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The actinopterygian fish fauna of the Late Kimmeridgian and Early Tithonian 'Plattenkalke' near Solnhofen (Bavaria, Germany): state of the art

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Abstract

An overview is presented of the actinopterygian fishes from the Late Jurassic (Late Kimmeridgian and Early Tithonian) 'Plattenkalke' near Solnhofen (Solnhofen lithographic limestone), Bavaria, Germany. The fish fauna is very diverse, with the palaeonisciform *Coccolepis*, halecostomes such as *Lepidotes*, *Heterostrophus*, three genera of macrosemiids and six genera of pycnodontiforms, halecomorphs including two genera of caturids, two genera of amiids, *Ophiopsis*, '*Furo*', *Ionoscopus*, *Brachyichthys*, *Callopterus*, *Liodesmus*, ?*Lophiurus*, five genera of pachycormids, three genera of pholidophorids, *Pleuropholis*, two genera of aspidorhynchids and eleven genera of basal teleosts. Although several groups have been subject of revision, most of the fauna remains poorly known. Study of this rich fauna will provide a lot of information on the phylogeny and interrelationships of halecostome fishes.

Introduction

The Late Jurassic (Late Kimmeridgian and Early Tithonian) 'Plattenkalke' limestones of Bavaria, also known as the 'Solnhofen lithographic limestone', are famous because of the diversity and preservation of their fossils. Especially well known is *Archaeopteryx lithographica*, the first known bird, of which seven specimens have been found so far. The Late Kimmeridgian limestones from Nusplingen (Baden-Württemberg) yield roughly the same spectrum of fossils, although not in the same amount and not of the same diversity as Solnhofen. Outside Germany, the Late Kimmeridgian lithographic limestones at Cerin (France) have a fossil content that is similar to that of the German localities, although the similarity is predominantly on genus level (see Wenz et al. 1993). This might well be due to the rather old taxonomic knowledge of the fossils from these localities. Revision of the material will certainly lead to other views on similarity, both on generic and species level. From Canjuers (France), an Early Tithonian limestone is known with a similar floral and faunal composition (Roman et al. 1993).

The fish fauna

The most recent species list published about the Solnhofen fossils (Kuhn 1961) contains 142 species, but this list has multiple entries of species under different genera and contains several synonyms. Since 1961, several papers on or including Late Jurassic fishes have been published and a new list of the Actinopterygii can be compiled, reflecting the modern state of the art. The 94 species are listed in Table 1. In the present contribution, they are compared with the faunas from Cerin (Saint-Seine 1949, Wenz et al. 1993) and Nusplingen (Heineke 1906, Heimberg 1949). The few fishes from the Early Tithonian at Canjuers have, except for the teleost *Naiaethalon okkidion* (Poyato-Ariza & Wenz 1994), been identified at genus level only; these genera are also known from Solnhofen (Roman et al. 1993).

Table 1. List of actinopterygians from the Solnhofen lithographic limestone. Compare this list with the lists of fishes from Cerin (Wenz et al. 1993), Nusplingen (Heineke 1906) and Canjuers (Roman et al. 1993).

CHONDROSTEI
Coccolepidae
Coccolepis bucklandi
HALECOSTOMI
Semionotidae
Lepidotes decoratus
Lepidotes intermedius
Lepidotes maximus
Lepidotes notopterus
Lepidotes oblongus
Lepidotes pustulosus
Lepidotes subovatus
Lepidotes unguiculatus
Macrosemiidae
Histionotus oberndorferi
Macrosemius rostratus
Notagogus decoratus
Notagogus denticulatus
Propterus elongatus
Propterus microstomus
?Eusemius beatae
Pycnodontiformes
Gyrodus hexagonus
Gyrodus circularis
Mesturus verrucosus
Eomesodon gibbosus
Mesturid gen. nov.
Proscinetes elegans
Proscinetes formosus
Macromesodon macropterus
?Macromesodon heckeli

Pachycormidae
Asthenocormus titanius
Hypsocormus insignis
'Hypsocormus' macrodon
Orthocormus cornutus
Pseudoasth. retrodorsalis
Sauropsis longimanus
Sauropsis depressus
***Halecostomi* inc. sed.**
Heterostrophus latus

HALECOMORPHI
Amiidae
Amiopsis lepidota
Solnhofenamia elongata
Caturidae
Caturus furcatus
Caturus giganteus
Amblysemius bellicianus
Amblysemius pachyurus
Liodesmus gracilis
Liodesmus sprattiformis
Liodesmus sp.
Ionoscopidae
Ionoscopus cyprinoides
Ionoscopus esocinus
Ionoscopus münsteri
Ionoscopus striatissimus
Ophiopsidae
Ophiopsis attenuata
Ophiopsis procera

Furidae
'Furo' angustus
'Furo' latimanus
'Furo' longiserratus
'Furo' microlepidotes
'Furo' münsteri
***Halecomorphi* inc. sed.**
Brach. radiato-punctatus
Brachyichthys typicus
Callopterus agassizzi
?Lophiurus minutus

TELEOSTEI
Pholidophoridae
Pholidophorus macrocephalus
Pholidophorus microps
Pholidophorus falcifer
?Pholidophorus armatus
?Pholidophorus diagonalis
?Pholidophorus sculptus
Pholidophoristion micronyx
Pholidophoristion ovatus
Ankylophorus sp.
Eurycormus speciosus
Pleuropholidae
Pleuropholis laevissima
?Pleuropholis pompecki
?Pleuropholis wagneri
Aspidorhynchidae
Aspidorhynchus acutirostris
Belonostomus münsteri
Belonostomus tenuirostris
Allothrissopidae
Allothrissops mesogaster
Allothrissops salmoneus
Pachythrissops propterus
Thrissops formosus
Thrissops subovatus
Anaethalionidae
Anaethalion angustissimus
Anaethalion angustus
Anaethalion knorri
Anaethalion cf. *subovatus*
Elopidae
Elops-like sp. 1
Elops-like sp. 2
Elops-like sp. 3
Orthogonikleithridae
Leptolepides haerteisi
Leptolepides sprattiformis
Orthogonikleithrus hoelli
Orthogonikleithrus leichi
Ostariophysi
Tischlingerichtys viohli
***Clupeocephala* inc. sed.**
Daitingichthys tischlingeri
***Elopocephala* inc. sed.**
Eichstättia mayri
***Teleostei* inc. sed.**
Ascalabos voithii
Tharsis dubius

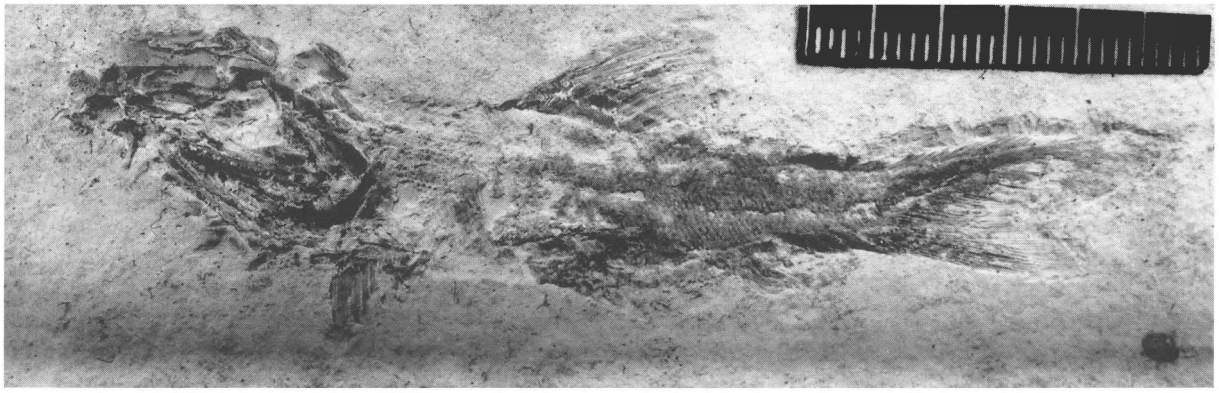

Figure 1. Coccolepis bucklandi. Specimen from Eichstätt in the Geological Institute, Dresden. Scale bar = 3 cm.

