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The European Adapid Primates *Agerina* and *Pronycticebus*

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ABSTRACT

The entire sample of *Agerina roselli* Crusafont-Pairo, 1967, from late early Eocene sediments of the Ager Basin, Spain, is described and compared with its nearest relatives, species of *Protoadapis*, *Pelycodus*, and *Pronycticebus gaudryi*. *Agerina* is not a necrolemurid as suggested by its describer, but is clearly a member of the Adapidae.

Two additional genera, described by Crusafont-Pairo in 1967 as omomyids, *Arisella* and *Pivetonia*, bear no particular resemblance to that group. The type specimen of *Arisella* appears to be an adapid, possibly that of *Agerina* or *Protoadapis*, whereas the sample described as *Pivetonia isabena* may be near *Pseudoloris parvulus*. Generic distinction from *Pseudoloris* is not warranted, although *Pseudoloris isabena* may be specifically distinct from *Pseudoloris parvulus*.

A reevaluation of the cranium of *Pronycticebus gaudryi* confirms the view that this taxon is a primitive adapid.

INTRODUCTION

In 1967 Crusafont-Pairo reported the presence of several known and some new genera of primates from the Ager, Isábena, Noguera Pallaresa, and Vich-Moià basins of northern Spain.

In addition to *Agerina roselli*, new genus and new species, from the Ager

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Basin, Crusafont-Pairo described *Pivetonia isabena*, new genus and new species, ?*Arisella capellae*, new genus and new species, and reported *Adapis priscus* Stehlin from the Isábena Basin. From the Noguera Pallaresa Basin he reported *Necrolemur erinaceus*, *Adapis* sp., and *Pseudoloris parvulus*, and from the Vich-Moià Basin described *Pseudoloris reguanti*, new species, and reported the presence of *Microchoerus ornatus* Stehlin, *Necrolemur* sp., and an adapid, indetermined. Although I have briefly examined these primates and reached some conclusions as to their relationships, I will restrict my comments to *Agerina* and to the two genera described by Crusafont-Pairo, *Arisella* and *Pivetonia*.

Both *Arisella* and *Pivetonia* were classified within the Omomyidae, a view I cannot accept. *Arisella*, based on a single third upper molar, is distinctly adapid in appearance. Recovery of additional specimens of this taxon may very well prove *Arisella* to be a synonym of one of the European Eocene adapids, *Protoadapis* or *Agerina* in particular. *Pivetonia*, in my opinion, does not warrant generic separation from *Pseudoloris*, whether specific distinctness of *Pivetonia isabena* from *Pseudoloris parvulus* is proved or not.

The purpose of the present paper is primarily to describe and re-evaluate *Agerina* Crusafont-Pairo, 1967, and to discuss briefly some problems related to close relatives of *Agerina*, *Protoadapis* and *Pronycticebus*. When Crusafont-Pairo (1967, p. 618) reported the genus he illustrated only a single molar and gave a brief diagnosis. A relatively large sample of this taxon graciously lent me by Professor Crusafont-Pairo, however, allowed a more detailed analysis of *Agerina roselli*.

I would like to express my sincere thanks to Prof. M. Crusafont-Pairo for the loan of the material described herein. He has not only given me his kind permission to study the undescribed specimens but he also allowed the description of the entire sample of *Agerina*. I thank Dr. Malcolm C. McKenna and Miss Susan Koelle for critical reading of the manuscript, Miss Biruta Ackerbergs who prepared figures 7, 12, and 13, and Mr. Spence Gustav who photographed figures 1-6. I am grateful for technical assistance to Miss Daria Dykyj for her help with the illustrations, and to Miss Miriam Siroky for her aid with the manuscript.

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ABBREVIATIONS

A.W., anterior width
L., length
N., number of specimens included in the sample

O.R., observed range
P.W., posterior width
 \bar{X} , mean

SYSTEMATICS

ORDER PRIMATES LINNAEUS, 1758

INFRAORDER LEMURIFORMES GREGORY, 1915

SUPERFAMILY LEMUROIDEA GRAY, 1821

FAMILY ADAPIDAE TROUESSART, 1879

SUBFAMILY ADAPINAE TROUESSART, 1879

AGERINA CRUSAFONT-PAIRO, 1967*Agerina* CRUSAFONT-PAIRO, 1967, p. 618.TYPE SPECIES: *Agerina roselli* Crusafont-Pairo, 1967, p. 618.

INCLUDED SPECIES: Type species only.

DISTRIBUTION: Cuisian, late early Eocene.

GENERIC DIAGNOSIS: The adapine adapid *Agerina* differs from all known species of *Protoadapis* in having P_3 and P_4 subequal in height, and in lacking a distinct, anteroposteriorly oriented cristid obliqua on P_4 talonid.

Unlike the trigonids of *Protoadapis* or *Pronycticebus*, those of *Agerina* are sealed off lingually by the union of the metaconid mesially and the paracristid distally. Although the paracristid is very low in *Agerina*, this crest invariably extends lingually almost to the limits of the metaconid, whereas in *Pronycticebus* the paracristid extends only midway on M_1 and slightly more lingually on M_2 and M_3 . Differences between *Agerina* and *Adapis* are most noticeable in the complete absence of a metastylid on the lower molars of the former.

