

# Osteoglossomorphs of the marine Lower Eocene of Denmark – with remarks on other Eocene taxa and their importance for palaeobiogeography

NIELS BONDE

*Institute of Geography and Geology, Øster Voldgade 10, DK-1350 Copenhagen K and Fur Museum, DK-7884 Fur, Denmark (e-mail: nielsb@geol.ku.dk; niels.bonde@mail.tele.dk)*

**Abstract:** The geological, faunal and palaeoecological conditions of the marine deposits from lowermost Eocene in North Jutland are briefly reviewed as background for the descriptions of six species of osteoglossiform fishes from the Stolle Klint Clay and the overlying Mo-clay (Ølst and Fur Formations respectively). Four of these primitive teleosteans are referred to new genera and species (one based on an almost complete skeleton, three others on skull material, one very incomplete), and the two most fragmentary specimens are referred to *Brychaetus* sp. and an indeterminate osteoglossiform. The phylogenetic relationships of these fossils are evaluated in the framework of two different models of osteoglossomorph phylogeny provided earlier by Taverne and Hilton. Despite differences in both data bases, methodologies and results given by the two models (the former based on c. 300 characters in an intuitive, qualitative phylogenetic parsimony analysis, the latter on 72 characters in a critical, rigorous, quantitative cladistic analysis) the phylogenetic positions of four of the fossil species are very similar in the two models concerning the relations to the recent forms. The other two species, rather fragmentary, but similar in many ways to the Eocene phareodonts (paraphyletic group), end up very differently in relation to extant forms in the two models. The phylogenetic systematics of all the marine, fossil osteoglossiforms (including *Brychaetus*, *Opsithrissops* and Monte Bolca forms) is evaluated as background for interpretation of their (palaeo-)biogeographic significance as marine members of a group, Osteoglossomorpha (of which the recent forms are prime examples of 'primary division freshwater fishes', and of which the extant osteoglossiforms have a classical 'Gondwana distribution'. There are 9 marine, Eocene taxa (plus an otolith from the Maastrichtian of USA) and none of the 9 appear more closely-related to any other marine form in either model: they might constitute 9 separate migrations from freshwater into the sea. The phylogenetic results strongly suggest instead, that the extant osteoglossiforms have independently entered freshwater from the sea on two, perhaps even three occasions. This may have happened as late as the Eocene, and phareodonts could be yet another independent invasion of freshwater in the Late Cretaceous. The mormyriforms most likely had an independent invasion into freshwater (in one model even with notopterids as a separate migration from the sea by Mid or Early Cretaceous). Because all the closest outgroups of the Osteoglossomorpha are marine, the group obviously originated in the sea, probably by the Late Jurassic, and it is not impossible that Hiodontiforms in NE Asia and North America underwent another independent freshwater invasion very early in the Cretaceous. What then is wanting? The expected Cretaceous, marine osteoglossomorphs are not found (but note the above otolith).

## Geology, 'ash-series' and faunas

This 'ash-series' comprises the main series of ash falls of the Palaeogene of NW Europe. The Palaeocene–Eocene ash falls were recognized as three distinctive 'phases' (Knox 1996, 1997; Knox & Morton 1988, 1990) of which the second one constitutes the main phase (phase 2.1–2.2b in Knox 1996, 1997 correction sheet p. 10x), which was deposited in the Danish Stolle Klint Clay (of the Ølst Clay facies, Heilmann-Clausen 1996) and the overlying Mo-clay (Fur Formation proper, Pedersen & Surlyk 1983 as modified by Heilmann-Clausen *et al.* 1985; Bonde 1997; Heilmann-Clausen

2006). These two deposits are well exposed only in NW Jutland round the western Limfjorden region, but tiny exposures of 'Mo-clay like' layers with ash can be found in a few places further south in East Jutland, and Stolle Klint Clay seems to correspond to the basal part of the Ølst Clay Formation exposed south of Limfjorden and in East Jutland (Andersen 1937; Nielsen 1994), NW Sealand (Petersen 1973) and also to the lower part of the Sele Formation in the North Sea (Schiøler *et al.* 2007).

Prinz & von Ermengen (1883) described and figured the so-called 'black sand' from limestone boulders of the Mo-clay as volcanic ash (tuffs),

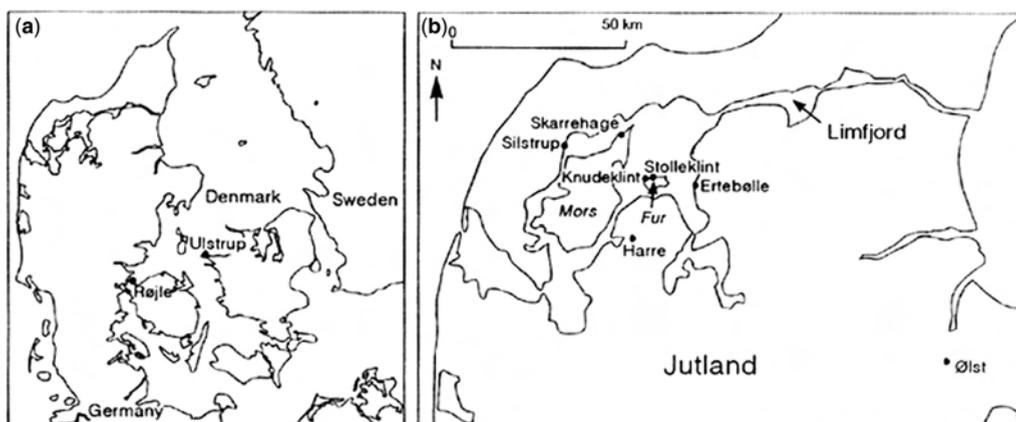


Fig. 1. Localities of the Mo-clay region (modified from Bonde 1997).

which, however was only recognized in Denmark by 1902. Professor N.V. Ussing immediately sent the young O.B. Bøggild to all known localities with such layers in Jutland (Bøggild 1903). Ussing also numbered the upper part of the ash series from +1 to +140 in a footnote to his major work on end moraines in Jutland (1907). After Ussing's death in 1910, Bøggild took over both the professorship and the investigation of the ash layers, which, after some delay, was published as his famous monograph in 1918. In this he continued the numbering of the ash layers downwards from -1 to -39 in the lower half of the Mo-clay (in which the ash layers are much less frequent). In those days many of the now-conspicuous sea cliffs were covered by scree and grass, due to less coastal erosion in the Limfjorden, and the industrial exploitation of the Mo-clay in the many clay pits had hardly begun early in the century, the initiation being the founding of 'Skarrehage Molérværk' (now 'Skamol') by 1912 on the Isle of Mors (see Bonde 1987 at the 75th anniversary of Skamol; Pedersen *et al.* 1994). It is estimated from measurements made on Isle of Fur in the 1920s of the horizontal mine shaft into the Stolle Klint (= cliff; originally dug about 1800 in search for coal, the black volcanic ashes) that, since then, at least 50 m of the seaward face of the cliff has eroded away. The Knudeklint, now type locality of Fur Formation (Pedersen & Surlyk 1983), was early in the 20th century mostly covered by grass and had a wide low foreland protecting part of the cliff from the sea.

#### Stolle Klint Clay (bottom of Ølst Fm)

Stolle Klint Clay (= SKC; which was informally named by Heilmann-Clausen 1996) is a

blackish-greyish, laminated mudstone with a few thin, hardened and silicified beds, and it contains a few of the earliest and numbered ash layers -34 to -39 (Bøggild 1918; Pedersen & Surlyk 1983; Heilmann-Clausen *et al.* 1985; Nielsen 1994). The 10–15 cm thick and whitish ash layer -33 is at the upper boundary of SKC. The fossils, plant debris, fishes, shrimps and insects are found mainly in the hardened layers, locally called 'shale' (Danish: 'skifer'; and therefore likely to be confused with the silicified layers in the Mo-clay originally called 'skifer' by Gry (1940) from around the level of ash layer -20, low in the Fur Formation; see Bonde 1997; Andersen & Sjørring 1997). The SKC contains few, if any, diatoms (Homann 1991). The fish fauna in North Jutland is clearly from open marine water (Bonde 1997), but Köthe (1990) indicates that this basal part of the ash series, at least in the North German region, seems to show a brackish influence as based upon the dinoflagellates.

No doubt the North Sea basin at this time (corresponding to the lower part of Sele Formation in the central North Sea, see Heilmann-Clausen 1985; Schiøler *et al.* 2007) was very restricted and nearly or completely landlocked by the 'Thulean land-bridge' (in the SW from Greenland via the Faroes to Scotland) combined with the closed 'Channel' and by the Spitzbergen-Barents shelf (in the north) in the narrow region between Greenland and the 'Scandinavian Continent' (Fig. 2; Bonde 1979, 1997; Schmitz *et al.* 1996; Ziegler 1990). This closure of the basin may be due to a combination of low global sea level and upheaval of the Thulean land-bridge area above the 'Icelandic hot spot' (Heilmann-Clausen 2006). Some indicate that the entire rift zone along the East Greenlandic coast and the Mohn Ridge may have been about one km above sea level (Larsen 1988) before the

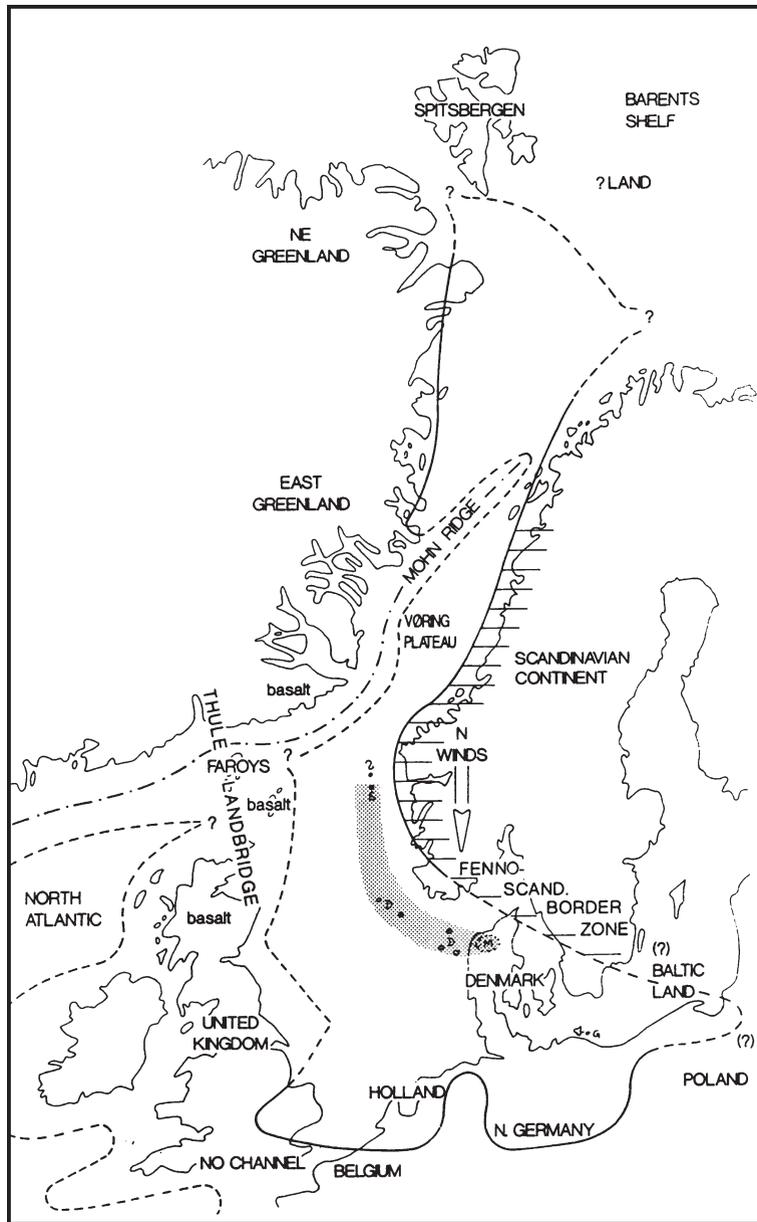


Fig. 2. Palaeogeography of the Mo-clay Basin modified from Bonde 1997. At the deposition of Stolle Klint Clay the basin was even more restricted, presumably a totally landlocked sea. Diatomite stippled.

sea floor spreading with its gigantic volcanism collapsed the rift zone beginning about 55.5 ma.

It is notable that the few complete fish which have been found in cores from the ash series below the central North Sea (Bonde 1979, 1982, 1987, 1997) are all preserved in dark, hardened, laminated mudstones very similar to the shales of the SKC. Only one is from the upper part of the

ash series corresponding to Balder Fm, while the others are from the underlying Sele Fm (though not necessarily from its lower part). Apparently this hardened mudstone is the normal facies in the main ash series of the North Sea (e.g. Frodesen *et al.* 1981; Thomsen & Danielsen 1994).

In these dark mudstones most fishes are preserved as extremely detailed imprints (Bonde

1997, fig. 4; this *Sardinella*-like clupeid was the only species well-known from the 'shales' until collection began more intensively in the 1990s), but larger fish may be preserved with parts of the skeleton intact and apparently little changed apart from becoming dark and brownish to more or less disintegrated as a dark, crumbling, carbonaceous material (see *Xosteoglossid* below). In some cases the bone and teeth may be preserved with a bluish to whitish colour, presumably due to silicification or opalisation of the skeleton (e.g. cf. *Brychaetus*, below).

### Mo-clay (Fur Fm)

The so-called 'Mo-clay' (Danish: 'Molér') is a true diatomite about 50 m thick composed of diatom skeletons mixed with about 30% clay and 10% volcanic dust (Pedersen *et al.* 2004) and for much of especially its lower part well-laminated (Pedersen 1981), thereby indicating anoxic conditions at the bottom (Bonde 1973). This is probably combined with a wind driven and coast parallel upwelling zone producing the rich plankton (diatoms, silicoflagellates and radiolaria; while calciferous microplankton was dissolved in the slightly acidic bottom water; see Bonde 1973, 1979). The predicted extent of the diatomaceous facies further towards the NW below the North Sea was confirmed by Thomsen & Danielsen (1994). The main part of the ash series is intercalated in this diatomite, constituting the Fur Formation proper (Pedersen & Surlyk 1983, as modified by Heilmann-Clausen *et al.* 1985). The basin is much expanded due to a high stand in the global oceans probably increasing the depth of the basin by some 150 m (Heilmann-Clausen 2006), but Bonde (1997) estimated 'a few hundred metres', perhaps 500 m (see below, e.g. the 'deep sea fish'), in order to explain how new, more oceanic fishes could invade the basin (Bonde 1997). This depth estimate is not unlikely, since the Holmehus Clay below the SKC (Heilmann-Clausen 2006) has a similar estimate, and the overlying Røsnæs Clay has benthic foraminifera indicating up to 600 m depth or more (Schmitz *et al.* 1996) even though the North Sea was on the continental shelf. In the North Sea drillings the Mo-clay corresponds to the upper part of the Sele Fm and the lower part of the Balder Fm (Heilmann-Clausen 1985; Michelsen *et al.* 1998; Schiøler *et al.* 2007).

Bøggild (1918) described, correlated and numbered the ash beds from +140 at the top, to -33 at the bottom (Fig. 3; also Andersen & Sjørring 1997, fig. 12), and at most localities the basal part below ash layer -17 is much more dark and clayey, and there seems to be a rather gradual

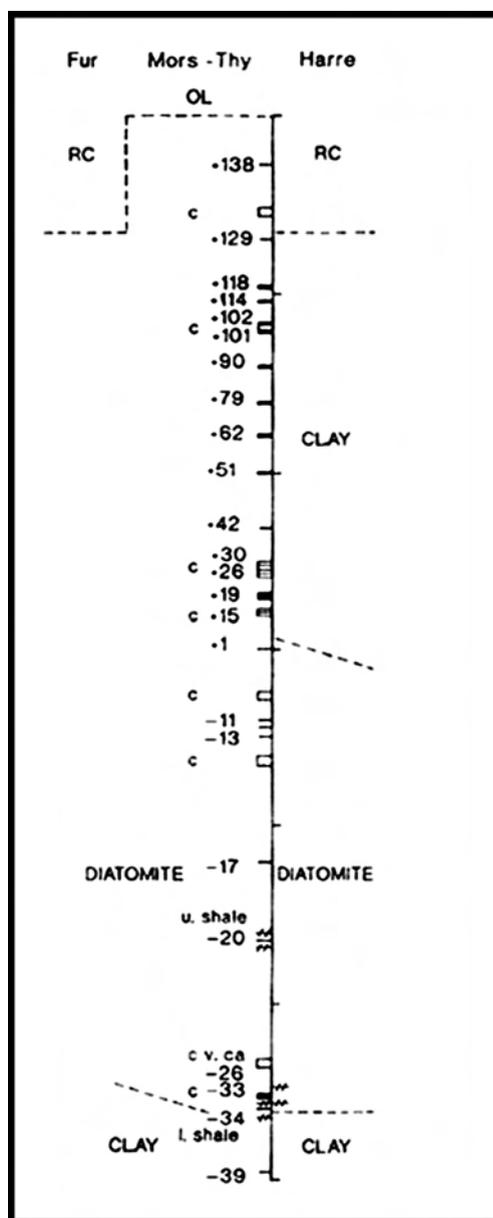


Fig. 3. Stratigraphy of the ash series modified from Bonde 1997. Numbers of the most significant ash layers, thickness per 10 m at right and cementstone levels as small boxes and the two levels for the hardened 'shales' are indicated. Harre is a borehole. OL, Oligocene; RC, Røsnæs clay; l. shale is SKC.

transition from the SKC into the Mo-clay (pers. obs.) above the thick ash layer -33. The thickest ash layer +19 is nearly 20 cm thick in NW Jutland and can be recognized in all of the North

Sea region, west of Ireland, in the Bay of Biscay and even in Austria (Egger *et al.* 2000). Bonde (2003a) and Egger & Brückl (2006) have estimated the amount of ash from that eruption to be thousands of cubic kilometres – an order of magnitude larger than any known from the recent historical period. The light colour of the soft diatomite, Mo-clay, is obviously a diagenetic feature due to weathering. Originally the sediment must have been an organic-rich, dark grey or black mud.

The diatomite is now light coloured (whitish to yellowish to beige/light grey) and porous with no lime, but in a few narrow horizons calcite has precipitated as lens-shaped limestone boulders, so-called cementstones, less than one metre thick (Fig. 3). Only in one level round ashes +101 and +102 was a continuous limestone bed formed, while, for example, the boulders containing –33 are far spread with perhaps 50–100 m between them and only known from the type locality for Fur Fm, Knudeklint, Fur (e.g. *Furichthys*, below). The precipitation of lime is probably conditioned by bacterial activity (Pedersen & Buchardt 1996), and would have taken place less than one metre below the sea floor. Therefore this makes a lot of difference in terms of preservation of the sediments and the fossils. The cementstones are dark grey (preserving much more of the original colour of the dark, anoxic mud) and the ash grains in them are almost perfectly fresh and they contain un-weathered glasses and mineral grains (Bøggild 1918; Larsen *et al.* 2003) and the diatoms are perfect and beautiful opal skeletons (Møller 1892; Pedersen 1981; Bonde 1987, Homann 1991; Pedersen *et al.* 1994). Chitinous skeletons of insects are preserved as a dark matter, and often colour marks can be seen as dark spots on the wings (Rust 1999; Madsen & Rust 2000; Bonde *et al.* 2007) and sometimes also on the fins of fishes (Bonde 1987, p. 21, 41).

Skeletons of vertebrates are preserved in the cementstones as calcium phosphate and can therefore be prepared out by weak acetic acid (sometimes the remaining, sticky clay can be nearly impossible to remove from the bones when the latter are small and fragile) resulting in extremely well-exposed fossils, especially of birds with skulls preserved in 3D (Bonde 1987; Kristoffersen 2002a, b). In one level of cementstones containing ash +15 sometimes the fishes (and fish coprolites) are preserved not completely flattened, but with the interior of the body between the scales from left and right with a perfect skeleton that is not filled by sediment or secondary calcite (see Bonde 1987; Pedersen *et al.* 1994) and with the skull not entirely crushed but showing a braincase with only very limited secondary calcite in its cavities. A large near complete tarpon over 1 m long was

found recently in a cementstone and has the braincase preserved in 3D, which has been removed by acetic acid (Bonde *et al.* 2007).

In the soft diatomite, the Mo-clay, insects are rarely preserved and all the fish skeletons and invertebrates like snails, bivalves, starfish and brittle stars (Rasmussen 1972) are completely dissolved leaving, however, in general perfect imprints (Bonde 1987, 1997, figs 5–6). Only rather large and strong bones may be partly-preserved in the diatomite, but most often as a dark, crumbling, carbonaceous material, which should rather be removed to expose the fine imprints (like *Heterosteglossum*, below). Moulds in silicone or latex material of the fine imprints is a distinct possibility for the larger fossils, but with the many overlapping layers or sheets of imprints, there is obviously a risk of damaging the fossils by removing important details (if the rubber material penetrates below the thin sheets and into deep cavities in the fragile clay matrix.)

## Ages

The stratigraphic age of the ash series and the Mo-clay has been controversial since 1900, sometimes recognized as Upper Paleocene, sometimes as lowermost Eocene, the problem being the lack of calciferous microplankton and correlation to the standard Palaeogene zonation (Heilmann-Clausen 1982). This was apparently overcome by Knox (1984), who could correlate the ash series to the nanoplankton zonation in the Eastern Atlantic to show that the main part of the ash series corresponds to lower part of the NP 10 zone, while part of the negative numbered ashes and SKC correlate to the Sele Formation and most of NP 9 (Schjøler *et al.* 2007). The very distinctive ash layer –17 is close to the base of NP 10 and has a radiometric age of *c.* 54.5 ma (Knox 1997), lately revised to 55.1 ma by Storey *et al.* (2007) with SKC beginning about 0.5 ma earlier. Recently it has been decided, by a stratigraphic sub-commission, that the lower boundary of the Eocene is defined as the base of the temperature optimum to be globally recognized (see below Crouch *et al.* 2001; Aubry & Ouda 2003; Gradstein *et al.* 2004) and implying that the stratigraphic age of the Stolle Klint Clay is the very earliest Eocene date. The positive ash series (ash +1 – 140) correlates to lower Balder Fm in the North Sea and the total duration of the ash series (phase 2.1–2.2b) is about 1.5 ma (Knox 1997; Beyer *et al.* 2001), with the intensive ash falls of the positive series distributed over a period of about 300000 years (Knox 1997) between 54–55 ma. The ash series also marks the initiation of the volcanism and the seafloor spreading along the

East Greenlandic coast, which can be precisely correlated with these ash falls (Heister *et al.* 2001).

### Faunas

Both of these deposits, Stolle Klint Clay and Mo-clay contain rich marine fish faunas (Nielsen 1960; Bonde 1987, 1997; Bonde *et al.* 2007), very poor faunas of marine invertebrates (Bonde 1979), but abundant faunas of insects – presumably blown out from the northern Scandinavian continent (described by Willmann (1990) and several of his students subsequently in Meyniana, summarized by Rust's thesis (1999); in total over 20000 specimens according to Madsen & Rust (2000); see also Andersen (1998) and Archibald & Markarkin (2006)). The Mo-clay has further provided a few planktonic crustacea (Garassino & Jakobsen 2005) and marine reptiles (Nielsen 1963; Hoch 1975) and quite a number of land birds (Kristoffersen 1999, 2002a, b; Dyke *et al.* 2004; Leonard *et al.* 2005; Lindow & Dyke 2006; Bonde *et al.* 2008).

### Environments at the Paleocene–Eocene boundary

Between SKC and the underlying Holmehus Clay there is a small hiatus, some places are partly infilled by a few metres of grey, more sandy clay indicating reduced depth (Nielsen & Heilmann-Clausen 1986; Beyer *et al.* 2001). The significance of this period of (almost) non-deposition is difficult to evaluate. Perhaps the 'Proto-Icelandic hot spot dome' elevated the entire North Sea region above sea level (Heilmann-Clausen 2006). Corresponding shallow water sediments could be Woolwich Beds and freshwater deposits could be the English Reading Clay and French–Belgian Sparnacian (see Beyer *et al.* 2001).

A similar, mostly small hiatus above the Mo-clay and below the Røsnæs Clay (e.g. on Fur) is equally difficult to interpret – in the westernmost Mo-clay localities this hiatus is enormous as the diatomaceous clay conformably overlying the Mo-clay is of Late Oligocene age (Heilmann-Clausen 1997) about 30 ma younger.

SKC was deposited as an anoxic, laminated mud in a much reduced and entirely closed basin (Bonde 1979, 1997; Ziegler 1990; Heilmann-Clausen 2006, figs 10-2, even smaller than in Fig. 2) during a short period beginning nearly 56 ma ago (based on Storey *et al.* 2007) and lasting around 200000 years (according to Röhl *et al.* 2000) of increased temperature as indicated by carbon isotope studies (Norris & Röhl 1999; Heilmann-Clausen & Schmitz 2000; Crouch *et al.* 2001; Zachos *et al.* 2003; Wing *et al.* 2005). This basin seem to have

a marine, pelagic fish fauna enclosed with no clear cut representatives from a freshwater environment. However, a single fossil of a possible 'percopiform' (listed with doubts by Bonde 1997) and some rare finds of the very osteoglossomorphs to be discussed below, obviously cannot entirely be excluded as being transported from rivers running into the basin. This basin was, according to Heilmann-Clausen & Schmitz (2000) and Heilmann-Clausen (2006, fig. 10-2), less than 200 m deep. Plant material in SKC must have been transported from land, presumably mainly by rivers. However, the general impression of the fish fauna is of a marine one comprising about 25 forms with only a few among these indicating possible affinities to benthic or near coastal fishes: a muraenid, an ariid (?) and some perhaps among the five species of clupeids and small aulostomoids, although one of each of these two groups survive into the Mo-clay basin (Bonde 1997, 2003a).

After this brief temperature optimum (increase 5–10°C, Wing *et al.* 2005) the warmth decreased a little during the deposition of the Mo-clay, perhaps from tropical to subtropical climate (Heilmann-Clausen 2006, fig. 10-2), and the basin increased in size and water depth. The transition to this larger and deeper basin, still almost land-locked, seems gradual as judged from the diatomaceous sediment, which, in the lower half of the Fur Fm, is dominated by periods of laminated mud deposition under anoxic conditions at the bottom (Bonde 1979; Pedersen 1981), where the stagnant and acid water was poisoned by hydrogen sulphide preventing all life but bacteria. In contrast to this, the planktonic life at the surface was rich especially in a zone paralleling the coast and governed by wind driven upwelling along the low Scandinavian continent (Bonde 1973, 1979, 1987, 1997; Thomsen & Danielsen 1994). Such upwelling in the upper 100–200 m (moving south into the closed basin by frequent and strong northern winds, as indicated by the distribution of the ash falls), was combined with a deeper counter current and below this the stagnant water was locked. The entire system probably demanded at least 500 m of water, but possible connections to the neighbouring basins may have been very narrow (through the Channel, between the Faroes and Scotland, along the Norwegian NW coast, and perhaps between NE Greenland and Spitsbergen; see Fig. 2).

Supported at the surface was a rich life of abundant oceanic, pelagic fishes, some of which ended as more or less complete skeletons in the laminated mud, undisturbed by scavengers and under very slow putrefaction, leaving the fossils sometimes with colour markings on the fin membranes (Bonde 1987). Upwards in the sedimentation, laminated periods became less frequent due

to the infilling of the basin low and therefore fewer periods with stagnant water according to Pedersen (1981). Usually no lime was precipitated because of the subacidity, but sometimes for short periods the chemical environment, controlled by bacterial activity a short distance below the surface, allowed calcite to precipitate as large, flat and lens shaped concretions, or cementstones, (Pedersen & Buchardt 1996).

The change in the fish fauna between SKC and Mo-clay indicates that some connection to the surrounding oceans was established allowing more oceanic, pelagic fish to enter the basin, which, however, for most of the time may have been nearly land locked (fig. 2; Bonde 1997). The more permanent opening of the Atlantic connection through the Channel later in Early Eocene introduced southern and warmer ocean currents, even with nummulite immigration, and probably this influx destroyed at least the southern region of the upwelling zone and thereby the deposition of diatomaceous sediment in the Danish region (Bonde 1979, 1987). After this only the finest clay particles (smectite, indicating that it is a result of weathering volcanic material) reached the centre of the basin to deposit the extremely fine grained so-called 'plastic clays' of Denmark, first Røsnæs Clay then followed by Lillebælt Clay into Middle Eocene and finally the Søvind Marl ending the Eocene sedimentation in the Danish region (Fig. 4; Heilmann-Clausen *et al.* 1985; Graversen 1993; Heilmann-Clausen 1996, 2006; Michelsen *et al.* 1998).