Chondrostei

Palaeonisciformes

Finds in Solnhofen of this taxon include only the Coccolepidae.

Coccolepidae

This family (Figure 1) is represented in Solnhofen by only one extremely rare and poorly known species, *Coccolepis bucklandi*. It has been described by Wagner (1863), Vetter (1881) and Woodward (1891). Coccolepidae are usually classified among the order Palaeonisciformes, which group is considered a paraphyletic taxon of Palaeozoic actinopterygians (Coates 1993, and references therein). Several species of *Coccolepis* are known from deposits ranging from the Early Jurassic up to the Early Cretaceous. The systematics of the Coccolepidae remain to be examined.

Halecostomi

Finds in Solnhofen of this taxon include the following:
- Pycnodontiformes
- Pachycormiformes
- rest-group Halecostomi *incertae sedis*
- Halecomorphi
- Teleostei

Semionotiformes

Finds in Solnhofen of this taxon include the two following families:
- Semionotidae
- Macrosemiidae

Semionotidae

Semionotidae are represented in Solnhofen by the genus *Lepidotes*. According to Olsen & McCune (1991), *Lepidotes* and *Semionotus* form a monophyletic group, sharing with the Macrosemiidae two or more lacrimal bones, and forming with them the sister group of the Teleostei. Gardiner et al. (1996) also consider the Semionotidae a monophyletic group with the Macrosemiidae, but they classify them as the sister group of the Halecomorphi, sharing with them, among other things, enlarged basal and fringing fulcra in the tail. Indeed, *Lepidotes* and – to a lesser degree – macrosemiids have large fulcra on the tail lobes, but it is doubtful whether these, in being enlarged, are homologous with the fulcra in halecomorphs. Tail fulcra in halecomorphs are not as well developed as in semionotiforms and are, relatively, not much larger than in other halecostomes such as *Tetragonolepis*. Moreover, tail fulcra, similar to those in halecomorphs such as *Caturus* occur in several genera: apart from *Woodthorpea* and *Acentrophorus* (mentioned by Gardiner et al. 1996) also in the Early Cretaceous *Ligulella* and *Catervariolus* (pers. obs. of several specimens in the 'Koninklijk Museum voor Midden-Afrika' at Tervuren, Belgium). Before 'enlarged-tail fulcra' can be defined as an apomorphic characteristic, the distribution of this characteristic among halecomorphs had better be examined first.

The fishes of the genus *Lepidotes* in Solnhofen remain imperfectly known systematically (see Thies & Zapp 1997). Weitzel (1930) described a large specimen of *L. maximus,* and Jain (1983, 1985) commented on some Late Jurassic species and briefly described *L. maximus* (reaching 2 m in length). Thies & Zapp (1997) described a specimen of *Lepidotes* from the Kimmeridgian 'Plattenkalke' at Schamhaupten, near Kehlheim; this find could not be assigned to any species because of the poor knowledge of this genus. Specimens assigned to *Lepidotes* have been found in several Jurassic and Cretaceous outcrops. The species known from Solnhofen might be similar to the ones known from Cerin, but there is no certainty about this without revision of the genus. Synonymy follows Woodward (1895); see also Thies & Zapp (1997).

Macrosemiidae

This monophyletic family has been reviewed by Bartram (1977). It is defined by the presence of up to nine tubular infraorbitals and a very small interoperculum, removed from the lower jaw. In addition to these characters, macrosemiids appear to have large, broad scutes in front of the ventral lobe of the caudal fin. The systematic position of this group is discussed with the Semionotidae (see above). *Eusemius* (Vetter 1881) might be a juvenile macrosemiid specimen. The only specimen of this species was lost. All genera and species known from Solnhofen also occur in Cerin. Synonymy follows Bartram (1977).

Pycnodontiformes

Pycnodontiformes constitute a distinct group of fishes, ranging from the Late Triassic into the Eocene; they have 21 derived characters in common (Nursall 1996),

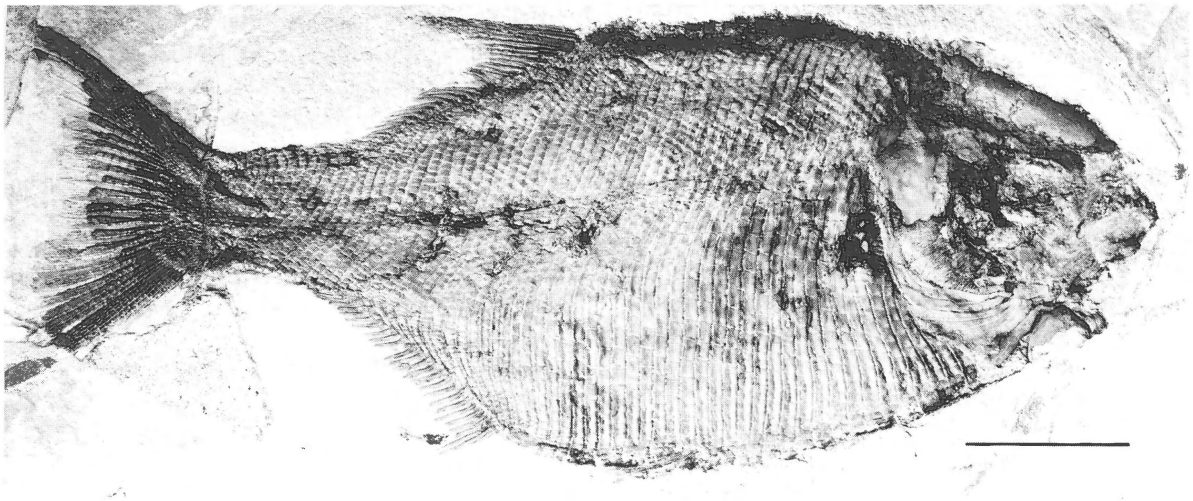

Figure 2. Heterostrophus latus. Specimen CM 4762 from Solnhofen, Carnegie Museum, Pittsburgh. Scale bar = 6 cm.

including the absence of a supramaxilla, absence of dentition on the maxilla, a broad preoperculum and small operculum, large and broad cleithrum and an anterior flange on neural and haemal spines. The first two and the last of these are also known from several other taxa. Most conspicuous is the presence of a specialized crushing dentition consisting of tritoral teeth arranged in longitudinal, parallel rows on the median vomer and the large paired prearticulars.

