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Occurrence of skeletal remains of Channids (Teleostean Fishes) in the Ottnangian (Lower Miocene) of Langenau, near Ulm (Württemberg, Germany)

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Abstract

During the construction of the A7 highway, in 1976, a new fossiliferous locality was found in the Lower Miocene (Ottnangian) in the surroundings of Langenau. Many of the fish remains from this locality belong to the family Channidae, which is represented by two species. From the shape of the opercula, at least one of these species differs from that represented by the articulated skeleton formerly described in the coeval locality of Illerkirchberg. The occurrence at Langenau of some bones of an undetermined Acanthopterygian which is also known in the Upper Miocene of Sahabi, Libya, is interpreted as suggesting a possible African origin for the Lower and Middle Miocene Channids of South-West Germany.
Keywords: Channidae, anatomy, biogeography, Lower Miocene (MN4b), Upper Freshwater Molasse, Brackish Water Molasse, Kirchberg-Schichten.

Zusammenfassung

Während des Baus der Bundesautobahn A7 wurde 1976 bei Langenau eine neue Fossillagerstätte des Untermiozäns (Ottnangium) entdeckt. Viele Fischreste dieser Fundstelle gehören zur Familie Channidae, die mit zwei Arten vertreten ist. Durch die Form des Operculums unterscheidet sich zumindest eine der beiden Arten von der bereits beschriebenen, durch ein Skelett repräsentierten Art von einer gleichalten Fundstelle bei Illerkirchberg. Die ebenfalls in Langenau gefundenen Knochen eines unbestimmten Acanthopterygiers, der auch aus dem Obermiozän von Sahabi in Libyen bekannt ist, lassen eine mögliche afrikanische Herkunft der unter- und mittelmiozänen Channiden Südwestdeutschlands vermuten.

Résumé

Un nouveau gisement fossilifère a été découvert en 1976 aux environs de Langenau, lors de la construction de l'autoroute A7. Parmi les débris de poissons trouvés dans ce gisement, un grand nombre provient de Channidae dont deux espèces différentes ont été distinguées. Comme le montre la forme des opercules, au moins l'une d'elles diffère de celle représentée par le squelette articulé décrit précédemment dans le gisement contemporain d'Illerkirchberg. La présence à Langenau de quelques os d'un Acanthoptérygien indéterminé, qui est également connu dans le Miocène supérieur de Sahabi, en Libye, est interprétée comme suggérant une possible origine africaine des Channidae du Miocène inférieur et moyen du sud-ouest de l'Allemagne.

1. Introduction

Channids are a specialized family of freshwater Acanthopterygians presently exhibiting a fragmented distribution in intertropical Africa and South-East Asia (from the Indian peninsula and the Indonesian archipelago to the North of China). Consequently, it was not expected that this family would be represented in the European fossil record. However, STINTON (1978) was the first to record the occurrence of fossil Channids in the European Tertiary when he assigned two otoliths from the Upper Eocene of his localities 3 and 33[1], in southern England, to the genus *Channa* SCOPOLI (nec BLOCH) as *C. antiqua* STINTON. Later, NOLF (1985) referred to the same genus two further fossil species, both founded on otoliths: *Otol.* (Cyprinodontidarum?) *ellipticus* VON SALIS, from the Upper Freshwater Molasse (Obere Süßwassermolasse) of Switzerland (VON SALIS 1967), and *Ot.* (inc. sed.) *rzehaki* BRZOBOHATÝ, from the Eggenburgian of Ivančice near Brno, Czech Republic (BRZOBOHATÝ 1969). REICHENBACHER (1988) subsequently recognised the occurrence of rare *Channa* otoliths in the upper part of the "Kirchberg-Schichten" of the Brackish Water Molasse ("Brackwassermolasse") and at the base of the Upper Freshwater Molasse ("Obere Süßwassermolasse"). She described them as *Channa rzehaki* (BRZOBOHATÝ). In the same paper, she reinterpreted the specimens described by MARTINI (1983) from Langenau as "*Morone moravica* WEILER", demonstrating that they are true channid otoliths.

Five years later, REICHENBACHER (1993) attributed the same specimens to *Channa elliptica* (VON SALIS), a species that she identified in four additional localities (Karpatian to Upper Badenian in age) from the Upper Freshwater Molasse of Switzerland.

The occurrence of bony remains of *Channa elliptica* (VON SALIS) was also reported by BÖHME (1999) from the Upper Freshwater Molasse of Sandelzhausen near Mainburg (Bavaria).

Finally, the first articulated channid skeleton was described from the "Kirchberg-Schichten" at Illerkirchberg (GAUDANT & REICHENBACHER 1998) (Fig. 1). Historically, this was not the first European find, however, as one of the two hitherto neglected fish skeletons found by FILHOL at Sansan is that of a Channid (GAUDANT 2000).

Three years ago, skeletal remains and otoliths of two species of channid fishes were described from two new Middle Miocene outcrops of the Upper Freshwater Molasse ("Obere Süßwassermolasse") (SACH et al. 2003). This confirms that the Western Paratethys was, during the Lower and Middle Miocene, an important area for the European channid fishes.

