

## Phylogeny and classification of early European *Mustelida* (*Mammalia: Carnivora*)

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A phylogenetic analysis of the Oligocene and some Neogene European arctoid carnivorans of the order-group taxon *Mustelida* is performed, based on characters of the skull and dentition. The following classification of the revised genera is proposed: *Simocyon* (*Ailurus*, *Amphictis*, *Bavarictis*, *Potamotherium* (*Pseudobassar* (*Angustictis* gen. n., *Broiliana*)) (*Mustelictis* ((*Franconictis* gen. n., *Stromeriella*) (*Bathygale* gen. n. (*Plesictis* (*Paragale*, *Plesiogale*)))))). *Potamotherium* is allied to phocids within the monophyletic *Pinnipedia*. *Pseudobassar*, *Angustictis* gen. n., and *Broiliana* are considered procyonids. *Mustelictis*, *Franconictis* gen. n., *Stromeriella*, *Bathygale* gen. n., *Plesictis*, and the mustelines *Paragale* and *Plesiogale* are placed in the *Mustelidae*. *Parailurus* is included in *Ailurus*, and *Ichneugale* (= *Viretius*, = *Alopecocyon*) is synonymized with *Amphictis*. Phylogenetic definitions and diagnoses are provided for the suprageneric taxa: *Carnivora*, *Caniformia*, *Arctoidea*, *Arctomorpha* (new), *Mustelida*, *Pinnipedia*, *Procyonidae*, *Mustelidae*, and *Mustelinae*.

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**Key words:** phylogenetic systematics, *Carnivora*, *Caniformia*, *Arctoidea*, *Arctomorpha*, *Mustelida*, *Simocyon*, *Ailurus*, *Amphictis*, *Bavarictis*, *Pinnipedia*, *Potamotherium*, *Procyonidae*, *Pseudobassar*, *Angustictis*, *Broiliana*, *Mustelidae*, *Mustelictis*, *Franconictis*, *Stromeriella*, *Bathygale*, *Plesictis*, *Mustelinae*, *Paragale*, *Plesiogale*, Oligocene, Neogene, Europe

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### Introduction

Early mustelidan carnivorans are apparently best documented from the European Tertiary. Especially the Oligocene and Early Miocene formations of France

and southern Germany, constituting a favoured field of research for many of our scientific predecessors, have yielded abundant material of primitive mustelidans. Studies of the European *Mustelida* have been carried out for more than 150 years, resulting in an impressive accumulation of bibliographic references. At present, however, it is often difficult to avoid misunderstanding when employing vague diagnoses of mustelidan taxa created during the epoch of the pioneers. Cladistics is now generally accepted as the philosophy and methodology of choice in phylogenetic inference and taxonomy. It is thus no longer possible to follow phylogenetic reconstructions and classifications proposed in the past as using overall similarity instead of special similarity, paraphyletic as opposed to monophyletic taxa, and taxonomic congruence rather than character congruence.

The first cladogram of the *Carnivora*, involving the major groups of mustelidans, was proposed by Tedford (1976). Although his hypothesis had been put forward in conflict with the premises of cladistic methodology (Wiig 1983), it was accepted at that time and played an important part, stimulating many systematists to further efforts to reconstruct the phylogeny of carnivorans, particularly pinnipeds.

Schmidt-Kittler (1981) presented a second attempt at distinguishing the major clades of mustelidan carnivorans. Through an analysis of primitive and derived features of the basicranium and dentition, he proposed a testable hypothesis of the phylogenetic relationships for non-marine mustelidans. His comparative analysis of the auditory region in many fossil and extant arctoids documented the phylogenetic significance of morphological transformations in this part of the cranium. Schmidt-Kittler's phylogeny of the *Mustelida*, based primarily on his pioneering interpretation of the transformation of the suprameatal fossa, represents an important step in the advancement of our understanding of the evolutionary history of this group. His study revealed a lack of knowledge of interrelationships among early mustelidans and the need for a taxonomic revision of these forms.

In the meantime, a number of alternative cladograms of the *Mustelida* have been proposed (Ginsburg 1982, Cirot 1988, 1992, Flynn *et al.* 1988, Baskin 1989, Wozencraft 1989, Wyss and Flynn 1993). However, though much has recently been written on phylogenetic relationships of mustelidan carnivorans, the critical Oligocene and Early Miocene forms have remained largely ignored.

This paper presents the results of a phylogenetic analysis of craniodental characters of the early European mustelidans and their taxonomic revision at a generic level, providing a new approach to mustelidan phylogeny and classification. To avoid terminological ambiguity, I use names "mustelidan" and "ursidan" for members of the *Mustelida* and the *Ursida*, respectively, employing "mustelid" and "ursid", as usually applied, to representatives of the families *Mustelidae* and *Ursidae*.

Chronostratigraphic units as used in this paper correspond to the following European land mammal ages and Mammal Paleogene (MP) and Neogene (MN) zones (Schmidt-Kittler *et al.* 1987, Mein 1990): Early Oligocene, Rupelian, MP 21–24; Late Oligocene, Chattian, MP 25–30; Early Miocene, Agenian plus Orleanian,

MN 1–5; Middle Miocene, Astaracian, MN 6–8; Late Miocene, Vallesian plus Turolian, MN 9–13; Early Pliocene, Ruscinian, MN 14–15; Late Pliocene, Villanyian, MN 16–17. For correlations of the European and North American land mammal ages see Lindsay and Tedford (1990).

## Material

### Abbreviations for collections

AMNH	American Museum of Natural History, New York, U.S.A.
BSP	Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany
FSL	Département des Sciences de la Terre, Université Claude Bernard, Lyon, France
FSM	Laboratoire de Géologie, Université de Provence, Marseille, France
IGM	Institut für Geowissenschaften, Johannes Gutenberg-Universität Mainz, Germany
ISE	Laboratoire d'Évolution des Vertébrés, Université des Sciences et Techniques du Languedoc, Montpellier, France
ISEZ	Instytut Systematyki i Ewolucji Zwierząt, Polska Akademia Nauk, Cracow, Poland
MGHN	Musée Guimet d'Histoire Naturelle, Lyon, France
MGL	Musée Géologique Cantonal, Lausanne, Switzerland
MHNM	Musée d'Histoire Naturelle, Montauban, France
MHNT	Muséum d'Histoire Naturelle, Toulouse, France
MNHN	Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France
MNHU	Museum für Naturkunde, Humboldt-Universität, Berlin, Germany
NHM	Natural History Museum, London, United Kingdom
NMB	Naturhistorisches Museum Basel, Switzerland
PDV	Private collection of D. Vidalenc, Saint Gaudens, France
PVPH	Laboratoire de Paléontologie des Vertébrés et Paléontologie Humaine, Université Pierre et Marie Curie, Paris, France
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany
SMN	Staatliches Museum für Naturkunde, Stuttgart, Germany
UK	Geologický a Paleontologický Ústav, Universita Karlova, Prague, Czech Republic
YPM	Yale Peabody Museum, Princeton University Collection, New Haven, U.S.A.
ZM	Zoologisk Museum, Copenhagen, Denmark
ZSM	Zoologische Staatssammlung, Munich, Germany

### Specimens examined

Materials of the following genera of the *Mustelida* formed the focus of the study:

*Simocyon* Wagner, 1858 (Late Miocene and Early Pliocene, Eurasia; Early Pliocene, North America) – Skulls plus mandibles: BSP AS II 52, NHM M9032a–h. Facial-palatal portion of skull: BSP AS II 51. Mandibles: BSP AS II 53, NHM M412 [cast].

*Ailurus* Cuvier, 1825 (Pliocene, Europe and North America; Pliocene to Recent, Asia) – Skulls plus mandibles: NHM 75.2338; NMB 10094; SMF 12743, 39290; ZSM 1953/98. Mandible: SMF W6301. Teeth: SMF W6142, W6144, W6148, W6219, W6239/1–6; UK OF65371, OF65372.

*Amphictis* Pomel, 1853 (Late Oligocene to Middle Miocene, Europe) – Skull: ISEZ MF2130/93. Cranium: BSP 1952 II 4769. Facial-palatal portion of skull: BSP 1952 II 21. Maxillae: BSP 1937 II 13357, 13371, 13392, 13393, 13399, 13402, 13545; FSL 97711, 212860 [cast], 213850 [cast]; MHNM Qu2; NMB GA5729 [cast]. Mandibles: BSP 1879 XV 74 (only mandible, not M<sup>1</sup>); BSP 1881 IX 15a, 571;

BSP 1937 II 13124–13132, 13134–13139, 13141–13145, 13147–13149, 13213–13215, 13221, 13222, 13227, 13228, 13243, 13248, 13250, 13257, 13419, 13516, 13607, 13608, 13895, 14883; FSL 4294 [old no.], 213846, 213848, 213849; FSM PQ283; ISE UM1841–1843; MGHN StG768, StG779–782, StG783 [cast]; MHNM MTB13, Qu1; MHNT GER259; MNHN Qu9238, Qu9240, Qu9242–9246, SG12307; NHM 31057, 31058, M1651, M1656, M2381, M9632; NMB GA5729 [cast], LM554, SG15495, SG19457. Teeth: BSP 1881 IX 28 [only M<sup>1</sup>, not M<sup>2</sup>], 572; BSP 1937 II 13708, 13710, 13711, 13723, 13726, 14484, 14488, 14523, 14529, 14531, 14735–14738, 14866, 14867, 14876, 14878–14882, 14927, 14946–14948, 14950, 14953, 14954, 14982, 14983, 14987; BSP 1947 III 4; BSP 1976 XXII 3423–3426, 3463, 3667; FSL 213048; ISEZ MF2129/93; NMB Cod5–7, LCh242, Pa1061; PDV Dp245, Dp247, Dp256, Mb43.

*Bavarictis* Mödden, 1991 (Late Oligocene, Europe) – Skull: BSP 1952 II 5. Facial-palatal portion of skull plus mandible: BSP 1952 II 8. Facial-palatal portions of skull: BSP 1952 II 6, 7. Maxilla: BSP 1952 II 10. Mandibles: BSP 1952 II 3336 [only dentary with P<sub>2</sub>, P<sub>4</sub>, and M<sub>1</sub>; not P<sub>3</sub>], NHM M9637. Teeth: BSP 1952 II 11, 12, 4770–4772.

*Potamotherium* Geoffroy Saint-Hilaire, 1833 (Late Oligocene to Late Miocene, Europe) – Skulls: BSP 1885 I 13, NMB Ph3653. Cranium: NMB MA905. Auditory portions of cranium: NMB MA1203, SG7539, SG18512, SG18513, SG20935. Facial-palatal portion of skull: NMB SG14041. Maxillae: NMB SG6922, SG11021. Mandibles: BSP 1885 I 501, 1964 I 225, 1967 I 224 [cast], 1972 I 12 [cast]; NMB MA703, MA915, SG227, SG3784, SG6941, SG10750, SG12302, SG12304, SG17382, SG17900. Teeth: NMB MA2972, MA2974–2976. Endocranial cast: BSP 1971 I 147.

*Pseudobassar* Pohle, 1917 (Late Oligocene, Europe) – Skull plus mandible: ZM 144. Skull: YPM 11455 [cast]. Maxillae: MHNT PHQ340; MNHN Qu8978; NHM M2361A, M2361C. Mandibles: BSP 1879 XV 713, 716, 718; MHNM Qu4–6; MNHN Qu9130, Qu9133, Qu9135; NMB QuB450, QuC66.

*Angustictis* gen. n. (Early Miocene, Europe) – Facial-palatal portion of skull plus mandible: BSP 1937 II 13281. Maxillae: BSP 1937 II 13556, 13576. Mandibles: BSP 1937 II 13260–13263, 13265, 13266, 13268–13272, 13274, 13276, 13278–13280, 13505–13511, 13513, 13626–13649, 13889, 13891–13893; BSP 1976 XXII 3416, 3417. Teeth: BSP 1937 II 13699–13705, 14884–14892, 14894–14903, 14905–14918, 14936, 14938; BSP 1976 XXII 3418, 3419, 3651–3653.

*Broiliana* Dehm, 1950 (Early Miocene, Europe) – Skulls: BSP 1937 II 13524, 13525. Crania: BSP 1937 II 13526–13532, 13537. Auditory portions of cranium: BSP 1937 II 13602–13604. Facial-palatal portion of skull plus mandible: BSP 1937 II 13555. Facial-palatal portion of skull: BSP 1937 II 13558. Maxillae: BSP 1937 II 13360–13367, 13548, 13550–13553, 13593–13595; BSP 1976 XXII 3475. Mandibles: BSP 1937 II 13151–13155, 13157, 13158, 13160–13166, 13169, 13172, 13173, 13176, 13178, 13181, 13182, 13184–13187, 13193, 13194, 13198–13200, 13202, 13203, 13205, 13207–13209, 13343, 13596, 13598. Teeth: BSP 1937 II 13009 [only M<sub>2</sub>, not dentary with P<sub>3</sub>–M<sub>1</sub>], 13159, 13167, 13168, 13177, 13179, 13180, 13183, 13188, 13195–13197, 13206, 13442, 13443, 13580, 13667–13678, 13681–13685, 14333–14371, 14373–14392, 14493, 14495, 14499, 14500, 14516–14522, 14524–14528, 14530, 14532–14549, 14551–14616, 14618–14642, 14647, 14667–14670, 14672–14676, 14678, 14680, 14682–14689, 14691, 14693, 14893; BSP 1976 XXII 3433–3446, 3450–3462, 3464, 3466–3468, 3476, 3477. Endocranial cast: BSP 1971 I 149.

*Mustelictis* Lange, 1969 (Early Oligocene, Europe) – Skulls: NHM M7490, PVPH unnumbered [holotype of *Mustelictis piveteaui*]. Mandibles: FSM PQ294; MHNM Qu3; MHNT PHQ169, PHQ348; MNHN Qu9121; NHM M1372; NMB QuB299, QuC77, QuC378; ZM 96.

*Franconictis* gen. n. (Early Miocene, Europe) – Crania: BSP 1937 II 13536, 13571, 13572. Auditory portion of cranium: BSP 1937 II 13605. Maxillae: BSP 1937 II 13379–13388, 13390, 13391, 13401, 13549. Mandibles: BSP 1937 II 13140, 13210–13212, 13216–13220, 13224–13226, 13229–13242, 13244–13247, 13249, 13251–13256, 13894; BSP 1976 XXII 3420, 3421. Teeth: BSP 1937 II 13389, 13691–13695, 13712–13714, 14864, 14865, 14868–14875, 14919–14926, 14928–14935, 14937, 14939–14944, 14979–14981, 14984–14986; BSP 1976 XXII 3427. Endocranial cast: BSP 1971 I 151.

*Stromeriella* Dehm, 1950 (Early Miocene, Europe) – Skulls: BSP 1937 II 13533, 13557. Crania: BSP 1937 II 13534, 13535, 13561. Auditory portion of cranium: BSP 1937 II 19604. Facial-palatal portion of skull: BSP 1937 II 13540. Maxillae: BSP 1937 II 13344–13355, 13358, 13359, 13541–13544,

13680, 14207, 14208; BSP 1976 XXII 3514. Mandibles: BSP 1937 II 13009 [only dentary with P<sub>3</sub>-M<sub>1</sub>, not M<sub>2</sub>], 10356, 13001-13008, 13010, 13011, 13013-13017, 13019-13035, 13037-13069, 13071-13074, 13133, 13156, 13609, 13612, 13613, 13616, 13621, 14237; FSM 750, 787, 788, LgM13, LgM14, LgM14a. Teeth: BSP 1937 II 13305, 13679, 13686-13688, 14108-14138, 14175-14193, 14195-14206, 14225-14236, 14238-14297, 14701, 14877; BSP 1976 XXII 3479-3484, 3486-3496, 3507-3513. Endocranial cast: BSP 1971 I 150.

*Bathygale* gen. n. (Early Miocene, Europe) – Skulls: MNHN SG3215-3218, NHM 31022. Crania: MNHN SG3195, MNHU MBMa29336. Mandibles: FSL 97710, 213854; MGHN StG772; MHNT GER260; MNHN SG3220, SG3222, SG3223, SG3227, SG3229, SG3233, SG3240-3242, SG3245; NHM M7646; NMB MA802, SG10732.

*Plesiictis* Pomel, 1846 (Late Oligocene to Early Miocene, Europe) – Skulls plus mandibles: AMNH 11001, NMB Chr2573. Skulls: FSL 97448, MGL 42043, MNHN LIM343, NMB Chr1168. Crania: NMB Bst3853, Cod2181. Maxillae: NMB Pa1044, Pa1045. Mandibles: FSL 7224 [old no.], 97708, 97709; FSM LgM15, LgM16; MNHN JC9, Qu9124, SG3240, SG12306; NMB Bst199, Pa1057-1060, QuB325, Sau1774, SG15496; PDV Dp244; PVPH Ph302, Ph304, Ph306-309, Ph311; ZM 93. Teeth: FSL CBr6067a-c; NMB Pa1046-1049, Pa1056, Pa1062-1065, Pa1068, Pa11878, Pa11884, Pa12120; PVPH Ph303.

*Paragale* Petter, 1967 (Early Miocene, Europe) – Skulls: NMB MA4641, Ph3638. Facial-palatal portion of skull: MNHN 3214a. Mandibles: MGHN StG769, StG825; MNHN 3214b; NMB MA2824, SG2098.

*Plesiogale* Pomel, 1847 (Early Miocene, Europe) – Skull: NMB SG2894. Mandibles: MNHN SG3191-3194, SG3203-3206; NMB MA4698, SG2895, SG2896, SG8094.

For purposes of the determination of character polarity, skulls and teeth of other fossil and Recent carnivorans housed in BSP, FSL, FSM, IGM, ISEZ, MGHN, MHNM, MNHN, MNHU, NHM, NMB, SMF, SMN, and ZSM were studied.

### Character analysis

Although 66 characters of the skull and dentition were originally sampled among the early mustelidans of Europe, the alternative states could be objectively defined for only 28 of them (Figs 1 – 6). The distribution of these character states across the genera analyzed is shown in Table 1.

