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The Turolian fossil artiodactyls from Scontrone (Abruzzo, Central Italy) and their paleoecological and paleogeographical implications

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ABSTRACT – In 1990, a rich fossiliferous site was found in the outskirts of Scontrone (L'Aquila), in the National Park of Abruzzo. The site yields fossil remains of reptiles and continental mammals, which are contained in Lower Tortonian marine calcarenites. The macromammals are similar to those found in a recent past in the karst fissure fillings of the Gargano peninsula, which raises an intriguing problem of Late Neogene paleogeography. The present is a preliminary description of the artiodactyls from Scontrone. At least seven hypothetical taxons are recognized; one of these is referred here to *Hoplitomeryx*, a genus known until now only from Gargano. The *hoplitomeryxids* are undoubtedly the most puzzling and mysterious of the fossil mammals found at Scontrone. In the literature these artiodactyls are classified as representatives of the *Cervoidea*. The writers find that these bizarre creatures show a mixture of cervid-, giraffid- and bovid-like features, together with characters which are absolutely autoapomorphic. Therefore, trying to force the *hoplitomeryxids* into the pigeon-holes of an established classification is probably premature or even inopportune. At the present state of knowledge, the most reasonable interpretation is to see the *hoplitomeryxids* as peculiarly adapted holdovers of the primitive ruminant stock. The characters of the *hoplitomeryxids* are suggestive of a life in a quite dense forest environment; the occurrence of warm and moist forests in the Abruzzo-Apulo domain is also documented by other multidisciplinary observations. An intriguing question is the source area of the Scontrone fauna. Two possible routes of immigration are suggested: one around, the other across the Adriatic sea, along the so called Apulo-Dalmatic archipelago. The former way of immigration seems however quite improbable in consideration of the fact that the Abruzzo-Gargano faunas are thoroughly distinct from the Miocene Romagna and Tuscan faunal associations.

RIASSUNTO – [Gli artiodattili fossili del Turoliano di Scontrone (Abruzzo) e loro implicazioni paleoecologiche e paleogeografiche] – Nel 1990 fu scoperto un ricco giacimento fossilifero nei dintorni di Scontrone (L'Aquila), nel Parco Nazionale d'Abruzzo. Il sito restituisce resti fossili di rettili e di mammiferi continentali, che sono contenuti in calcareniti marine del Tortoniano inferiore. I macromammiferi sono simili a quelli rinvenuti recentemente nei riempimenti di fessure carsiche della penisola del Gargano, cosa che fa sorgere un interessante problema di paleogeografia del Tardo Neogene. Quella presente è una descrizione preliminare degli artiodattili di Scontrone. Vengono riconosciuti almeno sette diversi taxa, uno di questi è qui riferito a *Hoplitomeryx*, un genere conosciuto finora solo dal Gargano. Gli *hoplitomeryxidi* sono senza dubbio i mammiferi più curiosi e misteriosi fra quelli trovati a Scontrone. Nella letteratura questi artiodattili vengono classificati come rappresentanti dei *Cervoidea*. Gli scriventi ritengono che queste bizzarre creature mostrino un insieme di caratteri di tipo cervide, giraffide e bovide, unitamente a caratteri assolutamente autoapomorfi. Perciò, cercare di forzare gli *hoplitomeryxidi* nelle caselle di una delle classificazioni esistenti è probabilmente prematuro o anche inopportuno. All'attuale stato delle conoscenze, l'interpretazione più ragionevole è di considerare gli *hoplitomeryxidi* come dei sopravvissuti di un ceppo ruminante primitivo caratterizzati da peculiari adattamenti. I caratteri degli *hoplitomeryxidi* suggeriscono una vita in ambiente di foresta piuttosto densa; la presenza di foreste calde e umide nel dominio apulo-abruzzese è anche documentata da altre osservazioni multidisciplinari. Un problema interessante è la zona di origine della fauna di Scontrone. Vengono suggerite due possibili rotte d'immigrazione: una attorno, l'altra attraverso il Mar Adriatico, lungo il cosiddetto arcipelago apulo-dalmatico. La prima via appare alquanto improbabile in considerazione del fatto che le faune Gargano-abruzzesi sono completamente diverse dalle associazioni faunistiche romagnole e toscane del Miocene.

INTRODUCTION

The discovery, in 1990, of a rich Vallesian (Lower Tortonian) vertebrate community at Scontrone, a small village located at the southern border of the National Park of Abruzzo, reopened intriguing paleoenvironmental and paleogeographical problems. The site yields fossil remains of reptiles (crocodiles and chelonians) and continental mammals, which are contained in Lower Tortonian marine calcarenites. The macromammals from Scontrone are very similar to the ones that were recovered from the Gargano fissure fillings in the

late 70s (Rustioni *et al.*, 1992). In Gargano, the macromammals are accompanied by several micromammals, such as *Prolagus*, *Microtia* and other rodents, while no micromammals have been found until now at Scontrone.

Scontrone is expected to provide a rich amount of information on the Miocene of Italy and, hopefully, of the Central Mediterranean as well.

Although so few, the fossil mammal material which has hitherto been freed from the calcarenites of Scontrone permitted the recognition of a lutrine carnivore and some artiodactyls, among which *Hoplitomeryx* Leinders 1983 and a larger-sized

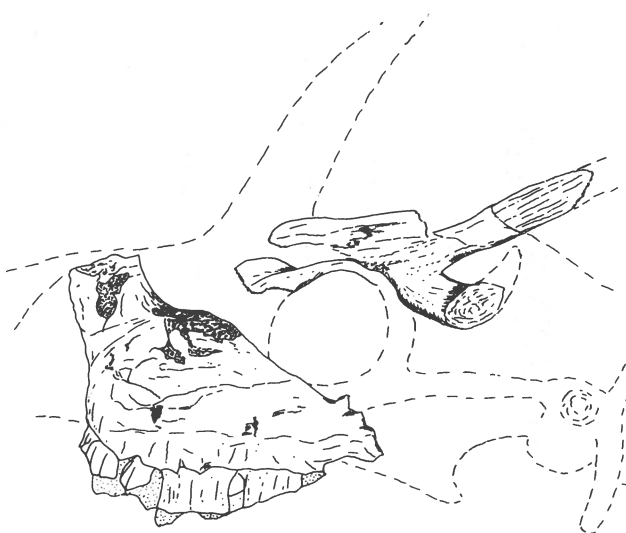
Amphimoschus-like cervid (Rustioni *et al.*, 1992). The ensuing is a detailed description of the artiodactyl material presently known from Scontrone.

