

The new fossil killifish genus *Aphanolebias* REICHENBACHER & GAUDANT, 2003 (Teleostei, Cyprinodontiformes) and its fossil record

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ABSTRACT. – We present the recently introduced fossil cyprinodontiform genus *Aphanolebias* REICHENBACHER & GAUDANT, 2003. Its type-species, formerly known as *Prolebias meyeri* AGASSIZ, was found in Lower Miocene deposits of the Northern Upper Rhinegraben area (Germany) and is well documented by skeletons with otoliths preserved *in situ*. The unique character of *Aphanolebias* is the combination of a *Prolebias*-like skeleton and dentition with *Aphanius*-like otoliths. We hypothesize that *Aphanolebias* may be considered as a “missing link” in the fossil record of cyprinodontiform fishes in the Old World.

Besides the type species, *Aphanolebias* is represented by the otolith based Miocene species *Aphanolebias* sp. 1 (REICHENBACHER 2000), *A. angulosus* (STEURBAUT, 1978), *A. chios* (MALZ, 1978), *A. konradi* (REICHENBACHER, 1988) and *A. gubleri* (REICHENBACHER, 1993). Those species were previously thought to be fossil *Aphanius* species. *Aphanius germaniae* WEILER, 1963 is a younger synonym of *Aphanolebias meyeri* (AGASSIZ).

KEYWORDS: *Aphanolebias*, *Prolebias*, *Aphanius*, Cyprinodontiformes, Miocene, stratigraphical range.

Introduction and historical review

The species *Lebias meyeri* was originally described by AGASSIZ (1839) from the Miocene of Frankfurt (Hanau Basin, Germany). It was based on abundant skeletal material that was collected when digging the well of the central cemetery (VON MEYER 1834). MALZ (1978) correctly recognized that the sediments yielding *Lebias meyeri* belong to the Upper Hydrobia Beds that can be placed in the late Lower Miocene (MARTINI 1987, REICHENBACHER 2000).

However, it was rather difficult to get an accurate understanding of *Lebias meyeri* AGASSIZ because its original description is incomplete and somewhat imprecise. Additionally, the original material, which belonged to von MEYER's private collection, was lost since that time, including the two syntypes figured by AGASSIZ (1839, V, Tab. 41, Figs 7–8).

According to SAUVAGE (1874), *Lebias meyeri* should be included in the fossil genus *Prolebias* SAUVAGE, 1874. It is worth to mention that the single “*P. meyeri*” skeleton, which is mentioned out of the Rhinegraben region (D’ERASMO 1929: Messinian from Senigallia, Italy), is probably a young specimen of *Aphanius crassicaudus* (AGASSIZ).

WEILER (1942) reported skeletons of so-called *Prolebias meyeri* from Upper Oligocene to Lower Miocene deposits of the borehole Baden 4 in the southern Upper Rhinegraben. He did not describe nor illustrate them, but noted that several skeletons were bearing round-shaped otoliths *in situ*, of which he described and figured one (WEILER 1942: 24, Pl. 1, Figs 11–12). Unfortunately, the material from the borehole Baden 4 is lost. Later, WEILER (1963) referred to the figured otolith from the borehole Baden 4 as “otolith-holotype of *Prolebias meyeri*”. In the same article, WEILER (1963: 25, pl. 2) described and figured skeletons from Upper Oligocene deposits of the borehole Dudenhofen in the southern Rhinegraben as *P. meyeri*. He mentioned two skeletons with *in situ* preserved otoliths and considered that they are similar to his “otolith-holotype of *P. meyeri*”. Additionally, WEILER (1963: Fig. 76–79) described and figured isolated otoliths as *P. meyeri*. However, only the two otoliths from the Upper Hydrobia Beds of the borehole Spöck 1 belong to that species (REICHENBACHER 2000: 73).