### Fish faunas and marine osteoglossomorphs

The fish faunas of the Stolle Klint Clay and the Mo-clay were mapped by Bonde (1997) indicating,

as mentioned above, that although fishes from both deposits are marine and pelagic in general, those from the Mo-clay appear much more oceanic with a tarpon, a paralepidid relative like *Holosteus*, 2–3 small zeiforms, a polymixiid, several lampridiforms, *Exellia*, probably two species of stromateoids, many scombrids, palaeorhynchids, a gempylid (euzaphlegid) and one carangid species, and a single 'true' deep sea fish, a *Rondeletia*-like cetomimiform (Bonde *et al.* 2007).

Apart from scales of the tarpon, none of these have been found in SKC: but, on the other hand, it has yielded such pelagic fishes as *Mene*, not occurring in the Mo-clay, and a small *Antigonia*-like fish (of which the occurrence in the negative series of the Mo-clay is a little uncertain) as well as another carangid species and a *Vomeropsis*-like species, presumably fully marine and pelagic fish. A few fishes from SKC might be considered more shallow water fishes, such as the three types of aulostomoids (two very small, the larger is also found in the Mo-clay) and the muraenid eel (and above was mentioned the dubious 'percopsiform', a freshwater group apart from a Cretaceous relative), but the fauna does not have strong littoral affinities.

The occurrence of several osteoglossid-like species (about 6) in the two near-contemporaneous, marine faunas is therefore remarkable, as all species of this group today live in freshwater and on the southern continents with a typical Gondwanan biogeographic distribution (cf. Darlington 1948, 1957): from South America (two genera: *Osteoglossum*, (2 species and *Arapaima gigas*) via Africa (*Heterotis* [= *Clupisudis*]) and *Pantodon* – both genera monospecific) to Australia and Indonesia (*Scleropages* with 6 species or subspecies [Pouyeaud *et al.* 2003]). Mostly these few species are referred to one family, Osteoglossidae, with *Pantodon* closest

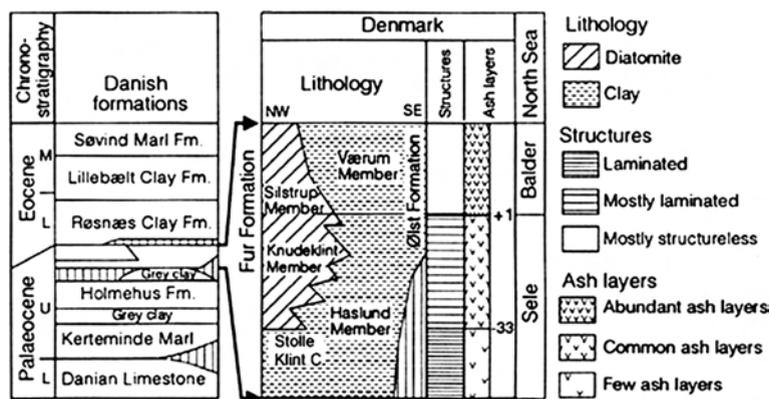


Fig. 4. Stratigraphy of Danish Eocene. Modified from Thomsen & Danielsen 1994 (with permission of the authors). Fur Fm. proper does not include Stolle Klint Clay, and both are considered Lower Eocene.

to Osteoglossinae (= *Osteoglossum* + *Scleropages*), but sometimes *Pantodon* is placed in its own family as sister-group to osteoglossids (see Taverne 1979, 1998; Nelson 1994; Li & Wilson 1996a, b; Li, Grande & Wilson 1997; Li, Wilson & Grande 1997, in contrast to Nelson 1968, 1969). Greenwood (1971) initially only specified that *Pantodon* is related to osteoglossids, and in 1973 placed Pantodontidae as sister-group to Osteoglossidae in osteoglossoids, and with all other osteoglossomorphs in its sister-group notopteroids. These remaining osteoglossomorph fishes (mormyrids, notopterids and hiodontids) today occur in respectively Africa, Africa plus South Asia and North America, and are sometimes indicated as a monophyletic sister-group to osteoglossids (Greenwood 1971, 1973). Or mormyrids plus notopterids are considered as related to osteoglossids, and hiodontids form the primitive sister-group of all the others (Li, Grande & Wilson 1997a; Taverne 1998 Nelson 1969) very tentatively held mormyrids and osteoglossids as closely-related and the sister-group to notopterids plus hiodontids. For this reason, the author remained uncertain concerning the placement of mormyrids (1996, fig. 4).

The last reviews of osteoglossomorphs that still consider that notopterids and/or mormyroid are most closely-related to hiodonts were by Patterson (1993) and Nelson (1994). Since the mid 1990s there seems to be general agreement that Hiodontiforms is the (plesiomorph) sister-group to all other osteoglossomorphs, constituting a large monophyletic taxon (Li & Wilson 1996a; Taverne 1998 and Hilton 2003), that is in need of a name. This group is called 'Osteoglossi' here (p. 297).

By the mid 1990s hiodontid-like fishes were known from middle Cretaceous (*Yanbiania*, Li 1987) and could have probably been established by mid Early Cretaceous (*Chetungichthys*, Chang & Chou 1977, accepted by Taverne 1979, and perhaps *Plesiolycoptera*, Chang & Chou 1976). Later Li, Wilson & Grande (1997) only accepted *Yanbiania* and *Plesiolycoptera* as hiodontids (and did not mention *Chetungichthys*). Cretaceous notopterids were known only from otoliths (Rana 1988), but have later acquired a better fossil record with *Palaeonotopterus* from late Early Cretaceous in Morocco (Forey 1997; Taverne & Maisey 1999), while mormyrids are generally believed to hardly have a fossil record at all. Ironically, *Palaeonotopterus* turns out perhaps to be a mormyrid relative than related to the notopterids (Cavin & Forey 2001; Hilton 2003, fig. 5), although the evidence is not that convincing, as Hilton left it unresolved (2003, p. 19, fig. 6).

Optimistically (1996, fig. 4), and probably wrongly (p. 280), I considered *Kipalaichthys* from mid Cretaceous in Congo (see Taverne 1976) as a

possible relative of *Pantodon* based on very little evidence (scale similarity), as the *Pantodon* lineage has little fossil record. This changed dramatically with Hilton's analysis (2003) resulting in both most parsimonious trees showing *Singida* as sister of *Pantodon*, and *Phareodus* as sister of those two. However, the support for this was meagre, (only homoplasies, four parallelisms and two reversals), (2003, p. 24). Such fragmentary mid Cretaceous fish, as *Paradercetis* (Taverne 1976) and *Chanopsis* (Taverne 1984), if they are osteoglossomorphs at all, could well be in the stem-group of *Pantodon* and osteoglossids. The same counts for the complete and very primitive looking *Laeliichthys* from Brazil (as judged by the reconstruction by Silva Santos 1985; here right spelling contrary to Bonde 1996, fig. 4; Taverne 1998, 136 ff; Hilton 2003, fig. 2), as I stated earlier (1996). It has sometimes been placed close to heterotines (Li 1996) or even as sistergroup of only *Heterotis* (Taverne 1979), despite its Early Cretaceous age (Aptian - and Brazilian colleagues now tell, that it is not even obvious that it is an osteoglossomorph, and indicate that the reconstruction is not so easy to reproduce from the many small fossils). Freshwater osteoglossids have been reported from the French Campanian (Sige *et al.* 1997).

Phareodontines, an extinct group of osteoglossids known from Late Cretaceous to Eocene (Taverne 1979; Grande 1984; Li, Grande & Wilson 1997) is usually, and firmly, based on several characters and placed in a stem-group position as closely related to Osteoglossinae. This is interesting because the phareodontines contain a marine member, *Brychaetus*, originally described from Early Eocene London Clay (Woodward 1901; Casier 1966; Roellig 1974; Taverne 1974); and, as indicated below, it probably occurs also in the Stolle Klint Clay. It is known from the Eocene Moroccan phosphates (Arambourg 1952), from Nigeria (Capetta 1972), and Taverne (1978) referred a caudal skeleton from the Paleocene (?) of Cabinda, Congo, to the same taxon as jaw fragments of a second species of *Brychaetus*. Later Weems & Horman (1983) identified jaw fragments from Maryland as *Brychaetus*, and Longbottom (1984) mentioned *Brychaetus* from Mali (enormous jaws, pers. obs. in NHM). All jaw fragments with teeth seem fairly trustworthy, because the large bony pedicles for the oval and pointed teeth, are smooth and conical with a small, distinct 'cap' closely set in the jaws seem very characteristic of *Brychaetus*.

Eocene marine otoliths from NW Europe have been referred to *Brychaetus* by Taverne (1978), but they do look more like heterotine than osteoglossine otoliths, and Nolf (1978) has described

osteoglossid otoliths from Belgian Paleocene. Considering the number of different osteoglossid-like taxa in the Danish lowermost Eocene it seems unwise to assign such otoliths to specified genera.

Late Cretaceous (Maastrichtian) marine osteoglossid otoliths have been described as *Osteoglossidarum taverni* by Nolf & Stringer (1996). It should also be noted that a tiny premaxilla from the marine Fish Clay (basal Danian at Stevns Cliff, Sealand) has been described as an osteoglossid (Bonde *et al.* 2008). The referrals of 'squamules' to *Brychaetus* (parts of reticulate scales when fragmented along the un-mineralised zones; see Meunier 1984) by, for example, Gayet & Meunier (1983) from Morocco are very uncertain. Slightly different squamules from continental Paleocene and Eocene of India and Pakistan are *Phareoides*, the genus known from the Australian mid Tertiary (Taverne 1978), but neither *Brychaetus* nor *Phareoides* has ever had their scale-structure analysed in any detail, and the former was generally, but incorrectly described with non-reticulate scales (see Bonde 1996). *Phareoides* (Li, Grande & Wilson 1997) is synonymized with *Phareodus*, as they do for *Brychaetus* (and Li [1996] has a similar suggestion for *Musperia* [Sanders 1934] from the Palaeogene of Sumatra). Li (1996) also described the oldest phareodontine, Late Cretaceous *Cretophareodus*, as primitive sister-group of all other taxa in the group (for more details about 'phareodontines', squamules and otoliths, see Taverne [1998, pp. 128–129, 136]). Recently, a *Brychaetus*-like phareodontine skull has been described as *Tavernichthys* from freshwater Paleocene in India (Kumar *et al.* 2005).

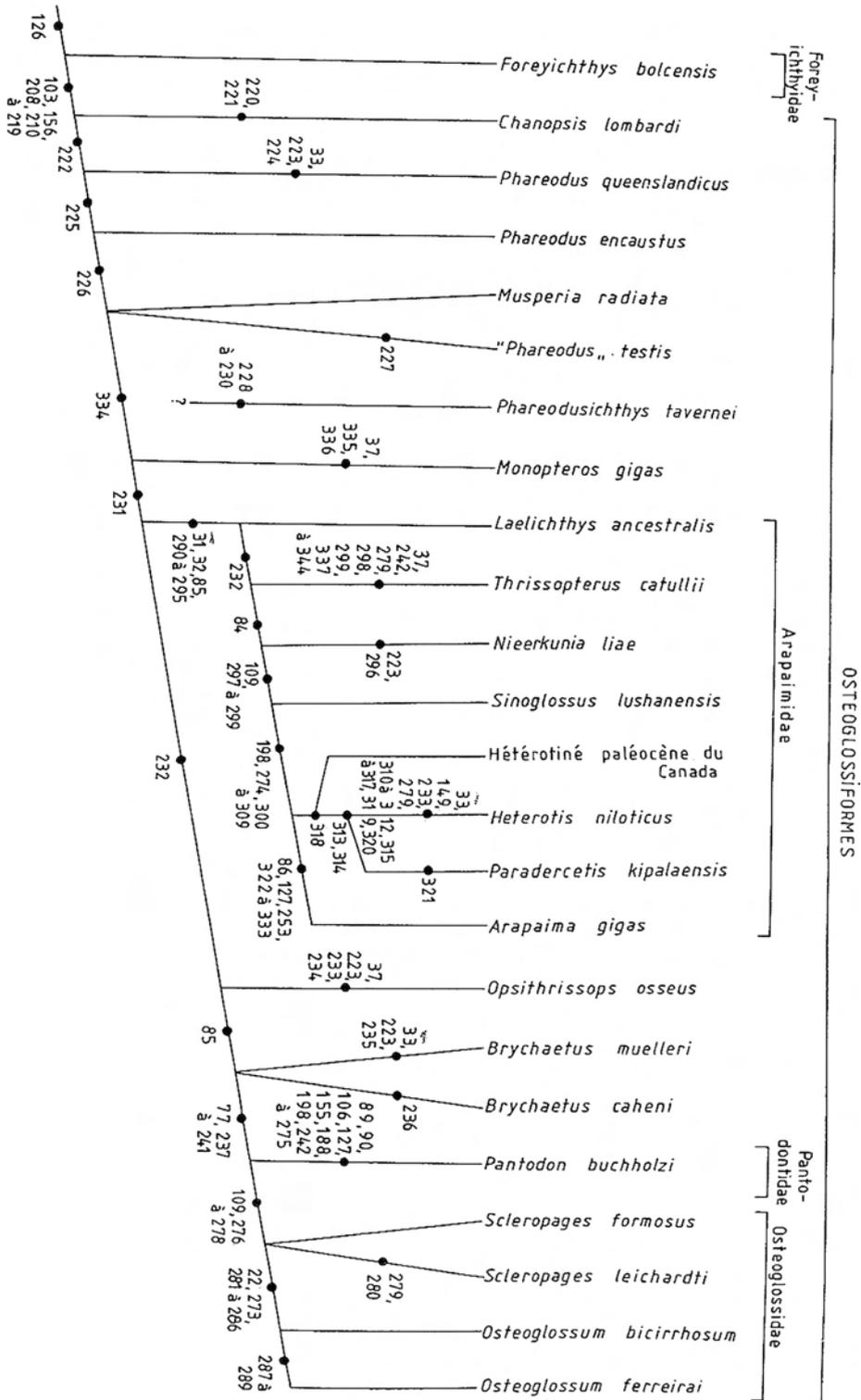
The synonymizing by Li, Grande & Wilson 1997 of five (or more) species within *Phareodus* is not necessarily the most informative, as there is a clear hierarchical structure indicating that the species *P. encaustus* and *P. queenslandicus* (Taverne's *Phareoides* [1973]) form a monophyletic group *Phareodus* with *Brychaetus* (2 spp.) as sister-group, and *Dapedoglossus testis* as sister-group of all the others (*Musperia* has not been reanalysed in this connection). So, here, I retain the generic name *Brychaetus* for the London Clay species and *B. muelleri* and the central African *B. caheni* (Taverne 1969). Two species are known to retain a small supramaxillary, *B. muelleri* (pers. obs.) and *P.* ('*Phareoides*') *queenslandicus*, presumably a primitive feature lost several times in osteoglossid evolution; (as it is also known from one of the Mo-clay species, from *Opsithrissops* (below), *Laellichthys* and most out-groups to osteoglossomorphs – most of which actually have two supramaxillae). To imply that the presence of a second supramaxilla is an 'apomorphic reversal' five times (Taverne 1998, trait no. 223;

see Fig. 5) does not seem well justified. Loss of supramaxillae has occurred independently many times in teleostean evolution. 'Dollo's law' should be obeyed here: a lost organ does not reappear.

Another marine osteoglossomorph contemporary with the forms in the ash series is *Opsithrissops* (Danil'chenko 1968; described as 'chirocentrid' meaning an ichthyodectid) from Danatinsk Series in Turkmenistan from the basal Eocene (Tyler & Bannikov 1992): it is a large osteoglossid (as pointed out by Patterson [1975] and Bonde [1975]). Taverne (1979) placed it in phareodontines near *Brychaetus*, although no phareodontine synapomorphies among the three that are claimed by Taverne (which *Brychaetus* also possesses) were demonstrated in *Opsithrissops*. Taverne (1979, fig. 13) gave a new and certainly better reconstruction based solely on Danil'chenko's reconstruction of the entire fish and his published photo of the skull. No further documentation appears to have been published about these big fish reaching 122 cm in length and known from three specimens (Danil'chenko 1968; 130 cm in length quoted by him in 1980).

Danil'chenko's drawings are not trustworthy in detail. They are very schematic, not showing nearly as much skeletal details, e.g. in the skulls, as can be observed in the fossils (I have closely scrutinized some lampridiforms from the Danatinsk deposits kindly brought to Copenhagen by Dr V. Fedotov). His reconstructions of caudal fins are usually unrealistic, even concerning the number of fin rays and his description (1968 in translation) and figure of *Opsithrissops* do not correspond, (the reconstruction has 23 principal caudal rays, which is very unlikely). None-the-less Taverne's interpretation is not unlikely – just unvalidated by facts.

Taverne recently (1998) completely abandoned his earlier views on *Phareodus* and other species by looking at the phylogeny of osteoglossomorphs from a non-quantitative, cladistic angle with arguments turning especially around parsimony and investigating around 300 features in a characterization of monophyletic groups in the entire osteoglossomorph hierarchy. He dissolved his subfamily phareodontines entirely (although it is also supported by Li & Wilson 1996a and Li, Wilson & Grande 1997 – which are, however, only briefly mentioned in Taverne's Appendices 1 & 2, not really discussed), distributing them as two paraphyletic groups of osteoglossiforms, one in stem-group position, the other more derived and related to *Pantodon* plus osteoglossines. The greatest difference concerns the genus *Phareodus* itself, which, instead of being an advanced relative of osteoglossines, now has a position as a very primitive, even paraphyletic, stem-group to crown-group osteoglossids (Taverne 1998, fig. 22; Fig. 5) as the



**Fig. 5.** Osteoglossiform phylogeny/cladogram' from Taverne (1998, fig. 22 – permission from the author). Concerning *Foreyichthys* it should be moved to a position as most advanced member of the Osteoglossid (+*Pantodon*) stem-group above *Brychaetus*. Numbers are traits; e.g. 223: supramax. present ('reversal').

first splits within Osteoglossiformes after the very incomplete, dubious and mid Cretaceous genus, *Chanopsis* (cf. my doubts in 1996). Now only *Opsithrissops* and *Brychaetus* are placed successively as relatives to osteoglossines (in his 1998 paper considered a family like its extant sister-group, Arapaimidae, earlier called 'heterotines'). Hilton's analysis (2003) gave the untraditional result, that *Phareodus* was closest to *Pantodon* (and *Singida* – see below), but he unfortunately did not include *Brychaetus* in his analysis (neither did he include *Opsithrissops*, *Phareoides*, *Musperia* nor other Eocene forms known from complete fossils like *Foreyichthys*, *Monopteros* and *Sinoglossus*).

Taverne's analysis (1998) was prompted by the description of three more marine osteoglossomorphs, all from the Monte Bolca fish fauna of Mid Eocene age, c. 5 younger than the Mo-clay. Of these forms the big and high-bodied *Monopteros* specimens are very poorly-preserved, hardly showing the precise outline of any skull bones (Taverne 1998, fig. 3 & pl. I; pers. obs.) nor any details of the caudal base. But it can be accepted as an osteoglossomorph with: its huge pectoral fins, tiny pelvic fins, 17 principal caudal rays, dorsal fin placed opposite the anal fin, many vertebrae and very long ribs, as well as cycloid scales of which some show superficial reticulation with tuberculated 'squamulae' (Taverne 1998, fig. 5), and they also have pores (pers. obs.). Although not well-preserved and fragmentary known *Monopteros* can be precisely placed (according to Taverne) as the most advanced member of the stem-group to crown-group osteoglossiforms (arapaimids + pantodontids + osteoglossids), based on the large number of vertebrae slightly more derived than *Dapedoglossum* [*Phareodus*] *testis* (by Cope 1877; Taverne 1998, fig. 22; Fig. 5).

### Foreyichthys

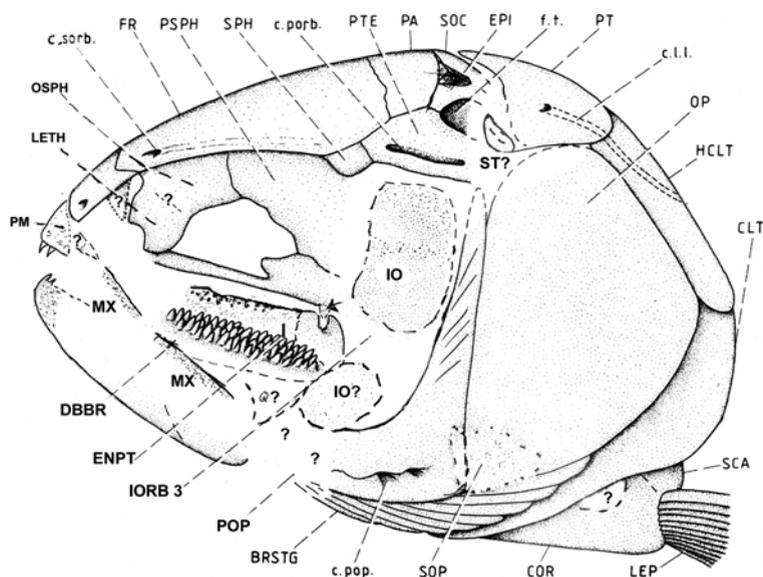
The small Bolca fossil *Foreyichthys bolcensis* (first named with a reconstruction and an overview of its description by Taverne 1979, before being mentioned in Forey's thesis (1970) as cf. *Platinx macropterus*) was finally described in detail (Taverne 1998, 91 ff. and photos of the only specimen having no counterpart, pl. VI & VII; NHM P 16.821). There is also an improved reconstruction (*ibid.*; fig. 12), and more details from the skull, caudal skeleton and part of a scale (*ibid.*; figs 13–15). I here add some details from notes and drawing made 1974 and 1992 and some checked in 2005: Taverne has shown one tooth at the symphysis of the lower jaw, although two seem preserved, and furthermore the proximal premaxilla with part of the ascending process and with two stout teeth can be seen even in his photo, pl. VI. The process nearly

reaches the tip of the nasal (presumably near the midline), of which the posterior boundary is difficult to see. There is a frontal with a laterally placed sensory canal and no indication of an anterior broad lappet. The proximal 'maxilla' fragment indicated by Taverne seems to be placed too far up and could instead be part of the premaxilla. Behind it, however, there appear to be more of a slim maxilla (dental margin not seen) reaching nearly to what seem to be traces of the quadrate below the posterior part of the orbit, although, admittedly, it is difficult to be sure of the exact position of the articulation and therefore the length of the lower jaw. This has consequences for estimating the length of the horizontal branch of the preopercular (not preserved) which I would estimate longer (and, therefore, more primitive) than reconstructed by Taverne. The posterior part of the endopterygoid shown by Taverne with a deep notch is perhaps metapterygoid (as in *Osteoglossum*), and in front of this a tooth patch of the endopterygoid (right) can be seen paralleling the parasphenoid. On the latter, just above the metapterygoid notch, there seems to be a weak trace of the basiptyergoid process partly hidden by some lime. The bones limiting the orbit are not so clear, and I believe the anteroventral part of Taverne's orbithosphenoïd is rather the parethmoid (Taverne, pers. com. 2007, does not agree) while his small 'lateral ethmoid' could as be the mesethmoid. Behind the orbit only the inner side of one large (right) infraorbital can be seen in between remains of crushed bone, while further down, level with the 'quadrate' (?) and the missing horizontal preopercular, another inner surface of a large flat bone seems exposed, perhaps part of a very large and deep infraorbital 3 (as in extant osteoglossiforms). There seems to be a trace of a narrow anterior infraorbital just below the parethmoid (like in osteoglossids). A pterotic with a canal/groove is seen with a subquadratic parietal above it and the temporal foramen, as indicated by Taverne, but between epiotic, parietal and supraoccipital there is also a matrix infill, which might hide a foramen or depression. Behind the epiotic a tiny triangular fragment perhaps, with a canal indicated is seen which might be a small supratemporal, and behind this is a large posttemporal (or perhaps extrascapular). The tiny subopercular is seen merely as an imprint on the inner side (not on the outside) of the opercular, which is large and D-shaped. The preopercular has striations on the narrow dorsal branch and near the corner, and a horizontal ledge hiding the slime canal, but the horizontal branch is not preserved and therefore of unknown length. Below the

ventral arm of the large cleithrum the coracoid is seen, perhaps with a large foramen indicated. There are about 70 vertebrae, half of these abdominal with a supraneural above each neural spine in front of the long, low dorsal fin opposed to a slightly shorter anal fin. Epineurals are seen in the anterior abdominal region, with no epipleurals, but very long, strong ribs. It cannot be said with certainty that hypural 3–5 are fused to each other and to ural 2, and it is difficult to see the free hypural 6, and to me parhypural and the hemal arch of preural 2 are probably autogenous – altogether a more primitive caudal fin than described by Taverne. The most remarkable feature, rightly reconstructed by Taverne, is the large path of very big and stumpy teeth in the bottom of the mouth, which must have been placed on the ‘tongue’.

My conviction is that, *Foreyichthys*, despite its more primitive caudal fin, is a little more osteoglossine-like than indicated by Taverne (who concluded that a monotypic family Foreyichthyidae is sister-group of all Osteoglossiformes [1998, fig. 22; Fig. 6], based on one synapomorphy the lack of basisphenoid, a feature

very difficult to confirm in a small, crushed, fossil braincase [and it might stay cartilaginous in that size of fish]). Of 13 features said certainly to link *Foreyichthys* to osteoglossiforms plus mormyriiforms (Taverne 1998, p. 143) I find only 3 of them (characters (ch.) 1, 3, 35) somewhat doubtful, and the same counts for 3–4 of the 13 ‘probable characters’ (ch. 41 [especially if Taverne’s boundary between the upper infraorbitals is correct], 45, 57 and perhaps 63), while character 44, the notch in endopterygoid, probably is in metapterygoid instead as mentioned above. On the other hand, three of the six osteoglossiform + mormyriiform characters said to be missing cannot easily be checked in *Foreyichthys* (ch. 103, 212, 216) and character 222 is a bit dubious being involved in a reversal. More advanced features found in *Foreyichthys* are large nasals meeting (ch. 226 – therefore reduced dermethmoid), a long, low body (ch. 232), high number of vertebrae, c. 70 (ch. 334), and – if Taverne is right, which I doubt – a caudal skeleton with fused ural 2 + hypural 3–5 (ch. 5), further loss of frontal expansion (ch. 237) and open (reopened in Taverne’s model) interorbital septum (ch. 238).



**Fig. 6.** An improved reconstruction of the skull of *Foreyichthys*, modified from Taverne 1998. BRSTG, branchiostegal ray; c.l.l., lateral line sensory canal; c.pop., preopercular sensory head canal; c.porb., postorbital sensory head canal; c.sorb., supraorbital sensory head canal; CLT, cleithrum; COR, coracoid; DBBR, dermobasibranchial; ENPT, endopterygoid (= endopterygoid); EPI, epiotic (= epioccipital); f.t., fosse temporale; FR, frontal; HCLT, hypercleithrum (= supracleithrum); IO, infraorbital; IORB, infraorbitals; LEP, lepidotrichia; LETH, lateral ethmoid; MX, maxilla; OP, opercular; OSPH, orbitosphenoid; PA, parietal; PM, premaxilla; POP, preopercular; PSPH, pleurosphenoid; PT, posttemporal; PTE, pterotic; Q, quadrate; SCA, scapula; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic (= autosphenotic); ST, supratemporal (= extrascapular). Arrow, ?basipterygoid process.

The latter two traits, both reversals, place *Foreyichthys* after *Brychaetus* at the base of *Pantodon* plus Osteoglossidae. Accordingly it should be placed in Taverne's implied classification (1998, figs 21, 22) as described below.

