SENCKENBERG
NATURFORSCHUNG

ORIGINAL PAPER

Diversity and function of the anterior dentitions in fossil and extant mammals

Wighart von Koenigswald[1] iD

Abstract

This paper reviews the morphological diversity of the anterior dentition (AD - incisors and canines) in fossil and extant mammals. The great diversity of the mammalian anterior dentition is due to mosaic evolution of different morphological features. The paper identifies twenty-one groups of genera that share specific features but are not phylogenetically related. These groups are referred to as clusters. Minor differences within the clusters are described as modifications that are found in the different mammalian orders. The clusters highlight convergent features as well as evolutionary trends that occur in different clusters, such as the reduction of antemolars, the formation of incisiform lower canines and of caniniform lower premolars. The different functions of the anterior teeth within these clusters are discussed. They suggest that adaptations for quite different functions have led to very similar structures. During evolution, the reduction of anterior teeth is rare in carnivores but common in herbivores. This illustrates the increasing importance of soft parts, such as lips, tongue and trunk for foraging. The setup of the clusters described here is not intended as an additional system to which taxa must be assigned, but as a framework for highlighting similarities in unrelated taxa.

Keywords Dental formula · Tooth reduction · Canine occlusion · Canine/premolar functional unit · Parallelism and convergence

Introduction

Mammalian teeth and dentition are a classic field of comparative morphology. Compared to their reptilian ancestors, mammals have greatly diversified their anterior dentition (AD), consisting of the incisors and canines and adapted it to the different functions. The primary function of the anterior dentition is to gain access to food. This is done by grasping plant material with the incisors, or by killing and/or holding prey with the canines. The second function is to shape the food for subsequent chewing and swallowing. A third function is their use as weapons in extra- and intraspecific displays or simply as indicators of individual strength (e.g. Romer et al. 1966, Thenius 1969, Iwasaki 2002, Rose 2006, Ungar 2010).

The structural similarities of the AD are the focus of this paper, but an analysis requires a classification of such structures. A morphological classification of molars has been proposed several times (e.g. Osborn 1910, Thenius 1969), but so far none for the AD.

This paper attempts such a classification by defining morphological categories or "clusters", that are based on morphological features and independent from the zoological classification. The term cluster is preferred to the term category here to emphasis the loose boundaries of clusters, because some taxa may be associated with different clusters. Nevertheless, the comparison within or between clusters highlights some fundamental evolutionary pathways that are less obvious when the focus is on taxonomic groups. The paper, thus, provides a new perspective on the diversity of the AD and its many examples of convergent evolution.

Compared to the molars the anterior dentition, formed by the incisors and canines, has received much less attention in the palaeontological literature. There are two reasons for this discrepancy. The anterior dentition is less often fully preserved. The single-rooted teeth fall out of the jaws easily

✉ Wighart von Koenigswald
koenigswald@uni-bonn.de

1   Universität Bonn, Bonner Institut für organismische
     Biologie, Paläontologie, Nussallee 8, 53115 Bonn, Germany

Springer

during maceration or fossilization, and when they are present, they are considered as less informative for phylogenetic studies because of the many cases of convergence. The poor documentation of the AD in fossil mammals also limits this qualitative survey.

Methods

The study was carried out on two levels. In order to recognise similar structures, it is necessary to identify the typical morphological structures and their variability. The different characters that comprise the first level are presented here as "features" and are indicated as FT. There are three groups of features: incisors (FT-1 to FT-18), canines (FT-30 to FT-43), and general features (FT-50 to FT-55) as listed in Table 1. These features occur in a mosaic of different combinations. These combinations features comprise the second level, the clusters. The most common combinations are classified as "clusters" (CL-1 to CL-21 in Table 2).

The most common features are the enlargement, reduction and loss of specific tooth loci in the incisors and canines. The upper and lower dentition often show very different numbers of teeth, different tooth types, and even different evolutionary trends. Therefore, the upper and lower dentition must be compared and classified as concordant or discordant.

"Clusters" are the second level of comparison. They include taxa that share similar combinations of specific characters. Clusters are independent of zoological classification and combine cases of homology and homoplasy. The twenty-one clusters established here are intended to cover the major differentiations of the AD in fossil and extant mammals. Their number could easily be increased if the definitions were more stringent. But a larger number would be confusing.

A clear separation of clusters is not always possible, as many characters occur in different combinations in different clusters. It is somewhat subjective which cluster a taxon belongs to. It is not affiliation that is the main concern of this approach, but the intention to compare across systematic boundaries.

Clusters are often named after one of the dominant features. The clusters and their names are arbitrary, but even in their preliminary form they have allowed some surprising observations.

The systematic affiliation of the taxa studied follows McKenna and Bell (1997) and partly "The Paleobiology Database" https://paleobiodb.org/classic/beginTaxonInfo.

Each chapter begins with a gallery of sketches representing the dentition of the cluster. The sketches are not to scale and the canines are darker than the incisors.

Table 1 List of relevant features and their occurrences in clusters

Features	Description	Cluster Examples
FT 1 to FT-18	**Incisors**	
FT-1	full number of incisors	Cl-1
FT-2	reduced number of incisors	CL-2
FT-3	pair of incisors	CL-8
FT-3a	upper incisors larger	CL-6, CL-11,
FT-3b	lower incisors larger	Cl-8
FT-4	concordant incisors	CL-3, CL-9
FT-5	discordant incisors	CL-5, CL-8
FT-6	enlarged incisors	CL-4, CL-9
FT-6a	central incisors enlarged	CL-4
FT-6b	lateral incisors enlarged	CL-12
FT-7	rooted incisors	CL-4
FT-8	euhypsodont	CL-6, CL-7, CL-9
FT-10	procumbent lower incisor	CL-6, CL-8
FT-11	reciprocal abrading	CL-6, CL-7, CL-9
FT-12	gliriform incisors	CL-9
FT-13	overbiting incisors	CL-5, CL-6
FT-14	Lemur tooth comb	CL-18
FT-15	ruminant incisor arcade (RIA)	CL-17
FT-16	incisor tusks	CL-11
FT-17a	occlusal angle incisors - 180°	CL-9
FT-17b	occlusal angle of incisors - 90°	CL-5, CL-6
FT-17c	occlusal angle of incisors low	CL-7
FT-18	no upper incisors	CL-17
FT-30 to FT-43	**Canines**	
FT-30	canine absent	CL-9
FT-31	concordant canines	CL-12
FT-32	small canines	CL-3
FT-33	adjusted canines	CL-13
FT-34	incisiform lower canines	CL-16, CL-17
FT-35	discordant canines	CL-10, CL-14, CL-15
FT-36	moderate canines	CL-12
FT-37	enlarged canines	CL-19
FT-38	upper canines larger	CL-12, CL-15, CL-16
FT-39	lower canines larger	CL-2,
FT-40	mutually abrading canines	CL-14
FT-41	euhypsodont canines	CL-14
FT-42	saberteeth	CL-15
FT-43	canine tusk	CL-11
FT-50 to FT-53	**General features**	
FT-50	homodont	CL-20
FT-51	premolar enlargement	CL-16
FT-52	antemolar reduction	CL-7, CL-8, CL-9
FT-53	diastema	CL-7, CL 17
FT-54	pigmented enamel	CL-8, CL-9
FT-55	significant reductions	CL-20

Table 2 The proposed clusters of the anterior dentition

	Name of the Clusters	Short description of the clusters	Typical features
PLESIOMORPHIC ANTERIOR DENTITIONS			
CL- 1	*Plesiomorphic pattern*	Undifferentiated therian dental pattern; e.g. *Didelphis*	FT-1
CL-2	*Unequal Incisors or Canines*	Unequally differentiated incisors or canines; e.g. *Tupaia*	FT-1 variable
INCISOR DOMINATED ANTERIOR DENTITIONS			
CL-3	*Concordant Incisors*	Concordant incisors and small canines; e.g. *Equus*	FT-1, (FT-31, FT-32)
CL-4	*Pair of Large Rooted Incisors*	Single pair of large and rooted Incisors; e.g. *Paraceratherium*	FT-3, FT-52
CL-5	*Rooted Overbite Incisors*	Rooted upper incisors truncating lowers; e.g. *Desmana*	FT-5, FT-6, FT-7, FT-13
CL-6	*Truncated Euhypsodont Lower Incisors*	Overbiting euhypsodont upper incisors truncating lower incisors; e.g., *Procavia*	FT-5, FT-6, FT-8, FT-13, FT-40, FT-52
CL-7	*Large Flat-Nose Pliers*	Large concordant incisors occluding at a low angle; e.g. *Vombatus*	FT-6 FT-8, FT-40, FT-53
CL-8	*Mandible with single procumbent incisor*	Mandible with a large procumbent incisor and a discordant antagonist e.g., *Sorex*	FT-2, FT-3a, FT-5, FT-6a, FT-52
CL-9	*Gliriform Incisors*	Pair of euhypsodont incisors with reciprocal sharpening; e.g. *Castor*	FT-2, FT-4, FT-6a, FT-8, FT-17a, FT-52, FT-53, FT-54
CL-10	*Special Incisors*	Special modifications of enlarged discordant incisors; e.g. *Tapirus*	variable
CL-11	*Dentin Tusks*	Extremely enlarged incisors or canines forming dentin tusks; e.g. *Gomphotherium*	FT-16, FT-43, FT-52, FT-53
CANINE DOMINATED ANTERIOR DENTITIONS			
CL-12	*Moderately Enlarged Canines*	Concordant canines, moderately enlarged; e.g. *Canis*	FT-31, FT-36
CL-13	*Adjusted Canines*	Concordant canines adjusted to the size of incisors and premolars; e.g. *Homo*	FT-1, FT-31, FT-33
CL-14	*Mutually Abrading Canines*	C/c functional unit; e.g. *Hippopotamus*	FT-30, FT-40
CL-15	*Saberteeth*	Extremely enlarged discordant upper canines; e.g. *Moschus*	FT-38, FT-42, FT-51, FT-53
CL-16	*Canine/premolar unit*	Concordant canines, FT-mutually abrading; e.g. *Leptoreodon*	FT-35, FT-42, FT-51
CL-17	*RIA*	Ruminant incisor arcade and toothless premaxilla; e.g. *Bos*	FT-15, FT-18, FT-34, FT-30
CL-18	*Lemuriform toothcomb*	Incisors and incisiform canines form the fan. No upper incisors; e.g. *Lemur*	FT-14, FT-34
CL-19	*Special Canines*	Uniquely modified canines	variable
CL-20	*Homodont Dentitions*	Homodont anterior dentitions; e.g. *Trusiops*	FT-50
CL-21	*Major Tooth Reductions*	AD with major tooth reductions, e.g. *Myrmecophaga*	FT-55

Terminology

Abutment: A step in the dentin facet or an additional upper tooth that stops the movement of the lower incisor (e.g. Plesiadapidae CL-8 or Lagomorpha CL-9)

Adjusted canines: Canines that are reduced in size and resemble premolars and incisors (i.e. in the human dentition) (FT-33).

Antemolars: The term antemolar (A/a) literally includes the teeth anterior to the first molar, but refers here to the teeth between the first molar and an enlarged incisor. Teeth in the antemolar area gradually reduced. The last premolars (P4/p4) are less affected by the reduction and often show a divergent development, e.g. in Soricidae, Lagomorpha, various Rodentia (except Myomorpha). When the number of antemolars is counted for taxonomic identification, the P4/p4 are excluded from the count (Rofes and Cuenca-Bescós 2009, Hugueney et al. 2012, Klietmann et al. 2013). The reduced teeth are often

unicuspid and their tooth loci are therefore difficult to identify.

Canines: Prominent canines are easy to recognise, because of the enlarged unicuspid morphology. The upper canine is defined by its position at the anterior edge of the maxilla. The lower canine occludes anteriorly to the upper canine. In certain clusters, the canines occur adjusted to the size of incisors.

Clusters: Each cluster focuses on specific dental structures in the AD (e.g. gliriform incisors) that occur independently in taxonomically unrelated groups. Clusters include several modifications that share certain features but differ in others. Clusters are named and numbered from CL-1 to CL-21 in Table 2.

Concordant and discordant: ADs are considered concordant when their upper and lower teeth are similar in morphology and number (e.g. *Canis* or *Homo*). They are discordant when upper and lower teeth differ significantly in size or number (e.g., in *Sorex* or in *Cervus*).

Euhypsodont and hypselodont: The term "euhypsodont" means continuously growing teeth. It was introduced by Mones (1982) to avoid the long-standing confusion between hypsodont and hypselodont.

Features: This term is used here for morphological characters that describe the clusters. The features are numbered in three groups: FT-1 to FT-18 for incisors, FT-30 to FT-43 for canines, and FT-50 to FT-55 for general features and listed in Table 1.

*Incisors***:** Incisors are all teeth in the premaxilla and in the dentary anterior to the lower canine.

Modifications: Modifications refer to a more specific morphology within a cluster. It describes the arrangement of the AD in a particular taxon or group (e.g. *Equus* modification). Several modifications that share significant morphological features form a cluster.

Mutual abrasion*:* Abrasion of antagonistic teeth that results in a synchronous sharpening of both teeth (FT-40) (e.g. canines of *Hippopotamus*).

Pair: The descriptive term "pair" is used here for enlarged teeth in the upper and lower dentition that function as antagonists (FT-3) (e.g. left upper and left lower incisor in Rodentia).

Positional terms: The different sides of the canines and the incisors are indicated as anterior and posterior, and lateral and mesial, according to their orientation in the jaws.

Reciprocal sharpening: Sharpening of the upper and lower incisors by two different movements, not synchronously as in mutual abrasion (FT-11) (e.g. rodent incisors).

Tooth classes: The tooth classes incisors (I/i), canines (C/c), premolars (P/p) and molars (M/m) are used in the traditional way according to Owen (1840−45), Hillson (1986), Luckett (1993) or Ungar (2010), although some details are still under discussion (Schwartz 1974).

Toothcomb: Procumbent and tightly aligned lower incisors that, in some taxa together with an incisiform lower canine, form a tool for fur grooming, bark gouging, and sab feeding (FT-14) (Coimbra-Filho 1978, Fleagle 1988).

Tooth loci: This study deals with the dentition of adult individuals. The traditional numbering within tooth classes is burdened with many unresolved details, especially when reduced tooth loci are counted or not. Traditional tooth counts are used, but other counts based on ontogenetic studies are mentioned because they are relevant when strict homology is considered. The adult dentition may include permanent teeth and retain persisting deciduous teeth. The gliriform incisors of Rodentia and Lagomorpha are such persisting deciduous teeth (Luckett 1985). In the unreduced dentition of most Placentalia, the first upper and first lower premolars are not replaced by permanent teeth, so they represent DP1 and dp1 (Ziegler 1971, Luckett 1993, Ungar 2010).

Tusks: The term "tusk" is not well defined in the literature. Here the term "tusk" is used for large dentin teeth that are only partially covered with enamel. They are usually euhypsodont (or continuously growing). The tusks may be formed by incisors and or canines (FT-16 and FT-43).

Materials

The number of extant and fossil mammalian taxa is very large and only a very limited number could be analysed in this initial survey (see Appendix). The aim of this paper is to highlight specific constellations of the AD that reoccur in taxa from different systematic units.

Data on the AD have been collected from various sources: direct observations in various museums (e.g. AMNH New York, FMC Chicago, MLP La Plata, ZFMK-Bonn, BSPG München, SF Frankfurt, SMNS-Stuttgart, MfN Berlin) and from illustrations in the scientific literature, textbooks, and papers on specific taxa.

The anterior dentition is often depicted in less detail than the post-canine teeth. There are two reasons for this: First, the anterior teeth are less well preserved in fossils. The single-rooted teeth are often detached in fossil and extant materials. Second, the AD is less informative for phylogenetic studies. General information on the AD is provided by textbooks and databases. Berkovitz and Shellis (2018) provide photographs of the skulls of nearly all extant mammals, but the anterior aspects are rare. Thenius (1989) provides very instructive drawings of the lateral aspects of fossil and extant skulls, as well as very informative comparisons of the frontal aspects of several mammalian groups. Other textbooks provide useful figures and information (e.g. Zittel 1897, Paula Couto 1979, Janis et al. 1998, 2008, Rose and Archibald 2005, Rose 2006,

Prothero and Foss 2007). Databases such as ADW (Animal Diversity Web - https://animaldiversity.org), Fossilworks (http://www.fossilworks.org/). Morphobank (https://morphobank.org), Morphosource (https://www.morphosource.org), Paleodiversity Database (https://paleobiodb.org/#/), UMORF (University of Michigan - https://animaldiversity.org/accounts/Mammalia), and Wikipedia provided additional information. The most important information on fossil taxa comes from the scientific descriptions consulted. A critical compilation of data from these sources was the basis for this study.

The study attempts to cover the mayor variations in the anterior dentitions found in fossil and extant Eutheria and Metatheria. Some allotherian Multituberculata are included because of their functional similarity to gliriforms. The selected clusters cover much of the diversity but certainly not all of it, so the result must be considered preliminary.

Technical abbreviations

AD	Anterior dentition
C, c	upper and lower canines
CL-1 to CL-21	clusters
dp1/dP1	deciduous lower/upper first premolar
FT-1 to FT-55	morphological features
I, i	upper and lower incisors
M, m	upper and lower molars
P, p	upper and lower premolars
Pmx	premaxilla
RIA	ruminant-incisor arcade

Institutional abbreviations

ADW	Animal Diversity Webb
AMNH	American Museum Natural History, New York,
BIOB-PAL	Bonner Institut für Organismische Biologie, Paläontologie
BSPG	Bayerische Staatssammlung für Paläontologie, München,
FMC	The Field Museum, Chicago,
MfN	Museum für Naturkunde, Berlin
MLP	Museo de La Plata, La Plata, Argentina.
MWNHS	Museum Wiesbaden - Naturhistorische Sammlungen
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NORPAL	Norvegian Center for Paleontology, Oslo
PBDB	Paleobiology Database
SF	Senckenberg Museum Frankfurt
SMNK	Staatliches Museum für Naturkunde Karlsruhe
SMNS	Staatliches Museum für Naturkunde Stuttgart
ZFMK	Leibniz-Institut zur Analyse des Biodiversitätswandels, Bonn

Clusters with indifferent dentitions

Cluster 1
"Plesiomorphic pattern" (CL-1)

Hypothetical plesiomorphic therian dental formula

The high diversity of anterior dention in the Paleogene, Neogene, and Quaternary Metatheria and Placentalia should be compared with the hypotheical plesiomorphic pattern of the last common ancestor. The common ancestor dates back to at least the Cretaceous, according to age estimates based on genetics (O'Leary et al. 2013), but it is not available for comparison because it has not been positively identified, and possible candidates are poorly preserved. Therefore, a few later species were selected that are thought to have retained the ancestral pattern as closely as possible.

Definition and occurrence: An anterior dentition is considered basic if it is concordant and contains the full number of incisors (FT-1), if the canines are significantly larger than the incisors, and if there are no large diastemata. None of the dentitions show enlargement or reduction of specific tooth loci.

As examples for this study, the Paleocene stem metatherian *Andinodelphis* (De Muizon and Ladevèze 2020) and the extant *Didelphis* represent the Metatheria. For Eutheria, the Upper Cretaceous *Asioryctes* and *Ukhaatherium* (Novacek et al. 2023) and the Paleocene pantodont *Alcidedorbignya* (De Muizon and Billet 2022) were chosen.

Examples of Marsupialia
***Didelphis* modification:** The extant *Didelphis* from the Americas (5.1.3.4/4.1.3.4) (Fig. 1.1a). is generally regarded as an unspecialised marsupial that retains many ancestral features. Upper and lower incisors are unicuspid. The central upper incisor (I1) is slightly longer than he other upper incisors (I2-I5), but much smaller than the upper canine (C). There is a short precanine diastema between I5 and C. The anterior premolars are somewhat reduced but have two roots. The mandible has four incisors (i1-i4) of varying size. The lower canine projects vertically and fits into the precanine diastema when the jaws are closed. In Didelphis, p2 is slightly enlarged and fits into a gap between P1 and P2 of the upper dentary. *Andinodelphys* is very similar to *Didelphis*. (Fig. 1.2).
***Nimbacinus* modification:** The AD of the thylacine marsupial *Nimbacinus dicksoni* (4.1.4.3/?3.1.4.3) (Fig. 1.1b) is incompletely preserved, but it has four alveoli for the upper incisors of which the I4 has the largest alveolus (Wroe and Musser 2001). In the lower dentition the i3 is crowded and staggered. The premaxillo-maxillary suture is anterior to the upper canine. The lower canine is significantly higher than the incisors and premolars. It shows a facet from the occlusion with the upper C.
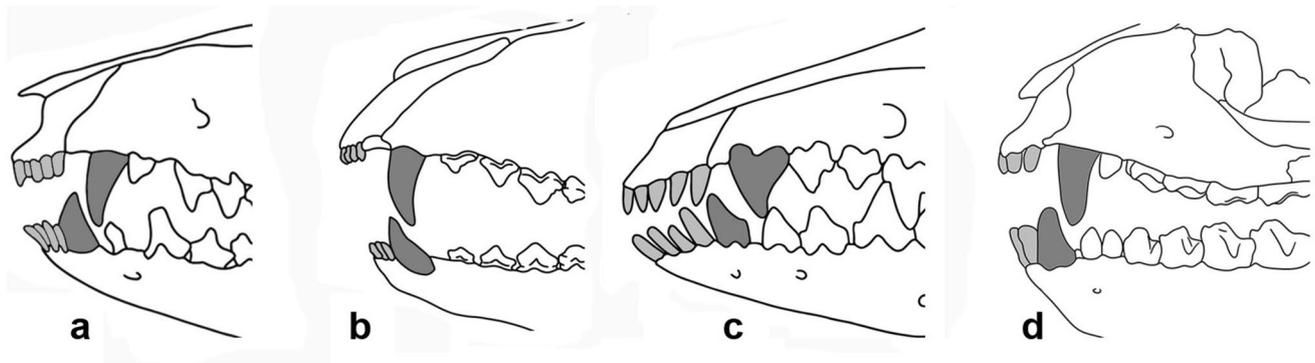
Fig. 1.1 "*Plesiomorphic Pattern*" (CL-1). **a** *Didelphis* (MARSU-PIALIA), **b** *Nimbacinus* (MARSUPIALIA), **c** *Asioryctes* (EUTHE-RIA), **d** *Alcidedorbignya* (PANTODONTA). (Modified from: **a** photo of BIOB-PAL, **b** Wroe and Musser 2001, **c** Wible et al. 2009 **d** De Muizon and Billet 2022). All sketches here and below are not to scale. Canines are shaded darker than incisors

Examples of Eutheria

***Asioryctes* and *Ukhaatherium* modification:** The AD of the Upper Cretaceous Euplacentalia is variable (Wible et al. 2009). *Zalambdestes* is characterised by an elongated very slender snout with diastemata between the upper incisors. The procumbent slender lower incisor is elongated (? FT-10), the lower c is small (Wible et al. 2009). *Asioryctes* (5.1.5.3/4.1.5.3) (Fig. 1.1c) and *Ukhaatherium* (5.1.5.3/4.1.5.3) from Mongolia are well documented (Novacek et al. 2023). The canines of *Asioryctes* are double-rooted, whereas the canines of *Ukhaatherium,* like most of the more modern Placentalia, have a single root. In both genera, the number of incisors is higher than in more modern Euplacentalia. But the number of molars, three, corresponds to modern Euplacentalia.

***Alcidedorbignya* modification:** The early Paleocene pantodont *Alcidedorbignya inopinata* (3.1.4.3./3.1.4.3.) (Fig. 1.1d and 1.2) from Argentina is perfectly preserved. Its dental formula corresponds to the unreduced formula of modern placentals (De Muizon and Billet 2022). Three incisors of similar size in the upper and lower dentition are typical, and the canines are slightly larger than the incisors. A small pre-canine diastema between I3 and C accommodates the lower canine when the jaws are closed.

Fig. 1.2 "*Plesiomorphic Pattern*" (CL-1). **a** (left) *Didelphis marsupialis* (MARSUPIALIA), **b** (right)*Alcidedorbignya inopinata* (PLACENTALIA). Their dentitions differ mainly in the number of incisors, as seen in the occlusal view of the upper and the lower AD. The i1 is present in *Alcidedrorbibignya*, but not in the figured specimen. (Modified from: **a** ADW, **b** De Muizon and Billet 2022)
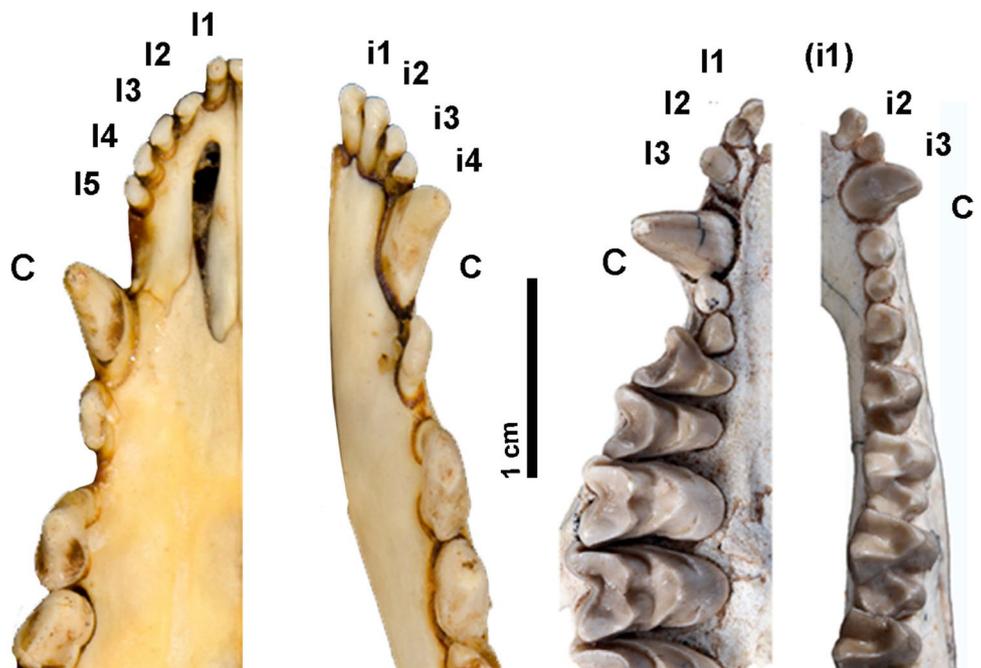
Discussion of CL-1 "Plesiomorphic pattern"

The cluster includes taxa that are considered to be similar to a hypothetical plesiomorphic pattern of the mammalian anterior dentition. Only a few taxa allow a vague reconstruction. Because of progressive evolution, the characters of the basic pattern have been intensively modified. Basic marsupials and basic eutherians differ in the number of incisors. *Didelphis* has 5 upper and 4 lower incisors, while *Alcidedorbignya* has 3 upper and 3 lower incisors, the typical number for eutherians (FT-1). Among the Mesozoic Euplacentalia, *Maelestes* has preserved 3 lower incisors. A small gap between i3 and c may indicate that a i4, present in *Asioryctes* and *Ukhaatherium* was reduced, as in all later placental mammals (Wible et al. 2009.13).

Cluster 2
"Unequal incisors or canines" (CL-2)

Unequally differentiated incisors or canines

Definition and occurrence: The cluster CL-2 "*Unequal Incisors or Canines*" is characterised by a limited enlargement of specific tooth loci, often discordant (FT-5, FT-35). The AD has an unreduced number of incisors, canines, and no diastema The number of mammals with a moderately modified anterior dentition is very large and this cluster could easily be subdivided indefinitely. I include the marsupial *Perameles* and a various placental insectivores and primates in this cluster (Fig. 2.1).

Examples of Marsupialia
Perameles modification: The Australian bandicot *Perameles* (5.1.3.4/3.1.3.4) (Fig.2.1a) has an elongated snout and thus, the three lower and five upper incisors are loosely arranged. separated by small diastemata. The diastemata between I4 and I5 and between the canines and the premolars are larger. The canines of *Perameles nasutus* show an unusual sexual differentiation (Freedman 1967). Males have unicuspid canines elevated well above the level of the premolars, whereas the canines of females are small and have additional cusps.

Examples of Insectivora
Amphilemurid variation: *Macrocranion* and *Pholidocercus* (Eocene, Europe) have a complete placental dental formula 3.1.4.3/3.1.4.3 and no diastema. The AD is characterised by teeth of similar size, but the I1, i3, C and the persistent dp1 are slightly enlarged. The lower c is slightly premolariform (Fig. 2.2) (Maier 1977, Koenigwald and Storch 1983, Lehmann, 2018). Due to a slightly discordant
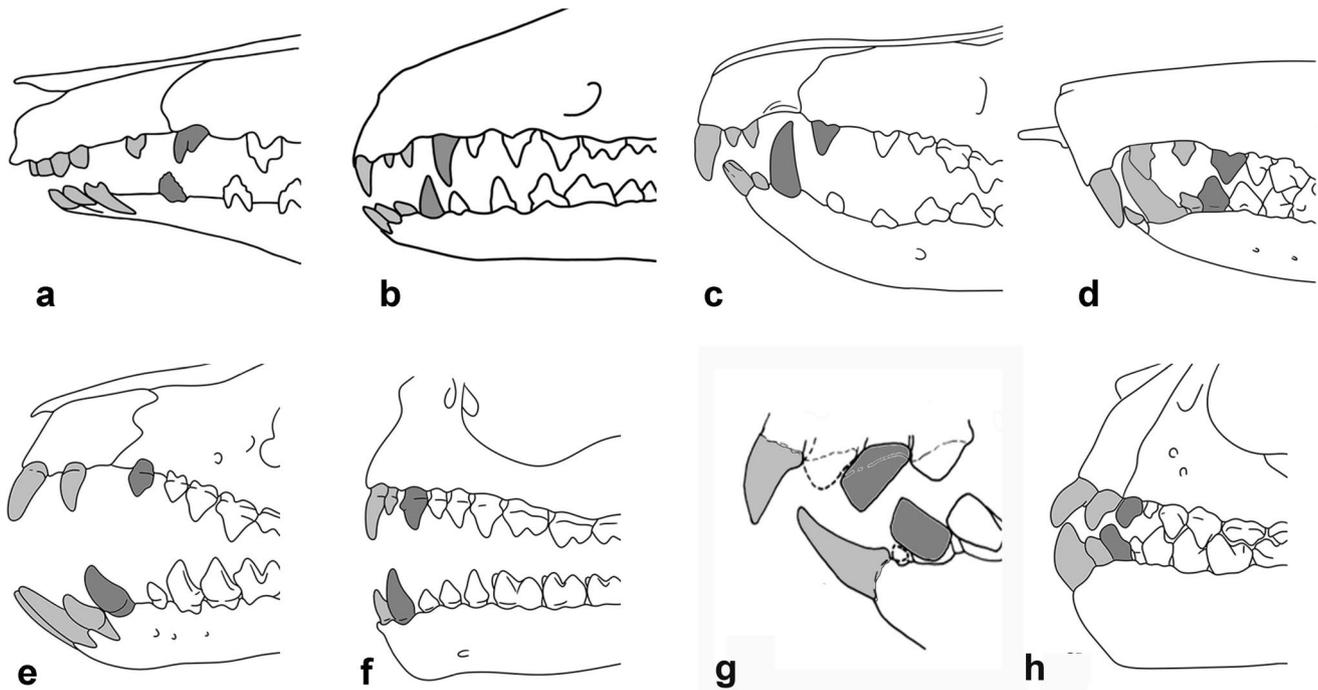

Fig. 2.1 "*Unequal Incisors or Canines*" (CL-2). **a** *Perameles* (MARSUPIALIA), **b** *Podogmynura* (EULIPOTYPHLA), **c** *Deinogalerix* (EULIPOTYPHLA), **d** *Solenodon* (EULIPOTYPHLA), **e** *Tupaia*, **f** *Tarsius*, **g** *Microchoerus*, **h** *Tetonius* (**e-h** PRIMATES). (Modified from: **a** ADW, **b** photo ZMFK, **c** Butler 1980, **d** Headdin 2014 (Wikimedia Common), **e** Thenius 1989, **f** Schultz 1971, **g** Roth 1985, **h** Szalay 1976).
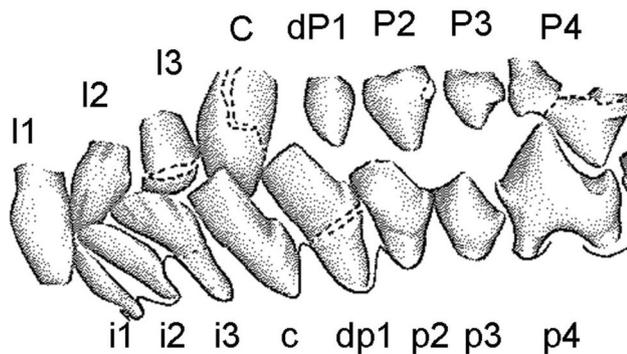
Fig. 2.2 "*Unequal Incisors or Canines*" (CL-2). *Pholidocercus hassiacus* (ANAGALIDA, Amphilemuridae), anterior dentition AD (from Koenigswald and Storch 1983]

differentiation and the small canines, Amphilemuridae are assigned to this cluster "*Unequal Incisors or Canines*".

Erinaceid modification: In the extant *Erinaceus* (3.1.3.3/2.1.2.3), the upper I1 and lower i2 are enlarged. The I1 is implanted vertically, the lower incisor is more procumbent. Two small incisors and a slightly larger double-rooted canine follow in the upper dentition. Two small premolars are followed by the enlarged P4. In the lower jaw, the large i2 is followed by a small i3, a small canine and p3. The p4 is broader and precedes to the square molars.

In *Podogymnura* (Fig. 2.1b) the dental formula is complete (3.1.4.3/3.1.4.3) (Heaney and Morgan 1982, Poduschka and Poduschka 1985). As in many erinaceids, the first upper incisor (I1) is slightly larger than the following I2 and I3. It points downward. The upper incisors, canines and premolars are separted by small distemeata. A prominent canine follows. In the dentary, the three incisors are smaller and anteriorly inclined. The lower canine is relatively large and fits into the precanine diastema between I3 and C.

The AD of *Echinosorex* (3.1.4.3/3.1.4.3) shows unevenly enlarged incisors, all are smaller than the canines. In the premaxillary, the first and second (I1 and I2) are slightly larger than the third (I3). The upper canine is significantly larger than I3 and the anterior premolars. There is a precanine diastema between the double-rooted C and the small I3, but no diastemata behind the canines. The mandible contains three incisors, i1 and i2 are slightly larger than i3. The lower canine is large and fits into the precanine diastema when the jaws are closed. Small premolars follow without a diastema.

The erinaceid *Deinogalerix* (3.1.4.3/?2.1.4.3) is an example of unequal enlargement of the upper and lower tooth loci (Fig. 2.1c). The snout of *Deinogalerix* is elongated. In the premaxilla the I1 (FT-3a) is enlarged and points downward. Two small incisors follow. They are separated from the upper canine by a wide precanine diastema. The upper

canine is double-rooted but small, almost of the same size as the anterior premolars. The lower incisors are incompletely preserved. An isolated bilobed tooth has been interpreted as i1 (Villier et al. 2013 Fig. 3 K). The lower canine is much larger than the upper (FT-39) and fits into the precanine diastema of the upper dentition (Butler 1980). In a three-dimensional model, that has been republished several times, the first lower incisor is large and procumbent. This was based on two isolated teeth tentatively interpreted as i1 (Freudenthal 1972). However, these teeth are most likely lower canines, while the lower incisors are small (Villier &Carnevale 2013).

In *Potamogale*, the upper I1 is enlarged and pointed, followed by two smaller incisors and a relatively large upper C. In the dentary, the incisors are all small, but the lower canine is enlarged.

Solenodon (3.1.3.3/3.1.3.3) (Fig. 2.1d) is an extant insectivore with an extremely elongated cartilaginous snout. Systematically, it has a plesiomorphic position (Wible 2008, Brace et al. 2016). Its dental formula is almost complete. The incisors are unequally enlarged. The upper I1 and the lower i2 are prominent (FT-1, FT-5), the others and the canines are small, as the anterior premolars. The second lower incisor is highly specialised, wih a deep groove through which the poisonous saliva flows from modified salivary glands in the lower jaw to be injected into the prey. - *Solenodon* is one of the few venomous mammals (Ligabue-Braun et al. 2012).

Examples of Scandentia

***Tupaia* modifications**: The dental formula 2.1.3.3/3.1.3.3 is slightly reduced and the incisors are differently specialised (FT-5) (Fig. 2.1e). The two upper incisors (I1 and I2) are peg-like and more or less vertical, whereas the three lower incisors are slender and elongated. They form a kind of tooth comb used for extracting sap from plants (Sorenson 1970) or for grooming (Martin 1981). The canines are small, and the first lower premolars are slightly larger. *Tupaia* fits best into the ckuster CL-2 "*Unequal Incisors or Canines*", the moderately modified plesiomorphic pattern.

Examples of Primates

***Tarsius*:** (2.1.3.3/1.1.3.3) has two pointed upper incisors, I1 is enlarged, I2 much smaller (Fig. 2.1f) (FT-5). The upper canine is smaller than I1, but higher than the following premolar. In the lower dentition, the canine is the largest. The identification of the tooth loci is under discussion (Fleagle 1988), but the unequal enlargement characterising this cluster (CL-2) is obvious.

Omomyid modifications: The anterior dentition of omomyids (tarsiform primates) is characterised by relatively small and pointed teeth. In *Microchoerus* (Fig. 2.1g) the first upper incisors are slightly procumbent and larger than

I2 (FT-2, FT-5). The upper C is premolariform. The lower i1 is pointed and procumbent, with facets of I1, I2, and C. The i2 is minute, the lower c premolariform (Roth 1985). In *Necrolemur* (2.1.3.3/2.1.3.3) the most anterior teeth are enlarged. They are followed by smaller teeth.

The North American omomyid *Tetonius* differs slightly from the European microchoerid *Necrolemur*. In *Tetonius* from Wyoming the enlarged first incisor (I2/i2) (FT-2, FT-5) and the I3/i3 is lost as in all Euprimates. The C/c are significantly smaller (Fig. 2.1h). A reduction of the antermolars can be observed in the lower dentition (Szalay 1976, Bown and Rose 1987). The canine and p3 and p4 are less affected, but p2 gradually disappears in the stratigraphic sequence. The reduction does not result in a diastema.

The dental formula is still discussed (Fleagle 1988), but a differentiation of the size of the anterior teeth qualifies both the Microchoeridae and the Omomyidae for CL-2.

Discussion of CL 2 "Unequal incisors or canines"

This cluster is morphologically heterogeneous. It is less characterised by a specific feature than other clusters presented in this paper. However, the cluster represents the multiple modification of the plesiomorphic patterns. No specific tooth locus is preferred for an enlargement or reduction. Enlargement of the anterior incisors is often accompanied by reduction of the antemolars. The formation of a wide diastema is rare in this cluster. The CL-2 "*Unequal Incisors or Canines*" shows that taxa of similar evolutionary trends come from different systematic groups.

The various modifications of the AD do not represent an adaptation for a specific function, but are mainly found in small mammals. The dentitions are suitable for catching and holding small prey that may be slippery or protected by a hard carapace. In either case, the pointed teeth are sufficient to hold and penetrate the prey. An unequally differentiated anterior dentition seems less suited to an herbivorous diet. However, molar morphology may indicate other dietary adaptations, as frugivory in omomyid primates (Fleagle 1988, Strait 2001).

Clusters with dominating incisors

Cluster 3
"Concordant incisors" (CL-3)

Concordant incisors and small canines

Definition and occurrence: The cluster CL 3 "*Concordant Incisors*" is characterised by the full number of concordant incisors and relatively small canines (FT-4, FT-32). Two evolutionary tendencies meet in CL-3, one is the reduction of

the canine size and the other is the increase of the diastemata between the canines and the premolars (FT-53). In addition, the teeth become increasingly hypsodont. The modifications of the CL-3 have been found in in the PERISSODACTYLA (Fig. 3.1) and in the mesotheriid NOTOUNGULATA

Examples of Perissodactyla
Hyrachyus modification: The Eocene *Hyrachyus* (Fig. 3.1a) is an early rhinocerotoid. The dental formula is complete (3.1.4.3/3.1.4.3) and concordant (FT-1, FT-4, FT-32, FT-53). The AD consists of three incisors that are separated from the canine by a small diastema that varies in size between species. The canine is slightly larger than the incisors, and there is a short diastema between the canine and the premolars (Bai et al. 2017). The AD of *Hyrachyus* is similar to the CL-1, but is included in this cluster due to the diastema. The Oligocene *Hyracodon* (3.1.4.3/3.1.4.3) (Fig. 3.1b) is similar to *Hyrachyus*, but the lower and upper canines are of the same size as the incisors (Radinsky 1967, Fig 17) (FT-1, FT-4, FT-32, FT-53). The diastemata are more prominent. The symphysis of *Hyracodon* is very massive and laterally constricted behind the incisiform canines. In the phylogenetically related *Ardynia* (Fig. 3.1c) the canine is also incisiform, but the subsequent diastema is longer (FT-1, FT-4, FT-34, FT-53).

During the evolution of rhinocerotids, the AD is strongly modified by the enlargement of selected incisors in a discordant mode as in *Trigonias* (see CL-10).

Hyracotherium modification: Perfect fossil skeletons of *Hyracotherium* from Wyoming and *Propalaeotherium* from Messel are well documented (Franzen 2007), but the arrangement of the upper incisors is difficult to determine due to fossilization that has distorted the skulls or isolated the teeth. Apparently, all members of the cluster CL-3 "*Concordant Incisors*" share three upper and three lower incisors. In the reconstruction of Savage et al. (1965) the incisors are loosely arranged, but not in Radinsky (1984). The lower canines are relatively small, slightly larger than incisors or premolars, the uppers slightly larger (Radinsky 1984) (FT-1 FT-4, FT-32, FT-53), but still not comparable to the moderately enlarged canines of Carnivora. The canines of *Hyracotherium* show a distinct sexual dimorphism (Gingerich 1981, Franzen 2007). Diastemata separate the canines from the premolars.

The Oligocene *Mesohippus* (Fig. 3.2a) has three incisors and a small canine in each quadrant. A large diastema extends between the small canines and the low-crowned cheek teeth. *Mesohippus* represents an intermediate stage between the *Hyracotherium* variation and the *Equus* modification with its hypsodont teeth.

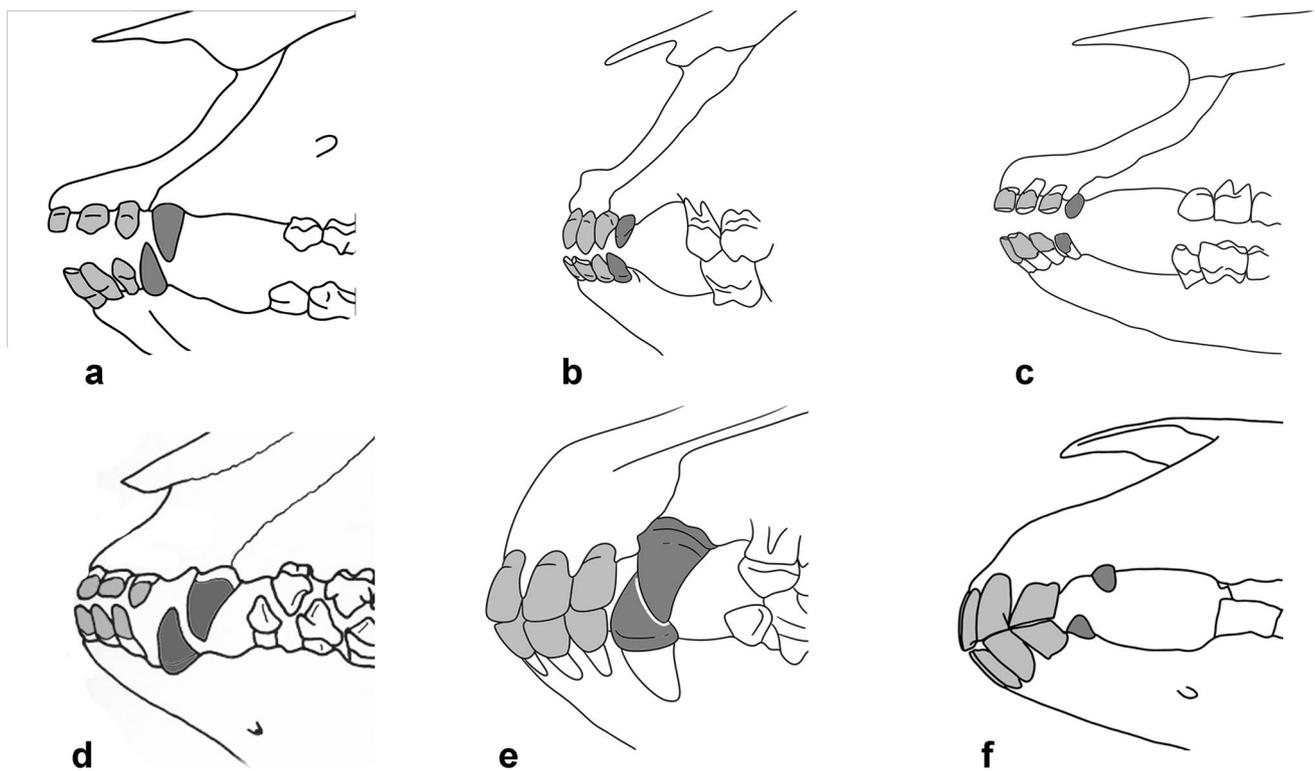In Eocene genera such as *Hallensia* (Fig. 3.1d) *Hyracotherium, Propalaeotherium, Palaeotherium* (Fig. 3.1e), the

Fig. 3.1 "*Concordant Incisors*" (CL-3). **a** *Hyrachyus,* **b** *Hyracodon,* **c** *Ardynia,* **d** *Hallensia*, **e** *Palaeotherium,* **f** *Equus.* (Modified from: **a, b**, and **c** Radinsky 1966, **d** Franzen 1990, **e** Remy 1992, **f** after photo ZMFK)

characteristic diastema is present, but the canines are small to moderately sized (Franzen, 2007, Remy 1992, Radinsky 1965, Scott 1891). These genera show the progressive reduction of canines during the Oligocene, while in *Hipparion* and *Equus* the incisors become increasingly enlarged and hypsodont (Dashzėvėg 1996, Bai et al. 2017).

Equus **modification:** The upper and lower anterior dentitions of *Equus* (Fig. 3.1f and 3-2b) are concordant and characterised by hypsodont teeth. The incisors are subequal in size (FT-1, FT-4). The three upper and lower incisors occlude with an occlusal surface flattened by wear (FT4, FT11). The enamel that surrounds the teeth and the islands
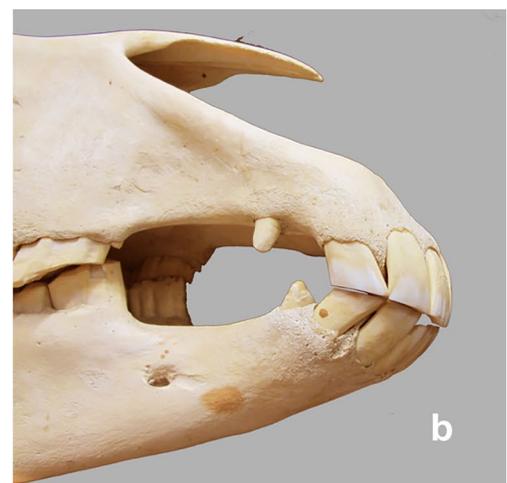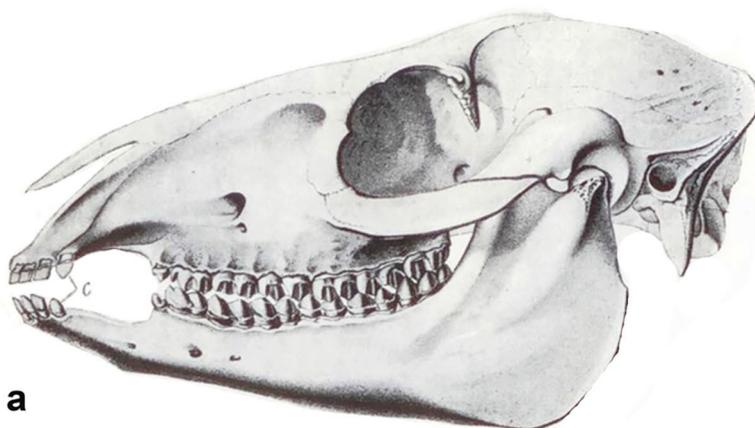
Fig. 3.2 "*Concordant Incisors*" (CL-3). **a** *Mesohippus bairdi,* **b** *Equus caballus* with large, concordant incisors and relatively small canines. (**a** Reproduced from Scott 1891, **b** ZMFK)

forms enamel ridges between the dentin and the cementum. These allow effective grasping and grinding of foliage. The occlusal pattern changes with increasing age. The upper and lower canines are relatively small (FT-32). but show a sexual dimorphism. The canines are separated from the premolars by distinct diastema (FT-53). The *Equus* modification with high-crowned incisors (and molars) is found, for example, in *Merychippus, Pliohippus, Hipparion*.

