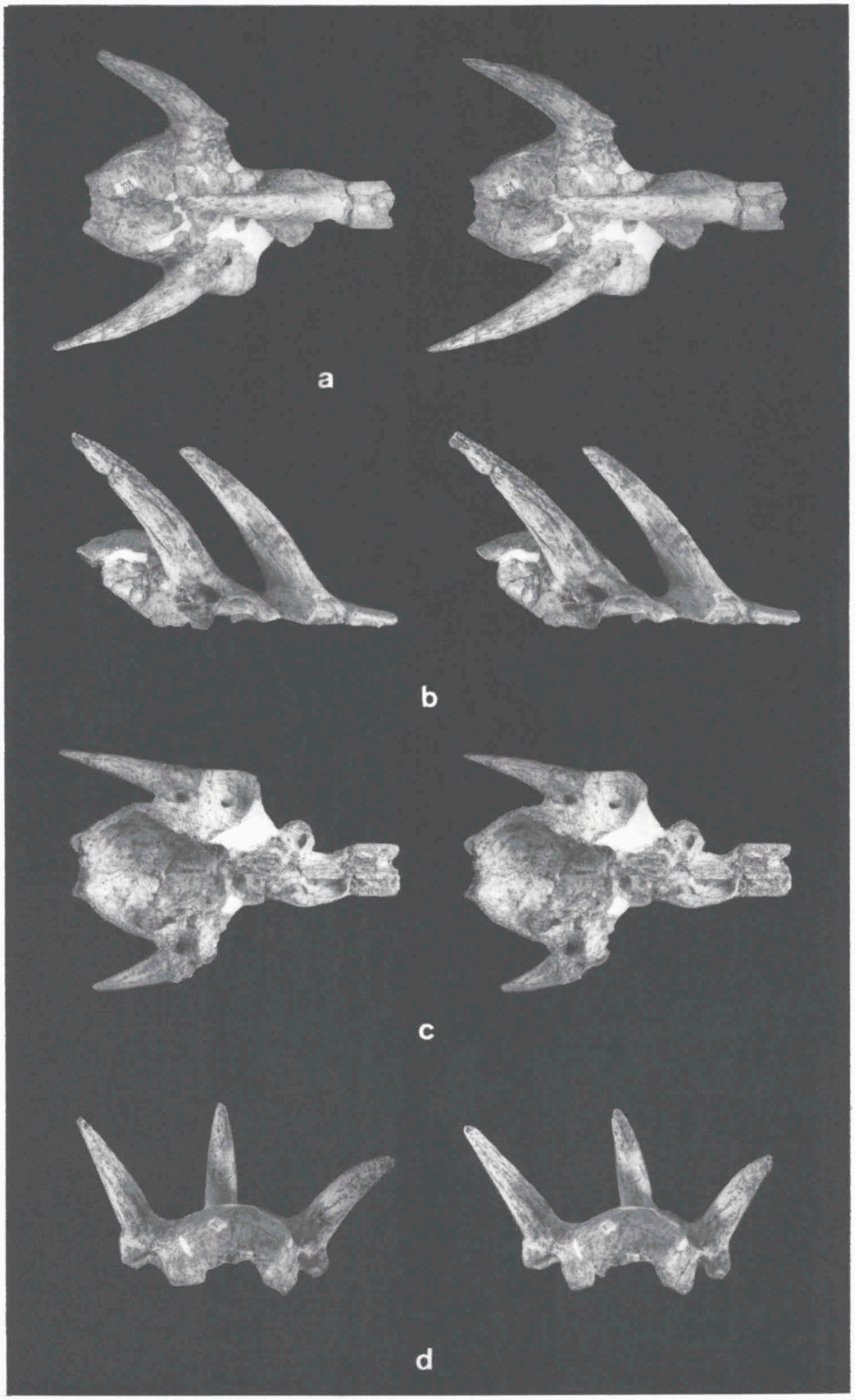


Plate 4

Hoplitomeryx horncore type II, RGM 260 945, orbital horncores sin., from San Giovannino 1.
A: lateral side; B: anterior side; C: posterior side.