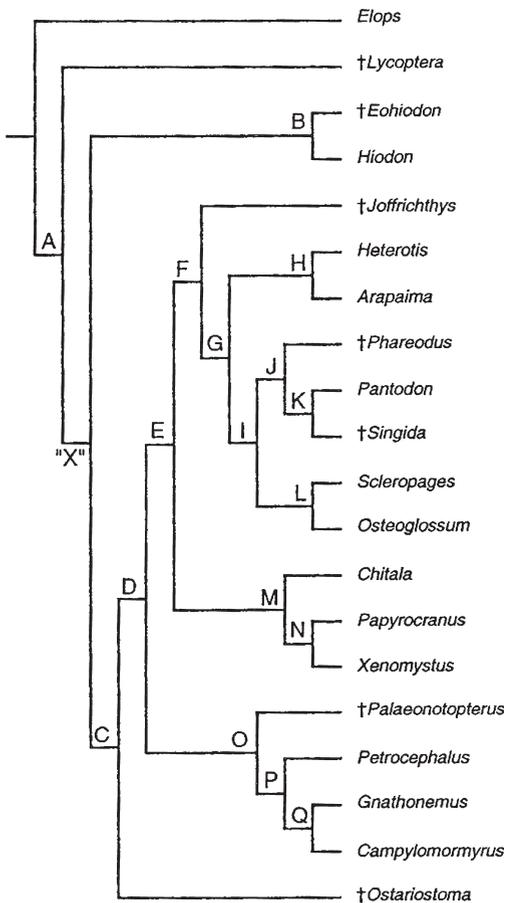
- Osteoglossomorpha
  - Hiodontiformes
    - †Ostariostomidae [*Ostariostoma*]
    - †Lycoperidae [2–3 gen.]
    - Hiodontidae [incl. 3–4 extinct genera]
    - †Huashiidae [2 gen.]
    - †*Kipalaichthys* [? – family unnecessary]
    - †*Singida* [ditto]
  - Mormyriiformes
    - †*Palaeonotopterus* [added in this study]
  - Notopteridae
  - Mormyroidei
    - Mormyridae
    - Gymnarchidae
  - Osteoglossiformes [†*Foreyichthys* more advanced, moved downwards]
    - †*Chanopsis* [?]
    - †‘*Phareodus*’ [= †*Phareoides*]
    - †*Phareodus*
    - Taxon A
      - †‘*Phareodus*’ [= †*Dapedoglossum*] mut.
    - †*Musperia* mut.
    - †*Phareodusichthys* mut.
    - Taxon B mut.
      - †*Monopteros*
    - Arapaimidae
      - †*Laeliichthys* [?]
      - †*Thrissopterus*
      - †*Nieerkunia*
      - †*Sinoglossus*
    - Arapaima*
    - Heterotinae
      - †*Joffrichthys* [= Taverne's ‘Paleocene Heterotina, Canada’]
      - †*Paradercites* [?]
      - Heterotis*
    - †*Opsithrissops*
    - †*Brychaetus* [2 species]
    - †*Foreyichthys* [placed here by me]
  - Pantodon[-tidae]
  - Osteoglossidae
    - Scleropages*
    - Osteoglossum*

† = extinct, ‘mut.’ means *mutabilis mutandis*, that those taxa can be interchanged due to lack of precise knowledge; [...] are author's changes or remarks, e.g. if the extinct taxa (†) have more than one species. This classification is strictly cladistic (phylogenetic) and without unnecessary absolute ranking, the convention

being that in a monophyletic group a taxon (fossil or recent) is sister-group to all groups listed (sequenced) below it at the same relative rank (here marked by identical indentation). If a taxon name is needed for mormyriiforms plus osteoglossiforms, those two groups should just be given ‘lower rank’ by extra indentation. This system could be made entirely non-Linnaean, if terminal taxa (species) were given only one name (e.g. the generic name without capitalizing – see Bonde & Westergaard 2004). If the very dubious taxa marked [?] (see also below) are removed from this classification, there remains very little inconsistency concerning stratigraphic age of the remaining taxa – and, therefore, there is no need for extremely long ‘ghost lineages’ (Norell 1992), apart from in Mormyriiformes, in which very few fossils are known (there is an Eocene–Oligocene notopterid and the mid Cretaceous *Palaeonotopterus* [perhaps a mormyrid?] and undescribed notopterids of the Early Cretaceous [Taverne, pers. comm. 2007]).

The third Bolca osteoglossomorph, the very slim *Thrissopterus*, has never been studied by me. It seems well described and analysed by Taverne (1998), who concludes that it is a primitive relative of his arapaimids (*Arapaima* plus *Heterotis*). It is slightly more advanced than mid Cretaceous *Laeliichthys* based on one synapomorphy shared with ‘higher’ arapaimids (reduced height of the body; and increase of vertebral number should be added – further critique in the phylogenetic discussion below). It has eight other apomorphies shared with arapaimids, three of which are reversals, one convergent, and one further, which *Thrissopterus* reverses together with three more reversed features. So its position is not so clear cut. The position of *Laeliichthys* is equally tenuous, being based on just the same features but one, although without the four last reversals, simply because it is so primitive. In 1996 I doubted its position as arapaimid, and I still do (see further sceptical remarks above). The only arapaimid stem-group member I have studied is the Eocene *Sinoglossus* (in prep.) and that may well be an arapaimid sharing the important fusion of antorbital and infraorbital I with such fishes, but, when checked against Li & Wilson's character lists from 1996a, and correcting their coding for wrong and ‘unlikely’ observations, it was discovered that it might equally be placed in osteoglossids, and is, therefore, of rather uncertain phylogenetic position.

Hilton's new cladistic analysis and classification (2003, fig. 7; Fig. 7) has notopterids as sister-group of osteoglossids (instead of mormyriids), and it comprises only few fossil taxa, but these, especially the osteoglossids, are placed in



**Fig. 7.** Hilton's cladogram (2003, fig 4B) (reproduced with permission of the author). A, Osteoglossomorpha; X, its crown group; C, Osteoglossiformes, its crown group; D, unnamed; F, Osteoglossidae, its crown group; G, unnamed; H, Heterotinae; I, Osteoglossinae (B, E, J–L, see p. 300).

very different relationships from those indicated by Taverne. *Joffrichthys* is sister-group of all other osteoglossids, and within these *Phareodus* and *Singida* are placed in osteoglossines related to *Pantodon* and *Osteoglossum* plus *Scleropages*. Further *Ostariostoma* is most closely-related to all crown-group osteoglossiformes, not to hiodontids. This analysis is based on 72 characters from 19 terminal taxa and one outgroup (*Elops*) with a consistency index of about 0.6, which is difficult to compare with Taverne's analysis. But the latter comprises 37 terminal taxa with three outgroups (Ichthyodectiforms, Elopomorphs and Clupeocephalans), and one can count about 50 parallelisms (= same number repeated) in his two trees (Figs 21, 22) based upon changes in about 300

different characters (somewhat difficult to count), presumably meaning 50 parallelisms out of 350 steps, which is about about 15%. To this should be added at least the same number of 'reversals' (even more difficult to count precisely, and mormyriiform and hiodontiform features not scrutinized in detail), adding up to at least 30–35% homoplasies in total. That is about same level as in Hilton's analysis (about 40%) – so the two may be 'equally good' in terms of parsimony.

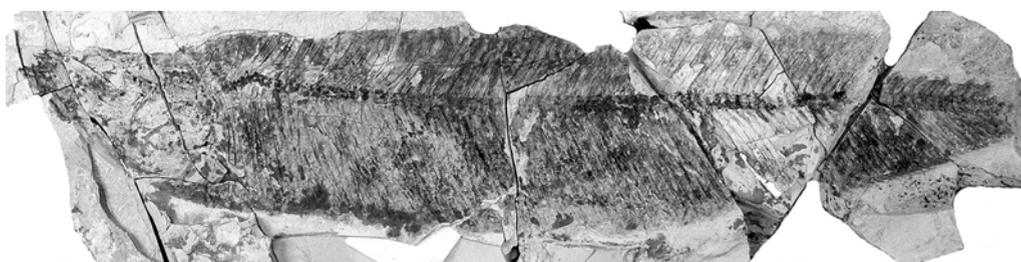
### Descriptions of Osteoglossomorphs

*Heterosteoglossum foreyi* n. gen. & sp.  
(Figs 8–14)

The generic name is a hybrid of *Heterotis* and *Osteoglossum*, alluding to its similarity to *Heterotis* in the shape of the short jaws and high mandible, the corresponding shape of the long ventral branch of the preopercular, the slight bend of the parasphenoid which may be toothless, the small pelvic fin and the position of the mesocoracoid, while the upturned mouth, the profile of the head, the very elongate body and the many vertebrae, the large pectoral fins, and to some degree the relation between dorsal and anal fins are more *Osteoglossum* like. The specific name is in honour of my friend and colleague Dr Peter Forey, Natural History Museum, London, UK, who for over three decades has enriched us with detailed descriptions and cladistic analyses of primitive teleosts, including osteoglossomorphs.

Diagnosis and phylogenetic relations are given below. (Diagnoses are here understood as [probable] autapomorphies and placed *after* their respective descriptions, because logically the diagnoses follow from the descriptions. The diagnoses are here not just abbreviated descriptions mixing plesiomorph and apomorph features. In fact it could well be argued that diagnoses are not possible before the phylogenetic analyses are finished, because from such analyses follows which features are accepted as autapomorphies).

*Holotype* MGUH 28.904 (DK 255). From laminated diatomite (Mo-clay) in the 'negative' ash series of the central mo-clay pit near the highest point, Stendal Høje, on the Isle of Fur, North Jutland, DK. Found *in situ* between the ash layers –13 and –17 in the wall of the quarry in 1997. Almost complete, lacking the posterior caudal region and fin and part of the dorsal fin, with less complete counterpart plate lacking more of the postero-dorsal body region. Over one metre long. Illustrated



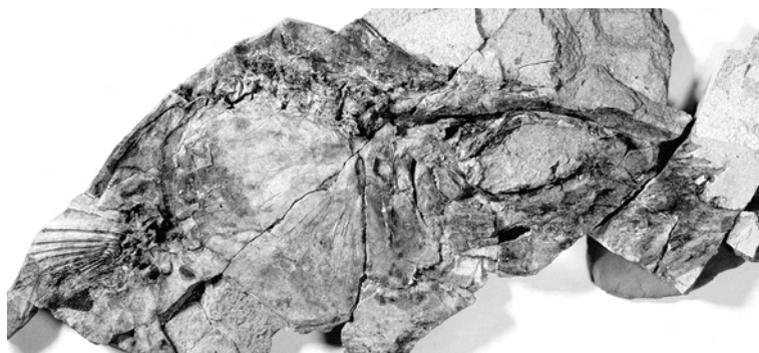
**Fig. 8.** *Heterosteoglossum foreyi*, holotype, MGUH 28.904 (DK 255), right side of the nearly complete fish. Imprint in diatomite, Mo-clay, between ash layers –17 and –13 in the lower part of Fur Formation. Mo-clay pit at Stendal Hills, Fur. Fish as preserved 89 cm.

also in Bonde *et al.* 2008. Age: Earliest Eocene, about 55 ma.

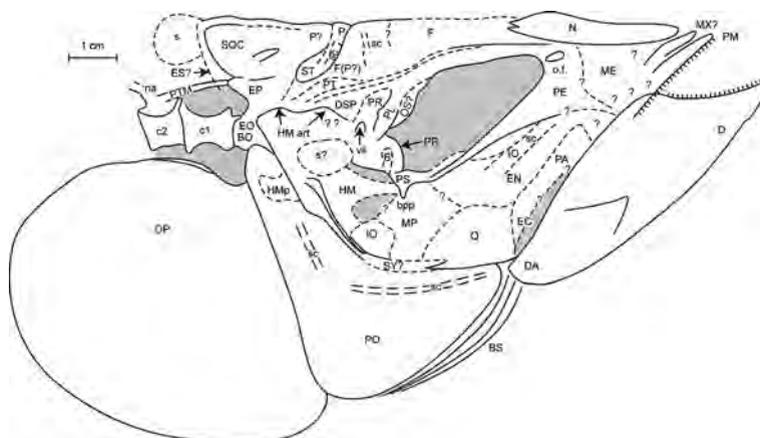
*Referred material.* The holotype is the only more or less complete specimen and comprises the only known skull. Two smaller caudal regions with the tail fin appear to be of the same species, NHM P.23946/47, (figured by Taverne [1998, fig. 17–18, Fig. 12] as an indeterminate osteoglossiform) found in 1938 by Walter Kühne around ash layer –18 in Skarrethage (northern) pit, northern Mors, N-Jutland, DK, and a corresponding specimen, also from the Skarrethage Quarry (southern pit at the time) found in the 1980s by Bent Søren Mikkelsen. Both caudal regions are with counterparts and preserved as imprints in laminated diatomite from the ‘negative’ ash series. They can be referred to this species entirely due to the reticulate scales (all other osteoglossiform fishes from the ash series have scales that are much less reticulated or not at all). Hundreds of isolated scales, rounded and oval, in the Mo-clay and cementstones as well as in Stolle Klint Clay are of this reticulate type, the largest nearly 5 cm high, many unregistered and several in the I. P. Andersen collection in

Geological Museum, Copenhagen, registered under 1954.469, some in the W. Kühne collections in GMC (registered under 1938.67) and four collected by him in NHML (one figured by Taverne 1998, fig. 16) and large numbers in Fur Museum and Molermuseet, Mors – this species must have been quite common despite the find of only the above three specimens of well articulated fossils. There is also a single scale from London Clay division B at Aveley, NHM P.65206, which on the label is referred to *Brychaetus*, but it seems to be fundamentally like scales of *Heterosteoglossum*, and not like those of the big skulls in the phosphatic concretions (derived from division D – see King 1981 and Beyer *et al.* 2001). Div. B (now Walton Mb.) is very low in the London Clay, just above division A comprising the Harwich ash layers, now the Harwich Fm, corresponding to part of ash series in the Mo-clay, so this scale is probably not much younger than the Danish specimens). Ages: *c.* 55.5 ma to *c.* 54 ma (or possibly slightly younger).

*Description.* The holotype (Figs 8–11) is an almost-complete fish, lacking part of the dorsal fin and the posterior caudal region with the caudal fin.



**Fig. 9.** *Heterosteoglossum foreyi* holotype, fragmentary counterpart to the skull preserved as a more detailed imprint than the main plate. Skull length *c.* 15 cm.



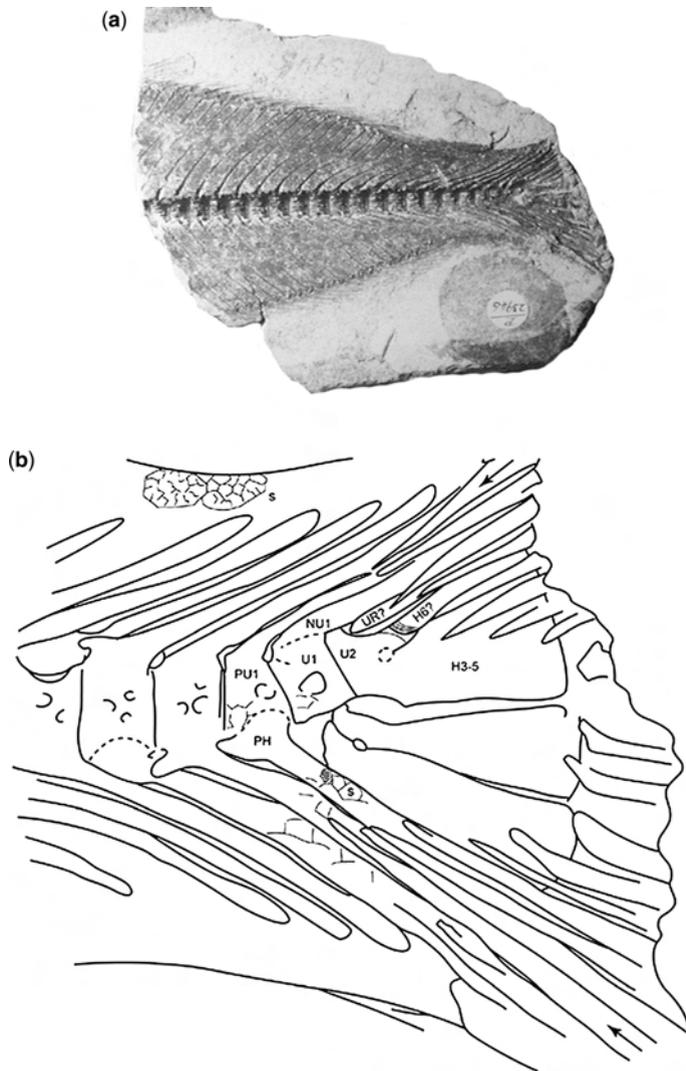
**Fig. 10.** *Heterosteoglossum foreyi*, reconstruction of the skull combined from both slabs, but based mainly on a camera lucida drawing of the left slab. Abbreviations used in the text and figures (excluding Figures 6 and 12): bpp, BP, basipterygoid process; c (1, 2), centra (no. 1, 2); na, neural arch; o.f., ophthalmic foramen; s, scale; sc, sensory canal; AN, angular; AR, articular; ASP, autosphenotic; B, basisphenoid; BH, basihyal; BO, basioccipital; BR, branchial element; BS, branchiostegal; D, dentary; DA, dermotic; DSP, dermosphenotic; EC, ectopterygoid; EN, endopterygoid; EO, exoccipital; EP, epioccipital; ES, 'extrascapular scale'; F, frontal; HM, hyomandibular; HMart, hyomandibular articulation; HMP, hyomandibular process; IO, infraorbital; L, left; ME, mesethmoid; MP, metapterygoid; MX?, maxilla?; N, nasal; OP, opercular; ORB, orbit; OS, orbitosphenoid; P, parietal; PA, palatine; PE, parietal; P-E, palato-ectopterygoid; PL, pleurosphenoid; PM, premaxilla; PO, preopercular; PR, prootic; PS, parasphenoid; PT, pterotic; PTM, posttemporal; Q, quadrate; R, right; RAR, right articular; SO, subopercular; SOC, supraoccipital crest; ST, supratemporal; SY, symplectic; V, vomer; VII, facialis foramen.

*Measurements.* The standard length is estimated about 100 cm, total length just over one metre. As it is preserved in several pieces the fossil is about 89 cm long, and missing probably c. 10 cm of the caudal vertebrae and hypurals, indicating about 100 cm standard length (which, with a caudal fin

estimated over 10 cm, gives a total length around 110 cm). The precaudal region is about 70 cm and, of this, c. 18 cm would be the head. Maximal body height is 16–17 cm, slightly more than the head (c. 15 cm). Orbit length 2.5–3 cm, postorbital skull c. 9 cm, and opercular width and height



**Fig. 11.** *Heterosteoglossum foreyi*, holotype, anterior region of the main plate. Skull length 15 cm.



**Fig. 12.** (a) *Heterosteoglossum foreyi*, NHM P. 23946, caudal region, right plate. Skarrebage Mo-clay Pit, North Mors, near ash layer -18; (b) NHM P. 23946, camera lucida drawing and interpretation of caudal base and scales (s), with the four last preural centra measuring c. 1 cm, H, hypural; NU, neural arch of ural vertebra; PH, parhypural; PU, preural centrum; U, ural centrum; UR, uroneural.

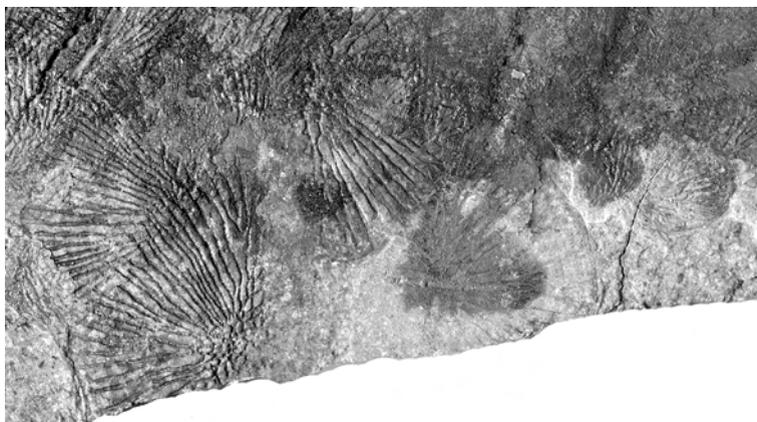
c. 5 × 7 cm. Scales are oval, a little higher than wide and from 1–1.5 cm high. Lower jaw length is c. 6.5 cm.

*Summary of meristics.* About 100 vertebrae (c. 87 preserved) of which c. 56 are abdominal.

*Fins:* Dorsal, about 35 rays, c. 16 cm base. Anal c. 45 rays, c. 22 cm base. Ventral, 7–8 rays, 4 cm long. Pectoral, 1 large plus 15, c. 10 cm long.

Caudal (from referred specimen), 9 + 9 principal rays.

*Skull (Figs 9–11).* As preserved the left side imprint seems a little more distinct than that of the right side. Little detail of the mesethmoid-vomer may be distinguished and no teeth be seen, and in some parts of the right preorbital region the surface with the imprint and a few millimetres of

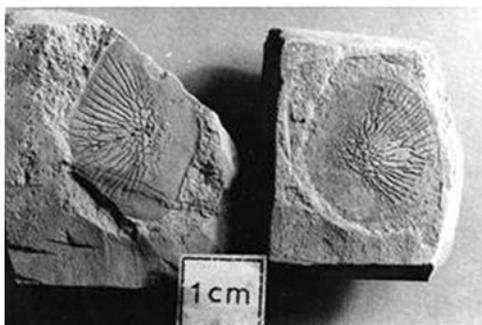


**Fig. 13.** *Heterosteoglossum foreyi*, holotype, scales from the ventral border. Scales c. 1.5 cm high.

sediment laminae have split off leaving no anatomical structure to be seen. The same has happened to part of the skull roof on the right side. The parethmoid is broad and obvious on the left side (almost destroyed on the right), but details are difficult to distinguish on its lateral face. Whether a dermal antorbital component is present, perhaps fused to the surface, seems uncertain as there is no trace of a sensory canal. There is a dorsally placed,

distinct, oval structure, which may represent the ophthalmic foramen. The basal part appears wide laterally and perhaps also at the medial end close to or at the parasphenoid, and to what degree a mesethmoid part is involved cannot be seen; that region appears low and smooth. Neither can the relation of the parethmoid to the infraorbitals be determined.

The parasphenoid is gently bent down in front, probably jointly with the (pre-)vomer, which however, may not be clearly distinguished (no teeth on either bone are seen). The parasphenoid is a rather straight and slim rod between the orbits, which are not closed by an interorbital septum or down-growths from the pleuro- and orbitosphenoids. The posterior, ascending part of parasphenoid, although impossible to outline in detail, bends up about  $135^\circ$ , and just above the bending there is a deep imprint of what has to be the basiptyergoid process pointing lateral and a little downwards. In the medium plane between the anterior edge of the ascending processes and/or that of the prootic is seen a subrectangular and smooth imprint of what most likely is a small vertical basisphenoid. This configuration would imply a rather high posterior myodome, and perhaps traces of the prootic bridge above it are visible. Above this ascending process is seen the lateral surface of the prootic with a dorsal depression, which is probably the foramen for the hyoid branch of the facialis. A little behind this the surface appears reticulate as if it (and possibly the anterior head of hyomandibular) were covered by a scale (or the bone surface has cracked?). Above the facialis foramen is a strong lateral process, which must be the dermosphenotic. In front of the prootic it is lined by pleurosphenoid, which has the anterior edge set off, or this part might be the orbitosphenoid in a very



**Fig. 14.** Two isolated scales of *Heterosteoglossum*, inside imprints in diatomite, from W. Kühne collection MGUH 1938.67, and one scale, external face, in cementstone MGUH 1935.32 (scale in mm).

posterior position – if not, there seem to be no obvious trace of an ossified orbitosphenoid, neither in the dorsal nor the anterior part of the orbit. Dorsally the orbit is covered by a long frontal of which the lateral edge gives a deep near perpendicular depression into the diatomite without showing any evidence of a supraorbital. A large and long nasal is pressed up in vertical position anterior to the frontal, and has a zig-zag suture against frontal rather than a straight one. Broad anterior frontals seem unlikely.

Below the orbit is a large and smooth (dorsal) surface of the endopterygoid adjacent to the parasphenoid, and darkened by the colour from the eye ball. In the anterior part of the endopterygoid a patch with small teeth is indicated on the right counterpart plate. Imprinted into its surface a distinct, squarish depression apparently is continued backwards with sub parallel edges, widening a little, then tapering off, and it is difficult to interpret, although it may be one of hypo- plus ceratohyals displaced into a very high position (see branchiostegals below). The remaining palate is difficult to distinguish, apart from the quadrate of the right side with its posterior process forming an angle about 100° with its anterior edge, along which the ectopterygoid area is weakly indicated and probably in continuation forward with the palatine, but no teeth are visible. A symplectic cannot be safely outlined. While the border between the metapterygoid and quadrate is vaguely distinguishable, the dorsal and anterior limits of the metapterygoid is very uncertain. The infraorbitals should cover this palatal region, but cannot be distinguished unless a rather straight groove on the right plate is the upper edge with the canal from the anterior of these bones, which in that case cannot have been very deep.

Above the sphenotic a long lateral edge of the pterotic is seen, and medial to that the broader posterior part of the frontal showing traces of the supraorbital sensory canal, perhaps with a branch toward the midline (unless this part is really the fairly long parietal [?] reaching the midline). Behind this is a nearly oval area apparently with an arched sensory canal also reaching the midline. This element most likely is a flat supratemporal, perhaps with the canal continued at the posterior edge of a small parietal (so the size of parietal is uncertain). The pterotic butts against the epi- and exoccipital area at its posterior end, and the former has a strong posterolateral point. Above that is a very flat, vertical area close to the dorsal outline of the skull, presumably a quite high supraoccipital crest, and in the region between this crest and epioccipital are impressions of what is most likely the dorsal branch of the posttemporal. The exoccipital area meets or combines with the

basioccipital to form the articulation for the first vertebral centrum, and the latter dorsally carries a forward pointing process reaching the exoccipital. Finally one should note that behind and above the supraoccipital crest is a narrow rim of what may be a large element like a huge, lateral, extrascapular scale covering most of the area behind the skull roof as in *Osteoglossum*, *Heterotis* and *Arapaima* figured by Taverne (1977).

On the left side in the postorbital region it is possible by a fine distinction between smooth and ornamented surfaces (pitted imprints) to differentiate between endo- and exoskeletal bones. In this way the smooth, long, triangular process on the anterior edge of hyomandibular can be seen pointing towards and just below the basipterygoid process on both plates. With a regular ornament of tiny tubercles a part of the large infraorbital behind the eye is vaguely outlined at a level slightly deeper, that is, lateral to the smooth process. While the anterior edge of the ventral branch of the hyomandibular is a strong deep imprint, the dorsal head is missing on the left plate and is only vaguely indicated by the shape of the articular areas of the pterotic behind and sphenotic (and pterotic?) in front. But the divided head is well indicated on the right plate just behind the deep print of dermosphenotic, and the opercular process is seen as a distinct imprint in the surface of the dorsal branch of the preopercular. This branch is rather narrow and smooth and continues ventrally bending slightly backwards along the opercular, then turning forward by a rounded posteroventral corner (seen best on left side), which has some few and weak ridges converging away from it indicating direction of growth, as also occur on the substantial and rather long horizontal branch, that reaches forward to the lower jaw. It seems as if the openings of the sensory canal are pushed back from the anterior edge by a broad, smooth bone lamella. The opercular is large, measuring c. 7 cm in height, and it is 5 cm wide and nearly oval, but with an almost straight anterior edge and fine ridges on the surface radiating from the articular area, again in the direction of growth. Sub- and interoperculars are not visible, and the region below the opercular most likely is occupied by the smooth surfaces of the anterior parts of cleithrum and coracoid (below).

On both sides the lower jaws are preserved with the articular region far posterior and a very short retroarticular process, and perhaps the outline of a rather short dermarticular (here used as a term for the combined articular, retroarticular and angular, which cannot be seen as separate elements in these Eocene fishes – but cf. *Furichthys* below). The two posterior pores for the mandibular canal can probably be seen as well as one pore in the

anterior half of the dentary. The lower jaw length is just above 6 cm, and the height of the posterior region is 2 cm and it is slightly higher in front. The anterior edge is strongly curved downwards and then forwards (in a very clupeid-like way) to a low and pointed symphyseal region, that is split open, and along the edge it carries small, pointed teeth in a single row. On the left side a shallow, elongate premaxillary is seen pointing forward with small teeth in a row on its ventral edge, and no dorsal ascending process to be seen. Just above it another slim bone points forward, presumably the anterior process of the maxilla, while the distal end of this bone is impossible to outline and no teeth are seen, perhaps the maxilla was quite small and more or less covered from the lateral side.

