On Prolebias meyeri (Agassiz) (Teleoistei, Cyprinodontiformes) from the Oligo-Miocene of the Upper Rhinegraben area, with the establishment of a new genus and a new species

Autor(en): **Reichenbacher, Bettina / Gaudant, Jean**

Objekttyp: **Article**

Zeitschrift: **Eclogae Geologicae Helvetiae**

Band (Jahr): **96 (2003)**

Heft 3

PDF erstellt am: **21.09.2024**

Persistenter Link: https://doi.org/10.5169/seals-169036

0012-9402/03/030509-12
DOI 10.1007/s00015-003-1098-x
Birkhäuser Verlag, Basel, 2003

Eclogae geol. Helv. 96 (2003) 509–520

On *Prolebias meyeri* (AGASSIZ) (Teleostei, Cyprinodontiformes) from the Oligo–Miocene of the Upper Rhinegraben area, with the establishment of a new genus and a new species

BETTINA REICHENBACHER[1] & JEAN GAUDANT[2]

Key words: Aphanolebias n. gen., *Prolebias, Aphanius,* Cyprinodontiformes, Oligocene, Miocene

ABSTRACT

The study of previously and newly collected skeletons with otoliths preserved *in situ* of the cyprinodontiform species *Prolebias meyeri* (AGASSIZ) from the Upper Hydrobia Beds of Frankfurt/Main (Early Miocene, Hanau Basin) enables us to propose an emended diagnosis of this species, which becomes the type-species of the new genus *Aphanolebias. Aphanolebias* nov. gen. differs from *Prolebias* SAUVAGE due to its triangular-shaped otoliths and from *Aphanius* NARDO due to its conical jaw teeth and the shape of its dentary. A younger synonym of *Aphanolebias meyeri* (AGASSIZ) is *Aphanius germaniae* WEILER 1963.

In addition, we have re-examined skeletons and otoliths of a *Prolebias* species from the Upper Oligocene and Lower Miocene of the Upper Rhinegraben and the Mainz and Hanau Basins, which was also assigned to *P. meyeri.* We introduce the new species *P. malzi* for it. We conclude that all otoliths determined as *P. meyeri* sensu Weiler (1942; 1963) belong to *P. malzi* n. sp. Slight differences in otolith morphology may occur between *P. malzi*-populations of different ages.

RESUME

L'étude de spécimens portant des otolithes *in situ*, à la fois anciens et nouvellement récoltés, de l'espèce de Cyprinodontiformes *Prolebias meyeri* (AGASSIZ), du Miocène inférieur de Francfort (Bassin de Hanau, Allemagne), nous conduit à en proposer une diagnose émendée pour cette espèce qui devient l'espèce-type du nouveau genre *Aphanolebias. Aphanolebias* nov. gen. diffère de *Prolebias* SAUVAGE par la forme triangulaire de ses otolithes et d'*Aphanius* NARDO notamment par la possession de dents coniques sur les mâchoires et par la forme du dentaire. Il est également établi que toutes les otolithes isolées désignées depuis Weiler (1963) comme *Aphanius germaniae* WEILER doivent être rapportées à l'espèce *Aphanolebias meyeri* (AGASSIZ).

On a également réexaminé les squelettes et les otolithes d'un matériel de véritables *Prolebias* de l'Oligocène supérieur et du Miocène inférieur du Fossé rhénan et des bassins de Mayence et de Hanau, qui avaient été décrits par erreur comme *P. meyeri* (AGASSIZ). La nouvelle espèce *P. malzi* n. sp. est créée pour ce matériel. Toutes les otolithes déterminées depuis Weiler (1942; 1963) comme *P. meyeri* (AGASSIZ) sont considérées comme appartenant réellement à l'espèce *P. malzi* n. sp. En outre, après avoir discuté la variabilité des otolithes de cette espèce, il est constaté que de légères différences peuvent exister entre des populations d'âge légèrement différent.

ZUSAMMENFASSUNG

Prolebias meyeri (AGASSIZ) (Cyprinodontiformes) aus den Oberen Hydrobien-Schichten von Frankfurt (Unter-Miozän, Hanauer Becken) wird anhand von Skeletten mit *in situ* erhaltenen Otolithen untersucht. Das Material stammt aus alten und neuen Aufsammlungen. Wir geben eine erweiterte Diagnose dieser Art und definieren sie als Typus-Art der neuen Gattung *Aphanolebias. Aphanolebias* nov. gen. ist von *Prolebias* SAUVAGE aufgrund seiner dreieckigen Otolithen und von *Aphanius* NARDO aufgrund seiner konischen Kieferzähne und der Form des Dentale unterschieden. Ein jüngeres Synonym von *Aphanolebias meyeri* (AGASSIZ) ist *Aphanius germaniae* WEILER.

Eine andere Art aus dem Ober-Oligozän und Unter-Miozän des Oberrheingrabens, des Mainzer und des Hanauer Beckens, die bisher für *Prolebias meyeri* gehalten worden war, wird als *P. malzi* neu definiert. Alle im Sinne von Weiler (1942; 1963) als *P. meyeri* bestimmte Otolithen gehören zu *P. malzi* n. sp. Zwischen *P. malzi*-Populationen unterschiedlicher stratigraphischer Herkunft sind kleine Unterschiede in der Otolithenmorphologie zu verzeichnen.

1. Introduction and historical review

The species *Lebias meyeri* was originally described by Agassiz (1839) from the Miocene of Frankfurt (Hanau Basin, Germany). It based on abundant skeletal material that was collected between 10 and 16 m depth when digging the well of the central cemetery (von Meyer 1834). Malz (1978: 444) correctly recognized that the sediments yielding *Lebias meyeri* belong to the Upper Hydrobia Beds that can be placed in the late Early Miocene (Martini 1987; Reichenbacher 2000).

However, it was rather difficult to get an accurate understanding of *Lebias meyeri* AGASSIZ because its original de-

[1] Department of Earth and Environmental Sciences & GeoBioCenter, Ludwig-Maximilans-Universität Munich, Richard-Wagner-Str. 10, D-80333 Munich. E-mail: b.reichenbacher@lrz.uni-muenchen.de
[2] 17, rue du Docteur Magnan, F-75013 Paris. E-mail: gaudant@ipgp.jussieu.fr

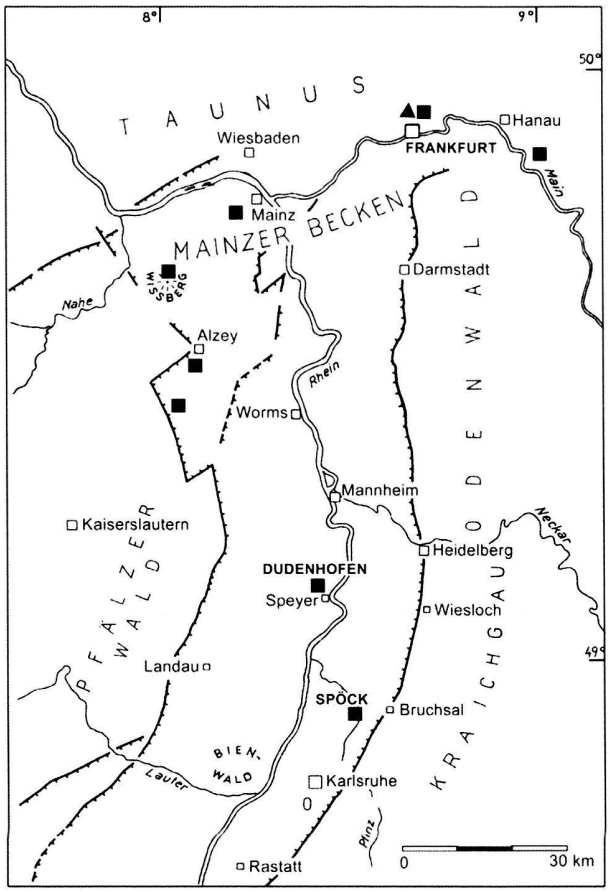


Fig. 1. Map showing the origin of the studied materials of *Aphanolebias meyeri* (AGASSIZ) and *Prolebias malzi* n.sp. (map from Weiler 1963, modified).

scription 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 one "*P. meyeri*" skeleton, which is mentioned out of the Rhinegraben region (d'Erasmo 1929: Messinian from Senigallia, Italy), probably is a young specimen of *Aphanius crassicaudus* (AGASSIZ).