Unfortunately, the cranial material and upper dentitions are represented, at the moment, only by a fragmental *Hoplitomeryx* skull, few maxillary fragments still bearing some cheek teeth and some isolated upper teeth. Most of these elements belong to young individuals. Adult or even aged individuals are represented in the quite more abundant and varied sample of mandibles and lower dentitions. Several morphotypes have been discriminated; however, any tentative to taxonomically assess the morphotypes is purely speculative at the moment. Also the postcranial remains are fairly well represented, but their possible relations with the cranial, mandibular and dental remains are obscure.

CRANIAL REMAINS AND UPPER DENTITIONS

SKULL SCT 17 (Text-fig. 1)

The most significant fragmental skull found at Scontrone is presently that figured by Rustioni *et al.* (1992) (SCT 17). It was referred to *Hoplitomeryx* Leinders because of the occurrence of a distinctive orbital horncore, typical of this genus. The specimen is still mostly embedded in the rock matrix; this prevents a full description of it. Six isolated *Hoplitomeryx* horncores have also been found at Scontrone, two nasal ones (one catalogued as SCT 28) and four orbital ones.



Text-fig. 1 - *Hoplitomeryx* sp.: Fragmentary skull SCT 17 with orbital horncores and tentative restoration of the specimen (redrawn from Rustioni *et al.*, 1992). About 1/2 natural size.

MAXILLARY SCT 18 (Pl. 1, fig. 1)

This specimen consists in a fragmentary left maxillary of a young, large-sized artiodactyl, more or less the size of a present-day fallow deer. The dentition preserved is represented by the emerging third upper premolar, by the last deciduous upper premolar, which is being replaced by the emerging fourth upper premolar, and by the first two molars. The teeth are brachyodont⁽¹⁾. The deciduous fourth upper premolar is molariform and is characterized by the occurrence of a very prominent paracone labial rib and by the complete absence of a metacone rib. The styles are well developed, especially the parastyle and, even more, the mesostyle, while the metastyle is somewhat weaker. The protocone is larger than the hypocone and its rear ala is fairly bent forwards. Wear causes the fusion of the rear alae of the paracone and protocone and of the anterior ala of the hypocone. A small entostyle occurs, while there are no cingula. The definitive third upper premolar shows prominent styles and paracone ribs on the labial enamel wall. The protocone is weak and fused to a robust hypocone. The metacone is just slightly developed. Two marked spurs issue from the lateral enamel walls of the lingual cusps, one from the anterior ala of the protocone, the other from the posterior ala of the hypocone. No cingula or entostyles occur. The lingual enamel wall is rougher than the labial one. The first upper molar bears a robust parastyle and an even stronger mesostyle; both structures are even more prominent than the considerably developed paracone rib. The metacone rib is lacking. The rear alae of the lingual crescents enlarge to some extent. No cingula or entostyles occur; on the contrary, the lingual crescents are separated by a very narrow fissure down to the enamel collar. The lingual enamel wall is rougher than the labial one. The second upper molar is practically an enlarged replica of the first molar.

ISOLATED UPPER TEETH

A certain number of isolated cheek teeth attest to the existence of other artiodactyls, smaller-sized than SCT 18. The teeth can be separated into two groups on morphological and dimensional grounds; therefore at least two other taxons seem to exist in

(1) The cheek teeth of all the specimens from Scontrone are worn. This prevented any quantitative assessment of brachyodontology and hypsodontology. Teeth are considered brachyodont if the labio-lingual breadth at the collar exceeds considerably the labio-lingual breadth at the occlusal plane; if the two breadths are comparable, the teeth are called hypsodont.

the present sample from Scontrone. One is represented by few isolated small-sized brachyodont molars, characterized by triangular, very acute lingual crescents, small entostyles, prominent styles and robust paracone and metacone ribs. These teeth bear no cingula.

The other taxon is smaller-sized than the former and is represented by few isolated deciduous teeth and few molars, all characterized by smooth buccal walls with no evidence of styles or ribs. The third and fourth upper deciduous teeth of this hypothetical taxon are similar. They have lingual cusps slightly more developed than the labial ones and a very weak entostyle on the mesial margin of the hypocones.

MANDIBLES AND LOWER DENTITIONS

Leinders (1983) only figured the mandibles and teeth of *Hoplitomeryx* and did not provide any further information. The only characteristic which he reported was that *Hoplitomeryx* lacks the second lower premolar. Therefore the lower cheek teeth formula is 2.3.

Three mandibles from Scontrone (SCT 16, SCT 29 and SCT 50) (Pl. 1, fig. 2) are similar to the specimen illustrated by Leinders. These mandibles are therefore tentatively referred to *Hoplitomeryx*.

These mandibles appear characteristically sinuous in dorsal and ventral view. In lateral view the horizontal ramus is slender, especially in the symphyseal area. On the contrary, the alveolar corpus is latero-medially massive. The pterygoid fossa is deep, while the masseterine one is quite shallow. The ventral border of the masseterine fossa is well marked. The condyle is short and directed obliquely backwards and outwards, and slightly inwards and downwards. The rear gonion is projected backwards beyond the condyle. The mandibular scissure is rather evident. The mental foramen is placed in a very dorsal position and is elongated forwards by a deep groove.

The teeth are fairly hypsodont. Wear tends to emphasize the difference in height of the cuspids. The buccal enamel surfaces of all the teeth are considerably rougher than the lingual ones.

The fourth premolar is unmolarized. The paraconid is very reduced. The metaconid appears just slightly split. The lophids connecting the metaconid with the protoconid and the entoconid with the hypoconid are directed obliquely backwards to some extent. The entostylid is slightly developed. On the buccal wall the transition from the trigonid to the talonid is marked by a shallow vertical groove. No cingula occur.

The molars lack the «pli-palaeomeryx». The lingual crescents are obliquely directed backwards and inwards. The labial crescents are triangular and slightly oblique backwards. The mesostylids are more developed than the parastylids and metastylids. The metaconid and entoconid ribs are fairly prominent. All the molars bear a small ectostylid between the protoconid and the hypoconid. No cingula are present. The third lobe of the third molar is characteristically bi-cusped.

