

THE EVOLUTION OF THE RODENT FAMILY CTENODACTYLIDAE

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ABSTRACT

The rodent family Ctenodactylidae, the four living genera of which are restricted to North Africa, is considered to have originated in Central Asia in the mid-Eocene and to have spread to South Asia (India and Pakistan), North Africa and Sardinia in the Miocene. The last known Asia ctenodactylid is from the Early Pliocene of India. Pleistocene members of the family are known from Morocco and Sicily. There is no evidence of close relationship with any other rodent lines, and the family was probably directly derived from Early Eocene Asiatic paramyids. The ctenodactylids have sometimes been associated with the Hystricognathi because of their hystricomorphy, but this is considered to have been acquired independently in the two groups, which could not have had a common ancestor later than Late Palaeocene. Parallelism also explains the presence in both groups of a number of other features, including the fusion of the malleus and incus, the development of multiseriate incisor enamel, the possible presence of a sacculus urethralis in the ctenodactylids, and the slightly delayed loss of the deciduous teeth in the Miocene ctenodactylid *Sardomys*.

INTRODUCTION

The rodent family Ctenodactylidae, the gundis, are at present restricted to North Africa (Fig. 1). They are one of a number of rodent families whose phylogenetic relationships have proven very difficult to disentangle. They are characterized by a hypertrophied masseter medialis muscle, which arises on the snout and passes through the enlarged infraorbital foramen, to insert on the mandible. This pattern of the muscle has long been known to characterize a considerable number of rodent families, and was used by Waterhouse (1839) as a basis for subdivision of the order and by Brandt (1855) as the formal diagnostic characteristic of the Suborder Hystricomorpha. The currently accepted Suborder Hystricognathi (Tullberg, 1899, as revised by Lavocat, 1973, and Wood, 1975) includes the Old World porcupines or Hystricidae; the Phiomorpha, a mid-Tertiary African radiation now greatly restricted; the Caviomorpha including 14 families of South American rodents; and the Paleocene to Eocene North American Franimorpha. All of these (except for some of the Franimorpha) are hystricomorphous, and without exception they are hystricognathous (i.e., the angle of the lower jaw arises lateral to the plane of the lower incisor). Like the Ctenodactylidae, the African families Anomaluridae and Pedetidae and the Eocene to Oligocene European Pseudosciuridae and Theridomyidae are hystricomorphous but sciurognathous (i.e., the angle arises in the plane of the lower incisor).

For many years, hystricomorphy was considered to be an indication of affinity, and all these forms were therefore united. As more has been learned about rodent evolution, it became more and more difficult to consider all of these forms related, and the current tendency among paleontologists (Wood, 1955, pp. 173-175; 1965a, p. 128; Lavocat, 1973, pp. 194-196; 1974) has been to eliminate the sciurognathous families from any possibility of relationship with the Hystricognathi. This paleontological consensus, however, has not received universal acceptance among neontologists, as indicated by Landry's conclusion (1957, p. 79) that the ctenodactylids are merely aberrant hystricognaths, and by the inclusion of the gundis as the only non-hystricognathous rodents discussed in the recent symposium, The biology of Hystricomorph Rodents, of the Zoological Society of London (George, 1974). A different solution was their placement by Grassé and Dekeyser (1955, p. 1419) as "beaucoup plus proches, en réalité, des Dipodoïdes" than to the hystricognaths.

Lockett (1971, pp. 166-168) has pointed out that there is great similarity of the fetal membranes of the Anomaluridae, Ctenodactylidae, Pedetidae, Aplodontidae and Sciuridae, which he interprets as independent retention of the primitive rodent condition, and not indicative of special relationships. This conclusion with regard to the ctenodactylids is similar to that reached by Tullberg (1899, p. 393 and phylogenetic tree on p. 481) and to that presented below.

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Over the last half century, considerable paleontological data have accumulated dealing with the Ctenodactylidae, and it is now clear (Wood, 1974a) that this family originated in Central Asia in the Eocene, continued its evolution there through the Oligocene, spread south of the Himalayas and into Africa and Sardinia in the Miocene, reached Sicily by the Pleistocene, and subsequently became restricted to North Africa (Fig. 1). The entire history, at least since the Middle Eocene, has been independent from that of all the Hystricognathi, and all the similarities between the ctenodactylids and the hystricognaths must, therefore, either be retained from their common Paleocene ancestors, or else have evolved as parallelisms.

The subject of this paper is particularly appropriate to the present volume, because the gundis originated in Central Asia, an area in whose paleontology Academician Orlov was much interested; one of the early descriptions of a fossil member of the family was from India

(Wood, 1937a); and I have been interested in the problem of the evolution of the hystricomorphous rodents for many years (Wood, 1950, 1968, 1972, 1973, 1974a, 1974c; Wood and Patterson, 1959, 1970; Patterson and Wood, in preparation) as well as in the concept of parallelism among rodents (Wood, 1937b, 1950).

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DEFINITION OF THE CTENODACTYLIDAE

The Family Ctenodactylidae may be defined as: sciurognathous but hystricomorphous rodents, with the masseter medialis arising as far forward as the premaxilla, at least in *Tataromys* and the recent genera; branch of the zygomatic arch lateral to the infraorbital foramen

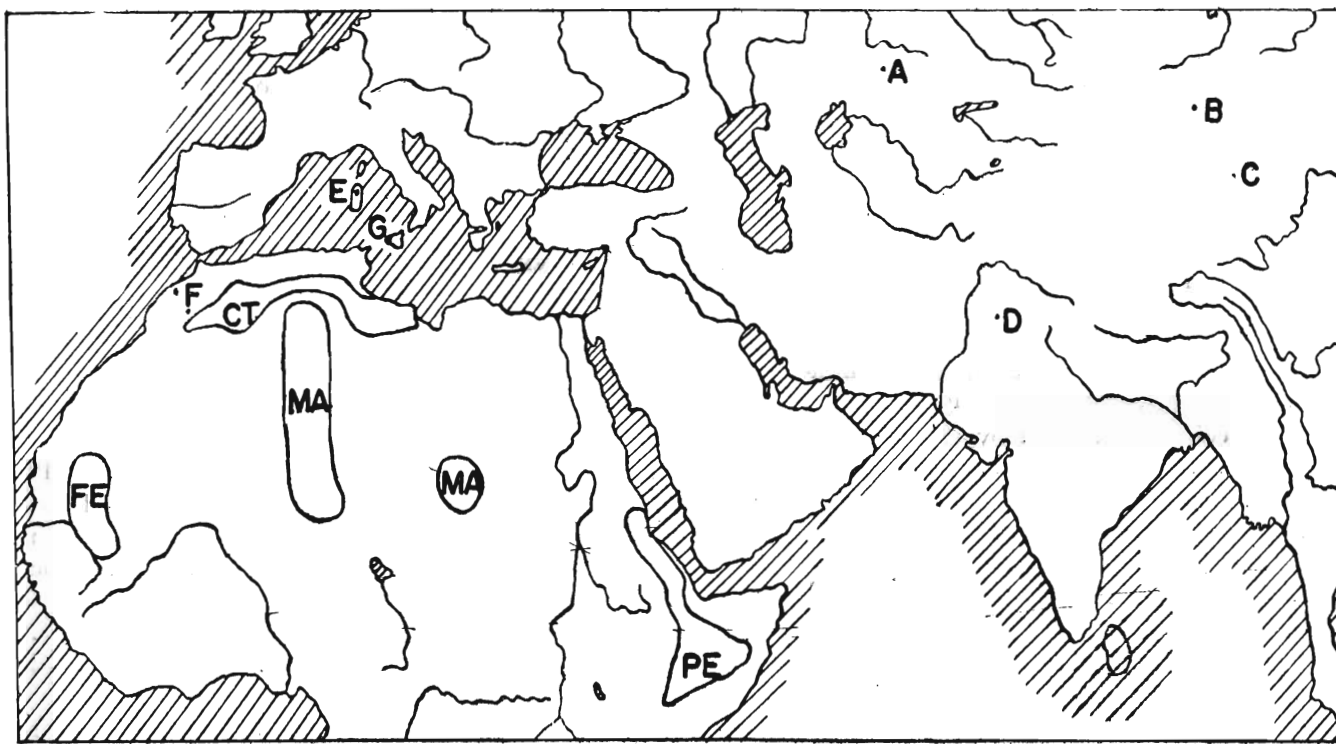


Fig. 1. Distribution of living and fossil ctenodactylids, redrawn from Shevyreva, 1971a, Fig. 2, with distribution of recent genera from Jaeger, 1971, Fig. 1, and with other genera added to complete the record.

- A. Lake Chelkar-Tenis and Zaisan Basin, Kazakhstan, USSR. *Saykanomys chalchae* and *Tamquammys tantillus*, Middle Eocene; *Terrarboreus arcanus* and *Woodomys chelharis*, Middle Oligocene.
- B. Mongolia, various localities. *Saykanomys chalchae*, Middle Eocene; *Advenimus burkei*, *A. bohlini* and Cf. *Advenimus* sp., Late Eocene; *Woodomys chelharis*, Middle Oligocene; *Karakoromys decessus*, *Tataromys plicidens*, *T. deflexus* and *T. sigmodon*, Late Oligocene.
- C. Kansu and Honan, People's Republic of China. *Tsinlingomys youngi*, Late Eocene; *Tataromys grangeri*, *T. sigmodon*, *T. plicidens*, *Yindertemys woodi* and *Leptotataromys gracilidens*, Late Oligocene; *Sayimys obliquidens*, mid-Miocene.
- D. Siwaliks, of northern India and Pakistan. *Africanomys sivalensis*, Late Miocene; *Sayimys perplexus*, Early Pliocene.
- E. Sardinia *Sardomys dawsonae*, *S. antonietae* and *Pireddamys rayi*, Miocene.
- F. Morocco. *Africanomys pulcher*, *Metasayimys curvidens*, Late Miocene; *Irhoudia bohlini*, Early Pleistocene.
- G. Sicily. *Pellegrinia panormensis*, Pleistocene.
- Known distribution of living genera: CT=Ctenodactylus; FE=Felovia; MA=Massouteria; and PE=Pectinator.

essentially vertical; inflated tympanic and mastoid bullae in modern genera and bulla slightly enlarged in the Late Oligocene *Tataromys* and more so in the Miocene *Sayimys obliquidens*; malleus and incus fused in living genera; mandible low, coronoid process progressively reduced or absent, and condyle progressively lowered to occlusal level of cheek teeth; no postglenoid process of the mandible for the insertion of the *Masseter lateralis profundus, pars posterior*, deep; cheek teeth reduced from a primitive P_1^2 $dp_1^{1 \text{ or } 2}$ M_3^3 to merely the molars in the adults of most of the Recent genera; teeth primitively brachydont and cuspidate, progressively crested, ultimately rootless with an extensive covering of cement; no mesocone, mesoloph or mesolophid, and mesoconid only in some Eocene genera; hypoconulid progressively enlarged; incisor enamel of the multiserial type at least since the Late Oligocene; lower incisors heavy, procumbent, usually short, generally ending beneath M_2 and often twisted in the alveolus; possibly a rudimentary Sacculus urethralis.

Recent ctenodactylids (Grassé and Dekeyser, 1955, pp. 1418–1420) inhabit desert to arid regions and are adapted to a rupestrian environment, and particularly to crevices in rocks in which they shelter themselves. They are climbers rather than burrowers. A tuft of heavy hairs on some of their digits are the “combs” from which the genus *Ctenodactylus* and the family acquired their names. The skull is flattened, with a long jugal, and the vertical branch of the zygomatic arch, lateral to the infraorbital foramen, is perpendicular to the horizontal one. The inflation of the bulla supports the view that such structures are desert rather than saltatorial adaptations.

