Pleuronectiform fishes from the Upper Badenian (Middle Miocene) of St. Margarethen (Austria)

By Bruno Chanet [1]) & Ortwin Schultz [2])

(With 10 Figures)

Summary

The aim of this paper is the study of the fossil pleuronectiform fishes from the Upper Badenian (Middle Miocene) of St. Margarethen (Austria). Two species have been recognized in this outcrop: *Rhombus heckeli* KNER in HECKEL & KNER, 1861, nomen dubium, a Pleuronectoidea incertae sedis, and *Miobothus weissi*, a new genus and a new species. The latter species has minute intermuscular bones apomorphic for Bothidae: myorhabdoi. *Miobothus weissi* is therefore the oldest representative of Bothidae, suggesting that the age of the dichotomy between the Bothidae and the remaining Pleuronectiformes occurred before the Upper Badenian or upper Middle Miocene, at least 14 Mill. years ago.

Keywords: Middle Miocene, St. Margarethen, Austria, Teleostei, Pleuronectiformes, Bothidae, *Rhombus heckeli*, *Miobothus weissi* nov. gen. nov. spec.

Zusammenfassung

Die Pleuronectiformes aus dem oberen Badenien, Mittelmiozän, der Fischfundstelle St. Margarethen, Österreich, werden einer Revision unterzogen: *Rhombus heckeli* KNER in HECKEL & KNER, 1861 kann der schlechten Erhaltung wegen nur als Pleuronectoidea incertae sedis bestimmt werden und muß als nomen dubium betrachtet werden. Myorhabdoi, winzige intermuskuläre Knöchelchen, sind nicht erhalten. – Neufunde werden als *Miobothus weissi* nov. gen. et nov. spec. beschrieben und zeichnen sich besonders durch den Besitz von Myorhabdoi aus. Zum ersten Mal können bei einem fossilen Vertreter der Pleuronectiformes diese taxonomisch so wichtigen Elemente festgestellt werden. Diese Myorhabdoi gelten als ein apomorphes Merkmal der Bothidae, sodaß *Miobothus weissi* zweifelsfrei zur Familie Bothidae zu zählen ist. Der Nachweis von Myorhabdoi bedeutet aber auch, daß *Miobothus weissi* als ältester Vertreter der Bothidae zu gelten hat und daß der Zeitraum der Abspaltung der Bothidae von den anderen Pleuronectiformes präzisiert werden kann: die Abspaltung muß früher als oberes Badenien bzw. früher als oberes Mittel-Miozän bzw. vor mehr als 14 Millionen Jahren angesetzt werden.

Schlüsselwörter: Mittel-Miozän, St. Margarethen, Österreich, Teleostei, Pleuronectiformes, Bothidae, *Rhombus heckeli*, *Miobothus weissi* nov. gen. nov. spec.

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Introduction

Since the mid-nineteenth century, the St. Margarethen locality (Burgenland, Austria) is known for its fossil fishes. The fossils are preserved in the laminated facies of the Leitha limestones of the Leitha mountains. These laminated marls and marly limestones in the KUMMER-quarry of St. Margarethen have been interpreted by DULLO 1983: 40 as being deposited in depressions inside a lagoonal environment (see also PILLER & KLEEMANN 1991: 23). The age of the fish-bearing layers corresponds to the Upper Badenian (Middle Miocene, approximately 14 Mill. years; BELLWOOD & SCHULTZ 1991). Many groups of fishes have been described from this facies: Labridae (MÜNSTER 1846, HECKEL 1856, KNER 1862), Clupeidae (HECKEL 1850), Scorpaenidae (KNER in HECKEL & KNER 1861, SCHULTZ 1993), Serranidae, Triglidae (HECKEL in HECKEL & KNER 1861), Myctophidae, Sparidae (KNER 1862), Carangidae (GORJANOVIC-KRAMBERGER 1902), Syngnathidae (BACHMAYER 1980), Cetorhinidae, Centriscidae, Lophiidae, Muraenidae (BELLWOOD & SCHULTZ 1991: 68), and Scaridae (BELLWOOD & SCHULTZ 1991). One pleuronectiform fish can be added to the list (HECKEL 1849, KNER in HECKEL & KNER 1861), and more recently some new excavations showed the existence of other specimens. Because of the rarity of pleuronectiform fossils, newly discovered specimens are an important source of information that can help our understanding of the history of one of the strangest teleostean orders. It has been clearly established that the Pleuronectiformes form a monophyletic group (CHAPLEAU 1993), but the relationships of pleuronectiforms to other percomorphs remain obscure (JOHNSON 1993). The aim of this study is to perfect the knowledge of Pleuronectiformes from St. Margarethen. Consequently, a revision of *"Rhombus" heckeli*, the already known pleuronectiform species from St. Margarethen, and a description of a new genus and a new species, *Miobothus weissi*, are proposed.

Material

For this study, two kinds of fossils have been examined:

– the pleuronectiform fossil fishes from the Upper Badenian (Middle Miocene) of St. Margarethen (Austria), preserved in the Naturhistorisches Museum in Vienna (Geologisch-Paläontologische Abteilung) and in two private collections. They are: *Rhombus heckeli* NHMWien 1979/2126; *Miobothus weissi* NHMWien 1988/140/23a and b, 1976/1812/99 (counterplate of 1976/1812/100), 1976/1812/100 (counterplate of 1976/1812/99), 1976/1812/101, 1976/1837/61, 1994/0005, and 1994/0007/0001. Additionally the latter species was represented by two specimens in the private collection of Mr. K. WEISS, Vienna, (one of them figured in FRICKHINGER 1991: 923), and by 11 specimens in the private collection of Mr. G. WANZENBÖCK, Gainfarn.

– various pleuronectiform fossil fishes for comparative purposes. They are: *Microchirus abropteryx* from the Messinian (Upper Miocene) of Oran (Algeria), specimens 67, 68, 71, 568, 1246, 1263, 1306 of the collection ARAMBOURG in the Muséum National d'Histoire Naturelle, Paris; *Microchirus abropteryx (= Rhombus abropteryx)* from the Messinian (Upper Miocene) of Licata (Italy) in the Muséum National d'Histoire Naturelle, Paris; *Citharichthys oranensis* from the Messinian (Upper Miocene) of Oran (Algeria), specimen 265 of the collection ARAMBOURG in the Muséum National d'Histoire Naturelle, Paris; *Rhombus sauvageus* from the Messinian (Upper Miocene) of Gabbro (Italy) from the Museum of Pisa,

but preserved in the Muséum National d'Histoire Naturelle, Paris; *Joleaudichthys sadeki* and *Turahbuglossus cuvillieri* from the Lower Mokkatam (= Upper Lutetian) of Djebel Turah (Egypt), in the Muséum National d'Histoire Naturelle, Paris; *Eobuglossus eocenicus* from the Lower Mokkatam (= Upper Lutetian) of Djebel Turah (Egypt), specimen P 14485, in the British Museum, London; *Imhoffius lutetianus* from the Lutetian of the Paris Basin (France), Syntype I and II in the Muséum National d'Histoire Naturelle, Paris; *Solea kirchbergana/antiqua* from the Upper Ottnangian (Lower Miocene) of Württemberg (Germany), specimens 36179, 36578, 35149, P 4972, 35520, 36178, P 39772 in the British Museum, London, and specimen 1857/XXVII/4 in the Naturhistorisches Museum, Vienna; *Eobothus minimus* from the Lutetian (Eocene) of Monte Bolca (Italy), specimen Bol 0113–114 in the Muséum National d'Histoire Naturelle, Paris, specimen NHMWien 1853/XXVII/7a and b in the Naturhistorisches Museum, Vienna, specimen BSP A I68 in the Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, specimens P 16753, P 16752, P 11099, P 3971, 1657 in the British Museum, London.