Weiler (1929) discussed and compared the skeletal characters of *P. meyeri* when introducing the Oligocene species *Prolebias praecursor* WEILER, but his comparison based only on the incomplete description by Agassiz (1839).

Weiler (1942) reported skeletons of *P. meyeri* from the borehole Baden 4 in the southern Upper Rhinegraben. He did neither 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). According to Weiler (1942), the skeletons and otoliths from the borehole Baden 4 originate from the "lower Hydrobia Beds" and the "boundary Corbicula/Hydrobia Beds". However, today it is well known that in the Rhinegraben area these strata truly belong to the Upper Cerithium Beds (Upper Oligocene to Lower Miocene) and to the underlying Middle Cerithium Beds (Upper Oligocene) (e.g., Reichenbacher 2000). Unfortunately, the material from the borehole Baden 4 cannot be located.

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 the Middle Cerithium Beds of the borehole Dudenhofen (890.5–895.3 m; Fig. 1) 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 (400.9–409.3 m; Fig. 1) belong to this species (Reichenbacher 2000: 73).

Reichenbacher & Mödden (1996), Reichenbacher (2000), and Reichenbacher & Sienknecht (2001) determined and figured isolated otoliths from several outcrops and boreholes in the Mainz and Hanau Basins (Fig. 1) as *P. meyeri*, referring to the determinations of Weiler (1942, 1963). These otoliths originate from the Landschneckenkalk and the overlying Upper Cerithium Beds and Rüssingen Formation (former Inflata Beds, Schäfer & Kadolsky 2002). They are absent in the overlying Wiesbaden-Formation (former Lower Hydrobia Beds, Reichenbacher & Keller 2002), but appear again in the overlying Upper Hydrobia Beds and Landschneckenmergel.

In the present study we demonstrate on basis of skeletons and otoliths that *P. meyeri* sensu Weiler (1942, 1963) does not agree with *P. meyeri* sensu Agassiz (1839).

2. Material and origin of material

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

Previous collection of *P. meyeri* sensu Agassiz (1839)

This material was collected by H. von Meyer and probably originates from the Upper Hydrobia Beds.

SMF P. 1687b: skeleton from Frankfurt, Alte Gasse; Fig. 2.2.
SMF P. 1686b: skeleton, probably from same locality as SMF P. 1687b; Fig. 2.1.
SMF P. 1686a: otolith, found *in situ* in the counterpart of SMF P. 1686b; mentioned by Malz (1978); Fig. 3.1.

New collection of *P. meyeri* sensu Agassiz (1839)

This material originates from the Upper Hydrobia Beds of Frankfurt, Senckenberganlage, and was collected by the amateur collectors K. Weiss, W. Ott, and M. Keller (Ott 2003). The fossiliferous layers were accessible during the

Tab. 1. Main characters of *Aphanolebias meyeri* (AGASSIZ 1839). All skeletons were found in the Upper Hydrobia Beds from the underground of Frankfurt/Main.

	previous collection SMFP. 1686ab, 1687b	new collection SMF P. 9612–16, 9620–27
standard length (SL)		up to 40 mm
maximum height of body	1/4 of SL	1/4 to 1/3.5 of SL
oral jaws	premaxilla with conical teeth	premaxilla with conical teeth
otolith	triangular	triangular
total number of vertebrae	28–29	28–29
number of postabdominal vertebrae	15	(15) 16 (17)
shape of caudal fin	convex	convex
number of principal rays of caudal fin	16	(15) 16
number of dorsal fin rays	10	9–12
number of pterygiophores of dorsal fin		9–10
number of anal fin rays	12	11–14
number of pterygiophores of anal fin	10	10–12
position of anal fin	slightly in front of origin of dorsal fin	almost opposed to dorsal fin
insertion of pelvic fins	slightly nearer to anal fin than to pectoral fins	slightly nearer to anal fin than to pectoral fins
number of pectoral fin rays		12–15
number of pelvic fin rays		6–7

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); Fig. 2.3.
SMF P. 9613: skeleton (collected by K. Weiss under the number Se 2-W4); Figs. 4, 6.1.
SMF P. 9614: skeleton (collected by W. Ott under the number Se 2a-4); Figs. 5, 6.2.
SMF P. 9615: skeleton (collected by K. Weiss under the number Se 2-W1); Fig. 6.3.
SMF P. 9616: skeleton (collected by W. Ott under the number Se 2-11); Fig. 6.4.
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); Fig. 3.3.
SMF PO. 64370–64372: otoliths found *in situ* (collected by M. Keller).

Collection of isolated otoliths of *Aphanius germaniae* WEILER 1963

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).
SMF P. 5554, 40 sagittae from the Upper Hydrobia Beds of Frankfurt/Main, borehole Mainzer Landstraße 156 (8 m depth) (mentioned in Malz 1978).
Further 450 sagittae are kept in the Senckenberg Museum (material of Malz 1978).

Collection of *Prolebias meyeri* sensu Weiler (1942, 1963)

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* n. sp.; Fig. 7.2.
SMF P. 3366A-B: skeleton; figured in Weiler (1963: Figs. 74a–b); paratype of *P. malzi* n. sp.; Figs. 7.1, 8.2, 8.4.
SMF P. 3572: skeleton; mentioned in Weiler (1963); Fig. 8.1.
SMF P. 3574: skeleton; mentioned in Weiler (1963).
SMF P. 9617: skeleton; Fig. 8.3.
SMF P. 9618a: skeleton and otolith embedded in the sediment; Fig. 9.
SMF P. 9618b–c: four skeletons.

B. From boreholes and outcrops in the Mainz and Hanau Basins, from boreholes in the Upper Rhinegraben
About 650 isolated otoliths (material of Reichenbacher & Mödden 1996; Reichenbacher 2000).

3. Re-examination of *Prolebias meyeri* sensu Agassiz (1839)

Previous collection (Figs. 2.1–2.2, 3.1, Tab. 1)

Specimen SMF P. 1687b (Fig. 2.2) is characterized by its elongate body, the maximum height of which equals slightly less than 1/4 of the standard length. Its rather short vertebral column consists of 28 or 29 vertebrae, 15 being postabdominal. Its caudal fin exhibits a convex posterior outline. The dorsal fin is opposed to the anal fin; it has about 10 rays. The anal fin begins slightly in front of the dorsal fin; its 12 rays are supported by about 10 pterygiophores. The pelvic fins are located slightly nearer to the origin of the anal fin than to the pectoral fins base. Specimen SMF P. 1686b (Fig. 2.1) provided additional information by showing some conical teeth in the premaxilla.

Malz (1978) isolated one *in situ* preserved otolith (Fig. 3.1) in the counterpart of SMF P. 1686b. It is a right sagitta exhibiting a symmetrical triangular shape and a rather prominent rostrum, slightly corroded at its tip. The sulcus, situated in the middle of the sagitta, displays a small and narrow ostium and a long cauda, which is strongly bent down and pointed at its distal end.