Agerina differs from *Caenopithecus* in having a larger metaconid on P_4 and in lacking a metastylid and any traces of an entoconid. Talonid cusps of *Agerina* are generally less bulbous than those of *Caenopithecus*.

Agerina differs from *Pelycodus* in lacking the distinct, cuspsate paraconid on M_1 and in the generally less bulbous nature of the talonid cusps.

Agerina roselli Crusafont-Pairo, 1967

Figures 1-7; Table 1

Agerina roselli CRUSAFONT-PAIRO, 1967, p. 618.

TYPE: There was no type specimen designated in the original report. Until official Sabadell Museum numbers are given to the specimens, Ager No. 1, left mandible fragment with M_{2-3} , of the present report is designated as the holotype.

HYPODIGM: Because museum numbers are lacking, the designations

used in this study refer to the numbers given specimens in the legends of the stereoscopic photographs. The following specimens are from the "Les Salares" (La Atmetella) locality of the Ager Basin: The type (Ager No. 1); Ager No. 2, right mandible fragment with M_{2-3} ; Ager No. 3, left mandible fragment with P_3-P_4 ; Ager No. 4, right M_1 ; Ager No. 5, right M_1 ; Ager No. 6, left mandible fragment with M_2 . One specimen from the "La Roca"

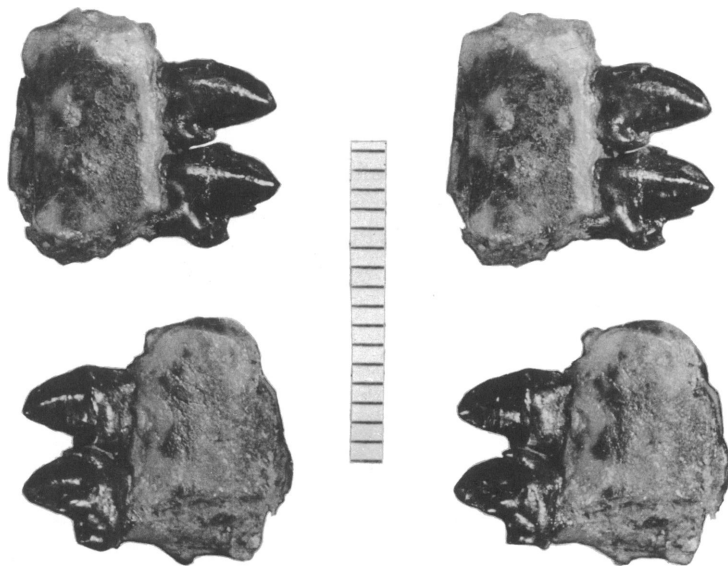


FIG. 1. *Agerina roselli*, Ager No. 3, left mandible fragment with P_3-P_4 ; buccal (above) and lingual (below) views. Scale in 0.5 mm. intervals.

locality of the Isábena Basin, Casa Picanton, is referred to as Isábena No. 1.

The fauna collected (Crusafont-Pairo, 1967) indicates an upper Lutetian or early Cuisian age of deposition for the "Les Salares" locality.

SPECIFIC DIAGNOSIS: Only known species of the genus.

DESCRIPTION: From the known fragments it is evident that the mandible was relatively deep. There are no teeth known anterior to the third premolar. P_3 and P_4 are of about equal height, both being distinctly taller than the molars behind them. P_3 is relatively short mesiodistally in comparison with P_4 and lacks a metaconid, whereas P_4 has a large one, about one-half the height of the protoconid. The cingulum is very faint on the buccal side of P_3 but stronger on P_4 . On the lingual side the cingula are strong on both premolars. The lingual cingulum is uninterrupted on P_3 ,

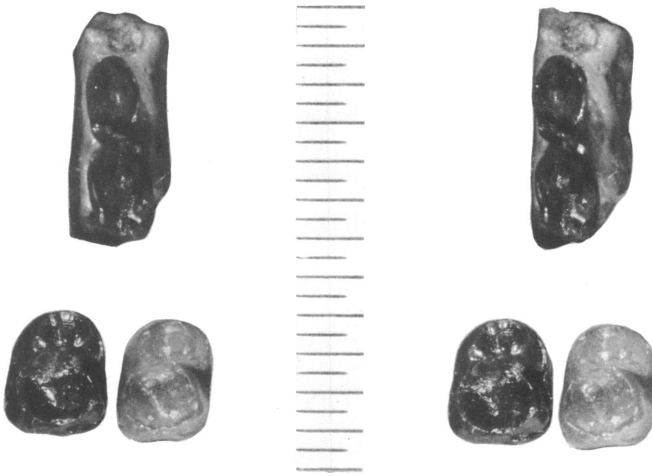


FIG. 2. *Agerina roselli*, Ager No. 3, left P_3-4 (above) and Ager No. 4 and 5 (below, from left to right), both right M_1 ; occlusal views. Scale in 0.5 mm. intervals.

where it turns sharply buccally to and into a single cusp representing the talonid homologue.

The talonid is more developed on P_4 than on P_3 , consisting of three cuspules and a small basin enclosed by them. Both P_3 and P_4 have gently



FIG. 3. *Agerina roselli*, Ager No. 1, holotype, left mandible fragment with M_{2-3} (left) and Ager No. 2, right mandible fragment with M_{2-3} (right); occlusal views. Scale in 0.5 mm. intervals.

