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Re-examination of the upper Miocene freshwater fish fauna from Höwenegg (Hegau, Germany)

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Abstract The fish fauna from the volcano-detritic sediments of Höwenegg has been known for more than half a century, when Tobien reported that cyprinid fishes are present at the site. Four years later, Jörg identified three genera: *Leuciscus*, *Tinca* and a catfish that he expected to describe. However, Jörg died in 1977 without having written the paper, although he had figured the catfish, which is the oldest one preserved as an articulated skeleton in the European Miocene, and a cyprinid: *Leuciscus* sp. The purpose of the present paper is to provide a better knowledge of these fishes and of their relationships; a new species, *Silurus joergi*, is created for the silurid.

Keywords Teleosts · Cyprinids · Silurids · Palaeoenvironment · Miocene · Germany

Introduction

Höwenegg is a basaltic maar belonging to the Hegau volcanic complex, extending from Immendingen to the vicinity of Singen (Südbaden) (Jörg et al. 1955). It is situated about 2.5 km south of Immendingen (Fig. 1). Its age was determined by radiometric analyses. The last ones produced an age of 10.3 ± 0.19 Ma (Swisher 1996), which is compatible with the MN 9 standard mammal zone corresponding to the lower part of the Vallesian continental stage.

The occurrence of fossil vertebrates at Höwenegg was first reported by Tobien (1938), who identified remains of *Hipparion* in the material found by a private collector. After World War II, the fossiliferous locality was intensively excavated during the years 1950–1963 under the leadership of Erwin Jörg, Director of the Landesammlungen für Naturkunde Karlsruhe—presently Staatliches Museum für Naturkunde Karlsruhe—and Heinz Tobien, then at the Hessisches Landesmuseum Darmstadt (Jörg and Rothausen 1991). It was during that time that the bulk of the fossil fish fauna was collected. An exceptionally well-preserved mammal fauna was also extracted, including articulated skeletons of *"Hipparion"*, *Aceratherium* and *Miotragocerus*, as well as bones and teeth of *Deinotherium*, *Chalicotherium*, *Machairodus*, etc., meaning that Höwenegg rapidly became a well-known fossiliferous locality, although its age remained uncertain, since, initially, Tobien (1951) considered it to be Lower Pliocene (in line with the old terminology employed at the time). Later, Bernor et al. (1980) established that Höwenegg really belongs to the lower part of the Vallesian (MN 9 standard mammal zone). This statement was confirmed by Woodburne et al. (1996).

Two decades later, sporadic excavations started again in 1985, in relation to a project of study of the hipparionine horses (Bernor et al. 1997). More recently, field work sessions were again organized from 2003 to 2006 (Munk et al. 2007). However, the only fish remains of interest found during the recent excavations comprise a small skull of *Silurus* (Fig. 9).

Origin of the fish skeletons

The position of the fossiliferous strata that yielded the fossil fishes was carefully described by Jörg (1954) who distinguished 48 beds in the sedimentary succession of Höwenegg. Among them, the fish stratum (no 20) has a

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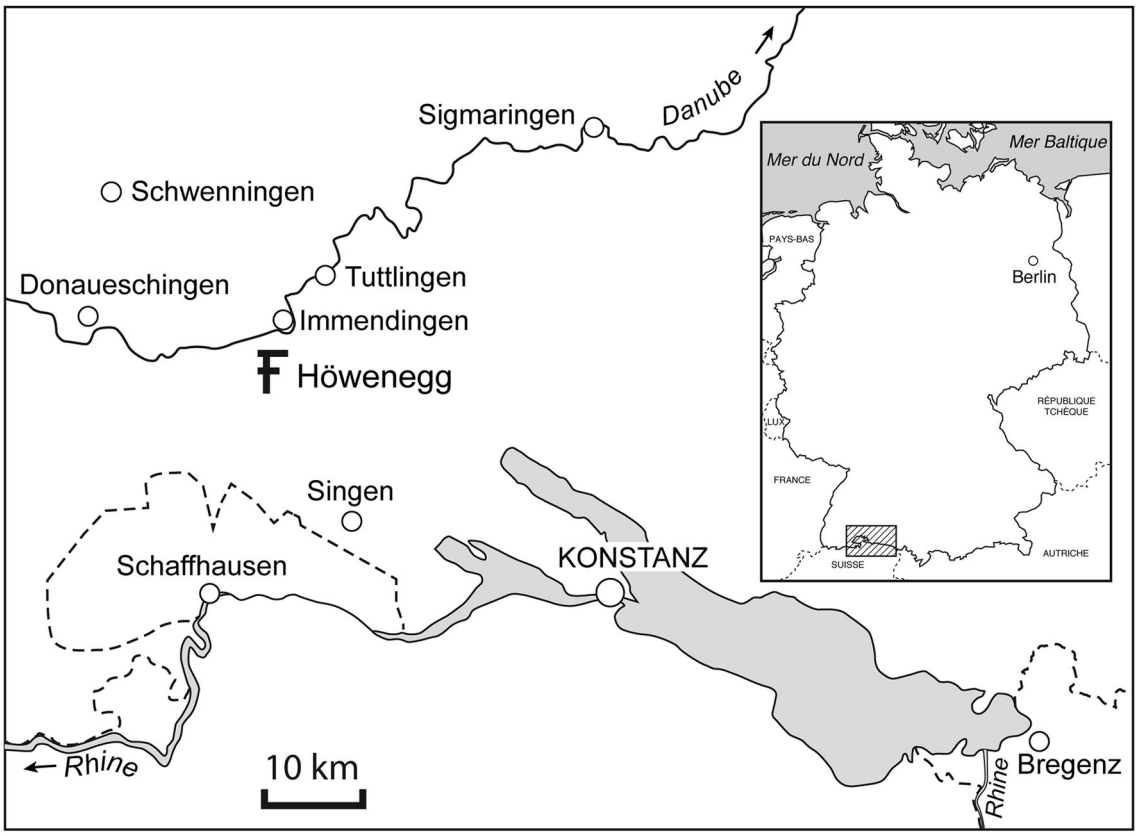

Fig. 1 Map showing the location of Höwenegg in Hegau (Südbaden, Germany)

thickness of 80 cm. It consists of a well-stratified white to light grey marl including several thin intercalations of paper shale and others of hard rust-coloured levels of tuffite. The upper half of the stratum has only yielded rather scarce isolated bones and pharyngeal teeth of small cyprinids. Underneath, Jörg (1954) distinguished several successive fish levels. Above, the first one has yielded numerous fish skeletons, their frequency being ca. 20 per square metre. Below, in two other levels having a reduced thickness (0.3 and 0.2 cm), there were only five skeletons per square metre. In the basal fourth level, Jörg remarked that the fossilization was somewhat different as the general outline of the bodies was visible. About 10–15 cm deeper, complete skeletons of larger fishes (tenches and catfishes) were found. Finally, the basal part of the fish stratum has only yielded parts of skeletons of the same fish species.