MANDIBLES SCT 73 AND SCT 77 (Pl. 1, figs. 3-4)

These fragmentary mandibles have sinuous horizontal rami. However, as compared to the supposed mandibles of *Hoplitomeryx*, the horizontal ramus is more depressed and more slender, especially in latero-medial direction, while the ventral border of the masseterine fossa and the mandibular scissure are far less evident. The ventral border of the horizontal ramus is sharp in ventral view.

The cheek teeth formula is 3.3. The teeth are more brachyodont than in *Hoplitomeryx*. The premolar row is decidedly reduced. The second and third premolars are not preserved in these specimens, but, judging by the dimensions of their roots, they must have been extremely small. The fourth premolar is unmolarized. The parastylid is robust, while the paraconid is extremely weak; the two structures fuse together with wear. The lophids connecting the metaconid with the protoconid and the entoconid with the hypoconid are approximately perpendicular to the sagittal axis of the tooth. The enamel surfaces are smooth. On the labial enamel wall a very deep vertical groove marks the transition from the trigonid to the talonid. No cingula occur in the fourth premolar. The molars have lingual crescents directed obliquely backwards like in *Hoplitomeryx*. All the molars bear ectostylids. The difference in height of the lingual and buccal cuspids is lesser than in the molars of *Hoplitomeryx*. The lingual walls of the molars are characterized by very robust ribs and stylids. The latter are wear-resistant structures, which give rise to a trough-like wear outline of the molars in medial view. Cingula occur at the base of the protoconids; they are particularly developed in the first molar. The buccal enamel walls are rough, while the lingual ones are smooth. The molars lack the «pli-palaeomeryx».

MANDIBLE SCT 51 (Pl. 1, fig. 5)

This fragmental right mandible still preserves its fourth premolar and most of its first molar. The teeth are very hypsodont. The fourth premolar is

unmolarized. Its paraconid and parastylid are fused together. The lophids connecting the metaconid with the protoconid and the entoconid with the hypoconid are obliquely directed backwards. The entostylid is well developed. No cingula occur. The outer enamel wall is rough and a very deep vertical groove separates the trigonid from the talonid. The first molar lacks its metaconid. The buccal crescents of this tooth are distinctly triangular, remarkably acute, and directed obliquely backwards. A small ectostylid occurs between the protoconid and hypoconid. The difference in height of the entoconid and hypoconid is lesser than in *Hoplitomeryx*. The lingual rib of the entoconid is fairly prominent. The metastylid is sharp, but not prominent lingually.

MANDIBLE SCT 20 (Pl. 1, fig. 6)

Rustioni *et al.* (1992) referred to this fragmental left mandible as to the «*Amphimoschus*-like» species. It is represented by a large-sized artiodactyl, approximately comparable in size with SCT 18. Few other isolated third lower molars of this taxon have been found at Scontrone at the moment. The mandible fragment preserves its complete molar row. The horizontal ramus is massive lateromedially. The molars are brachyodont. They all bear ectostylids, which grow progressively smaller from the first to the third molar. The lingual crescents are asymmetrical and directed obliquely backwards. Faint traces of cingula are present at the bases of the protoconids. The buccal enamel walls are rough, the lingual ones are smooth. The metaconid ribs are fairly prominent, while the entoconid ribs are slightly developed. The third lobe of the third molar is distinctly bi-cusped.

OTHER UNCATALOGUED FRAGMENTAL MANDIBLES

Three other uncatalogued mandible fragments, a right one and two left ones, seem to attest to the existence of still another artiodactyl species. Two of these specimens still preserve their second and third

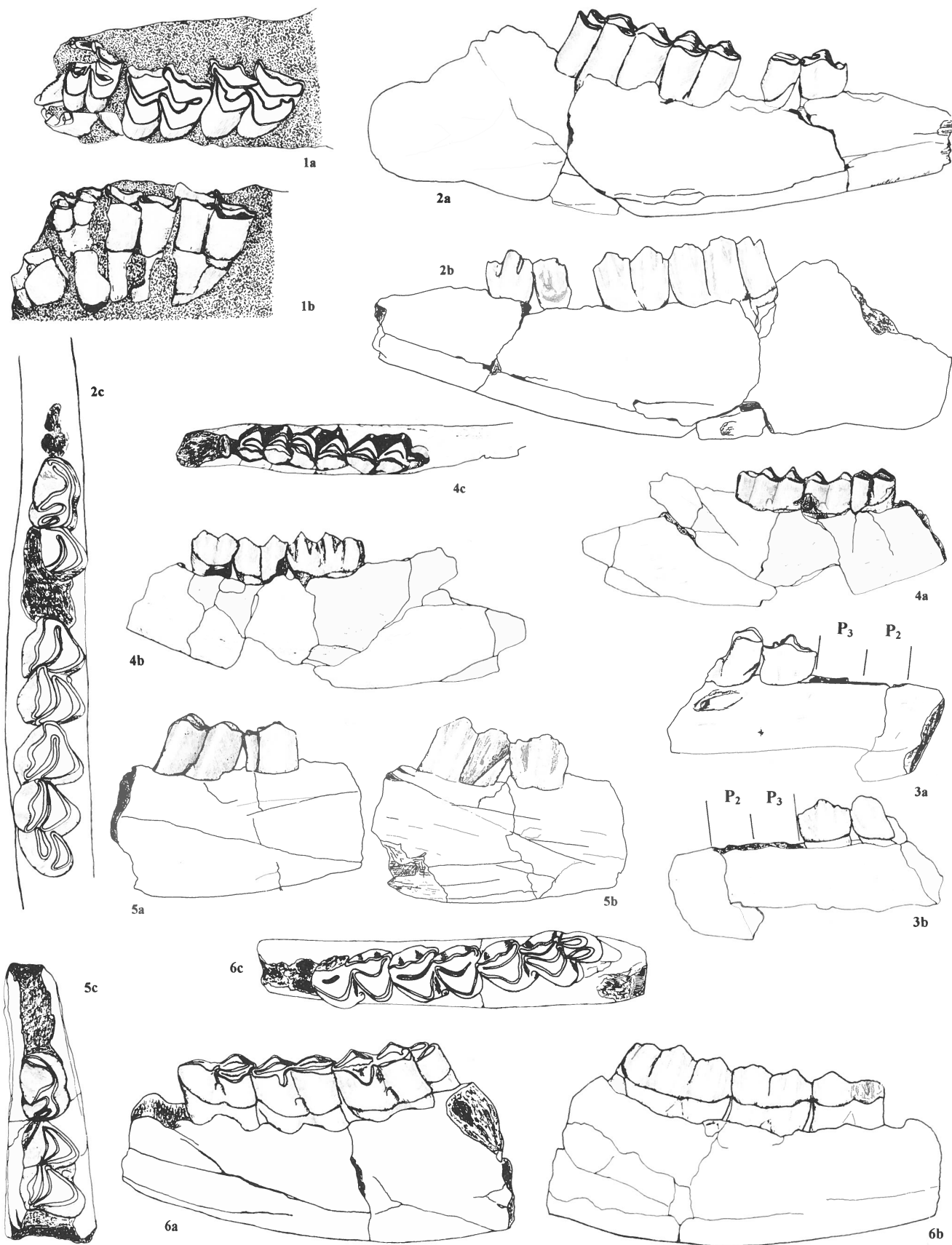
molars, the third one only the third molar. The most prominent feature of these fragmental mandibles is the unusually strong latero-medial depth of their rami; it could be described as a true pachyostosis. The teeth are brachyodont. No ectostylids occur. The lingual ribs are very weak. The lingual crescents are relatively less oblique than in the other specimens described above. The buccal enamel wall is rough, the lingual one is smooth. The lingual cuspid of the third lobe of the third molar is complete, while the buccal one forms a weak posterior loop.