Once Bohlin (1946) recognized that the mid-Tertiary representatives of the family belonged here, a recognition that had been delayed by the absence of fossils previously identified as ctenodactylids, the Tertiary history of the family seemed to fall into a relatively simple pattern. However, some authors (Schaub, 1958, p. 780; Lavocat, 1961, p. 52) have separated the earlier ctenodactylids as a separate Family Tataromyidae, attributed to Bohlin (1946). Dawson (1964, pp. 14–15) and Black (1972, p. 240) have already commented on this and have concluded: (a) that there is no justification for the use of the Family Tataromyidae, and (b) that in any case the family should not be credited to Bohlin. I agree with both conclusions. Bohlin (1946, pp. 75–146) discussed a group of rodents, identified at the start as the Family Ctenodactylidae. The same heading was used in his Table of Contents. His index does not contain the word Tataromyidae, although it does cite Ctenodactylidae. The term “Tataromyidae” was used a total of six times by Bohlin, three on each of pages 133 and 134, with no diagnosis, no listing of included genera, and always in quotation marks. In addition to the comments by Black (1972, p. 240), Bohlin stated (1946, p. 133) that “(1)

Karakoromys-Tataromys-Yindertemys; (2) *Leptotataromys*; (3) *Sayimys* . . . are specialized in such different ways that they may perhaps be considered as different subfamilies.” This, it seems to me, makes it perfectly clear that Bohlin was *not* trying to erect a Family Tataromyidae, but was using a convenient familiar reference term. As a further point, the use by Bohlin (1946, p. 108) of the word “tataromyoid” in the diagnosis of *Yindertemys* should not be interpreted to mean that he recognized a Superfamily Tataromyoidea.

Lavocat went even farther than Schaub, and erected the Subfamilies Tataromyinae (1961, p. 52) and Sayimyinae (1961, p. 58). I agree completely with Jaeger (1971, p. 133) that “aucun regroupement clair n'apparaît encore qui pourrait justifier soit la famille des Tataromyidés . . . soit la sous-famille des Tataromyinés [or Sayimyinae] de Lavocat (1961)”.

In summary, I believe the Ctenodactylidae, as here discussed, to be a reasonable and well defined family. I do not believe that present information warrants any attempt to subdivide the family at levels higher than the genus. The family is best either included in a monotypic Superfamily Ctenodactylloidea (Wood, 1955, p. 173) or left as an independent family (Wood, 1965a, p. 128).

EVOLUTION OF THE CTENODACTYLIDAE

EOCENE CTENODACTYLIDS

Rodents that I believe should be considered as the earliest recognized members of the Ctenodactylidae have been reported (Fig. 1) from the Middle Eocene of Kazakhstan and Mongolia (Shevyreva, 1972b, *Saykanomys*), the early Late Eocene of Honan (Li, 1963, *Tsinlingomys*), the late Eocene of Honan and Inner Mongolia (Li, 1975, *Yuomys*), and the Late Eocene of Mongolia (Dawson, 1964, *Advenimus*). Dawson referred her genus questionably to the Sciuravidae although she pointed out a number of ctenodactylid resemblances; Shevyreva and Li (1963) referred theirs to the Sciuravidae without question; and Li (1975) referred *Yuomys* questionably to the Paramyidae.

Saykanomys is characterized (Shevyreva, 1972b, Fig. 1 and pp. 134–135) by having a large infraorbital foramen, much larger than that of any known sciuravid (Shevyreva, 1972a, p. 1453; Shevyreva, 1972c, p. 12 stated that sciuravids may be either protrogomorphous or hystricomorphous); the fourth premolars, both upper and lower, are small in comparison to the molars (Figs. 2R, 3S); the cheek teeth are more cuspidate than in North American Early Eocene sciuravids, in all of which the cusps are beginning to unite in crests (Wood, 1965b); the hypoconulids are large and have expanded backward; the mesoconids are connected with the hypoconids; the entoconids

are extended as a crest toward the hypoconids; and the protoconids and metaconids unite along the anterior margin of the teeth in a metalophulid I (for this terminology, see Wood and Wilson, 1936, Fig. 2: 11, 12). In the upper teeth (Shevyreva, 1972b, Fig. 1 a), the hypocone appears to have developed in a manner very differ-

ent from the way it arose in the paramyids and sciuravids, where it formed from the point where the posterior cingulum joined the protocone. In *Saykanomys*, the hypocone is widely separated from the protocone, and is continuous with the posterior cingulum. As a result, the metaloph converges on the protocone, and there is a deep valley

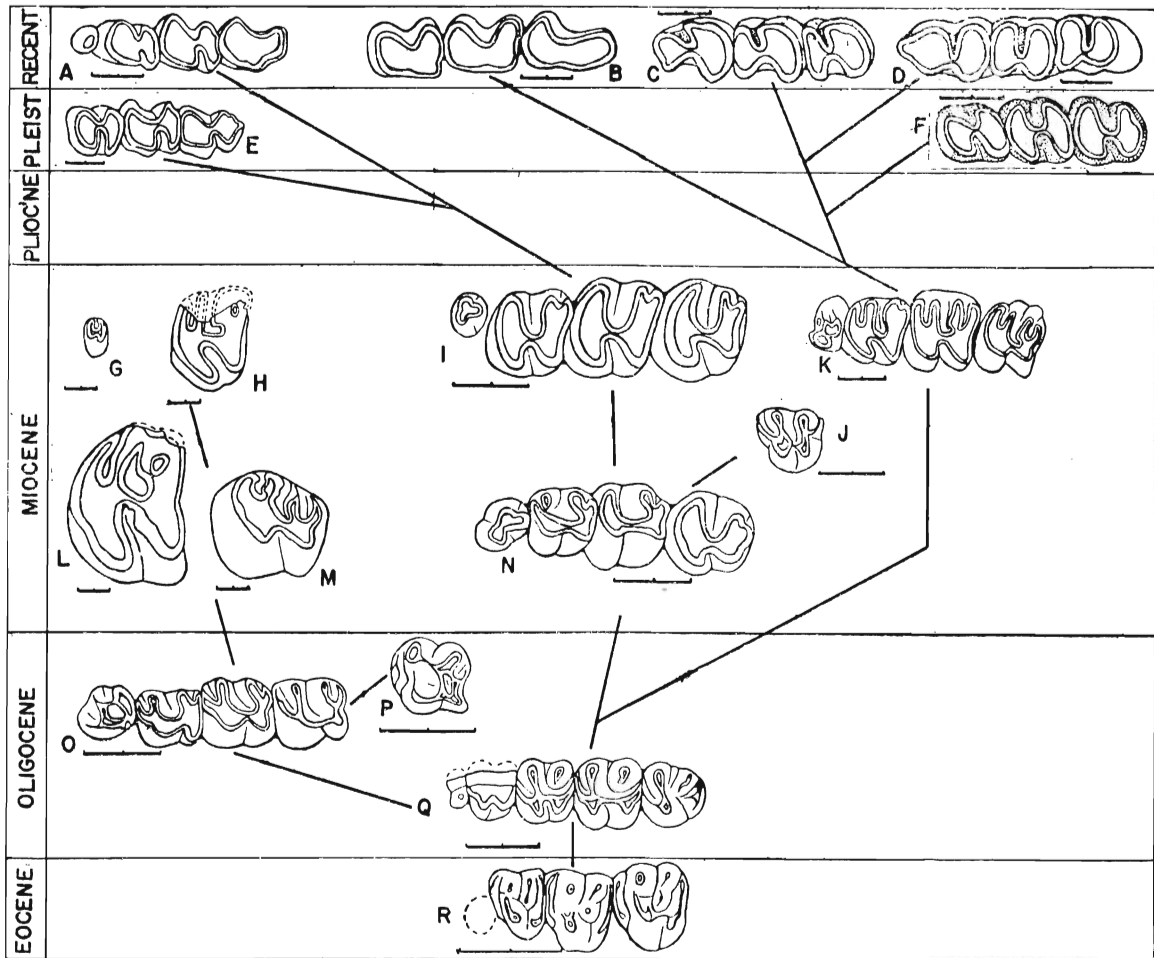


Fig. 2. Evolution of ctenodactylid upper cheek teeth. Scale bars (except Fig. 4 F) are 2 mm long. Figures redrawn from sources indicated.

- A. *Pectinator spekei*, RP⁴—M³ reversed, Jaeger, 1971, Fig. 3 C.
- B. *Ctenodactylus gundi*, RM¹⁻³ reversed, Jaeger, 1971, Fig. 3 D.
- C. *Felovia vae*, RM¹⁻³ reversed, Jaeger, 1971, Fig. 3 B.
- D. *Massouteria mzabi*, RM¹⁻³ reversed, Jaeger, 1971, Fig. 3 A.
- E. *Irhoudia bohlini*, LM¹⁻³, Jaeger, 1971, Pl. 1, Fig. 6.
- F. *Pellegrinia panormensis*, RM¹⁻³ reversed. Scale bar=4 mm.
- G. *Pireddamys rayi*, LP⁴, de Bruijn and Rümke, 1974, Pl. 3, Fig. 6.
- H. *P. rayi*, LM^{1 or 2}, de Bruijn and Rümke, 1974, Pl. 3, Fig. 8.
- I. *Metasayimys curvidens*, RP⁴—M³ reversed, Jaeger, 1971, Pl. 2, Fig. 5.
- J. *Africanomys sivalensis*, LM^{1 or 2}, de Bruijn and Rümke, 1974, Pl. 3, Fig. 4.
- K. *Sayimys obliquidens*, LP⁴—M³, Schaub, 1958, Fig. 212.
- L. *Sardomys dawsonae*, LM^{1 or 2}, de Bruijn and Rümke, 1974, Pl. 3, Fig. 1.
- M. *S. dawsonae*, LM², de Bruijn and Rümke, 1974, Pl. 3, Fig. 2 a.
- N. *Africanomys pulcher*, LM¹⁻², Jaeger, 1971, Pl. 1, Fig. 1; RP⁴ and RM³ reversed, *op. cit.*, Pl. 1, Fig. 3.
- O. *Tataromys plicidens*, RP⁴—M³ reversed, Bohlin 1937, Fig. 87.
- P. *Tindertemys woodi*, LM², Bohlin, 1946, Fig. 29 a".
- Q. *Terraroboreus arcanus*, LP³—M³, Shevyreva, 1971a, Fig. 7 b.
- R. *Saykanomys chalthae*, LP⁴—M³ and alveolus of LP³, Shevyreva, 1972a, Fig. 1 a.

between the protocone and hypocone. P^4 has essentially the same pattern as the molars. P^3 is represented only by its alveolus (Shevyreva, 1972b, Fig. 1 v).