Referring to the determinations of WEILER (1942, 1963), REICHENBACHER & MÖDDEN (1996), REICHENBACHER (2000), and REICHENBACHER & SIENKNECHT (2001) determined and figured isolated otoliths from the Upper Oligocene and Lower Miocene of the northern Upper Rhinegraben area (Mainz Basin, Hanau Basin) as *P. meyeri*. However, in the recent study of REICHENBACHER & GAUDANT (2003) it was demonstrated on basis of skeletons and otoliths from Dudenhofen that *P. meyeri* sensu WEILER (1942, 1963) does not agree with *P. meyeri* sensu AGASSIZ (1839), but belongs to the new species *Prolebias malzi* REICHENBACHER & GAUDANT, 2003.

Studied material

The studied material comes from previous and new collections and is kept in the sections Palaeozoology I (SMF P) and Micropalaeontology (SMF O) of the Senckenberg Museum Frankfurt.

Old collection of *P. meyeri* sensu AGASSIZ (1839) = *Aphanolebias meyeri* (AGASSIZ)

This material was collected by H. VON MEYER and probably originates from the Upper Hydrobia Beds (late Early Miocene).

SMF P. 1687b: skeleton from Frankfurt, Alte Gasse; see Fig. 1.2.

SMF P. 1686b: skeleton, probably from same locality as SMF P. 1687b; see Fig. 1.1.

SMF P. 1686a: otolith, found *in situ* in the counterpart of SMF P. 1686b; mentioned by MALZ (1978); see Fig. 2.1.

Recent collection of *P. meyeri* sensu AGASSIZ (1839) = *Aphanolebias meyeri* (AGASSIZ)

This material originates from the Upper Hydrobia Beds (late Early Miocene) of Frankfurt, Senckenberganlage, and was collected by the amateur collectors K. WEISS, W. OTT, and M. KELLER (see OTT 2003). The fossiliferous layers were accessible during the construction of the new metropolitan line U 4, uniting the central railway station to Bockenheimer Warte. Besides *P. meyeri*, some gobiid skeletons and one atherinid skeleton were found. According to its otoliths preserved *in situ*, the latter belongs to *Hemitrichas bartensteini* (MALZ). Gobiids do not occur in strata older than the Upper Hydrobia Beds and *H. bartensteini* is restricted to the Upper Hydrobia Beds (REICHENBACHER 2000). Thus, these taxa support the lithostratigraphic position of the fossiliferous layers.

SMF P. 9612: skeleton (collected by W. OTT under the number Se 2-6); see Fig. 1.3.
 SMF P. 9613: skeleton (collected by K. WEISS under the number Se 2-W4);
 SMF P. 9614: skeleton (collected by W. OTT under the number Se 2a-4);
 SMF P. 9615: skeleton (collected by K. WEISS under the number Se 2-W1);
 SMF P. 9616: skeleton (collected by W. OTT under the number Se 2-11);
 SMF P. 9620–9626: seven skeletons (collected by K. WEISS under the numbers Se 2-W2, -W3, -W6–10).
 SMF P. 9627, SMF PO. 64369: skeleton with both otoliths in situ (collected by M. KELLER); see Fig. 2.3.
 SMF PO. 64370–64372: otoliths found *in situ* (collected by M. KELLER).
 For more illustrations see REICHENBACHER & GAUDANT (2003).

Collection of isolated otoliths of *Aphanius germaniae* WEILER, 1963
 = *Aphanolebias meyeri* (AGASSIZ)

SMF P. 5553, 20 sagittae from the Upper Hydrobia Beds of Frankfurt/Main, borehole Mainzer Landstraße 148 (22.9 m depth) (mentioned in Malz 1978); see Fig. 2.4-5.
 SMF P. 5554, 40 sagittae from the Upper Hydrobia Beds of Frankfurt/Main, borehole Mainzer Landstraße 156 (8 m depth) (mentioned in Malz 1978); see Fig. 2.6-7.
 Further 450 sagittae are kept in the Senckenberg Museum (material of Malz 1978).

