

# Oldest mephitine cranium and its implications for the origin of skunks

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Recent molecular studies have recognized the skunks (Mephitinae) to be the sister taxon of a clade comprising the Procyonidae and Mustelidae. These findings are inconsistent with the traditional placement of the skunks among mustelids, which is based on morphological evidence from extant taxa. This paper reports on a well-preserved cranium of a young individual, recovered from the middle Miocene deposits (MN 7+8, about 11–12 Ma) of Steinheim am Albuch, Germany. The fossil is the holotype of *Palaeomephitis steinheimensis* Jäger, 1839, which is here recognized as a senior subjective synonym of *Trochotherium cyamoides* Fraas, 1870 (consequently, *Palaeomephitis* Jäger, 1839 is a senior subjective synonym of *Trochotherium* Fraas, 1870). The specimen is identified as the oldest and most primitive mephitine cranium known to date, approaching the primitive morphology for the Mephitinae. It exhibits a combination of mephitine (accessory middle-ear chamber, lateral swelling of the squamosal) and mustelid (mustelid suprameatal fossa) synapomorphies, corroborating the view that skunks are derived from a mustelid ancestor. Its auditory bulla shows a slightly inflated and relatively large caudal entotympanic, which indicates that the uninflated and relatively small caudal entotympanics of adult mephitines, as well as their hypertrophied ectotympanics, are not primitive (as hitherto assumed) but derived, providing a synapomorphy that supports a sister-group relationship between the Mephitinae and Lutrinae.

Key words: *Palaeomephitis*, *Trochotherium*, Mephitinae, Mustelidae, Carnivora, phylogeny, taxonomy, morphology.

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## Introduction

The skunks (Mephitinae, including stink badgers, *Mydaus*) have traditionally been included in the carnivoran family Mustelidae (most recently in a close relationship to the Lutrinae and Melinae), based on morphological data collected from extant taxa (Bryant *et al.* 1993, and references therein). Recently, however, molecular evidence

has been presented (Ledje & Árnason 1996a, 1996b; Dragoo & Honeycutt 1997), arguing for a sister-group relationship between the Mephitinae and a clade containing the Procyonidae and Mustelidae. Because the two databases derived from extant taxa have provided inconsistent results, phylogenetic information from early members of the Mephitinae is essential for solving the problem of mephitine origins, especially as the fossil record is the only source of direct evidence of past organismal history.

Here I report a well-preserved cranium recovered from the lacustrine deposits of Steinheim am Albuch, southern Germany. This locality has yielded a classic middle Miocene floral and faunal assemblage (Heizmann 1976) referred to MN zone 7+8 (Bruijn *et al.* 1992) which corresponds to the interval of 11.2–12.5 Ma (Steininger *et al.* 1996). The other hitherto recorded Tertiary crania of skunks are about 3–9 million years younger and come from upper Miocene and Pliocene strata of Eurasia (Gaudry 1862; Alexejew 1916; Pilgrim 1933; Zdansky 1937; Krokos 1939; He & Huang 1991). The Steinheim specimen represents the most primitive mephitine cranium known to date, plausibly approaching the primitive morphology for this group. It exhibits features neglected in the previous descriptions of the cranium (by Jäger 1839, Fraas 1870, and Helbing 1936), proving its mephitine status and shedding new light on the relationships of the skunks. These features are presented in this paper.

**Institutional abbreviations:** AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, USA; BMNH, The Natural History Museum, London, UK; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; FSL, Centre des Sciences de la Terre, Université Lyon I, Lyon, France; FSP, Laboratoire de Géobiologie, Biochronologie et Paléontologie humaine, Université de Poitiers, Poitiers, France; ISEZ, Instytut Systematyki i Ewolucji Zwierząt PAN, Cracow, Poland; NMB, Naturhistorisches Museum, Basle, Switzerland; PVPH, Laboratoire de Paléontologie des Vertébrés et Paléontologie humaine, Université Paris VI, Paris, France; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; YPM-PU, Yale Peabody Museum (Princeton University Collection), New Haven, USA; ZM, Zoologisk Museum, Københavns Universitet, Copenhagen, Denmark.

