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A New *Ruscinomys* (Mammalia, Rodentia) from the Late Tertiary (Pikermian) of Samos, Greece

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INTRODUCTION

During my recent visit to the United States, R. H. Tedford of the American Museum of Natural History kindly drew my attention to a fossil jaw from Samos which, in his opinion, might belong to *Ruscinomys*. The specimen (A.M.N.H. No. 20766) is listed as an upper jaw of a "small Artiodactyl?"; it was collected at "Quarry 4," Samos Island, Greece, by the American Museum of Natural History expedition in 1924, which was led by Barnum Brown.

The author examined the entire Samos collection in the American Museum in search of additional material, unfortunately, however, without success. In general the description of a new species on the basis of a single specimen is not desirable, but in this case it is justified because: 1) the specimen is well preserved; 2) it differs from the known species of *Ruscinomys* to a great degree; and 3) it produces valuable information on the phylogeny of this genus and on its geographical distribution for before this time the genus had been known only from France and Spain.

I am very much indebted to Dr. Tedford for putting the specimen at my disposal, and for rendering valuable information on its provenance. I wish to express my thanks to Mr. P. Mein at Lyon for helpful sugges-

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tions and for giving the manuscript a critical reading.

SYSTEMATICS

ORDER RODENTIA

FAMILY CRICETIDAE ROCHEBRUNE, 1883

SUBFAMILY CRICETODONTINAE STEHLIN AND SCHAUB, 1951

GENUS *RUSCINOMYS* DEPERET, 1890

***Ruscinomys hellenicus*, new species**

Figure 1

HOLOTYPE: Right maxilla with M^1 - M^3 , A.M.N.H. No. 20766.

TYPE LOCALITY: Quarry 4, Samos Island, Greece.

AGE: Pikermian (Crusafont, 1950).

DIAGNOSIS: Molars moderately hypsodont, with continuous longitudinal lophs; smaller than those of *R. europaeus*, about the size of *R. schaubi*; the most characteristic feature is the relative length of M^3 , which, compared to the lengths of M^1 and M^2 , is longer than it is in any of the known species of *Ruscinomys* or *Cricetodon*, *sensu stricto*.

MEASUREMENTS (IN TENTHS OF MILLIMETERS): M^1 , 41.3 x 24.2; M^2 , 28.4 x 22.7; M^3 , 25.9 x 20.4.

DESCRIPTION

M^1 : The anterocone is clearly divided into two parts; the labial part appears to be slightly larger than the lingual part. The labial cusp is connected to the anterior wall of the paracone by a loph that does not reach the height of the wear surface of the paracone. The lingual cusp of the anterocone is connected to the protocone; this connecting ridge sends a transversal spur toward the lingual border of the molar. Anterior to the protocone and the latter spur, the molar border is transverse, forming a right angle with the lingual border of the protocone on the one hand, and with the lingual border of the anterocone on the other. The posterior branch of the protocone is directed posterolabial, meeting the transverse anterior branch of the hypocone at a point labial to the central axis of the molar. The paracone surface is rather broadened by wear, but appears to be directed posterolingual, toward the same meeting point; the posterior part of the loph from paracone toward metacone is directed posterolabial and lies on a straight line with the posterior branch of the protocone; thus, the four mentioned elements form an X-pattern. It is not certain whether a mesoloph was present or not, because of the degree of wear of the molar. Hypocone and metacone form a continuous loop at the posterior end of the molar. The posterolabial spur

from the paracone does not reach the top of the metacone. The main lingual valley is deep and narrow; in a horizontal plan it is directed slightly backward. The two valleys in the center of the molar are wide and shallow. The walls of the main cusps are inclined anteriorly, and consequently so are the valleys. The molar probably has four roots.

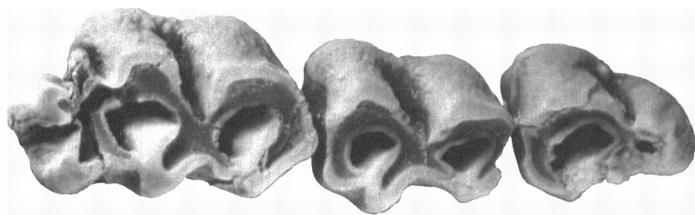


FIG. 1. Holotype of *Ruscinomys hellenicus*, new species, A.M.N.H. No. 20766, right M¹-M³. Occlusal view. Ca. $\times 10$.

M²: There is no trace of an anterocone. The protocone forms a crescent that reaches the anterior border of the molar and continues labially as a transverse crest along the anterior molar border. At its labial end this crest curves backward at a right angle and reaches the anterior wall of the paracone. The walls of the cusps are not so much inclined as they are in M¹; consequently the valleys are cut into the molar almost vertically. The main lingual valley is somewhat wider than in M¹. In all other features M² is identical to M¹. The posterior part of the molar is damaged (see fig. 1).