POSTCRANIAL ELEMENTS

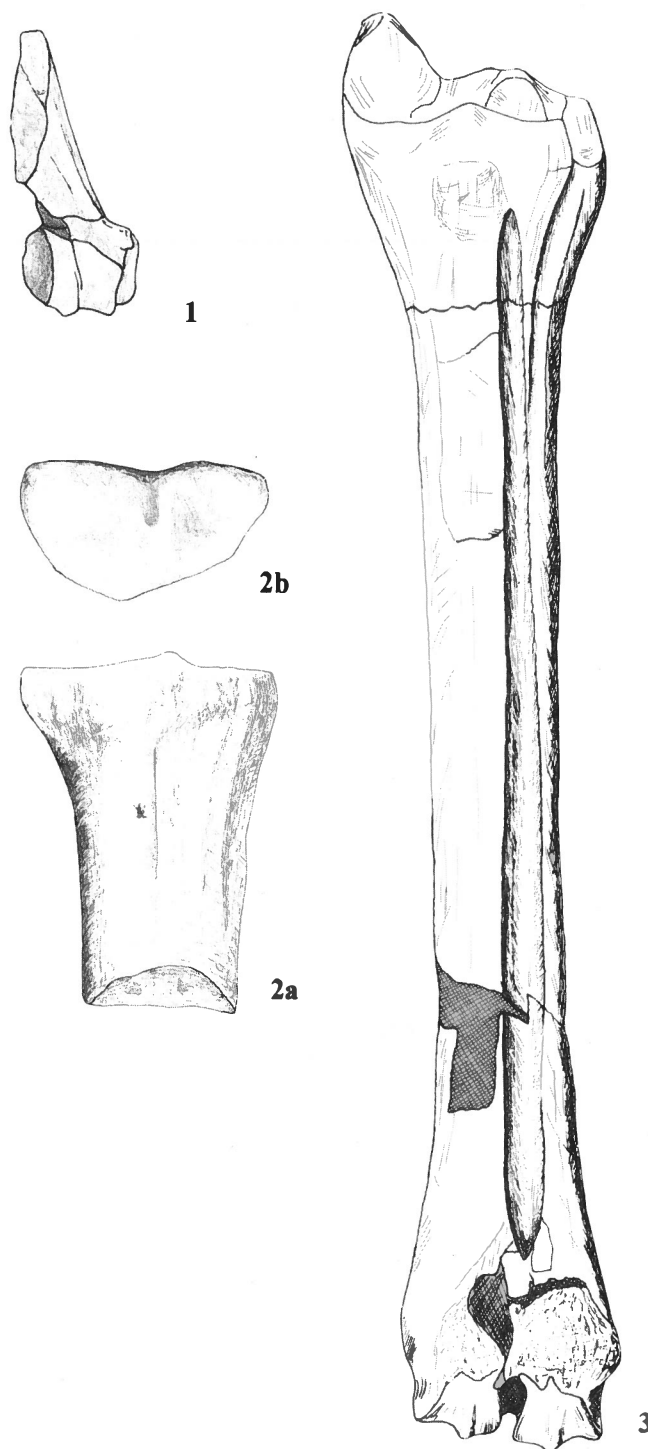
Two fragmental scapulae, a right, very large-sized one (SCT 30) and a left, much smaller, delicate one (SCT 21), are presently known from Scontrone. The former may belong to a large-sized taxon approximately the size of the fragmental maxillary SCT 18 or of the *Amphimoschus*-like fragmental mandible SCT 20, while the smaller one may be referred to *Hoplitomeryx* or to some of the other small-sized taxons described above. The larger scapula is massive. It preserves its glenoid cavity, but most of its blade is missing. The glenoid cavity is markedly oval in distal view. The supraglenoid tubercle is fairly salient, with a reduced coracoid process. The spine is not preserved, but it must have been rather well developed, judging by its base. It is so shifted cranially that the supraspinous fossa is reduced to a shallow groove. On the contrary the subspinous fossa is broad, but fairly shallow. A prominent relief stretches from the caudal margin of the blade obliquely towards the center of the lateral border of the glenoid cavity, verging upon the caudal face of the spine and separating the subspinous fossa from the neck of the scapula. The smaller scapula is very slender. Its glenoid cavity and most of its blade are not preserved. Also in this scapula the spine is quite shifted cranially, but in this case the supraspinal fossa, though narrow, is somewhat more developed. The subspinous fossa is