Systematical part

Order: Pleuronectiformes

Sub-order: Pleuronectoidea incertae sedis

nomen dubium: *Rhombus heckeli* KNER in HECKEL & KNER, 1861

(Figure 1)

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1849     Rhombus Fitzingeri – HECKEL: 500.
1861     Rhombus Heckelii KNER – HECKEL & KNER: 75–76, Pl. 10, Fig. 12.
1870     Rhombus Heckelii KNER – SAUVAGE: 5.
1879     Rhombus heckeli KNER – BASSANI: 89–91, 107–109.
1925     Rhombus Heckelii KNER – ARAMBOURG: 63–64 [99–100].
1927     R[hombus]. Heckeli KNER – ARAMBOURG: 61.
1927     M[icrochirus]? Heckeli – ARAMBOURG: 65.
non 1991 Scophthalmus heckeli (KNER) – FRICKHINGER: 923, Fig.
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H o l o t y p e : NHMWien 1979/2126.

T y p e   l o c a l i t y : Without exact locality, probably St. Margarethen, Vienna Basin, Austria.

S t r a t i g r a p h y : Upper Badenian, Middle Miocene.

R e m a r k s : Only one specimen of *Rhombus heckeli* is known; it is the holotype (one plate only, no counterplate) which is preserved in the Naturhistorisches Museum, Geologisch-Paläontologische Abteilung, Vienna.

D e s c r i p t i o n : *Rhombus heckeli* is a small dextral flatfish (total length = 72 mm; standard length = 62 mm). In the preserved view it is not possible to determine what side of the fish is visible.

Neurocranium

Few head bones are satisfactorily preserved. Only the shape of the neurocranium is visible. The upper orbit is preserved and is limited dorsally by an expansion of the skull (probably left frontal). Ventral to the upper orbit, a bony "bar-like" remain exists. It could be interpreted as a parasphenoid remain, but this bone would be more ventral, or it could be a piece of
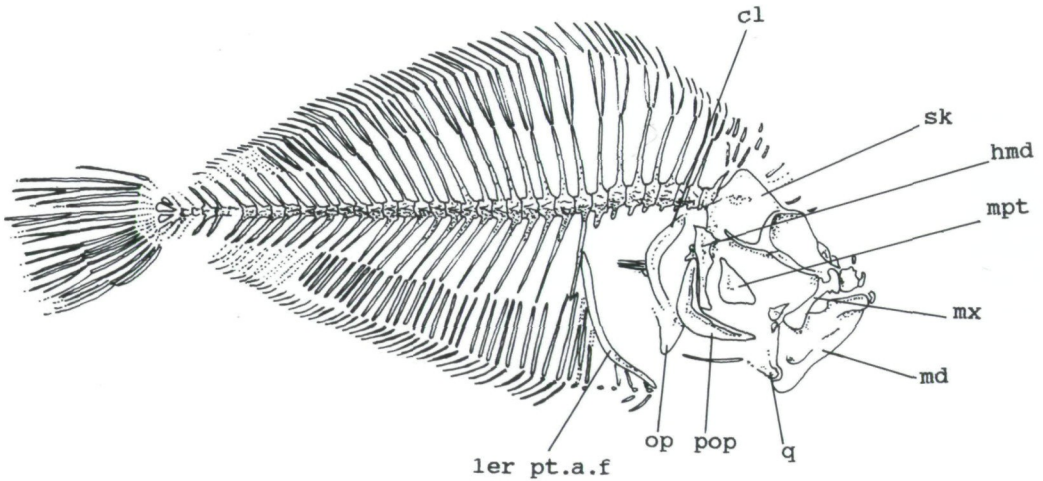
Fig. 1. *Rhombus heckeli* KNER in HECKEL & KNER, 1861, nomen dubium; no exact locality known, probably St. Margarethen, Vienna Basin; Upper Badenian, Middle Miocene. – Holotype, NHMWien 1979/2126. – 1.5x magnification.

the frontal forming the lower margin of the upper orbit. The position and the shape of the orbital bone indicate that the skull is asymmetric and that the eyes are on the right side.

Splanchnocranium

A hyomandibular is present (side unknown). Its postero-distal extremity is hidden by the preopercular. The hyomandibular is a large bone attached proximally to the skull. The shape of a large articulation facet with the skull is visible. A metapterygoid (side unknown) is present. The left mandible is broad, with a high coronoid process. The suture between the angulo-articular and dentary is not visible. Anteriorly, this mandible has teeth insertion traces. Below these traces an internal longitudinal ridge is observed. The articulation facet with the quadrate is preserved, with the distal part of the quadrate still visible. Posteriorly, a portion of a branchiostegal is present. Several bones of the upper jaw are visible. The right maxillary is the only identifiable bone. It is long, with its distal extremity flattened and plate-like. Anteriorly, two vertical processes are directed dorsally. Because the lower margin of the proximal extremity of the maxillary is broken, it is impossible to see if this bone was tooth-bearing. Anteriorly, a few pieces of a premaxillary (?) are present.

Opercular bones

The preopercular is preserved and is boomerang-like in shape, with a longer anterior portion. The two anterior edges are straight and form an angle slightly wider than 90°. The posterior edge is curved. Along the anterior edges, a trace of the preopercular canal is visible. This canal seems to terminate on the anterior tip of the bone. Posteriorly, some opercular or subopercular remains exist. There is no trace of fimbriation, and the side of these bones cannot be ascertained.

Paired fins and girdle

Elements of one paired fin and the corresponding girdle are preserved. These elements belong to a pectoral fin and its girdle (side unknown). A cleithrum with broken extremities is preserved. Three short fin rays are attached to the mid-posterior of the cleithrum.

Axial skeleton

Rhombus heckeli possesses 35 or 36 vertebrae: 8 precaudal vertebrae and 27 or 28 caudal vertebrae. The eighth precaudal centra has a complete haemal arch inclined posteriorly. From the first precaudal centrum to the eighth precaudal centrum, these arches are progressively longer and broader. The caudal vertebrae differ from the precaudal vertebrae in having a haemal spine. These spines are long and slender; their length decreases progressively from the first caudal centrum to the last (27th or 28th) caudal centrum. The last six haemal spines are poorly preserved. Each centrum has a neural spine. The longest neural spine is on the ninth centrum. From this spine, the anterior and the posterior neural spines progressively decrease in length. No intermuscular bones are observed or preserved. Pairs of proximal pterygiophores of the dorsal and anal fins are, respectively, attached to each neural and haemal spine. Both fins are long, extending along the whole body. The long dorsal fin extends along the entire upper margin of the body and is supported by 70 (at least) dorsal fin rays. The fin extends over the skull, with eight fin rays articulating on the cranium. They are oriented perpendicularly to the cranium. There is no trace of a long first pterygiophore of the dorsal fin. The anal fin extends along the lower margin of the body and is supported by 48 anal fin rays. The first pterygiophore of the anal fin is elongated. Postero-dorsally, this bone is in contact with the first haemal spine. Antero-ventrally, the first pterygiophore of the anal fin supports at least seven pterygiophores and the corresponding fin rays.