Vertebrate fossils were discovered during the construction of the A7 highway between Ulm and Würzburg, 2 km SW of Langenau and about 12 km NE of Ulm (HEIZMANN et al. 1980). This prompted the Staatliches Museum für Naturkunde Stuttgart to organize emergency excavations in 1976, concentrated in the foundations of the bridge which was to be built for the road uniting Langenau to a small village called Göttingen (Fig. 1). This locality is known as Langenau 1.

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[1] These localities are respectively: 3 = Hordle Cliff, Hampshire; 33 = Colwell Bay, West of the Isle of Wight (STINTON 1975).

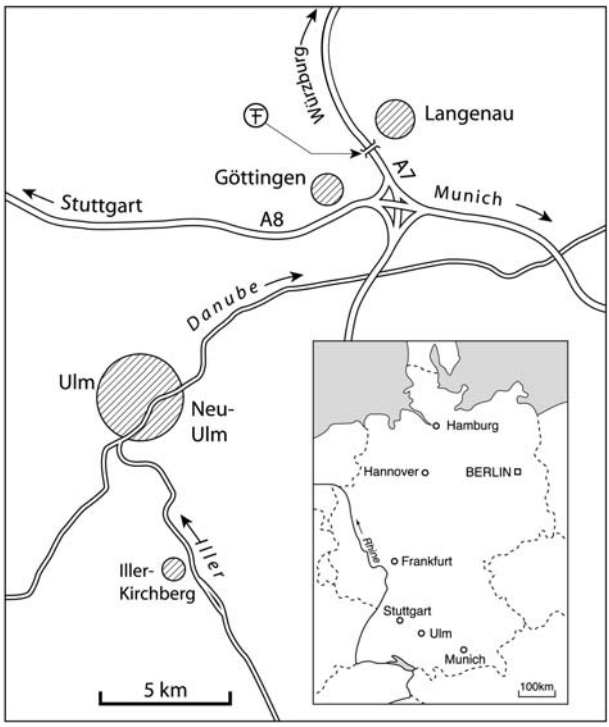

Fig. 1. Map showing the location of the fossiliferous locality of Langenau 1 excavated in 1976, during the construction of the A7 highway between Ulm and Würzburg.

It should be noted that all the studied material is held in the Staatliches Museum für Naturkunde Stuttgart (SMNS).

Acknowledgements

I wish to acknowledge Dr. R. BÖTTCHER who kindly informed me that Channid skeletal remains had been collected at Langenau by the staff of the Staatliches Museum für Naturkunde Stuttgart. I greatly appreciated his hospitality during my visit to the Museum, which made my research work much easier. Thanks are also due to the reviewers, Prof. Dr. B. REICHENBACHER (Munich) and Dr. L. TAVERNE (Brussels) for their useful remarks, and especially to Dr. C. DUFFIN (Sutton) who significantly improved the English of the original version of this paper.

As usual, the illustrations were prepared by Mr. J. DYON, using photographies made by Mr. D. SERRETTE and electrophotographies by Mrs. S. LAROCHE (all Paris).

2. Short account of the geology at Langenau 1

At Langenau 1 it was possible to recognize, in descending order, three superposed strata (BÖTTCHER 1987):

3. The "upper fossiliferous layer" ("Obere Fundstelle") corresponds to a yellowish to greyish marl with intercalated gravel layers. This proved to be the least productive level.

2. The "black layer" ("schwarze Schicht"), up to 2 m thick, is made of a dark blueish to black, partly pyritized clay channelling into the subjacent layer. It is rich in vertebrate remains, including the channid skeletal material described in the present paper. It has also yielded some complete, rather poorly preserved articulated skeletons of *Clupeonella humilis* (VON MEYER) (MARTINI 1983).

1. The "yellow layer" ("gelbe Schicht") consists of a yellow to brownish fossiliferous sandy marl, of unknown thickness. The fish remains collected from this layer include cephalic bones and vertebrae of undetermined Acanthopterygians. This layer has also produced several lachrymals of Mugilids (SMNS 87838, 87841, 87842) and some more or less complete preopercula of Moronids (SMNS 87835 and 87836).

The fossiliferous strata excavated at Langenau 1 belong to the Lower Miocene and more precisely to the MN4b mammal-zone (HEIZMANN et al. 1980, SACH & HEIZMANN 2001). They were deposited in a river coming from the north and flowing into the brackish sea of the "Kirchberg-Schichten" (BÖTTCHER 1987).

3. Anatomical description of the channid skeletal remains

The channid skeletal material from Langenau 1 includes mostly isolated cephalic bones, vertebrae and teeth[1], although one skull roof and a rather poorly preserved caudal fin, both found in the "black layer" ("schwarze Schicht"), are also present.

Skull roof: The skull roof (SMNS 80245; Figs. 2–3) is somewhat incomplete as the anterior third of the frontals is missing and has only left an imprecise print in the sediment. The upper surface of the frontals (Fr), which is rather smooth, is feebly ornamented with fine ridges radiating from a centre situated behind the orbital region. Lateral to the frontals are the sphenotics (Sph) and, behind them, the rather elongated and narrow pterotics (Ptot). The parietals (Pa), the lengths of which are approximately one third that of the frontals, are more or less trapezoidal. Their postero-lateral region exhibits a longitudinal depression for the articulation of the supratemporal. The two parietals are separated by the supraoccipital (Socc), the sharpened anterior part of which is inserted between the hind parts of the frontals. Posteriorly, the skull roof is delimited by the epiotics (Epot), the posterior edges of which are gently curved.