Examples of Notoungulata

Mesotherium modification: The Pleistocene notoungulate Mesotheriidae from South America (Fig. 3.3) are here included in this cluster, because of their concordant incisors, the relatively small canines and the diastema. The lateral incisors, however, become gradually reduced.

Trachytherus (2.1.4.3/2.1.4.3), *Typotheriops, Pseudotypotherium,* and *Mesotherium* (1.0.2.3/2.0.2.3) represent the specific evolution of this group (Ercoli and Armella, 2021). The euhypsodont central incisors (I1/i1) were progressively broadened in mesio-lateral direction. The lateral incisors were progressively reduced, and simultaneously the diastemata expanded (FT-2, FT-3a, FT-6a, FT-8, FT-30, FT-53). Canines are small in *Trachytherus* (FT-32) but completely reduced in *Mesotherium* (FT-30). The upper dentition is more progressive in favour the central incisors the than the lower. Lower incisors occlude with the broadened surface of the upper incisors.

It should be mentioned that the more derived mesotheriid *Thypotheriopsis* concentrates the function even more on the central upper and lower incisors with a wide diastema (Croft, 2016). These mesotheriid genera represent a stratigraphically late differentiation of this cluster (CL-3).

Discussion of the CL-3 "Concordant incisors"

The CL-3 *"Concordant Incisors"*, characterised by concordant incisors with large occlusal surfaces, evolved twice independently in Equoid and notoungulate Mesotheriidae herbivores. The battery of incisors is well suited for grasping plant material from the ground. Thus, this cluster is strictly related to herbivory. Plants are either cut by the enamel ridges on the incisors or pulled off squeezing between the lower and upper incisors. After plant material has been taken, the tongue moves it backwards into the premolar-molar region where it is disintegrated. The diastema marks the separation of the two functional areas. Horses have very tactile lips, and functionally the member united in CL-3 are distinctly different from other grazing mammals. The ruminants in CL-17 *"Ruminant Incisor Arcade"* have reduced their upper incisors and rely on lips or other soft parts to grasp foliage.

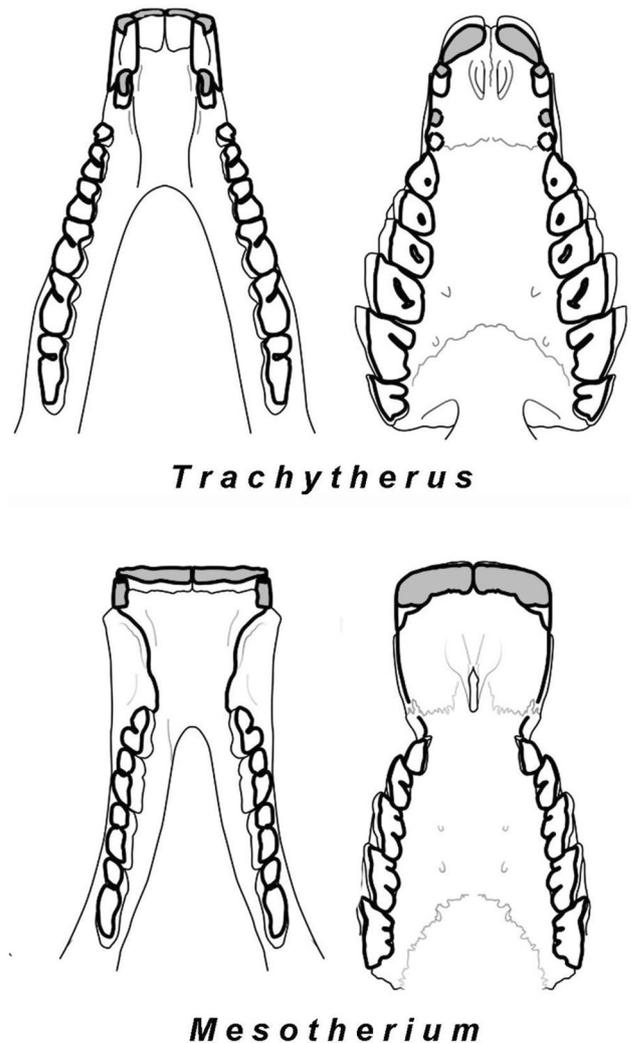The evolutionary lineages, Equoidea and Mesotheriidae show a different functional significance for their incisors

Fig. 3.3 *"Concordant Incisors"* (CL-3). Lower (left) and upper (right) dentitions in the notoungulate *Trachytherus* and *Mesotherium.* (From Ercoli and Armella 2021)

and canines. In the Mesotheriidae the incisors are greatly widened with a strict preference for the central incisors. The canines are reduced.

In Equoidea (sensu Franzen 2007) all incisors are of similar and the canines have little functional significance. Sexual dimorphism of the canine size has been found in some taxa (e.g. *Equus*), suggesting a social significance.

There are two evolutionary pathways. In the more conservative modifications (e.g. *Hyracotherium, Hipparion, Equus*), all three incisors are preserved and of equal size.

In the *Mesotherium* modification, the number of lateral incisors is reduced but the central incisor is dominant and of increasing size. The presence of large concordant incisors in the derived Equini and Hipparionini on the one hand, and the broadening of the central incisors in the Mesotherinae on the other, prove an independent evolution.

Cluster 4
"Pair of large rooted incisors" (CL-4)

Single pair of large and rooted incisors that are antagonists

Definition and occurrence: A single pair of enlarged and antagonistic incisors (FT-3) characterises the CL- 4 "*Pair of Large Rooted Incisors* ". Central incisors dominate (FT-6a); others are very small or lacking. Antemolars are reduced to a variable degree (FT-52) and often replaced by a diastema (FT-53).

Taxa representing CL-4 have been found in unrelated mammalian groups. MARSUPIALIA (T*hylacoleoFnotamacropus),* INSECTIVORA (*Brachyerix*), PERISSSODACTYLA (*Paraceratherium),* and most probably in PROBOSCIDEA (*Moeritherium*). Some Mesozoic Tritylodontia may also fit into the CL-4 "*Pair of Large Rooted Incisors*".

Examples of Marsupialia
Thylacoleo modification: The carnivorous diprotodont marsupial *Thylacoleo* (3.1.3.1/1.0.3.2) (Fig. 4.1a) has a pair of massive upper and lower incisors (I1/i1) (FT-2, FT-6a, FT-7, FT-8, FT-52). They are conical and pointed, covered with enamel and have well developed roots. In the upper jaw, three rudimentary teeth follow, which are two incisors and a small canine. The P1 and P2 are small. The huge P3 is elongated and has a sharp blade.

In the lower jaw the massive incisor is rooted and pointed, similar to the upper incisors. The gap between the incisor and the huge p3 may be filled by one or two small teeth, which are lost in many jaws. The p3 is trenchant with a longitudinal blade. It is sharpened by the enamel on the medial side (Owen 1871). The teeth of the antemolar region are strongly reduced, except for the huge last premolars (P3/p3). The reduction is more pronounced in the mandible than in the upper jaw. The enlarged blade-like third premolars (P3/p3) sharpen each other synchronously and form a convergence with the carnassial of Carnivora,

Examples of Insectivora
Brachyerix modification: The erinaceid *Brachyerix* (3.1.2.2/2.1.1.2) is – so far – the only small mammal assigned to the CL-4 "*Pair of Large Rooted Incisors*" (Fig. 4.1b) (FT-6a). It has strongly enlarged upper and lower first incisors, followed by two small incisors in the premaxilla and a double-rooted C, a small P3 and a large P4 in the maxilla. In the mandible the enlarged i1 is followed by a low but elongated tooth (i2) and another small tooth, which is a canine because it occludes with the anterior side of the upper canine (Rich and Rich 1971) (FT-32) The following tooth is a p4. *Brachyerix* fits well into this cluster.

Examples of Perissodactyla
Paraceratherium modification: The giant hyracodontid *Paraceratherium* (= *Indricotherium* following Wang et al. 2016) (1.0–1.4.0.4.3/1.0.3.3) has a pair of enlarged upper and lower incisors (I1 and i1) (Fig. 4.1c). These teeth are massive but short. The second and third incisors are reduced in both the upper and the lower jaws. An upper canine is occasionally present (Radinsky 1966, Fig. 3). The single incisor of the mandible is procumbent but sometimes turned slightly downward (Cooper 1924). Wide diastemata separate the incisors from the premolars (FT-2, FT-6a, FT-7, FT-8, FT-53). If the incisors occlude remains open in the different reconstruction of the dentition.

Examples of Proboscidea
Moeritherium modification: The Eocene proboscidean *Moeritherium* (3.1.3.3/2.0.3.3) has a pair of prominent incisors (I2/i2), which are enlarged but not euhypsodont (FT-6a, FT-7, FT-40, FT-53). They are covered with a thin enamel (Fig. 4.1d). The mesial I1/i1 are small but functional. Lower
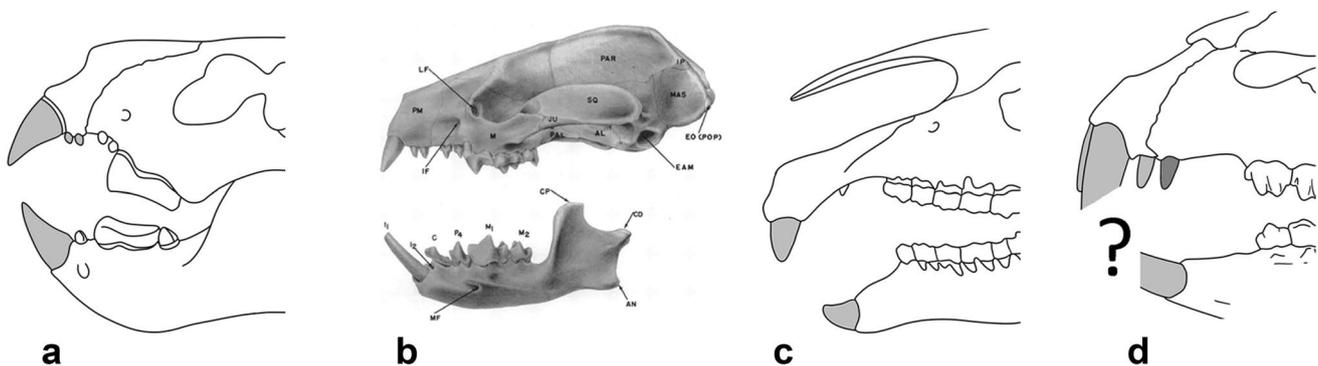

Fig. 4.1 "*Pair of Large Rooted Incisors*" (CL-4). **a** *Thylacoleo* (MARSUPIALIA), **b** *Brachyerix* (EULIPOTYPHLA), **c** *Paraceratherium* (PERISSIODACTYLA), **d** *Moeritherium* (PROBOSCIDEA). (Modified from: **a** Thenius 1989, **b** Rich and Rich 1971, **c** Radinsky 1966, **d** Andrews 1906)

canines are absent (Sanders et al. 2010a, b). A diastema separates the AD from the premolars. The tooth loci of the enlarged teeth (I2/i2) differ from those of Elephantiformes (I1/i2) (Tassy 1987, Gheerbrandt 2005, Gheerbrandt et al. 2005, Delmer 2009). The preservation of the occlusion pattern in the AD of *Moeritherium* is poor. Andrews (1906) reconstructed the enlarged incisors (I2/i2) as prominent tusks (which do not necessarily occlude). Osborn (1936) rejected the tusk hypothesis and described a facet over the entire cross-section of the upper I2, beveled by the lower i2. The reconstructed steep anterior facet on the lower i2 is reminiscent of an overbite with a truncated incisor, more similar to *Procavia* (CL-6). *Moeritherium chehbeurameuri* (Delmer et al. 2006) supports Osborn's interpretation to some degree. The proboscidean *Moeritherium* is included this cluster CL-4 because of its pair of enlarged incisors. The uncertain nature of their occlusion did not allow me to include *Moeritherium* in CL-11 like the other proboscideans.

Discussion of CL-4 "Pair of large rooted incisors"

Only few taxa have been found that have an AD fitting to CL-4. The homology of the enlarged incisors is uncertain. A pair of pointed incisors concentrates the biting forces, but the taxa included in the CL-4 "*Pair of Large Rooted Incisors*" are not restricted to any particular dietary category. *Brachyerix* is an insectivore. *Thylacoleo* was the largest marsupial carnivore and is interpreted as an ambush predator or scavenger. Although its enlarged incisors may have served to catch and kill prey (Turnbull 1978, Wroe et al. 2005), these teeth are is not comparable to the canines of felids and much less suitable for killing prey (Figueirido et al. 2016). The carnassial (P3/p3) of *Thylacoleo* are convergent with those of placental Carnivora. The carnivorous nature of this species has been supported by chemical analysis of the bones (Nedin 1991). The large *Paraceratherium* (=*Indricotherium*) was an herbivore. Its lower incisor is turned slightly downward, which excludes an occlusion with the upper incisor. Granger and Gregory (1936) concluded: "Osborn has also suggested that the enlarged upper incisors functioned as defensive tusks. Their primary function, however, was to assist in the sudden jerking loose of shrubs by downwards movements of the head and neck, since they are well placed to act as picks and levers, while the skull is braced to resist such stresses through its strong rostrum, down-curved zygomata and greatly emphasised basi-occipital eminence".

All taxa assigned to this cluster (CL-4) show a reduction of some or most antemolars, similar to taxa in CL-8 and CL-9. Thus, the enlargement of certain incisors seems to be related to the formation of a diastema.

Thus, the taxa with a concordant pair of enlarged incisors form a very heterogeneous cluster. This functional model does not seem to have been very successful.

Cluster 5
"Rooted overbite incisors" (CL-5)

Rooted overbite incisors, upper incisors truncate lowers

Definition and occurrence: In the cluster CL-5 "*Rooted Overbite Incisors*" the upper and lower incisor are discordant and occlude in an overbite mode (FT-6a). The upper incisor is more anterior and vertically aligned. The forward protruding lower incisor occludes with the posterior side of the anterior incisors. The angle between the tooth axes is large and reaches almost 90°. The cluster includes taxa with rooted upper incisors (Fig. 5.1). Taxa that have euhypsodont incisors are separated in CL-6 "*Euhypsodont Overbite Incisors*".

The overbite mode of the incisors (FT-13) is associated with the selective enlargement of certain incisors and the reduction of antemolars (FT-52) The CL-5 "*Rooted Overbite Incisors*" has been found in unrelated mammalian groups: INSECTIVORA (*Desmana, Galemys*), and NOTOUNGU-LATA (*Notostylops*),

Examples of Insectivora
***Desmana* modification:** The small, insectivorous-carnivorous talpid genera e.g. *Desmana*, *Galemys* (3.1.4.3/3.1.4.3) (Fig. 5.1a, 5.2), *Parascalops, Scapanus,* and *Scalopus* belong to this cluster, because they have an enlarged upper I1 (FT-6a.-FT-7, FT-13) that is implanted almost vertically, and occludes with the lower incisor on its posterior side (Niethammer and Krapp 1990). The I2 and I3 are small. The upper canines are small but slightly larger than the third incisor. There is no diastema in the upper or lower tooth row. Among the lower incisors, the i2 is the largest and occludes with the upper I1. The morphology of the i2 varies somewhat among the genera listed. In *Scapanus*, the lower incisors are almost equal in size (FT-4), whereas in *Desmana*, *Galemys*, and *Scalopus* the i2 is enlarged (FT-5) and slightly procumbent (ADW). The AD is characterised by the I1/i2
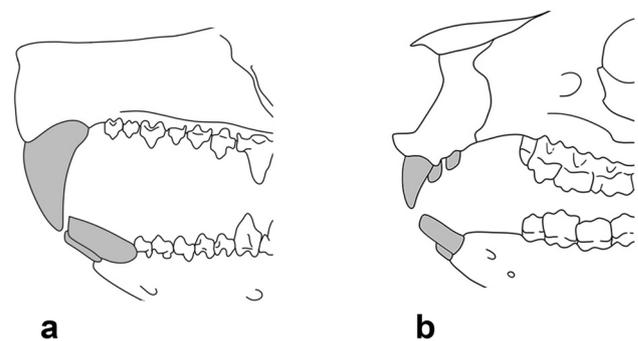

Fig. 5.1 "*Rooted Overbite Incisors*" (CL-5). **a** *Desmana* (SORICO-MORPHA), **b** *Notostylops* (NOTOUNGULATA). (Modified from: **a** Thenius 1989, **b** Simpson 1948)
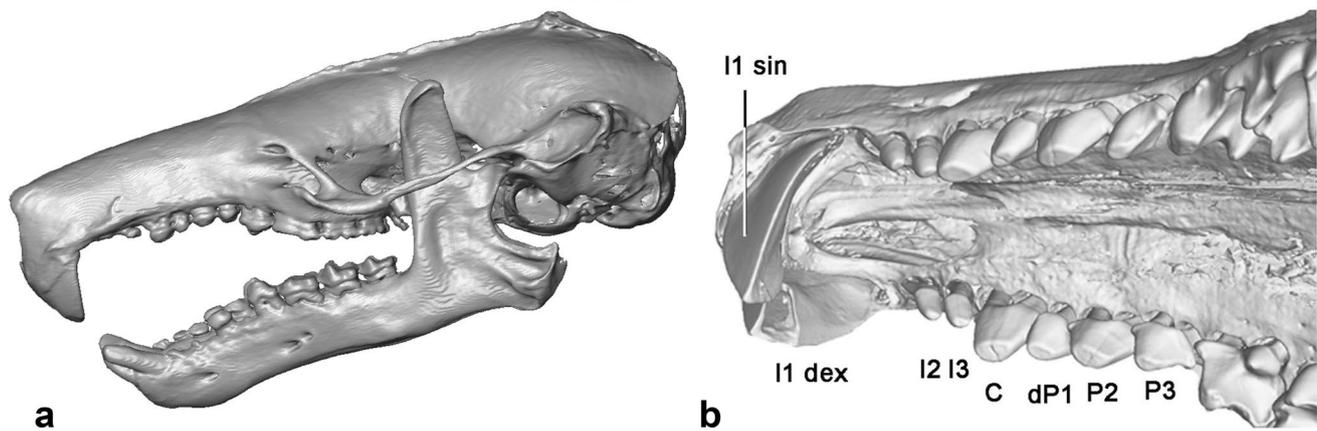
Fig. 5.2 *"Rooted Overbite Incisors"* (CL-5). **a** *Desmana moschata* (SORICOMORPHA) cranium with mandible. **c** *Galemys pyrenaicus* anterior dentition enlarged upper incisors. (**a** SMF - ZIN 98375, **b** µCT models BIOP-PAL)

functional complex. The AD of the other Talpidae is clearly different. The related genus *Talpa* is an example of the cluster CL-16 *"Canine-Premolar Unit"*.

Examples of Notoungulata

***Notostylops* modification:** In the notungulate genus *Notostylops* (Fig. 5.1b) the dental formula is quite variable. It has an enlarged pair of rooted incisors, formed by I1 and i2 (Simpson 1948) (FT-6a, FT-7, FT 13, FT-52). The upper incisor (I1) is vertically oriented and has a long facet on its posterior side, I2 and I3 are comparatively small. The canines and anterior premolars are largely reduced, leaving a considerable space for a large diastema. In the lower dentition, i1 is modest while i2 is about twice as large. Despite difference in size both lower incisors work against the posterior surfaces of the upper incisors at an almost right angle (Simpson 1948. 177). The i2 is vertically truncated, similar to *Procavia* (Simpson 1932a, b). Canines are absent from the upper and lower tooth rows, and a long diastema extends to the second premolars.

Discussion of CL-5 "Rooted overbite incisors"

As is generally the case in mammalian dentitions, the posterior side of the upper incisors functions with the anterior side of the lower incisors. This is exaggerated in CL-5, where the upper incisor shows a large facet which occludes and truncates the lower procumbent incisor. The characteristic feature of the overbite structure is the large, angle between the axes of the lower incisors, that may reach almost a right angle. The overbite is somewhat similar to the rodent occlusion (CL-9). But there the enlarged incisors are strongly curved and occlude more tip to tip with a much shorter facet in the upper incisor. The overbite mode occurs in two modifications, with

rooted or euhypsodont teeth (CL-6). The CL-5 *"Rooted Overbite Incisors"* seems to be rare, whereas the other with euhypsodont incisors evolved more common.

The two examples found to represent in the cluster CL-5 share the same enlarged tooth loci (*Desmana* and *Galemys*. I1/i2, *Notostylops*. I1/i2), but belong to unrelated mammalian lineages. Their corresponding tooth loci are most likely a coincidence, as the tooth loci in the euhypsodont incisors (CL-6) vary.

Cluster 6
"Euhypsodont overbite incisors" (CL-6)

Euhypsodont overbite upper incisors that truncate lower incisors

Definition and occurrence: The CL-6 *"Euhypsodont Overbite Incisors"* describes upper euhypsodont incisors that overbite and truncate the lower incisors (FT-8, FT-13). In contrast to CL-5, the overbite in CL-6 does not involve a single pair of incisors, but several selectively enlarged incisors. The euhypsodont incisors which have enamel mostly on the anterior side, occlude at an almost right angle and abrade each other in a specific way. The upper incisor is are steeply inclined, while the lower incisor is are more procumbent. The upper incisor truncates the lower incisor, while the lower incisor abrades the posterior surface of the upper incisor (Fig. 6.1). The modifications show different degrees of reduction (FT-52).

ADs related to cluster CL-6 *"Euhypsodont Overbite Incisors"* occur in several unrelated mammalian groups of. METATHERIA (*Phascolonus*). HYRACOIDEA (*Procavia, Dendrohyrax*), and NOTOUNGULATA (*Diadiaphorus, Nesodon* and *Hegetotherium*),
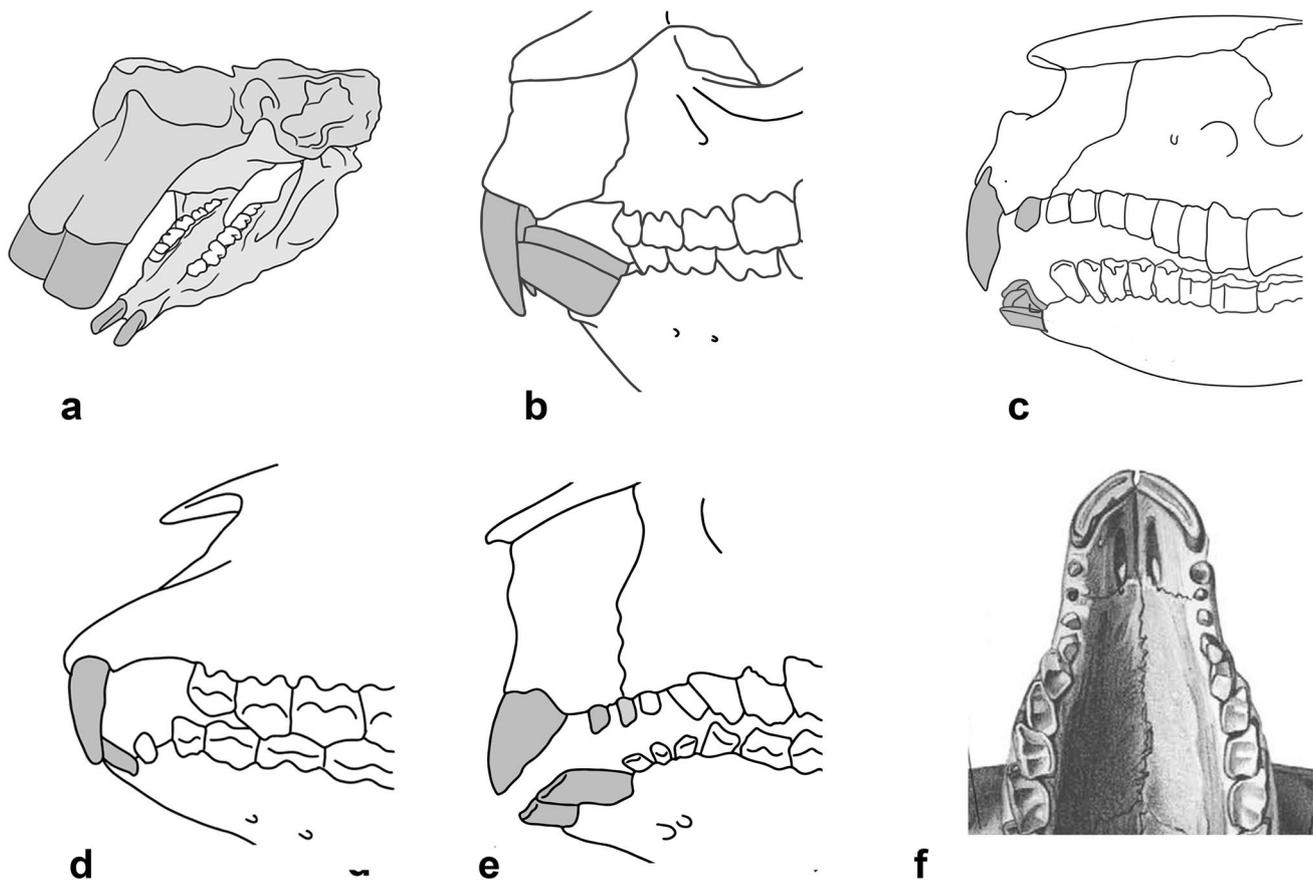
Fig. 6.1 "*Euhypsodont Overbite Incisors*" (CL-6). **a** *Phascolonus* (MARSUPIALIA), **b** *Procavia,* (HYRACOIDEA), **c** *Nesodon* (NOTOUNGULATA), **d** *Diadiaphorus*, **e** and **f** *Hegtotherium(d-f* NOTOUNGULATA). (Modified from: **a** 3D model in the Queensland Museum, **b** Schultz 1971, **c** Zittel 1893, **d** Scott 1910, **e** and **f** McCoy and Norris 2012)

Examples of Marsupialia

***Phascolonus m*odification:** The giant Pleistocene vombatid *Phascolonus* (1.0.1.4/1.0.1.4) (FT-2, FT-3a, FT-6a, FT-8, FT-13, FT-52, FT-53). has discordantly enlarged euhypsodont incisors (I1 and i1) (Fig. 6.1a and 6.2). The upper incisor is a flattened and very broad strap-like tooth, approximately 30 mm wide (Stirling and Zietz 1913). The lower incisor is more rounded and much smaller. Its cross-section is about 10 mm (Louys 2015, Owen 1872, Tedford 2002, https.//sketchfab.com). The distal side of the flattened upper incisor is slightly concave and has a broad facet abraded by the lower incisor. The lower incisor protrudes and is truncated by the posterior side of the broadened upper incisors (Lydekker 1891, Murray 1998). The incisors of *Phascolonus* occlude at an almost right angle. Murray (1998, Fig. 29) observed small additional facets, that may indicate the maximum lift of the lower incisor – similar to the break block in clusters CL-8 "*Mandible with Procumbent Incisor"* and CL-9 "*Gliriform Incisors".* Because of the large angle between the upper and lower incisors, the facets are oriented more similarly to *Procavia*

than to the related *Vombatus* or *Diprotodon* in CL-7 "*Large Flat-Nose Pliers*".

Examples of Hyracoidea

***Procavia* modification:** Extant *Procavia* (Fig. 6.1b) and *Dendrohyrax* (1.0.4.3/2.0.4.3) have a dominant pair of euhypsodont incisors (FT-3, FT-8, FT-13, FT-52) that is formed by the upper I1 and the lower i2 (Barrow et al. 2012, Asher et al. 2017). There is a distinct gap between the right and left upper incisors (I1). The I1 has a triangular cross-section with an anteriorly directed keel. The anterior surface is covered with enamel, while the distal side is exposed dentin. A large, almost vertical facet on the posterior side forms the sharp tip on the anterior keel. The facet documents the intensive abrasion by the lower incisor. The lower incisor (i2) is procumbent and vertically truncated by the upper incisor. The angle between the two teeth is about 90 degrees. Between the enlarged lower incisors (i2) of the right and left side, there are two small i1, corresponding to the gap between the right and left premaxillae. Canines are absent. A short diastema separates the upper incisors from the premolars.

Fig. 6.2 "*Euhypsodont Overbite Incisors*" (CL-6)**.** *Phascolonus* (MARSUPIALIA)*,* cranium with broad incisors. (Cast at the AMNH, photo courtesy John Wahlert)

Examples of Notoungulata

Adinotherium* modification: The AD of the notoungulate *Adinotherium* (3.1.4.3/3.1.4.3) is formed by three upper and three lower incisors. The upper I2 and the lower i3 are dominant, almost caniniform (Fig. 6.3) (FT-5, FT-6a, FT-13, FT-53). The upper I1 is pointed and directed downward (Sinclair 1909). The lower i3 is truncated. They abrade each other with a steep facet. The upper I1 and the lower i1 and i2 are much smaller but extend the facet, which may permit both, an orthal and a lateral shearing movement. The upper I3, C, and lower canine are reduced in size and do not participate in the shearing facet (Fig. 6.3 and 6.4). Sinclair (1909 pl. XVI) observed, that the size of the I2 increases with individual age. Upon full eruption, the tooth projects even more than the upper I1 and may serve a social function.

Nesodon (3.1.4.3/3.1.4.3) (Fig. 6.1c, Fig. 6.4) has a cutting device similar to that observed in *Adinotherium.* However*,* the upper I1 is slightly less broadened (Fig. 6.4) In both genera the central incisors are not enlarged (FT 8, FT-12, FT-13, FT-15, FT-28) as in many other herbivores.

Hegetotherium* modification: The notoungulate *Hegetotherium* (3.1.4.3/3.1.4) has significantly enlarged and euhypsodont first upper and lower incisors (I1and i1) (FT-2, FT-3, FT-6a, FT-10, FT-13, FT-52). The upper I1 is enlarged, and angled downward (McCoy and Norris 2012, Croft 2006). It also has a facet on its posterior side (Reguero and Cerdeno 2005). The upper I2 and I3 and the canine are reduced to cylindrical cones. In the lower dentition i1 and i2 are broadened and almost horizontally procumbent. They occlude with the large upper I1. The i3, the c and first premolar are minute. There is no diastema in either the upper or lower dentition (Croft 2006). Sinclair (1908: 68) compared the
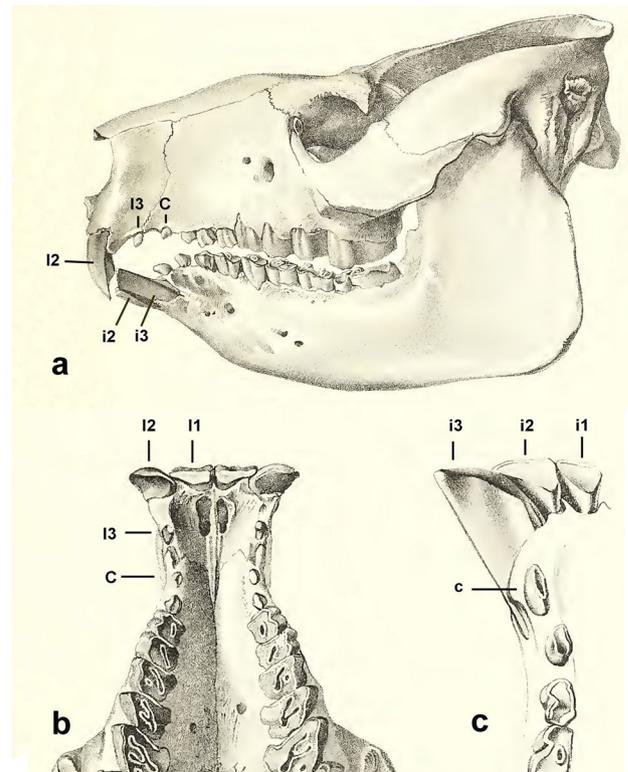

Fig. 6.3 "*Euhypsodont Overbite Incisors*" (CL-6)**. a** *Adinotherium* (NOTOUNGULATA), cranium, **b** and **c** anterior part of upper and lower dentition. (From Scott 1909-1928, Pl XIII+XX)
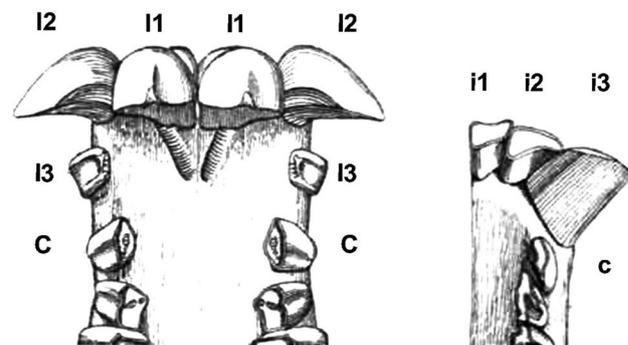

Fig. 6.4 "*Euhypsodont Overbite Incisors*" (CL-6). *Nesodon imbricatus* (NOTOUNGULATA), **a** – upper anterior dentition, **b** lower anterior dentition. (From Zittel 1899: Figs. 398 and 399)

incisor orientation of *Hegetotherium* with that of Hyracoidea. However, the upper incisor of *Hegetotherium* is not as massive as in Hyracoidea, but thin and lingually curved. McCoy and Norris (2012) postulated a woodpecker behaviour for *Hegetotherium*, based on cranial similarities with *Daubentonia*.

Examples of Litopterna

Litoptern modification: The litoptern genera *Proterotherium* and *Diadiaphorus* (Figs. 6.1d and 6.5) (1.0.4.3/2.1.4.3) (FT-2, FT-7, FT-13, FT-52) have a markedly enlarged upper incisor (Scott 1910). It is pointed and euhypsodont, growing from a persistent pulp. The tooth is curved and oriented almost vertically. The upper incisor has a trigonal cross-section. A large wear facet on the posterior side indicates the occlusion with the enlarged and procumbent lower incisor (i3). Due to the abrasion the anterior keel has formed a sharp point. The pair of enlarged incisors meet at an angle of approximately 90°. The left and right upper incisors are separated by a gap corresponding to the presence of a small lower incisor (i2). Scott indicated that the position of the single enlarged upper incisor is a I2, but this remains uncertain, due to the absence of other upper incisors and the canine. The lower AD contains a small i2 and a very small canine of minor functional importance. The Prototheriidae were included because of the euhypsodont upper incisor. However, the lower incisors are not mentioned as euhypsodont (Scott 1910).

Discussion of CL-6 "Euhypsodont Overbite Incisors"

The overbiting upper incisors that truncate the lower incisors are used for cutting herbivorous food. Several incisors may be involved, in contrast to CL-5 taxa that have only a single pair of overbiting incisors. Although the function of the overbiting incisors is similar in both clusters, no close relationship can be seen. They probable evolved independently.

Two different strategies can be observed in the euhypsodont incisors. A concentration on the central incisors is evident in the modifications represented by *Phascolonus, Procavia* and *Hegetotherium*, but the tooth loci differ. Furthermore, *Phascolonus* has a wider mouth and a more pointed jawline, than *Hegetotherium*. The second mode has a very wide mouth with

Fig. 6.5 "*Euhypsodont Overbite Incisors*" (CL-6). *Diadiaphorus* (LITOPTERNA). (From Scott 1910)

enlarged caniniform lateral incisors. It includes *Adinotherium, Nesodon,* and the litoptern *Diadiaphorus*. The two modes evolved independently in the different groups.

The truncated euhypsodont incisors serve as cutting tools, similar to those in CL-5 "*Rooted Overbite Incisors*", but they allow for more intensive abrasion, because the loss of material is compensated by the continuously growing teeth. In contrast to CL-9 "*Gliriform Incisors*" the abrasion is mutual (FT-40) and not reciprocal (FT-11). One distinctive feature of CL-6 "*Euhypsodont Overbite Incisors*" is the angle between the occlusal incisors (FT-17). Dentin forms the majority of the facets, with the enamel covering a minor component. It does not form a sharp cutting edge comparable to that of rodent incisors. Euhypsodont incisors require a regular abrasion. Unlike the gliriform incisors, the incisors in this cluster develop a sharp blade only on the upper tooth rather, than in both, upper and lower incisors as is the case with the Glires or *Daubentonia*.

Cluster 7
"Large flat-nose pliers" (CL-7)

Large concordant incisors occluding at a low angle

Definition and occurrence: Massive, euhypsodont, and procumbent incisors characterise the CL-7 "*Euhypsodont Overbite Incisors*" (Fig. 7.1). The number of enlarged incisors varies in the modifications, and may be reduced to one. The slightly curved incisors occlude at a low angle (FT-17c). The enamel is restricted to the anterior surface and usually does not form a sharp cutting edge. Antemolars are often reduced. A diastema separates the dominant incisors from the premolars (FT-52, FT-53).

Such teeth occur in MARSUPIALIA (*Diprotodon. Vombatus*, and *Lasiorhinus*), PYROTHERIA (*Pyrotherium*), and *Toxodon* (NOTOUNGULATA).

Examples of Marsupialia

***Diprotodon* modification:** In *Diprotodon* (3.0.1.4/1.0.1.4) (Figs. 7.1a, and 7.2) a pair of massive euhypsodont incisors dominates the anterior dentition (I1 and i1) (FT-2, FT-8, FT-13, FT-30, FT-53). The upper and lower first incisors are and have a massive dentin core with a thin enamel covering on the anterior surface. The incisors occlude at a low angle with an almost horizontal facet (FT-17c), similar to a pair of pliers. The occlusal facet of the upper incisor is twofold. The anterior side of the I1 is slightly overhanging, and the lower incisor rubs its posterior side. The more distal part of the I1-facet forms a more horizontal facet together with the following I2 and I3. Together, they form the more horizontal occlusal surface for the lower I1. A large diastema separates the incisors from the premolars (Sharp 2014).
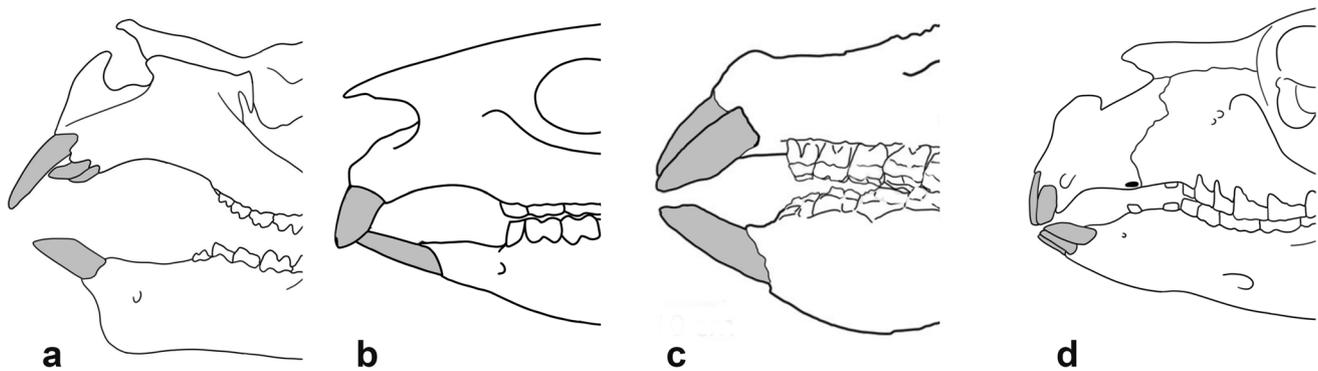
Fig. 7.1 *"Large Flat-Nose Pliers"* (CL-7). **a** *Diprotodon*, **b** *Vombatus* (**a** and **b** MARSUPIALIA), **c** *Pyrotherium* (PYROTHERIA), **d** *Toxodon* (NOTOUNGULATA). (Modified from: **a** Thenius 1989, **b** Sharp 2014, **c** Billet 2010, **d** Zittel 1893)

Fig. 7.2 *"Large Flat-Nose Pliers"* (CL-7). *Diprotodon* (MARSU-PIALIA), Cranium. (Courtesy of the John Fields/Australian Museum. Wikipedia)

The mandible has only one incisor. It is procumbent and euhypsodont. Its occlusal facet is almost horizontal and occludes with the horizontal facet in the upper incisors. The enamel band on the mesial side does not form a sharp cutting edge. The facets of the i1 and the combined facets upper incisors function like the lips of flat nose pliers.

The number of three upper incisors in *Diprotodon* is a reminiscent of the arcade in other diprotodont marsupials, as preserved in *Neohelos* (Murray et al. 2000). The reduction of the antemolars is in the upper dentition less than in the lower.

The ***Vombatus* modification** (1.0.1.4/1.0.1.4) (FT-2, FT-8, FT-13.,FT-17c, FT-30, Ft-33) has a pair of enlarged euhypsodont incisors (I1 and i1), which occlude with an almost horizontal facet (Fig. 7.1b). The angle between upper and lower incisors is low, significantly less than 90°. The enamel is restricted to the anterior surface, but does not form

a sharp blade. The other incisors and canines are reduced. A large diastema separates the AD from the premolars. All teeth are euhypsodont.

Examples of Pyrotheria
***Pyrotherium* modification:** *Pyrotherium* (2.0.3.3/1.0.2.3) has two upper incisors of similar size that are enlarged and procumbent (Fig. 7.1c) (FT 2, FT-5, FT-8, FT-17c, FT-40, FT-53). The mandible has one very strong procumbent incisor. The massive dentin teeth are covered by a band of enamel on their anterior sides. The teeth occlude at a low angle. A trunk is postulated due to the wide-open nasal aperture (Billet 2010).

The tooth loci of the two upper incisors and the single lower incisor are under discussion (MacFadden and Frailey 1984, Lucas 1986). If *Notostylops*, which belongs to the cluster CL-6 *"Euhypsodont Overbite Incisors"*, is considered a model for *Pyrotherium*, the procumbent lower incisor may be an i2 (Billet 2010).

Examples of Notoungulata
***Toxodon* modification:** *Toxodon* (2.0.4.3/3.0.3.3) has unequally enlarged incisors forming a plier-like grasping tool. (Fig. 7.1d) (FT-5, FT-6a). The central upper incisor (I2) is significantly wider and is accompanied by a much narrower I3. Both form a transverse cutting edge. In the lower dentition there are three procumbent incisors, i.e. the teeth are lamellarly arranged, one overlapping the other (Fig. 7.3). They have a broad almost horizontal wear facet, that acta as a Layer with the upper incisors. This qualifies *Toxodon* for the CL-7 *"Large Flat-Nose Pliers"*. Long diastemata separate the incisors from the premolars. A small canine has been occasionally observed (Owen 1837, Mones and Heintz 1992) but is more common in *Posnaskytherium* (Salas-Gismondi et al. 2023).

Fig. 7.3 *"Large Flat-Nose Pliers"* (CL-7). *Toxodon* (NOTOUNGULATA). **a** Cranium**, b** Occlusion of **i**ncisors. (Photos: **a** courtesy of the Bernardino Rivadavia Natural Sciences Museum, via Wikipedia, **b** courtesy of J. Hurum, NORPAL Oslo)

Discussion of CL-7 "Large Flat-Nose Pliers"

The enlarged incisors of *Vombatus, Diprotodon,* and *Pyrotherium* occlude at a low angle with their thick dentin bodies. Although the enamel is limited to a band on the anterior side, no sharp cutting edges are produced by abrasion. The incisors are less suitable for cutting but are used for pulling foliage from the ground. Mastication occurs in premolars and molars behind the diastema. *Vombat*us digs its underground den with its claws, but not with its teeth (Nowak 1999). The related *Phascolonus* is considered to belong to this cluster CL-7, because it has a strong overbite.

The dentition of *Toxodon* has been interpreted as specialised grazer. In southern Bolivia its main diet consisted of C4 grasses. However, in the forested Amazon Basin, however, *Toxodon* browsed on forest plants. *Toxodon* consumed a much more divers diet than expected from its molar morphology (Croft 2016).

Diprotodon and *Vombatus* most likely share the diprotodonty as a parallelism from a common ancestor. *Pyrotherium* and Vombatidae are not related, so the type of incisor occlusion is convergent. This includes the large diastema, resulting from the reduction of the antemolars.

Euhypsodont incisors require a constant abrasion. The enamel on the mesial side of the massive teeth does not provide a sharp cutting edge. Due to the low angle between the axes of the upper and lower incisors, there is no cutting device. The abrasion is clearly distinct from the gliriform incisors, which occlude at a very steep angle of about 180°.

Cluster 8
"Mandible with procumbent incisor" (CL-8)

Mandible with single procumbent incisor,
that has a discordant antagonist

Definition and occurrence: A single enlarged and procumbent lower incisor dominates the AD in CL-8 *"Mandible with Procumbent Incisor"* (Fig 8. 1). The well-rooted incisor is unicuspid and has no concordant antagonist (FT-2, FT-5, FT-7, FT-10). The central upper incisor may also be specialised, but in a different way. Wear of the rooted incisors is limited. Modifications show different stages of reduction of upper and lower antemolars. In diprotodont marsupials several upper incisors form an antagonistic arcade. In some genera the remaining antemolars are crowded, in others the antemolar region is replaced by a diastema. Most taxa in this group are small, with only a few marsupials (e.g. *Macropus*) reaching a considerable body size. In some families, such as the Soricidae, the enamel is often pigmented (FT-54).

The characteristics of this cluster *"Mandible with Procumbent Incisor"* have been found in several unrelated groups of mammals (Fig. 8. 1). EUHARAMYIDA: e.g. *Mirusodens,* MULTITUBERCULATA: e.g. *Kryptobaatar, Taeniolabis, Ptilodus, Barbatodon,* in AMERIDELPHIA: e.g. *Caenolestes,* in Australian DIPROTODONTIA: e.g. *Trichosurus, Macropus,* and in SORICOMORPHA: e.g. Soricidae (*Blarina, Neomys, Suncus),* Erinaceidae *(Amphechinus),* Apternodontidae *(Apternodus*), in APATOTHERIA, e.g. *Heterohyus,* PLESIADAPIFORMES, e.g. *Plesiadapis,*
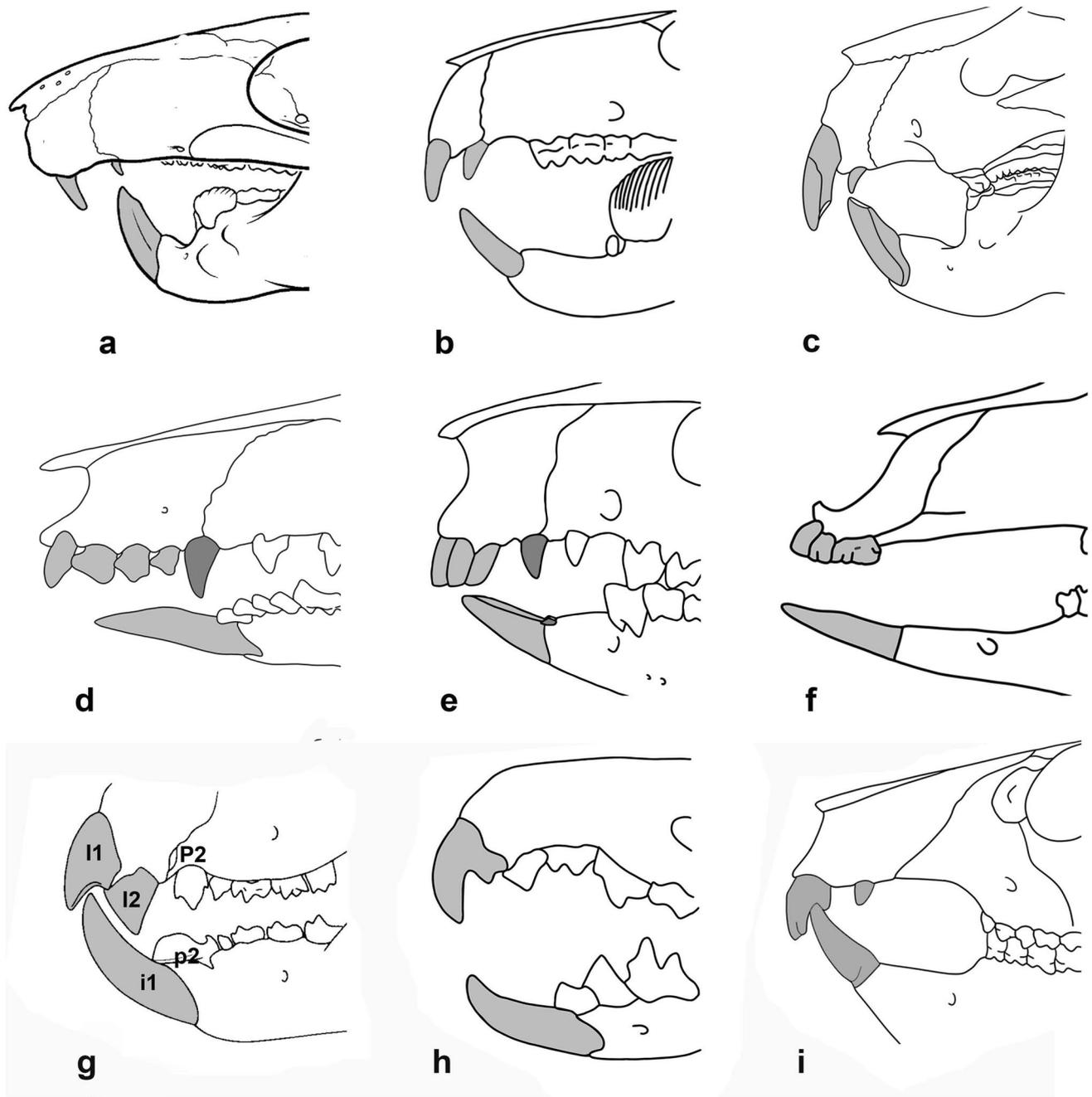
Fig. 8.1 "*Mandible with Procumbent Incisor*" (CL-8). **a** *Kryptobaatar* (Multituberculata), **b** *Ptilodus* (Multituberculata), **c** *Taeniolabis* (Multituberculata), **d** *Caenolestes* (Paucituberculata), **e** *Trichosurus* (MARSUPIALIA), **f** *Macropus* (MARSUPIALIA), **g** *Heterohyus* (APATOTHERIA), **h** *Suncus* (INSECTIVORA), **i** *Plesiadapis* (PRIMATES). (Modified from: **a** Wible and Rougier 2000, **b**, **d**, **e**, **f** and **i** Thenius 1989, **c** Granger and Simpson 1929, **h** Koenigswald 1990, **i** Gingerich 1976)

Mammals with enlarged but concordant incisors are excluded here and assigned to other clusters, e.g. Vombatidae cluster CL-7 *"Large Flat-Nose Pliers"*, Rodentia and Lagomorpha in cluster Cl-9 *"Gliriform Incisors"*.