In recent analyses, pycnodontiforms are either the primitive sister group of the Teleostei (Nursall 1996) or they form the sister group of the teleosts together with *Dapedium* (Gardiner et al. 1996). In some pycnodontiforms, the lower jaw joint involves the symplectic and quadrate, as in halecomorphs (Nursall & Maisey 1991, Gardiner et al. 1996, Nursall 1996). According to Nursall (1996), the situation in pycnodontiforms is homologous with halecomorphs, but Gardiner et al. (1996) interpret the pycnodontiform lower jaw joint as only superficially similar to the condition in halecomorphs.

Nursall (1996) presented a phylogeny of the order. In his analysis, *Eomesodon*, *Proscinetes* and *Macromesodon* belong to a monophyletic taxon, Pycnodontoidei, and among these to the Pycnodontidae; *Gyrodus*, *Mesturus* and a new genus, mesturid gen. nov. (Nursall 1996, see also Lambers 1992, *Mesturoides*) form the sister group of the Pycnodontoidei, i.e., the Gyrodontoidei. *Gyrodus* belongs to the Gyrodontidae and *Mesturus* and mesturid gen. nov. belong to the Mesturidae.

The Pycnodontiformes from Solnhofen are poorly known, except for the genus *Gyrodus*. Hennig (1906) and Lambers (1991) described *Gyrodus*, Hennig (1907) described *Eomesodon*, and Weitzel (1930) described *Gyrodus circularis*.

It is remarkable that *Gyrodus* is rather abundant in Solnhofen, while in Cerin *Proscinetes* is by far the most common pycnodontiform. Large forms such as *Mesturus* (specimens described as *Mesturus* by Saint-Seine 1949, belong to *Gyrodus*: see Lambers 1991), *Eomesodon* and *Gyrodus circularis* (also known from Nusplingen) are unknown in Cerin. *Gyrodus wagneri* from Cerin is unknown from Solnhofen; this species does, however, not belong to *Gyrodus*: most conspicuously it lacks the complete scale covering of *Gyrodus*. The intercalated anterior edges of the scales are visible almost up to the caudal fin, but complete scales are present only in the anteroventral trunk region. *Gyrodus wagneri* represents a distinct, undescribed genus (see also Lambers 1991). Mesturid gen. nov. was not found in Cerin.

Synonymy follows Woodward (1895), Hennig (1906), Lambers (1991) and personal observations.

Pachycormiformes

The Pachycormiformes are represented by five genera (see Wagner 1863, Vetter 1881, Eastman 1914, Weitzel 1930). Pachycormids could grow large: *Asthenocormus* (Vetter 1881) from the Solnhofen area up to 2.5 m; *Leedsichthys* from the Oxford Clay in England is estimated to have measured at least 13 m.

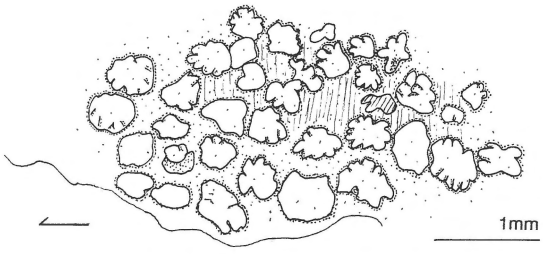

Figure 3. Heterostrophus latus. Schematic drawing showing the outline of the teeth anterior in the lower jaw in occlusal view, arrow points anteriorly. Specimen 10327 from Solnhofen, Teylers Museum, Haarlem.

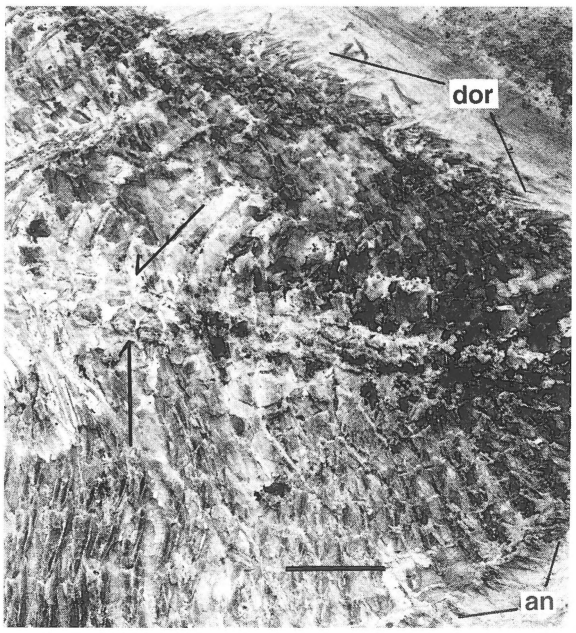

Figure 4. Heterostrophus latus. Hemichordacentra (arrows). Specimen 10327 from Solnhofen, Teylers Museum, Haarlem. Scale bar = 1 cm. an = anal fin; dor = dorsal fin.

Lambers (1988, 1992) described some pachycormid fishes, showed the monophyly of the group and presented a cladogram of the order. In this cladogram, *Hypsocormus* turns out to be non-monophyletic; *'H.' macrodon* is closely related to *Orthocormus*, sharing the shape of the pelvic plate and details of the premaxillary dentition. Genera such as *Hypsocormus* and *Sauropsis* need to be redescribed.

The Pachycormiformes have several unique characters: the presence of a rostrodermethmoid, absence of supraorbitals and the dorsal margin of the orbit formed by the dermosphenotic, nine infraorbitals behind the orbit, no extrascapulars and an enlarged dermopterotic containing the supratemporal commissural canal and a large, scythe-like pectoral fin with the fin rays only branching at their extreme ends. Since Patterson (1973), the Pachycormiformes were considered the most basal teleosts, because they supposedly had uroneurals, i.e., paired, median, modified uroneural arches in the tail; uroneurals are considered a teleost character. Arratia & Lambers (1996) showed, however, that the pachycormid uroneurals are median instead of paired and are not homologous with teleost uroneurals. Moreover, Thies (1991) described a supposed median uroneural in the tail of the halecostome *Tetragonolepis*, thus questioning the uniqueness of the teleost uroneural. In a phylogenetic analysis of some halecostome groups (Brito 1997), the Pachycormidae (or Pachycormiformes) turn out as:

- the sister group of the Teleostei, together with the Semionotidae, or
- the sister group of a monophyletic Semionotidae + Teleostei, or
- the sister group of a monophyletic Halecomorphi + Semionotidae.

The consensus tree of these three quite different topologies is an unresolved polychotomy of Halecomorphi, Semionotidae, Teleostei and Pachycormidae. The different topologies in Brito's analysis result from different interpretations whith respect to fused or unfused neurocranial bones, the presence of an ophistotic, the presence of an intercalar, the presence of a gular, and whether the symplectic is incorporated into the articulation of the jaw joint. These characteristics appear differently as homoplasies and reversals within each tree among several of the taxa. In any case, the Pachycormidae are not to be considered as teleosts.

The pachycormid fauna from Cerin consists of only *Orthocormus teyleri* (Lambers 1988) and an undetermined fragment of a vertebral column. *Asthenocormus*, *Sauropsis* and *Hypsocormus* are known from Late Jurassic localities in England, whereas *Hypsocormus* and *Pseudoasthenocormus* also occur in Nusplingen (Lambers 1992). *Sauropsis* has also been described from the Lower Jurassic of Holzmaden and Lyme Regis. Whether these Sauropsidae represent the same genus remains to be determined.