Urophore complex and caudal fin

This is the worst preserved part of the fish. Only the shape of some hypurals is visible; nothing precise can be said about them. Sixteen caudal fin rays are preserved.

Squamation

There is no trace of squamation on the whole body.

Interpretation

Rhombus heckeli shows the following features:
(1). dextral flatfish
(2). asymmetrical skull
(3). supracranial extension of the dorsal fin
(4). elongated first pterygiophore of the anal fin, supporting several fin rays
(5). first proximal pterygiophore of the dorsal fin without long anterior process
(6). no fimbriated opercule
(7). no myorhabdoi (but the preservation is very bad).

CHANET (1993) indicated that feature (1) is too variable to be used to assess the phylogenetic position of a fossil flatfish. Feature (2) is an apomorhhic character for the Pleuronectiformes (CHAPLEAU 1993). Features (3) and (4) are apomorphic characters for Pleuronectoidea (Pleuronectiformes except *Psettodes*) (CHAPLEAU 1993). Feature (5) shows that *Rhombus heckeli* is not a member of the Samarinae-Achiridae-Soleidae-Cynoglossidae assemblage within the Pleuronectoidea (CHAPLEAU 1993). In the fishes of this assemblage, the first proximal pterygiophore of the dorsal fin extends over the orbital region in an almost

parallel fashion; the dorsal edge of the orbital region supports the first pterygiophores of the dorsal fin (CHAPLEAU & KEAST 1988, CHAPLEAU 1993). No indentation of the opercle is visible (feature 6) (CHAPLEAU & KEAST 1988). Because the only flatfishes having a fimbriated opercle are Soleidae and Cynoglossidae (CHAPLEAU & KEAST 1988, CHAPLEAU 1993), *Rhombus heckeli* is neither a Soleidae nor a Cynoglossidae. Myorhabdoi (feature 7) are minute intermuscular bones (CHABANAUD 1949); these are only present in Bothidae (AMAOKA 1972, HENSLEY 1977, CHAPLEAU 1993). Consequently, *Rhombus heckeli* is not a Bothidae. The remaining known pleuronectiform families are Scophthalmidae, Paralichthyidae, Pleuronectidae, Poecilopsettinae. None of these families is defined on an apomorphic osteologic character, and the status of some of them is problematical (Paralichthyidae for instance (CHAPLEAU 1993)). Finally, *Rhombus heckeli* is too badly preserved to offer a more precise phylogenetic position than Pleuronectoidea incertae sedis for this Austrian Miocene fossil.

History and status of *Rhombus heckeli*

In 1849, HECKEL named *Rhombus Fitzingeri*, a pleuronectiform fish from the Miocene of the Leitha Mountains. In 1861, KNER in HECKEL & KNER described this fossil and *Rhombus Fitzingeri* became *Rhombus Heckelii*. This author compared it to the recent genus *Platessa* and to *Rhombus minimus* AGASSIZ, 1839–42 (= *Eobothus minimus* [EASTMAN 1910]) from the Upper Lutetian of Monte Bolca (Italy). He recognized *Rhombus heckeli* as an original species. In 1870, SAUVAGE differentiated *Rhombus heckeli* from *Rhombus abropteryx*, a Miocene flatfish from Gabbro (Italy). BASSANI 1880 thought that *R. heckeli, R. abropteryx* and *Rhombus (= Solea) antiqua/kirchbergana* (a fossil pleuronectiform fish from the Upper Ottnangian, Lower Miocene, of Germany) were three forms of the same species. But *R. abropteryx (= Microchirus abropteryx)* and *R. antiqua/kirchbergana (= Solea antiqua/kirchbergana)* are true soleid fishes (personnal observation), which is not the case in *Rhombus heckeli*. Moreover, the three fossil species are different in vertebral numbers: *Microchirus abropteryx*: 9 precaudal vertebrae and 27 caudal vertebrae, *Solea antiqua/kirchbergana*: 7 precaudal vertebrae and 24 caudal vertebrae, *Rhombus heckeli*: 8 precaudal vertebrae and 27 caudal vertebrae. In 1925, ARAMBOURG noted striking similitudes between *R. abropteryx* and *R. heckeli*, and he identified the Austrian fossil as a Soleidae. In 1927, the fossil became *Microchirus heckeli* (ARAMBOURG, 1927). Because *R. heckeli* is not a Soleidae, *Microchirus heckeli* is an invalid name. But *Rhombus* is not valid either. *Rhombus* is a genus name often given to pleuronectiform fossils in the nineteenth century. In 1914, EASTMAN wrote that "the term *Rhombus* as applied in 1800 by LACEPÈDE to genus of Butterfishes, or seven years before its employment by CUVIER for the Turbot; hence modern usage requires it to be replaced among flatfishes by the term *Bothus*, proposed in 1810 by RAFINESQUE". Consequently, EASTMAN created the new genus *Eobothus* for *Rhombus minimus* from the Lutetian (Middle Eocene) of Monte Bolca. *Eobothus minimus* differs from *Rhombus heckeli* in its number of vertebrae: all the *Eobothus minimus* specimens we have consulted possess 9 precaudal vertebrae and 20 caudal vertebrae (CHANET, in preparation). Can *Rhombus heckeli* become *Eobothus heckeli* ? No, because *R. heckeli* is too badly preserved for generic comparison. Thus, fossil 1979/2126 of the Naturhistorisches Museum in Vienna is *Rhombus heckeli* **nomen dubium**, Pleuronectoidea incertae sedis. The opinion of FRICKHINGER 1991: 923 that *Rhombus heckeli* is a member of *Scophthalmus* cannot therefore be supported (see also the remarks for *Miobothus* nov. gen.; see p. 101).

Sub-order: Pleuronectoidea

Family: Bothidae

Miobothus nov. gen.

D i a g n o s i s : With myorhabdoi. Urohyal (Fig. 6 and 7) like a fish-hook, with an elon-
gated and antero-dorsally curved sciatic portion. Caudal endoskeleton with hypurals 1 and
2 and hypurals 3 and 4 fused.

D e r i v a t i o   n o m i n i s : *Miobothus* means a *Bothus* from Miocene.

T y p e   s p e c i e s : *Miobothus weissi* nov. spec.

A d d i t i o n a l   s p e c i e s : none

S t r a t i g r a p h i c a l   d i s t r i b u t i o n : Upper Badenian, Middle Miocene.

R e m a r k s : The existence of minute intermuscular bones – myorhabdoi – are apomorphic
for Bothidae. Therefore *Miobothus* nov. gen., with its type species *weissi* nov. spec., is a
Bothidae.

Miobothus nov. gen., with its type species *weissi* nov. spec., is different from the recent
Bothidae by the shape of its urohyal (Fig. 7; for further details see AMAOKA 1969), by a dif-
ferent caudal endoskeleton (Fig. 9), and ordinarily by its number of vertebrae (the same
number of vertebrae[3] as in *Miobothus weissi* can be found in the recent bothids *Tarhops
oligolepis* BLEEKER, *Crossorhombus kobensis* JORDAN & STARKS, *Crossorhombus kanekonis*
TANAKA, *Engyprosopon longipelvis* AMAOKA).