The lower teeth and jaws (all that is known) of *Advenimus*, from the Late Eocene of Mongolia, are very similar to those of *Saykanomys* (Fig. 3R). Again, P_4 is smaller than the molars. Here the metaconid and protoconid are round cusps, with less cresting than in the earlier genus, a step toward such an Oligocene ctenodactylid as *Woodomys*. The mesoconids are much more closely related to the hypoconids than to the protoconids. The protoconids and metaconids of the molars are connected in a metalophulid I and there is little or no indication of a metalophulid II (Dawson, 1964, p. 10). The large hypoconulid, as in *Saykanomys*, is quite isolated from the hypoconid. The lower jaws of *Advenimus*, particularly that identified by Dawson as Cf. *Advenimus* sp. (1964, Fig. 8), are very similar to those of later ctenodactylids in the small vertical height of the ramus, the procumbent incisor, and the long, backwardly extended angular process (Bohlin, 1946, Fig. 31). Dawson (1964, p. 11) questionably referred *Advenimus* to the Sciuravidae, which she felt were the most similar rodents known at that time, but also (op. cit., p. 12) pointed out that the "characteristics that set *Advenimus* most clearly apart from other early rodents seem to associate this rodent with the Ctenodactylidae, rodents that first appear in the upper Oligocene of Mongolia." She particularly mentioned the increase in tooth size from P_4 to M_3 ; the reduction of the talonid (especially hypoconid) of P_4 ; the enlarged hypoconulid of the molars; and the strong ventral ridge of the masseteric fossa (op. cit., p. 12). The forward movement of the ectolophid-hypolophid junction that characterized the late Oligocene ctenodactylid had just begun in M_2 — M_3 of *M. burkei*. I feel that Dawson was very perceptive in recognizing the similarities between *Advenimus* and the ctenodactylids, and that the subsequent description of *Terrarboreus* and *Woodomys* from the Middle Oligocene supplies the necessary intermediates between *Advenimus* and the Late Oligocene genera with which she made comparisons. Black (1972, p. 243) reached conclusions generally similar to mine (Wood, 1974a; 1974c, p. 40) as to the taxonomic position of *Advenimus*. Jaeger (1971, p. 113, footnote 1) merely stated that Dawson considered that *Advenimus* might be a possible ancestor of the Ctenodactylidae, but, on p. 134, he stated that ctenodactylids are known since the Late Eocene of Asia, citing Dawson, 1964.

Since this paper was written, I received the paper by Li (1975) in which he described *Yuomys cavioides*, clearly another ctenodactylid, from the late Eocene of North China (two localities in Honan and one in Inner Mongolia). Li referred the genus questionably to the Paramyidae (following Black, 1968, he called it Family

Ischyromyidae,? Subfamily Paramyinae). Li stated that the skull was hystricomorphous, but the fossa for the origin of the *masseter medialis* was apparently limited to the maxillary portion of the snout, since Li stated (1975, p. 69) that this fossa measured ca. 6×6 mm, and a depression shown on his illustration (op. cit., Pl. 2, Fig. 2) that fits these measurements lies exclusively in the maxilla. *Yuomys* was therefore significantly more primitive than the Oligocene *Tataromys*. Unfortunately, although the Eocene *Saykanomys* and *Tamquammys* have enlarged infra-orbital foramina, neither snout is preserved, so that it is impossible to determine the forward extent of the masseter. The masseteric fossa of the lower jaw of *Yuomys* resembles that of *Saykanomys* (Li, 1975, p. 69).

The lower teeth are rather different from those of other Eocene ctenodactylids. There are no mesoconids, the entoconids are not isolated, the teeth do not differ appreciably in size, and, in particular, P_4 is not the smallest of the cheek teeth (Li, 1975, p. 61 and Fig. 1). However, the hypoconulids are prominently displaced backward and the metalophulid II is greatly reduced, as in *Saykanomys* and *Advenimus* (Fig. 3 R-S). As in these genera, there is a prominent metalophulid I forming the anterior margin of the teeth.

The upper cheek teeth have incomplete metalophs, the metaconule not being connected either to the hypocone or protocone (Li, 1975, Fig. 1). The hypocone seems to arise in the molars (it is absent on P^4) in a manner intermediate between that of *Saykanomys* and of the Paramyidae.

From Li's description and figures, it seems clear that *Yuomys* does not fit into any group of the Ischyromyoidea (including the Paramyidae) as now known. All of the known hystricomorphous paramyids are likewise hystricognathous, and have been placed in the hystricognath Infraorder Franimorpha (Wood, 1975, p. 78), whereas *Yuomys*, although hystricomorphous, is clearly sciurognathous. This indicates that it must be compared with the Theridomyoidea, Ctenodactylidae, Anomaluridae, Pedetidae or Dipodidae, the only other hystricomorphous sciurognaths known. The only real similarities seem to be with the ctenodactylids, which are also the only one of these groups known from the Eocene of Asia. I would therefore interpret *Yuomys* as a late Eocene survival of the mid-Eocene stock of the ctenodactylids. It probably represents a line distinct from all other known members of the family.

Tsinlingomys from the Late Eocene of Honan, China (Li, 1963) is a peculiar rodent (Fig. 3T). As pointed out by Dawson (1964, pp. 13-14), this genus "differs from North American sciuravids in having a complete metalophulid II and masseteric fossa below M_3 , which is more posterior than in other sciuravids." The teeth increase in size from P_4 to M_3 ; the talonid of P_4 is greatly

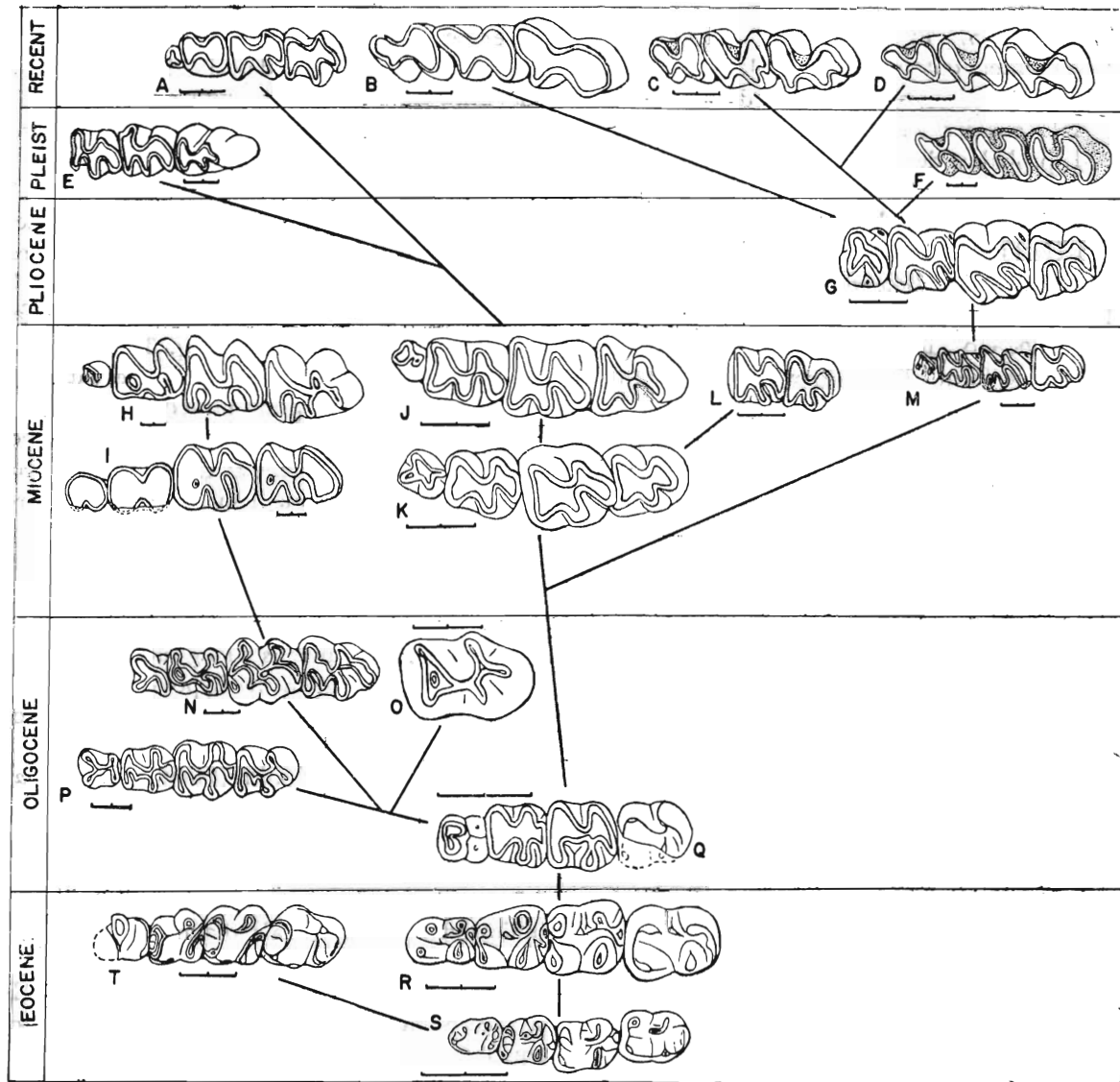


Fig. 3. Evolution of ctenodactylid lower cheek teeth. Scale bars (except Fig. 3 F) are 2 mm long. Figures redrawn from sources indicated.

- A. *Pectinator spekei*, RP₄—M₃, Jaeger, 1971, Fig. 3 C.
 B. *Ctenodactylus gundi*, RM₁₋₃, Jaeger, 1971, Fig. 3 D.
 C. *Felovia vae*, RM₁₋₃, Jaeger, 1971, Fig. 3 B.
 D. *Massouteria mzabi*, RM₁₋₃, Jaeger, 1971, Fig. 3 A.
 E. *Irhoudia bohlini*, RM₁, Jaeger, 1971, Pl. 1, Fig. 10; RM₂, *op. cit.*, Pl. 3, Fig. 2; LM₃ reversed, *op. cit.* Pl. 1, Fig. 9.
 F. *Pellegrinia panormensis*, RM₁₋₃. Scale bar=4 mm.
 G. *Sayimys perplexus*, LP₄—M₃, reversed, Wood, 1937a, Fig. 14.
 H. *Sardomys*; RP₄=*S. antontiettae*, de Bruijn and Rümke, 1974, Pl. 2, Fig. 3; RM₁₋₃=*S. dawsonae*, *op. cit.*, Pl. 2, Fig. 9.
 I. *Pireddamys rayi*, LP₄—M₃ reversed; de Bruijn and Rümke, 1974, Pl. 2, Fig. 1.
 J. *Metasayimys curvidens*, RP₄—M₃, Jaeger, 1971, Pl. 2, Fig. 4.
 K. *Africanomys pulcher*, LP₄—M₃ reversed, Jaeger, 1971, Pl. 1, Fig. 2.
 L. *A. sivalensis*, LM₂₋₃, reversed, Black, 1972, Fig. 1 e.
 M. *Sayimys obliquidens*, RP₄—M₂ and LM₃ reversed, Bohlin, 1946, Fig. 30 b, c.
 N. *Tataromys plicidens*, LP₄—M₃ reversed, Bohlin, 1946, Figs. 19-33 and 19-36.
 O. *Leptotataromys gracilidens*, LM₃ reversed, Bohlin, 1937, Fig. 101.
 P. *Karakoromys decessus*, RP₄—M₃, Schaub, 1958, Fig. 207 (after Matthew and Granger, 1923).
 Q. *Woodomys chelharis*, LP₄—M₂ reversed, Shevyreva, 1972a, Fig. 7 v, and LM₃ reversed, *op. cit.*, Fig. 7 g.
 R. *Adveninus burkei*, RP₄—M₂, Dawson, 1964, Fig. 2, and LM₃ reversed, *op. cit.*, Fig. 4.
 S. *Saykanomys chalchae*, LP₄—M₃ reversed, Shevyreva, 1972a, Fig. 1 g.
 T. *Tsinlingomys youngi*, RP₄—M₃, Li, 1963, Pl. 1, Figs. 1 b and f.

reduced; and the hypoconulids are enlarged on M_{1-2} (Li, 1963, pp. 153, 157; Pl. 1, Figs. 1 *b* and *f*). These features were pointed out by Dawson (1964, p. 12) as resemblances of *Advenimus* to the Ctenodactylidae. For these reasons I consider *Tsinlingomys* to be an aberrant ctenodactylid, probably derivable from an ancestor such as *Saykanomys* (compare Fig. 3, S and T), and with a precocious development of both metalophulid I and metalophulid II (Fig. 3 T), similar to but more advanced than the condition in *Karakoromys* and *Tataromys*. It does not seem possible that *Tsinlingomys* was ancestral to any known later ctenodactylids.

