A REVISION OF THE LARGE LAGOMERYCID ARTIODACTYLS OF EUROPE

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ABSTRACT. Large lagomerycids are only known in Europe from the Orleanian of the Loire Basin (France). At least three forms are recognized: *Ligeromeryx* gen. nov. *praestans*, *Heterocemas*? sp. and Lagomerycidae gen. et sp. indet. The genus *Lagomeryx* is restricted to small European species. If it is hypothesized that apophyseal appendages originated only once among cervoids, then a hypothetical brachyodont ruminant with divergent, supraorbital appendages bearing a small, distal fork which was cast from time to time, could be considered to be not only the common ancestor of lagomerycids and cervids, but also of merycodontines. Nevertheless, there is substantial evidence that appendages were acquired several times, and the possibility that lagomercyids are an entirely independent clade among cervoids is postulated. *Heterocemas* was the most primitive lagomerycid, having forked protoantlers with a prevalence of ramification by sprouting. The move evolved forms acquired multibranched construction (*Ligeromeryx*) and later, palmation at the protoantler basis (*Stephanocemas* and *Lagomeryx*). Small size, accompanied by a subsequent reduction of the protoantler size, could have been acquired secondarily by *Lagomeryx*, probably when the lagomerycids filled forest-browsing niches.

THE first ruminants provided with antler-like appendages appeared in Eurasia during the early Miocene. In the early Orleanian (MN 3), both lagomerycids and cervids (*Procervulus*, *Acteocemas*) were present in Europe. Lagomerycids were rare and represented by large to very small forms. Two large species have been recognized for a long time, *Ligeromeryx* gen. nov. *praestans* (Stehlin, 1937) and '*Stephanocemas*' *elegantulus* (Roger, 1904). The appendages of the latter show a coronet-like structure and a coarse surface and consequently this species has recently been removed from *Stephanocemas* and referred to a dicrocerine deer (Azanza and Menéndez 1990; Azanza 1993*b*). *Ligeromeryx praestans*, formerly placed with smaller species in the genus *Lagomeryx* Roger, 1904, was founded on the basis of only three appendage specimens coming from Chitenay. In recent decades, numerous appendage remains have been collected from other localities in the Loire basin, that allow us to undertake new research into the nature, growth and evolution of lagomerycine antler-like appendages. Some dental remains have also been attributed to large lagomerycids. A complete systematic revision of all this material is presented in this study. The controversial phylogenetic position of the Lagomerycidae among cervoids is discussed as are relationships within the group.

Institutional abbreviations used in this work are as follows. MB, Musée de Blois, Blois, Orléanais, France; MNHNP, Muséum National d'Histoire Naturelle, Paris, France; MO, Musée d'Orléans, Orléanais, France; MS, Musée de Savignéen, Savignée-sur-Lathan, France; NHMB, Naturhistorischen Museum, Basel, Switzerland.

GEOLOGICAL SETTING

In the Loire Basin, large lagomerycid remains have been found in various continental sands of Orleanian age (Stehlin 1907; Mayet 1908; Denizot 1927; Ginsburg 1972). The sands originate from the French Massif Central and are in the form of patches overlying the Beauce limestone plain. Material from Chitenay, apart from the specimens of the type series, is housed in the collections of the Musée de Blois and the Naturhistorischen Museum, Basel. A revised list of the faunal assemblage can be found in Ginsburg (1990). This fauna, slightly older than that of the German

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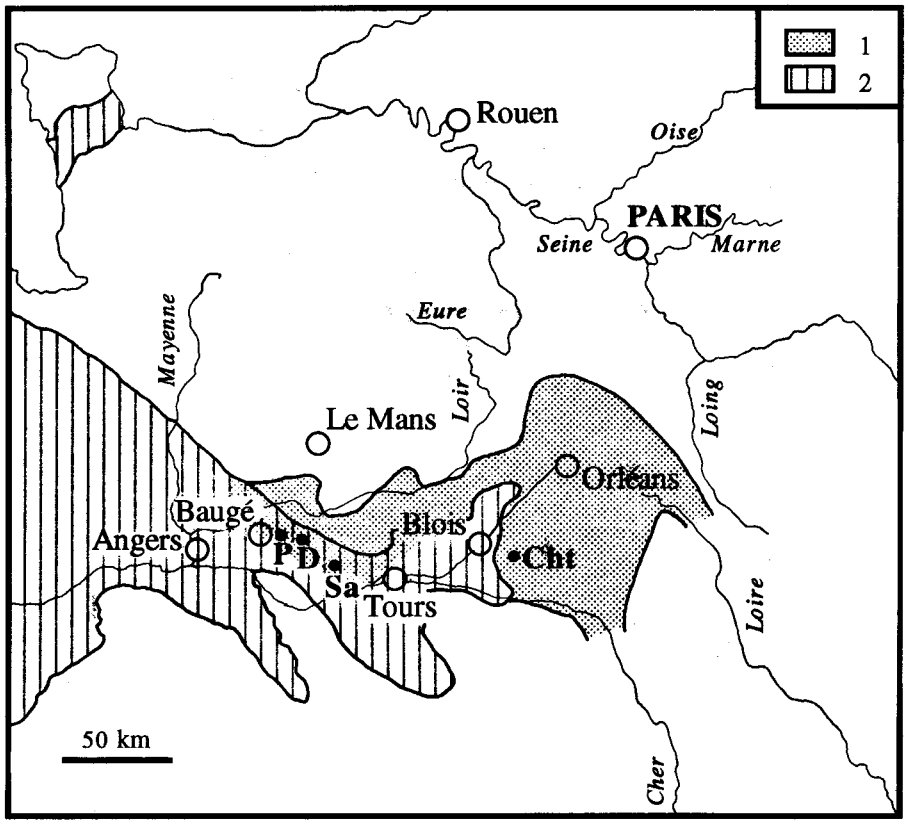
locality of Wintershof-West (MN 3), was placed at the lowermost part of the MN 3 (Ginsburg 1989, 1990; de Bruijn *et al.* 1992).

In Anjou, similar sands were deposited on the pre-existing Esvres syncline and later reworked by the first transgression of the Falun Sea. Some appendages and dental remains have been collected recently from several sites where rich mammal faunas can be found *in situ* (Text-fig. 1): Les



TEXT-FIG. 1. Geological sketch of the Loire Basin showing locations of the main sites from which large lagomerycid remains were examined. 1, continental sands, 2, marine Langhian Falun. Cht, Chitenay; D, Dénezé-sous-le-Lude; P, Pontigné; Sa, Savigné-sur-Lathan.

Beilleaux (parish of Savigné-sur-Lathan), La Brosse (parish of Dénezé-sous-le-Lude) and Pontigné (quarry of Buissoneaux). This material is housed at the Muséum National d'Histoire Naturelle, the Musée du Savignéen and some private collections. The associated fauna is listed in Ginsburg (1990). Apart from *L. praestans*, the species *Lagopsis spiracensis*, *Steneofiber depereti janvieri*, *Xenoyus venitor* and *Andegameryx andegaviensis* have never been found in the localities of the sands of Orléanais (MN 3b–4) nor in Wintershof-West. It seems that the sands of the Esvres syncline can be correlated with the sands of Chitenay.

The Langhian fauna of Anjou contains the remains of contemporaneous mammals mixed with older ones, reworked from the underlying continental sands. According to Ginsburg (1990), these reworked sands are mainly of the same age as the fauna of Chitenay, but some specimens from Pont Boutard, at the eastern end of the same basin, suggest a younger age (MN 4), so we cannot exclude the possibility that some reworked specimens of the large lagomerycids described herein could be of a younger age. These specimens are housed at the Muséum National d'Histoire Naturelle and Musée de Blois.

TERMINOLOGY

The antler-like appendage of lagomerycids is composed of two components: the long, proximal one or 'pedicle' and the branched distal one. This distal part was capable of spontaneous autotomy in its entirety, as indicated by the rugosely, concave ventral surface observed in some specimens. Thus, casting of the distal part could occur from time to time, despite no coronet-like structure being formed. Therefore, it seems appropriate to name it 'protoantler', following A. B. Bubenik (1990).

Protoantlers can branch by two mechanisms similar to those observed in deer antlers (A. B. Bubenik 1990). The first mechanism of branching is 'splitting', when the beam divides at the apex. However, they can also ramify through exostoses which form protuberances. Following A. B. Bubenik (1990), these cortical structures are termed 'sprouts' and the mechanism of ramification 'sprouting'. In this study, the structures resulting from the ramification are termed 'knobs', 'points' or 'branches' according to their relative importance.

SYSTEMATIC PALAEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Suborder RUMINANTIA Scopoli, 1777
Infraorder PECORA Linnaeus, 1758
Superfamily CERVOIDEA Simpson, 1931
Family LAGOMERYCIDAE Pilgrim, 1941

Genus LIGEROMERYX gen. nov.

1937 *Lagomeryx* Roger, 1904; Stehlin, p. 205, text-figs 10–12.

Derivation of name. From 'Liger', the Latin name for the Loire river. All the material belonging to this ruminant comes from the Loire basin.

Type species. Ligeromeryx praestans (Stehlin, 1937).

Diagnosis. That of the species.

Remarks. Individuals of this genus are larger than those of *Lagomeryx*. The pedicles bend forward and point outward more than in *Lagomeryx* or *Stephanocemas*. It also differs from *Stephanocemas* in its longer pedicles. The protoantler differs from that of *Lagomeryx* and *Stephanocemas* by the absence of a palmation, as occurs in *Heterocemas*, but the construction pattern is multibranched instead of forked. It differs from *Lagomeryx* also by a larger protoantler relative to the pedicle size and by the multibranched pattern, instead of being multipointed.

Ligeromeryx praestans (Stehlin, 1937)

Plates 1–2

1937 *Lagomeryx praestans* Stehlin, p. 205, text-figs. 10–12.

Lectotype. NHMB/SO-3020, partial right frontal with the appendage preserved to the branch bases (Text-fig. 2D–E), figured by Stehlin 1937, fig. 10 as a syntype, and designated the 'type specimen' (= lectotype) by Ginsburg *et al.* (1985).

Paralectotypes. Two cast protoantlers (NHMB/SO-5720 and SO-2078; Stehlin 1937, figs 11–12).

Diagnosis. A large lagomerycid in which the pedicles point outward in a plane very divergent to the sagittal one, and bend forward. The protoantler size is large relative to that of the pedicle. The

protoantler construction pattern is multibranched, without any true palmation being developed. The basic construction consists of three branches, two of which branch off closer together and generally more distally than the other. Commonly, there are accessory branches and knobs that modify this basic construction.

Type locality. Chitenay, France (Lower Miocene, MN 3).

Other localities. L. praestans has been found *in situ* in La Brosse and Les Beilleaux (Lower Miocene, MN 3) and reworked in several localities from Les Faluns (Middle Miocene, MN 5): Pontigné, Lasse, Denezé, Savigné, Noyant, Meigné-le-Vicomte, Chavaignes, Grand Trouvé, Pont Boutard. All of these are placed in the Loire basin (France).

