

External brain morphology of the late Oligocene musteloid carnivoran *Bavarictis gaimersheimensis*

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The carnivoran mammal *Bavarictis gaimersheimensis* is the type and only species of the genus, known from a single locality (Gaimersheim 1–2, MP 27–28, 24.5–26 Myr) in southern Germany. An endocranial cast of the holotype of this species indicates a low degree of posterior and ventral neopallial expansion (little overlap of the cerebellum and the piriform lobes by the neopallium, the middle portion of the rhinal fissure only slightly and smoothly elevated), and a distinctive pattern of neopallial convolutions, characterized by the presence of a Y-shaped fissure mediodorsally (consisting of the ansate sulcus anteromedially, the coronal sulcus anterolaterally, and the lateral sulcus posteriorly) and an arched suprasylvian sulcus lateroventrally. The status of the cruciate sulcus is uncertain because the corresponding part of the braincase is not preserved. The species is presently best placed *incertae sedis* among basal musteloids.

Key words: Musteloidea, Carnivora, brain, morphology, phylogeny, Oligocene.

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Introduction

The musteloid carnivoran *Bavarictis gaimersheimensis* Mödden, 1991 is the type and only known species of the genus *Bavarictis* Mödden, 1991. The material referred to this species contains a nearly complete skull and several skull and mandible fragments and isolated teeth (Mödden 1991; Wolsan 1993a: p. 348, all BSP specimens under *Bavarictis*). All specimens come from a fissure filling near Gaimersheim in Bavaria, southern Germany. The faunal assemblages collected from the upper Oligocene fissure fillings of Gaimersheim (referred to as Gaimersheim 1 and 2) have been assigned to Mammal Paleogene Reference Levels MP 28 and MP 27, respectively (Biochrom'97

1997), which correspond to the interval of 24.5–26 Myr within the Chattian (Schlunegger *et al.* 1996).

Although a good deal of information on skull, mandible, and dental morphologies of *Bavarictis gaimersheimensis* has been published (Schmidt-Kittler 1981, as *Musteloidarum* n. gen. n. sp.; Mödden 1991; Wolsan 1992, 1993a, 1999, as *Bavarictis*; Cirot & Bonis 1993, as *Bavarictis*; Wolsan & Lange-Badré 1996, as *Bavarictis*), its external brain morphology has remained undescribed. The purpose of this report is to redress this omission and provide new information useful in phylogeny reconstruction.

Material and methods

In carnivorans, the internal surfaces of the braincase conform to the topography of the brain, so that a cast of the inside of the braincase (endocranial cast or endocast) reproduces in detail the external morphology of the brain (e.g., Radinsky 1968, 1971). The only preserved braincase of *Bavarictis gaimersheimensis* is that of the holotype (BSP 1952II5). Its internal surface is exposed except for some dorsal portions which are either broken off (in front of the tentorium) or covered by the matrix present behind the tentorium. A cast of the inside of this braincase was made by filling the endocranial cavity with liquid latex.

Institutional abbreviations: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York, United States of America; BMNH, Natural History Museum, London, United Kingdom; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; FMNH, Geology Department, Field Museum of Natural History, Chicago, United States of America; FSL, Centre des Sciences de la Terre, Université Claude Bernard, Lyon, France; FSP, Laboratoire de Géobiologie, Biochronologie et Paléontologie humaine, Université de Poitiers, Poitiers, France; ISEZ, Instytut Systematyki i Ewolucji Zwierząt PAN, Cracow, Poland; MNHN, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris, France; NMB, Naturhistorisches Museum, Basel, Switzerland; PVPH, Laboratoire de Paléontologie des Vertébrés et Paléontologie humaine, Université Pierre et Marie Curie, Paris, France.