For more information on the situation of *Rhombus heckeli* KNER in HECKEL & KNER 1861,
which must be understood as a nomen dubium and as Pleuronectoidea incertae sedis, see the
first part of the present contribution, p. 90, and Table 1, p. 112.

In 1991, FRICKHINGER mentioned a new finding from St. Margarethen as *heckeli* and includ-
ed a short description and a photograph. The opinion of FRICKHINGER, that this specimen is
a representative of the recent genus *Scophthalmus* is false because myorhabdoi are absent
not only in *Scophthalmus* but also in the whole Scophthalmidae family. We had the oppor-
tunity to study FRICKHINGER's specimen (in the private collection of Mr. K. WEISS, Vienna):
myorhabdoi are not preserved, but the fossil actually presents some striking similitudes with
the better preserved specimens from the same outcrop described here as *Miobothus weissi*
nov. gen. et nov. sp. (Table 1).

Miobothus (with the type species *weissi*) differs from the other fossil Pleuronectiformes.
Firstly, some pleuronectiform fossils are clearly not related to *Miobothus*. Some of them are
true soleids: *Solea helvetica* from the Burdigalian of Switzerland (LERICHE 1927), *Micro-
chirus abropteryx* (ARAMBOURG, 1925; 1927), *Eobuglossus eocenicus* (CHABANAUD, 1937;
CHANET 1994), *Turahbuglossus cuvillieri* (CHABANAUD, 1937), *Solea kirchbergana/antiqua*
(von MEYER, 1851). Another one is related to the most plesiomorphic Pleuronectiformes
(i.e., the Psettodidae): *Joleaudichthys sadeki* (CHABANAUD, 1937). Secondly, others have
different osteologic features, such as the number of vertebrae: *Eobothus minimus* (EASTMAN,
1911) (nine precaudal vertebrae and twenty caudal vertebrae), *Rhombus sauvageus* (CAPEL-
LINI, 1878), *Citharichthys oranensis* (ARAMBOURG, 1927) (moreover in the latter two spe-

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[3]) Such a feature cannot be used in phylogenetic research; it is only used here to make an identification.

cies, the shapes of the preopercular and the hyomandibula are different), *Imhoffius lutetianus* (CHABANAUD, 1940b), *Rhombus stamatini* (PAUCA, 1933), *Scophthalmus pietriciensis* (CIOBANU, 1978) (both from the Oligocene of Piatra Neamt, Rumania), *Numidopleura enigmatica* (GAUDANT & GAUDANT, 1969) from the Eocene of Tunisia, the following Japanese fossil Pleuronectiformes; *Propsetta kubotai* (NIINO, 1951) – Cenozoic – , *Chibopsetta dolichurostyli* (SAKAMOTO & UYENO, 1988a) – Late Pleistocene – , *Hippoglossoides naritai* (SAKAMOTO & UYENO, 1989b) and *Hippoglossoides kumaishi* (SAKAMOTO & UYENO, 1991) – both Middle Miocene – , the following Californian fossil Pleuronectiformes from the Monterey Formation (Middle Miocene): *Evesthes jordani* (GILBERT, 1910), *Zororhombus veliger* (JORDAN & GILBERT, 1920), *Vorator (= Hippoglossoides) antiquus* (JORDAN, 1925), *Isomma pristina* (JORDAN, 1927). Thirdly, some fossils are too incomplete or incompletely described for any comparison. These fossils are: *Eobothus vialovi* from the Middle Eocene of Uzbekhistan (BERG, 1941), *Eobothus singhi* from the Lower Eocene of India (SAHNI & CHOUDHARI, 1927), *Rhombus bassanianus* and *R. parvulus* from the Sarmatian (Upper Miocene) of Vrabce and Dolje (Croatia) (KRAMBERGER 1883), the four following Japanese fossils: *Clidoderma asperrimum* (SAKAMOTO & UYENO, 1988b) – Pliocene – , *Platichthys miostellatus* (SAKAMOTO & UYENO, 1989a) – Miocene – , *Pseudorhombus* cf. *P. cinamoneus* (UYENO, SAKAMOTO & FUJII, 1990) – Neogene – and *Saitamapsetta nomurai* (SAKAMOTO & UYENO 1992) – Middle Miocene – , the two following Californian fossils from the Monterey Formation (Middle Miocene): *Diatomaeca zatima* (JORDAN & GILBERT, 1919), *Evesthes hooveri* (JORDAN, 1921). Consequently – apart from the partial considerable different stratigraphical distribution – , the pleuronectiform fishes from the Badenian of St. Margarethen appear to be different from the known Pleuronectiformes, and *Miobothus* nov. gen. is proposed here.

Miobothus weissi nov. spec.

(Figure 2–6, 7/I, 8–10)

non 1861   *Rhombus Heckelii* KNER – HECKEL & KNER: 75–76, Pl.10, Fig. 12.
v.   1991   *Scophthalmus heckeli* (KNER) – FRICKHINGER: 923 (short description), Fig.

H o l o t y p e : NHMWien 1988/140/23a and b (plate and counterplate). – see Figs. 3, 4, and 6.

A d d i t i o n a l   m a t e r i a l   (p a r a t y p e s) : 18 specimens, which are NHMWien: 5 specimens: 1976/1812/99[4]), 1976/1812/100[4]), 1976/1812/101, 1976/1837/61, 1994/0005, and 1994/0007/0001; from the private collection of Mr. Kurt WEISS, Vienna, one individual (plate and counterplate), of which one view was figured as *Scophthalmus heckeli* (KNER) by FRICKHINGER 1991: 923[5]), and one small specimen; 11 specimens from the private collection of Mr. G. WANZENBÖCK, Gainfarn.

T y p e   l o c a l i t y (Fig. 2): 47°48' N, 16°38' E: Leitha Limestone quarry KUMMER, operating company, St. Margarethen, Ruster Bergland, Burgenland, Austria.

Fig. 3. *Miobothus weissi* nov. gen. nov. spec., St. Margarethen, KUMMER-quarry; Bolivinen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene. – Holotype, NHMWien 1988/140/23a. – 2x magnification.

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[4]) 1976/1812/99 and 1976/1812/100 are plate and counterplate of one individual.
[5]) see also the remarks for *Miobothus* nov. gen.; some differences between *heckeli* KNER and *weissi* nov. sp. are demonstrated in Table 1.
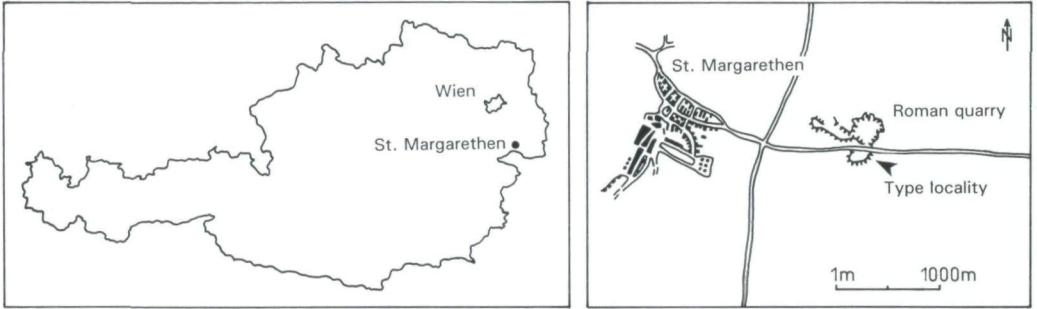
Fig. 2. The geographical locality of the type of *Miobothus weiss*i nov. gen. nov. spec. near St. Margarethen, Burgenland, Austria.