The fish fauna collected during the excavations made at Höwenegg by Jörg et al. (1955) includes three different genera. The most abundant is a rather small cyprinid belonging to the genus *Palaeoleuciscus* Obrhelová, whereas several specimens bear witness of the occurrence of a tench (*Tinca*) and a catfish (*Silurus*).

Systematic palaeontology

Family CYPRINIDAE Cuvier, 1817
Genus ***Palaeoleuciscus*** Obrhelová, 1969
Palaeoleuciscus cf. *etilius* Rückert-Ülkümen, 1965
(Figs. 2, 3, 4, 5 and 6)

Material: About 80 specimens were examined, mainly from the so-called fish strata.

This species is the most abundant one in the "fish strata" (Jörg 1954), in which it is represented by numerous specimens, the standard length of which ranges from 36 to 89 mm, with a maximum frequency between 55 and 70 mm (Fig. 2).

It is characterized by a slender body, the maximum height of which is generally included 4–5 times in the standard length (Fig. 3). As their state of preservation is not excellent, the anatomical description is rather incomplete.

The head of the specimen SMNK-PAL.6668 (Fig. 4) is characterized by the rather large size of the orbit, the horizontal diameter of which equals about one-third of the head length. The orbit is crossed in its middle part by the

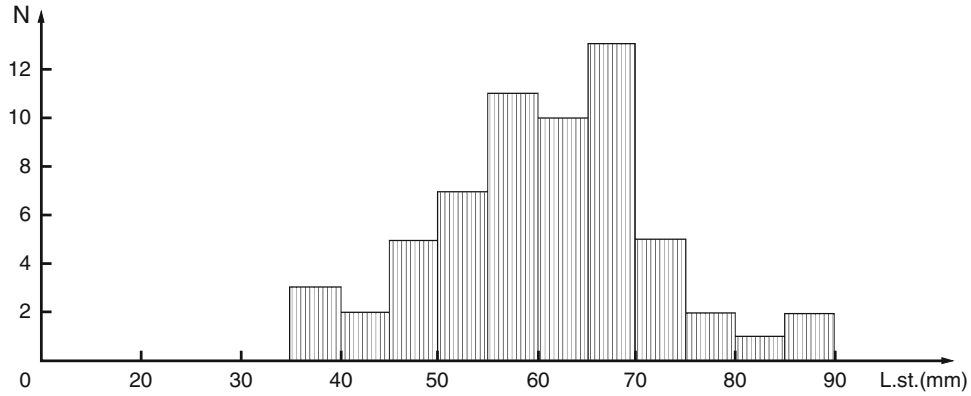

Fig. 2 *Palaeoleuciscus* cf. *etilius* Rückert-Ülkümen. Histogram of standard lengths of the fishes collected in the "fish stratum" of Höwenegg

Fig. 3 *Palaeoleuciscus* cf. *etilius* Rückert-Ülkümen. General view of body. **a** Specimen SMNK-PAL.6669 (figured by Jörg 1956, Taf. 2, Fig. 1), **b** Specimen SMNK-PAL. 6670

parasphenoid. The lachrymal and the infraorbitals are visible. Above the orbit, the skull roof is preserved. The supraorbital canal crosses longitudinally the large frontal above the posterior part of the orbit. Behind, the parietal, which is square, is crossed by the transverse commissure. Laterally, the dermopterotic is partly preserved. The maxillary and the oral process of the premaxillary are present, as well as the dentary and the articular. Behind the orbit, one can observe the hyomandibular. Between it and the operculum, the preoperculum shows its rather narrow vertical arm. Ventrally, the last two branchiostegals are preserved.

The subtrapezoidal operculum (Fig. 5) is remarkably broad: its width equals 85 % of the length of its anterior edge, which ends dorsally in a rather sharp prominent anterodorsal angle. The dorsal edge of the bone is straight.

Several pharyngeal teeth were extracted from the sediment. They are hook shaped ("Hakenzahn" of Rutte 1962).