Plate 4

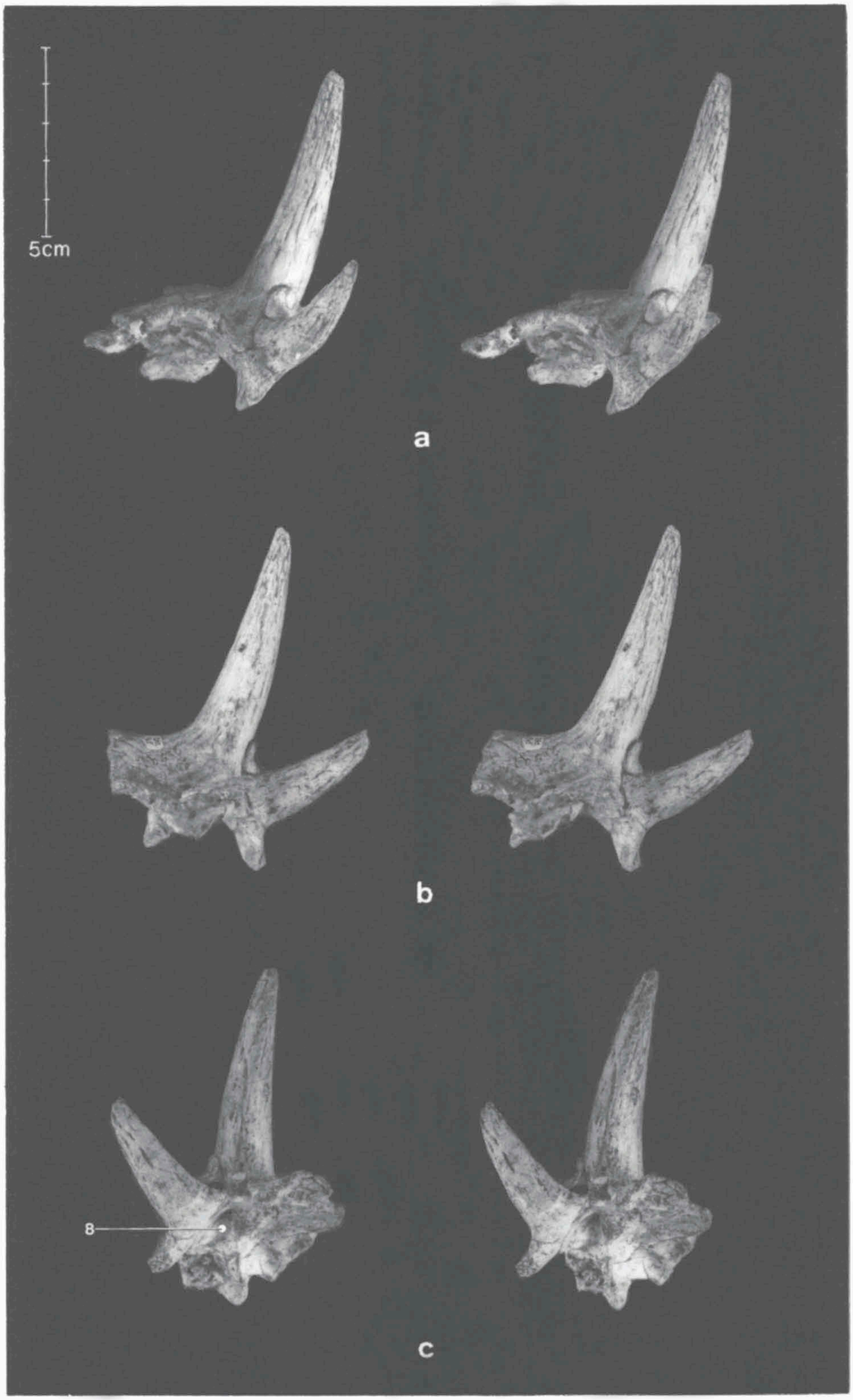


Plate 5

Horncores of hoplitomerycids.
A: RGM 260 898, h.c. type II ?, nasal horncore, left side, San Giovannino 1.
B: RGM 260 902, h.c. type II, nasal horncore, left side, San Giovannino 1.
C: RGM 260 922, h.c. type I, nasal horncore, left side, San Giovannino 1.
D: RGM 260 923, h.c. type I, nasal horncore, left side San Giovannino 1.
E: RGM 261 098, h.c. type III, nasal horncore, left side, Mobilio 1.
F: RGM 261 097, h.c. type III, orbital horncores dext., posterior view, San Nazario 4.
G: RGM 261 099, h.c. type IV, orbital horncores dext., posterior side, Pizzicoli 5.
H: RGM 178 286, h.c. type ?, orbital horncores sin., posterior side, Chiro 3.
I: RGM 260 926, h.c. type V, orbital horncores sin., posterior side, San Giovannino 1.