Imprints on the surface of the ventral part of the preopercular of a few long and slender branchiostegals perhaps make the interpretation of the very high position of the ceratohyals (above) less likely. Little is seen of the tongue and branchial skeleton, namely two elongate, near horizontal fragments just below the posterior orbit on the left plate; they must be epibranchials, and a small oval tooth plate seems attached to these elements.

*Girdles and fins.* There is a strong cleithrum of which the broad ventral branch can vaguely be seen on the right counterpart plate below the opercular that covers its dorsal edge as well as the anterior edge of its broad dorsal branch, which does not quite reach the level of the vertebral column. The dorsal end is overlapped by an elongate supracleithrum, apparently with a sensory canal indicated. The dorsal part of the bone is difficult to outline, probably being partly hidden by the opercular and partly obscured by the vertebrae. The posterior part of a strong, broad coracoid is seen on the left plate showing a distinct, oval fenestra near the posterior border where it meets the small, triangular scapula along the edge where its round foramen appears to be placed. At the anterodorsal part of the scapula is a deep and distinct, ovoid impression near the anterior edge of cleithrum; it must be the mesocoracoid arch in an anterior position as in *Heterotis* (Greenwood & Thomson 1960, fig. 2; Taverne 1977, fig. 111). Four radials seem mainly supported by the scapula, and they articulate against the strongly downward-bent bases of the pectoral fin rays. The anterior or upper fin ray is very large with the shaft *c.* 6 mm wide, unbranched but distally segmented, the second ray is not quite as big and this and the remaining *c.* 14 rays are branched and decrease in size. The length of the fin is *c.* 10 cm.

Although the pelvic (ventral) fin is not very big the pelvis is substantial, triangular-shaped, about 4 cm long and quite high, *c.* 2.5 cm near the

posterior border where there is a strong ridge from the fin articulation reaching the dorso-lateral corner. Furthermore there is a flat, smooth structure 'blurring' two sets of rib-imprints distally just behind the pelvis; probably this indicates an extensive, near vertical postpelvic process 2 cm long and 1.5 cm high. The pelvic fin is rather small for such a very long fish, the longest ray is only *c.* 4 cm long, and there are 7–8 fin rays, the lateral one segmented and unbranched and much stronger than the other branched rays, of which the internal one is branching nearly from the base. The fin articulation is placed below the 44th vertebral centrum.

The anal fin begins below centrum number 63 and has the anterior radial (pterygiophore) touching the hemal spine of number 57. There are *c.* 33 segmented rays preserved, but with 6–7 rays missing in front, and probably a few are missing at the posterior end. Only 21 rays are preserved in the referred specimen P. 23946 (Taverne 1998, fig. 17), but the two referred specimens show that the last anal ray is below preural centrum 7, and the posterior dorsal ray above preural 8. So the type must have had nearly 45 anal rays (and in front on first radial most likely were further 2–3 tiny unsegmented rays). The holotype shows the dorsal fin beginning above centrum no. 71, and with the strong first radial pointing to the neural spine of no. 66, which is the first one without a supraneural connected, so there are 65 of these. Only 3 tiny unsegmented rays and *ca.* seven longer rays are preserved as the unsegmented bases of *c.* 2 cm length (indicating rays about twice as long). A few radials are preserved above centrum no. 83, and combining P. 23946 with the estimated lack of about 10 vertebrae in the holotype, indicates that the dorsal fin probably had about 35 rays (26 are preserved in P. 23946). So both fins have a rather high number of rays compared to most osteoglossiforms (but there are more in *Osteoglossum*), but the fins are rather short and retreated in relation to the length of the fish because of the extended abdominal region.

*Axial skeleton (Figs 8, 12a, b).* The anterior vertebra articulates with the basioccipital and apparently has dorsal contact (zygapophyses?) on the exoccipital. The anterior centra are *c.* 1 cm long and almost as high, and in total about 87 vertebrae are preserved, and 10–12 posterior caudal vertebrae seem to be missing. So a total count of *c.* 100 vertebrae is most likely with *c.* 56 being abdominal, which means a very long abdominal region. The centra are 'primitive' with many thin ridges as horizontal, lateral lamellae and not very deep excavations (Fig. 12a). The ribs are very long and strong reaching the ventral border, and the first pair appears to articulate on the second centrum itself, while the following ribs are attached to

parapophyses at the anterior end of the centra. There are 'bunches' of epineurals at the anterior 31 vertebrae, 6–8 cm long and starting from the first vertebra, probably its neural arch, which is difficult to see, however. There are no epineurals in the caudal region, and no epipleurals are ossified. There are thin supraneurals with a slight backward bend in the dorsal end and approaching to the first 65 neural spines. Epineurals did not reach below the dorsal fin, and accordingly none of these bones can be seen on the referred caudal regions (Fig. 12; Taverne 1998, fig. 17).

The posterior caudal vertebrae are only preserved on the two referred caudal regions, P. 23946 (Fig. 12a) has 22 centra plus the separate second ural (U2; Fig. 12b), its counterpart P. 23947 has a few more vertebrae, but in very poor state of preservation, and the fossil from Mølmuseet has only about 14 vertebrae. Taverne's description (1998, fig. 17–18) is mostly confirmed (Fig. 12b): a separate second ural centrum (U2) is fused to a plate of 'fused hypurals 3–5' (H 3–5, if interpreted as by Taverne); the dorsal part of this element (H6?) appears separate, but the proximal 'dividing line' is perhaps only caused by the edge of a scale. But if this is interpreted as by Hilton (2003, 80) the two probable bones would be H3 and H4 (with no 'fusions', but U2 + H3), and a pattern like *Pantodon* (fig. also in Greenwood 1967). The narrow element above it in the first case could be a separate uroneural (UR? – or, as it seems unpaired, an eural; less likely according to Hilton [2003, 74–77]). The broad H1 and H2 are separate, the parhypural with a strong proximal head is autogenous like the hemal arches with long spines in front of it. The neural arches with long spines are fused to the centrum of a separate UI (?) and to the posterior preural centra (PU1, etc.). Arrows (Fig. 12b) are pointing to the fin rays likely to be the outer, unbranched principal rays giving a count of 18 principal rays (9 + 9). Branched elements are not actually preserved, and the shape of the fin is unknown.

*Scales (Figs 12–14).* The scales of the holotype are very characteristic and of a type found very often as isolated scales in both Mo-clay (Fig. 14) and Stolle Klint Clay in many different sizes from 0.5 to c. 5 cm in diameter. Those of the holotype (Fig. 13) vary from less than 1–1.5 cm in height, and they are rounded or oval (height greater than width/length); accordingly 5 cm scales indicate a much bigger fish, perhaps over three metres long. At the nucleus (centre) the scales are clearly reticulate as in most living osteoglossiforms, that is divided into small irregular and angular squamules by narrow, unossified fissures lined on the inner surface of the scale by thin ridges, so that each

squamule forms an angular dish with the edges turned in. Further there are tiny pores through the squamules ending on the inside surrounded by a small hill or tubercle on an otherwise smooth surface apart from the very fine concentric circuli (growth lines) crossing over the borders of the squamules. When the scale is just a few millimetres wide (<5 mm) the typical reticulation tends to disappear at the posterior, free margin (but the pores remain for a few millimetres), while the pattern of unossified zones changes to become irregular radial at the anterior (basal or covered) end. The external surface of the scales shows a very fine tuberculation and very fine circuli, while the same pattern of unossified zones show up as very narrow grooves. When preserved as imprints in Mo-clay the external surface has fine pits and a pattern of very narrow ridges, while the inner surface has a central area with small pits and reticulate grooves transforming into irregular fissures with very fine growth lines crossing them. The posterior (apical or free) area is covered by ornamentation of very fine tuberculation and only little reticulation if any.

On the referred specimens a few small scales (c. 3 mm long) are very evidently reticulate with very fine circuli. Two such scales are clearly seen above the posterior preural vertebrae at the dorsal margin of P. 23946 (Fig. 12b), and furthermore such reticulation is clearly visible imprinted onto the surface of many of the bones (in Fig. 12b only shown on parhypural). So I cannot at all agree with Taverne (1998, p. 101) that the scales are poorly preserved and show no reticulation. These small, reticulate scales are the sole reason for referring the two caudal specimens to the same species as the holotype, because the small scales correspond to the central fields of the larger scales – and no other form of osteoglossiform in the Mo-clay shows this typical reticulation of the scales. The closest match today would be *Pantodon* and mor-myrids as described by Hilton (2003, fig. 39) although not identical.

*Diagnosis.* Characteristics of the new taxon *Heterosteoglossum foreyi*, that is its autapomorphies, are the body proportions with c. 100 vertebrae and a very long abdominal region (far distal retreat of the anal and dorsal fins), the scales with central reticulation transformed through growth to a radiating pattern in the anterior field and tending to disappear in the posterior, free area. Probably also the large number of pectoral rays and possibly the very wide parethmoid (unless a feature of distortion?), and the bending down of the anterior parasphenoid. The gently angled preopercular with fine ridges, and probably the extremely short retroarticular process are also diagnostic features, as are the tiny teeth in the

jaws and the shape of the lower jaw (somewhat like *Heterotis*).

*Relationships.* The phylogenetic relations are discussed below. Features showing osteoglossiform affinities are the large first pectoral ray, the long ribs without epipleurals, and the large number of vertebrae with only epineurals. Likewise the reticulations of the juvenile scales, and remnants of dividing the scale into squamules with fine external tuberculation, and pores through to the inside ending on small hills. Further the basipterygoid process and the anterior hyomandibular process, as well as the possibly fused palato-ectopterygoid, and the large opercular and preopercular are typical for osteoglossiforms.

*Brief remarks on way of life.* *Heterosteoglossum* is a large fish, the holotype is over one metre long, and isolated scales indicate size over three metres with diminutive teeth. Today some osteoglossiforms take prey (fish, amphibians, insects and other invertebrates) by jumping out of the water after it (*Osteoglossum*, the arawana captures amphibians and insects both in and above the water, *Pantodon* perhaps also has similar behaviour). Such food objects must have been also targets for four of the Danish extinct species that had large teeth. Extant *Heterotis* with small teeth in the jaws and with short and high lower jaw is a plankton feeders with a suprabranchial organ forming a spiral over the slit between fourth and fifth branchial arches (see Taverne 1977, fig. 110). Here slime and plankton is concentrated before being swallowed. There is no trace of the posterior branchial arches preserved in *Heterosteoglossum*, so a similar way of feeding would be unsupported guesswork. On the other hand, this type of jaws and teeth found in *Heterosteoglossum* are hardly those of a piscivorous fish, and the gape of the mouth seems rather big. With the extremely rich plankton from an upwelling zone (Bonde 1979, 1996) as the source of the diatomite, life as an oceanic plankton feeder is a distinct possibility (perhaps supported by its very large size).

*Furichthys fieldsoei* n. gen. & sp. (Figs 15–19)

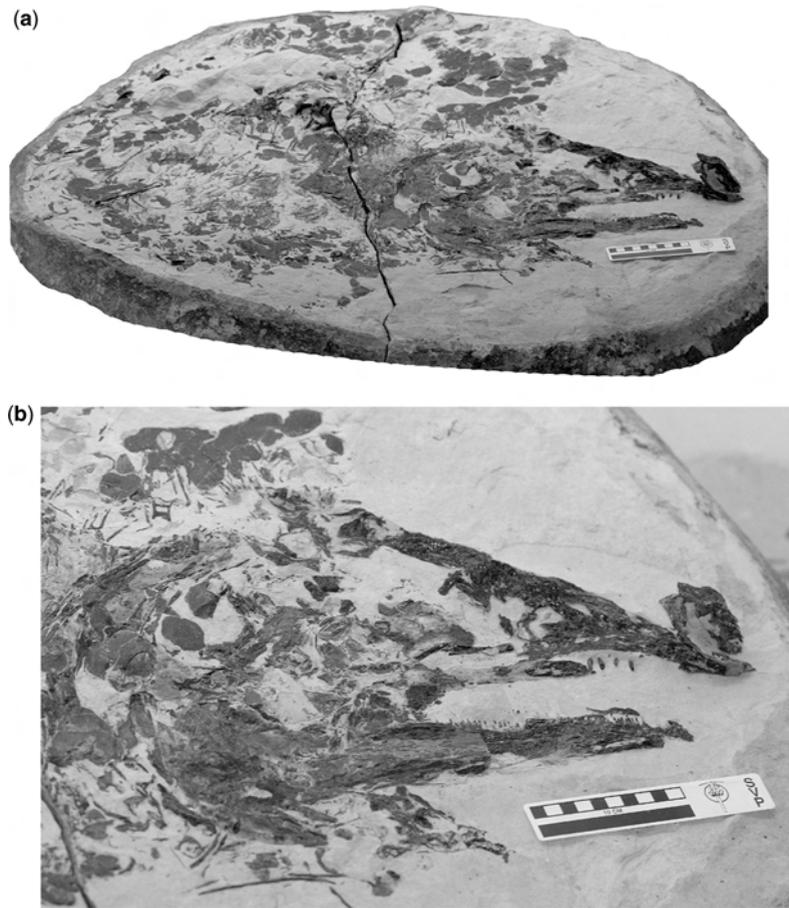
Named for the island Fur and the late Erik Fjeldsø Christensen (deceased 1996), palaeobotanist, once director of Fur Museum, collector of the larger part of the holotype and later the referred specimen; he traced the German finder of the holotype and borrowed it for the museum (that later bought this specimen through funding by 'Statens Museums-nævn'); he was a staunch supporter of the concept 'danekræ' (Bonde *et al.* 2008: 7, 204) since the 1980s (see note, p. 305).

*Holotype FUM-N 1427.* The large fish, with skull and scattered fragments of the abdominal region, found by a German collector in the 1980s on the beach at Knudeklint, Fur. It is preserved with counterpart in a cementstone containing ash layer –33 in Fur Museum. Referred specimen, FUM-N 1428, also in Fur Museum, posterior skull and anterior abdominal region in 'striped cementstone' including the ash layers around –25, at Stolle Klint, Fur; no counterpart.

*Age.* Earliest Eocene, about 55 ma. Illustrated also by Bonde (1987), Christensen (1994), Bonde *et al.* (2008: 7).

*Description.* The holotype is preserved in a large cementstone c. 85 cm in diameter (Fig. 15). It exposes almost all the bones of the flattened skull as exposed in the fossil, which means that in general the surfaces of the bones are not visible, making their precise identification difficult and outlines sometimes impossible to indicate with any certainty. The entire opercular region and pectoral girdle is not visible, some of it is hidden in the matrix. The better part of the skull with most of the thickness of the braincase is in the smaller right side counterpart of the stone (Figs 16–17). There are scattered vertebral centra, ribs and scales, but no indication of the shape of the body. The referred specimen is in a 72 cm long block, cut in two a little behind the pectoral girdle (and with a third small fragment). It shows the postorbital part of the skull, the pectoral region and part of the abdominal region with c. 35 vertebrae. Although incomplete both at the dorsal and ventral line the fossil confers the distinct impression of a rather high-bodied fish with a gentle arch to the dorsal profile and a deeper ventral profile (perhaps somewhat like *Phareodus*, but with a more horizontal skull roof and pointed snout). Its vertebrae indicate a fish that is probably about the same size as the type specimen, and it is estimated that the two fishes were between 1.5 and 2 m long.

*Skull (Figs 15b–18).* Lower jaw is c. 25 cm long and the skull roof c. 25 cm long (length of skull and braincase is difficult to estimate, but perhaps 30–35 cm long plus 7–8 cm opercular), height of the skull c. 25 cm (Figs 15–16). As preserved the braincase is about 5–6 cm wide, and although crushed by the sediment, it is difficult to escape the impression that the skull roof has been comparatively narrow, which seems somewhat at odds with the very heavy premaxillary (see below). As the braincase is split right through the skull roof, the sutures cannot be seen and the precise shape of the bones remains uncertain. There is, however, a



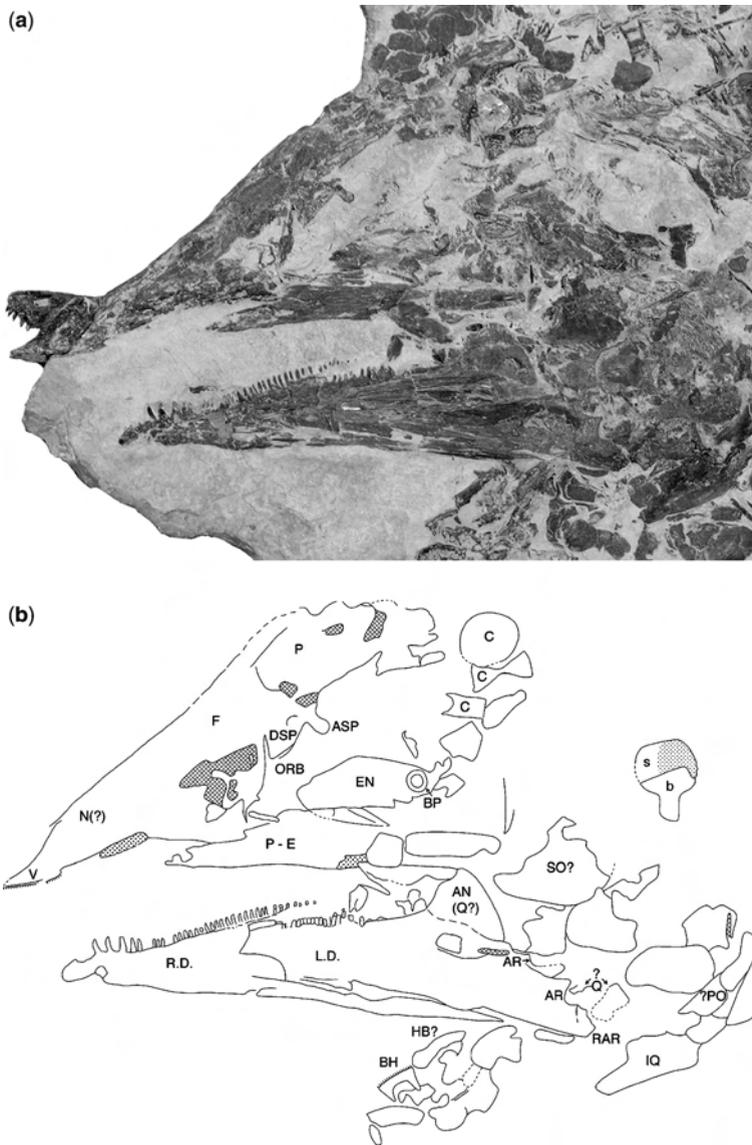
**Fig. 15.** (a) *Furichthys fjeldsoei*, holotype, Fur Museum, main block of cementstone c. 85 cm wide with left side; (b) *Furichthys fjeldsoei*, holotype, left side skull region with four strong teeth from left maxilla, and right premaxilla in original position. Scale = 10 cm.

strong ethmoid-vomer complex (Figs 15b–17) with a large path of tiny teeth on the vomer forming an elongate, oval tooth field (Fig. 17a, c). The extent of mes- and parthmoid is not obvious. Borders between nasal, frontal and parietal elements cannot be determined. Dermosphenotic and auto-sphenotic are indicated above the orbit, which is of very moderate size, and the remaining elements of the braincase cannot be outlined.

From the palate only the quadrate and the metapterygoid are partly-preserved. The parasphenoid may be represented by a toothpath of tiny teeth behind and a little above the vomer, but otherwise cannot be seen. A large part of endopterygoid is preserved (no visible teeth), and there is an excavation for the basiptyergoid process, which is itself cut

through. Much of the large palato-ectopterygoid is preserved with a part of its dentition of fine teeth seen in the posterior end. It seems uncertain where the quadrate is preserved. Some fragments of one may be seen on the right plate near the articular surface of the left jaw. On the same plate a triangular bone pressed on top of the lower jaw in front of the right articular may be the right quadrate – or perhaps rather a high ‘coronoid process’ of the angular (Fig. 16b, Q?).

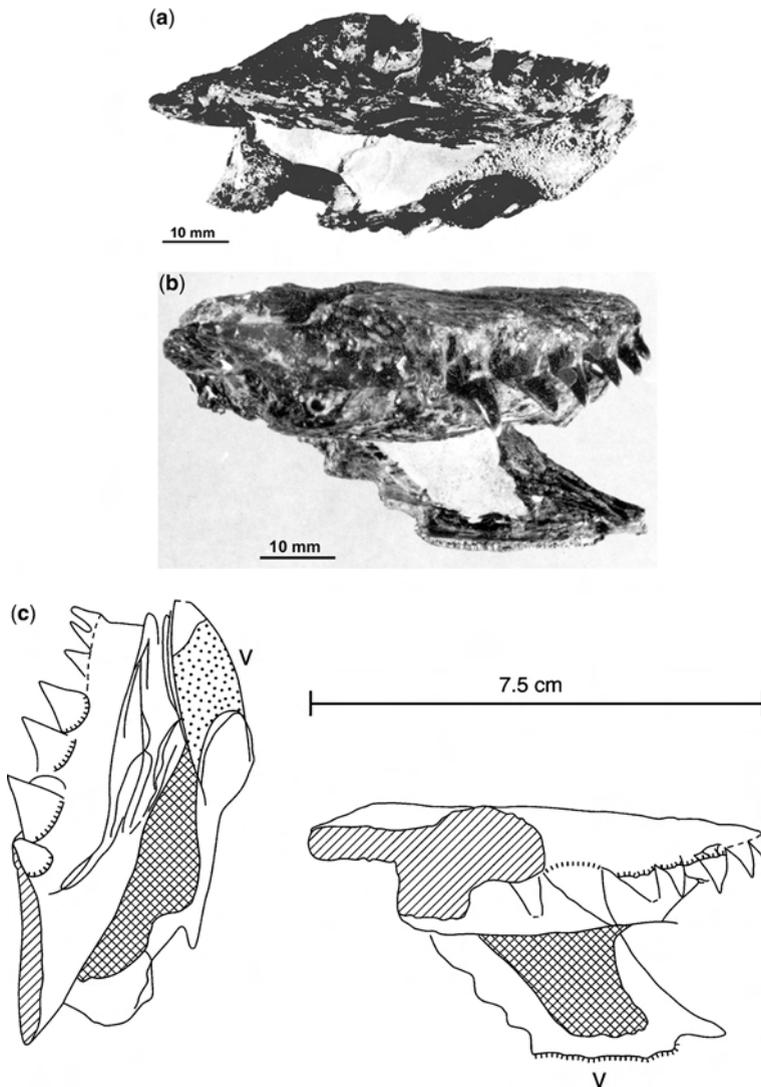
Of the upper jaw only part of the very strong right premaxilla is seen, it was acid prepared after being chiselled out of the block (Fig. 17), and its distal end has eroded away, so there must have been a few more teeth than preserved now (actually this heavy, black, eroded premaxilla was the bone



**Fig. 16.** (a) *Furichthys feldsoei*, holotype, Fur Museum, skull region, right side; (b) interpretative drawing of skull, right side. Lower jaw *c.* 25 cm long. HB?, perhaps hypobranchial; IO, interopercular; b, bone fragment; other abbreviations p. 268.

spotted by the collector on the surface of the stone). The proximal end is stuck into the large left plate, but not much can be hidden, so it is remarkable that this very heavy bone shows no traces of an ascending process. The thick body of the bone as preserved leans on a sloping surface of a strong ethmoid ossification, which appears fused to the vomer. The thickness of premaxillary as seen from above is near 4 cm, and the width of the dentigerous edge is 2 cm, about the same as the height

of the bone, which is not compact, but hollow. The two premaxillae must have formed a very strong 'rostrum' on the snout supported by a heavily ossified ethmoid, and here preserved a few centimeters above its natural position in relation to the vomer (Fig. 17). The premaxilla has a very heavy dentition with four smaller teeth in front (one [or more] still in the large block) increasing in size backwards, then follow three much stronger teeth, the largest *c.* 13 mm high and 9 mm wide at the base, and the



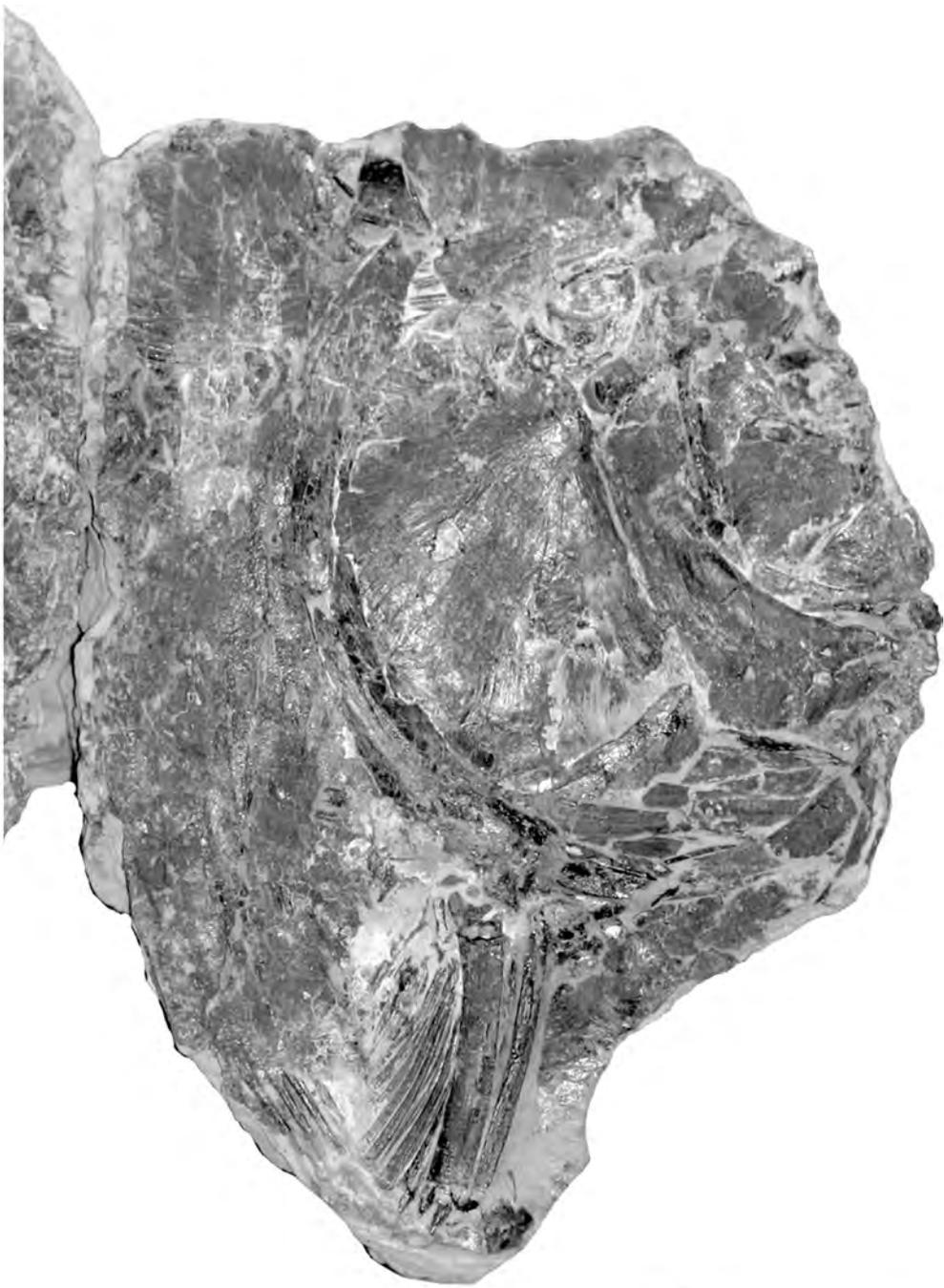
**Fig. 17.** (a) *Furichthys fjeldsoei*, holotype, right premaxilla and mesethmo-vomer ventral sight with vomerian tooth plate; (b) same, seen from right side; (c) interpretation of (a, b). V, vomerian toothplate; diagonal shading indicates sectioned bone; cross-hatching, matrix.

last to be seen is smaller again, but a few more (2–3?) are likely to have been lost by erosion. These teeth are robust, conical with smooth surface and indication of a cap-like point. They are carried on low bony pedicles. The tooth row is almost straight and its angle with the median plane (as defined by the elongate vomerian tooth field) is near 45°, and the incomplete premaxillary extends c. 4 cm lateral from the median plane. This means that when this right premaxillary-vomer complex is fitted onto the left plate and its vomer at the same time touches the right plate on its lateral face, the

angle at the symphysis would be about 90° making the snout quite broad, at least 10 cm at the posterior end of the bone, not narrow as expected from the skull roof. Four strong conical teeth of the left maxilla are visible, smaller and slimmer than the big premaxillary teeth, but nothing of the hidden bone itself can be seen as prepared at present.