New collection (Figs. 2.3, 3.2, 3.3, 4–6, Tab. 1)

These skeletons (Fig. 2.3, 6.1–6.3) correspond well with the skeletons from the previous collection and reveal some addi-

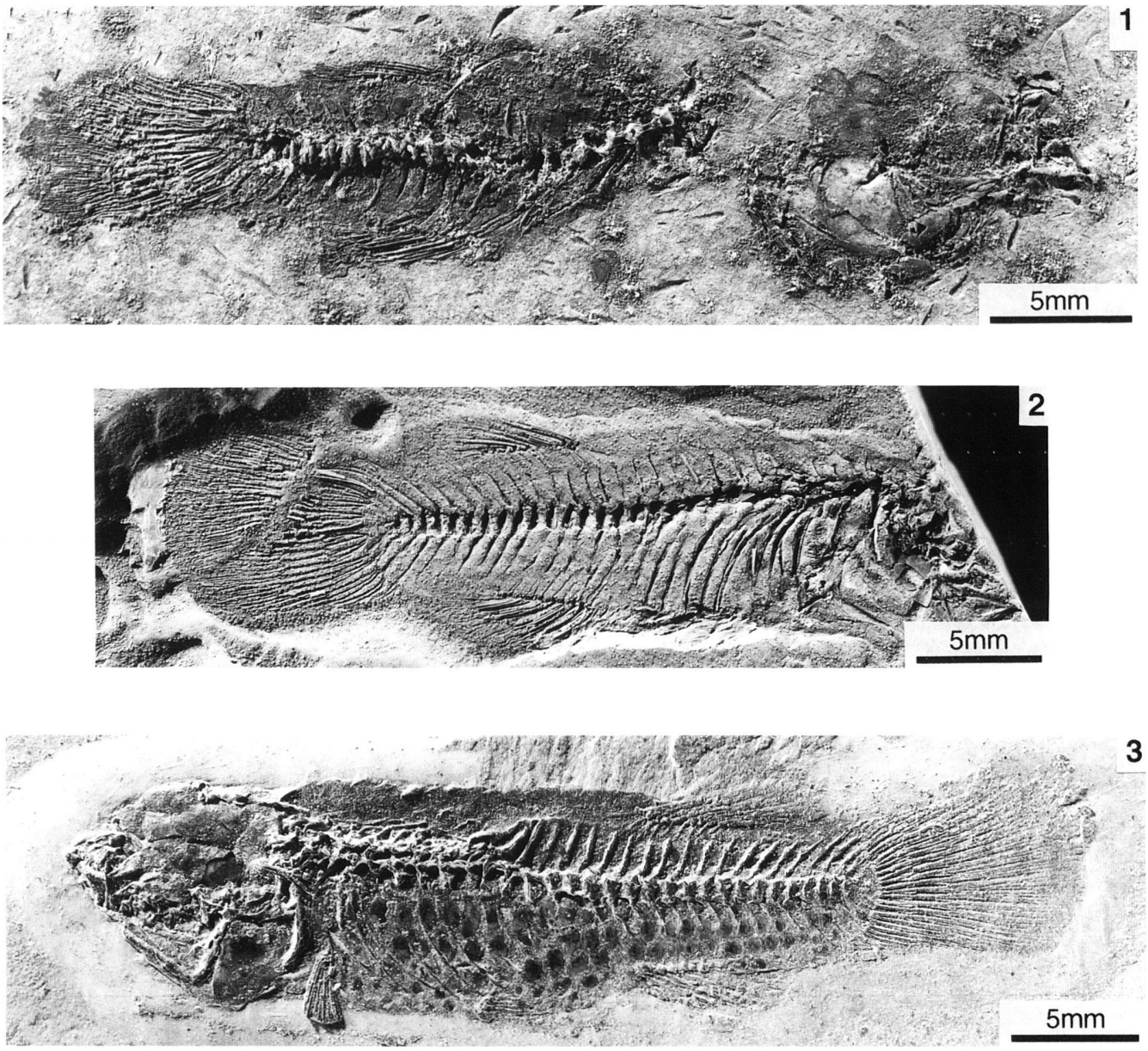


Fig. 2. *Aphanolebias meyeri* (AGASSIZ). General view of body of three specimens. Photographs D. Serrette.

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.

tional informations. They demonstrate jaws provided with many small conical teeth (Fig. 4) distributed in several rows, a dentary which is devoid of any spur-like medial process (Fig. 5), a relatively high number of principal caudal fin-rays (Figs. 2.3, 6.4) and two hypural plates incompletely fused (Fig. 6.4).

Some skeletons revealed *in situ* preserved otoliths (Figs. 3.2, 3.3). These otoliths (sagittae) are triangular with a prominent rostrum and display a sulcus with the distal end of the cauda bent down and pointed. A slight variability occurs relatively to the shape and length of the rostrum.

4. Discussion and introduction of *Aphanolebias* nov. gen.

The studied skeletons of *P. meyeri* sensu Agassiz (1839) 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 not

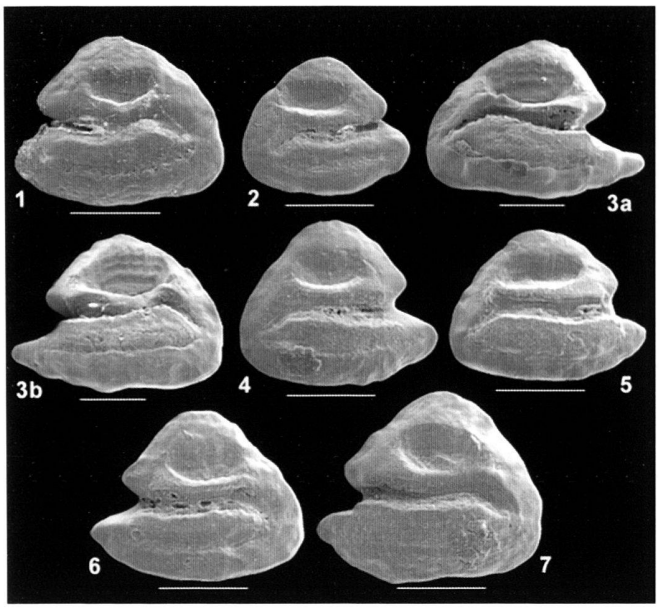


Fig. 3. *Aphanolebias meyeri* (AGASSIZ). Each scale bar = 0.5 mm. Photographs B. Reichenbacher.

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).

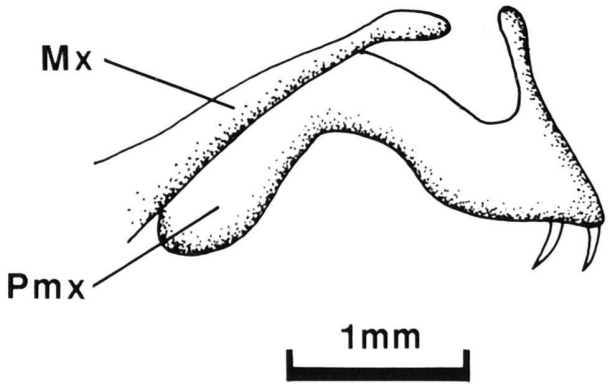


Fig. 4. *Aphanolebias meyeri* (AGASSIZ). Lateral view of the right upper jaw of specimen SMF P. 9613 from the Upper Hydrobia Beds, Senckenberganlage, Frankfurt/Main. Mx: maxilla; Pmx: premaxilla exhibiting two conical teeth.