Material. Apart from the type series, several mandible fragments are preserved from Chitenay. The material from La Brosse and Les Beilleaux comprises mainly dental remains; only a small protoantler fragment is preserved from Les Beilleaux. Among the appendage specimens from Les Faluns, are some frontal fragments which preserve the basal part of the pedicle, but the material mainly comprises protoantler specimens, none of which has branches preserved in their entirety. From Les Faluns there are also dental remains, generally isolated teeth. It must be pointed out that all dental remains found in the Loire basin are attributed here to *L. praestans*, usually the most abundant species, but the possibility cannot be excluded that some of them belong to another large lagomerycid.

Measurements. See Tables 1–3.

DESCRIPTION AND COMPARISONS

Frontal bone and appendages

The frontal bone is not well preserved. Only the upper region, from the orbital margin to the sagittal suture, remains. The supraorbital region is perforated by one supraorbital foramen without any depression being present. It is situated just anteromedially to the appendage base, being closer to the top of the frontal bone than in most primitive deer. The thick orbital rim in front of the appendages is nearly parallel to the sagittal plane. In cervids they converge anteriorly.

The cranial appendages are supported completely by the supraorbital process of the frontal bone (without extending onto the braincase), as in all primitive deer. Thus, they are separated from the braincase, as in *Lagomeryx*, *Procervulus ginsburgi* and *Acteocemas*.

Although the pedicles are vertically directed in lateral view, they point outward in a plane very divergent to the sagittal one (Text-fig. 2), more than in *Lagomeryx* and *Stephanocemas*. In most primitive cervids, they are parallel. The pedicle has a rounded cross section which can be flattened laterally in its distal part, just below the protoantler. It is noticeably bent anteriorly, whereas in *Lagomeryx* and *Stephanocemas* it slopes slightly posteriorly. It may also be slightly bend inwards in its distal part, as in *Lagomeryx*. Its surface is marked by very slight striations and by a deep groove that runs posteriorly to anteriorly on the medial side. It appears that there is very weak torsion. It is worth noting that the same morphology and disposition of pedicles also seem to be present in the Asiatic forms attributed to *Lagomeryx*, and in the problematical *Heterocemas*.

The protoantler size relative to that of the pedicle is larger than in *Lagomeryx*. Its construction pattern is multibranched, rather than the multipointed pattern of *Lagomeryx*. The basic branches point approximately from the protoantler base but, in contrast with *Stephanocemas* and *Lagomeryx*, no true palmation is developed.

The simplest protoantler morphology comprises three branches, as shown in the Chitenay specimens studied by Stehlin (1937). Their basal emplacements are situated approximately longitudinally according to the distal

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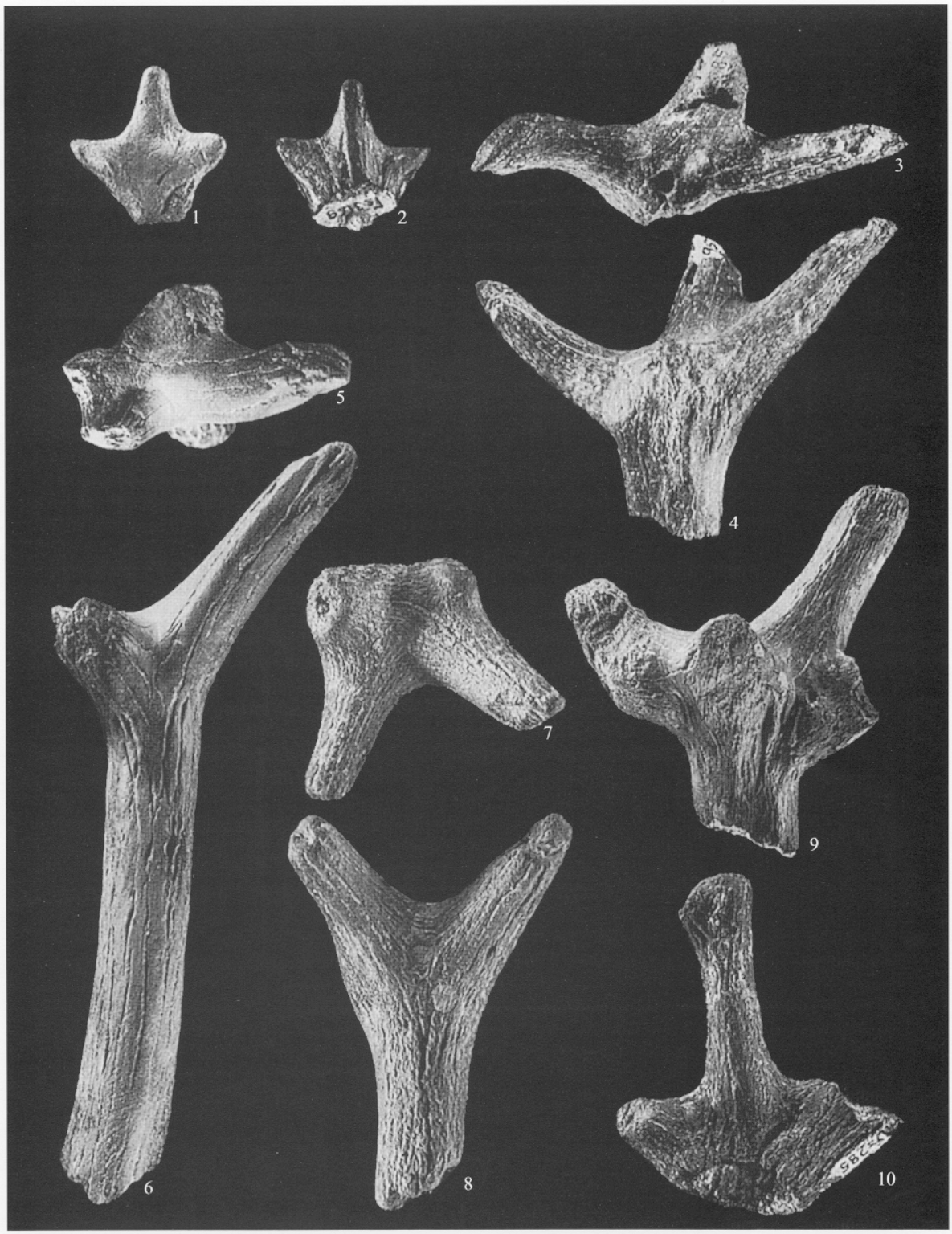
EXPLANATION OF PLATE 1

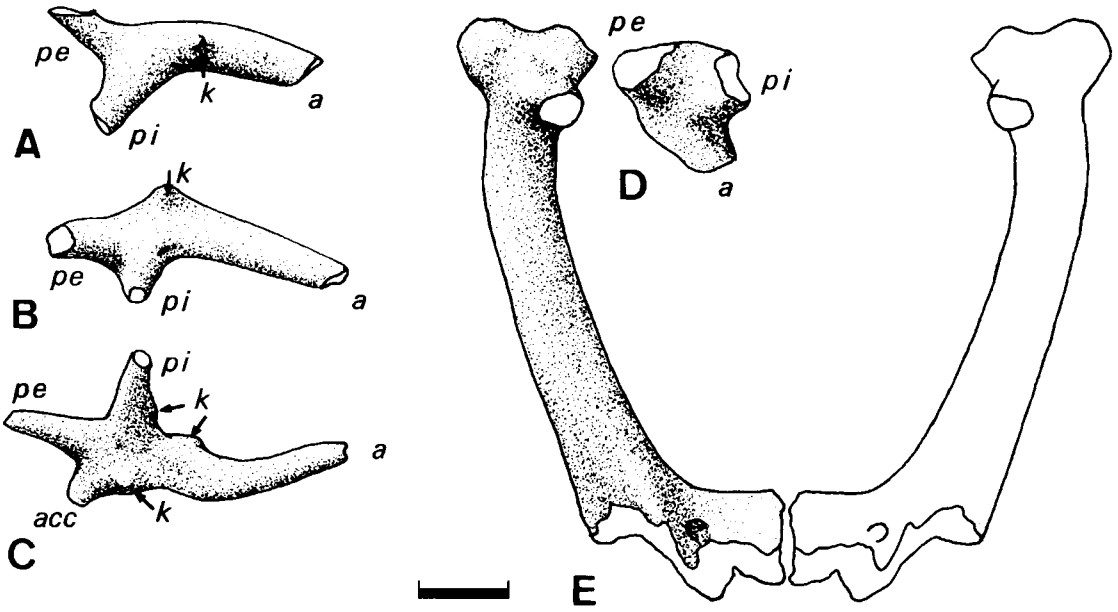
Figs 1–10. *Ligeromeryx praestans* (Stehlin, 1937). 1–2, MNHNP/Fs 3169; Pontigné; cast protoantler. 1, dorso-external view. 2, internal view. 3–4, MNHNP/Fs 295; Pontigné; fragment of left protoantler. 3, dorsal view. 4, external view. 5–6, MNHNP/Fs 283; Pontigné; fragment of left appendage. 5, dorsal view. 6, external view. 7–8, MNHNP/Fs 1626; Cléré-les-Pins; fragment of left protoantler. 7, dorsal view. 8, internal view. 9, MNHNP/Fs 2176; Dénezé/La Brosse; fragment of left protoantler, external view. 10, MNHNP/Fs 285; Pontigné; fragment of cast protoantler, internal view. All × 1.



AZANZA and GINSBURG, *Ligeromeryx*

TABLE 1. Dimensions (in mm) of the pedicle of large lagomerycids from the Loire Basin (France). L = maximal length; PAD = proximal anteroposterior depth; PTW = proximal transverse width; DAD = distal anteroposterior depth; DTW = distal transverse width.

