



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

Incus facet morphology in carnivorous mammals from different ecosystems: Taxonomy vs. habitat



Morphologie des facettes de l'enclume chez des mammifères carnassiers d'écosystèmes différents : taxonomie vs. habitat

Katharina Bastl^{a,b,*}, Doris Nagel^a, Floréal Solé^c^a Institut für Paläontologie, Universität Wien, Althanstraße 14, 1090 Vienna, Austria^b HNO-Klinik, Medizinische Universität Wien, Forschungsgruppe Aerobiologie und Polleninformation, Währinger Gürtel 18–20, 1090 Wien, Austria^c Directorate Earth and History of life, Royal Belgian Institute of Natural Sciences, rue Vautier 29, 1000 Brussels, Belgium

ARTICLE INFO

Article history:

Received 14 June 2016

Accepted after revision 25 November 2016

Available online 6 March 2017

Handled by Lars vanden Hoek OPstende

Keywords:

Carnivora

Hyaenodon

Incus

Incudo-malleolar facets

Mots clés :

Carnivores

Hyaenodon

Incus

Facettes incudo-malléaires

ABSTRACT

This study is prompted by the discovery of an incus of *Hyaenodon*, the first known auditory ossicle of this genus and thus of any hyaenodont mammal so far. A large set of incudes of recent Carnivora, including felids, hyaenids, viverrids, herpestids, nandiniid and canids of different ecosystems, was set up for morphological comparison. This study examines especially the incudo-malleolar facet. Typically, the incudo-malleolar facet is composed of: (1) three articular surfaces in felids, (2) a U-shaped surface in hyaenids and (3) four surfaces in canids. Both taxonomy (on family level) and habitat (open, closed or mixed habitat preference) might have an impact on the morphology of the incus facets, the former having a major impact in our sample. The *Hyaenodon* incus is small, delicate and possesses an incudo-malleolar facet of a general saddle-shape with two articulation facets, a large superior articulation area and a circular, inferior articulation area. Herein, its general morphology and facet shape is most similar to the felid incus morphology.

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R É S U M É

La découverte d'une enclume de *Hyaenodon*, le premier osselet auditif connu à ce jour pour ce genre et, de manière plus générale, pour les mammifères hyaenodontes, est à l'origine de la présente étude. La morphologie de l'enclume a été étudiée et comparée chez un large ensemble de carnivores récents (félidés, hyaenidés, viverridés, herpestidés, nandiniid et canidés) provenant d'écosystèmes variés. Cette étude s'intéresse tout particulièrement à la facette incudo-malléaire. En règle générale, la facette incudo-malléaire est composée de : (1) trois surfaces articulaires chez les félidés, (2) une surface en forme de U chez les hyaenidés et (3) quatre surfaces chez les canidés. Les facteurs taxonomiques (au niveau familial) et environnemental (milieu ouvert, fermé ou mixte) semblent avoir tous deux un impact sur la morphologie de l'enclume, le premier facteur ayant un impact plus important,

* Corresponding author. Institut für Paläontologie, Universität Wien, Althanstraße 14, 1090 Vienna, Austria.
E-mail address: katharina.bastl@meduniwien.ac.at (K. Bastl).

sur la base de notre échantillon. L'enclume de *Hyaenodon* est petite, délicate, et possède une facette incudo-malléaire en forme de selle avec deux facettes d'articulation, l'articulation supérieure possédant une grande surface, tandis que la zone d'articulation inférieure est circulaire. Au sein de notre échantillon, sa morphologie globale ainsi que la forme de sa facette se rapprochent de celles des félidés.

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1. Introduction

The incus of *Hyaenodon* described and compared herein is the first known auditory ossicle of the extinct group Hyaenodonta and thus of special interest due to its current uniqueness. This fossil specimen is affiliated with the species *Hyaenodon exiguus* from the Oligocene of Quercy (Lange-Badré, 1979). *Hyaenodon* was a successful predator of its time, distributed in North America, Europe and Asia from the late Eocene up into the beginning of the Miocene (Bastl et al., 2011; Lange-Badré, 1979; Mellett, 1977; Tsubamoto et al., 2008; Wang et al., 2005) and known for its carnivorous specialization (Bastl et al., 2012). It belongs to the order Hyaenodonta, that was formerly united with the family Oxyaenidae (now Oxyaenodonta) in the “Creodonta” (Solé, 2013); “Creodonta” was seen as sister group to Carnivora.

This study examines the morphology of the incudo-malleolar facets in different carnivoran taxa and one hyaenodont specimen of different habitats. There is a strong need for an increase in knowledge about especially such small elements, which exist in the fossil record, but receive up to now little attention. Thus, we provide here a first comparative dataset for taxa of Carnivora and Hyaenodonta as well as a guideline in possible analyses of the incus.

The auditory ossicles are also called ossicula auditus or tympani (Sarrat et al., 1988) and comprise the malleus (hammer), the incus (anvil) and the stapes (stirrup). The auditory ossicle chain serves for mechanical transmission and increases the sound pressure at the entrance to the inner ear (Toth and Csillag, 2005). The chain is connected via synovial joints and held in position by ligaments (Toth and Csillag, 2005). The tensor tympani muscle is connected to the manubrium of the malleus and the stapedia muscle to the stapes. The latter protects the middle ear from loud noises. The topology of the incus only is described in the present work, based on the canid incus (Getty, 1964) with general information from the human medical literature (Gulya, 2007; Toth and Csillag, 2005). The incus (Fig. 1) consists of the body, the articulation facet named the incudo-malleolar facet, the long and short processes and the lenticular process (Gulya, 2007). Due to the saddle-shaped articulation between the malleus and the incus, the latter is matched to the movements of the former (Gulya, 2007). The body of the incus shows the articulation area consisting of facets for the malleus (Gulya, 2007; Toth and Csillag, 2005). The incus body is situated in the epitympanic recess, with the short crus (short process, crus breve) connected via the posterior ligament to the fossa incudis (a depression in the posterolateral wall of the tympanic cavity; Toth and Csillag, 2005; = the posterior incudal recess in Gulya,

2007) and the crus longum extending into the tympanic cavity. The crus longum (long process, crus longum) articulates with the head of the stapes (Toth and Csillag, 2005). The long process ends in the lenticular process, which provides a convex surface for the concave head of the stapes (Gulya, 2007). The apophysis is fused to the end of the crus longum by means of a pedicle and then forms the processus lenticularis (Getty, 1964). The incus and most of the malleus are first branchial arch derivatives (Meckel's cartilage; O'Gorman, 2005). The superior ligament connects the body of the incus to the epitympanic recess (contra Gulya, 2007). More information of the evolutionary history of the middle ear is summarized in Maier and Ruf (2016).

The malleus and, especially, the malleus head including the facet has been more of a focus in previous studies than the incus, also in carnivorous samples (Fleischer, 1973, 1978; Segall, 1943). Auditory ossicles in Carnivora were subject to both phylogenetic (Hunt, 1991; Salles, 1992) and ecomorphological/functional studies (Fleischer, 1978; Huang et al., 2002; Puria and Steele, 2008; Solntseva, 2007). So far, only the projection of the head on the incus, various features on the malleus and the arrangement of the whole auditory ossicle chain were recognised to be of phylogenetic value (Hunt, 1991; Salles, 1992). Besides Holz (1931), Willi et al. (2002) worked on the topic of the incudo-malleolar joint, which is a synovial joint. That is a joint that is most mobile, with the union of the bones being surrounded by an articular capsule and the articulation areas covered by cartilage including the presence of synovial fluid. Willi et al. (2002) found that movement occurs at this joint. The most important vibrational component of the ossicular chain is the rotation around the axis through the short process of the incus and the head of the malleus. Relative motion in the incudo-malleolar joint occurs at 1–3 kHz (Willi et al., 2002; studied in humans). It is suggested that flexibility reduces the transmission of sound energy and protects the inner ear from high amplitude displacements (Mason and Farr, 2013). Summarizing, we assume that the incus underlies more phylogenetical than ecological constraints, which is the hypothesis tested in this study.

Herein, we test whether habitat or taxonomy has a stronger impact on the incus morphology, namely on the incudo-malleolar facets. We used the incus in this study because this auditory ossicle (1) seems to show less intraspecific variation than the other two ossicles (Sarrat et al., 1988), (2) is characteristic for every species and the incudo-malleolar complex shows little inter-individual variability in carnivores, artiodactyls and perissodactyls (Holz, 1931), (3) is important for phylogenetic reconstructions, because the ontogeny of this bone is up to now described as an undisturbed expression of basic controlling genetic factors (Rak and Clarke, 1979) and (4) the incus was the

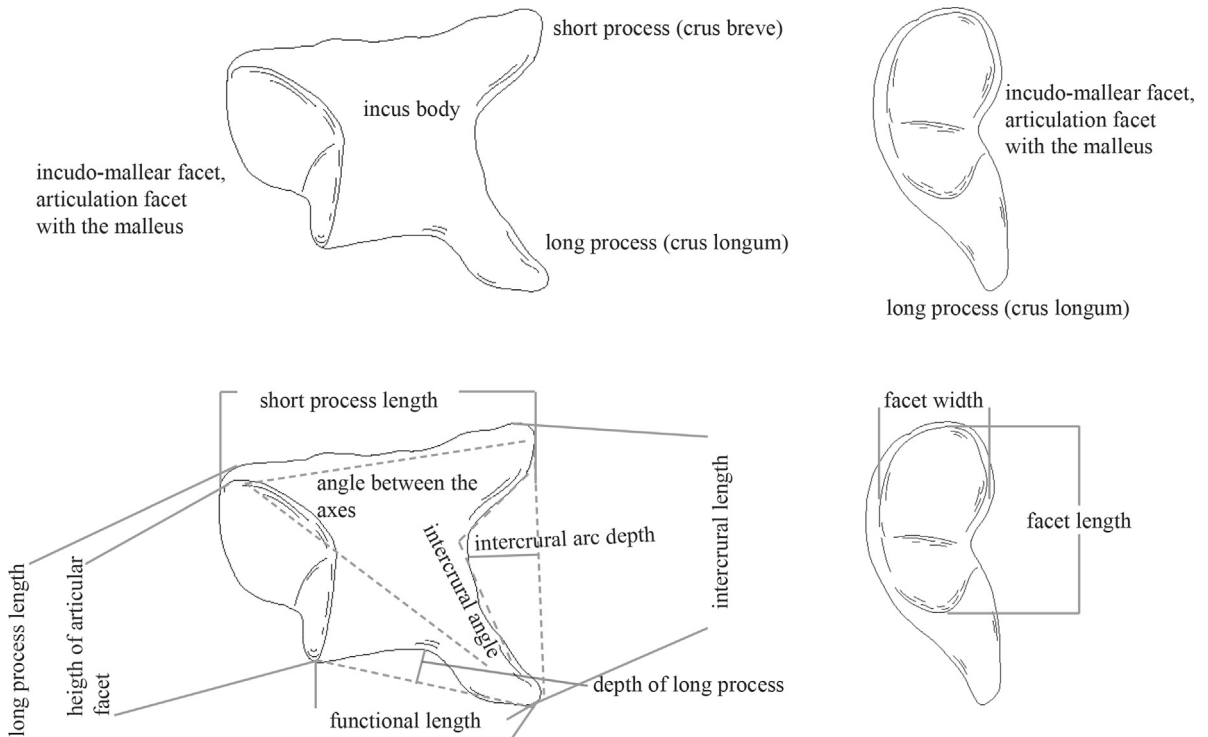


Fig. 1. Topology of the incus and measurements performed mostly after Quam and Rak (2008). See Section 2.1 for full explanation of each measurement.
Fig. 1. Topologie de l'enclume et mesures réalisées, principalement d'après Quam et Rak (2008). Voir Section 2.1 pour la description complète de chaque mesure.

only auditory ossicle available of the fossil taxon *Hyaenodon* included in this study.

2. Material and methods

Photos were taken with the Keyence VHX-1000 D (digital microscope connected to a profile measurement unit, the Keyence VHX-S15) at the IPUW. These photos were used as the basis for simple line drawings that were performed in Adobe® Illustrator CS5. For better illustration of the morphology, all drawings were made in the same size and are therefore not aligned to the same scale (Figs. 2–4). Measurements on the dimensions of the incus were also taken to sample data on incus size (Table 1). The unique incus of *Hyaenodon* was compared to a set of 23 different taxa of Carnivora: ten felid taxa, three hyaenid taxa, two viverrid taxa, one nandiniid taxon, one herpestid taxon and six canid taxa. Respective sample sizes of taxa are given in the description section. All ossicles were already loose and no skulls were destroyed by dissection. The specimen for *Felis domestica* is a nearly complete (except for the lenticular process), left incus. It was prepared from a skull of a four week old, female domestic cat. The bullae were not fused. Its morphology does not diverge from adult domestic cat incus (pers. obsv.), but was available for study. All other material is – if known – from adult animals. We decided to focus on feliform carnivore because a first pre-analysis revealed similarities of the *Hyaenodon* incus to the felid incus (Bastl, 2012).

