Freshwater fishes from the Pannonian of the Vienna Basin with special reference to the locality Sandberg near Götzendorf, Lower Austria

3 figures, 2 tables, 4 plates

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Zusammenfassung

Der wiederentdeckte Holotypus zu *Capitodus subtruncatus* MÜNSTER, 1842 wird beschrieben; seine taxonomische Stellung sowie der bisher unklare Locus typicus werden diskutiert. Aufgrund der Morphologie von Schlundknochen und -zähne ist *Capitodus* ein jüngeres Synonym zu *Barbus* CUVIER & CLOQUET 1816. Besonders Merkmale der Schlundzähne sind typisch für die Untergattung *Luciobarbus* HECKEL 1843. Der Locus typicus von *Barbus* ("*Luciobarbus*") *subtruncatus* (MÜNSTER 1843) ist mit hoher Wahrscheinlichkeit Brunn/Vösendorf (Pannonian E) im Wiener Becken.

Von der Lokalität Sandberg bei Götzendorf (Pannonian F) werden neun Arten von Süßwasserfischen (davon vier neue Arten) aus fünf Familien beschrieben: *Barbus* („*Bertinius*") *vindobonensis* nov. sp., *Tinca* sp., *Scardinius haueri* (Cyprinidae); *Cobitis martini* nov. sp., *Cobitis* nov. sp. (Cobitidae); *Heterobranchus austriacus* (Clariidae); *Silurus* nov. sp. (Siluridae); *Gobius* sp. (Gobiidae); aff. *Umbrina* sp. (Sciaenidae). Die Fundstelle lieferte somit die diverseste und am Besten dokumentierte Süßwasserfisch-Fauna des Vallesiums (MN9 und 10, unteres Obermiozän). Vier Arten sind Neueinwanderer zu Beginn des Obermiozäns. Ihre Paläobiogeographie zeigt südwestasiatische und afrikanische Affinitäten. Mit *Barbus* („*Bertinius*") *vindobonensis* wurde zum ersten Mal in einem europäischen Becken eine Adaptation an Malaccophagie innerhalb einer *Barbus* Linie nachgewiesen. Eine phylogenetische Linie von *Barbus subtruncatus* (Pannonian E, ~10.5 Ma) zu *B. vindobonensis* (Pannonian F, ~10.0 Ma) wird vermutet. Ein charakteristisches Merkmal der Götzendorfer Fischfauna ist, im Gegensatz zu mittelmiozänen Vergesellschaftungen, die Dominanz benthischer Arten. Eine mögliche Ursache ist das Vorkommen der zwei Wels-Arten. Als benthische Fischräuber erniedrigt ihr Fraßdruck die zwischenartliche Konkurrenz Benthos fressender Fische, was eine höhere Diversität auf dieser trophischen Ebene zur Folge hat. Es wird vermutet, dass biotische Events an der Mittel-/Obermiozän Grenze, namentlich das regionale Aussterben der Channidae (tagaktive Räuber mit visueller Beuteortung) und das Einwandern der Siluridae und Clariidae (nachtaktive Räuber mit olfaktorischer und mechanosensorischer Beuteortung) maßgebliche Auswirkungen auf die Struktur aquatischer Paläo-Ökosysteme hatte.

Abstract

The rediscovered holotype specimen of *Capitodus subtruncatus* MÜNSTER 1842 is described; the taxonomic setting as well as the hitherto obscure locus typicus are discussed. Based on the morphology of the pharyngeal bone and teeth, *Capitodus* MÜNSTER 1842 is a junior synonym of *Barbus* CUVIER & CLOQUET 1816. The morphology of the pharyngeal teeth are shared with the subgenus *Luciobarbus* HECKEL 1843. The locus typicus of *Barbus* ("*Luciobarbus*") *subtruncatus* (MÜNSTER 1842) is very probably Brunn/Vösendorf (Pannonian E) in the Vienna Basin.

Additionally, nine freshwater fish species representing five families are described from the locality Sandberg near Götzendorf (Pannonian F): *Barbus* ("*Bertinius*") *vindobonensis* nov.

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sp., *Tinca* sp., *Scardinius haueri* (Cyprinidae); *Cobitis martini* nov. sp., *Cobitis* nov. sp. (Cobitidae); *Heterobranchus austriacus* (Clariidae); *Silurus* nov. sp. (Siluridae); *Gobius* sp. (Gobiidae); aff. *Umbrina* sp. (Sciaenidae). Four taxa are new and until now this is the most divers and best documented freshwater fish fauna from the Vallesian (MN9 and MN10, lower Upper Miocene) of Europe. Four of the nine described taxa are unknown from pre-Vallesian sediments in Europe. They show Southwest Asian and African palaeobiogeographic affinities.

With *Barbus* ("*Bertinius*") *vindobonensis*, for the first time, from a European basin an adaption to molluscan diet in a lineage of *Barbus* is described. A phylogenetic lineage from *Barbus subtruncatus* (Pannonian E, ~10.5 Ma) to *B. vindobonensis* (Pannonian F, ~10.0 Ma) can be assumed. Furthermore, the autecology of the described taxa is discussed providing evidence that in contrast to Middle Miocene fish communities a characteristic feature of the Götzendorf fauna is the dominance of benthic species. A possible explanation is the presence of both catfishes as benthic piscivorous predators inducing through a top-down effect the high diversity of the benthivorous fishes suppressing the competition at the trophic level of their prey. It is hypothesized that the biotic events at the Middle/Upper Miocene transition, particularly the extinction of the Channidae (diurnal visual predator) and the immigration of the Siluridae and Clariidae (nocturnal olfactory and mechanosensory predators) altered the structure of the aquatic palaeo-ecosystems basically.

Keywords: freshwater fishes, *Barbus*, *Capitodus*, *Cobitis martini* nov. sp., Pannonian, palaeoecology

Introduction

Little is known about the freshwater fishes of the European Upper Miocene. This time span, which is characterized by important palaeoclimatic changes (the end of the Middle Miocene climatic optimum by an onset of Antarctic glaciation FLOWER & KENNETT 1994, BÖHME in prep.) and biogeographical reorganisations (AGUSTI 2000) play a specially role for studying the evolution of aquatic palaeoecosystems.

The first scientific work about fossil fishes from the Vienna Basin is dated back in 1842 by earl Georg zu MÜNSTER. Systematic studies on freshwater fishes are lacked until THENIUS (1952) and WEINFURTER (in PAPP & THENIUS 1954) described the fauna of Brunn-Vösendorf. Later, GAUDANT (1994) studied the new excavated freshwater fishes from Sandberg near Götzendorf (RÖGL et al.

1993). Since then additional material from this locality, especially from the private collection ULLRICH (Natural History Museum of Vienna), was available and a redescription of this freshwater fish fauna together with the newly rediscovered type specimen of *Capitodus subtruncatus* MÜNSTER 1842 seems necessarily.

Material and methods

The material described here is deposited in the Bavarian State Collection (holotype of *Capitodus subtruncatus* MÜNSTER 1842; acronym BSP) and in the Natural History Museum of Vienna (Ullrich Collection from Sandberg near Götzendorf; acronym NHMW). Additional material of *Scardinius haueri* (MÜNSTER 1842) from Vösendorf is deposited in the National Museum of Natural History Stuttgart (acronym SMNS). Comparative os-
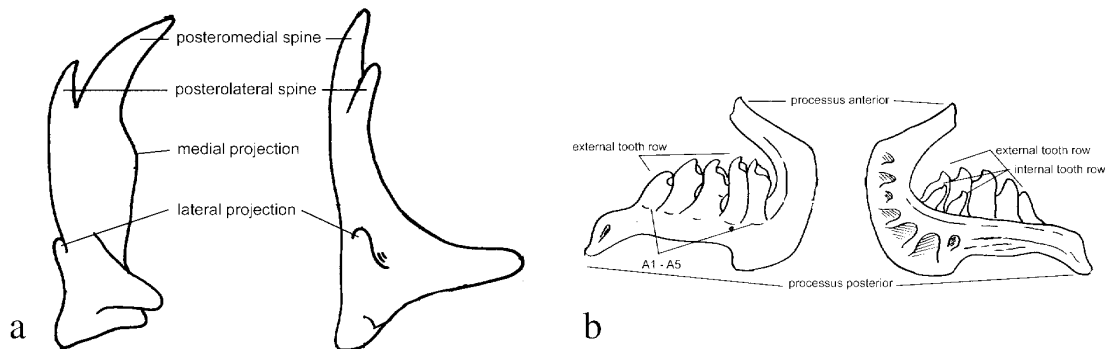

Fig. 1: Terminology of cobitid lateral ethmoids (after SYTCHEVSKAYA 1989) A and cyprinid pharyngeal bones B.

teological material of extant species are mainly from the private collection of the author (acronym PCB). The skeletons of West Asian barbs are from the collection of the Institute of Palaeoanatomy Munich (acronym IPM).

The terminology used follows FINE et al. 1997 for pectoral spines of Siluriformes, SYTCHEVSKAYA 1989 for the lateral ethmoids of Cobitidae (Fig. 1A) and NAKAJIMA 1984 for the pharyngeal dentition of Cyprinidae (Fig. 1B).

The genus *Capitodus* MÜNSTER 1842

As far back as 1842 earl Georg zu MÜNSTER described a collection of fish remains from the Vienna Basin. Among the fossils which have been collected by privy councillor HAUER at Vienna, was a bone fragment with teeth, on which Münster based a new genus and species: *Capitodus subtruncatus* MÜNSTER 1842 Fig. 2).