	L	PAD	PTW	DAD	DTW
Ligeromeryx praestans					
Chitenay					
NHMB/S.O. 3020	85·71	19·44	18·25	21·32	14·56
NHMB/S.O. 5720	—	—	—	17·65	11·91
NHMB/S.O. 2078	—	—	—	16·24	13·21
Pontigné					
MNHNP/Fs 298	—	12·77	12·6	—	—
MNHNP/Fs 294	—	17·88	18·24	—	—
MNHNP/Fs 296	—	—	—	19·62	10·92
MNHNP/Fs 301	—	—	—	19·1	16·11
MNHNP/Fs 300	—	—	—	15·21	12·49
MNHNP/Fs 285	—	—	—	21·65	10·22
MNHNP/M 3704	—	—	—	15·24	12·64
MNHNP/M 3162	—	—	—	14·82	11·35
MNHNP/MD 12	—	21·98	18·52	—	—
Cléré-les-Pins					
MNHNP/Fs 1626	—	—	—	20·25	18·59
Auverse					
MNHNP/M 4567	—	19·85	21·27	—	—
MNHNP/M 4571	—	—	—	17·62	12·02
MNHNP/M 4802	—	—	—	16·56	11·11
MNHNP/M 4801	—	—	—	14·8	9·89
Grand Trouvé					
MNHNP/MD 2	—	—	—	21·14	13·98
MNHNP/M 4133	—	—	—	23·97	16·19
Noyant-sous-le-Lude					
MNHNP/M 4135	—	—	—	12·62	8·2
MD 11	—	—	—	16·41	11·79
MNHNP/M 3339d	—	—	—	16·82	12·41
MNHNP/M 4134	—	—	—	19·62	12·53
Dénezé/La Brosse					
MNHNP/Fs 1609	—	—	—	15·93	12·68
MNHNP/Fs 2176	—	—	—	18·98	14·42
Lasse/Pont Brault					
MNHNP/Fs 1396	83	15·41	14·64	13·38	12·18
MNHNP/Fs 1395	—	—	—	18·93	14·34
Pont Boutard					
MNHNP/M 3222	—	—	—	20·34	12·12
Chavaignes					
MNHNP/Fs 5936	—	—	—	21·41	9·12
Heterocemas? *sp.*					
Pontigné					
MNHNP/M 3315g	—	—	—	16·99	12·11
MNHNP/Fs 304	—	—	—	14·72	10·39
Méon					
MNHNP/Fs 6414	—	—	—	15·69	12·13
Auverse					
MNHNP/M 4572	—	—	—	17·27	11·66
MNHNP/M 4569	—	—	—	17·98	16·05
Pont Boutard					
MNHNP/Fs 3914	—	—	—	18·13	14·99
Pontlevoy					
MNHNP/FP 3217	—	—	—	16·71	14·32
NHMB/CB1179	—	—	—	23·18	15·58



TEXT-FIG. 2. Protoantler terminology and orientation used in *Ligeromeryx praestans* (Stehlin, 1937). A, NHMB/SO-5720, paralectotype; Chitenay; cast protoantler, dorsal view. B, MNHNP/MD2; Grand Trouvé; protoantler fragment, dorsal view. C, MNHNP/M-3222; Pont Boutard; protoantler fragment, dorsal view. D–E, NHMB/SO-3020, lectotype; Chitenay; right frontal with the appendage. D, dorsal view. E, anterior view. *a* = anterior, *acc* = accessory, *pi* = postero-internal and *pe* = postero-external branches, *k* = knob. Scale bar represents 20 mm.

compression plane of the pedicle; this plane converges forward with the sagittal one, as can be seen in NHMB/SO-3020 (Stehlin 1937, fig. 10). The branches do not point equidistally. Two of them branch off closer together either more distally (morphotype A), or approximately from the protoantler base (morphotype B).

In NHMB/SO-3020 (Text-fig. 2D) the basal branch is situated anteriorly (*a*) pointing inwards, and the two distal branches posteriorly, one pointing inwards (*pi*) and the other outwards (*pe*). Similar orientation can be recognized in MNHNP/Fs-283 (Pl. 1, fig. 6) despite its four branches. Thus, it would seem logical to suppose that this orientation is the general condition. According to this interpretation, the orientation of NHMB/SO-5720 is the opposite to that suggested by Stehlin (1937, fig. 11).

It is noteworthy that Stehlin's specimens show great variability in (1) the relative size and morphology of the branches; (2) the disposition of the branches, which range from nearly horizontal to vertical; and (3) the distance between the basal and distal forks. Moreover, the number and position of accessory branches, points or protuberances must be added to obtain a picture of the enormous morphological variability found in the protoantler construction of this species. Hence, the same horizontal branch disposition of Stehlin's specimen NHMB/SO-5720 (morphotype B) is observed in the Grand Trouvé (MNHNP/MD2) and Pont Boutard (MNHNP/M3222) specimens, despite the differences in relative size and morphology of their basic branches (Text-fig. 2). Branch *a* is the largest, being curved in MNHNP/M3222 as in NHMB/SO-5720, but straight in MNHNP/MD2. In contrast, the smallest one is branch *pi* in NHMB/SO-5720, but branch *pe* in MNHNP/MD2. In MNHNP/M3222, both *pi* and *pe* branches are about the same size.

Nevertheless, the protoantler morphology of most of our specimens is referable to the vertical construction of NHMB/SO-2078, Stehlin's specimen (morphotype A), although the protoantler base is enlarged by the presence of, at least, an accessory point which may just be a knob as in MNHNP/Fs-295 or developed as a branch as in MNHNP/Fs-301 and MNHNP/Fs-283.

Ontogenetic growth. The nature of lagomerycid appendages has been discussed over a long time. Because of their relatively smooth surface and the absence of a coronet, they were interpreted as permanent skin-covered appendages (Stehlin 1939; Pilgrim 1941; Simpson 1945; Crusafont 1952;

Young 1964; Leinders 1983). However, as indicated by A. B. Bubenik (1983, 1990) and Vislobokova *et al.* (1989), their microstructure shows clearly that they are a direct outgrowth from the frontal bone, like deer antlers, and the presence of cast specimens has been demonstrated (Ginsburg 1985).

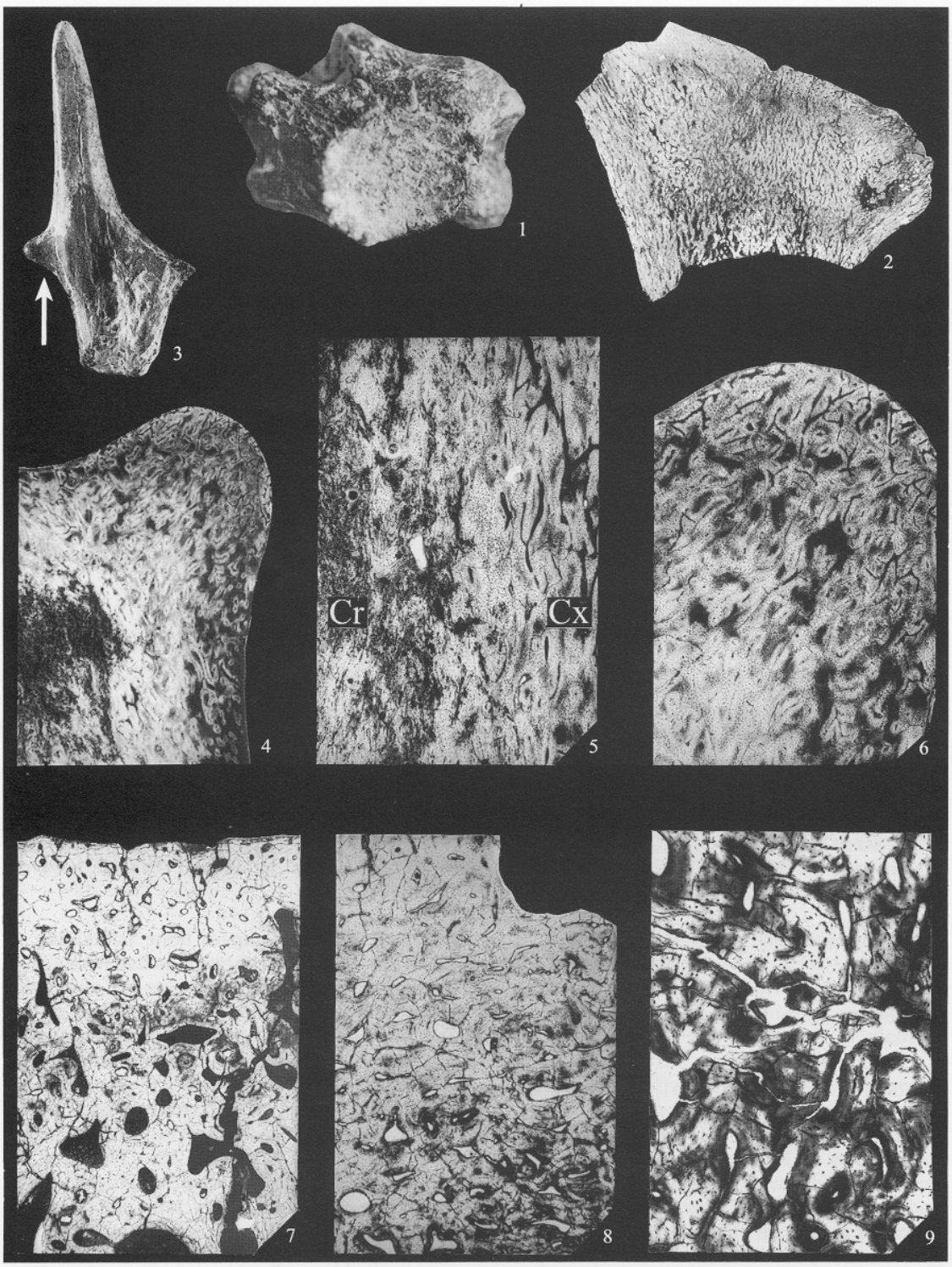
A perennial apophyseal appendage might grow in diameter and length by periodical apposition of new bony lamellae, like the pedicle of deer appendages (A. B. Bubenik 1990). In such a case, we would expect to find that all specimens, apart from yearlings, would show the same morphology with variability reduced to individual variation in size and certain proportions. Ontogenetic variability like this is found in merycodontids (Frick 1937; Voorhies 1969). However, the variability found in lagomerycid appendages exceeds this substantially. The variation is comparable to that of deciduous deer antlers, which change in size and complexity with age so that a lineal ontogenetic sequence can be designated. The variability shown by our material is so great that any lineal sequence can be proposed.

The growth mechanism of lagomerycid appendages seems to be more complex, and to explain this, their nature must be investigated by comparison with the most closely related extant appendage, the deer antler. Deer antlers are deciduous structures, the cycle and growth of which are dependent on the rise and fall of different androgen segregations, of which testosterone plays a dominant role (G. A. Bubenik 1990), therefore they develop in males in close relationship with their reproductive cycle. Nevertheless, if testosterone is substituted by some adrenal androgen, antlers can develop in both sexes. This seems to be the case of *Rangifer* (A. B. Bubenik 1975) and that of the Miocene *Dicrocerus* as we hypothesized (Ginsburg and Azanza 1991). It is possible that only the males of lagomerycids were provided with cranial appendages, as can be assumed from the complete skeletons found in Shanwang (China) It can be inferred that the role of testicular androgens in appendage development must be important, as is the rule in deer.

After growth is complete, the deer antler mineralizes throughout, induced by a sudden rise of testosterone secretion. The blood supply to the surface is cut off and the tissues above the pedicle die; simultaneously a compact bridge between antler and pedicle is built up (A. B. Bubenik 1983, 1990). As soon as the testosterone levels approach the minimum the bridge is demineralized and a narrow zone of bone at the junction of the living bone of the pedicle and the dead bone of the antler is simultaneously destroyed by numerous osteoclasts (Goss 1970). The points of attachment between the antler and the pedicle are so attenuated that the weight of the antler itself effects the detachment. The base of a shed antler shows numerous spicules of bone that are remnants of the osteoclastic erosion (Goss 1970, 1983). The hypothesis that the distal part of the lagomerycid appendage could have been spontaneously rejected is supported by the fact that the ventral surface of some protoantler specimens is concave and shows these spicules (Pl. 2, fig. 1). However, radiographs and longitudinal sections of these specimens (Pl. 2, fig. 2) show that their rejection was produced without the protective bridge at the joint with the pedicle, as noted by A. B. Bubenik (1990). Indeed, the mineralization was not sufficient to cut off the blood supply from the pedicle and consequently the protoantler tissues were still alive when their rejection occurred. A similar casting process of tines or distal parts has been observed in the antlers of castrated deer (A. B. Bubenik *et al.* 1990). The lagomerycid protoantler was rejected in its entirety; only one specimen could be interpreted as a cast partial protoantler.