The character polarity is established based on outgroup comparison (Watrous and Wheeler 1981, Farris 1982, Maddison *et al.* 1984), the paleontological method (Eldredge and Cracraft 1980), and the ontogenetic method (de Queiroz 1985). Bryant (1991) has recently shown that they are appropriate and equally valid procedures for determining polarity of character transformations in phylogenetic analyses.

There is general agreement on the bipartite division of the *Carnivora* into feliforms and caniforms, and the latter grouping into canoids (or cynoids) and arctoids. There is further agreement that arctoids related to ursids constitute the sister group to those related to mustelids (Tedford 1976, Flynn *et al.* 1988, Wyss and Flynn 1993). Accordingly, the following series of outgroups was used for polarity determination: (1) *Ursida*, defined as the most recent common ancestral species of ursids and *Ailuropoda* and all of its descendants, plus all arctomorphs that share an ancestral species with this clade, being not also common to the *Mustelida*; (2) *Amphicyonidae*, defined as the most recent common ancestral species

Table 1. Distribution of the states of 28 craniodental characters in 15 genera of early European mustelidans. The character states are defined in Figs 1–6; “a” designates the primitive state for each character; “b”, “c”, “d”, and “e” indicate derived states. In instances in which two different states of the same character could be scored for a genus, both the states are listed in the matrix according to the assumed sequence in which they appeared in the genus. Missing data are denoted by “?” (non-preservation) or “-” (non-applicable character).

Taxa	Characters																											
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
<i>Simocyon</i>	a	a	b	a	?	a	a	c	a	a	?	bc	a	a	a	a	a	b	a	a	b	a	c	a	a	a	a	a
<i>Ailurus</i>	a	a	b	a	ab	a	a	c	a	b	a	c	a	b	b	a	a	b	a	b	bc	a	a	d	a	a	a	b
<i>Amphictis</i>	a	a	b	a	a	a	a	ab	a	b	?	ab	a	a	a	a	a	b	a	ac	b	a	a	a	a	a	a	a
<i>Bavarictis</i>	a	a	a	a	a	a	a	b	a	b	a	b	a	b	a	b	a	b	a	ac	b	a	a	b	a	a	b	a
<i>Potamotherium</i>	b	a	b	b	a	b	b	c	b	b	a	b	a	a	a	b	d	ab	b	d	b	ab	ab	b	b	a	b	a
<i>Pseudobassar</i>	a	a	a	a	b	a	b	a	c	b	a	b	a	b	a	a	a	a	a	ac	b	a	a	b	a	a	ab	a
<i>Angustictis</i> gen. n.	?	?	a	?	?	?	?	?	?	?	?	b	a	b	a	a	a	b	a	c	ab	a	a	c	a	a	a	a
<i>Broiliana</i>	a	a	a	b	b	a	b	a	c	b	a	a	a	ab	a	a	a	b	a	a	ab	a	a	c	a	a	a	a
<i>Mustelictis</i>	a	a	a	a	a	a	a	a	d	b	a	b	a	b	a	a	a	ab	a	ac	b	a	a	ab	a	a	b	a
<i>Franconictis</i> gen. n.	?	a	?	b	b	a	b	b	d	b	b	?	a	b	a	a	a	b	a	c	b	a	a	a	a	a	a	a
<i>Stromeriella</i>	a	a	a	b	b	a	c	b	d	b	b	b	a	a	a	a	a	b	a	a	b	a	a	a	a	a	a	a
<i>Bathygale</i> gen. n.	a	b	b	b	b	a	bc	b	d	b	a	b	a	b	a	a	a	b	a	e	b	ab	b	b	ab	a	b	a
<i>Plesictis</i>	a	b	b	b	ba	a	b	b	d	b	a	b	a	b	a	a	b	b	a	de	b	ab	b	b	ab	a	b	a
<i>Paragale</i>	a	a	b	b	b	a	c	c	e	b	?	b	b	b	a	b	c	b	-	e	bc	b	c	b	b	a	b	a
<i>Plestogale</i>	a	a	b	b	b	?	?	b	e	b	b	bc	b	b	a	b	c	b	-	e	c	b	d	b	b	b	b	a

of amphicyonines and daphoenines and all of its descendants; (3) *Canoidea*, defined as the most recent common ancestral species of canids and all of its descendants, plus all caniforms that share an ancestral species with this clade, being not also common to the *Arctoidea*; (4) *Feliformia*, defined as the most recent common ancestral species of felids, viverrids, *Nandinia*, hyaenids, and herpestids, and all of its descendants, plus all carnivorans that share an ancestral species with this clade, being not also common to the *Caniformia*.

The justification for the polarity assigned is provided below. The characters are arranged according to anatomical region.

1. Form of postorbital region (Fig. 1) – Character state 1b characterizes most adult pinnipeds and some adult lutrines. Other carnivorans exhibit condition 1a. Hence state 1a is considered plesiomorphic for the *Mustelida*; 1b is derived.

2. Pattern of dorsal cranial crests (Fig. 1) – Configuration 2b is of rare occurrence among adult carnivorans. It applies to *Bathygale* gen. n., *Plesictis*, leptarctine

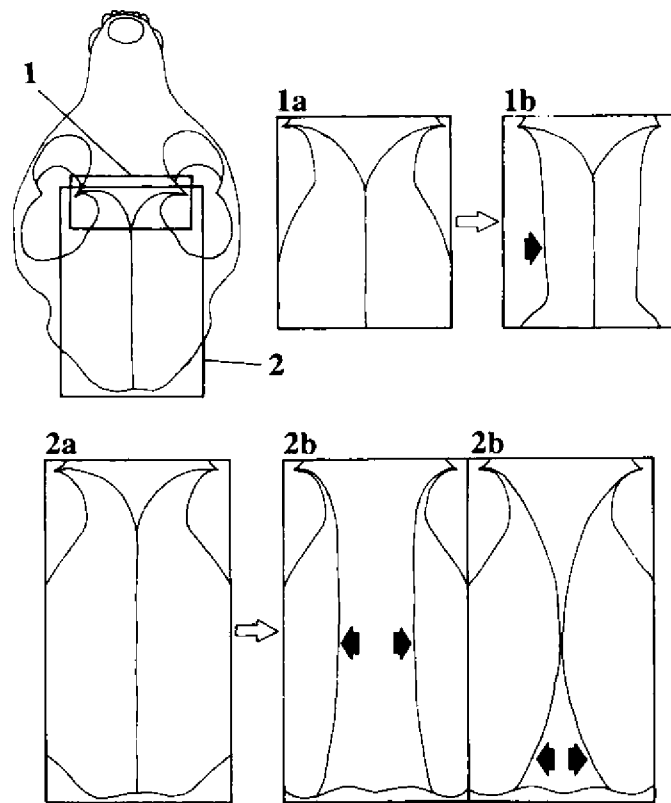


Fig. 1. Definitions of the states of characters 1 and 2 and the assigned polarity of their transformations in the early European mustelidans: 1a – postorbital region not elongated in adults, shorter than its greatest width, 1b – postorbital region greatly elongated in adults, longer than its greatest width; 2a – dorsal cranial crests Y-shaped in adults, sagittal crest present, 2b – dorsal cranial crests parallel to X-shaped in adults, strong parasagittal crests present.

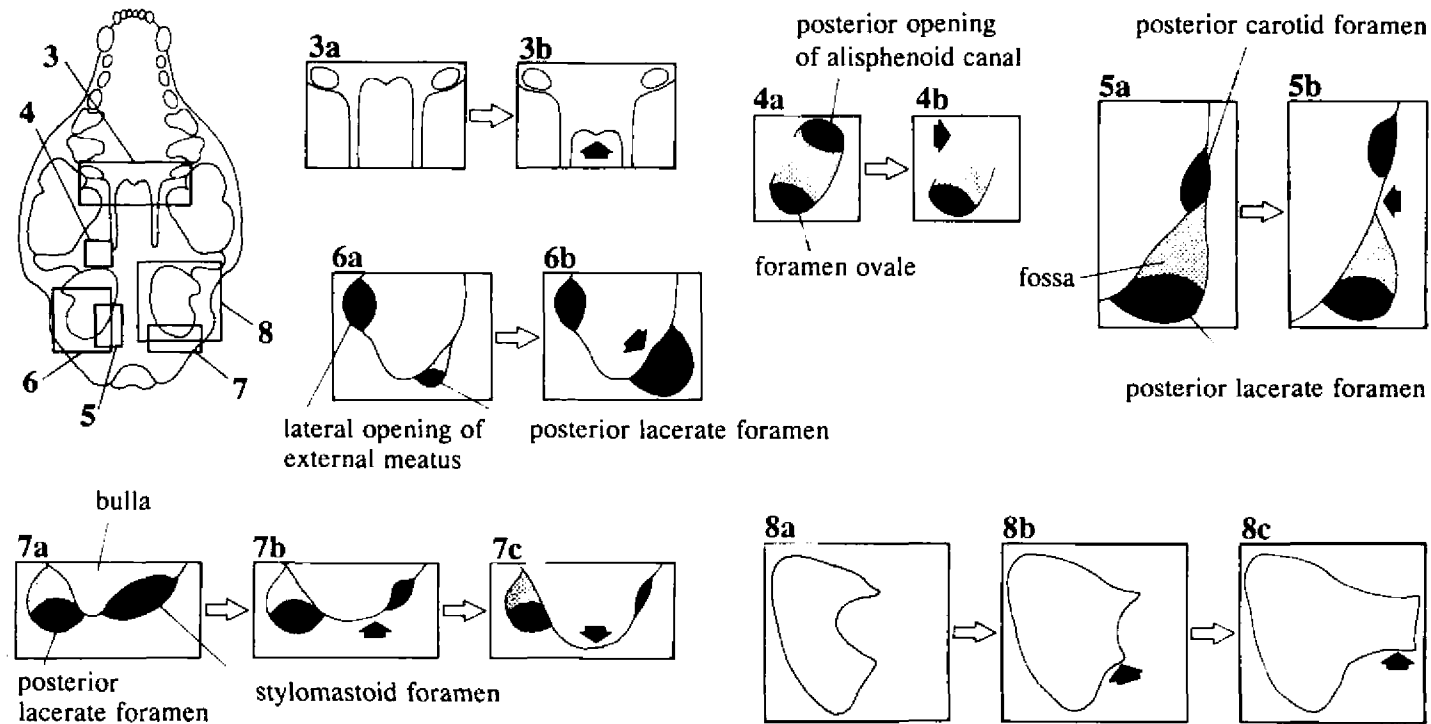


Fig. 2. Definitions of the states of characters 3–8 and the assigned polarity of their transformations in the early European mustelidans: 3a – posterior border of palate situated at level of posteriormost upper teeth, 3b – posterior border of palate situated behind posteriormost upper teeth; 4a – alisphenoid canal present, 4b – alisphenoid canal absent; 5a – posterior carotid foramen joined to fossa leading to posterior lacerate foramen, 5b – posterior carotid foramen separated from fossa leading to posterior lacerate foramen; 6a – posterior lacerate foramen not enlarged, smaller than lateral opening of external auditory meatus, 6b – posterior lacerate foramen greatly enlarged, greater than lateral opening of external auditory meatus; 7a – smallest width of auditory bulla between stylomastoid foramen and fossa leading to posterior lacerate foramen smaller than greatest diameter of stylomastoid foramen, 7b – smallest width of auditory bulla between stylomastoid foramen and fossa leading to posterior lacerate foramen greater than greatest diameter of stylomastoid foramen, posterior border of caudal entotympanic situated in front of that of fossa leading to posterior lacerate foramen, 7c – smallest width of auditory bulla between stylomastoid foramen and fossa leading to posterior lacerate foramen greater than greatest diameter of stylomastoid foramen, posterior border of caudal entotympanic situated behind that of fossa leading to posterior lacerate foramen; 8a – meatal trough of ossified ectotympanic not differentiated, 8b – meatal trough of ossified ectotympanic short, its smallest mediolateral dimension smaller than one-third of bullar width, 8c – meatal trough of ossified ectotympanic long, its smallest mediolateral dimension greater than one-third of bullar width.



mustelids (Qiu and Schmidt-Kittler 1982), and *Melogale* (= *Helictis*), being a variable feature in *Pliotaxidea* (Wagner 1976) and *Taxidea* (Heráñ 1974: fig. 3). Therefore state 2a is retained in the *Mustelida* ancestrally; condition 2b represents the derived configuration. State 2a is hypothesized to be secondarily derived in the *Mustelinae*.

3. Posterior extension of palate (Fig. 2) – Character state 3a is assumed to be ancestral for the *Mustelida* because it is characteristic of most canoids and Paleogene ursidans (*Amphicyonodon*, Cirot 1992: pl. VI/fig. 3; *Parictis*, Clark *et al.* 1967: fig. 10/2; *Cephalogale*, de Beaumont 1965: fig. 14a), some early pinnipeds (*Kolponomos*, Stirton 1960: fig. 3), the earliest known procyonids (*Pseudobassar*, *Angustictis* gen. n., *Broiliana*), and primitive mustelids (*Mustelictis*, *Bassariscus*, *Stromeriella*). Consequently, condition 3b is regarded as the derivative state.

4. Occurrence of alisphenoid canal (Fig. 2) – All canoids, amphicyonids, and ursidans except *Ailuropoda* display character state 4a. Thus state 4a occurs in the *Mustelida* ancestrally; 4b is derived.

5. Position of posterior carotid foramen (Fig. 2) – Outgroup comparisons with the *Ursida* and *Amphicyonidae* provide evidence that configuration 5a is primitive within the *Mustelida*, whereas condition 5b is derived. The appearance of configuration 5a in Early Miocene representatives of *Plesictis* (NMB Chr1168 and Chr2573) is clearly a secondary development, as evidenced by the presence of state 5b in the Late Oligocene members of this genus.

6. Size of posterior lacerate foramen (Fig. 2) – Among carnivorans, condition 6b is restricted in occurrence to pinnipeds and many lutrines. Hence state 6a is interpreted as primitive for the *Mustelida*, and 6b as derived.

7. Posterior extension of caudal entotympanic (Fig. 2) – Both outgroup comparisons with the ursidans and amphicyonids and evidence from the ontogeny of many extant mustelidans (Hunt 1974) demonstrate that a caudal entotympanic that is unexpanded posteriorad is primitive, whereas an expanded one is derived. Accordingly, configuration 7a is considered the ancestral condition for the *Mustelida*; 7b and 7c are derivative states, with 7b being unquestionably intermediate between 7a and 7c.

8. Lateral extension of ectotympanic (Fig. 2) – The ontogeny of the auditory bulla as observed in living carnivorans provides evidence that little or no lateral prolongation of the ossified ectotympanic component of the external auditory tube is primitive, and that a long tubular bony meatus is derived (Hunt 1974). Character state 8a is therefore ancestral for the mustelidans; conditions 8b and 8c, representing successive stages of the lateral expansion of ectotympanic, constitute apomorphic arrangements. State 8b plainly represents the intermediate configuration between conditions 8a and 8c.

9. Configuration of suprimeatal fossa (Fig. 3) – In all arctomorphs excepting post-Paleogene pinnipeds and advanced mephitines, the laterodorsal wall of the middle ear cavity is hollowed in the area adjoining the suture between squamosal and mastoid bones. This hollow was named the suprimeatal fossa by Segall (1943:

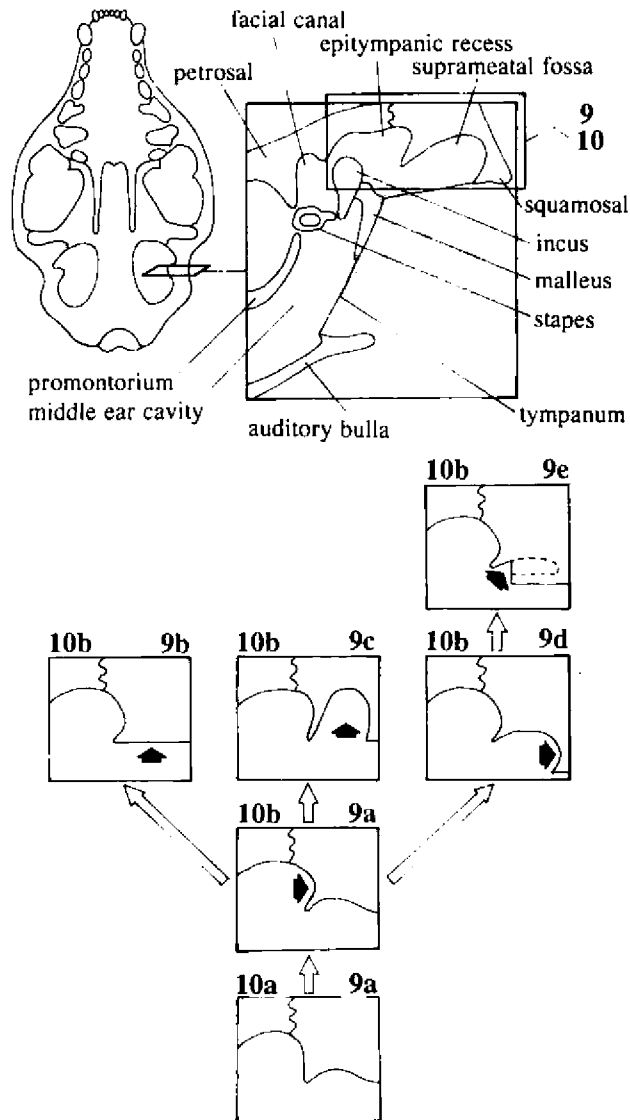


Fig. 3. Definitions of the states of characters 9 and 10 and the assigned polarity of their transformations in the early European mustelidans: 9a – anterior and lateral walls of suprameatal fossa neither excavated into squamosal nor perpendicular to meatal roof, 9b – suprameatal fossa absent, 9c – at least anterior or lateral wall of suprameatal fossa excavated into squamosal or perpendicular to meatal roof, ventral extension of medial wall of suprameatal fossa subequal to that of lateral wall, 9d – at least anterior or lateral wall of suprameatal fossa excavated into squamosal or perpendicular to meatal roof, medial wall of suprameatal fossa absent or its ventral extension considerably smaller than that of lateral wall, suprameatal fossa not closed anteriorly by posterior wall of meatal tube, 9e – lateral part of suprameatal fossa partially closed by posterior wall of meatal tube anteriorly; 10a – epitympanic recess anterior to fossa for incudal processus brevis not floored by squamosal, 10b – lateral part of epitympanic recess anterior to fossa for incudal processus brevis floored by squamosal.