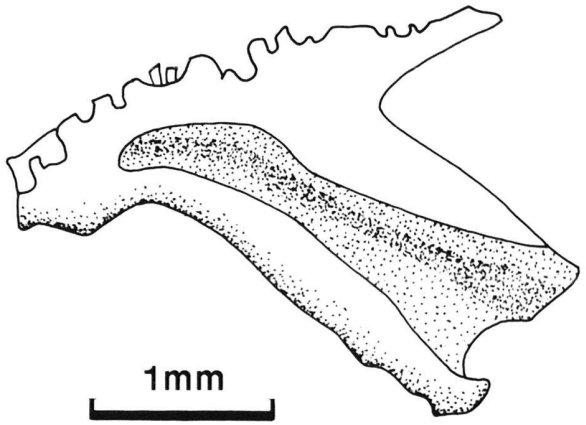


Fig. 5. *Aphanolebias meyeri* (AGASSIZ). Inner view of the right dentary of specimen SMF P. 9614 from the Upper Hydrobia Beds, Senckenberganlage, Frankfurt/Main.

any derived skeletal or dental character appears in *Prolebias*. Consequently, no definition of *Prolebias* from a phylogenetic point of view was given so far (Sethi 1960; Parenti 1981).

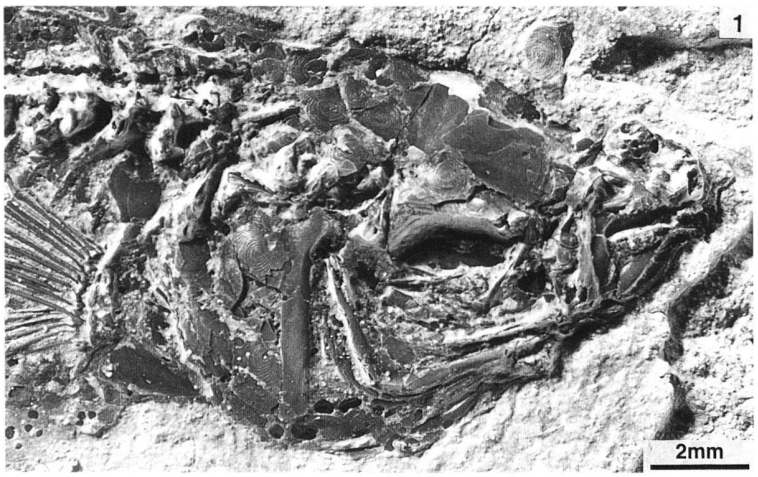
We consider the following characters of *Prolebias* SAUVAGE as most significant. Altogether, they allow to distinguish *Prolebias* from *Aphanius* NARDO and *Valencia* MYERS.

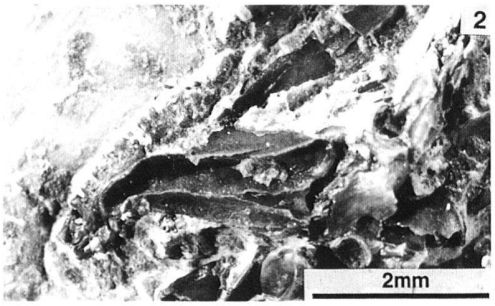
- jaws provided with conical teeth (tricuspid in *Aphanius*, conical in *Valencia*)
- dentary without any spur-like medial process (with process in *Aphanius*, without in *Valencia*)
- otolith with a dorsal tip and rounded (without dorsal tip and triangular in *Aphanius* and *Valencia*)

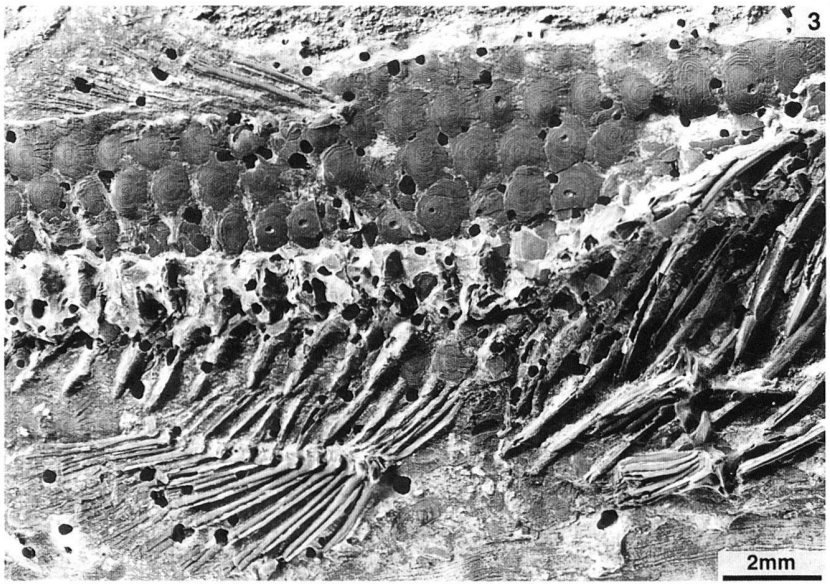
It should be added that the typical otoliths of *Prolebias* (with dorsal tip and rounded) have been found in several species *in situ*, e.g., in *P. hungaricus* GAUDANT 1991, in *P. cephalotes* (AGASSIZ) (unpublished data), and in *P.* aff. *weileri* (SALIS) (Gaudant & Reichenbacher 2002). The triangular-shaped otoliths of recent *Aphanius* species were illustrated by Malz (1978) and Reichenbacher & Sienknecht (2001). *Valencia* otoliths, which are also triangular-shaped, are described and illustrated in Sienknecht & Reichenbacher (in prep.).

It should also be added that *Valencia* is not known as fossil, whereas *Prolebias* is only known as fossil. *Aphanius* is known as fossil since the Early Miocene (Burdigalian, 17–18 Ma; Gaudant & Rovira-Sendrós 1998).

From our description of *P. meyeri* sensu Agassiz (1839) it is evident that this species 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, the conical teeth of its jaws, and the shape of the dentary are evidently typical for *Prolebias*. But contrary to *Prolebias*, its otoliths are triangular-shaped and resemble recent *Aphanius* and *Valencia* otoliths. Consequently, it is necessary to create a new genus for taking into account this unique combination.







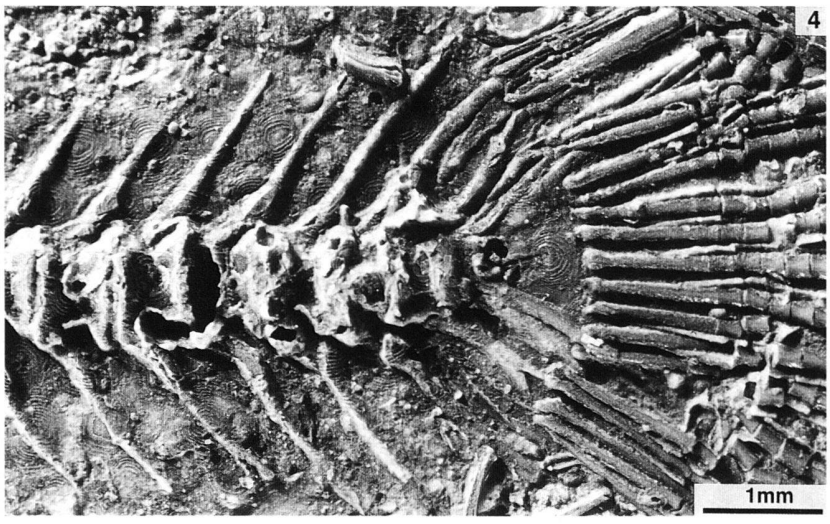


Fig. 6. *Aphanolebias meyeri* (AGASSIZ). Upper Hydrobia Beds, Senckenberganlage, Frankfurt/Main. Photographs D. Serrette.

1. Head of specimen SMF P. 9613.
2. Lower jaw of specimen SMF P. 9614.
3. Middle part of body of specimen SMF P. 9615.
4. Caudal axial skeleton of specimen SMF P. 9616.

Tab. 2. Comparison of *Aphanolebias meyeri* (AGASSIZ), *Prolebias malzi* n. sp., *P. praecursor* WEILER, and *P. rhenanus* GAUDANT.