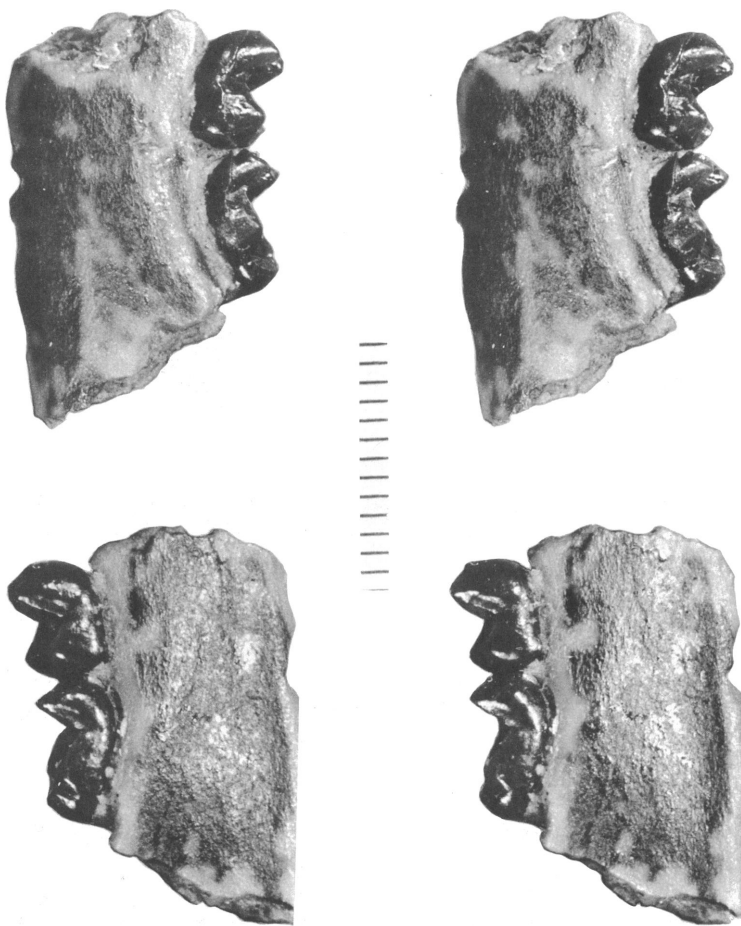


FIG. 4. *Agerina roselli*, Ager No. 1, holotype, left mandible fragment with M_{2-3} ; lateral view above and medial view below. Scale in 0.5 mm. intervals.

curving paracristids which have their sharp cutting edge facing toward the symphysis. On the anterolingual corner of the tooth on the cingulum there is a tiny cuspule, probably the paraconid.

The specimens labeled Ager Nos. 4 and 5 are interpreted to be first molars. The trigonid of the former teeth are different from those of the M_{2s} in Ager Nos. 1 and 2 in being lingually more open in consequence of the more buccal position of the paraconids relative to the metaconids. The trigonids become progressively more constricted anteroposteriorly

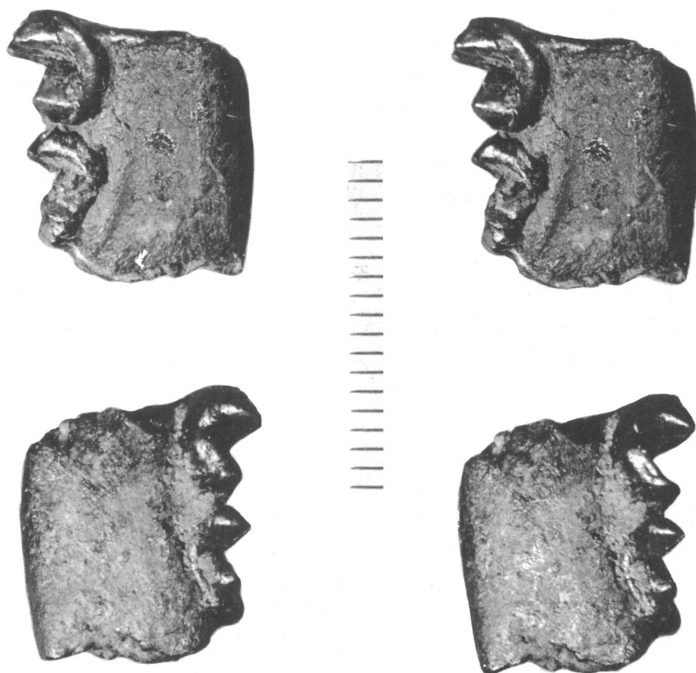


FIG. 5. *Agerina roselli*, Ager No. 2, right mandible fragment with M_2 - M_3 ; lateral view above and medial view below. Scale in 0.5 mm. intervals.

from M_1 to M_3 . The trigonids are low, the most important feature on them being the protocristid (protolophid), whereas the paracristid (paralophid) is relegated to the condition of a low shelf. The talonids of the first two molars are smoothly hollowed out. The hypoconid and entoconid are not cusperate, and are only slightly raised segments of the continuous crest surrounding the talonid basin. There are no traces of a hypoconulid. The talonid on the last molar has an enlarged hypoconulid and although this cusp is missing on the first two molars, M_3 has an extension that is the equivalent of the hypoconulid. Buccal cingula are relatively distinct on all three of the molars.