Both branches of the lower jaw (Figs 15–16) are well-preserved and some of the lateral surface of the right dentary is seen. The bone appears quite thin and narrow, and the lower jaws rather fit the

(a)



100 mm

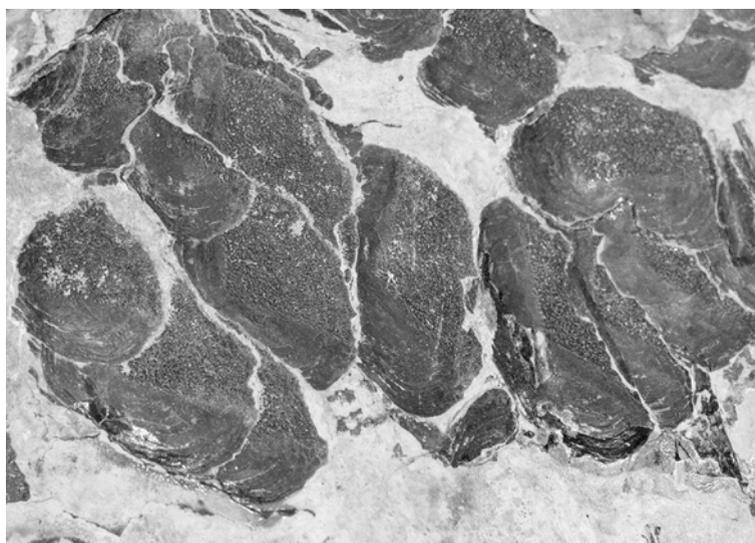
**Fig. 18.** (a) *Furichthys fjeldsoei*, referred specimen, Fur Museum, in 'striped cementstone', right lateral face of entire specimen; (b) interpretation (made from transparent paper on top of specimen) of (a) anterior part, opercular and pectoral region. CL, cleithrum; CO, coracoid; HY, hyoid arch; P1, first pectoral fin ray; SC, scapula; SCL, supracleithrum; other abbreviations p. 268.



Fig. 18. (b) (Continued).

picture of a narrow snout. The dentaries appear to have the symphyseal region preserved in front, and they are long, *c.* 25 cm, and low, *c.* 5 cm high, with numerous teeth in one row (about 40

teeth 7–8 mm high in the middle of the jaw, slightly decreasing in size backwards). All of these are sub-cylindrical with a distinct pointed 'cap', and they are attached directly to the jawbone without



**Fig. 19.** *Furichthys fjeldsoei*, holotype, scales, anterior left. The larger scales *c.* 4 cm high.

pedicles. There is a strong retroarticular process and a 'half-open' suture from the bottom of the posterior part of the articulation, indicating that the bone is only partly fused into the dermarterial. The 'glenoid' is directed backwards and upwards, curving nearly 180°. On both plates it is evident that the lower jaws are preserved in a position, where they cannot reach the tip of the upper jaw. They have to be moved forward *c.* 10 cm to close the gape.

Part of the tongue can be seen below the lower jaw, but which bones are represented seems very uncertain. One of them with many small teeth on its dorsal surface perhaps is a basihyal. A few thin bones below the articular end of the lower jaw presumably are branchiostegals. Of the cheek only few fragments are visible, probably part of a large rounded infraorbital, and perhaps fragments of preopercular and interopercular. Most of the bones of the right side could still be hidden in the stone, however, and part of a large bone has been prepared free. Several detached vertebral centra are scattered in the region behind the skull. They are *c.* 25 mm high and very short, only *c.* 13 mm long. Some rib fragments are seen, but none of the postcranial bones are in articulation.

The postorbital region is well exposed on the referred specimen, it has been cut just in front of the quadrate articulation and a little behind the eye, and apparently (nearly) all elements preserved are seen from the lateral, right side (Fig. 18a, b; the entire thickness of the fish being hidden in the stone). Part of the prootic is visible with some foramina difficult to interpret.

Above it the dermosphenotic region is not well delimited, but with the anterior articulation for hyomandibular, and the posterior part of the parietal (P – or frontal) grading into the pterotic, which forms the posterior hyomandibular articulation. Above the pterotic is a very large bone, probably an extrascapular which is incomplete towards the dorsal midline. A small narrow fragment on its surface might be part of a posttemporal, which is close to the upper end of a long rather narrow supracleithrum.

The hyomandibula is well exposed with a broad two headed articular end, a triangular flat process meeting the metapterygoid, a large process articulating against the opercular and a strong shaft supporting the upper end of preopercular. The symplectic is a rather small and narrow bone wedged into the quadrate. The preopercular is a strong rather narrow and vertical bone, 11 cm high, 2.5 cm wide, with a short ventral branch carrying a horizontal flange over the sensory canal, and apparently with a small, triangular process below the end of the hyomandibular shaft. There is a large, almost semi-rectangular opercular bone, 8 cm wide, with the subopercular appearing along the ventral border and not very reduced. Below the pre- and subopercular several ventral elements of the branchial arches are visible, probably with the broad and most ventral ones being ceratohyals (hyoid arch?), and there are fragments of some branchiostegals.

*Pectoral girdle and fin.* The long supracleithrum overlaps the dorsal and equally narrow end of the

cleithrum. This increases in width towards the scapular and coracoid region, which is not well exposed, and the ventral part of cleithrum is eroded away. Between the scapular articulation and the large anterior pectoral ray, fragments of the radials are seen. The coracoid may show traces of a foramen near its posterior end, but only a little of the bone is visible. The first pectoral ray is very strong and broad, *c.* 13 mm wide, and its two halves seem slightly separated. Behind it are seen 10–12 much thinner rays, but none of the rays are preserved in their full length.

*Axial skeleton* (Fig. 18). Between opercular, hyomandibular and pterotic in the referred specimen are seen the anterior three or probably four vertebral centra slightly disarticulated (and a scale; Fig. 18b), and behind the supracleithrum another three to four centra are exposed between the scales of the anterior block. The second part of the block with part of the abdominal region shows 26 articulated vertebral centra, which 'fade out' at the posterior end. There are about 35 vertebrae preserved in total. The centra are *c.* 13 mm long and partly covered by the heavy squamation, but one centrum is turned to show that the height is *c.* 25 mm. The ventral ends of four long ribs can be seen behind the pectoral fin, and many long ribs are visible further back. The neural spines gently bend backwards, and at the end of some of them supraneurals are indicated. There are long, thin epineurals, and several of them, nearly horizontal, can be seen crossing the fissure between the two parts of the block.

*Squamation* (Fig. 19). The scales of the referred specimen are big, *c.* 3–4 cm in diameter, thick, rounded to oval with a distinct ornamentation of small tubercles on the exposed field. They are smooth on the anterior part and show no reticulation. They appear similar to those of the holotype, and also here these scales are the sole reason for referring the two specimens to the same taxon. A large, round scale is well exposed besides some ribs on the small third fragment of the referred specimen and the ornamentation on its 'free' posterior region seems slightly weaker than on the scales of the holotype. There are somewhat more than 15 scales (perhaps near 20) in a vertical row behind the pectoral girdle. Where the maximal height is *c.* 15 cm above the vertebral column, the depth below the latter is probably *c.* 30 cm, indicating a body *c.* 0.5 m deep.

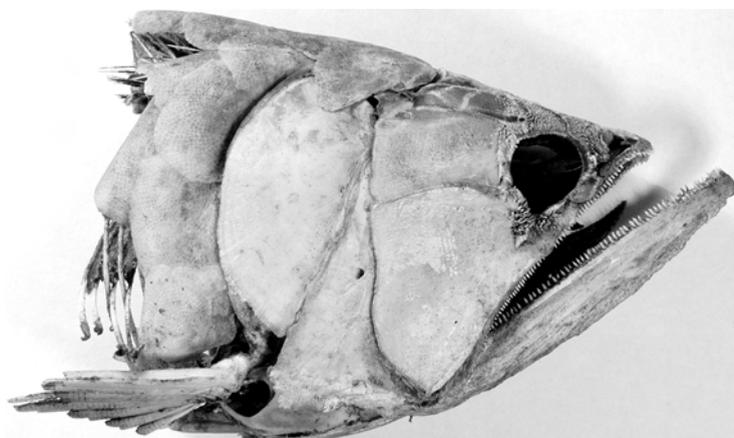
*Diagnosis.* *Furichthys* is a large-sized and deep-bodied osteoglossiform with large, non-reticulate scales. It has a pointed snout with long, slim lower jaws and very heavy premaxillaries with a

strong and differentiated dentition on very low pedicles with the three middle teeth the largest, conical, slightly bent, almost 1.5 cm high and 1 cm wide. The maxillary teeth are slimmer, *c.* 1 cm high, and the dentary teeth in front are a little smaller and decreasing backwards. There are tiny teeth covering (at least) vomer, palato-ectopterygoid and the tongue, and probably the (anterior) parasphenoid. The first pectoral ray is very large. Perhaps the heavy ethmo vomer complex is also characteristic.

The knowledge of *Furichthys*' anatomy is somewhat fragmentary, and known characteristic osteoglossomorph features are rather few. Most indicative is the dentition with the strong, conical to subcylindrical teeth on pedicles, although the differentiation of sizes does not occur in most relatives (some comparative remarks on osteoglossiform teeth below). But also the fused palato-ectopterygoid, the strong basipterygoid process, the shape and pores of the preopercular (like phareodonts), and the shape of the opercular point in that direction. The same counts for the huge first ray of the pectoral fin and the large number of the very short vertebrae, as well as the very long ribs and the lack of epipleurals – perhaps also for the fine tuberculation of the scales.

#### *Osteoglossiform teeth*

Because *Furichthys* and the following three 'bony tongue' fishes have quite characteristic teeth, a few remarks on such teeth seems relevant here. The typical osteoglossiform, *Osteoglossum bicirrhosum* is illustrated here (Fig. 20) for comparison with the fossils. Note that in this large adult specimen, almost 1 m long (precise length not known) from 'Danmarks Akvarium' near Copenhagen, the teeth are relatively much smaller than those of the smaller specimen (19 cm) figured by Taverne (1977, fig. 42). All the teeth of the jaws are placed on bony pedicles, and each has a quasi-cylindrical (slightly oval section perpendicular on the edge of the jaw), high, slim and hollow basal part of smooth dentine (this is called 'socle conique' by Taverne, 1977, 84) ending in an offset, small and slightly narrower, pointed and in-curved cap (Taverne: 'pointe très acérée'), nearly translucent, of acrodin (a hyper-mineralised dentine characteristic of actinopterygians). The pedicles here are about one fourth of the height of the teeth, and they are also hollow and somewhat 'bulbous'. Taverne paid only some little attention to details of the teeth, and he called them all 'grandes' (1977, pp. 84, 95) and even compared them to the huge teeth of *Brychaetus*, but called those of *Osteoglossum* 'exagéré à l'extrême' and 'encore plus évolué' with a 'socle énorme'. This is somewhat misleading, because it seems obvious



**Fig. 20.** Arawana, *Osteoglossum bicirrhosum*, skull and pectoral region of a c. 1 m long adult specimen.

that it is *Brychaetus* having the most extreme teeth (well shown by Taverne [1978, fig. 20] and Casier [1966] and Woodward [1901] and see the Danish jaw below), very large and with enormous bony pedicles, but such is now by Taverne (1978, p. 39) called 'très haut socle rugueux' [rough]. And the remainder of the tooth is described as 'une pointe cylindrique lisse' [smooth], and it is repeated that in *Osteoglossum* and *Scleropages* the 'socle' is more developed than in *Brychaetus*.

This is not true, in *Brychaetus* the pedicle/socle is up to almost half of the tooth, but much less in *Osteoglossum*. In the skull figured here the teeth are not 'grandes' at all, but quite small, and though both Taverne's small specimen and my specimen has about 10 teeth in the premaxilla, the numbers are very different in the maxilla (Taverne's about 50 positions, mine about 60, counting also positions with teeth fallen out) and dentary (Taverne shows about 50, mine has about 80). It seems that Taverne (1977, fig. 48) in section shows a smaller tooth inside the outer row in premaxilla, without mentioning it. On the contrary, in my specimen in the dentary there is a row of a dozen smaller teeth inside the external row at the symphysis (very similar in *Brychaetoides*, below). Nothing about two rows is mentioned by Taverne although in *Scleropages* he clearly shows two rows of teeth in the dentary (figs 82, 83), and seemingly also in the maxilla (fig. 71). Whether the difference in relative size of the teeth is simply age related, is not known, but the differences in numbers especially in the dentaries can hardly be explained in that way. The pedicle size is positively age correlated as shown by the London Clay *Brychaetus* and the huge jaws from

Malawi (Casier 1966, pl. 17 and pers. obs. in NHM, London).

The typical osteoglossiform jaw tooth thus has a hollow bony pedicle, a quasi-cylindrical/-conical, smooth dentine tooth with a small, pointed, offset tip or cap of clear acrodine. Differentiation in size of the teeth is not so evident in the extant ones as in some of the fossils.

*Xosteoglossid rebecca n. g. & sp.*

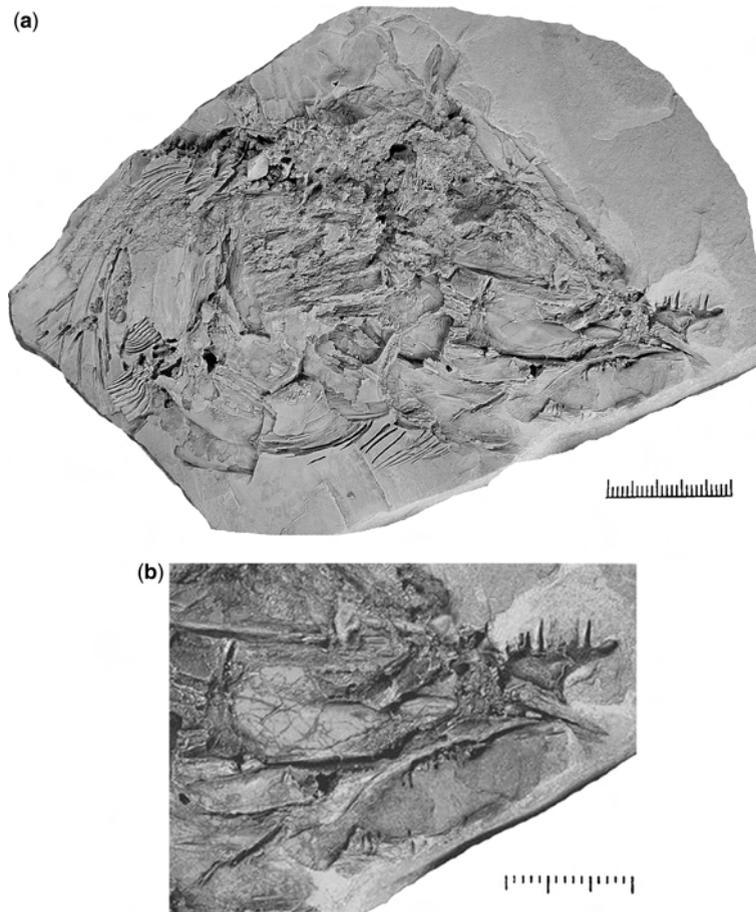
(Fig. 21a, b)

The generic name alluding to the somewhat uncertain or imprecise relation to other osteoglossids/osteoglossiforms (X = 'mystery' plus 'bony tongue'), and the specific name honouring the finder of this Danekrae no. 71 (see note, p. 305), Rebekka Madsen, Sejerslev, Mors, DK.

One specimen identified so far, the holotype DK 71 (MGUH 28.905 in counterparts), found in so-called 'shale', hardened (slightly silicified), laminated, dark grey mudstone of the Stolle Klint Clay on the beach at Stolle Klint, Fur. Collected in 1994. Length of the specimen c. 20 cm.

*Age.* Lowermost Eocene, at the bottom of the ash series, probably derived from the upper few metres below ash -33 (cf. Fig. 3 and Bøggild 1918; Bonde 1987, 1997). The fossil is briefly described and figured also by Bonde *et al.* (2008: 92).

*Description.* Incomplete fish (14 cm preserved) comprising the skull with anterior part of dentary missing, and the pectoral girdle and fin as well as some vertebrae, ribs and scales. The length of the skull is c. 10 cm (snout slightly disarranged). It is compressed to 2–5 mm thickness and preserved mainly as a very sharp and detailed imprint in the



**Fig. 21.** (a) *Xosteoglossid rebeccaе*, holotype, MGUH 28.905 (DK 71), skull and anterior abdominal region as partly imprint in hardened Stolle Klint Clay. Slight ammonium chloride dusting and 'reverse light direction' (from lower right); (b) upper jaw region to expose details of the state of preservation and the 'cracked' bones. Scales in mm.

ventral region, but with the crushed bones beautifully-preserved in most of the dorsal region with the braincase and some vertebrae. The branchial basket is a crumbling mass of disintegrating bone, difficult to interpret. The well-preserved bones appear as brittle, lamellar bone and airfilled spongiosa, perhaps as unchanged mineralization but for the dark brown colour. Bones of the braincase and branchial region are, unfortunately, split right through the bones leaving almost no external or internal surfaces visible on either part or counterpart. Imprints of the completely dissolved bones are left as empty cracks between hardened laminae of mud only fractions of a millimetre thick. The left and right surfaces of any bone are seen on the left and right counterparts respectively, and medial, horizontal structures like some tooth plates and the skull roof are squeezed into the vertical plane.

Roughened surfaces of endoskeletal bone, where they met cartilage can generally be recognized by their irregular structure, e.g. at the anterior end of the dermopalatine where it continues as the autopalatine, which may have been more or less completely cartilaginous (Fig. 21b).

*Skull.* The skull is c. 10 cm long (the rostral end is a little disturbed, the anterior half of the dentary is missing), the height (flattened) is 6–7 cm, in life probably a little less. The preorbital snout is c. 3 cm, the orbit c. 2 cm, and the opercular is c. 2.5 × 5 cm (lower edge not well defined). Snout to quadrate distance is c. 5 cm, approximately corresponding to jaw length, and height of the lower jaw is just over 1 cm. The skull roof comprises large frontals c. 4 cm long, which have been compressed by breaking them along the median suture (now

forming the 'dorsal line'), and the splitting of the fossil went through the sensory canal inside the left frontal of which the external table is on the left slab, the internal table on the right plate with most of the bone preserved as a spongy mass. Although difficult to judge, there is no indication that the anterior part of the frontals were very wide: rather, the contrary. The central division of the sensory canal is visible. The anterior and posterior borders against parietal and nasal are not obvious. The parietal is probably rather small and short, and a very deep, broad and arched imprint on the left slab is probably made by the transverse edge where the parietal bends down from the roof towards the occipital region. One of the nasals is displaced forward and down between the rotated premaxilla and the maxilla, and it appears to be a narrow, straight and flat bone presumably meeting its fellow and with a broad, open sensory canal and a bifid anterior point. A small, oval supratemporal with a sensory canal is displaced above the skull in the parietal region. Behind this is a smooth bone, which may be a supraoccipital crest, and at a level lateral to this is a large bone which most likely is a large 'extrascapular scale' (as in *Osteoglossum*).

The braincase is preserved partly as spongy bones split through, so that they are somewhat difficult to interpret, but preserved best on the left slab. There seem to be a closed interorbital septum mainly formed by the orbitosphenoid, but with a posterior component from the pleurosphenoid and a ventral part from the parasphenoid. The latter is a very straight bone but the ventral surface seems hidden, so a possible dentition cannot be observed. The parasphenoid shape may look like that of *Heterotis* (which lacks teeth). On both plates its basiptyergoid processes can be seen pointing backwards near a dorsal indentation in the metapterygoid (right slab), and the posterior parasphenoid does not seem to bend upwards in this region, while its ascending process is difficult to outline. In the mesh of spongy bone the sutures can be distinguished between orbito-, pleuro-, autosphenotic and pro- and pterotic, but no surface details of those bones are visible, and the latter's contact with epioccipital seems hidden. The latter clearly forms a posterolateral corner of the skull, and below it is a mesh of bone which must comprise ex- and basioccipital and possibly intercalar, but no sutures can be seen, apart from that between the latter two and the pterotic and prootic. The basioccipital (and perhaps exoccipital) is in contact with the first vertebral centrum, which has been displaced relative to the articulated row of other anterior centra preserved (see below).

In the snout region the parasphenoid seems to pass below the parethmoid and end rather abruptly

a short distance in front of it or be hidden below the anterior endopterygoid and palatine and a small subtriangular (?dermal) bone of uncertain affinities. The mesethmoid-vomer complex and a nasal has been moved down and a little forward, while the left premaxilla was rotated upwards and backwards 180° from the anterior maxillary process. The vomerian small and rounded tooth patch is turned 90° to make imprints from the small teeth into the right plate, and the bone just above it with 'cartilaginous structure' is from the ethmoid complex, probably the mesethmoid. The parethmoid shows no signs of having a lateral dermal bone attached to it. Unless the subtriangular bone or a smooth, oval surface below it and behind the mesethmoid (which most likely is part of endopterygoid) is part of the infraorbitals, no such bones are visible in this anterior region – they must have been quite small bones.

*Palate, jaws and visceral arches.* The length of the lower jaw is measured indirectly by the quadrate to snout length at 5–6 cm the anterior half of which is not preserved. Only *c.* 1.5 cm of the dentigerous edge of the dentary is preserved showing 3 mm high, upright and densely set teeth with small bony pedicles in one row. There are 14–15 teeth in the 15 mm jaw, indicating about 20 more teeth in the missing 2 cm in front in the left jaw, and the number hidden by maxilla can be estimated to about 10 teeth by comparison with the right jaw. So in total perhaps there were about 45–50 teeth in a lower jaw. There is a distinct retroarticular process behind the articulation, but it is difficult to judge whether it is a separate bone or fused into the dermartericular, which may occupy about half of the jaw. The lower jaw is not much over 1 cm high giving the impression of a narrow gape. While the two lower jaws almost precisely overlap each other, the upper jaws and the palate have been squeezed asymmetrically, so that the left parts are seen about 1 cm below and in front of the corresponding right part. The left premaxilla has been turned 180° backwards with the nine strong teeth now pointing up. They are about 4 mm high including about 1 mm pedicles, and a few imprints expose the pointed cap. The premaxilla is *c.* 2 cm long with a 7 mm high process in the middle, and the posterior end slimmer than the symphyseal part. The thin posterior branch should rest firmly against and below the 1 cm long and thin anterior process of the maxilla. In the right premaxilla one small replacement tooth is preserved as a thin cylinder with pointed cap of dentine (?acrodine) – the only tooth that has not been dissolved. The more distal 2.5 cm of maxilla has teeth a little weaker than the other jaw bones, only *c.* 2 mm high on little, if any, pedicles. About 10 teeth are

visible on the anterior centimetre, but even smaller teeth reach the posterior part of the bone, which is flattened and 7 mm broad. All teeth are relatively slim, sub conical with oval section basally (longer axes perpendicular to jaw length) and are pointed with a little cap. There is a large drop-shaped supramaxilla with a sharp point pointing forward. The arched maxilla and the way the upper jaw has been destroyed indicate some mobility, probably that this jaw could swing forward, when the mouth was opened allowing the gape to be bigger – presumably more so than as preserved. With the long, slim nasals and (apparently) frontals the fish must have had a narrow, pointed snout with large fangs in front in a much inclined and somewhat prognathous gape.

From the palate the large endopterygoids are well exposed, both left and right ones from their dorsal, smooth surfaces, which at the posterior edges are shaped as strong vertical and slightly arched ridges. Imprints of their covering of tiny teeth are seen on the opposite counterpart. The small vomerian toothplate is exposed on the right slab in front of endopterygoid and above the dense dentition of the anterior process of the palatine. The left endopterygoid is lined by a rather narrow palatine(-ectopterygoid, the latter hardly visible) covered with small teeth and with a distinct row along the lateral edge. It appears (though a parasphenoid dentition cannot be confirmed) that all of the palatal surface is covered by tiny teeth. The dermopalatine has a rostral process well ossified medially (right side is partly preserved as bone), but apparently covered by a cartilaginous autopalatine on its (dorso-)lateral face. The quadrate is well-exposed on both sides, and the articulation can be seen on the right side, where also the symplectic and a large metapterygoid are seen, the latter having a notch approached by both the basipterygoid process and the large triangular flange from the hyomandibula. The latter bone is well exposed on the right slab with some of its bone partly preserved and a large single headed articulation for the braincase and a very strong opercular process. Its long ventral shaft and a strong lateral ridge supporting the dorsal branch of preopercular is preserved.

In this region all four epibranchials of both sides seem to be preserved as straight and parallel rods lying just behind each other, and only partly overlapping number one of the left side onto number four of the right. Small fragments of a few pharyngobranchials are also seen, one is placed above epibranchial 2; all of these preserved as very crumbling bone, but all epibranchials remarkably uniform and slim in shape. Only number 4 may have a small postero-dorsal expansion, and above this a small, elongate bone in position as a

pharyngobranchial – perhaps it is a toothplate of the fourth arch (in modern relatives, Taverne [1977, 1978] found such toothplate in Osteoglossidae and some notoptyerids). Some of the ventral branchial elements are also visible as a jumble of bones exposed in a space between the right supramaxilla and endopterygoid. There is both a right and left hypobranchial and apparently some basi-branchials with small parts of toothplates indicated, but no large bony tongue. The large ceratohyals of both sides are seen with the posterior ossifications squeezed on top of each other – mainly visible on the left slab. Two small hypohyals are seen on both plates, and a small basihyal is indicated on the left slab. There are 17 branchiostegals, the anterior 13 are very slim, but the four posterior ones increase in width and probably all join the posterior ceratohyal.

*Infraorbitals and operculars.* Very little is seen of the infraorbitals, only part of a large right one on the left slab preserved as a smooth imprint of the medial face surrounding the two posterior ceratobranchials mentioned above (perhaps infraorbital 3). Part of the external surface of the same large bone may be seen on the right plate between the quadrate and metapterygoid, but the shape of this infraorbital cannot be determined. The large preopercular is only partly visible on the right plate with a high dorsal branch indicated by its anterior edge, and only the short anterior part of the ventral branch preserved with a clear indication of three to four large pores for the horizontal part of the sensory canal. The large right opercular has been detached from the hyomandibular articulation and has slid down on the outside to be placed partly below the skull (and with the ventral end out of the block). It has a vertical break in the middle, but its shape is well exposed with a rounded dorsal rim and sub parallel anterior and posterior edges. Although the ventral edge cannot be seen, the bone must have been about twice as high as wide, and it has a strong ridge on the inside supporting the articulation for hyomandibular. Sub- and interoperculars are not visible.

*Pectoral girdle and fin.* The broad anterior plate of the right cleithrum sutured to the coracoid is visible as imprint of the medial surface on the left plate, and further down is seen the lateral surface of the left coracoid. The inside of the cleithrum is continued upwards as a very broad vertical branch, cut off by imprints of the internal abdominal cavity, apparently filled with small fish debris from the last meal. On the right side the dorsal arm of cleithrum is approaching the vertebral column, where it overlaps the elongate and rather narrow supracleithrum. The right coracoid clearly shows a large fenestra close to

the posterior prong where it meets the deep imprint of the small, triangular scapula which has a small central foramen. Above the coracoid fenestra a strong, elongate mesocoracoid is placed in a vertical and anterior position. About five radials have been slightly disarranged between scapula and the bases of the pectoral fin rays, which evidently are from the right fin showing about 14 rays (crossing under the ribs on the right plate), while the left fin is pointing the opposite way exposing only 8 of the rays. The anterior ray is strongest, but not very much so, and the decrease in size of the rays backwards is even.