39). The presence of the suprameatal fossa is diagnostic of the *Arctomorpha*. Outgroup comparison with the *Ursida* provides evidence that character state 9a is retained by the mustelidans ancestrally. Condition 9b, shared by the post-Paleogene pinnipeds, is hypothesized to have originated by fusion of the developing external auditory tube to the roof of the 9a suprameatal fossa. The procyonid configuration (9c) evidently evolved as a result of a deep dorsal expansion of the roof of an initially shallow 9a suprameatal fossa. The early mustelid arrangement (9d) developed in consequence of great ventral extension of the lateral wall of the 9a suprameatal fossa. This statement is clearly supported by the transitional pattern of the suprameatal fossa as seen in *Mustelictis*. State 9e, exemplified by *Leptarctus* (Qiu and Schmidt-Kittler 1982: fig. 3) and early mustelines (*Paragale* and *Plesiogale*, Schmidt-Kittler 1981: figs 10, 11), constitutes the intermediary stage in evolution of the mustelid suprameatal fossa, in which the fossa is initially not floored (*Mustelictis*) or only partially floored laterally by the developing auditory tube (*Bassariscus*, Schmidt-Kittler 1981: fig. 7; *Franconictis* gen. n., *Stromeriella*, *Bathygale* gen. n., *Plesictis*) to be finally closed both ventrally and anteriorly by the posterior wall of this tube (*Melogale* and most mustelines, Schmidt-Kittler 1981: figs 12 – 15). Concluding, character state 9a is primitive; 9b, 9c, and 9d are independently derived from 9a; 9e is derived from 9d.

10. Lateral extension of epitympanic recess (Fig. 3) – Numerous examples from both ontogeny and phylogeny of extant and fossil carnivorans document that a middle ear cavity of small volume, unexpanded into the surrounding basicranium, is primitive, and that increase in relative volume of the middle ear cavity, either by bulla inflation and/or expansion into surrounding basicranial bones, is derived (Hunt 1974, 1987). Accordingly, condition 10a is assumed to be ancestral for the *Mustelida*, whereas state 10b is regarded as derived.

11. Occurrence of postlateral sulcus of brain (Fig. 4) – Examples from both phylogeny and ontogeny of carnivorans demonstrate that an unexpanded neocortex exposing a simple fissure pattern is primitive, and that the neocortical expansion in temporal and occipital areas accompanied by development of additional sulci is derived (Radinsky 1977). Therefore state 11a is retained in the *Mustelida* ancestrally; condition 11b is an evolutionary novelty.

12. Occurrence and form of P<sup>1</sup> (Fig. 4) – The general trend observed in dental evolution within the *Carnivora* is enlargement of the carnassials and simultaneous reduction of the remaining cheek teeth, including loss of the peripheral ones. Some of the lineages show a secondary hypertrophy of postcarnassial molars (e.g., post-Paleogene ursidans); however, no carnivoran is known to document an increased development of the anteriormost premolars. Accordingly, character state 12a is considered primitive; 12b and 12c are regarded as derivative conditions. State 12b is unquestionably intermediate between 12a and 12c.

13. Occurrence of P<sup>4</sup> carnassial notch (Fig. 4) – Character state 13a is characteristic of all carnivorans except for most mustelids that display condition 13b.

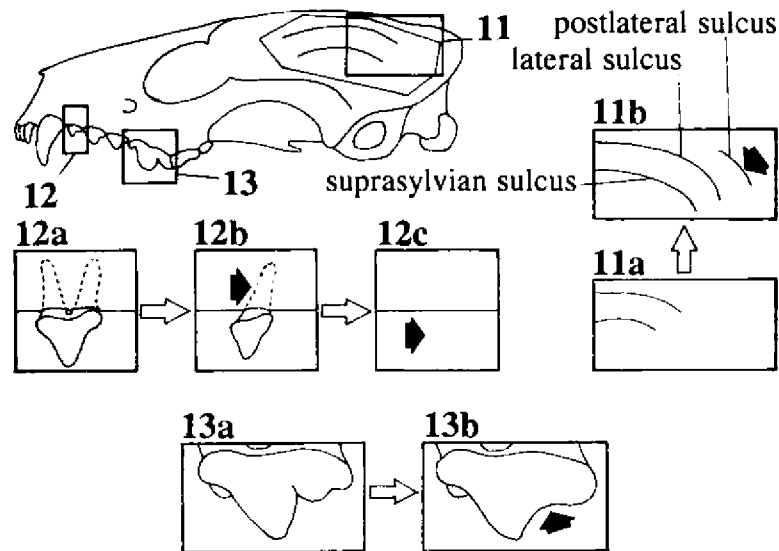


Fig. 4. Definitions of the states of characters 11–13 and the assigned polarity of their transformations in the early European mustelidans: 11a – postlateral sulcus of brain absent, 11b – postlateral sulcus of brain present; 12a –  $P^1$  two-rooted, 12b –  $P^1$  single-rooted, 12c –  $P^1$  absent; 13a –  $P^4$  carnassial notch present, 13b –  $P^4$  carnassial notch absent.

Thus state 13a is present in the *Mustelida* ancestrally; 13b is an evolutionary innovation.

14. Occurrence and form of  $P^4$  protocone (Fig. 5) – Outgroup comparisons with the ursidans and amphicyonids demonstrate that condition 14a is retained by the mustelidans ancestrally, and also confirms the derivative nature of state 14b.

15. Occurrence and form of  $P^4$  hypocone (Fig. 5) – Among mustelidans, *Ailurus* is unique in having configuration 15b. *Procyon* approaches this condition, but its  $P^4$  hypocone is always smaller than the protocone. In *Ailuropoda* the hypocone on  $P^4$  is even larger than the protocone, but the Paleogene ursidans (*Amphicynodon*, Cirot and de Bonis 1992; *Parictis*, Clark and Guensburg 1972; *Nothocyon*, Wang and Tedford 1992; *Cephalogale*, de Beaumont 1965), amphicyonids, and canoids, like most mustelidans, possess character state 15a. Thus state 15a occurs in the mustelidans ancestrally; 15b represents the apomorphous arrangement.

16. Size relation of  $M^1$  to  $P^4$  (Fig. 5) – Condition 16a is typical of canoids, amphicyonids, ursidans, and many early mustelidans (Table 1), which documents the primitive nature of this configuration and indicates that its alternative (16b) is an evolutionary novelty among mustelidans.

17. Pattern of  $M^1$  (Fig. 5) – Many canoids, amphicyonids (Springhorn 1977), and Paleogene ursidans (*Amphicynodon*, Cirot and de Bonis 1992; *Parictis*, Clark and Guensburg 1972; *Cephalogale*, de Beaumont 1965), as well as the Oligocene mustelidans except *Plesictis* exhibit condition 17a. Within the *Mustelida*, *Plesictis*

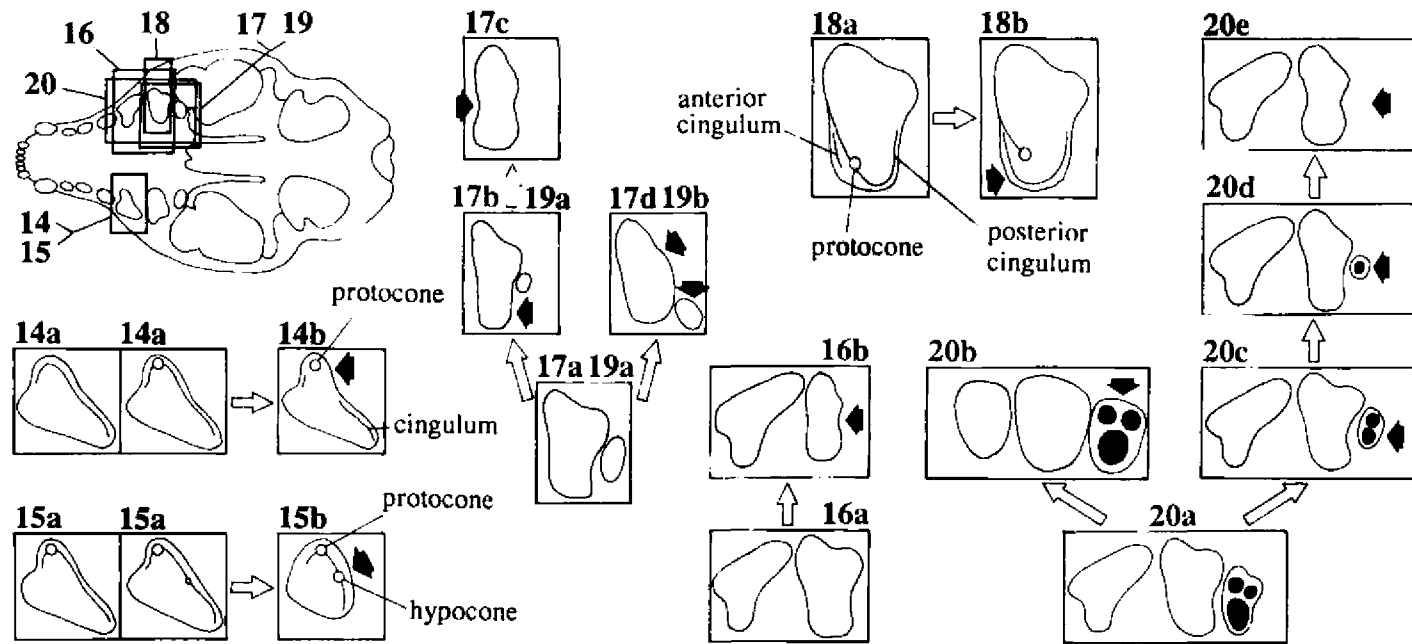


Fig. 5. Definitions of the states of characters 14–20 and the assigned polarity of their transformations in the early European mustelidans: 14a –  $P^4$  protocone not differentiated or crescentic, formed by cingulum entirely, 14b –  $P^4$  protocone conical, not formed by cingulum entirely; 15a –  $P^4$  hypocone notably smaller than protocone or not differentiated, 15b –  $P^4$  hypocone and protocone prominent and subequal in size; 16a –  $M^1$  larger than or equal in size to  $P^4$ , 16b –  $M^1$  smaller than  $P^4$ ; 17a – lingual half of  $M^1$  crown shorter than buccal half, anterior and posterior borders of lingual half not parallel to each other, 17b – lingual half of  $M^1$  crown shorter than buccal half, anterior and posterior borders of lingual half parallel to each other, 17c – lingual half of  $M^1$  crown about equal in length to or longer than buccal half, both halves separated from each other by anteroposterior constriction, 17d – lingual half of  $M^1$  crown subequal in length to buccal half, no anteroposterior constriction between both halves; 18a – anterior and posterior cingula of  $M^1$  not continuous around lingual base of protocone, 18b – anterior and posterior cingula of  $M^1$  continuous around lingual base of protocone; 19a – buccal border of  $M^2$  crown situated behind buccal half of  $M^1$ , 19b – buccal border of  $M^2$  crown situated behind lingual half of  $M^1$ ; 20a –  $M^2$  three-rooted and distinctly smaller than  $P^4$ , 20b –  $M^2$  three-rooted and subequal in size to  $P^4$ , 20c –  $M^2$  two-rooted, 20d –  $M^2$  single-rooted, 20e –  $M^2$  absent.

is unique in possessing state 17b that arose from 17a by reduction of the posterior part of the  $M^1$  talon and simultaneous enlargement of its anterior part. This transformation is well supported by the transitional pattern of  $M^1$ , as observed in the earliest known representatives of *Plesictis* (MGL 42043 and MNHN LIM343). Configuration 17c is diagnostic of the *Mustelinae*. It evidently evolved from state 17b as a result of the symmetric expansion of the talon of  $M^1$ , accompanied by reduction of the metacone wing of this tooth. The pattern of  $M^1$  in *Plesiogale*, with the lingual half of the crown being still shorter than the buccal one, is a good example for a transitional stage between configuration 17b and those shown by *Paragale* and other mustelids, in which the lingual half of the  $M^1$  crown is always longer than the buccal one. Condition 17d (*Potamotherium*), though theoretically derivable from an arrangement equivalent to that of *Plesictis*, is interpreted here as having originated from state 17a in consequence of great reduction of the  $M^1$  metacone wing. This inference is supported by the lingual position of  $M^2$  (19b) in *Potamotherium*, suggesting quite another pattern of upper molar reduction in this genus as compared to that of the non-pinniped mustelids. Accordingly, state 17a is primitive; 17b and 17d independently arose from 17a; 17b gave rise to 17c.

18. Occurrence of  $M^1$  lingual cingulum (Fig. 5) – Character state 18a is typical of the *Feliformia*, being variably present among canoids and amphicyonids (Springhorn 1977). It is unknown in ursids, but occurs in some mustelids, for instance in the earliest known procyonid *Pseudobassaris* and the earliest known mustelid *Mustelictis*. Hence condition 18a is considered plesiomorphic for the *Mustelida*; its alternative (18b) is derived.

19. Position of  $M^2$  (Fig. 5) – Among carnivorans possessing  $M^2$ , the earliest pinnipeds are unique in having state 19b (for discussion see Classification). Thus condition 19a is primitive; 19b is derived.

20. Occurrence, size, and form of  $M^2$  (Fig. 5) – Within the *Mustelida*, configuration 20b is exclusive of *Ailurus* and some procyonids. In most post-Paleogene representatives of the *Ursida* and *Amphicyonidae*,  $M^2$  is larger than  $P^4$ . However, the Paleogene ursids (*Amphicyonodon*, Cirot and de Bonis 1992; *Parictis*, Clark and Guensburg 1972; *Nothocyon*, Wang and Tedford 1992; *Cephalogale*, de Beaumont 1965) and amphicyonids (Springhorn 1977), like the canoids, are characterized by arrangement 20a. This supports the view that configuration 20a is plesiomorphic for the *Mustelida*, and that condition 20b arose from 20a and is therefore apomorphic within this taxon. The remaining states of this character represent succeeding steps in reduction of  $M^2$  and, according to this tendency, can be ordered in linear sequence as follows: 20a → 20c → 20d → 20e.

21. Occurrence and form of  $P_1$  (Fig. 6) – Character state 21a is primitive; states 21b and 21c are derived; 21b is intermediary between 21a and 21c. For argumentation justifying these statements see discussion of character 12.

22. Relation of  $M_1$  trigonid to talonid (Fig. 6) – Outgroup comparisons with the *Ursida*, *Amphicyonidae*, and *Canoidea* indicate that character state 22a is present in the *Mustelida* ancestrally, whereas its alternative (22b) is derived.

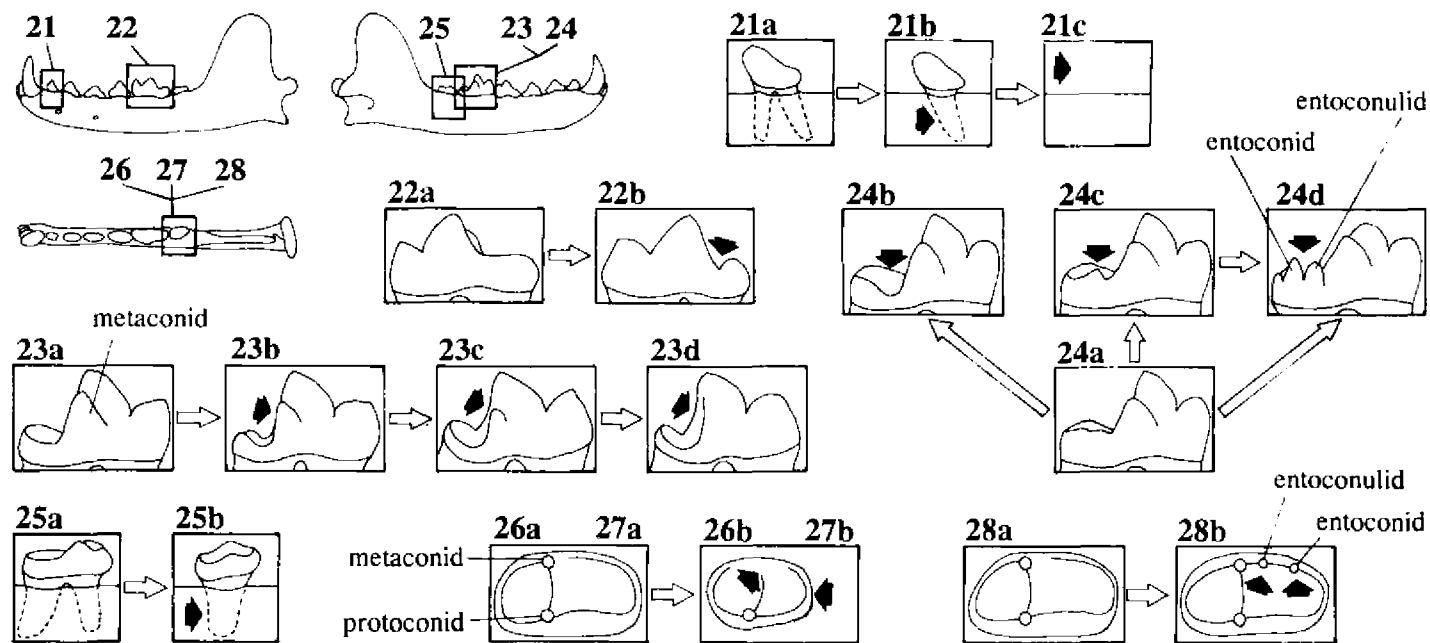


Fig. 6. Definitions of the states of characters 21–28 and the assigned polarity of their transformations in the early European mustelidans: 21a – P<sub>1</sub> two-rooted, 21b – P<sub>1</sub> single-rooted, 21c – P<sub>1</sub> absent; 22a – M<sub>1</sub> trigonid less than three times as long as talonid, 22b – M<sub>1</sub> trigonid more than three times as long as talonid; 23a – M<sub>1</sub> metaconid distinctly higher than paraconid, 23b – M<sub>1</sub> metaconid subequal in height to paraconid, 23c – M<sub>1</sub> metaconid distinctly lower than paraconid, 23d – M<sub>1</sub> metaconid not differentiated; 24a – M<sub>1</sub> entoconid and entoconulid poorly differentiated (ridge-like or cuspule-like), anterior and posterior halves of lingual wall of M<sub>1</sub> talonid subequal in height to each other, 24b – M<sub>1</sub> entoconid and entoconulid poorly differentiated (ridge-like or cuspule-like) or not differentiated, anterior half of lingual wall of M<sub>1</sub> talonid distinctly lower than posterior half, 24c – M<sub>1</sub> entoconid prominent (cusp-like), M<sub>1</sub> entoconulid poorly differentiated (ridge-like or cuspule-like) or not differentiated, 24d – M<sub>1</sub> entoconid and entoconulid prominent, cusp-like; 25a – M<sub>2</sub> two-rooted, 25b – M<sub>2</sub> single-rooted; 26a – M<sub>2</sub> metaconid present, 26b – M<sub>2</sub> metaconid not differentiated; 27a – talonid basin of M<sub>2</sub> distinctly longer than trigonid basin, 27b – talonid and trigonid basins of M<sub>2</sub> subequal in length; 28a – M<sub>2</sub> entoconid and entoconulid poorly differentiated (ridge-like or cuspule-like) or not differentiated, 28b – M<sub>2</sub> entoconid and entoconulid prominent, cusp-like.