DISCUSSION: I have extensively compared *Agerina* with all early Tertiary primates with possible relevance to the relationship of the genus. These comparisons did not uphold the conclusions of Crusafont-Pairo who suggested that the genus was a necrolemurid.

Without much doubt, *Agerina* shows affinities with the Adapidae in general and more particularly with the genera *Protoadapis*, *Pelycodus*, and

Pronycticebus. Consequently, most of the following discussion concerns itself with comparison between *Agerina* and pertinent adapids.

Both *Protoadapis* and *Pronycticebus* have received detailed treatment by Simons (1962) and Russell, Louis, and Savage (1967). A generic distinction between *Protoadapis* and *Pronycticebus* based on the lower molars was cited by Russell, Louis, and Savage (1967, p. 40). It seems that the otherwise very similar lower molars of these taxa can be differentiated on the basis of the strength and development of the protoconids and metaconids. The more inflated cusps in *Protoadapis* are separated by a narrower, V-shaped trigonid notch, whereas in *Pronycticebus* the space between the metaconid and protoconid is greater and U-shaped, due to the less bulbous nature of these cusps. It might be added that in this respect *Pelycodus* is more similar to *Protoadapis* than to *Pronycticebus* or *Agerina*, which share relatively non-bulbous metaconids and protoconids. Judged from all available morphology, however, the resemblances and hence probably the degree of relationship is very close between *Protoadapis* and *Pronycticebus*. The trigonid structures, except for the small differences mentioned above, are similar on the two genera, both showing about equal degree of trigonid opening lingually and the same degree of paraconid development.

The total number of premolars in the type of *Pronycticebus* (figs. 8 and 9) is four both in the maxilla and the mandible. The upper molars of *Pronycticebus* retain more primitive proportions than those of *Protoadapis* in having relatively greater transverse diameters. The major differences between *Agerina* and *Pronycticebus* are in the structure of molar trigonids and the proportions of the ultimate lower molar. In *Agerina* the paraconid is indistinct on M₁, whereas in *Pronycticebus* this cusp is well defined.

The differences between either the upper and lower molars and premolars of *Protoadapis*, *Pronycticebus*, or *Agerina*¹ on one hand and those of *Caenopithecus* on the other are not any more extensive than differences that might be found between early Eocene species of *Pelycodus* (including *Cantius*) and advanced medial Eocene species of *Notharctus*.

Russell, Louis, and Savage (1967, pp. 36–37) reported that the specimens of the genotype of *Protoadapis*, *P. curvicaudatus*, have well-developed metaconules and paraconules. This statement can be confirmed from their published illustrations. This fact is contrary to Simons's (1962, p. 29) assertion that the lack of metaconules also characterizes *Protoadapis* upper molars in addition to those of *Caenopithecus*.

¹ Only lower molars are known, although the genus *Arisella* described by Crusafont-Pairo, 1967, based on a single ultimate upper molar, and lacking a hypodigm other than the type, might conceivably be an upper tooth of *Agerina*.