EXPLANATION OF PLATE 1

- Fig. 1 - Fragmentary left maxillary SCT 18: a) occlusal view; b) lingual view. Both figures about natural size.
 Fig. 2 - *Hoplitomeryx* (?): fragmentary right mandible SCT 29: a) lateral view; b) lingual view; c) occlusal view. Figures 2a, b: about natural size; figure 2c: about 1.5 natural size.
 Fig. 3 - Fragmentary right mandible SCT 73: a) lateral view; b) lingual view. Both figures about natural size.
 Fig. 4 - Fragmentary right mandible SCT 77: a) lateral view; b) lingual view; c) occlusal view. All figures about natural size.
 Fig. 5 - Fragmentary right mandible SCT 51: a) lateral view; b) lingual view; c) occlusal view. All figures about natural size.
 Fig. 6 - Fragmentary left mandible SCT 20: a) lateral view; b) lingual view; c) occlusal view. All figures about natural size.



broad and not too deep. Also this scapula has an elongated relief running from the caudal margin of the blade to the glenoid cavity. The anterior stylopodials are only represented by the distal fragments of two small-sized left humeri (one of which catalogued as SCT 31). The most significant characteristic of these bones is the unusual arrangement of the articular surface, which is markedly inclined downwards and outwards. The medial lip of the articular surface is conical; the trough is fairly deep; the lateral lip prominent but blunt; the condyle robust and massive; a curious epicondylar tubercle occurs. Only two fragmental left radii have been found, both of relatively small-sized forms. One is represented by a portion of a proximal epiphysis, the other lacks its distal epiphysis and is still articulated to the ulna. The diaphysis of the latter specimen is markedly arcuated forwards and its surface is very angular and irregular. The ulna is sealed all along its length. The metacarpals are represented by three left specimens. Two belong to the small-sized representatives (one of which catalogued as SCT 32), the other (SCT 22) to one of the large-sized forms. The proximal articular surfaces are not very well sculptured in the small-sized specimens. The relief separating the two components of the proximal articular surface is placed laterally to the median trough. The palmar faces of all three the specimens are just slightly concave. In the large-sized specimen the palmar surface of the diaphysis is fairly concave and the distal articular surfaces are carinated anteriorly. The femurs are only represented by several small-sized isolated capita and by the distal condyles of a right femur of a very large-sized form. The capita show wide but shallow ligament fossae. Six astragali were found, all belonging to the small-sized representatives. They are all characterized by a deep fossa in the center of their dorsal face and by a marked depression on the lateral face. The postcranial sample includes a two astragali (SCT 15 and SCT 34), a complete left naviculocuboid-metatarsal cannon (SCT 35) and seven fragmental ones. The astragali belong to small-sized artiodactyls, approximately the size of *Hoplitomeryx*. They are regular in shape, only slightly compressed dorso-plantarly and show no torsion. The naviculocuboid-metatarsal cannons are the result of a peculiar fusion of the distal tarsal bones with the metatarsal cannon. They were first reported from the Gargano by Leinders and Sondaar (1974) and later attributed to *Hoplitomeryx* by Leinders (1983). The cannon bones have very angular and irregular surfaces and are separated by a deep and narrow dorsal groove, which enlarges distally. The groove is closed distally as occurs in the cervids, but



Text-fig. 2 - 1) Uncatalogued fragmentary distal portion of left humerus, cranial view. 2) Uncatalogued fragmented proximal half of left metacarpal bone: a) dorsal view; b) proximal view. 3) Uncatalogued left naviculocuboid-metatarsal cannon, dorsal view. All figures about 1.5 natural size.

the plantar surfaces of the cannons are completely flat or just slightly concave as those of bovids. The distal epiphyses are modestly expanded latero-medially. The distal articular surfaces are slightly prominent dorso-plantarly, but are keeled anteriorly; the keels slightly converge distally. The third metatarsal is more massive, but somewhat shorter, than the fourth one. Finally seven phalanges were found, five first ones and two second ones. All the specimens are slender and have a cervoid aspect. Two first phalanges belong to the large-sized representatives. On the volar faces of these bones there is a rough, elongated surface bounded by prominent, irregular margins. One of the large-sized phalanges bears a particularly broad distal articular surface; in the other specimen the same surface is narrower. The smaller-sized first phalanges are like reduced replicas of the former. The two second phalanges are very small-sized; although crushed latero-medially, they seem to have been rather thick dorso-ventrally in their proximal epiphyses.

OBSERVATIONS

The hoplitomerycids are undoubtedly the most puzzling and mysterious of the fossil mammals found at Scontrone. These bizarre creatures show a mixture of cervid-, giraffid- and bovid-like features, together with characters which are absolutely autoapomorphic. Leinders (1983) observed that the Hoplitomerycidae combine keratine-covered horns, a bovid characteristic, with others suggesting a cervid ancestry. On the basis of phylogenetic considerations and hypotheses, Leinders (1983) gave slight importance to cranial appendages in high-rank Ruminant classification and attributed considerable more weight to other characters. This reasoning led him to refer the hoplitomerycids to the Cervoidea because of their possessing two lacrimal orifices along the orbital rims and rear cannon bones with distally closed gullies. We find that these two characters alone may not be sufficient for substantiating this opinion. Primitive giraffid representatives, such as *Zarafa*, of the early Miocene of Africa, have paired lacrimal orifices; later representatives show only one. The Hoplitomerycidae show several of the giraffid characters listed by Ginsburg and Heintz (1966): non-deciduous, unbranched horncores which appear laterally compressed and fairly bent backwards; teeth with styles(-ids) relatively more developed than in cervids; humeri with rather deep trochlear troughs; metacarpal bones with the relief separating the two components of the proximal articular surface placed laterally to the median trough; cannon bones with flat volar surfaces. A very significant

SCT 18	Maxillary
D4/L	12
D4/l	12, 5
D4/Hl	5
D4/Hm	4, 8
P3/L	11, 6
P3/l	12
P3/H	7, 2
M1/L	16, 1
M1/l	
M1/Hpr	10, 1
M1/Hpa	
M1/Hm	
M1/Hh	11, 4
M2/L	13, 3
M2/l	
M2/Hpr	11, 1
M2/Hpa	
M2/Hm	
M2/Hh	9, 5