EXPLANATION OF PLATE 2

Figs 1–9. *Ligeromeryx praestans* (Stehlin, 1937). 1–2, MNHNP/Fs 302; Pontigné; cast protoantler. 1, ventral view; × 1·3. 2, longitudinal section; × 1·5. 3–6, MNHNP/Fs 1294; Lasse; protoantler fragment. 3, lateral view showing a knob indicated by the arrow; × 1. 4, longitudinal section of the knob; × 7. 5, detail of the cortex-centre transition (Cr: centre, Cx: cortex); × 16. 6, detail of the knob; × 16. 7–9 transversal sections of specimen MNHNP/Fs 295 (in Pl. 1, fig. 4). 7, section under the ramification; × 16. 8, section at the base of *pe-pi* branches; × 16. 9, detail of the centre part of the section of fig. 8; note the presence of secondary Haversian systems; × 52.



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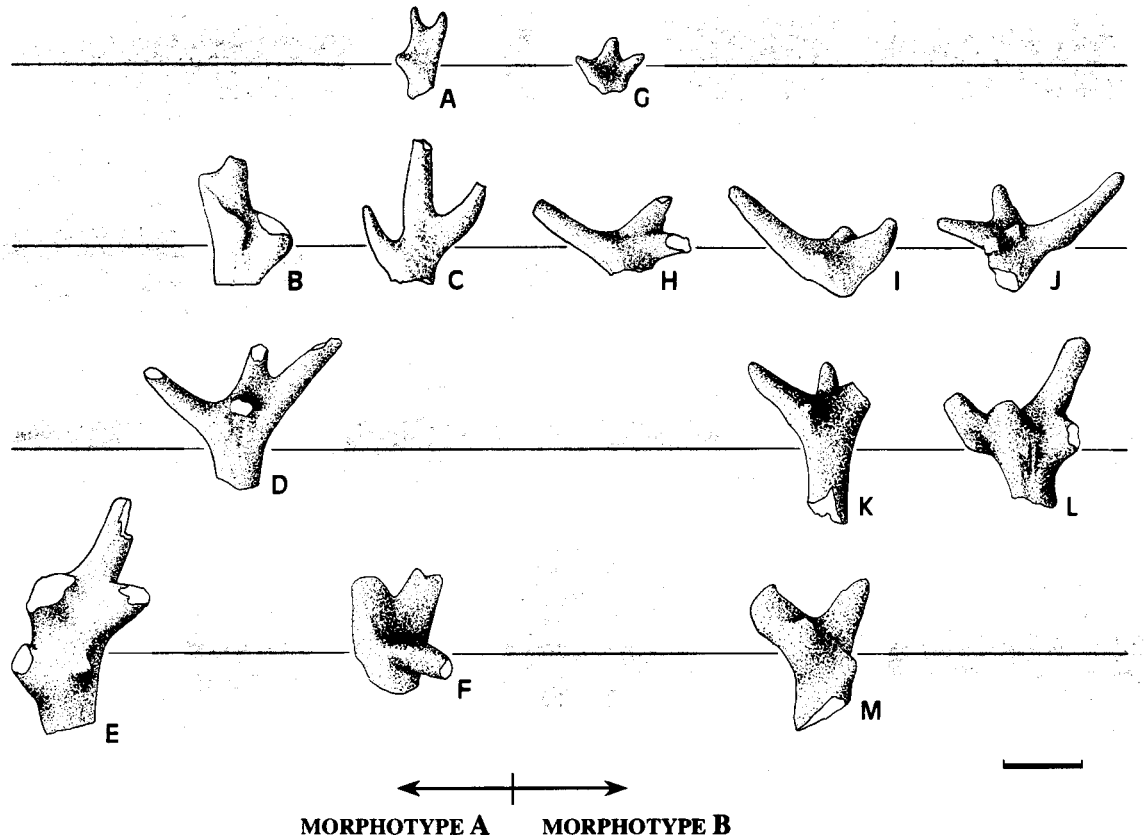


TEXT-FIG. 3. Hypothetical ontogenetic growth of *L. praestans* protoantler combining two mechanisms: the protoantler casting and its subsequent regrowth by beam splitting (from top to bottom) and the cortical growth by sprouting (from middle to sides). A–F protoantler specimens corresponding to morphotype A. A, MNHNP/M4135; Noyant. B, MNHNP/M4134; Noyant. C NMB/SO2078, paralectotype; Chitenay. D, MNHNP/Fs 295; Pontigné. E, MNHNP/M 4133; Grand Trouvé. F, MNHNP/Fs 301; Pontigné. G–M protoantler specimens corresponding to morphotype B. G, MNHNP/Fs 3169; Pontigné. H, NMB/SO 5720, paralectotype; Chitenay. I, MNHNP/MD2; Grand Trouvé. J, MNHNP/M-3222; Pont Boutard. K, MNHNP/Fs 1626; Cléré-les-Pins. L, MNHNP/Fs 2176; Dénezé. M, MNHNP/Fs 1395; Lasse or Pont Broult. Scale bar represents 30 mm.

The mature deer antler is made up of an outermost region of compact bone containing a Haversian system, and a central region of spongy bone formed by fewer, coarser lamellae with wider marrow spaces. Secondary and tertiary Haversian systems and interstitial lamellae are absent in deer antler, presumably because the life of the antler bone is limited and the antler is laid down annually in its entire width from the beginning (Chapman 1975). The lagomerycid protoantler is constructed of rather immature compact bone. Although the core is more porous than the cortex, spongious bone trabeculae typical of the antler core are not developed (Pl. 2, figs 8–9). The lamellae of the osteons of the cortex were not oriented in any particular direction in transverse sections of MNHNP/Fs-295 (Pl. 2, figs 7–8), and do not confirm the presence of appositional lamellae supposed by A. B. Bubenik and figured in *Cosoryx* (A. B. Bubenik 1990, text-fig. 16a). However, in the longitudinal section of MNHNP/Fs-1394 (Pl. 2, fig. 5), the lamellae are longitudinally oriented and a thin peripheral layer can be observed. Haversian osteons of secondary bone lamellae are observed mainly in the central region (Pl. 2, fig. 9), but a dense Haversian tissue with several generations of Haversian systems, superimposed as in lifelong appendages (Rothschild and Neuville

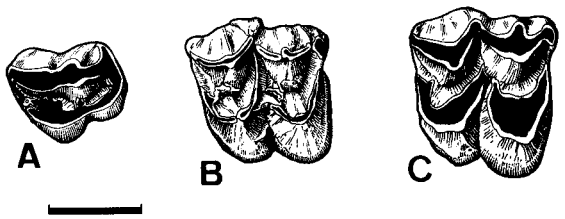
TEXT-FIG. 4. Dentition of large lagomerycids from the Loire Basin, France. A–B, MNHNP/Fs 3580; Pontigné; right upper canine. A, lingual view. B, labial view. C–E, MNHNP/Fs 2397; La Brosse; left mandibular ramus. C, occlusal view. D, labial view. E, lingual view. All $\times 1$.

TABLE 2. Dimensions (in mm) of the upper dentition of large lagomerycids from the Loire Basin (France). L = length; W = width.

		L	W			L	W
La Brosse				Dénezé			
MNHNP/Fs 2194	M1/	13·2	14·3	MNHNP/Fs 761	P2/	12·9	10·2
MNHNP/Fs 2189	M3/	14·2	15·8	MNHNP/Fs 2358	P4/	9·4	11·2
Les Beilleaux				Pontigné/Lasse			
BBX 63	P2/	12·5	10·0	MNHNP/Fs 225	C/	12·5	6·8
BBX 128	P4/	11·4	10·0	MNHNP/Fs 228	C/	12·8	6·1
BEI 534	M1/	15·0	14·8	MNHNP/M 200	C/	12·7	6·5
BEI 315	M2/	15·2	16·5	MNHNP/Fs 3980	C/	12·7	6·6
BBX 285	M3/	14·1	15·5	MNHNP/Fs 6159	C/	12·7	6·3
Cléré-les-Pins				MNHNP/Fs 5361	P2/	12·7	—
MNHNP/Fs 1942	P4/	9·7	12·1	MNHNP/Fs 3605	P4/	11·0	12·4
Savigné				MNHNP/Fs 3606	P4/	9·3	12·5
MNHNP/Fs 2145	P3/	11·7	10·3	MNHNP/Fs 5215	P4/	9·4	12·2
Pont Boutard				MNHNP/Fs 6143	P4/	10·2	12·0
MNHNP/Fs 3867	M3/	13·7	16·3	Noyant-sous-le-Lude			
				MNHNP/Fs 908	P4/	9·6	12·1
				MNHNP/Fs 3023	M2/	14·3	15·7

1910, pl. 6), is not developed. In contrast, it is developed in the pedicle bone. We conclude that protoantlers could be cast and regenerated without necessarily being annually deciduous.

Deer antlers grow by proliferating fibroblast in their apices. These cells later become cartilaginous and are eventually incorporated into the bone trabeculae which strengthen the shaft (Goss 1970). So, beam-splitting (dichotomous branching at the tip) is the usual mechanism of ramification. However, they can ramify also through exostoses, which form sprouts. Sprouting is present in



TEXT-FIG. 5. Upper dentition of large lagomerycids from the Loire Basin, France. A, MNHNP/Fs 2145, Savigné; right P^3. B, BEI 534, Les Beilleaux; right M^1. C, BBX 285, Les Beilleaux; right M^3, occlusal view. Scale bar represents 10 mm.

Rangifer, in the first antler of *Cervus elaphus*, in the second antler of North American *Alces* and the prong in *Odocoileus* (A. B. Bubenik 1990). As described above, the protoantler of *Ligeromeryx* shows numerous protuberances of knobs that are cortical structures (Pl. 2, figs 3–6). Possibly these knobs eventually developed as accessory branches. Some of them might have had a genetic basis, as they have frequently been found in the same position, but many others have not. It appears that sprouting might have been a very important process of ramification in lagomerycids, to judge by the frequency and versatility of the accessory branches and knobs.

If these interpretations of the nature of the lagomerycid appendage are correct, protoantler growth in *Ligeromeryx* was influenced by (1) total or partial protoantler casting and its subsequent regrowth by beam splitting; and (2) cortical growth by sprouting or appositional lamellae. We hypothesize that, if the first mechanism occurred, the protoantler morphology would reproduce the basic pattern with three or perhaps four branches, but if casting did not occur, then the second mechanism would modify this basic pattern resulting in the enormous variability of *Ligeromeryx* morphology.