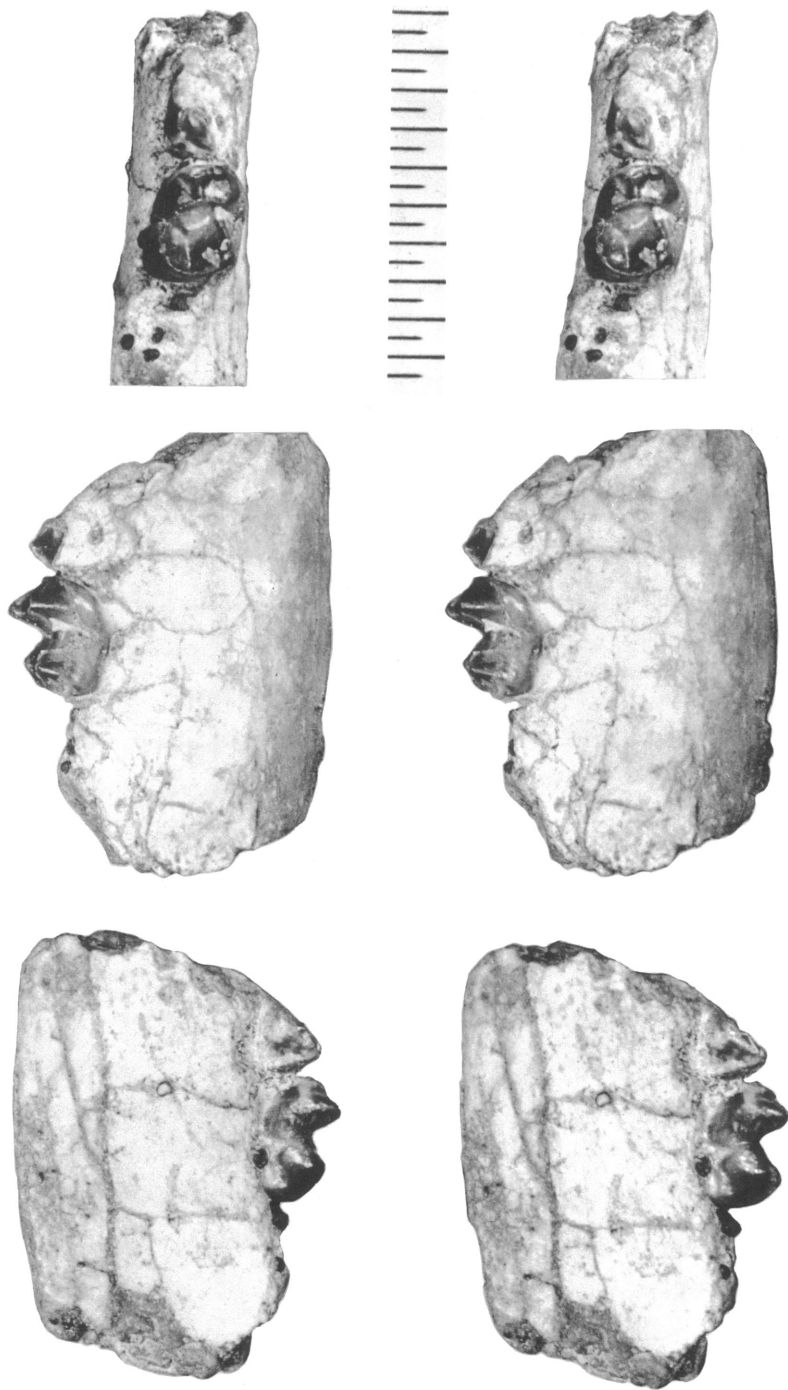


FIG. 6. *Agerina roselli*, Isábena No. 1, right mandible fragment with M_2 ; occlusal view above, buccal view middle, and lingual view below. Scale in 0.5 mm. intervals.

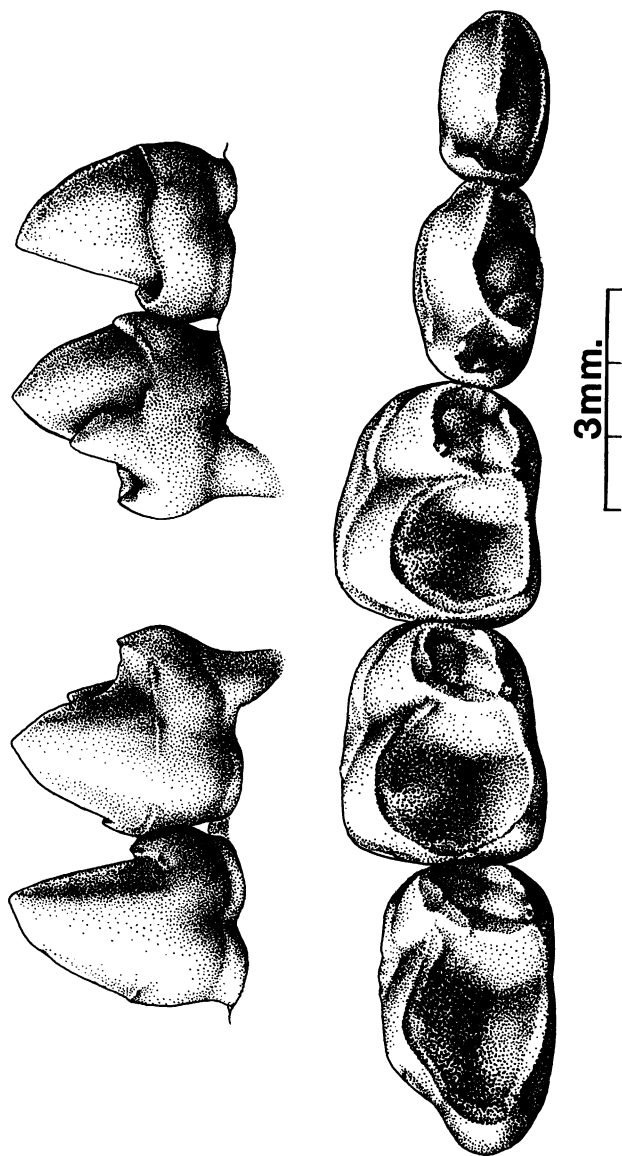


FIG. 7. *Agerina roselli*, composite lower dentition from P_3-M_3 ; occlusal view of P_3-M_3 below, buccal and lingual views of P_3-4 on the left and right respectively.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF THE TEETH OF *Agerina roselli* FROM THE AGER AND ISÁBENA BASINS, SPAIN

	Ager No. 1	Ager No. 2	Ager No. 3	Ager No. 4	Ager No. 5	Isábena No. 1	N	O.R.	\bar{X}
P ₃ L	—	—	2.22	—	—	—	1	—	2.22
PW	—	—	1.40	—	—	—	1	—	1.40
P ₄ L	—	—	2.72	—	—	—	1	—	2.72
PW	—	—	1.60	—	—	—	1	—	1.60
L	—	—	—	2.95	3.05	—	2	2.95-3.05	3.00
PW	—	—	—	2.50	2.45	—	2	2.45-2.50	2.47
AW	—	—	—	2.50	2.35	—	2	2.35-2.50	2.42
L	3.12	3.05	—	—	—	3.10	3	3.05-3.12	3.09
PW	2.58	2.65	—	—	—	2.65	3	2.58-2.65	2.63
AW	2.35	2.68	—	—	—	2.46	3	2.35-2.68	2.74
L	3.74	3.30	—	—	—	—	2	3.30-3.74	3.52
PW	2.24	1.95	—	—	—	—	2	1.95-2.24	2.15
AW	2.20	2.04	—	—	—	—	2	2.04-2.20	2.12