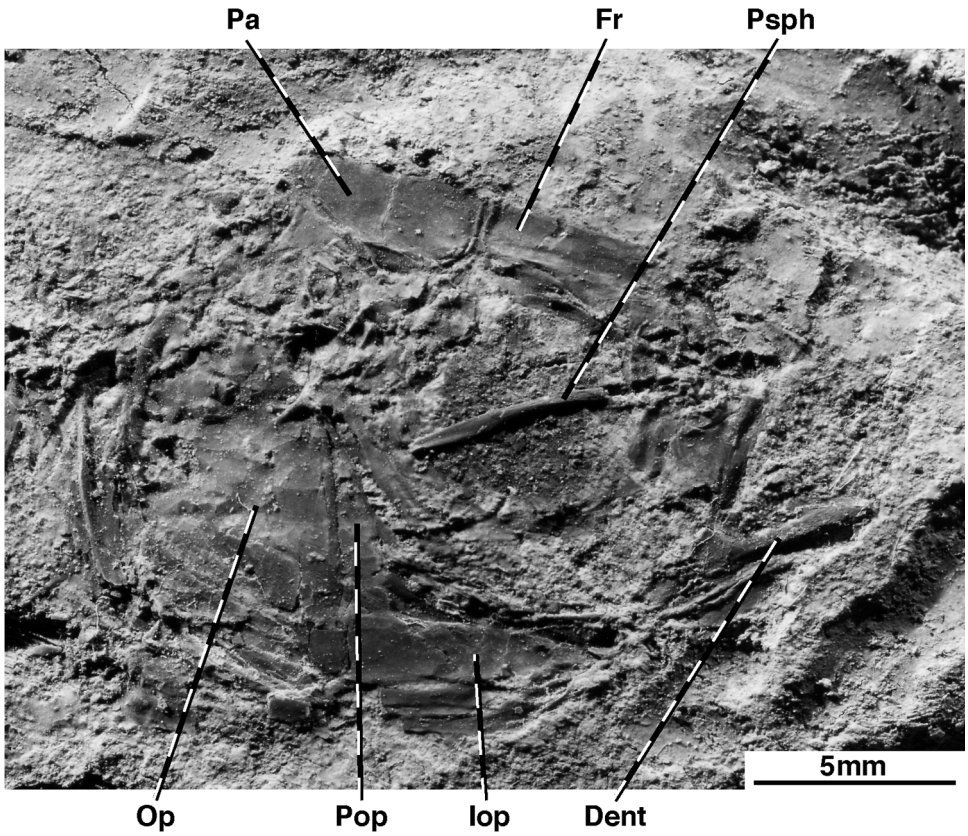

Fig. 4 *Palaeoleuciscus* cf. *etilius* Rückert-Ülkümen. Head of specimen SMNK-PAL.6668

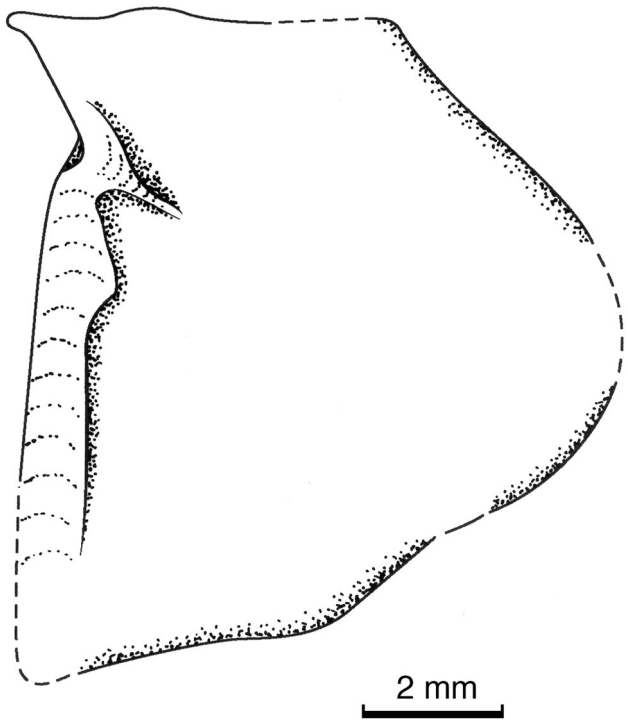

Fig. 5 *Palaeoleuciscus* cf. *etilius* Rückert-Ülkümen. Operculum of specimen SMNK-PAL.6669

Under the distal hook a rather long, well-developed concave chewing area ("Kaufläche of Rutte) is present (Fig. 6). It determines an angle of about 15° with the longitudinal axis of the crown and is delimited laterally by a crest made by a row of tubercles, whereas a low smooth crest is present on the opposite side.

The vertebral column is composed of 36–37 vertebrae, including the four anterior centra that make up the Weberian apparatus. The abdominal region comprises 19–20 vertebrae supporting about 14 pairs of pleural ribs. Epineuralia and epipleuralia are generally not preserved.

The caudal fin, which is deeply forked, has 19 principal rays; 17 of them are both articulated and furcated. Dorsally, there are 5–7 and ventrally about 6 marginal rays.

The caudal axial skeleton consists of three components: the posterior uro-terminal complex, supporting the hypurals and the parhypural. In front, two free preural centra bearing long neurapophyses and haemapophyses are present.

The dorsal fin is inserted slightly behind the middle of the body as the antedorsal distance is about 52–54 % of standard length. It is composed of 9–10 rays: two rather short anterior ones, a long articulated ray and 7–8 rays, which are both articulated and furcated. It is supported by 8–9 pterygiophores.

Fig. 6 *Palaeoleuciscus* cf. *etilius* Rückert-Ülkümen. Pharyngeal tooth from a left pharyngeal bone. Specimen SMNK-PAL.6671

The anal fin is situated posteriorly: the anteanal distance equals 68–70 % of standard length. It is composed of 12 or 13 rays: two short anterior ones, a long articulated ray and 9–11 rays, which are both articulated and furcated. Its endoskeleton is composed of 10–11 pterygiophores.

The pectoral fins, which are moderate in size, have generally 16 rays.

The relatively small pelvic fins are inserted slightly nearer to the origin of the anal than to the pectoral base. They have 8–9 rays.

The scales are not preserved.

Discussion

From the anatomical description, it clearly follows that these fishes belong to the Leuciscinae and also that the shape and the width of the operculum are indicative of the genus *Palaeoleuciscus* Obrhelová, which was rather abundant from Western Turkey to Central Europe during the Lower and the Middle Miocene. Two species were mainly present at that time: *Palaeoleuciscus etilius* (Rückert-Ülkümen) and *P. oeningensis* (Agassiz). The first one seems to have been mainly distributed during the Lower Miocene (Gaudant 1993, 1994a) and the second during the Middle Miocene (Badenian) (Gaudant 1980), although fishes showing affinities with *P. oeningensis* (Agassiz) have been recently described in the Lower Miocene (Burdigalian) of Frankfurt am Main (Gaudant 2014).

Taking now into consideration the *Palaeoleuciscus* from Höwenegg, although their vertebral column and their dorsal fin have the same composition as that of *P. etilius* (Rückert-Ülkümen) and *P. oeningensis* (Agassiz), the composition of the anal fin differs from that of *P. oeningensis* (Agassiz) in having a relatively smaller number of fin rays (cf. Table 1), so that they should be considered as being more directly related to the species *P. etilius* (Rückert-Ülkümen). For this reason, they may be described as *P.* cf. *etilius* (Rückert-Ülkümen), suggesting that this species survived in Central Europe until the Early Upper Miocene (Lower Vallesian).