*Axial skeleton.* 11–12 vertebral centra are preserved with the two anterior ones displaced onto the top of the fourth and fifth centra. Very long ribs running all the way to the ventral line are seen beginning from the fourth centrum directly without parapophyses. Parapophyses start from about the sixth centrum and are quite large and pointed. Only 5–6 of the neural arches are visible due to imprints of large dorsal scales. Whether the neural arches are paired is uncertain and one rod may be the anterior supraneural, but there is an indication of some horizontal epineurals low down near the centra. The centra are c. 5 mm long and 6–7 mm high with 1–2 rather strong lateral ridges, and are clearly hour glass shaped with just one of the chordal intercentral spaces filled in by calcite. It is estimated that, with the narrow, pointed snout and no indication of a deep abdomen, this fish had a long, low and compressed body of a fast hunter – and perhaps a ‘jumper’ – somewhat like *Osteoglossum* in shape and maybe in behaviour.

*Scales.* On the left slab a small patch of large oval scales is preserved on the nape. One scale behind the supraoccipital crest is seen in its entirety from its external surface. It is 17 mm high and c. 10 mm long with an even ornamentation of small, irregular tubercles on the ‘free’, posterior field, while the anterior, basal field is more smooth (but in reality is covered by the tiniest tubercles tending to be slightly elongated and arranged in a radiating pattern mirroring the growth direction). There are some well-spaced, very thin and crossing lines as indication of a possible reticulation on much of the scale, while other and stronger fissures must be cracks, especially on one scale around a puncture hole made by a bone fragment (apparently from the outside). The posterior (apical) field shows a number of pores in the surface. This scale shows part of its inside on the right counterpart, but while the broader cracks are clearly seen, the traces of reticulation and pores are not so convincing (which is unusual; they should be more

evident on the inside). One smaller scale, 5 × 5 mm, just below the left pectoral fin does, however, show a clearer reticulation by fissures, especially on the inside of the posterior field, while pores are only weakly indicated on the anterior field. The external ornamentation is of the same type, but the stronger ornamentation on the posterior part only occupies about one third of the scale. When evaluating these indications of reticulation it is worth noting, that many of the bones show an irregular pattern of sediment filled fissures which surely are cracks (Fig. 21b) and usually more ‘straight lined’ than proper reticulation – this is an obvious difficulty when looking for reticulation in the scales, which also seem to be cracked. The conclusion is that the scales show some weak indications of reticulation and pores as well as ornamentation typical of osteoglossiform scales.

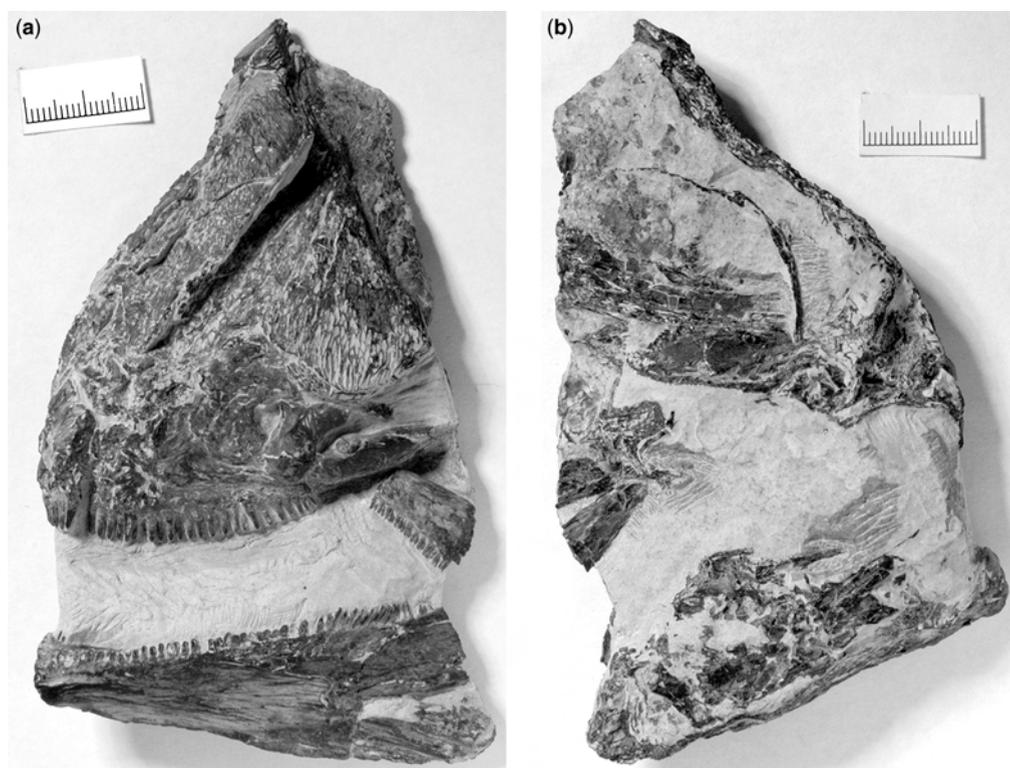
*Diagnosis.* Complete interorbital septum of orbitho-, pleuro- and parasphenoid. Rather narrow and high opercular and preopercular with short ventral branch with four large pores for the sensory canal. Marked supraoccipital crest and notch in metapterygoid (for basiptyergoid process and/or hyomandibular process?). Probably tiny teeth all over the mouth cavity (parasphenoid teeth unknown). Ribs beginning only from the fourth centrum without parapophyses (which start from about the sixth centrum). Differentiated dentition with the teeth on the premaxilla much bigger than the other jaw teeth.

The presence of a supramaxilla is an unusual feature among osteoglossiforms, but it is probably plesiomorphic – see text on marine forms above, and the phylogenetic analysis below. The latter shows *Xosteoglossid* to have many osteoglossomorph synapomorphies. Furthermore, there are nearly half of the characteristics present of the new ‘Osteoglossi’ (Mormyriiformes plus Osteoglossiformes), and several features to place it among osteoglossiforms and even high in the stem-group of the extant members of the group.

#### *Brychaetoides greenwoodi* n. gen. & sp.

(Fig. 22)

Meaning *Brychaetus*-like due to some superficial similarity to *Brychaetus* from the London Clay (Casier 1966), and named in honour of Dr P. H. Greenwood, late colleague in the Fish Department, Natural History Museum, London, a great connoisseur of osteoglossomorph fishes both extant and extinct. In 1973 he published his knowledge of the group, after the Linnaean Society meeting in 1972, which seriously introduced cladistics into fish systematics (see Bonde 1974, 1999, 2003b).



**Fig. 22.** (a) *Brychaetoides greenwoodi*, holotype, MGUH 28.906 (1954.469). Snout part in cementstone, left side; (b) right side of snout sectioned through the oral cavity exposing palate and tongue. Scales 2 cm.

*Holotype (only known specimen) MGUH 28.906 (former 1954.469).* Originally described by Bonde (1965, unpublished 'Gold Medal' thesis; summary 1966) a very fragmentary skull, pectoral bones and scales in a cementstone from the Fur Formation found in 1947 at the eastern part of Knudeklinten, Fur, presumably on the beach, by the late I. P. Andersen, Viborg. Four pieces said to be from the same fossil, preserved in a cementstone, light grey with some weak lamination. The level is unknown, but the limestone looks like the one having ash -33 through it from the very base of Fur Fm (same level and locality as the large *Fur-ichthys* described above, although it was recorded by this author [1997, p. 47], as 'Ost. 3', as level +25-30? from the upper part of the formation). The specimens consists of: (a) mainly the snout part with anterior end of the lower jaw and most of the orbital region, part of the palate and tongue; (b) part of a large flat skull bone, apparently an opercular with some crushed branchial arches attached to its inner surface, and some bony struts at one end of the elongate specimen could be the distal ends of branchiostegals; (c) a piece with strongly overlapping scales from both sides of the

fish with fragments of ribs in between and apparently part of a vertebral centrum and parts of bones from possibly the shoulder girdle. Those three parts of the fossil do not fit exactly onto each other. There is a fourth much smaller fragment (d) with some scales of just one side pressed together and a fragment of a rib - not even that fragment can be convincingly fitted onto one of the other parts. All fragments have sharp, freshly-broken edges, but apparently no more of the fossil was in I. P. Andersen collection, when the Geological (then Mineralogical) Museum acquired the collection (registered in 1954), which contains a large number of isolated scales, many of them osteoglossoid of the reticulate type known from *Heterosteoglossum*.

*Skull (Fig. 22a, b).* The skull (snout) of specimen 'a' has been laterally compressed and split in a near mid sagittal plane with most of the right half missing while exposing some of the palatal and tongue region. The frontals are broken through the orbital region, the posterior part (and the rest of skull roof and braincase) is missing, the left frontal is squeezed down into the left orbit, and

the anteromedial part of the right frontal is preserved. The antorbital is displaced forward, and the maxilla is broken in two and the distal end is missing. Most of left dentary and the rostral end of dermatarcular are preserved.

The snout part is *c.* 14 cm high and can probably be oriented by keeping the line from the vomer and the parasphenoid approximately horizontal, indicating that the fish did not have a near horizontal skull roof to snout line (like *Osteoglossum*, *Scleropages*, *Heterosteglossum*), but rather a profile like that of *Heterotis* or *Phareodus* (with a falling snout-line (a little over 45°) and an upward pointing dentary (less than 45°)). If the skull roof is kept horizontal and the mouth slit/upper jaw turned upward about 45°, the exposed dermatarcular would be unlikely long or the jaw (dentary *c.* 8 cm) very short compared to the entire fish.

Of the lower jaws (Fig. 22a) almost only the left dentary is preserved with a small part of the anterior point of dermatarcular mainly seen on the inside of dentary. The anteriormost few millimetres at the rather thick, and somewhat expanded, symphysis are missing. There is an inner row of about five small, cylindrical teeth, *c.* 2 mm high, one of which was actually pointing its cap the wrong way, outwards (but this cap was lost years ago). The main row of teeth numbers over 45 teeth and a few are missing at the symphysis and perhaps also distally, so around 50 teeth is a fair estimate. The teeth are 3–4 mm high, upright with a distinct, rounded cap pointing lingually, and with near parallel sides in labial view, but basally oval, almost twice as wide (linguo-labially) as long (meso-distally). The crowns are set on small bony pedicles comprising about one fourth of the height. They are hollow with 0.5 mm thick walls and height slightly decreasing distally, where they are inclined a little backwards. About 8 of the teeth have much thinner walls and are newer replacement teeth. The dentary is almost complete, *c.* 8 cm long, and *c.* 3 cm high distally, but the ventral border is broken off. Close to this the sensory canal runs at the lower bent-in edge with one anterior, narrow pore pointing downwards and the posterior pore to the side. Little can be observed of the anterior part of the exposed dermatarcular, but the sensory canal can be seen cut at the posterior end of the edge where the medial lamella bends in. The inside of the jaw is mostly hidden by parts of the tongue and a fragment of the medial side of the right dentary.

The premaxilla, nearly 4 cm long, has larger teeth *c.* 5 mm high and slightly more conical, upright with a cap, and set on pedicles 20–25% of the height. The teeth slightly decrease in size distally. The thickness of the dentine is only 0.3 mm in the largest teeth. There are 24 teeth in one row (a

full grown possible replacement tooth, pointing through from an inner position, is seen in fifth position in both sides, but the section of the right premaxillary after the seventh position does not show two rows of teeth – two other replacement teeth are in 16th and 23rd position). Quite differently, the broken off middle part of the maxillary dentition distinctly shows two rows of teeth, about 2.5 mm high, oval at the bases and set on very low pedicles in an alternate pattern, where the inner teeth point out between the outer teeth, so that all the pointed caps are in nearly one line.

Twenty-three teeth of both rows combined are preserved in a fragment less than 2 cm long so, if the upper and lower dentitions were approximately equally long, the maxillary may have had nearly twice that amount. The dentigerous part of the bone is narrow and only *c.* 1 cm high, with a dorsal edge indicating no attachment to the infraorbitals, and tapering in front, where it is broken from a strong anterior part, that has a big articular 'knob' for the antorbital (stronger than in osteoglossids). Behind this it has teeth pointing into the matrix and exposed on the reverse side of the slab. The most proximal end is a thinner process closely attached to the dorso-medial side of the slim posterior process of the premaxilla. The latter takes up about half the length of the bone, while its proximal half is much higher, nearly 2 cm, and has a blunt, dorsal process passing up between the nasal and the mesethmoid region.

In between the two premaxillae at the dorsal part of the symphysis a small part of a cartilage bone is visible, probably a hypethmoid ossification ('hypoethmoïde ventral' by Taverne 1977–1979, which may be fused to vomer). Between this region and the nasals/frontals is exposed a rim of the mesethmoid ossification of which the dorsal surface is ornamented like a dermal bone ('hypoethmoïde dorsal', Taverne). Between this and the anteromedial flanges of the frontals is a small, round supraethmoid bone. Lateral to the mesethmoid is a much bigger and oval nasal with a large lateral embayment for a nostril, and the bone has a small mid-ventral pore and probably receives the sensory canal at the postero-medial edge from the indentation, where it fits into the frontal. The nostril on its postero-lateral side is limited by a strongly ossified, pillar-like antorbital with a rounded ventral surface presumably to meet the 'knob' a little further back on maxilla, and the broader dorsal end meets the frontal. This antorbital distinctly appears to be an endoskeletal bone, and it is not obvious that it has a lateral, dermal component. There are some small, dorsal superficial pores and a small ventrally placed pore at a horizontal break in the bone, and another tiny one at the

ventral edge, but they do not really look like those from a sensory canal. The bone is no doubt what is called 'antorbital' by Taverne (1977–1979) in the fossil *Phareodus* and *Brychaetus*, where it, as in the present fossil, does not appear like the antorbitals of the recent osteoglossids, although the bone in *Osteoglossum*, *Scleropages* and *Pantodon* does have the same relation with an articulation onto the maxilla. The last two fossils mentioned and *Opsithrissops* (Danil'chenko 1968; Taverne 1979, 1998) may perhaps lack this dermal component or it may be fused completely into what looks more like some sort of (par-)ethmoid ossification. On the reverse side of the fossil (Fig. 22b), however, under the right nasal and lining the nasal cavity is seen the mesethmoid ossification in conjunction with a near vertical ridge, that must be part of the true parethmoid. This continues toward the orbital side as thick, spongy bone. These strong ethmoids seem not to be co-ossified with the thin vomerian tooth plate, which closely follows their ventral surface.

The frontal, to accommodate the supraethmoid, nasal and antorbital has a wavy anterior border, which continues laterally in a broad and ornamented lappet, behind which the snout is cut off. It appears likely that this lappet is wider than the frontals, in general similar to the condition in *Brychaetus* and *Phareodus*, and the lappet has been pressed down into the left orbit and onto the side of the orbitosphenoid with a thin sclerotic ossification squeezed in between the two. The course of the sensory canals is not very evident in these dermal bones, although it perhaps can be traced in the right frontal as a slit near the broken edge, and in the left bone as a narrow slit in a near symmetrical position, and it appears to end at the notch into which the nasal fits. At the top end of the right frontal is a fragment of a more posterior bone, presumably the pterotic, and if so, approximately indicating the width of the skull roof at this region, namely much narrower than the anterior frontal lappets.

On the reverse side of the fossil where it is cut through the right frontal, nasal and premaxilla, the section cuts through the mouth cavity (Fig. 22b) and the visceral arches. In the snout the mesethmoid is cut, and below it is attached a thin plate, perhaps Taverne's ventral hypethmoid. Closely below the latter is a very thin plate of vomer, totally covered by tiny teeth. Behind the mesethmoid is an upright strut or wall, presumably the mentioned parethmoid with a postero-ventral extension butting against some dermal bone, either endopterygoid or dermopalatine. Part of two plates of the sclerotic ring is cutting down behind this region, and a flat bone posterior to this is likely to be the

dorsal part of endopterygoid (dorsal surface of right side), while the straight bone cut below it carrying tiny teeth on its ventral surface is probably the corresponding toothplate (or could it be the parasphenoid with a displaced endopterygoid border above it?). Above this 'endopterygoid' is another flat bone with indistinct borders above and a nearly straight border below within the orbit that might be the parasphenoid with a dorsal lamella partly closing the interorbital fenestra. It seems uncertain whether the said 'parasphenoid' carried teeth although none is seen in the section of its ventral rim.

In the dorsal region of the mouth cavity is a stout cartilage bone with thin dermal plates, presumably dorsal elements of the first gill arch, and ventrally in the mouth cavity some unossified element of the tongue is sectioned showing tiny teeth on two surfaces. A large endoskeletal bone is pressed into the innerside of left dentary, presumably the ceratohyal, and it is worth noting, that it carries tiny toothplates on the lateral side facing the lower jaw. Such dentition is not described by Taverne (1977–1979) for any of the living osteoglossiforms, and it may be unique within teleosteans. So perhaps most of the cavities in the mouth were lined with thin tooth plates covered with tiny teeth.

Specimen 'b' shows a fragment of a strong, flat dermal bone, most likely an opercular, or perhaps an infraorbital, with a rather smooth surface, but no edges of the bone exposed. The 'pieces c and d' have many large and fragmented scales tightly squeezed together, so that limits of individual scales are difficult to observe. They appear laminated with 3–4 thin layers penetrated by pores which end in small, very low raised areas on the inside of the scales as in many osteoglossiforms. No very obvious reticulation is visible, but the squeezed scales have thin and sometimes wider breaks forming a pattern reminiscent of squamulae, and the external surface is ornamented with fine tubercles and ridges upon which is overprinted a larger pattern of low, crossing grooves also a bit reticulation like.

Specimen 'c' has a vertebral centrum *c.* 2 cm in diameter (therefore probably between 1–2 cm in length) and somewhere between 50–100 centra can be estimated for the vertebral column, so its body length would be 0.5–2 m. Specimen 'a' has over 6 cm long frontals, and accordingly would have a braincase over 10 cm, meaning a total length of the fish (with tail) would be between 70 cm and (if elongate like *Osteoglossum* or *Heterosteoglossum*) 2 m.

*Diagnosis.* Premaxilla with a large number of strong, closely set teeth, over 20 teeth in one row,

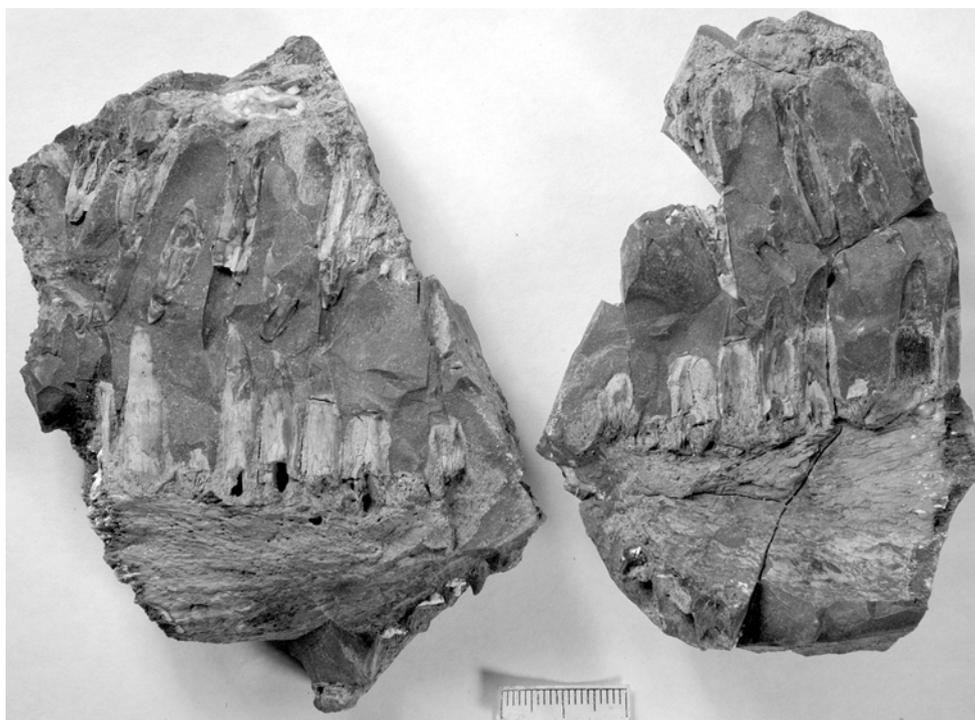
decreasing in size distally, and a plumb ascending process near the midline touching the mesethmoid. Maxilla with similar, but smaller teeth closely set rather in two rows with alternating teeth. The dentary has numerous closely set teeth, around 50 in number, of the same type in one row with a short inner row of about five small, pointed, cylindrical teeth near the expanded symphysis. The larger teeth set on strong bony pedicles, which are relatively very low for the smaller teeth. This specific pattern of differentiated dentition of osteoglossiform-like teeth is characteristic of this taxon, and the tooth plates apparently on the ceratohyal seems unique. Scales are thin, laminar with many pores each ending on a tubercle on the inside (inner surface otherwise smooth), and dense ornamentation of tiny tubercles and ridges are present on external surface, also where they overlap in three or four layers. No, or very little, typical reticulation. Both the scales and the specific pattern of dentition of typical osteoglossiform teeth may well be autapomorphic for *Brychaetoides*. The medium large rounded nasals fitting into rounded excavations of the frontals, and not meeting in midline, as well as the dermal supraethmoid visible between nasals and frontals, and the

mesethmoid exposed between nasals and premaxillaries, may well be autapomorphies also.

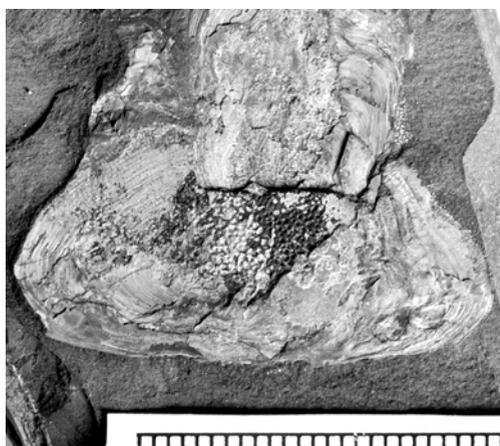
The following features have a somewhat wider, but still narrow distribution among osteoglossomorphs (see below): Frontals very broad in front of the orbit (a phareodont feature); sclerotic ossifications present; antorbital (perhaps), without a dermal component, but it has a very strong articulation for the proximal maxillary process; all exposed bones of the mouth cavity may have small, densely set teeth (not known with certainty for parasphenoid), and there is a rather large, separate vomerine tooth plate with tiny teeth.

cf. *Brychaetus* sp. (Figs 23, 24)

Several parts of (probably) the same individual of a large osteoglossiform fish. Some of these have been valuated as Danekræ, namely part and counterpart of a fragment of the symphyseal part of lower jaw and premaxilla with huge teeth Danekræ 177 (MGUH 28.907) and several fragments of strong, segmented fin rays and many large scales Danekræ 181 (MGUH 28.908a–h). All preserved in hardened (silicified), dark grey to black mudstone found on the beach near Stolle Klint, Fur, that is from Stolle Klint



**Fig. 23.** cf. *Brychaetus* sp. in hardened Stolle Klint Clay, MGUH 28.907 (DK 177), near symphyseal parts of right upper and lower jaw, part and counterpart. Scale 2 cm.



**Fig. 24.** cf. *Brychaetus* sp., part of same specimen as Figure 23. MGUH 28.908 (DK 181), large scales seen from the lateral side. Scale in mm.

Clay, age earliest Eocene. Found by C. Sönderby and N. Christensen; some fragments in Moler museet, Mors and other fragments said to be in private collections. The bone is preserved in both jaw bones, teeth, fin rays and scales with the spongy bone often filled with secondary chert (opal?) of a whitish-bluish colour. These fossils are not here described in any detail, the two figures are just referred to. The teeth indicate a very large fish when compared to the big skulls known from the London Clay (Casier 1966), probably over 2 m long. In the *Brychaetus* sp. from Mali, mentioned by Longbottom (1984) some jaw fragments have even bigger teeth (pers. obs. in NHM).

**Jaws and teeth (Fig. 23).** The 7 cm long lower jaw fragment is only 3 cm high at the end cut off furthest away from the symphysis, and it has 3 cm high teeth. This indicates a rather low and slim lower jaw. The teeth in the premaxilla are about 4 cm high, and all the big jaw teeth have pedicles

covering about half their height and the dentine continues inside the pedicles.

**Scales (Fig. 24).** The scales have a fine external ornamentation of irregular tubercles and small ridges with tiny pores penetrating the laminated scale in the posterior area and ending on small protuberances on the otherwise smooth internal surface. There are no clear signs of proper reticulation, despite some cracks giving such impression.

**Characteristics.** The huge teeth with very high bony pedicles are typical for *Brychaetus*. The same counts for the comparatively weak and low mandible, despite its large teeth. Perhaps also the scales are characteristic with pores only through the posterior, ornamented part of the scale, but without reticulation (*B. muelleri* scales seem to be weakly reticulate [Bonde 1996], but Taverne disagrees [1978, p. 45–46] although his Figure 25 appears to show squamulae). The difference in scale structure may indicate different species. Considering the age difference from earliest Eocene to late Early Eocene in the North Sea Basin, it is a bit surprising that *Brychaetus* has not been found in the Mo-clay of intermediate age – but perhaps *Brychaetus* was simply rare in the earliest Eocene North Sea. This genus is known from Eocene deposits in Europe, eastern USA and northern and central Africa.

#### *Osteoglossiform indet.*

A small fish comprising part of the abdominal region and part of the skull, that is cut off in front of the hyomandibular. It is preserved in a cementstone without counterpart, probably at the level of ashlayer +15 in the upper half of Fur Formation. The fragment is 43 mm long, and the height of the body and the skull is 13 mm. About 3 cm of the abdominal region is preserved behind the opercular,



**Fig. 25.** Small osteoglossiform indet. MGUH 28.909. Opercular and anterior abdominal region of juvenile (?) fish. Fossil 43 mm long.

and apparently nothing of the caudal region. Only a few details of this fish will be described.

**Skull.** Very little detail is visible of the braincase and the large hyomandibular. The preopercular is incomplete, the rostral part of the horizontal branch is missing, but it appears to have been about as long as the vertical branch, which is *c.* 8 mm high, the angle of the bone being about 100°, and its maximal width is 3 mm. The large, rounded opercular is 10 mm high and 8 mm wide and has both a rough radiating ornamentation and very evident concentric growth lines. A small subopercular is visible at the preopercular corner. The missing snout is due to a break in the stone, the skull of the fossil may well have been complete and *c.* 3 cm long.

**Pectoral girdle and fin.** A rather broad cleithrum, broken at the dorsal end, and a strong, horizontal coracoid – probably with a hole near the posterior border – frame the opercular behind and below. The supracleithrum is not well preserved and the small scapular shows no details. The pectoral fin is 10 mm long and appears to be folded, because only about 8 rays can be seen. The upper ray is large, but not extremely so.

**Abdominal region.** Only the anterior part of the abdominal region is preserved, and there is no trace of the unpaired fins. Thirty-six vertebrae are visible behind the opercular, and 32 pairs of *c.* 10 mm long and strong ribs reach the ventral border, and they attach directly to the centra behind quite well-developed parapophyses at least in the anterior part. The neural spines of the anterior 20 or so vertebrae are strongly backwards inclined, and neither supra-neurals nor epineurals are seen above them, so the dorsal musculature must have been very low. The posterior part of the vent has been entirely torn away, leaving the ribs near the end bent away from each other, and the last four vertebrae are without ribs. It may well be that the hind end of the animal was bitten off before the cadaver ended in the diatomaceous ooze. All the vertebral centra are as high as they are long, and vertebral column, ribs, opercular region etc. are well ossified, so perhaps only the lack of ossification of supra- and epineurals as well as the small size indicates, that the animal is in fact a juvenile. The pelvic region is not preserved, which suggests that the fish may well have had twice the number of vertebrae as preserved.

**Scales.** The scales are small, smooth and round with concentric growth lines and no trace of reticulation, which might also be a juvenile feature. It appears unlikely, however, that this little fish is a juvenile *Heterosteglossum*.

**Relations.** The huge opercular, large preopercular, very long ribs and rather strong first pectoral ray and elongate body with (presumably) many vertebrae are features found in most 'higher' osteoglossomorphs. Although not strictly diagnostic of these fishes, there seems no better alternative. The little that can be performed of comparative analysis (below) tends to place it rather high in the osteoglossiforms, but obviously this is very tentative.