He placed *Capitodus* together with additional new species within the family Pycnodontidae. This assignment was lasting a long time. Then ZITTEL (1887-1890) recognized that the fossil remain represents a pharyngeal bone of a cyprinid, comparing it with *Chondrostoma* and *Tinca*. In the past century the genus was mentioned only seldom, usually in synopsises (at last by CARROLL, 1987). A revision has been never done and the original after all has been taken as lost (WEINFURTER, 1954).

The rediscovery of the type specimen of MÜNSTER in the Bavarian State Collection of Palaeontology and Geology at Munich enables for the first time a more precise knowledge of the systematic position of *Capitodus subtruncatus* MÜNSTER 1842. ZITTEL's designation as Cyprinidae is confirmed to be correct, moreover a close relationship to *Barbus* CUVIER & CLOQUET 1816 can be ascertained.

MÜNSTER described altogether in the two papers 1842 and 1846 five species of the genus *Capitodus*, beside the abovementioned *Capitodus subtruncatus*, further *C. truncatus*, *C. angustus*, *C. dubius*, and *C. ? interruptus*. The original specimens of all these species could be investigated at the Bavarian State Collection of Palaeontology and Historical Geology. I found that the letter four abovementioned species belong not to the Cyprinidae but to the Sparidae (see synonymy list). Except *Capitodus ? interruptus* - a praemaxillaria-fragment, the three other species are based on isolated teeth. Two types of teeth can be distinguished: spatula shaped teeth (*C. truncatus*, *C. dubius*) and pin- to cone-shaped teeth (*C. subtruncatus* - pro parte, *C. angustus*). Both types of teeth occur among diverse genera of Sparidae. SCHULTZ (1998) referred, investigating the fish fauna of the Korneuburg Basin (Karpatian), special spatula shaped teeth to the genus *Diplodus*, and some pin- to cone-shaped teeth to Sparidae gen. et sp. indet.

Thus, *Capitodus subtruncatus* MÜNSTER 1842 is the unique valid species of the cyprinid genus *Capitodus* MÜNSTER, 1842.
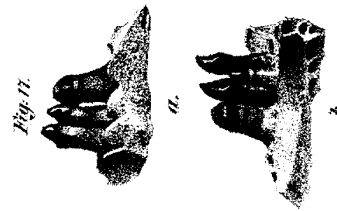

Fig. 2: Original figure from the type of *Capitodus subtruncatus* MÜNSTER 1842 (MÜNSTER 1842: pl. 6, fig. 17).

Provenance of the holotype specimen

In the original description of MÜNSTER (1842: 68) no place of discovery is given for the specimen which he created as holotype of *Capitodus subtruncatus*. At the beginning of his work he mentions as provenance of all the described specimens "Tertiär-Becken von Wien". On the other hand, MÜNSTER gives more precise information regarding other species. They stem chiefly from Neudörfl (= Neudorf an der March, = Devinska Nova Ves), Nußdorf, Enzersdorf and Brunn (= Vösendorf/Brunn). In a subsequent work (MÜNSTER, 1846: Taf. I, Fig. 2a-d) he figured specimens referred to *Capitodus subtruncatus* from Neudörfl, which are also housed at Munich, but belong all to sparide teeth (see synonymy list).

On the attached label of the holotype also Neudörfl an der March is recorded as place of discovery. Already WEINFURTER (1954) expressed doubt on the correctness of this assignment reasoning the state of preservation. He supposed Brunn/Vösendorf as locus typicus based on the frequent occurrence of *Capitodus*-like remains in this outcrop.

Nowadays, distinct localities are referred to the old name Neudörfl (= Neudorf an der March, = Devinska Nova Ves) encompassing differential fossils and showing varied genesis (FEJFAR, 1990). On the one side Neudorf fissure 1-3 (Karst fissure fillings with terrestrial tetrapods), on the other side Devinska Nova Ves - Bonanza (submarine cave filling with marine and terrestrial vertebrates), and Neudorf - Sandberg (littoral sands with marine and terrestrial vertebrates). Both, according to the time of discovery (the holotype has been collected about 1840) as well as the ecology of the recorded fish fauna (exclusively marine fishes at Bonanza and Neudorf-Sandberg; SCHUBERT, 1906; HOLEC, 1973; HOLEC et al. 1987), none of the abovementioned localities can be assumed.

Furthermore, also Nußdorf and Enzersdorf yielded a pure marine (shark) fauna (MÜNSTER, 1842 und 1846).

Since MÜNSTER had in hand certainly material from Brunn/Vösendorf at the time of his first description in 1842 (additional cyprinids and sparids) and WEINFURTER (1954) mentioned a frequent occurrence of *Capitodus subtruncatus* like teeth from this locality, Brunn/Vösendorf can be assumed only as locus typicus beyond question.

Synonymy of the genus *Capitodus* MÜNSTER 1842

Capitodus MÜNSTER, 1842

v   1842 *Capitodus subtruncatus* nov. sp. – MÜNSTER,
              Beiträge zur Petrefaktenkunde, V: Taf. VI,
              Fig. 17a, b.

v, non 1842 *Capitodus truncatus* nov. spec. – MÜNSTER,
              Beiträge zur Petrefaktenkunde, V: Taf. VI,
              Fig. 13a, b, c; 14.

v, non 1842 *Capitodus angustus* nov. spec. – MÜNSTER,
              Beiträge zur Petrefaktenkunde, V: Taf. XV,
              Fig. 8a, b.

v, non 1846 *Capitodus subtruncatus* MÜNSTER - MÜNSTER,
              Beiträge zur Petrefaktenkunde, VII: Taf. I,
              Fig. 2a-d; Taf. II, Fig. 1, 7, 8.

v, non 1846 *Capitodus truncatus* MÜNSTER – MÜNSTER,
              Beiträge zur Petrefaktenkunde, VII: Taf. II,
              Fig. 2.

v, non 1846 *Capitodus* MÜNSTER – MÜNSTER, Beiträge zur
              Petrefaktenkunde, VII: Taf. II, Fig. 3-6.

v, non 1846 *Capitodus* ? *interruptus* nov. spec. – MÜNSTER,
              Beiträge zur Petrefaktenkunde, VII: Taf. I, Fig.
              3 a-c.

v, non 1846 *Capitodus dubius* nov. spec. – MÜNSTER,
              Beiträge zur Petrefaktenkunde, VII: Taf. II,
              Fig. 10-16.

Type and only species: *Capitodus subtruncatus* MÜNSTER 1842: pl. 6, fig. 17a,b. BSP AS-VII-998.

Description of the holotype specimen

Cyprinidae

Barbus CUVIER & CLOQUET 1816

Barbus ("*Luciobarbus*") *subtruncatus*
(MÜNSTER 1842)
pl. 1, fig. 1-3

v   1842 *Capitodus subtruncatus* nov. sp. – MÜNSTER,
              Beiträge zur Petrefaktenkunde: Taf. 6,
              Fig. 17a, b.

v, non 1846 *Capitodus subtruncatus* MÜNSTER – MÜNSTER,
              Beiträge zur Petrefaktenkunde, VII: Taf. I,
              Fig. 2a-d; Taf. II, Fig. 1, 7, 8.

nv   1954 Cyprinide gen. et sp. indet. – WEINFURTER in
              PAPP und THENIUS: Vösendorf – ein
              Lebensbild etc., S. 32 f.

Locus typicus: Brunn/Vösendorf near Wien (see PAPP & THENIUS 1954)

Stratum typicum: Pannonian E (*Congeria sub-globosa* zone) of the biozonation of the Vienna Basin (after PAPP 1985); absolut age of the type locality ~10.5 Ma (after DAXNER-HÖCK 2001).

Material: Only the holotype of *Capitodus subtruncatus* MÜNSTER 1842, a right pharyngeal bone with teeth (BSP AS-VII-998).

Diagnosis: Pharyngeal teeth in three rows – pharyngeal tooth formula 5.3.2.. The A1 (?), A2 and B1 teeth

are molariform. The A2 is not much enlarged and shows a weak hook at the tip. The A1 was like the B1 reduced to a small accessorial tooth. The A3 and A4 teeth are cylindrically, slightly crescent shaped with a curved groove on the posterior crown flank and a hook at the outer side of the tip. Processus anterior of the pharyngeal bone short and massive. Neither an anterior nor a posterior edge of the pharyngeal bone is developed.

Description: The delivered pharyngeal bone is completely preserved except the processus posterior. In ventral view, three rows of pharyngeal teeth can be seen (pl. 1, fig. 2). The external row carries five teeth from which two (A2 and A3) are still preserved and three can be viewed as tooth bases (A1, A4, and A5). On the figure of the holotype by MÜNSTER the tooth A4 was present yet (Fig. 3). The A2 is molariform and slightly hooked. The diameter of the dental base of the A1 measures only a third of the A2 indicating a small accessory tooth sized as the B1. Certainly, its crown was also molariform.

The A3 and A4 teeth are cylindrical, slightly crescent shaped with a curved groove on the posterior crown flank and a hook at the external side of the tip. The angle between the masticatory plane and the longitudinal axis of both tooth is about 60°. On the original figure by MÜNSTER, the A4 has essentially a similar morphology as the A3 (see Fig. 3).

The A5 lies on the outermost lateral flank of the pharyngeal bone. Its dental base points to a slim, rudimentary tooth with a diameter like the C2.