Frontal: A right frontal (SMNS 59266; Pl. 1, Fig. 1) has a maximum width which is less than half its length. Its anterior region is narrower than the remaining part of the bone which is crossed longitudinally by the supraorbital canal which runs toward the parietal. Near the centre of the bone, the supraorbital canal produces a short postero-lateral branch which opens distally by a rather large pore.

Premaxillary: The anterior part of a left premaxillary (SMNS 53874/1; Pl. 1, Figs. 2–3) exhibits the proximal part of the ascending process, the somewhat rounded articular process for the maxillary and the widened oral process which is covered by many bases of small villiform teeth.

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[1] The robust arch-shaped teeth found at Langenau 1 both in the "black layer" and in the "yellow layer" were referred by MARTINI (1983) to the Sciaenid *Atractoscion* sp. because six otoliths of *Atractoscion* GILL have been identified by him in the "yellow layer". However, it is not impossible that these teeth belong to a Channid.

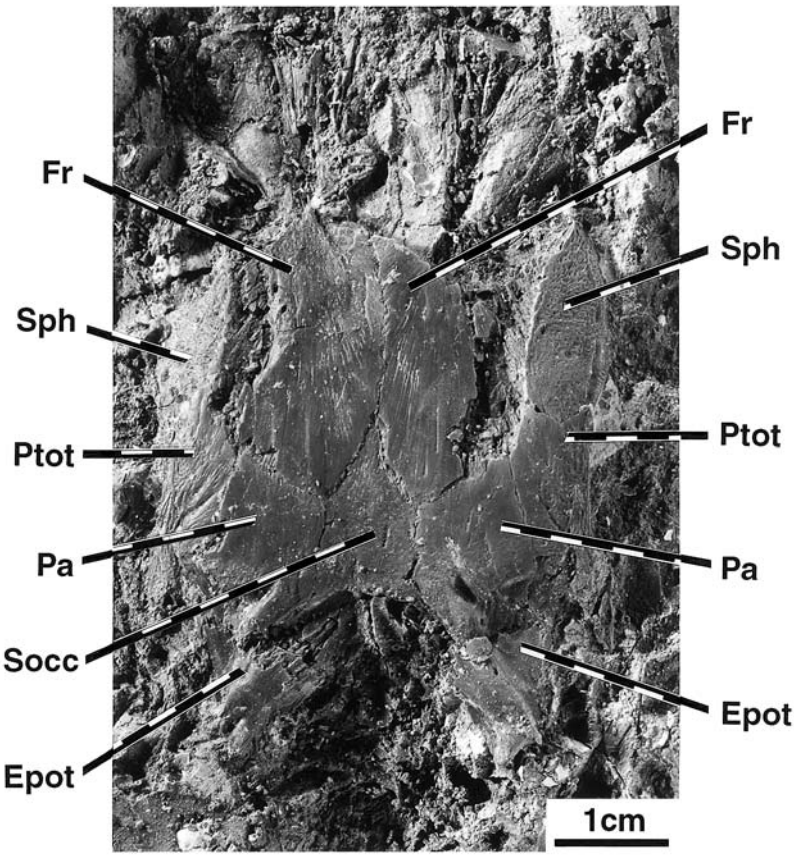

Fig. 2. Channidae indet. sp.; skull roof found in the "black layer" at Langenau 1; SMNS 80245. Epot: epiotic; Fr: frontal; Pa: parietal; Ptot: pterotic; Socc: supraoccipital; Sph: sphenotic.

Maxillary: A left maxillary (SMNS 53868/1; Pl. 1, Fig. 4), the posterior part of which is missing, is feebly arch shaped. It has a subcircular transverse section. Its articular process is made of a convex prominent roll articulating with the articular process of the premaxillary. It is produced anteriorly into an elongated vertical lamina.

Dentary: The anterior part of a right dentary (SMNS 53874/2; Pl. 1, Fig. 5) shows that several pores of the mandibular canal open laterally near the symphysis which is abruptly cut. Additionally, an accessory pore is present near the oral process at a short distance from the symphysis. The oral process itself (Pl. 1, Fig. 6) is enlarged in the symphyseal region where it is covered by many bases of small villiform teeth. Posteriorly, its width decreases. Two tooth sockets and the bases of two large teeth are present on its lingual side, whereas the bases of small villiform teeth are present on its labial side.

Angulo-articular: A right angulo-articular (SMNS 53862/1; Pl. 1, Fig. 7) exhibits a lateral surface which is ornamented with thin longitudinal ridges. It is anteriorly indented for articulation with a posterior process of the dentary. The articular

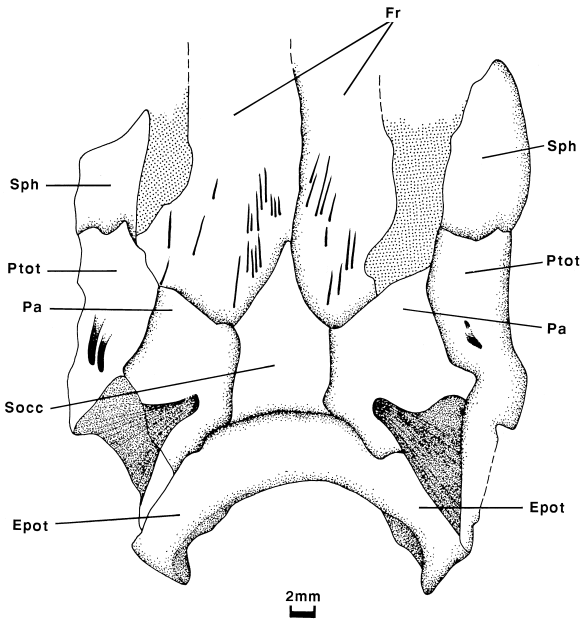

Fig. 3. Channidae indet. sp.; interpretative drawing of Fig. 2. Abbreviations cf. Fig. 2.