Description

As evidenced by the endocranial cast (Fig. 1), the brain of *Bavarictis gaimersheimensis* was anteroposteriorly elongated and dorsoventrally flattened. Its length from a line connecting the anterior ends of the olfactory bulbs to the posterior end of the cerebellum was approximately 47 mm, the greatest width (across the piriform lobes) was 30.5 mm, and the greatest height measured from the dorsal surface of the neopallium to a line joining the ventral ends of the piriform lobes was about 23 mm. The combined olfactory bulbs were 13.5 mm long, 16.5 mm broad, and approximately 18 mm high. The cerebellum was apparently widely exposed, and so were the voluminous piriform lobes, indicating little posterior and ventral neopallial expansion. The neopallium was about 32 mm long and 30.5 mm broad. It exhibited a Y-shaped fissure mediadorsally

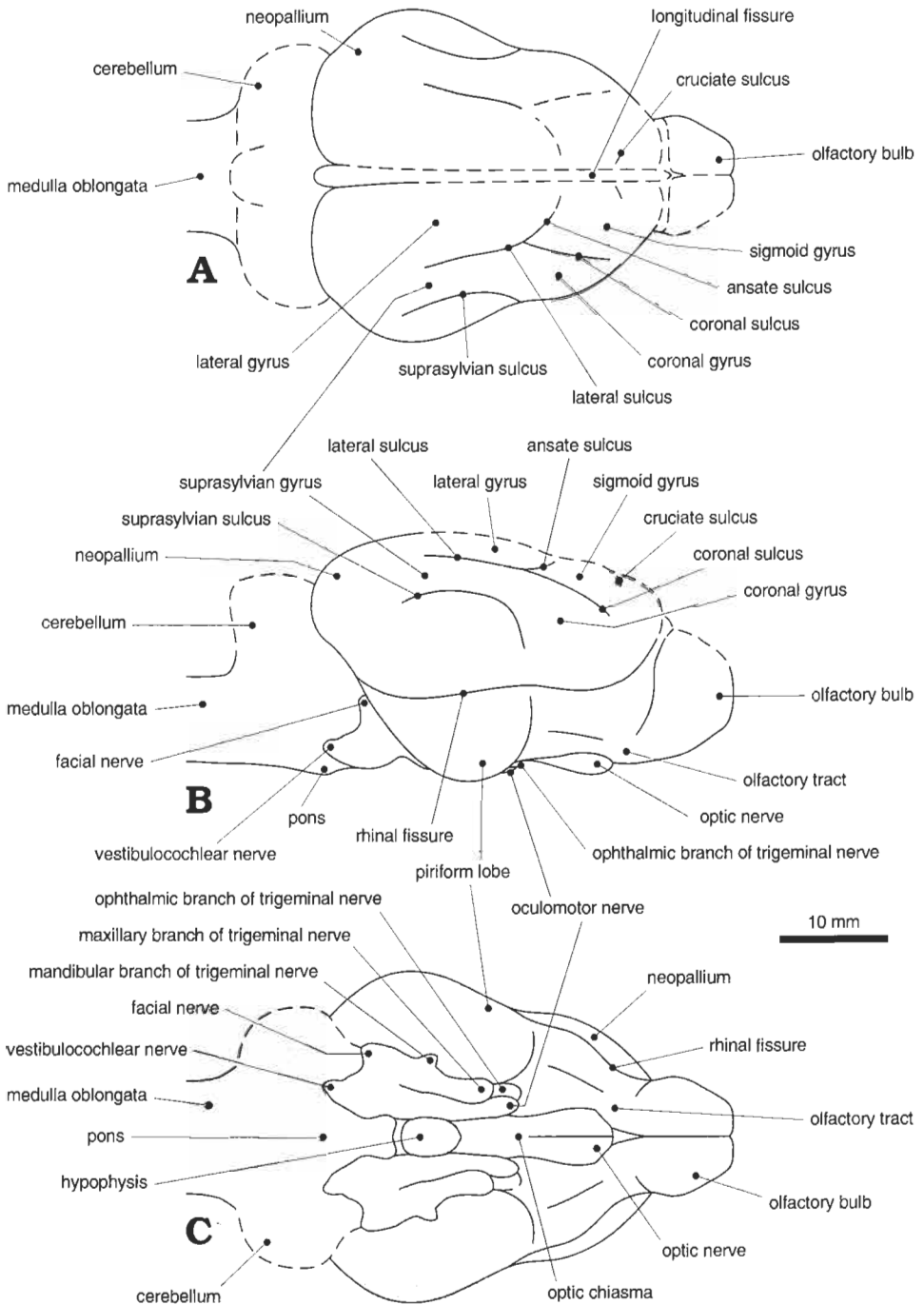


Fig. 1. A restoration of the external brain morphology in *Bavarictis gaimersheimensis*, based on an endocranial cast of the holotype (BSP 1952II5), in dorsal (A), right lateral (B), and ventral (C) views. Shaded areas and solid lines denote, respectively, surfaces and contours or grooves evidenced by the endocranial cast.