The second row of teeth carries three teeth. The B1 is morphologically similar to the more as half as bigger A2. He is molariform but without a accentuated hook (pl. 1, fig. 3). The not preserved B2 and B3 are smaller regarding their diameter than the B1.

The third row carries two teeth but only the bases are visible. The C1 was thick in proportion (diameter like the B2). In contrast, the C2 seem to have been a rudimentary tooth. Beside the A5, he was the most slender of the whole pharyngeal dentary. The pharyngeal teeth formula of holotype is 5.3.2.

The pharyngeal bone posses a short but massive processus anterior. In the latitude of the A2 he stopped to reduce to a smaller scale, and his flanks stretch hereon parallel. The processus goes over to the central bone area without any indication of an anterior or posterior pharyngeal bone edge.

Comparison: The tooth formula 5.3.2., the short and massive processus anterior of the pharyngeal bone and the absence of an anterior and posterior edge of the pharyngeal bone point to a taxonomical position within *Barbus* CUVIER & CLOQUET 1816 (= *Barbus* sensu latu). The development of both strong but not very enlarged, hooked molariform A2 teeth and cylindrical, slightly crescent shaped A3 and A4 teeth with a curved groove on the posterior crown flank and a hook at the external side of the tip are shared with the subgenus *Luciobarbus*

HECKEL 1843 (DOADRIO 1990; see e.g. the Iberian *B.* (*Luciobarbus*) *graellsii* on pl. 1, fig. 4, 5 and the West Asian *Barbus* (*Luciobarbus*) *barbulus* on pl. 1, fig. 6). *Barbus*("*Luciobarbus*") *subtruncatus* differ from *Barbus* ("*Bertinius*") *vindobonensis* nov. sp. by the hooked and less enlarged and molarized A2.

Discussion: The subgenus *Luciobarbus* HECKEL 1843 is based on morphological evidence and includes North African, West Asian, South-East European and Iberian species. Whereas BERREBI (1995) had some doubt about its monophylety, MACHORDOM & DOADRIO (2001) confirmed the monophylety by means of mtDNA investigatation, but did not include West Asian species. According to the latter authors, the genus *Barbus* sensu latu can be divided in five main mitochondrial lineages, one of them *Barbus* sensu strictu (tetraploid barbels of the Palaearctic) with the subgenera *Barbus* and *Luciobarbus*.

Moreover, TSIGENOPOULOS et al. (1999) have shown among North Mediterranean *Barbus* s.s. lineages that ecophaenotypes (e.g. rheophile and fluvio-lacustrine species groups) appear to be paraphyletic. Thus, the adaptation to distinct ecological niches (e.g. mountain or lowland waters, molluscan or piscivorous diet) gaves rise to a similar phenotype of independent taxa by convergence (see also NAGELKERKE & SIBBING 2001 for African barbels). The similar morphology of the pharyngeal teeth of the investigated species of *Luciobarbus* and *Barbus* ("*Luciobarbus*") *subtruncatus* can be a convergent evolution induced by a similar type of food. Therefore this subgenus is used here not in a phylogenetical sense, but in quotation marks to signalize these trophic relationships. Beside these similarities in the A2-A4 teeth, a molariform B1 tooth as in *Barbus* ("*Luciobarbus*") *subtruncatus* is unknown from all investigated *Barbus* species.

Autecology: The members of *Luciobarbus* (species list see DOADRIO 1990) inhabit slow running waters of lowland streams and some species are able to tolerate brackish water conditions. It seems that they are unspecialised bottom feeders (molluscs, insect larvae), but detailed studies are lacking.

The freshwater fish fauna from Sandberg near Götzendorf, Lower Austria

Cyprinidae

Barbus CUVIER & CLOQUET 1816

Barbus ("*Bertinius*") *vindobonensis* nov. sp.
pl. 2, fig. 1-16

v 1994 *Palaeocarassius* sp. – GAUDANT, pl. 2, fig. 1-5
v 1994 *Barbus* sp. – GAUDANT, pl. 1, fig. 16

Material: 13 molariform (A2) teeth, 30 spatulate (A3, A4) teeth, 5 molariform/ mammiliform (A1, B1) teeth, 3 cylindrical (A5, B2, B3, C1, C2) teeth, 1 pharyngeal bone fragment, 1 dorsal spine.

Holotype: Pharyngeal bone fragment (pl. 2, fig. 13; NHMW2002z0002/0001).

Paratypes: Two molariform A2 teeth (NHMW2002z 0002/0002, 0003; pl. 2, fig. 1, 2), two molariform/ mammilliform A1/B1 teeth (NHMW2002z 0002/0004, 0005; pl. 2, fig. 11, 12), four spatulate A3/A4 teeth (NHMW2002z0002/0006-0009; pl. 2, fig. 3-6), four cylindrical B2/B3/C1/C2 teeth (NHMW2002z0002/ 0010-0013; pl. 2, fig. 7-10), one dorsal spine (NHMW 2002z0002/0014; pl. 2, fig. 14-16).

Locus typicus: Sandberg near Götzendorf (Lower Austria), Vienna Basin.

Stratum typicum: Pannonian F (*Congeria neumayri/C. zahalkai* zone) of the biozonation of the Vienna Basin (after PAPP 1985); absolut age of the type locality ~10.0 Ma (after DAXNER-HÖCK 2001).

Derivatio nominis: From the latin name for Vienna (lat.: Vindobona)

Diagnosis: A new species of the genus *Barbus* CUVIER & CLOQUET 1816 with a serrated dorsal spine and a strong heterodonty (molariform A2 tooth; molariform/mammiliform A1, B1 teeth; spatulate A3, A4 teeth; cylindrical B2, B3, C1, C2 teeth; hooked teeth in juveniles) similar to the extant *Barbus lorteti, B. longiceps, B. xanthopterus* and *B. subquincunciatus*. It differs from these species by the unreduced tooth formula 5.3.2.

Description: The genus *Bertinius* was erected by FANG (1943) on *Barbus lorteti*, characterized mainly by an enlarged, molariform A1 teeth. Later KARAMAN (1971) referred *Barbus longiceps, B. lorteti* and *B. subquincunciatus* to *Bertinius* based on this feature. KRUPP (1985a) regarded *Bertinius* as a junior synonym of *Barbus*, due to the convergent evolution of enlarged, molariform teeth in the external row in different lineages of *Barbus*. The name *Bertinius* is used here in the sense of a paraphyletical taxon characterized by enlarged, molariform teeth.

As stated by KRUPP (1985a, b), the pharyngeal teeth of the aforementioned species are highly heterodontous. Therefore and due to the isolated preservation of the material, the morphotypes are described separately.

Molariform teeth (pl. 2, fig. 1, 2): The smooth crowns are round to slightly oval. The maximal diameter is 5.5 mm. The crown height varies between 45% and 60% of the value ot the diameter. In some specimens the masticatory surface is markedly rubbed off. These teeth are regarded as A2 teeth. Some smaller molariform teeth (up to 2 mm in diameter) show a slight mammiliform hook on the centre of the crown (pl. 2, fig. 11, 12). These teeth are regarded as A1 or B1. That the A1 is a small molariform tooth show the holotype (pl. 2, fig. 13), a pharyngeal bone fragment with a small molariform/

mammiliform A1 and a typical tooth base at the position of a big molariform A2.

Spatulate teeth (= crescent shaped of DOADRIO 1990): (pl. 2, fig. 3-6) The plate like crowns are broadened distally and are only slightly concave. The crowns bend to the internal side from the tooth base (pl. 2, fig. 6). The cross-section of the tooth is crescently (visible on the masticatory facet), mainly from tear to comma shaped (pl. 2, fig. 3, 4). On unmasticated crowns a slight hook is visible on the external site (pl. 2, fig. 5). The maximal diameter of the crown is 5.5 mm. These teeth are regarded as A3 (tear shaped cross-section) or A4 teeth (comma shaped cross-section).

Cylindrical teeth: (pl. 2, fig.7-10) The crowns are more or less cylindrical, not broadened distally and sharply concave bended on the inner side. The tooth crown is attached nearly straight on the tooth base. The top of unmasticated crowns (pl. 2, fig. 8, 9) is asymmetrically and on the external side slightly hooked. On the posterior crown flank a curved groove is developed. The maximal diameter of the crown is 4.5 mm. These teeth are regarded as A5. Smaller teeth (up to 1.5 mm) of the same morphology are regarded as B2, B3, C1 or C2 teeth (see GAUDANT 1994: pl. 2, fig. 2).

Hooked teeth: (see GAUDANT 1994, pl. 1, fig. 16) These teeth are of typical *Barbus*-like morphology: slender, round in cross-section, with a concave and rough masticatory area, and a strong and hooked tip.

Comparison: The cylindrical, sharply bended teeth are a common feature of species of *Capoeta* and *Varicorhinus*, but they are never associated with molariform and spatulate teeth. The coexistence of big molariform with spatulate and cylindrical teeth indicates strong similarities with the West Asian molluscivorous *Barbus* species *B. lorteti* (Fig. 3A), *B. longiceps* (Fig. 3B), *B. subquincunciatus* (pl. 1, fig. 7, 8) and *B. xanthopterus* (pl. 1, fig. 9, 10), formerly united under the genus *Bertinius* FANG 1943. All these species share a reduced tooth formula of 4.3.2. or 3.3.2. (the ancestral one within *Barbus* is 5.3.2.), as a result by a reduction of the first (and last in *B. subquincunciatus*) tooth of the external row. The big molariform tooth is therefore the A1. In *B.* ("*Bertinius*") *vindobonensis* the first tooth of the external row is not fully reduced (pl. 2, fig. 13), the big molariform tooth is the A2 and the tooth formula was probably like that of the ancestral type 5.3.2.