Genus ***Tinca*** Cuvier, 1817
Tinca cf. *furcata* Agassiz, 1839
(Figs. 7, 8, 9)

Material: This species is documented at Höwenegg by several specimens from the "fish strata": a complete one (SMNK-PAL.6416) having a standard length of 245 mm, a second, poorly preserved one without head, having an estimated standard length of about 210 mm, a third one showing the body and an incomplete head (estimated standard length about 140 mm), and a fragment of abdominal region showing large oval scales bearing concentric circuli and a small number of radii.

An opercular region (SMNK-PAL.6666, Fig. 7) shows an operculum characterized by a very prominent posterodorsal angle, separated from the anterodorsal angle by a rounded depression.

Two isolated pharyngeal teeth have also been observed (SMNK-PAL.6672, Fig. 8A, B). Both show distally a more or less developed hook and an elongated chewing depression ("Kaufläche" of Rutte 1962) making with the longitudinal axis of the tooth an angle of 60° in the first one (Fig. 8A) and 80° in the second (Fig. 8B), which was probably the posterior one.

The best preserved specimen (Fig. 9) exhibits the characters of a male, as shown by the thickened outer ray of the pelvic fin. The head is very poorly preserved. The body is rather elongate: its maximum height is included 3.5 times in the standard length. The vertebral column consists of 37 vertebrae, including the modified anterior vertebrae that take part in the Weberian apparatus. There are 15 postabdominal vertebrae.

The caudal fin is feebly indented posteriorly: the length of the axial rays is about three-fourth of that of the longest

Table 1 Comparison of the meristic characters of the *Palaeoleuciscus* from Höwenegg with those of four Miocene localities which have yielded this genus

	P. etilius (Rückert-Ülkumen) Etili	*P.* cf. *etilius* (Rückert-Ülkümen) Dietrichsberg	*P.* cf. *etilius* (Rückert-Ülkümen) Höwenegg	*P.* aff. *oeningensis* (Agassiz) Frankfurt a. M.	*P. oeningensis* (Agassiz) Öhningen
Vertebrae (total)	36–38 (39)	34–36 (37?)	36–37	35	35–38
Abdominal vertebrae	19–21	18–20	17	18	19–20
Postabdominal vertebrae	17–19	16–17 (18)	19–20	17	15–19
Dorsal fin rays	i–ii + I + 7–8	ii + I + (6) 7–8	ii + I + 7–8	i + I + 9	ii + I + 7–9
Dorsal pterygiophores	8–9	(7) 8 (9)	8–9	9	8–9
Anal fin rays	ii + I + 8–11	ii + I + (8) 9–10	ii + I + 9–10	ii + I + 11	ii + I + 9–13
Anal pterygiophores	9–12	(9) 10–11	10?–11	13	11–13
Pectoral fin rays	I + 13–15	I + 13–14 (15)	16	–	12–15
Pelvic fin rays	I + 7–8	I + 6–8	8–9	–	7–9

Etili, Turkey: undetermined Miocene (cf. Gaudant 1993); Dietrichsberg, Germany: Lower or Middle Miocene (cf. Gaudant 1994a; Frankfurt am Main, Germany: Lower Miocene (cf. Gaudant 2014); Öhningen, Germany: Middle Miocene (cf. Gaudant 1980)

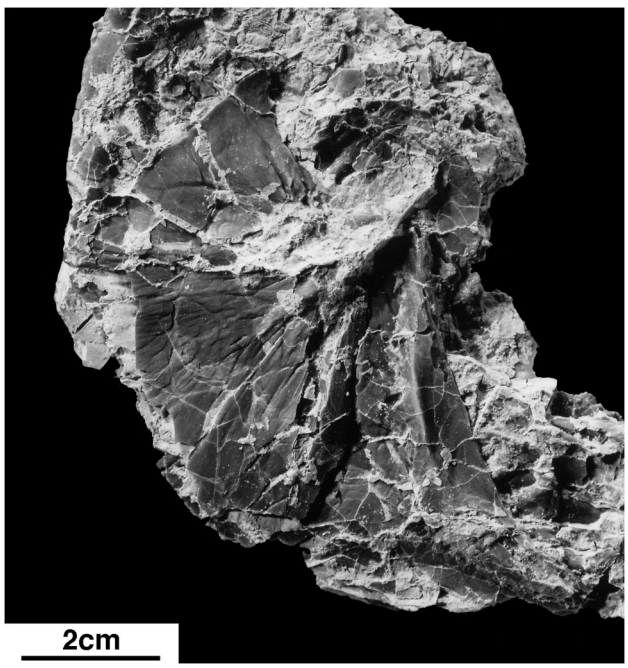

Fig. 7 *Tinca* cf. *furcata* Agassiz. Preoperculum and Operculum. Specimen SMNK-PAL.6666

ray of the ventral lobe of the fin. It consists of 19 principal rays; 17 of them are both articulated and furcated. It should be noted that the dorsal unbranched principal ray is made of rather broad articles.

The dorsal fin is inserted slightly behind the middle of body (the antedorsal distance reaches 54.7 % of standard length); it is composed of three anterior articulated rays,

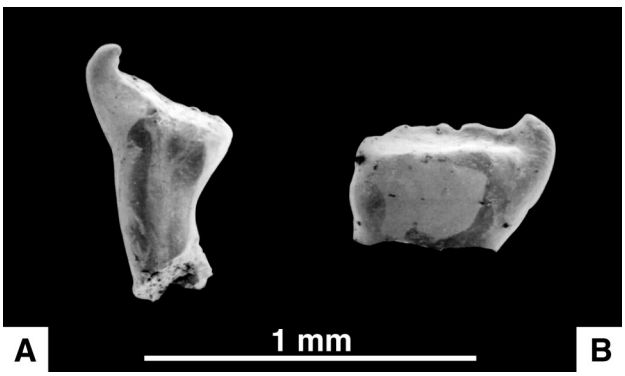

Fig. 8 *Tinca* cf. *furcata* Agassiz. Two isolated pharyngeal teeth. Specimen SMNK-PAL.6672

one long articulated ray and eight rays that are both articulated and furcated. It is supported by 9 pterygiophores.