23. Occurrence and size of M<sub>1</sub> metaconid (Fig. 6) – The presence of state 23a in Paleogene amphicyonids (Springhorn 1977) and ursidans (*Amphicyonodon* and *Pachycynodon*, Cirot 1992; *Parictis*, Clark and Guensburg 1972; *Cephalogale*, de Beaumont 1965) as well as its widespread distribution among Oligocene mustelidans (Table 1) support the conclusion that this state is plesiomorphic for the *Mustelida*. Character states 23b, 23c, and 23d represent consecutive stages in reduction of the M<sub>1</sub> metaconid and are regarded as derivative conditions. State 23c is unquestionably intermediate between 23b and 23d.

24. Pattern of M<sub>1</sub> talonid (Fig. 6) – Most amphicyonids (Springhorn 1977) and the Paleogene ursidans (*Amphicyonodon* and *Pachycynodon*, Cirot 1992; *Parictis*, Clark and Guensburg 1972; *Cephalogale*, de Beaumont 1965) display character state 24a. It is thus hypothesized to constitute the ancestral arrangement for the *Mustelida*. Condition 24b is assumed to be derived from 24a by gradual decrease in height of the anterior part of the lingual wall of M<sub>1</sub> talonid. This transformation seems to be associated with the anteroposterior contraction of the talonid, affecting all involved forms. State 24c is interpreted to have originated from 24a as a result of the enlargement of the entoconid. Configuration 24d is derivable both from 24a by simultaneous increase in size of the entoconid and entoconulid and from 24c by enlargement of the entoconulid. Concluding, state 24a is primitive; 24b and 24c represent independently derived conditions; 24d arose from 24a or 24c.

25. Number of M<sub>2</sub> roots (Fig. 6) – Outgroup comparisons with the *Ursida*, *Amphicyonidae*, and *Canoidea* provide evidence that state 25a is retained by the mustelidans ancestrally, whereas 25b is derived.

26. Occurrence of M<sub>2</sub> metaconid (Fig. 6) – All ursidans and Oligocene mustelidans (Table 1) possess character state 26a. It is therefore considered primitive for the *Mustelida*; its alternative (26b) is derived.

27. Relation of M<sub>2</sub> trigonid to talonid (Fig. 6) – Character state 27a occurs in many canoids and amphicyonids as well as in all ursidans. Hence it is assumed to be present in the *Mustelida* ancestrally; 27b is thus an apomorphic condition.

28. Occurrence and form of M<sub>2</sub> entoconid and entoconulid (Fig. 6) – Configuration 28b is characteristic of *Ailurus*. Most other mustelidans, the Paleogene ursidans (*Amphicyonodon* and *Pachycynodon*, Cirot 1992; *Parictis*, Clark and Guensburg 1972; *Nothocyon*, Wang and Tedford 1992; *Cephalogale*, de Beaumont 1965), the amphicyonids, and the canoids show character state 28a. Thus state 28a is considered ancestral for the *Mustelida*; 28b represents the derived condition.

### Phylogenetic reconstruction

Although the use of parsimony as an operational principle in scientific inference is justified, it is unclear which of various methods based on parsimony is the most appropriate for producing cladograms. It is often believed that minimum-step algorithms represent the only parsimonious procedures in cladistic analysis. In



fact, however, Farris' (1983) definition of parsimony also provides the rationale for other methods, including character weighting and character compatibility analysis (Bryant 1989).

In contrast to numerical cladists, I believe that the monophyly of a group defined by the unanimous possession, among its members, of a single derived feature that does not also occur within two or more successive outgroups is better supported than one in which the members are united by a number of features that also occur in taxa outside of the group. Classifications of numerical cladists, resulting from minimum-step cladograms in which nodes are diagnosed by numerous unweighted features, are often subject to dramatic changes when a set of characters analyzed is altered; with regard to this, the most-recent classifications of the *Carnivora* (Wozencraft 1989 *versus* Wyss and Flynn 1993) may serve as a good example. On the contrary, a classification in which taxa are distinguished on the basis of single but "strong" derived features seems to be more stable.

For the above reasons, a character weighting procedure has been applied in the present approach to phylogeny of the *Mustelida*. Fig. 7 presents the outcome of an iterative process of generating, testing, and corroboration of subsequent hypotheses of the interrelationships among the early European mustelidans in order to find the topology that best accounts for the distribution of the analyzed character states among the 15 genera under study and in other known members of the *Mustelida*. In cases of conflicts among the 28 characters analyzed, the subjectively established 38 characters of the skull and dentition were also taken into account. Although the cladogram of Fig. 7 does not constitute the most parsimonious solution based exclusively on the character state matrix of Table 1, it is believed to approach more reliably the real relationships within the *Mustelida*.

### Classification

The principal objective of this study was to identify monophyletic taxa in the sense of Hennig (1966); paraphyletic and polyphyletic groups have been rejected. Apart from diagnoses based on apomorphies, phylogenetic definitions of taxa (de Queiroz and Gauthier 1990) are also provided. Although I am well aware that the corresponding supraspecific categories of the Linnaean system of hierarchy are not equivalent as commonly applied to groups of organisms (e.g., the family of mustelids *versus* the family of amphicyonids), I use their names in this classification because of their widely accepted usage; however, I do not introduce new names for "missing" categories. I have retained previously named taxa, and have left most previously unrecognized suprageneric taxa unnamed; the latter are informally referred to as Clades A, B, C, D, E, and F.

The proposed classification of 15 genera of early European mustelidans, reflecting the topology of the cladogram of Fig. 7 and the pattern of interrelationships among the outgroups, is presented below.

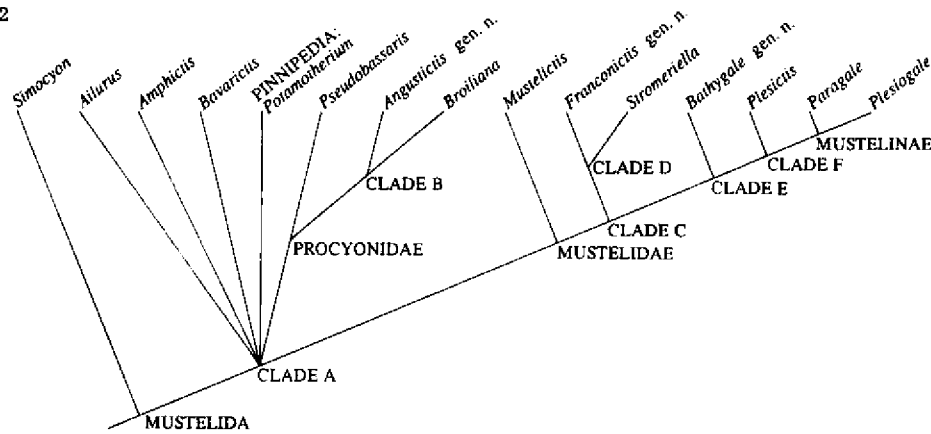


Fig. 7. Hypothesis of the phylogenetic relationships among the early European mustelidans based on an analysis of craniodental characters. *Ailurus*, *Amphictis*, *Bavarictis*, *Pinnipedia*, *Procyonidae*, and *Mustelidae* are interpreted as originated independently from a common ancestral group within Clade A because no unique synapomorphy could be identified to give secure grounds for a hypothesis concerning interrelationships among these taxa.

The derived character states for the taxa are summarized below. Their definitions are provided in Figs 1–6. The character states inferred to be uniquely derived within the *Arctoidea*, and thus believed to constitute strong support for the suggested relationship, are denoted by exclamation marks. In each instance of variable occurrence of the alternative states in a terminal taxon, that of them which is regarded as derived within the taxon is given in parentheses. Asterisks indicate derived states that are present in the analyzed European genera included in a suprageneric taxon, but that are not considered synapomorphies for that suprageneric taxon, for example the genus *Potamotherium* versus the suprageneric taxon *Pinnipedia*. Reversals are designated by a negative sign preceding the character number.

*Mustelida*: M<sub>3</sub> absent!

*Simocyon*: 3b, 8c, 12b(c), 18b, 21b, 23c

Clade A: 10b

*Ailurus*: 3b, 5(b), 8c, 12c, 14b, 15b, 18b, 20b, 21b(c), 24d, 28b

*Amphictis*: 3b, 8(b), 12(b), 18b, 20(c), 21b

*Bavarictis*: 8b, 12b, 14b, 16b, 18b, 20(c), 21b, 24b, 27b

*Pinnipedia* – *Potamotherium*: 1b\*, 3b\*, 4b\*, 6b, 7b, 8c\*, 9b\*, 12b, 16b\*, 17d\*, 18(b), 19b!, 20d\*, 21b, 22(b), 23(b), 24b\*, 25b\*, 27b

*Procyonidae*: 5b, 7b, 9c!

*Pseudobassaris*: 12b, 14b, 20(c), 21b, 24b, 27(b)

Clade B: 4b, 18b\*, 24c

*Angustictis* gen. n.: 12b, 14b, 20c, 21(b)

*Broiliana*: 14(b), 21(b)

*Mustelidae*: 9d!, 12b, 21b

*Mustelictis*: 14b, 18(b), 20(c), 24(b), 27b

Clade C: 4b, 5b\*, 7b, 8b, 18b\*

Clade D: 11b

*Franconictis* gen. n.: 14b, 20c, 27b

*Stromeriella*: 7c

Clade E: 2b!, 3b, 14b\*, 20d, 23b, 24b, 27b

*Bathygale* gen. n.: 7(c), 20e, 22(b), 25(b)

Clade F: 17b!

*Plesictis*: –5(a), 20(e), 22(b), 25(b)

*Mustelinae*: –2a, 7c, 9e, 11b, 13b, 16b, 17c!, 20e, 22b, 23c, 25b

*Paragale*: 8c, 21(c)

*Plesiogale*: 12(c), 21c, 23d, 26b

Order *Carnivora* Bowdich 1821: 33

**D e f i n i t i o n** – The most recent common ancestral species of feliforms and caniforms and all of its descendants, plus all carnivorans that share an ancestral species with this clade, being not also common to the *Creodonta*.

**D i a g n o s i s** – Eutherian mammals differing from all other *Eutheria* in the following derived features: P<sup>4</sup> and M<sub>1</sub> modified as the only carnassial teeth in the permanent dentition; P<sup>4</sup> protocone situated anterolingual to the paracone.

Suborder *Caniformia* Kretzoi 1945: 62

**D e f i n i t i o n** – The most recent common ancestral species of canoids and arctoids and all of its descendants, plus all caniforms that share an ancestral species with this clade, being not also common to the *Feliformia*.

**D i a g n o s i s** – Carnivorans differing from all other *Carnivora* in the derived enlargement and ramification of maxilloturbinals excluding nasoturbinals from the narial cavity.

Infraorder *Arctoidea* Flower 1869: 15

**D e f i n i t i o n** – The most recent common ancestral species of amphicyonids and arctomorphs and all of its descendants, plus all arctoids that share an ancestral species with this clade, being not also common to the *Canoidea*.

**D i a g n o s i s** – Caniforms differing from all other *Caniformia* in the derived enlargement of the inferior petrosal sinus and creation of the postscapular fossa.

*Arctomorpha*, new order-group taxon

(ranked between infraorder and category of taxon *Mustelida*)

**D e f i n i t i o n** – The most recent common ancestral species of ursidans and mustelidans and all of its descendants, plus all arctomorphs that share an ancestral species with this clade, being not also common to the *Amphicyonidae*.

**D i a g n o s i s** – Arctoids differing from all other *Arctoidea* in the derived creation of the suprimeatal fossa. The absence of M<sup>3</sup> is a supplementary synapomorphy of the *Arctomorpha*, evolved in some non-arctomorph arctoids independently.

**D i s c u s s i o n** – Flynn *et al.* (1988: fig. 4.7) have recently presented three alternative hypotheses for the relationships of the amphicyonids within the *Arctoidea*: A, (*Amphicyonidae*, *Ursida*, *Mustelida*); B, ((*Amphicyonidae*, *Ursida*) *Mustelida*); and C, (*Amphicyonidae* (*Ursida*, *Mustelida*)). No synapomorphy supports hypothesis B; it must be therefore rejected. However, there are two synapomorphies supporting hypothesis C: presence of the suprimeatal fossa and absence of M<sup>3</sup>. Although the suprimeatal fossa occurs in some feliforms (*Herpestides*, Hunt 1991), it is absent in the canoids and amphicyonids (Springhorn 1976, Hunt 1977), which confirms its derivative nature for the taxon encompassing ursidans and mustelidans. The amphicyonids retained M<sup>3</sup> that was subsequently lost in some later genera (Flynn *et al.* 1988). On the other hand, no ursidan or mustelidan is known to have M<sup>3</sup>. Thus the

absence of this tooth may be considered a supplementary synapomorphy of the taxon *Ursida* plus *Mustelida*.

Though I am aware of the inconvenience of introducing a new order-group name, I also feel the advantage of taking this action for facility of reference to the group including the ursidans and mustelidans, especially since its monophyly seems to be well supported.

#### Order-group taxon *Mustelida* Tedford 1976: 372

(ranked between categories of taxon *Arctomorpha* and Clade A)

**D e f i n i t i o n** – The most recent common ancestral species of *Ailurus*, pinnipeds, procyonids, and mustelids and all of its descendants, plus all mustelidans that share an ancestral species with this clade, being not also common to the *Ursida*.

**D i a g n o s i s** – Arctomorphs differing from all other *Arctomorpha* in the derived loss of M<sub>3</sub>.

**D i s c u s s i o n** – Although it seems to be hardly probable that loss of M<sub>3</sub> has occurred only once during arctomorph evolution, I follow here the diagnosis of *Musteloidea* as proposed by Schmidt-Kittler (1981) because of the absence of evidence to the contrary. I prefer the order-group name *Mustelida* to the family-group name *Musteloidea* to preserve the widely used name *Pinnipedia*, avoiding an infringement of the generally accepted convention that taxa of the higher categorical rank are not to be contained within taxa of the lower category.

#### Genus *Simocyon* Wagner, 1858

*Pseudocyon* Wagner 1857: 128 [not *Pseudocyon* Lartet 1851: 16].

*Simocyon* Wagner 1858: 366. Renaming of *Pseudocyon* Wagner, 1857.

*Metarctos* Gaudry 1860: 927. Type species – *Gulo diaphorus* Kaup 1832: 150, by monotypy.

Synonymized with *Simocyon* Wagner, 1858 by Lydekker (1885: 145).

*Amphalopex* Kaup 1861: 15. Type species – *Gulo diaphorus* Kaup 1832: 150, by monotypy.

*Pliocyon* Thorpe 1921: 477 [not *Pliocyon* Matthew 1918: 190]. Type species – *Pliocyon marshi* Thorpe 1921: 477, by monotypy.

*Aræocyon* Thorpe 1922: 97. Renaming of *Pliocyon* Thorpe, 1921. Synonymized with *Simocyon* Wagner, 1858 by Zdansky (1924: 9).

*Protursus* Crusafont Pairó and Kurtén in Crusafont Pairó 1971: 155. Nomen nudum.

*Protursus* Crusafont Pairó and Kurtén in Crusafont Pairó 1973: 59. Nomen nudum.

*Protursus* Crusafont Pairó and Kurtén 1976: 22. Type species – *Protursus simpsoni* Crusafont Pairó and Kurtén 1976: 22, by original designation. Synonymized with *Simocyon* Wagner, 1858 by Thenius (1977: 40).

**T y p e s p e c i e s** – *Simocyon primigenius* (Roth and Wagner, 1854) [*Canis lupus primigenius* Roth and Wagner in Wagner 1854: 339], by monotypy.