Examples of Allotheria

***Mirusodens* modification:** The Upper Triassic euharamyid *Mirusodens caii* (1.0.3.2/3.0.1.2) can be assigned to a very early occurrence of this cluster (FT-2, −5, FT-3b, FT-6, FT-7

FT-10, FT-53). It is exceptionally well preserved (Mao et al. 2023) and displays the characteristic single enlarged and pointed lower incisor (i1), which is procumbent and has a long root. A diastema extends to the large p4, which has a trigonal aspect and serrated margins. Two molars follow. The antagonist of the pointed lower i1 is the enlarged I2, which has a broad and basined occlusal surface with cusps along the lateral side. After a short diastema two multi-cusped premolars (P2 and P3) follow. The cusps have a similar height. P4 is enlarged and provides a basin-like occlusal surface with many cusps of different sizes. Two upper molars are present.

Examples of Multituberculata
Multituberculate modification: Multituberculata (e.g. *Kryptobaatar* Fig. 8.1a, *Ptilodus* Fig. 8. 1b) (2.0.1.2/1.0.4.2)*, and *Taeniolabis* (Figs. 8.1c) are characterised by greatly enlarged lower incisors separated from the premolars by a diastema (FT-2, FT-5, FT-6a, FT-7, FT.10, FT-30, FT-52, FT-53) (Kielan-Javorowska and Hurum 2001, Kielan-Javorowska et al. 2005). Two comparatively small incisors are located in the premaxilla. A diastema separates the incisors from the premolars. Canines and anterior premolars are absent due to antemolar reduction (Simpson 1933).

Multituberculates have been compared to rodents, but the small upper incisors, such as those of *Ptilodus* are less suitable for gnawing. Together with the reconstructed musculature the anterior teeth suggest a more omnivorous diet (Krause et al. 1986, Wall and Krause 1992).

The Late Cretaceous/Paleocene genus *Taeniolabis* (Fig. 8.1c) (2.0.1.2/1.0.1.2) reached a relatively large body size (Krause et al. 2021, Rose 2006). The procumbent lower incisor is very hypsodont but not euhypsodont (Granger and Simpson 1929). A large diastema separates i1 from the shearing premolar (p4). Two multicuspid molars follow. The two upper incisors are different in size. Their tooth positions have been identified as I2 and I3 (Greenwald 1988). The upper I2 is the same size as the lower i1 and functions as an antagonist. The I3 is much smaller than the I2 and peg-like (Granger and Simpson 1929, Krause 1986, Krause et al. 2020). A long diastema extends between I3 and the small P4. The incisors are enamel-covered, but the enamel is much thicker on the anterior side, exposing the shearing blades by mutual abrasion.

An enhanced gnawing function has been suggested for *Taeniolabis,* but unlike the gliriform incisors of rodents (CL-9), the two enlarged incisor (I2/i1) are not euhypsodont and do not allow for the same intense abrasion. However, the rooted incisors of *Taeniolabis* may represent the way in which euhypsodont incisors evolved.

The Late Cretaceous *Barbatodon* from Europe has an elongated lower incisor separated from the plagiaulacoid premolar by a wide diastema. All antemolars in the lower tooth row are reduced. In the dentition the reduction is nearly complete with two incisors but no canine, four premolars and two molars. *Barbatodon* is mentioned here, because the enamel of all tooth tips is iron pigmented (Smith and Codrea 2015), convergent with Glires and some Soricidae (FT-54).

Examples of Paucituberculata
Paucituberculate modification: The extant marsupial Paucituberculata (e.g. *Caenolestes* and *Lestoros* (4.1.3.4/4-3.1.1.1.1.3.4) (FT-2, FT-5, FT-7, FT10, FT-52) from South America have two of very elongated and procumbent lower incisors (Fig. 8.1d). Their upper side is formed by a trenchant margin. The dominant lower incisor is followed by five small and single-cusped antemolars anterior to p3. There is no diastema. A lower canine is not recognisable. The upper first incisor is slightly higher than the three small following incisors. The upper canine is slightly larger and located on the border between the premaxilla and the maxilla. Three upper premolars follow, separated by small diastema. They do not occlude with the lower antemolars. The upper dentition does not provide an enlarged tooth as an antagonist. The upper incisors together with the slightly larger canine (C) form a narrow arcade, e.g. in *Caenolestes conveltus* (ADW). This arcade surrounds the two lower incisors when fully occluded. Paucituberculata show the enlarged lower incisors, but only a limited reduction of the antemolars.

Fossil Polydolopidae are compared to extant Caenolestidae, because of their enlarged and procumbent incisors. However, *Epidolops ameghinoi*, has three lower incisors in each ramus (Paula Couto 1952, Beck 2017). Thus, the concentration of bite force is less concentrated on the anterior incisor than in extant Paucituberculata.

Examples of Diprotodontia
*Petaurus m*odification: The diprotodont *Petaurus* (3.1.3.4/1.0.4.4) (FT-2, FT-5, FT-7, FT-10, FT-52., FT-53) has the large lower incisor (i1) followed by three small antemolars and a slightly larger p3. The upper teeth are variable in size. The I1 is peg-shaped and larger than the following two incisors. The upper canine is again large, much larger than the two following P1 and P2 (Berkovitz and Shellis 2018). The P3 is enlarged and shares a small facet with the p3, which has been observed similarly in *Plesiadapids* (Gingerich 1974). *Trichosuchus* (Fig. 8.1e) is similar and is affiliated here.

Macropodid modification: In *Macropus* (3.1.3.4./1.0.2.4) (FT-2, FT-5, FT-7, FT-10, FT-52, FT-53) and other macropodids (Fig. 8.1f), the single lower incisor is very long, well rooted and procumbent. pointed. The abrasion produces a sharp cutting edge on the dorsal margin of the tooth. long diastema extends between i1 and p3. In the upper dentition

are three incisors of which last one (I3) is elongated antero-posteriorly. The three incisors on either side form a closed arcade that accommodates the lower incisor when they rest on the palate during cheek tooth occlusion. The elongation of I3 increases the area of contact with i1 during food intake, which appears to be particularly beneficial for vegetative items (Prideaux and Warburton 2010). The functional significance of this specific occlusion has been described in detail for *Macropus (Notamacropus) eugenii* (Crompton et al. 2008). Plant material formatted by the incisors is moved to the cheek teeth by the tongue.

The macropodid modification is widespread in other diprotodontids and shows minor changes in the AD. In the more primitive macropodid *Balbaroo* from the Oligocene of Queensland, the antemolars are less reduced. An i2 and an upper canine are still present (Black et al. 2014). More severe evolutionary changes occur in the cheek teeth, such as the development of a plagiaulacoid last premolar (P3/p3).

Macropodid marsupials share a closed arcade of incisors that provides a perfect antagonist structure for the enlarged lower incisors. In placental mammals, usually each enlarged lower incisor has only a single antagonist.

Examples of Apatotheria

Heterohyus modification: The AD of *Heterohys* (2.0.2.3/1.0.2.3) (Figs. 8.1g and 8.2) or *Apatemys* (FT-2, FT-5, FT-6a, FT-7, FT-10, FT-52) are characterised by a single procumbent enlarged lower incisor, considered as i1. The first upper incisor is discordant, enlarged, but smaller than the lower one. It is biscuspid and in some species it has a small additional cusp (mediocone) on the mesial side (Russel 1964). The antemolars are modified differently from the other members of this cluster "*Mandible with Procumbent Incisor*". In the upper dentition the first antemolar (I2) is greatly enlarged and forms a trigon in the lateral view. Obviously, its anterior facet occludes with the posterior side of i1 (Fig. 8.2). The following two antemolars are considered as P2 and P4 both teeth are small. In the lower dentition a large p2 follows the procumbent i1. This p2 is elongated in antero-distal direction and forms a blade. The p4 is minuite. Canines are absent. The identification of the tooth loci is under discussion (Gingerich and Rose 1982, Koenigswald 1990, Koenigswald et. al. 2005, Silcox et al. 2010). The number of antemolars is reduced to two in the upper and one in the lower dentition (excluding P4/p4).

The apatemyid modification differs from the soricid modification in the upper I2 and the lower p2, but shares the general reduction of the antemolars (FT-52), both more pronounced in the lower than in the upper dentition.

Examples of Eulipotyphla

Soricid modification: Soricidae and the related fossil Heterosoricidae are typical for CL-8 "*Mandible with Procumbent Incisor*". *Sorex* has a single enlarged and pointed lower

Fig. 8.2 "*Mandible with Procumbent Incisor*" (CL-8). The AD of *Apatemys chardini* (CIMOLESTA), Wyoming. (From Koenigswald et al. 2005)

incisor and the discordant upper incisor (3.0.1.4.3/1.0.2.3) (FT-2, FT-5, FT-6a, FT-7, FT-10, FT-52, FT-54) (Fig. 8.1h and 8.3b). The tooth loci of the enlarged incisors are accepted as i1/I1 (Kindahl 1959, Storch and Qui 2004). The dominant lower incisor (i1) is elongate, procumbent and well rooted in all fossil and extant genera (Repenning 1967). In some genera the elongated dorsal side has small cusps (e.g. *Sorex*).

The first upper incisor (I1) is bicuspid, with a pointed main cusp (anterocone) and a strong heel at the base of the crown (posterocone), using the terminology coined for the dentition of *Plesiadapidis* by Gingerich (1976) (Fig. 8.3a). A small mediocone may occur on the mesial side of the anterocone in "fissident" soricids, such as in the Pleistocene *Beremendia fissidens*.

Antemolars are mostly unicuspid, with the exception of P4/p4. The first upper antemolar (I2) is slightly enlarged, e.g. in *Crocidura*, *Scutisorex* and *Suncus*, but never reaches the size of the I1. The antemolars show different stages of the general trend of antemolar reduction (FT-52) which is more progressive in the lower dentition than in the upper dentition. *Sorex coronatus* 5/1, *Blarina* 5/1, *Petenyia* and *Suncus* 4/1, *Notiosorex* and *Megasorex* 3/1, and *Corcidura* 2/1 (Hugueney et al. 2012. Klietmann et al. 2013), and in the heterosoricine *Lusorex taishanensis* 4/4 (Qui and Storch 2005). Counting the antemolars (excluding the P4/p4) is important for the phylogenetic reconstruction (Hugueney et al. 2012. Klietmann et al. 2013).

The tooth loci of antemolars are often difficult to identify. The upper canine has been identified in some extant taxa, by observing the margin between the premaxilla and maxilla in young individuals (Hutterer 2005). This method is not applicable to most other soricids.

Several but not all genera of the Soricidae have a pigmented enamel (FT-54) due to the presence of iron (Dötsch and Koenigswald 1978). The families also differ in the Schmelzmuster (enamel microstructure) of their molars. However, the pigmentation and the enamel microstructure are independent features (Koenigswald and Reumer 2020).

***Amphechinus* modification:** The Miocene erinaceid *Amphechinus* (3.1.3.3/2.1.2.3) (FT2, FT-5, FT-7, FT-10, FT-52) differs from most Erinaceidae in having an enlarged and procumbent lower incisor, which qualifies this genus for the CL-8 "*Mandible with Procumbent Incisor*". The lower incisor is procumbent and pointed. It is followed by three antemolars and a prominent p4. In the upper jaw, the I1 is unicuspid and pointed as in many erinaceids, but it is much more enlarged and directed downward. Such an upper incisor is a unique feature in this cluster. A small diastema in the premaxilla is followed by a small I2. The I3 is of similar size as the upper C. Two small premolars and a large P4 follow (Viret 1938, Thenius 1969). The reduction of the antemolar region is more pronounced in the lower tooth row than in the upper dentition.

***Apternodus* modification:** *Apternodus* (2.1.3.3/3.1.3.3) (FT-2, FT-5, FT-7, FT-10) Eocene-Oligocene eulipotyphlan from North America, has an enlarged procumbent lower incisor. The special adaptation of *Apternodus* consists of bulbous teeth following the enlarged incisors (I1/i1), suitable for crushing arthropod carapaces. The procumbent lower incisor
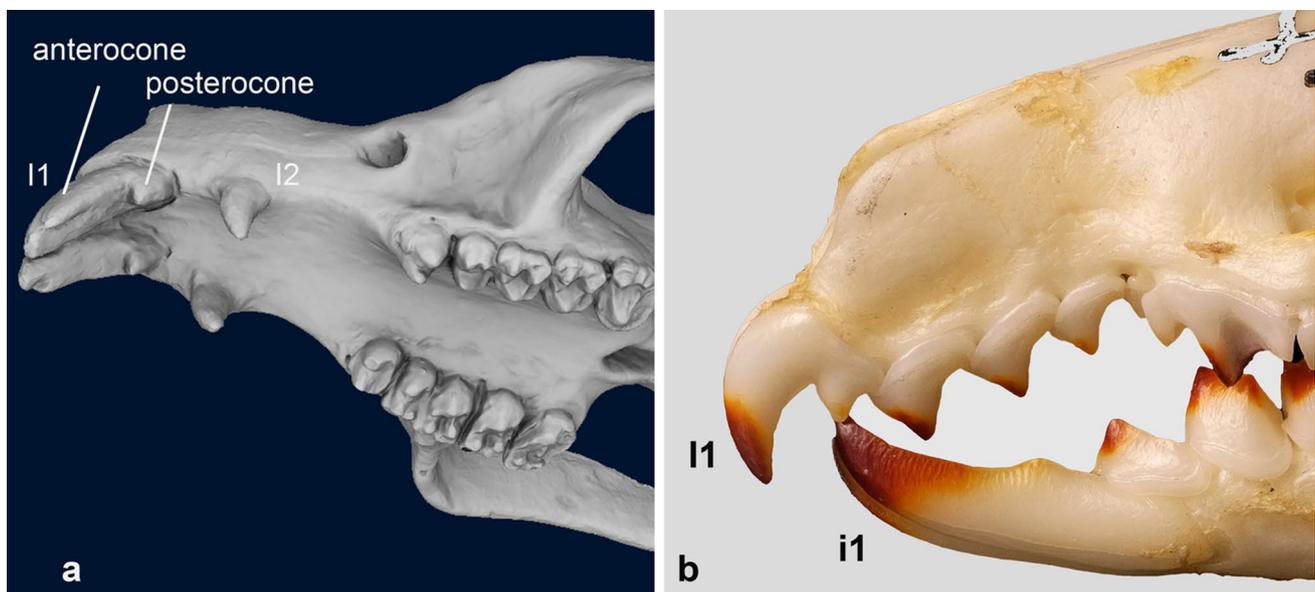
Fig. 8.3 "*Mandible with Procumbent Incisor*" (CL-8). **a** *Plesiadapis* (PRIMATES), 3D Modell, upper dentition, with a strong posterocone on the upper incisor (I1), **b.** *Neomys fodiens* (EULIPOTYPHLA).

Anterior dentition with discordant incisors and pigmented tooth tips (**a** 3D modell UMORF, courtesy of P.D. Gingerich, **b** ZMFK 2010 18555.314, photo: M. Kunz)

(i1) has an elongated but slender crown. Half of the length of this crown contacts the antagonist incisor (Asher et al. 2002). The lower i2 is diminutive and wedged between the i1 and the i3 inf. The i3 and the second premolar are enlarged and bulbous. The discordant upper dentition contains only two incisors. The I1 is unicuspid. The upper canine is very bulbous and has two or three roots. The upper C and the P2 are antagonists for the bulbous lower teeth. Molars are zalambdodont. Teeth are pigmented (FT-54). *Apternodus* forms a its own modification of this cluster because of its bulbous teeth.

Examples of Primates – Plesiadapiformes

Plesiadapid modification: Plesiadapidae belong to this cluster because the mandible bears a single enlarged lower incisor (FT-2, FT-5, FT-7, FT-10). The antagonist is bicuspid upper incisor (Fig. 8.3a). Plesiadapids occurred during the Paleocene and Eocene in the northern hemisphere and are related to primates. The late Paleocene *Carpolestes simpsoni* from Montana (Bloch and Gingerich 1994) is compared with *Plesiadapis* tricuspidens from North America and Europe (Russel 1964, Gingerich 1976). They represent two different levels of reduction and specialization in the AD.

Carpolestes (3.0.3.3/2.1.1.3) has a procumbent lower incisor that is laterally compressed (Bloch and Silcox 2006). Two strongly reduced antemolars (considered as i2 and c) follow anteriorly to the extraordinarily enlarged and trenching p4. No diastema is present. The upper dentition has three incisors, the first two of which are large and bicuspid. They are followed by two smaller unicuspid antemolars, identified as I3 and P2. The P3 and P4 have trenching buccal sides that form antagonists to the specialised lower p4.

The dentition of *Plesiadapis* (2.0.3.3/1.0.2.3) (Fig. 8. 1i) (FT-2, FT-5, FT-7, FT-10) is more reduced, with a wide diastema in the lower jaw between the enlarged lower incisor (i1) and the more massive p3. The large upper incisor is heel-shaped and has a differentiated occlusal surface with four cusps, typical of Plesiadapidae (Gingerich 1976, Rose et al. 1993). The prominent posterocone at the base of the crown serves as a abutment for the maximum movement (Fig. 8.3a). Both incisors show small facets caused by a limited wear (Gingerich 1976).

Discussion of CL-8 "Mandible with Procumbent Incisor"

Cluster CL-8, characterised by a single procumbent lower incisor and discordant upper incisors. Both teeth form an antagonistic pair. Although its dental locus of the enlarged lower incisor is usually given as i1, its dental locus was rarely confirmed by detailed study. For diprotodont marsupials Hershkovitz (1982) argued for an i3.

The cluster CL-8 is more widespread than any other and occurs in very different mammalian groups such as

ALLOTHERIA, METATHERIA and PLACENTALIA. The enlarged lower incisor evolved independently. Even within these groups multiple convergent occurrences are plausible, e.g. in the South American Paucituberculata and in the Australian Diprotodontia (Ride 1962, Beck 2017).

The basic function of a pair of antagonistic and pointed incisors, as found in placentals, is a precision grip to catch small prey. This structure is less suitable for gnawing. An increasing specialization of placentals to an herbivorous diet may have reduced the abundance of this cluster during the Neogene. Some marsupials, e.g. Macropodidae, retained a greater number of upper incisors. They are more similar and are modified into an arcade that surrounds the lower incisors when the mouth is closed. This (and the lack of hoofed mammals) probably allowed these marsupials to specialise in an herbivorous diet.

The examples discussed for the CL-8 have discordant dentitions. The powerful lower incisor is deeply rooted in the mandible and has no concordant antagonist. In contrast, in gliriform dentitions (CL-9) upper and lower incisor are concordant. The marsupial Vombatidae modified the upper incisors to forms an antagonistic structure. In Multituberculata the antagonistic upper incisors are generally small. Only in late forms do the upper incisors reach a size adequate for the lower incisor. It indicates the evolutionary trend.

The various modifications of CL-8 "*Mandible with Procumbent Incisor*" found in Eulipothyphla, Apatotheria and Plesiadapidae represent a striking functional solution with the single upper incisor. In addition to the main cusp, the anterocone, a posterocone evolved as an abutment at the base of the posterior side of the I1. It most likely evolved convergently in the different groups (e.g. in Plesiadapidae and Soricidae). Their functional significance is underlined by the occurrence of comparable structures in the cluster of CL-9 "Gliriform Incisors".

The stratigraphic occurrence of the cluster is very uneven. It was very abundant in the Paleogene but in the extant fauna it is restricted to diprotodont marsupials and to Soricidae in placental mammals in.

Cluster 9
"Gliriform incisors" (CL-9)

Antagonistic pair of euhypsodont incisors with reciprocal sharpening

Definition and occurrence: The cluster CL-9 *"Gliriform Incisors"* is characterised by an antagonistic pair of concordant and euhypsodont incisors (Fig. 9.1). Other incisors are reduced or absent. In gliriform incisors the enamel is restricted to a band on the anterior surface. It forms a cutting edge that is reciprocally sharpened by abrasion. In addition, the canines are absent and the premolars show variable
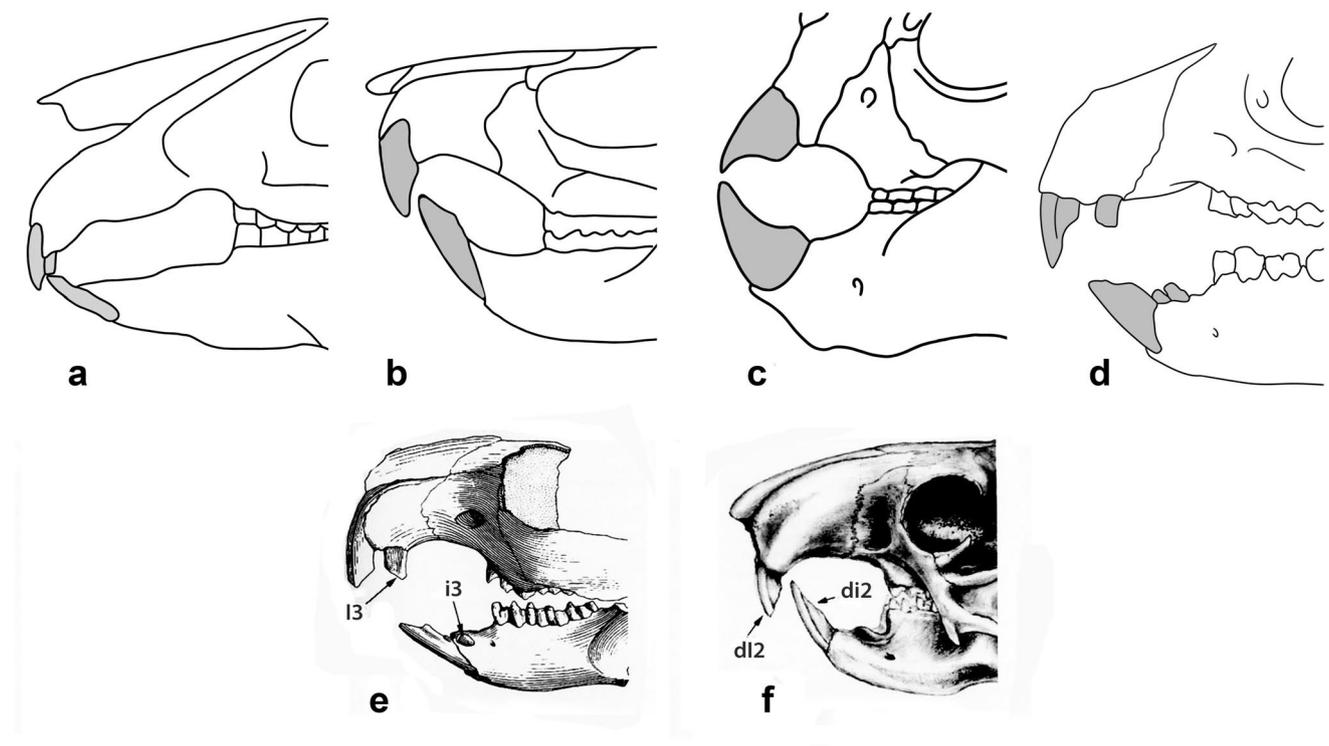
Fig. 9.1 *"Gliriform Incisors"* (CL-9). **a** *Oryctolagus* (Lagomorpha), **b** *Thisbemys* (Rodentia), **c** *Daubentonia* (Primates), **d** *Trogosus* (Tillodonta), **e** *Mimotona* (LAGOMORPHA), **f** *Rhombomylus* (RODENTIA). (Modified from: **a** and **b** Thenius 1989, **c** Schultz 1971, **d** Gazin 1953, **e** and **f** Rose and Archibald 2005)

degrees of reduction. A large diastema separates the incisor from premolars and molars, depending on the degree of antemolar reduction. The common features are therefore FT-2, FT-3, FT-4, FT-8, FT-12, FT-52, FT-53 in some taxa FT-54. In addition, the incisors share the reciprocal abrasion (FT-11).

CL-9 *"Gliriform Incisors"* has been found in GLIRES, Rodentia and Lagomorpha, in systematically isolated genera of PRIMATES (*Daubentonia*), TILLODONTIA (*Trogosus*) and MARSUPIALIA (*Yalkaparidon*). The South American marsupial *Groeberia* is a potential candidate for the CL-9 *"Gliriform Incisors"*.

Examples of Lagomorpha
Lagomorph modification: *Lepus* (2.0.3.3/1.0.2.3) has an antagonistic pair of gnawing incisors in the upper and lower dentition (Fig. 9.1a). These teeth are euhypsodont and have an enamel band on the mesial side. They are identified as dI2 and di2 and not shed (Luckett 1985). The function of the teeth and the reciprocal sharpening of the main incisors is comparable to that of rodents. The upper dI2 is regularly notched, whereas the lower is flat. Lagomorphs differ from rodents in that they have a second upper incisor (I3) positioned behind the behind the dI1. The I3 has a deciduous precursor which is shed. It functions as an abutment for the

lower incisor Canines are absent. There are large diastemata between the incisors and the premolars. Three upper and two lower premolars remain as antemolars. Compared to rodents, the reduction of the antemolars is less intense and, similar to taxa in CL-8, the reduction of the lower dentition is more progressive. The schmelzmuster of the incisors is one-layered in most Lagomorpha, in contrast to the two-layered schmelzmuster in Rodentia (Korvenkontio 1934, Koenigswald 1995).

Mimotona (2.0.3.3/2.0.2–3.3.2.3) (Fig. 9.1e) has typical gliriform incisors in the upper and lower jaw with enamel restricted to the anterior surface The upper incisor (I1) is notched. There is a second euhypsodont incisor (I3) originating from the premaxilla. Both characters are shared with the lagomorph modification. However, the large lower incisor (i2) is followed by a small i3, not present in Lagomorpha. The upper I3 and the lower i3 can be interpreted as remnants of the reduced antemolars. Large diastemata separate the incisors from the premolars. (Li and Tang 1993, Rose and Archibald 2005).

Examples of Rodentia
Rodent modification: Rodents (Fig. 9.1b) are represented by more than 2000 extant species belonging to about 500 genera. All are very similar in their anterior dentition,

lacking canines, but differ in the number of unreduced premolars. The euhypsodont upper and lower incisors have been identified as permanent milk teeth, dI2 and di2 (Luckett 1985). Rodentia are present since the Paleocene and despite their large number and long history, the pattern of the AD was not changed. Antemolars, expected in the ancestral dentition of placentals, are largely reduced during rodent evolution. The P3 and P4/p4 are preserved in the Eocene *Paramys*. Most sciuromorphs have a P4/p4, and most Myomorpha have completely reduced premolars. The antemolar region is occupied by large diastemata in the upper and lower jaws.

The use of the incisors causes intense wear, which has to be compensated by a very fast eruption of the euhypsodont teeth. The dentinal wear facets are wedge-shaped and concave with the enamel at the tip. Reciprocal sharpening ensures the continuous wear.

The enamel band on the anterior side of the teeth forms a cutting edge that is constantly sharpened. The cross section of the incisors determines the function. A flattened mesial surface produces a brought blade, especially in tooth digging species (Kalthoff and Mörs 2021), a strongly curved mesial surface a sharp pointed edge, e.g. in *Myoxus*. The upper incisors show a variety of longitudinal notches or grooves (Kalthoff, 2000), but their functional significance remains uncertain. The enamel band has a two-layered schmelzmuster that characterises the different rodent groups (Korvenkontio 1934, Wahlert 1968, Martin 1992, Koenigswald 1993, 1995, Kalthoff, 2000, Kalthoff and Mörs, 2021). The enamel band has a reddish pigmentation due to iron in the outermost layer (Dötsch and Koenigswald 1978).

Rhombomylus (1.0.2.3/1.0.2.3) (Fig. 9.1f) has been discussed as possibly related to rodents (Meng et al. 2003). In the anterior dentition the euhypsodont di2 and dI2 are separated by diastemata from the premolars. Thus, *Rhombomylus* thus fits the rodent modification.

Examples of Primates

Daubentonia modification: The anterior dentition of the lemur *Daubentionia* (1.0.1.2/1.0.1.2) (Fig. 9.1c) shows a classic convergence of rodent incisors. All the characteristic features of the CL-9 "*Gliriform incisors*" are present. The incisors are separated from premolars by a wide diastema, and canines are absent. The incisors are euhypsodont and laterally compressed. They are permanent teeth (Ankel-Simons 1996) and not milk teeth as proposed by Lucket and Maier (1986). Enamel is restricted to the anterior surface. Due to the narrow and rounded anterior surface, the cutting edge is pointed, concentrating the chewing force. The concave facets in the upper and lower incisors indicate reciprocal sharpening, similar to that in rodents. This sharpening requires the mandible to move far forward. Accordingly, the cranial articulation facet for the mandible is very flat allowing the mandible to move very freely, especially anteriorly.

Examples of Tillodontia

Tillodont modification: The tillodont *Trogosus* (2.1.2.3/3.1.2.3) (Fig. 9.1d) is characterised by concordant and enlarged second incisors (I2/i2). The upper I1 is reduced (Gazin 1953). In the mandible, small i1 and i3 are located on either side of the enlarged i2. Concave facets indicate mutual abrasion of the euhypsodont incisors. The enamel of these teeth is restricted to the anterior surface. Diastemata extend between the small canines and the premolars (P2/p2) (Gazin 1953, Marsh 1875, Simons 1960, Lucas and Schoch 1998a).

In the related *Tillodon*, the reduction of the anterior dentition is somewhat more progressive, as lower i1 and i3 are missing. Moderate diastemata separate the upper canine from I3 and P2. The lower canine is well separated from p2 (Lucas and Schoch 1998a). *Trogosus* and *Tillodon* fit well into CL-9 "*Gliriform Incisors*", although the anterior dentition is not strictly congruent due to the presence of an i3 and a small lower canine.

Examples of Marsupialia

Yalkaparidon (Fig. 9.2a) represents a separate marsupial order, Yalkaparidontia, from the Middle Miocene (Archer et al. 1988, Beck, 2023, Beck et al. 2014). The upper and lower dentition have enlarged euhypsodont incisors (I1/i1). In the upper dentition two smaller incisors (I2 and I3) are located behind the enlarged I1. These teeth have no enamel. After a short diastema, the canine follows and after another diastema, the alveolus indicates the P3. In the lower jaw, a large euhypsodont incisor (i1) is followed by two single-rooted teeth, inferred from the alveolus, and four molars (Beck et al. 2014). Despite some uncertainties, the antemolar reduction feature is more progressive in the lower than in the upper jaw.

The large incisors are euhypsodont and have enamel only on their anterior surfaces. The two additional upper incisors are short and appear to be an abutment for the lower incisor and form a functional equivalent of I3 in Lagomorpha (Fig. 9.2b). According to the figures, the large incisors have a concave facet, suggesting reciprocal sharpening. *Yalkaparidon* thus represents the CL 9 "*Gliriform Incisors*".

Questionable candidates for the cluster Gliriform Incisors – Marsupialia

Groeberia (2.1.3.4/1.1.1.4) characterised by euhypsodont incisors, two in the premaxilla and one in the mandible (FT.3, FT-5, FT-8, FT-52). Canines are present and premolars and molars follow closely without a diastema. The anterior dentition is similar to the cluster *Gliriform incisors* in having euhypsodont upper and lower incisors, but the second upper incisor makes the dentition discordant. The antemolars are more reduced in the mandible than in the maxilla. The dentition of *Groeberia* is so far unique and does not fit well

Fig. 9.2 *"Gliriform Incisors"* (CL-9) **a** *Yalkaparidon* (MARSUPIALIA) **b** *Lepus europaeus* (LAGOMORPHA). Incisors posterior to the I1 has an abutment for the maximum lift of the lower incisor. (**a** Photo by courtesy of R.D.M Beck, **b** Photo G. Oleschinski, BIOB)
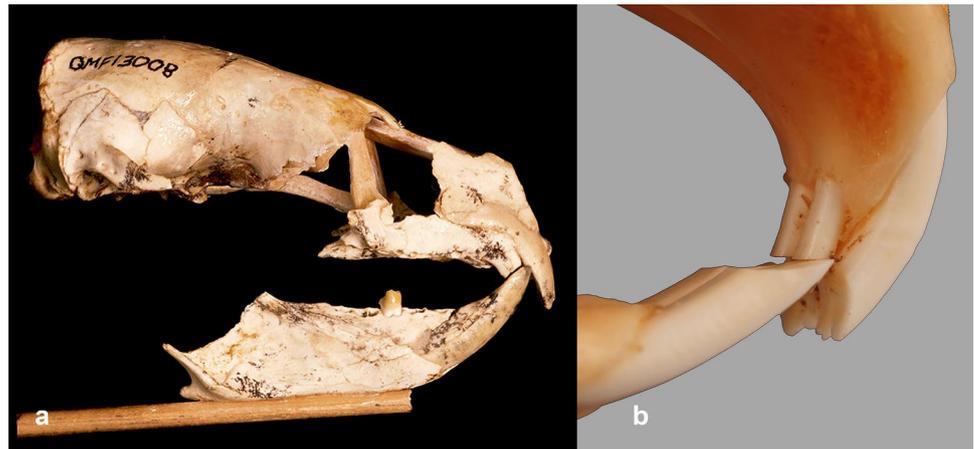
into any of the proposed clusters. The systematic position of *Greoberia* from South America has been intensively discussed and recently described as a marsupial (Zimicz and Goin, 2020).

Other South American taxa, such as the gondwantherian genera *Patagonia* or *Sudamerica* (Chimento et al. 2014, Goin and Abello, 2013) are known from mandibles with euhypsodont lower incisors, making them candidates for the cluster CL-9 *"Gliriform incisors"*. The occlusal facets of the lower incisors are concave and may indicate a reciprocal sharpening. However, until the upper anterior dentition is sufficiently known, they should not be classified.

Questionable candidates for the cluster Gliriform Incisors – Gondwanatheria

Adalatherium and *Vintana* from the Late Cretaceous of Madagascar may be other members of this cluster. *Adalatherium* has two upper and one lower incisor. I2 is larger than I1, but in contrast to the lagomorphs. It does not form an abutment for the lower incisor, but has a facet on its mesial side (Krause et al. 2020). The upper dentition of *Vintana* lacks incisors, but shows the two long and curved alveoli for two gliriform and probably euhypsodont incisors on each side (Krause 2014).

Discussion of CL-9. "Gliriform Incisors"

The euhypsodont incisors of *Groeberia*, *Daubentonia* and *Tillodon* are certainly cases of convergent evolution. Whether these teeth in Lagomorpha and Rodentia represent a a case of parallel evolution is uncertain. Both orders are monophyletic (Mein 2003), but the common ancestor is still unknown and therefore its incisors cannot be studied. The enamel band of the incisors has been strengthened by decussating enamel prisms in both orders, but differently (Korvenkontio 1934, Wahlert 1968) suggesting a convergent evolution in the schmelzmuster.

All members of this cluster, show an antemolar reduction. It concentrates the biting forces on the antagonistic pair of enlarged incisors, that are concordant in contrast to the incisors in cluster 8. The antemolar reduction reached the most advanced stages in Glires, in Rodentia even more than in Lagomorpha. The presence of an I3 can be interpreted as a trace of antemolar reduction (FT-52). The similar more progressive reduction in the mandible than in the upper jaw has been observed in several clusters, such as CL-8 *"Mandible with Procumbent Incisor"*. The concordant incisors in CL-9 may have evolved from discordant incisors, as in CL-8. Multituberculata may serve as a model for this transformation. *Ptilodus* (Fig. 8.1b) has peg-like upper incisors, whereas *Taeniolabis* developed very hypsodont upper incisors with cutting blades. In contrast, the large bicuspid upper incisors of Plesiadapidae, Sorcidae and Apatemyidae seem to have resisted further transformation.

The antagonistic pair of enlarged incisors is a perfect tool for gnawing, digging and fighting. They act as end cutting pliers and the blades have been termed "nipper facets" (Koenigswald 2016a). The dentition of rodents and lagomorphs has two separate functional sections separated by the large diastema as a result of antemolar dentition. Both sections do not function simultaneously. Because of the shape of the lower jaw, the incisors do not come into contact when the molars chew. Also, the molars do not occlude when the incisors are active, either for gnawing or for sharpening.

The functionality of the euhypsodont incisors in CL-9 is ensured by a balance between rapid eruption, abrasion, and sharpening. Abrasion occurs in two modes. In the first mode the entire cross-sections of both antagonistic teeth are abraded on a flat facet. The marginal enamel can form a sharp edge. Abrasion of the upper and lower teeth occurs simultaneously and is called "mutual abrasion", e.g. in canines (see CL-14). In a second mode, as in the glirid incisors, the enamel is exposed as a blade, while the dentin is excavated. The enamel bands on the mesial sides of
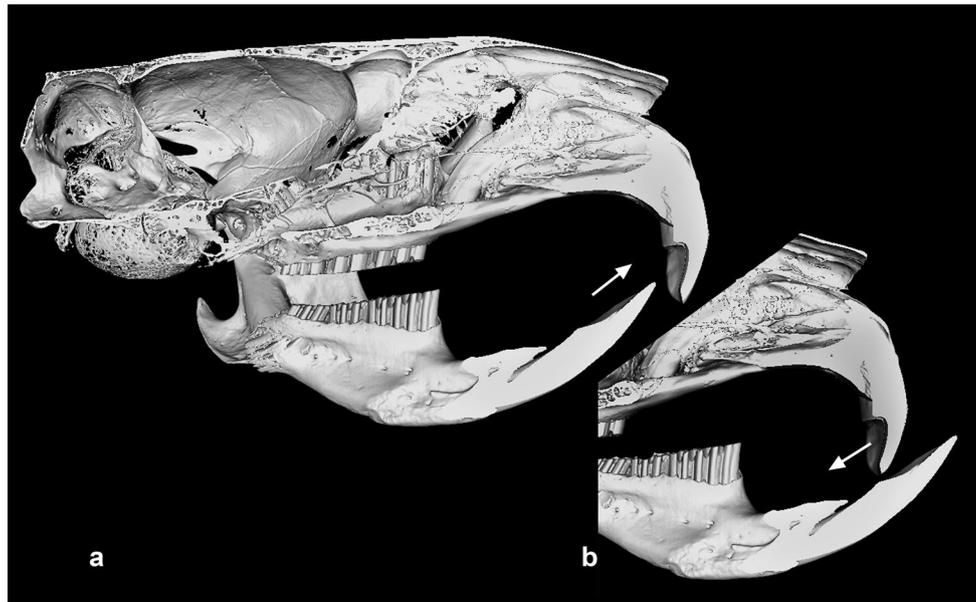
Fig. 9.3 *"Gliriform Incisors"* (CL-9). *Microtus gregalis* (RODEN-TIA). The reciprocal sharpening of gliriform incisors is demonstrated by the median section. **a** During a normal occlusion of the mandible, the lower incisor sharpens the upper incisor. Note the excavated notch on the posterior side of the upper incisor. It is an abutment that limits the maximum adduction of the lower incisor. **b** Position to sharpen the lower incisor, the mandible must be pushed forward to allow the upper incisor to abrade the entire length of the facet. (BIOB-PAL M 1004 µCT model)

the incisors form such blades, and the dentin has a concave facet. The upper and the lower incisors sharpen each other with two different movements. This way of sharpening is called here a "reciprocal sharpening".

The upper incisor is sharpened during the normal raising of the mandible. The lower incisor scrapes the dentin on the distal side of the upper incisor and exposes its enamel band. The maximum lift of the lower incisors is marked by an abutment. The I3 in Lagomorpha (Fig. 9.2b) and I2 and I3 *Yalkaparidon* perform the same function (Fig. 9.2a). In many rodents the distal facet of the upper incisor ends smoothly, but in others, such as *Microtus*, it has an abrupt step forming an abutment (Fig. 9.3a). This abutment in the upper incisor has some taxonomic value in some extant rodents (Miller 1912, Niethammer 1978). The I3 in Lago-morpha as well as the step in the facet of rodent incisors, are a functional equivalent of the posterocone on the upper incisors found in Plesiadapidae (Fig. 8.3a) (Gingerich 1976) and many other members assigned to CL-8.

The sharpening of the lower incisor requires a significant forward movement of mandible (Abel 1911. 506). During this movement, the upper incisor scrapes the dentin along the entire length of the facet on the lower incisor (Fig. 9 3b). A characteristic concave facet reflects this reciprocal sharpening. The specific movement of the lower incisor requires an elongated condylar joint that is open in the anterior-posterior direction.

Cluster 10
"Special incisors" (CL-10)

Special modifications of enlarged discordant incisors

Definition and occurrence: The CL-10 *"Special Incisors"* unites some mammalian dentitions that share unusually enlarged incisors, but do not fit into any of the categories proposed here. They each represent unique modifications for which no convergent pattern was found in the great diversity of mammalian dentition (Fig. 10.1). However, they are important in terms of diversity. They include the metatherian *Argyrolagus*, the vampire bat *Desmodus*, Rhinocerotiodae with their unique shearing between incisors and *Tapirus,* which has a specific incisor pattern.

Examples of Metatheria
***Argyrolagus* modification:** The South American marsupial *Argyrolagus* (2.0.1.4/2.0.1.4) is a leaping animal with long hind legs (Abello and Candela 2020). In the skull, the pre-maxilla and the nasals protrude forward, well beyond the two upper incisors (I1 and I2). The I1 has a trigonal cross-section and is recumbent. The I2 is slightly larger and more procumbent. I1 and I2 are enameled in the labial side. The enlarged lower i1 is procumbent with an almost horizontal wear facet. The i2 is significantly smaller and parallel to the i1. Both form a continuous wear facet. The upper and lower
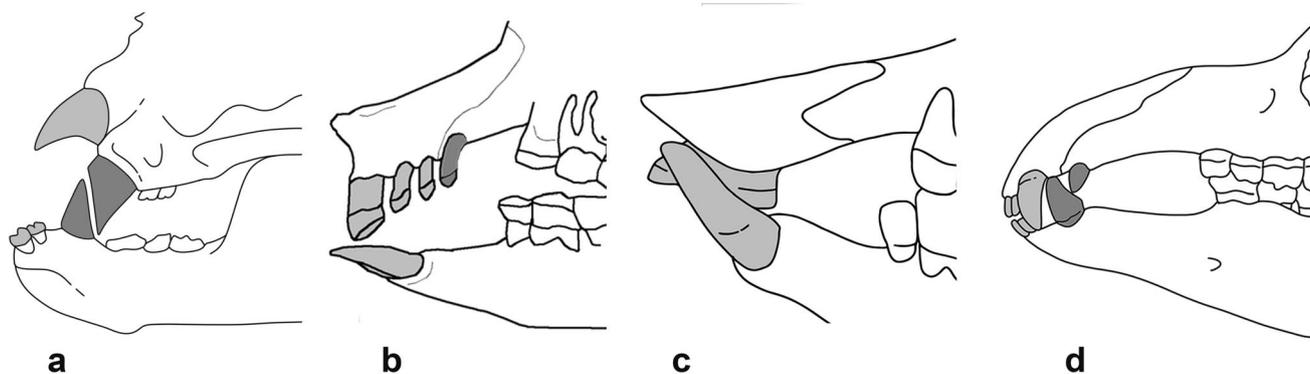
Fig. 10.1 "*Special Incisors*" (CL-10). **a** - *Desmodus rotuntus* (CHIROPTERA), **b** *Trigonias,* **c** *Aceratherium,* **d** *Tapirus* (**b, c,** and d PERISSO-DACTYLA). (Modified from: **a** Thenius 1989, **b** Radinsky 1966, **c** Hünermann 1982, **d** Radinsky 1965)

incisors form a "a pinching apparatus" (Simpson 1970.3). *Argyrolagus* shares the enlarged lower incisor with other marsupials, such as Paucituberculata and Diprotodontia, but differs not only in the number of upper incisors but also in the way the incisors occlude.

Examples of Chiroptera

Desmodus modification: The vampire bat, *Desmodus* (1.1.1.1/2.1.2.1) (Fig. 10.1a) has a huge upper incisor that protrudes as a sharp and pointed blade. It has no antagonist. The tip is constantly sharpened by the tongue, which abrades the distal side, exposing the enamel on the anterior side. The small and bicuspid lower incisors do not act as antagonists. When the mouth is closed, the tip of the upper incisor dips into a pocket in the gum behind the lower incisors. The blade of the upper incisor performs the cutting function, assisted by the blades of the lower and upper canines. Both canines form large triangles that abrade each other with a long facet to keep the tips sharp. These facets are on the posterior side

of the lower canine and the anterior side of the upper canine. The lingual side of the upper canine shows scratches from abrasion against the anterior slightly elongated lower premolar (Vierhaus 1983). The contact of the upper canine with the lower premolar is reminiscent of the cluster CL-16 "*C/p Functional Unit*" perhaps even a convergence. - The function of the upper incisor is to cut into the skin of its prey to extract blood. The related genus *Diaemus* has a similar dentition (Thenius 1989). The AD has the following conspicuous features: FT-2, FT-5. FT-6a, FT-7 and FT-37-

Examples of Perissodactyla

Rhinocerotid modification: Some derived rhinocerotids, such as *Aceratherium* ((2-1.0.4.3/2-1.0..4.3)1 or the extant *Dicerorhinus sumatrensis* (Fig. 10.2) (FT-2, FT-5, FT-10, FT-40) show a very specific occlusion pattern of the upper I1 and the lower i2, termed the "basic incisor shearing mechanism" (Radinsky 1966). The lower i2 is strongly elongated and procumbent. It is enamel-covered on the antero-buccal
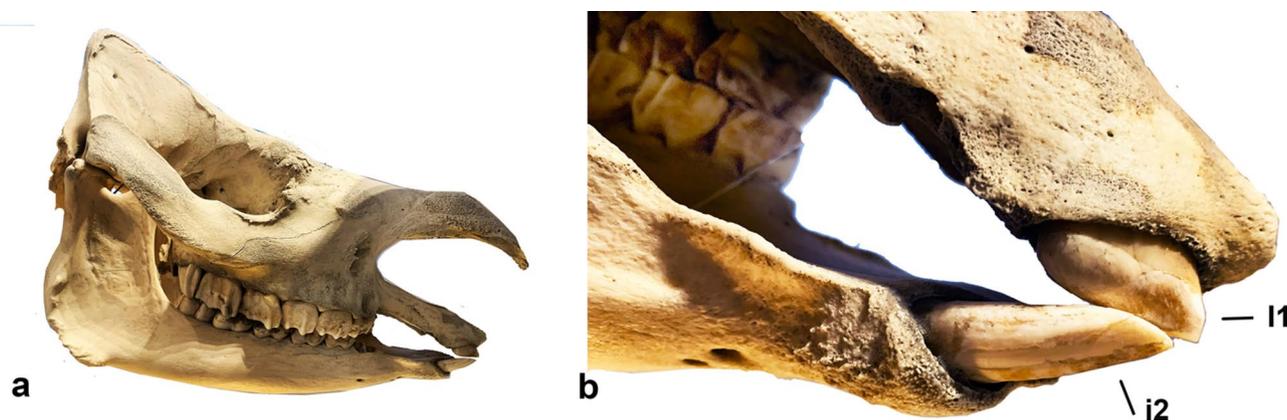

Fig. 10.2 "*Special Incisors*" (CL-10). *Dicerorhinus sumatrensis* (Rhinocerotidae): **a** cranium and **b** occlusion of the abrading incisors (HLMD-M-1257). (Photos courtesy of J. Köhler, HLMD)

side and has a large, almost vertical facet on the antero-lingual side. When the cross-section is triangular, the inclined facet forms a sharp tip. The antagonist of this facet is the upper I1. It is elongated in the antero-distal direction and has a strong root. On the buccal side, it has a large wear facet for the lower i1. The wear facet exposes a large field of dentin. The enamel of the mesial side forms a cutting edge (Hünermann 1982). The antemolars become increasingly reduced during the phylogeny. The specific arrangement of I1 and i2 is already found in the Oligocene *Trigonias* (3.1.4.3/3.0.4.3) (Fig. 10.1 b) although the antemolars less reduced. The larger upper incisor (I1)is followed by two small incisors and an unimpressive small upper canine. The enlarged lower incisor (i2) is located between the tiny i1 and i3, a lower canine is missing ((FT-5, 3b. 10, (53)) (Lucas 1900, Tissier et al. 2020). These teeth mark the loci of the enlarged teeth in later rhinoceroses. Concentration on the incisor shearing mechanism of (I1/i2) is more intense in the Miocene *Teleoceras* (2.0.3.3/2.0.3.3) from North America and the European *Aceratherium* (Fig. 10. 1c). The antemolars between the enlarged I2 and the premolars are progressively reduced, more so in the mandible than in the maxilla.