The anal fin is situated posteriorly (the anteanal distance is 76 % of standard length). It consists of three anterior rays, one long articulated ray and seven rays, which are articulated and furcated. It is supported by at least 7 pterygiophores.

The pectoral fins are not preserved.

The pelvic fins are inserted slightly in front of the dorsal fin (the antepelvic distance equals 52.6 % of the standard length) and in the middle between the pectoral base and the origin of the anal fin. The morphology of the lateral fin ray of specimen SMNK-PAL.6665, which is made of a series of wide and short articles (Fig. 9b), indicates that this skeleton is from a male.

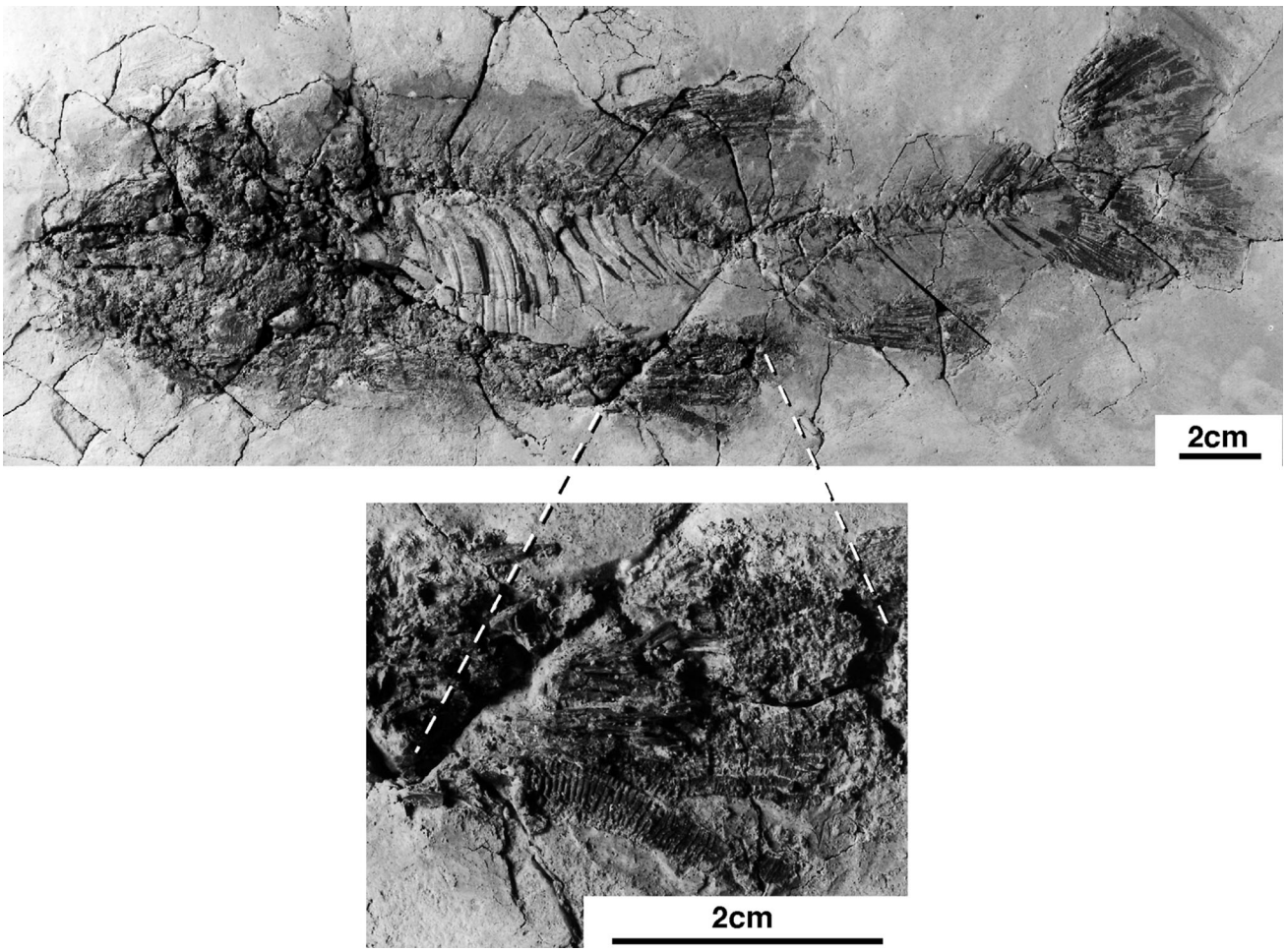

Fig. 9 *Tinca* cf. *furcata* Agassiz. General view of a male specimen with close-up view of the pelvic fin. Specimen SMNK-PAL.6416

An uncatalogued fragment shows well preserved rather large cycloid scales ornamented with concentric circuli and showing a rather small number of radii on their posterior field.

Discussion

The articulated skeleton of the male specimen which is described above exhibits meristic characters that are very similar to those of the species *Tinca furcata* Agassiz, from the Middle Miocene (Badenian) of Öhningen (Gaudant, 1980), and of the more or less coeval *Tinca micropygoptera* Agassiz from Steinheim am Albuch (Gaudant 1989): the vertebral column includes 37 vertebrae (22 + 15), against 35–37 (generally 20–21 + 15–16) in *T. furcata*, and 35–38 (19–21 + 15–17) in *T. micropygoptera*; the dorsal fin is composed of 12 rays (8 branched), supported by 9 pterygiophores, against 10–13 (7–9 branched) and 9 pterygiophores in *T. furcata*, and 10–12 (7–8 branched) and 8–9 pterygiophores in *T. micropygoptera*; the anal fin consists of 11 rays (8 of them being probably branched), supported by at least 7 pterygiophores, instead of 9–11 (7–8 branched) and 8 pterygiophores in *T. furcata*, and 9–11 (8–9 branched) and 8–9 pterygiophores in *T. micropygoptera*.