Formation: Laminated facies of Leitha Limestone.

Stratigraphy: Bolivinen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene, approximately 14 Mill. years.

Derivatio nominis: The name *weissi* refers to Mr. Kurt WEISS, Vienna, the cooperative private collector meritorious with the fossil fishes from St. Margarethen.

Description

Miobothus weissi is a small sinistral flatfish. Each of the specimens enumerated above offered some information about the skeleton of *Miobothus weissi*, and the reconstitution proposed here is a compendium of observations on all specimens of the NHMWien enumerated above.
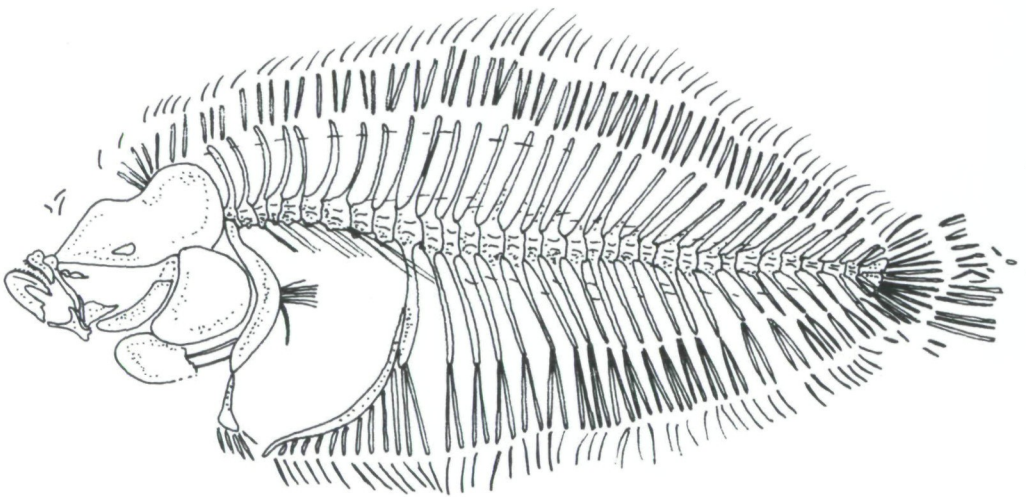
Fig. 4. *Miobothus weissi* nov. gen. nov. spec., St. Margarethen, KUMMER-quarry; Bolivinen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene. – Reconstitution based mainly on the holotype, NHMWien 1988/140/23a and b; *d, pmx, mx,* and *pal* based mainly on NHMWien 1976/1812/101. – 2x magnification.

Fig. 5. *Miobothus weissi* nov. gen. nov. spec., St. Margarethen, KUMMER-quarry; Bolivinen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene. – NHMWien 1976/1812/101. – 4x magnification of the head.

Neurocranium

Only the approximate shape of the neurocranium is preserved; no complete bone is visible. In the orbital region, the frontals develop a high, shell-like blade supporting the upper orbit. On the blind side (right side) of NHMWien 1976/1812/101, there is a trace of a supraorbital sensory canal (s.o.c.). Ventrally, close to the parasphenoid, an ellipsoid hole represents the "false-orbit", the fenestra between the ethmoid and the sphenoid (where the lower part of the right eye was prior to its migration). The ethmoid region is not preserved.

Splanchnocranium

The right hyomandibular is preserved. It appears to be an elongated bone; the main part of the bone is hidden by the preopercular. The quadrates are present; they have a long postero-dorsal spine. The articulation facet with the angulo-articular is not well developed. The quadrate is larger on the eyed-side than on the blind-side. Dorsal to the blind-side quadrate lies a big rhomboid metapterygoid. Close to either quadrate, a broad ectopterygoid is present. The angle between the two portions of the bone is about 120°. At the anterior tip of the blind-side ectopterygoid, the palatine is observed. Five fine and long branchiostegals extend after the cleithrum.
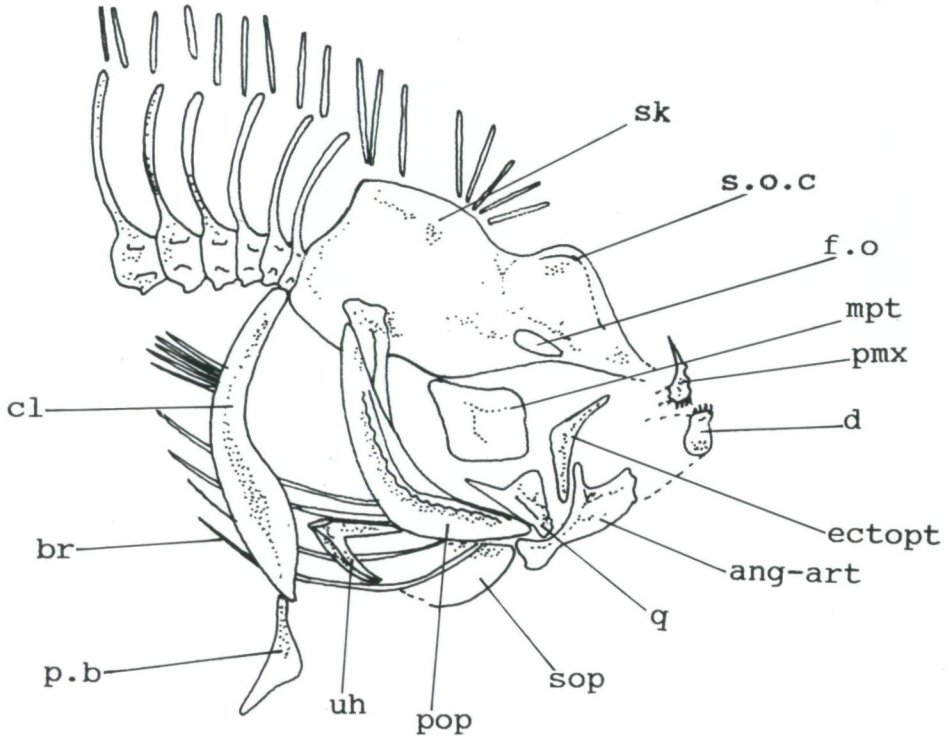
Fig. 6a. Blind-side of the head of *Miobothus weissi* nov. gen. nov. spec.; St. Margarethen, KUMMER-quarry; Boli-vinen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene. – Reconstitution based mainly on the holo-type, NHMWien 1988/140/23a and b; *d, pmx, mx,* and *pal* based mainly on NHMWien 1976/1812/101. – 4x magnification.

The urohyal is present and well preserved (NHMWien 1994/0005; see Fig. 6a and 7). This bone is fish-hook like, with an elongated and antero-dorsally curved sciatic portion. The cli-dian angle[6]) is 40°. Posteriorly, this bone is prolonged by a thin septal flange, while the para-ortic portion is massive, horizontal and straight. The septal flange is curved with an oval, flattened depression over it.