A final Eocene form, *Tamquammys* from the Middle Eocene of Kazakhstan (Shevyreva, 1971*b*) possibly is a ctenodactylid because of its rather large infraorbital foramen (Shevyreva, 1971*b*, Fig. 1 *b*, *v*; p. 745). However, the material is very fragmentary; there is apparently no certain association of the teeth and the maxillary fragment; the teeth (identified as P^3 and P^4) are not very diagnostic. If I interpret Shevyreva correctly, the holotype, P. I. N. no. 2976-11, is the isolated P^4 ; catalog numbers of the other specimens are not given. The genus seems to me, on the basis of Shevyreva's illustrations and description, to be indeterminate. I feel, as indicated previously (Wood, 1974*c*, p. 40) that the *Tamquammys* maxilla (Shevyreva, 1971*b*, Fig. 1 *a*, *b*, *v*) is probably ctenodactylid, whatever the isolated teeth might be.

OLIGOCENE CTENODACTYLIDS

In the Oligocene, the ctenodactylids are known only from Mongolia, Kansu and Kazakhstan (Fig. 1). Most of the known species (*Tataromys* sp. div., *Karakoromys*, Fig. 3 N, P) possess a typical ctenodactylid lower premolar, considerably smaller than the molars, and molars that, although either low crowned or of medium height, show the basic ctenodactylid pattern (Matthew and Granger, 1923, Figs. 6-7; Stehlin and Schaub, 1951, Figs. 179-181, 494-497). The lower premolar has a quadritubercular pattern, with the cusps uniting in the centre of the tooth, fundamentally a pattern analogous to the X-pattern of perognathine heteromyids (Wood, 1935, p. 88). In ctenodactylids, this pattern presumably consists of an anterior pair of cusps, the protoconid and metaconid, and a posterior pair, the hypoconid and entoconid, by analogy with most other rodents. However, Li's figure of *Tsinlingomys* (reproduced here as Fig. 3 T) suggests other possibilities. Shevyreva's suggestion (1971*a* p. 84) that one of the anterior cusps is the paraconid does not seem reasonable; if this were correct, it would mean that the ctenodactylids could not be related to any other known rodents, which seems highly unlikely. The lower premolar, in these Oligocene genera, is following the evolutionary sequence that developed in the molars, but,

because it started from a more primitive situation, it never achieved a similar pattern.

Shevyreva (1971*a*) described two new genera from the Middle Oligocene of Chelkar-Tenis, Kazakhstan: *Terrarboreus*, based on a maxilla, she referred to the Sciuravidae; *Woodomys*¹ based on two lower jaws from Chelkar-Tenis and two jaw fragments from Tatal Gol, Mongolia, she referred to the Ctenodactylidae.

There can be no question but that *Woodomys* is a ctenodactylid although it is much more brachydont than any genus previously referred to the family. The premolar is reduced in size (Fig. 3 Q). The protoconid and metaconid, in the stage of preservation of the only known specimen of P_4 , are united into a transverse crest, with the hypoconid and entoconid isolated cusps. They are, however, connected with the anterior crest by a ridge that runs through the centre of the crown, as in other ctenodactylids. The lower molars have a protoconid and metaconid connected along the anterior margin of the crown as a metalophulid I; the well developed and united hypoconid and entoconid are fairly far forward on the tooth; and there is a longitudinal crest (ectolophid) from the protoconid to the hypolophid to the prominent hypoconulid. Halfway between the metalophid and hypolophid there is, in unworn teeth, a very faint irregularity in the ectolophid (Shevyreva, 1971*a*, Fig. 8*d*) which may be a mesoconid but is more probably the point where the tip of the posterior arm of the protoconid meets the ectolophid.

Terrarboreus certainly is not a typical sciuravid, as indicated by Shevyreva's diagnosis (translated as: "Infraorbital foramen very large, of oval form, the tooth row medial to it, the masseteric area—on the ventral surface of the horizontal malar arch. Hypocone almost equal to the size of the protocone, metaloph incomplete." Shevyreva, 1971*a*, p. 81). In addition, Middle Oligocene genera should not be accepted as sciuravids without strong supporting evidence, the family being Eocene. The infraorbital foramen (Shevyreva, 1971*a*, Fig. 7 *g*) is large, as in *Saykanomys*, and much larger than in *Sciuravus* (Matthew, 1910, Fig. 13; Dawson, 1961, p. 3), although it may have been almost as large in *Knightomys* (Wood, 1965*b*, p. 128). The masseteric fossa extends much farther back on the zygomatic arch than in *Sciuravus* (compare Shevyreva, 1971*a*, Fig. 7 *a* and *b* with Dawson, 1961, Pls. 2, 3 and 4); P^3 is very small and P^4 is reduced; the metalophs are directed toward the protocones as in

¹ Shevyreva, 1968, pp. 155-156, briefly cited a new genus and species of rodent from the Oligocene of Kazakhstan, *Woodomys chelkaris*, but with no definition, designation of a type, description of the genotype species, or illustration. This was, of course, a *nomen nudum*, as she herself recognized (1971*a*, p. 83). The name dates from the second paper, Shevyreva 1971*a*, p. 83, where she used the spelling given here. Jaeger (1971, p. 133, footnote), writing before the appearance of Shevyreva's second publication, cited her original paper and used her original spelling, incorrectly as it turned out.

Saykanomys, but are even less complete, the metacone being widely separated from both the protocone and hypocone. The anteroloph seems to be an outgrowth from the protocone rather than an independent entity (Shevyreva, 1971a, Fig. 7 b). There is no trace of a mesoloph or mesocone (Fig. 2 Q). The upper molars are longer than wide in contrast to the situation in sciuravids. *Terrarboreus* agrees with the later ctenodactylids in the enlarged infraorbital foramen, the shape of the molars, the reduction of the premolars, the characters of the anteroloph, and the absence of mesocone and mesoloph. The main changes that would be needed to derive the upper teeth of unquestioned ctenodactylids from those of *Terrarboreus* would be to develop a connection from the metacone to the posteroloph, as in *Tataromys* (Fig. 2 O), and the loss or near loss of P³. In her text, Shevyreva (1971a, p. 81) considered that the large size of the infraorbital foramen might require the removal of *Terrarboreus* from the Sciuravidae, but considered it best to leave it as a progressive member of that family. She did not raise the possibility that it might be primitive ctenodactylid. The following year (1972a, p. 1453) she suggested relationships between *Terrarboreus* (and *Tamquammys*) and the European paramyids *Pseudoparamys*, *Meldimys* and *Ailuravus*. Any such relationships must be quite distant, although *Ailuravus* agrees with the ctenodactylids in having a short lower incisor (Wood, 1976, p. 125-128).

It seems very possible that *Terrarboreus* and *Woodomys* are the upper and lower dentitions of the same genus. However, the two should not be considered synonyms until associated upper and lower dentitions are found, and until it is fully demonstrated that *Terrarboreus* was a ctenodactylid.

Four genera from the Late Oligocene of Mongolia and China have been recognized as undoubted ctenodactylids since Bohlin's detailed study (1946). *Tataromys*, with four described species, is the best known, being represented by skulls, jaws, skeletal material and numerous teeth (Bohlin, 1946, pp. 95-99, 168-197). The infraorbital foramen is fully enlarged, transmitting a large masseter medialis (Bohlin, 1946, p. 77); although Bohlin does not say so, his illustration (1946, Fig. 17A) makes it clear that the fossa for the muscle extended onto the premaxilla; the posterior end of the palate is thickened into a very peculiar mass of bone, 6 mm in vertical thickness and extending well back of the rear of M³, as in *Massouteria*, *Felovia* and *Ctenodactylus*. Unfortunately, this area is known in very few fossil ctenodactylids. The bulla was enlarged, but not hypertrophied. The coronoid is small, but it and the condylar process rise distinctly above the level of the occlusal plane. The skeleton indicates "that in its proportions *Tataromys* must have been very like *Ctenodactylus*" (Bohlin, 1946, p. 196).

In the lower molars of *Tataromys*, *Leptotataromys* and

Karakoromys, there is a feature not seen in *Woodomys*—a definite crest between the metalophid and the hypo-lophid, paralleling them and directed toward the metaconid (Fig. 3, N, O, P). It is more probable that this is an elongate posterior arm of the protoconid than that it is a mesolophid, especially in view of its tendency to swing toward the metaconid, where it almost forms a metalophid II. If this interpretation is correct, there is, presumably, no mesolophid in any ctenodactylid. *Leptotataromys*, known from a single specimen (although Stehlin and Schaub, 1951, Fig. 497 and p. 291, wonder whether a lower jaw, Basel Mo 21624, might belong here), is an isolated form of uncertain phylogenetic position.

The upper teeth of *Tataromys* show the metacone firmly connected with the posteroloph and no suggestion of any metacone-protocone connection (Fig. 2 O), agreeing with all later ctenodactylids. This is the first step toward the double-lobed pattern of the Pleistocene and Recent genera (Fig. 2 A-F). *Yindertemys* is known from a single isolated M³ (Fig. 2 P), which is a most peculiar tooth, with an isolated anterocone and numerous unusual connections between crests in the posterior half of the tooth. Perhaps the pattern could have been derived from one like that of *Tataromys*; the tooth is, however, lower crowned than that genus (Bohlin, 1946, p. 109), and must represent either a highly specialised type of ctenodactylid or a highly anomalous individual. It could not be congeneric with *Leptotataromys*.

In both *Tataromys* and *Leptotataromys* the lower incisor is long, for ctenodactylids, reaching to the rear of M₃ (Bohlin, 1946, pp. 85 and 108).

MIocene AND PLIOCENE CTENODACTYLIDS

More ctenodactylids are known from the Miocene than from any other epoch, presumably because by this time the family was present not only in Central Asia but also south of the Himalayas, in Africa and in Sardinia. The relationships of the Miocene forms to the known Oligocene ctenodactylids is in all instances somewhat uncertain, but attempts to suggest possible relationships have been made in Figs. 2-3.

The largest collection of Miocene ctenodactylids is from Beni Mellal, Morocco. Material from here was described by Lavocat (1961, pp. 52-64 and 66-67) as *Africanomys pulcher*, *A. incertus*, *Sayimys jebeli*, *Metasayimys curvidens* and *Dubiomys mellali*. Following Schaub (1958, p. 780), he accepted the Family Tataromyidae Bohlin, 1946 (see above, p. 122), to which he referred all but *Dubiomys* (which he left Rodentia, *incertae sedis*). Black (1972, p. 243) concluded: "From Lavocat's descriptions and illustrations, it appears possible that only a single genus of ctenodactylid is actually present in the Beni Mellal fauna and this is *Africanomys*." Jaeger revised the Beni Mellal ctenodactylids, with the help of "un matériel

nouveau et abondant" (1971, p. 113, Résumé). He concluded that only two of Lavocat's five species, representing the genera *Metasayimys* and *Africanomys*, were valid.