M³: The anterior part of the molar, comprising protocone and paracone, is relatively and absolutely longer than it is in M². The protocone and its two branches form a very broad crescent. The posterior part of the molar is very short and narrow, being little more than a simple cone with a fossette in the top.

REMARKS

This species is referred to the genus *Ruscinomys*, but it might be referred to the genus *Cricetodon*, as well. Arguments for placing it in the genus *Ruscinomys* are based on its large size and on the fact that the labial lophs in all three upper molars are complete. Arguments for placing it in *Cricetodon* are based on the low degree of hypsodonty and on the fact that M¹ probably has only four roots. It is not worthwhile, however, to dwell on this problem unduly as it will be pointed out below the definition of these two genera is, in fact, a subjective matter at the present time.

COMPOSITION OF THE GENUS *Ruscinomys* Deperet, 1890

GENOTYPE: *Ruscinomys europaeus* Deperet, 1890, from the Pliocene of Serrat d'en Vacquer near Perpignan (France). Thaler (1966) described *R. europaeus* from Sète and Nîmes (France).

REFERRED SPECIES: (1) *R. schaubi* Villalta and Crusafont, 1956, from the Turolian of Los Mansuetos (Spain). Adrover (1963) cited this species from Los Aljezares near Teruel, from several localities near Concud and from Castralvo (all Calatayud-Teruel Basin, Spain). (2) *R. thaleri* Hartenberger, 1966, from the Vallesian of Can Llobateres (Spain). (3) *R. lavocati* (Freudenthal), 1966, from the "Vindobonian" of Hostalets de Pierola (Spain). The original description is based on material from the beds without *Hipparion* of Hostalets, and it placed this species in the genus *Cricetodon*. Hartenberger (1967) described a specimen from the beds with *Hipparion* (Vallesian) of Hostalets and referred the species to the genus *Ruscinomys*. It will be pointed out in the following discussion that it is not certain whether or not the material from the "Vindobonian" and the Vallesian represent the same species. (4) *Ruscinomys* aff. *europaeus* Thaler, Crusafont, and Adrover, 1965, from the Pliocene of Alcoy (Spain), which is stated to be of the size of *R. schaubi* and of the evolutionary stage of *R. europaeus*. (5) *Ruscinomys hellenicus*, a new species from the Pikermian of Samos.

During the past few years the number of species described within, or referred to, the genus *Ruscinomys* has risen from two to six. It is evident that this complex is closely related to the genus *Cricetodon*, as various authors have suggested. In fact, there is no well-defined limit between the two genera and several species may be placed in either of the two, depending on the personal conception of the various authors. This makes a redefinition of these genera desirable. However, this is impossible without a better knowledge of the phylogeny of *Cricetodon* and *Ruscinomys*. In the discussion following I will try to outline some of the problems involved.

DISCUSSION

As far as the phylogeny of *Ruscinomys* is concerned, two theories are current. The first was developed by Hartenberger and Thaler (1963), Thaler (1966), and Hartenberger (1966). It views the evolutionary lineage *Cricetodon decedens* → (?) → *R. thaleri* → *R. schaubi* → *R. europaeus*. The second theory is by Freudenthal (1966) and proposes the lineage *C. sansaniensis* → *C. lavocati* → *R. schaubi* → *R. europaeus*. Both theories imply a monophyletic origin of the genus *Ruscinomys*, and differ only in

the assumption as to which species of *Cricetodon* should be considered the direct ancestor.

The new species from Samos makes it necessary to revise these ideas. The extreme length of M^3 of *R. hellenicus* is a feature absent in all known species of *Cricetodon*, and, unless we assume a reversal of the general tendency of reduction of M^3 , this implies that the ancestor of *R. hellenicus* is unknown. Thus, the genus *Ruscinomys* has arisen from at least two different sources.

In my 1966 publication on *Cricetodon* and *Ruscinomys* I considered *C. lavocati* (later referred to *Ruscinomys* by Hartenberger, 1967) as the ancestor of *R. schaubi*. However, although these two species are closely related, I now think they are not exactly in the same lineage, because the labial lophs on the upper molars of *C. lavocati* are constructed slightly differently from those of *R. schaubi*. The pattern in *R. schaubi* cannot have been derived from the pattern in *C. lavocati*.