Tab. 1 - Measurements of maxillary SCT 18

character, whose importance was apparently overlooked by Leinders, is the peculiar occurrence of a nasal horncore; among fossil and living ungulates, only *Giraffa* has an unpaired forehead protuberance, which, however, is by no means comparable. Another character in common with the giraffids is the particular prominence of the occiput. Together with primitive, non-molarized fourth lower premolars, which distinguish them from the giraffids, bovids and specialized cervids, the hoplitomerycids have progressed metatarsal bones, characterized by anteriorly carinated distal articular surfaces. The fusion of the naviculocuboids with the rear cannon bones is certainly autoapomorphic, although primitive ungulates show a marked tendency towards the partial to total fusion of the tarsal bones. We believe that the distal closure of the dorsal gullies of the metatarsal cannons may be the result of convergence with the cervids and not necessarily the proof of a direct relation with the latter. Like cervids, and unlike bovids and giraffids, *Hoplitomeryx* shows small, roundish ante-orbital cavities; on the other hand, like bovids, and unlike cervids and giraffids, it shows no trace of ethmoidal vacuities. Its tympanic bullae are considerably developed. At the moment it is by no means possible to ascertain whether the fragmental humeri with the odd distal articular surfaces inclined downward and outward do belong to the hoplitomerycids or to one of the

other ungulates represented in the sample from Scontrone. In case, this further autoapomorphy would raise additional problems to the interpretation of the eco-ethology of these animals. Leinders (1983) included the Hoplitomerycidae in the Cervoidea, together with the Moschidae, Antilocapridae, Dromomerycidae and Cervidae; his proposed classification and phylogeny are illustrated in fig. 4, pag. 43. In this figure Leinders united the named families, with the exclusion of the Moschidae, in a general group which he called Cervidae, distinguished from the Bovoidea and the Moschidae by having two lacrimal orifices in place of one. These Cervidae should have all gone through an unantlered «Hydropotes stage». Then four lines arose: the Antilocapridae, which developed two non-deciduous, branched cranial appendages, covered by a keratine sheath; the Hoplitomerycidae, which developed five non-deciduous cranial appendages, covered by a keratine sheath; the Dromomerycidae, which appeared in what Leinders called the «Pre-antler stage», characterized by the development of non-deciduous, branched cranial appendages covered by skin; the Cervidae, which developed true deciduous antlers. Carroll (1988) proposed a quite different classification. He included four families in the Cervoidea: the Palaeomerycidae, among which he mentioned the genus *Dromomeryx*; the Moschidae; the Cervidae, which comprises not only the antlered genera, but also primitive, unantlered forms, such as *Hydropotes*; the Giraffidae. By definition, the Family Cervidae should include only ruminants with paired, deciduous, branched frontal appendages – the antlers; any other use of this name is improper and misleading. Leinders correctly separated the Hoplitomerycidae as a completely distinct family, but the use of the name Cervidae in a broader sense may perhaps be confusing. We even query whether it is opportune to include the Hoplitomerycidae into the Superfamily of the Cervoidea altogether, since, as we have seen in the foregoing descriptions, these ruminants show far more differences from the cervids than they show affinities, while they share a number of characters in common with the giraffids. Trying to force the hoplitomerycids into the pigeonholes of an established classification is probably premature or even inopportune. Ginsburg and Heintz (1966, pag. 4) expressed the opinion that the «...soi-disant Cervidés sans bois de la fin de l'Oligocène (*Amphitragulus*, *Dremotherium*, *Blastomerycinés*) ne representent pas, non des Cervidés primitifs, mais le stock commun d'où sortiront à l'époque suivante les Cervidés, d'une part, et les Giraffoidea, d'autre part». We agree with this view, in the sense that a pool of primitive ruminants

with heterogeneous and mixed characters existed in the Oligocene-early Miocene which should not be classified as cervids or even as Cervoidea. Several lines arose from this pool, the three main ones leading to the true cervids, giraffids and bovids, which certainly are related taxons, plus others represented by forms without or with non-deciduous cranial appendages, which would deserve to be distinguished into separated taxonomic units. The hoplitomerycids show remote affinities with *Eumeryx*, in the unmolarized lower premolars and in the prominence of the tooth ribs; with the leptomerycids, in the bi-cusped third lower molars; with the tragulids and gelocids, in the fusion of the tarsal elements. At the present state of knowledge, the most reasonable interpretation is to see the hoplitomerycids as peculiarly adapted holdovers of the primitive ruminant stock.

PALEOENVIRONMENTAL INFERENCES

Although still imperfectly known, the Scontrone macrofaunal community provides an interesting insight on the possible paleoenvironmental conditions of the area during the Late Miocene.

The crocodiles, chelonians and lutrine indicate the presence water. The crocodiles and chelonians also attest relatively high temperatures.

Hoplitomeryx had a short, massive muzzle and orbits faced more forwards than other artiodactyls; moreover, it must have had a fairly acute hearing, judging by its well-developed tympanic bullae. This contrasts with what is generally observed in open-space dwelling ungulates, which tend to develop lateral rather than stereoscopic vision and elongated muzzles and reduced tympanic bullae, as a consequence of their increased olfactory powers and of their relatively less keen sense of hearing. Most of the artiodactyl postcranial elements from Scontrone belong to sturdy animals. This applies especially to the ones tentatively attributed to *Hoplitomeryx*. These bones are generally short, massive elements. The elbow joint and tarsal region are very peculiar: the former was somewhat awkwardly projected sideways from the body, while the distal row of the tarsal bones are fused to the metatarsal cannon. Moreover, the radial tuberosity of the radius appears shifted in a quite distal position. Limbs so structured are unsuitable for running and unable to zigzag, while they are perfectly modelled for powerful thrusts.

Leinders (1983) supposed that the horns of *Hoplitomeryx* were a necessary defence against endemic giant birds of prey which lived in the Gargano

Tab. 2 - Measurements of mandibles SCT 16, SCT 20, SCT 29, SCT 51, SCT 77, SCT 50, SCT 73.

area: «...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» (pag. 47). We do not share Leinders' opinion. Scontrone has provided a rich amount of specimens, but not a single bone of bird has been found until now. In spite of this, *Hoplitomeryx* shows the same horn arrangement as the at least 4-million-years-younger representatives from Gargano. The lack of evidence is certainly not a conclusive argument against the actual presence of birds of prey at Scontrone. However, even more important is that Leinders' hypothesis finds no correspondence in present-day ruminants. Ruminants generally use horns for sexual display or for intraspecific fights; a use for defence from predators is exceptional, for example for the defence of young (S. Lovari, pers. comm., 1996; cf. Locati, 1990; Côté *et al.*, in press). Birds of prey actually concentrate their attacks on young ruminants, most of all because of their size and not because of their lack of horns. Size, and thus weight, of the prey is the critical factor limiting the activity of birds, because killing strategy consists in seizing the prey, raising it in air and finally tossing it to the ground. Horns are very slightly efficacious against this kind of strategy. Moreover, on anatomical grounds, the structure of the occipital region of *Hoplitomeryx*, characterized by condyles and foramen magnum arranged

obliquely downwards and backwards with respect to the main axis of the head, suggests that the animal probably bore its head uplifted. In case *Hoplitomeryx* had a fairly mobile head-neck complex, it may have been able to lower its head in the vertical plane to gore a frontal challenger and to swing it laterally as giraffes do today during ritual combats. These possible movements seem a reasonable explanation, in our view, of the occurrence of the backward projected horns and of the lateral orbital horns, respectively.