Only one tooth (of 600 investigated) is of the hooked type. This small tooth (1,8 mm in diameter) is interpreted as originated from a juvenil individual, since in the extant molluscivorous *Barbus* the tooth morphology of juvenile specimens differ not from typical *Barbus* (KRUPP 1985a).

Barbus ("*Bertinius*") *vindobonensis* nov. sp. differ from *Barbus* ("*Luciobarbus*") *subtruncatus* by the smooth, more enlarged, and molarized A2.
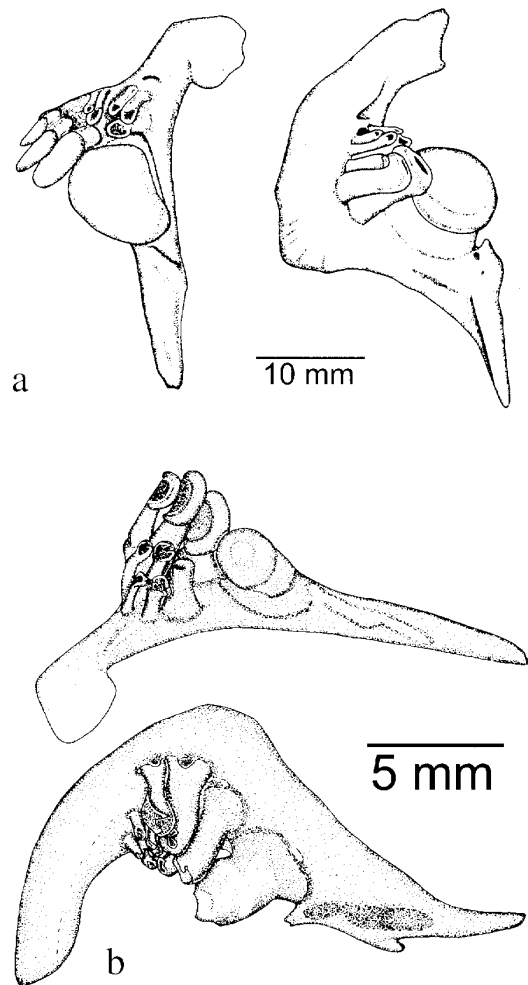

Fig. 3: A: Pharyngeal bone of *Barbus lorteti* SAUVAGE 1882, from KRUPP 1985 a; B: Pharyngeal bone from *Barbus longiceps* VALENCIENNES in CUVIER & VALENCIENNES 1842, from KRUPP 1985 b.

The spatulate teeth of *Barbus* ("*Bertinius*") *vindobonensis* nov. sp. are regarded as *Palaeocarassius* OBRHELOVA 1969 by GAUDANT (1994). They differ from *Palaeocarassius* by the following features (see BÖHME 1999: fig. 2): the bigger size, the lesser compressed crown (up to tear shaped in cross-section), the more bended connection of the crown to the tooth base, and the lesser degree of distal crown broadening. The genus *Palaeocarassius* extincts at the Middle/Upper Miocene boundary and is known in Western and Central Europe from the upper Lower Miocene (MN3/4) to the uppermost Middle Miocene (MN8).

Discussion: The morphology of the pharyngeal teeth of *Barbus* ("*Bertinius*") *vindobonensis* nov. spec. shows strong similarities with the extant West Asian species *Barbus lorteti*, *B. longiceps*, *B. xanthopterus* and *B. subquincunciatus*. These taxa are probably members of the

subgenus *Luciobarbus* HECKEL 1843, but genetical investigations are not done. The most outstanding feature, which is shared by all taxa, is an enlarged molariform teeth in the external row. This modification is regarded by KRUPP (1985a, b) and BANISTER & CLARKE (1980) as an adaptation to a molluscan diet. Therefore, the occurrence of this feature points to a convergent origin, to ecophenotypes, and do not reflect a monophyletic origin. KRUPP (1985a) described molariform crowns of pharyngeal teeth from Pliocene lake deposits in the Ghab Basin (Syria) and referred them to a molluscivorous *Barbus* species. These sediments are very rich on endemic *Viviparus*, *Melanopsis* and *Dreissena* species (KINZELBACH 1980, KRUPP 1985a) like the sediments of Sandberg near Götzendorf (RÖGL et al. 1993). Now, for the first time, from a European basin an adaptation to molluscan diet in a lineage of *Barbus* is described. It is noteworthy that except of the Tigris-Euphrat drainage system most extant molluscivorous *Barbus* species occur allopatrically. Each basin is inhabited by at least one species of *Barbus* which is specialized on a molluscan diet (KRUPP 1985a), e.g. *Barbus longiceps* in the Jordan Basin, *B. lorteti* in the Orontes Basin, or as an African example *B. eurystomus* in the Malawi Basin (BANISTER & CLARKE 1980). Only the Tigris-Euphrat basin yielded with *B. subquincunciatus* and *B. xanthopterus* two (probably non-related) species with enlarged molariform teeth.

Barbus ("*Luciobarbus*") *subtruncatus* from little older sediments at Brunn-Vösendorf is similarly in some aspects (morphology of the A3 and A4) to *B.* ("*Bertinius*") *vindobonensis*, but in regard to the adaptation on molluscan diet his A2 shows a lesser degree of molarification and displays therefore a more primitive condition. A phylogenetic lineage from *Barbus subtruncatus* (Pannonian E, ~10.5 Ma) to *B. vindobonensis* (Pannonian F, ~10.0 Ma) can be assumed.

Stratigraphical and biogeographical distribution: Up to now only known from the locus typicus.

Autecology: Based on the tooth morphology this fishes are adapted on molluscan diet. The extant representatives of this food type are riverine fishes, this can also be assumed for *Barbus vindobonensis* nov. sp.

Tinca sp.
pl. 3, fig. 9-12

v 1994 *Tinca* sp. – GAUDANT, pl. 1, fig. 10-12

Material: 10 isolated teeth (NHMW2002z0003/0001-0003, 0005); one pharyngeal bone fragment (NHMW 2002z0003/0004).

Description: The cross-section of these blunt and stout teeth is oval (pl. 3, fig. 11). The masticatory surface bend to the tooth axis by 50°-60°. On the external side, beneath the rudimentary tip of the tooth, a small incision is developed (pl. 3, fig. 9, 10). This incision can be ex-

tended into the masticatory surface (pl. 3, fig. 11). The pharyngeal bone fragments show a slightly curved, broad and stout processus posterior and an anteriorly directed expansion of the lateral edge of the bone (pl. 3, fig. 12). The tooth formula is 4.0.

Comparison: The morphology of the pharyngeal teeth and bone and the tooth formula closely resemble that of the extant green tench *Tinca tinca*. They differ only slightly by a stronger and more extended incision on the external tooth side and a stronger anteriorly directed expansion of the lateral edge of the pharyngeal bone. The pharyngeal teeth and bone of the fossil genus *Palaeotinca* OBRHELOVA 1969 differ by a more prominent developed tooth-tip, a stronger bended masticatory surface and in some specimens by one tooth on the second tooth row (tooth formula 4-5.0-1.).

Discussion: The fossil history of tenches in Europe can be traced back to the beginning of the Upper Oligocene (MP25). During the Upper Oligocene and Lower Miocene the genus *Palaeotinca*, which contains three species, is common especially in fluviatile sediments. After a gap during most parts of the Middle Miocene (MN5-MN6), the first representatives of *Tinca* occur in the upper Middle Miocene (MN7). In contrast to the riverine *Palaeotinca*, *Tinca* occurs mainly in stillwater habitats.

Stratigraphical and biogeographical distribution: The extant genus *Tinca* is known in Europe since the upper Middle Miocene (MN7 at Steinheim).

Autecology: The extant tench is a strictly limnophilous fish. Its typical habitat are meso- or eutrophic shallow lakes in which they live mainly near the bottom. The oxygene requirement is low. They feed on different types of zoobenthos (e.g. the so called tench-snail *Bithynia tentaculata* but also arthropods).

Scardinius BONAPARTE 1837

Scardinius haueri (MÜNSTER 1842)
pl. 3, fig. 1-6, 8

v   1842 *Soricidens haueri* nov. sp. – MÜNSTER, pl. 6, fig. 5-11
nv 1949 *Leuciscus haueri* (MÜNSTER) – WEINFURTER
nv 1954 *Leuciscus haueri* (MÜNSTER) – WEINFURTER in PAPP & THENIUS, p. 32-33
v   1994 *Rutilus* sp. – GAUDANT, pl. 1, fig. 13-15
v   1994 *Scardinius* nov. sp. – GAUDANT, pl. 1, fig. 1-9

Material: 27 isolated teeth (NHMW2002z0004/0001-0004, 0008) and three pharyngeal bone fragments (NHMW2002z0004/0005-0007); aditional material (14 isolated teeth) from the type locality Vösendorf (SMNS-80555)

Description: These slender teeth show typically

knoblike to conical spines along the internal side of the masticatory surface (pl. 3, fig. 3, 4). The up to eight spines are visible only on unmasticated teeth. On masticated teeth, the internal side is wavily. The external side is smooth, and posses beneath the tip of the tooth a small horizontal incision (pl. 3, fig. 2). The top of the tooth is blunt. The very slender processus anterior of the pharyngeal bone bends strongly by an obtuse angel of approximate 75°. The tooth formula is 5.2. (pl. 3, fig. 6) or 5.0. (pl. 3, fig. 5, 8).