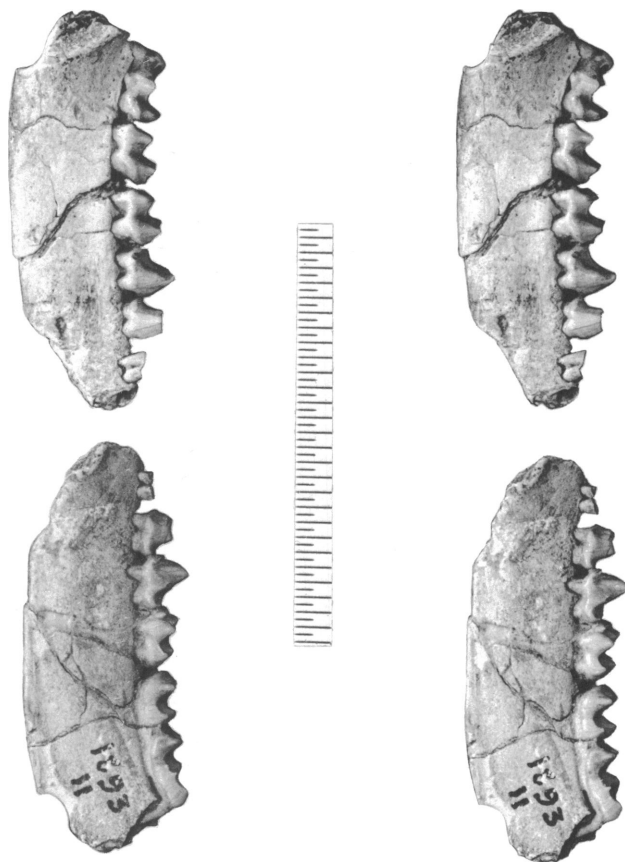


FIG. 8. *Pronycticebus gaudryi*, holotype, right mandible fragment with roots of P_2 , and P_3 – M_3 ; lateral view above and medial view below. Scale in 0.5 mm. intervals.

The height difference between P_3 and P_4 of *Protoadapis* does not appear to be a very reliable generic character although in most cases of the three valid species of *Protoadapis* [*P. curvicauspiciens* Lemoine, 1878; *P. klatti* (Weigelt, 1933); *P. angustidens* (Filhol, 1888)], P_3 is distinctly taller than P_4 .

EARLY ADAPIDS AND LORISOID EVOLUTION

Since the naming of *Pronycticebus*, controversy has surrounded the degree of relationship of the genus to the living lorisooids. With the exception of Gregory, Stehlin, Abel, Weber, and others who at one time or another considered *Pronycticebus* tarsiooid or lemuroid-like, agreement has been



FIG. 9. *Pronycticebus guadryi*, holotype, right mandible fragment with roots of P_2 , and P_3 - M_3 ; occlusal view. Scale in 0.5 mm. intervals.

general since LeGros Clark's study of 1934 that *Pronycticebus* is either an adapid of very close ties to genera of that predominately Eocene family, or possibly related to lorisoids (Simons, 1962). The question remained whether *Pronycticebus*¹ was an adapid with a slightly distinctive (in many ways more primitive) dentition and palate shape, or that the genus shared homologous specializations with lorisoids, thus possibly qualifying the taxon to be representative of the ancestry of living lorisoids.

The doubts and puzzles concerning the origin and level of organization of lorisoids have been among the most vexing problems for students of primate evolution. It was Simons's (1962) restudy of *Pronycticebus* which gave impetus to the notion that certain characters of the basicranium are lorisoid-like, an assertion made in spite of the detailed and careful study of LeGros Clark (1934) who showed this genus to be decisively lemuroid. Simons did not reconsider most of the features of the basicranium nor the

¹ Although Simons (1962) has contributed additional careful observations on the cranium of *Pronycticebus* to LeGros Clark's (1934) study, and both Simons (1962) and Russell, Louis, and Savage (1967) made pertinent comparisons of the dentition of *Pronycticebus* to related genera, the illustrations available in the literature of this important genus have not been completely satisfactory. In addition to stereoscopic photographs of the two unique specimens of *Pronycticebus*, I take the opportunity to publish a restoration of this primate. Although the reconstructions are hopefully clearer, more detailed, and accurate than previous drawings of the cranium, they are partly based on the confirmed researches shown by the valuable figures published by LeGros Clark (1934), Simons (1962), and Russell (1964).