Halecostomi incertae sedis

Heterostrophus – This genus (Figures 2–4), which was described as *Homoeolepis* by Eastman (1914), is rare. It is usually classified among the deep-bodied forms that were supposed to belong to the semionotiforms and that were grouped together as Dapediidae

(e.g. *Dapedium* and *Tetragonolepis*; see Lehman 1966). It is only known from the Solnhofen area.

Woodward (1929) described a rather complete specimen of *H. typicus* from the lithographic limestone, together with *H. phillipsi* from the Oxford Clay at Peterborough. Specimen 10327 in Teylers Museum (at Haarlem) shows that the dentition of *H. typicus* consists of more than a hundred small tritoral teeth with characteristically undulating outline on the vomer and lower jaw (Figure 3). The vertebral column consists of hemichordacentra (Figure 4).

Recent cladistic analysis has shown that the Dapediidae do not belong to the semionotiforms. The position of *Dapedium* appears to be close to the teleosts and pycnodontiforms instead (Gardiner et al. 1996, Nursall 1996). Without revision of both *Dapedium* and *Heterostrophus*, the position of the latter remains unclear, however, and it is labelled therefore as Halecostomi *incertae sedis*.

Halecomorphi

Halecomorphi are characterized by a double jaw joint in the lower jaw, including quadrate and symplectic (Patterson 1973). Grande & Bemis (1998) in their analysis also listed a posterior notch in the maxilla and a single supramaxilla. Recent phylogenies of halecomorphs have been published by Lambers (1995), Gardiner et al. (1996) and Grande & Bemis (1998). This subdivision of the Halecostomi comprises the following orders found at Solnhofen:

- Amiiformes
- Ionoscopiformes
- a group of Halecomorphi *incertae sedis*.

Amiiformes

The Amiiformes found in Solnhofen comprise the following two families:

- Amiidae
- Caturidae

Amiidae

Lange (1968) revised the genus *Urocles*; he recognized seven species. In a revision of amiid fishes, Grande & Bemis (1998) concluded that *Urocles* is a junior synonym of *Amiopsis* and that only two of the species ascribed to *Urocles* are valid; one of these (*U. elongatus*) belongs to a new genus, *Solnhofenamia* Grande & Bemis 1998, and the other (*U. lepidotes*) to *Amiopsis*. In their analysis of the phylogeny of the Amiidae, *Amiopsis* is the sister group of all other amiids (Amiida) and *Solnhofenamia* is among the Amiida the sister group of the remaining amiids (Amiista). *Amiopsis* is known from Cerin and Early Cretaceous deposits from Europe, North and South America as well, whereas *Solnhofenamia* is only known of the Solnhofen area.

Caturidae

Among the Amiiformes, the Caturidae are the sistergroup of the Amiidae (Lambers 1992, 1995, Grande & Bemis 1998). They are known from several Jurassic and Early Cretaceous deposits. Two genera can be recognized, *Caturus* and *Amblysemius*, each with two species. *Amblysemius* was known as *C. pachyurus* and *C. bellicianus* from Cerin, but it has been shown that they form a different caturid genus, *Amblysemius*, which is only known from Solnhofen and Cerin (Lambers 1992, 1994).

Caturidae can be recognized by the slender maxilla, a high number of branchiostegal rays, block-like ural neural arches, haemal spines shaped broadly spatulate in the transverse plane and the ural neural spines and haemal arches being inclined towards the horizontal (Lambers 1992, 1994, 1995, Grande & Bemis 1998). The latter two characteristics seem also to be present in *Liodesmus*. *C. giganteus* reaches 1 m in length, but *C. furcatus* specimens measuring about 1 m in length are also known.

Liodesmus – This supposedly amiiform genus (Figure 5) is known only from the Solnhofen area. They are very small fishes, with a standard length of about 9 cm. They are characterized by the presence of very large rectangular urodermals covering the upturned lobe of the tail and absence of suborbitals (Lambers in prep.). They have three supraorbitals, of which the anterior one is the largest and the middle one is the smallest; the scales are elasmoid, vertebral centra are absent.

The systematics of the genus remains unclear. Two species are known, the type species *L. gracilis*, and *L. sprattiformis*. Nybelin (1963) described a tail of a fish that he named *Liodesmus* sp. It is difficult to establish the differences between *L. sprattiformis* and *L. gracilis* with the available material, as the type specimen of *L. gracilis* was poorly preserved and it is unclear if other fishes assigned to this species are similar to the type specimen. The specimen described by Nybelin (1963) is considerably larger than the other

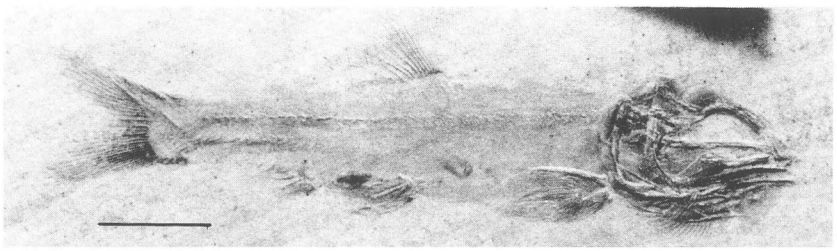

Figure 5. Liodesmus sprattiformis. Specimen 1986.XV.113 from Zandt, Bayerische Staatssammlung für Paläontologie und historische Geologie, München. Scale bar = 1 cm.

two forms and apparently does not belong to any of these although it may still belong to the genus. It has a slightly asymmetrical tail, with a rounded lower lobe. *Liodesmus* might be closely related to the Caturidae, with which it possibly shares the inclination of the neural and haemal spines and the broadly spatulate haemal spines.

Ionoscopiformes

Of this order the following families are found in Solnhofen:
- Ionoscopidae
- Ophiopsidae
- Furidae

Ionoscopidae

According to Grande & Bemis (1998), the Ionoscopidae form a clade Ionoscopiformes with the Oshuniidae (from the Lower Cretaceous of Brazil) and the Ophiopsidae. The Ionoscopiformes are the sister group of the Amiiformes in their cladogram. They are represented by the genus *Ionoscopus*. The genus is in need of revision, as several species, possibly synonyms, are known from the lithographic limestone and no proper descriptions are available. It is even unclear whether the Late Jurassic *Ionoscopus* belongs to the same genus as the Cretaceous *Ionoscopus* from Italy, of which *Ionoscopus pietraroiae* in fact represents the type species of the genus. *Ionoscopus* is known from Late Jurassic and Early Cretaceous localities in Europe and in North and South-America. In Grande & Bemis' analysis, *I. cyprinoides* is the only *Ionoscopus* examined. Data on the phylogenetic position of Ionoscopidae are still tentative, awaiting a revision of all *Ionoscopus* and possibly related forms (e.g., *Spathiurus*). The largest specimens of *Ionoscopus* reached about 1 m in length.

Ophiopsidae

Ophiopsidae are known from Middle Triassic up to Early Cretaceous deposits in Europe, Africa and North and South America. Bartram (1975) presented a revision of the family. He described two species from the lithographic limestone, but these species may be diagnosed on meristic characters only. *Ophiopsis* shows the halecomorph double joint in the lower jaw (specimen Mbf 1377 in the Museum für Naturkunde, Berlin). The genus is characterized by a ventrally projected hook anterior on the maxilla. The Ophiosidae contain *Ophiopsis* and *Macrepistius* (Bartram 1975, Lambers 1995, Grande & Bemis 1998) and possibly genera such as *Teoichthys*, *Brachyichthys*, *Heterolepidotes* and *Osteorhachis*.