The specimen of *Hyaenodon* is a nearly complete, left incus. It was found together with two skull fragments, one of which exhibited a completely preserved auditory bulla (MNHN.F.Qu8594 left fragment; MNHN.F.Qu8593 right fragment) and is stored in the Quercy collection at the “Muséum national d'histoire naturelle” in Paris (France). The auditory bulla and the inner ear of that specimen were described in Bastl (2012) and Pfaff et al. (2016). No more precise information on the provenance of the fossils is indicated than Quercy (late Eocene/Oligocene) for the specimens. However, the small and leptorhynch species is only known from the Oligocene of Europe (Bastl et al., 2011; Lange-Badré, 1979).

2.1. Incus measurements

Most of the measurements follow those of Quam and Rak (2008) provided for the human incus. Quam and Rak (2008) modified measurements from Masali (1964) and provided figures and tables to describe them. Before performing the measurements, the ossicles are oriented: the incus is lying on its medial aspect; thus, in most cases, the majority of the facet is visible and the long process is pointing downwards. In the following, these measurements are explained (Fig. 1):

Explanation of measurements performed on the incus (Table 2 and Fig. 2, both p. 418 in Quam and Rak, 2008; Measurement Number 9–16; Fig. 1, Table 1 herein):

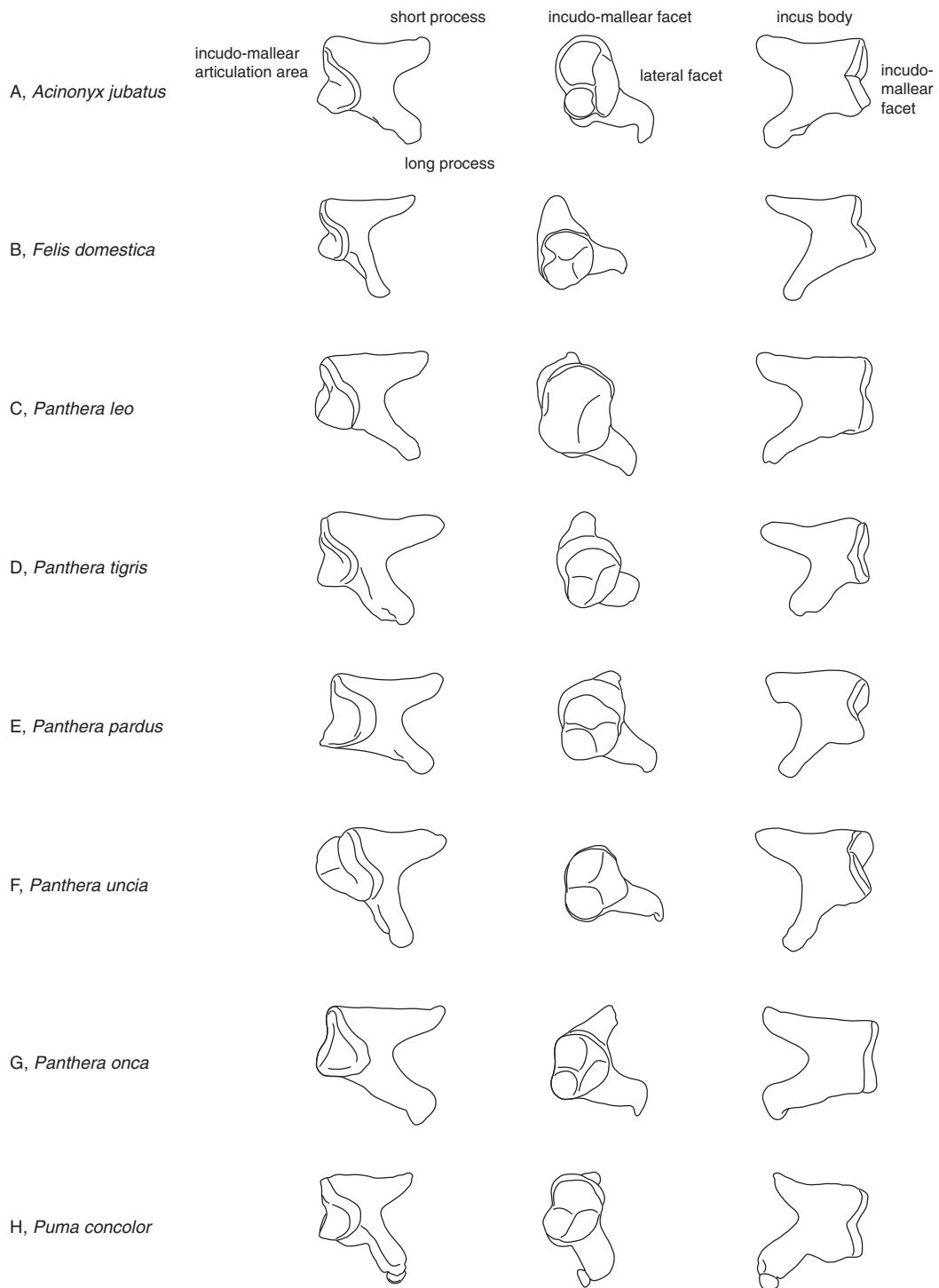


Fig. 2. Line drawings of the incus of felid Carnivora in medial (left), occlusal (with the incudo-malleolar facet in focus; middle) and lateral (right) view. A: *Acinonyx jubatus*; B: *Felis domestica*; C: *Panthera leo*; D: *Panthera tigris*; E: *Panthera pardus*; F: *Panthera uncia*; G: *Panthera onca*; H: *Puma concolor*. Note the saddle-shaped morphology and the extension of a lateral facet. Some of the specimens, where possible, are shown complete with the lenticular apophysis in place.

Fig. 2. Dessin des enclumes des carnivores félinés en vues médiale (à gauche), occlusale (avec focalisation sur la facette incudo-malléaire ; au milieu) et latérale (à droite). A : *Acinonyx jubatus* ; B : *Felis domestica* ; C : *Panthera leo* ; D : *Panthera tigris* ; E : *Panthera pardus* ; F : *Panthera uncia* ; G : *Panthera onca* ; H : *Puma concolor*. Remarquez la morphologie en forme de selle et l'extension de la facette latérale. Quand cela est possible, les spécimens sont présentés en entier, avec l'apophyse lenticulaire en place.

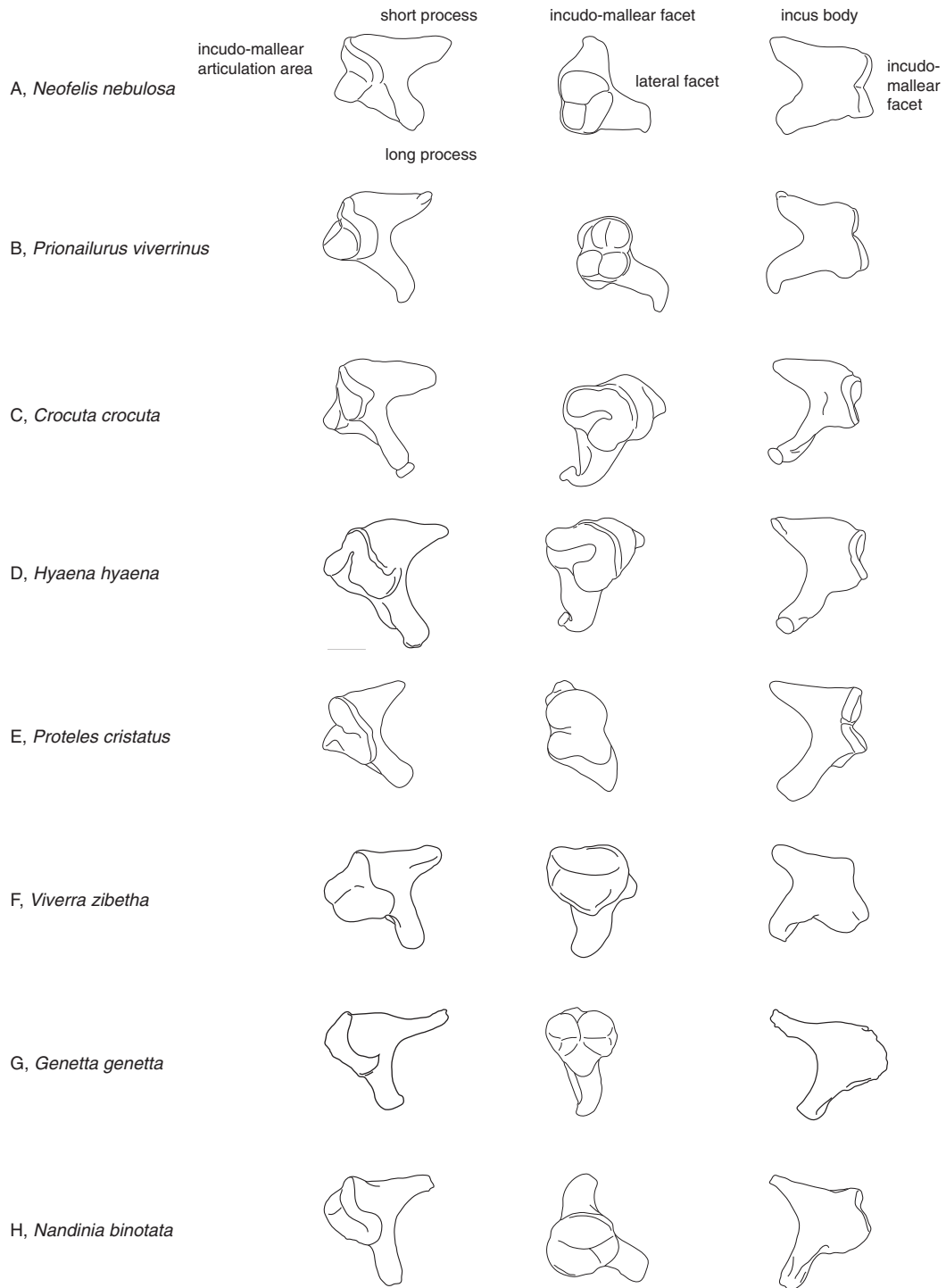


Fig. 3. Line drawings of the incus of felid, hyaenid, viverrid and nandiniid Carnivora in medial (left), occlusal (with the incudo-malleolar facet in focus; middle) and lateral (right) view. A: *Neofelis nebulosa*; B: *Prionailurus viverrinus*; C: *Crocuta crocuta*; D: *Hyaena hyaena*; E: *Proteles cristatus*; F: *Viverra zibetha*; G: *Genetta genetta*; H: *Nandinia binotata*. Note the U-shaped facet in hyaenids. Some of the specimens, where possible, are shown complete with the lenticular apophysis in place.

Fig. 3. Dessin des enclumes des carnivores félinés, hyaenidés, viverridés, et nandiniidés en vues médiale (à gauche), occlusale (avec focalisation sur la facette incudo-malléaire ; au milieu) et latérale (à droite). A : *Neofelis nebulosa* ; B : *Prionailurus viverrinus* ; C : *Crocuta crocuta* ; D : *Hyaena hyaena* ; E : *Proteles cristatus* ; F : *Viverra zibetha* ; G : *Genetta genetta* ; H : *Nandinia binotata*. Remarquez la morphologie en U chez les hyaenidés. Quand cela est possible, les spécimens sont présentés en entier, avec l'apophyse lenticulaire en place.