Specimens that correspond to both the vertical and horizontal patterns are ordered in Text-figure 3 according to a hypothetical ontogenetic sequence that combines these two mechanisms. The youngest state is attributed to small three-pointed specimens, the morphology of which resembles that of the more adult specimens. Among the material from the Pontigné-Savigné Basin there are some unbranched specimens. MNHNP/M4800 from Les Beilleaux is a complete appendage that, in contrast with other slender pedicle fragments (MNHNP/Fs 298), is less divergent, right in frontal and lateral views and without any trace of torsion. In our opinion, it is not attributable to *Ligeromeryx praestans* but to *Lagomeryx ruetimeyeri*.

A few peculiar specimens cannot be placed in this scheme. Their taxonomic position is discussed later.

Upper dentition

The upper canine (Text-fig. 4A–B) is very long, slender and curved downward and backward. Its anterior edge is thicker than the posterior one, where both the labial and lingual faces join bevelled to form a sharp ridge. The labial face bulges anteriorly while the lingual one is flatter and shows a weak longitudinal groove that runs along its posterior part from the base to within 18–31 mm of the apex, depending on the individual. This confers a sigmoidal profile on the lingual face.

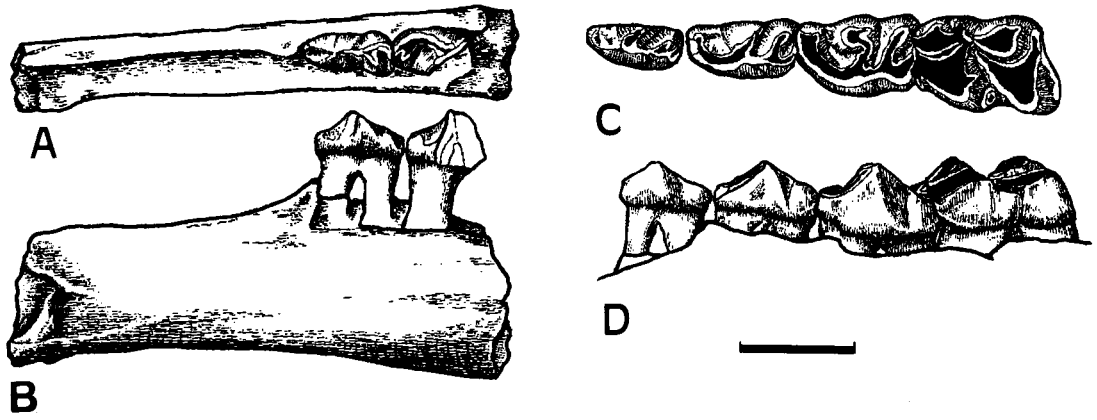
P^2 is a long thin tooth. On the labial wall, the parastyle and the paracone protrude, but less than in *Procervulus* or *Dicrocerus*, and are joined basally. The labial side of the metacone is flatter and is separated from the paracone by a groove. On the lingual lobe, the slightly protruding protocone is in a central position as in *Procervulus*, but the tooth is much longer.

P^3 resembles P^2 but both the parastyle and the paracone are less divergent on the labial wall. The protocone is more protruding on the lingual lobe than in P^2 and the hypocone seems consequently to be slightly thrown back (Text-fig. 5A). According to this, the difference between P^2 and P^3 appears to be clear. However, study of the rich material of *Dicrocerus elegans* from Sansan leads to the conclusion that these features are variable and are sometimes reversed. Only teeth observed *in situ* on the maxillary can be identified with certainty.

P^4 is a short wide tooth. It is almost symmetrical, the protocone being approximately in a central position on the lingual lobe. The parastyle, paracone and metastyle protrude from the labial wall. A medial fold is present. The lingual cingulum is weak, sometimes reduced to a basal bulge.

TABLE 3. Dimensions (in mm) and statistics of the lower dentition of large lagomerycids from the Loire Basin (France). L = length; W = width.

	P/2		P/3		P/4		M/1		M/2		M/3	
	L	W	L	W	L	W	L	W	L	W	L	W
Chitenay												
NHMB/SO 2060	—	—	10·7	5·8	12·4	7·3	12·25	9·0	13·6	10·0	20·3	9·8
NHMB/SO 3027	7·8	3·7	9·7	5·3	10·65	6·4	—	8·5	13·05	9·6	19·2	9·5
NHMB/SO	—	—	—	—	11·4	6·8	—	—	—	—	—	—
MB/M 3199	8·85	3·9	—	—	—	—	—	—	—	—	—	—
MB/M 3193a	9·4	4·0	10·4	5·5	11·8	7·8	12·3	9·1	—	—	—	—
MB/M 3193b	—	—	—	—	—	—	—	—	12·9	9·75	19·9	9·85
MB/M 3193c	—	—	—	—	—	—	—	—	13·4	9·9	20·2	9·7
MNHNP/CHT4	—	—	—	—	—	—	—	—	13·6	8·9	—	—
n	3	3	3	3	4	4	2	3	5	5	4	4
min.	7·80	3·70	9·70	5·30	10·65	6·40	12·25	8·50	12·90	8·90	19·20	9·50
max.	9·40	4·00	10·70	5·80	12·40	7·80	12·30	9·10	13·60	10·00	20·30	9·85
mean	8·68	3·87	10·27	5·53	11·56	7·07	12·27	8·87	13·31	9·63	19·90	9·71
La Brosse												
n	—	—	—	—	2	2	3	3	2	3	2	3
min.	—	—	—	—	11·40	6·75	11·70	8·70	12·70	8·70	17·90	9·50
max.	—	—	—	—	11·40	7·0	12·45	9·40	13·80	10·80	19·80	9·90
mean	—	—	—	—	11·40	6·88	12·20	8·97	13·25	9·62	18·85	9·70
Pontigné												
n	—	—	3	3	7	7	5	5	13	13	11	11
min.	—	—	10·10	5·20	11·40	6·85	11·90	8·00	12·00	7·40	18·60	8·80
max.	—	—	12·00	6·20	13·10	7·70	12·55	9·40	14·90	10·20	21·40	10·30
mean	—	—	10·98	5·58	12·80	7·21	12·31	8·77	13·61	9·57	19·51	9·61
Lasse												
n	—	—	1	1	—	—	—	—	—	—	2	2
min.	—	—	—	—	—	—	—	—	—	—	18·80	9·40
max.	—	—	—	—	—	—	—	—	—	—	20·20	10·45
mean	—	—	11·10	5·40	—	—	—	—	—	—	19·50	9·92
Lasse/Pontigné												
n	—	—	1	1	6	6	1	1	9	9	1	1
min.	—	—	—	—	11·50	6·60	—	—	12·10	8·60	—	—
max.	—	—	—	—	12·90	7·20	—	—	14·60	10·40	—	—
mean	—	—	10·70	6·10	12·18	6·85	11·5	9·10	13·21	9·46	19·25	9·85
Pont Boutard												
n	—	—	—	—	1	1	—	—	3	3	—	—
min.	—	—	—	—	—	—	—	—	13·10	9·25	—	—
max.	—	—	—	—	—	—	—	—	13·55	9·70	—	—
mean	—	—	—	—	11·70	7·00	—	—	13·33	9·42	—	—
Denezé												
n	—	—	—	—	4	3	1	1	3	3	2	2
min.	—	—	—	—	11·60	7·30	—	—	12·70	8·80	18·00	9·40
max.	—	—	—	—	12·70	7·60	—	—	13·90	10·30	19·15	9·95
mean	—	—	—	—	12·15	7·47	11·9	8·7	13·83	9·57	18·58	9·67
Noyant												
n	—	—	—	1	1	1	2	2	1	1	5	5
min.	—	—	—	—	—	—	11·40	9·70	—	—	18·25	9·15
max.	—	—	—	—	—	—	12·10	10·00	—	—	19·70	10·00
mean	—	—	—	6·50	12·60	7·30	11·75	9·85	13·50	10·00	19·01	9·76



TEXT-FIG. 6. Lower dentition attributed to *Ligeromeryx praestans* from the type locality. A–B, MB/M 3199; fragment of right mandible ramus with P_2 and fragment of P_3. A, occlusal view. *B*, lingual view. C–D, MB/M 3193a; left P_2-M_1. C, occlusal view. D, labial view. Scale bar represents 10 mm.

The upper molars have an approximately square outline. The external wall relief is strong, as in *Procervulus* and *Dicrocerus*, with the metastyle much more protruding than the metacone, but very weak in comparison with the parastyle, the paracone and the mesostyle. The anterior and posterior lobes are parallel but somewhat oblique to the longitudinal axis in M^1 (Text-fig. 5B). The posterior lobe is moved slightly outwards in comparison with the anterior one. This character decreases from M^1 to M^3, reaching the same level. The lingual cones are developed, the protocone being more pronounced than the metaconule from M^1 to M^3. A very weak central fold-like structure is present only in M^1. The postprotocrista (= protoconal fold in Heintz 1970) is short in M^1 but is more developed in M^2 and M^3 turning labially (Text-fig. 5C). The endostyle is in general strong and the development of the cingulum is variable.

Lower dentition

There is no P_1 as in most cervoids (Text-fig. 6A). P_2 has two roots (Text-fig. 6B, D) and is small, low, long and very thin. The paraconid is pointed and turned lingually. The crest coming down forward from the protoconid takes up a position approximately on the longitudinal axis. The anterior valley is shallow and broad. The metaconid, when present, is very small and attached to the postero-lingual side of the protoconid (Text-fig. 6C). A broad external groove is insinuated.

P_3 is long and thinner than in *Procervulus* and much more so than in *Dicrocerus*. The biggest specimens have the anterior elements differentiated; the paraconid is well developed but close to the parastyle, so it is not visible if the tooth is moderately worn. The anterior valley is deep and wide. The metaconid is not individualized from the short oblique cristid (Text-fig. 6C). The entoconid and the entostylid are well developed and reach the postero-lingual corner. The external groove is weak, but deeper than in *Dicrocerus*. On the external wall, the hypoconid shows a basal bulge on the P_3 of the mandible from Les Beilleaux.

P_4 is thicker and somewhat longer than in P_3. However, it is shorter than in *Dicrocerus* and *Procervulus* because of the reduction of its anterior part. The anterior valley and the anterior crest of the protoconid are consequently shorter than in *Dicrocerus* and *Procervulus*. It is not molarized. The metaconid is individualized from the short oblique cristid and is usually almost opposite the protoconid and develops a short postero-lingual crest (Text-figs 4C, 6C). The metaconid on the P_4 from Les Beilleaux and in some specimens from Les Faluns, protrudes on the lingual profile and is placed thrown back developing no postero-lingual crest. The entoconid is well developed, closing the posterior valley. The external groove is deep whilst the protoconid is very delimited on the external wall. The hypoconid may bulge toward its base in some specimens.