However, it should be noted that the maximum height of the body of the best preserved specimen from Höwenegg is included 3.5 times in the standard length, a situation which is similar to that known in *Tinca furcata* Agassiz, whereas this ratio is generally less than 1/4 in *Tinca micropygoptera* (Agassiz). For this reason, the tenches from Höwenegg may be considered as probably belonging to the species *Tinca furcata* Agassiz.

Family SILURIDAE Cuvier, 1817
Genus ***Silurus*** Linnaeus, 1766
Silurus joergi n. sp.
(Figs. 10, 11, 12, 13, 14)

Short diagnosis: *Silurus* of moderate size having a vertebral column is composed of about 50 vertebrae (about 13 + 37) behind the Weberian apparatus. Anal fin having about 45 rays.

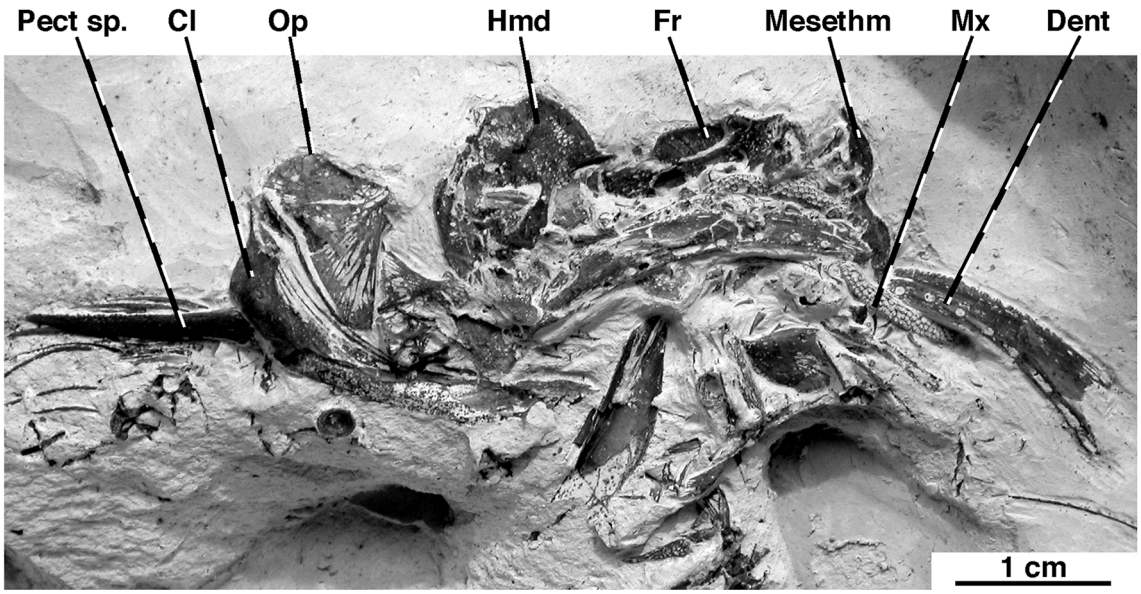

Fig. 10 *Silurus joergi* n. sp. Lateral view of the head. Specimen SMNS 95177 kept in the Staatliches Museum für Naturkunde Stuttgart (by courtesy of Dr. Ronald Böttcher, Stuttgart)

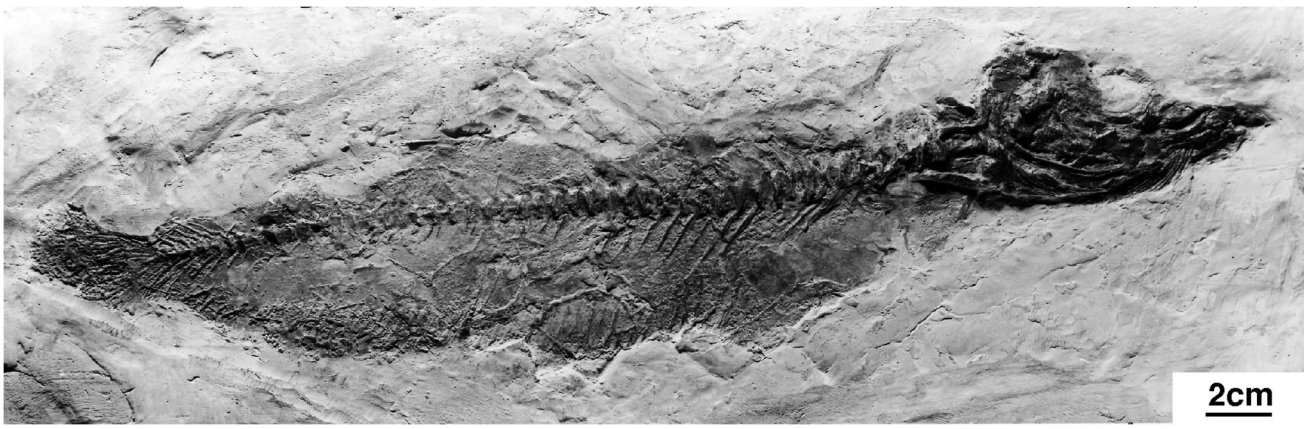

Fig. 11 *Silurus joergi* n. sp. General view of body. Specimen SMNK-PAL.6662

Holotype articulated skeleton SMNK-PAL.6662, kept in the Staatliches Museum für Naturkunde Karlsruhe.

Origin of the name: Species dedicated to Dr. Ernst Jörg (1917–1977), former director of the Landessammlungen für Naturkunde Karlsruhe, who was active from 1951 to 1963, together with Heinz Tobien, in excavating the maar of Höwenegg and initiated the study of its fish fauna.

Material: This genus is documented by two complete specimens, and some fragments including a cleithrum with the pectoral spine in connexion. Additionally, a well-preserved head of a young fish, which is curated in the palaeontological collections of the Staatliches Museum für Naturkunde, Stuttgart, was found during the excavations made in June, 2005 (R. Böttcher *in litt.*).