## Taxonomic history and status

The reported cranium (Fig. 1A–C) was collected over 160 years ago and first described by Jäger (1839), who found it similar to those of extant *Conepatus* (a part of his *Mephitis*) and *Mephitis*, and accordingly named the fossil *Palaeomephitis Steinheimensis*. Fraas (1870) and Helbing (1936) redescribed the specimen; the former believed it represented a viverrid (his *Viverra Steinheimensis*), while the latter referred it to the alleged mephitine *Trocharion albanense*. Qiu & Schmidt-Kittler (1982) identified *Trocharion* as a leptarctine mustelid, and they (Schmidt-Kittler 1981; Qiu & Schmidt-Kittler 1982) consequently excluded the cranium from placement in this genus, assuming its affiliation with *Trochotherium cyamoides*, originally described by Fraas (1870) from the same deposits and also recorded from a few other European localities of middle Miocene age (Wegner 1913; Viret 1935; Wolsan & Engesser 1997).

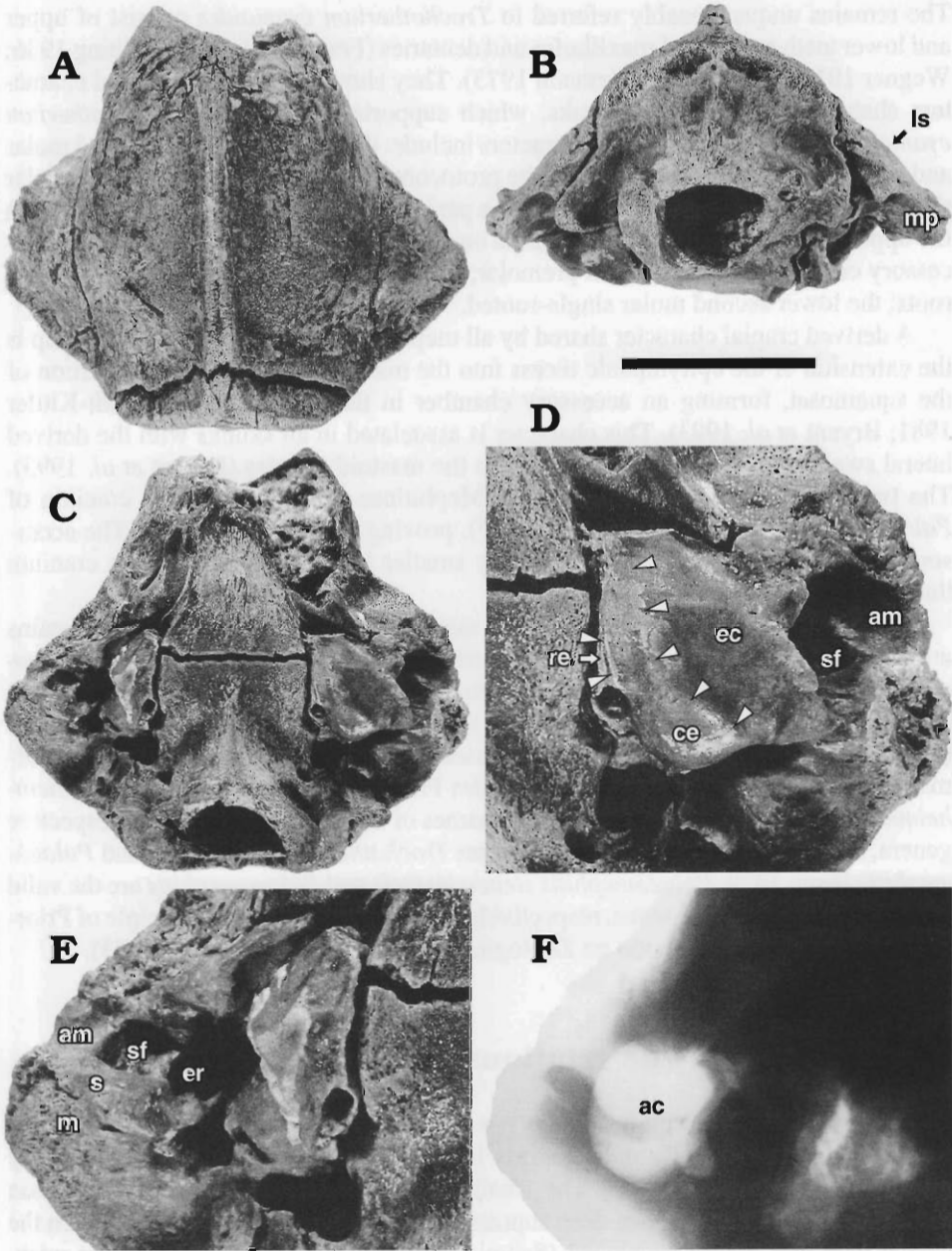


Fig. 1. Holotype cranium (SMNS 4743a) of *Palaeomephitis steinheimensis* in dorsal (A), posterior (B), and ventral (C) views, its left ear region in ventral view (D), and its right ear region (E) and a radiograph of this region (F) in ventral view. Abbreviations: ac, accessory chamber of the middle ear; am, roof of the external auditory meatus; ce, caudal entotympanic; ec, ectotympanic; er, epitympanic recess; ls, lateral swelling of the squamosal; m, mastoid; mp, mastoid process; re, rostral entotympanic; s, squamosal; sf, suprameatal fossa. White triangles indicate the suture between the rostral and caudal entotympanics (D, left) and an approximate border (the suture is fused and partly obliterated) between the caudal entotympanic and ectotympanic (D, right). Scale bar: A-C, 20 mm; D-F, 9 mm.

The remains unquestionably referred to *Trochotherium cyamoides* consist of upper and lower teeth and partial maxillaries and dentaries (Fraas 1870, 1885; Helbing 1936; Wegner 1913; Viret 1935; Heizmann 1973). They show a number of derived characters shared with the living skunks, which supports the view that *Trochotherium cyamoides* is a mephitine. These characters include: the lack of the upper second molar and upper and lower first premolars; the protocone wing of the upper fourth premolar shelf-like and positioned at the level of the paracone; the upper first molar larger than the upper fourth premolar; no metacone on the upper first molar and no posterior accessory cusp on the lower fourth premolar; the lower first molar with more than two roots; the lower second molar single-rooted.