The Ophiopsidae are supposedly related to the Ionoscopidae and the Oshuniidae, jointly forming the Ionoscopiformes (Grande & Bemis 1998, see above). *Ophiopsis*, *Macrepistius* and *Oshunia* share the presence of a lateral line canal in the maxilla (Grande & Bemis 1998). Also some '*Furo*' species are related to the Ophiopsidae, as *'Furo' longiserratus* has a maxilla housing a lateral line canal (Lambers 1995, 1998).

Furidae

It can be concluded from a brief overview of the Late Jurassic '*Furo*' that it does not constitute a monophyletic taxon (Lambers 1998). Because the genus *Furo* is not monophyletic, it is referred to as '*Furo*'. The genus is known from Early and Late Jurassic deposits in England, Germany and France.

'Furo' is generally thought to be related to *Caturus*. The monophyly of the former genus has, however, never been shown, nor has the relation of *'Furo'* with *Caturus* ever been demonstrated. *'F.' microlepidotes* appears more closely related to the Caturidae, sharing a similar slender maxilla; *'F.' longiserratus* is related to the Ophiopsidae (see also Lambers 1995) and the Oshuniidae, having a sensory canal in the maxilla. This feature is also known from *Lepidotes*

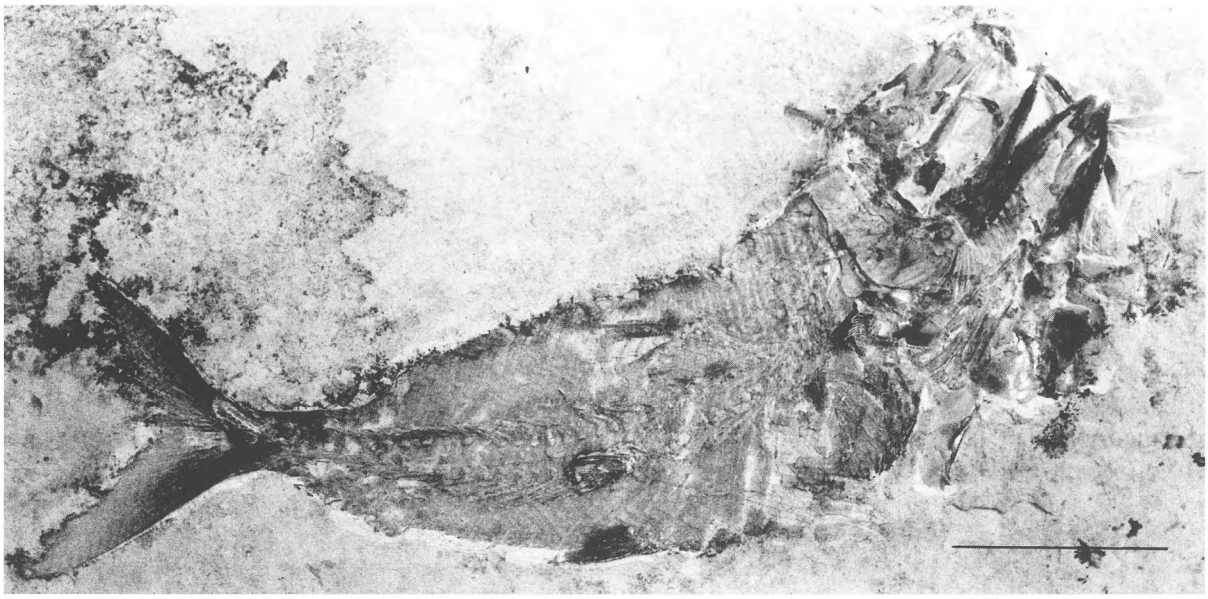

Figure 6. ?*Ankylophorus similis*. Specimen 13305 from Solnhofen, Teylers Museum, Haarlem. Scale bar = 2 cm.

(Thies 1989). '*F.*' *angustus*, '*F.*' *münsteri* and '*F.*' *aldingeri* (from Nusplingen: Heimberg 1949) probably form a monophyletic group. The position of '*F.*' *latimanus* remains unclear.

Halecomorphi incertae sedis
This 'rest group' is represented in the Solnhofen 'Plattenkalke' by three genera:
- *Brachyichthys*
- *Callopterus*
- *Lophiurus.*

Brachyichthys – This very rare genus was described by Winkler (1862), and has two species, only known from Solnhofen. Since the original descriptions by Winkler (1862) and Wagner (1863, *B. radiatopunctatus*), only Woodward (1895) briefly described the type specimen of *B. typicus*, and its anatomy remains poorly known.

According to Gardiner et al. (1996), the genus is the sister group of *Ophiopsis+Macrepistius*, sharing with them lateral line ossicles in the tail, the shape of the rostral and relative size of the dermopterotic. According to Grande & Bemis (1998), the presence of lateral line ossicles in the tail is more widespread among halecomorphs, and because of its poor fossilization potential of no use in phylogenetic analysis.

Callopterus – This is a rare fish genus characterized by small, ganoin-covered scales in front of the tail. The fish is otherwise without scales. *Callopterus* has the halecomorph lower jaw joint, with the symplectic articulating in the lower jaw, but its position among the halecomorphs remains unknown. The vertebral column consists of hemichordacentra. Large *Callopterus* specimens can reach 1 m in length.

Callopterus is more common in Cerin than in Solnhofen; specimens ascribed to *Callopterus* from the Upper Jurassic of Orbagnoux (Sauvage 1893) and the Lower Cretaceous of Bernissart (Traquair 1910) do not belong to this genus (pers. obs.). The material from Bernissart is poorly preserved and – as far as can be judged – does not show any resemblance with the Late Jurassic *Callopterus*.

Lophiurus – *Lophiurus minutus* has been described by Vetter (1881) after a small, juvenile specimen in the Geological Institute in Dresden. According to Woodward (1895), the species might belong to *Liodesmus*, but the ventral and dorsal hemicentra appear to surround the notochord partly, which is not the case in *Liodesmus* (pers. obs.). The species is poorly known and its position among the halecostomes or halecomorphs is unknown.

Teleostei

The Teleostei are represented by:
- Aspidorhynchidae

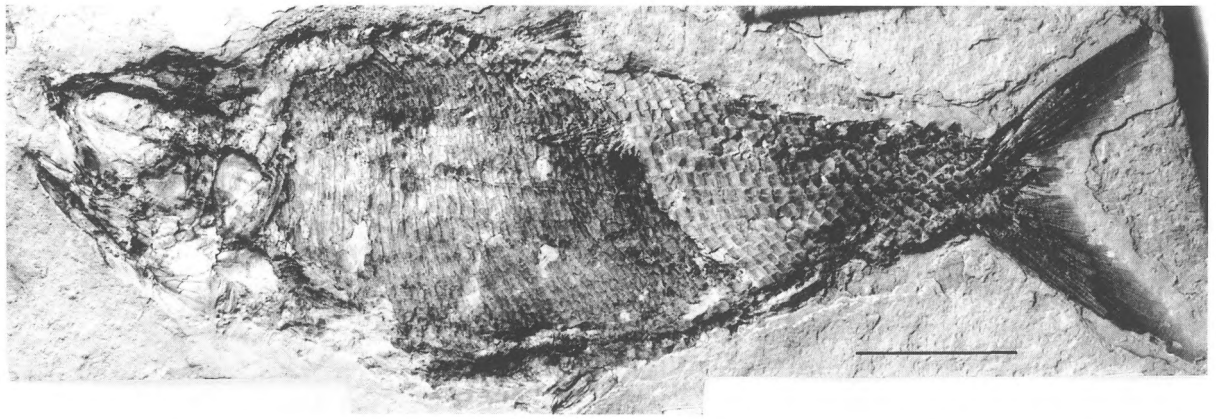

Figure 7. Pholidophorus macrocephalus. Specimen AS VII 873 from Eichstätt, Bayerische Staatssammlung für Paläontologie und historische Geologie, München. Holotype of *Pholidophorus latus* Agassiz. Scale bar = 4 cm.