**D i a g n o s i s** (Fig. 7) – Mustelidans of a paraphyletic group that differs from all other *Mustelida* in the retention of the epitympanic recess that is not floored by the squamosal anterior to the fossa for the incudal processus brevis (Fig. 3: 10a); distinguished from other taxa of this paraphyletic group by the following autapomorphies: posterior border of the palate situated behind the posteriormost upper teeth (Fig. 2: 3b); meatal trough of ossified ectotympanic long, with its

smallest mediolateral dimension greater than one-third of the bulla width (Fig. 2: 8c);  $P^1$  single-rooted or absent (Fig. 4: 12b, c); anterior and posterior cingula of  $M^1$  continuous around the lingual base of the protocone (Fig. 5: 18b);  $P_1$  single-rooted (Fig. 6: 21b);  $M_1$  metaconid distinctly lower than the paraconid (Fig. 6: 23c).

**D i s c u s s i o n** – During most of its taxonomic history, *Simocyon* has subjectively been placed among either canoids or amphiocyonids. De Beaumont (1964) was the first who suggested mustelidan affinities of this genus, including it within the *Mustelidae*, and later (1968) in the *Procyonidae*. Although none of the features mentioned by him can be regarded as mustelid synapomorphies, and those supporting the affiliation with the procyonids were erroneously assumed, I leave this genus within the *Mustelida* because of the absence of  $M_3$ .

### Clade A

(taxon unnamed, ranked between categories of taxa *Mustelida* and *Pinnipedia*)

**D i a g n o s i s** (Fig. 7) – Mustelidans differing from all other *Mustelida* in the derived configuration of the epitympanic recess the lateral part of which is floored by the squamosal anterior to the fossa for the incudal processus brevis (Fig. 3: 10b).

#### Genus *Ailurus* F. Cuvier in Geoffroy Saint-Hilaire and Cuvier 1825: 3

*Arctaelurus* Gloger 1841: 55. Renaming of *Ailurus* Cuvier, 1825.

*Aelurus* Agassiz 1846: 9 [not *Aelurus* Klug 1842: 42]. Emendation of *Ailurus* Cuvier, 1825.

*Parailurus* Schlosser 1899: 73. Type species – *Ailurus anglicus* Dawkins 1888: 229, by monotypy.

*Ailurus* Cuvier, 1825 and *Parailurus* Schlosser, 1899 are monotypic genera (Roberts and Gittleman 1984, Kurtén and Anderson 1980). Schlosser (1899) and Tedford and Gustafson (1977) provided evidence that *Ailurus fulgens* Cuvier, 1825 and *Ailurus anglicus* Dawkins, 1888 are sister species. Thus I synonymize *Parailurus* Schlosser, 1899 with *Ailurus* Cuvier, 1825, in order to maintain the monophyly of the latter taxon and make the taxonomy more informative by reducing the number of monotypic genera.

**T y p e s p e c i e s** – *Ailurus fulgens* Cuvier, 1825 [*Ailurus Fulgens* F. Cuvier in Geoffroy Saint-Hilaire and Cuvier 1825: 3], by monotypy.

**D i a g n o s i s** (Fig. 7) – Mustelidans of Clade A, distinguished from all other taxa included in this clade by the derived enlargement of the  $P^4$  hypocone that is prominent and subequal in size to the protocone (Fig. 5: 15b). Supplementary autapomorphies of *Ailurus*, presumed to be developed in some other taxa of Clade A independently, include the following features: posterior border of the palate situated behind the posteriormost upper teeth (Fig. 2: 3b); meatal trough of ossified ectotympanic long, with its smallest mediolateral dimension greater than one-third of the bulla width (Fig. 2: 8c);  $P^1$  absent (Fig. 4: 12c);  $P^4$  protocone conical: not formed by the cingulum entirely (Fig. 5: 14b); anterior and posterior cingula of  $M^1$  continuous around the lingual base of the protocone (Fig. 5: 18b);  $M^2$  three-rooted and subequal in size to  $P^4$  (Fig. 5: 20b);  $P_1$  single-rooted or absent (Fig. 6: 21b, c); entoconid and entoconulid on  $M_1$  and  $M_2$  prominent, cusp-like (Fig. 6: 24d, 28b).

**D i s c u s s i o n** – The question of the affinities of *Ailurus* has been controversial since the discovery of the red panda. This genus has previously been considered an ursid or procyonid, grouped with *Ailuropoda* in their own family, or relegated to a monotypic family. Its phylogenetic relationships to other arctoids have recently been analyzed by Schmidt-Kittler (1981), Ginsburg (1982), Wozencraft (1989), Cirot (1992), and Wyss and Flynn (1993).

Schmidt-Kittler (1981: fig. 27) nested *Ailurus* within *Musteloidea* based on the absence of  $M_3$ , regarding this genus as a living descendant of a paraphyletic group of stem musteloids. Cirot (1992: fig. 126) followed this assignment.

Ginsburg (1982: fig. 12) recognized *Ailurus* as a member of *Ailuridae*, being a sister group to the taxon encompassing ursids, *Ailuropoda*, and otariids (including *Odobenus*). However, his evidence for this relationship included no synapomorphies (Flynn *et al.* 1988).

Wozencraft (1989: fig. 18.2) placed *Ailurus* together with *Ailuropoda* and living ursids in *Ursidae* and interpreted them as the sister family to *Otariidae* (including *Odobenus*). For the so-constituted *Ursoidea* he proposed 10 features as synapomorphies. As shown in appendix 18.1 to Wozencraft's paper, five of them also occur within his *Canoidea*, a sister taxon to the *Ursoidea*. Below I make comments on the remaining five features, coded by him as 4(1), 23(1), 29(1), 39(1), and 40(1+2). Feature 4(1), or "posterior width of palate nearly equal to width at canines", is, in fact, of widespread occurrence among Wozencraft's *Canoidea*. Feature 23(1), or "petrosal widely separated from basioccipital", though present in otariids, is also seen in phocids and *Potamotherium*, being rare in ursidans and absent in *Ailurus*. Feature 29(1), or "ectotympanic not inflated", is plausibly primitive for the caniforms; besides, this bone in the mephitine and lutrine mustelids is not more inflated than that of *Ailurus*. Feature 39(1), or "hypomastoid fossa present", applies to many of Wozencraft's *Canoidea* but not to *Ailurus*. Feature 40(1+2), or "inferior petrosal sinus large" to "very large": this sinus is also relatively large in some fossil mustelidans (e.g., *Stromeriella*) and in *Nasua* and *Potos*.

Wozencraft (1989) recorded nine features to support his hypothesis of the monophyly of *Ailurus*, *Ailuropoda*, and extant ursids. However, only four of them, coded 8(1), 11(1), 20(1), and 78(1), were interpreted by Wozencraft as exclusive of the so-constituted *Ursidae*. Feature 8(1), or "lacrimal vestigial, restricted to area around lacrimal foramen": indeed, within Wozencraft's *Ursidae* the lacrimal is variable not only in size and occurrence but also in shape, enclosing the lacrimal foramen or constituting only a part of its border, when present; in mustelidans, this bone may be relatively large, surrounding the lacrimal foramen (e.g., *Nasua*), as in canids, or it is vestigial or lacking (e.g. otariids, Wyss 1987: 16). Feature 11, or "inferior oblique muscle fossa widely separated from lacrimal foramen" (0) or "closely adjacent to lacrimal foramen" (1), is variable in both *Ailurus* and ursids. Feature 20(1), or "suprameatal fossa present, dorsal to external meatus": in many arctoids, including the disputed *Ursidae*, the suprameatal fossa is placed both dorsal and posterodorsal to the external meatus, which corresponds exactly to

Wozencraft's definition of feature 20(2), supposed by him to be exclusive of the procyonids. Feature 78(1), or "M<sup>2</sup> hypocone present", is seen also in *Broiliana*, being of variable occurrence in *Nasua* and *Procyon*.

Wyss and Flynn (1993: fig. 4.3) paired *Ailurus* into a sister-group relationship with *Ursida* (including pinnipeds) on the basis of five hypothesized synapomorphies, coded by these authors 12(0), 16(2 to 1), 22(1), 29(0), and 47(1). There is no doubt that feature 12(0), or "alisphenoid canal present", has independently been lost at least several times within the *Arctomorpha*; however, no carnivoran lineage has hitherto been demonstrated to evidence the regeneration of this primitive condition convincingly. Feature 16, or "posterior entrance of carotid artery into auditory capsule: 1 = posterior entry, artery enclosed in tube; 2 = anterior entry, artery enclosed in osseous tube": both these conditions occur among mustelidans (Table 1, character states 5a and 5b). Wyss and Flynn (1993) interpreted the occurrence of feature 29(0), or "major a4 arterial shunt absent", in their clades *Ailurus* plus *Ursida* and the mephitines plus lutrines as independent reversals; however, they provided no valid argument to support this statement. For comments on features 22(1), or "excavation in basioccipital accommodating inferior petrosal sinus large, excavation highly distinct", and 47(1), or "M<sup>2</sup> hypocone present", see discussion of Wozencraft's features 40(1+2) and 78(1), above.

Concluding, Wozencraft (1989) and Wyss and Flynn (1993) presented no unequivocal synapomorphy to warrant the rejection of Schmidt-Kittler's (1981) hypothesis that *Ailurus* is a mustelidan.

#### Genus *Amphictis* Pomel 1853: 99

*Ichneugales* Jourdan 1861: 1012. Nomen nudum.

*Ichneugales* Jourdan 1862: 132. Nomen nudum.

*Ichneugale* Jourdan in Filhol 1883: 69. Type species – *Viverra leptorhyncha* Filhol 1883: 67, by monotypy. Thenius (1949: 723) included "*Cephalogale*" *gaillardi* Wegner, 1913 in the synonymy of "*Viverra*" *leptorhyncha* Filhol, 1883. If *Ichneugale* Jourdan, 1883 were recognized, *Amphictis* Pomel, 1853 would be paraphyletic. Thus I synonymize the former with the latter name and thereby avoid a paraphyletic taxon.

*Alopecodon* Viret 1933: 9 [not *Alopecodon* Broom 1908: 361]. Type species – *Cephalogale Gaillardi* Wegner 1913: 226, by original designation.

*Viretius* Kretzoi, 1947: 286. Renaming of *Alopecodon* Viret, 1933.

*Alopecocyon* Viret 1951: 23. Renaming of *Alopecodon* Viret, 1933.

Type species – *Amphictis antiqua* Pomel, 1853 [*Amphictis antiquus* Pomel 1853: 99], by subsequent designation of Dehm (1950: 60).

Diagnosis – Mustelidans of Clade A, characterized by a combination of the following features: postorbital region shorter than broad (Fig. 1: 1a); sagittal crest present in adults, so that the dorsal cranial crests are Y-shaped (Fig. 1: 2a); posterior border of the palate situated behind the posteriormost upper teeth (autapomorphy; Figs 7 and 2: 3b); alisphenoid canal present (Fig. 2: 4a); posterior carotid foramen joined to the fossa leading to the posterior lacerate foramen (Fig. 2: 5a); posterior lacerate foramen smaller than the lateral opening of the external auditory meatus (Fig. 2: 6a); smallest width of the auditory bulla between the

stylomastoid foramen and fossa leading to the posterior lacerate foramen smaller than the greatest diameter of the stylomastoid foramen (Fig. 2: 7a); meatal trough of ossified ectotympanic not differentiated or short, with its smallest mediolateral dimension smaller than one-third of the bulla width (Fig. 2: 8a, b); anterior and lateral walls of the suprimeatal fossa neither excavated into the squamosal nor perpendicular to the roof of the external auditory meatus (Fig. 3: 9a);  $P^1$  two-rooted or single-rooted (Fig. 4: 12a, b);  $P^4$  carnassial notch present (Fig. 4: 13a);  $P^4$  protocone not differentiated or crescentic: completely formed by the cingulum (Fig. 5: 14a);  $P^4$  hypocone notably smaller than the protocone or absent (Fig. 5: 15a);  $M^1$  not smaller than  $P^4$  (Fig. 5: 16a);  $M^1$  crown with its lingual half shorter than the buccal half, and the anterior and posterior borders of the lingual half being not parallel to each other (Fig. 5: 17a); anterior and posterior cingula of  $M^1$  continuous around the lingual base of the protocone (autapomorphy; Figs 7 and 5: 18b); buccal border of the  $M^2$  crown positioned behind the buccal half of  $M^1$  (Fig. 5: 19a);  $M^2$  three-rooted or double-rooted, and distinctly smaller than  $P^4$  (Fig. 5: 20a, c);  $P_1$  single-rooted (autapomorphy; Figs 7 and 6: 21b);  $M_1$  trigonid less than three times as long as the talonid (Fig. 6: 22a);  $M_1$  metaconid distinctly higher than the paraconid (Fig. 6: 23a);  $M_1$  entoconid and entoconulid poorly differentiated (ridge-like or cuspule-like), and the anterior and posterior halves of the lingual wall of the  $M_1$  talonid subequal in height to each other (Fig. 6: 24a);  $M_2$  double-rooted (Fig. 6: 25a);  $M_2$  metaconid present (Fig. 6: 26a); talonid basin of  $M_2$  distinctly longer than the trigonid basin (Fig. 6: 27a);  $M_2$  entoconid and entoconulid poorly developed (ridge-like or cuspule-like) or not differentiated (Fig. 6: 28a).

**D i s c u s s i o n** – This genus has variously been referred to the viverrids (e.g., Pomel 1853), miacids (Pohle 1920), canids (e.g., Ginsburg 1961), amphicyonids (Ginsburg 1966), mustelids (e.g., de Bonis 1973), and procyonids (e.g., Roth 1987). Winge (1895) erected a new family with *Amphictis* as its type genus. De Bonis (1976) suggested that this genus was a representative of the ancestral stock of both the procyonids and mustelids. The phylogenetic arrangements of Schmidt-Kittler (1981: fig. 27) and Cirot (1992: fig. 126) nested *Amphictis* within *Musteloidea* (loss of  $M_3$ ) as one of the earliest offshoots from the main stem.

#### Genus *Bavarictis* Mödden 1991: 128

**T y p e s p e c i e s** – *Bavarictis gaimersheimensis* Mödden 1991: 129, by original designation.

**D i a g n o s i s** – Mustelidans of Clade A, distinguished by a combination of the following features: postorbital region shorter than wide (Fig. 1: 1a); sagittal crest present in adults: the dorsal cranial crests Y-shaped (Fig. 1: 2a); posterior border of the palate situated at level of the posteriormost upper teeth (Fig. 2: 3a); alisphenoid canal present (Fig. 2: 4a); posterior carotid foramen joined to the fossa leading to the posterior lacerate foramen (Fig. 2: 5a); posterior lacerate foramen smaller than the lateral opening of the external auditory meatus (Fig. 2: 6a);



smallest width of the auditory bulla between the stylomastoid foramen and fossa leading to the posterior lacerate foramen smaller than the greatest diameter of the stylomastoid foramen (Fig. 2: 7a); meatal trough of ossified ectotympanic short, with its smallest mediolateral dimension smaller than one-third of the bulla width (autapomorphy; Figs 7 and 2: 8b); anterior and lateral walls of the suprameatal fossa neither excavated into the squamosal nor perpendicular to the roof of the external auditory meatus (Fig. 3: 9a); postlateral sulcus of the brain absent (Fig. 4: 11a);  $P^1$  single-rooted (autapomorphy; Figs 7 and 4: 12b);  $P^4$  carnassial notch present (Fig. 4: 13a);  $P^4$  protocone conical: not formed by the cingulum entirely (autapomorphy; Figs 7 and 5: 14b);  $P^4$  hypocone absent (Fig. 5: 15a);  $M^1$  smaller than  $P^4$  (autapomorphy; Figs 7 and 5: 16b);  $M^1$  crown with its lingual half shorter than the buccal half, and the anterior and posterior borders of the lingual half being not parallel to each other (Fig. 5: 17a); anterior and posterior cingula of  $M^1$  continuous around the lingual base of the protocone (autapomorphy; Figs 7 and 5: 18b); buccal border of the  $M^2$  crown located behind the buccal half of  $M^1$  (Fig. 5: 19a);  $M^2$  having three or two roots and being distinctly smaller than  $P^4$  (Fig. 5: 20a, c);  $P_1$  single-rooted (autapomorphy; Figs 7 and 6: 21b);  $M_1$  trigonid less than three times as long as the talonid (Fig. 6: 22a);  $M_1$  metaconid distinctly higher than the paraconid (Fig. 6: 23a);  $M_1$  entoconid and entoconulid poorly differentiated (ridge-like or cuspule-like) or not differentiated, and the anterior half of the lingual wall of the  $M_1$  talonid distinctly lower than the posterior half (autapomorphy; Figs 7 and 6: 24b);  $M_2$  double-rooted (Fig. 6: 25a);  $M_2$  metaconid present (Fig. 6: 26a); talonid and trigonid basins of  $M_2$  subequal in length (autapomorphy; Figs 7 and 6: 27b);  $M_2$  entoconid and entoconulid not differentiated (Fig. 6: 28a).

**D i s c u s s i o n** – Mödden (1991) followed Schmidt-Kittler (1981), who placed this genus in a paraphyletic stem group of *Musteloidea*.

#### Order-group Taxon *Pinnipedia* Illiger 1811: 138

(ranked between category of Clade A and superfamily)

**D e f i n i t i o n** – The most recent common ancestral species of otariids, odobenids, and phocids, plus all of its descendants.

**D i a g n o s i s** (Fig. 7) – Mustelidans of Clade A, differing from all other taxa included in this clade in the derived displacement of  $M^2$  linguad (subsequently lost), making the buccal border of its crown positioned behind the lingual half of  $M^1$  (Fig. 5: 19b). Supplementary synapomorphies of the *Pinnipedia*, assumed to be developed in some other taxa of Clade A independently, include the following features: posterior lacerate foramen greatly enlarged, so that it is greater than the lateral opening of the external auditory meatus (Fig. 2: 6b); smallest width of the auditory bulla between the stylomastoid foramen and fossa leading to the posterior lacerate foramen greater than the greatest diameter of the stylomastoid foramen, and the posterior border of the caudal entotympanic situated in front of that of the fossa leading to the posterior lacerate foramen (Fig. 2: 7b);  $P^1$  and  $P_1$

single-rooted (Figs 4: 12b, 6: 21b); M<sub>2</sub> talonid and trigonid basins subequal in length (Fig. 6: 27b).