The functional significance of the scissor-like facets between the upper I1 and lower I2 is, probably less related to food preparation (Prothero 1998a, 1998b) but important as a social organ. The length of the lower incisor is used for social dominance or as a weapon. According to Dinerstein (1991), males of *Rhinoceros unicornis* often suffer severe wounds from the lower incisors (i2) of their rivals during fights.

Chilotherium, a Miocene rhinoceros, has an enlarged lower incisor, but no antagonists in the upper jaw. Nevertheless, the tooth is pointed and constantly sharpened. Enamel covers the antero-buccal side, forming a vertical cutting edge along the abraded dentin.

In the extant fauna, the Asian rhinoceroses *Rhinoceros unicornis* and *Dicerorhinus sondaicus* retain the basic shearing mechanism of the incisors between I1 and i2, while the African genera *Diceros* and *Ceratotherium* lack frontal teeth altogether (see CL-21 "*Mayor Tooth Reductions*"). Their social interaction does not require enlarged lower incisors.

Tapirus **modification:** Both extant tapirs, the Asian and the South American *Tapirus* (3.1.4.3/3.1.4.3) (Fig.10. 1 d) have an unusual arrangement in their discordant AD (FT-5, FT-35, FT 53). The size of the upper incisors increases from I1 to i3 (FT-6b), while the lower i3 is the smallest incisor of the tooth row (FT-6a). The lower canine is large and occludes mainly with the upper I3 and only marginally with the reduced upper canine (FT-35). The C and I3 form a functional unit with a large facet between them. It is important to note, that when the jaws are closed, the small i3 makes room for the large upper I3 (Fig. 10.3).
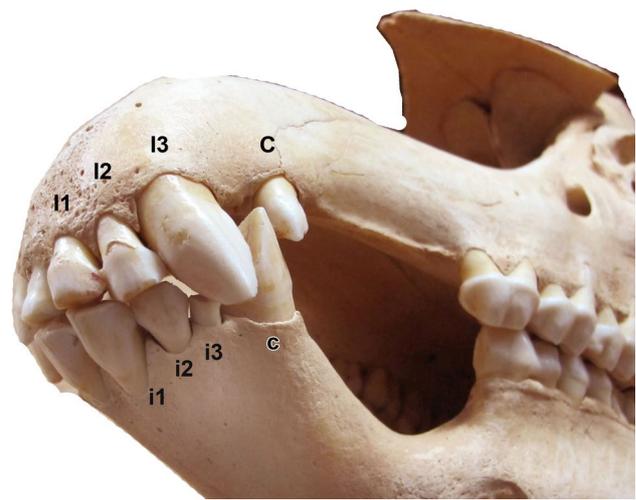

Fig. 10.3 "*Special Incisors*" (CL-10). *Tapirus indicus*, AD with unequal large incisors and a small upper canine. (ZMFK MAM 1938-0016 - authors photo)

The specific *Tapirus* modification has been found in Pleistocene tapirs from Florida (Hulbert 2010). Schultz et al. (1975: Fig. 5) have observed an increasing dwarfism of the lower i3 in the North American tapirs (e.g. in *Protapirus, Miotapirus and Tapiravus*). Thus, the *Tapirus* modification evolved gradually between the Oligocene and Pleistocene (Schultz et al. 1975, Hulbert 2010).

The specific function of the *Tapirus* modification is not obvious. The facets between I3 and c are most likely involved in food grasping. The large I3 contacting the large lower canine is somewhat reminiscent to the fork (I3-c-C) described for Carnivora. However, this fork has a different structure, because it includes a large upper canine, which is very small in tapirs. Tapirs are herbivores and do not need for a fork to hold prey.

Discussion of cluster 10 "Special incisors"

The taxa included in this cluster differ in the morphology and dental loci of dental adaptations. In *Desmodus* the upper incisor cuts into the victim without an antagonist. In Rhinos, the special facets between antagonistic incisors cut antero-distally rather than transversely as in most other dentitions. The enlarged lower incisor has two independent functions, firstly to cut with the antagonist, and secondly to be used for display and as a weapon. The second function It is maintained, even when the antagonist is reduced, as in *Chilotherium*. The facet of the lower incisor has sharp edges, formed by the enamel. The tooth has no antagonist, but the upper lips wear away the dentin and expose the sharp edges formed by the cross-section of the enamel. A similar sharpening has been postulated for the saberteeth in *Thylacosmilus* or *Pomelomeryx* (Koenigswald and Goin 2000).

Cluster 11
"Dentin tusks" (CL-11)

Extremely enlarged incisors or canines forming dentin tusks

Definition and occurrence: "Dentin Tusks" protrude from the skull silhouette. The dentin tusks are either enlarged incisors (FT-16) or enlarged canines (FT-43) and are mostly discordant. Incisor tusks originate either in the mandible or in the premaxilla. Canine tusks arise from the maxilla (Fig. 11.1). Such teeth primarily are found in the upper and lower jaw, but in later stages are reduced either in the upper or the lower jaw. The teeth are euhypsodont with an open pulp. The enamel is gradually reduced. Wear is limited and therefore tusks can provide life history data. Common features are among others FT-2, FT-5, FT-6a, FT-8, FT-52. Dentin Tusks have been found in PROBOSCIDEA (e.g. *Deinotherium, Elephas, Mammut,*), CARNIVORA (*Odobenus*), CETACEA (*Monodon*), and DESMOSTYLIA (*Behemotops*), but not in Marsupialia. The tooth loci involved in tusk formation are incisors or canines and differ between groups.

Examples of Proboscidea
***Elephas* modification:** Proboscideans are characterised by their ivory tusks formed by enlarged upper and or incisors. The number and position of the enlarged incisors varies between genera. The original number of three incisors was reduced during phylogeny, with the lower incisors being reduced more than the upper ones. The enamel, which should have been present at an early stage, was reduced to an enamel band or to a small enamel cap present in very young individuals. In some genera the enamel is completely lost. The curvature of the upper tusks increased in some taxa to a large spiral (Fig. 11.2). These modifications occurred independently in the different proboscidean lineages.

Numidotherium and *Moeritherium* have three upper and two lower incisors (Gheerbrant et al. 2005). One of these teeth was enlarged in Elephantiformes and became an euhypsodont dentin tusk. The identification of their loci has been hotly debated. Delmer (2009. 574) concluded that the lower tusk is the i1 with a deciduous precursor (di1), and the upper tusk is the I2 (di2). Thus, the upper and lower tusks do not represent a functional pair.

Some of the Eocene proboscidean genera from Africa still have two incisors each in their lower jaws. The middle incisor (i1) is already reduced at this stage of differentiation (e.g. in *Arcanotherium*, *Daotherium* and *Moeritherium*) (Sanders et al. 2010a, b, Gheerbrant 2005, Delmer 2009). The second upper incisor (I2) and second lower incisor (i2) tend to become larger and develop into tusks.

The Deinotheriidae (*Prodeinotherium* and *Deinotherium*) have a unique tusk pattern (Fig. 11.1a) (FT-2, FT-3b, FT-16, FT-18, FT-53). The lower incisors are massive and recurving downward, while the upper incisors are completely reduced. In contrast Mammutidae, and Gomphotheriidae (Fig. 11.1b) have had enlarged upper and smaller lower tusks in early phylogenetic stages, but independently reduced the lower tusks (FT-2, FT-3a, FT-5, FT-16., FT-53). In Elephantidae lower tusks are generally smaller than the upper ones. In some Gomphotheriidae, however, the lower tusks, are widened into shovels, as in *Platybelodon* (Shoshani and Tassy 1996). The lower tusks of Mammutidae and Gomphotheriidae were reduced independently during the Late Miocene. Upper tusks became thicker and longer (Lucas 2013).

The dentin tusks were initially covered with enamel, which was gradually reduced to a band of enamel running along the tooth in gomphotheres and mammutids. In the South American gomphothere genera *Rhynchotherium* and *Cuvieronius*, the enamel band (and the tooth structure) is spiral (Mothé et al. 2016).

The function of the enamel band is uncertain. It does not form a shearing edge. Mothé et al. (2016) proposed a possible
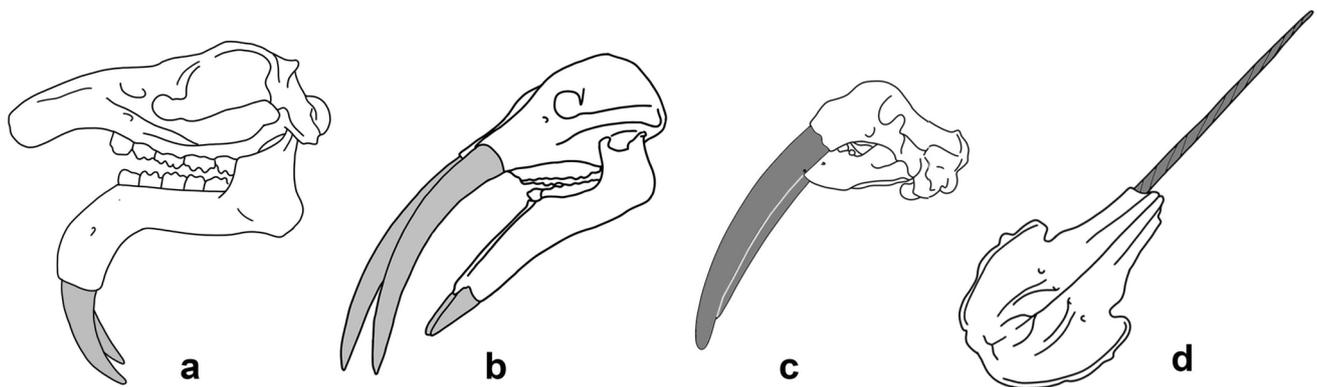

Fig. 11.1 "*Dentin Tusks*" (CL-11). **a** *Deinotherium*, **b** *Gomphotherium* (**a** and **b** PROBOSCIDEA), **c** *Odobenus* (CARNIVORA), **d** *Monodon* (CETACEA). (Modified from: **a** Zittel 1893, **b** Göhlich 1999, **c** Photo, ZFMK, **d** Thenius 1989)

thermal regulation, a hypothesis that requires further evidence. During further differentiation the enamel band disappeared in terminal taxa of Mammutidae (*Mammut americanum*) and Gomphotheriidae (*Anancus*) in parallel evolution (Göhlich 1999, 2010, Koenigswald et al. 2023). In extant Elephantidae (FT-2, FT-3a, FT-5, FT-16. FT-19, FT-53), a tiny enamel cap occurs as a reminiscence in unworn teeth of extant elephants (Koenigswald 2011, 2016a and b).

Mammutidae, Gomphotheriidae and Elephantidae share a specific cross-hatching pattern in the ivory called the "Schreger-pattern" or "Schreger-lines", which is caused by the arrangement of collagen fibres. It is best seen in the cross-section of tusks. The lines cross each other at a species-specific angle (Palombo and Villa 2001, Virag 2012). They reinforce the rigid inorganic matrix and give the material some elasticity (Virag 2012). The *Deinotherium* ivory lacks the Schreger-pattern. It is unclear, whether the structure evolved independently in the different families.

Examples of Carnivora

Odobenus modification: The extant walrus, *Odobenus rosmarus* (Fig. 11.1c), is characterised by its by its robust upper tusks projecting downward from the maxilla (Kastelein and Gerrits 1990) (FT-2, FT-5, FT-43). They are canine tusks and the only dentin tusks produced by Carnivora.

The tusks of the genus *Odobenus* are euhypsodont dentin teeth with a funnel-shaped open pulp, similar to elephant tusks. Only at a very early ontogenetic stage do they bear an enamel cap (Fay 1982, 1985). The teeth have a core of globular dentin (Boessenecker and Churchill 2013). Adult individuals lack almost all incisors, with only one I3 located lingually of the upper canine. A lower canine may be present but very small. It disappears when the symphysis is fully formed (Harington et al. 1993, Kryukova 2012). The canine tusk of odobenids has been known since the Late Miocene (Boessnecker et al. 2023), but at this evolutionary stage the upper canines are rooted and lack globular dentin, e.g.in *Osodobenus* (Biewer et al. 2020).

Examples of Cetacea

Monodon modification: The narwhal, *Monodon monoceros* (Fig. 11.1d), is best known for its single long and straight tusk that is helically twisted to the left. The euhypsodont tooth has been discussed as an incisor or a canine (Berkovitz and Shellis 2018, Nasoori 2020). The tusk originates in the maxilla and therefore it is a canine tusk (FT-43) (Nweia et al. 2012). Normally, only the left tusk grows out of the skull, while the right tusk remains as a germ in the crypt. Very rarely, both tusks are fully developed. Male tusks tend to be longer and are used for used for ritualized command fights. Tusk length is a social signal. Males with long tusks are preferred by females (Graham et al. 2020). The tooth consists of a core of dentin and covered by a thick layer of cementum. There is no convincing interpretation of the spiral structure (Kingsley and Ramsay 1988). Nweia et al. (2014) have discovered structures for innervation, making the tusk an important sensory organ. The single tusk is one of the very rare right-left asymmetries occurring in mammalian dentition.

Odobenocetops modification: *Odobenocetops* from the Mio-Pliocene of Peru is morphologically similar to *Monodon* because of its straight tusk. However, the similarity is superficial. In *Odobenocetops* both tusks, the right and the left one, are present, but of different length. They originate from the premaxilla and are therefore incisors rather than canines (FT-16). In addition, in *Odobenocetops* the premaxilla is turned ventrally and the tusks are directed posteriorly more or less parallel to the body (De Muizon 1993, De Muizon et al. 2002). No other teeth are present, neither in the mandible nor in the maxilla. Structural details of the dentin core were not observed, so it remains open whether these tusks served as a sensory organ as in *Monodon*.

Examples of Sirenia

Dugon modification: In Sirenia, the Dugonidae have small tusks, whereas extant Trichechidae lack functional incisors. The Sirenian AD has been progressively reduced (Abel 1904, Domning 2018). Canines are present in fossil taxa such as *Protosiren* (Domning and Gingerich 1994), but not in extant species.

In *Dugon*, the permanent upper incisor (I1) is an euhypsodont dentin tooth with the typical open pulp and occasionally some traces of enamel (Marsh 1980). In *Dugon* males, these tusks protrude only a few centimeters from the rostrum (premaxilla) (FT-16). They are used for sexual encounters and environmental exploration, but have no apparent role in feeding (Domning 2001, Marshall et al. 2003). The tusks follow a small deciduous dI1.

Examples of Desmostylia

Behemotops modification: Early desmostylians (e.g. *Behemotops*) had strong lower incisors and canines (Domning et al. 1986). The massive lower canines extend well beyond the incisors. The upper canines are much smaller. The tusks do not fit exactly in the category of tusks as used in this paper, because of a thin enamel cover and a possible late root formation (Domning et al. 1986). Compared to other tusked mammals, desmostylians gradually reduced their tusks during the evolution. The Miocene *Vanderhoofus* has no anterior teeth in either the upper or lower jaw (Inuzuka et al. 1994).

Extraordinary tusks

Hippopotamus: The canines of *Hippopotamus* are discussed in CL-14. Its incisors, however, are protruding dentin teeth, similar to dentin tusks but they are not typical tusks, because

they barely protrude from the mouth. The two lower incisors protrude forward, almost horizontally. The two upper incisors face downward leaving a large gap between them for the lower incisors when the mouth is closed. The upper and lower incisors pass each other without a regular occlusion. - The pigmy hippopotamus *Choeropsis* has a very similar AD, but lacks one lower incisor. The fossil hexaprotodont hippos had less reduced incisors.

Mesoplodon*:* The xiphdon whale *Mesoplodon layardii* has only one large tooth that originates in the lower jaw, known as the „mandibular tusk" (Lambert et al. 2018: Fig.9). The orientation of this tooth is very unusual. It curves strongly posteriorly and covers the upper jaw. The tooth locus of this unique tusk-like tooth has been identified as a p3 (Abel 1944).

Nihohae matakoi, an Oligocene cetacean from the of New Zealand, has been described as a dolphin with tusk-like incisors (Coste et al. 2023). The premaxilla has three elongated incisors with roots twice as long as the crown. The canine is a similarly shaped. These teeth are procumbent, and the crowns are covered with enamel. Thus, this taxon – and other members of the Waipatiidae - do not fit exactly into the CD-11 "Dentin Tusks" as discussed here, but may indicate how tusks evolved in cetaceans.

Discussion of CL-11 "Dentin Tusks"

The term tusk is used in a variety of ways, and there is no clear definition for tusks (Biewer et al. 2020). Ungar (2010) uses the term tusk to refer to enlarged, specialised anterior teeth, in which most of the elongated crown protrudes from the mouth when the mouth is closed. Nasoori (2020) classified tusks according to their environmental exposure, in the

atmosphere, or in water. Despite their different origins, the internal structure of all euhypsodont tusks reflects the same additive growth. Cylindrical layers of dentin are added to an open funnel-shaped pulp. The additive growth of the dentin provides some kind of a calendar. Tusks generally show little wear and the preserved annual layers in the dentin provide information about lifestyle and the individual history, as demonstrated for *Mammut americanum* (Fisher et al. 2014).

Dentin tusks from the in different mammal groups and are not homologous, not even the incisor tusks come from the same tooth locus. Tusks are rarely used for foraging. Their function is primarily for display, so sexual differences are quite common. In addition tusks are used as weapons or, together with the trunk, as a tool for moving large objects.

In Proboscidea the evolution of tusks correlates with the reduction of canines and other incisors. The development of a trunk freed the front to bring nourishing plant material into the mouth. Thus, the remaining incisors, modified into powerful tusks, are used primarily as organs of social communication in display, defence and attack (Haynes 1991). The use of the unique lower tusks of *Deinotherium*, that are directed caudoventrally, and the length of its trunk are still debated (Nabavizadeh 2024).

Gomphotheres and Mammutidae were separated when they emerged from Africa in the Early Miocene. As they evolved in Eurasia and the Americas, several features of the tusk evolved in parallel and almost simultaneously. Each reduced the enamel to a band covering one side of the dentin tusk. During the Late Miocene, this band disappeared independently in both families. Only the South American *Cuvieronius* retained its spiral enamel band into the Pleistocene (Mothé et al. 2016). During the Miocene both families have had lower incisors. They are reduced and the symphysis is

Fig. 11.2 "*Dentin Tusks*" (CL-11) in Proboscidea. **a** *"Mammut" borsoni*, straight tusks of 5 m length from Milia, **b** *Mammuthus pimigenius*, a spiraled tusk from Siberia. (Photos courtesy of D. Mol)

shortened in both families independently in the Late Miocene (Göhlich 1999, Koenigswald et al. 2023).

During The Plio-Pleistocene some taxa of European mammutids and gomphotheres have extremely elongated and straight upper tusks. The tusks of the gomphotheriid *Anancus* from Europe and the Siwaliks reached a length of 2.7 m (Kurten 1968, Akbar Khan et al. 2011) and the "*Mammut*" *borsoni* from Greece even reached a length of 5 m (Tsoukala and Mol 2016) (Fig. 11.2a).

During the Pleistocene, there is another parallelism in time between the Mammutidae (*Mammut americanum)* and the Elephantidae *(Mammuthus primigenius)*. In both, the upper incisors were independently elongated and strongly spiraled upwards (Fig. 11.2b).

Observations of canine dominated dentitions

Cluster 12
"Moderate Canines" (C12)

Concordant canines, moderately enlarged

Definition and occurrence: Strong but not exaggerated canines characterise the cluster CL-12 "*Moderate Canines*".

The canines are conical in shape, single pointed, with one root and occur almost concordantly in the upper and lower dentition (FT-36). Strong canines are often combined with a gradual reduction of the anterior premolars (FT-52) The lower canine is generally set more anteriorly than the upper canine (Fig. 12.1). The canines occlude often only slightly, and when they do, they abrade with their sidewalls. The number of incisors is not usually reduced. In general, the size of the incisors increases I1/i1 to I3/i3 (FT- 6b).

Moderately enlarged canines are a plesiomorphic element of the mammalian dentition, so they occur in all groups of mammals, regardless of whether they are carnivorous, omnivorous or herbivorous mammals (Fig. 12.1). The peculiarities are the concordant enlargement of the canines and the preservation of the entire set of incisors. The number of mammals with moderately enlarged canines is so great that only a few examples representing the different groups will be discussed. METATHERIA (e.g. *Borhyaena*, *Dasyurus, Thylacinus*), AFROINSECTIPHiLIA (*Tenrec*), PANTODONTA (e.g. *Titanoides*, *Kopidodon*), PANTOLESTA (e.g. *Buxolestes, Palaeosinopa*), CHIROPTERA, CONDYLARTHRA (e.g. *Carsioptychus*, *Arctocyonides, Arctocyon*), HYAENIDONTA (e.g. *Hyaenodon, Megistotherium),* PERISSODACTYLA (e.g. *Hyracotherium*, *Thomashuxleya, Phenacodus, Megacerops*), and in ARTIODACTYLA (e.g.
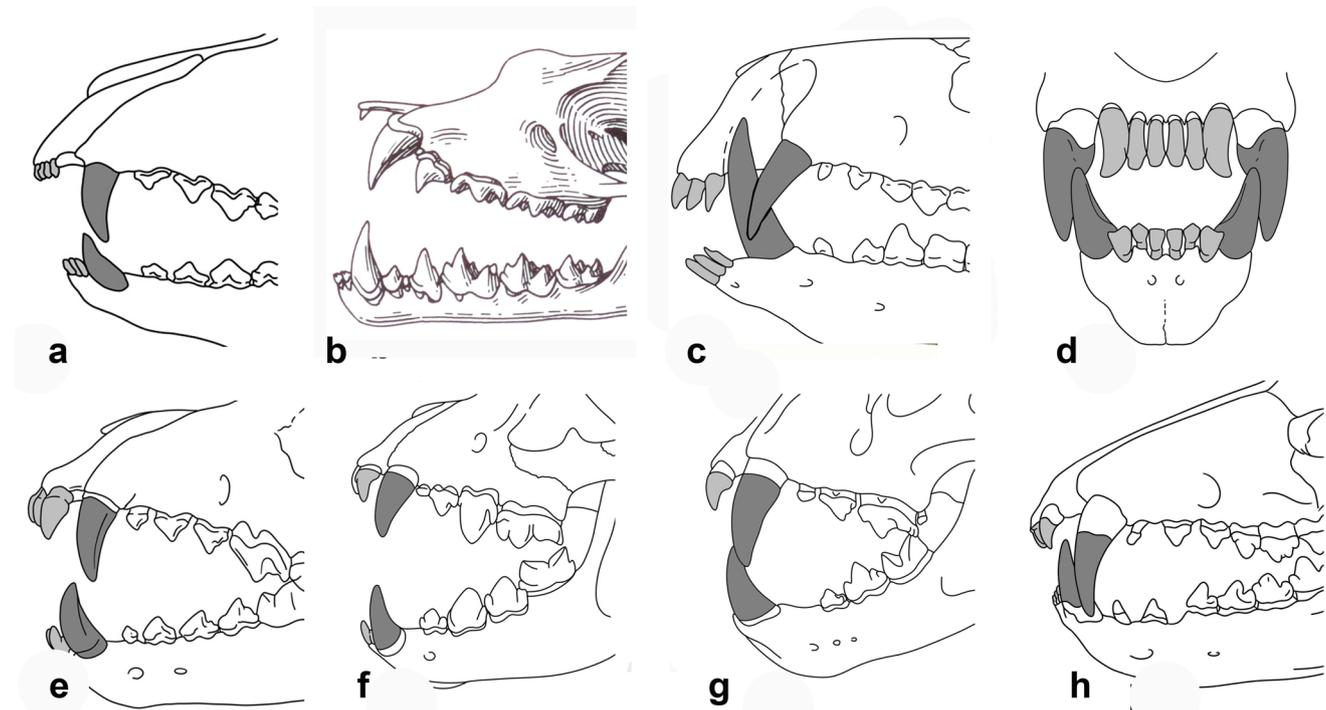
Fig. 12.1 "*Moderate Canines*" (CL-12). **a** *Thylacinus* (MARSUPIALIA), **b** *Rhinolophus* (CHIROPTERA), **c** *Arctocyon* (CONDYLARTHRA), **d** *Gulo gulo,* **e** *Canis,* **f** *Crocuta,* **g** *Panthera* (**d** -**g** CARNIVORA), **h** *Sionyx* (MESONYCHIA). (Modified from: **a, b, d, e, f, g, h** Thenius 1989, **c** Russel 1964)

Homacodon, Archaenodon, Hypertragulus, MESONYCHIA (*Archaeotherium, Sinonyx, Daeodon* and perhaps *Andrewsarchus*). Almost all CARNIVORA, even the smallest, represent this CD-12 "Moderate Canines".

Examples of Sparassodenta

Borhyaenid modifications: The extinct borhyaenids from South America (e.g. *Borhyaena* (3.1.3.4/3.1.3.4), *Cladosictis* (4.1.3.4/4.1.3.4) and *Prothylacinus*) have massive canines. They have 4 or 3 upper and 3 lower incisors. In *Arctodictis* (Miocene, Argentina) the lower incisors are laterally compressed and staggered between the very robust canines (Forasiepi et al. 2004). In *Thylacosmilus* the upper canines are discordant and are modified into saberteeth (CL-15) (Janis et al. 2020).

Dasyurid modification: The dentition of *Thylacinus* (4.1.2.4/3.1.3.4) (Fig. 12.1a) has moderate upper and lower canines and 4 incisors in the upper and 3 in the lower jaw. In *Dasyurus* (4.1.3.4/3.1.3.4) and other dasyurines the central upper incisor (I1) is enlarged, whereas the lateral incisors (I4) is significantly larger in thylacinines (Tate 1947, Archer 1976, Archer and Hand 2006).

Examples of Lipotyphla

***Tenrec* modification**: The AD of the extant *Tenrec* (2.1.3.3./3.1.3.3, Madagascar) is modified by the elongated snout. There are two incisors in the upper jaw, and three in the lower jaw (Fig. 12.2). The lateral one is specialised. The canines are relatively large and accordingly there is a large canine fossa in the premaxilla. The upper and lower canines are followed by large diastemata which correlate with the elongation of the skull.

Examples of Chiroptera

Chiropteran modifications: Chiroptera are generally characterised by relatively large upper and lower canines (Fig. 12.1b) Some Megadermoptera have canines with small additional cusps (e.g. *Pteropus*). The incisors, two upper
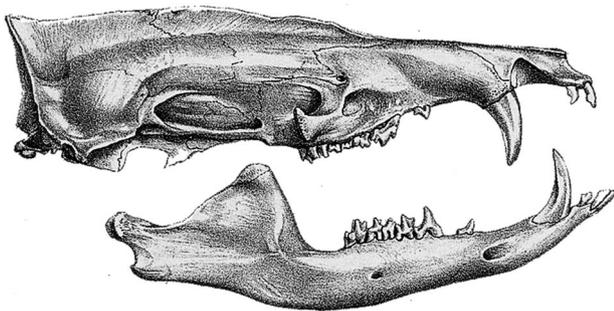
Fig. 12.2 "*Moderate Canines*" (CL-12). *Tenrec ecaudatus* (AFROSORICIDA) that has a large precanine diastema for the large lower canine. (From Dobson 1883 via Wikimedia)

and three lower, are mostly small. The I1 and P1 and p1 are always reduced (Miller 1907). Chiroptera have developed very different types of dentitions. Thenius (1989.99) counted about 50 different types, differing mainly in the massive reduction of specific tooth loci and in the molar morphology. The great variability will not be discussed here, because they do not share convergent structures with other mammals. Because of their large canines all can be included into this CL-12. As an exception vampire bats (e.g. *Desmodus*) have been placed in CL-10 "Special Incisors", unsimilar to most mammals.

Examples of Pantodonta

Pantodont modification: Pantodonts belong the Cl-12 "*Moderate Canines*" because their canines are mostly higher than the incisors and premolars. The Paleocene *Alcidedorbignya* was mentioned in the CL-1 "*Plesiomorphic Pattern*" (De Muizon et al. 2015) because of its similarity to *Didelphis*. It shows the smooth transition between CL-1 and CL-12.

The European *Kopidodon* (Koenigswald 1983, Clemens and Koenigswald 1993) and most of the North American genera have medium-sized canines. The molars do not indicate a specialization in carnivory. In *Titanoides*, the higher upper canine is extremely elongated but not curved (Simpson 1960). In *Coryphodon* the strong canines abrade each other, making this genus a member of the cluster CL-14 "*Mutually Abrading Canines*".

Examples of Pantolesta

Pantolestid modification: Pantolestids (3.1.4.3/3.1.4.3) have moderately enlarged canines, with the upper canine is slightly larger than the lower. The lower incisors are relatively small and more equal, but in the upper tooth row the I3 is larger than I1 and I2 and more caniniform. The European *Buxolestes* and the very similar *Palaeosinopa* from Wyoming are at least facultatively piscivorous, according to their preserved stomach contents (Koenigswald 1980, Rose and Koenigswald 2005).

Examples of Condylarthra

***Arctocyon* modification*:* The Paleocene *Arctocyon* (3.1.4.3/3.1.4.3) (Fig. 12.1c) has strong canines. The lower is slightly larger than the upper. Despite the well-developed canines *Arctocyon* must be considered as omnivorous because of its broadened and bunodont molars (Russel 1964).

Examples of Carnivora

Carnivora modification: The Carnivora (e.g. Canidae, Felidae, Mustelidae, Ursidae) can generally be assigned to CL-12, because their AD is dominated by moderately enlarged canines (Figs. 12.1d-g). The canines are concordant in the upper and lower tooth row, although the uppers are

mostly slightly larger. The pointed canines are usually well rooted and show little wear. Sexual dimorphism is common (Meachen-Samuels and Binder 2009). This pattern is very conservative and is present in small (e.g. *Mustela nivalis*) or large (e.g. *Panthera leo*) animals.

Between the prominent canines there are much smaller incisors. Their full number is three on each side of the upper and lower dentition. The size of the incisors usually increases from the central (i1 or I1) to the lateral incisor (i3 or I3). This results in a very specific functional construction in some genera. If the I3 is canine-like, this tooth and the upper canine form two strong points. The lower canine fits into the gap between the two teeth and completes the tool. This "fork" enhances the ability to hold the prey. It is found in several Carnivora (Fig. 12.3).

The conservatism of the AD is most evident in the hyaenid *Proteles* (Fig. 12.4a). Its premolars and molars are almost completely reduced, as is often the case in mammals specialised on eusocial insects. However, in contrast to the cheek teeth, the AD is well developed with incisors and dominant canines (Berkovitz and Shellis 2018).

Canines are important social organs in rivals. This may be one of the reasons why canines have been retained in omnivorous and herbivorous members of the order Carnivora, such as *Ursus* or *Meles*. Although such canines have lost their significance for catching or killing prey, they may be used for display. The canines of the (mostly) herbivorous cave bear (*Ursus spelaeus*) show a marked sexual dimorphism (Kurten 1955).

In general, the canines of carnivores show little wear. In the herbivore *Ursus spelaeus*, some canines may be heavily worn, and others may show horizontal furrows around the base of the canine. Such unusual wear facets are caused by blades of grass being drawn between the teeth (Breuer 1933).

Examples of Perissodactyla

***Heptodon* modification:** Early perissodactyls, e.g. *Hyracotherium,* an early equid, and *Homogalax,* an early Eocene tapiroid, show a moderately enlarged canine (FT-26) and no diastema (Radinsky 1963 1965). They fit well into CL-12. In *Heptodon* (3.1.4.3/3.1.4.3), an Eocene tapiroid, the upper canine is slightly larger than the lower, and a diastema separates canines from the premolars (Radinsky 1965).

During the perissodactyl evolution the size of the canines shrinks and the diastema expands.

Extant equids belong to CL-3 "*Concordant incisors*", extant *Tapirus* is discussed in CL-10 "Special Incisors".

Examples of Artiodactyla

Artiodactyls are mostly herbivorous and these families have reduced or missing canines. In Ruminantia the lower canines are incisiform (CL-17). In some genera the upper canines are enlarged as prominent social organs (CL-14 and 16). Large and massive canines in the extinct Mesonychidae are interpreted as indicative of carnivory.

Entelodontid modification: Entelodontids (e.g. *Archaeotherium* (Fig. 12.5), *Daeodon, Entelodon*) have relatively strong canines. Their frontal dentition is peculiar in that in some taxa the incisors arranged with diastemas between them, rather than close together. The size of the incisors increases from i1/I1 to i3/I3 (FT-5). The lateral incisor may reach half the height of the canines (Effinger 1998). The canines are large and massive in *Daeodon* but comparable in the upper and lower jaws. The molars are bunodont. In
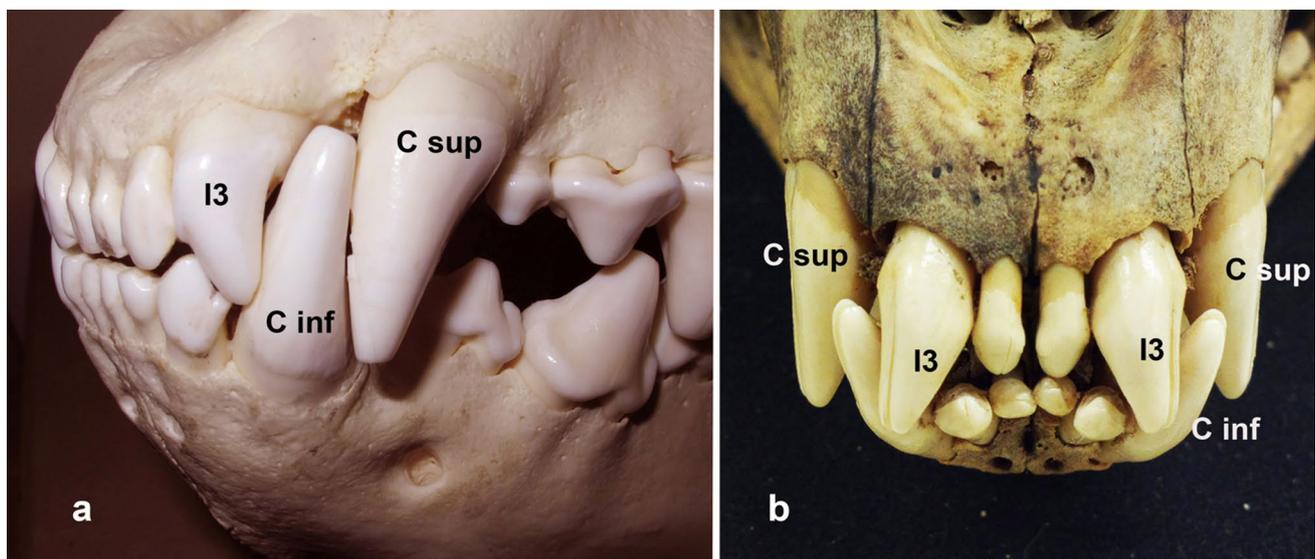

Fig. 12.3 "*Moderate Canines*" (CL-12). **a** *Crocuta crocuta* (Hyaenidae) and **b** *Leptonychotes* (Phocidae). The enlarged I3 forms together with the upper (C) and lower canines (c) a grasping tool ("fork"). (**a** ZFMK 2016-0130, **b** photo courtesy of L. Jernval)

Fig. 12.4 "*Moderate Canines*" (CL-12): **a** *Proteles cristata* (Hyaenidae), note the full anterior dentition and the reduced molar dentition **b** *Sinonyx jiashanensis* (Mesonychidae), distinct canines in a carnivorous artiodactyl. (**a**, ZMFK 79.72 **b** UMMP-NH VP 118345 – UMORF reconstruction Zhou et al 1995)

the European *Elomeryx,* the canines are relatively small (Hellmund 1991). The spacing of the subsequent premolars is related to the elongated facial cranium, but this does not explain the spacing of the canines. Enteledonts are omnivores and occasionally scavengers, or even hunters (Joekel 1990). The wear on the large canines of *Daeodon* has been interpreted as a trace of bone crushing.

Examples of Mesonychia

Mesonychian modification: Mesonychians are carnivorous Artiodactyla with massive canines e.g. in *Sinonyx* (Figs. 12.1h and 12.4b)*, Mesonyx.* These teeth are certainly useful for catching and holding prey. Molars are trenchant, but not as much as in true Carnivora. Mesonychids show marked sexual dimorphism (O'Leary et al. 2000). *Sinonyx*

Fig. 12.5 "*Moderate Canines*" (CL-12): Cranium of *Archaeotherium mortoni* (Anoplotheriidae), an omnivorous or carnivorous artiodactyl with large canines. (SMNK-PAL 8445, photo Mathias Vielsäcker)

(3.1.4.3/3.1.4.3, Paleocene, China) is unique in having very slender elongated canines. The slender canines are not comparable with saberteeth, because they are concordant in the upper and lower dentition (Zhou et al. 1995). The giant *Andrewsarchus* belongs to this morphological cluster (Osborn and Olson 1924). Its systematic position is discussed as a mesonychid or an artiodactyl (Geisler and Theodor 2009, Spaulding et al. 2009).

Discussion of CL-12 "Moderate canines"

Large canines are a plesiomorphic element of the mammalian dentition. Their size and function have undergone many changes during evolution in different lineages. Moderately enlarged canines occur in carnivorous, omnivorous and herbivorous taxa and are thought to be as ancestral to the various differentiations. They derived from the ancestral pattern with relatively small canines, such as in *Didelphis* (CL-1). Canines are primarily weapons for catching and killing prey, but the power of canines made them important social organs for rivalry and display.

In general, canines are single-pointed and have only one root. The lower canine closes more anteriorly than the upper. Only in some early mammals, canines do have two roots. Only in some early mammals do have canines with two roots.

Depending on the height of the lower canine, a diastema between the I3 and the upper canine is necessary to close the jaw. This is called precanine or paracanine diastema, which may form a canine fossa in the premaxilla and is very prominent in *Tenrec* (Fig 12.2) or *Arctocyon* (Fig. 12.1c). In some herbivores the canines are reduced to the size of premolars and incisors (CL-13).

The occlusion of the lower canine anterior to the upper canine is a very conservative pattern. However, it has been broken several times when the lower canine has become incisiform as in CL-17 "*Ruminant Incisor Arcade*", or in CL-16 "*C/p Functional Unit*".

Canines are important social organs, either as weapons or for display. Their excess height is of functional importance, as weapons or for display. Wear occurs manly on the side walls.

In carnivores the main function of canines is to catch or hold prey, but display functions are also important.

In herbivores and omnivores, the social aspect is of is great importance and controls the size of the canine. Sexual dimorphism is common. Some herbivores have evolved extremely elongated upper canines resembling saberteeth (CL-15). Other herbivores have massive upper and lower canines that abraded each other (CL-14). In both cases the teeth are used for social functions food and less for foraging.

During evolution the importance of canines in the plesiomorphic pattern was independently replaced by enlarged incisors as in placentals and marsupials (CL-8). In other groups the size of the canines became adjusted to the size of the incisors and premolars in (CL-13).

Cluster. 13
"Adjusted canines" (CL-13)

Concordant canines adjusted to the size of incisors and premolars

Definition and occurrence: The CL 13 "*Adjusted Canines*" is characterised by upper and lower canines that are fully integrated into the toothrow and are similar in size and height to the incisors and premolars. The toothrow is generally complete without major diastemata (Fig. 13.1). Adjusted canines occur with various modifications in almost all placental orders, but always only in selected groups. The human dentition is a typical example The adjusted size of the canines is a derived condition, since in most ancestral therians, canines are the largest features the AD. Common
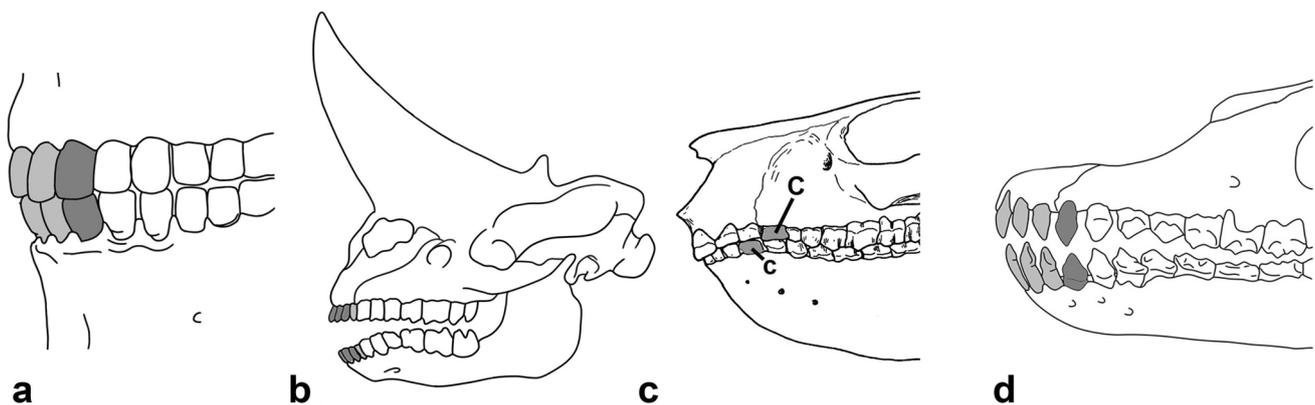

Fig. 13.1 "Adjusted Canines" (CL-13): **a** *Homo* (PRIMATES), **b** *Arsinoitherium* (EMBRITHOPODA), **c** *Notopithecus* (NOTOUNGULATA), **d** *Theosodon* (LITOPTERNA). (Modified from **a** artificial model, **b** Andrews 1906, **c** Simpson 1932b, **d** Scott 1910)

morphological features are the concordant incisors and canines that are of similar size (FT-1, FT-31, and FT-33), and the absence of diastemata." Adjusted Canines" have been observed in e.g. DERMOPTERA (*Cynocephalus*), in PRIMATES (*Australopithecus*, *Homo*), CONDYLARTHRA (e.g. *Hyopsodus),* EMBRITHOPODA (e.g. *Arsinoitherium*), ARCTOSTYLOPIDA (A*rctostylops*), NOTOUNGULATA (e.g. *Protypotherium*), LITOPTERNA (e.g. *Macrauchenia*), and several early ARTIODACTYLA (e.g. *Dichobune*).

Examples of Dermoptera

***Cynocephalus* modification**. The extant *Cynocephalus* (2.1.2.3/2.1.2.3) has a highly differentiated AD. The lower canine has a central point but is not much higher than the incisors and premolars The lower incisors (i1 and i2) are multicusped with several spines, forming a toothcomb. The i3 is slightly more robust with only three spines. The upper I2 is very small, but has three points. The I3 and the lower canine are triangular when viewed from the side. These two triangles embrace the central cusp of the lower c when the mouth is closed. The triangles thus form an effective tool, for cutting captured insects (Stafford and Szalay 2000).

Plagiomene (??−1.4.3/3.1.4.3) has been assigned to DERMOPTERA. The lower canine is small and projects only very little beyond the premolars and incisors. The three lower incisors are slightly procumbent and have bicuspid crowns (MacPhee et al. 1989, Rose 1973, 1982).

Examples of Primates

***Australopithecus* modification**: Primates generally have well-developed canines. The Hominini with *Australopithecus* and *Homo* (Fig. 13.1a) are an exception with canines of almost equal height and width with incisors and premolars (FT-1, FT-33). The modification is limited, whereas the closest relatives within the Homininae such as *Gorilla* and *Pan* have fairly massive canines (CL-12).

Examples of Condylarthra

***Hyopsodus* modification**: The Eocene *Hyopsodus* is an early ungulate and associated with Perissodactyla (Orliac et al. 2012) (FT-1, FT-33). It has a complete dentition without large diastemata. Canines and incisors are of similar size. The genus is therefore placed in this cluster. In general, canine size is quite variable in early perissodactyls (Simpson 1932a, b, Thenius 1989, Janis et al. 1998).

Examples of Embrithopoda

***Arsinoitherium* modification:** The dentition of *Arsinoitherium* (Fig. 13.1b) is characterised by a continuous tooth row with the full set incisors, canines, premolars, and molars (3.1.4.3./3.1.4.3) (Sanders et al. 2010a, b). All teeth are of the same height. The frontal dentition with the adjusted canines is a perfect representation of CL-13.

Examples of Arctostylopida

Arctosylopid modification: Arctostylopidae are a very restricted group of archaic ungulates (3.1.4.3./3.1.4.3) that is known from the Paleocene and early Eocene of China (e.g. *Gashatostylops, Palaeostylops*) and North America (e.g. *Microstylops*) (Rose 2006). They share reduced canines of similar height to the incisors or anterior premolars. Thus, the group of rabbit-sized mammals is added to Cl-13 "*Adjusted Canines*".

Examples of Notoungulata

Notoungulata are very diverse in their AD. Typical examples of the cluster Adjusted Canines (CL-13) are found e.g. in the in the toxodont *Homalodotherium*, and in the typotheres *Oldfieldthomasia*, *Notopithecus* (Fig. 13.1c)*,* and *Protypotherium* (Fig. 13.2).

The occlusion pattern of the Eocene *Notopithecus* is remarkable. Incisors and canines have broadened crowns. The lower i1 and i2 occlude mainly with the upper I1. The lower i3 occludes only with the I2, and the lower canine with the I3. The first lower premolar is the antagonist of the upper canine. This unusual occlusion pattern is slightly repeated in cluster CL-16 "*C/p Functional Unit*". The position of the P3 is less abnormal, it occludes between p2 and p3 as usual (Simpson 1932a.10).

Examples of Litopterna

In litopterns *Macrauchenia* and *Theosodon* (Fig. 13.1d) have adjusted canines but differ slightly. In *Macrauchenia* (3.1.4.3./3.1.4.3) (FT-1, FT-33) the anterior teeth are sectorial and closely aligned. In *Theosodon* (3.1.4.3/3.1.4.3), the incisors, canines and first premolars are pointed and small diastemata separate the teeth. In conjunction with the elongated neck, this particular pattern may be an adaptation for stripping leaves high off the ground (Croft 2016).

Examples of Artiodactyla

Artiodactyl modifications: In some early artiodactyls, the upper and lower canines are adjusted to the size of the incisors and premolars. Examples include Diplobunidae (such as
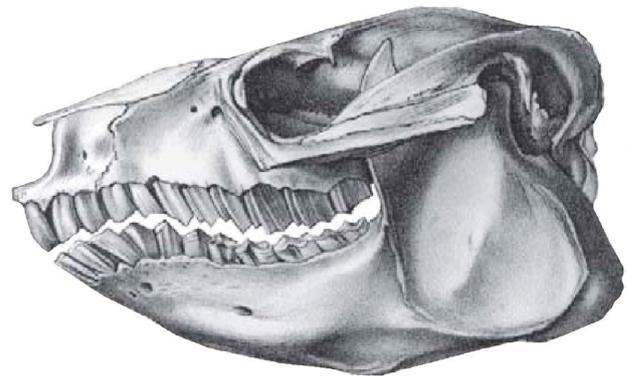

Fig. 13.2 "Adjusted Canines" (CL-13): *Protypotherium* (NOTOUNGULATA) (from Sinclair 1908)

*Diacodexis***,** *Dichobune, and Cainotherium),* Anoplotheriidae (*Anoplotherium*), Oromerycidae (*Eotylopus* and *Montanatylopus*) and early Camelidae (*Protylopus).* Later camelids such as *Poebrotherium* also have small canines as well, but diastemata occur between the teeth (Thenius 1989, Prothero 1998a, b, Wall and Hauptmann 2001).

Discussion of CL-13 "Adjusted canines"

Adjusted canines occur with various modifications in almost all placental orders, but have not been found in Metatheria. This feature (FT-33) is restricted selected groups. A typical example is the human dentition, compared to other primates (Fig. 13.1). The adjusted size of the canines is a derived condition, since in most ancestral therians, the canines are the largest feature in the AD. For a carnivorous lifestyle the absence of a functional canine offers no obvious advantage. Adjusted canines are preferable in herbivorous or omnivorous mammals. They unify the dentition and increase the total amount of the occlusal surface in use simultaneously. Most taxa are of medium the body size. An exception is *Arsinoitherium* with a body mass of 2.5 tonnes (Sander et al. 2010).

The reduced size of the canines suggests that three specific functions of canines are lacking. their use for catching or holding prey, the use as a weapon and their importance for display. The occurrence of adjusted canines is well documented in a limited group of higher Primates. Cercopithecidae and Cebiidae and most Hominidae, e.g. *Pongo, Gorilla* and *Pan,* have prominent canines, often with a marked sexual dimorphism. In Hominini (*Australopithecus* and *Homo*), however, the sexual dimorphism in the canines is greatly reduced but still present. A change in the preferred food may have been one reason for the reduction in canines, but perhaps the social organization also changed, requiring less general male dominance and less rivalry.