socket for the articulation of the quadratum is situated in the upper third of the bone, just in front of which a rather large elongated pore of the mandibular canal is located. The inner surface of the bone (Pl. 1, Fig. 8) is strengthened by a rod-like thickening which widens backwards and is slightly projected under the articular socket. A second angulo-articular (SMNS 53862/2) has a truncated postero-ventral angle which accommodated a triangular dermarticular.

Quadratum: A triangular-shaped right quadratum (SMNS 53879/3; Pl. 1, Fig. 9) exhibits a robust articular process. The posterior part of the bone is rather deeply indented for the articulation of the symplectic.

Ceratohyal: A left ceratohyal (SMNS 53879/2; Pl. 1, Fig. 10) is made of two components which are tightly connected by a zigzag suture. The proximal ceratohyal (epihyal), the ventral part of which is slightly broken, bears a rounded prominent process proximally for articulation with the interhyal. Only the widened proximal part of the distal ceratohyal is preserved.

Interoperculum: SMNS 59265 is a more or less triangular shaped right interoperculum (Pl. 2, Fig. 1), the postero-dorsal angle of which is hollowed. Its height is approximately 2/3 of its length.

Operculum: A left operculum (SMNS 80247; Pl. 2, Fig. 2), triangular in shape, is characterized by its width which equals 1.3 times the maximum height. A second operculum (SMNS 80243) is also obviously wider than high.

Basioccipital: SMNS 53870/1 is the posterior part of a basioccipital. Its ventral surface (Pl. 2, Fig. 5) exhibits an axial region which is ornamented with a series of longitudinal ridges, and two lateral moderately expanded wings bearing a fine, more or less transverse ornamentation. In lateral view, a deep oval shaped depression is present in the posterior part of the bone (Pl. 2, Fig. 6). Posteriorly, the bone exhibits

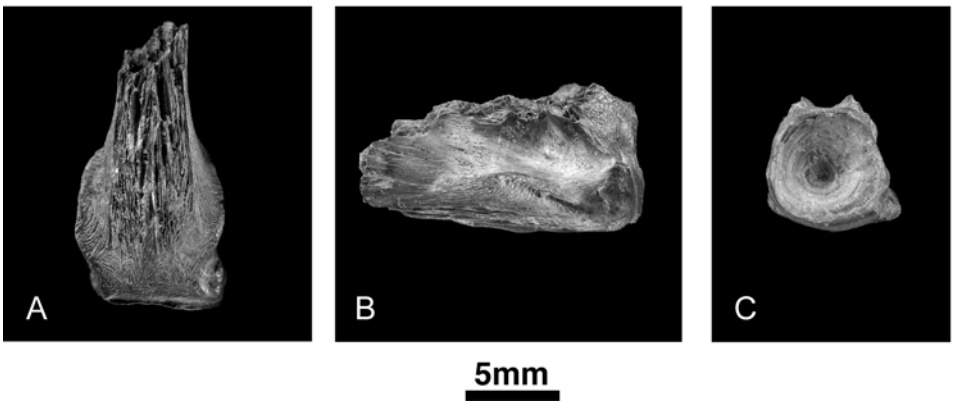

Fig. 4. Channidae indet. sp. 2; basioccipital found in the "black layer" at Langenau 1; SMNS 53870/2. **A:** ventral view; **B:** left lateral view; **C:** posterior view.

a concave surface to which the two latero-ventral wings give a more or less triangular general outline (Pl. 2, Fig. 7).

It should be noted that, although the basioccipitals found in the "black layer" most frequently conform to the morphology described above, a second type has also been found in the same layer. As shown by SMNS 53870/2, this is characterized in ventral view by more reduced lateral wings (Fig. 4A), such that the maximum width of the bone is not significantly larger than the width of its posterior face (Fig. 4C). It should be noted that the reduced size of the lateral wings of this specimen obviously exceeds the variability observed among all the other basioccipitals found in the "black layer" of Langenau 1. Consequently, we consider that this basioccipital is indicative of the presence of a second Channid species in this locality, a situation which is similar to that already noted in the Middle Miocene of Wannenwaldtobel 2 (SACH et al. 2002).

Pharyngeal bones: Several fragments of pharyngeal bones are also present in the material. SMNS 80605 (Pl. 2, Fig. 4) is an incomplete left lower pharyngeal bone. Some small blunt grinding teeth are still present in the central region of the specimen, and the whole surface of the bone is covered with a great number of sockets of small teeth. Their size increases toward the posterior edge of the bone along which are larger flattened sockets.