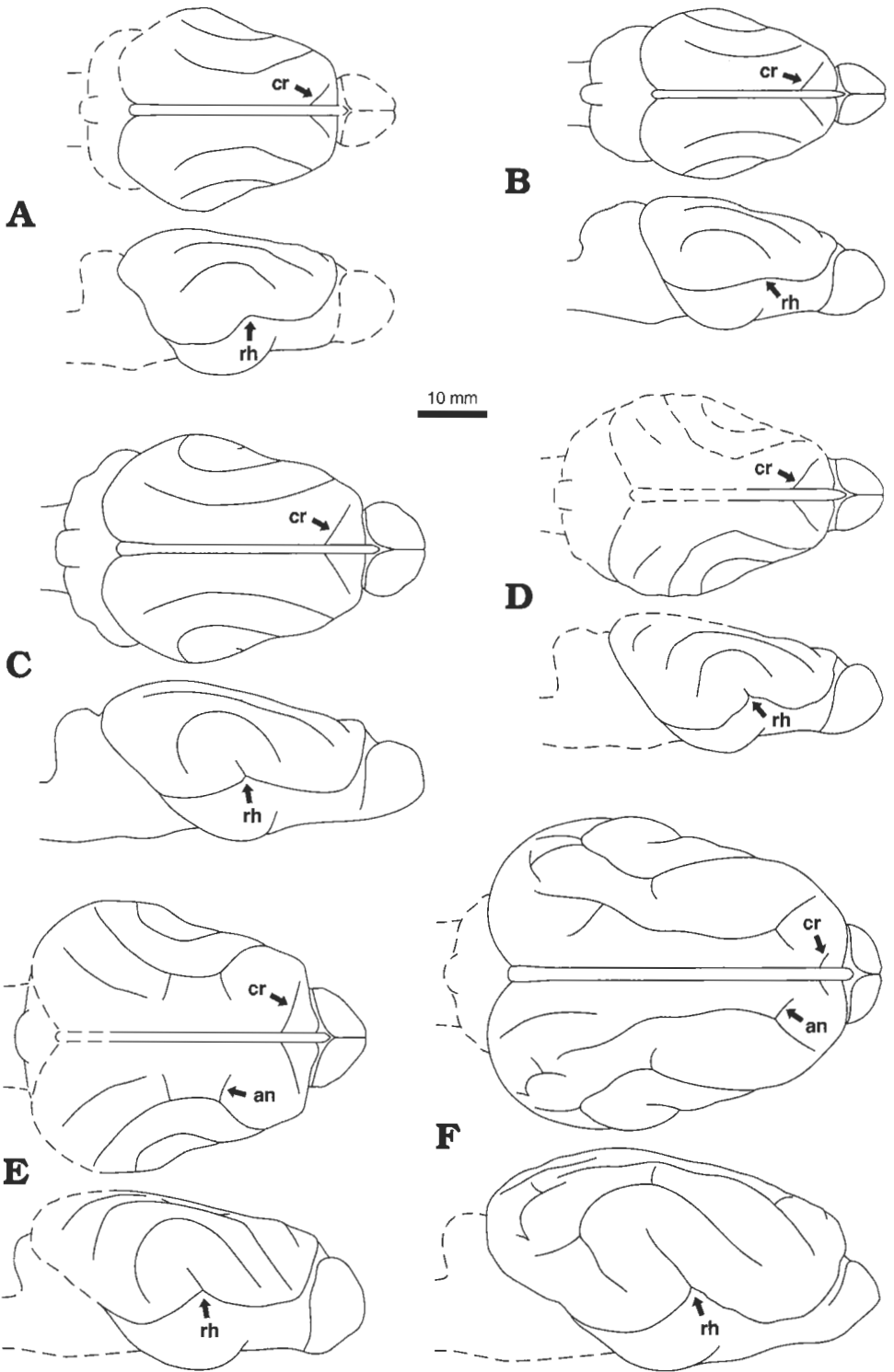
(composed of the ansate sulcus anteromedially, the coronal sulcus anterolaterally, and the lateral sulcus posteriorly) and an arched suprasylvian sulcus lateroventrally. The anterior limb of the suprasylvian sulcus was ventrally continuous with a marked depression that extended to the slightly and smoothly elevated middle portion of the rhinal fissure, and farther on the ventral surface of the brain, where it anteriorly delimited the piriform lobe. The sulci divided the anterior and central parts of the neopallium into the sigmoid and coronal gyri anteriorly and the lateral and suprasylvian gyri posteriorly. The status of the cruciate sulcus is uncertain because the corresponding part of the braincase is not preserved. We assume the presence of this sulcus in *Bavarictis gaimersheimensis* based on its occurrence in most early musteloids (Fig. 2; Filhol 1889; Piveteau 1951, 1961; Beaumont 1968; Radinsky 1968, 1971).