In the lower molars, lobe disposition is variable, although in most cases they tend to be disposed obliquely. The lobes are bulging on the internal wall, whose relief is well developed, while the mesostylid is prominent (Text-fig. 4E). The relief is not very well developed on the molars of the mandible from Les Beilleaux and some specimens from Les Faluns, the mesostylid being less protruding than in *Dicrocerus*. The *Palaeomeryx*-fold is strong. The ectostylid and the cingulum are weaker from M_1 to M_3. The internal cristids are relatively long but never overlapping. A diagonal connection forms the interlobular union. The postmetacristid and the

prehypocristid tend to be joined to this connection. The third lobe of M_3 is long and placed on the longitudinal axis so that there is an inflection on the lingual wall.

Genus HETEROCEMAS Young, 1937

Heterocemas? sp.

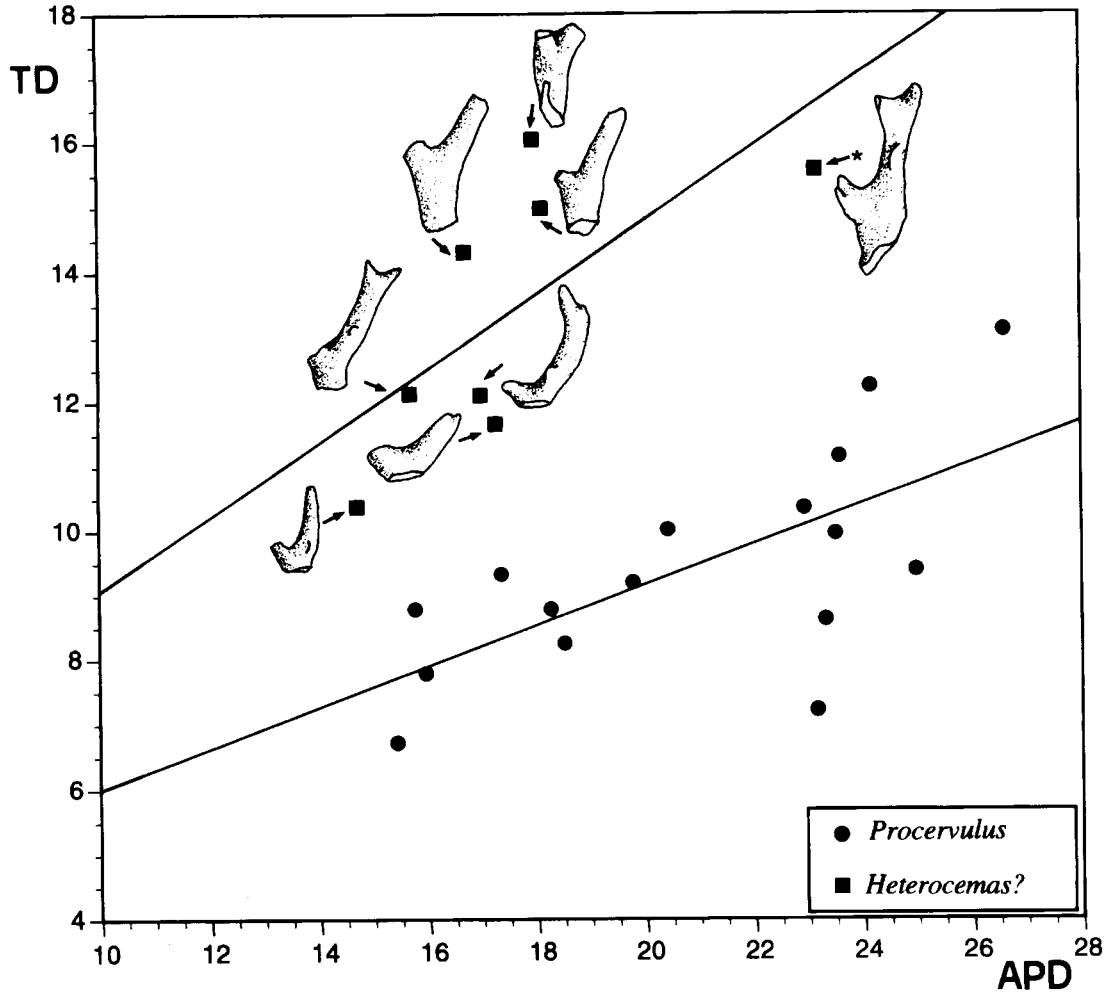
Material. Twelve appendage fragments from Méon, Pontigné, Pont Brault, Pont Poutard, Auverse, Chalonnes and Meigné-le-Vicomte, housed at the MNHNP. From Pontlevoy, MNHNP/Fp 3217 and probably NHMB/Bourgeois collection-1179 also belong to this form.

Description and comparisons. The protoantler specimens included in this form correspond to a basic forked construction in which one branch (probably the posterior) is distinctly longer than the other, sometimes also having the tip forked. This morphology is clearly shown by MNHNP/Fs 6414 which is also sharply bent inward (Text-fig. 7A–B). The presence of knobs is the rule as in *L. praestans*. There is usually a knob on the

TEXT-FIG. 7. *Heterocemas*? sp. from the Loire Basin, France. A–B, MNHNP/6414; Méon; left protoantler. A, anterior view. B, external view. C, MNHNP/Fs 304; Pontigné; left protoantler presumably juvenile, external view. D, MNHNP/M 3315g; Pontigné; left protoantler, external view. All ×1.

posterior branch situated on its lower part (Text-fig. 7B–D) or in the middle (in NHMB/1179, MNHNP/Fs1391). Only MNHNP/M4569 from Auverse has sufficient preserved structure below the main fork to be certain that it is the pedicle.

The size of these specimens is comparable to that of *L. praestans* and to *Procervulus dichotomus*, but the section of the protoantler just below the main fork is rounded instead of elliptical as in *Procervulus* (Text-fig. 8). MNHNP/Fs 304 (Text-fig. 7C) from Pontigné is very small and is presumably a juvenile protoantler. The



TEXT-FIG. 8. Scatter plot of transverse/antero-posterior diameters of the protoantler (measured just below the main fork) of *Heterocemas*? sp. versus *Procervulus dichotomus* from the Loire Basin. (* Pontlevoy specimen referred to *Procervulus aurelianensis* by Mayet 1908).

Pontlevoy specimen NHMB/1179 (figured as *Procervulus aurelianensis* by Gaudry 1878, text-fig. 100c and Mayet 1908, text-fig. 94c) is much bigger and the anterior branch is also forked, and must probably belong to an old individual.

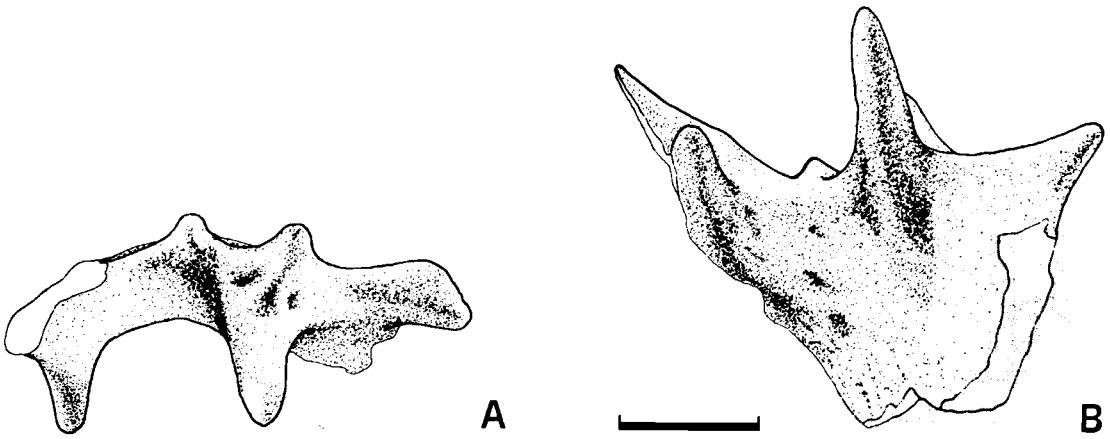
These specimens cannot be considered as belonging to *L. praestans*, despite the versatility assumed for their protoantler morphology. Certainly there is a prevalence of branching by sprouting and the morphology seems to represent the extreme of morphotype A. Nevertheless, the forked and multibranched patterns can be clearly separated. In contrast, they resemble greatly the problematical *Heterocemas simpsoni* Young, 1937 and to a

lesser extent *Heterocemas gracilis* (Vislobokova, 1983). In our view, it seems feasible that a form closely related to these Asian species was present in the Loire basin.

Lagomerycidae gen. et sp. indet.

Material. One distal fragment of protoantler (MB specimen) from Chitenay. Two fragments from Fay-aux-Loges belonging to the same cast specimen (MO/827), one of which was figured by Mayet (1908, pl. 4, fig. 17).

Description and comparisons. The Chitenay specimen (Text-fig. 9) shows a very unusual multibranched pattern



TEXT-FIG. 9. Lagomerycidae gen. and sp. indet. A–B, MB; Chitenay; distal fragment of the protoantler. A, dorsal view. B, lateral view. Scale bar represents 20 mm.

not referable to any of the described lagomerycid forms. The protoantler is flattened, showing a tendency to form a vertical palmation, the distal border of which bristles with two ranges of branches or knobs. It is possible that this specimen is an aberrant protoantler, as is from time to time found in deer appendages. Nevertheless, it should be pointed out that this morphology resembles that of the merycodontid *Ramoceros* (*Merriamoceros*) (Frick 1937, text-figs 35A, 40A), suggesting that it might really correspond to an as yet incompletely known form. Two other fragments of cast specimens show a flattened scar suggesting that they might also belong to this form.

DISCUSSION

As described above, we recognize at least three forms among the remains of large lagomerycids found in the Loire basin. The most abundant, *Ligeromeryx praestans*, was included for many years in *Lagomeryx* Roger, 1904. This genus was defined as small ruminants with antler-like appendages that are constituted by a long pedicle supporting a rather small protoantler built by a palmation surrounded by a crown of small points (multipointed construction). Its taxonomic status has been revised recently by Gentry and Heizmann (1993) who exposed the problem concerning the species type and asked the International Commission on Zoological Nomenclature to designate *L. ruetimeyeri* Thenius, 1948 as the type species, the holotype being the Reisenburg left appendage illustrated by Rütimeyer (1880, pl. 1, figs 2–3). Other smaller species included in the genus are *L. parvulus* Roger, 1904 and *L. pumilo* Roger, 1904. *L. simplicicornis* Schlosser (1904) was described as a *Lagomeryx* with unbranched appendages, nevertheless, the specimen illustrated by Schlosser (1904, pl. 26, fig. 1a) corresponds to a pedicle whose protoantler was cast (Antunes *et al.* 1994). Some other large Asian forms have also been referred to this genus but, as discussed below, the protoantler construction is not the same and it should be excluded from the genus.