Vertebrae: Several vertebrae have been observed in the material. One of these (SMNS 53886/1) is an anterior (possibly the second) abdominal vertebra. In lateral view (Pl. 2, Fig. 8), the centrum shows a deep large depression laterally. It is surmounted by a robust neurapophysis which, laterally, is slightly flattened. A prominent epiprezygapophysis is present in front of its base. The anterior (Pl. 2, Fig. 9) and posterior (Pl. 2, Fig. 10) faces of the centrum are oval-shaped, the width of the centrum being approximately 1.5 times its height. Ventrally, the centrum bears two lateral facets for the articulation of the pleural ribs.

Scales: As shown by SMNS 87833 (Pl. 2, Fig. 3), the scales have their surface ornamented with concentric oval-shaped circuli.

Caudal fin: A poorly preserved caudal fin is present on specimen SMNS 80246 (Fig. 5). Although several postabdominal vertebrae have left their cast in the sedi-

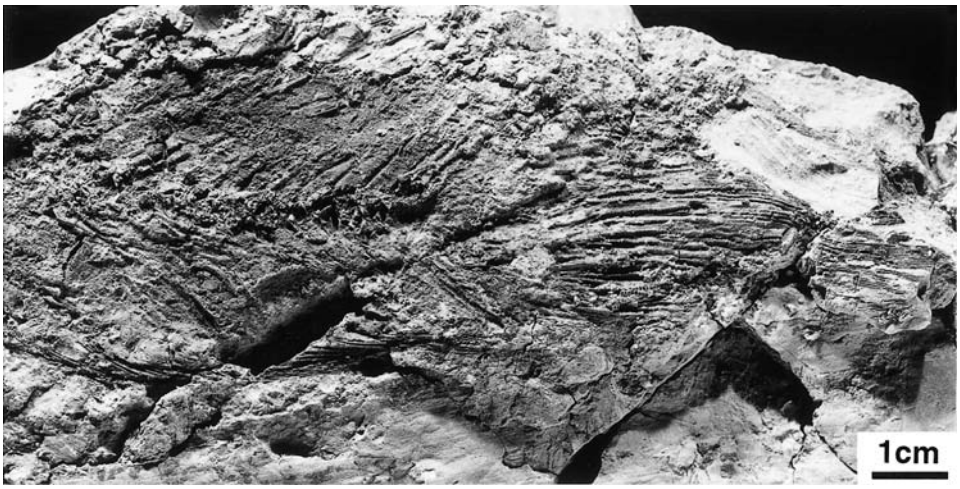

Fig. 5. Channidae indet. sp.; articulated caudal region found in the "black layer" at Langenau 1; SMNS 80246.

ment, the caudal axial skeleton is not preserved. There are about six rays in the upper half of the caudal fin. The base of the last ray of the dorsal fin is inserted very near the base of the first dorsal marginal ray of the caudal fin, so that the length of the postdorsal diastem is only approximately half the height of the caudal pedicle.

4. Conclusion

The examination of the skeletal fish remains collected from the "black layer" at Langenau 1 has shown that channid remains dominate the fauna at this level. It

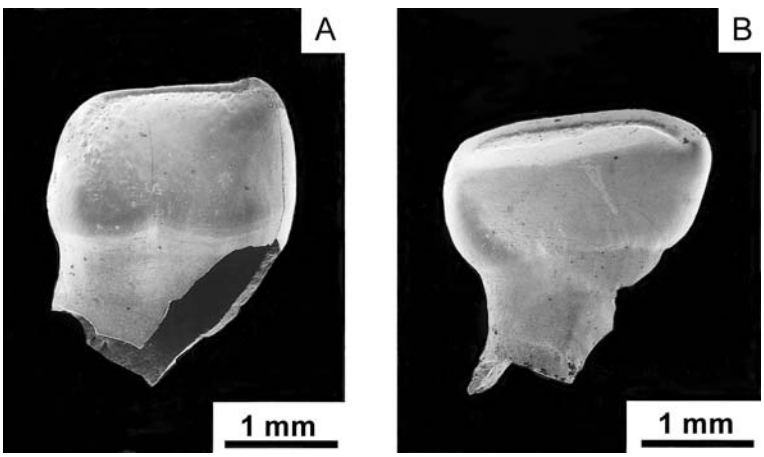

Fig. 6. *Palaeocarassius* sp.; isolated pharyngeal teeth found in the "black layer" at Langenau 1. **A:** SMNS 53863/2; **B:** 53863/1.

should be noted, however, that articulated skeletons of *Clupeonella humilis* (VON MEYER) have also been collected from the same level which has also yielded pharyngeal teeth of the Cyprinid genera *Palaeocarassius* OBRHELOVÁ (Fig. 6) and possibly *Rutilus* RAFINESQUE, and also at least two more or less complete lachrymals of a Mugilid (SMNS 87839 and 87840).

According to MARTINI (1983), the situation is quite different amongst the otoliths; only three otoliths of Channids (wrongly determined as "*Morone moravica* WEILER") have been collected in the "black layer", as compared with 22 sagittae belonging to the genus *Dapalis* GISTEL, 2 of Gobiids and 9 lapilli of Cyprinids.

Although their conditions of preservation are quite different (isolated bones vs. articulated skeletons) we can try to determine whether or not the Channids from Langenau – or at least one of their two suspected species – belong to the species already identified at Illerkirchberg by GAUDANT & REICHENBACHER (1998). For that, the only available argument is the shape of the operculum. We have already noted that the two opercula found in the "black layer" at Langenau are characterized by their width which obviously exceeds their height. By contrast, the operculum of the articulated skeleton found at Illerkirchberg has a height which is larger than its width (Fig. 7). Consequently, the opercula found at Langenau cannot belong to the Channid species already known at Illerkirchberg.