The hypophysis (or pituitary gland) and several cranial nerves are clearly reproduced on the ventral surface of the endocranial cast (Fig. 1C). The optic chiasma was situated at the level where the ansate, coronal, and lateral sulci met.

Phylogenetic implications

Although the musteloid status of *Bavarictis gaimersheimensis* is well supported (Schmidt-Kittler 1981, as *Musteloidarum* n. gen. n. sp.; Mödden 1991; Wolsan 1993a; Wolsan & Lange-Badré 1996) and has not been questioned, the phylogenetic relationships of this species within Musteloidea remain uncertain. *Bavarictis gaimersheimensis* has been considered a basal musteloid of indefinite affinities (Schmidt-Kittler 1981, as *Musteloidarum* n. gen. n. sp.; Mödden 1991; Wolsan 1992, 1999), placed in an unresolved multichotomy with *Ailurus*, *Amphictis*, *Potamotherium*, Mustelidae (containing *Mustelictis*, *Paragale*, *Plesictis*, and *Plesiogale*), and Procyonidae (Wolsan 1993a), recognized as basal within a clade comprising *Paragale*, *Plesictis*, and *Plesiogale* but not *Amphictis* and *Mustelictis* (Ciot & Bonis 1993), or regarded as a procyonid (McKenna & Bell 1997). Since McKenna & Bell (1997) presented no supporting evidence for the suggested relationship, and *Bavarictis gaimersheimensis* indeed shows none of the unequivocal synapomorphies of Procyonidae (Wolsan 1993a, b, 1994, 1996a, b, 1997a, b, 1998, 1999; Wolsan & Lange-Badré 1996), the only currently available hypothesis that proposes the resolved phylogenetic relationships of *Bavarictis gaimersheimensis* is that of Ciot & Bonis (1993).

Fig. 2. Restorations of dorsal (top) and lateral (bottom) views of brains of early musteloids, based on endocranial casts. **A.** *Mustelictis piveteaui*, PVPH PVQ69-1, early Oligocene (cf. Lange 1969: fig. [A, B], 1970: figs. 2, 3). **B.** *Plesictis branssatensis*, FSL 97448 (endocast FMNH PM57182), latest Oligocene–earliest Miocene (cf. Radinsky 1971: fig. 2B, 1977: figs. 5C, 7 [*Plesictis*]). **C.** *Paragale huerzeleri*, NMB MA4641 (endocast FMNH PM58910), early Miocene (cf. Radinsky 1971: fig. 2D). **D.** *Plesiogale angustifrons*, NMB SG2894 (endocast FMNH PM58911, reversed), early Miocene (cf. Beaumont 1968: fig. 3). **E.** *Promartes* sp., FMNH P25233, late Oligocene–early Miocene (cf. Radinsky 1971: fig. 2E). **F.** *Potamotherium valletoni*, AMNH 22520B (endocast FMNH PM58906), late Oligocene–early Miocene (cf. Filhol 1889: figs. 1, 2; Friant 1942: fig. [2]; Piveteau 1951: figs. 17, 18, 1961: fig. 199; Savage 1957: fig. 13a–c, pl. 2 [c], 1977: fig. 8G; Radinsky 1968: fig. 5C, 1971: fig. 2C). Shaded areas and solid lines denote, respectively, surfaces and contours or grooves evidenced by the endocranial casts. Arrows indicate the ansate sulcus (**an**), the cruciate sulcus (**cr**), and an excavation between the anterior and posterior limbs of the rhinal fissure (**rh**).