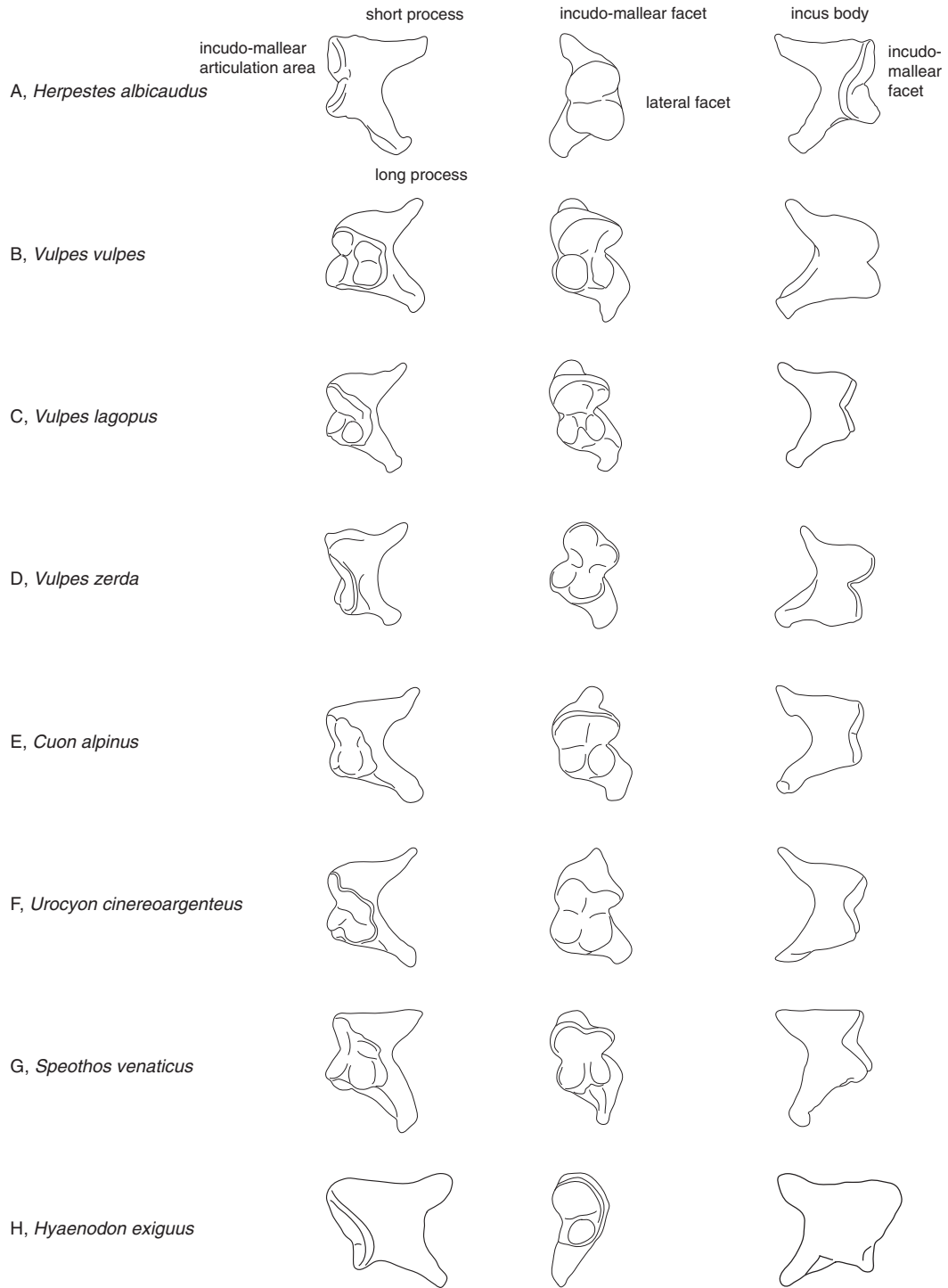


Fig. 4. Line drawings of the incus of herpestid, canid Carnivora and the fossil specimen of *Hyaenodon* in medial (left), occlusal (with the incudo-malleolar facet in focus; middle) and lateral (right) view. A: *Herpestes albicaudus*; B: *Vulpes vulpes*; C: *Vulpes lagopus*; D: *Vulpes zerda*; E: *Cuon alpinus*; F: *Urocyon cinereoargenteus*; G: *Speothos venaticus*; H: *Hyaenodon exiguus*. Note the clover-leaf like facet in canids. Some of the specimens, where possible, are shown complete with the lenticular apophysis in place.

Fig. 4. Dessin des enclumes des carnivores herpestidés, canidés et un spécimen fossile de *Hyaenodon* en vues médiale (à gauche), occlusale (avec focalisation sur la facette incudo-malléaire ; au milieu) et latérale (à droite). A : *Herpestes albicaudus* ; B : *Vulpes vulpes* ; C : *Vulpes lagopus* ; D : *Vulpes zerda* ; E : *Cuon alpinus* ; F : *Urocyon cinereoargenteus* ; G : *Speothos venaticus* ; H : *Hyaenodon exiguus*. Remarquez la morphologie en forme de trèfle chez les canidés. Quand cela est possible, les spécimens sont présentés en entier, avec l'apophyse lenticulaire en place.

Table 1

Measurements of the incus (in mm) of all specimens under study (where such measurements could be performed). Most of them follow [Quam and Rak \(2008\)](#). For explication of each measurement see Section 2.1. Incus mass in mg, measurements 1–7 and 9–10 in mm, 8 and 11 are angles.

Tableau 1

Mesures de l'enclume (en mm) pour tous les spécimens étudiés (quand il était possible de les réaliser). La plupart des mesures suivent [Quam et Rak \(2008\)](#). Les mesures sont expliquées dans la Section 2.1. Masse de l'enclume en mg, mesures 1–7 et 9–10 en mm, mesures 8 et 11 en degrés.

Specimen	Taxon	Mass	1	2	3	4	5	6	7	8 (°)	9	10	11 (°)
ZMB.MAM.105487	<i>Acinonyx jubatus</i>	11.0	3.72	4.33	2.19	2.6	0.23	3.38	1.41	46.6	2.14	1.73	66.1
ZMB.MAM.105487	<i>Acinonyx jubatus</i>	11.8	3.81	4.14	2.01	2.36	0.31	3.36	0.95	58.1	2.19	1.61	84.1
ZMB.MAM.105487	<i>Acinonyx jubatus</i>	11.5	3.8	3.91	2.26	2.21	0.16	3.28	1.28	49.1	2.32	1.66	77.5
ZMB.MAM.105487	<i>Acinonyx jubatus</i>	12.0	3.67	4.27	2.18	2.44	0.19	3.26	1.37	45.8	2.12	1.75	71.9
ZMB.MAM.105487	<i>Acinonyx jubatus</i>	12.0	3.71	3.98	2.08	2.37	0.24	3.18	1.31	50.2	2.31	1.87	76.8
IPUW 2973/1	<i>Felis catus</i>	1.9	2.58	2.99	1.4	1.5	0.21	2.81	0.93	58.4	1.38	1.21	109.5
ZMB.MAM.105491	<i>Panthera leo</i>	27.3	4.94	6.07	3.32	3.24	0.44	4.79	1.78	52.9	3.27	2.59	79.5
ZMB.MAM.56046	<i>Panthera tigris</i>	17.8	3.2	3.91	2.02	2.33	0.26	3.54	1.09	63	2.1	1.58	101.7
ZMB.MAM.56046	<i>Panthera tigris</i>	18.2	2.59	3.2	1.68	1.83	0.23	2.9	0.84	64.7	1.67	1.42	107.3
ZMB.MAM.105500	<i>Panthera tigris</i>	25.9	3.1	3.58	1.76	2.09	0.37	3.15	1.06	59	2.03	1.58	93.7
ZMB.MAM.28793	<i>Panthera tigris</i>	20.1	2.76	3.25	1.71	1.75	0.36	2.91	0.96	66.3	1.85	1.64	101
ZMB.MAM.14368	<i>Panthera tigris</i>	24.4	3.05	3.28	1.66	1.92	0.29	2.86	1.07	58.8	1.8	1.54	85.2
ZMB.MAM.14369	<i>Panthera tigris</i>	23.3	2.87	3.27	1.72	1.81	0.27	2.79	1.04	56.8	1.88	1.52	83.3
ZMB.MAM.105495	<i>Panthera pardus</i>	13.0	3.04	3.73	1.87	2.19	0.27	3.31	1.02	64.6	1.85	1.67	95.5
ZMB.MAM.105496	<i>Panthera pardus</i>	14.1	2.44	3.02	1.62	1.84	0.26	2.6	0.68	57.6	1.54	1.21	99.6
ZMB.MAM.105497	<i>Panthera pardus</i>	13.8	2.64	2.8	1.56	1.6	0.16	2.38	0.75	60.4	1.58	1.24	97.2
ZMB.MAM.5560	<i>Panthera pardus</i>	14.9	2.36	2.85	1.49	1.69	0.24	2.4	0.71	53.5	1.54	1.33	94.5
ZMB.MAM.56404	<i>Panthera pardus</i>	14.7	2.39	2.74	1.49	1.5	0.21	2.49	0.74	58.6	1.64	1.49	93.9
ZMB.MAM.56404	<i>Panthera pardus</i>	14.7	2.32	2.8	1.51	1.46	0.19	2.47	0.76	59.8	1.61	1.36	94.5
ZMB.MAM.105503	<i>Panthera uncia</i>	11.2	3.04	3.29	1.96	1.81	0.23	2.93	0.87	54	2.16	1.84	98.4
ZMB.MAM.105504	<i>Panthera uncia</i>	11.5	3.36	4.01	2.32	1.84	0.40	3.68	0.99	64.5	2.6	2.1	107.7
ZMB.MAM.105504	<i>Panthera uncia</i>	11.6	3.31	4.15	2.18	2.01	0.45	3.68	0.99	64.4	2.47	2.19	105.6
ZMB.MAM.105505	<i>Panthera uncia</i>	11.8	2.79	3.09	1.67					61.6	1.94	1.56	107.9
ZMB.MAM.105506	<i>Panthera uncia</i>	12.6	3.44	4.09	2.31	2.06	0.35	3.5	1.18	63	2.37	2.02	90.2
ZMB.MAM.105494	<i>Panthera onca</i>	16.8	3.1	4.05	2.08	2.12	0.34	3.39	1.06	56.4	2.23	1.83	82.2
ZMB.MAM.56263	<i>Panthera onca</i>	21.8	3.54	4.09	2.04	2.38	0.35	3.3	1.15	52.2	2.25	1.84	86.1
ZMB.MAM.105492	<i>Panthera onca</i>	13.9	3.07	3.81	1.85	2.12	0.22	3.13	1.22	49.9	1.96	1.59	83.6
ZMB.MAM.1208	<i>Panthera onca</i>	16.8	3.35	3.71	2.01	2	0.26	3.37	1.15	58.2	2.14	1.74	94
ZMB.MAM.105493	<i>Panthera onca</i>	19.2	3.68	4.35	2.32	2.62	0.34	3.51	1.36	50.2	2.36	2.12	72.5
ZMB.MAM.56238	<i>Puma concolor</i>	14.9	2.83	3.72	1.91	2.04	0.52	3.2	0.85	56.6	1.93	1.56	99
ZMB.MAM.15780	<i>Puma concolor</i>	11.8	2.6	3.26	1.67	1.84	0.36	2.94	0.79	59.8	1.77	1.46	104.6
ZMB.MAM.38701	<i>Puma concolor</i>	12.4	2.67	3.37	1.69	2.04	0.13	2.88	0.95	64.5	1.66	1.27	102.6
ZMB.MAM.105509	<i>Puma concolor</i>	10.0	2.55	3.31	1.83	1.81	0.12	2.88	0.92	60.3	1.77	1.31	92.4
ZMB.MAM.29161	<i>Puma concolor</i>	11.7	2.77	3.39	1.82	2.18	0.21	2.9	1.04	55.4	1.93	1.35	96.5
ZMB.MAM.105510	<i>Puma concolor</i>	14.4	2.77	3.62	1.84	2.04	0.51	3.12	1.12	61.7	2.02	1.44	109.1
ZMB.MAM.105510	<i>Puma concolor</i>	12.1	2.62	3.31	1.63	1.96	0.35	3.03	0.78	64.9	1.8	1.36	106.5
ZMB.MAM.105510	<i>Puma concolor</i>	11.7	2.53	3.5	1.67	2.17	0.28	3.13	0.78	69.4	1.67	1.41	109.5
ZMB.MAM.105510	<i>Puma concolor</i>	11.5	2.67	3.32	1.72	1.93	0.17	2.94	0.89	62.5	1.86	1.39	107.8
ZMB.MAM.105488	<i>Neofelis nebulosa</i>	6.9	3.03	3.39	1.65	1.95	0.21	3.24	0.82	70.1	1.75	1.59	111.9
ZMB.MAM.105489	<i>Neofelis nebulosa</i>	7.7	3.11	3.27	1.87	1.93	0.16	3.03	0.9	59.7	1.81	1.72	103.2
ZMB.MAM.105489	<i>Neofelis nebulosa</i>	6.0	3.12	3.47	1.89	1.97	0.28	3.17	0.87	64.5	1.85	1.38	108.6
ZMB.MAM.105489	<i>Neofelis nebulosa</i>	7.7	3.01	3.21	1.65	2.05	0.17	2.99	0.97	62.2	1.62	1.6	93.4
ZMB.MAM.105507	<i>Prionailurus viverrinus</i>	6.6	2.51	3.18	1.81	1.92	0.38	2.79	0.88	57.9	1.94	1.52	85.8
ZMB.MAM.105508	<i>Prionailurus viverrinus</i>	6.9	2.98	3.32	1.51	1.77	0.28	3.32	0.93	70.9	1.89	1.48	98.7
ZMB.MAM.105508	<i>Prionailurus viverrinus</i>	6.6	2.92	3.3	1.76	1.76	0.33	3.15	0.95	64.7	2	1.54	87.2
IPUW without number	<i>Crocota crocuta</i>	22.1	3.58	5.13	2.7	2.56	0.42	5.24	1.4	66.6	2.96	2.48	141.8
IPUW 73149	<i>Crocota crocuta</i>	29.5	3.06	4.08	1.92	1.99	0.45	3.73	1.15	65.5	1.82	1.81	103.7
IPUW 73149	<i>Crocota crocuta</i>	29.1	3.14	3.85	1.8	2.11	0.37	3.36	1.26	65.7	1.66	2.17	89.1
IPUW A 168.10	<i>Hyaena hyaena</i>	14.3	3.08	4.05	2.24	1.77	0.38	3.72	1.04	69.9	1.8	2.26	107.3
IPUW A 168.10	<i>Hyaena hyaena</i>	14.2	1.65	2.14	1.2	0.94	0.13	1.98	0.53	69.6	1.14	1.23	114.1
IPUW 2398	<i>Proteles cristatus</i>	6.8	2.61	3.59	2.41	1.4	0.07	3.53	0.92	65.4	2.09	1.81	142.8
NMW 1159	<i>Viverra zibetha</i>	0.5	1.28	1.66	1.01	0.65	0.35	1.52	0.32	65.1	1	1.18	126.1
NMW 32680	<i>Genetta genetta</i>	0.5	2.09	1.66	1.06	0.76	0.06	1.94	0.53	74.6	1.08	1.1	106.6
NMW5479/B5118	<i>Nandinia binotata</i>	0.9	1.38	1.81	1.1	0.73	0.08	1.79	0.38	78.4	0.85	1.08	125.5
NMW 1169	<i>Ichneumia albicauda</i>	1.2	1.52	2.11	1.16	1.23	0.17	1.9	0.57	66.8	1.26	0.86	104.2
NMW 1973	<i>Vulpes vulpes</i>	5.7	2.48	3.21	1.58	1.28	0.2	3.12	0.81	65	1.7	1.58	119.3
NMW 4007	<i>Vulpes lagopus</i>	3.4	2.17	2.89	1.82	1.07	0.14	2.95	0.63	70.1	1.46	1.37	122
NMW B4817	<i>Vulpes zerda</i>	4.2	1.88	2.54	1.68	0.89	0.15	2.34	0.57	54.1	1.93	1.64	129.8
NMW 4254/B4719	<i>Cuon alpinus</i>	6.5	2.35	3.19	1.75	1.3	0.16	2.84	0.9	61.3	1.61	1.62	126.4
NMW 2876	<i>Urocyon cinereoargenteus</i>	3.7	2.28	3.03	1.78	1.21	0.15	2.97	0.95	70.2	1.53	1.53	135.4
NMW 1287	<i>Speothos venaticus</i>	5.3	2.37	3.58	1.93	1.48	0.28	3.24	0.75	62.2	1.8	1.71	109.7
MNHN.F. Qu 8594	<i>Hyaenodon exiguus</i>		2.4	2.9	1.5	1.24	0.27	2.18	0.48	44	1.43	0.98	139.8