The upper jaws are preserved (Figs. 5 and 6 a+b). On the eyed-side, the premaxillary and the maxillary are present. The premaxillary is tooth-bearing on its ventral margin. This bone shows a very strong anterior process which is perpendicular to the rest of the bone. The maxillary is very elongated and extends postero-ventrally to the angulo-articular. On the blind-side, only the premaxillary is preserved. This bone is broken posteriorly and shows a high and perpendicular, spine-like ascendant process. The ventral margin of the bone bears some little teeth. The blind-side mandible is poorly preserved, but it probably has a high coronoid process as in the eyed-side mandible. On the blind-side mandible, the angulo-artic-

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[6]) The angle between the ventral edge of the paraortic portion and the anterior edge of the sciatic portion (CHA-BANAUD 1940a).
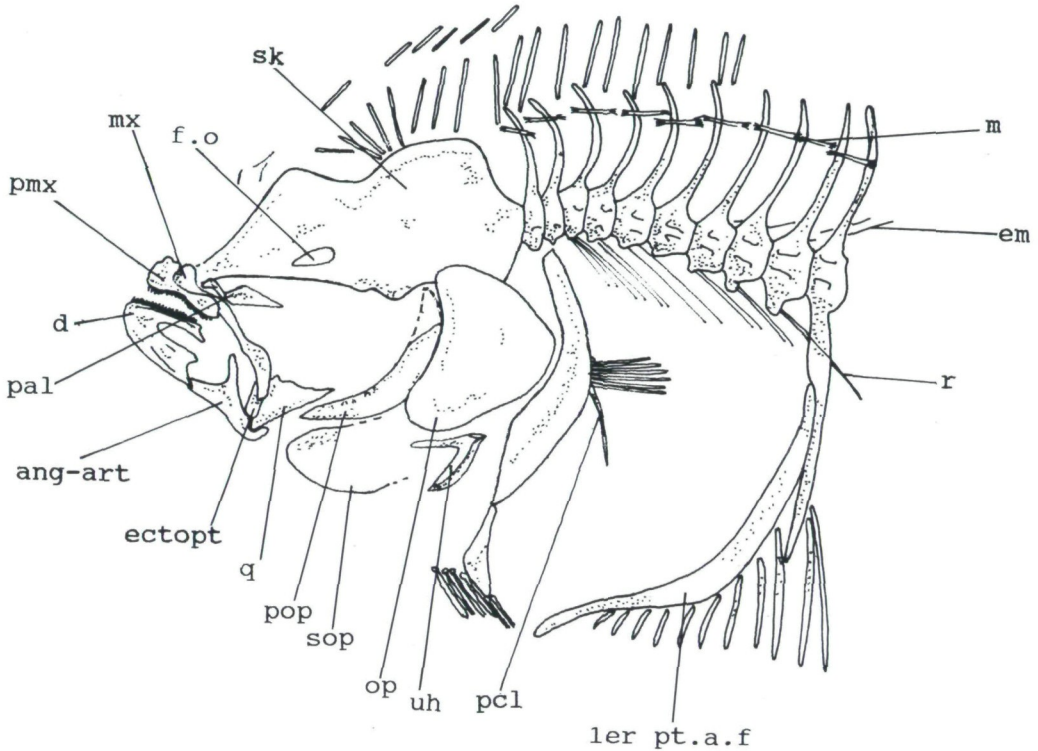
Fig. 6b. Eyed-side of the head of *Miobothus weissi* nov. gen. nov. spec.; St. Margarethen, KUMMER-quarry; Bolivinen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene. – Reconstitution based mainly on the holotype, NHMWien 1988/140/23a and b. – 3.4x magnification.

ular is present, and only the most anterior region of the left dentary is preserved. This piece is tooth-bearing. On each side, the angulo-articular possesses a strong retroarticular process. On the eyed-side, the two bones (angulo-articular and dentary) are preserved. The eyed-side mandible (Figs. 5 and 6b) is more complete and broader than the blind-side mandible. The dentary is well preserved, with numerous teeth.

Opercular bones (Fig. 6a+b)

On the blind-side, the preopercular is the only preserved bone of the opercular series. It is a large, crescentic-shaped bone with a curved posterior edge. The preopercular canal is present, it runs along the bone and apparently stops on the anterior tip of the bone. Ventral to the preopercular, a bony remain may be the subopercular. The eyed-side opercular series is more complete, with the preopercular, opercular and an incomplete subopercular. The preopercular is not well preserved. Its proximal extremity is broken. The bone is crescentic-shaped as well, but is shorter than the blind-side preopercular. Few traces of the preopercular sensory canal are present on the anterior edge of the bone. Posteriorly, a large opercular is present and ventrally the anterior part of a subopercular is visible.
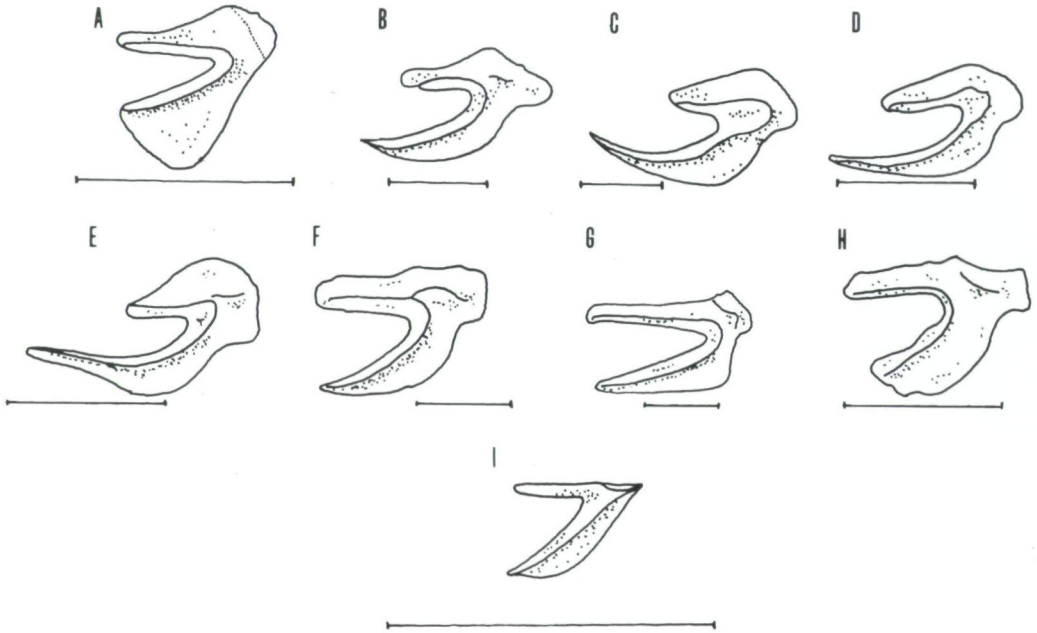
Fig. 7. Lateral aspect of the urohyals in some recent Bothidae (after AMAOKA 1969) and in *Miobothus weissi* nov. gen. nov. spec. – A. *Tarhops oligolepis* BLEEKER; B. *Crossorhombus kobensis* JORDAN & STARKS; C. *Crossorhombus kanekonis* TANAKA; D. *Engyprosopon longipelvis* AMAOKA; E. *Bothus myriaster* TEMMINK & SCHLEGEL; F. *Psettina gigantea* AMAOKA; G. *Arnoglossus japonicus* HUBBS; H. *Taeniopsetta ocellata* GÜNTHER; I. *Miobothus weissi* nov. gen. nov. spec., NHMWien 1994/0005 (don. G. WANZENBÖCK). – The scales indicate 10 mm.