Cluster 14
"Mutually abrading canines" (CL-14)

Concordant canines, mutually abrading

Definition and occurrence: The CL-14 "*Mutually Abrading Canines*" is defined by large and massive canines that abrade each other on large and plain facets (Fig. 14.1). The edges of the wear facets are often very sharp due to the exposed cross-section of the enamel layer. Upper and lower canines are often concordant and euhypsodont. Such teeth are used as weapons and for display rather than for food acquisition. Modifications differ in the orientation of the canines and the facets between them. The canines are either sagittal oriented (e.g. *Hippoptamus*) or divergently projecting laterally from the mouth (e.g. *Phacochoerus*). Common morphological features include enlarged canines that abrading each other on a steep facet (FT-40). Examples of this CL-14 are found in PANTODONTA (*Coryphodon*), ARTIODACTYLA (*Hippopotamus* and various Suidae), PERISSODACTYLA (*Metamynodon*), and ASTRAPOTHERIA (*Astrapotherium*). All are herbivores.

Examples of Pantodonta
***Coryphodon* modification**: The Paleocene/Eocene pantodont *Coryphodon* from North America and Europe has a broad skull with large and massive premaxillae. The enlarged canines are hypsodont but not euhypsodont. The lower canines are slightly flaring outwards, while the upper ones are almost vertical (Cope 1877. 211, Simons 1960, Lucas 1989:46). The enlarged canines grind against each other on their sidewalls. Wear facets are located on the posterior side of the lower canines and on the mesio-anterior side of the upper canines. The incisors are relatively small and are implanted with interdental spaces suitable for grasping aquatic plants. Sexual dimorphism in canine size has been
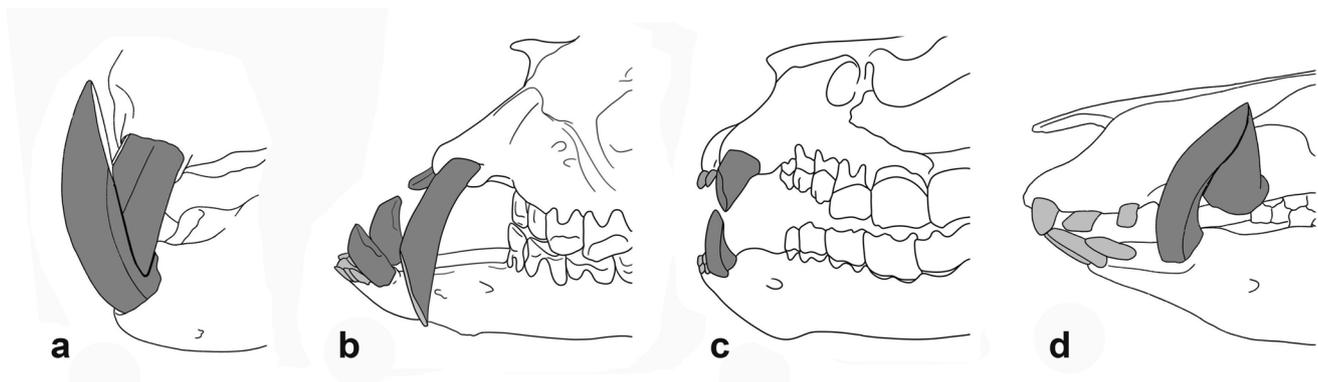

Fig. 14.1 "*Mutually Abrading Canines*" (CL-14): **a** *Hippopotamus* (ARTIODACTYLA)*,* **b** *Astrapotherium* (ASTRAPOTHERIA), **c** *Metamynodon* (PERISSODACTYLA), **d** *Sus scofa* (ARTIODACTYLA). (Modified from: **a** and **d** own photos, **b** Riggs 1935, **c** Thenius 1989)

measured (Uhen and Gingerich 1995). *Coryphodon* was herbivorous and probably semi-aquatic (Eberle et al. 2010).

Examples of Artiodactyla

***Hippopotamus* modification:** In the extant *Hippopotamus* (2.1.4.3/2.1.4.3), the powerful upper and lower canines are euhypsodont (Fig. 14.1a). Both upper and lower canines are aligned in the same sagittal plane (Fig. 14.2b). The highly curved teeth abrade each other on flat, almost vertical facets (FT-40). These facets extend over the entire cross-section. Because of these facets, the enormous canines do not limit the lateral movement of the mandible during mastication (Avedik et al. 2023). The facets are surrounded by sharp edges formed by the hard enamel. The lower canine has a trigonal cross-section with a keel on the anterior side. As the facet is inclined posteriorly, the enamel on the anterior side forms a sharp tip pointing upwards. In the upper canine the facet ends with two points on the posterior side, which are associated with a deep concave groove on the distal side of the tooth (Thenius 1989, Koenigswald 2020). The canines sharpen each other mutually as the mandible closes. This regular sharpening does not require any additional movement of the mandible and therefore differs from reciprocal sharpening in rodents or lagomorphs. In addition to the massive canines, the *Hippopotamus* has two straight incisors per quadrant, which are pure dentin teeth (see CL-11).

Suid modifications: Two types of canine orientation occur in suids. In the more plesiomorphic one, the canines are oriented sagittal and abrade each other in an almost vertical facet, as in the Tayassuidae. In a more derived version, the upper and lower canines are divergent and oriented more laterally. They abrade each other much less, allowing the upper canines to reach an impressive length (Orilac et al. 2010). Very good examples are the extant *Tayassu* (Fig. 14.2c) and the Pleistocene genera *Platygonus* and *Mylohyus*. The canines are oriented sagittally, almost vertically, and have little curvature. They occlude with a very steep facet over the entire cross-section. In the premaxilla there are two incisors, the central one being much wider and curved towards the midline. In the mandible there are three procumbent incisors, the two central ones forming a common cutting surface, the lateral one (i3) being much shorter (Hulbert 2001, Berkovitz and Shellis 2018).

The AD is more derived in *Sus* (3.1.4.4/3.1.4.3) or *Phacochoerus* (1.1.3.3/2-3.1.2.3) (Fig. 14 1 d and 14. 2a). Canines are long and strongly divergently curved. The upper canine is more massive. It has a facet for the lower canine on its anterior surface. This facet does not truncate the tooth, allowing the upper canine to grow continuously past the lower canine. The lower canine is shorter and truncated by the wear facet. Due to the triangular cross section of the lower canine and the inclination of the facet, the lower canine may have a sharp tip on its anterior side.

The upper and lower jaws have three incisors. The lower incisors are procumbent, while the upper incisors are downward facing. The I1 is rooted and has a laterally curved occlusal surface. The three lower incisors are elongated and procumbent. The three upper incisors are wider and curved mesially. They occlude with the lower incisors when the mandible is protruded (Herring 1972). The occlusion of the incisors is similar to that of the Tayassuidae (Herring 1972).

An impressive example of this modification with divergent canines is the Miocene *Listriodon* (3.1.3.3/3.1.3.3) from Europe. In the Pleistocene *Celebochoerus* from Celebes the upper canines reach an enormous length (Hooijer 1948).
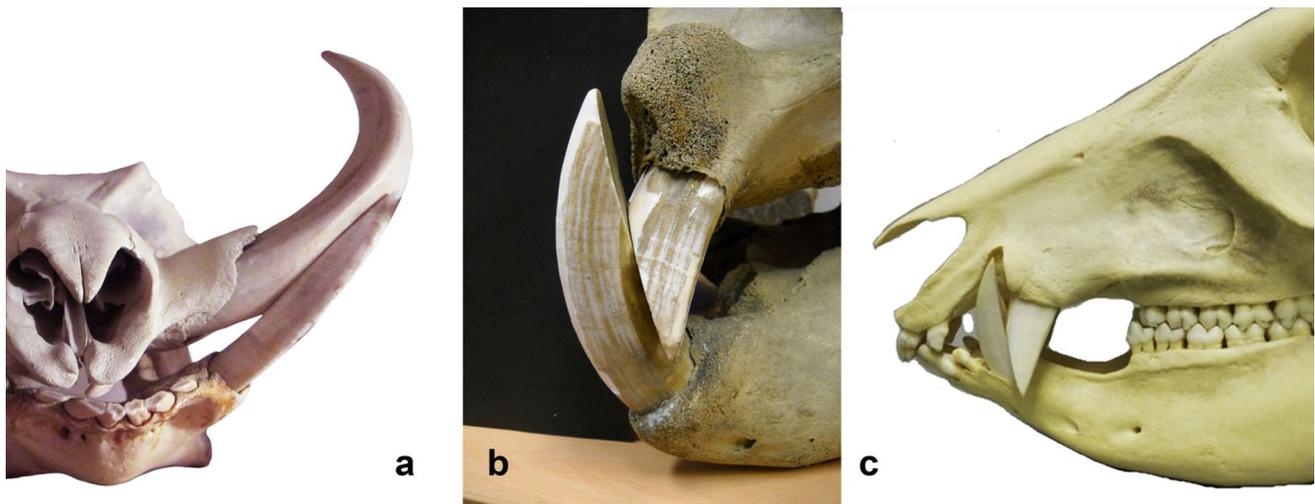

Fig. 14.2 "*Mutually Abrading Canines*" (CL-14): **a** *Phacochoerus*, **b** *Hippopotamus* **c** *Tayassu* (**a, b**, and **c** ARTIODACTYLA). The orientation of the canines is divergent in **a**, but sagittal in **b** and **c**. (**a** ZMFK 2024-0304, **b** BIOB-PAL M2365, photo G. Oleschinski)

Examples of Astrapotheria

Astrapotherium **modification**: The upper and lower canines of *Astrapotherium* are euhypsodont and abrade each other (Fig. 14.1b). The upper canines are oriented almost sagittally and have a vertical wear facet with a cutting edge on the lower margin (Fig. 14.3a). The lower canine is strongly divergent and laterally curved. Its wear facet is on the posterior side (FT-40). As the tooth grows laterally, the facet shifts medially. Thus, in contrast to Suidae, it is the lower canine rather than the upper canine that forms a strong protruding weapon (Riggs 1935, Scott 1912, 1937) (Fig. 14.3b). The less derived astrapothere *Trigonostylops* has a very similar arrangement of the rooted canines (MacPhee et al. 2021).

Examples of Perissodactyla

Metamynodon **modification**: The Oligocene perissodactyl *Metamynodon* (3.1.3.3/2.1.2.3) has strong mutually abrading canines (FT-40). Only the upper canine may be euhypsodont (Fig. 14.1c). The orientation of the canines is sagittal with a lateral twist. The wear facet of the lower canine is on the antero-lateral side, the wear facet of the upper canine is on the postero-labial side. The facets affects the entire cross-section. The canines are slightly rotated outwards, but do not exaggerate laterally due to the mutual abrasion. (Scott 1887, Wall and Heinbaugh 1999, Thenius 1989).

Examples of Xenarthra

Choelopus **modification**: The extant xenarthran *Choelopus didactylus* is often discussed because of the canine-like nature of the most anterior teeth (McAfee and Naples 2012, Hautier et al. 2016). These are euhypsodont dentin teeth with no enamel, but an outer layer of hyper-mineralized orthodentin that produces sharp edges (Kalthoff 2011). The canine-like teeth abrade each other on an almost vertical facet. The tooth loci remain uncertain, mainly because the upper tooth is more anterior than the lower, exactly the opposite of the usual canine occlusion. Functionally, the teeth are similar to CL-14. However, if the lower tooth is a homologue of a first premolar, the constellation of *Choelopus* would to some degree resemble the CL-16 "C/*p* Functional Complex".

Discussion of CL-14 "Mutually Abrading Canines"

The large and flat wear facets found in CL-14 indicate that they were abraded during the normal jaw movement. This differs from the abrasion of the incisors in gliriform incisors, which are abraded by two different positions of the mandible, one for gnawing and one for sharpening (see CL-9).

The enlarged canines in this cluster occur in different mammalian lineages and their similarity is due to a multiple convergent evolution. All taxa in the CL-14 are herbivores, and their canines are not, or only rarely used for foraging or shaping food. They may be used as weapons against predators or in intraspecific rivalry. A weapon function is plausible, because the tips of the canines are kept very sharp by mutual abrasion. It is interesting, that neither the incisors nor the premolars share any function with the enlarged canines. The formation of such large teeth may be costly, but their social significance seems to be important. The orientation of the canines is vertical or divergent, never anterior as in tusks. The large canines do not interfere with the lateral movement of the jaws during mastication (Avedik et. al. 2023). The curved canines are unsuitable for digging. Some Suidae are
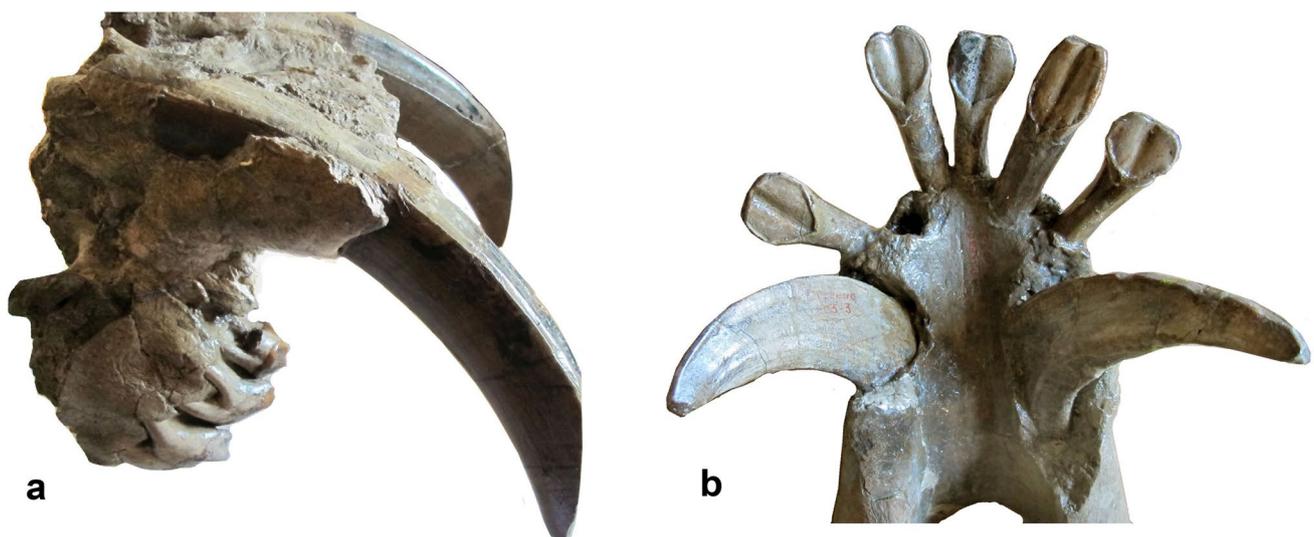

Fig. 14.3 "*Mutually Abrading Canines*" (CL-14): *Astrapotherium holmbergi*. **a** fragmented maxilla with canines, **b** symphysis with diverging canines (MNHN COL 10, own photos)

known to dig into the ground for food but such digging is mainly done with the trunk-like nose. The burrows used by *Phacocoerus* for shelter are dug by other animals.

Within the Suidae different evolutionary stages can be observed within this cluster, a simple one with straight canines in *Tayassu*, a more derived one with curved canines in *Phacocoerus*, and finally the orientation of the upper canine in *Babyrousa,* which is so anomalous that it is discussed in CL-19 "*Special canines*".

Cluster 15
"Saberteeth" (CL-15)

Extremely enlarged discordant upper canines

Definition and occurrence: Saberteeth are conspicuous, elongated upper canines. Despite their long roots, they are generally not euhypsodont (Fig. 15.1). The teeth are usually laterally compressed and often have serrated margins, if they are covered with enamel. The lower canines and all incisors are relatively small. Most carnivorous and some herbivorous taxa have a prominent flange on the anterior mandible for protection. The common morphological features are FT-38,

FT-42, and often FT-53. Saberteeth occur in the metatherian SPARASSODONTA (*Thylacosmilus*) and in several placental mammals. DINOCERATA (*Uintatherium*)*,* CREODONTA (*Machaeroides*), CARNIVORA (Nimravidae, Felidae), ARTIODACTYLA (Anthracotheriidae, e.g. *Microbunodon,* Protoceratidae. *Syndoceras),* RUMINANTIA (Moschidae, Tragulidae, Cervidae). Thus, saberteeth occur in both carnivorous and herbivorous mammals (Werdelin 2024).

Examples of Metatheria

Thylacosmilus **modification:** The South American Pleistocene *Thylacosmilus* belongs to Sparasssodonta, Metatheria, but was often called as a "marsupial sabertooth predator". It has often been cited as a typical example of convergent evolution with sabertoothed placental Carnivora such as *Smilodon*. In *Thylacosmilus* (0.1.2.4/1.1.2.4) (Fig. 15.2a) the upper canine has a scimitar-like shape, is laterally flattened and has sharp margins. It has a slightly triangular cross-section, with a keel on the buccal side and a flat lingual side. When the mouth is closed, the large and pointed blade extents far downwards. The long blade is secured by a sizable flange in the mandibular bone. The root of the large canine remains open throughout life (Simpson 1948,
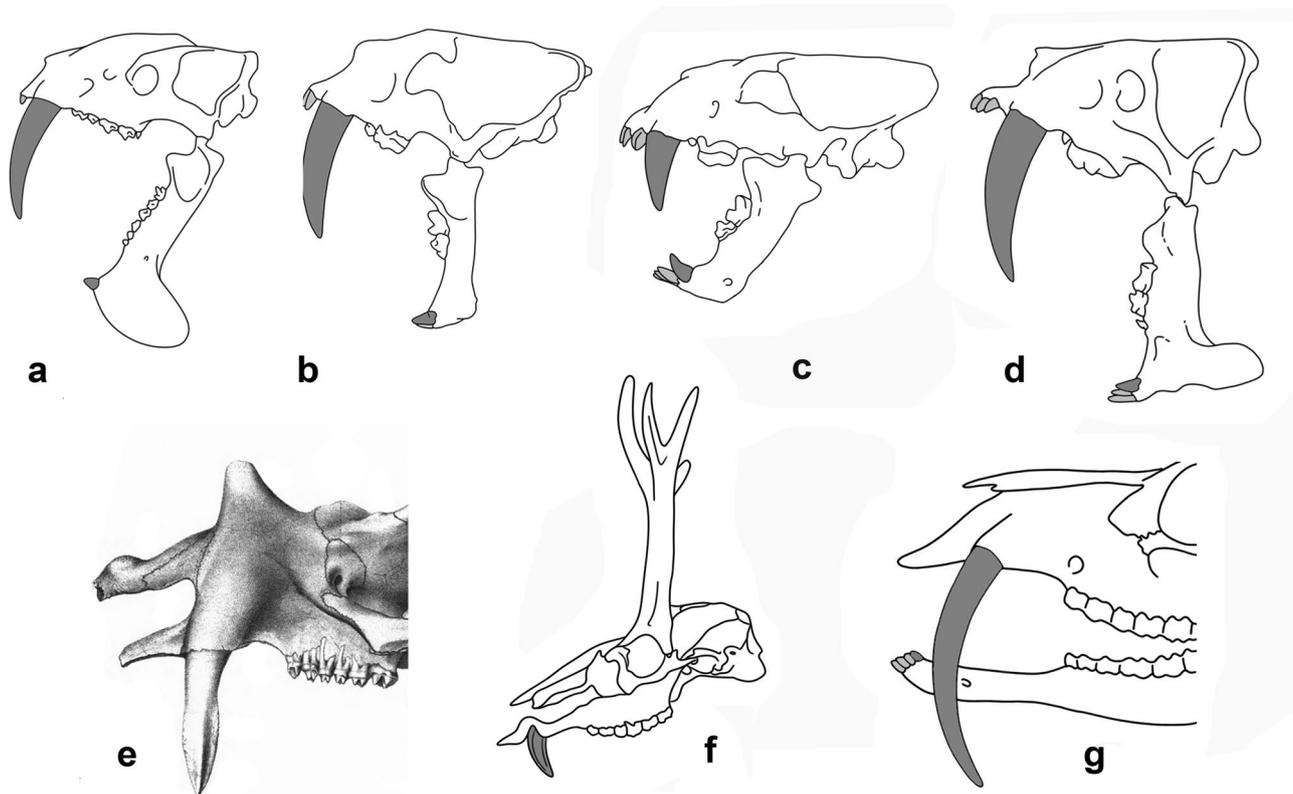
Fig. 15.1 *"Saberteeth"* (CL-15): **a** *Thylacolsmilus* (METATHERIA), **b** *Smilodon* (Carnivora: Felidae), **c** *Xenosmilus* (Carnivora)*,* **d** *Barbourofelis* (Carnivora), **e** *Uintatherium* (DINOCERATA), **f** *Procervulus* (ARTIODACTYLA), **g** *Moschus* (ARTIODACTYLA). (Modified from **a** Goin and Pascual 1987, **b** and **d** Martin 1981, **c** Naples et al. 2011, **e** Marsh 1886, **f** Thenius 1989, **g** Gentry et al. 1999)

Fig. 15.2 *"Saberteeth"* (CL-15): **a** *Thylacosmilus atrox*, **b** *Hoplophoneus*. Comparable saberteeth and protective flanges in MARSUPIALIA and CARNIVORA. (**a** from Riggs 1934, **b** SMNK-PAL 8444, photo M. Vielsäcker)
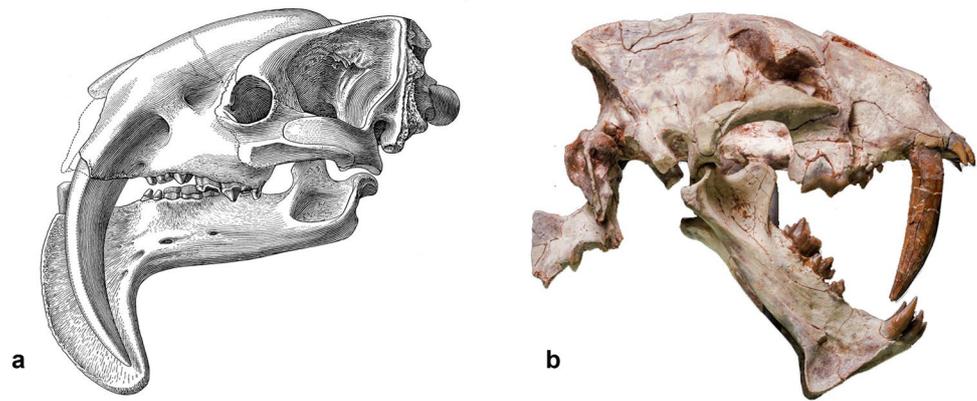
Marshall 1978, Goin and Pasqual 1987, Babot et al. 2002). The upper incisors are reduced (Janis et al. 2020). The lower canine is high-crowned but small, not comparable to the upper canine.

Despite being called a "marsupial sabertooth predator," *Thylacosmilus* primarily fed on existing cadavers rather than killing them (Janis et al. 2020). The large canines have been used to open carcasses.

The upper canines are sharpened by the abrasion on the lingual side. It exposes the dentin core with sharp anterior and posterior edges formed by the enamel from the buccal side. The abrasion was interpreted as being caused by the lower canine. A sharpening is not necessarily due to an antagonist, but rather to the contact with the leathery lips, as a similar sharpening occurs in sabertoothed *Pomelomeryx,* where no antagonist is present (Koenigswald and Goin 2000).

Examples of Carnivores

Carnivore modifications: Saberteeth are highly enlarged upper canines that occur in several genera of Creodonta, and Carnivora (Nimravidae and among Felidae the Machairodontinae). An example for the Creodonta is *Machaeroides* (3.1.4.2/2–3. 1.4.2) from the Eocene of North America (Dawson et al. 1986).

Three types of saberteeth are distinguished, varying in length and cross-section. In scimitar-toothed cats, such as *Homotherium* (Machairodontinae). Canines are relatively short, broad, and coarsely serrated. Their limbs are slender. In dirk-toothed cats, such as the *Barbourofelis* and *Hoplophoneus* (Nimravidae) (Fig. 15.2b) or *Megateron, Smilodon* (Fig. 15.1b), *Machairodon* (Felidae - Machairodontinae), the canines are much longer, laterally compressed and non-serrated to finely serrated. A prominent diastema extends between the upper canine and I3 (Kurtén 1968, Martin 1980). The limbs are massive in dirk-toothed cats. A third group, named the "cookie-cutting cat", is represented by the Pleistocene *Xenosmilus* (Fig. 15. 1c) from Florida, which combines the scimitar-toothed canine with the short, massive limbs of a dirk-toothed predator. The morphology

of the saberteeth and body posture allow for an objective interpretation of the hunting behaviour of sabertoothed cats (Marshall 1980, Martin 1981, Martin et al. 2000, 2008, Naples et al. 2011). The flange in the anterior mandible may provide a protective sheath for the upper canine when the mouth is closed. Its size varies, being large in *Barbourofelis* (Fig. 15.1d) and small in the felid *Smilodon* (Turnbull 1978). In Carnivora the saber-toothed cats have retained their upper and lower incisors. These saberteeth have evolved independently several times, e.g.in Nimravidae and even within the machairodont Felidae (Barrett et al. 2021, Werdelin et al. 2010, Werdelin 2024).

Examples of Dinocerata

Uintatherium modification: The dinocerates *Probathyopsis* and *Uintatherium* (0.1.3.3/3.1.3.3) (Figs. 15.1e and 15.3) both from the late Paleocene and Eocene of North America

Fig. 15.3 *"Saberteeth"* (CL-15): Cranium of the herbivorous *Uintatherium anceps* (DINOCERATA). Cast of the skull in the NMNH, Paris. (Photo, Jebulon via Wikipedia https://de.wikipedia.org/wiki/Uintatherium#/media/Datei:Dinoceras_mirabile_Marsh_MNHN.jpg)

and China, are characterised by their extremely elongate upper canines that place Dinocerata among sabertoothed mammals (Marsh 1886, Wheeler 1961, Turnbull 2002). The premaxilla of *Uintatherium* is toothless, but Wheeler reports vestigial roots of the upper incisors in one individual, suggesting progressive reduction of the upper incisors. The number of premolars varies in the upper and lower jaws. The mandible has three incisors and a small canine. The front part of the mandible has a substantial flange that shields the upper canine when the mouth is closed.

The enlarged upper canine is rooted and less curved than in typical saber-toothed mammals. It has a flattened cross-section with a buccal keel, especially near the tip. The pointed canines are considered to be weapons, used not only for defense against predators but also for offensive attacks against live rivals (Simpson 1941: 10). Both sexes have large upper canines, although those of the female are smaller, indicating limited sexual dimorphism.

The degree of sexual dimorphism varies among taxa and is particularly pronounced in *Probathyopsis* (Thewissen and Gingerich 1987).

Examples of Artiodactyla

***Microbunodon* modification:** The upper canines of the anthracothere genus *Microbunodon* show a distinct sexual dimorphism (Fig. 15.4) with small teeth in females and large and blade-like canines in males (Stehlin 1910, Lihoreau 2004). A well-preserved skull from Switzerland is reconstructed with small upper canines (Hünermann 1967). The lower canines are not incisiform. Enlarged sabertooth-like upper canines are known from France from the late

Oligocene (Renevier 1879). The best example is a skull fragment of *Microbunodon* comes from the Eocene of China (Fig. 15 4a). It has both transversely flattened upper canines that are slightly laterally oriented (Tsubamoto 2010). Despite the enormous size of the upper canine no diastema is present.

Sabertooth modifications in Ruminantia: In ruminants the lower canine is incisiform and thus morphologically insignificant. The size of the upper canine varies greatly and it becomes sabertooth-like in some families. Some of the basal ruminants have medium-sized upper canines (e.g. *Archaeomeryx*), while others have only rudimentary canines (e.g. *Leptomeryx*). The extant Giraffidae, Antilocapridae and Bovidae have reduced the upper canines. However, extremely elongate canines are present in several fossil and extant genera related to Cervoidea. Tragulidae (e.g. *Dorcatherium* and extant *Tragulus*), Moschidae (e.g. *Micromeryx, Procervulus* (Fig. 15.1f) and extant *Moschus* (Fig. 15.1g) and Cervidae (e.g. extant *Muntiacus* and the capreoline *Hydropotes*) (Vislobokova 2001, Prothero 2007, Rössner 2007, 2010).

Discussion of CL-15 "Saberteeth"

The term "saberteeth" was used in an extended form by Werdelin (2024), who coined the term "hypercanine". In addition to the classic examples of saberteeth, he includes some taxa with euhypsodont lower and upper canines that are not blade-like. Because they differ significantly in morphology and function from the examples in CL-15. They are excluded and discussed, for example, in CL-14 (*Astrapotherium*) and CL-19 (*Babyrousa*).
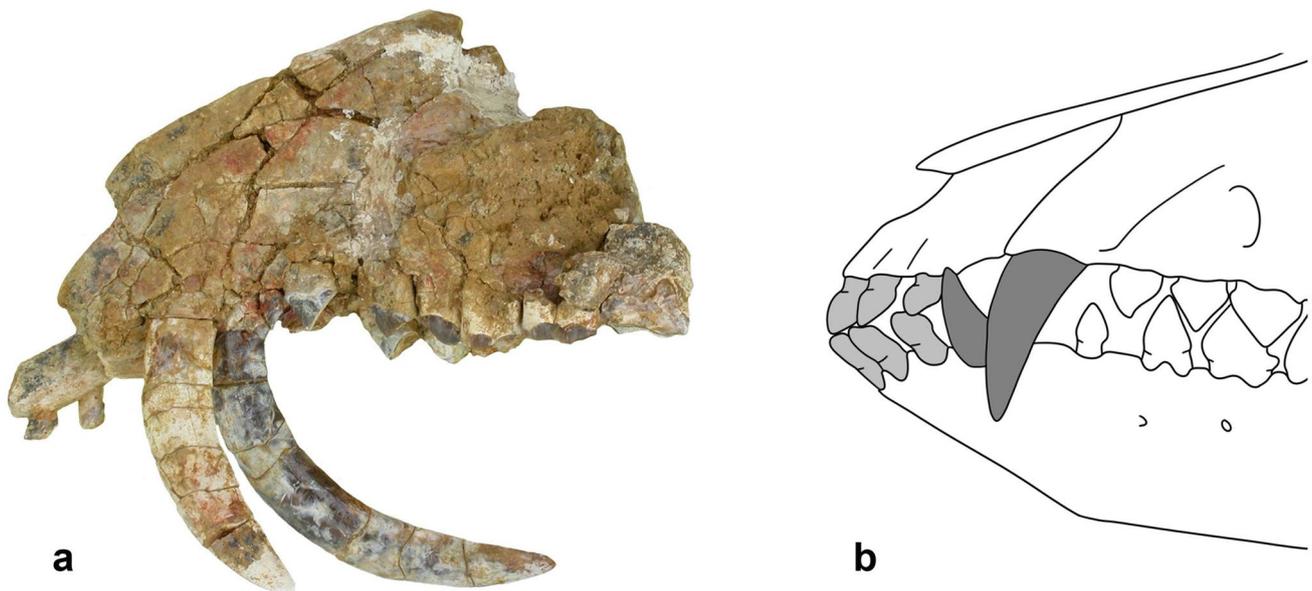

Fig. 15.4 *"Saberteeth"* (CL-15): **a** *Microbunodon* sp. from China, **b** *Microbunodon minus* from Europe (Anthracotheriidae). The sizes of the canines mark – most probably – a significant sexual dimorphism. (**a** Photo courtesy of T. Tsubamoto, **b** modified from Hünermann 1967)

Functional aspects

In carnivorous species, saberteeth indicate a more specialised hunting and killing technique. This can even be distinguished between the different types of saberteeth. The main goal is a killing bite that cuts the throat when the powerful claws immobilise the prey (McHenry 2007, Naples et al. 2011). The sharp edge on the posterior side of the canines allows for cutting when the head is pulled back after impact. The long blades were also very useful for opening carcasses. The large canines served an additional important purpose as a social organ for threatening or indicating personal strength. However, it is noteworthy that *Smilodon fatalis* shows little or no sexual dimorphism (Valkenburgh and Sacco 2002).

In herbivores, saberteeth are not used for foraging, but are important weapons in fights with other species and within species (Gentry et.al. 1999). Sexual dimorphism is observed in several taxa. In *Uintatherium* saberteeth have been interpreted as weapons, both against predators and in offensive attacks on live rivals (Simpson 1941.10).

Among extant Artiodactyla saberteeth occur in Tragulidae, Moschidae, and Cervidae (Aitchinson 1946). *Munitacus* shows a pronounced sexual dimorphism in its saberteeth (Chapman et al. 1985, Aiglstorfer et al. 2023), suggesting a social significance. During the evolution of the Cervidae, the social importance of the saberteeth was reduced as the antlers took over the function as a social organ (Cabrera and Stankowich 2020). The Miocene *Procervulus* (Fig. 15.1f) having elongated canines, is one of the earliest cervids to evolve delicate antlers (Gentry et al. 1999).

In extant *Muntiacus* and *Hydropotes* the saberteeth are characterised by their loose implantation in the sockets (Aitchinson 1946, Wheeler 1961). This allows them to slide backwards during feeding and prevents them from breaking when saberteeth are used as weapons.

The edges of the enamel-covered canines are crenulated in several carnivores. As the enamel on the lingual side wears away, the enamel on the buccal side forms sharp margins. The process of resharpening could be reconstructed from an upper canine of the moschid *Pomelomeryx*. Due to abrasion, the dentin is exposed on the lingual side and the anterior and posterior margins of the saberteeth are formed by the cross-section of the buccal enamel. Similar to the canine in *Thylacosmilus* the lingual side is abraded by the skin of the mandible (Koenigswald and Goin 2000).

Saberteeth evolved independently in different mammalian group, such as Sparassodonta (METATHERIA), Carnivora, various Artiodactyla and in Dinocerata (PLACENTALIA), for different functions (Werdelin 2024). Within the Carnivora saberteeth evolved several times, even within the family Felidae. Similarly canine elongation evolved independently several times in Artiodactyla (Janis and Scott 1987, Aiglstorfer et al. 2023). However, all saberteeth are enlarged upper canines, so the question of their homology is irrelevant.

Sabertoothed mammals reduced the incisors between the enlarged canines, e.g. the metatherian *Thylacosmilus* and the placental *Astrapotherium*. In *Astraponotus* the premaxilla is so small that no incisors are expected (Kramarz et al. 2011). The dinocerates *Bathyopsis, Gobiatherium, Tetheopsis, Eobasileus* have toothless premaxillae. But in In *Uintatherium,* however*,* vestigial roots of the upper incisors were found (Wheeler 1961), indicating an incomplete reduction of the upper incisors (Osborn and Granger 1932, Lucas and Schoch 1998b). The reduction occurred independently in the different classes and may represent a convergence induced by space problems.

Several sabertoothed taxa have developed a characteristic flange in the anterior part of the mandible. It is interpreted as a shield to protect the enlarged canines when the mouth is closed. This flange evolved independently as a convergent character. It is noteworthy that such a flange is absent in sabertoothed ruminants, but present in the herbivore *Uintatherium.*

The evolution of the saberteeth the different groups of herbivores and carnivores is definitely convergent and is not an adaptation that optimises a single function.

Moderately or greatly enlarged canines often occur together with a postcanine diastema - examples were discussed in CL-12 "*Moderate canines*" and CL-15 "*Saberteeth*". But these two features are not necessarily related, as shown in *Microbunodon.*

Cluster 16
"Canine/Premolar functional unit" (CL-16)

C/p Functional Unit. Caniniform lower premolar occludes with upper canine, lower canine is incisiform

Definition and occurrence: The CL-16 "*C/p Functional Unit*" describes the articulation between the upper canine and a caniniform most anterior premolar (Fig. 16 1). The lower canine is incisiform and is no part of this functional unit (FT-51). The posterior side of the upper canine, contacts the first lower premolar. The caniniform premolar thus functionally replaces the lower canine. This tooth is usually the dp1, but in Primates it is replaced by the p2 or p3. The first upper premolar (dP1), if present, is double-rooted and may contribute to the "*C/p Functional Unit*". - The lower canine is small or incisiform and has little or no functional relationship with the upper canine.

The most important common morphological features of this CL-16 *"C/p Functional Unit"* are the caniniform premolars and the reduced lower canine (FT-34, FT-38, FT-51). The included modifications differ in the size of the facets between the upper canine and the first lower premolar.

Stevens and Stevens (2007) observed the occlusion of the enlarged premolar with the upper canine in Merycoidodontidae
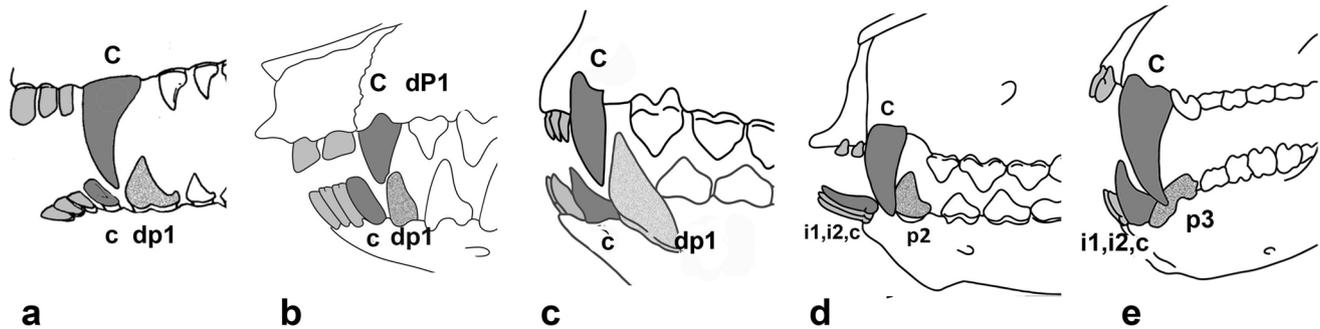
Fig. 16.1 "C/p Functional Unit" (CL-16). **a** *Talpa* (EULIPOTYPHLA), **b** *Leptictis* (LEPICTIDA), **c** *Eporeodon* (ARTIODACTYLA), **d** *Lemur* (PRIMATES), **e** *Papio* (PRIMATES). (Modified from: **a** Luckett 1993, **b** Novacek 1986, **c** Thorpe 1937, **d** Thenius 1989, **e** photo BIOB-PAL)

and named the structure "C/p1 caniniform pair". This term is modified here to "*C/p Functional Unit"* because the involved premolar is either a deciduous premolar (dp1), or in Primates a p2 or a p3 (Koenigswald et al. 2025).

CL-16 "*C/p Functional Unit"* has been observed in PANTODONTA (*Caenolambda*), EULIPOTYPHLA (*Talpa*), ARTIODACTYLA (e.g. *Hypertragulus*, *Masillabune*, Merycoidodontidae, Protoceratidae) PRIMATES (e.g. *Lemur*, *Papio*) and probably in *Rhychocyon* and *Leptictidium.*

Examples of Eulipotyphla

***Talpa* modification:** In *Talpa europaea* (3.1.4.3/3.1.4.3) the upper C is large and pointed (Fig. 16.1a). The lower canine is incisiform and joins the three lower incisors. The lower dp1 is caniniform and double-rooted. The upper canine has a sharp distal flange corresponding to the anterior edge of the dp1. The dp1, although considerably smaller than the C, has taken over the canine function in the lower jaw (Niethammer 1990). However, no facet is visible on dp1. The upper DP1 is small and does not contribute to the "*C/p Functional Unit"*. In Talpidae this modification occurs, e.g. in *Mogera, Parascaptor* and *Euroscaptor* (ADW), but other talpid genera (e.g. *Desmana*) have a completely different tooth constellation with enlarged mesial incisors (CL-5 "*Rooted Overbite Incisors*").

Examples of Leptictida

***Leptictis* modification:** *Leptictis* (2.1.4.3/3.1.4.3) has only two upper incisors (Fig. 16.1b). The upper canine is slightly higher than the premolars. The DP1 is small. In the mandible there are three incisors and an incisiform lower canine. The dp1 is as large as the canine, but slightly smaller than the double-rooted p2 (Novacek 1986, Gunnel et al. 2008). The extent to which the dp1 functionally cooperates with the upper C remains to be investigated. *Leptictis* is not typical of the CL-16 "*C/p Functional Unit"*, but may represent an early stage of this differentiation.

Examples of Pantodonta

***Caenolambda* modification**: The pantodont *Caenolambda jepseni* has a large upper canine that occludes with the lower canine, but also with the highly elongated dp1. "It performs a shearing action against the postero-internal face of the upper canine, suggesting that this type of cutting mechanism has a particularly useful adaptive function in pantodont function in the pantodont phylum" (Simons 1960, Lucas 1998. Fig 5). According to the given figure, only in *Caenolambda* does the dp1 have a large facet on its anterior side. Therefore, *Caenolambda* is provisionally included in CL-16, but none of the other pantodont genera.

Examples of Artiodactyla

***Archaeomeryx* modification**: *Archaeomeryx* (3.1.3.3/3.1.4.3) is an early ruminant of the middle Eocene represented by several skeletons from Inner Mongolia (Vislobokova and Trofimov 2002). The lower canine is incisiform, and separated from the dp1 by a diastema. This tooth is single-rooted and slightly higher than the canine and the premolars. The upper canine is not large, its anterior edge is rounded, but its posterior edge is sharp. In some individuals, the first lower premolar has a facet on its anterior side. This can only be related to the occlusion with the upper canine (Vislobokova and Trofimov 2002). Thus, *Archaeomeryx* thus represents a lower level of the *"C/p functional Unit".*

***Masillabune* modification**: The early artiodactyl choeropotamid *Masillabune* (3.1.4.3/3.1.4.3) has large as the upper canine, whereas the lower canine is incisiform. The first lower premolar (dp1) is caniniform (Tobien 1980 1985). The upper canine and the dp1 are laterally compressed and have crests on their anterior and posterior sides (Koenigswald et al. 2025). The diastemata between C and dP1 and between lower c and dp1 accommodate the pair of the enlarged teeth, when the jaws are in full occlusion. The first upper premolar (dP1) is double-rooted and contributes to the "*C/p Functional Unit"*. Other genera of the Choeropotamidae may

have the "*C/p Functional Unit*" as well, because of their incisiform lower canines and the enlarged dp1, but the upper dentition is only partially known (Lehmann and Ruf 2018, Hooker and Thomas 2001).

Hypertragulus **modification**: The early ruminant *Hypertragulus* (0.1.4.3/3.1.4.3) has a toothless premaxilla (Fig. 16.2). The upper canine is long and pointed. After a short diastema, the two-rooted DP1 follows. It is separated from the following premolars (P2-P4) by another diastema. In the mandible three incisors and the incisiform lower canine are closely set. A caniniform dp1 follows after a short diastema. It is slender and prominent. Its anterior side occludes with the upper canine, and it fits into the diastema between C and DP1 when the jaws are closed. Another diastema separates the dp1 from the p2 (Janis and Scott 1987, Rose 2006). *Hypertragulus* belongs to CL-16 because of the occlusion between the upper canine and the caniniform dp1. As an early ruminant, *Hypertragulus* has a ruminant incisor arcade (RIA) and a toothless premaxilla.
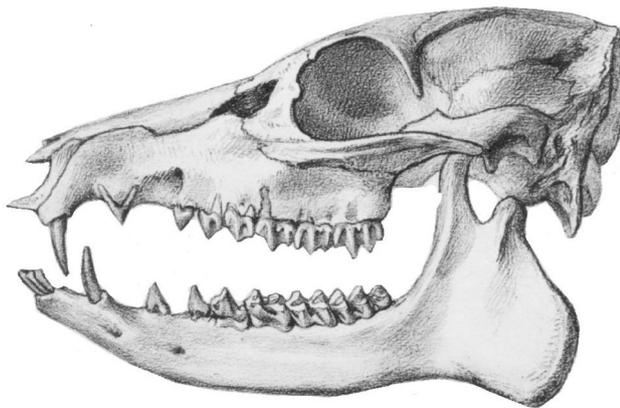
Fig. 16.2 "*C/p Functional Unit*" (CL-16). *Hypertragulus* (ARTIODACTYLA) (from Scott 1940)
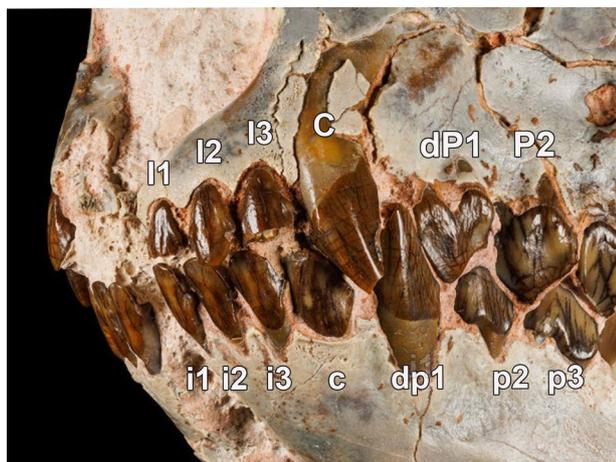
Merycoidodon **modification**: The most typical CL-16 "*C/p Functional Unit*" is found in the artiodactyl Merycoidodontidae (Figs. 16.1c and 16.3). The family diversified extensively in North America during the Oligocene and Miocene (Thorpe 1937, Schultz and Falkenbach 1968, Patton and Taylor 1973, Stevens and Stevens 2007, Prothero and Ludtke 2007). Most genera illustrated share an upper canine that occludes mainly with the caniniform dp1, but only marginally or not at all with the lower canine, which is incisiform. The dp1 is narrow in its linguo-buccal direction. Thus, the facet with the upper C is narrow. The observed striations indicate a transversal movement over the broad facet of the upper canine. The first upper premolar is double-rooted and may contact the posterior side of the lower dp1.

Protoceratid modification: Another typical "*C/p Functional Unit*" has been well documented in the protoceratid genera *Protoceras* and *Leptoreodon* (Wortmann 1898) (Fig. 16.4). The upper canine and the caniniform dp1 are large. The lower canine is incisiform and well separated from the subsequent lower dp1 by a diastema (Patton and Taylor 1973). The first upper premolar is small.

The phylogenetic position of the protoceratid *Leptoreodon* (Fig.16. 1c) is controversial (Prothero and Foss 2007, Janis and Scott 1987). Wortmann (1898) published a cranium and mandible of *Leptoreodon marshi.* However, the fine and delicate figure is misleading. According to the numbers given in the figure, Wortmann correctly identified the tooth loci. The mandible was found detached from the cranium, and in the figure the mandible has been misplaced. There, the enlarged caniniform premolar is placed in front of the upper canine, obscuring the perfect "*C/p Functional Unit*" and simulating a normal occlusion of the upper and lower canines. The original fossils in the AMNH show that the isolated mandible fits the upper jaw perfectly when the CL-16 "*C/p Functional Unit*" is taken into account (personal
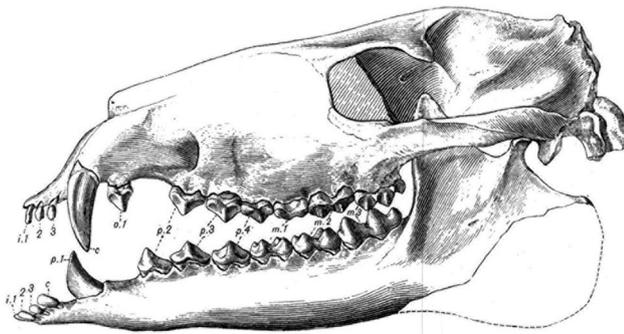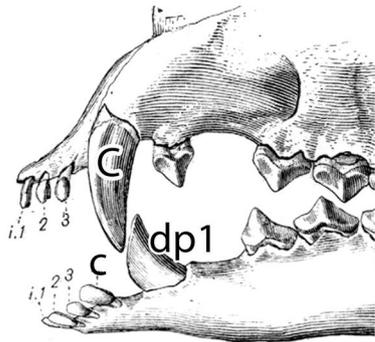

Fig. 16.3 "*C/p Functional Unit*" (CL-16). **a** *Merycoidodon* sp., **b** *Eporeodon montanus* (**a** and **b** ARTIODACTYLA). (**a** SMNK – Pal 70328, photo Mathias Vielsäcker, **b** from Thorpe 1937, fig 40)
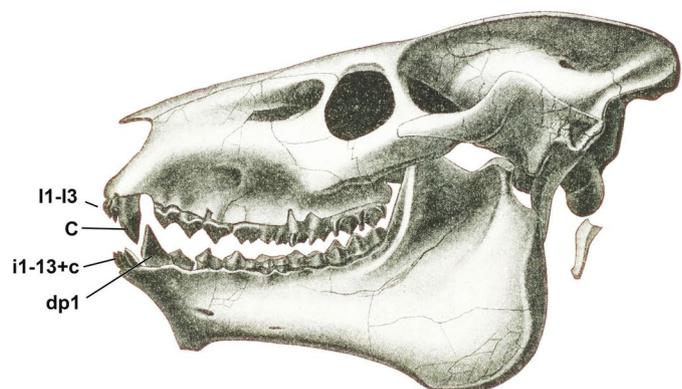
Fig. 16.4 "*C/p Functional Unit*" (CL-16). *Leptoreodon marshi* (Protoceratidae), **a** ancient reconstruction from Wortmann 1898, based on AMNH 2064. The teeth are correctly identified, but the mandible is shifted forward obscuring the characterising CL-16 "*C/p Functional Unit*", **b** repositioned mandible demonstrating the correct occlusion pattern. (**a** and **b** modified from Wortmann 1898, Fig. 1)

Fig. 16.5 "*C/p Functional Unit*" (CL-16). *Papio* (Primates) has a large lower canine, that is unusual for CL-16. (BIOB-PAL M 280, photo G. Oleschinski)

communication of John Wahlert, Dec. 2023). Wortmann's misleading figure has been republished in several textbooks.