Another comparison should be made between the isolated bones of Channids found at Langenau and in two slightly younger localities of Württemberg: Edelbeuren-Maurerkopf (MN5 mammal-zone) and Wannenwaldtobel 2 (transition MN5/6 mammal-zones). As already noted by SACH et al. (2003), the most frequent type of basioccipital found at Langenau is similar to the basioccipitals from Edelbeuren-Maurerkopf and Wannenwaldtobel 2, figured respectively by SACH et al. (2003, pl. 1, figs. 8–10 and pl. 2, figs. 10–12). For this reason, we suspect that the same species of Channid has been surviving in SW Germany from the Ottnangian to the

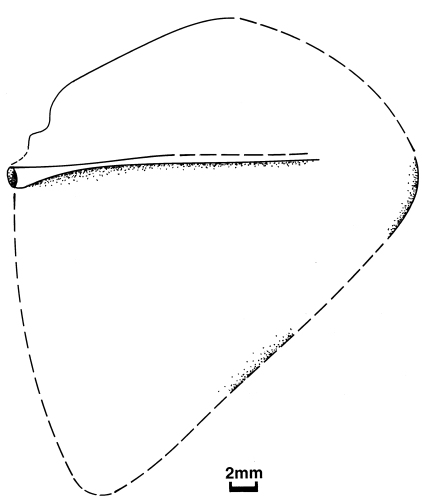

Fig. 7. Channidae indet. sp.; operculum of the articulated skeleton found in the "Kirchberg-Schichten" at Illerkirchberg; original kept in the Heimatmuseum, Neu-Ulm.

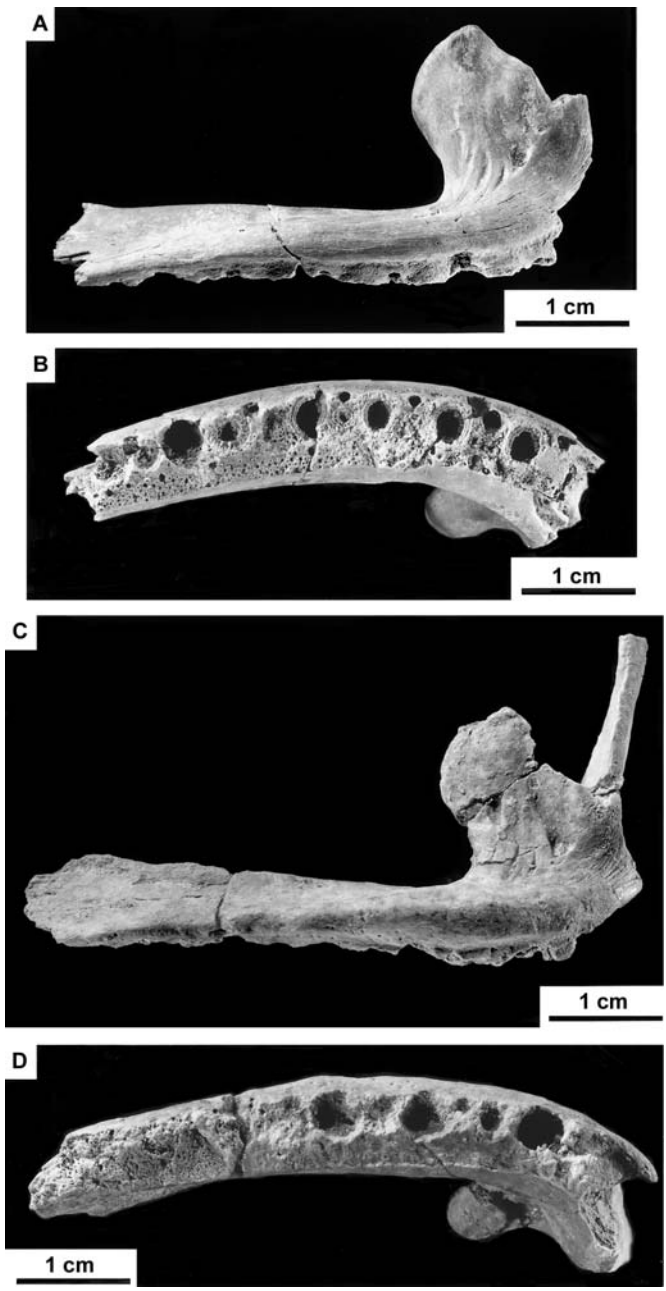

Fig. 8. Undetermined Acanthopterygian; premaxillaries found in the "yellow layer" at Langenau 1. **A–B:** SMNS 53926; **A:** lateral view; **B:** oral view. **C–D:** SMNS 53843/1; **C:** lateral view; **D:** oral view.

Badenian. We already know that Channids survived into the Upper Badenian in Switzerland (REICHENBACHER 1993, GAUDANT 2003).