The length of this head (SMNS 95177) reaches about 40 mm (Fig. 10). Although it is rather strongly crushed, it shows the two elongate dentaries (Dent) exhibiting the pores of the mandibular sensory canal. On their oral edge, no tooth is preserved. The oral process of the maxillaries (Mx) is covered with several longitudinal rows of small tooth sockets. Of the mesethmoid (Mesethm), one can see the typical shape of its anterolateral processes. The left frontal (Fr) may be partly observed by its ventral surface. The massive articular head of the hyomandibular (Hmd) is visible. The operculum (Op) is triangular; its maximum width, which reaches about two-third of the maximum

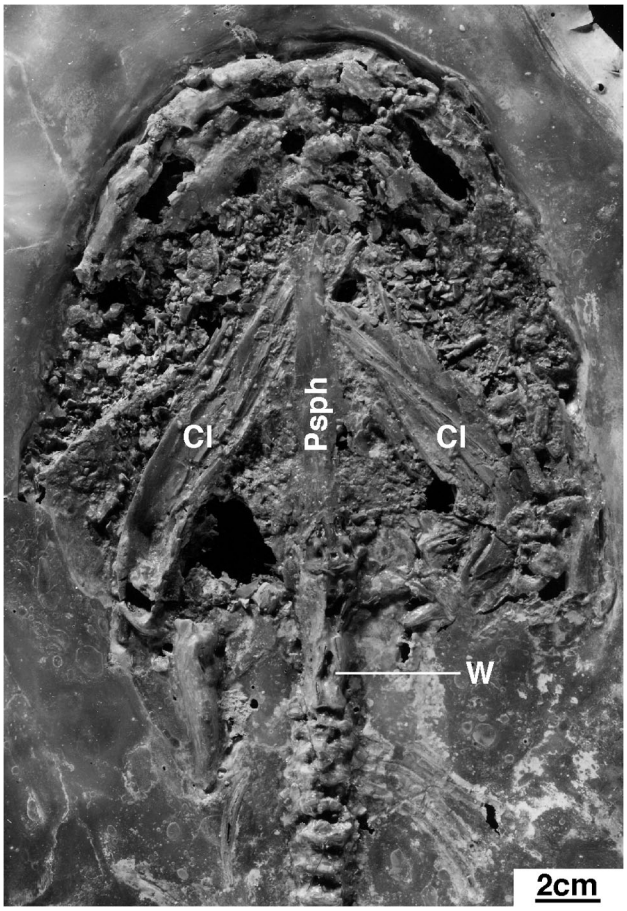

Fig. 12 *Silurus joergi* n. sp. Lower surface of the head showing the Weberian apparatus. Specimen SMNK-PAL.6661. *Cl* cleithrum, *Psph* parasphenoid, *W* Weberian apparatus

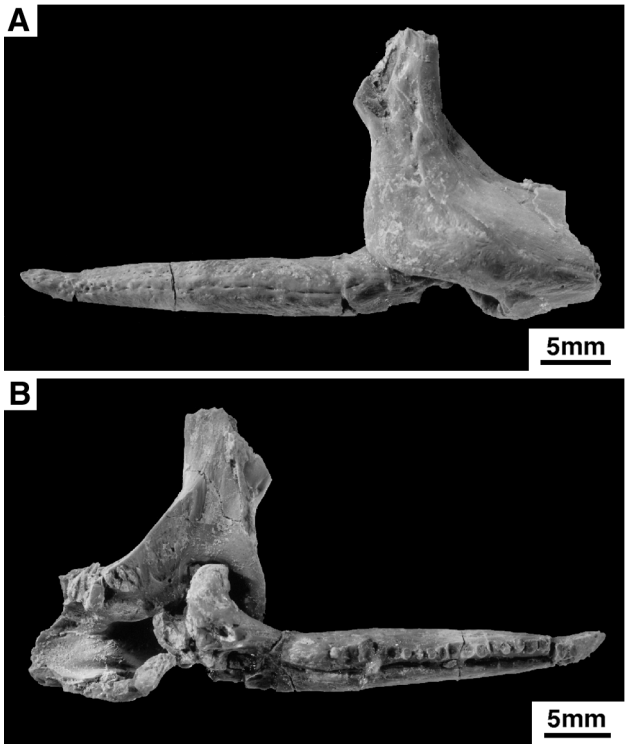

Fig. 13 *Silurus joergi* n. sp. Right cleithrum with articulated pectoral spine. Specimen SMNK-PAL.6663

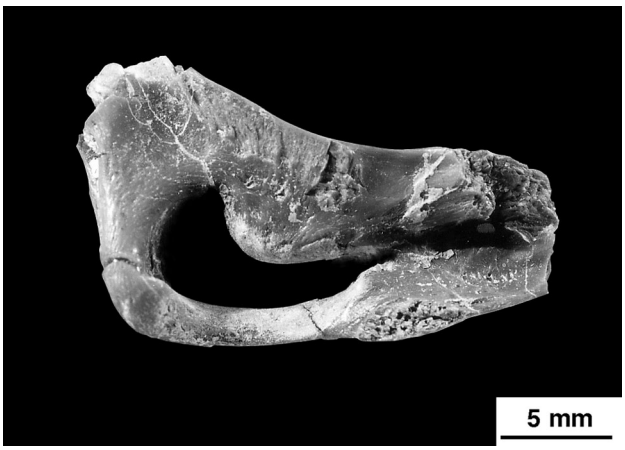

Fig. 14 *Silurus joergi* n. sp. Inner surface of a left cleithrum showing the cavity for the articulation of the pectoral spine. Specimen SMNK-PAL6664

height, is situated in its upper part. The anteroventral part of its lateral surface is ornamented with ridges radiating from the anterodorsal part of the bone. The right cleithrum (Cl), which is arch-shaped, articulates with the pectoral spine (Pect sp.), which exhibits small denticulations on its upper part.

A rather well-preserved specimen which has been prepared by the transfer method into an epoxy resin is the best preserved silurid skeleton found at Höwenegg (SMNK-PAL.6662; Fig. 11). It has a standard length of 355 mm. The head length is included about 4.5 times in standard length, whereas the maximum height of body is included 5 times in the same measurement. The head is rather elongate, its height being included about two times in its length.