	Aphanolebias meyeri (AGASSIZ) (see Tab. 1)	*Prolebias malzi* n. sp. [= *P. meyeri* sensu Weiler 1942, 1963]	*Prolebias praecursor* WEILER 1929 (?*Hemitrichas*)	*Prolebias rhenanus* GAUDANT 1981
Standard length (SL)	up to 40 mm	up to 29 mm	about 40 mm	up to 27 mm
maximum height of body	1/4 to 1/3.5 of SL	1/4 to 1/4.5 of SL	not known	1/3 to 1/4.5 of SL
jaws	premaxilla with conical teeth	not known	not known	not known
otolith	triangular	rounded	not known	not known
total number of vertebrae	28–29	30	31	28–29
number of postabdominal vertebrae	(15) 16 (17)	18–19	17–18	16–17
shape of caudal fin	convex	truncated	indented	truncated
number of principal rays of caudal fin	(15) 16	10–12	14–16	12
number of dorsal fin rays	9–12 (7–9 branched)	7–8	9	9–11
number of pterygiophores of dorsal fin	9–10	7–8	not known	9–10
number of anal fin rays	11–14 (9–11 branched)	14–17	11–12	12–13
number of pterygiophores of anal fin	10–12	13–15	not known	11–12
position of anal fin	almost exactly opposed to dorsal fin	significantly in front of origin of dorsal fin	in front of origin of dorsal fin	slightly in front of origin of dorsal fin
insertion of pelvic fins	slightly nearer to anal fin than to pectoral fins	nearer to pectoral fins than to anal fin	nearer to anal fin than to pectoral fins	very near to anal fin
number of pectoral fin rays	12–15	10–11	not known	13–14
number of pelvic fin rays	6–7	6, sometimes with claw-like distal ends	not known	6

Aphanolebias nov. gen.

Derivatio nominis
Compound name emphasizing the unique combination of characters.

Type species
Lebias meyeri AGASSIZ 1839.

Synonymy of the type species
Prolebias meyeri (AGASSIZ) (not *P. meyeri* sensu Weiler 1942, 1963, see below), *Aphanius germaniae* WEILER.

Type locality
Frankfurt/Main (Hanau Basin, Germany).

Other localities
Boreholes in the Upper Rhinegraben (as *A. germaniae* WEILER, Reichenbacher 2000: Fig. 33).

Type formation
Upper Hydrobia Beds.

Other formations
Landschneckenmergel, which overly the Upper Hydrobia Beds.

Age and stratigraphic range
Late Early Miocene (Burdigalian), probably 19–20 Ma (Martini 1987, Reichenbacher 2000).

Diagnosis
Skeletal characters like those of *Prolebias* SAUVAGE, but otoliths are triangular-shaped and similar to those of *Aphanius* NARDO and *Valencia* MYERS.

Description of the type species (Table 1)
Small cyprinodontiform, the standard length does not exceed 40 mm. Body elongated, its maximum height equals 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) tri-

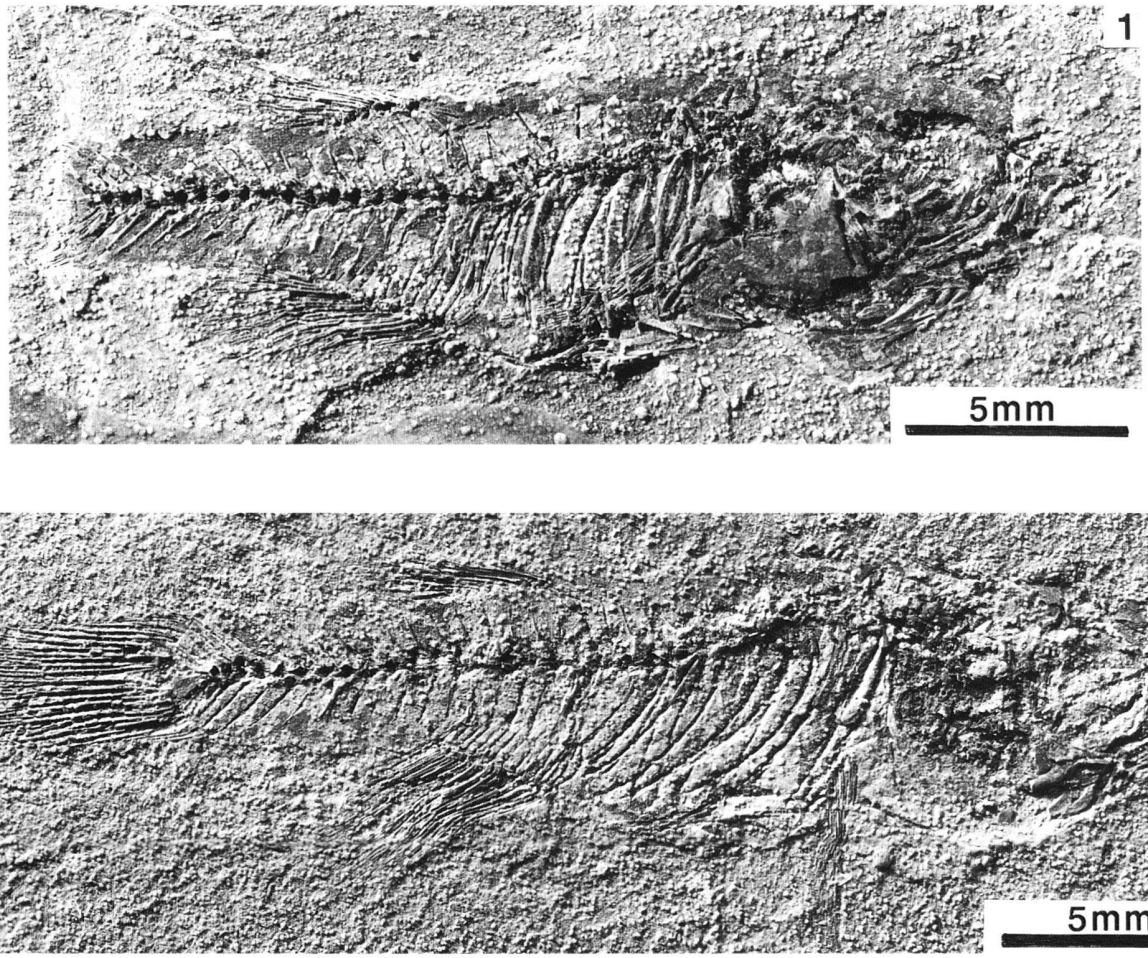


Fig. 7. *Prolebias malzi* n. sp. Middle Cerithium Beds (Upper Oligocene), borehole Dudenhofen 1 (southern Upper Rhinegraben). Photographs D. Serrette.

1. Specimen SMF P. 3366A, paratype.
2. Specimen SMF P. 3509, holotype.

angular-shaped with a prominent rostrum and a cauda distinctly bent down and pointed at its distal end.

Synonymies

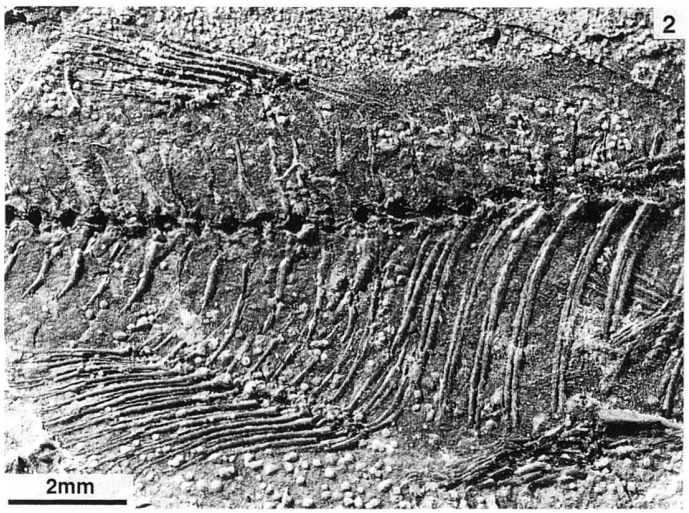
The otoliths of *Aphanolebias meyeri* (AGASSIZ) correspond perfectly with *Aphanius germaniae* WEILER 1963 (Figs. 3.4–3.7), which is an otolith based-species.