- 1 (“Short process length”; Quam and Rak, 2008) describes the maximum distance from the most extruding point of the body to the opposite tip of the short process.
- 2 (“Long process length”; Quam and Rak, 2008) describes the maximum distance from the most salient point of the body to the opposite tip of the long process.
- 3 (“Height of articular facet”; Quam and Rak, 2008) describes the maximum diameter of the facet.
- 4 (“Functional length”; Quam and Rak, 2008) the shape of the incus in Carnivora is different from a human one; therefore, this length was modified: herein, it is the maximum distance between the tip of the long process and the lowermost point of the articular facet.
- 5 (“Depth of long process”; Quam and Rak, 2008) describes the maximum depth of the arc of the long process, measured perpendicular to a line connecting the outermost part of the lower part of the articular facet to the tip of the long process.
- 6 (“Intercrural length”; Quam and Rak, 2008) explains the maximum distance between the most salient point of the superior border of the short process to the tip of the long process.
- 7 (“Intercrural arc depth”; Quam and Rak, 2008) describes the maximum depth of the curvature, measured perpendicular to a line drawn from the tip of the short process to the tip of the long process.
- 8 (“Angle between the axes”; Quam and Rak, 2008) explains the angle between the short and long process with those transformed into straight lines.

Additional measurements added herein are:

- 9 (“Facet length”) is measured when the articular facet is in full view. This explains the maximum distance from the upper to the lower border of the articular facet (the same axis as from the short to the long process).
- 10 (“Facet width”) is measured in the same position as the former. It describes the maximum width of the articular facet measured perpendicular to “facet length”.
- 11 (“Intercrural angle”) is measured in the same orientation as most of the measurements (incus lying on its

medial aspect). It depicts the angle between the short and long process.

For Figs. 2–4, we mirrored some of the drawings to present all drawings in the same way (as left incus).

2.2. Habitat classification

In order to define the habitat preference of the taxa under study, we used the commonly used habitat classification: open, mixed and closed. There are many ways to classify the ecology of a species, even within the three categories mentioned above (Meloro et al., 2013). We decided to use the database of the World Wide Fund for Nature (WWF) to meet the criterion of a simple, comprehensible and repeatable source (Table 2). Usually, studies are focused on only one or two families. We downloaded all habitat types of the recent species from the WWF Wildfinder (<http://worldwildlife.org/science/wildfinder/>) and assigned those habitats to rather closed or rather open environments (Tables 2 and 3). Information on included material is found in Table 4. All ecoregions in which a recent species occurs were included. The ratio of each species' occurrence in a rather open and rather closed habitat was calculated (Table 3). If the lesser of the two percentages exceeded the threshold of 30%, the species was classified as preferring a “mixed” habitat. In most cases, this approach is in good accordance with literature. Habitat descriptions from the literature can be found below (Species' descriptions), together with the recent distribution (Wozencraft, 2005).

During the study, we established six different morphological facet types of the incus (see Section 3.1 and Table 3). We mapped these types onto a simplified phylogeny that includes only the carnivorous mammals (carnivorans and *Hyaenodon*) studied in the present article (Fig. 5). The phylogenetic relationships among carnivorans are based on Agnarsson et al. (2010), a molecular phylogeny at the species-level of the carnivorans, and on Bardeleben et al. (2005), a molecular phylogeny of the Canidae.

Table 2

Classification from WWF Wildfinder showing the WWF Code, the biome and the definition of habitat type (either closed or open), that was used for gathering ecological information.

Tableau 2

Classification tirée de la WWF Wildfinder montrant le WWF Code, le biome et la définition du type d'habitat (soit fermé, soit ouvert), qui a été utilisé pour collecter les informations sur l'écologie.

WWF CODE	BIOME	Habitat type
1	Tropical and subtropical moist broadleaf forests	Closed
2	Tropical and subtropical dry broadleaf forests	Closed
3	Tropical and subtropical coniferous forests	Closed
4	Temperate broadleaf and mixed forests	Closed
5	Temperate coniferous forests	Closed
6	Boreal forests/Taiga	Closed
7	Tropical and subtropical grasslands, savannahs, and shrublands	Open
8	Temperate grasslands, savannahs, and shrublands	Open
9	Flooded grasslands and savannahs	Open
10	Montane grasslands and shrublands	Open
11	Tundra	Open
12	Mediterranean forests, woodlands, and scrub	Closed
13	Deserts and xeric shrublands	Open
14	Mangroves	Closed

Table 3

Calculation of closed to open habitats per taxon based on the WWF Wildfinder (Table 2). If the threshold of 30% is exceeded, the taxon is defined as preferring a mixed habitat type. Data matrix for statistical analysis, that shows the taxon, its familiar affiliation, the habitat preference (open, mixed, closed) and the morphological type of the incudo-malleolar facets (1–6) with 1: two facets and an additional lateral inclination; 2: four facets; 3: U-shaped facet; 4: two sloping facets; 5: four tectiform facets and 6: two simple facets.

Tableau 3

Calcul des habitats (fermés ou ouverts) pour chaque taxon à partir du WWF Wildfinder (Tableau 2). Si le seuil de 30 % est dépassé, le taxon est défini comme préférant un habitat mixte. La matrice de données pour l'analyse statistique inclut pour chaque taxon son affiliation familiale, son habitat de prédilection (ouvert, mixte, fermé) et le type morphologique des facettes incudo-malléaires (1–6), avec 1 : deux facettes et une inclinaison latérale additionnelle ; 2 : quatre facettes ; 3 : facette en forme de U ; 4 : deux facettes inclinées ; 5 : quatre facettes tectiformes ; et 6 : deux facettes simples.

Taxon	Family	Percentage closed: open habitat (WWF)	Classification	Morphological type
<i>Acinonyx jubatus</i>	Felidae	12.7%: 87.3%	Open	1
<i>Felis domestica</i>		34.3%: 65.7%	Mixed	1
<i>Panthera leo</i>		16.2%: 83.8%	Open	1
<i>Panthera tigris</i>		92%: 8%	Closed	1
<i>Panthera pardus</i>		56.2%: 43.8%	Mixed	1
<i>Panthera uncia</i>		28.3%: 71.7%	Open	1
<i>Panthera onca</i>		86.4%: 13.6%	Closed	1
<i>Puma concolor</i>		71.6%: 28.4%	Closed	1
<i>Neofelis nebulosa</i>		96.3%: 3.7%	Closed	1
<i>Prionailurus viverrinus</i>		98.3%: 1.7%	Closed	2
<i>Crocuta crocuta</i>	Hyaenidae	4.8%: 95.2%	Open	3
<i>Hyaena hyaena</i>		0%: 100%	Open	3
<i>Proteles cristatus</i>		3.7%: 96.3%	Open	3
<i>Viverra zibetha</i>	Viverridae	94.3%: 5.7%	Closed	4
<i>Genetta genetta</i>		27.3%: 72.7%	Open	5
<i>Nandinia binotata</i>	Nandiniidae	63.3%: 36.7%	Mixed	1
<i>Ichneumia albicauda</i>	Herpestidae	16.7%: 83.3%	Open	6
<i>Vulpes vulpes</i>	Canidae	60.2%: 39.8%	Mixed	2
<i>Vulpes lagopus</i>		40.8%: 59.2%	Mixed	2
<i>Vulpes zerda</i>		0%: 100%	Open	2
<i>Cuon alpinus</i>		73.6%: 26.4%	Closed	2
<i>Urocyon cinereoargenteus</i>		71.2%: 28.8%	Closed	2
<i>Speothos venaticus</i>		82.9%: 17.1%	Closed	2
<i>Hyaenodon exiguus</i>	Hyaenodontidae	Fossil	Mixed	1

Table 4

Information on included specimens per species and sample size.

Tableau 4

Information sur les spécimens étudiés par espèce et par taille des échantillons.