Collection of *Prolebias meyeri* sensu WEILER (1942, 1963)
 = *Prolebias malzi* REICHENBACHER & GAUDANT, 2003

A. From Middle Cerithium-Beds of the borehole Dudenhofen 1 (890.5–895.3 m depth)
 SMF P. 3509: skeleton; figured in WEILER (1963: Pl. 2, Fig. 5); holotype of *P. malzi* sp. nov.;
 SMF P. 3366A-B: skeleton; figured in WEILER (1963: Figs. 74a–b); paratype of *P. malzi* sp. nov.;
 SMF P. 3572: skeleton; mentioned in WEILER (1963);
 SMF P. 3574: skeleton; mentioned in WEILER (1963);
 SMF P. 9617: skeleton;
 SMF P. 9618a: skeleton and otolith embedded in the sediment;
 SMF P. 9618b–c: four skeletons.

For illustrations see REICHENBACHER & GAUDANT (2003).

B. From boreholes and outcrops in the Mainz and Hanau Basins, from boreholes in the Upper Rhinegraben

About 650 isolated otoliths (material illustrated in REICHENBACHER & MÖDDEN 1996, REICHENBACHER 2000).

Presentation of *Aphanolebias* REICHENBACHER & GAUDANT and its
 systematic position versus *Prolebias* SAUVAGE

Aphanolebias REICHENBACHER & GAUDANT, 2003, bears characters that neither allow to assign it to *Prolebias* SAUVAGE, nor to include it in the genus *Aphanius* NARDO or *Valencia* MYERS. Its general osteology (Fig. 1), the conical teeth of its jaws, and the shape of the dentary are evidently typical for *Prolebias*. But opposite to *Prolebias*, its otoliths are triangular-shaped (Fig. 2) and resemble Recent *Aphanius* and *Valencia* otoliths. However, contrary to *Aphanius* and *Valencia* otoliths, the sulcus of *Aphanolebias* otoliths is sharply bent down at its end. Consequently, the genus *Aphanolebias* REICHENBACHER & GAUDANT was created for taking into account this unique combination. The type species was described as follows: Small cyprinodontiform fish, the standard length does not exceed 40 mm. Body elongated, its maximum height equals