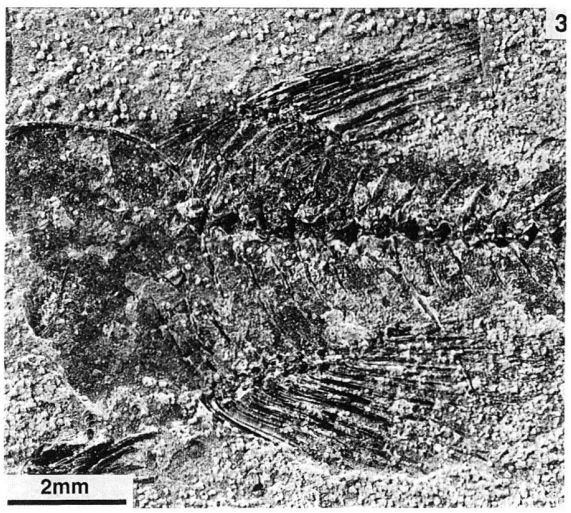
5. Re-examination of *Prolebias meyeri* sensu Weiler (1942, 1963)

5.1 Skeletons and otoliths from the boreholes Dudenhofen 1 and Baden 4

Skeletons and otoliths from the Middle and Upper Cerithium Beds of the boreholes Dudenhofen 1 and Baden 4 (southern Upper Rhinegraben) were determined by Weiler (1942, 1963) as *Prolebias meyeri* (AGASSIZ). However, this material reveals skeletal characters and otoliths, which are clearly different from *Prolebias meyeri* (AGASSIZ) (Tab. 2).

The skeletons from the borehole Dudenhofen 1 (Figs. 7–8) have a standard length ranging from 13.5 to 29 mm. Their maximum height of body equals 1/4 to 1/4.5 of standard length. The head (Fig. 8.1) exhibits characters that are well known for the genus *Prolebias* SAUVAGE, especially a dentary without spur-like process. The vertebral column consists of about 30 vertebrae, 18–19 being postabdominal. The caudal fin is posteriorly truncated and includes 10–12 principal rays (articulated and furcated) and, both ventrally and dorsally, 7–8 procurrent rays. It is supported by a caudal axial skeleton in which two distinct hypural plates are present (Fig. 8.4). The dorsal fin consists of i–ii+I+7– (rarely 8) rays, its principal rays are articulated and furcated. It is supported by 7 or 8 pterygiophores (Figs. 8.2, 8.3). The anal fin begins rather significantly in front of the origin of the dorsal fin (Figs. 8.2, 8.3); the anteanal distance generally ranges from 59 to 62.5% of standard length, whereas the antedorsal distance ranges from 62 to 63.5%. The anal fin consists of ii+I+11–14, its principal rays are articulated





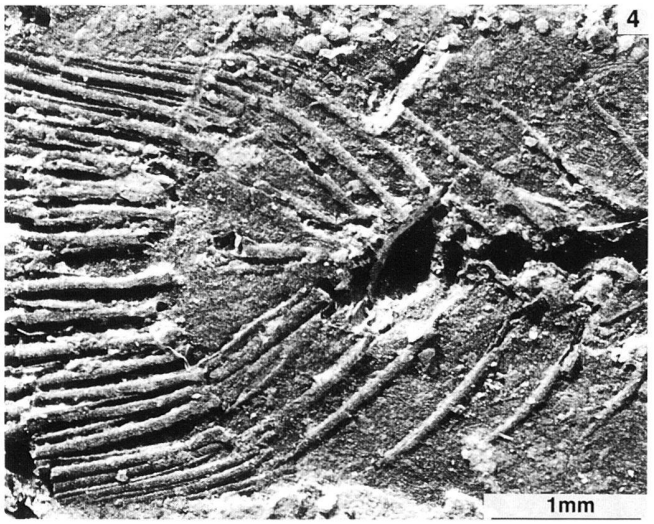


Fig. 8. *Prolebias malzi* n. sp. Middle Cerithium Beds (Upper Oligocene), borehole Dudenhofen 1, (southern Upper Rhinegraben). Photographs D. Serrette.

1. Anterior part of body of specimen SMF P. 3572.
2. Middle part of body of specimen SMF P. 3366B.
3. Middle part of body of specimen SMF P. 9617.
4. Caudal axial skeleton of specimen SMF P. 3366B.

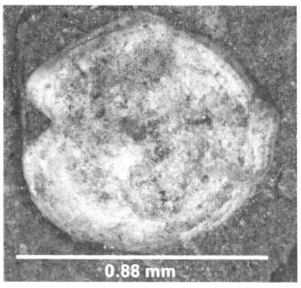


Fig. 9. Left sagitta of *P. malzi* n. sp., embedded in the sediment of the core of the borehole Dudenhofen 1 (SMF P. 9618a). Photograph B. Reichenbacher.

and furcated. It is supported by 13–15 pterygiophores. The three anteriormost pterygiophores – the first one being arch-shaped – take place in front of the hemapophyse of the first postabdominal vertebra. The pectoral fins have about ten rays; the distal end of the longest reaches the base of the pelvic fins (Fig. 8.1). The pelvic fins are obviously situated nearer to the base of the pectorals than to the origin of the anal fin (Fig. 8.2). Six rays make up the pelvic fins. In some fishes, the pelvic rays are not articulated and exhibit claw-like distal ends, as shown by specimen SMF P. 3366A. The body is covered with cycloid scales, the surface of which bears concentric circuli.

Weiler (1963: Fig. 75) mentioned and figured rather corroded otoliths preserved *in situ* in the skeletons. According to him, these otoliths have a round shape, a broadly rounded, short rostrum, and a pointed antirostrum. Unfortunately, we found them strongly corroded and not suited for any figure or more detailed description.

However, we found a slightly flattened, but well-preserved otolith (sagitta) in the core material, embedded in the sediment with the inner face down (Fig. 9). The shape of this otolith is round with a dorsal rim showing a slight median tip. The posterior rim, well rounded, presents a slight edge in the middle. The rostrum is moderately rounded and shows a slight tip in its upper part. It is not longer than the pointed antirostrum. Length of otolith is 0.88 mm and height is 0.83 mm. This otolith corresponds well with the so-called otolith-holotype of *P. meyeri* sensu Weiler (1942) from the borehole Baden 4. On the other hand, it seems to be somewhat more rounded in shape than the otolith found in the skeleton SMF P. 3509 *in situ* (Weiler 1963: Fig. 75), but this may result from the bad preservation of the latter. Taking also into account that no other fish species occurs in the cores of the borehole Dudenhofen 1 (890.5–895.3 m), we assume that our otolith belongs to the *Prolebias* species described above.

5.2 Isolated otoliths from the Mainz and Hanau Basins

Isolated otoliths revealing a rounded shape and a slight median tip, as described above, are well known from Upper Oligocene and Lower Miocene sediments of the Mainz and Hanau Basins. A few specimens were also found in the Upper Rhinegraben (Weiler 1963).

Referring to Weiler (1942, 1963), all these otoliths were determined as *P. meyeri* (AGASSIZ) in subsequent publications (e.g., Wiesner 1967; Best 1975; Reichenbacher & Weidmann 1992; Reichenbacher & Mödden 1996; Reichenbacher 2000). However, on basis of their rounded shape it is clear that they cannot belong to *P. meyeri* (AGASSIZ), because that species, which is now *Aphanolebias meyeri*, has triangular-shaped otoliths (Fig. 3).