Cirot & Bonis (1993) recorded two features to support a close relationship among *Bavarictis*, *Paragale*, *Plesictis*, and *Plesiogale*. They defined these features as (1) '[f]ossa muscularis major au niveau des deux autres fosses de l'oreille moyenne', or '[t]hree fossae of the middle ear (suprameatal fossa, recessus epitympanicus, fossa muscularis major) on the same right line', and (2) 'ébauche du conduit auditif externe ossifié', or 'beginning of an ossified external auditory tube' (Cirot & Bonis 1993: p. 1332). Although the ossified external auditory meatus is indeed apomorphically better developed in *Bavarictis*, *Paragale*, *Plesictis*, and *Plesiogale* than it is in *Mustelictis* and primitively in *Amphictis* (Wolsan 1993a), our survey of all available basicrania representing species of *Amphictis* (BSP 1952II4769, FSP PFRA28, ISEZ MF2130/93), *Bavarictis* (BSP 1952II5), *Mustelictis* (BMNH M7490, FSP MGB60, PVPH PVQ69-1), *Paragale* (NMB MA4641, NMB Ph3638), *Plesictis* (AMNH 11001, FSL 97448, MNHN LIM343, NMB Bst3853, NMB Cod2181, NMB Chr1168, NMB Chr2573), and *Plesiogale* (NMB SG2894) has not revealed any significant difference in the positional interrelationship among the suprameatal fossa, epitympanic recess, and fossa muscularis major between either *Amphictis* or *Mustelictis*, on the one hand, and any one of *Bavarictis*, *Paragale*, *Plesictis*, or *Plesiogale*, on the other. We therefore regard Cirot & Bonis' (1993) hypothesis as supported by a single feature only (i.e., an advanced ossification of the external auditory meatus).

A comparison of the details of brain morphology reproduced by the endocranial cast of *Bavarictis gaimersheimensis* (Fig. 1) with those of other early musteloids (Fig. 2; Filhol 1889: figs. 1, 2, 1890: fig. 1; Friant 1942: fig. [2]; Piveteau 1951: figs. 10, 11, 14–18, 1961: figs. 197–199; Savage 1957: fig. 13a–c, pl. 2 [c, d], 1977: fig. 8G; Beaumont 1968: fig. 3; Radinsky 1968: fig. 5C, 1971: fig. 2B–E, 1977: figs. 5C, 7 [*Plesictis*]; Lange 1969: fig. [A, B], 1970: figs. 1–3; Wolsan 1997b) indicates that *Bavarictis gaimersheimensis*, *Potamotherium valletoni*, and *Promartes* sp. are derived in possessing the ansate sulcus, and that *Bavarictis gaimersheimensis* and *Plesictis branssatensis* are most primitive with respect to ventral neopallial expansion (the two species show the least overlap of the piriform lobes by the neopallium and the least marked excavation between the anterior and posterior limbs of the rhinal fissure). The differences in the degree of ventral neopallial expansion provide evidence in conflict with Cirot & Bonis' (1993) hypothesis and suggest that *Mustelictis piveteaui*, *Paragale huerzeleri*, *Plesiogale angustifrons*, *Potamotherium valletoni*, and *Promartes* sp. may have shared a common ancestor not shared with *Bavarictis gaimersheimensis* and *Plesictis branssatensis*. On the other hand, the distribution of the ansate sulcus among early musteloids supports an alternative hypothesis that *Bavarictis gaimersheimensis*, *Potamotherium valletoni*, and *Promartes* sp. are more closely related to one another than to any of the remaining species. The first alternative supported by brain morphology implies parallel developments of the ansate sulcus in *Bavarictis gaimersheimensis* and within a hypothetical clade containing *Potamotherium valletoni* and *Promartes* sp., whereas the second alternative requires parallel ventral expansion of the neopallium in that clade and within a hypothetical clade comprising *Mustelictis piveteaui*, *Paragale huerzeleri*, and *Plesiogale angustifrons*.