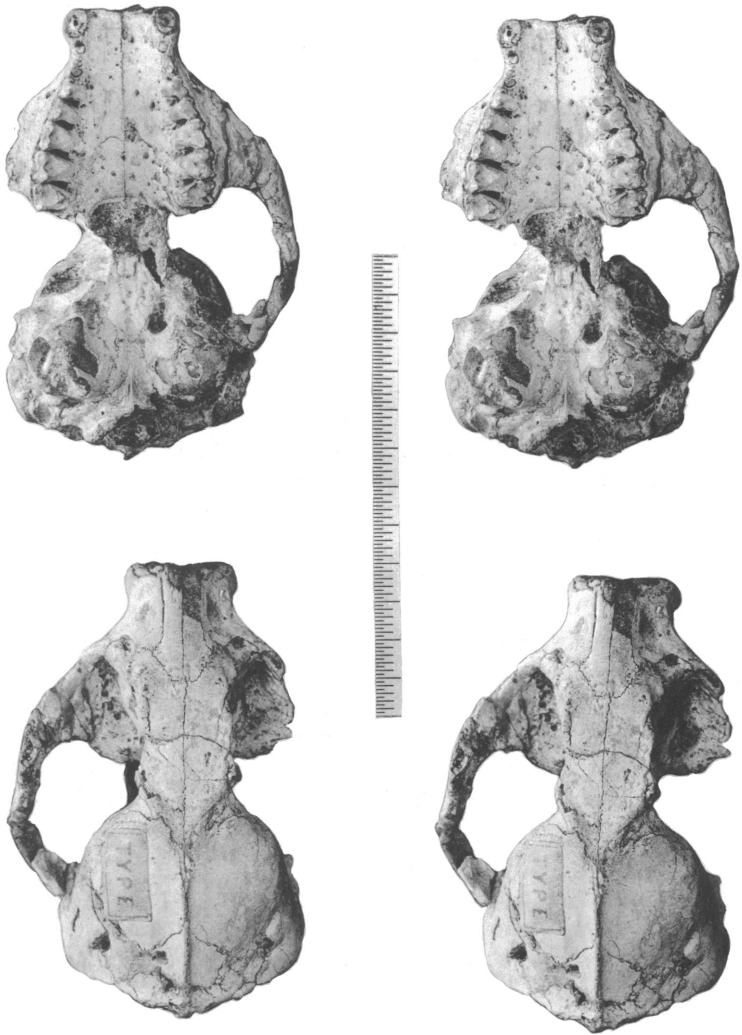


FIG. 10. *Pronycticebus gaudryi*, holotype, nearly complete cranium; ventral view above, dorsal view below. Scale in 0.5 mm. intervals.

distinct details which are shared by lemuroids, adapids as well as lemurids, and that are unlike the particulars of lorisooid basicrania.

What have been the characters specifically advocated to show affinities with lorisooids? Simons (1962), who has cleaned a small part of the calcite-filled auditory bulla, noted in particular that there was a shelf (smaller



FIG. 11. *Pronycticebus gaudryi*, holotype, occlusal view of the upper dentition of the cranium. Scale in 0.5 mm. intervals.

than that in *Adapis*, according to Simons) for the support of the annulus membrane. He subsequently stated (pp. 18–19) that in *Loris tardigradus*, *vide* a reference to Hill (1953), the annulus was “reduced” only to a slightly greater degree than in *Pronycticebus*. Simons noted (p. 19), concerning the relatively close position of the tympanic ring (which is inside the bulla as in all known lemuriforms) to the border of the external meatus in *Pronycticebus*, that this might be an indication of affinity between this genus and lorisooids. The fact that he considered the proximally (to the external auditory meatus) situated annulus in *Pronycticebus* indicative of special lorisooid ties, but thought *Pronycticebus* to be an adapid (as lorisooids do not have the ectotympanic enclosed in the bulla), would mean that the lorisooid condition is implied to be the specialized one. In fact Simons (p. 34) did specifically remark, in line with the traditionally accepted lemuroid-lorisooid relationships, that the lorisooid-like characters of *Pronycticebus* might indicate “. . . the differentiation of the lorisoiform pro-

simians from the general stock of the Adapidae (s.l.).” In a quasi-ancestral lorisoid, such as *Pronycticebus* is implied to be, it would be expected, then, that the position of the annulus would be intermediate between the ancestors (lemuroids) and descendents (lorisoids).

Simons appears to have rejected LeGros Clark’s astute analysis of the tympanic region. LeGros Clark’s statement (p. 26) is fully warranted even today by all the available comparative evidence. He noted that “*Pronycticebus* is definitely excluded from a close relationship with the Loris-

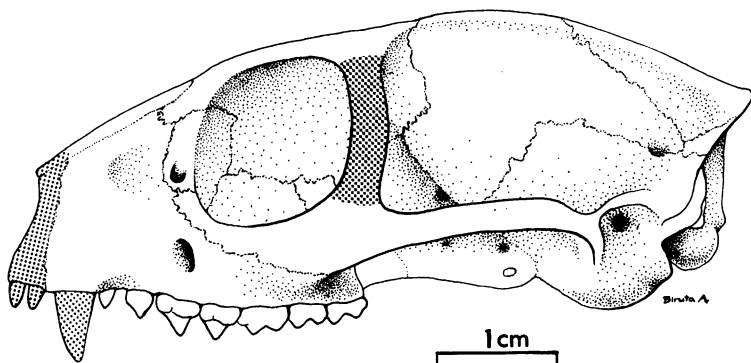


FIG. 12. *Pronycticebus gaudryi*, lateral view of reconstructed cranium. Uniformly stippled areas represent parts missing.

formes in the features of the tympanic region, including the absence of the foramen lacerum medium. On these grounds alone it seems unlikely that it can represent a precursor of recent lorisiforms, for the lemuriform structure of the tympanic region is almost certainly to be regarded as a specialization which could hardly have given rise to the (in many respects) more primitive lorisiform type.” It must be remembered that LeGros Clark’s efforts were concentrated on evaluating the degree of relationships of *Pronycticebus* to living lorisiforms and known lemuriforms. His conclusions that *Pronycticebus* shared undoubted lemuroid specializations (rather than primitive retentions)¹ with lemuriform primates are confirmed.