Comparison: The knoblike to conical spines along the internal side of the masticatory surface and the strongly bended slender processus anterior of the pharyngeal bone point to the genus *Scardinius*. Similar teeth exist also within the genus *Rutilus*, but only at the position A4 to A6, whereas the remaining teeth are smooth at the inner side. Furthermore, the processus anterior of the pharyngeal bone is in *Rutilus rutilus* much more robust and bends only by an angel of 45°. The teeth differ from the extant *Scardinius erythmophtalmus* by their more robustness, the higher count of knoblike spines and a more reduced tooth formula (5.3. in *S. erythmophtalmus*).

Discussion: *Scardinius* and *Rutilus* are morphologically closely related genera. In juvenile *Rutilus rutilus* the pharyngeal teeth are in two rows, the pharyngeal bone and the teeth show the same morphology as the adult *Scardinius erythmophtalmus*, thus a paedomorphic relationship can not be excluded (personal observation). HOWES (1981) regards *Scardinius* BONAPARTE 1837 as a junior synonym of *Rutilus* RAFINESQUE 1820, but this is not supported by genetical investigations (BRIOLAY et al. 1998, ZARDOYA et al. 1999, ZARDOYA & DOADRIO 1999). Both genera are genetically widely separated into different clades (ZARDOYA et al. 1999: fig. 4). This can be regarded as a further example of convergent evolution within the cyprinids. A phylogenetical relationship between *Scardinius haueri* and *S. erythmophtalmus* can not be proved, but based on similar pharyngeal bone and tooth morphology, both species represent probably the same ecophenotype.

Stratigraphical and biogeographical distribution: Pannonian E and F (after PAPP 1985) of the Vienna Basin.

Autecology: The rudd *Scardinius erythmophtalmus* is a limnophilous fish which inhabits standing or slow running waters rich on submerse plants. It is a typical phytophagous fish (HOLČÍK & BASTL 1976). Older individuals feed also on benthos, but this is more typically for the roach *Rutilus rutilus* which is specialized on molluscs (e.g. the so called roach-snail *Valvata piscinalis*, *Planorbis* ssp., *Dreissena polymorpha*, *Cardium* sp.; HEUSCHMANN 1962). Compared with the rudd, the greater robustness of the teeth and the reduced tooth-formula suggest an intermediate food type for the fossil species.

Cobitidae

Cobitis martinii nov. sp.
pl. 3, 14-19

Holotype: Lateral ethmoid (pl. 3, fig. 14, 15; NHMW 2002z0005/0001).

Paratypes: Two lateral ethmoids (pl. 3, fig. 16-19; NHMW 2002z0005/0002, 0003).

Locus typicus: Sandberg near Götzendorf (Lower Austria), Vienna Basin.

Stratum typicum: Pannonian F (*Congeria neumayri / C. zahalkai* zone of the biozonation of the Vienna Basin; after PAPP 1985); absolute age of the type locality ~10.0 Ma (after DAXNER-HÖCK 2001).

Derivatio nominis: Dedicated to Prof. Dr. ERLEND MARTINI.

Diagnosis: The shape of the lateral ethmoid is generally straight and slender. The posteromedial spine is robust and less bended, the posterolateral spine is stout and short, the medial projection is only sparsely pronounced, and the lateral projection is small.

Comparison: All European fossil loaches, especially the spined loaches of the genus *Cobitis* are described on complete skeletons. In all specimens a lateral ethmoid is not preserved. SYTCHEVSKAYA (1989) used this characteristic bone first for taxonomical investigation in fossils. She described five species of spined loaches based on the lateral ethmoid (*Cobitis zaisanica*, *C. ichberchae*, *C. centralasiae*, *C.* cf. *simplicispina*, *Sabanajewa shargaensis*) from the Miocene and Pliocene of Sibiria and Mongolia. I can distinguish three species of *Cobitis*, here named as *Cobitis* sp. A, B and C, in the Middle Miocene of the South German Alpine Molasse Basin. A detailed comparison of all taxa is shown on Tab. 1.

Discussion: *Cobitis martini* nov. sp. differs from all fossil *Cobitis* species which are based on lateral ethmoids (tab. 1). A comparison with *Cobitis ioannis* OBRHELOVA 1990 from the Lower Miocene of the North Bohemian Browncoal Basin and with *C. centrochir* AGASSIZ 1843 from the Middle Miocene of Oehningen is not possible because both taxa are based on complete skeletons where the lateral ethmoids are not preserved (personal observation).

Cobitis nov. sp.
pl. 3, fig. 20, 21

Material: 1 lateral ethmoid (pl. 3, fig. 20, 21; NHMW 2002z0006/0001).

Description: The shape of the lateral ethmoid is generally straight and robust. The posteromedial spine is lesser robust and bended medially, the posterolateral spine is stout and longer, the medial projection is pronounced, and the lateral projection is big.

Tab. 1: Morphological comparison of the lateral ethmoids of Mongolian, Sibirian, and Central European Miocene *Cobitis* species (from SYTCHEVSTKAYA 1989 and personal observation).

	General shape	posteromedial spine	posterolateral spine	medial projection	lateral projection
Sabanajewa shargaensis	bended, robust	robust, long, bended	slender, long	pronounced	big
C. cf. *simplicispina*	straight, slender	slender, long, not very bended	reduced	not very pronounced	small
C. centralasiae	straight, slender	slender, long, not very bended	slender, long	not very pronounced	small
C. ichberchae	straight, slender	slender, long, not very bended	slender, short	not very pronounced	small
Cobitis zaisanica	bended, robust	robust, long, bended	slender, long	not very pronounced	big
Cobitis sp. A	straight, stout	robust, short, not very bended	stout, short	pronounced	small
Cobitis sp. B	straight, slender	slender, long, not very bended	slender, long	not very pronounced	small
Cobitis sp. C	bended, slender	slender, long, bended	stout, short	not very pronounced	very small
Cobitis martini nov. sp.	straight, slender	robust, long, not very bended	stout, short	not very pronounced	very small
Cobitis nov. sp.	straight, robust	not very robust, bended	stout, long	pronounced	big

Comparison: This species differs from *Cobitis martinii* nov. sp. by its more robust shape, the more slender and bended posteromedial spine, the longer posterolateral spine, the more pronounced medial projection and the big lateral projection. It differs from all Sibirian, Mongolian and Bavarian species (see tab. 1) and represents clearly a new species. This species will be named if more material is available.

Autecology: All species of the genus *Cobitis* (in Europe more than ten) live benthic in clear, oxygene rich waters with sandy, sometimes rocky bottom. The best known species, *C. taenia,* prefers small, sandy and oligotrophic rivers or brooks with medium stream velocity (STERBA 1962). Spiny loaches are nocturnal and feed on detritus and zoobenthos.

Siluriformes
Clariidae

Heterobranchus austriacus THENIUS 1952
pl. 4, fig. 1-3, 6

Material: 11 pectoral spines (NHMW2002z0009/0001, 0002)

Description: The pectoral spine is slender and curved slightly posterior. The shaft bears on its postaxial margin a series of proximal directed, blunt dentations, which are more or less regular, with the largest one at the central region of the shaft. The anterior margin of the shaft shows on its proximal part some very small dentations, the distal part is smooth. Most proximal at the posterior margin of the shaft, a small distally restricted groove is developed. The three processes on the spine base (dorsal, ventral and anterior process) articulate with the pectoral girdle. The dorsal process points dorsolaterally showing an angel between the spine shaft and the process of 50° to 60° (pl.

4, fig. 2, 3). The shape of the dorsal process is broad and crescent shaped and bears numerous ridges at the surface. Both, ventral and anterior process are well developed but medium sized.

Comparison: The pectoral spines resemble in all details those of *Heterobranchus austriacus* described by THENIUS (1952) from Vösendorf. THENIUS claimed, that in contrast to African *Clarias* species, the dentation of the postaxial margin is a characteristic feature for all Asian Clariidae. *Clarias batrachus* from Thailand (pl. 4, fig. 4) shows that like in *Heterobranchus austriacus* both margins are denticulated. In African clariids (*Clarias anguillaris* vel *lacerta* from Egypt) the dentition is situated on the anterior shaft margin (pl. 4, fig. 5). The opinion of THENIUS that the fossil pectoral spines are similar to those of the extant *Heterobranchus* species (he compared with *H. longifilis, H. bidorsalis* and H. *boulengeri*) must be adopted without checking because no recent *Heterobranchus* skeleton was available for study.

Discussion: Extant members of the Clariidae are widely distributed in the tropical and subtropical Africa and Asia. The genus *Heterobranchus* is restricted to Africa. The generic assignment of the fossils to *Heterobranchus* is based mainly on more characteristic skull elements (THENIUS 1952), thus *Heterobranchus austriacus* can be regarded as an African immigrant during the Vallesian faunal turnover.