Examples of Primates
Some primates share a similar occlusion between the upper canine and the most anterior premolar. Because of the premolar reductions in Primates, the upper canine occludes with the p2 in lemurs and with the p3 in cercopithecids.
Lemur **modification:** In *Lemur* (2.1.4.3/2.1.4.3), as in most Primates (Fig. 16.1d), the number of upper and lower incisors is reduced to two. The upper canine is rather large and triangular in its lateral aspect. It has a functional correlation with the enlarged anterior premolar, which in lemurs is the p2 (Marivaux et. al. 2013). The lower canine is incisiform and part of the lemuriform toothcomb. Although the Lemuridae fit well into the CL-16 "*C/p Functional Unit*" they are discussed in CL-18, because of their toothcomb.
Papio **modification:** In the Cercopithecidae, particularly *Papio* (Figs. 16.1e and 16.5), the most anterior premolar (p3) is enlarged and, with its elongated blade, forms the antagonist for the large upper canine. The anterior slope of the p3 has a large facet (e.g. in *Macaca* and *Cercopithecus*) (Berkowitz and Shellis 2018, Zingeser 1969). The structure

is similar to the C/p functional unit but the dp1 is replaced by the p3, due to premolar reduction in Primates. In contrast to the reduced lower canine, that is common in the "*C/p Functional Unit*", as in Merycoidodontidae, the lower canine of *Papio* is large and fits into the diastema between C and I3. The upper and lower canines form an impressive weapon.

Possible candidates – Macroscelidea
***Rhynchocyon* modification**: The extant *Rhynchocyon* (0–1.1.1.4.2/3.1.4.2) is a leptictid. Its AD has an enlarged upper canine corresponding to an enlarged lower first premolar (Fig. 16. 6a). This tooth erupts relatively late and has no successor, so it is a deciduous tooth (dp1). The lower canine is small but not fully incisiform. It is separated from i3 by a small diastema (Allen 1922). This combination indicates a less derived "*C/p Functional Unit*", as the facets between
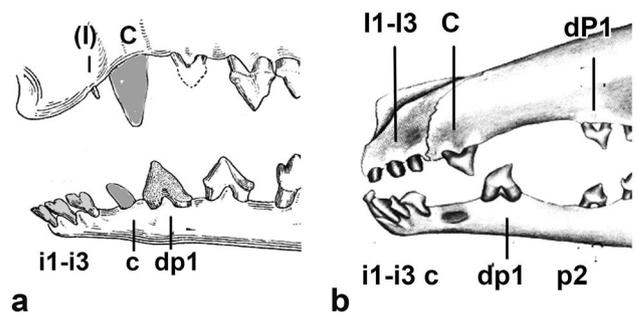

Fig. 16.6 "*C/p Functional Unit*" (CL-16).). Anterior dentition in **a** *Rhynchocyon,* **b** *Leptictidium nasutum* (LEPTICTIDA).(Modified from: **a** Allen 1922, **b** Stroch and Lister 1985)

these two teeth appear to be limited. The AD shows another peculiarity. The upper incisors are reduced, only one small one is occasionally present. The three lower incisors are bifid.

***Leptictidium* modification:** The Eocene *Leptictidium nasutum* (3.1.4.3/3.1.4.3) has an elongate snout (Storch and Lister 1985, Koenigswald and Storch 1987) (Fig. 16.6b). The premaxilla has three incisors. The upper canine is double-rooted and considerably larger but not taller. It is separated from the double-rooted DP1 by a long diastema. In the mandible there are three incisors and the lower canine is incompletely preserved, but incisiform and closely attached to the i3. It is considerably smaller than the upper canine. A long diastema separates the c from the much larger dp1.

The incisiform lower canine, the large upper canine and the large dp1 resemble the "*C/p Functional Unit*", but a functional contact between the upper canine (C) and the dp1 is questionable. Both may have functioned as a holding point rather than for cutting of a piece of prey.

Discussion of CL-16 "Canine/premolar Functional Unit"

The caniniform first lower premolar is one of the characterising features of the "*C/p Functional Unit*". It evolved independently in different groups. It differs in the intensity of the canine/premolar articulation. The occlusion of the C with the premolar is different in Primates. It is the p2 in lemurs and the p3 in cercopithecids, corresponding reduction of premolars in Primates. The different dental locus between lemurs and cercopithecids indicates that the formation of the CL-16 evolved independently and at different stages of the premolar reduction. In addition the lower canine of *Papio* is not incisiform but large (Fig. 16.5). These observations prove the independent and frequent formation of the "*C/p Functional Unit*".

The "*C/p Functional Unit*" is useful for holding prey and perforating insect armor. However, a functional advantage in comparison to the more plesiomorphic unit of upper and lower canines, as in CL-1, is not obvious. The more primitive subcluster, as in *Talpa* and *Leptictis* (Fig. 16.1),

is insectivorous and omnivorous. The enlargement of the facet in the more derived subcluster as in *Merycoidodon* (Fig. 16.3), may be an adaptation for cutting foliage. It is certainly involved in the comminution of the food. The specific function of the enlarged premolar (p3) in *Papio* (Fig. 16.5) may be to sharpen the upper canine, but wear facets need to be tested. The "*C/p Functional Unit*" in lemurs has less functional significance than the lemuriform toothcomb.

Cluster 17
"Ruminant incisor arcade" (CL-17)

Ruminant incisor arcade "RIA" and toothless premaxilla

Definition and occurrence: The ruminant dentition is characterised by a ruminant incisor arcade (RIA) including an incisiform lower canine, and the toothless premaxilla (Fig. 17.1) (FT-15; FT-18, and FT-34). The three lower incisors and the incisiform canine are spatulate. The central incisor (i1) is often laterally extended. The teeth are well rooted. A large diastema separates the lower canine from the premolars. Because of the toothless premaxilla, the teeth of the RIA have no dental antagonists for cutting. The palate is covered with a horny pad. Upper canines may be present, and in some genera may even be saber-toothed. The term ruminant incisor arcade (RIA) is derived from (Gordon and Illius 1988). The RIA is a synapomorphy of the RUMINANTIA (e.g, Tragulidae, Antilocapridae, Cervidae, and Bovidae) and is slightly modified with a remaining upper incisor in Camelidae.

Examples of Artiodactyla
Ruminantia modification. All ruminants share the RIA and a toothless premaxilla (Fig. 17. 1) (0.1.3.3/3.1.3.3) (FT-15 and FT-18). Camelidae share the RIA, but retain a single incisor in the premaxilla (0.1.3–2.3/3.1.3–2.3). The RIA is a very conservative structure and shows only few changes in its incisors or canines.

Of the three incisors within the RIA, the central incisor (i1) is somewhat accentuated (e.g. in *Capra* or *Cervus*

Fig. 17.1 "*Ruminant Incisor Arcade*" (CL-17): *Cervus elaphus* (ZMFK).**a** dorsal and **b** lateral aspects of the ruminant incisor arcade (RIA). Canines are shaded darker than incisors. (Redrawn from authors' photos)
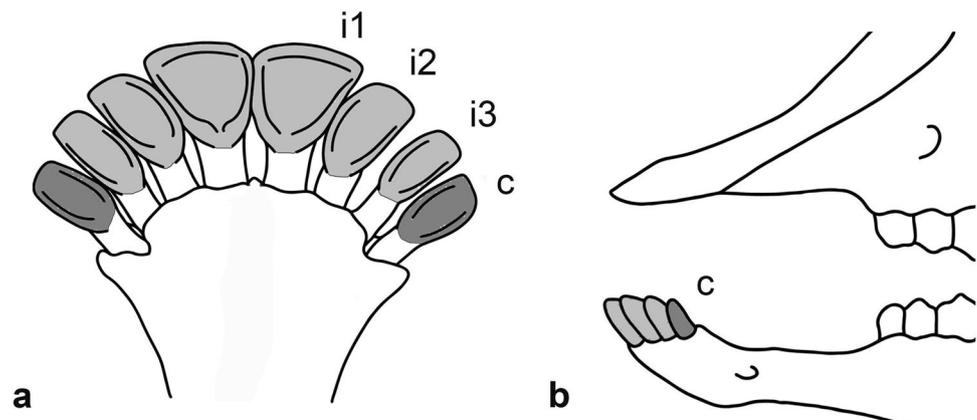
elaphus (Fig. 17.1a and 17. 2b). In other taxa, the i1 is asymmetrically widened to the lateral side, such as in the gazelle *Nanger* (Fig. 17.2a and 17.2d). Such a fan-shaped i1 occurs in several unrelated bovids (e.g. *Oryx*), tragulids (e.g. *Tragulus*), and in some cervids (*Cervus nippon*, but not in *C. elpahus*) (Rössner 2007). A well-documented example from the Miocene is the tragulid *Dorcatherium* (Aiglstorter et al. 2014). The specialised central (lower) incisors are considered an ecological indicator (Gordon and Illius 1988). In general, the lower canine is incisiform, only in giraffes it is enlarged antero-distally and has a second cusp (Thenius 1989) (Fig 17.2e).

The central incisor of the small *Leptomeryx* from the Oligocene of Wyoming was described as tusk-like because it is a strongly procumbent (Taylor and Webb 1976, Webb and Taylor 1980). (But this tooth does not fit to the term "tusk" as used in this paper).

The upper canine is either rudimentary or enlarged to form a sabertooth. Bovidae and Giraffidae generally lack an upper canine. Some cervids such as *Cervus elaphus* (Fig. 17.2c) have a rudimentary upper canine, but other cervids as the extant *Muntiacus* and *Hydropotes* have enlarged upper canines. Saberteeth are common in Tragulidae and Moschidae as discussed in CL-15. The size of the upper canine is often controlled by a sexual dimorphism.

Myotragus modifications: The RIA is a very stable construction and the number of modifications is very limited. In the Pleistocene island-bovid *Myotragus,* the RIA is reduced to a single, enlarged and euhypsodont tooth (0.0.2.3./1.0.2–1.3.2.3). The enlargement of the central incisor
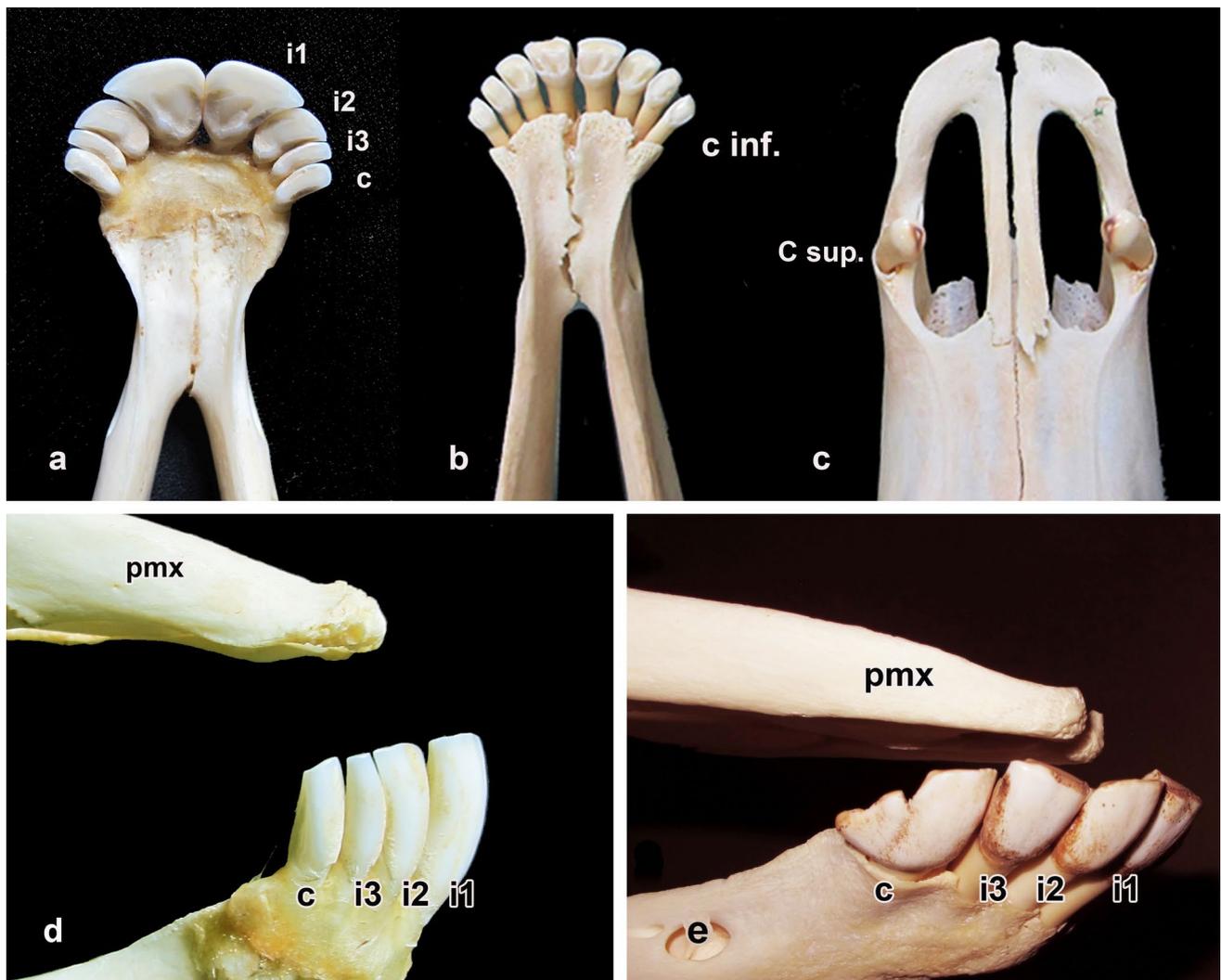
Fig. 17.2 "*Ruminant Incisor Arcade*" (CL-17): **a** and **d** *Nanger granti* (ZMFK 1935-0335A), **b** and **c** *Cervus elaphus* (ZFMK 2016-0646), **e** *Giraffa camelopardalis* (ZMFK). The RIA includes the lower i1-i3 and the lower canine (**a, b,** and **d**) and has no antagonist. The width of the i1 is broadened in *Nager* (**a**) but much less in *Cervus* (**b**). The lower canine is incisiform (**a, b** and **c**), but in *Camelus* the lower canine it is mesiodistally enlarged (**e**)

corresponds to the widening of the i1 in various cervids and bovids. However, its tooth locus has been interpreted as a deciduous second incisor (di2) (Bover and Alcover 1999). The procumbent tooth has an almost horizontal abrasion surface exposing a large area of dentin with a sharp cutting edge formed by the enamel band on the mesial side of the tooth.

The RIA of the hypertragulid *Hypisodus* (0.0.3.3/3.1.3.3) is very unusual, because it contains five teeth instead of four: three incisors, the incisiform canine, and one incisiform first premolar. Its RIA is separated from the other premolars by a long diastema (Meehan and Martin 2004).

Discussion of CL 17 "Ruminant incisor arcade"

The RIA is present in most primitive Ruminantia, including the Hypertragulidae and it characterises this group as a synapomorphic feature (Loomis 1914, Scott 1940, Webb and Taylor 1980, Métais and Vislobolka 2007). Early Eocene *Archaeomeryx* represents a less derived stage in the preservation of upper incisors (3.1.3.3/3.1.4.3) (Webb and Taylor 1980).

A prerequisite for an incisiform lower canine in the RIA of all Ruminantia and Giraffa, is a functional separation of the upper and lower canines. The same dissolution of the traditional C/c unit occurs when a caniniform premolar functionally replaces the lower canine (CL-16). As described by Scott and Jepson (1940. 509), "the lower canine is incisiform. The first premolar takes its place in function and shape and bites behind the upper canine". In contrast to the extant ruminants, the Oligocene *Hypertragulus* shows both specializations (FT-15 and FT-51) simultaneously. It is discussed in CL-16 "*C/p Functional Unit*".

The function of the RIA is unique but difficult to understand because the teeth of the RIA have no antagonists. Therefore, the selected foliage cannot be cut. Baumont et al.

(2006. 345) describe the foraging habits of domestic ruminants. "At pasture, ruminants gather and manipulate herbage in the sward with their tongues (cattle) and lips (sheep and goats), grasping the herbage between their incisors and upper dental pad and severing it from the sward, often but not always with a jerk of the head. The herbage severed by the bite is then manipulated, chewed, and formed into a bolus before being swallowed". The importance of the tongue and lips in grasping food (foliage, herbage, grass, or twigs) is evident in all ruminants. In summary, the RIA is a highly efficient tool and enabled the Ruminantia to become a very successful group of herbivores. Camelids also evolved an RIA, but their premaxilla retained one upper incisor.

Cluster 18
"Lemuriform toothcomb"

An incisiform lower canine and two incisors form the lemurian toothcomb. The dp2 is enlarged

Definition and occurrence: The CL-18 "*Lemuriform Toothcomb*" is characterised by a lower dentition with two lower incisors and the incisiform lower canine, which is closely attached (Fig. 18.1). Upper incisors are small. The *"Lemuriform Toothcomb"* is found in Lemuridae and Lorisidae. a structure, similar in function, has been found in *Thryptacodon* (PROCREODI)

Examples of Primates
Lemuriform toothcomb: In *Lemur* (2.1.4.3/2.1.4.3), as in most Lemuridae, the number of upper and lower incisors is reduced to two. The two lower incisors together with the incisiform lower canines from the lemuriform toothcomb (Fig. 18.1). The incisors and the canine are elongated and
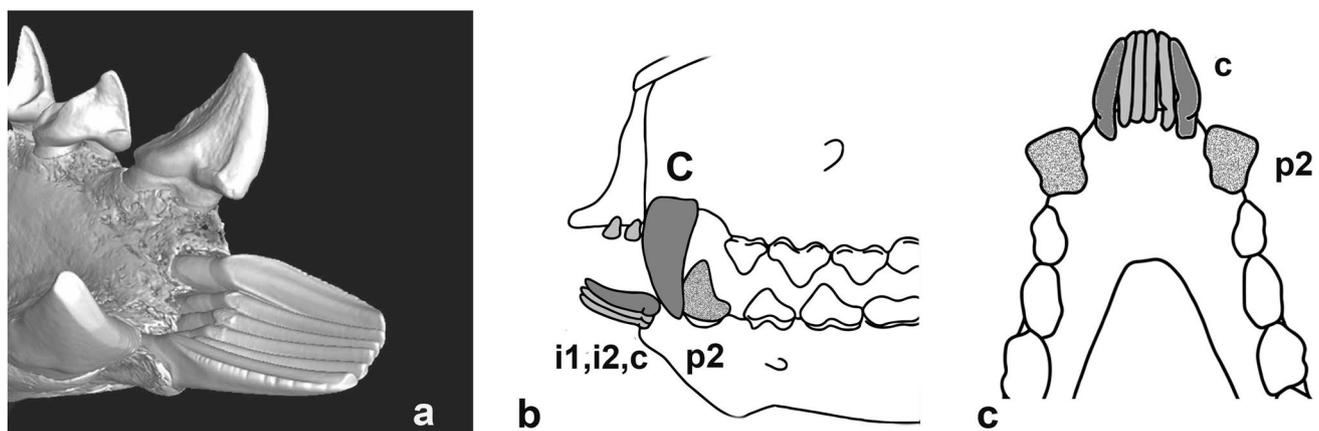

Fig. 18.1 "*Lemuriform Toothcomb*" (CL-18): *Lemur catta* (PRIMATES), **a** the lower premolar has a distinct facet for the upper canine; the lower incisors show the marks of fur grooming **b** lateral aspect of the AD, **c** dorsal aspect of the tooth comb in *Lemur* with the enlarged p2. (**a** from Koenigswald 2011; **b** and **c** modified from Thenius 1989)

well rooted. The canine is thicker than the two incisors. The teeth of the toothcomb are horizontally procumbent and closely aligned. The tooth loci of the two incisors are indicated as i1 and i2 (López-Torres et al. 2020). The two upper incisors in the premaxilla are vertically implanted and do not form proper antagonists. They occlude marginally with the side of the lower canine.

The enlarged lower p2 is separated from the toothcomb by a short diastema. It occludes with a distinct facet on its anterior side with the upper canine (Fig. 18.1a) and forms together with the upper canine a typical CL-16 *"C/p Functional Unit"*.

In Lemuridae (e.g. *Lemur, Hapalemur, Varecia*) and Lorisidae (e.g. *Perodicticus, Nycticebus*) the typical lemuriform toothcomb with three teeth is found (Szalay and Seligmann 1977, Fleagle 1988, Ealgen 1980). In Indriidae (e.g. *Avahi* and *Propithecus*), the toothcomb contains only two teeth per quadrant. Either one of the incisors (Schwartz 1974) or the canine (Gingerich 1977) is reduced, but the toothcomb has the same function. The number of incisors involved varies in the giant lemur *Megaladapis*. Its AD is less procumbent, but the tooth-comb is functional (Godfrey et al. 2010).

The earliest lemuriform toothcomb has been observed in *Karanisia* from the middle Eocene of Egypt. It contains an incisiform canine making the toothcomb six-toothed (Seiffert et al. 2003, Tattersall 2006, López-Torres et al. 2020). Marivaux et al. (2013) described the primate *Djebelemur* from the Eocene of Tunisia. Based on the canine-premolar complex, they suggested a "pre-toothcomb stage" leading to the typical adaptation in crown strepsirrhines.

Examples of Procreodi
Thryptacodon modification: The Eocene condylarth *Thryptacodon* is discussed here, because the three elongated and procumbent lower incisors form a toothcomb comparable to the lemurian toothcomb. The upper incisors are loosely arranged with small diastemata and vary in size and the canines large. The toothcomb has been discussed as a grooming device in comparison to lemurs (Gingerich and Rose 1979). The six-toothed toothcomb of *Thryptacodon* contains incisors only and no incisiform canine. There is no *C/p Functional Unit*. Because of the distinct canines *Thryptacodon* could also be discussed as CL-12 "*Moderate Canines*".

Discussion of CL-18 "Lemuriform toothcomb"

The lemuriform toothcomb is used for two purposes. Some species gouge bark for sab feeding. More common is the grooming of fer. Mutual grooming is an important social activity within the group. Grooming is reflected in the wear pattern by narrow forehead grooves perpendicular to the tooth axis, especially in the canines (Fig. 18.1a) (Rose et al. 1981). Sap feeding is quite common in small arboreal mammals and the toothcomb is a perfect tool for scraping or gouging the bark (Coimbra-Filho 1978, Martin 1979, 1981). Two hypotheses for the origin of the toothcomb are discussed, emphasizing grooming or sap or gum consumption as the driving components. Both activities are not mutually exclusive and both have been postulated for *Karanisia* (López-Torres et al. 2020).

In contrast to the lemurian tooth with narrow grooves on the lateral side of the canines, the lower i1 in hyraxes shows vertical marks on their anterior side, that derived from grooming.

The toothcomb is a monophyletic feature shared by Lemuridae and Lorisidae (Rosenberger and Strasser 1985). However, the toothcomb in the unrelated Thryptacodon is an example of convergent evolution.

Cluster 19
"Special canines" (CL-19)

Uniquely modified canines

Definition and occurrence: In CL-19 *"Special Canines"* some ADs are united that do not fit into any of the canine categories. They are characterised by enlarged discordant canines (FT-35, FT-37) They are discussed here, because they add to the diversity of the AD.

Examples of Suidae
Babyrousa modification: The extant suid *Babyrousa babyrussa* (2.1.3.3/2.1.3.3) (Fig. 19 1a), endemic to Sulawesi, has a unique orientation of its upper canines. The euhypsodont teeth are relatively thin and made entirely of dentin. They are unusually long and curve in a large arch towards the forehead (Macdonald et al. 2016). The alveoli of the upper canines in the maxilla are unusually rotated upward. As a result, the upper canines grow through the skin next to the nose. The lower canines are long, thin and slightly divergent. This specific orientation of the canines generally prevents any contact between the upper and lower canines and any mutual abrasion. Therefore, the canines show no facets, which are typical for most Suidae (CL-14).

The canines are not used for food acquisition but as social organs. The upper canines show a pronounced sexual dimorphism and are often broken in males, due to intense fighting. The extraordinary canines are often malpositioned (Macdonald 2018).

Examples of Taeniodiodonta
Stylinodon modification: Taeniodont dentitions are canine-dominated. *Leptoganus* (Fig. 19.1b) and *Stylinodon*
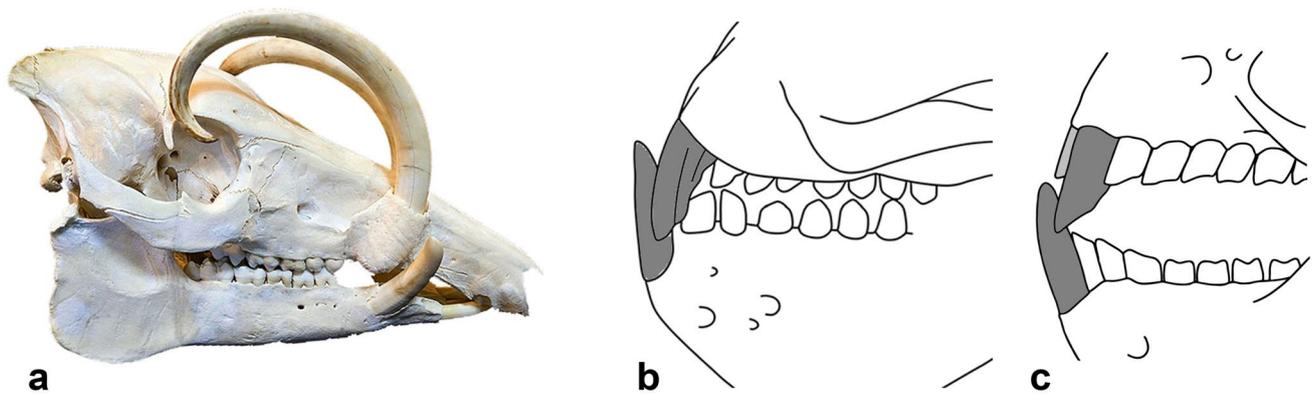
Fig. 19.1 *"Special Canines"* (CL-19): **a** *Babyrousa celebensis* (ARTIODACTYLA); **b** *Leptoganus;* **c** *Stylinodon* (both TAENIODONTA). (Modified from **a** photo by Didier Descouens via Wikimedia, **b** and **c** from Schoch 1986)

(Fig. 19.1c) (2.1.4.3/1.1.4.3) developed euhypsodont teeth. Incisors are partially reduced. The lower canines normally occlude, before the upper canines, but they are more mesial than the upper canines. The occlusion pattern has been interpreted differently (Schoch 1986, Turnbull 2004). The upper canines have a differentiated occlusal surface. The anterior part with the enamel-bearing surface forms a tip, while the posterior part half forms a flat grinding surface, that occludes with the elongated first lower premolar.

These canines are somewhat similar to gliriform incisors, but they are not as exposed, because the canines stand in a closed tooth-row without a diastema. This is a unique modification for euhypsodont canines with mutual abrasion. The occlusion of the upper canine with the lower first premolar is vaguely reminiscent of CL-16, but differs in many details.

Discussion of CL-19 "Special Canines"

Babyrousa shares with other Suidae the strongly curved canines and the procumbent lower incisors. This suggests that the special arrangement of canines in *Babyrousa* is derived from suid ancestors belonging to CL-14 *"Mutually Abrading Canines"*.

The very peculiar AD of *Leptoganus* and *Stylinodon* differentiated most likely from a form belonging to the cluster characterised by moderately enlarged canines (CL-12). The Conoryctidae, a less derived taeniodont family, represent an AD with the full number of incisors and moderate canines.

Cluster 20
"Homodont dentitions" (CL-20)

Homodont teeth in the dentition

Definition and occurrence: In completely homodont dentitions the tooth classes are not differentiated, and the unicuspid teeth are present along the entire length of the tooth row (FT-50). Here I include dentitions with homodont teeth only in the anterior part and those with typical dentin teeth. Homodont teeth are simplified and occur in three different types. Two of them retain teeth that are at least partially covered by enamel and the third has dentin teeth. In dentitions of the first type, unicuspid, homodont teeth occur only in the anterior part of the dentition (e.g. *Durodon*, Fig. 20.1a). In the second mode such teeth occur throughout the dentition (e.g. *Trusiops,* Fig. 20.1b) These two types are typical of CETACEA. In the third type (e.g. *Megatherium* Fig. 20.1c) the columnar teeth have no enamel but a modified dentin (e.g. in XENARTHRA and TUBULIDENTATA).

Examples of Cetacea

Odontocete modification: Most extant Odontoceti represent the second type of homodont dentition (Fig. 20.1a). The upper and lower dentitions are concordant. All tooth classes (incisors, canines, premolars, and molars) are homodont: one-rooted and cone-shaped (FT-50). Therefore, the tooth classes cannot be distinguished (Armfield et al. 2013). Typical examples are the genera *Orcinus*, *Delphinus*, *Inia,* and *Trusiops* (Fig. 21. 1a). Upper and lower teeth alternatively occlude, and sometimes the teeth abrade each other on the sides (Fig. 20. 2). Homodonty is often associated with polydonty (Armfield et al. 2013). In some genera the number of teeth increased dramatically. Some dolphins, such as *Platanista* or *Inia*, have more than 30 teeth per quadrant (Jefferson et al. 1993). The extant *Physeter* has a discordant dentition. The upper jaw is toothless, while the lower jaw has strong dentin teeth with tiny enamel caps when they erupt.

***Durodon* modification**: In early whales representing the *Durodon* modification (Fig. 20.1a), the dentition is not fully homodont, and to some extent heterodont (Uhen 2004). The tooth classes are still recognisable (3.1.4.3/3.1.4.3). The incisors, canines and the first premolars are cone-shaped
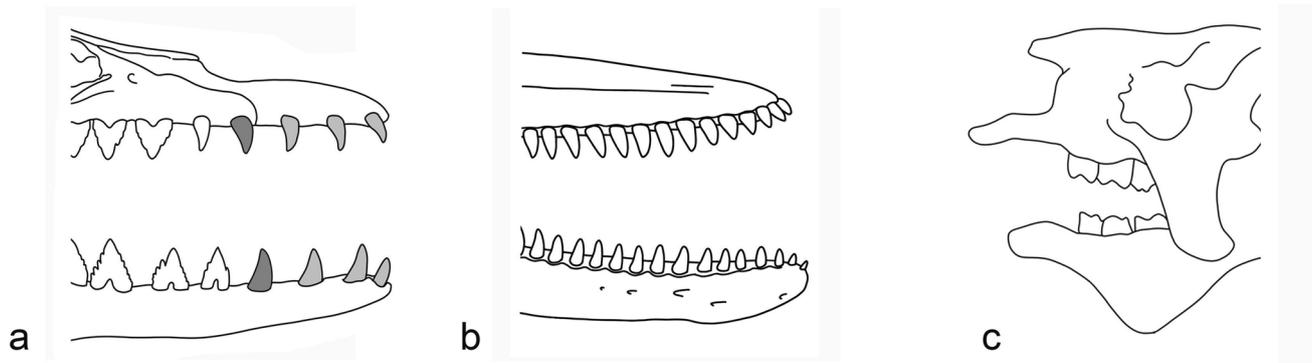
Fig. 20.1 "*Homodont Dentitions*" (CL-20): **a** *Durodon* (ARCHAEOCETI)*;* **b** *Trusiops* (ODONTOCETI); **c** *Megatherium* (XENARTRA). (Modified from: **a** Uhen 2004; **b** and **c** Thenius 1989)

Fig. 20.2 "*Homodont Dentitions*" (CL-20). *Orcinus orca*, SMF. Some of the homodont teeth show intensive abrasion marks on their lateral side (authors photo)

teeth and show typical homodont features. The posterior premolars and molars are leaf-shaped and have small accessory cusps on their sides (Uhen 2004). The teeth are completely enamel coated (Sahni and Koenigswald 1997). The *Durodon* modification is present in the Eocene odontocetids e.g. in *Pakicetus, Durodon, Basilosaurus* and *Zygorhiza.* They represent the first stage of adaptation of a homodont dentition.

Examples of Tubulidentata

***Orycteropus* modification:** The tubulidentate *Orycteropus* (0.0.2—3.3/0.0.2.3) represents the different type of homodonty. It has no teeth in the anterior part of the jaws and homodont columnar teeth in the back. The enamel-free dentin teeth are composed out of prismatic columns, each with its own pulp (Schmidt 1940). *Orycteropus* feeds mainly on colonial insects and some plant material collected with an extremely long tongue.

Examples of Xenarthra

Xenarthran modifications: In xenarthrans, the incisors and canines are reduced and leaving the anterior parts of the both jaws toothless. The posterior parts have columnar teeth that are euhypsodont and never separated by diastemata (Vizcaíno 2009). The number of teeth is limited to five per quadrant (Berkovitz and Shellis 2018). Upper and lower teeth are concordant and formed only by dentin. Traces of enamel are found in the fossil *Utae*tus (Simpson et al. 1932a), suggesting a secondary reduction of the enamel.

In Cingulata (e.g. in *Dasypus, Euphractus*) the anterior part of the elongated jaws is toothless, but the posterior part has homodont dentin teeth. The number of the euhypsodont teeth exceeds the traditional number of premolars and molars. The cylindrical teeth are usually simple columns, that are worn flat. In *Glyptodon, however,* the cross-section of the teeth is a differentiated (Soibelzon et al. 2006). The occlusal surface shows a slight profile, due to the differentiation of the dentin, which increases the effectiveness of grinding (Kalthoff 2011, Green and Kalthoff 2015).

The tardigrad *Megatherium* (0.0.3/0.0.4) (Fig. 20. 1c) has massive bilophodont dentin teeth. Their profile allows a differentiated occlusion with a steep phase one, directed anteriorly (Bargo 2001, Koenigswald et al. 2013).

Vermilingua a group of the xenarthan Pilosa reduced their teeth completely and specialised in feeding social insects (Redford 1985).

Discussion of CL-20 "Homodont Teeth"

Homodont teeth are secondary in mammals. They result from a general simplification of the tooth morphology (Peredo et al. 2018). Homodont dentitions evolved independently in CETACEA, TUBULIDENTATA, and XENARTHRA, these are undeniable cases of convergence. The different taxa have very different diets. The functional advantage is obvious for piscivorous and insectivorous mammals, but not so for the large herbivorous Xenarthra. Nevertheless, they managed

to cope with phylogenetic inheritance of dentin teeth and certainly used the tongue to grasp foliage.

The morphological differentiation of teeth was a very successful adaptation in early mammals. However, in some lineages this achievement was reversed during evolution. The odontocete modification is a perfect adaptation for catching fish or squid. The homodont unicuspid teeth are mainly used to hold and puncture the slippery prey until it can be swallowed. As there is no chewing, precise occlusion is not necessary. *Orycteropus* (Tubulidentata) collects social insects with its extremely long tongue. The dentin teeth can be used for crushing. Dentin teeth in Xenarthra, are used for a more omnivorous diet, and for a more herbivorous diet in Cingulata and in Pilosa.

Cluster 21
"Major tooth reductions" (CL-21)

Anterior dentitions with major tooth reductions

Definition and occurrence: Although the food intake is the primary function of the AD, several mammalian species have reduced the number of tooth loci in their AD. The reductions occur independently in the different taxa, but with similar modifications. The reduction of the anterior teeth is compensated for by soft organs, such as specialised lips or a trunk for ingestion and/or shaping of food. Four types of reduction can be distinguished.

Progressive loss of antemolars in the upper and lower dentitions (FT-52)

Enlargement of certain incisors in different clusters, such as CL-8, CL-9, and CL-11, is usually associated with a progressive loss of antemolars. It affects the teeth between an enlarged incisor and the first molar in the upper and lower dentition. The P4/p4 are often excluded. diprotodont METATHERIA, MULTITUBERCULATA and PLACENTALIA (e.g. in Adapisoricidae, Apatemyiade, and Soricidae) are typical examples (CL-8). They show the progressive loss of tooth loci independently. The highest degree of reduction occurs in the cluster of Gliriform Incisors (CL-9). Rodents have only one upper and one lower incisor. In lagomorphs, the premaxilla has a second incisor as a reminder of reduced antemolars. It is noteworthy that the reduction of the antemolars is discordant and often more progressive in the lower than in the upper dentition. The different lineages of proboscideans developed tusks, but in in different tooth loci and reduced others (CL-11). The pattern is generally discordant.

A discordant reduction resulting in a toothless premaxilla

All ruminants that form the CL-17 "Ruminant Incisor Arcade" are characterised by a discordant tooth reduction (e.g. *Cervus*, Fig. 21.1a). The premaxilla is toothless, but the dentary retains three incisors and an incisiform lower canine. The gum of the toothless premaxilla is protected by a horny plate. The preservation of a single upper incisor in Camelidae (e.g. *Camelus*, Fig. 21.1b) marks an intermediate stage of the reduction. The upper canine is affected in a different way. *Hypertragulus* (Fig. 16.2), an early ruminant, has a toothless premaxilla but a large upper canine (CL-17). Some ruminants retained the upper canine as a tooth, showing some sexual dimorphism (*Cervus elaphus*) or evolved the upper canine into a saber-like weapon, such as *Muntiacus* (CL-15).

A toothless premaxilla occurs independently in several mammalian lineages. The perissodactyl *Moropus* (0.0.3.3/3.0.3.3) (Fig. 21.1c), a Miocene chalicothere, evolved a toothless premaxilla very similar to the RIA in Ruminantia, but independently. The dentary has three incisors, lower and upper canines are absent (Holland and Petersen 1914, Coombs 1978).

In Dinocerata the genera *Bathyopsis, Uintatherium, Tetheopsis,* and *Eobasileus* share a toothless premaxilla. *Uintatherium* has sabertoothed canines (CL-15), whereas *Gobiatherium* (0.0.3.3/3.1.3.3) has reduced upper canines (Osborn and Granger 1932, Schoch and Lucas 1985, Lucas 2001). The toothed whale *Physeter* (CETACEA) has a toothless upper jaw (Fig. 21.1e). The marsupial *Thylacosmilus* (0.1.3.4/1.1.2–3.3.2.3–4.3) lacks upper incisors between the huge, sabertoothed upper canines (CL-15), but retained one lower incisor.

All these examples indicate a discordant reduction of upper teeth in the premaxilla. In the lower jaw such reductions are rare, but may occur in some sirenians.

Concordant reduction forming edentulous regions

A concordant reduction of the entire AD is characteristic of XENARTHRA, but also occurs in some derived Rhinocerotidae (e.g. *Elasmotherium*, Fig. 21.2a) (PERISSODACTYLA).

The dentition of xenarthrans is characterised by euhypsodont dentin teeth, which are not directly comparable in morphology and in their tooth loci with the teeth of other mammals. Nevertheless, some trends, such as the reduction of anterior teeth, are similar to those in other mammals. The giant fossil xenarthans, such as *Mylodon* (Fig. 21 2b), *Megatherium,* and *Glossotherium* have no anterior teeth, although they were herbivorous and required large amounts of plant material on a daily basis. For food acquisition or ingestion, the lack of teeth was compensated by their lips and the tongue, which allowed them to pull out enough grass and herbaceous plants (Bargo and Vizcaíno 2008).

Rhinocerotidae show a complex pattern of reductions and enlargements in specific incisor tooth loci in some lineages (Tissier et al. 2020) (see CL-10 "Special Incisors"). In some Pleistocene rhinoceroses e.g. *Elasmotherium* (Fig. 21 2a),
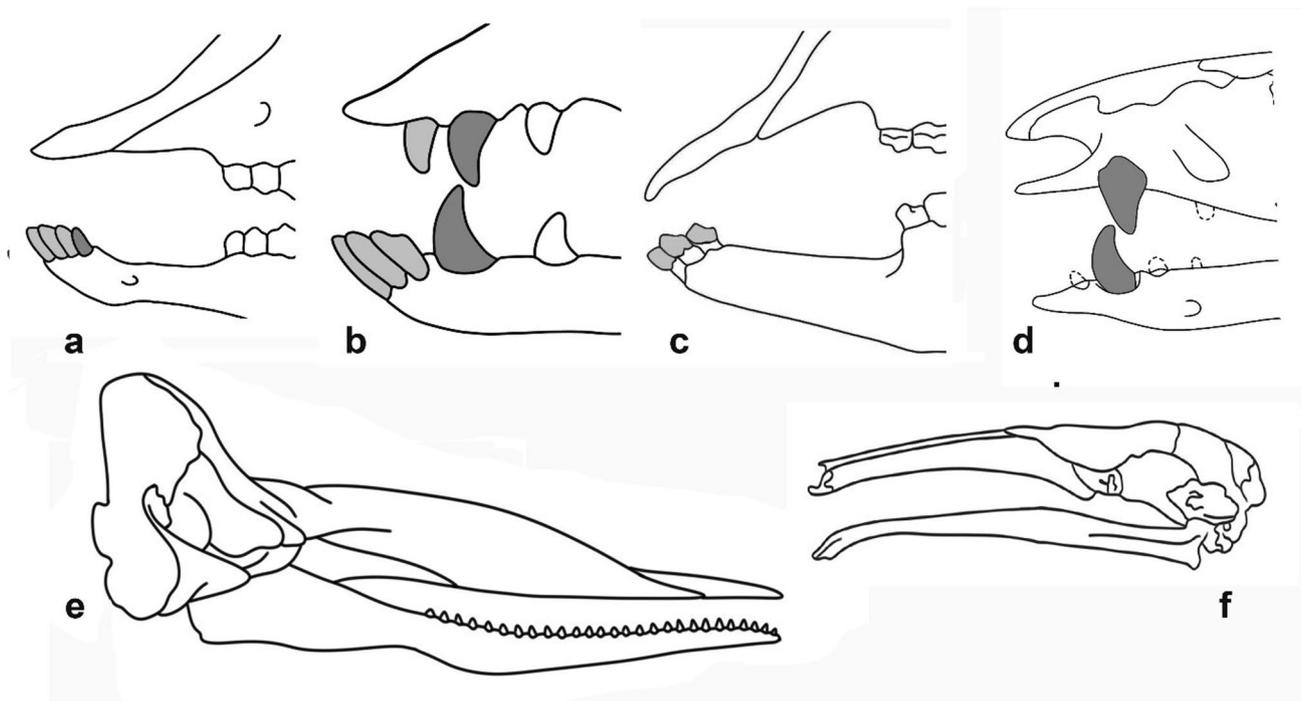
Fig. 21.1 *"Major Tooth Reductions"* (CL-20): **a** *Cervus elaphus* (ARTIODACTYLA) Ruminant incisor arcade with toothless premaxilla, **b** *Camelus* (ARTIODACTYLA) upper incisor, except one reduced, **c** *Moropus elatus* (PERISSODACTYLA) toothless premaxilla, **d** *Metacheiromys* (PALAEANODONTA), most incisors reduced, but heavy canines present, **e** *Physeter* (CETACEA) upper jaw toothless, **f** *Myrmecophaga* (XENARTHRA) toothless jaws. (Modified from **a** and **c** photos ZMFK, b Simpson 1931, **d** Coombs, 1978, **e** and **f** Thenius 1989)

Stephanorhinus, and *Coelodonta* and the extant African genera *Diceros* and *Ceratotherium* the anterior teeth are completely reduced.

Despite their common feature, the absent teeth in anterior region, they differ in their preferred diet. The black rhino*, Diceros,* is a herbivorous browser preferring leafy plants, twigs, branches, shoots, thorny wood bushes, small trees, fruits, and grass (Rivals et al. 2020). It gathers the plants with the support of the finger-like e upper lips (Buk et al. 2012). The white rhino, *Ceratotherium simum,* has a broad square upper lip for grazing. The extant species demonstrate the importance of the lips for gathering different types of plant material. The two Pleistocene examples were certainly grazers in a cold environment (Kurten 1968).

The Miocene rhinoceroses *Chilotherium* from Eurasia and *Aphelops* from North America provide an intermediate level of reduction that anticipates the toothless AD. They reduced the upper incisor but retained the large lower incisor (i2), which certainly functioned as a social organ (Prothero and Schoch 2003, Mihlbachler 2003).

The total loss of teeth

During the specialization of mammals for specific diets the dentition was modified. Foraging on social insects does not require teeth and therefore different mammalian lineages reduced their teeth including the AD. The examples in the extant fauna (Manidae and Tubulidentata) from Africa and Europe, and MYRMECOPHAGA (Fig. 21.1f) from South America are well known as cases of convergent evolution. Their number must be increased by the Eocene PALEANODONTA (Rose 2006, 2008, Rose et al. 1992). *Metacheiromys* (Fig. 21.1d) may fit into this group, although its canines show no reduction (Simpson et al. 1931).

Discussion of CL-21 "Major tooth reductions"

The above examples show that teeth of very different dental loci and regions are reduced, both in a concordant and discordant patterns. The large tooth reductions in the AD may be somewhat surprising, as the impression is that the loss of teeth might reduce the ability to ingest food. The reduction in the AD occurs in many herbivores but much less so in carnivores.

Avedik et al (2023) correlate the tooth reduction in the AD in herbivores with a lateral jaw movement during mastication. A large canine would certainly prevent a wide lateral excursion of the mandible, but the amount of the lateral movement is open. It is only effective for grinding as long as the molars/premolars of the mandible and maxilla are in contact, so its amount is limited.

On the other hand, the soft tissues of the frontal region differentiated into delicate organs in herbivores, much more so than in carnivores. In some taxa the lips became highly tactile, in others the tongue became elongated and flexible, and in some lineages the nose was transformed into a trunk. The evolution of such organs, which are usually not preserved in the fossil record, may sometimes have been neglected, although there are clues. Muscle attachments on the front of the skull may indicate differentiated soft parts, such as lips or a trunk (Bargo and Vizciáno 2008, Nabavizadeh 2024).

These soft tissues around the mouth, became increasingly involved in techniques of grasping and collecting foliage and functionally replaced the teeth of the AD. The preference for soft organs seems to correlate with the ingestion of large quantities of uniform plant material, such as leaves or grasses. Large quantities of uniform food items are provided by social insects. Mammals that specialised in social insects are characterised by their elongated and slender skulls with toothless jaws. Such skulls evolved independently, e.g. in XENARTHRA (*Myrmecopha*). PHOLIDOTA (*Manis*), and PALAEANODONTA (*Eurotamandua*) (Rose 2006, 2008).

Results and general considerations

The attempt to classify recent and fossil mammals based on their anterior dentition resulted in 21 clusters (Fig. 22). For clarity, each cluster is represented here by only one example, although it includes examples from very different groups, as shown in the previous chapters. The members of a cluster are characterised by common morphological and functional features. The great diversity of the mammalian anterior dentition (AD) is due to a mosaic evolution of different morphological features. Although our survey is still incomplete, the 21 clusters proposed intend to cover the diversity of the AD.

Fig. 22 A synopsis of the proposed clusters of the AD, including the ▶ plesiomorphic ones (CL-1 and CL-2), those with dominant incisors (CL-3 to CL-11), those with dominant canines (CL-12 to CL-19), those with homodont teeth (CL-20) and those with significant reductions (CL-21). Each cluster is represented by a single example. The various modifications are indicated in the different chapters

Each cluster is discussed separately following the description of related taxa. In this chapter, the interrelationship between the different clusters is highlighted, as they reveal some general features that only become apparent in such a comparison.

Forming clusters: In order to provide a basis for comparing the great diversity in mammalian AD, clusters have been proposed. They are characterised by conspicuous morphological features and are independent of any phylogenetic system. The choice of characterising features is somewhat subjective, as most genera have several features, and even important features, such as incisiform incisors, are not restricted to one cluster but may occur in genera assigned to different clusters. This arrangement of clusters is therefore somewhat preliminarily. Nevertheless, it is a reasonable means of comparison.

In the appendix the genera are listed in their systematic position, with their main characters and their assignment to a particular cluster.