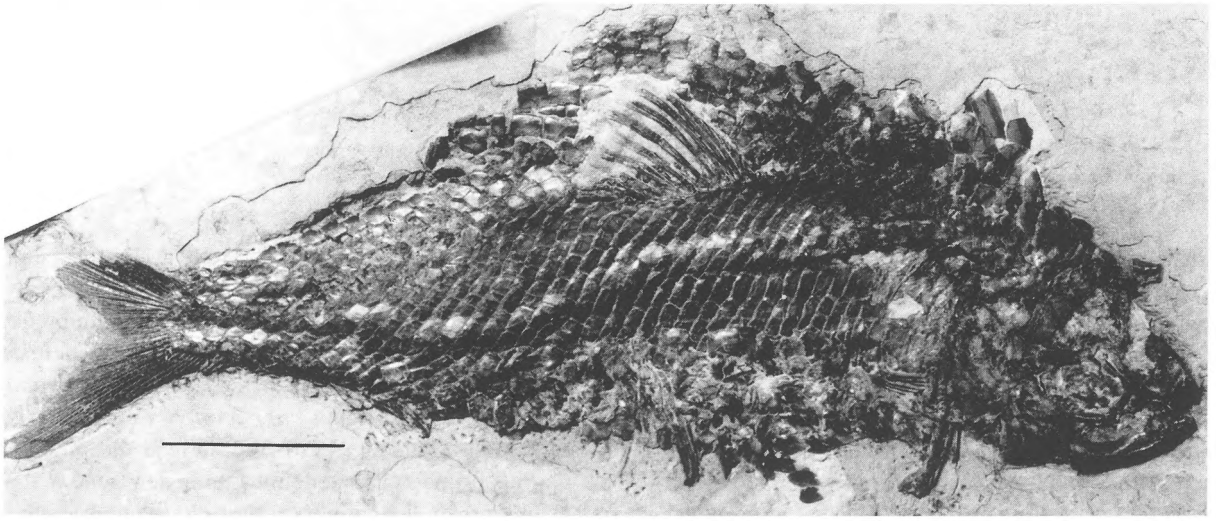

Figure 8. Pholidophorus microps. Holotype, specimen AS I 635 from Solnhofen, Bayerische Staatssammlung für Paläontologie und historische Geologie, München. Scale bar = 2 cm.

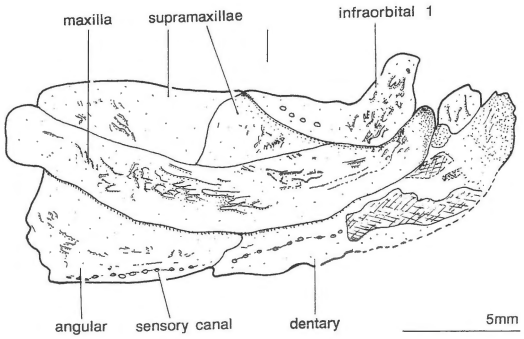

Figure 9. Pholidophorus microps. Upper jaw and lower jaw and associated bones, showing the shape of the maxilla and the relative size and shape of the angular. Specimen 7150 from Nusplingen, Geologisches und Paläontologisches Institut der Universität Tübingen.

- Pholidophoridae
- Pleuropholidae
- a diverse group referred to as basal teleosts (cf. Arratia 1996)

Aspidorhynchidae

The Aspidorhynchidae are represented by the genera *Aspidorhynchus* and *Belonostomus*. These are known worldwide from Late Jurassic and Cretaceous localities, although the species known from the lithographic limestone have elsewhere only been recorded from Cerin and Nusplingen.

Since the original descriptions of the species belonging to these genera, the aspidorhynchids have been redescribed briefly by Assmann (1906). Patterson (1977) and Patterson & Rosen (1977) interpreted

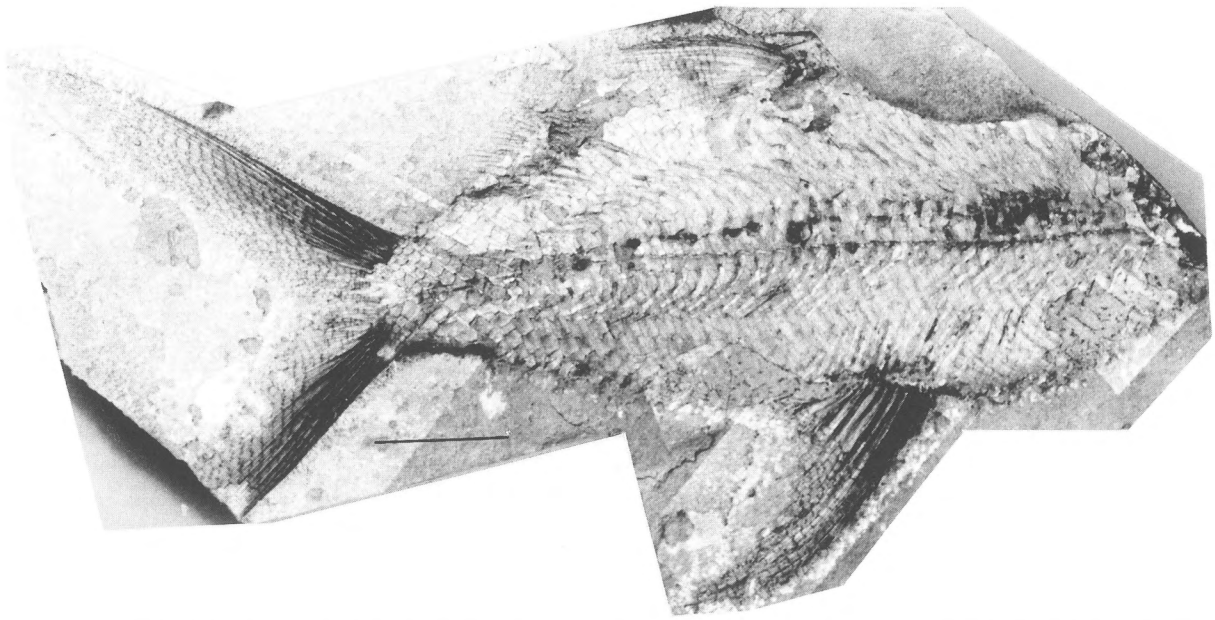

Figure 10. Pholidophorus falcifer. Holotype, specimen AS VII 266 from Kelheim, Bayerische Staatssammlung für Paläontologie und historische Geologie, München. Scale bar = 2 cm.

the Aspidorhynchidae as basal teleosts, based on the presence of paired uroneurals in the tail. Brito (1997) published a revision of the Aspidorhynchidae, mainly focusing on the Early Cretaceous *Vinctifer* from Brazil. Brito recognized *Aspidorhynchus acutirostris*, *Belonostomus tenuirostris* and *B. münsteri* as valid species. In his analysis, the Aspidorhynchidae constitute a monophyletic taxon within the Teleostei. The monophyly of the group is based on the presence of an occipital process on the neurocranium consisting of the intercalar and the autopterotic, the 'rostral tube' of the premaxilla being inserted in the ethmoidal region of the neurocranium, the posterior position of the sensory canal in the preoperculum, the presence of a toothed predentary bone and the absence of the interoperculum (see also Lambers 1992).