Plate 5

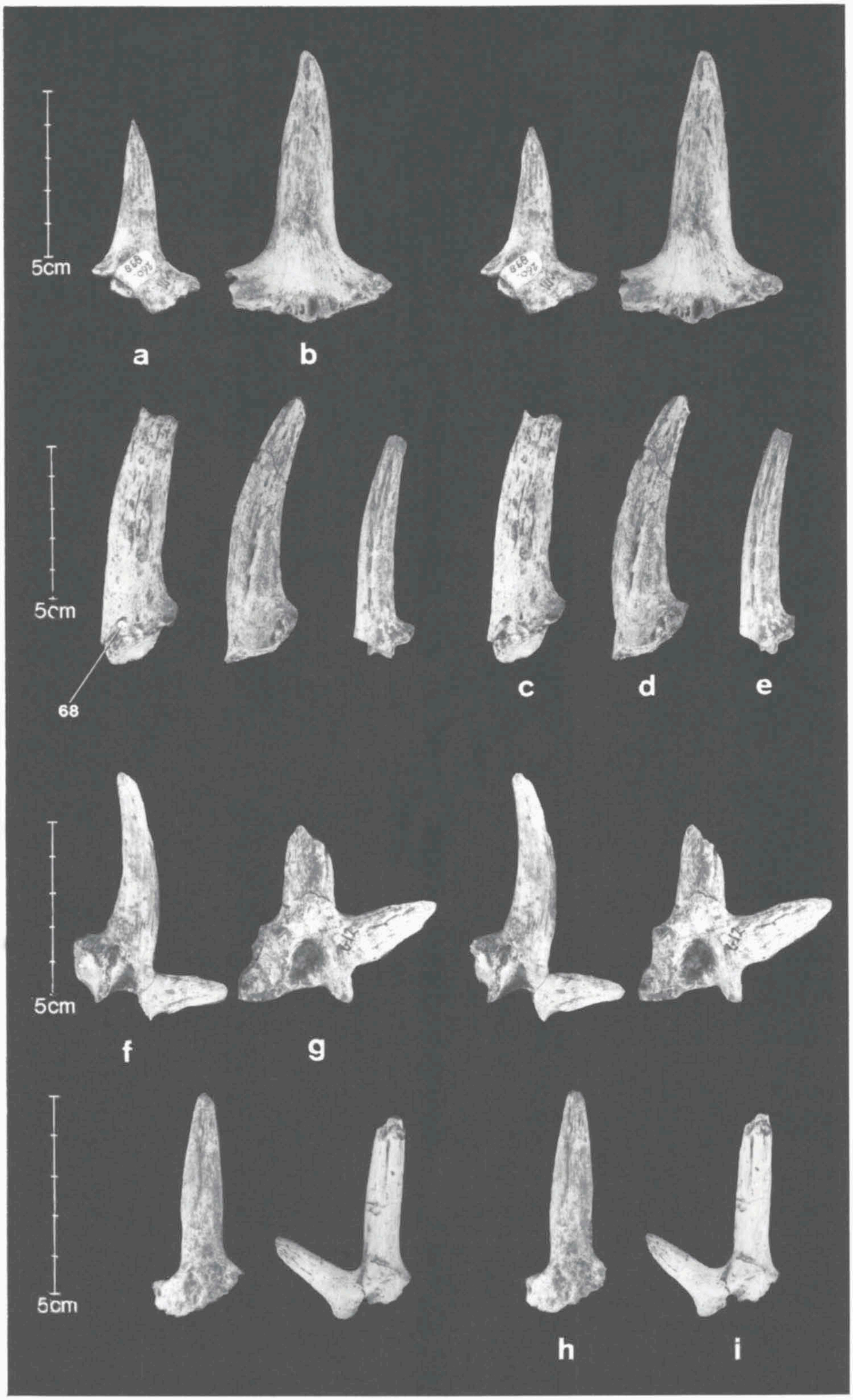
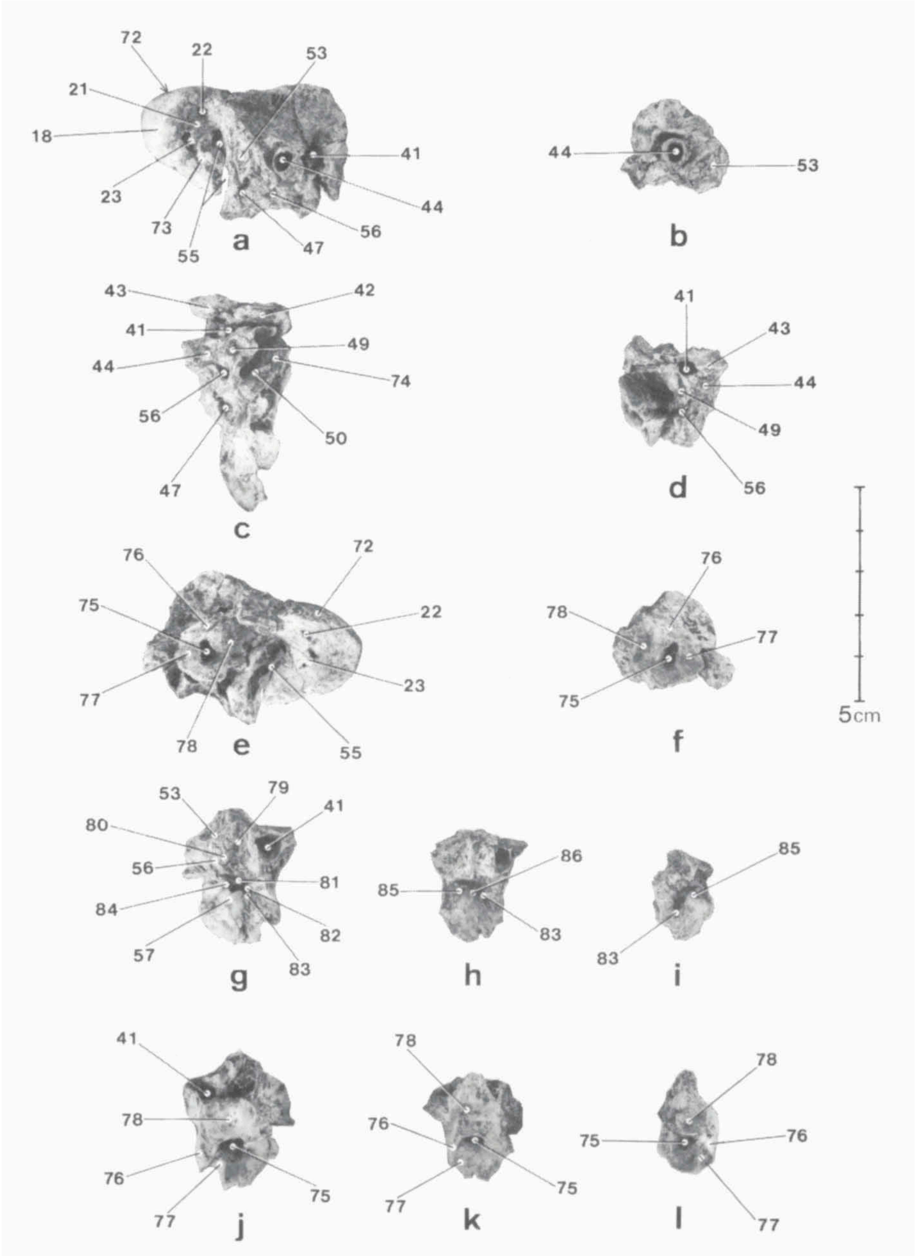