Convergence or parallelism: The features that characterise the clusters evolved independently in the different orders and are considered to be convergent, if parallel evolution is defined as a similarity that evolved from the same ancestral feature (McGhee 2011, Powell and Mariscal 2014). The different mammalian orders may have radiated around or shortly after the Cretaceous-Paleocene boundary (Rose and Archibald 2005, O'Leary at al. 2013). The anterior dentition of the early members is often incompletely known or
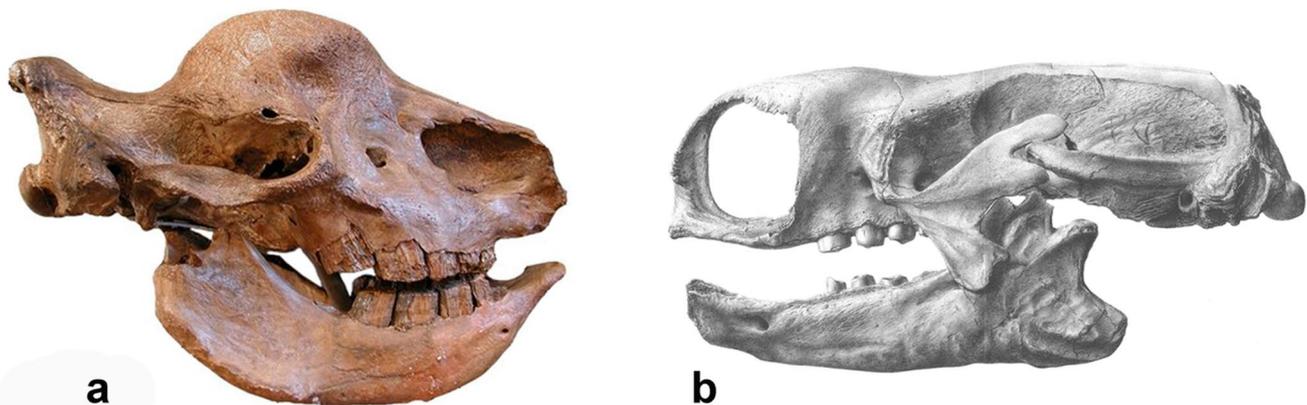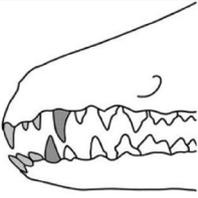
Fig. 21.2 *"Major Tooth Reductions"* (CD-21) Skulls of **a** *Elasmotherium sibiricum* (PERISSODACTYLA) and **b** *Mylodon darwini* (NOTOUNGULATA) have euhypsodont molar dentitions, but are toothless in the anterior region. Intensive lip or trunk activity is required for food intake. (**a** Photo courtesy of R. Uchytel, Kiew, **b** from Reinhardt 1879)

CLUSTERS WITH A PLESIOMORPHIC ANTERIOR DENTITION

CL-1: *Plesiomorphic Pattern*

CL-2: *Unequal Incisors or Canines*

CLUSTERS OF THE ANTERIOR DENTITION WITH DOMINATING INCISORS
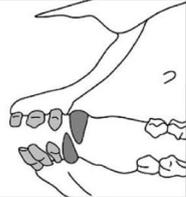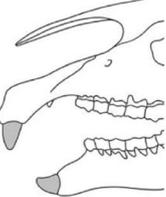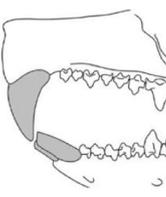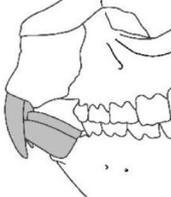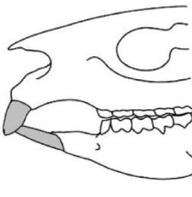
CL-3: *Concordant Incisors*

CL-4: *Pair of Large Rooted Incisors*

CL-5: *Rooted Overbite Incisors*

CL-6: *Truncated Euhypsodont Lower Incisors*

CL-7: *Large Flat-Nose Pliers*
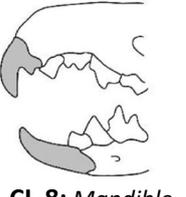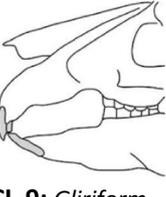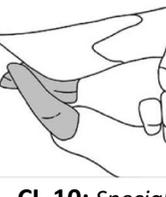
CL-8: *Mandible with Single Procumbent Incisor*

CL-9: *Gliriform Incisors*

CL-10: *Special Incisors*

CL-11: *Dentin Tusks*

CLUSTERS OF THE ANTERIOR DENTITION WITH DOMINATING CANINES OR WITH REDUCTIONS
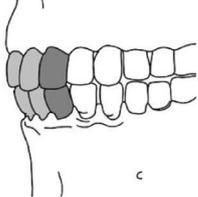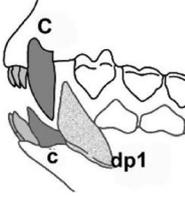
CL-12: *Moderately Enlarged Canines*

CL-13: *Adjusted Canines*

CL-14: *Mutually Abrading Canines*

CL-15 *Saberteeth*

CL-16: *C/p Functional Unit*
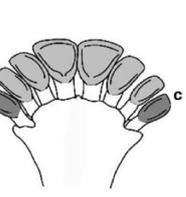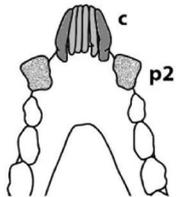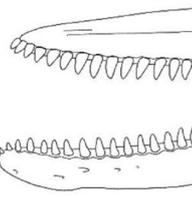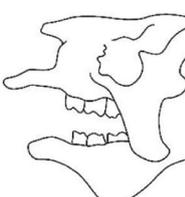
CL-17: *RIA*

CL-18: *Lemuriform Toothcomb*

CL-19: *Special Canines*

CL-20: *Homodont Dentitions*

CL-21: *Major Tooth Reductions*

missing altogether. As a result, the ancestral state cannot be tested and thus potential parallelisms cannot be proven. The similarity of rodent and lagomorph incisors can only be considered as parallelism, because the monophyly of Glires has been accepted (Meng & Wyss 2001, Meng et al. 2003). It is not the purpose of this paper to separate convergence from parallel evolution, but it may stimulate further investigation.

Discordant AD and antemolar reduction: In many genera the number and morphology of the teeth in the upper and the lower AD are different. Such a condition is called discordant. These differences are well known and illustrated in many textbooks (Ungar 2010), but rarely interpreted.

One reason for the differences in the AD is the completely different function of the upper and lower jaws. The mandible is very mobile due to the highly differentiated musculature that connects it to the cranium. These muscles drive the bite. The upper dentition row is passive. However, when the upper canines are enlarged and used for display or as a weapon, the entire skull must move, driven by the neck muscles. "*Saberteeth*" (CL-15) are a very obvious example.

Many small mammals of the early Tertiary have another type of discordant incisors and/or canines (FT-5 and FT-35). Their mandibles have an enlarged lower incisor, that has no equivalent antagonist. Nevertheless, the two inadequate teeth function as forceps. Soricidae, Apatemyidae and Plesiadapidae (Gingerich 1976) are a few examples that are discussed in CL-8. The discordance of the upper and lower AD is increased by an discordant antemolar reduction.

The antemolar reduction: The reduction of antemolars, teeth between the enlarged incisors and the molars, is an often-discussed phenomenon in the dentition of Soricidae (Hugueney et al. 2012, Klietmann et al. 2013). A very similar reduction of antemolars has been found in the AD of MULTITUBERCULATA, LAGOMORPHA, RODENTIA, EULIPOTYPHLA and even in METATHERIA (see CL-8). The gradual reduction follows similar rules in the different mammalian lineages.

The reduced teeth may leave room for a diastema, as in Multituberculata, or the remaining teeth are crowded, as in Soricidae (Repenning 1967, Hugueney et al. 2012). The last premolars (P4/p4) are often excluded. Glires provide an instructive example. In the dentition of *Lepus* Lagomorpha (2.0.3.3/1.0.2.3) the upper jaw has one incisor and one premolar more than the lower jaw. The upper I3 and the P3 can be regarded as a remnant of the former antemolars. In Rodentia the reduction eliminated the extra incisors, and in some genera, such as *Cricetus,* even all the premolars. The most surprising observation is that in most of the genera studied, the reduction of the antemolars is more progressive in lower jaw than in the upper dentition.

Modification of the incisors: Enlarged incisors (FT-6) occur at different tooth loci and are therefore not homologous. An AD with a single enlarged lower incisor and a discordant upper incisor occurs mostly in small mammals, CL-8 "*Mandible with Procumbent Incisor*". This pattern evolved independently in different mammalian groups, including ALLOTHERIA, METATHERIA, and EUTHERIA. The pointed teeth of the AD are well suited for catching small prey, but less so for feeding on vegetation. This cluster was very common during the Late Cretaceous and Early Tertiary. In the extant placental fauna, however, it is restricted to the single family of Soricidae. This may illustrate a correlation between specific dental clusters and preferred diets.

Gliriforms (CL-9) have a similar pair of incisors, but upper and lower incisors are concordant (FT-4) and euhypsodont (FT-8). Such incisors are perfect for cutting plant material. The blades of the intensively worn incisors are continuously sharpened by the reciprocal abrasion (FT-11).

Few examples have been found in which the AD is characterised by a set of large concordant incisors and relatively small canines (CL-3). Dentitions with a single pair of large concordant upper and lower incisors (CL-4) are also rare.

The upper incisors may overbite the lower incisors (FT-13). Those with rooted incisors are rare (CL-5), but others with euhypsodont incisors are common in several placental and in some diprotodont marsupial lineages (CL-6). The thick and euhypsodont incisors, which are not strongly curved, tend to form a grasping tool, which is comparable to flat-nosed pliers (CL-7) that occur independently in placentals and marsupials. Such teeth show a simple mutual abrasion (FT-40) in contrast the reciprocal abrasion in gliriform incisors.

Tusks have been evolved in different groups (CL-11 "*Dentin Tusks*") This survey covers only dentin tusks, which can be formed by either canines or incisors. Incisors from different tooth loci may be involved. Dentin tusks are generally less used for food gathering, but are important social organs.

Tooth loci of large incisors: Several Eulipoyphla, Apatotheria and Plesiadapidae have an enlarged lower incisor that usually is labelled I1/i1, but the identification of the tooth position in fossil taxa is often tentative and not necessarily homologous. The possibility of persistent deciduous teeth must be considered because they persist in rodents and lagomorphs. According to ontogenetic studies, the cutting incisors have been identified as di2 and dI2 (Lucket, 1985). In contrast, the small I3 of lagomorphs that forms an abutment, is a permanent tooth that follows a deciduous tooth. This difference reflects their different functions.

In Multituberculata the enlarged incisors have been identified as I2/i1 (Greenwald 1988). In the marsupial Paucituberculata and Diprotodontia the two enlarged teeth are traditionally assigned as I1/i1, although a former central lower incisor has been reduced. For this reason, and because of the staggered arrangement of the lower incisors, Hershkovitz (1982) argued for the identification of the enlarged lower incisor as i3, but his arguments have never been totally

falsified, and the prominent tooth is usually referred to as i1 (e.g. Black et al. 2014). No specific tooth position can be identified in the incisors for either enlargement or reduction and therefore, the enlarged incisors are not homologous.

Modifications of canines: The primary function of canines is to catch or collect food items and to convert it into a digestible form. Most canines also have a secondary function as social organs if they are large enough. They can be used as weapons against predators or for display. Canines often shrink in size or disappear entirely when these functions are not required.

Moderately enlarged canines serve both functions in the various carnivorous groups, but as part of the general equipment of the mammalian dentition such canines also occur in basal herbivores (CD-12), where they are often reduced during evolution.

The most impressive canine modification is the slender blade of saberteeth (FT-42). They evolved independently in different placental and marsupial lineages (CL-15 "*Sabertteeth*"). In carnivores the saberteeth function as powerful weapons and for display. Similar saberteeth occur independently in some herbivores, such as some Artiodactyla and Dinocerata. In these taxa the display function is dominant.

Other herbivores (e.g. Cl-14 "*Mutually Abrading Canines*") have enlarged canines that are massive. They are used less for foraging than as social organs, as in *Hippopotamus*. They have specific types of abrasion that produce sharp-edged or pointed weapons (FT-40).

On the other hand, canines may become reduced when an incisor dominates the dentition, as in CL-8 and CL-9. In several independent groups, the canines are not enlarged, but adjusted (FT-33) to the size of the incisors and premolars (CL-13). They make the toothrow more uniform and increase the total occlusal surface. The canines lose their potential as a weapon or display organ.

Upper and lower canines have a very conservative interaction. The lower canine is set anterior to the upper canine. This pattern is modified in three different ways when the lower canine is incisiform (CL-16, CL-17, and CL-18). In all three clusters both the lower canine is adjusted to the incisors and lost its function as an antagonist of the upper canine. In the CL-16 "*C/p Functional Unit*" the most anterior lower premolar is caniniform and functionally replaces the lower canine. The CL-17 "*Ruminant Incisor Arcade"* lacks the upper incisors and commonly the upper canines (FT-15). The loss of antagonistic teeth is compensated for by highly mobile lips. In some ruminant taxa the upper canine is not reduced but used for display. In the CL-18 "*Lemuriform Toothcomb*" the lower canine is part of the toothcomb and occludes with the two upper incisors.

Sharpening of teeth: Intense wear limits the function of the teeth. The abrasion caused by a carnivorous diet is less intense than that caused by an herbivorous diet.

In carnivorous mammals the wear is usually limited, and even the canines are not sharpened. However, the enamel blades of the carnassial (p4/M1) are sharpened. The antagonists move over each other as in the normal chewing, but with little or no food in between. In this way, they sharpen the enamels on the luv side synchronously by mutual abrasion.

Such a synchronous grinding by tooth-tooth contact is common in herbivorous molars and premolars. It is also found in some incisors (CL-6) and canines CL-14 "*Mutually Abrading Canines*" which have a flat facet that is constantly reground. The surrounding enamel forms sharp edges. The canines of *Hippopotamus* are a good example of such a synchronous sharpening. The hypothetical thegosis, that postulates independent movements for sharpening of molar teeth, has been rejected (Murray and Sanson 1998). The only movement for sharpening that is not related to chewing or cutting, was found in gliriform dentitions, CL-9 "*Gliriform Incisors*". The upper and lower incisors sharpen each other reciprocally. The upper incisor is sharpened by the lower incisor. This process begins when the two teeth meet tip to tip. When the mandible is raised, the enamel of the lower incisor grinds along the posterior side of the upper incisor. It scrapes the dentin in a concave facet that sometimes ends in an abutment. To sharpen the lower incisor, the mandible is pulled forward, which allows the enamel of the upper incisor to grind the dentin of the lower incisor from tip to base. The facet on the lower incisor extends over the posterior side of the dentin core without an abutment (Fig. 9.3). These concave facets on both teeth are characteristic of the reciprocal sharpening of gliriform incisors.

The conspicuous saberteeth usually have no antagonist for sharpening, but serrated edges keep the sabers functional. The sparassodont *Thylacosmilus* forms an exception. The lingual side of the canines is abraded by the soft or horny tissue of the mandible exposing the sharp cross-section of the buccal enamel (Koenigswald and Goin 2000).

Different evolutionary trends in the AD of carnivores and herbivores: In Carnivora, AD is very conservative. The concordant pattern of three incisors and a moderately enlarged canine (CL-12 "*Moderate Canines*") has been maintained unchanged over time. Such an AD is optimal for the function of biting or cutting out pieces of the killed prey. – However, the AD of herbivores, has undergone major changes during evolution. Many herbivores have reduced part of the AD, such as the largest group of Artiodactyla, the ruminants, which have reduced all teeth in the premaxilla and often the upper canines (CL-17 "*Ruminant Incisor Arcade"*). Most Xenarthra have no teeth in the anterior parts of the upper and lower jaws. These herbivores must have developed additional equipment for grasping food from the ground or from trees. Such additional tools are provided by soft tissues, such as the tongue, lips, or a trunk (Bargo et al. 2006). Although such structures are difficult to reconstruct from fossils, they

must always be considered when the anterior dentition is discussed.

Data availability Data have been collected from various sources, direct observations in various museums and from illustrations in the scientific literature, textbooks, and papers on specific taxa and additional data from databases (please see chapter "Materials").

Declarations

Conflict of Interest The author declares that he has no conflict of interest.

References

Abel, O. (1904). Die Sirenen der mediterranen Tertiärbildungen Österreichs. *Abhandlungen Geologische Reichsanstalt*, *19*, 1–223.

Abel, O. (1911). *Palaeobiologie* (pp. 1-708). Stuttgart: Schweizerbart.

Abel, O. (1944). Studie über vergrößerte Einzelzähne des Vordergebisses der Wirbeltiere und deren Funktion. *Palaeobiologie* 8/1: 1–112.

Abello, M. A., & Candela., A. M. (2020). Paleobiology of *Argyrolagus* (Marsupialia, Argyrolagidae), an astonishing case of bipedalism among South American mammals. *Journal of Mammalian Evolution*, *27*, 419–444.

Aiglstorfer, M., Rössner, G., E., & Böhme, M. (2014). *Dorcatherium naui* and pecoran ruminants from the late Middle Miocene Gratkorn locality (Austria). In M. Böhme, M. Gross, & J. Prieto (Eds.), *The Sarmatian vertebrate locality Gratkorn, Styrian Basin. Palaeobiodiversity and Palaeoenvironments, 94*(1), 83–123.

Aiglstorfer, M., Sánchez, I. M., Wang, S. Q., Morales, J., Li, C., Mayda, S., & Mennecart, B. (2023). Musk deer on the run – dispersal of Miocene moschidae in the context of environmental changes. In I. Casanovas, L. W. van den Hoek-Ostende, C. M. Janis, & J. Saarinen (Eds.), *Evolution of Cenozoic land mammal faunas and ecosystems, 25 years of the NOW database of fossil mammals* (pp. 165–187). Cham: Springer International Publishing.

Aitchison, J. (1946). Hinged teeth in mammals, a study of the tusks of muntjacs (*Muntiacus*) and Chinese water deer (*Hydropotes inermis*). *Proceedings of the Zoological Society of London, 116*, 329–338.

Akbar Khan, M., Iliopoulos, G., Akhtar, M., & Ghaffar, A. (2011). The longest tusk of cf. *Anancus sivalensis* (Proboscidea, Mammalia) from the Tatrot Formation of the Siwaliks, Pakistan. *Current Science* (*00113891*), *100*(2).

Allen, J. A. (1922). The American Museum Congo Expedition collection of Insectivora. *Bulletin of the American Museum of Natural History, 47*, 1–38.

Andrews, C. W. (1906). *A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt* (pp.xxxvii + pp. 1–324). London: British Museum (Natural History).

Ankel-Simons, F. (1996). Deciduous dentition of the Aye Aye, *Daubentonia madagascariensis*. *American Journal of Primatology, 39*, 87–97.

Archer, M. (1976). The dasyurid dentition and its relationships to that of didelphids, thylacinids, borhyaenids (Marsupicarnivora) and peramelids (Peramelina, Marsupialia). *Australian Journal of Zoology Supplementary Series*, *24*(39), 1–34.

Archer, M., & Hand, S. (2006). The Australian marsupial radiation. In J. R. Merrick, M. Archer, G. M. Hickey, & M. S. Y. Lee (Eds.), *Evolution and Biogeography of Australasian Vertebrates* (pp. 633–808). Sydney: Australian Scientific Publishing.

Archer, M., Hand, S., & Godthelp, H. (1988). A new order of Tertiary zalambdodont marsupials. *Science 239* (4847), 1528–1531.

Armfield, B., A, Zheng, Z., Bajpai, S., Vinyard, C., J., & Thewissen, J., G., M. (2013). Development and evolution of the unique cetacean dentition. *PeerJ, 1*, e24.

Asher, R., J., Gunnell, G., F., Seiffert, E., R., Pattinson, D., Tabuce, R., Hautier, L., & Sallam, H., M. (2017). Dental eruption and growth in Hyracoidea (Mammalia, Afrotheria). *Journal of vertebrate Paleontology, 37*(3), e1317638.

Asher, R. J., McKenna, M. C., Emry, R. J., Tabrum, A. R., & Kron, D. G. (2002). Morphology and relationships of *Apternodus* and other extinct, zalambdodont, placental mammals. *Bulletin of the American Museum of Natural History*, *2002*(273), 1–117.

Avedik, A., Duque-Correa, M. J., & Clauss, M. (2023). Avoiding the lockdown, Morphological facilitation of transversal chewing movements in mammals. *Journal of Morphology*, *284*, e21554.

Babot, M. J, Powell, J. E, & de Muizon, C. (2002). *Callistoe vincei*, a new Proborhyaenidae (Borhyaenoidea, Metatheria, Mammalia) from the early Eocene of Argentina. *Geobios*, *35*(5), 615–629.

Bai, B., Meng, J., Wang, Y. Q., Wang, H. B., & Holbrook, L. (2017). Osteology of the middle Eocene ceratomorph Hyrachyus

modestus (Mammalia, Perissodactyla). Bulletin of the American Museum of Natural History, 2017(413), 1–70

Bargo, M. S. (2001). The ground sloth *Megatherium americanum*, skull shape, bite forces, and diet. *Acta Palaeontologica Polonica*, *46*(2).

Bargo, M. S, & Vizcaíno, S. F (2008). Paleobiology of Pleistocene ground sloths (Xenarthra, Tardigrada), biomechanics, morphogeometry and ecomorphology applied to the masticatory apparatus. *Ameghiniana*, *45*(1), 175-196.

Bargo, M. S, Toledo, N., & Vizcaíno, S. F. (2006). Muzzle of South American Pleistocene ground sloths (Xenarthra, Tardigrada) *Journal of Morphology*, *267*(2), 248–263.

Barrett, P. Z., Hopkins, S. S., & Price, S. A (2021). How many sabertooths? Reevaluating the number of carnivoran sabertooth lineages with total-evidence Bayesian techniques and a novel origin of the Miocene Nimravidae. *Journal of Vertebrate Paleontology, 41*(1), e1923523.

Barrow, E. C., Seifert, E. R., & Simons, E. L (2012). Cranial morphology of *Thyrohyrax domorictus* (Mammalia, Hyracoidea) from the early Oligocene of Egypt. *Journal of Vertebrate Paleontology, 32*(1), 166–17.

Baumont, R., Doreau, M., Ingrand, S., & Veissie, I. (2006). Feeding and mastication behavior in ruminants (pp 241-262). In V. Bels (Ed.). Feeding in Domestic Vertebrates. *Wallingford*: *CABI Publishing.*

Beck, R., Travouillon, K. J., Aplin, K. P., Godthelp, H., & Archer, M. (2014) The osteology and systematics of the enigmatic Australian Oligo-Miocene metatherian *Yalkaparidon* (Yalkaparidontidae, Yalkaparidontia, ?Australidelphia, Marsupialia). *Journal of Mammalian Evolution*, *21*(2), 127–172.

Beck, R. M. (2017). The skull of *Epidolops ameghinoi* from the early Eocene Itaboraí fauna, southeastern Brazil, and the affinities of the extinct marsupialiform order Polydolopimorphia. *Journal of Mammalian Evolution*, *24*(4), 373–414.

Beck, R. M. (2023). Diversity and phylogeny of marsupials and their stem relatives (Metatheria). In N. C. Cáceres, C. R. Dickman (Eds.), *American and Australasian marsupials: An evolutionary, biogeographical, and ecological approach* (pp. 1–66). Cham: Springer International Publishing.

Berkovitz B, & Shellis, P. (2018). *The teeth of mammalian vertebrates*. Academic press.

Biewer, J. N., Velez-Juarben, J., & Parham, J. F. (2020). Insights on the dental evolution of walruses based on new fossil specimens from California. *Journal of Vertebrate Paleontology*, *40*(5), e1833896.

Billet, G. (2010). New observations on the skull of *Pyrotherium* (Pyrotheria, Mammalia) and new phylogenetic hypotheses on South American ungulates. *Journal of Mammalian Evolution, 17*, 21–59.

Black, K. H., Travouillon, K. J, Den Boer, W., Kear, B. P, Cooke, B. N., et al. (2014). A new species of the basal ''Kangaroo'' *Balbaroo* and a re-evaluation of stem macropodiform interrelationships. *PLoS ONE, 9*(11), e112705. https://doi.org/10.1371/journal.pone.0112705

Bloch, J. I., Gingerich, P. D. (1994). New species of *Carpolestes* (Mammalia, Proprimates) from Clarkforkian late Paleocene limestones of the Clarks Fork Basin, Wyoming, teeth, skulls, and femur. *Journal Vertebrate Paleontology, 14,* 17Ae18A.

Bloch, J. I. Silcox, M. T. (2006). Cranial anatomy of the Paleocene plesiadapiform *Carpolestes simpsoni* (Mammalia, Primates) using ultra high-resolution X-ray computed tomography, and the relationships of plesiadapiforms to Euprimates. *Journal of Human Evolution, 50*(1), 1–35.

Boessenecker, R. W., Churchill, M. (2013). A reevaluation of the morphology, paleoecology, and phylogenetic relationships of the enigmatic walrus. *Pelagiarctos*. *PLoS One, 8*(1), e54311.

Boessenecker, R. W., Poust, A. W., Boessenecker, S. J., & Churchill, M. (2023). Tusked walruses (Carnivora, Odobenidae) from the Miocene–Pliocene Purisima Formation of Santa Cruz, California (USA), a new species of the toothless walrus *Valenictus* and the oldest records of Odobeninae and Odobenini. *Journal of Vertebrate Paleontology*, e2296567.

Bover, P., & Alcover, J. A (1999). The evolution and ontogeny of the dentition of *Myotragus balearicus* Bate, 1909 (Artiodactyla, Caprinae), evidence from new fossil data. *Biological Journal of the Linnean Society, 68*(3), 401–428.

Bown, T. M., & Rose, K. D. (1987). Patterns of dental evolution in early Eocene anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. *Memoir (The Paleontological Society), 23,* 1–162.

Brace, S. J. A., Thomas, L., Dalén, J., Burger, R. D. E., MacPhee, R. D., Barnes, I., & Turvey, S., T. (2016) Evolutionary history of the Nesophontidae, the last unplaced Recent mammal family. *Molecular Biology and Evolution, 33*(12). https://doi.org/10.1093/molbev/msw186

Breuer, R. (1933). Über das Vorkommen sogenannter keilförmiger Defekte an den Zähnen von *Ursus spelaeus* und deren Bedeutung für die Paläobiologie. *Paläobiologica, 5*, 103–114.

Buk, K. G, & Knight, M. H. (2012). Seasonal diet preference of black rhinoceros in three arid South African Natitional Parks. *African Journal of Ecology, 42*(4), *82–93.*

Butler, P. M. (1980). The giant erinaceid insectivore, *Deinogalerix* Freudenthal, from the upper Miocene of Gargano, Italy. *Scripta Geologica*, *57*, 1–72.

Cabrera, D. & Stankowich, T. (2020). Stabbing slinkers, tusk evolution among artiodactyls. *Journal of Mammalian Evolution*, *27*(2), 265–272.

Chapman, D. I, Chapman, N. G., & Colles, C. M. (1985). Tooth eruption in Reeves' muntjac (*Muntiacus reevesi*) and its use as a method of age estimation (Mammalia, Cervidae). *Journal of Zoology*, *205*(2), 205–221.

Chimento, N., Agnolin, F. L., & Novas, F. E. (2014). The bizarre 'metatherians' *Groeberia* and *Patagonia*, late surviving members of gondwanatherian mammals. *Historical Biology, 27*(5). https://doi.org/10.1080/08912963.2014.903945

Clemens, W. A., & Koenigswald, W. von (1993). A new skeleton of *Kopidodon macrognathus* from the Middle Eocene of Messel and the relationships of paroxyclaenids and pantolestids based on postcranial evidence. *Kaupia, 3*, 57–73.

Coimbra-Filho, A. F. (1978). Tree-gouging, exudate-eating and" shorttusked" condition in *Callithrix* and *Cebuella*. *The biology and conservation of the Callitrichidae* (pp. 105-115). Washington DC: Smithsonian Institution Press.

Coombs, M. C. (1978). A premaxilla of *Moropus elatus* Marsh, and evolution of Chalicotherioid anterior dentition. *Journal of Paleontology*, 118–121.

Cooper, C. F. (1924). IX. On the skull and dentition of *Paraceratherium bugtiense*, a genus of aberrant rhinoceroses from the lower Miocene deposits of Dera Bugti. *Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character*, *212* (391-401), 369–394.

Cope, E. D. (1877). *Report upon the extinct vertebrata obtained in New Mexico by parties of the expedition of 1874*. (*Vol. 4).* US Government Printing Office.

Coste, A., Fordyce, R. E., & Loch, C. (2023). A new dolphin with tusk-like teeth from the late Oligocene of New Zealand indicates evolution of novel feeding strategies. *Proceedings of the Royal Society B, 290*, 20230873. https://doi.org/10.1098/rspb.2023.0873

Croft, D. A (2006). Do marsupials make good predators? Insights from predator–prey diversity ratios. *Evolutionary Ecology Research, 8*(7), 1193–1214.

Croft, D. A (2016). *Horned armadillos and rafting monkeys, the fascinating fossil mammals of South America.* Bloomington: Indiana University Press. ISBN 978-0-253-02084-0.

Crompton, A. W., Barnet, J., Lieberman, D. E., Owerkowiczc, T., Skinner, J., & Baudinette, R. V. (2008), Control of jaw movements in two species of macropodines (*Macropus eugenii* and *Macropus rufus*). *Comparative Biochemistry and Physiology, Part A,* 109–123.

Dashzėvėg, D. C. (1996). A new hyracodontid (Perissodactyla, Rhinocerotoidea) from the Ergilin Dzo Formation (Oligocene, Quarry 1) in Dzamyn Ude, eastern Gobi Desert, Mongolia. *American Museum novitates*, no. 3178.

Dawson, M. R., Stucky, R. K., Krishtalka, L. & Black, C. C. (1986). *Machaeroides simpsoni*, new species, oldest known sabertooth creodont (Mammalia), of the Lost Cabin Eocene. *Contributions to Geology*, *University of Wyoming, Special Paper, 3,* 177–182.

De Muizon, C. (1993). Walrus-like feeding adaptation in a new cetacean from the Pliocene of Peru. *Nature*, *365*, 745–748. https://doi.org/10.1038/365745a0

De Muizon, C., & Billet, G. (2022). Dental ontogeny in the early Paleocene placental mammal *Alcidedorbignya inopinata* (Pantodonta) from Tiupampa (Bolivia). *Geodiversitas, 44*(32), 989–1050.

De Muizon, C., & Ladevèze, S. (2020). Cranial anatomy of *Andinodelphys cochabambensis*, a stem metatherian from the early Palaeocene of Bolivia. *Geodiversitas*, *42*(30), 597–739

De Muizon, C., Domning, D. P., & Ketten, D. R. (2002). *Odobenocetops peruvianus*, the walrus-convergent delphinoid (Mammalia, Cetacea) from the early Pliocene of Peru. *Smithsonian Contributions to Paleobiology*, *93*, 223–261.

De Muizon, C., Billet, G., Argot, C., Ladevèze, S., & Goussard, F. (2015). *Alcidedorbignya inopinata*, a basal pantodont (Placentalia, Mammalia) from the early Palaeocene of Bolivia, anatomy, phylogeny and palaeobiology. *Geodiversitas*, *37*(4), 397–634.

Delmer, C. (2009). Reassessment of the generic attribution of *Numidotherium savagei* and the homologies of lower incisors in proboscideans. *Acta Palaeontologica Polonica, 54*(4) 561–580.

Delmer, C., Mahboubi, M., Tabuce, R., & Tassy, P. (2006). A new species of *Moeritherium* (Proboscidea, Mammalia) from the Eocene of Algeria, new perspectives on the ancestral morphotype of the genus. *Palaeontology, 49*(2), 421–434.

Dinerstein, E. (1991). Sexual dimorphism in the greater one-horned rhinoceros (*Rhinoceros unicornis*). *Journal of Mammalogy*, *72*(3), 450–457.

Dobson, G. E. (1883). *A monograph of the Insectivora, systematic and anatomical. Part I*. London: John Van Voorst.

Domning, D. P. (2001). Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. *Palaeogeogaphy, Palaeoclimtology, Paleaoecology, 166*, 27–50.

Domning, D. P. (2018). Sirenian evolution. In Perrin, W. F., Würsig, B., & Thewissen, J. G. M. (Eds.), *Encyclopedia of marine mammals* (pp. 856–859), Academic Press.

Domning, D. P., & Gingerich, P. D. (1994). *Protosiren smithae*, new species (Mammalia, Sirenia), from the late middle Eocene of Wadi Hitan, Egypt. *Contributions from the Museum of Paleontology*, *University of Michigan*, 29, 69–87.

Domning, D. P., Ray, C. E., & McKenna, M. C. (1986). Two new Oligocene desmostylians and a discussion of tethytherian systematics. *Smithsonian Contributions to Paleobiology, 59*, 1–56.

Dötsch, C., & Koenigswald, W. von (1978). Zur Rotfärbung der Soricidenzähne. *Zeitschrift für Säugetierkunde, 43*, 65–70.

Eaglen, R. H. (1980). Toothcomb homology and toothcomb function in extant strepsirhines. *International Journal of Primatology 1*, 275–286 (1980). https://doi.org/10.1007/BF02692275

Eberle, J. J., Fricke, H. C., Humphrey, J. D., Hackett, L., Newbery, M. G., & Hutison. J. H. (2010). Seasonal variability in Arctic temperatures during early Eocene time. *Earth and Planetary Science letters, 296*, 481–486

Effinger, J. A. (1998). Enteledontidae. In C. M. Janis, M. K. Scott, L. L. Jacobs (1998), *Evolution of Tertiary mammals of North America* (pp. 375–380). *Cambridge University Press*.

Ercoli, M. D., Armella, M. A. (2021). Snout shape and masticatory apparatus of the rodent-like mesotheriid ungulates (Notoungulata, Typotheria), exploring evolutionary trends in dietary strategies through ancestral reconstructions. *Palaeontology*, *64*(3), 385–408.

Fay, F. H. (1982). Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *North American Fauna, 74*, 1–279.

Fay, F. H. (1985*). Odobenus rosmarus*. *Mammalian Species, 238*, 1–7.

Figueirido, B., Martín-Serra, A., & Janis, C. M. (2016). Ecomorphological determinations in the absence of living analogues, the predatory behavior of the marsupial lion (*Thylacoleo carnifex*) as revealed by elbow joint morphology. *Paleobiology*, *42*(3), 508–531.

Fisher, D. C. Cherney, M. D. Newton, C. Rountrey, A. N., Calamari, Z. T., Stucky, R. K., Lucking, C., Petrie, L. (2014), Taxonomic overview and tusk grown analyses of Ziegler Reservoir proboscideans. *Quternary Resarch 82*, 518–532.

Fleagle, J. G. (1988) *Primate adaptation and evolution*. Academic Press.

Forasiepi, A., Goin, F. J., & Tauber, A. A. (2004). Las especies de *Arctodictis mercerat*, 1891 (Metatheria, Borhyaenidae), grandes carnívoros del Mioceno de América del Sur. *Spanish Journal of Palaeontology*, *19*(1), 1–22.

Franzen, J. L. (1990). *Hallensia* (Mammalia, Perissodactyla) aus Messel und dem Pariser Becken sowie Nachträge aus dem Geiseltal. *Bulletin del Institut Royal des Sciences Naturelles de Belgique. Science de la Terre, 60*, 175–201.

Franzen, J. L. (2007). Eozäne Equoidea (Mammalia, Perissodactyla) aus der Grube Messel bei Darmstadt (Deutschland) Funde der Jahre 1969-2000. *Schweizer Paläontologische Abhandlungen, 127*, 1–245.

Freedman, L. (1967). Skull and tooth variation in the genus *Perameles*. Part I, anatomical features. *Records of the Australian Museum*, *27*(6), 147–165.

Freudenthal, M. (1972). *Deinogalerix koenigswaldi* nov. gen., nov. sp., a giant insectivore from the Neogene of Italy. *Scripta Geologica, 14*, 1–19.

Gazin, C. L. (1953). The Tillodontia, an early Tertiary order of mammals. *Smithsonian Miscellaneous Collections, 121*(10), 1–110.

Geisler, J. H., & Theodor, J. M. (2009). *Hippopotamus* and whale phylogeny. *Nature*, *458*(7236), E1-E4.

Gentry, A. W., Roessner, G. E., & Heizmann, P. J. (1999). Suborder Ruminantia. In G. E. Rössner, & K. Heissig (Eds.), *The Miocene land mammals of Europe* (pp 225–258). München: Verlag Dr. Friedrich Pfeil.

Gheerbrant, E., Sudre, J., Tassy, P., Amaghzaz, M., Bouya, B., & Iarochène, M. (2005). Nouvelles données sur *Phosphatherium escuilliei* (Mammalia, Proboscidea) de l'Éocène inférieur du Maroc, apports à la phylogénie des Proboscidea et des ongulés lophodontes. *Geodiversitas, 27*(2), 239-333.

Gingerich, P. D. (1974). *Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates)*. Yale University.

Gingerich, P. D. (1976). Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Papers in Paleontology 15*. Ann Arbor: Museum of Paleontology, The University of Michigan.

Gingerich, P. D. (1977). Homologies of the anterior teeth in Indriidae and a functional basis for dental reduction in primates. *American Journal of Physical Anthropology, 47*, 387–393.

Gingerich, P. D. (1981). Variation, sexual dimorphism, and social structure in the early Eocene horse *Hyracotherium* (Mammalia, Perissodactyla). *Paleontology*, *7*(4) 443–455.

Gingerich, P. D., & Rose, K. D. (1979). Anterior dentition of the Eocene Condylarth *Thryptacodon*, convergence with the tooth comb of lemurs. *Journal of Mammalogy, 60*, 16–22. https://doi.org/10.2307/1379754

Gingerich, P. D., & Rose, K. D. (1982). Studies on Paleocene and Early Eocene Apatemyidae (Mammalia, Insectivora) - I. Dentition of Clarkforkian *Labidolemur* kayi. II. *Labidolemur* and *Apatemys* from the Early Wasatchian of the Clark's Fork Basin, Wyoming. *Contributions from the Museum of Paleontology, University of Michigan, 26*(4), 49–69.

Godfrey, L. R., Jungers, W. L., & Burney, D. A. (2010). Subfossil lemurs of Madagascar. In L. Werdelin & W. J. Sanders (Eds.), *Cenozoic mammals of Africa* (pp. 351–367). University of California Press.

Göhlich, U. B. (1999). Order Proboscidea. In G. E. Rössner & K. Heissig (Eds.), *The Miocene Land Mammals of Europe* (pp. 157–168). München: Verlag Dr. Friedrich Pfeil.

Göhlich, U. B. (2010). Tertiäre Urelefantenfunde aus Deutschland. In H. Meller (Ed.). *Elefantenreich* (pp. 363–372). Halle: Landesmuseum für Vorgeschichte.

Goin, F. J., & Abello, M. A. (2013). Los metetheria Sudamericanos de Cimienzos dell Neógeno (Mioceno temprano, edad mamífero Colhuehuapense), Microbiotheria y Poplydolopimorphia. *Ameghiniana, 50*, 51–78.

Goin, F. J., & Pascual, R. (1987). News on the biology and taxonomy of the marsupials Thylacosmilidae (Late Terciary of Argentina). *Anales de la Academia Nacional de Ciencias Exactas, Físicas y Naturales de Buenos Aires, 39*, 219–246.

Gordon, I. J., & Illius, A. W. (1988). Incisor arcade structure and diet selection in ruminants. *Functional ecology, 1988*, 15–22.

Graham, Z. A., Garde, E., Heide-Jørgensen, M. P., & Palaoro, A. V. (2020). The longer the better, evidence that narwhal tusks are sexually selected. *Biology Letters*, *16*(3), 20190950. https://doi.org/10.1098/rsbl.2019.0950

Granger, W., & Gregory, W. K. (1936). Further notes on the gigantic extinct rhinoceros, *Baluchitherium*, from the Oligocene of Mongolia. *Bulletin of the American Museum of Natural History, 72*, 1–73.

Granger, W., & Simpson, G. G. (1929). *A revision of the Tertiary Multituberculata.* American Museum of Natural History.

Green, J. L., & Kalthoff, D. C. (2015). Xenarthran dental microstructure and dental microwear analyses, with new data for *Megatherium americanum* (Megatheriidae). *Journal of Mammalogy, 96(*4), 645–657.

Greenwald, N. S. (1988). Patterns of tooth eruption and replacement in multituberculate mammals. *Journal of Vertebrate Paleontology*, *8*(3), 265–277.

Gunnel, G. F., Bown, T. M., & Bloch, J. I. (2008). 6. Leptictida. In C. M. Janis, G. F. Gunnell, & M. D. Uhen (Eds.), *Evolution of Tertiary Mammals of North America*, Vol. 2. (pp 82–88). Cambridge University Press.

Harington, C. R., Anderson, T. W., & Rodrigues, C. G. (1993). Pleistocene walrus (*Odobenus rosmarus*) from Forteau, Labrador. *Géographie physique et Quaternaire*, *47*, 111–118.

Hautier, L., Gomes Rodrigues, H., Billet, G., & Asher, R. J. (2016). The hidden teeth of sloths, evolutionary vestiges and the development of a simplified dentition. *Scientific Reports*, *6*(1), 1–9.

Haynes, G. (1991). *Mammoths, mastodonts, and elephants, biology, behaviour, and the fossil record*. New York: Cambridge University Press.

Headdon, N. (2014). https://www.deviantart.com/qilong/art/The-Venomous-Mammal-441303049

Heaney, L. R., & Morgan, G. S. (1982). A new species of gymnure, *Podogymnura* (Mammalia, Erinaceidae) from Dinagat Island, Philippines. *Proceedings of the Biologial Society Washington 95*(1), 13–26.

Hellmund, M. (1991). Revision der europäischen Species der Gattung *Elomeryx* Marsch 1894 (Anthracotheriidae, Artiodactyla, Mammalia) - odontologische Untersuchungen. *Palaeontographica A, 220*(1-3), 1–101.

Herring, S. W. (1972). The role of canine morphology in the evolutionary divergence of pigs and peccaries. *Journal of Mammalogy, 53*(3), 500–512.

Hershkovitz, P. (1982). The staggered marsupial lower third incisor (i3). *Geobios mémoire special, 6*, 191–200.

Hillson, S. (1986). Teeth. *Cambridge manuals in Archeology*. Cambridge University Press.

Holland, W. J., & Peterson, O. A. (1914). The osteology of the Chalicotheroidea, with special reference to a mounted skeleton of *Moropus elatus* Marsh, now installed in the Carnegie Museum. *Memoirs of the Carnegie Museum, 3*, 189–406.

Hooijer, D. A. (1948). Pleistocene vertebrates from Celebes I. *Celebochoerus heekereni* nov. gen. nov. spec. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, *51*, 1024–1032.

Hooker, J. J., & Thomas, K. M. (2001). A new species of *Amphirhagatherium* (Choeropotamidae, Artiodactyla, Mammalia) from the late Eocene Headon Hill Formation of southern England and phylogeny of endemic European 'anthracotherioids'. *Palaeontology*, *44*(5), 827–853.

Hugueney, M., Mein, P., & Maridet, O. (2012). Revision and new data on the Early and Middle Miocene soricids (Soricomorpha, Mammalia) from central and south-eastern France. *Swiss Journal of Palaeontology*, *131*(1), 23–49.

Hulbert, H. C. (2001). *The Fossil Vertebrates of Florida*. University Press of Florida.

Hulbert Jr., R. C. (2010). A new Early Pleistocene tapir (Mammalia, Perissodactyla) from Florida, with a review from Blancan tapirs from the state. *Bulletin of the Florida Museum of Natural History, 49*(3), 67–126.

Hünermann, K. A. (1967). Der Schädel von *Microbunodon minus* (Cuvier) (Artiodacryla, Anthracotheriidae) aus dem Chatt (Oligozän). *Eclogae geologicae Helvetiae, 60*, 661–688.

Hünermann, K. A. (1982). Rekonstruktion des *Aceratherium* (Mammalia, Perissodactyla, Rhinocerotidae) aus dem Jungtertiär von Höwenegg/Hegau (Baden-Württemberg). *Zeitschrift für geologische Wissenschaften*, *10*(7), 929–942.

Hutterer, R. (2005). Homology of unicuspid and tooth nomenclature in shrews. *Special publications. International Society of Shrew Biologists. 1*, 397–404.

Inuzuka, N., Domning, D. P., & Ray, C. E. (1994). Summary of taxa and morphological adaptations of the *Desmostylia*. *Island Arc*, *3*(4), 522–537.

Iwasaki, S. I. (2002). Evolution of the structure and function of the vertebrate tongue. *Journal of anatomy 201*(1), 1–13.

Janis, C. M. Scott, K. M. (1987). The interrelationships of higher ruminant families with special emphasis on the members of the Cervoidea. *American Museum novitates*, *2893*, 1–85.

Janis, C. M., Scott, K. M., & Jacobs, L. L. (Eds.) (1998). Evolution of Tertiary mammals in North America. Vol. 1 *Terrestrial carnivores, Ungulates and ungulate-like mammals.* Cambridge University Press.

Janis, C. M., Gunnell, G. G., & Uhen, M. D. (2008). Evolution of Tertiary mammals in North America. *Vol. 2 Small mammals, xenarthrans and marine mammals*. Cambridge University Press.

Janis, C. M., Figueirido, B., DeSantis, L., & Lautenschlager, S. (2020). An eye for a tooth: Thylacosmilus was not a marsupial "sabertooth predator". *PeerJ*, *8*, e9346.

Jefferson, T. A., Leatherwood, S., Webber, M. A (1993). *Marine mammals of the world*. Food and Agriculture Organization.

Joeckel, R. M. (1990). A functional interpretation of the masticatory system and paleoecology of entelodonts. *Paleobiology*, *16*(4), 459–482.

Kalthoff, D. C. (2000). Die Schmelzmikrostruktur in den Incisiven der hamsterartigen Nagetiere und anderer Myomorpha (Rodentia, Mammalia). *Palaeontographica, A 259*, 1–193.

Kalthoff, D. C. (2011). Microstructure of dental hard tissues in fossil and recent Xenarthrans (Mammalia, Folivora and Cingulata). *Journal of Morphology*, 272, 641–661.

Kalthoff, D. C., Mörs, T. (2021). Biomechanical adaptations for burrowing in the incisor enamel microstructure of Geomyidae and Heteromyidae (Rodentia, Geomyoidea). *Ecology and Evolution*, *11*(14), 9447–9459.

Kastelein, R. A., & Gerrits, N. M. (1990). The anatomy of the Walrus head (*Odobenus rosmarus*) Part, 1. *Aquatic Mammals 1990*, 16.3, 101–119.

Kielan-Jaworowska, Z., Hurum, J. H. (2001). Phylogeny and systematics of multituberculate mammals. *Palaeontology*, *44*(3), 389–429.

Kielan-Jaworowska, Z., Hurum, J. H., & Lopatin, A. V. (2005). Skull structure in *Catopsbaatar* and the zygomatic ridges in multituberculate mammals. *Acta Palaeontologica Polonica*, *50*(3), 487–512.

Kindahl, M. (1959). Some aspects of the tooth development in Soricidae. *Acta Odontologica Scandinavica, 17*(2), 203–237.

Kingsley, M. C. S., & Ramsay, M. A. (1988). The Spiral in the Tusk of the Narwhal. *Arctic*, *41*(3), 236–238.

Klietmann, J., Nagel, D., Rummel, M., & Hoek Ostende, L. W., van den (2013). Tiny teeth of consequence, vestigial antemolars provide key to Early Miocene soricid taxonomy (Eulipotyphla, Soricidae). *Comptes Rendus Palevol*, *12*(5), 257–267.

Koenigswald, W. von (1980). Das Skelett eines Pantolestiden (Proteuthria, Mamm.) aus dem mittleren Eozän von Messel bei Darmstadt. *Paläontologische Zeitschrift, 54*, 267–287.

Koenigswald, W. von (1983), Skelettfunde von *Kopidodon* (Condylarthra, Mammalia) aus dem mitteleozänen Ölschiefer von Messel bei Darmstadt. *Neues Jahrbuch Geologie Paläontologie, Abhandlungen*, *167*, 1–39.

Koenigswald, W. von (1990). Die Paläobiologie der Apatemyiden (Insectivora s.l.) und die Ausdeutung der Skelettfunde von *Heterohyus nanus* aus dem Mitteleozän von Messel bei Darmstadt. *Palaeontographica A, 210,* 41–77.

Koenigswald, W. von (1993). Die Schmelzmuster in den Schneidezähnen der Gl234iroidea (Gliridae und Seleviniidae, Rodentia, Mammalia) und ihre systematische Bedeutung. *Zeitschrift für Säugetierkunde*, *58*, 92–115.

Koenigswald, W. von (1995). Lagomorpha versus Rodentia, The number of layers in incisor enamel. *Neues Jahrbuch Geologie Paläontologie Monatshefte, 1995*(10), 605–613.

Koenigswald, W. von (2011). Diversity of hypsodont teeth in mammalian dentitions - construction and classification. *Palaeontographica A, 294*, 63–94.

Koenigswald, W. von (2016a), Specialized wear facets and late ontogeny in mammalian dentitions. *Historical Biology, 30*, 7–29. https://doi.org/10.1080/08912963.2016.1256399

Koenigswald, W. von (2016b). The diversity of the mastication patters in the Neogene and Quaternary Proboscideans. *Palaeontographica A, 307*, 1–41.

Koenigswald, W. von (2020). Construction and wear of mammalian teeth in terms of heterochrony. In T. Martin, & W. von Koenigswald (Eds.), *Mammalian teeth, form and function* (pp.171–186). München: Verlag Dr. Friedrich Pfeil.

Koenigswald, W. von, & Goin, F. (2000). Enamel differentiation in South American marsupials and a comparison of placental and marsupial enamel. *Palaeontographica A, 255*, 129–168.

Koenigswald, W. von, & Reumer, J. (2020). The enamel microstructure of fossil and extant shrews (Soricidae and Heterosoricidae, Mammalia) and its taxonomical significance. *Palaeontographica A, 316,* 79–163.

Koenigswald, W. von, & Storch, G. (1983). Messel, Nr. 36, *Pholidocercus hassiacus*, ein Amphilemuride aus dem Eozän der «Grube Messel» bei Darmstadt (Mammalia, Lipotyphla). *Senckenbergiana lethaea*, *64*(5-6), 447–495.

Koenigswald, W. von, & Storch, G. (1987). *Lepticidum tobieni* n. sp. ein dritter Pseudorhynchocyonide (Proteuthria, Mammalia) aus dem Eozän von Messel. *Courier Forschungsinstutut Senckenberg, 91*, 107–116.

Koenigswald, W. von, Rose, K., D., Grande, L., & Martin, R., D. (2005). First apatemyid skeleton from the lower Eocene Fossil Butte Member, Wyoming, compared to the European apatemyid from Messel, Germany. *Palaeontographica A, 272*, 149–169.