Taxon	Specimen numbers	Sample size
<i>Acinonyx jubatus</i>	ZMB.MAM.105487	5
<i>Felis domestica</i>	IPUW 2073/1	1
<i>Panthera leo</i>	ZMB.MAM.105491	1
<i>Panthera tigris</i>	ZMB.MAM.5604, .105500, .28793, .14358, .14369	7
<i>Panthera pardus</i>	ZMB.MAM.105495, .105496, .105497, .5560, .56404 ZMB.MAM.105504, .105505, .105506, .105503	6
<i>Panthera uncia</i>	ZMB.MAM.105494, .56263, .105492, .1208, .105493	
<i>Panthera onca</i>	ZMB.MAM.56238, .15780, .38701, .105509, .29161, .105510 ZMB.MAM.105488, .105489	5
<i>Puma concolor</i>	ZMB.MAM.105507, .105508	5
<i>Neofelis nebulosa</i>		9
<i>Prionailurus viverrinus</i>		4
<i>Crocuta crocuta</i>	IPUW 73149, without number	3
<i>Hyaena hyaena</i>	IPUW A168.10	2
<i>Proteles cristatus</i>	IPUW 2398	1
<i>Viverra zibetha</i>	NMW 1159	1
<i>Genetta genetta</i>	NMW 32680	1
<i>Nandinia binotata</i>	NMW 5479b5118	1
<i>Ichneumia albicauda</i>	NMW 1169	1
<i>Vulpes vulpes</i>	NMW 1073	1
<i>Vulpes lagopus</i>	NMW 4007	1
<i>Vulpes zerda</i>	NMW B4817	1
<i>Cuon alpinus</i>	NMW 4254/B4719	1
<i>Urocyon cinereoargenteus</i>	NMW 2876	1
<i>Speothos venaticus</i>	NMW 1287	1
<i>Hyaenodon exiguus</i>	MNH.N.F. Qu8594	1

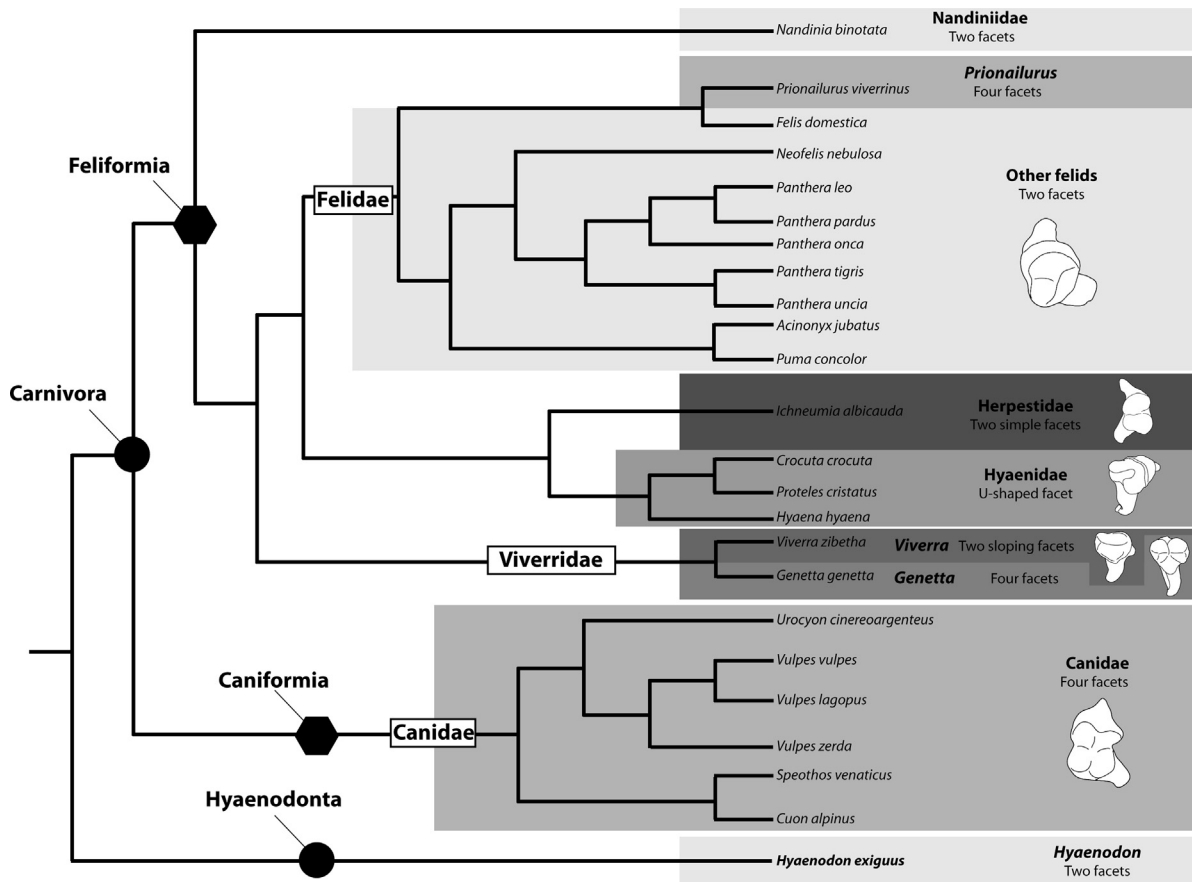


Fig. 5. Simplified phylogenetic tree illustrating the relationships between the carnivorous mammals studied in the present paper, with indication of their morphological incus types (see text). The relationships are based on Bardeleben et al. (2005) and Agnarsson et al. (2010).

Fig. 5. Phylogénie simplifiée illustrant les relations de parenté entre les mammifères carnassiers étudiés dans l'article, avec indications de type morphologique sur leur enclume (voir dans le texte). Les relations de parenté sont tirées de Bardeleben et al. (2005) et Agnarsson et al. (2010).

2.3. Statistical analysis

We performed a principal component analysis (=PCA) on the incus measurements we took (Table 1) in order to explore the variance between these data. We applied the PCA on the measurements (all in mm) and angles (11 variables; n=61); the data has been normalized. The results have been compared to taxonomy (species) and ecology (open, closed, mixed habitat), as well as to the different morphological types of incus established herein (Figs. 6–8; Table 5). The function software R version 3.2.3 (The R Development Core Team, 2015; <http://www.R-project.org/>) package FactoMineR (<http://factominer.free.fr/>; Lê et al., 2008) was used. We calculated the barycentre and 95% confidence ellipse for each type of data (open/mixed/closed habitats; morphological type; taxonomic groups). For the analysis regarding the morphological facet types of the incus, we have removed the Herpestidae and Viverridae, since the incus facet type is represented only by a single specimen only (11 variables; n=58); hence, no confidence ellipse could be reconstructed. We have represented the barycentres and confidence ellipses on the latter system (Fig. 7), because the coordinate system that resulted from this analysis

is almost entirely identical to the one based on all the data.

The procedure for calculating the barycentre and confidence ellipse was slightly modified in the analysis of the influence of the taxonomic classification (Fig. 7): the families represented only by one specimen (i.e. Herpestidae,

Table 5

Squared cosines of the measurements for the first three axes. The highest values for each measurement are in bold.

Tableau 5

Cosinus carré pour chaque mesure sur les trois premiers axes. Les valeurs les plus hautes pour chaque mesure sont en gras.

	F1	F2	F3
Measurement 1	0.904	0.018	0.005
Measurement 2	0.958	0.010	0.001
Measurement 3	0.856	0.035	0.042
Measurement 4	0.826	0.047	0.007
Measurement 5	0.304	0.055	0.618
Measurement 6	0.812	0.139	0.006
Measurement 7	0.866	0.014	0.018
Measurement 8	0.196	0.490	0.003
Measurement 9	0.877	0.009	0.003
Measurement 10	0.719	0.116	0.003
Measurement 11	0.254	0.529	0.034

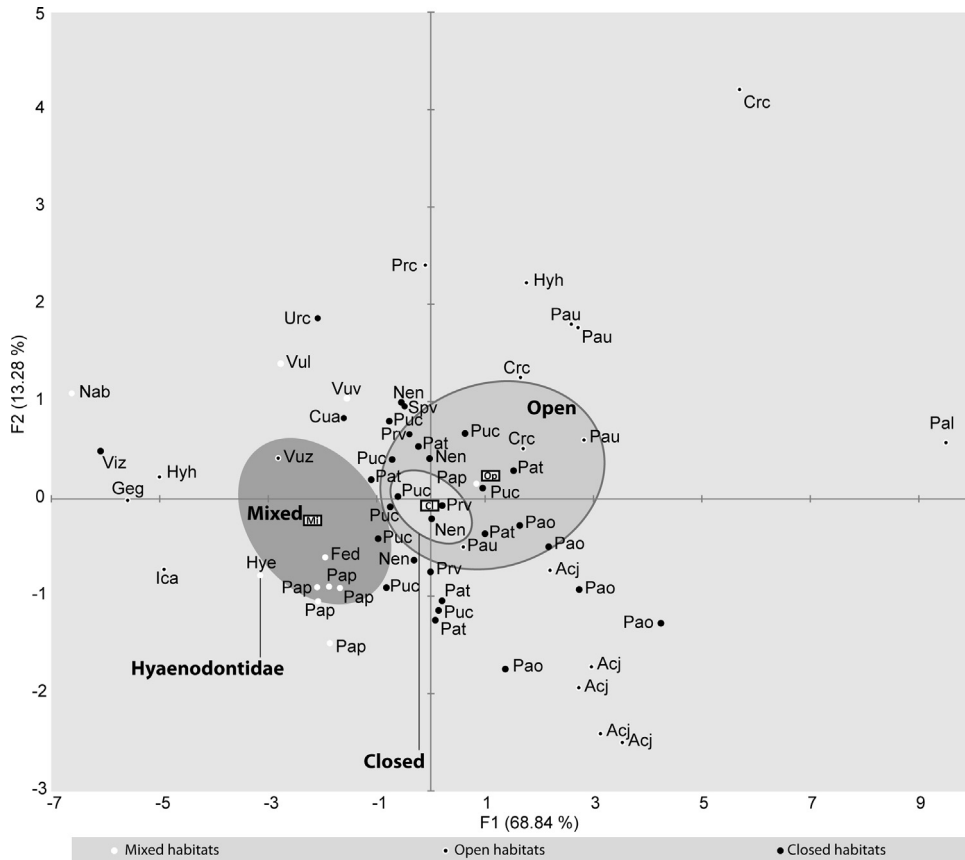


Fig. 6. PCA Analysis. Biplot of the first two components of the PCA. We mapped the barycentres and confidence ellipses calculated for each type of habitats (open/mixed/closed). Acj: *Acinonyx jubatus*; Crc: *Crocota crocota*; Cua: *Cuon alpinus*; Fed: *Felis domestica*; Ges: *Genetta genetta*; Hye: *Hyaenodon exiguus*; Hyh: *Hyaena hyaena*; lca: *Ichneumia albicauda*; Nab: *Nandinia binotata*; Nen: *Neofelis nebulosa*; Pal: *Panthera leo*; Pao: *Panthera onca*; Pap: *Panther pardus*; Pat: *Panthera tigris*; Pau: *Panthera uncia*; Prv: *Prionailurus viverrinus*; Prc: *Proteles cristatus*; Puc: *Puma concolor*; Spv: *Speothos venaticus*; Urc: *Urocyon cinereoargenteus*; Viz: *Viverra zibetha*; Vul: *Vulpes lagopus*; Vuv: *Vulpes vulpes*; Vuz: *Vulpes zerda*.

Fig. 6. Analyse ACP. Sont représentés les deux premiers axes de l'ACP. Les barycentres et ellipses de confiance calculés pour chaque type d'habitat (ouvert/mixte/fermé) sont indiqués. Acj : *Acinonyx jubatus* ; Crc : *Crocota crocota* ; Cua : *Cuon alpinus* ; Fed : *Felis domestica* ; Ges : *Genetta genetta* ; Hye : *Hyaenodon exiguus* ; Hyh : *Hyaena hyaena* ; lca : *Ichneumia albicauda* ; Nab : *Nandinia binotata* ; Nen : *Neofelis nebulosa* ; Pal : *Panthera leo* ; Pao : *Panthera onca* ; Pap : *Panther pardus* ; Pat : *Panthera tigris* ; Pau : *Panthera uncia* ; Prv : *Prionailurus viverrinus* ; Prc : *Proteles cristatus* ; Puc : *Puma concolor* ; Spv : *Speothos venaticus* ; Urc : *Urocyon cinereoargenteus* ; Viz : *Viverra zibetha* ; Vul : *Vulpes lagopus* ; Vuv : *Vulpes vulpes* ; Vuz : *Vulpes zerda*.

Nandiniidae, Hyaenodontidae) were not incorporated. Furthermore, one analysis was performed that did not include one of the two specimens of *Hyaena hyaena* (IPUW A 168.10) in order to observe its effect on the confidence

ellipse of the Hyaenidae (Figs. 6–8). The results provided by the latter two analyses are not different from those of the PCA including all specimens (i.e. the axes and repartition of the specimens are similar), and are thus represented in the

Table 6
Matrix of the Pearson's correlation coefficient. The values above 0.9 are in bold.

Tableau 6
Matrice présentant les coefficients de corrélation de Pearson. Les valeurs supérieures à 0,9 sont en gras.