It is not impossible that two different species of *Ruscinomys* (resp. *Cricetodon*) did exist at Can Llobateres. Most of the first upper molars from this locality are clustered in the lower part of the field of variation, and only one specimen (the holotype of *R. thaleri*) is much larger. If two species exist, the name *thaleri* should be applied to the larger one. The exact pattern of M^1 of *R. thaleri* cannot be ascertained in full detail from the original description and figure. If, however, *R. thaleri* descends from *C. lavocati* (which is highly probable because of their geographical and stratigraphical proximity) the foregoing arguments tend to exclude *R. thaleri* from the ancestry of *R. schaubi*, as it is assumed that its ancestor *C. lavocati* already represented a sideline. Thus, the direct ancestor of *R. schaubi* is unknown, but most probably *C. lavocati* and *R. thaleri* are closely related to it. Their common ancestor probably had a short M^3 , unlike that in the ancestor of *R. hellenicus*.

Ruscinomys schaubi and *R. hellenicus* descend from two different species, and whether these species are called *Cricetodon* or *Ruscinomys* will depend on the drawing of an arbitrary line between these two genera. The criteria used up to the present by various authors to delimit *Cricetodon* and *Ruscinomys* are hypsodonty, the formation of labial lophs in the upper molars, and size. None of these features can solve the difficulty which has arisen as a result of the finding of *R. hellenicus*. The genus *Ruscinomys* is not a phylogenetic unit but a group of independent descendants from different species of *Cricetodon*, which resemble one another through parallel evolutionary trends. One of these parallel trends, not heretofore recognized, is found in the upper incisors.

As far as I know, the upper incisors of all "Burdigalian" and "Vin-

dobonian" species of *Cricetodon* have a smooth anterior face. ["Burdigalian" and "Vindobonian" are meant here as comprising the *Megacricetodon collongensis*-Zone and *Heteroxerus grivensis*-Zone as defined by De Bruijn (in press; De Bruijn and Van Meurs, 1967), thus excluding all localities in the *Hipparion* Range-Zone.] This is true, at least, for the *Cricetodon* species from Manchones, Arroyo del Val (prov. Zaragoza, Spain), Sansan (Gers, France), Vieux-Collonges (Rhône, France) according to a personal communication by P. Mein (Lyon), and all of the different fissures at La Grive-St. Alban (Isère, France). On the other hand, all species of *Cricetodon* and *Ruscinomys* from the Vallesian and Turolian of the Calatayud-Teruel Basin (Spain) have upper incisors with a groove in the anterior surface, which separates that surface into two steps, exactly as is the case in the Dipodoidea. This same feature can be seen on plate 3, figure a in Hartenberger (1967), a skull which Hartenberger refers to *R. lavocati* but which might as well belong to *R. thaleri*. I have not seen incisors from the Montredon or from Can Llobateres, but probably these are grooved too.

The upper incisors of *R. europaeus* are smooth, which excludes *R. schaubi* from the ancestry of *R. europaeus*. The upper incisor of *R. hellenicus* is not known.

We may conclude that prior to the appearance of *Hipparion* in western Europe all *Cricetodon* species have smooth incisors, whereas most of their descendants have the dipodoid type of incisor (as far as these incisors are known). Neither *R. europaeus*, the typical *Ruscinomys*, nor *R. hellenicus* can be regarded as a direct descendant of any known species of *Cricetodon*.

The evolution of *Cricetodon* and *Ruscinomys* at the Mio-Pliocene boundary is marked by the following features (some of which may be lacking in one or more lineages): development of labial lophs in upper molars; increase of hypsodonty; increase in size; grooved incisors; increased number of roots in M^1 . These features develop independently in a number of different lineages. It is evident that these lineages should be distinguished as different genera or subgenera in order to stress their different phylogenetic origin. This certainly is not yet possible as none of these lineages is sufficiently known. The present author intends to deal with this problem in more detail in a revised classification of the Miocene Cricetodontinae and the Cricetinae in collaboration with P. Mein at Lyon (to be published in the Leidse Geologische Mededelingen).

I have grouped in related units the known species of *Cricetodon* and *Ruscinomys* from Vallesian and higher levels in the following manner (see table 1). These groups may give an indication of the number and

TABLE 1
STRATIGRAPHIC DISTRIBUTION OF *Cricetodon* AND *Ruscinomys* IN EUROPE

Age	Group 1	Western Europe Group 2	Group 3	Greece Group 4
"Pliocene"	<i>R. europaeus</i>			
Turolian (Pikermian in Greece)		<i>C. sp. 1</i> <i>C. sp. 2</i> <i>R. thaleri</i> , <i>pro parte</i> <i>C. aragonensis</i> <i>C. nombrevillae</i>	<i>R. schaubi</i>	<i>R. hellenicus</i>
Vallesian			<i>R. thaleri</i> , <i>pro parte</i>	
<i>grivensis</i> -Zone		<i>C. decedens</i> <i>C. meini</i>	<i>C. lavocati</i> <i>C. sansaniensis</i>	
<i>collongensis</i> -Zone		<i>C. meini</i>	<i>C. sp.</i>	

the composition of the genera and subgenera to be distinguished in the future.