Plate 6



Fragments of the ear region of hoplitomerycids.
A, C, E: RGM 261 092, e.r. type II, skull fragment dext., San Nazario 4.
A: lateral side; B: ventral side; C: medial side.

B, D, F: RGM 261 093, e.r. type II, ear region fragment sin., San Nazario 4.
B: lateral side; D: ventral side; F: medial side.

G, J: RGM 260 933, e.r. type III, petrosal dext., San Giovannino 1.
G: lateral side; J: medial side.

H, K: RGM 261 100, e.r. type II ?, petrosal dext., Gar. 4.
H: lateral side; K: medial side.

I, L: RGM 261 096, e.r. type IV, petrosal sin., San Nazario 4.
I: lateral side; L: medial side.

Plate 6

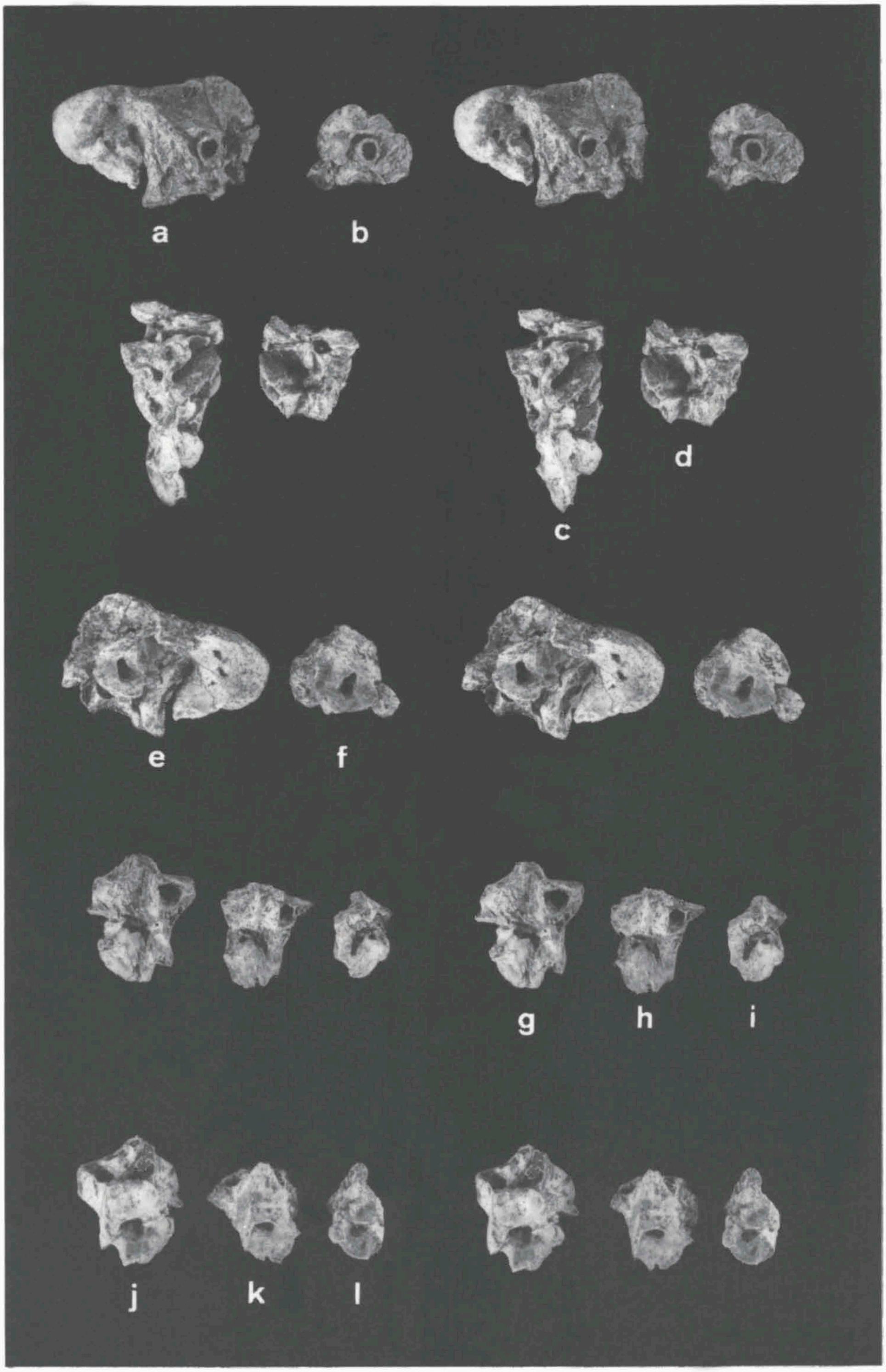
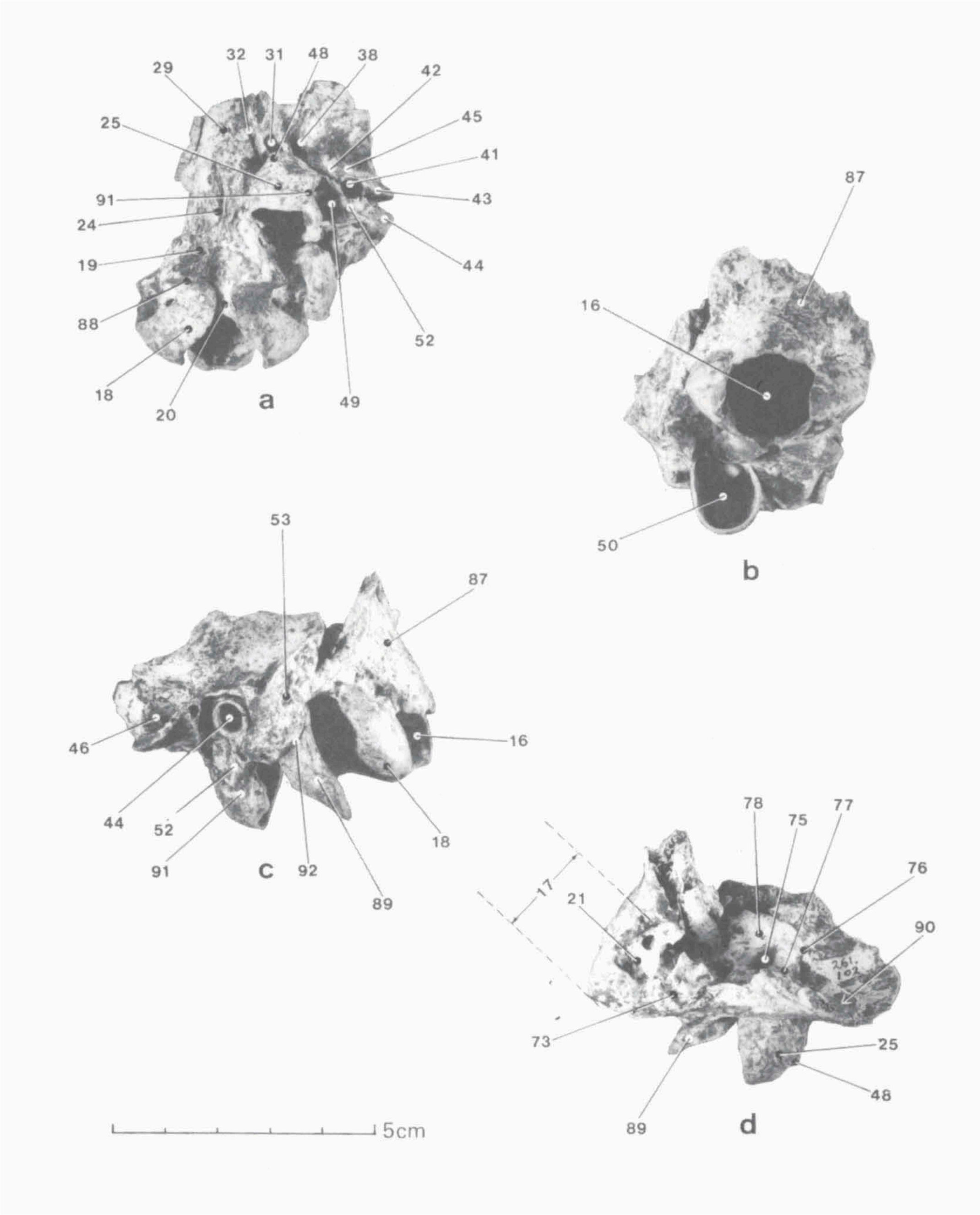


Plate 7



RGM 261 102, e.r. type V, basicranium and ear region sin., Gervasio quarry.
A: ventral side; B: nuchal side; C: lateral side; D: medial side.