A derived cranial character shared by all mephitines and exclusive to this group is the extension of the epitympanic recess into the mastoid and the posterior portion of the squamosal, forming an accessory chamber in the middle ear (Schmidt-Kittler 1981; Bryant *et al.* 1993). This character is associated in all skunks with the derived lateral swelling of the squamosal dorsal to the mastoid process (Bryant *et al.* 1993). The two unique synapomorphies of the Mephitinae are present in the cranium of *Palaeomephitis steinheimensis* (Fig. 1B, F), proving its mephitine status. The accessory middle-ear chamber is proportionally smaller (more primitive) in this cranium than it is in the living skunks.

Their mephitine status, presence at the same locality, and the fact that the remains attributed to *Trochotherium cyamoides* correspond in size to the cranium of *Palaeomephitis steinheimensis* support the view that the two names represent the same species. This view has already been expressed by Wolsan (1993a) and Wolsan & Engesser (1997), but no evidence was provided. Based on the evidence presented here, I formally synonymize *Trochotherium cyamoides* Fraas, 1870 with *Palaeomephitis steinheimensis* Jäger, 1839. Because these are names of the type species of their respective genera, I also synonymize the generic names *Trochotherium* Fraas, 1870 and *Palaeomephitis* Jäger, 1839. *Palaeomephitis steinheimensis* and *Palaeomephitis* are the valid names of the species and genus, respectively, in conformity with the Principle of Priority (International Commission on Zoological Nomenclature 1985: Article 23).

## Implications for the relationships of skunks

All extant mustelids except mephitines possess a suprameatal fossa that is partially or completely closed ventrally and anteriorly by the ossified tube of the external auditory meatus (Schmidt-Kittler 1981). The fossil record shows that this middle-ear fossa evolved from the entirely open deep suprameatal fossa of early mustelids in which the meatal tube was poorly developed (Schmidt-Kittler 1981; Wolsan 1993a). An open, deep suprameatal fossa is also characteristic of procyonids (Schmidt-Kittler 1981), but (contrary to Schmidt-Kittler 1981) it displays an essentially different configuration and its origin is distinct from that in mustelids. As evidenced by crania of Oligocene and early Miocene musteloids, the procyonid suprameatal fossa originated in consequence of a deep dorsal expansion of the primitively shallow fossa seen in stem musteloids (*Bavarictis*, *Brachypsalis*, *Mustelavus*, *Mustelictis*, *Oligobunis*, *Promartes*) and ailurids (*Ailurus*, *Amphictis*, *Simocyon*), and thereby preserved about equally extended lateral