Autecology: Members of the family Clariidae are characterized by the possession of an air-breathing organ arising from the branchial arch. This apparatus enabels these fishes to live in very oxygene-deficient waters, even out of water moving some distances and hours on land. That probably depends upon the atmospheric humidity, since the moving over land occurs mostly during the rainy season (personal observation on *Clarias*

	Heterobranchus austriacus	*Silurus* nov. sp.
shape of the pectoral spine	slender, slightly curved posterior	robust, nearly straight
postaxial shaft margin	blunt regular dentation	spiny irregular dentation
anterior shaft margin	very small dentation proximal	small dentation at the entire lenght
position of the proximal groove	posteriorly	ventrally
proximal groove	distally restricted	distally expanded
dorsal process	points dorsolaterally	points dorsally
shape of dorsal process	crescent	subangular
surface of the dorsal process	ridged	smooth
ventral process	medium sized	big sized
anterior process	medium sized	not developed

Tab. 2: Morphological comparison of the pectoral spines of *Heterobranchus austriacus* THENIUS 1952 and *Silurus* nov. sp. from Sandberg near Götzendorf.

batrachus in Thailand). Members of the family are carnivorous (piscivorous) and are found in various types of waters, in ponds and rivers, but especially in relict and swampy waters. During the dry season some species live buried into mud (STERBA 1990).

Siluridae

Silurus nov. sp.
pl. 4, fig. 9-13, 15

v 1994 *Silurus* sp. – GAUDANT, pl. 1, fig. 6-11

Material: 24 pectoral spines (NHMW2002z0010/ 0001-0003)

Description: The pectoral spine is robust and nearly straight, only in adult individuals slightly curved posterior (pl. 4, fig. 12, 13). The surface of the spine is smooth in juveniles and striated in adults. The postaxial margin of the shaft is smooth in young individuals (pl. 4, fig. 9-11), in older individuals irregular and pointed spines are developed (pl. 4, fig. 12, 13). The anterior margin of the shaft bears small irregularly shaped dentations which become also more prominent in adult individuals. Most proximal at the ventral margin of the shaft a triangular, distally expanded groove is developed. In adults this groove divides the shaft in its entire length (pl. 4, fig. 13). The dorsal process points dorsally (not dorsolaterally) showing an angel between the spine shaft and the process of 80° to 90° (pl. 4, fig. 9-11, 13). The shape of the dorsal process is broad and subangular and its surface is smooth (pl. 4, fig. 15). The ventral process is extraordinarily developed and curved slightly posterior at the tip (pl. 4, fig. 15). An anterior process is not developed.

Comparison: The morphology of the pectoral spines closely resembles that of the extant *Silurus glanis* (pl. 4, fig. 14, 16) differing by a slightly more laterally elongated dorsal process (compare pl. 4, fig. 15 and 16), by a striated spine surface and by a dentigerous anterior shaft margin. This features indicate a new species of *Silurus*. The dentation of the pectoral spines of *Silurus glanis* appears very late in ontogeny. On pl. 4, fig 14 a smooth pectoral spine of an individual of 50 cm total length is shown in comparison with a pectoral spine of *Silurus* nov. sp. of the same length (pl. 4, fig. 13). In *Silurus glanis*,

probably at 100 cm total length, an irregular spine dentation is developed on the postaxial shaft margin. Regarding individuals of probably 200 cm total length (material at the private collection, not shown here) an indistinct dentation is developed also on the anterior shaft margin, but much lesser distinct as in adults of *Silurus* nov. sp.. This indicates a faster growth of the extant species up to more than 300 cm total length, thus a paedomorphic relationship between the two species can be assumed. The adult size of *Silurus* nov. sp. reaches probably not more than 50 cm.

Discussion: The new species occurs also in other Central European localities of the mammal biozone MN9 (e.g. Hammerschmiede, Höwenegg – personal observation). It is not named here, because the complete skeletons from Höwenegg are more appropriate for describing the species. However, *Silurus* nov. sp. is the oldest representative of the genus in Europe and probably the oldest known in the world, because in East Asia the first *Silurus* species occurs in sediments dated as Upper Miocene to Lower Pliocene (SYTCHEVSKAYA 1989). About eighteen extant species are known with a disjunctive distribution in Central Europe, Southeast Europe, Siberia (Amur Basin), the Caucasian and South Asian regions. The European *Silurus* species probably immigrated from Southwest Asia (BANARESCU 1960) during the Vallesian faunal turnover.

Autecology: The European *Silurus glanis* is a benthic, nocturnal species which inhabits mainly lakes and slowly running waters in the lowland of large streams. The feeding type is strictly piscivorous. Not much is known about the ecology of the small sized South Asian species.

Percomorpha
Gobiidae

Gobiidae indet.
pl. 3, fig. 23

Material: One right dentary (NHMW2002z0008/ 0001)

Description and Comparison: The curved dentary is nearly complete and shows typical multi-

rowed tooth bases on the dorsal to dorsolateral side. Near the symphysal area, three tooth rows are developed followed by two rows on the middle and a single tooth row on the posterior part of the dentary. A big mental foramen is developed at the labial side.

Little is known about the osteology of fossil gobiids. The taxonomy is based mostly on otoliths. Some dentaries from the lower Middle Miocene freshwater species *Gobius helveticus* are available for comparison. In contrast to *Gobius* sp. indet. from Götzendorf, the tooth density is much higher, beginning with four rows in the symphysal area and ending with two rows at the posterior region of the dentary. Furthermore, the labial sided mental foramen is smaller than in the Upper Miocene species.

Discussion: Only based on a dentary, a more precise taxonomic determination is not possible.

Autecology: Gobiids, especially brackish and freshwater gobiids, live in various near-shore habitats but mostly in running water. Some species enter the lower stretches of rivers. They are specialized bottom feeders and can be regarded as zoobenthophagous. Some species are specialized on molluscs like the pontian *Neogobio melanostomus* on the zebra mussel *Dreissena polymorpha* (RAY & CORKUM 1997).

Sciaenidae

aff. *Umbrina* sp.
pl. 3, fig. 22

v 1994 Percoidei indet. – GAUDANT, pl. 2, fig. 9

Material: four teeth (NHMW2002z0007/0001, 0002), some fin spines (NHMW 1994/216).

Description and Comparison: The teeth are broad conically and slightly curved, the cross-section is round and the tip is formed by a small dentin cusp. All teeth show signs of mechanical abrasion. They differ from the in some respects similar looking teeth of channids (snakehead fishes) by their broad conical shape, their bigger size and their uniform appearance (channid teeth are heterodontous). Concerning the description of the fin spine see GAUDANT (1994). The fin spines and the teeth morphology are typically for fishes of the sciaenid family within the percomorph group. BRZOBOHATY (1992) described sciaenid otolithes from Götzendorf as "genus aff. *Umbrina" kokeni* (SCHUBERT 1902). Following this determination the osteological remains are named as aff. *Umbrina* sp.

Discussion: BRZOBOHATY (1992) has described the otolithes from Götzendorf, but without a clear allocation of the position of the samples in the profile. He found otoliths only from the family Sciaenidae, apart from some juveniles, 469 otolithes determined as "genus aff. *Umbrina" kokeni*. This high quantity of otolithes (from about 230 individuals) contrasts significantly with the low number of osteological sciaenid remains. Additionally, the lack of cyprinid, cobitid, silurid or gobiid otolithes leads to the reasonable assumption that both samples are not identical originating from different layers in the outcrop.

Autecology: The Sciaenidae (croakers or drums) occupy continental shelves and estuaries of tropical and temperate oceans. Some of the total, about 210 species, enter particularly the brackish- or freshwaters as feeding ground to be the nursery of the young (TALWAR & JHINGRAN 1992). 11 genera comprising 17 species of drums are known from the Indian inland waters (TALWAR & JHINGRAN 1992). One species is restricted to freshwaters of North- and Central America (PAGE & BURR 1991) and three genera with usually riverine species to the freshwaters of the Brazilian region of South America, from where also fossil freshwater sciaenids are known (CIONE & CASCIOTTA 1995). Most species are active piscivorous predators of the mid to upper water column.

General discussion

The freshwater fish fauna from the locality Sandberg near Götzendorf comprises nine species from five families: *Barbus* ("*Bertinius*") *vindobonensis* nov. sp., *Tinca* sp., *Scardinius haueri* (Cyprinidae); *Cobitis martini* nov. sp., *Cobitis* nov. sp. (Cobitidae); *Heterobranchus austriacus* (Clariidae); *Silurus* nov. sp. (Siluridae); *Gobius* sp. (Gobiidae); aff. *Umbrina* sp. (Sciaenidae). Until now this is the best documented freshwater fish fauna from the Vallesian (MN9 and MN10, lower Upper Miocene) of Europe. The base of the Vallesian is defined by a palearctic mammal dispersal event, the so called Vallesian dispersal event of the equid *Hipparion* (AGUSTI et al. 2000). The results presented here provide that this dispersal event incorporates also fishes. Four of the nine described taxa are unknown from pre-Vallesian sediments in Europe. These are the malacophagous barbs, the genus *Scardinius* and both catfish families Clariidae and Siluridae. Their palaeobiogeographic affinities do not support an immigration from East (Northwest Asia, Siberia) but rather from Southeast (Southwest Asia). One species, *Heterobranchus austriacus*, is probably an African immigrant.