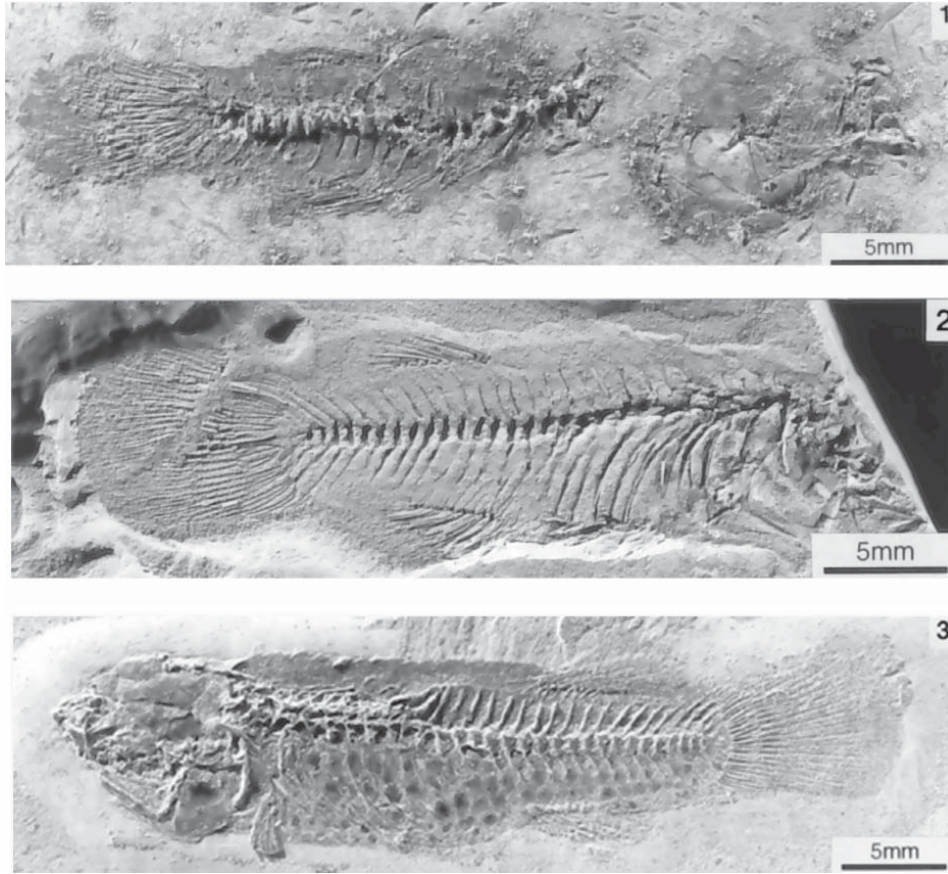


Fig. 1. *Aphanolebias meyeri* (AGASSIZ). General view of body of three specimens. – **1**, Specimen SMF P. 1686b. Upper Hydrobia Beds, probably Alte Gasse, Frankfurt/Main; **2**, Specimen SMF P. 1687b. Upper Hydrobia Beds, Alte Gasse, Frankfurt/Main; **3**, Specimen SMF P. 9612. Upper Hydrobia Beds, Senckenberganlage, Frankfurt/Main. (Photographs D. Serrette.)

1/5 to 1/3.5 of standard length. Vertebral column consists of about 28–30 vertebrae, 15–16 postabdominal. Caudal fin rounded, with 15–16 principal rays. Dorsal fin consisting of i–ii+I+7–9 rays supported by 9–10 pterygiophores. Anal fin beginning more or less exactly opposed to dorsal fin and consisting of i–ii+I+9–11 rays supported by 10–12 pterygiophores. Antedorsal and anteanal distance generally ranging from 69 to 72% of standard length. Pelvic fins situated nearer to the origin of the anal fin than to the base of the pectorals. Dentary and premaxilla provided with small conical teeth distributed in several rows. Otoliths (sagitta) triangular-shaped with a prominent rostrum and a cauda distinctly bent down and pointed at its distal end.

From the above given description it is evident that *Aphanolebias* skeletons display skeletal and dental characters that are well known from fossil *Prolebias* species (e.g., GAUDANT 1981, 1989, 1991, 1998, GAUDANT & REICHENBACHER 2002). However, it seems that in *Prolebias* not any derived skeletal or dental character appears. Consequently, no definition of *Prolebias* from a phylogenetic point of view was given so far

(SETHI 1960, PARENTI 1981). Based on the fossil record, the following characters of *Prolebias* SAUVAGE can be considered as most significant. Altogether they allow to distinguish *Prolebias* from *Aphanius* NARDO, *Valencia* MYERS and *Aphanolebias* REICHENBACHER & GAUDANT.

- jaws provided with conical teeth (tricuspid in *Aphanius*, conical in *Valencia*)
- dentary without any spur-like medial process (with process in *Aphanius*, without in *Valencia*)
- otolith rounded and with a dorsal tip (triangular and without dorsal tip in *Aphanius* and *Valencia*)

Otoliths of *Prolebias* (rounded and with dorsal tip) have been found in several species *in situ*, e.g., in *P. hungaricus* GAUDANT 1991, in *P. cephalotes* (AGASSIZ) (unpublished data), and in *P. aff. weileri* (SALIS) (GAUDANT & REICHENBACHER 2002). The triangular-shaped otoliths of Recent *Aphanius* species were illustrated by MALZ (1978) and REICHENBACHER & SIENKNECHT (2001). *Valencia* otoliths, which are also triangular-shaped, will be described and illustrated in a future study.