All in all, *Hoplitomeryx* seems fit for living in a fairly closed forest, woodland or in a relatively thick bush. Its acute hearing and its dreadful horns apparently depict *Hoplitomeryx* as a watchful and aggressive animal which may have fiercely challenged outsiders.

The other artiodactyl elements found until now at Scontrone and described above attest to the occurrence of at least other six different taxons, two relatively large-sized representatives and four smaller ones. The cheek teeth of most of these animals are brachyodont and most lack cingula. No cementum occurs in any of these supposed taxons. The dentitions of these representatives recall those of present-day fallow or roe deer, therefore of browser and browser/grazer rather than true grazer artiodactyls, which is not in contrast with the supposed ecology of *Hoplitomeryx*.

SCT 21	Scapula	SCT 34	Astragalus
DB	40	L	23,7
CS	26,9	l	15,6
LG	27,9	T	14,2
BG	21,5	SCT 35	Naviculo-metatarsal bone
SCT 22	Metacarpal bone	L	128,8
BS	19,1	BP	24,6
DS	12,2	DP	18,3
BD	31,4	BS	11,2
DD	16,1	DS	9,3
SCT 32	Metacarpal bone	BD	19,8
BP	21,5	BDA	18
DP	12,3	DD	11
BS	13,5	SCT 23	First phalanx
		L	24
		BP	9,3
		DP	12,8
		BD	9,2
		DD	8,7

Tab. 3 - Measurements of postcranial elements: scapula SCT 21; metacarpal bones SCT 22 and SCT 32; astragalus SCT 34; naviculo-metatarsal bone SCT 35; first phalanx SCT 23.

The Gargano finds also provide valuable paleoenvironmental information. Crocodiles, chelonians, a lutrine and several artiodactyls, among which *Hoplitomeryx*, are present here too, along with several other taxons not reported, at least until now, from Scontrone, such as amphibians, snakes, lizards, birds, insectivores, several rodents and lagomorphs (Freudenthal, 1971, 1973, 1976; De Giuli & Torre, 1984). Some faunal elements, such as the amphibians, crocodiles and chelonians attest relatively high temperatures, and these same taxons, together with the lutrine, confirm the presence of water. The insectivores include crocidurines, small galericines (De Giuli *et al.*, 1986b) and the giant *Deinogalerix koenigswaldi* (Freudenthal, 1972; Butler, 1981). The two subfamilies may suggest a humid forest environment (De Giuli *et al.*, 1985b, 1986a). The giant *Deinogalerix* perhaps represented the ecological substitute of a similar sized carnivore; middle- to large-sized carnivorous mammals were absent from the Gargano community. Freudenthal (1972) considered *Deinogalerix* a slow-moving animal capable to prey, at most, on rodents and lagomorphs, but he also supposed that *Deinogalerix* may have been a scavenger. We rather agree with the latter view, since we find that the giant insectivore from the Gargano appears to have been slightly able to snatch and firmly hold a struggling prey, but its long, slender body structure and its short, sturdy limbs seem to make it particularly fit for penetrating through thick shrubs. We acknowledge, however, that, given its features, *Deinogalerix* may have well occupied also the niche of a fish-eating predator, and might have thus been somehow linked with an aquatic environment.

According to De Giuli *et al.* (1985b, 1986a), the rodents from the Gargano indicate a transition from a moist forest to drier and more open environmental conditions. De Giuli & Torre (1984) and De Giuli *et al.* (1985a, b, c, 1986a, b, 1987) concluded that during the Messinian - earliest Pliocene an archipelago existed in the Apulo-Dalmatic realm, inhabited by a fauna that went through a rapid and strong endemization, as testified by the gigantism of micromammals and the absence of large carnivorous mammals.

For a number of considerations, Freudenthal (1971, 1972, 1976) dated the Gargano finds to the Middle-Late Miocene, De Giuli & Torre (1984), De Giuli *et al.* (1985a, b, c; 1986a, b; 1987) and Valleri (1984) to the Early Pliocene. Later on Freudenthal (1985) stressed that the micromammals probably colonized the Gargano in an age that «may be equal to, or somewhat older than, the age of the Crevillente faunas» (pag. 62). Freudenthal observed that there

are strict similarities between some distinctive components of the two faunas, such as between, respectively, *Cricetulodon* sp. and *C. fahlbuschi*; *Cricetus* sp. and *Hattomys* sp., from the Gargano, and *C. kormosi*, from Crevillente; *Apodemus* sp. and *Apodemus* cf. *primaevus*; and that *Stephanomys* from Crevillente is this most probable ancestor of *Microtia*. Mazza *et al.* (1995), on the basis of paleontological, stratigraphical and paleogeographical arguments, suppose that the only possible moments for the colonization of the Abruzzo-Apulian area by the micromammals are either the Late Oligocene - Early Miocene, or the Early Messinian, when wide-scale regressions occurred.

The laterites embedding the Gargano fossil vertebrates, the so-called «Terre Rosse», are podzolic soils. Today these soils, poor in humus, form under humid, sub-tropical climates, characterized by warm summers and mild winters, which favor intense bacterial activity, and support tropical to temperate rainforests. The red color of these sediments is due to staining, with the formation of iron hydroxides. It is true that pedogenesis may have occurred after the fissures had already been filled up or that the fissures may have been partially and repeatedly emptied and filled up in a number of following cycles. The latter would make us suspect that the fossil community from Gargano may not be homogeneous and that it may thus provide a misleading ecological and stratigraphical information, which is not the case of Scontrone, because all the fossils come from few closely packed layers. A detailed analysis of the facies characteristics of the fissure fillings from Gargano would likely dispel all doubts.