After Lavocat (1961, p. 59) had defined the new genus *Metasayimys*, he then described the new species, *Metasayimys curvidens*, whose diagnosis was "Celle du genre. Dents de petites dimensions." Since no further species of the genus were defined, *M. curvidens* is the genotype of *Metasayimys* by monotypy. Jaeger (1971, p. 123) listed *Sayimys jebeli* Lavocat 1961, *Africanomys incertus* Lavocat 1961 (in part), *Africanomys pulcher* Lavocat 1961 (in part), *Metasayimys curvidens* Lavocat 1961, and *Dubiomys mellali* Lavocat 1961, as synonyms, an action that seems very reasonable. However, Jaeger selected, without explanation, the species *jebeli*, placed by Lavocat in *Sayimys*, as the valid species, perhaps because it had page priority. Since *M. curvidens* Lavocat 1961 was a validly proposed name for the genotype species of *Metasayimys*, the International Rules dictate that it *must* be the valid species, assuming the synonymy given above to be correct and that the surviving species belongs to *Metasayimys*. I therefore use the species name *M. curvidens* for the Beni Mellal *Metasayimys*, and consider the other forms listed above as its synonyms.

The lower deciduous tooth shown here in Fig. 5 C, identified by Lavocat as *Africanomys incertus* and by Jaeger as *Metasayimys jebeli* (= *M. curvidens*), seems to have nothing to do with the deciduous tooth identified by Lavocat as *M. curvidens* (shown here as Fig. 5 E), but to be closely related to the tooth figured by Jaeger as *Africanomys pulcher* (Fig. 5 D). It is, perhaps, a second species of *Africanomys*; it must surely belong to that genus (Black, 1972, p. 243). An attempt to suggest relationships among the poorly known deciduous teeth of ctenodactylids is shown in Figs. 4 and 5.

The lower molars of *Metasayimys* and *Africanomys* (Fig. 3, j, k) have three lingual lobes. None of the material illustrated by Jaeger (1971) suggests any separate metalophulid II, as do those of *Tataromys* and *Karakoromys* (Fig. 3, N, P), although on p. 127 Jaeger stated that a "pseudomesolophid" (= metalophulid II) is present on M_1 , but is lower on M_2 , of *Metasayimys*. On p. 133 he indicated that such a crest was present in *Africanomys*, but again none is shown on any of his figures. I would interpret this to mean that a distinct metalophulid II is very transitory in *Africanomys* and *Metasayimys*, even more so than in *Sayimys* (Fig. 3 M). The crests of the lower molars are nearly transverse, differing in this from those of *Sayimys*. P_4 is large, for a ctenodactylid, and that of *Africanomys*, at least, could have been derived from one like that of *Woodomys* without great difficulty. Cement is present in the valleys of M_{2-3} of *Metasayimys* (Jaeger, 1971, Pl. 2, Figs. 4 and 8), a progressive character.

The upper teeth of both genera are bilobed (Fig. 2), with a strong tendency, especially in *Metasayimys*, for the crests of each lobe to unite soon after wear begins. P^4 of *Africanomys* is large for a ctenodactylid; that of *Metasayimys*

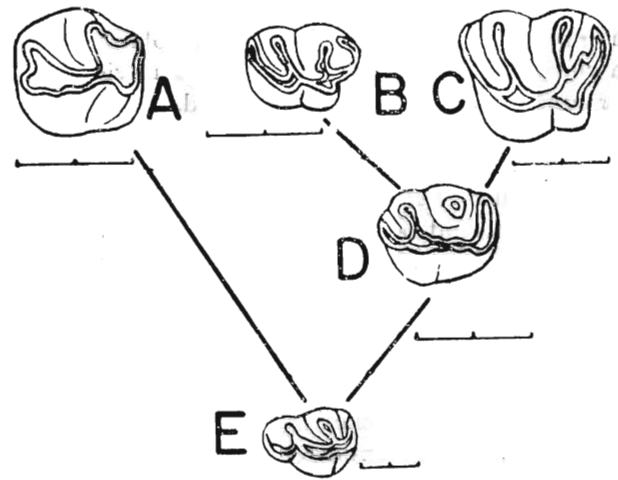


Fig. 4. Ctenodactylid upper deciduous teeth. Scale bars are 2 mm long. Figures redrawn from sources indicated.

- A. *Irhoudia bohlini*, RdP⁴ reversed, Jaeger, 1971, Pl. 1, Fig. 7.
- B. *Metasayimys curvidens*, RdP⁴ reversed, Jaeger, 1971, Pl. 2, Fig. 6.
- C. RdP⁴ (reversed) identified by Lavocat, 1961, as *Africanomys pulcher*, and by Jaeger, 1971, as *Metasayimys jebeli* (= *M. curvidens*); Lavocat, 1961, Pl. 6, Fig. 6.
- D. *Africanomys pulcher*, RdP⁴ reversed, Jaeger, 1971, Pl. 1, Fig. 4.
- E. *Tataromys plicidens*, LdP⁴, Bohlin, 1937, Fig. 88.

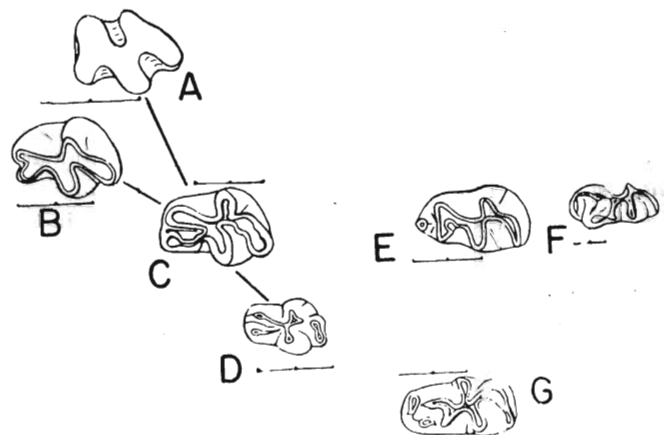


Fig. 5. Ctenodactylid lower deciduous teeth. Scale bars are 2 mm long. Figures redrawn from sources indicated.

- A. *Pectinator* sp., RdP₄, Jaeger, 1971, Fig. 4.
- B. *Irhoudia bohlini* LdP₄ reversed, Jaeger, 1971, Pl. 1, Fig. 8.
- C. RdP₄ identified by Lavocat, 1961, as *Africanomys pulcher*, and by Jaeger, 1971, as *Metasayimys jebeli* (= *M. curvidens*); Lavocat, 1961, Fig. 13 C.
- D. *Africanomys pulcher*, Jaeger, 1971, Pl. 1, Fig. 5.
- E. *Metasayimys curvidens*, LdP₄ reversed, identified by Lavocat, 1961, as *Dubiomys mellali*; Lavocat, 1961, Fig. 13 B.
- F. *Sardomys dawsonae*, RdP₄, de Bruijn and Rümke, 1974, Pl. 2, Fig. 7.
- G. *Tataromys cf. plicidens*, LdP₄ reversed; Lavocat, 1961, Fig. 13 A, after Bohlin, 1946, Fig. 19-27.

is somewhat reduced. Jaeger stated (1971, p. 124) that a greatly reduced P^3 is present in *Metasayimys*, and that it is shed at the same time as dP^4 . This suggests the possibility that the tooth may have been dP^3 rather than P^3 , especially in view of the general uncertainty among rodents as to which tooth is present (Wood, 1970, pp. 244-246). As Jaeger pointed out (1971, p. 127), *Metasayimys* and *Sayimys obliquidens* developed cheek tooth hypsodonty in rather diverse manners, which supports reference of the latter to *Sayimys*. The upper incisor of *Metasayimys* is grooved. It does not seem possible, at present, to make sense of the distribution of this characteristic among ctenodactylids, due to the absence of information for most fossil genera. The lower incisor of *Africanomys* may have been longer than usual in ctenodactylids, perhaps extending beyond M_2 (Jaeger, 1971, p. 131). The posterior end of the hard palate of *Africanomys* extends behind M^3 , reminiscent of *Tataromys*, *Ctenodactylus*, *Felovia* and *Massouteria* (Jaeger, 1971, p. 128).

Although the two genera were sympatric and contemporaneous, *Africanomys* was certainly structurally ancestral to *Metasayimys*, and must have had, in turn, an ancestor not very different from *Woodomys* (Figs. 2, 3).

De Bruijn (de Bruijn and Rümke, 1974, p. 54) thought that the morphology of the Sardinian ctenodactylids suggests that the family "reached Africa at least as early as the Late Oligocene." I doubt very much that they arrived there before the Burdigalian.

The two genera *Sardomys* and *Pireddamys* from the Miocene of Sardinia (de Bruijn and Rümke, 1974) seem to stand in the same relationship to each other as do *Africanomys* and *Metasayimys*. They are strikingly different from the Beni Mellal genera, however, in that the lower molars have four lobes on the lingual side, a feature that connects these genera with the Late Oligocene Asiatic ones (de Bruijn and Rümke, 1974, p. 54). The second of these lobes (Fig. 3 H, I) was directed toward the posterior or posterobuccal side of the metaconid, in a manner that I interpret as indicating the crest to be an incomplete metalophulid II, a conclusion in agreement with that of de Bruijn (de Bruijn and Rümke, 1974, p. 48), who, however, calls this crest a metalophid. I believe that the situation in the ctenodactylids shows the value of the more precise terminology proposed by Wood and Wilson (1936, Fig. 2: 11, 12). Although it is impossible to be certain, due to the wear of the teeth, the second crest in *Sardomys* (Fig. 3 I) seems to have been a metalophulid II: that in *Pireddamys* could not have been a metalophid, since it did not reach the metaconid (Fig. 3 H, all molars, but specially M_{2-3}). It could be called either a metalophulid II or the posterior arm of the protoconid. Cement is present in the valleys of M_{2-3} of *Sardomys* (de Bruijn and Rümke, 1974, p. 54). Both upper and lower incisors of *Sardomys* were grooved. The lower incisor of *Pireddamys*

ends below M_2 . The peculiar wear surface of the upper incisor (de Bruijn and Rümke, 1974, p. 53), common, as they state, among ctenodactylids, is an unusual but by no means unknown occurrence in a wide variety of other rodents.

In the upper molars, these Sardinian genera have less union of the anterior and posterior pairs of crests into two lobes than is the case in the genera from Morocco. Although the upper teeth are also reminiscent of those of the Late Oligocene Asiatic genera, the difference from their contemporaries in Africa is less striking than in the lower teeth.

In conclusion (based especially on the lower teeth, which are better known), *Sardomys* and *Pireddamys* could readily have been derived from ancestors similar to the Oligocene Asiatic genera *Karakoromys* and *Tataromys*, but they are very different from the known Moroccan genera (de Bruijn and Rümke, 1974, p. 54). This suggests the possibility that the ctenodactylids might have reached Sardinia from some source other than North Africa.

Sayimys perplexus, from the Early Pliocene Nagri Zone of the Indian Siwaliks (Wood, 1937a, pp. 73-76) represents a third line of ctenodactylids. Still known only from a single lower jaw (Fig. 3 G), it is characterized by a large (for a ctenodactylid) P_4 , and molars with three lingual lobes that are diagonally directed, in contrast to the transverse lobes of *Africanomys* and *Metasayimys*. A very notable feature of the teeth is the presence of a large posterobuccal cingular cusp on P_4-M_2 .