### Stratigraphic distribution of the Danish fossils

Two of the six Danish osteoglossomorph taxa, *Xosteoglossid* and *Brychaetus*, are known exclusively from the Stolle Klint Clay, that is from a low stand and landlocked marine basin. Two other taxa, *Furichthys* and *Brychaetoides*, have so far been found only in the very earliest Mo-clay (between ash layers –33 and –25). The indeterminate little osteoglossiform is known only from near the middle of the Mo-clay, and only *Heterosteglossum* is found in both deposits and is quite common as judged by the many finds of scales (in fact also found in the lower London Clay).

### Relationships of the Danish fossils

The relationships of the Danish Eocene osteoglossomorphs will be discussed in the framework of the recent reviews by Taverne (1998) and Hilton (2003) with some remarks also on the paper by Li & Wilson (1996a). I will accept these ideas as different models of the evolutionary history of osteoglossomorphs discussed in phylogenetic systematic or cladistic terms (for a distinction see Bonde 1977) to scrutinize what they mean for the phylogenetic positions of the Danish fossils. The fossils shall first be interpreted within Taverne's model, which is based on more than 300 characters, and which included all known fossils.

The discussion below is not 'quantified' by including the Danish taxa in a matrix, because there are serious problems with the many missing characters. It is more reasonable to confront the features themselves as they are used in the phylogenetic models by Taverne (1998) and by Hilton (2003) based on very different methodologies. Quantifications, in my opinion, tend to hide the real problems about comparing the single features, because whatever the data there are always some consensus models appearing according to some mathematical considerations and assumptions, which may have little to do with the empirical (real) world. So this study checks every feature among the postulated synapomorphies.

### Heterosteoglossum

It is an osteoglossomorph possessing the following features of Taverne (1998, p. 104, character number indicated by \*; see Fig. 5): interbuccal dentition – only a little is visible on several bones (1\*); no supraorbital (4\*); reduced number of epurals, perhaps none (10\*); complete npu1 (11\*); 18 (or less) principal caudal ray (12\*); Dorsal fin inserted very distally (ibid, p. 105); perhaps has no interhyal (7\*) – at least none is observable.

Like forms more 'advanced' than *Hiodontiforms* it has: large opercular, nearly oval (24\*); only 6 hypurals or less (29\*); complete nu1 (28\*); probably also no 'free' epural (27\*); reduced subopercular (25\*) – none seen.

Of those features shared also by *Singida* and more advanced forms it has: large nasals sutured to frontals (40\*); large infraorbital 3 & 4 (42\*) and quite likely also only four infraorbitals (41\*); Further enlarged coracoid and pectoral fin (46\*); less than two uroneurals (47\*), and it seems to show notch in endopterygoid for basipterygoid process (44\*); it definitely has neither short ventral branch of preopercular (long ventral arm as a reversal in Taverne's model) (45\*) nor less than 18 principal caudal rays (48\*); (the 18 rays in Taverne's model would represent a reversal from a more advanced osteoglossiform stage to a more primitive one).

Of Osteoglossiform plus Mormyriiform synapomorphies it has: u2 with 3 dorsal hypurals fused in (65\*); scales partly reticulated with ornamented squamules (66\*); it probably also shows epineurals not fused to neural arches (63\*); only one uroneural (64\*); it seems not to have large ossified orbitosphenoid (58\*); retroarticular excluded from the articulation (60\*) – a debatable feature.

Because of the above two supposed reversals by Taverne it shares apomorphies with mormyroids caudal with 18 principal rays (12\*); long ventral arm of preopercular (32\*). It is more disturbing, however, that the few osteoglossiform synapomorphies, which can be checked, are not present: supraclithrum without sensory canal (103\*); lack of basisphenoid bone (126\*); interorbital septum (156\*); paired orbitosphenoid bones (208\*); teeth with pedicles (211\* – but teeth too small to judge) and another characteristic trait not mentioned by Taverne: premaxilla with a broad, medial, ascending process. Several of these features are, admittedly, not found in one or another 'advanced' osteoglossiform, especially in *Pantodon*, and neither in its close relatives *Osteoglossum* and *Scleropages*. Furthermore *Heterosteoglossum* seems also to be lacking the few controllable apomorphies shared by phareodonts and the more advanced osteoglossiforms: it probably has neither the broad antero-lateral expansion of frontals (214\*); nor lack of membranous supratemporal (219\*); and it is uncertain

whether it lacks teeth on the middle part of parasphenoid (215\*). On the other hand it does have large nasals which presumably meet in the midline (226\*), a feature of more advanced osteoglossiforms (and some 'phareodonts'). It also has a feature shared by *Opsithrissops* and more 'advanced forms': a longer and lower body with more vertebrae (232\*); and, like *Brychaetus* it has dorsal hypurals 3–5 fused to u2 (if the caudal skeleton referred to is really from *Brychaetus*).

Even more important are the advanced traits shared with the extant osteoglossiforms of which one lineage comprises the Osteoglossidae: *Osteoglossum*, *Scleropages* and *Pantodon*. With those three the fossil shares no bony interorbital septum (reversal; 238\*); and possibly derm- and retroarticular fused (79\*); several parallelisms), while it does not have the elongation of lower jaw (239\*). There are no important similarities specifically with *Pantodon*, but one with the lineage of *Osteoglossum*/*Scleropages* (277\*: orbitosphenoid not ossified), which is countered by the lack of 109\* (reduced number of principal caudal rays). Significant similarities with *Osteoglossum* alone could be very long body with more than 80 vertebrae (282\*), possibly coupled with elongation of the dorsal (283\*) and anal fin (284\*), and also long first pelvic fin ray (285\*). Primitive retentions are the lack of: lateral ethmoid loss (281\*); 5 hypurals or fewer (22\*); fewer than 10 branched caudal rays (286\*).

There are also apomorphies jointly with fossil and Recent Arapaimidae, namely two coupled features: short mandible (31\*); and long ventral arm of preopercular (reversal) (32\*); while others are lacking: deep infraorbital 1–2 (291\*); nu1 thin or short (294\*); and uroneurals are small ridges on top of hypural 6 (295\*). Shared with Eocene *Sinoglossus* and living arapaimids it has elongate dorsal (298\*) and anal (299\*) fins, but it lacks reduced caudal fin (109\*), and probably also the unique fusion of antorbital and infraorbital 1 (297\*). With the crown-group *Arapaima* plus *Heterotis* it shares further elongation of the body and dorsal and anal fins (307–309\*); and probably retroarticular as part of the articulation (274\*); while it seems not to have reduced myodome (302\*); and there is no indication of a descending lamina on nasals (303\*). Important traits shared with *Heterotis* alone are: reduced teeth in the short, rather high mandible (318\*); but there are no traces of apomorphies like suprabranchial organ (316\*); epipleurals (233\*); or very large haemal arches (320\*). A slim body, short upturned mouth with a short, high lower jaw, rather weak teeth and preopercular with a long ventral arm is also characteristic of the primitive arapaimid *Thrissopterus* (and for that matter also for the mid Cretaceous *Laeliichthys*, should it really be a very primitive arapaimid, which is doubtful [Bonde 1996]).

*Arapaima* specializations are lacking and there are only vague similarities with the two large Eocene, marine osteoglossiforms from Monte Bolca, *Monopteros* and *Thrissopterus*, those are reduced pelvis and pelvic fins (37\*); and long dorsal and anal fins (298–299\*). Likewise the only specific similarity with *Foreyichthys* seems insignificant, only one uroneural (64\*).

Summing up these comparisons, there are significant similarities with advanced osteoglossiforms, but this concerns features combined from Osteoglossidae and *Heterotis* (of Arapaimidae), so *Heterosteoglossum* should probably be placed in Taverne's 'cladogram' as an advanced member of the stemgroup for Osteoglossidae plus Arapaimidae, that is about the same position as *Foreyichthys* was given above, especially due to the open interorbital fenestra, but with no special relationship with *Heterotis* and *Heterosteoglossum*. In the corresponding classification as outlined below *Heterosteoglossum* could be placed as the most advanced stem-group member of the Osteoglossidae (if it has unossified orbithosphenoid this might even place it as sister-group to the Osteoglossinae, because *Pantodon* has a pair of medium-sized orbithosphenoid ossifications in the anterior part of the orbit, which otherwise has cartilage almost closing the interorbital fenestra). Only a very conservative standpoint would place it as *sedis mutabilis* with the two families because of the character-conflict relating it to those two groups, which would imply that the just mentioned special similarities with crown-group osteoglossids would be due to convergence.

### Furichthys

*Furichthys*, as presently preserved and prepared, is difficult to relate precisely to other osteoglossiforms due to the lack of information. Of its osteoglossomorph features only (1\*) the interbuccal dentition can be assumed – but it is probably a primitive feature. Of 'higher osteoglossomorph' traits (non *Hiodon*-like) it has a the large opercular (24\*); and perhaps subopercular (slightly) reduced (25\*); There seem also to be large nasals meeting (40\*); and presumably a notch in endopterygoid for the basipterygoid process (44\*); and preopercular with short ventral branch (45\*). Likewise it has a large pectoral fin combined with some enlargement of the coracoid (46\*).

It may have osteoglossiform–mormyriiform specialisations such as strongly ossified ethmoid region (56\*); and fused palato-ectopterygoid (59\*), but it seems to lack retroarticular exclusion from the articulation (60\*), and it probably has an ossified basihyal (contra 61\*) and shows no reticulation of the scales (part of 66\*).

The only osteoglossiform features shown by *Furichthys* is pedicles of the teeth (211\*), but only small ones and only in premaxilla, which seems to lack the characteristic ascending process. And given the symmetrical shape of the possible basihyal with its tooth plate the bone is hardly fused to several more posterior elements forming a long bony tongue (218\*). *Furichthys* does not have a long and low body like *Opsithrissops* and most advanced osteoglossiforms (232\*), and the *Brychaetus* autapomorphies which can be checked (33\*, 235\*, 236\*) are not present.

It does have a few of the osteoglossid synapomorphies, such as 239\* long lower jaw and 79\* articular fused to angular (a dermoticular), but none from the subdivisions of the group, nor from arapaimids including fossils.

In conclusion *Furichthys* seems to be a primitive relative of Osteoglossiformes plus Mormyriiformes. It does not have very convincing features of osteoglossiforms, and apparently has no feature of any constituent subgroup apart from the 'long lower jaw' (osteoglossid-like), and there is no indication of close relationship to any of the known fossils. According to Taverne's model (1979, 1998) it occupies, based on one or two synapomorphies, a position just above *Singida* as an advanced member of the stem-group for the Osteoglossiformes/Mormyriiformes, but it seems to lack 1–3 (?) specializations of this crown-group (Osteoglossi – named below).

### Xosteoglossid

This fossil exhibits some more details, especially from the skull, and it can easily be recognized as a 'non-Hiodont', that is as more advanced osteoglossomorph having about 10 of the about 18 synapomorphies characteristic of the level, where *Singida* branches off in the stem-group of the osteoglossiform–mormyriiform crown-group. (It only lacks one trait, the presumed loss of the last supramaxilla, which demands several reversals of this bone reappearing later in the history – see the introduction). It has about six of the about 14 further synapomorphies of this crown-group, but of these two features seem not to be present: the lack of ossification of the basihyal (60\*) and the ventral hypohyal (61\*) and it is, as mentioned above, not obvious that the scales are divided into squamules (reticulate; 66\*). All three are features with difficulties of interpretation.

It does have a few of the osteoglossiform specialisations: 'divided' teeth on pedicles (211\*), interorbital septum (156\*) and the latter may not leave space for a separate basisphenoid (126\*). But it appears not to have features of phareodonts (paraphyletic) and more advanced forms, neither antero-lateral expansion of frontals (214\*), nor

large, fused toothplate on the tongue (218\*; it should have been visible in this type of detailed preservation), nor supratemporal without membrane bone (219\*). It shows the questionable 'reversal' of a large supramaxillary (223\*), but it is believed to be primitive. Of more advanced osteoglossiform traits it shares large meeting nasals (226\*) placing it above *Phareodus sensu stricto*, and the diminished, more narrow ascending process on the premaxilla (231\*), indicating a position at or above *Opsithrissops* and *Brychaetus*. If the lack of frontal expansion is really a loss (237\*; a reversal), this might indicate an even higher position as an advanced member of the stemgroup of living (crown group) Osteoglossiformes. (The inferred body and likely fin proportions would agree with such position – and here *Laeliichthys* should be left out of the discussion at this level, as almost none of its claimed shared specialisations [290–295\*] can be checked with certainty in these only 5 cm long fishes).

There is a character conflict between the long, prognathous jaws of osteoglossids (239\*) and the free, movable maxilla of arapaimids (290\*), the only features it possesses from these crown-group members. So it could be placed *sedis mutabilis* alongside Osteoglossidae and Arapaimidae. The alternatives are such, that if it is really an arapaimid relative, then it is quite primitive in this lineage. If it is an osteoglossid, it must be close to the split between *Osteoglossum/Scleropages* and *Pantodon*, and therefore also close to *Foreyichthys*, which shows a partly open interorbital septum (238\*) perhaps only as a juvenile feature. But *Xosteoglossid* seems to share no important apomorphies with any of the fossils close to this position, neither to *Opsithrissops*, *Brychaetus*, *Foreyichthys* itself, nor *Heterosteoglossum* (with which it might share the inferred long, narrow body and head profile, but with a very different lower jaw).

### *Brychaetoides*

This fragmentary fossil only shows a few features to indicate its relationships: extensive interbuccal dentition (1\*) and no indication of supraorbital (4\*) indicate its osteoglossomorph status. Another clue might be a large opercular (? 24\*), and the *Singida*-level is indicated by large nasals meeting frontals (40\*), and perhaps some partly open sensory canals (?43\*). The ossification pattern of the ethmoids could be of a type (56\*) found in the osteoglossiform–mormyrid group, while it is very uncertain whether there is a reticulate scale pattern (66\* – but there are pores through the tubercles on the inner surface).

The teeth are clearly osteoglossiform (211\*), and perhaps the parasphenoid part of an interorbital septum is visible (? 156\*), and it has the broad,

medial ascending process of primitive osteoglossiforms (and therefore not the *Opsithrissops* level; 231\*). Frontals are evidently with lateral expansion like phareodonts (214\*; therefore not 237\* the more advanced loss of this trait, a reversal), but another feature is the lack of nasals meeting (226\*) as they do in advanced osteoglossiforms. It probably has a long lower jaw as in living Osteoglossidae (239\*; but has not lost the ossified parethmoid like *Osteoglossum*; 281\*). The maxilla was not attached firmly to infraorbitals, and it may have had some mobility (290\* partly) like in arapaimids, but with a longer mandible (not 31\*). Its own specializations, e.g. the pattern of dentition, would lead to the conclusion that it seems to be a primitive osteoglossiform branch at the level below *Phareodus sensu stricto*.

The relations of cf. *Brychaetus* are quite obviously based on the characteristic and huge teeth, while its scales are not entirely similar to the London Clay species. The small indeterminate 'osteoglossiform' has the large rounded opercular of advanced osteoglossomorphs (24\*), and large coracoid of even more advanced forms (46\*). However, it does not have the concomitant very large pectoral fin, neither short ventral arm of preopercular (45\*; characterizing the level above *Singida*, but reversed in arapaimids), and it lacks the reticulate scales (66\*) as do most of the Danish osteoglossiforms. Its most significant feature may be its apparently long, low body (232\*) with almost 40 vertebrae seemingly in front of the pelvic region (perhaps twice that number in total). This could indicate a level of *Opsithrissops* or higher on the osteoglossid lineage, and the above number is exceeded only by *Osteoglossum* and *Heterosteoglossum*. If the long ventral arm of the preopercular is interpreted as a reversal, it is an arapaimid characteristic (32\* – but on the other hand also shared with *Heterosteoglossum*), and these also have rather long bodies (307\*) with a similar number of vertebrae, c. 80, in *Arapaima*. The conclusion must be that this fossil probably is a 'higher' (derived) osteoglossiform, but very imprecise as *sedis mutabilis* (with perhaps a tendency for the arapaimid lineage, which only more complete fossils can test).

Finally it should not be overlooked, that in Taverne's model both *Opsithrissops* and *Brychaetus* are placed on the osteoglossid stemlineage based on very weak arguments, namely two consecutive apomorphies (elongate body, 232\* and hypural 3–5 fused to u2, 85\*), which are paralleled immediately during the first two steps of the arapaimid lineage. Only because the very dubious *Laeliichthys* is placed as a primitive arapaimid (based on 9 synapomorphies of which three are reversals, two or perhaps three are parallelisms with Hiodonts and Early Cretaceous Huashiidae, and the

remaining three traits are impossible or very unlikely to be observed with certainty in such tiny fossils [5 cm fish, cf. my scepticisms above]), the aforementioned features 232\* and 85\* are not reconstructed already for the morphotype (last common ancestor) of arapaimids and osteoglossids. If this ancestor was supposed to have those features *Opsithrissops* and *Brychaetus* should be placed either with uncertainty at, or even below, this ancestor in the osteoglossiform stem-group. And in the same way also *Foreyichthys* and *Heterosteoglossum* should be placed near this ancestor, but presumably still as stem-group osteoglossids. The net result would be that the osteoglossiform crown-group would be characterized by some extra synapomorphies, namely the above 232\* and 85\*, but further also the reduction of the lateral expansion of frontals (237\*) and the loss of supramaxilla (23\*; see p. 261). With this bone 'retained' in all of *Opsithrissops*, *Brychaetus* and *Xosteoglossid* around the level of this common ancestor, and also in *Phareoides* as the most primitive osteoglossiform stem-group member (actually also *Laeliichthys* has a supramaxilla), then it is much more likely to be a plesiomorph feature, and not several reversals, violating 'Dollo's law'. The supramaxilla undoubtedly has instead been lost in many osteoglossomorph lineages, as it is the case in many other groups of fishes.

#### *Summary of interrelationships based on Taverne's model*

All of the Danish Early Eocene bony tongues seem in the framework of Taverne's model (1998, which is almost unchanged since 1979, only the fossil Ichthyodectiforms have been left outside Osteoglossomorpha following Patterson & Rosen 1977) to be osteoglossomorphs more 'advanced' than Hiodontids or rather related to the recent sister-group of the latter (that is Osteoglossi relatives, below). Only *Furichthys* is so primitive as to be an advanced member of the stemgroup of Osteoglossi, all the others are osteoglossiforms. *Brychaetoides* may belong in the osteoglossiform stem-group as a non-Mormyriiform, while the four others are possibly crown-group members (or nearly so) with *Xosteoglossid* and the small form in uncertain positions between the two recent subgroups Arapaimidae and Osteoglossidae. *Brychaetus* and *Heterosteoglossum* are in advanced positions in the osteoglossid stem-group (where *Foreyichthys* should also be placed), but none appear to be truly a member of the crown-group Osteoglossidae. Only one species is known in many details including postcranium, namely *Heterosteoglossum foreyi*, but it does not seem to be especially closely-related to any of the other fossil marine forms, while it has a few *Heterotis*-like features in the jaws, which might

suggest behaviour as plankton feeder like the extant *Heterotis*.

#### *A new name: Osteoglossi*

As is readily seen in the above discussion, there is an obvious need of a name for the monophyletic group of Osteoglossiformes and Mormyriiformes (= mormyroids plus notoapteroids), which Taverne did not include in his 1979 classification, neither in 1998. Here it is suggested that taxon name is Osteoglossi for that clade, which seems to be recognized in all of the more comprehensive recent reviews (despite disagreements over the precise interrelationships within this group). Taverne (1998) and Li & Wilson (1996a, b) suggest the relation above, while Hilton (2003) is the first to argue that notoapteroids are most closely-related to the osteoglossiform (his osteoglossid) group with the sister-group of the being mormyroids (Mormyridae plus Gymnarchidae). Hilton calls this larger group [Mormyrids [Notopterids + Osteoglossids]] characterised at his node 'D' (see 2003, figs 4 and 7 – and here his fig. 4B is used as Fig. 7) an 'unnamed group', but it is quite obvious that this crown-group should have a name as sister-group to extant *Hiodon*, a crown-group containing two living species.

This taxon, Osteoglossi, is not identical to Hilton's Osteoglossiformes, which also contains fossil *Ostariostoma* (a problematic relationship) and therefore is a 'stem-based' taxon as opposed to the crown-group Osteoglossi (a 'node based' taxon – see de Queiroz & Gauthier 1992 and Bonde & Westergaard 2004). It is remarkable that Hilton, a neontologist, nearly always names taxa inclusive of stem-group fossils (2003), while he refrains from giving formal names to the corresponding, well-established living crown-groups. Is this the 'Simpsonian' legacy? Evolutionary tradition may destroy proper biological systematics by always insisting on fossils and 'ancestors' in order to make phylogenies and their reflected classifications more objective (or 'less hypothetical' as it was claimed – see Bonde 1977). The same story is behind the eternal quarrels over the 'true meaning' of birds, the taxon Aves, and this has very important consequences for discussing the age and origin of a group, whether one talks about the crown-group or the crown- plus stem-group – or somewhere in-between (as is usually done by palaeontologists, e.g. in the case of Aves or *Hiodon*).

#### *New classification of the Osteoglossomorpha*

Below is a classification of Osteoglossomorpha, based on the cladogram from Taverne (1998, fig. 22); but changed for *Foreyichthys*, here placed after *Brychaetus* at the base of *Pantodon* plus Osteoglossidae, as above. Also *Palaenototeropterus*

and the six Danish osteoglossiforms have been introduced (underlined in the classification below) in their proper positions, and *Joffrichthys* has been moved to conform with Li & Wilson (1996b). The taxon name Osteoglossi is coined for crown-group of osteoglossiforms plus mormyriiforms. Here also (minimum) ages are added to give an immediate idea of the minimum ages of the nodes (splits, speciations), which can, in fact, be used as both a relative and absolute rank, especially if ages are given as millions of years (see Bonde & Westergaard 2004).

The most dubious taxa, marked [?] in the above classification of Taverner's trees (1998, figs 21, 22; Fig. 5) have been removed (they could perhaps be reinstalled as Osteoglossomorpha *incertae sedis*), and superfluous taxon names are avoided, like monotypic families (e.g. †*Singida* instead of †Singidae). On the other hand a few intermediate taxa are indicated as taxon A, B etc., they are not all strictly necessary as formal taxa. 'Taxon D' is a total group, that is, crown-group Osteoglossidae plus its entire stem-group (back to the split from Arapaimidae), and a taxon name seems necessary to express that this taxon is interchangeable (shown as mut.) at the same level with Arapaimidae (total group), and the two Danish fossils, *Xosteoglossid* and the 'small indet osteoglossiform'. In the same way 'taxon B' needs a name for expressing that at a higher level in the hierarchy this group is

interchangeable with *Musperia*, *Phaerodusichthys* and *Dapedoglossum* (all indicated mut.) at this level. But 'taxon A' is not strictly necessary, as it only gives a name to the latter level where all members have a certain synapomorphy, in this case character 226, although unknown for *Phaerodusichthys*, which is known only from jaw fragments. The latter has been placed here by Taverner (1998, 131) only due to its strong ascending process of premaxilla, which thus is similar to phareodonts (see also Gayet *et al.* 2001 – and like *Brychaetoides*). It is, however, problematic at which stage this heavy process at the symphysis was developed because, in the mormyriiform sister-group there is such process on the rather small premaxillae in notopterids (Taverner 1978), but the premaxilla is not known for the next more basal branches, *Singida* and *Kipalaichthys* (Greenwood & Patterson 1967; Taverner 1976), and the small Huashiidae have reduced upper jaws and the premaxilla of Hiodonts is a thin bone without an ascending process (Taverner 1977; Hilton 2002). So the strong ascending process may have been characteristic even in the stem-group of Osteoglossi, and does not indicate a very precise level for the position of *Phaerodusichthys*. Whether it belongs exactly at this level or not does not change the fact, that the mutually interchangeable groups could just have been sequenced between *Phareodus* and *Monopteros* without creating a name for taxon A.

#### New classification of Osteoglossomorpha, including all marine fossils

##### Osteoglossomorpha

###### Hiodontiformes

†*Ostariostoma*, L. Cretaceous/E. Paleocene

†Lycoperidae [3+ gen.], E. Cretaceous

Hiodontidae [*Hiodon*, L. Eocene & 3–4 extinct genera, since E. Cretaceous, with *Eohiodon*, M. Eocene]

†Huashiidae [2 gen.], L. Cretaceous

†*Singida*, Eocene

†*Furichthys*, Eocene

###### Osteoglossi, new crown-group

###### Mormyriiformes (total group)

†*Palaeonopterus* [added here], M. Cretaceous

Notopteridae, Eocene-Oligocene

###### Mormyroidei

###### *Gymnarchus*

Mormyridae [c. 14 gen.], Pliocene

###### Osteoglossiformes (total group)

† *Brychaetoides*, Eocene

†*Phareoides* [= †'*Phareodus*'], Eocene

†*Phareodus*, Paleocene

###### Taxon A

†*Dapedoglossus* [= †'*Phareodus*'], Eocene, mut.

†*Musperia*, Eocene/Oligocene, mut.

†*Phaerodusichthys*, Paleocene, mut.

## Taxon B mut.

†*Monopteros*, Eocene

## Taxon C

†*Xosteoglossid*, Eocene, mut.†'small indet. osteoglossiform' (Mo-clay), Eocene, mut. (aff. Arapaimidae?)

## Arapaimidae, mut.

†*Joffrichthys*, Paleocene†*Trissopterus*, Eocene†*Sinoglossus*, Eocene*Arapaima*, Pliocene?*Heterotis*

## Taxon D, mut. (total group)

†*Opsithrissops*, Eocene†*Brychaetus* [2 spp.], Paleocene – Eocene†*Foreyichthys*, Eocene†*Heterosteoglossum*, Eocene

## Osteoglossidae (s.l.)

*Pantodon**Scleropages* (? Eocene/Oligocene)*Osteoglossum*

Symbols, abbreviations and position of †*Foreyichthys* as in the classification on p. 265. The most dubious taxa from Taverne's classification (1998) removed. †*Joffrichthys* placed according to Li & Wilson (1996b) and Taverne (1998, Addendum 1). Danish taxa underlined. [. . .] remarks about content of a taxon, synonyms and diversity of fossil taxa. Taxon C represents the Osteoglossiformes crown group with two Danish fossils in uncertain position; they may be in the stem group as listed, but could be inside the proper crown group (Arapaimidae plus Osteoglossidae).

It is obvious, that because the three more dubious osteoglossiform genera from Lower to mid. Cretaceous, marked [?] in the classification p. 265, are removed, then the need of very long 'ghost lineages' (Norell 1992) is greatly diminished, the only ones being those between *Plesiolycoptera* and *Eohiodon* from Early Cretaceous to mid Eocene (c. 70 ma), for *Palaeonotopterus* to Notopteridae from mid-Cretaceous to Eocene–Oligocene (c. 65 ma), for *Ostariostoma* from Early to latest Cretaceous (c. 60 ma), and those for *Arapaima* Paleocene to Pliocene (c. 55 ma), and for Mormyroidei, *Pantodon* and *Osteoglossum*, all Eocene–Oligocene to Recent (c. 40 ma). It is seen that all known fossil or recent genera of Osteoglossiforms (of the crown-group) are not older than Paleocene (minimum ages), contrary to the implications of Taverne's placement of *Paradercetus* as sister-group to *Heterotis* giving both that lineage and that of *Arapaima* (both actually comprising only one species) a minimum age about 100 ma.

The relative high ages of Recent genera also in this phylogenetic classification with the mentioned lower to mid Cretaceous fossils removed to an uncertain position (perhaps as stem-group osteoglossiforms as discussed by Bonde 1996), namely Paleocene for *Heterotis* and accordingly also for *Arapaima*, and mid-Eocene for *Hiodon* (indicated as minimum ages by *Joffrichthys* and *Eohiodon*

respectively), may be an artifact of the traditional way of naming such monophyletic taxa including part of their stemgroup as 'genera.' If taxon names were instead only used for crown-groups (since last common ancestor of extant members), then the two extant species of *Hiodon* alone would define that name for the (crown) genus, which might be very young, perhaps from the Pleistocene, as defined by their speciation (node or separation from each other).