In the Solnhofen limestone, *Aspidorhynchus* is the most abundant genus, while in Cerin *Belonostomus* is the most common form and *Aspidorhynchus* is very rare. According to Wenz et al. (1993), the few fossils from Cerin identified as *Aspidorhynchus* are too poorly preserved to enable a specific identification.

Pholidophoridae

Pholidophorids (Figures 6–11) are known from the Late Triassic to the Cretaceous, but certainly not all these pholidophorids form a monophyletic taxon. Many pholidophorids from Solnhofen have been described, but the pholidophorids are in need of revision. Woodward (1895) put some species into synonymy, but later Biese (1927) caused confusion again by describing several new, poorly described and defined species. Woodward (1941) defined *Pholidophoristion*, to which *Ph. ovatus* and *Ph. micronyx* were supposed to belong. Gaudant (1978) redescribed the pholidophorids from Cerin and defined three new genera, *Ankylophorus*, *Lehmanophorus* and *Pholidophorichthys*. These genera do not appear in the Solnhofen area, with the possible exception of the genus *Ankylophorus*. Specimen 13305 in Teylers Museum, Haarlem might belong to this genus (Figure 6; Lambers, in prep.). Gaudant (1978) also described a specimen of *Pholidophoristion* ?cf. *ovatus* from Cerin; *Pholidophoristion ovatus* was originally described after specimens from Solnhofen.

Patterson (1973, 1975) provided information on the neurocranium and associated bones of several *Pholidophorus*, without drawing taxonomic conclusions. *Ph. macrocephalus* (Figure 7), *Ph. microps* (Figures 8–9), *Ph. falcifer* (Figure 10) and *Pholidophoristion micronyx* (Figure 11) are listed here as distinct species (cf. Lambers in prep.); the validity of the remaining species has to be determined. *Ph. microps* has a round maxilla and the dentary and angular are almost equal in length; the suture between dentary and angular is very distinctive, halfway the

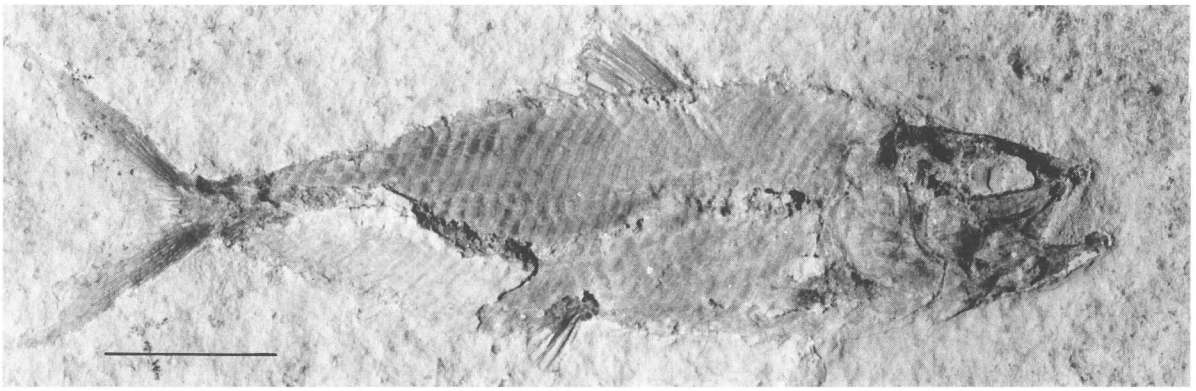

Figure 11. Pholidophoristion micronyx. Specimen SOS 2817 from Blumenberg, Jura-Museum, Eichstätt. Scale bar = 2 cm.

length of the lower jaw (Figure 9); in *Pholidophoristion micronyx*, the maxilla is straight and the posterior border of the maxilla slopes obliquely dorsoventrally (Figure 12), while the angular is much smaller than the dentary and the suture between both is situated posteriorly in the lower jaw. *Ph. macrocephalus* is a fish of medium size (maximum 30 cm in length) with a curved maxilla; details of the lower jaw are unknown.

Ph. microps is possibly a small *Ph. macrocephalus*. The holotype of *Ph. latus* Agassiz (Figure 7), is a pecies that I provisionally consider a junior synonym of *Ph. macrocephalus*. Virtually nothing is known about *Ph. falcifer*. Most conspicuous in this species is the deeply forked caudal fin with long dorsal and ventral lobes (Figure 9). The validity of the three species described by Biese (1927) is debatable, as his descriptions are not very clear, the drawings are very schematic and the differences between the species are not well founded. Whether the various species of *Pholidophorus* belong to the same genus remains to be determined.

Eurycormus – The genus *Eurycormus* (Figure 13a, b) was originally considered a caturid. Lund (1967) interpreted *E. speciosus* as a leptolepid. Patterson (1973) showed the affinities of this species with the pholidophorids. Other species of *Eurycormus* – such as *E. grande* from Nusplingen (Heineke 1906) and species from the Jurassic of England – are halecomorphs, showing the halecomorph double jaw joint. The tail of *Eurycormus* has been described by Nybelin (1963) and Lund (1967).

Pleuropholidae

The Pleuropholidae are a monophyletic taxon, characterized by deep flank scales and a distinctive curved maxilla. The best known members of this family come from the Early Cretaceous of Zaire (*Austropleuropholis* and *Parapleuropholis*, Saint-Seine 1955).

Patterson (1973) sketched the general anatomy of *Pleuropholis* and concluded that the Pleuropholidae belong to the Teleostei, as they possess uroneurals. The systematic position of the Pleuropholidae among the primitive teleosts remains unknown. Wagner (1863), Woodward (1895), Johnston (1909) and Biese (1927) described specimens from Solnhofen. The validity of the species described by Biese (1927) remains to be examined.

Basal teleosts

In the lithographic limestone, eleven genera of basal teleosts have been found. Several species were originally described as *Leptolepis*. The basal teleosts have been the subject of many publications during the last thirty years (by, a.o., Nybelin 1964, 1967, 1974; Taverne 1975a, b, 1977, 1981; Arratia 1987a, b, 1996). Nybelin, in revisions of the genera *Thrissops* (1964), *Anaethalion* (1967) and *Leptolepis* (1974), defined the genera *Allothrissops* (formerly among *Thrissops*), *Ascalabos*, *Leptolepides* and *Tharsis* (all three formerly among *Leptolepis*). Arratia (1987a, b, 1996) described four new genera (*Daitingichthys*, *Eichstättia*, *Tischlingerichthys* and *Orthogonikleithrus*), a new species of *Leptolepides*, and recognized several *Elops*-like forms. Arratia (1996) extensively revised the taxonomy of basal teleosts and the list of basal teleosts is taken from this revision. In her analysis, *Ascalabos* and *Tharsis* are Teleostei *incertae sedis*; *Thrissops*, *Pachythrissops* and *Allothrissops* belong to the Allothrissopidae among the Ichthyodectiformes; *Anaethalion* and *Elops*-like forms belong to

the Elopiformes; *Leptolepides* and *Orthogonikleithrus* belong to the Orthogonikleithridae among the Salmoniformes. *Tischlingerichthys* is an ostariophysean fish.