Hinton (1933, p. 622) briefly described (without illustration) a rodent from the Late Miocene Chinji Zone of the Siwaliks of Pakistan as *Pectinator sivalensis*. Fortunately, Hinton's specimen has been illustrated and described by Black (1972, pp. 241-242 and Fig. 1), who transferred the species to *Sayimys*, as *S. sivalensis*, and considered it to be more primitive than but directly ancestral to *S. perplexus* (1972, p. 242 and Fig. 11). There are, however, differences between the two species that seem to me to be significant, and which mitigate against the close relationship postulated by Black. The crests and valleys of M_{2-3} of *S. sivalensis* are directed transversely and there is no trace of a cingular cusp on M_2 (Fig. 3 L; Black, 1972, Fig. 1 e). The same holds true for the lower molar that de Bruijn (de Bruijn and Rümke, 1974, Pl. 2, Fig. 5) referred to this species. Moreover, Black (1972, p. 241) states that there is "only [a] faint posterior shelf, or cingulum, on M_2 ", which clearly is much weaker than in *S. perplexus*, as it does not show on either the lateral or occlusal drawings of the tooth (Black, 1972, Fig. 1 c, e). The lower incisor is short, ending below M_2 (Black, 1972, p. 242). The teeth of *S. sivalensis* are of about the same height of crown as are those of *Africanomys pulcher*, the pattern is very similar (Figs. 2 J and N; 3 K and L), and the jaw seems equally, primitive.

The description of *S. sivalensis* by Black (1972, p. 242) agrees very closely with the illustrations and description of *Africanomys pulcher* (Jaeger, 1971, Figs. 11-13; Pl. 1, Figs. 1-5; Pl. 3, Figs. 3-5; pp. 128-133), which were not available when Black wrote his paper. I feel that the best treatment of the Chinji species, until much better material is available, is to refer it to *Africanomys* as *A. sivalensis* (Figs. 2-3).

De Bruijn (de Bruijn and Rümke, 1974, Pl. 3, Fig. 4) illustrated an upper molar from the Chinji of Pakistan, redrawn here as Fig. 2 J, as *Sayimys sivalensis* [sic]. This tooth is bilobed, and clearly had no mesocone or mesoloph. The metaloph is complete, with the posterior cingulum arising from the middle of the loph. As in the case of the lower teeth, this tooth seems very similar to the corresponding teeth of *Africanomys*, although perhaps it is more primitive, and supports the identification of this species as *Africanomys sivalensis*. The Pakistani species seems much too primitive to be placed in *Metasayimys*.

Bohlin described material from beds at Taben-buluk, later than the extensive Yinderte fauna (Bohlin, 1946, p. 248). Thenius (1959, p. 121, footnote) considered these to be Late Miocene. Among the fossils were a skull, maxillae and jaws described by Bohlin as *Sayimys obliquidens* (1946, pp. 109-125). The coronoid process was weak, passing the alveolar border behind M_3 (op. cit., p. 113). The palate extended slightly behind M^3 , but not so much so as in *Tataromys*, nor was it so thick (op. cit., p. 111). The lower molars of this species have diagonal crests, as in *S. perplexus* (Fig. 3 M) and there is a strong postero-buccal basal cingular cusp on P_4-M_2 (Fig. 3 M). The crowns are of intermediate height. These features, I believe, together with all the detailed similarities pointed out by Bohlin (1946, pp. 114-116), indicate a close relationship between *S. obliquidens* and *S. perplexus*, and justify Bohlin's placing them in the same genus. These features are also marked differences from *Metasayimys*, and indicate that Jaeger (1971, p. 123) was wrong in referring *S. obliquidens* to that genus. I believe that the Moroccan genera are not far removed from *Sayimys*, however, as indicated by their placement on Figs. 2 and 3. On a little worn lower molar of *Sayimys*, the anterior lobe clearly is double (Fig. 3 M; Bohlin, 1946, Fig. 30 c) as in *Africanomys* and *Metasayimys* (Jaeger, 1971, pp. 127, 133), but was much less persistent than in *Sardomys* and *Pireddamys*. Perhaps this feature was present in the unworn teeth of all Miocene ctenodactylids, but disappeared more quickly with wear in some lines than in others. In *Africanomys*, *Metasayimys* and *Sayimys* there does not seem to have been any tendency to form a lake in the anterior part of the tooth, as is the case in the Sardinian genera (Fig. 3 H, I). The posterior end of the lower incisor of *S. obliquidens* lies below the anterior half of M_2 (Bohlin, 1946, p. 114).

The upper teeth of *S. obliquidens* are fundamentally bilobed, as in other ctenodactylids. The subdivision of the lobes into the basic four crests is not obliterated by wear quite so rapidly as in *Africanomys* and *Metasayimys*. The metacone is offset (Fig. 2 K) from the metaloph, as in *Africanomys* (Fig. 2 N). Both upper and lower incisors were keeled.

In general, all the Miocene-Pliocene ctenodactylids have upper teeth whose crowns have begun to develop strong unilateral hypsodonty (Bohlin, 1946, Figs. 30d, d'', e, e'; 35; Lavocat, 1961, Figs. 9 A₃; 10 G₂, G₄; Pl. 6, Figs. 1, 4; Jaeger, 1971, Fig. 9; de Bruijn and Rümke, 1974, Pl. 3, Fig. 2 b), with relatively low crowned buccal sides and hypsodont lingual ones. This is a normal pattern for the development of hypsodonty in many diverse types of rodents. The teeth of these forms are never, however, evergrowing. Cement fills the valleys of M_{2-3} of *Metasayimys* and *Sardomys*. So far as I am aware, these are the only pre-Pleistocene ctenodactylids in which cement has been reported.

PLEISTOCENE CTENODACTYLIDS

There has been, until recently, a complete absence of generally recognized ctenodactylids from the Pleistocene. Jaeger (1971) described *Irhoudia* as a new genus of ctenodactylid from the Villafranchian of Morocco. *Pellegrinia* from the Pleistocene of Sicily was first considered a ctenodactylid by Tullberg (1899, p. 395); later by Forsyth-Major (in Vaufrey, 1929, p. 47); and, apparently independently, by Bohlin (1946, Fig. 90). Otherwise it was generally forgotten. Schaub (1958, p. 719) erected a Family Pellegriniidae, of uncertain relationships, for this genus. More recently, Jaeger (1971, pp. 133-134, Fig. 14) has discussed *Pellegrinia* and again referred it to the Ctenodactylidae, where it unquestionably belongs. Thaler (1972) accepts *Pellegrinia* as a ctenodactylid without question.

The shape of the sciurognathous lower jaw of *Pellegrinia* is very similar to that of other ctenodactylids (Fig. 6 A), in the great elongation and vertical shallowness of the jaw, the absence of a coronoid process, the condyle level with the occlusal plane of the cheek teeth, and the small size of the mental foramen. The masseteric crest is more continuous (Fig. 6 A) than indicated by Jaeger (1971, p. 133), and runs into a ridge that extends back to the condyle (Fig. 6 C). The symphysis is highly rugose, and there is a very large genioglossal pit (Fig. 6 B).

As pointed out by Jaeger (1971, p. 133), the large incisive foramina (Fig. 6 D, E) extend back nearly to the level of M^1 , and are continued back by paired gutters along each side of the narrow palate. There are two pair of posterior palatine foramina (Fig. 6 D), the anterior one in the maxillary near the front of M^1 , and the pos-

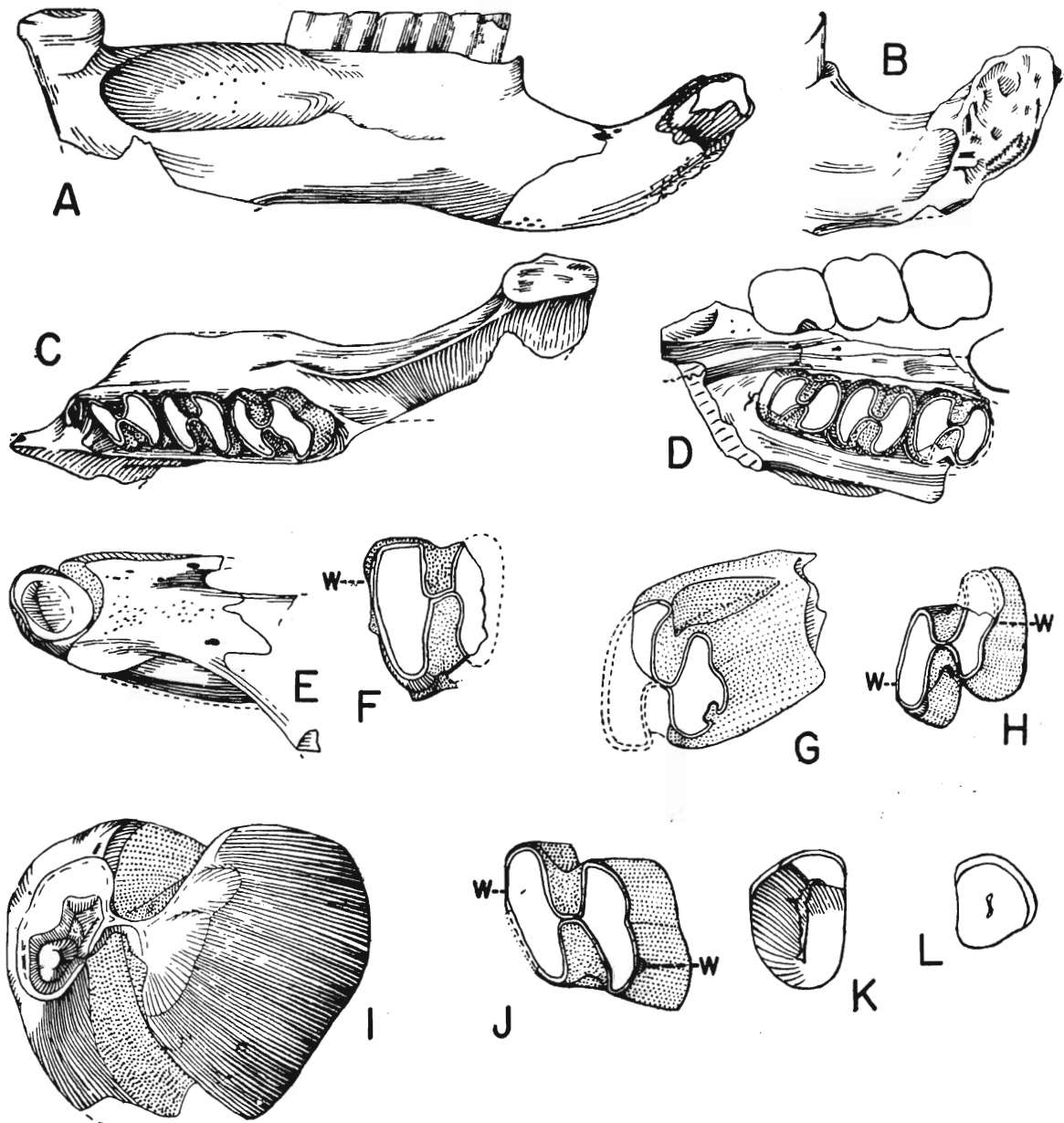


Fig. 6. Bones and teeth of *Pellegrinia panormensis*. Anterior ends of isolated teeth to the left. W=interdental wear facet. A-D $\times 2.5$; I $\times 10$; others $\times 5$.