6. Discussion and definition of *Prolebias malzi* n. sp.

From the preceding descriptions, it clearly appears that *Prolebias meyeri* sensu Weiler (1942, 1963) differs from *Aphanolebias meyeri* (AGASSIZ) from the Upper Hydrobia Beds. As it can be seen from Tab. 2, *Aphanolebias meyeri* has less postabdominal vertebrae, a smaller anal fin having only 11–14 rays and 10–12 pterygiophores, pelvic fins situated slightly nearer to the origin of the anal fin than to the base of the pectoral fins, and triangular-shaped otoliths. Consequently, the skeletons and otoliths, so far determined as *Prolebias meyeri* sensu Weiler (1942, 1963), belong to a new species, *Prolebias malzi* n. sp.

Prolebias malzi n. sp. – Figs. 7–9

Derivatio nominis
: This species is dedicated to Dr. HEINZ MALZ (Bramsche), who was the first to question Weiler's determination of this material (Malz 1978: 455).

Holotype
: Specimen SMF P. 3509 (Fig. 7.2), already figured by Weiler (1963, Pl. 2, Fig. 5).

Type locality
: Borehole Dudenhofen 1 (890.5–895.3 m), southern Upper Rhinegraben (Fig. 1).

Other localities
: Boreholes Grünstadt and Spöck 1 in the Upper Rhinegraben, boreholes and outcrops in the Mainz and Hanau Basins (as *P. meyeri* sensu WEILER 1942, 1963; e.g., Reichenbacher 2000: 73).

Type formation
: Middle Cerithium Beds.

Other formations
: Landschneckenkalk, Upper Cerithium Beds, Rüssingen Formation (former Inflata Beds), Upper Hydrobia Beds, Landschneckenmergel (Reichenbacher 2000: 73).

Age and chronostratigraphic range
: Upper Oligocene (24–24.5 Ma) until Late Early Miocene (19–20 Ma).

Definition and description
: Body elongate with a standard length up to 30 mm, a maximum height, which equals 1/4 to 1/4.5 of standard length, and comprising about 30 vertebrae, 18–19 being postabdominal. The caudal fin is truncated and consists of 10–12

principal rays. The dorsal fin is opposed to the anal fin and consists of 7–8 rays supported by 7–8 pterygiophores. The anal fin, which begins rather significantly in front of the dorsal fin, displays 14–17 rays supported by 13–15 pterygiophores. The pectoral fins consist of 10 rays and are of moderate size. The pelvic fins are situated nearer to the pectoral fins than to the origin of the anal fin; they consist of 6 rays having sometimes claw-like extremities. Body covered with cycloid scales. Otoliths of rounded shape with a slight dorsal tip and a rostrum, which is not or only slightly longer than the antirostrum.

Comparison with other species

The holotype and only known specimen of *Prolebias praecursor* WEILER 1929 was found in Upper Oligocene sediments near Alzey in the Mainz Basin, either in the Cyrena Marls, or the so-called Süßwasserschichten, or the Upper Cerithium Beds (Reichenbacher 2000: 15). Unfortunately, the holotype is lost. According to the short description given by Weiler (1929) (Tab. 2), the most significant characters of *P. praecursor* are the dorsal fin with 9 long rays (instead of 7–8 in *P. malzi*), the number of rays in the anal fin (11–12, instead of 14–17 in *P. malzi*), and the position of the pelvic fins, which are situated nearer to the anal fin than to the pectoral fins (instead of the contrary in *P. malzi*).

It is worth mentioning that according to Weiler (1929), the caudal fin of *P. praecursor* is rather deeply furcated because this can be hardly expected within the genus *Prolebias* SAUVAGE. Moreover, our re-examination of *P.* cf. *praecursor* from the Cerithium Beds of the borehole Gundersheim 13, determined by Weiler (1963), revealed that this specimen has **two** dorsal fins, the first one being made of short thin spines. Consequently, *P.* cf. *praecursor* cannot belong to the genus *Prolebias*, but may be a species of the genus *Hemitrichas* PETERS, which is widely distributed in the Mainz Basin and the Hanau Basin (Micklich 1996, Ott 2001, Keller et al. 2002).

Prolebias rhenanus GAUDANT 1981 is known from the Lower Oligocene of Kleinkems (near Baden) in the southern Upper Rhinegraben. This species, whose characters are summarized in Tab. 2, clearly differs from *P. malzi* because of its smaller anal fin consisting of 12–13 rays (instead of 14–17 in *P. malzi*), and its pelvic fins, which are smaller and situated nearer to the anal fin than to the pectoral fins (instead of the contrary in *P. malzi*).

7. Otolith variability of *Prolebias malzi* n. sp.

We have investigated the angle of the excisura in populations of *P. malzi* otoliths from the Upper Cerithium Beds and the overlying Rüssingen Formation (former Inflata Beds). The excisura angle tends to be narrower in older specimens (Fig. 10). This fits well with the fact that the excisura angle is most narrow (114°) in the otolith from the Middle Cerithium Beds of Dudenhofen (Fig. 9). Also the antirostrum displays changes in shape and dimensions from the older to the younger populations (Reichenbacher 2000: Fig. 17). Following the actualistic studies on the Recent Mediterranean species *Aphanius iberus* (VALENCIENNES in CUVIER & VALENCIENNES) (Reichenbacher & Sienknecht 2001), such changes in otolith morphology may point to a genetic divergence between *Prolebias malzi* populations of different stratigraphic ages.

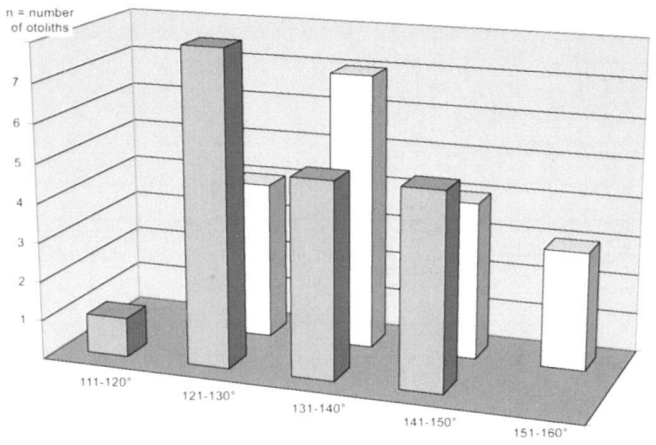


Fig. 10. Distribution patterns of excisura angles of *Prolebias malzi* n. sp. from the Upper Cerithium Beds (dark columns, n = 16) and the overlying Rüssingen Formation (light columns, n = 18).

Acknowledgements

We are grateful to W. Ott (Offenbach), K. Weiss (Fischbach), and M. Keller (Frankfurt), who made available their newly collected cyprinodontiform fishes and donated the most important specimens to the Senckenberg Museum. We are grateful to Dr. N. Micklich (Hessisches Landesmuseum Darmstadt) and Prof. Dr. G. Stringer (The University of Louisiana at Monroe) for their critical review of the manuscript. We thank Dr. G. Plodowski and Dr. T. Jellinek (both Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main) for the loan of material. Sincere thanks go to D. Serrette (Paris) for the photographs of the fish skeletons and to J. Dyon (Paris) for preparing the illustrations of Figs. 4–5. SEM-pictures were made at the Laboratorium für Elektronenmikroskopie of the University Karlsruhe, we thank V. Zibat for his assistance. This study was kindly supported by the Deutsche Forschungsgemeinschaft (Re 1113/6-1).

REFERENCES

AGASSIZ, L. 1839: Recherches sur les Poissons fossiles, 5(1-2), 1–122, 1–160, Neuchâtel (Petitpierre).

BEST, G. 1975: Feinstratigraphie der Hydrobien-Schichten (Untermiozän, Mainzer Becken). Mainzer geowiss. Mitt. 4, 75–138, Mainz.