Fossil record of *Aphanolebias*

Prolebias is an extinct genus that thrived from Oligocene to Middle Miocene times in euryhaline habitats of France and Spain (e.g., GAUDANT 1981, 1989, 1998), the western Paratethys region (e.g., VON SALIS 1967, REICHENBACHER & WEIDMANN 1992, REICHENBACHER 1993), the eastern Paratethys (e.g., GAUDANT 1991), and the Upper Rhinegraben area (e.g., WEILER 1963, REICHENBACHER 2000). *Aphanius* is known as fossil since the Early Miocene (Burdigalian, 17–18 Ma; GAUDANT & ROVIRA-SENDRÓS 1998) whereas *Valencia* is not known as fossil. We consider the following species as belonging to *Aphanolebias*.

- *Aphanolebias angulosus* (STEURBAUT) from the Early Miocene (approximately 21 Ma) of the Aquitaine Basin in SW-France (STEURBAUT 1978, as “genus Cyprinodontidarum”);
- *Aphanolebias chios* (MALZ) from the Miocene of the island Chios, Greece (MALZ 1978, as *Aphanius*);
- *Aphanolebias* sp. 1 from the Early Miocene (approximately 22 Ma) of the Upper Rhinegraben area of Germany (REICHENBACHER 2000, as *Aphanius*);
- *Aphanolebias konradi* (REICHENBACHER) from the late Early Miocene of the Northalpine Foreland Basin (approximately 17,5 – 16,4 Ma) (REICHENBACHER 1988, 1993, as *Aphanius*);
- *Aphanolebias gubleri* (REICHENBACHER) from the late Early Miocene of the Northalpine Foreland Basin (approximately 17,3 – 16,4 Ma) (REICHENBACHER 1988, 1993, as *Aphanius*);

Additionally, *Aphanius germaniae* WEILER, 1963 is a younger synonym of *Aphanolebias meyeri* (AGASSIZ).

In all, *Aphanolebias* is recorded so far from the Early Miocene (Aquitainian) of France, the Upper Rhinegraben area, and the Early Karpatian Miocene (Otnangian to Karpatian) of the Western Paratethys. In several localities, *Aphanolebias* species occur sympatrically with *Prolebias* species, e.g., with *Prolebias weileri* VON SALIS, 1967.