Measurement	1	2	3	4	5	6	7	8	9	10	11
1	1	-	-	-	-	-	-	-	-	-	-
2	0.914	1	-	-	-	-	-	-	-	-	-
3	0.842	0.932	1	-	-	-	-	-	-	-	-
4	0.901	0.887	0.750	1	-	-	-	-	-	-	-
5	0.427	0.543	0.414	0.486	1	-	-	-	-	-	-
6	0.817	0.936	0.893	0.764	0.512	1	-	-	-	-	-
7	0.906	0.899	0.826	0.868	0.368	0.816	1	-	-	-	-
8	-0.463	-0.379	-0.353	-0.466	-0.119	-0.114	-0.427	1	-	-	-
9	0.866	0.905	0.922	0.793	0.509	0.862	0.813	-0.414	1	-	-
10	0.746	0.829	0.858	0.613	0.504	0.850	0.761	-0.159	0.819	1	-
11	-0.582	-0.392	-0.267	-0.634	-0.198	-0.175	-0.570	0.518	-0.360	-0.224	1

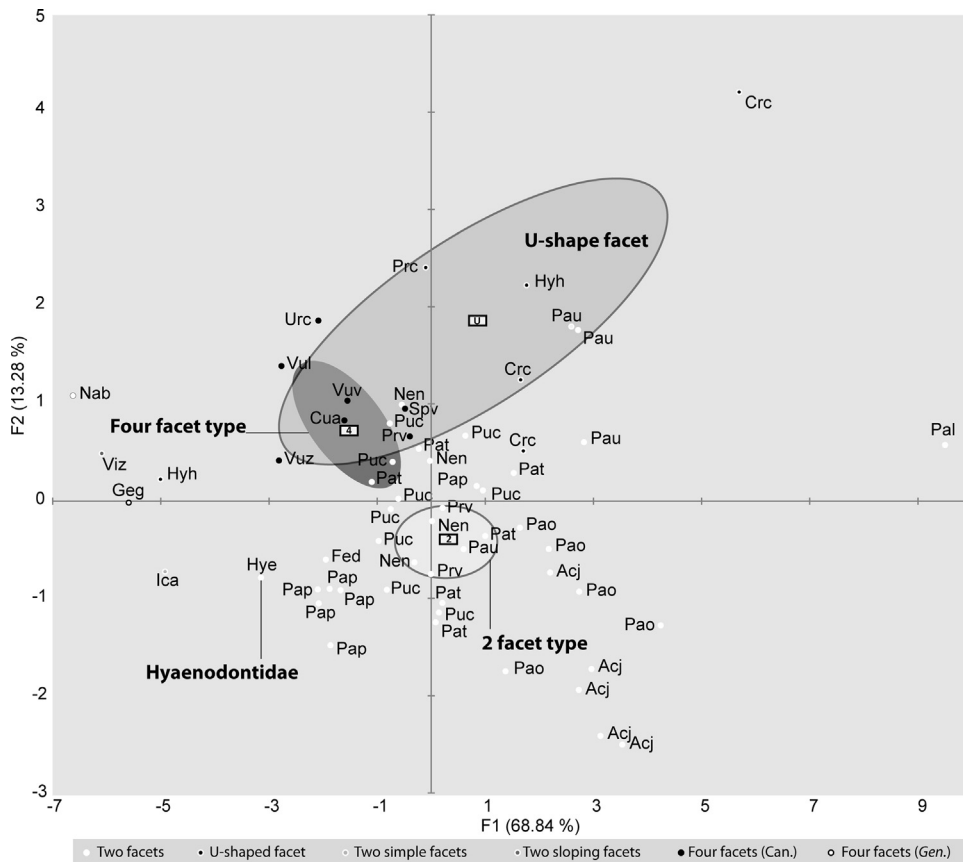


Fig. 7. PCA Analysis. Biplot of the first two components of the PCA. The values are identical to those in Fig. 6. We mapped the barycentres and confidence ellipses calculated for each type of morphological facet except for the two sloping facet (*Viverra*), the four tectiform facet (*Genetta*) and the two simple facet (herpestids) because they are each represented by one specimen. Acj: *Acinonyx jubatus*; Crc: *Crocota crocuta*; Cua: *Cuon alpinus*; Fed: *Felis domestica*; Ges: *Genetta genetta*; Hye: *Hyaenodon exiguus*; Hyh: *Hyaena hyaena*; Ica: *Ichneumia albicauda*; Nab: *Nandinia binotata*; Nen: *Neofelis nebulosa*; Pal: *Panthera leo*; Pao: *Panthera onca*; Pap: *Panther pardus*; Pat: *Panthera tigris*; Pau: *Panthera uncia*; Prv: *Prionailurus viverrinus*; Prc: *Proteles cristatus*; Puc: *Puma concolor*; Spv: *Speothos venaticus*; Urc: *Urocyon cinereoargenteus*; Viz: *Viverra zibetha*; Vuv: *Vulpes lagopus*; Vuv: *Vulpes vulpes*; Vuz: *Vulpes zerda*.

Fig. 7. Analyse ACP. Sont représentés les deux premiers axes de l'ACP. Les valeurs sont identiques à celles de la Fig. 6. Les barycentres et ellipses de confiance calculés pour chaque type morphologique sont indiqués, excepté pour les morphologies de type « deux facettes inclinées » (*Viverra*), « quatre facettes tectiformes » (*Genetta*) et « deux facettes simples » (herpestidés), car ces types ne sont représentés que par un individu. Acj : *Acinonyx jubatus* ; Crc : *Crocota crocuta* ; Cua : *Cuon alpinus* ; Fed : *Felis domestica* ; Ges : *Genetta genetta* ; Hye : *Hyaenodon exiguus* ; Hyh : *Hyaena hyaena* ; Ica : *Ichneumia albicauda* ; Nab : *Nandinia binotata* ; Nen : *Neofelis nebulosa* ; Pal : *Panthera leo* ; Pao : *Panthera onca* ; Pap : *Panther pardus* ; Pat : *Panthera tigris* ; Pau : *Panthera uncia* ; Prv : *Prionailurus viverrinus* ; Prc : *Proteles cristatus* ; Puc : *Puma concolor* ; Spv : *Speothos venaticus* ; Urc : *Urocyon cinereoargenteus* ; Viz : *Viverra zibetha* ; Vuv : *Vulpes lagopus* ; Vuv : *Vulpes vulpes* ; Vuz : *Vulpes zerda*.

system reconstructed based on all data. Finally, the matrix of the Pearson's correlation coefficient was calculated with XLSTAT 2015.6 (Table 6).

Institutional abbreviations

- IPUW: Institut für Paläontologie, Universität Wien, Austria.
- MNHN.F.Qu: Quercy collection at the “Muséum national d'histoire naturelle”, Paris, France.
- NMW: Säugetiersammlung, Naturhistorisches Museum Wien, Austria.
- ZMB.MAM: mammal collection of the Zoological Museum Berlin, Museum für Naturkunde, Berlin, Germany.

Other abbreviations

Species were abbreviated in the PCA plots (Figs. 6–8) by the first two letters of the genus and the first letter of

the species name, respectively; all are listed in alphabetical order with the description for the respective figure.

3. Results

3.1. Anatomical descriptions

The general incus morphology is described for the respective family followed by remarks on interspecific variations. No trace of a ligament attachment can be found on the ossicle directly. Unless stated otherwise, the morphology of the incus was the same in the whole sample. Measurements are given in Table 1.

Felid incus (Fig. 2A–G, 3A–B): The crus breve is more or less straight or slightly convex curved. The crus longum is of approximately equal length and both crura are rather robust. The border surrounding the facet is distinct. With the exception of one species (*Prionailurus viverrinus*) (see

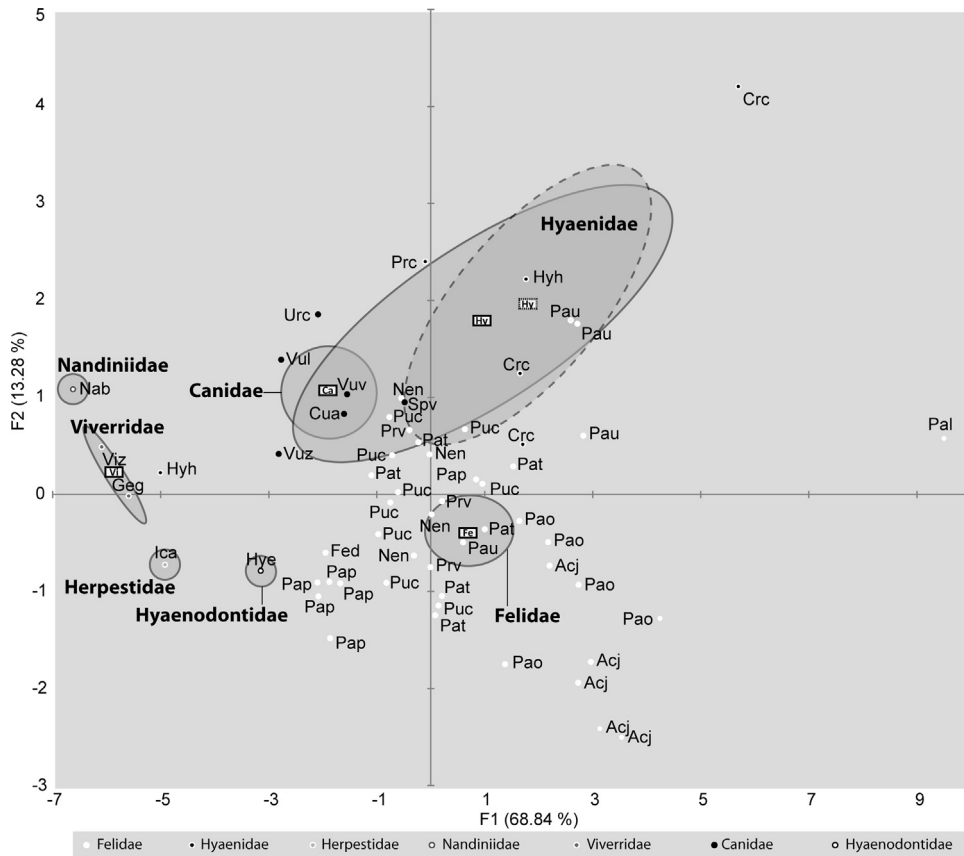


Fig. 8. PCA Analysis. Biplot of the first two components of the PCA. The values are identical to Fig. 6. We mapped the barycentres and confidence ellipses calculated for each family except for the Nandiniidae and Herpestidae because they are each represented by one specimen. Acj: *Acinonyx jubatus*; Crc: *Crocota crocuta*; Cua: *Cuon alpinus*; Fed: *Felis domestica*; Ges: *Genetta genetta*; Hye: *Hyaenodon exiguus*; Hyh: *Hyaena hyaena*; Ica: *Ichneumia albicauda*; Nab: *Nandinia binotata*; Nen: *Neofelis nebulosa*; Pal: *Panthera leo*; Pao: *Panthera onca*; Pap: *Panthera pardus*; Pat: *Panthera tigris*; Pau: *Panthera uncia*; Prv: *Prionailurus viverrinus*; Prc: *Proteles cristatus*; Puc: *Puma concolor*; Spv: *Speothos venaticus*; Urc: *Urocyon cinereoargenteus*; Viz: *Viverra zibetha*; Vul: *Vulpes lagopus*; Vuv: *Vulpes vulpes*; Vuz: *Vulpes zerda*.

Fig. 8. Analyse ACP. Sont représentés les deux premiers axes de l'ACP. Les valeurs sont identiques à celles de la Fig. 6. Les barycentres et ellipses de confiance calculés pour chaque famille sont indiqués, excepté pour les nandiniidés et les herpestidés, car ces groupes ne sont représentés que par un individu. Acj : *Acinonyx jubatus*; Crc : *Crocota crocuta*; Cua : *Cuon alpinus*; Fed : *Felis domestica*; Ges : *Genetta genetta*; Hye : *Hyaenodon exiguus*; Hyh : *Hyaena hyaena*; Ica : *Ichneumia albicauda*; Nab : *Nandinia binotata*; Nen : *Neofelis nebulosa*; Pal : *Panthera leo*; Pao : *Panthera onca*; Pap : *Panthera pardus*; Pat : *Panthera tigris*; Pau : *Panthera uncia*; Prv : *Prionailurus viverrinus*; Prc : *Proteles cristatus*; Puc : *Puma concolor*; Spv : *Speothos venaticus*; Urc : *Urocyon cinereoargenteus*; Viz : *Viverra zibetha*; Vul : *Vulpes lagopus*; Vuv : *Vulpes vulpes*; Vuz : *Vulpes zerda*.

below), the incudo-malleolar articulation area is divided into three surfaces: a superior larger, an inferior smaller and an inclined one. The inferior facet often shows a round shape. The lateral facet is inclined acutely in comparison to the other facets. A lateral indentation can be present on the superior articulation area. A narrow groove that separates the superior from the inferior facet can be present. The border surrounding the facet is distinct.

Remarks: The groove between the facets is most pronounced in *Acinonyx jubatus*, *Panthera tigris*, *P. uncia* and *P. onca*, but can be also completely missing as in *Panthera leo*. The inclined lateral articulation area can be traced in all examined species, but is most steeply inclined in *A. jubatus*. The long process is twisted in some taxa (e.g., *F. domestica*), more robust (*Panthera tigris*, *Panthera onca*, *Neofelis nebulosa*) or longer than the crus breve (*Panthera pardus*, *Puma concolor*). The exception to the general description is *P. viverrinus* with an incudo-malleolar facet

divided into two superior and two inferior articulation areas. They are arranged like a roof to each other, resulting in a lateral sloping constellation. The inferior articulation areas are round in shape, and separated from the superior ones by a groove. The superior ones are of semilunar shape.