Girdles and paired fins

Six or seven fin rays form the pectoral fin. This fin is attached on the mid-dorsal margin of the cleithrum. There is no difference between the cleithra of each side. The post-cleithrum of the eyed-side pectoral fin is preserved. It is a spine-like bone directed ventrally and attached near the pectoral fin. Both cleithra are large curved bones. There is no trace of any other bone of the pectoral girdle, particularly of the bones attaching the girdle to the skull. At the distal extremity of the cleithra, the pelvic girdles are present. Each is composed of a triangular pelvic bone supporting five or six rays ventrally. The pelvic fins are in a jugular position.

Axial skeleton (Figs. 3 and 4)

Miobothus weissi possesses 33 vertebrae: 9 precaudal vertebrae and 24 caudal vertebrae. The precaudal vertebrae become increasingly broad from the first to the ninth centrum. Each precaudal centrum bears a complete haemal arch. These are longer and broader posteriorly. The centra three to nine possess fine and straight ribs. A neural spine is present on each centrum (precaudal and caudal). The first are long, curved and slender. From the first precaudal centrum to the first caudal centrum, the length of the spines increases progressively. Subsequently, from the first caudal centrum to the last caudal centrum, these spines become progressively shorter. Each caudal centrum bears a long haemal spine, the first being the long-

est; posteriorly, spine length decreases progressively. These spines, haemal and neural, bear two pterygiophores, those of the anal fin for haemal spines and those of the dorsal fin for neural spines. These two fins extend, respectively, on the upper and lower margins of the body. The anal fin is supported by 57 rays. The first haemal spine supports the first pterygiophore of the anal fin. The latter is a broad, curved and elongated bone which supports the first nine anal fin rays. A minimum of 73 rays form the dorsal fin. This fin extends over the skull, with eight pterygiophores on the orbital region. These narrow bones are perpendicular to the cranium. Three fin rays lie in front of the first preserved pterygiophore.

Urophore complex and caudal fin (Figs. 8 and 9)

Four plate-like elements form the caudal endoskeleton. The lower lobe is composed of a free parhypural, supported by the haemal spine of PU2, and by hypurals 1 and 2 fused together. The latter plate is in contact with the last centrum (PU1). The two remaining plates form the upper lobe of the caudal skeleton. The lower plate of the upper lobe is formed by hypurals 3 and 4 fused together and fused with the last centrum (PU1). The upper one is the result of the fusion of hypural 5 with one epural; this latter plate is supported by the neural spine of PU2. The structure of the caudal endoskeleton corresponds to pattern 6 (HENSLEY & AHLSTROM 1984). Seventeen caudal fin rays are supported by this endoskeleton. Each outermost ray is unbranched; there are eight branched rays in the upper lobe and seven in the lower.

Fig. 8. *Miobothus weissi* nov. gen. nov. spec., St. Margarethen, KUMMER-quarry; Bolivinen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene. – Caudal endoskeleton, NHMWien 1988/1837/61. – 6x magnification.
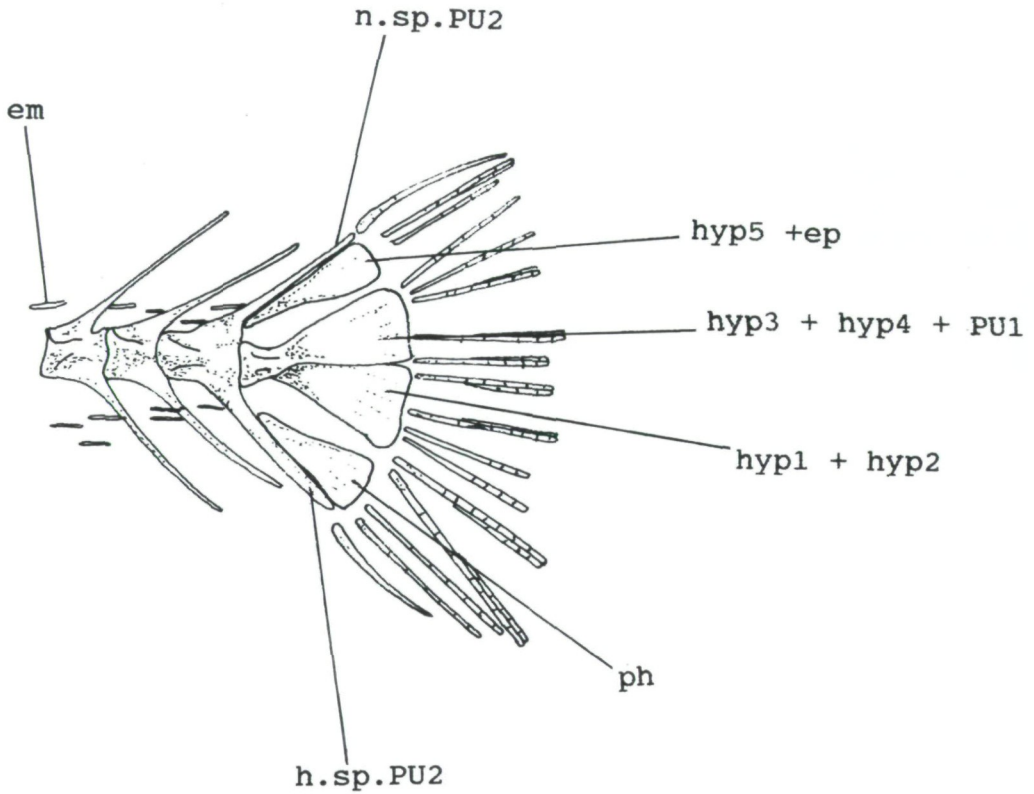
Fig. 9. Caudal endoskeleton of *Miobothus weissi* nov. gen. nov. spec.; St. Margarethen, KUMMER-quarry; Bolivi-nen-Buliminen-Zone resp. NN6, Upper Badenian, Middle Miocene. – Reconstitution based mainly on the speci-men NHMWien 1976/1837/61. – 5.77x magnification.

Intermuscular bones (Fig. 10)

Epimerals are present close to each caudal centrum. These minute bones are positioned ven-tral and dorsal to the vertebrae. Some "brush-like", highly branched, little bones lie close to the tip of neural spines. These bones are myorhabdoi; they are especially visible in the pre-caudal region.

Squamation

Some fragments of a thin filaceous layer are preserved in most specimens. The shape and the characteristics of the scales are undeterminable.