**D i s c u s s i o n** – The controversy over pinniped origin(s) and relationships has extensively been discussed elsewhere (Wyss 1987, Flynn *et al.* 1988, Wozencraft 1989). The present paper provides a new support for the monophyly of this group, including it within the *Mustelida* based on the absence of M<sub>3</sub> shared by all pinnipeds.

Among carnivorans, M<sup>2</sup> with its buccal margin located behind the lingual half of M<sup>1</sup> (Fig. 5: 19b) is exclusive of *Kolponomos* (Stirton 1960: fig. 3), or an enigmatic arctomorph of the earliest Miocene (Tedford *et al.* 1991); *Amphicticeps* (Matthew and Granger 1924: fig. 4), or a Late Oligocene arctomorph of elusive affinities (Schmidt-Kittler 1981); the enaliarctine otariids *Enaliarctos* (Mitchell and Tedford 1973: fig. 5A) and *Pteronarctos* (Barnes 1989: fig. 5); and *Potamotherium* (Savage 1957: pl. 1/a). This lingual displacement of M<sup>2</sup> is evidently associated with a different pattern of posterior reduction in the tooth row as compared to that of other carnivorans. No pinniped is known to show the alternative state (Fig. 5: 19a). It seems therefore that the hypothesis considering the lingual position of M<sup>2</sup> to be synapomorphic for the *Pinnipedia* has sufficiently strong basis to be put forward in spite of the fact that most pinnipeds lack M<sup>2</sup>.

#### Genus *Potamotherium* Geoffroy Saint-Hilaire, 1833

*potamotherium* Geoffroy Saint-Hilaire 1833: 80 [not *Potamotherium* Gloger 1841: 127].

*Lutricitis* Pomel 1847: 380. Type species – *lutra valletoni* Geoffroy Saint-Hilaire 1833: 80, by monotypy.

*Stephanodon* von Meyer 1847: 183. Type species – *Stephanodon Mombachensis* von Meyer 1847: 183, by monotypy. Synonymized with *Potamotherium* Geoffroy Saint-Hilaire, 1833 by Gervais (1852, p. 11 in explanations to pls XXVI–XXVIII).

*Potamophilus* Gervais 1852: 2nd unnumbered page in explanations to pl. XXII [not *Potamophilus* Germar 1811: 41; not *Potamophilus* Latreille in Desmarest 1826: 97; not *Potamophilus* Muller 1838: 140]. Type species – *lutra valletoni* Geoffroy Saint-Hilaire 1833: 80, by monotypy.

**T y p e s p e c i e s** – *Potamotherium valletoni* (Geoffroy Saint-Hilaire, 1833) [*lutra valletoni* Geoffroy Saint-Hilaire 1833: 80], by monotypy.

**D i a g n o s i s** – Pinnipeds distinguished from other members of the *Pinnipedia* by a combination of the following features: postorbital region greatly elongated in adults, longer than its greatest width (Fig. 1: 1b); posterior border of the palate situated behind the posteriormost upper teeth (Fig. 2: 3b); alisphenoid canal absent (Fig. 2: 4b); meatal trough of ossified ectotympanic long, with its smallest mediolateral dimension greater than one-third of the bulla width (Fig. 2: 8c); suprameatal fossa absent (Fig. 3: 9b); M<sup>1</sup> smaller than P<sup>4</sup> (Fig. 5: 16b); M<sup>1</sup> crown broader buccolingually than long anteroposteriorly, with its lingual and buccal halves subequal in length to each other (autapomorphy; Figs 7 and 5: 17d); M<sup>2</sup> single-rooted (Fig. 5: 20d); M<sub>1</sub> metaconid higher than or subequal to the paraconid (Fig. 6: 23a, b); anterior half of the lingual wall of the M<sub>1</sub> talonid distinctly lower than the posterior half (Fig. 6: 24b); M<sub>2</sub> single-rooted (Fig. 6: 25b); M<sub>2</sub> metaconid present (Fig. 6: 26a).

**D i s c u s s i o n** – Most earlier students of *Potamotherium* grouped the genus with lutrines, although some of them (e.g., Savage 1957) paid attention to its morphological similarities to phocids. These resemblances induced Tedford (1976) to transfer this genus to the *Phocidae*. Schmidt-Kittler (1981) also excluded *Potamotherium* from the lutrines, based on the absence of the suprimeatal fossa in the former; however, though he identified the corresponding arrangement in the auditory region of *Phoca*, he recognized *Potamotherium* as a separate offshoot of the musteloid stem group. The present paper supports the unique common ancestry of *Potamotherium* and phocids, as distinguished from all other pinnipeds by the derived loss of the alisphenoid canal.

#### Family *Procyonidae* Gray 1825: 339

**D e f i n i t i o n** – The most recent common ancestral species of *Bassaricyon*, *Nasua*, *Nasuella*, *Potos*, and *Procyon*, and all of its descendants.

**D i a g n o s i s** (Fig. 7) – Mustelidans of Clade A, distinguished from all other taxa included in this clade by the derived configuration of the suprimeatal fossa the ventral extension of the medial wall of which is subequal to that of the lateral wall and at least its anterior or lateral wall is perpendicular to the roof of the external auditory meatus or excavated into the squamosal (Fig. 3: 9c). Supplementary synapomorphies of the *Procyonidae*, presumed to be developed in some other taxa of Clade A independently, include the following features: posterior carotid foramen separated from the fossa leading to the posterior lacerate foramen (Fig. 2: 5b); smallest width of the auditory bulla between the stylomastoid foramen and fossa leading to the posterior lacerate foramen greater than the greatest diameter of the stylomastoid foramen, and the posterior border of the caudal entotympanic situated in front of that of the fossa leading to the posterior lacerate foramen (Fig. 2: 7b).

**D i s c u s s i o n** – After the description of the suprimeatal fossa in *Procyon*, *Potos*, and *Bassariscus* by Segall (1943), this structure was often employed, especially recently, to diagnose the *Procyonidae*. At first, the presence of the fossa was regarded as characteristic of this family (e.g., Hough 1948); later, its deepness in procyonids was contrasted with the shallowness seen in many other arctomorphs (e.g., Schmidt-Kittler 1981). The present paper provides another attempt to define states of this character (Fig. 3: 9a–e), to use them at distinguishing the major mustelidan clades. According to these definitions, the procyonids are the only arctoids that possess state 9c.

Numerous other features of the skull and dentition have recently been proposed to support the monophyletic status of the procyonids (Baskin 1982, 1989, Ginsburg 1982, Cirot 1988, 1992, Flynn *et al.* 1988, Wozencraft 1989, Decker and Wozencraft 1991, Wyss and Flynn 1993). All of them, however, also occur within the non-procyonid *Mustelida* and seem to be, therefore, of less relevance to the question of the relationship advocated here.

Genus *Pseudobassaris* Pohle 1917: 408

**T y p e s p e c i e s** – *Pseudobassaris riggsi* Pohle 1917: 409, by original designation.

**D i a g n o s i s** (Fig. 7) – Procyonids differing from all other *Procyonidae* in the retention of the alisphenoid canal (Fig. 2: 4a) and in the autapomorphically developed  $M_1$ , in which the entoconid and entoconulid are poorly differentiated (ridge-like or cuspule-like) or not differentiated and the anterior half of the lingual wall of the talonid is distinctly lower than the posterior half (Fig. 6: 24b). Supplementary autapomorphies of *Pseudobassaris*, derived by some other procyonids independently, include the following features:  $P^1$  and  $P_1$  single-rooted (Figs 4: 12b, 6: 21b);  $P^4$  protocone conical: not formed by the cingulum entirely (Fig. 5: 14b).

**D i s c u s s i o n** – Pohle (1917) described this genus as a procyonid, mainly because of its believed resemblance to *Bassariscus*. Subsequent systematists consistently doubted this placement (e.g., Simpson 1945: 226). Hough (1948) included *Pseudobassaris* in *Plesictis* while Schmidt-Kittler (1981) synonymized it with *Mustelictis*. Mödden (1991) pointed out that the suprameatal fossa in *Pseudobassaris* is deep, whereas that of *Mustelictis* is shallow, and treated both the genera separately; however, he did not suggest their relationships. I follow the original allocation of *Pseudobassaris* to the *Procyonidae* because this genus shares the unique synapomorphy of the family.

## Clade B

(taxon unnamed, ranked between family and genus)

**D i a g n o s i s** (Fig. 7) – Procyonids differing from all other *Procyonidae* in the following derived features: alisphenoid canal absent (Fig. 2: 4b);  $M_1$  entoconid prominent (cusp-like) while  $M_1$  entoconulid poorly developed (ridge-like or cuspule-like) or not differentiated (Fig. 6: 24c).

*Angustictis*, new genus

**T y p e s p e c i e s** – *Angustictis mayri* (Dehm, 1950) [*Plesictis mayri* Dehm 1950: 46].

**E t y m o l o g y** – Latin *angustus*, narrow, and *ictis* (Greek ἰκτίς), weasel-like carnivorous animal; in allusion to great transverse elongation of the upper molars; feminine in gender.

**D i a g n o s i s** – Procyonids of Clade B, distinguished by a combination of the following features: posterior border of the palate situated at level of the posterior-most upper teeth (Fig. 2: 3a);  $P^1$  single-rooted (autapomorphy; Figs 7 and 4: 12b);  $P^4$  protocone conical: not formed by the cingulum entirely (autapomorphy; Figs 7 and 5: 14b);  $P^4$  hypocone absent (Fig. 5: 15a); anterior and posterior cingula of  $M^1$  continuous around the lingual base of the protocone (Fig. 5: 18b);  $M^2$  two-rooted (autapomorphy; Figs 7 and 5: 20c).

*Angustictis* gen. n. differs from *Broiliana* in the following features: P<sup>1</sup> single-rooted; P<sup>4</sup> protocone wing proportionally smaller; M<sup>1</sup> shorter relative to its width; M<sup>1</sup> parastyle wing better developed while M<sup>1</sup> metacone wing less well developed; metaconule on M<sup>1</sup> vestigial or absent; M<sup>1</sup> hypocone not differentiated; M<sup>2</sup> smaller relative to M<sup>1</sup> and P<sup>4</sup>, double-rooted, with a less complicated occlusal pattern; M<sub>2</sub> smaller relative to M<sub>1</sub>.

#### Genus *Broiliana* Dehm 1950: 80

Type species – *Broiliana nobilis* Dehm 1950: 81, by original designation.

Diagnosis – Procyonids of Clade B, characterized by a combination of the following features: posterior border of the palate situated at level of the posterior-most upper teeth (Fig. 2: 3a); meatal trough of ossified ectotympanic not differentiated (Fig. 2: 8a); P<sup>1</sup> two-rooted (Fig. 4: 12a); P<sup>4</sup> hypocone considerably smaller than the protocone or not differentiated (Fig. 5: 15a); anterior and posterior cingula of M<sup>1</sup> continuous around the lingual base of the protocone (Fig. 5: 18b); M<sup>2</sup> three-rooted and distinctly smaller than P<sup>4</sup> (Fig. 5: 20a); M<sub>1</sub> metaconid distinctly higher than the paraconid (Fig. 6: 23a).

*Broiliana* differs from *Angustictis* gen. n. in the following features: P<sup>1</sup> double-rooted; P<sup>4</sup> protocone wing proportionally larger; M<sup>1</sup> longer relative to its width; M<sup>1</sup> parastyle wing less well developed while M<sup>1</sup> metacone wing better developed; metaconule and hypocone on M<sup>1</sup> prominent; M<sup>2</sup> larger relative to M<sup>1</sup> and P<sup>4</sup>, three-rooted, with a more complicated occlusal pattern; M<sub>2</sub> larger relative to M<sub>1</sub>.

Discussion – *Broiliana* was originally classified by Dehm (1950) as a meline mustelid in its own tribe. De Beaumont (1964) rose this tribe to the subfamily level within the *Mustelidae*, and later (1968) moved it to the *Procyonidae* on the basis of morphological similarities in the auditory region. The incorporation of *Broiliana* in the procyonids has been followed by most subsequent students of this genus.

#### Family *Mustelidae* Fischer von Waldheim 1817: 372

Definition – The most recent common ancestral species of *Bassariscus*, mephitines, lutrines, melines, and mustelines (including mellivorines), and all of its descendants.

Diagnosis (Fig. 7) – Mustelidans of Clade A, differing from all other taxa included in this clade in the derived configuration of the suprimeatal fossa the medial wall of which is absent or its ventral extension is considerably smaller than that of the lateral wall and at least its anterior or lateral wall is perpendicular to the roof of the external auditory meatus or excavated into the squamosal (Fig. 3: 9d). The single-rooted P<sup>1</sup> and P<sub>1</sub> (Figs 4: 12b, 6: 21b) are supplementary synapomorphies of the *Mustelidae*, presumed to be developed in some other taxa of Clade A independently.

Discussion – Several features have been employed to support the monophyly of the *Mustelidae* (Tedford 1976, Schmidt-Kittler 1981, Qiu and Schmidt-

-Kittler 1982, de Muizon 1982, Cirot 1988, 1992, Flynn *et al.* 1988, Wozencraft 1989, Wyss and Flynn 1993); however, their synapomorphic status has been questioned, directly or indirectly, by other investigators (Schmidt-Kittler 1981, Wiig 1983, Wyss 1987, Wozencraft 1989, Wyss and Flynn 1993). I discuss below two of these features, the notchless shearing blade of P<sup>4</sup> (Wortman 1901) and the ventrally closed suprameatal fossa (Schmidt-Kittler 1981), because they seem to be best founded. The former feature has generally been accepted as the unquestionable synapomorphy of the mustelids; no objective argument has hitherto been presented contrary to the latter feature.

The carnassial notch on P<sup>4</sup> has independently been lost at least four times during mustelid evolution: within the *Mephitinae*, as evidenced by its retention in *Miomephitis* and *Palaeomephitis* (= *Trochotherium*) of the European Miocene and in *Mydaus* (= *Suillotaxus*); within the *Lutrinae*, as indicated by its occurrence in *Enhydra*; among leptarctines (Qiu and Schmidt-Kittler 1982); and in the mustelines. Thus this feature cannot be regarded as a synapomorphy of the *Mustelidae*.

The suprameatal fossa that is partially or completely closed anteriorly by the posterior wall of auditory tube is exclusive of the mustelines, lutrines, melines, and leptarctines (Schmidt-Kittler 1981, Qiu and Schmidt-Kittler 1982). Even if the mustelines, lutrines, and melines indeed constitute the monophyletic grouping as suggested by Schmidt-Kittler (1981, 1984) and Qiu and Schmidt-Kittler (1982), the sister-group relationship of the so-constituted clade with the *Leptarctinae* appears to be uncertain. On the other hand, the disputed feature excludes from the *Mustelidae* a number of genera that are plausibly related to the ancestors of both leptarctines and modern mustelids, leaving them within a paraphyletic assemblage. It seems, therefore, to be sufficiently warranted to rediagnose this family, with the 9d suprameatal fossa (Fig. 3) as the major synapomorphy, especially insofar as this feature is evidently uniquely derived within the *Caniformia*.

#### Genus *Mustelictis* Lange 1969: 2870

**Type species** – *Mustelictis piveteaui* Lange 1969: 2870, by monotypy.

**Diagnosis** (Fig. 7) – Mustelids of a paraphyletic group that differs from all other *Mustelidae* in retaining the following plesiomorphies: the alisphenoid canal present (Fig. 2: 4a), the smallest width of the auditory bulla between the stylomastoid foramen and fossa leading to the posterior lacerate foramen smaller than the greatest diameter of the stylomastoid foramen (Fig. 2: 7a), and the meatal trough of ossified ectotympanic not differentiated (Fig. 2: 8a); distinguished from other taxa of this paraphyletic group by the following autapomorphies: P<sup>4</sup> protocone conical, not formed by the cingulum entirely (Fig. 5: 14b); talonid and trigonid basins of M<sub>2</sub> subequal in length (Fig. 6: 27b).

**Discussion** – Lange (1969, 1970) recognized *Mustelictis* as a musteline. Schmidt-Kittler (1981) and Cirot (1992) considered it as an early musteloid offshoot of the ancestral stock of procyonids and mustelids.

## Clade C

(taxon unnamed, ranked between family and higher of categories  
of Clades D and E)

**D i a g n o s i s** (Fig. 7) – Mustelids distinguished from all other *Mustelidae* by the following derived features: alisphenoid canal absent (Fig. 2: 4b); smallest width of the auditory bulla between the stylomastoid foramen and fossa leading to the posterior lacerate foramen greater than the greatest diameter of the stylomastoid foramen, and the posterior border of the caudal entotympanic situated in front of that of the fossa leading to the posterior lacerate foramen (Fig. 2: 7b); meatal trough of ossified ectotympanic short, with its smallest mediolateral dimension smaller than one-third of the bulla width (Fig. 2: 8b).

## Clade D

(taxon unnamed, ranked between category of Clade C and genus)

**D i a g n o s i s** (Fig. 7) – Mustelids of Clade C, belonging to a paraphyletic group that differs from all other taxa included in Clade C in having the following features: posterior border of the palate situated at level of the posteriormost upper teeth (Fig. 2: 3a);  $M^2$  with three to two roots (Fig. 5: 20a, c);  $M_1$  metaconid distinctly higher than the paraconid (Fig. 6: 23a); anterior and posterior halves of the lingual wall of the  $M_1$  talonid subequal in height to each other (Fig. 6: 24a). The derived creation of the postlateral sulcus on the brain (Fig. 4: 11b) distinguishes members of Clade D from all other taxa of this paraphyletic group.

*Franconictis*, new genus

**T y p e s p e c i e s** – *Franconictis humilidens* (Dehm, 1950) [*Plesictis? humilidens* Dehm 1950: 54].

**E t y m o l o g y** – After the medieval duchy Franconia, including the area from where the type species of the genus was described; Latin *ictis* (Greek ἰκτίς), weasel-like carnivorous animal; feminine in gender.