«Terre Rosse» sediments have been encountered and sampled at the base of the exposed sequence of Capo di Fiume quarry, near Palena, Maiella Mountains, from the Messinian layers of which an almost complete *Prolagus* skeleton was recently recovered (Mazza *et al.*, 1995). These sediments seem to be in a stratigraphical position more or less comparable with the vertebrate-bearing layers of Scontrone. Pedologic observations of these «Terre Rosse» sediments, carried out for us by Prof. Donatello Magaldi, agronomist of the University of L'Aquila with a past experience in paleo-pedology, confirmed that the staining is indeed primary, but obviously not datable. However, palinspastic maps published by Dercourt *et al.* (1986) show that Abruzzi-Apulian domain actually layed in a sub-tropical climatic belt during the Tortonian.

In summary, the Scontrone-Gargano paleobiogeographic province seems to have been characterized by tropical to sub-tropical conditions and to have been rather densely covered by shrubs or

woodlands for at least the whole time lapse running from the Early Miocene up to the earliest Messinian; then, as the climate became more temperate, drier conditions set up and landscapes opened up considerably (Mazza *et al.*, 1995).

We believe that the endemism of the Scontrone-Gargano faunas not necessarily attests the existence of an Apulo-Dalmatic archipelago, but may well result from the occurrence of a dense vegetation cover, which would have acted as a filter to the distribution of middle - to large-sized carnivores, with the indirect effect of causing the gigantism of the micromammals. We question if such a dense forest cover and if a fauna with so delicate and unstable ecological equilibriums could last for as long as about 6 million years without any marked evidence of change. This implicitly repropose the problem of the dating of the Gargano fauna.

SOURCE AREAS

An intriguing question is the source area of the Scontrone fauna. The primitive artiodactyl stock from which the hoplitomerycids may have arose was distributed in North America, Eurasia and Africa. Two possible routes of immigration have been suggested by Rustioni *et al.* (1992): one around, the other across the Adriatic sea, along the so called Apulo-Dalmatic archipelago. The former way of immigration seems however quite improbable in consideration of the fact that the Abruzzi-Gargano faunas are thoroughly distinct from the Miocene Romagna and Tuscan faunal associations.

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APPENDIX

TABLE CAPTIONS

Upper cheek teeth

D4/L - length of the fourth upper deciduous tooth

D4/I - breadth of the fourth upper deciduous tooth

D4/HI - buccal height of the fourth upper deciduous tooth

P3/L - length of the third upper premolar

P3/I - breadth of the third upper premolar

P3/H - height of the third upper premolar

M1/L - length of the first upper molar

M1/I - breadth of the first upper molar

M1/Hpr - greatest height of the protocone of the first upper molar

M1/Hpa - greatest height of the paracone of the first upper molar

M1/Hm - greatest height of the metacone of the first upper molar

M1/Hh - greatest height of the hypocone of the first upper molar

M2/L - length of the second upper molar

M2/I - breadth of the second upper molar

M2/Hpr - greatest height of the protocone of the second upper molar

M2/Hpa - greatest height of the paracone of the second upper molar

M2/Hm - greatest height of the metacone of the second upper molar

M2/Hh - greatest height of the hypocone of the second upper molar

Mandible and lower dentition

LP/3-M/3 - length of the lower toothrow from P/3 to M/3

LP/4-M/3 - length of the lower toothrow from P/4 to M/3

LM tot - length of the lower molar row: M/1 - M/3

P/3L - length of the third lower premolar

P/3I - breadth of the third lower premolar

P/3HI - buccal height of the third lower premolar

P/3Hm - lingual height of the third lower premolar

P/4L - length of the fourth lower premolar

P/4I - breadth of the fourth lower premolar

P/4HI - buccal height of the fourth lower premolar

P/4Hm - lingual height of the fourth lower premolar

M/1L - length of the first lower molar

M/1I - breadth of the first lower molar

M/1Hp - greatest height of the protoconid of the first lower molar

M/1Hm - greatest height of the metaconid of the first lower molar

M/1He - greatest height of the entoconid of the first lower molar

M/1Hh - greatest height of the hypoconid of the first lower molar

M/2L - length of the second lower molar

M/2I - breadth of the second lower molar

M/2Hp - greatest height of the protoconid of the second lower molar

M/2Hm - greatest height of the metaconid of the second lower molar

M/2He - greatest height of the entoconid of the second lower molar
M/2Hh - greatest height of the hypoconid of the second lower molar
M/3L - length of the third lower molar
M/3I - breadth of the third lower molar
M/3Hp - greatest height of the protoconid of the third lower molar
M/3Hm - greatest height of the metaconid of the third lower molar
M/3He - greatest height of the entoconid of the third lower molar
M/3Hh - greatest height of the hypoconid of the third lower molar
HM/3 - height of the horizontal ramus under M/3
HM/1 - height of the horizontal ramus under M/1
HP/4 - height of the horizontal ramus under P/4
Tmax - maximum thickness
Lsym-con - symphysis-condyle length
Lsym-gc - symphysis-gonion caudale length
Hgv-con - gonion ventrale - condyle height
Hsgm-gv - gonion ventrale - sigmoidal incisure height
DIP/3 - length of the diastema from the incisor area to the oral border of P/3

Scapula

DB - distal breadth
CS - breadth of the collum scapulae
LG - length of the glenoid cavity
BG - breadth of the glenoid cavity

Metacarpal bone

BP - breadth of the proximal epiphysis
DP - depth of the proximal epiphysis
BS - breadth of the diaphysis
DS - depth of the diaphysis
BD - breadth of the distal epiphysis
DD - depth of the distal epiphysis

Naviculo-metatarsal bone

L - greatest length
BP - breadth of the proximal epiphysis
DP - depth of the proximal epiphysis

BS - breadth of the diaphysis
DS - depth of the diaphysis
BD - breadth of the distal epiphysis
BDa - breadth of the distal articular surface
DD - depth of the distal epiphysis

Astragalus

L - greatest length
I - greatest breadth
T - greatest depth

First phalanx

L - greatest length
BP - breadth of the proximal epiphysis
DP - depth of the proximal epiphysis
BD - breadth of the distal epiphysis
DD - depth of the distal epiphysis

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