As the distribution area of the family Channidae is presently disjointed, two hypotheses are plausible concerning their possible origin, which may be either Asiatic or African. The first hypothesis is suggested by the occurrence of the oldest known Channid (*Eochanna chorlakkiensis* ROE) in the Lower Eocene (Ypresian) of Pakistan (PATTERSON 1993). Additionally, the fact that channid skeletal remains have been described by SYTCHEVSKAYA (1989) in the Lower and Middle Miocene of the Zaissan depression (Eastern Kazakhstan) might be indicative of an Asiatic origin for these fishes. However, concerning the biogeographical significance of the channid remains from Langenau 1 it is interesting to take into consideration the fact that the "yellow layer" ("gelbe Schicht"), underlying the "black layer" at Langenau 1, has yielded some bones of an undetermined Acanthopterygian. Amongst these are two premaxillaries (Fig. 8) which exhibit a striking similarity to a specimen found in the Upper Miocene of Sahabi, Libya (GAUDANT 1987, figs. 4C, D). This fact may be interpreted as suggesting a possible African origin for the Miocene Channids of SW Germany, as it confirms the information furnished by the occurrence of the African Characiform genus *Alestes* MÜLLER & TROSCHEL, together with channid remains, in the Middle Miocene of Sansan (Gers, France) (GAUDANT 2000).

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Plate 1

Channidae indet. sp.
All the material figured in Plate 1 was collected from the "black layer" at Langenau 1.

Fig. 1. Right frontal, upper view; SMNS 59266.

Figs. 2–3. Left premaxillary; SMNS 53874/1; **Fig. 2:** labial view; **Fig. 3:** oral view.

Fig. 4. Left maxillary, lateral view; SMNS 53868/1.

Figs. 5–6. Right dentary; SMNS 53874/2; **Fig. 5:** labial view; **Fig. 6:** oral view.

Figs. 7–8. Right angulo-articular; SMNS 53862/1; **Fig. 7:** labial view; **Fig. 8:** lingual view.

Fig. 9. Right quadratum, lateral view; SMNS 53879/3.

Fig. 10. Left ceratohyal, lateral view; SMNS 53879/2.

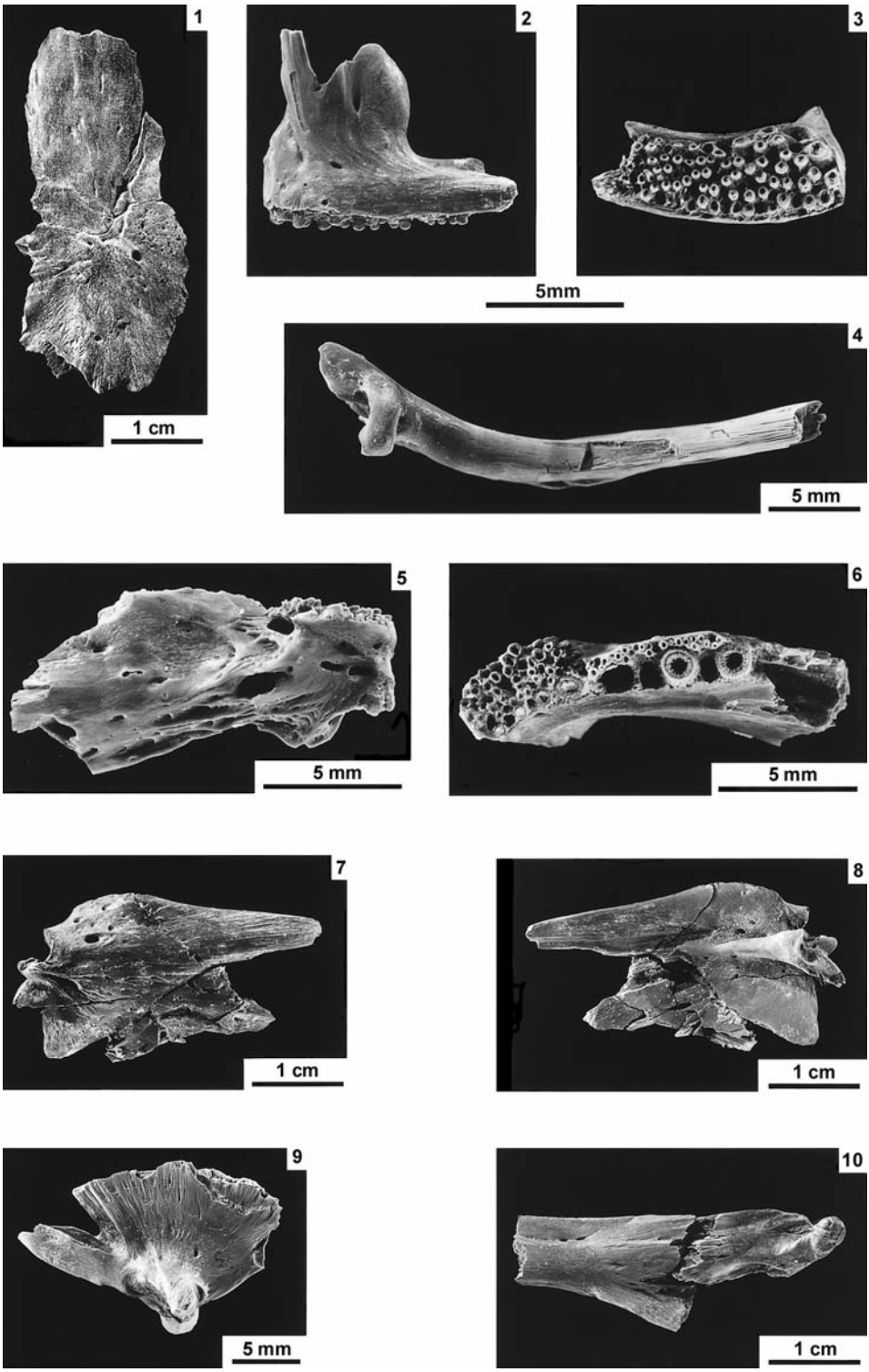
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Plate 2

Channidae indet. sp.
All the material figured in Plate 2 was collected from the "black layer" at Langenau 1.