GROUP 1: (1) *Ruscinomys europaeus* Deperet, 1890, from Serrat d'en Vacquer, is the only true *Ruscinomys* now known. *Ruscinomys schaubi*, generally considered the direct ancestor of *R. europaeus*, cannot be so because it belongs to a different lineage. *Ruscinomys europaeus* is characterized by smooth incisors, well-developed labial lophs, very large size, and a high degree of hypsodonty. All species but *R. hellenicus* can be excluded as possible ancestors.

GROUP 2: (1) *Cricetodon nombrevillae* Freudenthal, 1966, from Nombrevilla. (2) *Cricetodon aragonensis* Freudenthal, 1966, from Pedregueras II C. (3) *Cricetodon* sp. 1 in Freudenthal (1966) from Masia del Barbo II. (4) *Cricetodon* sp. 2 in Freudenthal (1966) from Masia del Barbo II. (5) *Ruscinomys thaleri* Hartenberger, 1966, *pro parte*? (if the material from Can Llobateres contains two species, the smaller one belongs to this group).

REMARKS: Phylogenetically these species are still isolated; none can be placed in an evolutionary lineage; additional material from other localities may prove that group 2 represents more than one group. A possible ancestor of group 2 (or of part of group 2) is *Cricetodon decedens* Schaub, 1925, from La Grive-St. Alban. All species within this group are of relatively small size; they have grooved incisors, moderately developed labial lophs in the upper molars, and moderate hypsodonty.

GROUP 3: (1) *Ruscinomys schaubi* Villalta and Crusafont, 1956, from

Los Mansuetos. (2) *Ruscinomys thaleri* Hartenberger, 1966, *pro parte?* (if the material from Can Llobateres represents two species, the larger one, including the holotype of *R. thaleri*, belongs to this group). (3) *Cricetodon lavocati* Freudenthal, 1966, from Hostalets ("Vindobonian").

REMARKS: The upper incisor of *lavocati* is unknown; if it is grooved, *lavocati* would be the only "Vindobonian" species with grooved incisors. Freudenthal (1966) supposed the presence of *C. lavocati* in levels with *Hipparion* (Viladecabals, Vallès-Penedès; compare also Schaub, 1947, p. 62). This material may belong to *R. thaleri*. The skull of *R. lavocati*, described by Hartenberger (1967) from Hostalets (Vallesian) certainly has grooved incisors. Maybe it belongs to *R. thaleri*. *Ruscinomys schaubi* also has grooved incisors. *Cricetodon lavocati* and *R. thaleri* are closely related to the ancestor of *R. schaubi*. *Ruscinomys schaubi* can no longer be considered to be the ancestor of *R. europaeus* with its smooth incisors. *Cricetodon sansaniensis* Lartet, 1851, may be the ancestor of group 3.

GROUP 4: (1) *Ruscinomys hellenicus*, new species from Samos. Evidently the ancestor of this species is not known, but it must have had a long M^3 . It therefore cannot be placed in group 2 or group 3, which are probably derived from species with a short M^3 . We cannot exclude the possibility, although this is a mere hypothesis, that *R. hellenicus* is close to the ancestor of *R. europaeus*.

SPECIES OF UNCERTAIN POSITION: (1) *Ruscinomys* or *Cricetodon* from Montredon. (2) *Ruscinomys* cf. *europaeus* from Alcoy. No material of these species was available.

Obviously, our present knowledge is insufficient to solve a number of problems. Therefore the author refrains from naming new genera or subgenera; it would not be advisable to introduce new names before the evolutionary lineages that they should represent are better known. For the same reason it is not yet possible to delimit *Cricetodon* and *Ruscinomys* against each other, or to judge the taxonomic value of the different groups. Three possibilities may be considered: (1) *Cricetodon*, *Ruscinomys*, *sensu stricto*, and each of the other groups mentioned to be recognized as separate genera; (2) *Cricetodon* and *Ruscinomys*, *sensu stricto*, to be considered separate genera, each comprising one or more subgenera; (3) *Ruscinomys*, *sensu stricto*, and all other units to be considered as subgenera of *Cricetodon*. A decision on one of these possibilities will be made in a future publication, in collaboration with Mr. P. Mein.

SUMMARY

A jaw of *Ruscinomys* (Mammalia, Rodentia) from the Pikermian of Samos is described as *Ruscinomys hellenicus*, new species. It proves the

complex origin of the genus *Ruscinomys*, which is not a phylogenetic unit, but which consists of a number of parallel evolutionary lineages. Each lineage should be distinguished as a separate genus or subgenus. However, none of these lineages is as yet sufficiently known at the present time to permit the erection of new genera or subgenera. The species described so far are grouped in an attempt to outline the composition of the genera or subgenera yet to be described.

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