- A. Lateral view of right lower jaw, Basel Br 586; anterior portion reversed from Basel Br 581.
- B. Medial view of symphysis, Basel Br 581.
- C. Occlusal view of RM_{1-3} with lower jaw, Basel Br 586.
- D. Palate of Basel Br 583; outline of left cheek teeth reversed from right side; posterior end of hard palate drawn from Basel Br 584.
- E. Ventral view of premaxilla and incisor, Basel Br 383.
- F. RM_2 , Basel Br 378.
- G. LM_2 , Basel Br 375.
- H. LM_2 , Basel Br 379.
- I. LM_1 or $_2$, unerupted, Basel Br 380.
- J. RM_4 , Basel Br 377.
- K. RI_1 , wear surface, Basel Br 384.
- L. Broken anterior end of LI_1 , Basel B 386.

terior one in the palatine near the back of M^1 . As Jaeger stated, the posterior end of the bony palate is not preserved on Basel Br. 583, but it is shown on Fig. 6 D slightly behind the middle of M^3 , based on Basel Br. 584, a very badly damaged palate. The palate differs notably from those of *Tataromys* (Bohlin, 1946, Fig. 17 b) and *Sayimys obliquidens* (Bohlin, 1946, Fig. 30 a''), as well as from those of *Ctenodactylus*, *Felovia* and *Massouteria*, in all of which the palate has been produced backward a considerable distance. *Pellegrinia* is primitive in this respect.

The cheek teeth (M^3_3) are all hypselodont, and are completely covered with a heavy layer of cement (Fig. 6 C, D, F-J), much more prominent than the cement in any other ctenodactylid, since it completely surrounds the crowns. Most of the teeth, both uppers and lowers, of *Pellegrinia* in the Basel collection merely show the typical double invagination, giving a figure-8 enamel pattern (Fig. 6 C, D). One slightly worn M^3 , however, preserves the notch between the posterior cingulum and the metacone, that is rather characteristic of ctenodactylids (Fig. 6 G). Several lower teeth (Fig. 6 C, M^3_3 ; H, I), show an indentation on the posterior side, marking the buccal edge of the hypoconulid. The crests are diagonally oriented, the lowers more so than the uppers, as in *Sayimys*, *Felovia* and *Massouteria*.

A completely unworn and presumably unerupted lower molar (LM^1_1 or $_2$) shows a number of interesting features (Fig. 6 I). The cement clearly neither entirely surrounded the tooth nor covered the crown, before eruption, at least not with a macroscopically visible layer. The anterior lobe consists of a marginal crest, briefly interrupted on the posterior side, and thickened lingually and anteriorly in what would seem to be a protoconid and an anteroconid. This crest surrounds a basin, near the lingual side of which is a large, isolated metaconid. There are clearly two transverse trigonid crests, best called the metalophulids I and II. The preservation of any trace of these as distinct crests would be even more transitory than in *Sayimys obliquidens*. Near the centre of the tooth, the trigonid is connected to the talonid by a narrow ridge, with no trace of a mesoconid. The talonid is compressed anteroposteriorly, in contrast with most ctenodactylids, and shows no trace of the usual hypoconulid flare. What seem to be the entoconid, hypoconulid and hypoconid are aligned, with only faint notches separating them.

The incisors (Fig. 6 E, K, L) are subtriangular in outline, the lower with thicker enamel than the upper. There is some variation in shape of the upper incisors with wear, a young one (Basel Br. 383, Fig. 6 E) showing a sulcus, and the incisor of what seems, because of the very irregular pulp cavity, to have belonged to a senescent individual (Wood, 1974b, p. 33, Fig. 14 C) having a

smooth anterior face. Age variation presumably accounts for the rather pronounced size variation. The enamel extends well onto the lateral side of the lower incisor (Fig. 6 A, L), and is heavier than that of the upper teeth. There is a pocket in the dentine of one upper incisor (Fig. 6 E) that would have received the tip of the lower incisor, as in *Pireddamys* (de Bruijn and Rümke, 1974, p. 53). The outline of the lower incisor is similar to that of *Tataromys* (Bohlin, 1946, Fig. 16 j, l-q) and rather different from that of *Sayimys* (Bohlin, 1946, Fig. 30 b'''). The lower incisor is short, as in other ctenodactylids and in the Eocene paramyid *Ailuravus* (Wood, 1976, 125-128), extending back only to a point beneath the rear of M^2_2 .

Jaeger (1971, p. 134) considered *Pellegrinia* to have been close to the living genera *Felovia* and *Massouteria* and to the Pleistocene *Irhoudia*. I agree with him that *Pellegrinia* is close to the two Recent genera, but, as pointed out below, I believe it to be rather different from *Irhoudia*, as shown on Figs. 2 and 3. Its primitive palate may indicate, however, that *Pellegrinia* had had a much longer independent ancestry.

The described material of *Pellegrinia* leaves many questions to be answered by the study of better material. A note by Stehlin with the Basel specimens states "Das Museum in Palermo besitzt viel besserer und reichlicher Material als das von de Gregorio bearbeitet", and Dr. Johannes Hürzeler informed me that there is beautiful material, including a good skull, of *Pellegrinia* in the Instituto di Geologia y Palaeontologia de l'Universita Pisa.

Irhoudia, from the Villafranchian of Morocco, is much more primitive than *Pellegrinia*. The teeth are high crowned but rooted. The lower molars have three lingual and two buccal lobes, transversely oriented, and the uppers two of each. No P^4 is preserved, but one specimen shows a small alveolus, presumably for this tooth. There is no evidence that there was a P^4 but one may have been present. A specimen with dP^4 has no trace of an alveolus for P^3 or dP^3 (Jaeger, 1971, p. 119). Even an unworn M^1_1 (Jaeger, 1971, Fig. 6) shows no trace of a separate metalophulid II.

Jaeger (1971, p. 122) considered *Irhoudia* to be close to the ancestry of both *Pectinator* and *Felovia*, but not directly ancestral to either. However, the distinction between ctenodactylids with transversely directed lobes of the lower molars, as *Pectinator*, *Irhoudia*, *Metasayimys* and *Africanomys*, and those with diagonal ones, as *Sayimys*, *Pellegrinia*, *Ctenodactylus*, *Felovia* and *Massouteria*, seems to me a rather fundamental one. This, together with the fact that *Pectinator* and *Irhoudia* possess functional, though small, premolars and have no cement, suggests a close relationship of *Irhoudia* to *Pectinator* (Figs. 2 A, E; 3 A, E).

RECENT CTENODACTYLIDS

The four genera of living ctenodactylids, *Pectinator*, *Ctenodactylus*, *Massouteria* and *Felovia*, are all limited to arid areas of North Africa (Fig. 1). The details of the tooth pattern are rapidly lost with wear in all living genera, all (Grassé and Dekeyser, 1955, p. 1419) having rootless molars, although Tullberg (1899, p. 154) reported that *Ctenodactylus* ultimately forms roots. The teeth of *Massouteria* and *Felovia* possess cement.

The dental formula for *Pectinator* given by Jaeger (1971, p. 116, following Stehlin and Schaub, 1951, p. 292 and Fig. 500) must surely be in error in including two lower premolars, since no rodent has ever been demonstrated to have more than a single lower premolar, leaving aside the situation in the Bathyergidae in which, whatever the supernumerary teeth may be, they clearly result from a relatively recent duplication of one sort or another. Schaub (Stehlin and Schaub, 1950, p. 292) considered *Pectinator* to have a tooth in front of P_4 . However, from the figure (Stehlin and Schaub, 1951, Fig. 500), it seems probable that this structure is part of an anterior root of dP_4 . Jaeger reported (1971, p. 116, footnote) the presence of P^3 in a specimen of *Pectinator*. If he is correct that this was P^3 and not dP^3 , it would mean either that this tooth was shed very early in life in all post-Eocene ctenodactylids or that *Pectinator* has no known ancestors later than Eocene. The unworn teeth of *Pectinator* figured by Lavocat (1961, Pl. 6, Fig. 3) which Jaeger (1971, p. 116) called P^3 , dP^4 and M^1 must be something else, if I interpret Lavocat's stereophotographs correctly. The posterior tooth is certainly M^1 ; the large tooth in front of it seems to be less worn than M^1 , and should, therefore, be P^1 . The structure in front of P^4 shows no detail on the plates; I wonder whether it might be an anterior root of dP^4 , especially since Jaeger said it is reduced to a stump (1971, p. 116).

Pectinator seems derivable from *Africanomys* and *Metasayimys*, except for the presence of cement in the valleys of the latter. It is separable from the other living genera by the short palate, that ends by the middle of M^3 ; the separate palatines; the flat upper incisors; and the transverse crests of the lower molars.

Massouteria, *Felovia* and *Ctenodactylus* agree in a number of features. The hard palate is produced well behind M^3 as in *Tataromys*; the functional cheek teeth are reduced to M_3^3 (Jaeger, 1971, p. 117, reports that P^4 of *Felovia* is very small and barely pierces the bone, that one is present in *Massouteria*, and that very ephemeral premolars, both upper and lower, are present in *Ctenodactylus*); and the crests of the lower molars are diagonal. The first two genera agree in being more hypsodont than *Ctenodactylus*, in having grooved upper incisors, and in having cement that seems to be restricted to the buccal embayment of the lower teeth. From Jaeger's

figure (1971, Fig. 3) cement seems to be present only in the lingual embayment of the upper molars. However, Schaub (Stehlin and Schaub, 1951, p. 371) says of the upper molars of *Massouteria*: "Beide Buchten sind mit Zement erfüllt." *Massouteria* and *Ctenodactylus* have hypertrophied bullae. It seems to me that all three genera were perhaps derived from a common ancestor something like *Sayimys*, and that *Felovia*, *Massouteria* and *Pellegrinia* are more closely related to each other than any is to *Ctenodactylus* (Figs. 2, 3).

PARALLELISM BETWEEN THE CTENODACTYLIDAE AND THE HYSTRICOGNATHI

If the thesis presented above, that the Ctenodactylidae have an independent evolutionary history that can be traced back to the Middle Eocene of Central Asia, is anywhere near correct, it becomes clear that this family can have no close ties with any members of the Hystricognathi as defined by Lavocat (1974, p. 8) or by Wood (1975). The earliest member of the Ctenodactylidae accepted in this paper, *Saykanomys*, could not have been close to any hystricognathous form, including the reithroparamyine paramyids. Its ancestry is, at present, uncertain, but seems to me more probably to have been paramyine or microparamyine than sciuravid.

The features that the Ctenodactylidae share with the Hystricognathi include: (1) the enlarged infraorbital foramen through which the *medialis* branch of the masseter muscle passes from its origin on the snout to its insertion on the mandible; (2) fusion of the malleus and incus; and (3) multiserial incisor enamel. In addition, it has been suggested that there is a rudimentary Sacculus urethralis in *Ctenodactylus* and de Bruijn has proposed that retention of deciduous teeth is a character shared by ctenodactylids and hystricognaths.

Some features markedly separate the ctenodactylids from the hystricognaths. There is never any suggestion in ctenodactylids of the lateral shifting of the angular process of the mandible that is the diagnostic feature of the Hystricognathi. The ctenodactylids do not seem ever to have had a *Masseter lateralis profundus, pars posterior*, deep, a muscle present in all living hystricognaths (Woods, 1972, pp. 127-128). The ctenodactylid tooth pattern has, I believe, evolved without either a mesoloph or a mesolophid, structures that are present at least in the early members of the Old World Hystricognathi, whatever may have been the situation in the New World Caviomorpha (for varying interpretations of the tooth structure in the latter, see Wood and Patterson 1959 and 1970, and Lavocat 1973 and 1974). Since incipient hystricognathy was present in the Late Paleocene *Franimys* (Wood, 1975, p. 78), the separation between the Ctenodactylidae and the Hystricognathi must go back at least that far.

HYSTRICOMORPHY

The most striking parallelism between the Ctenodactylidae and the Hystricognathi is the development of hystricomorphy—the enlargement of the infraorbital foramen and the forward migration through that opening of the origin of the *Masseter medialis*, shifting its origin from the inner surface of the zygomatic arch forward onto the snout, and resulting in a much greater anteroposterior component of the pull of this muscle.