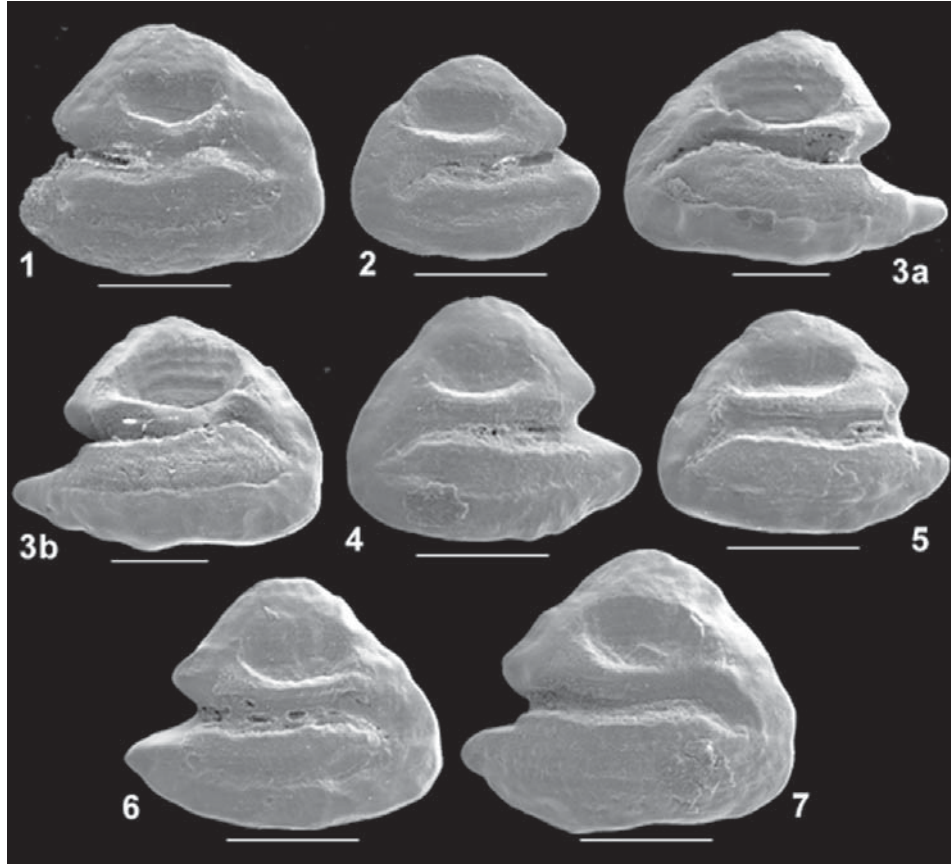


Fig. 2. *Aphanolebias meyeri* (AGASSIZ): 1–3. Otoliths preserved *in situ* in skeletons. – 1, Specimen SMF P. 1686a, right sagitta from the counterpart of specimen SMF P. 1686b (see Fig. 2.1). Upper Hydrobia Beds, probably Alte Gasse, Frankfurt/Main; 2, Left sagitta from specimen Se 2-14 of W. Ott's private collection. Upper Hydrobia Beds, Senckenberganlage, Frankfurt/Main; 3, Specimen SMF PO. 64369. Left (3a) and right (3b) sagitta from specimen SMF P. 9627. Upper Hydrobia Beds, Senckenberganlage, Frankfurt/Main. 4–7. Isolated otoliths, previously determined as *Aphanius germaniae* WEILER. – 4–5, Specimens SMF P. 5553, left sagittae from the Upper Hydrobia Beds of Frankfurt/Main, borehole Mainzer Landstraße 148 (22.9 m depth) (from Malz 1978); 6–7, Specimens SMF P. 5554a-b, right sagittae from the Upper Hydrobia Beds of Frankfurt/Main, borehole Mainzer Landstraße 156 (8 m depth) (from Malz 1978). Each scale bar = 0.5 mm, Photographs B. Reichenbacher.

Conclusions

In a recent study, VILLWOCK (1999) proposed *Prolebias* to be an ancestor of *Valencia* due to the conical jaw teeth distributed in several rows in both genera. However, it is obvious that the new fossil genus *Aphanolebias* intermediates between the *Prolebias*-type, which can be considered as conservative or plesiomorph, and the more advanced *Aphanius/Valencia*-types. Additionally, *Aphanolebias* appears 4-5 Ma before the first appearance of *Aphanius*. Consequently we hypothesize that *Aphanolebias* may be considered as a “missing link” in the fossil record of cyprinodontiform fishes in the Old World. At the present state of knowledge it is not clear whether *Aphanolebias* can be directly related with *Aphanius* or *Valencia*.

Zusammenfassung

In dieser Studie wird die kürzlich eingeführte fossile Gattung *Aphanolebias* REICHENBACHER & GAUDANT, 2003 (Teleostei, Cyprinodontiformes) vorgestellt. Die Typusart, bisher bekannt als *Prolebias meyeri* AGASSIZ, stammt aus Sedimenten des Unter-Miozäns des nördlichen Oberrheingraben und ist aufgrund von Skeletten mit *in situ* erhaltenen Otolithen sehr gut dokumentiert. Das besondere Merkmal von *Aphanolebias* ist die Kombination eines *Prolebias*-artigen Skelettes und -Bezahnung mit *Aphanius*-artigen Otolithen. Wir vermuten, dass *Aphanolebias* die Rolle eines „missing link“ in der fossilen Überlieferung der altweltlichen Zahnkärpflinge einnimmt.

Außer der Typusart gehören zu *Aphanolebias* die fossilen, auf Otolithen basierenden miozänen Arten *Aphanolebias* sp. 1 (REICHENBACHER 2000), *A. angulosus* (STEURBAUT), *A. chios* (MALZ), *A. konradi* (REICHENBACHER) und *A. gubleri* (REICHENBACHER), die bislang für fossile *Aphanius*-Arten gehalten wurden. *Aphanius germaniae* WEILER, 1963 ist ein jüngeres Synonym von *Aphanolebias meyeri* (AGASSIZ).

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