Orientation

This question can be resolved up especially with specimen NHMWien 1976/1812/101. The main preserved part of the specimen is a left half of the fish, but the preserved outer part of a supraorbital bone undoubtedly shows the supraorbital sensory canal (s.o.c.) of the right side (undistorted convexity !). Because this canal is found at the same place on the blind-side of the supraorbital bones of recent species as well, the fossil specimen must be a sin-
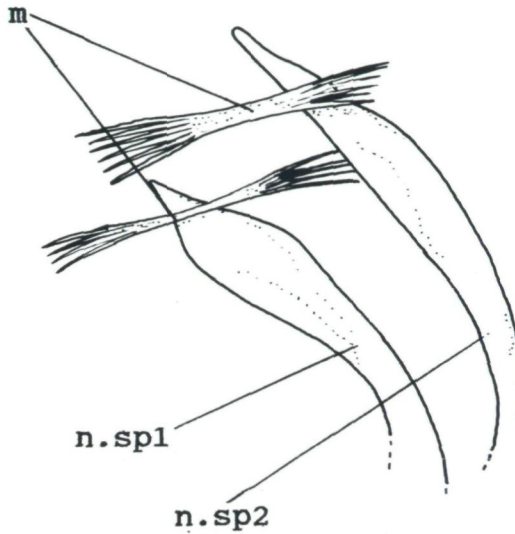
Fig. 10. Myorhabdoi of *Miobothus weissi* nov. gen. nov. spec.; St. Margarethen, KUMMER-quarry; Bolivinen-Buli-minen-Zone resp. NN6, Upper Badenian, Middle Miocene. – Specimen NHMWien 1976/1812/99. – 12x mag-nification.

istral fish. The other fossil specimens also appear to be sinistral individuals. Sinistrality is found in recent species of several flatfish families (Bothidae, Cynoglossidae...).

Interpretation:

Miobothus weissi shows the following features:

(1) asymmetrical skull
(2) sinistral flatfish
(3) supracranial extension of the dorsal fin
(4) elongated sciatic portion of urohyal
(5) parhypural free from PU1
(6) elongated anteriormost proximal pterygiophore of the anal fin
(7) first proximal pterygiophores of the dorsal fin perpendicular to the cranium
(8) hypurals 3 and 4 and hypurals 1 and 2 are fused
(9) fusion of hypurals 3 and 4 to the centrum of PU1
(10) myorhabdoi present

Features (1) and (3) are apomorphic characters for Pleuronectiformes (CHAPLEAU 1993). Feature (2) cannot provide phylogenetic data as this character is variable in the recent fauna. Because fossil Pleuronectiformes are too rare and isolated, it is impossible to use this char-acter to determine the phylogenetic position of a fossil (CHANET 1993). Features (4), (5) and (6) are apomorphic characters for Pleuronectoidea (Pleuronectiformes except Psettodidae) (CHAPLEAU 1993). In the Psettodidae, the sciatic portion of the urohyal is not well devel-oped, the parhypural articulates with the centrum of PU1, and the anteriormost proximal pterygiophore is short and supports one fin ray. These character states are plesiomorphic.

Within Pleuronectoidea, reverse characters exist, in *Brachypleura* (a recent Pleuronectoidea) for feature (6) (AMAOKA 1972, CHAPLEAU 1993), and in *Lepidoblepharon* (a recent Pleuronectoidea too) for feature (5) (CHAPLEAU 1993). Feature (7) is the plesiomorphic character state within Pleuronectiformes. In fact, a long first proximal pterygiophore of the dorsal fin extending over the cranium in an almost parallel fashion is an apomorphic character for the Soleidae-Cynoglossidae-Samarinae-Achiridae assemblage. Consequently, *Miobothus weissi* cannot be a member of this assemblage. Features (8) and (9) are apomorphic characters for *Brachypleura*, Scophthalmidae, Paralichthyidae (except *Thysannopsetta* and *Tephrinectes*), Bothidae (except *Mancopsetta*) and Pleuronectinae (CHAPLEAU 1993). Feature (10) is apomorphic for Bothidae (AMAOKA 1972, CHAPLEAU 1993). The Bothidae are unique within Pleuronectoidea in having these minute intermuscular bones. This indicates that *Miobothus weissi* is probably a Bothidae. Because the intrarelationships within the Bothidae are unclear (CHAPLEAU 1993), *Miobothus weissi* is a Bothidae incertae sedis.

Some differences between *Rhombus heckeli* KNER and *Miobothus weissi* nov. gen. et nov. sp. are given in Table 1:

Table 1: Differences between *Rhombus heckeli* KNER and *Miobothus weissi* nov. gen. et nov. sp.

	Rhombus heckeli	*Miobothus weissi*
vertebral number	8 precaudal + 26-27 caudal vertebrae	9 precaudal + 24 caudal vertebrae
mandible	massive	slender
insertion of the first pterygiophore of anal fin on the first haemal spine	the tip of the pterygiophore is in contact with the first haemal spine	a large part of the dorsal edge of the pterygiophore is in contact with the first haemal spine
shape of the first neural spines	straight	curved

Some pleuronectiform fossils have already been recognized as bothids: *Eobothus minimus*, *Eobothus vialovi* from the Eocene of Uzbekhistan (BERG 1941), *Eobothus singhi* from the Eocene of Rajasthan (India) (SAHNI & CHOUDHARY 1972), *Arnoglossus sauvageus* from the Messinian of Gabbro (Italy) (LANDINI 1982). The latter is superficially described; *Eobothus vialovi* and *Eobothus singhi* may not be Bothidae or even Pleuronectiformes (PATTERSON 1993). None of the specimens of *Eobothus minimus* we have examined possesses any myorhabdoi. Bothidae were defined on three apomorphic characters (HENSLEY & AHLSTROM 1984): asymmetrical states of the ventral fin morphology, loss of the blind-side preorbital, presence of myorhabdoi. The first two, however, are not unique to the Bothidae (CHAPLEAU 1993), while myorhabdoi are unique to Bothidae (AMAOKA 1969, HENSLEY 1977, HENSLEY & AHLSTROM 1984). The status of *Eobothus minimus* is unclear, with more study being needed. *Miobothus weissi* is the first fossil showing an apomorphic character (myorhabdoi) of the Bothidae. As a consequence, it is reasonable to hypothesize that the dichotomy between the Bothidae and its sister group (still hypothetical within Pleuronectoidea [CHAPLEAU 1993]) occurred before the Upper Badenian or the upper Middle Miocene or before 14 Mill. years.

Conclusion

The pleuronectiform fossil fishes from St. Margarethen are important in so far as they are original and that their study provides information about the history of certain taxa within the Percomorpha. Some representatives of the Upper Badenian (Middle Miocene) are true Bothidae, and the separation of Bothidae from the remaining Pleuronectiformes occurred before this period.

Because pleuronectiform fossils are not abundant, the outcrop of St. Margarethen is an "open window" towards the upper Middle Miocene, and for the history of pleuronectiform fishes.

Abbreviations

NHMWien: Naturhistorisches Museum Wien, Geologisch-Paläontologische Abteilung. – 1er pt.a.f: first pterygiophore of the anal fin. – ang-art: angulo-articular. – br: branchiostegal ray. – cl: cleithrum. – d: dentary. – ectopt: ectopterygoid. – sop: subopercular. – em: epimeral. – ep: epural. – f.o: false orbit. – h.sp: haemal spine. – hmd: hyomandibular. – hyp: hypural. – m: myorhabdoi. – md: mandible. – mpt: metapterygoid. – mx: maxillary. – n.sp: neural spine. – pal: palatine. – pmx: premaxillary. – p.b: pelvic bone. – pcl: post-cleithrum. – ph: parhypural. – pop: preopercular. – PU: preural centrum. – q: quadrate. – r: rib. – s.o.c.: supra-orbital canal. – sk: skull. – uh: urohyal.

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