Of all these forms, *Ascalabos*, *Leptolepides*, *Tharsis*, *Thrissops*, *Allothrissops* and *Anaethalion* also occur in the deposits of Cerin. The genera recently described by Arratia (1987a, b, 1996) are unknown in Cerin, but it is possible that representatives of these forms can be recognized after reexamination of the teleost material from Cerin. For extensive discussions and references to relevant literature, the reader is referred to Arratia (1996).

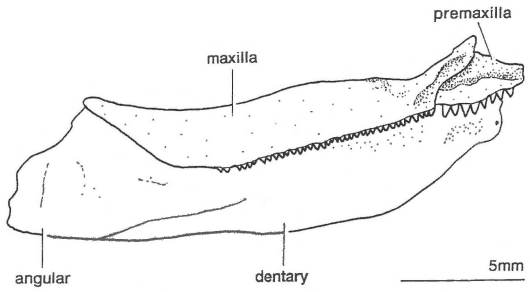

Figure 12. Pholidophoristion micronyx. Upper and lower jaw, showing the shape of the maxilla and the relative size and shape of the angular. Specimen from Nusplingen, Geologisches und Paläontologisches Institut der Universität Tübingen.

Discussion

The actinopterygian fish fauna of the lithographic limestones of Bavaria is very diverse. Some genera are also known from the localities at Cerin and Nusplingen. Especially Cerin is similar with respect to the genera, but there is a difference with Solnhofen at species level (compare with the list in Wenz et al. 1993). This difference might be due to the poor knowledge of several taxa; the faunas might turn out to be more similar after revisions of these taxa. Notable are the absence of *Coccolepis* from Cerin, the abundance of pachycormids in Solnhofen compared to Cerin, the different distribution of the aspidorhynchidae, the different composition of the diverse pycnodontiform fauna and the less diverse fauna of basal teleosts in Cerin.

Several large forms are known from the Solnhofen area, measuring 1–2 m in standard length, e.g., large *Lepidotes* (up to 2 m), *Gyrodus*, *Callopterus*, *Caturus*, *Ionoscopus* (these four up to 1 m) and several pachycormids (*Asthenocormus* reaching 2.5 m in length). The largest actinopterygian from Cerin is *Orthocormus teyleri*, measuring not more than 54 cm standard length (Lambers 1988, 1992). The large specimens are, however, not common; the predominant size in Solnhofen lies between 10 and 20 cm. The large forms were not living in the area of deposition, but most probably entered the lagoon coincidentally .

Conclusions

Although some groups have been restudied during the last twenty years, most of the fauna remains poorly known. New studies of the fishes from Solnhofen will present much new information concerning the interrelationships, phylogeny and evolution of halecostome fishes and primitive teleosts. A large spectrum of the former Holostei is represented in the Solnhofen fauna, together with many primitive and basal teleosts.

Furthermore, the material is most suitable for acid-preparation, enabling fine preparation that can reveal lots of detail. All this makes the fish fauna of the Solnhofen lithographic limestone a unique source of information.

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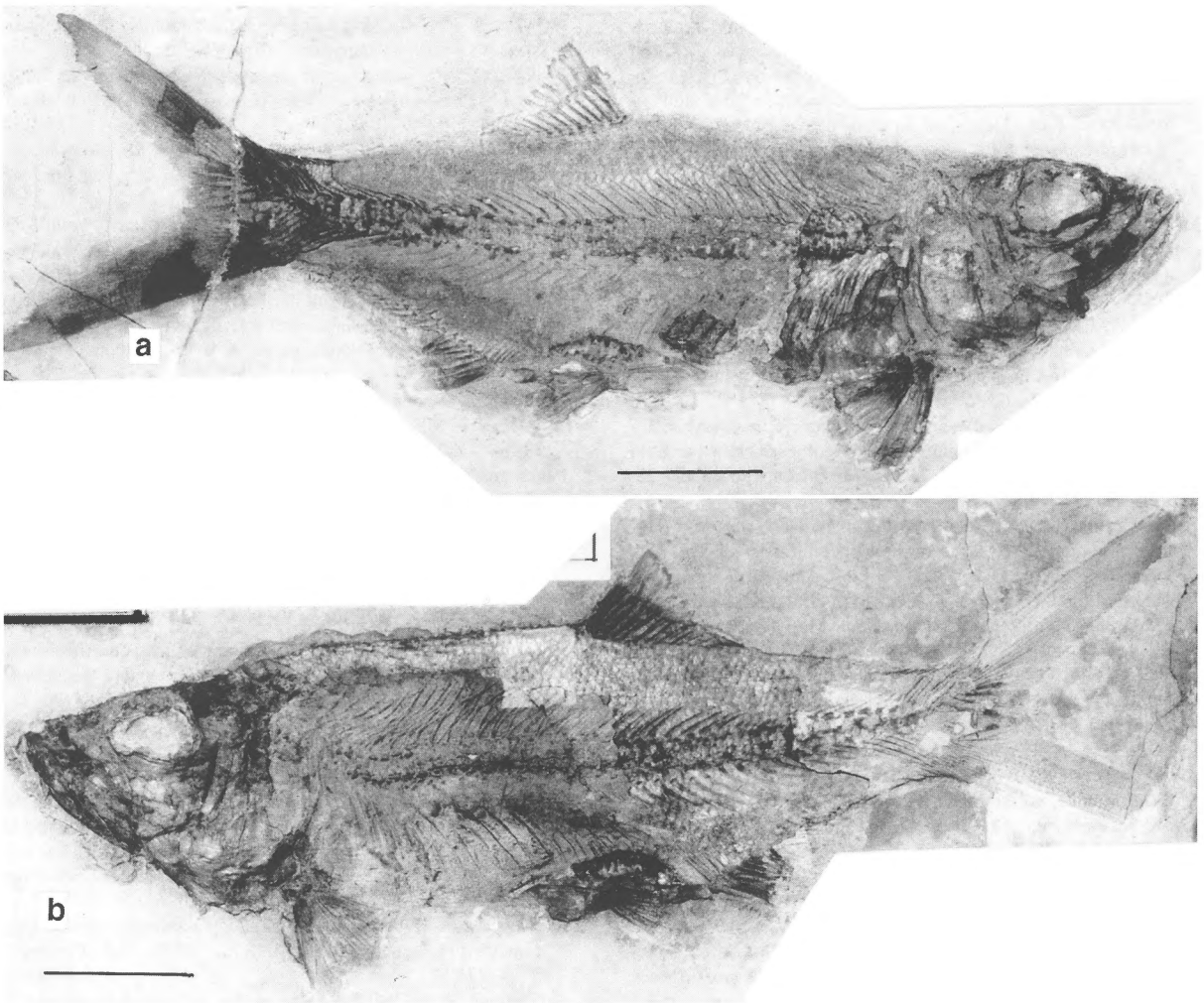

Figure 13a, b. Eurycormus speciosus. Holotype, part and counterpart; specimen AS V 510 from Eichstätt, Bayerische Staatssammlung für Paläontologie und historische Geologie, München. Scale bar = 3 cm.

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