For the first time in an European basin, a malacophagous *Barbus* species (*B. vindobonensis*) is described from the Pannonian F at Götzendorf (10.0 Ma). As mentioned above, this species probably evolved from *B. subtruncatus* from the Pannonian E at Vösendorf (10.5 Ma). The high abundance and diversity of freshwater molluscs in the Vienna Basin as well as the probably altered structure of Upper Miocene ecosystems (see below) gave rise to the evolution of diet specialists in *Barbus*. This corresponds with the results of TSIGENOPOULOS et al. (1999) that similar ecophenotypes of barbs are not necessarily phylogenetically related and that different

ecophenotypes can evolve from one parental population in every colonized drainage systeme.

A characteristic feature of the Götzendorf fish community is the dominance of benthic species. Seven of nine investigated taxa were bottom dwellers or lived in the lower water column whereby five are bentivorous (*Barbus vindobonensis* nov. sp., *Tinca* sp., *Cobitis martini* nov. sp., *Cobitis* sp., *Gobius* sp.), two are piscivorous fishes *(Heterobranchus austriacus, Silurus* nov. sp.) which used olfactory and mechanosensory cues to localize moving prey (POHLMANN et al. 2001). Only two taxa (the phytophagous *Scardinus haueri*, the piscivorous predator aff. *Umbrina* sp.) lived in the mid-water or upper water column.

In contrast, only one or two benthic fish species (Cobitidae, Gobiidae) are recorded sympatrically in Middle Miocene freshwater fish communities (BÖHME in prep.). The typical and usually sole piscivorous predator of these communities is the snakehead fish (Channidae), a visual predator who occupied the mid-water or upper water column.

A high predation pressure within a lotic fish assemblage causes not necessarily a vertical segregation to microhabitat use (GROSSMAN et al. 1987). It appears plausible that the two catfishes may be act as keystone predators (BOND 1993). Regarding the Götzendorf community such a scenario implies that the benthic piscivorous predators induce through a top-down effect the high diversity of the benthivorous fishes suppressing the competition at the trophic level of their prey.

It is hypothesized that the biotic events at the Middle/Upper Miocene transition, particularly the extinction of the Channidae (diurnal visual predator) and the immigration of the Siluridae and Clariidae (nocturnal olfactory and mechanosensory predators) altered the structure of the aquatic ecosystems basically.

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Plates 1–4

Plate 1

Fig. 1-3: *Barbus("Luciobarbus") subtrunctatus* (Münster 1842), Vösendorf: pharyngeal bone in dorsolateral, dorsal and lateral view, holotype - BSP AS-VII-998;

Fig. 4, 5: *Barbus graellsi,* Rio Arga near Miranda, Spain: pharyngeal bone - IPM;

Fig. 6: *Barbus barbulus,* Dokan reservoir, Iraq: pharyngeal bone - IPM;

Fig. 7-8: *Barbus subquincuitatus*, Lake Assad, Syria: pharyngeal bone - IPM;

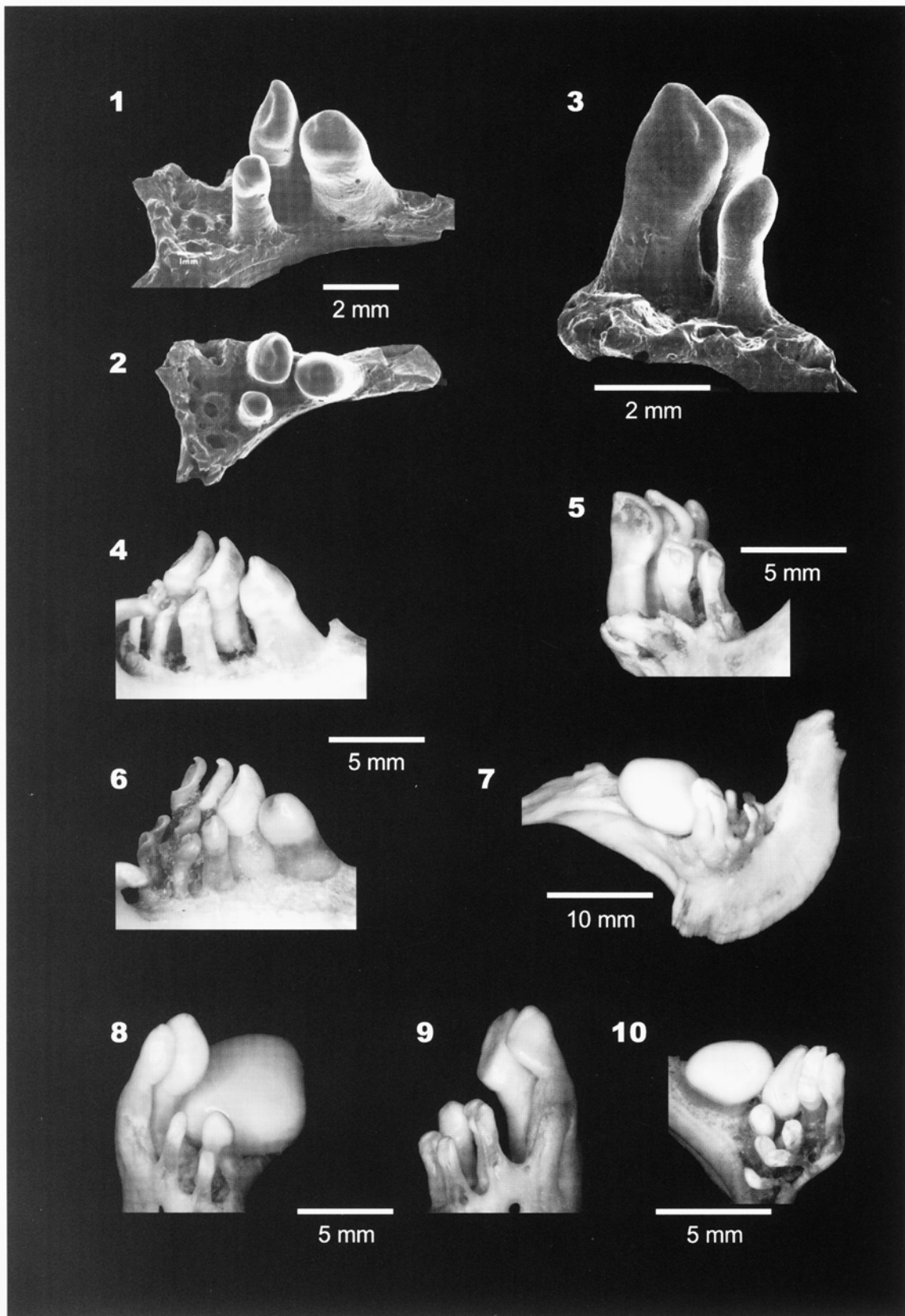**Fig: 9-10:** *Barbus xantopterus*, river Tigris near Baghdad, Iraq: pharyngeal bone – IPM.

Plate 1

Plate 2

Fig. 1-14: *Barbus* ("*Bertinius*") *vindebonensis* nov. sp., Sandberg near Götzendorf:

Fig. 1: molariform A2 tooth, dorsal view – NHMW 002;

Fig. 2: molariform A2 tooth, dorsal view – NHMW 003;

Fig. 3: spatulate A4 tooth, dorsal view – NHMW 004;

Fig. 4: spatulate A3 tooth, dorsal view – NHMW 005;

Fig. 5: spatulate A4 tooth, lateral view – NHMW 006;

Fig. 6: spatulate A3 tooth, lateral view – NHMW 007;

Fig. 7: cylindrical A5 tooth, lateral view – NHMW 008;

Fig. 8: cylindrical A5 tooth, lateral view – NHMW 009;

Fig. 9: cylindrical A5 tooth, lateral view – NHMW 010;

Fig. 10: cylindrical A5 tooth, lateral view – NHMW 011;

Fig. 11: mammiliform A1 or B1 tooth – NHMW 012;

Fig. 12: mammiliform A1 or B1 tooth – NHMW 013;

Fig. 13: pharyngeal bone fragment, holotype – NHMW 001;