and medial walls (Wolsan 1992, 1993a, 1993b, 1994, 1996, 1997a, 1997b; Wolsan & Lange-Badré 1996). In addition, the suprimeatal fossa and epitympanic recess are about equally extended dorsally (apomorphy), and the epitympanic recess is laterally excavated into the squamosal in front of the suprimeatal fossa (apomorphy) because there is no place for it over the fossa (Wolsan 1998). In contrast, the mustelid suprimeatal fossa developed from the primitive shallow fossa through ventral elongation of its lateral wall, so that the lateral wall apomorphically extends further ventrally than the medial wall, which may not be differentiated at all (Wolsan 1992, 1993a, 1993b, 1994, 1996; Wolsan & Lange-Badré 1996). The mustelid suprimeatal fossa extends less dorsally than the epitympanic recess (plesiomorphy), and the epitympanic recess is laterally excavated into the squamosal over the suprimeatal fossa (plesiomorphy). The early mustelid arrangement is unknown outside of the Mustelidae. This arrangement is also seen in *Palaeomephitis steinheimensis* (Fig. 1E), which indicates that the mustelid suprimeatal fossa was primitively present in the Mephitinae, and therefore argues for the mustelid status of the skunks. In the reported cranium the suprimeatal fossa is posteriorly deeply excavated into and partly floored by the medial part of the mastoid process, its medial wall is not differentiated, and the anterior and lateral walls are about perpendicular to the meatal roof (Fig. 1E). This form of the suprimeatal fossa conforms to that exhibited by the oldest and most primitive known, completely developed mustelid suprimeatal fossae (seen in late Oligocene members of *Plesictis*: AMNH 11001, NMB Bst3853, NMB Cod2181), with the exception that the lateral wall of the fossa in *Palaeomephitis steinheimensis* is less extended ventrally and the anterior wall is better developed. The loss of the suprimeatal fossa within the Mephitinae was apparently caused by the development of a long ectotympanic tube of the external auditory meatus, which is a characteristic feature of late Miocene to Recent skunks. In *Palaeomephitis steinheimensis* this tube is still short and incompletely developed, so that the meatus is roofed by the squamosal (Fig. 1D, E).

Among extant mustelids, the mephitines and lutrines are unique in having auditory bullae with an uninflated caudal entotympanic that is small relative to the ectotympanic (which is hypertrophied) and rostral entotympanic (Hunt 1974). This configuration has generally been considered primitive, following Hunt (1974), who relied on general evidence from carnivoran ontogeny. However, in the cranium of *Palaeomephitis steinheimensis* the caudal entotympanic is slightly inflated and much larger, and the ectotympanic is less well developed (Fig. 1D). The size relations between the two bones approach those seen among stem musteloids (e.g., the late Oligocene *Bavarictis*: BSP 1952II5) and in the earliest known ailurids (the late Oligocene to middle Miocene *Amphictis*: FSP PFRA28, ISEZ MF2130), the earliest known procyonids (the late Oligocene *Pseudobassar*: BMNH M9647, PVPH PVQ70-2, YPM-PU 11455, ZM 144), and the earliest known mustelids (the late Oligocene to early Miocene *Plesictis*: AMNH 11001, FSL 97448, NMB Bst3853, NMB Cod2181). Although the ossification of the reported cranium had not been completed before the end of the animal's life (as evidenced by numerous unfused sutures between bones; Fig. 1A–E), and therefore some ontogenetic changes in inflation and size proportions between the bullar bones could have occurred if the animal had lived longer, it is evident that the uninflated and small caudal entotympanics of late Miocene to Recent skunks, as well as their hypertrophied ectotympanics, are not primitive but derived. As the adult mor-

phology of the auditory bulla in *Palaeomephitis steinheimensis* is uncertain, and in all other known mephitines the apomorphic condition is present, I consider this condition apomorphic for the whole subfamily and therefore regard it as supporting a sister-group relationship between the Mephitinae and Lutrinae.

## Conclusions

- *Palaeomephitis steinheimensis* Jäger, 1839 is a senior subjective synonym of *Trochotherium cyamoides* Fraas, 1870 and the valid name for the species.
- *Palaeomephitis* Jäger, 1839 is a senior subjective synonym of *Trochotherium* Fraas, 1870 and the valid name for the genus.
- *Palaeomephitis steinheimensis* is a mephitine.
- The mephitines are mustelids.
- The Mephitinae and Lutrinae are sister taxa.