Hyaenid incus (Fig. 3C–E): The crus breve is clearly shorter than the crus longum, straight and ends in a narrow tip. The crus longum is more robust than the crus breve. The excavation between the crura is deep. The articulation surface is large and broad. The superior facet (near the crus breve) is the more extensive, while the lower one fades towards the lateral side and decreases in length. The articulation area is shaped into one band (U-shaped). The border surrounding the facet is distinct. The incus in general is thick and extremely robust.

Remarks: The crus breve is distally twisted in *Hyaena hyaena*. The articulation facet in *Proteles cristatus* is divergent, because it does not describe a clear u-shape,

but is more disbanded (the centre of the facet is not set apart as in the other hyaenids).

Viverrid incus (Fig. 3F): The crus breve is slimmer than the crus longum. The crus longum is shorter and more robust. The articulation area is consisting of facets, but there is no groove separating them present. The border surrounding the facet is weakly developed. The incus itself is delicate.

Remarks: The articulation facet is of different shape in the two examined taxa. It consists of two articulation areas in *Viverra zibetha* (an equally developed superior and inferior one) and of five areas that are clearly set apart from each other (the superior and inferior areas consist of two areas building a roof and a rounded articulation area is inclined laterally) in *Genetta genetta*.

Nandiniid incus (Fig. 3H): The crus breve is relatively short and slim. The crus longum is more robust and indented at its basis. The incudo-malleolar facet is composed of a larger superior, a smaller inferior and a laterally sloping articulation area. The inferior one is merging into the lateral one by showing a distinct crest. The border surrounding the facet is distinct.

Remarks: Because the family consists of only one species, *Nandinia* was the only taxon examined.

Herpestid incus (Fig. 4A): The crus breve is shorter in length compared to the crus longum. The outline of its border is relatively straight with an upwards curved tip. The crus longum shows a distal twist of the crus. The incudo-malleolar facet is composed of one superior and one inferior articulation area. They are partly separated by a narrow groove. Both of them are sloping laterally to nearly merge into each other. The superior facet is convex, whereas the inferior one is concave. The border surrounding the facet is distinct.

Remarks: *Ichneumia albicauda* is the only taxon under study here for this family.

Canid incus (Fig. 4B–G): The crus breve is curved upwards with a slim tip. The long process is rather short compared to the crus breve and more robust. The facet is divided in four articulation areas of which at least one of the inferior ones is circular in shape. A vertical groove separating the lateral and medial articular surfaces can be found in most taxa. In general, the facet is twisted laterally with all articular surfaces facing lateral, except for the inferior, circular one on the medial side.

Remarks: The crus breve is straight in *Speothos venaticus*. The long process is shorter than the crus breve in *Vulpes zerda*. The shape of the articulation area of the facets varies, but sticks to the general pattern of four articulation areas. A groove is not present in *Cuon alpinus* and *Urocyon cinereoargenteus*. In *S. venaticus*, this groove is very long and in *Vulpes lagopus* it separates only the inferior circular articulation area from the other areas.

Fossil case study:

Hyaenodon exiguus (sample size: 1; MNHN.F.Qu 8594; Fig. 4H)

The incus itself appears small in comparison to the extant dataset (e.g., to that of *Vulpes vulpes*, purportedly an animal of similar size; Lange-Badré, 1979). The processes

are short and rather fragile. The long process is slimmer than the short process. The superior border of the crus breve is not straight: it is concave with the tip of the crus breve curved upwards. The long process is very short, comparable to the crus breve. The former is twisted. In lateral view, much of the facet is seen. The facet is very long, occupying most of the length of the whole incus. It is divided into two main articulation surfaces. The superior one is larger. The lower one is quite small and oval in outline. It is projecting. A narrow groove separates the two surfaces. A striking feature is seen in the medial view: the facet is not simply saddle-shaped (with the two areas mentioned above), but is steeply inclined – showing an additional, broadened and lower articulation surface. The body of the incus is stout and compact.

3.2. PCA results taxonomy vs. habitat

Concerning the methodology the following, it should be stated beforehand that there are only six cases where the literature (noted in brackets) seems to suggest a different habitat type classification (Gaubert, 2009; Gilchrist et al., 2009; Holekamp and Kolowski, 2009; Jennings and Veron, 2009; Sillero-Zubiri, 2009; Sunquist and Sunquist, 2009), namely: (1) *Panthera uncia* mixed (instead of closed), (2) *P. concolor* mixed (instead of closed), (3) *P. viverrinus* mixed (instead of closed), (4) *G. genetta* mixed (instead of open), (5) *I. albicauda* mixed (instead of open) and (6) *Vulpes lagopus* open (instead of mixed). All of those suggestions concern the category “mixed”. Clearly, it is difficult to define clear definitions for the category “mixed”. Thus, some variation in opinions has to be tolerated. We are confident that this approach is feasible, as the IUCN cat specialist group (2009) gave the same classification for all of the felid taxa studied here, except for the puma. *P. concolor*, which was classified as “mixed” (IUCN, 2009). However, there is no intensive contradiction, as the percentage of open environments (28.4%) almost reaches our threshold of 30%. The advantage of this approach is the easy application to all species under investigation that are affiliated with various families.

The three main components that are reconstructed by the PCA dealing with the incus measurements (11 variables; $n = 61$) explain 88.84% of variance (68.84, 13.28, and 6.72%) (Figs. 6–9). The first axis is correlated with the measurements 1–4, 6, 7, 9 and 10 (Table 6). The second axis is correlated with the angles 8 (“angle between the axes”) and 11 (“intercrural angle”), while the third axis is surprisingly related with the “depth of the long process” (measurement 5) (Table 5). The Pearson’s Correlation Coefficients (Table 6) support these three groups of positive correlation. The variables that show the highest linear relationship are notably: the long process length (measurement 2) with the intercrural length (measurement 6), the height of articular facet (measurement 3) with the facet length (measurement 9); the long process length (measurement 2) is also correlated with the short process length (measurement 1) (Table 6).

One can have the impression, based on these results, that the morphology of the incus in this dataset seems to diverge mainly in two ways: in its overall size and in the angle between the short and long processes. Several

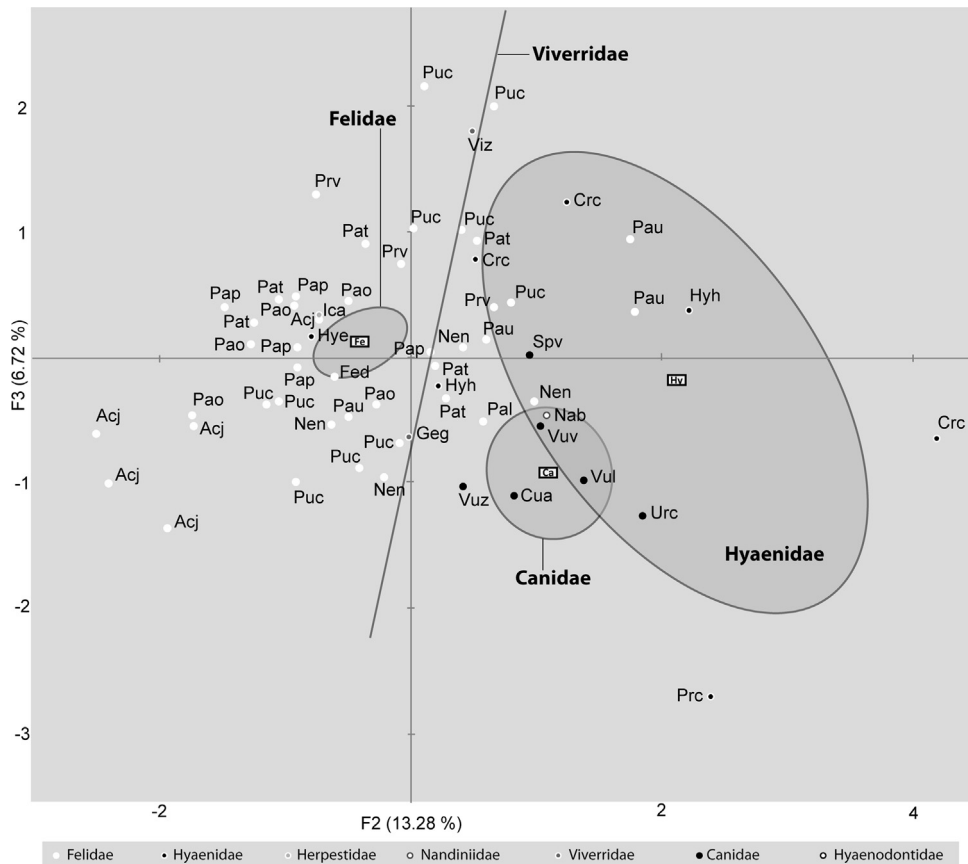


Fig. 9. PCA Analysis. Biplot of the second and third components of the PCA. We mapped the barycentres and confidence ellipses calculated for each family except for the Nandiniidae and Herpestidae because they are each represented by one specimen. Acj: *Acinonyx jubatus*; Crc: *Crocota crocuta*; Cua: *Cuon alpinus*; Fed: *Felis domestica*; Ges: *Genetta genetta*; Hye: *Hyaenodon exiguus*; Hyh: *Hyaena hyaena*; Ica: *Ichneumia albicauda*; Nab: *Nandinia binotata*; Nen: *Neofelis nebulosa*; Pal: *Panthera leo*; Pao: *Panthera onca*; Pap: *Panther pardus*; Pat: *Panthera tigris*; Pau: *Panthera uncia*; Prv: *Prionailurus viverrinus*; Prc: *Proteles cristatus*; Puc: *Puma concolor*; Spv: *Speothos venaticus*; Urc: *Urocyon cinereoargenteus*; Viz: *Viverra zibetha*; Vul: *Vulpes lagopus*; Vuv: *Vulpes vulpes*; Vuz: *Vulpes zerda*.

Fig. 9. Analyse ACP. Sont représentés les deuxième et troisième axes de l'ACP. Les barycentres et ellipses de confiance calculés pour chaque famille sont indiqués, excepté pour les nandiniidés et les herpestidés, car ces groupes ne sont représentés que par un individu. Acj : *Acinonyx jubatus* ; Crc : *Crocota crocuta* ; Cua : *Cuon alpinus* ; Fed : *Felis domestica* ; Ges : *Genetta genetta* ; Hye : *Hyaenodon exiguus* ; Hyh : *Hyaena hyaena* ; Ica : *Ichneumia albicauda* ; Nab : *Nandinia binotata* ; Nen : *Neofelis nebulosa* ; Pal : *Panthera leo* ; Pao : *Panthera onca* ; Pap : *Panther pardus* ; Pat : *Panthera tigris* ; Pau : *Panthera uncia* ; Prv : *Prionailurus viverrinus* ; Prc : *Proteles cristatus* ; Puc : *Puma concolor* ; Spv : *Speothos venaticus* ; Urc : *Urocyon cinereoargenteus* ; Viz : *Viverra zibetha* ; Vul : *Vulpes lagopus* ; Vuv : *Vulpes vulpes* ; Vuz : *Vulpes zerda*.

features are very closely related such as those that concern the facets (measurements 3, 9 and 10), the angles (measurements 8 and 11), and the length (measurements 1, 2, 4, and 7) (Table 5). Only the depth of the long process (measurement 5) is relatively variable in comparison with the other measurements.

These results have been compared to the habitats (Fig. 6), to the morphological type of the incus (Fig. 7), and to the taxonomic classification (Fig. 8). The ecology is not well separated by the first two components (Fig. 6): the confidence region of the open habitats is the largest one and totally overlaps that of the closed habitats. One can note that the axis 1 however separates the taxa that inhabit in mixed environments from those that live in closed and open environments (Fig. 6).

When looking at repartition of the incus morphological type on the new coordinate system, we can see that the second axis discriminate the different type of facets, notably

the 2-facet type from the 4-facet type and the U-shape type (Fig. 7). It is worth reminding that this axis mainly explains the angle between the short and long processes.

The families are far better discriminated by the combination of the two axes, but there is an overlap between the Hyaenidae and Canidae (Fig. 8). The Hyaenidae are remarkable in the large region they cover. This region is more reduced and does not overlap that of the Canidae when one of the two specimens of *H. hyaena* (IPUW A 168.10) is removed (Fig. 8; dashed line). However, it still represents the largest area of the PCA. This observation is the more remarkable when considering the limited number of specimens measured ($n=5$); by comparison, the Canidae are represented by six specimens and have a more restricted distribution. The first axis separates the large predators (canids, felids and hyaenids) from the small ones (herpestids, viverrids, and nandiniids). The second axis discriminates mainly the herpestids,

viverrids, as well as the Felidae from the Hyaenidae and Canidae.