Along with *Lagomeryx*, most authors have included *Procervulus* Gaudry, 1878 and *Climacoceras* MacInnes, 1936 in the family Lagomerycidae Pilgrim, 1941. In contrast to lagomerycids, splitting of the beam is the predominant process of branching in the protoantler construction of the European *Procervulus*; moreover, the protoantler is ornamented and the upper molars show a clear central fold. These features place *Procervulus* closer to true deer (Ginsburg, 1985; Azanza 1993*b*). In *Climacoceras*, it appears that sprouting is the predominant process of branching of its appendages, although they have no differentiated pedicle and are perennial. Other dental and postcranial features placed *Climacoceras* closer to giraffoids (Hamilton 1978; Janis and Scott 1987).

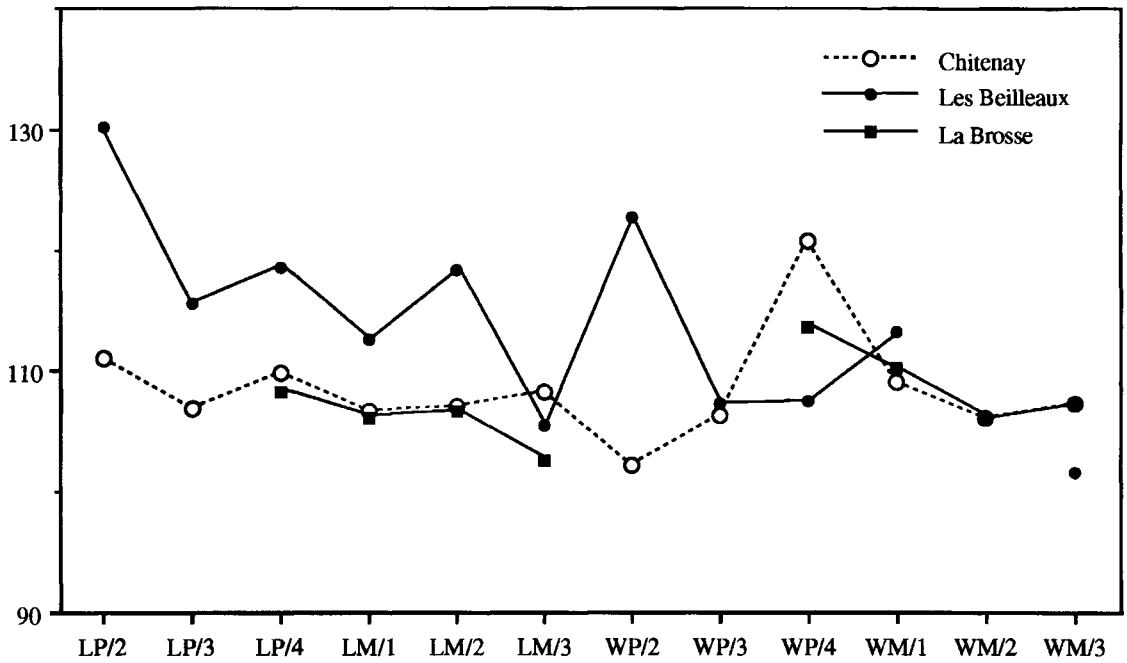
By contrast, a form very close to *Lagomeryx* is the Asian *Stephanocemas* Colbert, 1936, as noted by Ginsburg (1985). It comprises medium to large forms in which the morphology of the appendages resembles that of *Lagomeryx*. The protoantler is built also by palmation but is surrounded by a crown of branches (multibranched construction) instead of points. Moreover, the pedicle is relatively short (at least in the type species) whilst the protoantler is very large. Along with the type species, *Stephanocemas thomsoni* Colbert, 1936 from Tung Gur, we recognize *S. tsaidamensis* Bohlin, 1937 (including the material described by Bohlin as Cervidae sp.), *S. aralensis* Beliajeva, 1974, and *S. rucha* Ginsburg and Ukkakimapan, 1983. Two European species have been included in this genus for a long time, *Acteocemas infans* (Stehlin, 1939) and *Stehlinoceros elegantulus* (Roger, 1904). They have a coronet-like surrounding to the protoantler base and the surface is ornamented, so they are considered to be closer to *Dicrocerus* (Azanza 1993*b*). *Paradicrocerus flerovi* Gabounia, 1959 was described on the basis of only one specimen (Gabounia 1973, pl. 8, fig. 3) showing a multibranched construction resembling that of *Stehlinoceros elegantulus*. This could be an aberrant specimen of *Dicrocerus*, also represented in Belometchescaya, exhibiting a construction similar to that found in extant *Muntiacus*. Nevertheless this morphotype is not present in the rich population of *Dicrocerus* from Sansan. Moreover, a cranium that Gabounia (1973, pl. 8, fig. 2) illustrated as *Dicrocerus* sp. belongs to *P. flerovi*. It shows short divergent pedicles very distant from each other and the supraorbital foramen is very close to the frontal roof. This morphology is not present in *Dicrocerus* but is in *Stehlinoceros elegantulus*. It is possible that *Stehlinoceros* Azanza and Menéndez, 1990 is a junior synonym of *Paradicrocerus*.

The large French lagomerycid *Ligeromeryx praestans* differs from both *Lagomeryx* and *Stephanocemas* because there is not true palmation at the protoantler basis. Its protoantlers are multibranched, as in *Stephanocemas*, but not multipointed as in *Lagomeryx*. Moreover, the size proportion between the protoantler and the pedicle is bigger than in *Lagomeryx*. These features are also shared by some Asian species referred either to *Stephanocemas* or to *Lagomeryx*. They are *L. triacuminatus* (Colbert, 1936) and *L. colberti* (Young, 1937) (= *L. teilhardi* Young, 1964). They show a more complex morphology of protoantlers but their dentition is more primitive, with P_1 still preserved (Chow and Shih 1978; Vislobokova *et al.* 1989). It seems that it could be related to *Ligeromeryx* but this matter needs further study.

It is worth mentioning that the protoantlers of the problematical *Heterocemas* Young, 1937, resemble those of *Ligeromeryx* in the absence of a palmation but their construction is not multibranched but rather forked. Vislovokova (1983) included *Heterocemas* in *Procervulus*, but the former has very divergent curved pedicles and the surface of the appendage is smooth, as in lagomerycids. As described above, some incomplete specimens found also in the Pontigné-Savigné Basin show a similar morphology but the first branch is more reduced and the presence of knobs seems more predominant. Probably, the enigmatic specimen from Pontlevoy NHMB/1179 (figured as *Procervulus aurelianensis* by Gaudry 1878 and Mayet 1908) belongs to this form. Although larger and with a more complex morphology, this specimen could be placed into a sequence of ontogenetic development comparable to that hypothesized for *L. praestans*. These specimens might belong to *Heterocemas* but the material is not sufficiently well preserved to be certain.

Finally, we note the possibility that there is a greater diversity of lagomerycid forms among our material. Despite the versatile construction that we assume for the protoantler of *Ligeromeryx*, the peculiar specimens described as Lagomerycidae gen. et sp. indet. cannot be feasibly ascribed to it. The material is too incomplete to lead to any conclusions.

There is also great variability in the dentition attributed to large lagomerycids. The mandible from Les Beilleaux described by Ginsburg *et al.* (1985) is bigger than that of Chitenay and La Brosse; the premolars are longer and thinner (Text-fig. 10) and with a relatively simple morphology.



TEXT-FIG. 10. Comparative measurements of the lower dentitions of large lagomerycid from the Loire Basin. (100 = *Procervulus ginsburgi* from Artesilla, Spain).

The molars are also long with the inner cristids in line and a weak metastylid. By contrast, the morphology of the teeth from Chitenay and La Brosse is more like that of cervids. A slight difference of age has been argued to explain these differences (Ginsburg 1990).

PHYLOGENETIC RELATIONSHIPS

The lagomerycids have been one of the most controversial ruminant groups because of the different interpretations about the nature of their appendages. They have been considered to be aberrant giraffoids, either a separate lineage or a junior synonym of the Palaeomerycidae (Pilgrim 1941; Simpson 1945; Young 1964), or cervoids. Their cervoid affinities now seem to be firmly established by cranial and postcranial features (Chow and Shih 1978; Leinders and Heintz 1980; Vislobokova *et al.* 1989) but there is no consensus over the phylogenetic position within that group. Thus, they have been considered to be a group (1) that represents the perennial stage or the 'pre-antler stage' in the evolution of antlered cervids (Crusafont 1952; Leinders 1983; Gentry 1994); (2) included into the family Cervidae either as a separate subfamily (Vislobokova *et al.* 1989) or as a junior synonym of Muntiacinae (Chow and Shih 1978); (3) more closely related to antilocaprids (Ginsburg 1985; Solounias 1988); or (4) that represents a possible independent clade (G. A. Bubenik and A. B. Bubenik 1986; Azanza 1993*b*).

The fact that *Procervulus*, the most primitive cervid (Ginsburg 1985; Azanza 1993*b*), has been included among lagomerycids for a long time, and even its synonymy with *Heterocemas* proposed (Vislobokova 1983), demonstrates the great resemblances between the procervuline and lagomerycid

protoantlers. Both appendages show: (1) long upright pedicles above the orbits; (2) absence of a coronet (or any structure resembling one) and no evidence of 'velvet' shedding, in contrast with other primitive deer lineages such as the dicrocerines (Azanza 1993*b*); (3) presence of cast specimens indicating occasional protoantler rejection, which occurred presumably when the tissue was still alive.

We noticed that the procervuline protoantler has a remarkably ornamented surface and its predominant process of branching is by splitting of the beam tip (Ginsburg 1985; Azanza 1993*b*). These features indicate that, as in true antlers, growth occurs at the tip and presumably requires a more intense vascularization of the 'velvet' than in the lagomerycid protoantler (Azanza 1993*b*). In contrast, the most important feature of the lagomerycid protoantler is the predominance of branching by sprouting which translates into enormous versatility of protoantler construction. Branching by sprouting indicates a highly active cortex and could be linked to the protoantler structure because mineralization progresses centrifugally (A. B. Bubenik 1990). It must be pointed out that in dicrocerines the mineralization is clearly centrifugal, but nevertheless the presence of sprouts is a rarity. Sprouts are hardly ever present in primitive procervulines (Azanza 1993*a*), as well as in some extant deer (A. B. Bubenik 1990). Azanza (1993*b*) emphasized the prevalence of branching by sprouting in the growth of lagomerycid appendages and considered this feature to be a useful synapomorphy to define this family.

Although belonging to cervoid ruminants, Ginsburg (1985) considered the Lagomerycidae more closely related to the Antilocapridae. This argument is based on the great similarity in appendage construction between one of the most ancient antilocaprids, the merycodontine *Ramoceros*, and *Ligeromeryx praestans*. Both taxa have a similar three-branched structure of the protoantler and the pedicles are divergent, long and inwardly curved. Concerning dental features, the upper molars lack the central fold and the lingual cingulum is absent or very weak.