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## Najstarsza mózgowca przedstawiciela skunksów i jej znaczenie dla wyjaśnienia pochodzenia tej grupy

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### Streszczenie

Pochodzenie skunksów (Mephitinae) jest obecnie przedmiotem kontrowersji. Podczas gdy badania morfologiczne współczesnych taksonów potwierdzają tradycyjne umiejscowienie skunksów w obrębie ssaków drapieżnych z rodziny łasicowatych (Mustelidae), w bliskim pokrewieństwie do wydr (Lutrinae) i borsuków (Melinae), to wyniki badań molekularnych sugerują, że skunksy są grupą siostrzaną kładu obejmującego łasicowate i szopowate (Procyonidae). W tej sytuacji sprzeczności pomiędzy wynikami uzyskanymi na podstawie obu baz danych opartych na żyjących taksonach, dane paleontologiczne z wczesnych etapów ewolucji skunksów mogą mieć znaczenie decydujące dla ustalenia pozycji filogenetycznej tej podrodziny.

Najstarszą i najbardziej prymitywną znaną mózgowcą skunksa jest holotyp gatunku *Palaeomephitis steinheimensis* Jäger, 1839 (Fig. 1A–C). Mózgowca tę wydobyto ze środkowioceńskich (MN 7+8, ok. 11–12 mln lat temu) osadów Steinheim am Albuch w południowych Niemczech. Reprezentuje ona młodego osobnika, o czym świadczą liczne niezrośnięte szwy między kośćmi oraz ukształtowanie powierzchni kości (Fig. 1A–E).

Za młodszy subiektywny synonim *Palaeomephitis steinheimensis* uznano tutaj *Trochotherium cyamoides* Fraas, 1870, opisane z tych samych osadów i znane również z kilku innych środkowioceńskich stanowisk w Europie. Ponieważ obie nazwy dotyczą gatunków typowych swoich rodzajów, *Trochotherium* Fraas, 1870 jest młodszym subiektywnym synonimem nazwy *Palaeomephitis* Jäger, 1839.

Mózgowca *Palaeomephitis steinheimensis* posiada dodatkową komorę w uchu środkowym (Fig. 1F: ac) i boczną wypukłość kości łuskowej ponad wyrostkiem sutkowym (Fig. 1B: ls). Cechy te są unikalnymi synapomorfiami skunksów i świadczą o przynależności *Palaeomephitis steinheimensis* do tej podrodziny. Chociaż u współczesnych skunksów brak jest w uchu środkowym dołu nadprzewodowego (*fossa suprameatale*), w mózgowcu *Palaeomephitis steinheimensis* zagłębienie to występuje (Fig. 1E: sf) i jest wykształcone w sposób charakterystyczny dla najstarszych znanych łasicowatych i synapomorficzny dla tej rodziny. Wskazuje to na plezjomorficzną obecność tej cechy w obrębie podrodziny skunksów i przemawia za ich przynależnością do łasicowatych.

Spośród współczesnych łasicowatych, jedynie u skunksów i wydr kość wewnątrzbębenkowa tylna (*entotympanicum caudale*) nie jest wydęta i jest mała w stosunku do kości zewnątrzbębenkowej (*ectotympanicum*), która jest silnie rozwinięta, i kości wewnątrzbębenkowej przedniej (*entotympanicum rostrale*). Tak ukształtowane puszki bębenkowe skunksów i wydr traktowano dotąd jako cechę plezjomorficzną. W mózgowcu *Palaeomephitis steinheimensis* kość wewnątrzbębenkowa tylna jest jednak nieco wydęta i dość duża (Fig. 1D: ce), a kość zewnątrzbębenkowa jest stosunkowo mała (Fig. 1D: ec), zbliżając się względnymi rozmiarami do stosunków panujących u najstarszych znanych łasicowatych, szopowatych i małych pand (Ailuridae), a także w wymarłych rodzajach z pnia tych rodzin. Przemawia to za apomorficznością ukształtowania puszki bębenkowej skunksów, dostarczając w ten sposób synapomorfii na poparcie siostrzanego pokrewieństwa pomiędzy podrodzinaми skunksów i wydr.