Only a fossil referred to one of those two extant species would indicate min. age of that speciation, and therefore of *Hiodon* in the restricted sense. The *Hiodon consteniorum* from Lower Eocene is in a stem-group position, and therefore of no relevance for the age of the *Hiodon* crown-group. Furthermore, lineages with only one species today like *Heterotis* and *Arapaima*, cannot really give an estimate of the age of their respective 'crown group lineages' because no splits (or nodes) are known (and a single species is at the limit of usual definitions of a [monophyletic] group). There may well have been some so far unknown and extinct species split away from these lineages and having evolved characteristics to indicate a different species and thereby a (crown) group (to be referred to by a generic name if such fossils were found) of minimum age as the fossil taxa. The possible Pliocene scales (Taverne 1979)

might do the trick for *Arapaima*. The same arguments count for *Pantodon* and osteoglossids, the latter comprising two crown-group genera each with two species, but there are no fossils to indicate their ages, which for all of them might be very young (even a Pleistocene distribution pattern – across the ‘Wallace line’ – might well be a possibility for the species of *Scleropages*) – completely in disagreement with the molecular analyses by Kumazawa & Nishida (2000), which are said to indicate the split among the species of *Scleropages* in SE Asia and New Guinea–North Australia (*S. formosus* and *S. leichardti* respectively) to be of Early Cretaceous age (Pouyaud *et al.* 2003 recognised six ‘species’ within *S. formosus*!). From a palaeontological viewpoint this age appears to be very unlikely, even if one accepts that some scales can actually be identified with confidence as *Scleropages* from Eocene–Oligocene on Sumatra (Sanders 1934) or otoliths and fragments from Palaeocene in Belgium (Taverne *et al.* 2007) (see the biogeographical discussion).

#### *Relationships in Hilton’s model*

If Hilton’s hypothesis of osteoglossomorph interrelationships is accepted as a framework for interpreting the Danish fossils it remains to be seen if it makes a significant difference for the position of those fossils (specifically if any group of the marine genera should emerge as a clade). This could have some bearing upon their (palaeo-) biogeographic significance, because in the extreme case that all marine genera formed a single monophyletic group, this would facilitate the hypothesis that at least the Osteoglossi is a ‘primary freshwater group’ with a Gondwana origin and spreading only by freshwater routes – apart from that single excursion into marine waters.

Hilton’s model(s) from 2003 (Fig. 7) are based on very thorough discussions of every single character used to generate his cladograms. It is one of the largest osteoglossomorph datasets to be employed in a cladistic analysis based upon 19 terminal taxa (and only one outgroup, *Elops*) and 72 characters carefully selected (several of those used in Taverne’s analysis [1998 and above] were discarded for reasons stated in detail). Unfortunately only few fossils were included (*Lycoptera*, *Eohiodon*, *Ostariostoma*, *Joffrichthys*, *Phareodus*, *Brychaetus*, *Palaeonotopterus* and a fossil species of *Notopterus*, *N. primaevus* but the latter and *Brychaetus* do not appear in Hilton’s trees).

The latter taxon was considered synonymous with *Phareodus*, and that genus alone (then based on three species, two of which are from freshwater deposits) was coded (e.g. Hilton 2003, p. 57 and App. I). A surprising number of features were

considered unknown for *Phareodus*, actually the most well-known of all fossil osteoglossiforms, of which even-acid prepared specimens exist. It is also unfortunate that Hilton used only one outgroup, although many primitive teleosteans were discussed, and a few of those from clupeocephalans and/or euteleosts or perhaps Jurassic teleosts could easily have been added to the matrix. It is also a little disturbing that state 0 is not always the most plesiomorph state, even when that information is well established.

The comparisons below refer to Hilton’s (2003, p. 25–27) characterizations of the nodes of his tree, fig. 4B (Fig. 7) by listing the relevant character number, which are described in detail by Hilton (p. 27–82). The states are only given, when they are different from [1] and advanced (i.e., if the state is not given with the character number then it is advanced and assumed to be [1]).

*Heterosteoglossum* fits node A, Osteoglossomorpha, by possessing characters 20, 22, 28 [0] (perhaps primitive), 56 [0] (quite likely a primitive trait), 65, 68, 69 [0] out of the 15 features listed for this node. From node X (all taxa but *Lycoptera*, based on 4 traits) it possesses 37, probably 36, but not 7. Of six hiodontid features, node B, it may have something like the postpelvic bone (62). From node C, Osteoglossiformes [including *Ostariostoma* plus the recent crown-group (much more inclusive than Taverne’s taxon name)], it possesses 60, 66 and 71 [2] and of the 17 features it may also show 5[0] and possess several, which are not preserved, but it does not have 7 [2], 43 and 58. Of the five traits for D, above called Osteoglossi, it has 68 [2], but probably not 41.

Among 7 features for node E, Hilton’s new ‘Osteoglossoidae’ (=Osteoglossidae plus Notopteridae) it possesses only 6 [2] and 67, but not 37 [0] and 65 [2], and perhaps not 32 [2] and 2. (This lack of many synapomorphies seems odd here). From Hilton’s 10 characters of his *sensu lato* Osteoglossidae, node F, it possesses 7 [3], 29, 41 [0] and perhaps 24 [0] and 25, but apparently does not show 2 [2], 21 [0] and 49. Node G (unnamed, corresponds to his Osteoglossidae crown-group, should clearly have a name as above), with three traits sharing 9 [0] with *Heterosteoglossum*, but not 72 [2] (the fully reticulate scales), and 35 (subopercular size) is uncertain. Hilton’s node H, Heterotinae (=Taverne’s Arapaimidae, above) has 10 features, of which *Heterosteoglossum* may have 32 [0] and 43 [0] (both primitive), while it lacks 23, 28 and probably 42 [2]. From the sister-group at node I, Osteoglossinae (Taverne’s Osteoglossidae plus Pantodontidae), with 4 traits it has 61, 63 and probably 3, but not 33. From node J, unnamed, with 6 traits ‘shared’ by *Pantodon*, *Phareodus* and *Singida* (most are unknown for one or both fossils)

it has 58 [0] ('presumably plesiomorph' Hilton, p. 71) and uncertainty about all others. With node K (unnamed for *Pantodon* plus *Singida*, for the latter only one trait is known), having 8 features, it only may be said to share 72 (the scales with both reticulate and radial furrows), but does not have 29 [0], other features uncertain. Node L is Hilton's unnamed group for *Scleropages* plus *Osteoglossum* (Taverne's Osteoglossidae) with five synapomorphies and only sharing 12 and 37 with *Heterosteoglossum*, others unknown.

Summing up this distribution of features which are recognizable in *Heterosteoglossum* the pattern in Table 1 appears. But how can we interpret this pattern in terms of relationships? *Heterosteoglossum* clearly has some basic osteoglossomorph features, although two of them are primitive teleostean traits, and some evidence for the next level on the tree. There are also several special similarities with specific subgroups such as *Osteoglossum* plus *Scleropages* (Osteoglossidae of the preceding discussion) and the next higher level (Hilton's Osteoglossinae including *Pantodon*). But between this level and the basic level there is a suspicious lack of supporting characters, (actually more characters are known *not* to be present [17] than supporting ones [13]). This implies a lot of homoplasy because of the missing synapomorphies at several levels, if *Heterosteoglossum* is placed within Hilton's framework. Although *Heterosteoglossum* appears best interpreted as related to Hilton's osteoglossines based on 5 synapomorphies, the lack of 20 synapomorphies (from the *c.* 50 that are possible to verify in the fossil) is troublesome. Also some of the 'synapomorphies' at different levels are really primitive retentions (e.g. the two heterotinae 'synapomorphies'), made possible in Hilton's analysis due to the lack of more outgroups. One should note, that the conclusion here for *Heterosteoglossum* is exactly the same as when using Taverne's model, and almost 100 features were checked.

*Furichthys* shares the following traits with Hilton's nodes:

Node A: 20 (no supraorbital) and all others unknown.

Node X: 37 (only slightly developed proc. asc. on premaxilla), but not 7.

Node B; Hiodonts: none known.

Node C: Osteoglossiformes: perhaps 30 (palato-ectopterygoid), but probably not 43, others unknown.

Node D: Osteoglossi (new name): not 41, others unknown.

Node E: probably 6 [2] (nasals meeting), but not 37, the rest unknown.

Node F: Osteoglossidae: 41 [0] (primitive), probably 7 [3] (nasals flat, broad) and 21 [0] (primitive), but not 44.

Table 1. *Heterosteoglossum* features 'mapped' on Hilton's model

Node	Number of characters <i>Heterosteoglossum</i> possesses/does not have	My comments in parentheses; Hilton's taxonomy	Total number of 'node-apomorphies'	My systematic conclusion
A	6		15	Osteoglossomorph
X	2	(two traits plesiomorphic)	4	Osteoglossomorph crown-group
B	1	Osteoglossomorpha excl. stem (dubious homology: postpelvic)	6	not hiodont
C	3	Osteoglossiformes	17	? Osteoglossiform
D	1	Osteoglossiformes crown-group	5	? Osteoglossi new
E	2	new Osteoglossoidae	7	?
F	4	'Osteoglossidae'	10	?
G	1	Osteoglossidae crown-group	3	? not related
H	2	'Heterotinae'	10	Osteoglossin/-id
I	3	'Osteoglossinae'	4	(primitive feature)
J	1	<i>Pantodon</i> + 2 fossils	6	(parallelism)
K	1	<i>Pantodon</i> + <i>Singida</i>	8	? closely-related
L	2	Osteoglossinae + <i>Scleropages</i>	5	
Total	29		100	

Node G: 9 [0] (? primitive), but not 72 [2].

Node H: apparently 43 [0] (primitive), but not 42 [2] and 47.

Node I: Osteoglossinae: perhaps 3 (equal frontal width).

Node J: *Pantodon* plus fossils, nothing is known.

Node K: only 43 [0] (primitive), the rest unknown.

Node L: 37, but the lack of an ascending process on the huge, very specialized premaxilla in *Furichthys* is probably not the same as the lack of such process on the tiny premaxilla in osteoglossines; nothing else known.

Comparison with notopterids and mormyroids is of no relevance, *Furichthys* appears to be a very primitive osteoglossid (*sensu* Hilton), with synapomorphies no higher than node F, or perhaps even no higher than node E in the stem-group of his new clade, combined notopterids + osteoglossids. This corresponds approximately to the position in the stem-group of Osteoglossi in the analysis based upon Taverne's model (where also mormyriforms are included in the crown-group), where the level would correspond to node D.

There are many characters of *Xosteoglossid* to relate to the Hilton model – it has the following characterizing his nodes:

Node A: 20, 22, 28 [0], 31, but not 40 (lack of supramaxilla, which is coded incorrectly anyway).

Node X: it probably has 36, but not 7.

Node B: it shows no hiodontid features.

Node C: it has 5 and 66, and probably 30, but not 7 [2] and probably not 43.

Node D: those five features are unknown in the fossil.

Node E: it has 10 and 37 [0], but not 32 [2] and probably not 2.

Node F: it has 7 [3], 21 [0], 25, 29, 41, but not 2 [2] and probably not 49.

Node G: it has 9 [0].

Node H: it has 32 [0] and probably 39, but not 23 and 28.

Node I: it has 61 and probably 3 and 33.

Node J: it has no information on those features.

Node K: it may have 72 (the reticulate scale character weakly developed), but not 29 [0].

Node L: it does not have 12 and 37; Node M etc, notopterids and mormyrids, are not relevant.

*Concluding remarks.* *Xosteoglossid* has some features up to the levels of node I (osteoglossines) and node H, (heterotines) but it lacks a few from the latter group. Concerning the lower nodes *Xosteoglossid* shows most of the characteristic features (with only one or two traits lacking at some levels), but it has no hiodontid traits. Again, as in Taverne's model, the conflicting features from osteoglossines and heterotines (osteoglossids and

arapaimids in his terms) gives an uncertain position (*sed. mut.*) between those two groups. So it may belong to the crown-group osteoglossids (osteoglossiforms for Taverne) or just outside as an advanced member of the stem-group.

The few characters that can be checked for *Brychaetoides* indicate that from node A it has character 6 and perhaps 44. From node X it lacks 7, and it has none of the hiodontid features of node B. From node C it has 6 [0], but may lack 44 [0]. It does not give information on node D features, but from node E it has 37 [0], but not 6 [2]. From node F it can only be seen to show 41 [0], while it lacks 7 [3]. Node G features are unknown, and from node H it just lacks 23 with the rest unknown. It gives no information on node I and J characters, but from node K (*Pantodon*) it has 6 and perhaps 21. It is unknown for node L traits.

It can thus be confirmed for *Brychaetoides* that it shows a few traits related to the *Pantodon* group and thereby to osteoglossines, but shows no features from heterotines. From more basal nodes, if it shows any of the characters, it generally has one and lacks another at each level, and it shows two features of the most basal osteoglossomorph node. To conclude, *Brychaetoides* should (in accordance with its advanced features) be placed near *Pantodon*. This seems quite different from the more basal position indicated in Taverne's model. But one should note that in Hilton's model, not very surprisingly, *Phareodus* is closely-related to *Pantodon* (and *Singida*), causing *Brychaetoides* to shift up into the crown-group of osteoglossiforms/-glossids past *Xosteoglossid*. In the original description of *Singida*, and shortly after (Greenwood & Patterson 1967; Nelson 1969; Murray & Wilson 2005), a relationship to *Pantodon* was seriously discussed, and in the analysis of *Phareodus* by Li *et al.* (1997) phareodonts (including *Brychaetus*), *Pantodon* and *Singida* appear as consecutive branches on the way towards *Osteoglossum/Scleropages* with only 1–2 steps between those branches. Li *et al.* (1997) conclude their research with a model of the osteoglossomorph interrelationships that, for the recent forms, is exactly the same as Taverne's model.

*Brychaetus* is synonymized with *Phareodus* in the Hilton model, as done by Li *et al.* (1997), and it would therefore also be moved in the system. The small indet. osteoglossiform can only be related to a few characters in Hilton's scheme. It probably has 56 of node A (epipleurals absent) and 60 from node C (coracoid fenestra), and it does not have the osteoglossine feature of a very deep opercular (no. 33 of node I). Accordingly it should be placed somewhere between node C and node I. This is also where it ended up with a little

more precision in Taverne's model, namely at the node leading to heterotines and osteoglossines, or as an osteoglossid *incerta sedis* (using Hilton terms corresponding to node G).

Also with Hilton's model as framework the six Danish fossils are distributed over the cladogram from the stemgroup of non-Hiodont osteoglossomorphs (*Furichthys*) to inside the crown-group of the osteoglossines/osteoglossids proper (*Heterosteoglossum*) or just high in their stemgroup, and with none of them closely related to each other or to other marine osteoglossiforms (the latter, however, 'hidden' under synonymy in Hilton's model).

Hilton (2003) found after profound discussion several severe problems in the phylogenetic analysis by Li & Wilson (1996a), which could otherwise also have been used for comparisons with the Danish fossils, so although the latter included as much as 14 fossil taxa and three living outgroups plus the Jurassic fossil *Leptolepis*, I refrained from using their model. My own experience (in prep.) trying to relate *Sinoglossus* from the Chinese Eocene to their model is also that there are many problems with both their interpretation and coding of characters, so their model of relationships is not very easy to use.

The more recent quantitative, cladistic analysis of osteoglossomorph interrelationships by Zhang (2006; acquired after submitting this paper) is based on 65 characters and has exactly the same relation between the living forms as in Taverne's model. Zhang includes many Chinese fossils, not in the models mentioned above, but has no other Asian fossils, none of the European, marine forms apart from *Brychaetus*, no African fossils but *Singida*, and none from South America. Zhang keeps the phareodonts including *Brychaetus* together with *Singida* as a sister-group to osteoglossids including *Pantodon*, and those two groups combined as sistergroup to arapaimids. Therefore comparison with the Danish fossils is unlikely to give a result very different from the above comparison with Taverne's model, apart from the obvious one that *Brychaetus* is placed in a monophyletic phareodont group.

### Phylogeny and distribution

The marine, fossil osteoglossomorphs are of special interest to zoogeographers because they are related to one of the groups of fishes, which today comprises only so called 'primary freshwater fish' (Myers 1949, also used in biogeographic texts like Darlington 1948, 1957, 1965), which appear to be completely intolerant of saltwater, so that their present distribution cannot be explained by migrations via seawater. To reconstruct past distributional history of a group in any reasonable way,

a secure phylogenetic background is mandatory with precise knowledge of the interrelationships of the members of the group and of the group to its most closely-related taxa (Nelson 1969, 1976; Patterson 1975, 1981; Gayet 1987; Grande & Bemis 1999). During the period of these studies the concept 'vicariance biogeography' was developed by Nelson and his colleagues (see Rosen 1978; Nelson & Platnick 1981; Nelson & Rosen 1981) as a method which corresponded better to a world knowledgeable of continental drift.

The experience of using Taverne's (1998) and Hilton's (2003) respective phylogenetic models, which have been constructed in different ways, perhaps to be characterized as 'qualitative-intuitive' and 'quantitative-rigorous' respectively, has shown the following. For the position of the six taxa of Danish fossils within osteoglossiforms the results are very similar for four of these taxa, the three with most information present, *Heterosteoglossum*, *Xosteoglossid* and *Furichthys*, and the small indeterminate form: *Heterosteoglossum* is just inside the crown-group Osteoglossidae (Taverne's taxonomy) on the lineage to *Osteoglossum/Scleropages*, or just outside as an advanced member of the stemgroup. *Xosteoglossid* can be placed best in an uncertain relationship with the two families Osteoglossidae and Arapaimidae, and be classified *sedis mutabilis* with these families. *Furichthys* seems much more primitive, and belongs in the stem-group for Osteoglossi (Osteoglossiforms plus Mormyriiforms including notoapterids; Taverne's terms) as an advanced member more derived than the *Singida* branch, although in Hilton's model it tends to be placed slightly 'higher' in the stem of a less inclusive clade, his new Osteoglossoidei, or even in the stemgroup of his Osteoglossidae (osteoglossines plus heterotines). On the contrary the small osteoglossiform seems placed with greater precision in Taverne's model, namely at the node for crown osteoglossiforms, perhaps even near the base of the branch to arapaimids. In Hilton's model it can, due to the very few (only 3) of his characters that can be observed, only be placed somewhere between node C and I (six splits – that is as an osteoglossiform no more advanced than a stem-group osteoglossine in his terms).

There is a greater difference concerning *Brychaetus* (by Hilton coded as *Phareodus*) and *Brychaetoides*. In Taverne's model *Brychaetus* is an advanced member of the osteoglossid *sensu stricto* stem-group far 'above' *Phareodus*, while in Hilton's model the two are coded together and end up 'one step higher' inside the osteoglossine crown-group as closely-related to *Pantodon* (and *Singida*). The difference is much more drastic for *Brychaetoides*, in Taverne's model placed in the stem-group of

osteoglossiforms (= Hilton's osteoglossids) just 'below' *Phareodus sensu stricto*. But, because the latter in Hilton's model has moved many 'steps up' (six nodes higher), into the lineage of *Pantodon*, then *Brychaetoides* apparently moves with it. In this model this new genus is placed very close to *Brychaetus/Phareodus*.

Hilton's model comprises no marine forms, but by the addition of the Danish fossils in six (at least five) different positions in the osteoglossiform part of the tree, each of these positions in an evolutionary context will constitute separate excursions into the sea. The same is true for Taverne's model, which already included five marine forms, all at different branches of the osteoglossomorph tree. By adding the Danish marine fossils there will be yet six more marine branches on the tree (or at the very least four, if both *Xosteoglossid* and the small form here placed near the split between arapaimids and osteoglossids could be shown to join another marine lineage).

This demands a closer analyses of the implication for the minimum number of osteoglossomorph excursions into the sea because, in the most parsimonious model for the ecological preferences and changes of habitats of these fishes, several neighbouring marine branches could be interpreted as first one migration into the sea with several consecutive branches living there, and then one (or more) later re-invasion(s) of freshwater.

Before these Danish additions, the tree by Taverne (Fig. 5) – especially if *Laelichthys* is removed from its uncertain position as a basal arapaimid – implies that the last common ancestor of his arapaimids and osteoglossids (including *Pantodon*) is most likely to have been marine. This is because on all sides of this ancestor node there are exclusively marine branches (*Monopteros*, *Thrissopterus*, *Opsithrissops* and *Brychaetus* and it is suggested that *Foreyichthys* is more derived than *Brychaetus*). So the most parsimonious solution for the habitat of this ancestor of the two families is the sea, which was invaded before the *Monopteros* branch. The arapaimids then re-invaded freshwater after the *Thrissopterus* split, and *Joffrichthys* gives the minimum date of that as Paleocene. The osteoglossids did the same after the split with *Foreyichthys* (or *Brychaetus*) and, if there really are *Scleropages* scales in the Eocene of Sumatra (Sanders 1934) and otoliths and skeletal fragments in the Belgian Palaeocene (Taverne *et al.* 2007), it would have had to be earlier than that.

Even if the criticism above is not acceptable concerning the position of *Opsithrissops* and *Brychaetus* on the osteoglossid lineage, and they should be relegated down to just above *Monopteros* in the top of the stem-group for osteoglossiforms, this would make no difference for the two families. They would still have marine forms at their bases

(*Thrissopterus* and *Foreyichthys* respectively), and several marine forms in the top of their stem-group.

It is quite clear, that the addition of the Danish marine forms to the tree makes this hypothesis much more evident, because both *Xosteoglossid* and the small form are placed somewhere near this ancestral node. Furthermore *Heterosteoglossum* is placed near the top of the osteoglossid stemgroup, if not inside the crown group on the *Osteoglossum/Scleropages* lineage. The latter position would imply that both that lineage and *Pantodon* were separate re-invasions of freshwater. These invasions may not be older than Eocene, in fact they might well be younger (unless it is really a *Scleropages* [stem group, presumably] described by Taverne *et al.* 2007 – above).

*Furichthys* and *Brychaetoides* are not so well known anatomically and therefore probably not quite as safely placed in the phylogeny, but most likely they occupy positions near and probably below respectively above the 'common ancestor node' for the two lineages of osteoglossiforms and mormyriforms (including notopterids). *Furichthys* is 'high' in the stem-group, and *Brychaetoides* near the base of the osteoglossiform lineage. The implication of this is clearly that the common ancestor of those two lineages was also marine. This would be even much more evident if it were right that *Phareodus sensu lato* is a natural group comprising both *Phareoides* and *Dapedoglossum* (whether *Brychaetus* and perhaps *Musperia* are included or not is unimportant for this argument – it may complicate the model a little though). In that case this genus, *Phareodus (sensu lato)* may constitute just one branch and one re-invasion of freshwater by Late Cretaceous, and the entire stem-lineage for osteoglossiforms would evidently have been marine including the node from which it originated by splitting from mormyriforms by the mid Cretaceous or earlier.

If we look at the base of the osteoglossomorph tree it is clear that all the closest outgroups of this clade are marine, whether one prefers the Patterson & Rosen model (1977) with osteoglossomorphs as sistergroup of all other living teleosts, or Arratia's model (e.g. 1997, 2000) with elopomorphs in that basal position. All the early teleosts from the Jurassic at the top of their stem-group are also marine (Arratia 1997; Patterson & Rosen 1977, 2000), so osteoglossomorphs originated in the sea, we just have not yet found or recognized the earliest osteoglossomorphs. This carries the implication that also the hiodontiforms might be a separate migration from sea- to freshwater (by Early Cretaceous), especially because of the somewhat uncertain position of the other early freshwater branches in the tree, such as Huashiids, *Kipalaichthys* and *Singida*. If they were placed differently, either on the hiodontiform lineage or on that of the

mormyriforms (or if one or more of them are not osteoglossomorphs at all), then the simplest model could well be, that the entire stem-lineage from the root of the tree and up to the node for osteoglossids was better interpreted as marine. Such interpretation is entirely dependent on the phylogenetic positions of the many new marine members of the group.

When there was only one anomaly, *Brychaetus*, one could almost forget about it (or raise questions about its relations like Nelson 1969), and in Patterson's model (1975) a single marine form did not make much difference. But by now when there are 9 marine taxa placed in as many different positions in the tree, they cannot be ignored (unless they were all members of just one or two marine clades). They paint the entire picture in very different colours than before, and we will have to re-think the history of the bony-tongues, and wonder why they are all today so intolerant of salt water as Myers (1949) would claim (and which perhaps is not entirely true according to Taverne *et al.* 2007).

After the findings and/or reinterpretations of all the Eocene marine osteoglossiforms, there are evidently good arguments for abandoning the classical idea of osteoglossiform fishes as primary freshwater fishes clearly of Gondwanan origin with a potential of linking widespread continental areas in a comprehensive vicariance biogeographic model. Early on this was done exclusively in 'dispersalist' models like Darlington's (1948, 1957, 1965) or other 'evolutionists'. But this was not very different from 'progression' models by Hennig (e.g. 1966) and Brundin (1966) both in a phylogenetic systematic framework criticising Darlington and his 'school'. Today much historical biogeography is done with a background in vicariance theory as developed by Nelson, Rosen, Platnick and others firmly based in cladistic theory (Nelson 1969; Patterson 1981; Nelson & Platnick 1981; Nelson & Rosen 1981). In such analyses precise phylogenetic models are required in the attempts to reconstruct ancient distribution patterns of many different natural groups.

In fact, looking at a single group is not optimal, unless there are several subgroups which can complement each other. The classical single group approach, like here, as done both by 'evolutionists' of the Mayr-Simpson-Darlington school and the early 'hennigians' is often open for interpretations in terms of dispersal. As done early on also by Nelson (1975), it is dependent on the tendency of the organisms to move, migrate and disperse. One attempts to reconstruct the simplest possible migrations from one area to another, often assuming a 'need' to expand the area of occupation. A vicariance approach suggests that the land (or sea for that matter) moves or become divided with the

organisms passively moving with their habitats. Seen in a worldview of known continental drift and origin of physical dispersal barriers, this makes one less assumption about behaviour of the organisms.

But most of these models should 'face the real world', that is be tested by data, and here fossil distributions force themselves upon the interpreter in unexpected and sometimes inexplicable ways. We did not know this great diversity of marine osteoglossomorphs before testing. In an analogous way, a scientific study gave us the disturbing fact that there appears to be an Eocene anteater in Europe (Storch 1981, 1984). Should that number increase to several Old World anteaters, the history of the edentates would certainly have to be drastically rewritten – like that of the osteoglossomorphs, which should now be given up as primary freshwater fish.

## Conclusion

The description of several new marine osteoglossiforms of the Danish Eocene dramatically increases the diversity of this group. The phylogenetic positions of these marine forms on the phylogenetic tree necessitates total re-evaluation of the biogeographic history of the group, because they make it quite clear that Osteoglossomorpha is not a primary freshwater fish group with osteoglossiforms having a typical Gondwana distribution and vicariance history. Instead several subgroups of the osteoglossomorphs are separate invaders into freshwater from the sea. Both the osteoglossids (perhaps at two occasions) and the arapaimids are separate invasions, and the same may be true for the mormyriforms and probably even the hiodontiforms.

Without the findings of these many marine fossils such interpretations would never have been possible. But where would the missing marine, (Late Jurassic-) Cretaceous osteoglossiforms have been? Perhaps in the Pacific round 'Pacifica' (Melville 1966), the mythical and disintegrating continent in the middle of the ocean (which Gayet [1987] also invoked to explain osteoglossomorph distribution) from which slivers of land were squeezed into the surrounding continents mainly by subduction, so much of these marine deposits have been lost forever (including their fossils). Search in Andean Cretaceous to Palaeogene sediments and perhaps corresponding rocks in Japan or Alaska might produce some answers (and one should remember that the North American Maastrichtian has produced marine 'osteoglossid' otoliths [Nolf & Stringer 1996]).

Danekræ comprise exceptional Danish natural objects (meteorites, fossils, minerals etc.) which

when found must, following a law of 1990, be offered to the state (Hald 1993). If approved by the Geological Museum as a danekræ the finder receives a reward. The large *Furichthys* described herein, found by a German collector in about 1985, was instrumental in the process of convincing politicians to pass this legislation through the Danish parliament. The story of the danekræ and descriptions and photographs of the 200 most important danekræ (c. 500 approved since 1990) are given in Bonde *et al.* 2008.

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Institutions: FUM, Fur Museum; MGUH, Geological Museum, Copenhagen; NHM, Natural History Museum, London.

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