Koenigswald, W. von, Anders, U., Engels, S., Schultz, J. A., & Kullmer, O. (2013). Jaw movement in fossil mammals, analysis, description and visualization. *Paläontologische Zeitschrift, 87*, 141–159.

Koenigswald, W. von, Widga, C., & Göhlich, U., B. (2023). New mammutids (Proboscidea) from the Clarendonian and Hemphillian of Oregon – a survey of Mio-Pliocene mammutids from North America. *University of Oregon Museum Bulletin, 30*, 1–63.

Koenigswald, W. von, Lehmann, T., & Wappler, T. (2025). Extraordinary occlusion of caniniforms in the Eocene *Masillabune martini* from Messel. In Julia A. Schultz & Achim H. Schwermann (Eds.), *Palaeobiological Contributions in honour of Thomas Martin. Palaeobiodiversity and Palaeoenvironments, 105*(4). https://doi.org/10.1007/s12549-025-00672-3

Korvenkontio, A. (1934). Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmelzstruktur der Backenzähne. *Annales Botanici Societatis Zoologicae-Botanicae Fennicae Vanamo, 2*, 1–274.

Kramarz, A.,G., Bond, M., & Forasiepi, A., M (2011). New remains of *Astraponotus* (Mammalia, Astrapotheria) and considerations on astrapothere cranial evolution. *Paläontologische Zeitschrift, 85*, 185–200.

Krause, D. W. (1986). Competitive exclusion and taxonomic displacement in the fossil record, the case of rodents and multituberculates in North America. *Rocky Mountain Geology, 24* (special paper 3), 95–117.

Krause, D. W. (2014). Dental morphology of Vintana sertichi (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology, 34(sup1), 137–165.

Krause, D. W., Hoffmann, S., Lyson, T. R., Dougan, L. G, Petermann, H., Tecza, A., Chester, S. G. B., & Miller, I. M. (2020). New skull material of *Taeniolabis taoensis* (Multituberculata, Taeniolabididae) from the Early Paleocene (Danian) of the Denver Basin (Colorado). *Journal of Mammalian Evolution, 28*(4), 1083–1143.1

Kryukova, N., V (2012). Dentition in pacific walrus (*Odobenus rosmarus divergens*) Calves of the year. *Biology Bulletin, 39*(7), 618–626.

Kurtén, B. (1955). Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmüller and Heinroth. *Acta Zoologica Fennica, 90*, 1–46.

Kurtén, B. (1968). *Pleistocene mammals of Europe*. London: Weidenfeld and Nicolson.

Lambert, O., de Muizon, C., Duhame, I., G, & Plicht, J., van der (2018). Neogene and Quaternary fossil remains of beaked whales (Cetacea, Odontoceti, Ziphiidae) from deep-sea deposits off Crozet and Kerguelen islands, Southern Ocean. *Geodiversitas*, *40*(6), 135–160.

Lehmann, T. (2018). Mit oder ohne Stacheln - die Igel Verwandten. In S. F. K. Schaal, K. T. Smith, & J. Habersetzer, *Messel ein fossiles Tropenökosystem* (pp. 234–239). Frankfurt am Main: Senckenberg Gesellschaft für Naturforschung.

Lehmann, T., & Ruf, I. (2018). Das Aufkommen der Paarhufer. In S. F. K. Schaal, K. T. Smith, & J. Habersetzer, *Messel ein fossiles Tropenökosystem* (pp. 285–291). Frankfurt am Main: Senckenberg Gesellschaft für Naturforschung.

Li, C-K., & Ting, S. Y. (1993). New cranial and postcranial evidence for the affinities of the eurymylids (Rodentia) and mimotonids (Lagomorpha). In F. S. Szalay, M. J. Novacek, & M. C. McKenna (Eds.), *Mammal phylogeny Placentals* (pp. 151–158). New York: Springer.

Ligabue-Braun, R., Verli, H., & Carlini, C. R. (2012). Venomous mammals, a review. *Toxicon, 59*(7-8), 680–695.

Lihoreau, F., Blondel, C., Barry, J., & Brune M. (2004). A new species of the genus *Microbunodon* (Anthracotheriidae, Artiodactyla) from the Miocene of Pakistan, genus revision, phylogenetic relationships and palaeobiogeography. *Zoologica Scripta, 33*, 97–115.

Loomis, F. B. (1914). *The Deseado Formation of Patagonia*. Rumford Press.

López-Torres. S., Selig, K. R., Burrows, A. M., Silcox, M. T. (2020). Chapter 6, The Toothcomb of *Karanisia clarki*, was this species an exudate-feeder? In A. I., Nekaris & A. M. Borrows (Eds.), *Evolution, ecology and conservation of lorises and pottos* (pp. 67–75). Cambridge: University Press.

Louys, J. (2015). Wombats (Vombatidae, Marsupialia) from the Pliocene Chinchilla Sand, southeast Queensland, Australia. *Alcheringa, 39*, 394–406.

Lucas, F. A. (1900). A new rhinoceros, *Trigonias osborni*, from the Miocene of South Dakota. *Proceedings of the United States National Museum, 23*, 221–224.

Lucas, S. G. (1986). Pyrothere systematics and a Caribbean route for land-mammal dispersal during the Paleocene. *Revista Geologica de America Central 5*, 1–35.

Lucas, S. G. (1989), *Coryphodon* (Mammalia, Pantodonta) from the Hannold Hill Formation Eocene of Trans-Pecos Texas. *Pearce-Sellards Series, 46*, 1–16.

Lucas, S. G. (1998). Pantodonta. In C. M. Janis, G. F. Gunnell, & M. D. Uhen (Eds.), *Evolution of Tertiary Mammals of North America* (pp. 274–283). Cambridge University Press.

Lucas, S. G. (2001). *Gobiatherium* (Mammalia, Dinocerata) from the Middle Eocene of Asia, Taxonomy and biochronological significance. *Paläontologiasche Zeitschrift, 74*, 591–600.

Lucas, S. G. (2013). The palaeobiogeography of South American gomphotheres. *Journal of Palaeogeography, 2*(1), 19–40.

Lucas, S. G., & Schoch, R. M. (1998a). Tillodontia. In C. M. Janis, K. M. Scott, & L. I. Jacobs (Eds.), *Evolution of Tertiary Mammals of North America* (pp. 268–283). Cambridge University Press.

Lucas, S. G., & Schoch, R. M. (1998b). Dinocerata. In C. M. Janis, K. M.Scott, & L. I. (Eds.), *Evolution of Tertiary Mammals of North America* (pp. 284–291). Cambridge University Press.

Luckett, W. P. (1985). Superordinal and intraordinal affinities of rodents, developmental evidence from the dentition and placentation. In W. P. Luckett & J-L. Hartenberger (Eds.), *Evolutionary relationships among rodents, a multidisciplinary analysis* (pp. 227–276). *NATO ASI Serie A*, 92.

Luckett, W. P. (1993). An ontogenetic assessment of dental homologies in therian mammals. In F. S. Szalay, M. J. Novacek, & M. C. McKenna (Eds.), *Mammal phylogeny, Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials* (pp. 182–204). New York: Springer-Verlag.

Luckett, W. P., & Maier, W. (1986). Developmental evidence for anterior tooth homologies in the Aye *Aye, Daubentonia. American Journal of Physical Anthropology*, 69, 233.

Lydekker, R. (1891). II. On the generic identity of *Sceparnodon* and *Phascolonus. Proceedings of the Royal Society of London*, 49(296-301), 60–64.

Macdonald, A. (2018). Aberrant growth of maxillary canine teeth in male babirusa (genus *Babyrousa*). *Comptes rendus biologies, 341*(4), 245–255.

Macdonald, A., Leus, K., & Hoare, H. (2016). Maxillary canine tooth growth in babirusa (genus *Babyrousa*). *Journal of Zoo and Aquarium Research, 4*(1), 22–29.

MacFadden, B. J., Frailes, C. D. (1984). *Pyrotherium*, a large enigmatic ungulate (Mammalia, incertae sedis) from the Deseadan (Oligocene) of Salla, Bolivia. *Palaeontology, 27*(4), 867–874.

MacPhee, R. D. E., Cartmill, M., & Rose, K. D. (1989). Craniodental morphology and relationships of the supposed Eocene dermopteran *Plagiomene* (Mammalia). *Journal of Vertebrate Paleontology, 9*(3), 329–349.

MacPhee, R. D. E., Del Pino, S., H., Kramarz, A., Forasiepi, A. M., Bond, M., & Sulser, R. B. (2021) Cranial morphology and phylogenetic relationships of *Trigonostylops wortmani*, an Eocene South American Native Ungulate. *Bulletin of the American Museum of Natural History, 449*(1), 1–183.

Maier, W. (1977). *Macrocranion tupaiodon* Weitzel, 1949,– ein igelartiger Insektivor aus dem Eozän von Messel und seine Beziehungen zum Ursprung der Primaten. *Journal of Zoological Systematics and Evolutionary Research, 15*(4), 311–318.

Mao, F., Li, Z., Hooker, & J. J, Meng, J. (2023). A new euharamiyidan, *Mirusodens caii* (Mammalia, Euharamiyida), from the Jurassic Yanliao Biota and evolution of allotherian mammals. *Zoological Journal of the Linnean Society, 2023*, XX, 1–28.

Marivaux, L., Ramdarshan, A., El Mabrouk Essid, Marzougui, W., Ammar, H. K., Lebrun, R., Marandat, Merzeraud, G., Tabuce, R., & Vianey-Liaud, M. (2013). *Djebelemur*, a tiny pre-toothcombed primate from the Eocene of Tunisia, A glimpse into the origin of crown strepsirhines. *PLoS ONE, 2013, 8*(12), e80778.

Marsh, H. (1980). *Age determination of the dugong (Dugong dugon (Muller)) in northern Australia and its biological implications* (pp. 181-201). Zoology Department, James Cook University of North Queensland.

Marsh, O. C. (1875). Notice of new Tertiary mammals, IV. *American Journal of Science, 9*(51), 239–250.

Marsh, O. C. (1886). Dinocerata, a monograph of an extinct order of gigantic mammals. *Monographs of the United States Geological Survey 10*.

Marshall, C. D., Neada, H., Iwata, M-, Furuta. M., Asano, S., & Rosas, F. (2003). Orofacial morphology and feeding behavior of the dugong, Amazonian, West African and Antillean manatees (Mammalia, Sirenia), functional morphology of the muscular-vibrissal complex. *Journal of Zoology, 259*, 245–260.

Marshall, L. D. (1978). Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *University of California Publications in Geological Sciences, 117*, 1–89.

Marshall, L. D. (1980). Functional morphology and the evolution of cats. *Transactions of the Nebraska Academy of Science*, 8, 141–154.

Martin, L. D., Bibiarz, J. P., Naples, V. L., & Hearst, J. (2000). Three ways to be a saber-toothed cat. *Naturwissenschaften, 87*, 41–44.

Martin, L. D, Naples, V. L., Babiarz, J. P. (2008). Cookie-Cutter cats, another saber-toothed morphotype. *Journal of Vertebrate Paleontology, 28*, 112A.

Martin, R. D. (1979). Phylogenetic aspects of prosimian behavior. In G. A. Doyle & R.D. Martin (Eds.), *The study of Prosimian behavior* (pp 45–77). New York: Academic Press.

Martin, R. D. (1981). Well-groomed predecessors. *Nature, 289*, 536–536.

Martin, T. (1992). Schmelzmikrostruktur in den Inzisiven alt- und neuweltlicher hystricognather Nagetiere. *Palaeovertebrata, Mémoire extraordinaire*, 1–168.

McAfee, R. K., & Naples, V. L. (2012). Notice on the occurrence of supernumerary teeth in the two-toed sloths *Choloepus didactylus* and *C. hoffmanni*. *Mastozoología Neotropical*, *19*(2), 339–344.

McCoy, D. E., & Norris, C. A. (2012). The cranial anatomy of the Miocene notoungulate *Hegetotherium mirabile* (Notoungulata, Hegetotheriidae). with preliminary observations on diet and method of feeding. *Bulletin of the Peabody Museum of Natural History, 53*(2), 355–374.

McGhee, G. R. (2011), *Convergent evolution, limited forms most beautiful*. MIT press.

McHenry, C. S., Wroe, S., Clausen, P., Moreno, K., & Cunningham, E. (2007). Supermodeled sabercat, predatory behavior in *Smilodon fatalis* revealed by high-resolution 3D computer simulation. *Proceedings of the National Academy of Sciences*, *104*(41),16010–16015.

McKenna, M. C., & Bell, S. K. (1997). *Classification of mammals: above the species level*. Columbia University Press.

Meachen-Samuels, L., & Binder, W. (2009). Sexual dimorphism and ontogenetic growth in the American lion and sabertoothed cat from Rancho La Brea. *Journal of Zoology, 280*(3), 271–279.

Meehan, T. J., & Martin, L. D. (2004). Emended genus description and a new species of *Hypisodus* (Artiodactyla), Ruminantia, Hypertragulidae). In S. G. Lucas, K. E. Zeigler, & P. E. Kondrashov (Eds.), *Paleogene Mammals. New Mexico Museum of Natural History and Science Bulletin*, *26*, 137–144.

Mein, P. (2003). Über neogene Nagetiere Eurasiens: Verbreitung und Wanderungen. *Deinsea, 10*(1), 407–418.

Meng, J., & Wyss, A. R. (2001). The morphology of *Tribosphenomys* (Rodentiaformes, Mammalia), phylogenetic implications for basal Glires. *Journal of Mammalian Evolution, 8*(1), 1–71.

Meng, J. Hu, Y., & Li, C. (2003). The osteology of *Rhombomylus* (Mammalia, Glires), implications for phylogeny and evolution of Glires. *Bulletin of the American Museum of Natural History, 275*, 1–247.

Métais, G. M., & Vislobolka, I. A. (2007). Basal ruminants. In D. R. Prothero & S. E. Foss (Eds.), *The evolution of artiodactyls* (pp. 189–212), Baltimore: Johns Hopkins University Press.

Mihlbachler, M. C. (2003). Demography of late Miocene rhinoceroses (*Teleoceras proterum* and *Aphelops malacorhinus*) from Florida, linking mortality and sociality in fossil assemblages, *Paleobiology, 29*(3), 412–428.

Miller, G. S (1907). The families and genera of bats. *Bulletin U.S. national Museum Washington 57, 1-282.*

Miller, G. S. (1912). *Catalogue of the mammals of Western Europe*. London: British Museum Natural History.

Mones, A. (1982). An equivocal nomenclature: what means hypsodonty?. *Paläontologische Zeitschrift, 56*(1), 107–111.

Mones. A., & Heintz, N. (1992). *Catalogue of the Conrad Møller collection of Cenozoic mammals from Uruguay*. Paleontological Museum, University of Oslo, No. 375.

Mothé, D. Ferretti, M. P., & Avilla, L. S. (2016). The dance of tusks, Rediscovery of lower Incisors in the PanAmerican proboscidean *Cuvieronius hyodon* revises incisor evolution in Elephantimorpha. *PLoS ONE, 11*(1). e0147009. https://doi.org/10.1371/journal.pone.0147009

Murray, P. F. (1998). Palaeontology and palaeobiology of wombats. In R. T. Wells and P. A. Pridmore (Eds.), *Wombats* (pp. 1–33). Norton, N.S.W: Surrey Beatty and Sons in association with the Royal Zoological Society of South Australia.

Murray, C. G., & Sanson, G. D. (1998). Thegosis-A critical review. *Australian Dental Journal*, *43*(3), 192–198.

Murray, P. F., Megirian, D., Rich, T., Plane, M., Black, K., Archer, M-, Vickers-Rich, P. (2000). Morphology, systematics, and evolution of the marsupial genus *Neohelos stirton* (Diprotodontidae, Zygomaturinae). *Museums and Art Galleries of the Northern Territory Research Report*, *6*(6), 1–141.

Nabavizadeh, A. (2024). Of tusks and trunks, A review of craniofacial evolutionary anatomy in elephants and extinct Proboscidea. *Anatomical Record 2024*, 1–20.

Naples, V. L., Martin, L. D., & Babiarz, J. P. (Eds.), (2011). *The other saber-tooths, scimitar-tooth cats of the Western Hemisphere*. Baltimore: Johns Hopkins University Press.

Nasoori, A. (2020). Tusks, the extra-oral teeth. *Archives of Oral Biology*, *117*, 104835.

Nedin, C. (1991). The dietary niche of the extinct Australian marsupial lion, *Thylacoleo carnifex* Owen. *Lethaia*, *24*(1), 115–118.

Niethammer, J. (1978). Nagetiere 1. *Handbuch der Säugetiere Europas*. Wiesbaden: Akademische Verlagsgesellschaft.

Niethammer, J., & Krapp, F. (1990). *Insektenfresser, Primaten.* Handbuch der Säugetiere Europas 3/1. Wiesbaden: Aula Verlag.

Novacek, M. J. (1986). The skull of leptictid insectivorans and the higher-level classification of eutherian mammals. *Bulletin of the American Museum of Natural History, 183*, 1–112.

Novacek, M. J., Hoffman, E. A., & O'Leary, M. A. (2023). First occurrence of the eutherian mammal *Asioryctes nemegtensis* from the Upper Cretaceous Djadokhta Formation, Gobi Desert, Mongolia, and a revised alpha taxonomy based on the skull and dentition. *Journal of Vertebrate Paleontology 42*(4), e2196320.

Nowak, R. M. (1999). *Walker's mammals species of the world*. Baltimore: Johns Hopkins University Press.

Nweia, M. T., Eichmiller, F. C., Hauschka, P. V., Tyler, E., Mead, J. G., Potter, C. W., Angnatsiak, D. P., Richard, P. R., Orr, J. R., & Black, S. R. (2012). Vestigial tooth anatomy and tusk nomenclature for *Monodon monoceros*. *The Anatomical Record*, *295*, 1006–1016.

Nweia, M. T., Eichmiller, F. C., Hauschka, P. V., Donahue, G. A., Orr, J. R., Ferguson, S. H., Watt, C. A., Mead, J. G., Potter, C. W., Dietz, R., Giuseppetti, A. A., Black, S. R., Trachtenberg, A. J., & Kuo, W. P. (2014). Sensory ability in the narwhal tooth organ system. *Anatomical Record, Advances in Integrative Anatomy and Evolutionary Biology, 297*, 599–617.

O'Leary, M. A., Lucas, S. G., & Williamson, T. E. (2000). A new specimen of *Ankalagon* (Mammalia, Mesonychia) and evidence of sexual dimorphism in mesonychians. *Journal of Vertebrate Paleontology, 20*, 387–393.

O'Leary, M. A., Bloch, J. I., Flynn, J. J., Gaudin, T, J., Giallombardo, A., Giannini, N, P., Goldberg, S. L., Kraatz, B. P., Luo, Z. X, Meng, J., Ni, X., Novakm, M. J., Perini, F. A, Randall, Z. S., Rougier, G. W., Sargis, E. J., Silcox, M. T., Simmons, N. B., Spaudling, M., Vélazco, P. M., Weksler, M., Wible, J. R., & Cirranello, A. L. (2013). The placental mammal ancestor and the post–K-Pg radiation of placentals. *Science*, *339*(6120), 662–667.

Orliac, M. J., Antoine, P-O., & Ducrocq, S. (2010). Phylogenetic relationships of the Suidae (Mammalia, Cetartiodactyla), new insights on the relationships within Suoidea. *Zoologica Scripta*, *39*, 315–330.

Orliac, M. J., Argo, C., & Gilissen, E. (2012). Digital cranial endocast of *Hyopsodus* (Mammalia,"Condylarthra"), a case of Paleogene terrestrial echolocation? *PLoS One,* 7(2), e30000.

Osborn, H. F. (1910). *The age of mammals in Europe, Asia and North America.* New York: Macmillan.

Osborn, H. F. (1936). *Proboscidea*. New York: American Museum Natural History.

Osborn, H. F., Olsen, G (1924). *Andrewsarchus*, giant mesonychid of Mongolia. *American Museum Novitates*, *146*.

Osborn, H. F., & Granger, W. (1932). Coryphodonts and Uintatheres from the Mongolian expedition of 1930. *American Museum novitates, 552*, 1–16.

Owen, R. (1837). A description of the cranium of the *Toxodon platensis*, a gigantic extinct mammiferous species, referable by its dentition to the Rodentia, but with affinities to the Pachydermata and the herbivorous Cetacea. *Proceedings of the Geological Society of London, 2,* 541–542.

Owen, R. (1840-1845). *Odontography.* London: Hippolyte.

Owen, R. (1871). IX. On the fossil mammals of Australia. — Part IV. Dentition and mandible of *Thylacoleo carnifex* , with remarks on the arguments for its herbivory. *Philosophical Transactions of the Royal Society of London 161*, 213–266.

Owen, R. (1872). IX. On the fossil mammals of Australia–Part VI. Genus *Phascolomys*, geoffr. *Philosophical Transactions of the Royal Society of London*, *162*, 173–196.

Palombo, M. R., & Villa, P. (2001). Schreger lines as support in the Elephantidae identification. In G. Cavarretta, P. Gioia, M. Mussi, & M. R. Palombo (Eds.), *The World of Elephants* (pp 656–660), Proceedings of the 1st International Congress. Rome: Consigilio Nazionale delle Ricerche.

Patton, T, H., & Taylor, B, E. (1973). The Protoceratinae (Mammalia, Tylopoda) and the systematics of Protoceratidae. *Bulletin of the American Museum of Natural History, 150*(4), 352–413.

Paula Couto, C. de (1952). Fossil mammals from the beginning of the Cenozoic in Brazil. Marsupialia, Polydolopidae and Borhyaenidae. *American Museum novitates, 1559, 1*–27.

Paula Couto, C. de (1979). *Tradado de Paleomastozoologia.* Rio de Janeiro: Academia Brasiliera de Ciencias.

Peredo, C. M., Peredo, J. S., & Pyenson, N. D. (2018). Convergence on dental simplification in the evolution of whales. *Paleobiology, 44*(3), 434–443.

Poduschka, V. W., & Poduschka, C. (1985). Beitrage zur Kenntnis der Gattung *Podogymnura* Mearns 1905 (Insectivora, Echinosoricinae). *Zeitschrift für Säugetierkunde*, *50*, 1–21.

Powell, R., & Mariscal, C. (2014). There is grandeur in this view of life, the bio-philosophical implications of convergent evolution. *Acta Bitheroretica, 62*, 113–121.

Prideaux, G. J., & Warburton, N. M. (2010). An osteology-based appraisal of the phylogenyand evolution of kangaroos and wallabies (Macropodidae, Marsupialia). *Zoological Journal of the Linnean Society, 159*, 954–987.

Prothero, D. R. (1998a). Oromerycidae. In C. M. Janis, K. M. Scott, & J. L. Jacobs (Eds.), *Evolution of Tertiary mammals of North America*, Vol. 1, (pp. 426-430), Cambridge University Press.

Prothero, D. R. (1998b). Rhinocerotidae. In C. M. Janis, K. M. Scott, & J. L. Jacobs (Eds.), *Evolution of Tertiary Mammals of North America*, Vol. 1, (pp. 595–605), Cambridge University Press.

Prothero, D. R. (2007). Family Moschidae. In D. R. Prothero & S. E. Foss (Eds.), (2007). *The evolution of artiodactyls,* (pp. 221–226), Baltimore: Johns Hopkins University Press.

Prothero, D. R. & Foss, S. E. (Eds.) (2007). The evolution of artiodactyls. Baltimore: Johns Hopkins University Press.

Prothero, D. R. Ludtke, J. A. (2007). Family Protoceratidae. In D. R. Prothero & D. E. Foss (Eds.), *The evolution of artiodactyls* (pp. 169–176). Baltimore: Johns Hopkins University Press.

Prothero, D. R., & Schoch, R. M. (2003). *Horns, tusks, and flippers. The evolution of hoofed mammals.* Baltimore: Johns Hopkins University Press.

Qiu, Z., & Storch, G. (2005). The fossil record of the Eurasian Neogene insectivores (Erinaceomorpha, Soricomorpha, Mammalia), Part I.: China. *Scripta Geologica. Special Issue, 5*, 37–50.

Radinsky, L. B. (1963). Origin and early evolution of North American Tapiroidea. *Peabody Museum of Natural History, Yale University, Bulletin 17.*

Radinsky, L. B. (1965). Evolution of the tapiroid skeleton from *Heptodon* to *Tapirus*. *Bulletin of the Museum of Comparative Zoology*, *134*(3), 69–106.

Radinsky, L. B. (1966). The families of the Rhinocerotoidea (Mammalia, Perissodactyla). *Journal of Mammalogy*, *47*(4), 631–639.

Radinsky, L. B. (1967). *Hyrachyus, Chasmotherium* und die frühe Evolution der Helaletiden-Tapiroidea. *American Museum Novitates, No. 2313.*

Radinsky, L. B. (1984). Ontogeny and phylogeny in horse skull evolution. *Evolution 38*(1), 1–15.

Redford, K. H. (1985). Feeding and food preference in captive and wild giant anteaters (*Myrmecophaga tridactyla*). *Journal of* Zoology *205*(4), 559–572.

Reguero, M., & Cerdeno, E. (2005) New Late Oligocene Hegetotheriidae (Mammalia, Notoungulata) from Salla, Bolivia. *Journal of Vertebrate Paleontology, 25*, 674–684.

Reinhardt, J. T. (1879). Description of the skull of a giant sloth, *Grypotherium darwini. Videnskavernes Selskabs Skrifter, 5*, 351–381.

Remy, J-A. (1992). Observations sur l'anatomie crânienne du genre *Palaeotherium* (Perissodactyla, Mammalia), mise en évidence d'un nouveau sous-genre, *Franzenitherium. Palaeovertebrata, 21*(3-4), 203–224.

Renevier, E. (1879). Les *Anthracotherium* de Rochette. *Bulletin de la Société Vaudienne de Sciences Naturelles, 16*, 140–148.

Repenning, C. A. (1967). Subfamilies and genera of the Soricidae. *Geol. Surv. Professional papers* 565.

Rich, T. H., & Rich, P. V. (1971). *Brachyerix*, a Miocene hedgehog from western North America, with a description of the tympanic regions of *Paraechinus* and *Podogymnura. American Museum novitates 2477.*

Ride, W. D. (1962). On the- evolution of Australian Marsupials. In G. W. Leeper (1962). *The evolution of living organisms* (pp.281–306). Melbourne: University Press.

Riggs, E. S. (1934). A new marsupial saber-tooth from the Pliocene of Argentina and its relationships to other South American predacious marsupials. *Transactions of the American Philosophical Society*, *24*(1), 1–32.

Riggs, E. S. (1935). A skeleton of *Astrapotherium. Geological Series 6* (13), 167–176. Chicago*:* Field Museum of Natural History.

Rivals, F., Prilepskaya, N. E., Belyaev, R. I., & Pervushov, E. M. (2020). Dramatic change in the diet of a late Pleistocene *Elasmotherium* population during its last days of life, Implications for its catastrophic mortality in the Saratov region of Russia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *556*, 109898.

Rofes, J., Cuenca-Bescos, G. (2009) A new genus of red-toothed shrew (Mammalia, Soricidae) from the Early Pleistocene of Gran Dolina (Atapuerca, Burgos, Spain), and a phylogenetic approach to the Eurasiatic Soricinae. *Zoological Journal of the Linnean Society*, *155*(4), 904–925.

Romer, A. S., Frick, H., & Starck, D. (1966). *Vergleichende Anatomie der Wirbeltiere*. Hamburg: P. Parey.

Rose, K. D. (1973). The mandibular dentition of *Plagiomene* (Dermoptera, Plagiomenidae). *Breviora, 411*, 1–17.

Rose, K. D (1982). Anterior dentition of the early Eocene plagiomenid dermopteran *Worlandia. Journal of Mammalogy*, *63*(1), 179–183.

Rose, K. D. (2006). *The beginning of the age of mammals* (pp. 1–428). Baltimore: Johns Hopkins University Press.

Rose, K. D. (2008). Palaeanodonta and pholidota. In P. D. Polly (Ed.), *Evolution of Tertiary mammals of North America, Volume 2, small Mammals, xenarthrans, and marine mammals* (pp. 135–146). Cambridge University Press.

Rose, K. D., & Archibald, J. D. (2005). *The rise of placental mammals, origins and relationships of the major extant clades* (pp. 1–239). Baltimore: Johns Hopkins University Press.

Rose, K. D., & Koenigswald, W. von (2005). An exceptionally complete skeleton of *Palaeosinopa* (Mammalia, Cimolesta, Pantolestidae) from the Green River Formation, and other postcranial elements of the Pantolestidae from the Eocene of Wyoming. *Palaeontographica, A273*, 55-96.

Rose, K. D., Walker, A., & Jacobs, L. L. (1981). Function of the mandibular tooth comb in living and extinct mammals. *Nature*, *289*(5798), 583–585.

Rose, K. D., Emry, R. J., & Gingerich, P. D. (1992). Skeleton of *Alocodontulum atopum*, an early Eocene epoicotheriid (Mammalia, Palaeanodonta) from the Bighorn basin, Wyoming. *Contributons from the Museum of Paleontology. The University of Michigan,* 28, 221–245.

Rose, K. D., Beard, K., C., & Houde, P. (1993). Exceptional new dentitions of the diminutive plesiadapiforms *Tinimomys* and *Niptomomys* (Mammalia), with comments on the upper incisors of Plesiadapiformes. *Annals of Carnegie Museum, 62*(4), 351–361.

Rosenberger, A. L., & Strasser, E. (1985). Toothcomb origins: support for the grooming hypothesis. *Primates, 26*(1), 73–84.

Rössner, G. E. (2007). Family Tragulidae. In D. R. Prothero & S. E. Foss (Eds.), *The evolution of artiodactyls* (pp.213–220). Baltimore: Johns Hopkins University Press .

Rössner, G. E. (2010). Systematics and palaeoecology of Ruminantia (Artiodactyla, Mammalia) from the Miocene of Sandelzhausen (southern Germany, northern Alpine Foreland basin). *Paläontologische Zeitschrift, 84*, 123–162.

Roth, C. (1985) Kauzyklus und Usurfacetten von *Microchoerus* WOOD, 1844 (Omomyiformes, Primates). *Mainzer Geowissenschaftliche Mitteilungen, 14*, 287–306.

Russel, D. E. (1964). *Les mammifères paléocènes d'Europe* (pp. 1-324). Muséum national d'Histoire naturelle. Serie C, Sciences de la Terre, 13.

Sahni, A., & Koenigswald, W. von (1997). The enamel structure of some fossil and recent whales from the Indian subcontinent. In W. v. Koenigswald, & P. M. Sander (Eds.), *Tooth Enamel Microstructure* (pp. 177–191). Rotterdam: Balkema.

Salas-Gismondi, R., Ochoa, D., Gamarra, J., Pujos, F., Foster, D. A., &, Tejada, J. V. (2023). Pliocene pre-GABI herbivorous mammals from Espinar, Peruvian Andean plateau. *Journal of Vertebrate Paleontology, 43*(1), e2237079.

Sanders, W. J., Rasmussen, D. T., & Kappelmann, J. (2010a), Embrithopoda. In L. Werdelin & W. J. Sanders (Eds.), *Cenozoic mammals of Africa* (pp. 115–122). Berkeley, London, New York: University of California Press.

Sanders, W. J., Gheerbrant, E., Harris, J. M., Saegusa,H., & Delmer, C. (2010b). Proboscidea. In L. Werdelin & W. J. Sanders (Eds.), *Cenozoic mammals of Africa* (pp. 161–251). Berkeley, London, New York: University of California Press.

Savage, D. E., Russell, D. E., & Louis, P. (1965). *European Eocene Equidae (Perissodactyla)*. University of California Press.

Schmidt, W. J. (1940). Polarisationsoptische Untersuchung des Zahnbeins von *Orycteropus*. *Zeitschrift für Zellforschung und Mikroskopische Anatomie Abt. A, 30*, 598–614.

Schoch, R. M. (1986). Systematics, functional morphology and macroevolution of the extinct mammalian order Taeniodonta. *Yale University Peabody Museum of Natural History Bulletin, 42*, 1–307.

Schoch, R. M., & Lucas, S. G. (1985). The phylogeny and classification of the Dinocerata (Mammalia, Eutheria). *Bulletin of the Geological Institutions of the University of Uppsala, 11*, 31–58.

Schultz, A. H. (1971) Die Primaten. *Die Enzyklopedie de Natur*. Lausanne: Editions Rencontre.

Schultz, C. B., & Falkenbach, C. H. (1968). The phylogeny of the oreodonts. *Bulletin of the American Museum of Natural History, 139*.

Schultz, C. B., Martin, L. D., & Corner, R. G. (1975). Middle and Late Cenozoic Tapirs from Nebraska. (1975). *Bulletin of the University of Nebraska State Museum*, 100.

Schwartz, J. H. (1974). Observations on the dentition of the Indriidae. *American Journal of Physical Anthropology, 41*(1), 107–114.

Scott, W. B. (1887). Preliminary account of the fossil mammals from the White River Formations. *Bulletin of the Museum of Comparative Zoology, 13*, 165–169.

Scott, W. B. (1891). On the osteology of *Mesohippus* and *Leptomeryx* with observations on the modes and factors of evolution in the Mammalia. *Journal of Morphology, 5*, 301–466.

Scott, W. B. (1909-1928). *Reports of the Princeton University expeditions to Patagonia 1896–1899*. Princeton University.

Scott, W. B. (1910). Mammalia of the Santa Cruz Breds. Part I, Litopterna. *Reports of the Princeton University Expeditions to Patagonia, 1896–1899, 1* (pp. 1–156). Princeton University.

Scott, W. B. (1912). Mammalia of the Santa Cruz Breds. Part II, Toxodonta, Entelonychia, Astrapotheria. *Reports of the Princeton University Expeditions to Patagonia, 1896–1899, 6*, 111–238. Princeton University.

Scott, W. B. (1937). The Astrapotheria. *Proceedings of the American Philosophical Society*, 309–393.

Scott, W. B. (1940). The mammalian fauna of the White River Oligocene. Part IV, Artiodactyla, *Transactions of the American Philosophical Society, 28*, 524–537.

Scott, W. B., Jepsen, G. L. (1940). The mammalian fauna of the White River Oligocene, Part IV. Artiodactyla. *Transactions of the American Philosophical Society, 28*(4), 363–746.

Seiffert, E. R., Simons, E. L., &, Attia, Y. (2003). Fossil evidence for an ancient divergence of lorises and galagos. *Nature, 422*(6930), 421–424.

Sharp, A. C. (2014). Three-dimensional digital reconstruction of the jaw adductor musculature of the extinct marsupial giant *Diprotodon optatum*. *PeerJ, 2*, e514.

Shoshani, J., & Tassy, P. (Eds.) (1996). *The Proboscidea. Evolution and palaeoecology of the elephants and their relatives*. Oxford, New York, Tokyo: Oxford University Press.

Silcox, M. T., Bloch, J. I., Boyer, D. M., & Houde, P. (2010). Cranial anatomy of Paleocene and Eocene Labidolemur kayi (Mammalia: Apatotheria), and the relationships of the Apatemyidae to other mammals. Zoological Journal of the Linnean Society, 160(4), 773–825.

Simons, E. L. (1960). The Paleocene Pantodonta. *Trans American Philosophical Society 50*(6), 3–99.

Simpson, G. G. (1931). *Metacheiromys* and the Edentata. *Bulletin of the American Museum of Natural History, 59*, 295–381.

Simpson, G. G. (1932a). Enamel on the teeth of an Eocene edentate. *American Museum novitates 567*, 1–4.

Simpson, G. G. (1932b). Skulls and brains of some mammals from the *Notostylops* beds of Patagonia. *American Museum novitates, 578.*

Simpson, G. G. (1933). The" plagiaulacoid" type of mammalian dentition a study of convergence. *Journal of Mammalogy, 14*(2), 97–107.

Simpson, G. G. (1941). The function of saber-like canines in carnivorous mammals. *American Museum novitates, 1130*.

Simpson, G. G. (1948). The beginning of the age of mammals in South America. Part 1, Introduction, Systematics, Marsupialia, Edentata, Condylarthra, Litopterna and Notioprogonia. *Bulletin of the American Museum Natural History, 91*(1).

Simpson, G. G. (1960). The beginning of the age of mammals in South America. *Bulletin of the American Museum Natural History, 137*, 1–259.

Simpson, G. G. (1970). The Argyrolagidae, extinct South American marsupials. *Bulletin of the Museum of Comparative Zoology, 139*, 1–86.

Simpson, G. G., Granger, W., & Wortman, J. L. (1931). *Metacheiromys* and the Edentata. *Bulletin of the American Museum Natural History, 59*, 297–380.

Sinclair, W. J. (1908). The Santa Cruz Typotheria. *Proceedings of the American Philosophical Society, 47*(188), 64–78.

Sinclair, W. J. (1909). Mammalia of the Santa Cruz Beds, Typotheria. In W. B. Scott (Ed.), *Reports of the Princeton University Expeditions to Patagonia, 1896–1899*. Princeton University.

Smith, T., & Codrea, V. (2015). Red iron pigmented tooth enamel in a Multituberculate – Mammal from the Late Cretaceous Transylvanian "Haţeg Island". *PLoS One*, *10*(7), e0132550.

Soibelzon, E., Zurita, A. E., & Carlini, A. A. (2006). *Glyptodon munizi* Ameghino (Mammalia, Cingulata, Glyptodontidae), redescripción y anatomía. *Ameghiniana*, *43*(2), 377–384.

Sorenson, M. W. (1970). Behavior of tree shrews. *Primate behavior, developments in field and laboratory research*, *1*, 141–194.

Spaulding, M., O'Leary, M. A., & Gatesy, J. (2009). Relationships of Cetacea (Artiodactyla) among mammals, increased taxon sampling alters interpretations of key fossils and character evolution. *PloS One*, *4*(9), e7062.

Stafford, B. J., & Szalay, F. S. (2000). Craniodental functional morphology and taxonomy of dermopterans. *Journal of mammalogy*, *81*(2), 360–385.

Strait, S. G. (2001). Dietary reconstruction of small-bodied omomyoid primates. *Journal of Vertebrate Paleontology*, *21*(2), 322–334.

Stehlin, H. G. (1910). Zur Revision der Europäischen Anthracotherien. *Verhandlungen der Naturforschenden Gesellschaft zu Basel, 21*, 165–185.

Stevens, M. S, & Stevens. J. B. (2007). Family Merycoidodontidae. In D. R. Prothero & S. E. Foss (Eds.), *The evolution of artiodactyls* (pp.157–168). Baltimore: Johns Hopkins University Press.

Stirling, E. C., & Zietz, A. H. C. (1913). *Fossil remains of Lake Callabonna*. Adelaide: W. C. Rigby.

Storch, G., Lister, A. (1985). *Leptictidium nasutum* – ein Pseudorhyncocyonide aus dem Eozän der Grube Messel bei Darmstadt (Mammalia, Proteutheria). *Senckenbergiana lethaea, 66*, 1–37.

Storch, G., & Qiu, Z. (2004). First complete heterosoricine shrew, a new genus and species from the Miocene of China. *Acta Palaeontologica Polonica*, *49*(3), 357–363.

Szalay, F. S. (1976). Systematik der Omomyidae (Tarsiiformes, Primaten): Taxonomie, Phylogenie und Anpassungen. *Bulletin of the American Museum of Natural History 156*, article 3.

Szalay, F., & Seligmann, D. (1977). Why did the strepsirhine tooth comb develop? *Folia Primatologica, 27*, 75–82.

Tassy, P. (1987). A hypothesis on the homology of proboscidean tusks based on paleontological data. *American Museum Novitates, 2895*, 1–28.

Tate, G. H. H. (1947). On the anatomy and classification of the Dasyuridae (Marsupialia). *Bulletin of the American Museum Natural History, 88*, 97–156.

Tattersall, I. (2006). Chapter 1, Origin of the Malagasy strepsirhine primates. In L. Gould, & M. L. Sauther (Eds.), *Lemurs, ecology and adaptation* (pp. 3–20). Springer, ISBN 978-0-387-34585-7.

Taylor, B. E., & Webb, S. D. (1976). Miocene Leptomerycidae (Artiodactyla, Ruminantia) and their relationships. *American Museum Novitates, 2596*, 1–159.

Tedford, R. H. (2002). The basicranium of the giant wombat *Phascolonus gigas* Owen (Vombatidae, Marsupialia) and its significance in phylogeny. *Smithsonian Contributions to Paleobiology*, *93, 39*–47.

Thenius, E. (1969). *Phylogenie der Mammalia, Stammesgeschichte der Säugetiere* [einschliessl. d. Hominiden]. Berlin: de Gruyter.

Thenius, E. (1989). Zähne und Gebiss der Säugetiere. *Handbuch der Säugetiere (Mammalia), 8*, 56.

Thewissen, J. G. M., & Gingerich, P. D. (1987). Systematics and evolution of *Probathyopsis* (Mammalia, Dinocerata) from the Late Paleocene and Early Eocene of Western North America. *Contributions from the Museum of Paleontology, University of Michigan*, *27*, 195–219.

Thorpe, M. R. (1937) The Merycoidodontidae an extinct group of mammals. *Memoires Peabody Museum Natural History, 3*(4), 1–428.

Tissier, J., Antoine, P-O., & Becker, D. (2020) New material of *Epiaceratherium* and a new species of *Mesaceratherium* clear up the phylogeny of early Rhinocerotidae Perissodactyla. *Royal Society Open Science 7*(7), 200633.

Tobien, H. (1980). Ein anthracotherioider Paarhufer (Artiodactyla, Mammalia) aus dem Eozän von Messel bei Darmstadt (Hessen). *Geologisches Jahrbuch Hessen*, *113*, 5–58.

Tobien, H. (1985). Zur Osteologie von *Masillabune* (Mammalia, Artiodactyla, Haplobunodontidae) aus dem Mitteleozän der Fossilfundstätte Messel bei Darmstadt (S-Hessen, Bundesrepublik Deutschland). *Geologisches Jahrbuch Hessen*, *113*, 5–58.

Tsoukala, E., & Mol, D. (2016). The Proboscidea of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Quaternary International 406*, 4–24.

Tsubamoto, T. (2010). Recognition of *Microbunodon* (Artiodactyla, Anthracotheriidae) from the Eocene of China. *Paleontological Research*, *14*(2), 161–165.

Turnbull, W. D. (1978). Another look at dental specialization in the extinct saber-toothed marsupial, *Thylacosmilus*, compared with its placental counterparts. In P. Butler, J. Milton, & A, Kenneth (Eds.), *Development, function and evolution of teeth* (pp. 399–414). New York, London: Academic Press.

Turnbull, W. D. (2002). The mammalian faunas of the Washakie Formation, Eocene Age, of Southern Wyoming. Part IV. The Uintatheres. *Fieldiana, 47*, 1–189.

Turnbull, W. D. (2004). Taeniodonta of the Washakie Formation, southwestern Wyoming. *Bulletin of the Carnegie Museum of Natural History*, *36*, 302–333.

Uhen, M. D. (2004). Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea), an archaeocete from the middle to late Eocene of Egypt. *Paleontogical Papers*, *34*, 1–222. Baltimore: University of Michigan.

Uhen, M. D., & Gingerich, P. D. (1995). Evolution of *Coryphodon* (Mammalia, Pantodonta) in the Late Paleocene and Early Eocene of northwestern Wyoming. *Contributions from the museum of Paleontology*. Baltimore: University of Michigan.

Ungar, P. S. (2010). *Mammal teeth, origin, evolution, diversity*. Baltimore: Johns Hopkins University Press.

Van Valkenburgh, B., & Sacco, T. (2002). Sexual dimorphism, social behavior, and intrasexual competition in large Pleistocene carnivorans. *Journal of Vertebrate Paleontology*, *22*(1), 164–169.

Vierhaus, H. (1983). Wie Vampirfledermäuse (*Desmodus rotundus*) ihre Zähne schärfen. *Zeitschrift für Säugetierkunde*, *48*(5), 269–277.

Villier, B., & Carnevale, G. (2013), A new skeleton of the giant hedgehog *Deinogalerix* from the Miocene of Gargano, southern Italy. *Journal of Vertebrate Paleontology*, *33*(4), 902–923.

Virag, A. (2012). Histogenesis of the unique morphology of proboscidean ivory. *Journal of Morphology, 273*, 1406–1423.

Viret, J. (1938). Étude sur quelques Erinacéidés fossiles spécialement sur le genre *Palaerinaceus*. *Travaux et Documents des Laboratoires de Géologie de Lyon, 34*(28), 1–32.

Vislobokova, I. A. (2001). Evolution and classification of Tragulina (Ruminantia, Artiodactyla). *Paleontological Journal*, *35*(2), 69–145.

Vislobokova, I. A., & Trofimov, B. A. (2002). *Archaeomeryx* (Archaeomerycidae, Ruminantia), morphology, ecology, and role in the evolution of the Artiodactyla. *Paleontological Journal ISSNL, 36, Suppl5*.

Vizcaíno, S. F. (2009). The teeth of the "toothless", novelties and key innovations in the evolution of xenarthrans (Mammalia, Xenarthra). *Paleobiology*, *35*(3), 343–366.

Wahlert, J. H. (1968), Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and recent rodent groups. *Breviora, Museum Comparative Zoology, 309*, 1–18.

Wall, C., & Krause, D. W. (1992). A biomechanical analysis of the masticatory apparatus of *Ptilodus* (Multituberculata). *Journal of Vertebrate Paleontology*, *12*(2), 172–187.

Wall, W. P., & Hauptman, J. A. (2001). A craniodental interpretation of the dietary habits of *Poebrotherium wilsoni* (Camelidae) from the Oligocene of Badlands National Park, South Dakota. In V. Santucci & L. McClelland (Eds.), *Proceedings of the 6th Fossil Resource Conference* (pp. 76–82), *Geologic Resources Division Technical Report NPS/NRGRD/GRDTR-01/01).*

Wall, W. P., & Heinbaugh, K. L. (1999). Locomotor adaptations in *Metamynodon planifrons* compared to other amynodontids (Perissodactyla, Rhinocerotoidea). *National Parks Paleontological Research, 4*, 8–17.

Wang, H., Bai, B., Meng, J., & Wang, Y. (2016). Earliest known unequivocal rhinocerotoid sheds new light on the origin of Giant Rhinos and phylogeny of early rhinocerotoids. *Scientific reports, 6*(1), 39607.

Webb, S. D., & Taylor, B. E. (1980). The phylogeny of hornless ruminants and a description of the cranium of *Archaeomeryx*. *Bulletin of the American Museum of Natural History, 167*, 1–157.

Werdelin, L. (2024). Hypercanines, not just for sabertooths. *The Anatomical Record, 1-12*. https://doi.org/10.1002/ar.25510

Werdelin, L., Yamaguchi, N., Johnson, W. E., & O'Brien, S. J. (2010). Phylogeny and evolution of cats (Felidae). *Biology and conservation of wild felids*, 59–82.

Wheeler, W. H. (1961). Revision of the Uintatheres. *Bulletin of the Peabody Museum of Natural History Yale University, 14*, 1–93.

Wible, J. R. (2008). On the cranial osteology of the Hispaniolan Solenodon, *Solenodon paradoxus* Brandt, 1833 (Mammalia, Lipotyphla, Solenodontidae). *Annals of Carnegie Museum, 77*, 321–402.

Wible, J. R., & Rougier, G. W. (2000). Cranial anatomy of *Kryptobaatar dashzevegi* (Mammalia, Multituberculata), and its bearing on the evolution of mammalian characters. *Bulletin of the American Museum of Natural History, 247*, 1–120.

Wible, J. R., Rougier, G. W., Novacek, M. J., & Asher, R. J. (2009). The eutherian mammal *Maelestes gobiensis* from the Late Cretaceous of Mongolia and the phylogeny of Cretaceous Eutheria. *Bulletin of the American Museum of Natural History, 327*, 1–123.

Wortman, J. L .(1898). The extinct Camelidae of North America and some associated forms. *Bulletin of the American Museum of Natural History, 10*(7).

Wroe, S., & Musser, A. (2001). The skull of *Nimbacinus dicksoni* (Thylacinidae, Marsupialia). *Australian Journal of Zoology, 49*(5), 487–514.

Wroe, S., McHenry, C., & Thomason, J. (2005). Bite club, comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society B, Biological Sciences, 272*(1563), 619–625.

Zhou, X., Zhai, R., Gingerich, P.D., & Chen, L. (1995). Skull of a new mesonychid (Mammalia, Mesonychia) from the late Paleocene of China. *Journal of Vertebrate Paleontology, 15*(2), 387–400.

Ziegler, A. C. (1971). A theory of the evolution of therian dental formulas and replacement patterns. *Quarterly Review of Biology, 46*, 226–249.

Zimicz, A. N., & Goin, F. J. (2020). A reassessment of the genus *Groeberia* Patterson, 1952 (Mammalia, Metatheria), functional and phylogenetic implications. *Journal of Systematic Palaeontology, 18*(12), 975–992.

Zingeser, M. R. (1969). Cercopithecoid canine tooth honing mechanisms. *American Journal of Physical Anthropology, 31*(2), 205.

Zittel, K. (1897). *Handbuch der Palaeontologie 1. Abteilung, Palaeozoologie. IV, Vertebrata* (pp 1–799). München: R. Oldenburg.