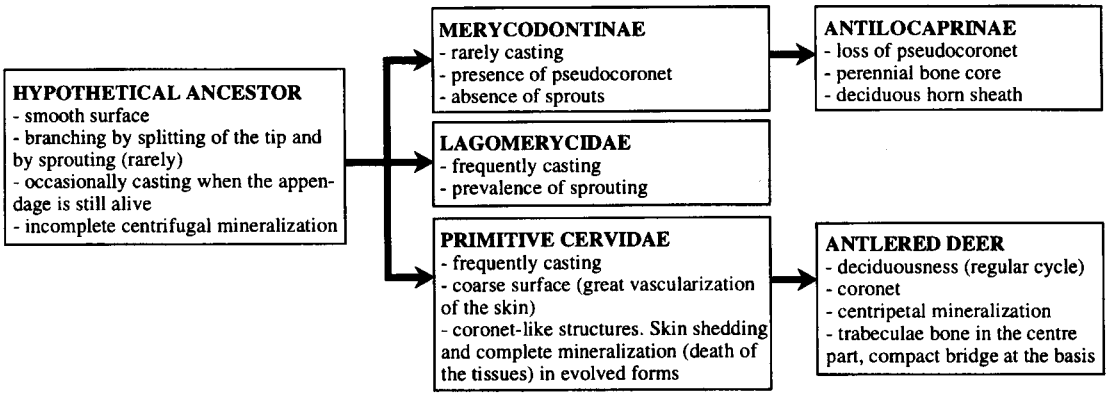
Despite these resemblances, merycodontines differ from lagomerycids in the following features.

1. A simple ontogenetic sequence: small yearling appendages and adult specimens have the same morphology, the variability being reduced to an individual variation in size and certain proportions (Frick 1937; Voorhies 1969).
2. The total absence of sprouts.
3. The common presence of one or several pseudocoronets that are not homologous to the coronets of antlers. They can be asymmetrical in both appendages of the same individual and can be developed either over the pedicle or over the branches. This structure has been variously interpreted. Voorhies (1969) suggested that it is related to a periodic regression of the skin anticipating the casting of the horn sheath in Antilocaprinae. He argued that the skin would have been present only during the period of additive growth and regenerated over the whole, bare and dead appendage but this is difficult to accept (A. B. Bubenik 1990). According to A. B. Bubenik (1990), they might have evolved when the distal part of the appendage was sequestered, or at a stage to be lost as a situation similar to that known in deer prior to the velvet shedding. This interpretation is surprising when it is taken into account that this structure is the rule and the cast appendages the exception.
4. Little evidence of casting. According to A. B. Bubenik (1990), a few pedicles with a bare surface above the uppermost pseudocoronet exit (e.g. the right appendage of F: A.M. 32895 figured by Frick 1937, fig. 27). Surprisingly there is no evidence of cast protoantlers.
5. Unenlarged upper canines occasionally retained, hypsodont cheek teeth, *Paleomeryx*-fold and metastylid lost, complete postentocristid.
6. Lacrimal depression absent, nasals and muzzle extremely enlarged, inflated auditory bullae, lateral metacarpal partially retained occasionally (Frick 1937).

It could be argued that these differences are autapomorphies and do not exclude a closer relationship between them. The origination of merycodontines may have occurred by geographical speciation. This conspicuous speciation event could have taken place when the ancestors migrated from Eurasia during the latest early Miocene. Prior to this date no evidence of merycodontines or ancestral taxa has been found in the North American palaeontological record. Merycodontines

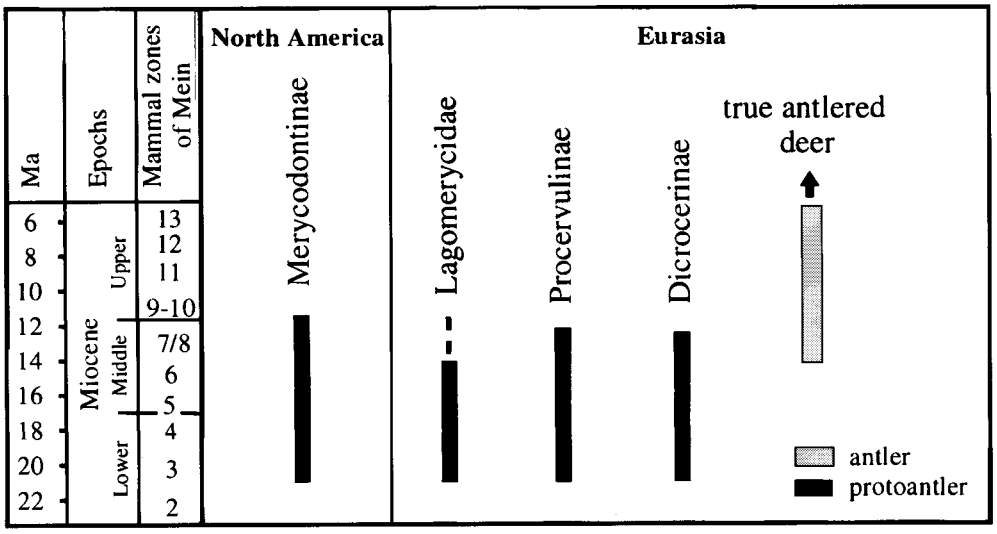
quickly acquired hypsodonty, as well as the other characteristic cranial and postcranial features; their descendants acquired the horn sheath. It must be pointed out that during the mid Miocene hypsodonty was acquired by other groups like the equids in North America while their Eurasiatic counterparts remained brachyodont.

A hypothetical brachyodont ruminant provided with divergent, supraorbital appendages whose rather small, distal fork could or could not be cast from time to time, is considered tentatively as a common ancestor of both groups and also to cervids. This was inferred from the resemblances of the appendage construction of the most primitive representatives of each group: *Paracosoryx*, *Heterocemas* and *Procervulus*. Apart from the forked, occasionally deciduous protoantler, no apomorphy is shared among them (Text-fig. 11). In addition, the differences should not be



TEXT-FIG. 11. Morphostructural features and physiological processes of the different antler-like appendages.

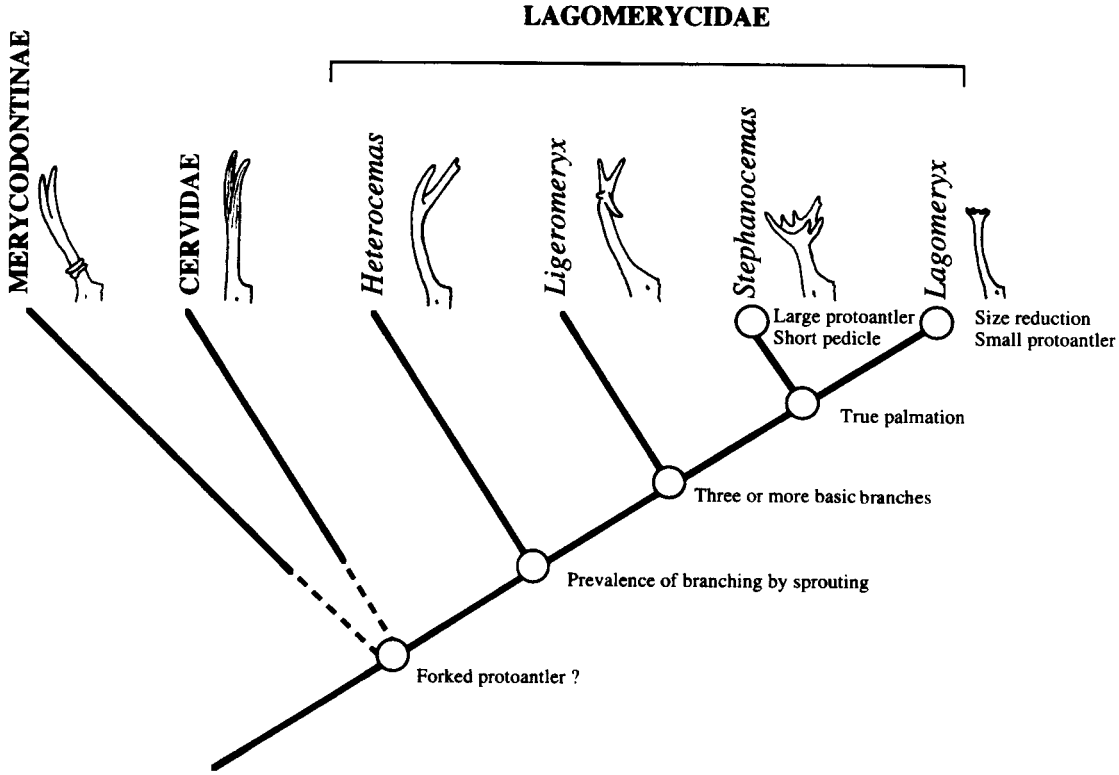
overlooked on the above mentioned morphostructural features. These are correlated with differences in physiological processes suggesting that they correspond to separate types of protoantlers. Lagomerycids and procervulines, as well as dicrocerines (*Acteocemas*), appeared in Europe during the early Miocene, MN 3 (Text-fig. 12). The first record of merycodontines is



TEXT-FIG. 12. Biochronological distribution of the antler-like appendages.

Paracosoryx (*'Merycodus' prodomus* Cook, 1934) in the uppermost Arikareean (Tedford *et al.* 1987) correlated with the lower part of the MN 3 (Steininger *et al.* 1985). At precisely the same time, frontal appendages were developed in different lineages of artiodactyls, induced by the onset of marked seasonality (Morales *et al.* 1994). In this context, the independent evolution of protoantlers in each group seems feasible.

As discussed above, we recognize four protoantler morphologies typifying four genera: *Heterocemas*, *Ligeromeryx*, *Stephanocemas* and *Lagomeryx*. The hypothesis of phylogenetic relationships among them is illustrated by the cladogram of Text-figure 13. In our view, it is feasible



TEXT-FIG. 13. Phylogenetic relationships of the Lagomerycidae.

that the most primitive morphology of the lagomerycid protoantler was a forked construction with a prevalence of ramification by sprouting. The protoantler of *Heterocemas* seems to correspond well with this construction. All the other lagomerycids shared the presence of three or more branches, i.e. they acquired the multibranched construction as is preserved in *Ligeromeryx*. The more evolved forms (*Stephanocemas* and *Lagomeryx*) acquired palmation at the protoantler basis. It seems feasible that the small size and the reduction of the protoantler size were acquired secondarily by *Lagomeryx*, so the multipointed construction could be related to it and be considered to derive from the multibranched construction. The reduction of size, accompanied by a subsequent reduction of the protoantler size, is a trend also found in the South American deer genera *Mazama* and *Pudu*, which have radiated to fill forest-browsing niches in a manner comparable to that shown by the forest duikers in Africa and the muntjaks of Asia (Eisenberg 1987). This interpretation could explain the almost total absence of small lagomerycids in the faunas from the Spanish central basins (Antunes *et al.* 1994), where a greater predominance has been detected of inhabitants of open

habitats than the contemporaneous faunas of the Vallés-Penedés and other European basins (Alberdi *et al.* 1985).

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