Plate 7

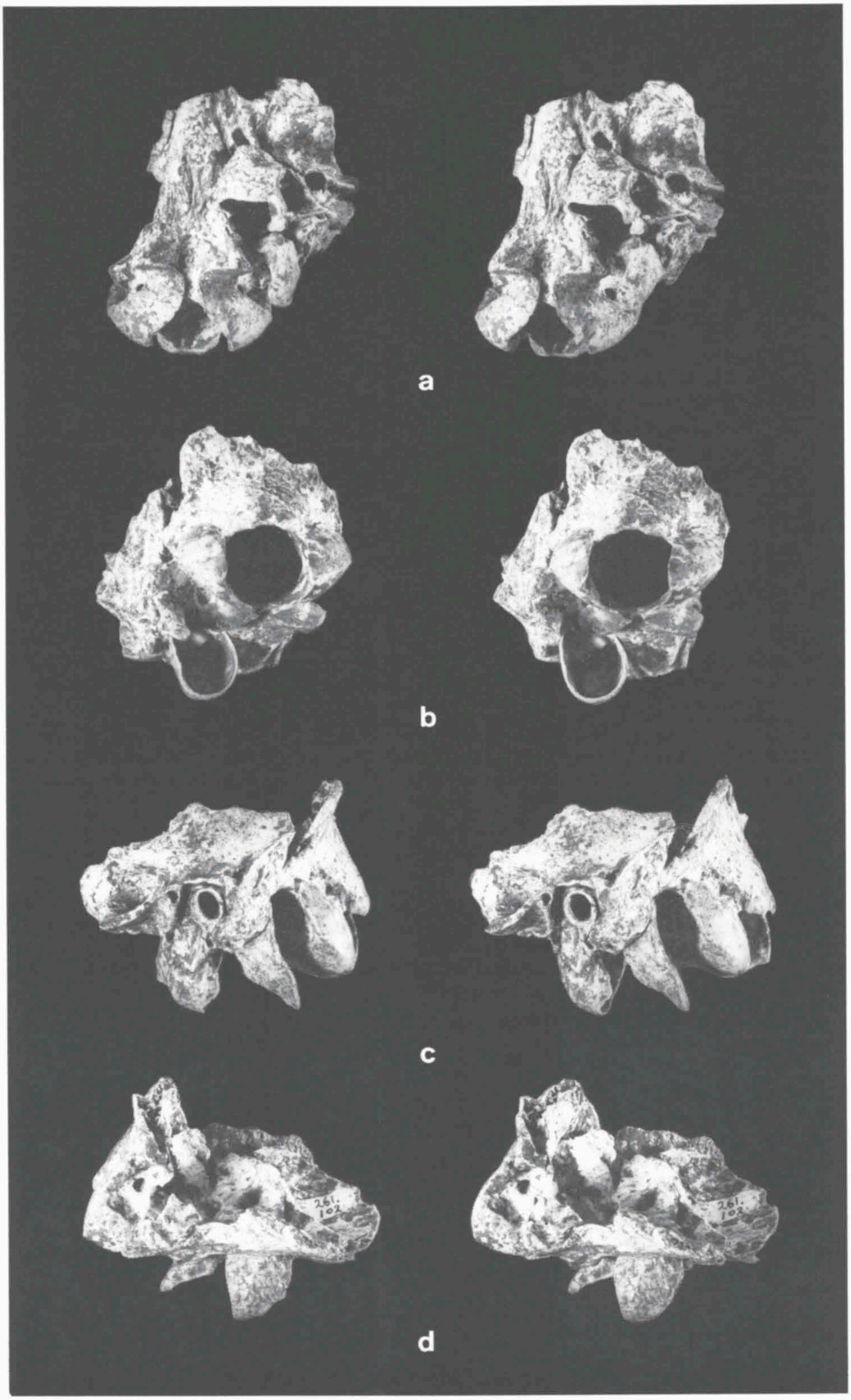
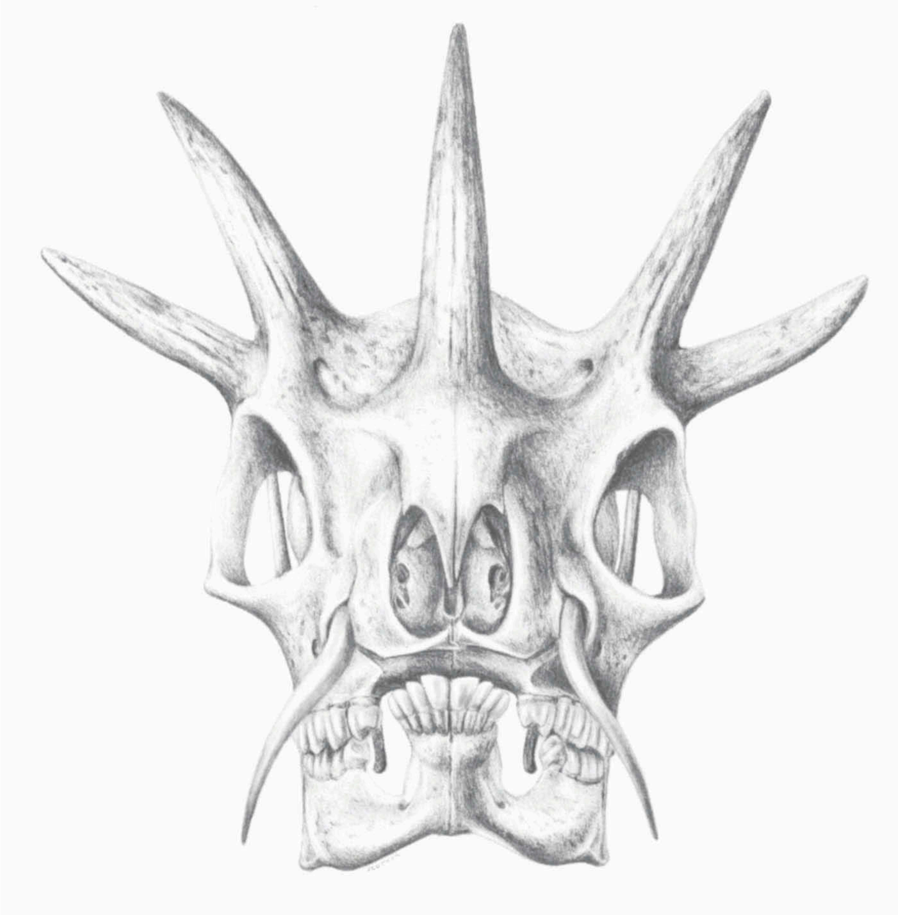