In view of the conflicting distribution of the brain characters among *Bavarictis gaimersheimensis* and other early musteloids, of the weakness of support for Cirot & Bonis' (1993) hypothesis (which is based on a single basicranial character that is in

conflict with one brain character), of the lack of support for McKenna & Bell's (1997) placement of *Bavarictis gaimersheimensis* within Procyonidae, and of the plesiomorphic status of most cranial, dental, and brain features in *Bavarictis gaimersheimensis* (Schmidt-Kittler 1981, as *Musteloidarum* n. gen. n. sp.; Mödden 1991; Wolsan 1992, 1993a; Wolsan & Lange-Badré 1996; this paper), the species is presently best placed *incertae sedis* among basal musteloids.

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Externe Gehirnmorphologie des oberoligozänen musteloiden Raubtiers *Bavarictis gaimersheimensis*

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Zusammenfassung

Bavarictis gaimersheimensis Mödden, 1991 ist eine monotypische Gattung innerhalb der musteloiden Carnivora. Das bekannte Material dieser Art stammt ausschliesslich aus der süd-deutschen Spaltenfüllung Gaimersheim 1–2 (MP 27–28, 24.5–26 Myr). Ein Ausguss des Endocraniums des Holotyps der Art (Fig. 1) zeigt für das Neopallium, neben einem geringen Grad an Ausdehnung nach posterior und ventral, auch ein Furchungsmuer, das durch den bogenförmigen Sulcus suprasylvius und den Y-förmigen Verlauf von Sulcus lateralis, ansatus und coronalis charakterisiert wird. Konkrete Aussagen zum Sulcus cruciatus sind nicht möglich, weil der entsprechende Teil des Schädels nicht überliefert ist.

Sein Vorhandensein wird jedoch in der Rekonstruktion des Gehirns von *Bavarictis gaimersheimensis* angenommen (Fig. 1), weil er bei den meisten frühen Vertretern der Musteloidea auftritt (Fig. 2). Ein Vergleich mit den Rekonstruktionen der Gehirne anderer frühen Vertreter der Musteloidea (Fig. 2) zeigt, dass *Bavarictis gaimersheimensis*, *Potamotherium valletoni* und *Promartes* sp. durch den Besitz des Sulcus ansatus als evoluiert anzusehen sind, wohingegen *Bavarictis gaimersheimensis* und *Plesictis branssatensis* bezüglich der Ausdehnung des Neopalliums als am primitivsten anzusehen sind. Die Differenzen in der Ausdehnung des ventralen Neopalliums legen den Verdacht nahe, dass *Mustelictis piveteaui*, *Paragale huerzeleri*, *Plesiogale angustifrons*, *Potamotherium valletoni* und *Promartes* sp. einen gemeinsamen Vorfahren gehabt haben, den sie nicht mit *Bavarictis gaimersheimensis* und *Plesictis branssatensis* geteilt haben. Auf der anderen Seite wird durch die Verteilung des Auftretens eines Sulcus ansatus unter den frühen Musteloiden die Hypothese gestützt, dass *Bavarictis gaimersheimensis*, *Potamotherium valletoni* und *Promartes* sp. innerhalb dieser Gruppe als nächstverwandt anzusehen sind. Die erste Alternative impliziert eine voneinander unabhängige Entstehung des Sulcus ansatus bei *Bavarictis gaimersheimensis* und innerhalb einer hypothetischen Entwicklungslinie, die *Potamotherium valletoni* und *Promartes* sp. umfasst. Die zweite Alternative setzt eine voneinander unabhängige Entstehung der Ausdehnung des ventralen Neopalliums bei der letztgenannten Entwicklungslinie und bei einer hypothetischen Entwicklungslinie voraus, die *Mustelictis piveteaui*, *Paragale huerzeleri* und *Plesiogale angustifrons* umfasst. Angesichts des Konfliktes bei der Bewertung dieser Merkmale für die phylogenetischen Beziehungen von *Bavarictis gaimersheimensis* und angesichts des plesiomorphen Charakters der meisten Merkmale an Schädel, Bezahnung und Gehirn bei dieser Art, sollte *Bavarictis gaimersheimensis* weiterhin als incertae sedis innerhalb der basalen Musteloidea betrachtet werden.