The vertebral column consists of about 50 vertebrae; 37 of them are postabdominal. The caudal fin, which is incompletely preserved, is small.

Of the dorsal fin, only two rays are visible. Although the anal fin is destroyed, it is possible to estimate its composition because its endoskeleton is composed of about 45 pterygiophores.

A strong spine is present in the pelvic fin. It is ornamented with a row of small tubercles.

A second, almost complete, specimen has been transferred onto Lackfilm (SMNK-PAL.6661; Fig. 12). It shows the ventral side of a large head, which is dorsoventrally compressed. It has a length of about 90 mm. The ventral arms of the cleithra and the parasphenoid are exposed on the ventral surface. In front of the first abdominal

vertebrae, the main component of the Weber apparatus is present. Its ventral surface is characterized by the presence of a long and rather narrow longitudinal ventral fossa.

An incomplete right cleithrum is fossilized in connection with a robust pectoral spine, which is ornamented by a row of tubercles (SMNK-PAL.6663; Fig. 13).

Additionally, a fragment of a left cleithrum (SMNK-PAL.6664) shows on its mesial surface the characteristic arch-shaped articular socket, which is penetrated by the articular process of the pectoral spine.

Discussion

From the preceding description, especially from that of the small isolated head (SMNS 95177), there is no doubt that the silurid skeletons found at Höwenegg belong to the genus *Silurus* Linnaeus. In fact, the morphology of the dentary, of the mesethmoid, of the hyomandibular, of the operculum and of the cleithrum is quite similar to that of the homologous bones of the recent species *Silurus glanis* Linnaeus. However, the fossil silurids from Höwenegg differ from the two living European species of the genus *Silurus* Linnaeus by at least two meristic characters:

1. Their shorter vertebral column is composed of 50–55 vertebral free centra behind the Weberian apparatus, whereas they are about 68 in *Silurus glanis* Linnaeus.
2. Their smaller anal fin, which is supported by about 45 pterygiophores, corresponding to less than 50 anal fin rays, against more than 80 in *S. glanis* Linnaeus and about 70 in *S. aristotelis* Garman (Kottelat and Freyhof 2007).

For these reasons, the skeletons of the genus *Silurus* Linnaeus found at Höwenegg may be considered to represent a new species for which the name *Silurus joergi* n. sp. is given, in honour of Dr. Ernst Jörg (1917–1977). It is the oldest known European occurrence of a silurid.

This species differs from the living and fossil European species of the genus *Silurus* Linnaeus by its shorter vertebral column composed of 50–55 centra and by its relatively smaller anal fin in which the number of fin rays was about 45. The holotype of this species is the specimen SMNK-PAL.6662 (Fig. 10), embedded in epoxy resin.

It should be noted that articulated skeletons of another *Silurus* were found in Upper Miocene diatomites worked in the Montagne d'Andance quarry, at Saint-Bauzile (Ardèche, France) (Mein et al. 1983). Although this material remains hitherto unstudied, it is evidently different from the silurid species described above as it is characterized by a long anal fin composed of at least 75 rays (unpublished).

Conclusion

The re-examination of the fish fauna from the Lower Vallesian maar of Höwenegg has complemented the original information published by Jörg (1956). First, it was possible to propose a more precise identification for the cyprinids originally named "*Leuciscus*", which should be considered as belonging to a population which does not significantly differ from the species *Palaeoleuciscus etilius* (Rückert-Ülkümen). Second, the occurrence of the genus *Tinca* Cuvier is confirmed at Höwenegg, and it is suggested that it is represented by the species *T. furcata* Agassiz, which is already known in the Middle Miocene (Badenian) of Öhningen. However, the most important information consists in the determination of the relationship of the siluriform from Höwenegg as the find of the head of a small specimen has clearly shown that it belongs to the recent genus *Silurus* Linnaeus, although the meristic characters observed in the two articulated skeletons demonstrate that this species differs significantly from the recent species *Silurus glanis* Linnaeus. For this reason, the new species *Silurus joergi* is created for the silurid skeletons of Höwenegg.

Consequently, Höwenegg is a significant locality for the knowledge of the Upper Miocene fish fauna of Central Europe, which was hitherto rather poorly documented. The most diversified Vallesian fauna is that of Sandberg near Götzendorf an der Leitha, in the Vienna basin, which is a fluviatile one, belonging to the "Pannonian F". It has an age estimated at about 10.0 Ma (Daxner-Hock 2001). According to Gaudant (1994a, b), Böhme (2002) and Schultz (2013), this fish fauna, which is composed of disarticulated bones and isolated pharyngeal teeth of cyprinids, includes at least *Barbus vindobonensis* Böhme, 2002, *Scardinius haueri* (Münster, 1842), *Tinca* sp., *Cobitis martinii* Böhme, 2002, a gobiid, an undetermined perciform, and *Silurus* sp. *Heterobranchus austriacus* Thenius, 1952, an African siluriform immigrant, which had been previously identified by Thenius (1952) in the nearby locality of Brunn-Vösendorf is also present.

It should be also noted that the poorly preserved articulated skeleton of a freshwater "gadiid", *Lota hulai* Pietschmann, had been reported by Pietschmann (1934) from a claypit located in Vienna, near the Ober-Laa railway station. However, its re-examination in the Vienna Museum of Natural History has shown that its poor state of preservation does not allow any reliable determination, even at the family level (Gaudant 2002).

Although no Upper Miocene freshwater fish fauna is known in Central Europe, one is present at Saint-Bauzile (Ardèche, France) in the Turolian diatomitic filling of a maar which is worked in the Andance quarry. The mammal

fauna is indicative of the upper part of the MN 11 (Demarcq et al. 1989). Although this fish fauna remains only partly studied, its main component belongs to the genus *Palaeoleuciscus* Obrhelová (unpublished information). A still undescribed species of the genus *Silurus* Linnaeus is also present, as well as a representative of the genus *Barbus* Cuvier and a fluviatile blenniid.

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