Plate 8



Hoplitomeryx matthei. Reconstruction of the cranium, anterior view. The morphology of the anterior part of the nasalia, the premaxillae, the zygomatic arch, and the postorbital bar is not known and is inferred from the skull morphology of Recent pecorans.

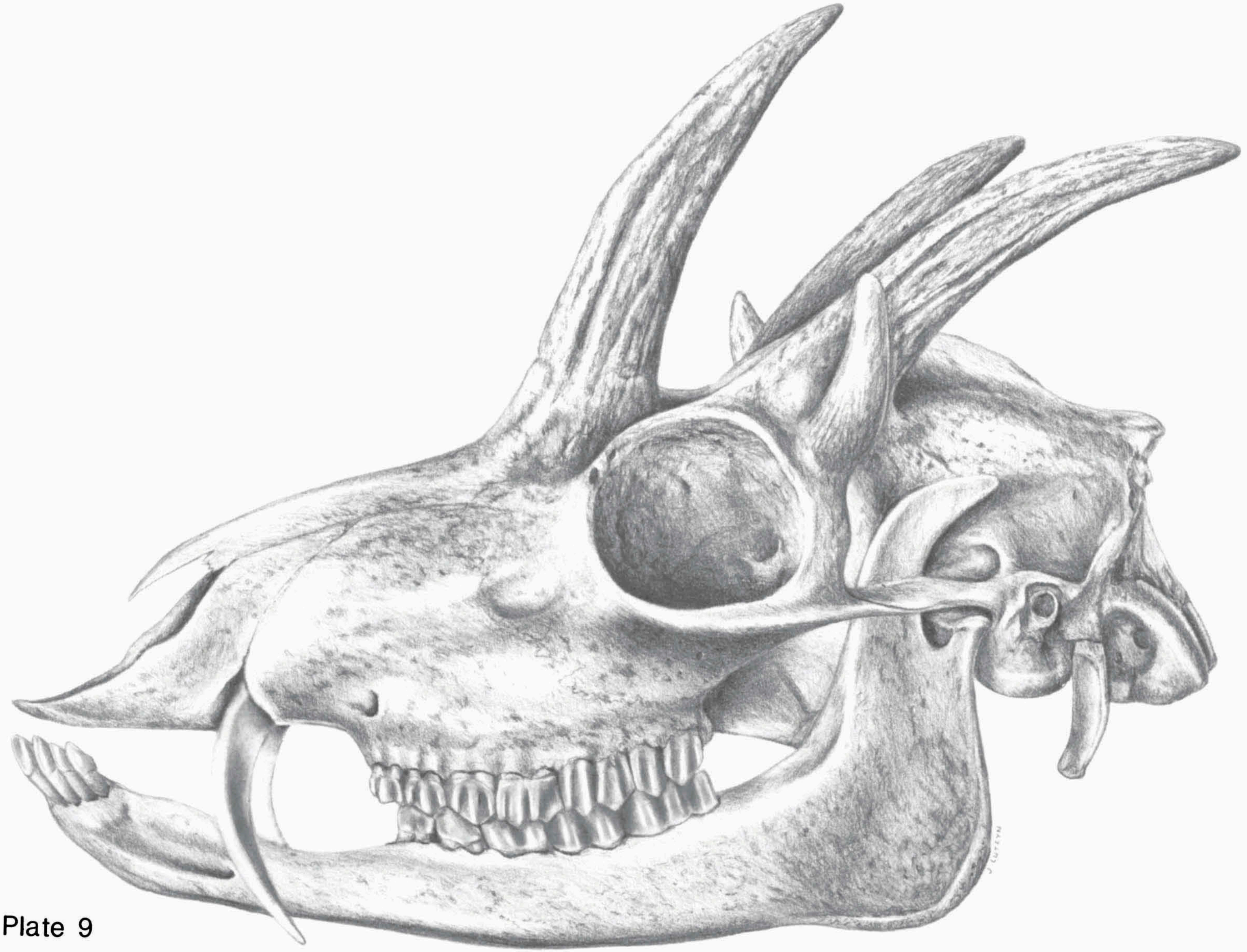


Plate 9