Morfologia mózgu późnooligocenijskiego ssaka drapieznego *Bavarictis gaimersheimensis*

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Streszczenie

Wczesny musteloid *Bavarictis gaimersheimensis* Mödden, 1991 jest typowym i jedynym znanym gatunkiem rodzaju *Bavarictis* Mödden, 1991. Całość materiału reprezentującego ten gatunek pochodzi z pojedynczego stanowiska (Gaimersheim 1–2) w południowych Niemczech, datowanego na późny oligocen (MP 27–28, 24,5–26 mln lat temu). Odlew wnętrza mózgowcaszki holotypu *Bavarictis gaimersheimensis* (Fig. 1) wskazuje na niewielki zasięg kory nowej (*neocortex*) w okolicy ciemieniowo-potylicznej i skroniowej mózgu (znaczące odstąpienie mózdzku – *cerebellum* i płatów gruszkowatych – *lobi piriformes*, nieznaczne i łagodnie przebiegające wzniesienie środkowej części szczeliny węchowej – *fissura rhinalis*), a także na obecność czterech bruzd w obrębie kory nowej: bruzdy pętlowatej (*sulcus ansatus*), koronowej (*sulcus coronalis*) i bocznej (*sulcus lateralis*), połączonych w kształcie litery Y, oraz łukowatej bruzdy suprasylwialnej (*sulcus suprasylvius*). Stan zachowania mózgowcaszki nie umożliwia stwierdzenia obecności czy braku bruzdy krzyżowej (*sulcus cruciatus*). Założenie obecności tej bruzdy w rekonstrukcji mózgu *Bavarictis gaimersheimensis* (Fig. 1) oparte jest na jej

występowaniu u większości wczesnych przedstawicieli Musteloidea (Fig. 2). Z porównania z rekonstrukcjami mózgow innych wczesnych musteloidów (Fig. 2) wynika, że *Bavarictis gaimersheimensis*, *Potamotherium valletoni* i *Promartes* sp. łączy apomorficzna obecność bruzdy pętlowatej, oraz że *Bavarictis gaimersheimensis* i *Plesictis branssatensis* są najprymitywniejszymi znanymi musteloidami pod względem zasięgu kory nowej w części skroniowej (najbardziej odsłonięte płaty gruszkowate, najslabiej zaznaczone wzniesienie w środkowej części szczeliny węchowej). Podczas gdy różnice w zasięgach kory nowej sugerują, że *Mustelictis piveteaui*, *Paragale huerzeleri*, *Plesiogale angustifrons*, *Potamotherium valletoni* i *Promartes* sp. miały wspólnego przodka, którego nie dzieliły z *Bavarictis gaimersheimensis* i *Plesictis branssatensis*, to występowanie bruzdy pętlowatej przemawia za bliskim pokrewieństwem między *Bavarictis gaimersheimensis*, *Potamotherium valletoni* i *Promartes* sp. Pierwsza z hipotez zakłada niezależny rozwój bruzdy pętlowatej u *Bavarictis gaimersheimensis* oraz w obrębie hipotetycznego kladu zawierającego *Potamotherium valletoni* i *Promartes* sp., natomiast druga hipoteza wymaga niezależnego powiększenia kory nowej w tym kladzie oraz w innym hipotetycznym kladzie, zawierającym *Mustelictis piveteaui*, *Paragale huerzeleri* i *Plesiogale angustifrons*. Wobec tej sprzeczności i braku lub słabości poparcia dla wcześniejszych hipotez o powiązaniach filogenetycznych *Bavarictis gaimersheimensis* (dyskutowanych w pracy), a także przy plezjomorficzności większości cech czaszki, uzębienia i mózgu tego gatunku, brak uzasadnienia dla jego innej pozycji niż *incertae sedis* w obrębie bazalnych Musteloidea.