The basicranial evidence from *Pronycticebus*, however, coupled with the dental evidence, might be interpreted in another way. It must be remembered that the total evidence of the basicranium as presented by

¹ Whether the “foramen lacerum medium” is a primitive, shared advanced, or convergent character that both the lorisoids and the lemroids *Cheirogealus* and *Microcebus* possess is a question that will be pursued elsewhere.

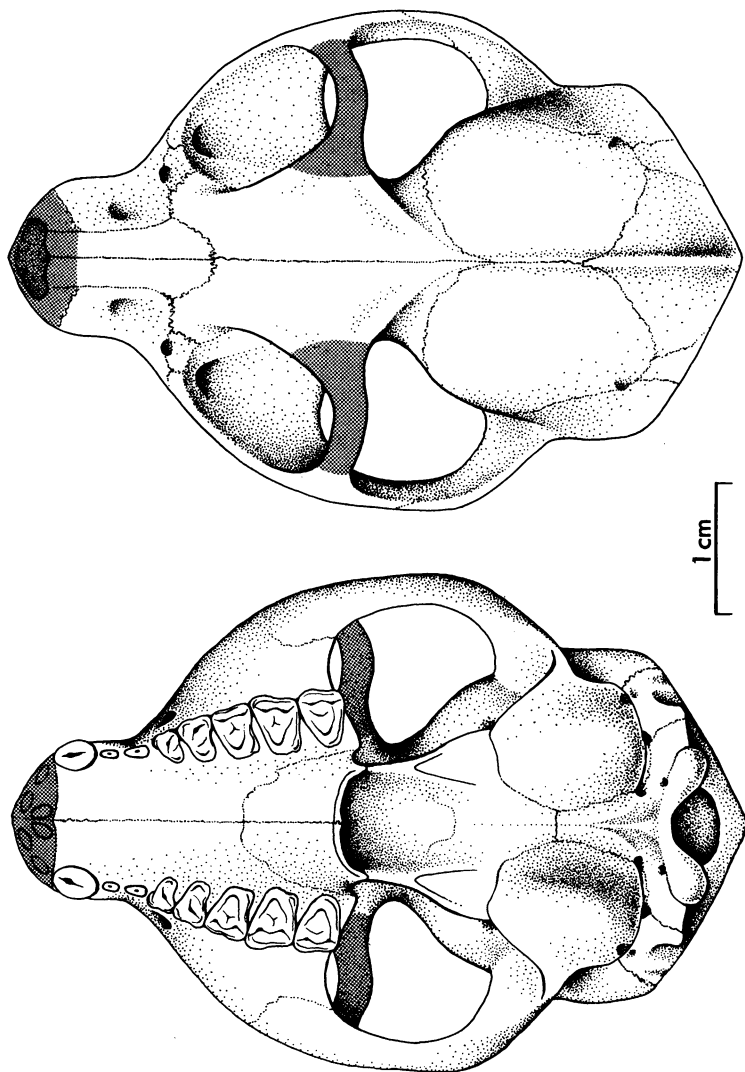


FIG. 13. *Pronycticebus gaudryi*, ventral (left) and dorsal (right) views of reconstructed cranium. Uniformly stippled areas represent parts missing.

LeGros Clark (1934) shows clearly the lemuroid combination of characters. Yet, it is not unusual in the fossil record that relatively primitive genera are recovered from younger rocks than are many advanced members of a family. Thus the relatively primitive upper teeth, the conformation of the palate, the large caniniform canine (as inferred from the alveoli), and the proximity of the annulus to the external meatus might show a very primitive adapid. Furthermore, the primitive condition from which the position of the tympanic ring was derived might have been the ectotympanic external to the bulla as in lorisooids, tarsiooids, plesiadapoids,¹ catarrhines, and platyrrhines.

It is then not inconceivable that lorisooids, in spite of some specializations of the middle ear such as the numerous air chambers, retain a more primitive condition of the ectotympanic and are more primitive than lemuroids in having only the stapedial, but not the promontory artery, enclosed in a bony tube.

It may be more meaningful, I believe, to consider *Pronycticebus* as a primitive lemuroid, with a number of genus specific characters, possibly derived from a very primitive ancestry which might have had features (a combination of primitive and advanced) that would now be considered lorisooid were they known in a fossil.

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¹ In a paper (in press) I unite the predominantly Paleocene families Paromomyidae, Picrodontidae, Plesiadapidae, and Carpolestidae in the superfamily Plesiadapoidea. Van Valen's (1969) concept of Microsyopoidea, in which he united the four families listed and the Eocene Microsyopidae, is rejected on the ground of lack of ordinal affinities between the microsyopids and the Paleocene primates.