We plot the specimens on the second and third axes (Fig. 9) in order to see how they explain the variation. The third axis only discriminates the families: the Canidae are well separated from the Felidae, but one can note that the hyaenids and viverrids have large distributions and are thus poorly discriminated. The third axis appears to be unrelated to difference either in incus morphological type or in ecology: all the barycentres are overlapped and close to 0 when considering the third axis (data not shown here). Consequently, it seems possible to use the depth of the long process (the sole measurement correlated with axis 3) only to discriminate families.

4. Discussion

A distinct pattern emerges when different families of Carnivora are examined: the morphology of the incudomalleolar facet can set clearly apart canids, hyaenids and felids from each other (with the exception of *Prionailurus*; Figs. 2–4). We found six different morphological facet types: 1) two facets with a lateral slope (felids, nandiniid and *Hyaenodon*), 2) four facets (canids and *Prionailurus*), 3) U-shaped facet (hyaenids), 4) two sloping facets (*Viverra*), 5) four tectiform facets (*Genetta*) and 6) two simple facets (herpestids; Figs. 2–4). These types seem to be related to the taxonomy (Fig. 5). It should be noted that *Proteles* is clearly different from other extant hyaenids in its ecology (insect eater) and ear morphology. For example, it shows enlarged bullae (ventrally strongly inflated) and a septum divides the bulla into an anterior and posterior chamber (personal observation KB). However, the morphology of the incudomalleolar facet is still similar to *Crocuta* and *Hyaena*. The U-shaped facet seems to be a shared feature of hyaenids. *Ichneumia* is most similar to hyaenids. *Nandinia* is similar to viverrids. *Prionailurus*, the fish cat, is completely different from other felids and is reminiscent of canids instead.

In *Hyaenodon*, the incus shows a large upper articulation surface and a lower circular area. This articulation facet is completely unlike those seen in canids: all of the canid specimens show a facet composed in various types by four articulation surfaces. Hyaenids are also showing a different formed facet (U-shaped). From this sample, the felids are most comparable to *Hyaenodon*: the malleo-incudal joint shows three articulation surfaces of the facet in (sub)equal development. The upper one is convex and the lower two are concave. Especially, the domestic cat and the cheetah have includes similar to the fossil predator *Hyaenodon*. In *Hyaenodon*, the inferior articulation surface is circular-oval and shows a lateral inclination. Both in the cat and in *Hyaenodon*, the incus is small and delicate. The long process is short in relation to the crus breve in *Hyaenodon* – this was not observed in any other taxa of this comparative carnivoran dataset. The crus breve is curved and, in this character, the *Hyaenodon* incus is most similar to that of the fox *Vulpes vulpes*. As no other hyaenodont ossicle is known up to now, further insight cannot be provided at present.

To conclude, the morphology of the incudo-malleolar facets can set apart several carnivoran clades (e.g., hyaenids and felids), hence it may be used when reconstructing the

relationships among Carnivora. The six different morphological facet types established herein can be viewed as potential character states.

4.1. Limitations

Prior to discussion of the interpretation of the outcome of this study, methodological effects should be noted. The approach of categorization of the habitat has an advantage of objectivity, but does not take into account species population density and that areas (biomes) are not independent from each other (due to being small and/or geographically adjacent). Thus, a certain bias of the approach cannot be excluded. Overall, the validity of the approach has not to be doubted in a major extent, because it was tested with literature and came to congruent assessments in most cases (see Section 2.2). Holz (1931) stated that the incus is specific for each species; this study provides further evidence for this finding. We observed no obvious intraspecific variability concerning especially the articulation facets. Furthermore, we propose a thorough study of auditory ossicles of modern taxa before drawing palaeobiological conclusions. Hence, there is a considerable number of recent taxa of high interest for this aim (other families of Carnivora, e.g., Mustelidae) not included in this study, which shall be seen only as a first step in this direction.

4.2. Influence of taxonomy on the morphology of the incus facets

The results from the PCA suggest a strong impact of phylogenetic relationships (family groups) on the incus facet morphology in our sample. However, both phylogeny (in terms of taxonomy) and ecology (in terms of habitat type) are considered to have influence on the morphology of the auditory ossicles (e.g., morphology of ossicles in subterranean rodents; Burda et al., 1992). The influence of factors other than taxonomic affiliations is apparent in some cases (e.g., *P. viverrinus*). We assume that the divergent morphology seen in *Prionailurus* could be explained by its different ecologic needs apart from habitat preference (e.g., hunting habits in water). Although in this study the influence of close taxonomic relationships (family groups) seems to appear more clearly (Figs. 5 and 8), a stronger influence of ecological than phylogenetic factors can be traced in other studies, e.g., in long bone ratios and ecomorphospaces by Meloro (2011) and Jones (2003). It should be noted that the sample consists only of a couple of families of recent Carnivora and is biased in favour for felids (see also Section 4.1 above). More felids were analysed due to the findings and the similarity to felids in the pre-analysis in Bastl (2012). However, despite their few numbers, canids are not dispersed, supporting the importance of the phylogenetic factors, as well as the consistency of the sample. It is worth noting, that the incus of the Mustelidae *Lutra lutra*, *Martes martes*, *Meles meles*, and *Mustela nivalis* (Paul, 2014) seem to exhibit a morphology of the facet not particularly similar to any morphology observed in the sample used herein, although CT reconstructions are shown which complicate a direct comparison.

The analysis of the variation of the incus facet morphology through a PCA based on measurements show that the global morphology seems to be better explained by the taxonomy than by the habitat (Figs. 5–7). However, the fact that our study shows a discrimination between the predators that live in mixed habitats and those from closed and open habitats indicates that there is nevertheless an influence of the ecology on the morphology of the incus. Moreover, it is worth noting, that the approach for classification of habitats here is objective, but does not take into account, that low population densities in different habitats located next to each other are valued as much as high population densities in one homogenous habitat, which could distort the picture.

The differences evidenced by the PCA are less striking than those visible on the incudo-malleal facet – as indicated above at least six types of facets can be recognized. The PCA shows that the morphology of the incus varies according to two ways: by modification of the overall size (measurements 1–4, 6–7, 9, 10), and by variation in the angle between the short and long process (measurements 8 and 11). The first feature appears to be related to both taxonomy and ecology, while the second way of transformation seems to be related only to taxonomy – and also to the incudo-malleal facet.

The importance of the correlation between almost all the measurements probably means that the modification of the incus is fairly tightly constrained and that the variation of its global morphology is restricted. Only hyaenids show a high variation for the incus. The crucial role of this ossicle in the mechanical transmission and the increasing of the sound may explain these limitations.

In order to better understand the relations between the morphology of the incus facets, incus measurements and taxonomy, it will be unavoidable to analyse these data using phylogenetic comparative methods such as phylogenetically independent contrasts. However, this will require an increase of the sample for both carnivorans (e.g., mustelids, ursids, phocids) and hyaenodonts (e.g., primitive hyaenodonts).

4.3. Inferences for *Hyaenodon*

It is noticed that *Hyaenodon* appears in the space covered by the feliforms of this sample in the PCA (Fig. 8). This extinct species is notably placed in proximity to the felids *Panthera pardus* (leopard) and *F. domestica*, and to the herpestid *I. albicauda* (white-tailed mongoose).

In the absence of knowledge about the morphology of the rest of the ossicular chain (e.g., arrangement with the malleus, the malleus and the stapes itself or development of ligaments, see above), the malleo-incudal articulation surface may at least give an idea on hearing inference (Fleischer, 1973). It should be noted that the *Hyaenodon* incus is the first known auditory ossicle in this taxon and also the first known within Hyaenodontidae and Hyaenodontia. The articulation facet gives a clue on the counterpart on the malleus. Therefore, we can assume that the malleus is saddle-shaped, showing two main articulation surfaces. The incus of *Hyaenodon* is small compared to the body size of the individual. Although the incus

size is approaching the incus size of the smaller cat, it is smaller than the incus of *Vulpes vulpes*, which has approximately the same body size for this species of *Hyaenodon* (Lange-Badré, 1979). However, the incus is known to be allometrically correlated to body size, namely negatively and proportionally smaller with in large-sized animals (Mason, 2001; Nummela, 1995) and up to now it remains unknown if relative incus size is unusual or not. A comparison to taxa more related to *Hyaenodon* would be of great interest, because the incus provides phylogenetic information (Quam and Rak, 2008; Rak and Clarke, 1979) as indicated here as well. As a comparative set of hyaenodont ossicles is hitherto not available, this topic awaits future discussion. There is no living relative of *Hyaenodon* left as the whole order died out during the Miocene. Therefore, basal carnivores like *Nandinia binotata* seem to be the best choice for a comparison as long as no other fossil material is unravelled. In fact, *Nandinia* and *Hyaenodon* share some morphological features, such as an articulation area made up by two facets and a lateral inclining one. However, those features are shared with most felids and *Hyaenodon* shows in addition a clearly set apart and circular round inferior facet as seen in *Acinonyx*. Concerning the possible habitat of *Hyaenodon*, it is assumed that it dwelled in more closed habitats in the Eocene and more open habitats in the Oligocene (Mellett, 1977). For the Oligocene species *H. exiguus* of the Quercy a subdesert to desert environment has been reconstructed (Legendre, 1986). In the PCA, *Hyaenodon* appears close to the taxa that live in mixed habitats (Fig. 6). However, results from the inner ear of the same fossil specimen of *Hyaenodon* plot close to *Genetta genetta* and show proximity to taxa living in a closed habitat (Pfaff et al., 2016). It was shown that the inner ear provides a phylogenetic signal in Carnivora-like musteloids, whereas the shape of the bony labyrinth gives a significant ecological signal (Grohé et al., 2016) and that the middle ear serves as a proxy by varying less intraspecifically than interspecifically in carnivorous taxa (Mustelidae: Rozen-Rechels et al., 2016). Concluding, the findings of data from the middle ear region of hyaenodont taxa analysed by modern CT-methods should be awaited to propose a specific reconstruction of behaviour, habitat and taxonomy of a fossil taxon.

Finally, the shape of the incus in respect to its function in *Hyaenodon* cannot be interpreted in detail (as Puria and Steele, 2008 did for other taxa). However, some significant clues give information on the hearing in *Hyaenodon*. An enlarged bulla is functionally linked to better low-frequency hearing as it increases middle ear compliance (Mason, 2016). There is no sign of specialisation to low-frequency hearing, as none of the characteristics like a large, inflated bulla, an enlarged incus, a flat articular surface of the incus (Argyle and Mason, 2008; Burda et al., 1992) is present in *Hyaenodon* (Bastl, 2012; Lange-Badré, 1979; Mellett, 1977). The auditory bulla is not greatly inflated like in the fennec fox or the hyaenid *Proteles*. Carnivora are known to have a wide frequency range, especially in felids (Peters, 1987), which is a useful adaptation for a predator. Cats are known to show a great sensitivity to high frequencies (Decraemer et al., 1989; Phillips et al., 1985). Similar frequency dependence was detected in the

lion and the domestic cat with lower sound pressures in the lion (Huang et al., 1997). The incus of *Hyaenodon* is most comparable to the cat, the leopard (PCA) and the cheetah (facet morphology). However, it is not known if such a similarity implies that *Hyaenodon* is capable of hearing a relative wide range of frequencies extending up values comparable to felids.

Author contributions

K. Bastl took the lead of the study and collected the specimens, took the measurements, prepared part of the tables and figures, designed the drawings and drafted the manuscript. D. Nagel gave advice through all processes and took part in drafting the manuscript. F. Solé performed the statistical analyses (e.g., PCAs), prepared part of the tables and figures and took part in writing the manuscript.

Disclosure of interest

The authors declare that they have no competing interest.

Acknowledgements

Kind thanks to the Institut für Paläontologie (Universität Wien) for providing facilities, tools, material and room. The University of Vienna supported one of us (KB) with travel grants (Awards of advancement scholarships of the University of Vienna, used for travel costs) for Paris. The Federal Science Policy Office of Belgium (Belspo Brain project BR/121/A3/PALEURAFRICA) supported the research of FS.

Christine Argot (MNHN) gave access to the Quercy collections and granted the loan of the specimens. Anita Gamauf (NMW) gave access to the collections of the NMW and granted a loan of comparative carnivore (canid) specimens. Jürgen Kriwet gave permission to work on the digital microscope and Rica Stepanek kindly introduced us to using this device. We thank Cathrin Pfaff for fruitful discussion. We are grateful for valuable input of two anonymous reviewers.

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