This similarity was the basis for the Suborder Hystricomorpha as foreshadowed by Waterhouse (1839) and officially erected by Brandt (1855). But Tullberg (1899) divided rodents, on the basis of the angular process of the mandible, into Sciurognathi and Hystricognathi, and was very uncertain about the correct taxonomic position of the sciurognathous hystricomorphs (Ctenodactylidae, Anomaluridae, Pedetidae), an uncertainty that has continued to the present time.

Studies of the Eocene-Oligocene European Theridomyoidea (Theridomyidae + Pseudosciuridae) convinced almost all workers (Lavocat, 1951, pp. 66-70; 1955; Wood, 1955, pp. 173-175; 1965a, p. 128; Thaler, 1966, Fig. 1) that these families had nothing to do with the hystricognaths or with the other sciurognathous hystricomorphs. The only recent suggestion of a relationship of any sciurognath with the Hystricognathi was the inclusion by George (1974) of the ctenodactylids in the Zoological Society of London symposium on hystricomorphs.

According to the phylogeny of the Ctenodactylidae proposed in this paper, their Middle Eocene ancestors already had a somewhat enlarged infraorbital foramen, but show no trace of hystricognathy. The snouts of the Middle Eocene *Tamquammys* and *Saykanomys* are not preserved (Shevyreva, 1971b, Fig. 1 b, v; 1972b, Fig. 1 b), so that it cannot be determined whether the masseter had as yet invaded the enlarged infraorbital foramen, but in the late Eocene *Yuomys* the muscle clearly arose on the maxilla in front of the infraorbital foramen. Among the Hystricognathi, there is no evidence of enlargement of the foramen before the Late Eocene (Wood, 1975, p. 78; Wahlert, 1973), so that the Middle Eocene ctenodactylids were more advanced in this respect than was any known hystricognath.

Hystricomorphy must have developed independently a minimum of four times (Ctenodactylidae, Franimorpha Theridomyoidea and Anomaluridae + Pedetidae if these two are related, which I doubt), and perhaps three or more additional times among the Franimorpha or their descendants. This extreme parallelism was due, I believe, to a very strong selective pressure for an increase in the anteroposterior component of pull of the masseter muscle for more efficient gnawing. The strength of this selective pressure resulted in the rapid elimination, beginning

in the Late Eocene or Early Oligocene, of rodents that had not modified the masseter muscle in one of the hystricomorphous, myomorphous or sciuromorphous manners. As a result, only a single genus with the primitive type of musculature (*Aplodontia*) has survived to the present.

FUSION OF MALLEUS AND INCUS

These bones are fused in all living Old World hystricognaths, in most (but not all) living Caviomorpha (New World hystricognaths), and in the living ctenodactylids, and are not fused but so closely appressed as to eliminate motion between them in the living *Pedetes*. Unfortunately these bones are essentially unrepresented among fossils. The only instances of which I am aware are the report of non-fused ossicles in *Theridomys* (Lavocat, 1967), and of fused ones in the Miocene hystricognathous phiomorph *Paraphiomys* (Lavocat, 1973, pp. 33-34) and in the Miocene caviomorph "*Olenopsis*" (Fields, 1957, p. 343). Because of the rarity of fossil ossicles, it is impossible to determine the dates at which fusion originated, but the absence of fusion in a number of recent caviomorphs (Wood and Patterson, 1959, pp. 292-293; Wood, 1975, Fig. 1) suggests that fusion may have developed several times, independently, within that group.

Since I do not know the selective advantage of fused ear ossicles, it is exceedingly difficult to arrive at any idea as to when or why fusion occurred in the various lines that have developed this feature. But the assumption that hystricognaths and ctenodactylids inherit fusion of ossicles from a common Paleocene ancestor seems to me to be so improbable as not to be worth consideration.

MULTISERIAL INCISOR ENAMEL

Korvenkontio (1934, Table pp. 116-123; his studies were extended by Wahlert, 1968) pointed out that multiserial incisor enamel characterizes all living hystricognaths. This feature is present in all the known Oligocene to Recent members of the group, both the Old World Hystricomorpha and Phiomorpha and the New World Caviomorpha. However, all of the Paleocene to Eocene North American Franimorpha that have been studied had the primitive type of enamel, the pauciserial type. The living ctenodactylids and pedetids alone among sciurognathous rodents have multiserial enamel (Wahlert, 1968, p. 17; Wood, 1975, Fig. 1).

Bohlin (1946, pp. 143-146) sectioned incisor enamel of *Taiaromys* and *Sayimys*, both of which had multiserial enamel. The enamel of *Sayimys* is very similar to that of *Ctenodactylus*, whereas in *Taiaromys* the lamellae are much heavier than in *Ctenodactylus* and with a much larger number of prisms.

The modification of the incisor enamel from the pauciserial type was probably related to resisting the increased pressure of the masseter muscle involved in

the gnawing mechanism (Wilson, 1972, pp. 220-221). Therefore, the development of multiserial enamel should have proceeded *pari passu* with the migration of the masseter muscle through the infraorbital foramen. There is no evidence as to why some groups of rodents acquired multiserial enamel, whereas most sciurognaths changed to uniserial enamel.

SACculus URETHRALIS

The Sacculus urethralis is a structure of unknown function, characteristic of the Hystricognathi. Tullberg (1899, p. 70) stated "Unter der Öffnung der Urethra findet sich am Penis stets ein Blindschlauch, den ich Sacculus urethralis nennen will." His description of the conditions in various hystricognaths shows that there is considerable variation in this structure. It may be a long groove on the ventral side of the penis, ending posteriorly in a deep sac (*Hystrix*, op. cit., p. 88); a shallow groove with a small sac (*Georychus*, op. cit., pp. 78-79); or a sac without any groove (*Coelogenys*, op. cit., p. 95 and, apparently, *Cavia*, op. cit., p. 103).

Tullberg reported that the Sacculus urethralis occurred in all forms that he included in the Hystricognathi, if adequately preserved males were available to him. Apparently, however, the structure is absent in *Lagostomus* (Wood and Patterson, 1959, p. 414, footnote³⁴).

Tullberg found a groove on the ventral side of the penis of *Ctenodactylus*. He said "Glans penis ... ist nach vorn etwas zugespitzt, mit einer ziemlich langen und tiefen, unter die Spitze gehenden Spalte, in deren distales Ende die Urethra mündet. Einen wirklichen Blindschlauch unter die Spitze, wie bei *Hystricomorphi*, giebt es hierz war nicht, diese Spalte dürfte jedoch möglicherweise als der Anfang einer solcher zu betrachten sein." (Tullberg, 1899, p. 158).

If the groove in *Ctenodactylus* is homologous to the structure in the hystricognaths (such a structure is unknown elsewhere in the order), it has presumably been acquired independently, just as it presumably was secondarily lost in *Lagostomus*. In the absence of any known function for either the groove or the sac, no explanation can be given for its independent acquisition.

RETENTION OF DECIDUOUS TEETH

Deciduous teeth have been retained, independently, in a considerable number of rodent groups. All known members of the Phiomorpha, beginning with the Early Oligocene (Wood, 1968) possessed deciduous teeth that were retained for much of the animal's life time; in all Miocene and later genera, these teeth were never replaced. The Recent Bathyergidae are unique among rodents in the large number of cheek teeth that may be present. There has been, so far as I am aware, no satisfactory study of these teeth, but it seems highly probable

that the series includes both permanent and deciduous premolars, sometimes, probably, duplicated. There is, however, no trace of retention of deciduous teeth in the Old World Hystricidae, so the trend must have started after the separation of the Hystricidae and Phiomorpha—possibly after the arrival of the ancestral phiomorphs in Africa.

Retention of deciduous teeth occurs in some of the Caviomorpha. But here it is very clear that it was not characteristic of the Early Oligocene members of the infraorder, but developed subsequently, within South America, only in the Colhuéhuapian and later echimyids (Wood, 1975, Fig. 1).

Among the Pedetidae, the situation is highly unusual (Wood, 1975, Fig. 1). Of the three known genera, there was normal replacement in the Miocene *Parapedetes*; probably the deciduous tooth was retained in the Miocene *Megapedetes* (Wood, 1974c, p. 41); in the living *Pedetes*, the hypselodont premolar is never replaced and seems not to replace a deciduous tooth. I know of no method of determining whether or not it is a retained deciduous premolar.

I do not believe that any ctenodactylid can be characterized as having retained deciduous teeth. De Bruijn (de Bruijn and Rümke, 1974, p. 51) stated that retention occurred in *Tataromys*, *Sardomys*, *Africanomys*, *Sayimys* and *Metasayimys*. I feel that he must have either misinterpreted what happened in these genera or have a very different understanding from mine of what is meant by retained deciduous teeth. He said (de Bruijn and Rümke, 1974, p. 51) "Judging from the *Tartaromys* [sic] dentitions figured by Bohlin (see Bohlin, 1946, fig. 19, no. 32 and 33) retention of DP₄ also occurred in this genus." But these figures of Bohlin's show P₄ well worn, though less so than M₁ and perhaps less so than M₂. I would interpret them to indicate that P₄ was lower crowned than M₁ and wore away faster, but that it erupted at the usual mammalian time. Bohlin (1946, Figs. 22 and 23) plotted the measurements of the available teeth of *Tataromys*. He included 23 specimens of P₄, 2 of dP₄, 19 of P₄ and 2 of dP₄, which are about the proportions to be expected among mammals with normal replacement. Neither Bohlin (1946, pp. 114-116, 122-124) nor Wood (1937a, pp. 73-76) reported deciduous teeth in *Sayimys*; clearly they were replaced at the normal time. I can find no indication either in the text or in the plates (Lavoocat, 1961; Jaeger, 1971) that either *Africanomys* or *Metasayimys* retained the deciduous teeth longer than normal.

However, replacement of the deciduous teeth was apparently somewhat delayed in *Sardomys*, since de Bruijn reports that both known lower jaws contain dP₄, and two of five isolated premolars are deciduous. P₄ is considerably less worn in the type of *Sardomys antonietae* than is M₁, which de Bruijn thought showed it to be

delayed in eruption. But one would expect P_4 to be less worn than M_1 , and de Bruijn's figures (de Bruijn and Rümke, 1974, Pl. 1, Fig. 1 a, 3 a) show P_4 to be much lower crowned than the molars in both *Sardomys* and *Pireddamys*, which would make it difficult to determine relative eruption dates from stages of wear. It should also be pointed out that the pattern of P_4 of *Pireddamys* was reduced to a circle of enamel at a time when M_1 still retained the buccal embayment (de Bruijn and Rümke, 1974, Pl. 2, Figs. 1, 2).

CONCLUSIONS

The rodent family Ctenodactylidae, now restricted to North Africa, can be traced back with certainty to Middle Oligocene, and probably to Middle Eocene, ancestors that inhabited Central Asia. The family presumably originated in Central Asia from an Early Eocene paramyid stock. One of the initial events in its evolution was the enlargement of the infraorbital foramen. By the Miocene, the family had spread into South Asia, North Africa and Sardinia. Enough is known of the structure of the Oligocene and Miocene genera to show them to have been ctenodactylids, but not enough to clarify the trends within the family. A suggested phylogeny of the family is presented in Figs. 2-3. However, several other arrangements would be equally logical. The family is best considered an independent Family Ctenodactylidae or the only family within an independent Superfamily Ctenodactyloidea.

The ctenodactylids have acquired hystricomorphy independently of any other rodents. The same is true for the fusion of the malleus and incus and the development of multiseriate incisor enamel. The suggested Sacculus urethralis in the male urogenital system, if it really is one, is another instance of parallelism.

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