Fig. 14-16: fin spine – NHMW 014. (all Figures except Fig. 13 are paratypes).
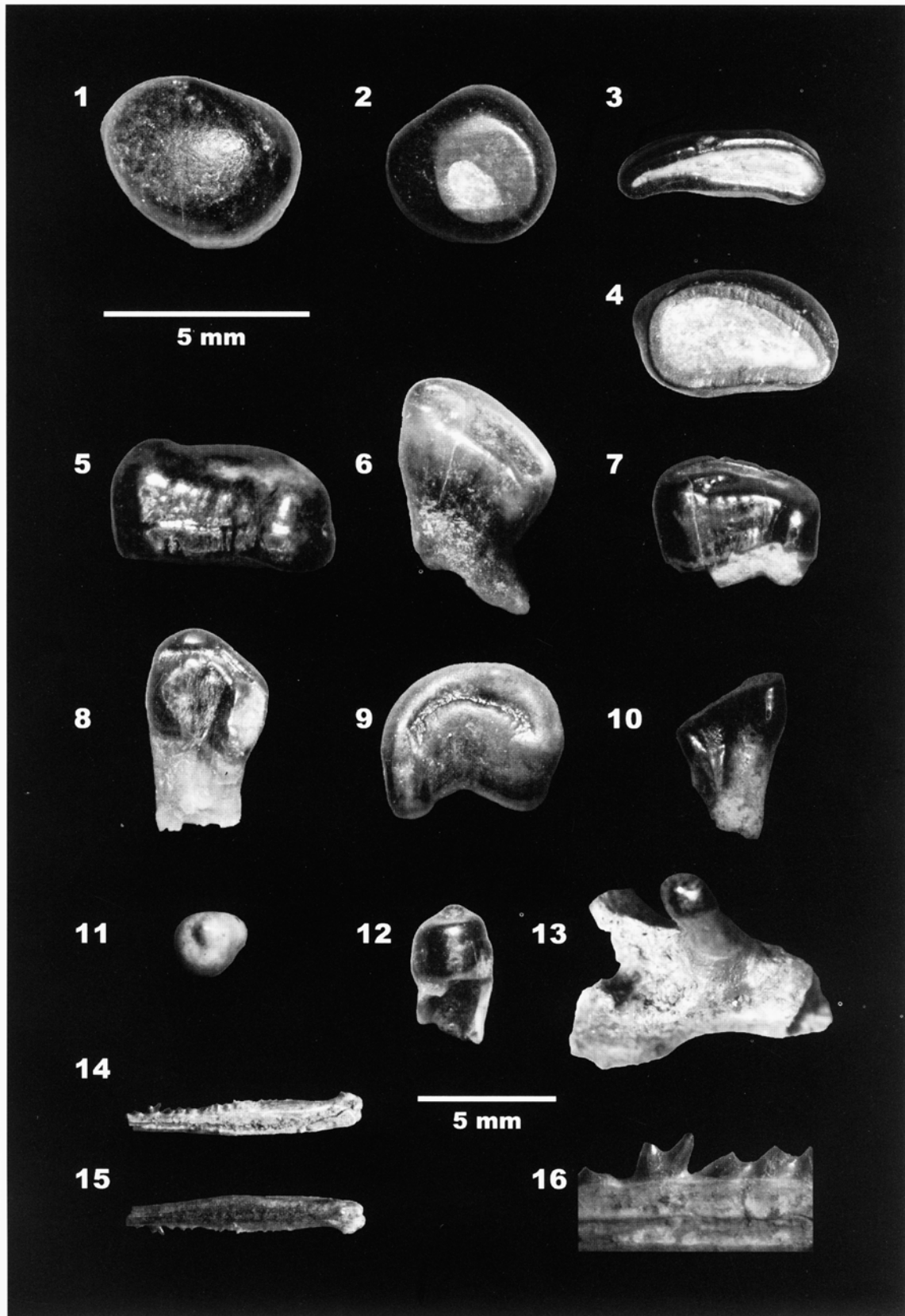
Plate 2

Plate 3

Fig. 1-6, 8: *Scardinius haueri* (MÜNSTER 1842), Sandberg near Götzendorf: Fig. 1 isolated tooth, external side – NHMW 020, Fig. 2 isolated tooth, external side – NHMW 021, Fig. 3 isolated unmasticate tooth, lateral view – NHMW 022, Fig. 4 isolated unmasticate tooth, lateral view – NHMW 023, Fig. 5 pharyngeal bone fragment – NHMW 025, Fig. 6 pharyngeal bone fragment – NHMW 026, Fig. 8 pharyngeal bone fragment – NHMW 027;

Fig. 7: *Scardinius erythmophtalmus,* Koncia river, Bulgaria: pharyngeal bone PCB;

Fig. 9-12: *Tinca* sp., Sandberg near Götzendorf: Fig. 9 isolated tooth, external side – NHMW 015, Fig. 10 isolated tooth, external side – NHMW 016, Fig. 11 isolated tooth, dorsal view - NHMW 017, Fig. 12 pharyngeal bone fragment - NHMW 019;

Fig. 13: *Tinca tinca,* Germany: pharyngeal bone- PCB;

Fig. 14-19: *Cobitis martinii* nov. sp., Sandberg near Götzendorf: Fig. 14, 15 lateral ethmoid, lateral and dorsal side – NHMW 028 (holotype), Fig. 16, 17 lateral ethmoid, lateral and dorsal side – NHMW 029 (paratype), Fig. 18, 19 lateral ethmoid, lateral and dorsal side – NHMW 030 (paratype);

Fig. 20, 21: *Cobitis* nov. sp., Sandberg near Götzendorf: lateral ethmoid, lateral and dorsal side – NHMW 031;

Fig. 22: aff. *Umbrina* sp., Sandberg near Götzendorf: isolated tooth – NHMW 032;

Fig. 23: *Gobius* sp., Sandberg near Götzendorf: right dentary – NHMW 034.
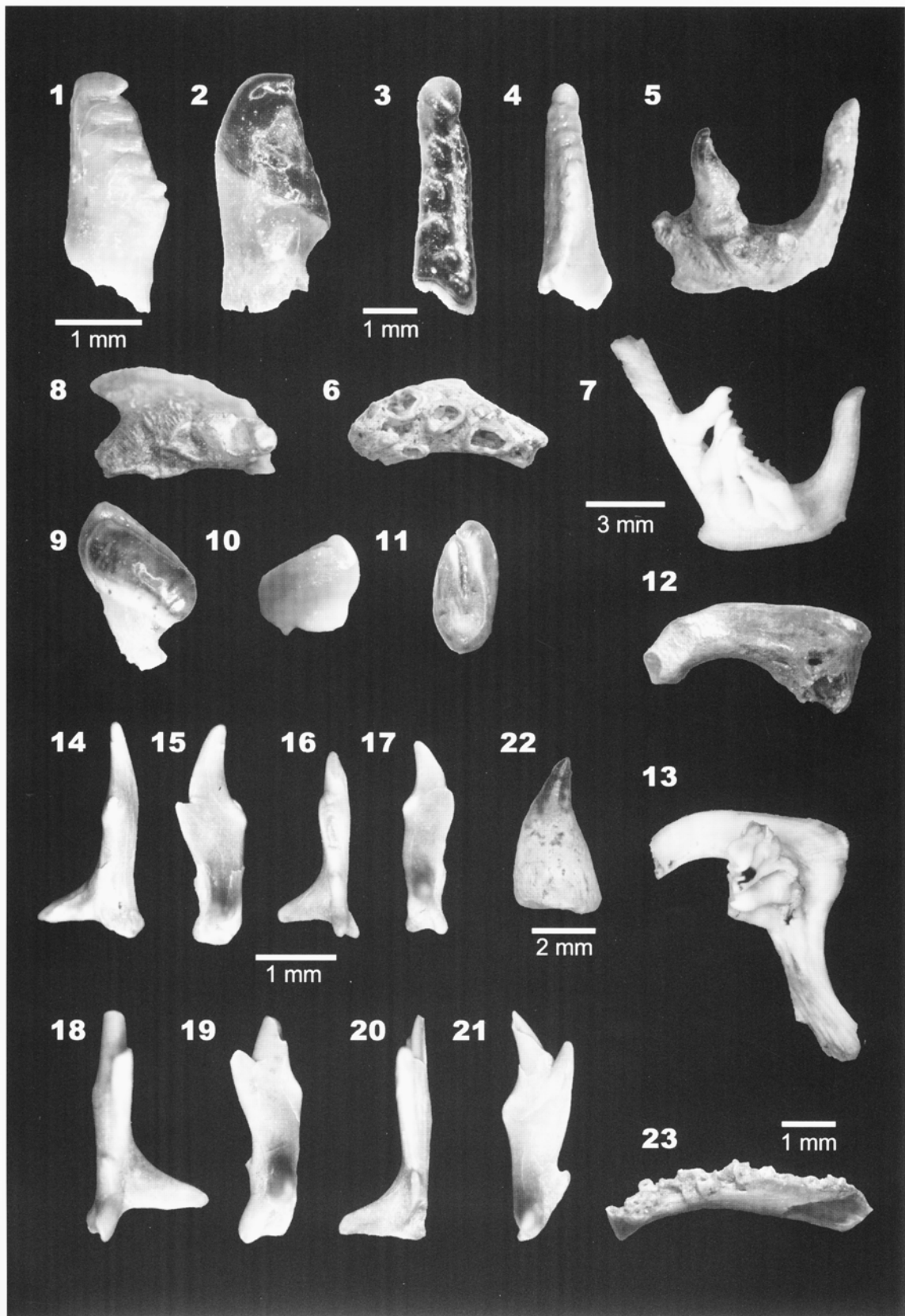
Plate 3

Plate 4

fig. 1-3, 6: *Heterobranchus austriacus,* Sandberg near Götzendorf: left pectoral spine, fig. 1 dorsal view, fig. 2 lateral view, fig. 3 ventral view, fig. 6 proximal articulation surface – NHMW 035; **fig. 4, 7:** *Clarias batrachus,* Phuket, Thailand: left pectoral spine, fig. 4 dorsal view, fig. 7 proximal articulation surface – PCB;

fig. 5, 8: *Clarias anguillaris* vel *lacera,* River Nile near Assuan, Egypt: right pectoral spine, fig. 5 dorsal view, fig. 8 proximal articulation surface – PCB;

fig. 9-13, 15: *Silurus* nov. sp., Sandberg near Götzendorf: left juvenile pectoral spine in anterior view (fig. 9), posterior view (fig. 10), ventral view (fig. 11), proximal articulation surface (fig. 15) – NHMW 037; fig, 12 left adult pectoral spine in dorsal view – NHMW 038; fig. 13 left adult pectoral spine in ventral view – NHMW 039;

fig. 14, 16: *Silurus glanis,* Germany: fig. 14 left pectoral spine in ventral view; fig. 16 proximal articulation surface – PCB. (fig. 9-14 same scale; abbreviations: dp – dorsal process, vp – ventral process, ap – anterior process).

Plate 4