**D i a g n o s i s** (Fig. 7) – Mustelids of Clade D, distinguished from other representatives of this clade by the following autapomorphies:  $P^4$  protocone conical, not formed by the cingulum entirely (Fig. 5: 14b);  $M^2$  two-rooted (Fig. 5: 20c);  $M_2$  talonid and trigonid basins subequal in length (Fig. 6: 27b).

*Franconictis* gen. n. differs from *Stromeriella* in the following features: infraorbital foramina relatively smaller; braincase about as high as the occiput; auditory bullae less well inflated and subtriangular in outline, with a better developed meatal tube; caudal entotympanic expanded posteriorad less extensively (Fig. 2: 7b); medial wall of the suprimeatal fossa less well developed; lateral extension of the anterior part of the epitympanic recess into squamosal less extensive while its dorsal excavation into petrosal wider;  $P^4$  protocone wing proportionally smaller, with a conical protocone (Fig. 5: 14b);  $M^1$  shorter relative to its width;  $M^1$  parastyle

wing better developed while  $M^1$  metacone wing less well developed;  $M^2$  smaller relative to  $M^1$  and  $P^4$ , double-rooted, with a less complicated occlusal pattern;  $M_1$  talonid smaller relative to the trigonid; talonid basin of  $M_2$  about equal in length to the trigonid basin (Fig. 6: 27b).

#### Genus *Stromeriella* Dehm 1950: 99

**Type species** – *Stromeriella franconica* Dehm 1950: 100, by original designation.

**Diagnosis** (Fig. 7) – Mustelids of Clade D, distinguished from other members of this clade by the autapomorphically expanded caudal entotympanic that terminates posteriorly behind the fossa leading to the posterior lacerate foramen (Fig. 2: 7c).

*Stromeriella* differs from *Franconictis* gen. n. in the following features: infra-orbital foramina relatively larger; braincase distinctly higher than the occiput; auditory bullae better inflated and subellipsoidal in outline, with a less well developed meatal tube; caudal entotympanic expanded posteriorad more extensively (Fig. 2: 7c); medial wall of the suprameatal fossa better developed; lateral excavation of the anterior part of the epitympanic recess into squamosal more spacious while its dorsal extension into petrosal less extensive;  $P^4$  protocone wing proportionally larger, with a crescentic protocone (Fig. 5: 14a);  $M^1$  longer relative to its width;  $M^1$  parastyle wing less well developed while  $M^1$  metacone wing better developed;  $M^2$  larger relative to  $M^1$  and  $P^4$ , three-rooted, with a more complicated occlusal pattern;  $M_1$  talonid larger relative to the trigonid; talonid basin of  $M_2$  distinctly longer than the trigonid basin (Fig. 6: 27a).

**Discussion** – Dehm (1950) allied *Stromeriella* with *Broiliana* and placed them among melines. De Beaumont (1964) excluded these genera from the *Melinae*, and later (1968) concluded that they are procyonids based on the comparison of their auditory regions with that of *Bassariscus*. Most subsequent authors have accepted the inclusion of *Stromeriella* in the *Procyonidae*. The present paper, however, unites this genus with the *Mustelidae*, principally because of the condition of the suprameatal fossa.

#### Clade E

(taxon unnamed, ranked between categories of Clades C and F)

**Diagnosis** (Fig. 7) – Mustelids of Clade C, differing from all other taxa included in this clade in the following derived features: strong parasagittal crests present in adults, so that the dorsal cranial crests are parallel to X-shaped (Fig. 1: 2b); posterior border of the palate situated behind the posteriormost upper teeth (Fig. 2: 3b);  $M^2$  single-rooted (Fig. 5: 20d);  $M_1$  metaconid subequal in height to the paraconid (Fig. 6: 23b); anterior half of the lingual wall of the  $M_1$  talonid distinctly lower than the posterior half (Fig. 6: 24b);  $M_2$  talonid and trigonid basins subequal in length (Fig. 6: 27b).



*Bathygale*, new genus

**Type species** – *Bathygale lemanensis* (Pomel, 1853) [*Plesictis lemanensis* Pomel 1853: 97].

**Etymology** – Greek βαθύς, deep, and γαλέη or γαλή, small carnivorous animal; in reference to great dorsal extension of the epitympanic recess; feminine in gender.

**Diagnosis** – Mustelids of Clade E, distinguished by a combination of the following features: posterior carotid foramen separated from the fossa leading to the posterior lacerate foramen (Fig. 2: 5b); absence of the postlateral sulcus on the brain surface (Fig. 4: 11a); P<sup>4</sup> carnassial notch present (Fig. 4: 13a); P<sup>4</sup> protocone conical: not formed by the cingulum entirely (Fig. 5: 14b); P<sup>4</sup> hypocone absent (Fig. 5: 15a); M<sup>1</sup> not smaller than P<sup>4</sup> (Fig. 5: 16a); lingual half of the M<sup>1</sup> crown shorter than the buccal half, and the anterior and posterior borders of the lingual half not parallel to each other (Fig. 5: 17a); M<sup>2</sup> absent (autapomorphy; Figs 7 and 5: 20e); M<sub>2</sub> metaconid present (Fig. 6: 26a).

*Bathygale* gen. n. differs from *Plesictis* in the following features: anterior and posterior margins of the lingual half of M<sup>1</sup> not parallel to each other, and the posterolingual portion of the M<sup>1</sup> cingulum better developed than the anterolingual one (Fig. 5: 17a); auditory bullae better inflated (autapomorphy) and less compressed mediolaterally; anterior part of the epitympanic recess expanded dorsad into the petrosal more extensively (autapomorphy).

## Clade F

(taxon unnamed, ranked between category of Clade E and subfamily)

**Diagnosis** (Fig. 7) – Mustelids of Clade E, differing from all other taxa included in this clade by the derived configuration of M<sup>1</sup>, in which the lingual half of the crown is shorter than the buccal half, and the anterior and posterior borders of the lingual half are parallel to each other (Fig. 5: 17b).

Genus *Plesictis* Pomel 1846b: 366

*Plesictis* Pomel 1846a: 199. Nomen nudum.

**Type species** – *Plesictis plesictis* (de Laizer and de Parieu, 1839) [*Martes plesictis* de Laizer and de Parieu in Anonymous 1839: 43], by monotypy.

**Diagnosis** – Mustelids of Clade F, distinguished by a combination of the following features: postlateral sulcus of the brain absent (Fig. 4: 11a); P<sup>4</sup> carnassial notch present (Fig. 4: 13a); P<sup>4</sup> protocone conical: not formed by the cingulum entirely (Fig. 5: 14b); P<sup>4</sup> hypocone absent (Fig. 5: 15a); M<sup>1</sup> not smaller than P<sup>4</sup> (Fig. 5: 16a); M<sub>2</sub> metaconid present (Fig. 6: 26a).

*Plesictis* differs from *Bathygale* gen. n. in the following features: anterior and posterior borders of the lingual half of M<sup>1</sup> parallel to each other, and the anterolingual and posterolingual portions of the cingulum subequal to each other in development (Fig. 5: 17b); auditory bullae more compressed mediolaterally (autapomorphy) and

less well inflated; anterior part of the epitympanic recess excavated dorsad into the petrosal less extensively.

**D i s c u s s i o n** – The earliest students of *Plesictis* (e.g., Pomel 1853) regarded it as a viverrid, but most later authors associated this genus with mustelids. Hough (1948) was the first to suggest placement of *Plesictis* in the *Procyonidae* because of a deep suprimeatal fossa. Although some subsequent workers, particularly in recent years (e.g., Roth 1987), have followed this assignment, others did not accept it (e.g., Lavocat 1952).

#### Subfamily *Mustelinae* Fischer von Waldheim 1817: 372

**D e f i n i t i o n** – The most recent common ancestral species of *Eira*, *Galictis*, *Gulo*, *Ictonyx*, *Lyncodon*, *Martes*, *Mellivora*, *Mustela*, *Poecilictis*, *Poecilogale*, and *Vormela* and all of its descendants.

**D i a g n o s i s** (Fig. 7) – Mustelids of Clade F, differing from all other taxa included in this clade by the following derived features: sagittal crest present in adults, so that the dorsal cranial crests are Y-shaped (reversal; Fig. 1: 2a); posterior border of the caudal entotympanic situated behind that of the fossa leading to the posterior lacerate foramen (Fig. 2: 7c); lateral part of the suprimeatal fossa partially closed by the posterior wall of the meatal tube anteriorly (Fig. 3: 9e); postlateral sulcus of the brain present (Fig. 4: 11b); P<sup>4</sup> carnassial notch absent (Fig. 4: 13b); M<sup>1</sup> smaller than P<sup>4</sup> (Fig. 5: 16b); lingual half of the M<sup>1</sup> crown about equal in length to or longer than the buccal one, and both the halves separated from each other by an anteroposterior constriction (Fig. 5: 17c); M<sub>1</sub> metaconid distinctly lower than the paraconid (Fig. 6: 23c). Supplementary synapomorphies of the *Mustelinae*, evolved in some other taxa of Clade F independently, include the following features: M<sup>2</sup> absent (Fig. 5: 20e); M<sub>1</sub> trigonid more than three times as long as the talonid (Fig. 6: 22b); M<sub>2</sub> single-rooted (Fig. 6: 25b).

#### Genus *Paragale* Petter 1967: 19

**T y p e s p e c i e s** – *Paragale huerzeleri* Petter, 1967 [*Paragale hürzeleri* Petter 1967: 19], by monotypy.

**D i a g n o s i s** (Fig. 7) – Mustelines differing from all other *Mustelinae* except *Plesiogale* in the retention of the suprimeatal fossa that is only partially closed by the posterior wall of the meatal tube anteriorly (Fig. 3: 9e); characterized by the autapomorphically elongated meatal trough of ossified ectotympanic, making its smallest mediolateral dimension greater than one-third of the bulla width (Fig. 2: 8c), and the plesiomorphically retained metaconid on M<sub>2</sub> (Fig. 6: 26a).

**D i s c u s s i o n** – Petter (1967) described *Paragale* as a mustelid, and de Muizon (1982) affiliated it to the *Mustelinae*.

#### Genus *Plesiogale* Pomel 1847: 380

**T y p e s p e c i e s** – *Plesiogale angustifrons* Pomel 1847: 385, by monotypy.

**D i a g n o s i s** (Fig. 7) – Mustelines differing from all other *Mustelinae* in M<sup>1</sup> the trigon of which is plesiomorphically longer than the talon, and from all other

mustelines but not *Paragale* in the retention of the suprameatal fossa that is only partially closed by the posterior wall of the meatal tube anteriorly (Fig. 3: 9e); distinguished by the autapomorphically lost P<sub>1</sub> (Fig. 6: 21c) and metaconid on both M<sub>1</sub> and M<sub>2</sub> (Fig. 6: 23d, 26b).

**D i s c u s s i o n** – This genus, though confused with *Palaeogale* during almost the half of its taxonomic history (Simpson 1946), has consistently been classified in the *Mustelidae*, being usually assigned to the mustelines.

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## References

- Agassiz L. 1846. Nomenclatoris zoologici. Index universalis, continens nomina systematica classium, ordinum, familiarum et generum animalium omnium, tam viventium quam fossilium, secundum ordinem alphabeticum unicum disposita, adjectis homonymiis plantarum, nec non variis adnotationibus et emendationibus. Jent et Gassmann, Solothurn: I – VIII + 1 – 393.
- Anonymous 1839. Marte fossile. L'Écho du Monde Savant 5: 42 – 43.
- Barnes L. G. 1989. A new enaliarctine pinniped from the Astoria Formation, Oregon, and a classification of the *Otariidae* (Mammalia: Carnivora). Contr. Sci. nat. Hist. Mus. Los Angeles County 403: 1 – 26.
- Baskin J. A. 1982. Tertiary *Procyoninae* (Mammalia: Carnivora) of North America. J. Vertebr. Paleont. 2: 71 – 93.
- Baskin J. A. 1989. Comments on New World Tertiary *Procyonidae* (Mammalia: Carnivora). J. Vertebr. Paleont. 9: 110 – 117.
- Beaumont G. de 1964. Essai sur la position taxonomique des genres *Alopecocyon* Viret et *Simocyon* Wagner (Carnivora). Eclog. geol. Helv. 57: 829 – 836.
- Beaumont G. de 1965. Contribution à l'étude du genre *Cephalogale* Jourdan (Carnivora). Schweiz. paläont. Abh. 82: 1 – 34.
- Beaumont G. de 1968. Note sur la région auditive de quelques Carnivores. Arch. Sci., Genève 21: 213 – 223.
- Bonis L. de 1973. Contribution à l'étude des Mammifères de l'Aquitainien de l'Agenais. Rongeurs – Carnivores – Périssodactyles. Mém. Mus. natn. Hist. nat., Paris, N. Sér. (C) 28: 1 – 192.
- Bonis L. de 1976. Découverte d'un crâne d'*Amphictis* (Mammalia, Carnivora) dans l'Oligocène supérieur des Phosphorites du Quercy (Lot). C. R. Séanc. Acad. Sci., Paris (D) 283: 327 – 330.
- Bowdich T. E. 1821. An analysis of the natural classifications of *Mammalia*, for the use of students and travellers. J. Smith, Paris: 1 – 115.
- Broom R. 1908. On some new Therocephalian reptiles. Ann. S. Afr. Mus. 4: 361 – 367.
- Bryant H. N. 1989. An evaluation of cladistic and character analyses as hypothetico-deductive procedures, and the consequences for character weighting. Syst. Zool. 38: 214 – 227.
- Bryant H. N. 1991. The polarization of character transformations in phylogenetic systematics: role of axiomatic and auxiliary assumptions. Syst. Zool. 40: 433 – 445.
- Cirot E. 1988. Caractères et classification des Fissipèdes: exemple du genre *Amphicyonodon* (Oligocène inférieur des Phosphorites du Quercy). Mém. DEA, Lab. Paléont. Vertébr. Paléont. hum. Univ. P. et M. Curie, Paris: 1 – 46.

- Cirot E. 1992. Étude phylogénétique de quelques genres d'*Arctoidea* de l'Oligocène eurasiatique. Comparaison des données morphologiques et moléculaires. Vols 1, 2. Ph. D. Diss., Fac. Sci. fondament. appl. Univ. Poitiers, Poitiers: 1 – 152.
- Cirot E. and de Bonis L. 1992. Révision du genre *Amphicyonodon*, Carnivore de l'Oligocène. *Palaeontographica (A)* 220: 103 – 130.
- Clark J., Beerbower J. R., and Kietzke K. K. 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology in the Big Badlands of South Dakota. *Fieldiana, Geol. Mem.* 5: I – VIII + 5 – 158.
- Clark J. and Guensburg T. E. 1972. Arctoid genetic characters as related to the genus *Parictis*. *Fieldiana, Geol.* 26: 1 – 76.
- Crusafont Pairó M. 1971. Estado actual de los estudios paleomastológicos en España. *Mem. r. Acad. Cienc. Artes Barcelona, Tercera Época* 41: 139 – 159.
- Crusafont Pairó M. 1973. *Mammalia tertiaria Hispaniae*. [In: *Fossilium catalogus*, 1 (121). F. Westphal, ed.]. W. Junk b. v., the Hague: I – IV + 1 – 198.
- Crusafont Pairó M. and Kurtén B. 1976. Bears and bear-dogs from the Vallesian of the Vallés-Penedés basin, Spain. *Acta zool. fenn.* 144: 1 – 29.
- Dawkins W. B. 1888. On *Ailurus anglicus*, a new carnivore from the Red Crag. *Q. J. geol. Soc. Lond.* 44: 228 – 230.
- Decker D. M. and Wozencraft W. C. 1991. Phylogenetic analysis of Recent procyonid genera. *J. Mamm.* 72: 42 – 55.
- Dehm R. 1950. Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. *Abh. Bayer. Akad. Wiss., Math.-naturw. Kl., N. F.* 58: 1 – 141.
- Desmarest A. G. 1826. Potamophile, *Potamophilus*. (Crust.). [In: *Dictionnaire des sciences naturelles, dans lequel on traite méthodiquement des différens êtres de la nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement à l'utilité qu'en peuvent retirer la médecine, l'agriculture, le commerce et les arts*]. F. G. Levrault, Strasbourg: 97.
- Eldredge N. and Cracraft J. 1980. Phylogenetic patterns and the evolutionary process. *Method and theory in comparative biology*. Columbia Univ. Press, New York: i – x + 1 – 349.
- Farris J. S. 1982. Outgroups and parsimony. *Syst. Zool.* 31: 328 – 334.
- Farris J. S. 1983. The logical basis of phylogenetic analysis. [In: *Advances in cladistics, volume 2. Proceedings of the second meeting of the Willi Hennig Society*. N. I. Platnick and V. A. Funk, eds]. Columbia Univ. Press, New York: 7 – 36.
- Filhol H. 1883. Notes sur quelques mammifères fossiles de l'époque miocène. *Arch. Mus. Hist. nat. Lyon* 3: 1 – 97.
- Fischer [von Waldheim] G. 1817. *Adversaria zoologica*. *Mém. Soc. imp. Nat. Moscou* 5: 357 – 472.
- Flower W. H. 1869. On the value of the characters of the base of the cranium in the classification of the order *Carnivora*, and on the systematic position of *Bassaris* and other disputed forms. *Proc. scient. Meet. zool. Soc. Lond.* 1869: 4 – 37.
- Flynn J. J., Neff N. A., and Tedford R. H. 1988. Phylogeny of the *Carnivora*. [In: *The phylogeny and classification of the tetrapods*, 2. M. J. Benton, ed.]. *Syst. Ass. spec. Vol. 35B*. Clarendon Press, Oxford: 73 – 115.
- Gaudry A. 1860. Résultats des fouilles entreprises en Grèce sous les auspices de l'Académie. (Suite.). *C. R. hebd. Séanc. Acad. Sci., Paris* 51: 926 – 929.
- Geoffroy Saint-Hilaire [É.] 1833. Palaeontographie. Considérations sur des ossemens fossiles la plupart inconnus, trouvés et observés dans les bassins de l'Auvergne. *Rev. encycl.* 59: 76 – 95.
- Geoffroy Saint-Hilaire [É.] and Cuvier F. 1825. Panda. [In: *Histoire naturelle des Mammifères, avec des figures originales, coloriées, dessinées d'après des animaux vivans*, 3 (50). [É.] Geoffroy Saint-Hilaire and F. Cuvier]. A. Belin, Paris: 1 – 3.
- Germar E. F. 1811. Eine neue Käfergattung *Potamophilus*. *N. Schr. naturf. Ges. Halle* 1 (6): 39 – 46.
- Gervais P. 1852. *Zoologie et paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France*, 2. Arthus Bertrand, Paris 1848 – 1852: 1 – 16 + 1 – 8 + 1 – 8 + 1 – 8 + 1 – 12 + 1 – 8 + 1 – 14 + 1 – 16.