Fig. 1. Right interoperculum, lateral view; SMNS 59265.

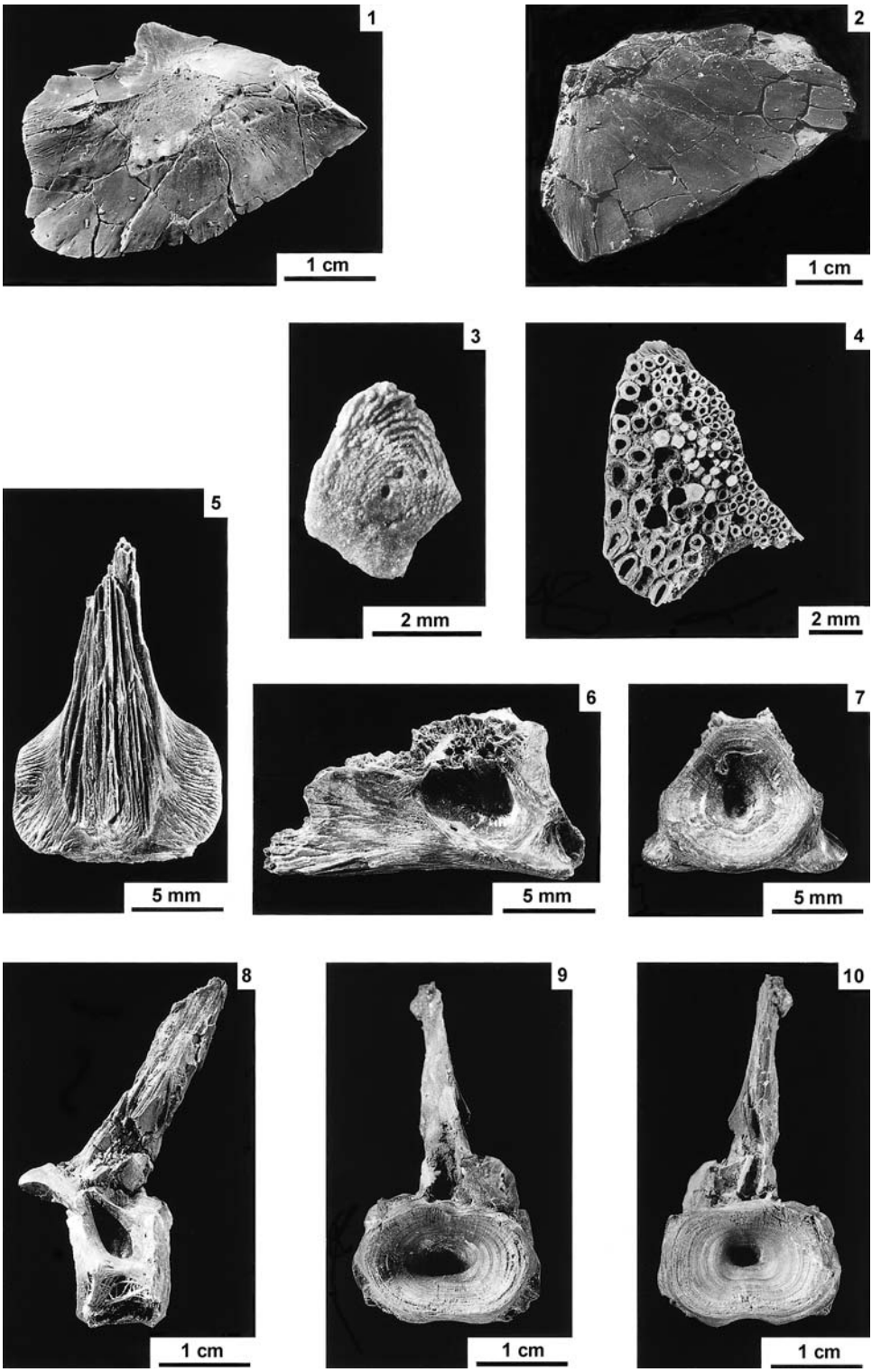
Fig. 2. Left operculum, lateral view; SMNS 80247.

Fig. 3. Incomplete scale, external surface; SMNS 87833.

Fig. 4. Left lower pharyngeal bone, upper surface; SMNS 80605.

Fig. 5–7. Channidae indet. sp. 1, basioccipital; SMNS 53870/1; **Fig. 5:** ventral view; **Fig. 6:** left lateral view; **Fig. 7:** posterior view.

Fig. 8–10. Abdominal vertebra; SMNS 53886/1; **Fig. 8:** left lateral view; **Fig. 9:** anterior view; **Fig. 10:** posterior view.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