Hoplitomeryx matthei. Reconstruction of the cranium, left side. The morphology of the anterior part of the nasalia, the premaxillae, the dorsal part of the maxillae, the zygomatic arch, the postorbital bar, and the paroccipital process is not known and is inferred from the skull morphology of Recent pecorans.

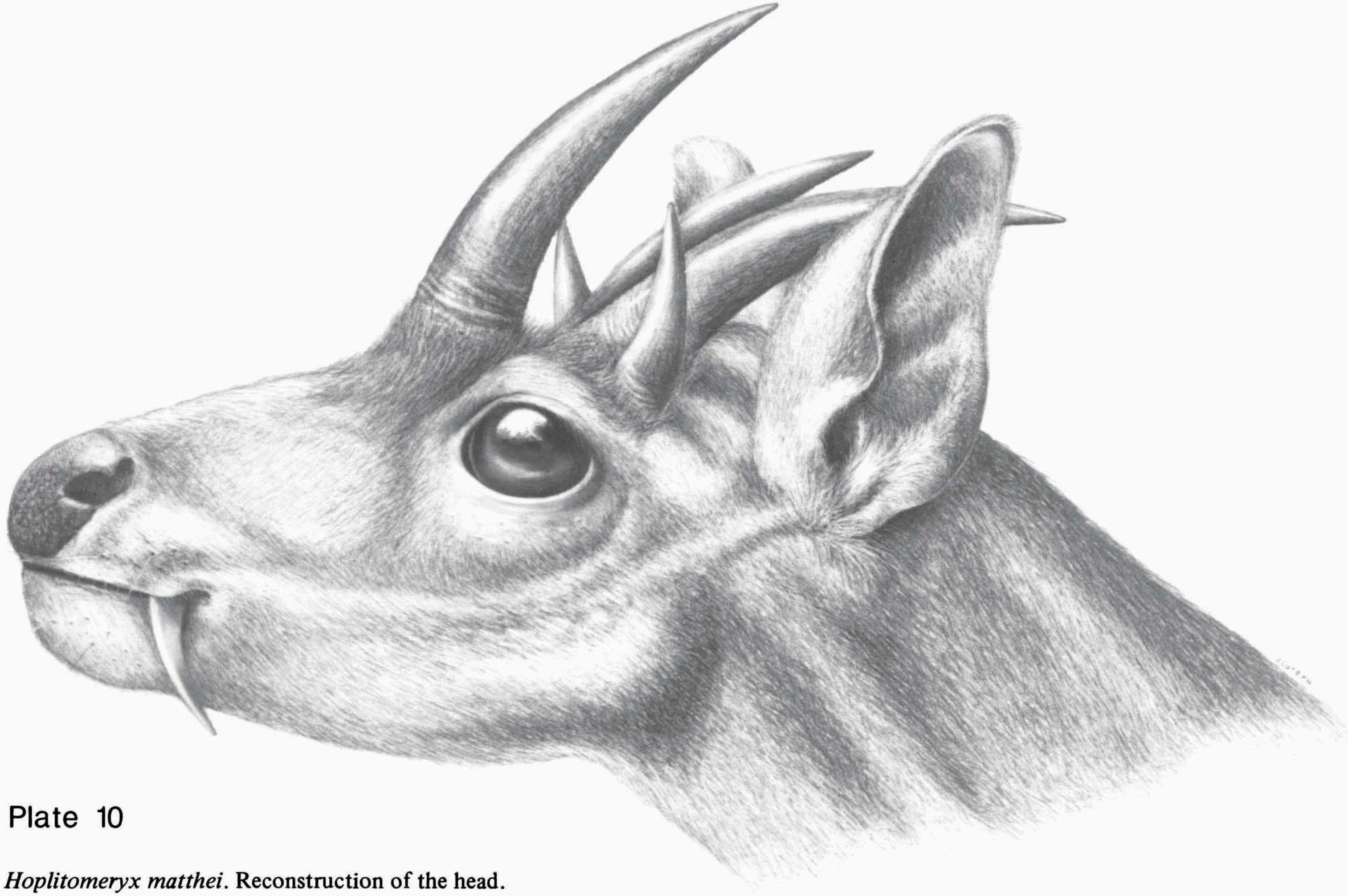


Plate 10

Hoplitomeryx matthei. Reconstruction of the head.