- Ginsburg L. 1961. La faune des Carnivores miocènes de Sansan (Gers). Mém. Mus. natn. Hist. nat., Paris, N. Sér. (C) 9: 1 – 190.
- Ginsburg L. 1966. Les Amphicyons des Phosphorites du Quercy. Ann. Paléont., Vertébr. 52: 21 – 64.
- Ginsburg L. 1982. Sur la position systématique du petit Panda, *Ailurus fulgens* (Carnivora, Mammalia). Géobios, Mém. spéc. 6: 247 – 258.
- Gloger C. W. L. 1841: Gemeinnütziges Hand- und Hilfsbuch der Naturgeschichte. Für gebildete Leser aller Stände, besonders für die reifere Jugend und ihre Lehrer, 1. Verl. v. A. Schulz & Comp., Wroclaw 1841 – 1842: I – XXXIV + 1 – 495.
- Gray J. E. 1825. An outline of an attempt at the disposition of *Mammalia* into tribes and families with a list of the genera apparently appertaining to each tribe. Ann. Philos., N. Ser. 10: 337 – 344.
- Hennig W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana: 1 – 263.
- Heráň I. 1974. Poznámky k výskytu sagitálního hřebene (crista sagittalis externa) u kunovitých šelem. Lynx, Ser. n. 16: 101 – 111.
- Hough J. R. 1948. The auditory region in some members of the *Procyonidae*, *Canidae*, and *Ursidae*. Its significance in the phylogeny of the *Carnivora*. Bull. am. Mus. nat. Hist. 92: 67 – 118.
- Hunt R. M., Jr 1974. The auditory bulla in *Carnivora*: an anatomical basis for reappraisal of carnivore evolution. J. Morph. 143: 21 – 75.
- Hunt R. M., Jr 1977. Basicranial anatomy of *Cynelos* Jourdan (*Mammalia: Carnivora*), an Aquitanian amphicyonid from the Allier Basin, France. J. Paleont. 51: 826 – 843.
- Hunt R. M., Jr 1987. Evolution of the aeluroid *Carnivora*: significance of auditory structure in the nimravid cat *Dinictis*. Am. Mus. Novit. 2886: 1 – 74.
- Hunt R. M., Jr 1991. Evolution of the aeluroid *Carnivora*: viverrid affinities of the Miocene carnivoran *Herpestides*. Am. Mus. Novit. 3023: 1 – 34.
- Illiger C. 1811. Prodrum systematis mammalium et avium additis terminis zoographicis utriusque classis. C. Salfeld, Berlin: I – XVIII + 1 – 302.
- Jourdan [C.] 1861. Des terrains sidérolitiques. C. R. hebd. Séanc. Acad. Sci., Paris 53: 1009 – 1014.
- Jourdan [C.] 1862. Des terrains sidérolitiques. Rev. Soc. sav., Sci. math. phys. nat. 1: 130 – 133.
- Kaup J. 1832. Vier neue Arten urweltlicher Raubthiere, welche im zoologischen Museum zu Darmstadt aufbewahrt werden. Arch. Miner. Geogn. Bergb. Hüttenk. 5: 150 – 158.
- Kaup J. 1861. Beitrage zur naeheren Kenntniss der urweltlichen Saeugethiere, 5. Eduard Zernin, Darmstadt: 1 – 32.
- Klug F. 1842. Über die Insectenfamilie *Heterogyna* Lat. und die Gattung *Thynnus* F. insbesondere. Abh. k. Akad. Wiss. Berlin, Phys.-math. Kl. 1840: 1 – 44.
- Kretzoi M. 1945. Bemerkungen über das Raubtiersystem. Ann. hist.-nat. Mus. natn. hung. 38: 59 – 83.
- Kretzoi M. 1947. New names for mammals. Ann. hist.-nat. Mus. natn. hung. 40: 285 – 287.
- Kurtén B. and Anderson E. 1980. Pleistocene mammals of North America. Columbia Univ. Press, New York, i – xviii + 1 – 443.
- Lange B. 1969. Un nouveau Musteliné des Phosphorites du Quercy, *Mustelictis piveteaui*. C. R. Séanc. Acad. Sci., Paris (D) 268: 2870 – 2872.
- Lange B. 1970. *Mustelictis piveteaui*, mustélidé nouveau des Phosphorites du Quercy. Ann. Paléont., Vertébr. 56: 73 – 91.
- Lartet E. 1851. Notice sur la colline de Sansan, suivie d'une récapitulation des diverses espèces d'animaux vertébrés fossiles, trouvés soit à Sansan, soit dans d'autres gisements du terrain tertiaire miocène dans le bassin sous-pyrénéen. J.-A. Portes, Auch: 1 – 42.
- Lavocat R. 1952. Sur les affinités de quelques carnassiers de l'oligocène d'Europe, notamment du genre *Plesictis* Pomel et du genre *Proailurus* Filhol. Mammalia 16: 62 – 72.
- Lindsay E. H. and Tedford R. H. 1990. Development and application of land mammal ages in North America and Europe, a comparison. [In: European Neogene mammal chronology. E. H. Lindsay, V. Fahlbusch, and P. Mein, eds]. NATO ASI Ser. (A) 180. Plenum Press, New York: 601 – 624.

- Lydekker R. 1885. Catalogue of the Fossil *Mammalia* in the British Museum, (Natural History) Cromwell Road, S. W. Part I. Containing the Orders *Primates*, *Chiroptera*, *Insectivora*, *Carnivora*, and *Rodentia*. Order Trustees, London: i - xxx + 1 - 268.
- Maddison W. P., Donoghue M. J., and Maddison D. R. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33: 83 - 103.
- Matthew W. D. 1918. Contributions to the Snake Creek fauna. With notes upon the Pleistocene of western Nebraska. American Museum Expedition of 1916. *Bull. am. Mus. nat. Hist.* 38: 183 - 229.
- Matthew W. D. and Granger W. 1924. New *Carnivora* from the Tertiary of Mongolia. *Am. Mus. Novit.* 104: 1 - 9.
- Mein P. 1990. Updating of MN zones. [In: European Neogene mammal chronology. E. H. Lindsay, V. Fahlbusch, and P. Mein, eds]. NATO ASI Ser. (A) 180. Plenum Press, New York: 73 - 90.
- Meyer H. von 1847. Frankfurt a. M., 4. Januar 1847. [...]. *N. Jb. Miner. Geogn. Geol. Petrefakten-K.* 1847: 181 - 196.
- Mitchell E. and Tedford R. H. 1973. The *Enaliarctinae*, a new group of extinct aquatic *Carnivora* and a consideration of the origin of the *Otariidae*. *Bull. am. Mus. nat. Hist.* 151: 201 - 284.
- Mödden C. 1991. *Bavarietis gaimersheimensis* n. gen. n. sp., ein früher Mustelide aus der oberoligozänen Spaltenfüllung Gaimersheim bei Ingolstadt. *Mitt. bayer. Staatssamml. Paläont. hist. Geol.* 31: 125 - 147.
- Muizon C. de 1982. Les relations phylogénétiques des *Lutrinae* (*Mustelidae*, *Mammalia*). *Géobios*, *Mém. spéc.* 6: 259 - 277.
- Muller S. 1838. Over eenige nieuwe zoogdieren van Borneo. *Tijdschr. natuurl. Geschied. Physiol.* 5 (1838 - 1839): 134 - 150.
- Petter G. 1967. *Paragale hürzeleri* nov. gen., nov. sp., Mustélidé nouveau de l'Aquitaniens de l'Allier. *Bull. Soc. géol. Fr.* (7) 9: 19 - 23.
- Pohle H. 1917. *Pseudobassaris riggsi*, gen. n., spec. nov. für *Amphictis* spec. Riggs. *Sber. Ges. naturf. Freunde Berl.* 1917: 403 - 411.
- Pohle H. 1920. Zur Kenntnis der Raubtiere. II. Die Stellung der Gattungen *Amphictis* und *Nandinia*. *Sber. Ges. naturf. Freunde Berl.* 1920: 48 - 62.
- Pomel A. 1846a. Quelques nouvelles considérations sur la paléontologie de l'Auvergne. *Bull. Soc. géol. Fr.* (2) 3 (1845 - 1846): 198 - 231.
- Pomel A. 1846b. Mémoire pour servir à la géologie paléontologique des terrains tertiaires du département de l'Allier. *Bull. Soc. géol. Fr.* (2) 3 (1845 - 1846): 353 - 373.
- Pomel A. 1847. Note sur des animaux fossiles découverts dans le département de l'Allier. *Bull. Soc. géol. Fr.* (2) 4 (1846 - 1847): 378 - 385.
- [Pomel A.] 1853. Catalogue des vertébrés fossiles (suite.). *Ann. scient. litt. ind. Auvergne* 26: 81 - 229.
- Qiu Z. and Schmidt-Kittler N. 1982. On the phylogeny and zoogeography of the leptarctines (*Carnivora*, *Mammalia*). *Paläont. Z.* 56: 131 - 145.
- Queiroz K. de 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. *Syst. Zool.* 34: 280 - 299.
- Queiroz K. de and Gauthier J. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Syst. Zool.* 39: 307 - 322.
- Radinsky L. 1977. Brains of early carnivores. *Paleobiology* 3: 333 - 349.
- Roberts M. S. and Gittleman J. L. 1984. *Ailurus fulgens*. *Mamm. Spec.* 222: 1 - 8.
- Roth C. 1987. Die Raubtierfauna der miozänen Spaltenfüllungen Petersbuch 2 und Erkertshofen 2. Taxonomie - Stratigraphie - Ökologie. Ph. D. Diss., Inst. Geowiss. Univ. Mainz, Mainz: 1 - 252.
- Savage R. J. G. 1957. The anatomy of *Potamotherium*, an Oligocene lutrine. *Proc. zool. Soc. Lond.* 129: 151 - 244.
- Schlosser M. 1899. *Parailurus anglicus* und *Ursus Böckhi* aus den Ligniten von Baróth-Kőpecz, Comitát Háromszék in Ungarn. *Mitt. Jb. k. ung. geol. Anst.* 13: 67 - 95.
- Schmidt-Kittler N. 1981. Zur Stammesgeschichte der marderverwandten Raubtiergruppen (*Musteloidea*, *Carnivora*). *Eclog. geol. Helv.* 74: 753 - 801.

- Schmidt-Kittler N. 1984. On the phylogenetic and biogeographic history of the musteloid carnivores in east and southeast Asia. [In: The evolution of the east Asian environment, 2. R. O. Whyte, T.-N. Chiu, C.-K. Leung, and C.-L. So, eds]. Cent. asian Stud. occ. Pap. Monogr. 59. Univ. Hong Kong, Hong Kong: 710 – 723.
- Schmidt-Kittler N., Godinot M., Franzen J. L., Hooker J. J., Legendre S., Brunet M., and Vianey-Liaud M. 1987. European reference levels and correlation tables. [In: International Symposium on Mammalian Biostratigraphy and Paleocology of the European Paleogene – Mainz, February 18th – 21st 1987. N. Schmidt-Kittler, ed]. Münchn. geowiss. Abh. (A) 10: 13 – 31.
- Segall W. 1943. The auditory region of the arctoid carnivores. Zool. Ser. Field Mus. nat. Hist. 29: 33 – 59.
- Simpson G. G. 1945. The principles of classification and a classification of mammals. Bull. am. Mus. nat. Hist. 85: I – XVI + 1 – 350.
- Simpson G. G. 1946. *Palaeogale* and allied early mustelids. Am. Mus. Novit. 1320: 1 – 14.
- Springhorn R. 1976. Zur Craniologie südfranzösischer oligozäner *Amphicyonidae* (*Carnivora*, *Mammalia*). Palaeontographica (A) 152: 1 – 13.
- Springhorn R. 1977. Revision der alttertiären europäischen *Amphicyonidae* (*Carnivora*, *Mammalia*). Palaeontographica (A) 158: 26 – 113.
- Stirton R. A. 1960. A marine carnivore from the Clallam Miocene formation, Washington. Its correlation with nonmarine faunas. Univ. Calif. Publ. geol. Sci. 36: 345 – 368.
- Tedford R. H. 1976. Relationship of pinnipeds to other carnivores (*Mammalia*). Syst. Zool. 25: 363 – 374.
- Tedford R. H., Barnes L. G., and Ray C. E. 1991. Earliest Miocene littoral arctoid, *Kolponomos*. J. Vertebr. Paleont. 11 (3, suppl.): 57A.
- Tedford R. H. and Gustafson E. P. 1977. First North American record of the extinct panda *Parailurus*. Nature 265: 621 – 623.
- Thenius E. 1949. Die Carnivoren von Göriach (Steiermark). Beiträge zur Kenntnis der Säugetierreste des steirischen Tertiärs IV. Sber. öst. Akad. Wiss., Math.-naturw. Kl. (I) 158: 695 – 762.
- Thenius E. 1977. Zur systematischen Stellung von *Protursus* (*Carnivora*, *Mammalia*). Anz. math.-naturw. Kl. öst. Akad. Wiss. 1977 (3): 37 – 41.
- Thorpe M. R. 1921. Two new fossil *Carnivora*. Am. J. Sci. (5) 1: 477 – 483.
- Thorpe M. R. 1922. A new generic name for *Pliocyon Marshi*. Am. J. Sci. (5) 3: 97.
- Viret J. 1933. Contribution à l'étude des carnassiers miocènes de la Grive-Saint-Alban (Isère). Trav. Lab. Géol. Fac. Sci. Lyon 21 (18): 1 – 37.
- Viret J. 1951. Catalogue critique de la faune des Mammifères miocènes de la Grive Saint-Alban (Isère). Première partie: Chiroptères, Carnivores, Édentés Pholidotes. N. Arch. Mus. Hist. nat. Lyon 3: 1 – 104.
- Wagner A. 1854. Bericht über die urweltlichen Arten von Wirbelthieren, deren Knochen-Ueberreste durch die von dem Herrn Akademiker Dr. Johannes Roth bei Pikermi in Griechenland während des Winters 1852/53 unternommenen Ausgrabungen aufgefunden wurden. Gelehrte Anzeigen (Bull. k. bayer. Akad. Wiss. 10) 38: 337 – 343.
- Wagner A. 1857. Neue Beiträge zur Kenntniss der fossilen Säugethier-Ueberreste von Pikermi. Abh. k. bayer. Akad. Wiss. (II) 8: 109 – 158.
- Wagner A. 1858. Geschichte der Urwelt, mit besonderer Berücksichtigung der Menschenrassen und des mosaïschen Schöpfungsberichtes, 2. 2nd ed. Verl. Leopold Voss, Leipzig: I – VI + 1 – 528.
- Wagner H. 1976. A new species of *Pliotaxidea* (*Mustelidae*: *Carnivora*) from California. J. Paleont. 50: 107 – 127.
- Wang X. and Tedford R. H. 1992. The status of genus *Nothocyon* Matthew, 1899 (*Carnivora*): an arctoid not a canid. J. Vertebr. Paleont. 12: 223 – 229.
- Watrous L. E. and Wheeler Q. D. 1981. The out-group comparison method of character analysis. Syst. Zool. 30: 1 – 11.

- Wegner R. N. 1913. Tertiaer und umgelagerte Kreide bei Oppeln (Oberschlesien). *Palaeontographica* 60: 175 – 274.
- Wiig Ø. 1983. On the relationship of pinnipeds to other carnivores. *Zool. Scr.* 12: 225 – 227.
- Winge H. 1895. Jordfundne og nulevende Rovdyr (*Carnivora*) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Rovdyrenes indbyrdes Slaegtskab. [In: *E Museo Lundii. En Samling af Afhandlinger om de i det indre Brasiliens Kalkstenshuler af Professor Dr. Peter Vilhelm Lund udgravede og i den Lundske palaeontologiske Afdeling af Københavns Universitets zoologiske Museum opbevarede Dyr- og Menneskeknogler*, 2 (2, IV). C. F. Lütken, ed]. H. Hagerups Boghandel, Copenhagen: 1 – 130.
- Wortman J. L. 1901. Studies of Eocene *Mammalia* in the Marsh collection, Peabody Museum. *Am. J. Sci.* (4) 12: 143 – 154.
- Wozencraft W. C. 1989. The phylogeny of the Recent *Carnivora*. [In: *Carnivore behavior, ecology, and evolution*. J. L. Gittleman, ed]. Cornell Univ. Press, Ithaca: 495 – 535.
- Wyss A. R. 1987. The walrus auditory region and the monophyly of pinnipeds. *Am. Mus. Novit.* 2871: 1 – 31.
- Wyss A. R. and Flynn J. J. 1993. A phylogenetic analysis and definition of the *Carnivora*. [In: *Mammal phylogeny: Placentals*. F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds]. Springer-Verl., New York: 32 – 52.
- Zdansky O. 1924. Jungtertiäre Carnivoren Chinas. *Palaeont. sin.* (C) 2 (1): 1 – 155.

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