ERASMO, G. D' 1929: L'Ittiofauna fossile di Senigallia. Atti della R. Accademia delle Scienze fisische e matematiche di Napoli 18, 1–83.

GAUDANT, J. 1981: Un nouveau Cyprinodontidae (Poisson téléostéen) de l'Oligocène inférieur de Kleinkems (Pays de Bade, Allemagne): *Prolebias rhenanus* nov. sp. Sci. Geol. Bull. 34(1), 3–12.

GAUDANT, J. 1989: Découverte d'une nouvelle espèce de poissons cyprinodontiformes (*Prolebias delphinensis* nov. sp.) dans l'Oligocène du bassin de Montbrun-les-Bains (Drôme). Géol. méditerr. 16, 355–370, Marseille.

GAUDANT, J. 1991: *Prolebias hungaricus* nov. sp.: une nouvelle espèce de Poissons Cyprinodontidae des diatomites miocènes de Szurdokpüspöki (Comté de Nograd, Hongrie). Magyar All. Földt. Int. Evi Jel. 1989, 481–493.

GAUDANT, J. 1998: L'ichthyofaune des eaux continentales miocènes de Serbie (Yougoslavie): une revision. N. Jb. Geol. Paläont. Abh. 207(1), 107–123.

GAUDANT, J. & ROVIRA-SENDRÓS, J. 1998: Découverte de la plus ancienne espèce connue du genre *Aphanius* NARDO (Poissons téléostéens) dans le Miocène inférieur évaporitique de la Catalogne. Batalleria 8, 55–60.

GAUDANT, J. & REICHENBACHER, B. 2002: Anatomie et affinités des *Prolebias* aff. *weileri* VON SALIS (Poissons téléostéens, Cyprinodontidae) du Miocène inférieur à moyen du Randecker Maar (Wurtemberg, Allemagne). Stuttgarter Beitr. Naturkde. B 331, 1–11.

KELLER, T., REICHENBACHER, B., GAUDANT, J. 2002: Erstnachweis von Atheriniden-Skeletten (Pisces, Teleostei, Atheriniformes) mit Otolithen *in situ* aus den Unteren Hydrobien-Schichten (Wiesbaden-Formation) des Mainzer Beckens, mit einem Beitrag zur Sedimentologie und Paläoökologie. Cour. Forsch.-Inst. Senckenberg 237, 319–343.

MALZ, H. 1978: Vergleichend-morphologische Untersuchungen an aquitanen Fisch-Otolithen aus dem Untergrund von Frankfurt am Main. Senckenberg. lethaea 59(4/6), 441–481.

MARTINI, E. 1987: Nannoplankton aus den Oberen Hydrobien-Schichten des Hanauer Beckens (Miozän). Geol. Jb. Hessen 115, 217–226.

MEYER, H. v. 1834: Vorkommen des *Lebias meyeri*, AGASS., eines fossilen Fisches, im Thone von Frankfurt a.M. Mus. Senckenbergianum 1, 282–285.

MICKLICH, N. 1996: Sexual dimorphism in a lower Miocene moronid? Pal. Z. 70(3/4), 547–554.

OTT, W. 2001: Baustellen: Fenster in die Erdgeschichte. 2. Mitteilung: Baustelle "Westhafen", Frankfurt am Main. Ber. Offb. Ver. Naturkde 101, 28–35.

– 2003: Baustellen: Fenster in die Erdgeschichte. 3. Mitteilung: Neubau der U-Bahnstation Senckenberganlage, Frankfurt am Main-Bockenheim. Eine ergiebige Fundstelle fossiler Fischskelette in den Oberen Hydrobien-Schichten. Ber. Offb. Ver. Naturkde 103 (in press).

PARENTI, L. R. 1981: A phylogenetic and biogeographic analysis of Cyprinodontiform fishes (Teleostei, Atherinomorpha). Bull. Amer. Mus. Nat. Hist. 168(4), 335–557.

REICHENBACHER, B. 2000: Das brackisch-lakustrine Oligozän und Unter-Miozän im Mainzer Becken und Hanauer Becken: Fischfaunen, Paläoökologie, Biostratigraphie, Paläogeographie. Cour. Forsch.-Inst. Senckenberg 222, 1–143.

REICHENBACHER, B. & KELLER, T. 2002: Neudefinition von stratigraphischen Einheiten im Tertiär des Mainzer und Hanauer Beckens (Deutschland, Oligozän – Miozän). Teil 2: Wiesbaden-Formation [= Untere Hydrobien-Schichten]. Mainzer geowiss. Mitt. 31, 99–122.

REICHENBACHER, B. & MÖDDEN, C. 1996: Biostratigraphie und Paläoökologie aufgrund von Fisch-Otolithen in den Oberen Cerithienschichten (Unter-Miozän) bei Göllheim (Mainzer Becken). Mainzer geowiss. Mitt. 25, 89–110.

REICHENBACHER, B. & SIENKNECHT, U. 2001: Allopatric divergence and genetic diversity of recent *Aphanius iberus* and fossil *Prolebias meyeri* (Teleostei, Cyprinodontidae) from southwest and western Europe, as indicated by otoliths. Geobios 34(1), 69–83.

REICHENBACHER, B. & WEIDMANN, M. 1992: Fisch-Otolithen aus der oligo-/miozänen Molasse der West-Schweiz und der Haute-Savoie (Frankreich). Stuttgarter Beitr. Naturkde. B 184, 1–83.

SAUVAGE, H.E. 1874: Notice sur les Poissons tertiaires de l'Auvergne. Bull. Soc. Hist. nat. Toulouse 8 (1873–1874), 171–198.

SCHÄFER, P. & KADOLKSY, D. 2002: Neudefinition von stratigraphischen Einheiten im Tertiär des Mainzer und Hanauer Beckens (Deutschland, Oligozän – Miozän), Teil 1: Oberrad-Formation [= Obere Cerithienschichten, oberer Teil] und Rüssingen-Formation [= *Inflata*-Schichten]. Mainzer geowiss. Mitt. 31, 73–98.

SETHI, R.P. 1960: Osteology and Phylogeny of Oviparous Cyprinodont Fishes (Order Cyprinodontiformes). Diss. Univ. Florida, 11–274.

SIENKNECHT, U. & REICHENBACHER, B. (in prep.): Otolith affinities of *Valencia* MYERS and *Aphanolebias* REICHENBACHER & GAUDANT and phylogenetic conclusions.

VILLWOCK W. 1999: Biogeography of the Cyprinodontiform fishes (Teleostei: Cyprinodontidae) of the Mediterranean region. In: Generalitat Valenciana, (Ed. by CONSELLERIA DE MEDIO AMBIENTE) - Peces Ciprinodóntidos Ibéricos Fartet y Samaruc, Monografía: 13–31.

WEILER, W. 1929: *Prolebias praecursor* sp. n. aus den Süsswasserschichten des Cyrenenmergels im Mainzer Becken. Notizbl. Ver. Erdk. 5(12), 110–111.

WEILER, W. 1942: Die Otolithen des rheinischen und nordwestdeutschen Tertiärs. Abh. Reichsamt Bodenforsch. N. F. 206, 5–140.

WEILER, W. 1963: Die Fischfauna des Tertiärs im oberrheinischen Graben, des Mainzer Beckens, des unteren Maintales und der Wetterau, unter besonderer Berücksichtigung des Untermiozäns. Abh. Senckenberg. naturforsch. Ges. 504, 1–75.

WIESNER, E. 1967: Das Miozän im östlichen Mainzer Becken unter besonderer Berücksichtigung der Mikrofauna. – Unpublished Thesis, 1–111, Geol.-Paläont. Inst., Univ. Frankfurt/Main.

Manuscript received February 16, 2003
Revision accepted September 28, 2003