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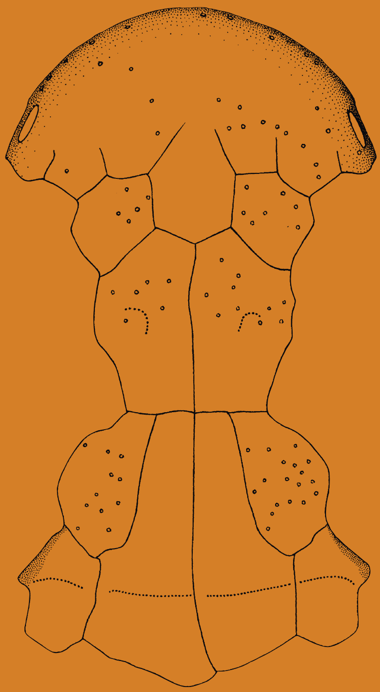
# Morphology, phylogeny and taxonomy of osteolepiform fish



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*by*

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# Morphology, phylogeny and taxonomy of osteolepiform fish

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Material of six osteolepiform genera is described, including *Askerichthys* n. gen., a new Late Carboniferous genus from Norway, *Megalichthys* Agassiz, 1835 from the Carboniferous of Great Britain, *Latvius* Jarvik, 1948 from the Late Devonian of Germany and Latvia, and *Osteolepis* Agassiz, 1835 and *Gyroptychius* McCoy, 1848 from the Middle Devonian of Great Britain and northeast Greenland. New information on *Eusthenopteron foordi* Whiteaves, 1881 from the Late Devonian of Canada is presented in the morphologic discussions. On the basis of the descriptions and previous studies morphologic variation in osteolepiforms is recorded, and it is discussed whether these variations are taxonomic or intraspecific. Morphologic clines are described and it is discussed whether they are trends. When possible, functional implications of the morphologic variations are suggested. In the phylogenetic and taxonomic section different types of characters as well as use of these characters when reconstructing phylogeny and taxonomy, is discussed. Consideration has been given as to whether diagnoses can be constructed in a more informative way by stating whether characters are necessary, sufficient or indicative. A tentative phylogenetic model based on the morphologic information in this and other works is presented. This phylogeny leads to a taxonomic model that is expressed as a review of osteolepiform taxa with diagnoses formulated as stated above. The order Osteolepiformes Woodward, 1932 is divided into two suborders, Osteolepidoidei Moy-Thomas & Miles, 1971 and Cyclolepidoidei n. suborder. Osteolepidoidei includes the families Osteolepididae Cope, 1889, Thursiidae n. fam. and Megalichthyidae Hay, 1902. Osteolepididae is divided into Glyptopominae Goodrich, 1909 and Osteolepidinae Cope, 1889. Megalichthyidae is divided into the subfamilies Ectosteorhachinae n. subfam., Megalichthyinae n. subfam. and Askerichthyinae n. subfam. Cyclolepidoidei includes Eopodoidea n. superfamily, Parapodoidea n. superfamily, and Rhizodontoidea. Eopodoidea includes the families Gyroptychiidae n. fam., Panderichthyidae Vorobyeva, 1968, Chrysolepididae n. fam. and Eusthenopteridae Berg, 1955. Parapodoidea includes the families Canowindridae Young, Long & Ritchie, 1992 and Medoevididae n. fam. Panderichthyidae is divided into Panderichthyinae n. subfam. and Elpistosteginae n. subfam. New species erected in this paper are the megalichthyids *Askerichthys heintzi* and *Megalichthys syndentolaminaris*.

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## Introduction

The group of fishes called Osteolepiformes is of great interest as they are generally accepted ancestors of probably all tetrapods. Since also considered relatively primitive (Jarvik 1968a, p. 506) it is a central group in the study of vertebrate evolution.

This work includes the following: (1) an introductory part discussing the general taxonomy of osteolepiforms, as used by other authors and as used in this work; terminological problems; a review of the stratigraphic background as well as surrounding fauna and flora of a new probably Late Carboniferous genus from Norway, and a review of material and methods; (2) a descriptive part treating macrostructures of mainly four groups: the new probably Late Carboniferous Norwegian taxon, Carboniferous material from Great Britain referred to *Megalichthys* Agassiz, 1835, Late Devonian material from Balticum and Bergisch Gladbach in Germany referred to different species of *Latvius* Jarvik, 1948, and Middle Devonian material from Great Britain and northeast Greenland referred, respectively, to *Osteolepis macrolepidotus* Agassiz, 1835, *Gyroptychius milleri* Jarvik, 1948 and *Gyroptychius groenlandicus* Jarvik, 1950a; (3) a discussion of variation and possible trends in osteolepiform morphology as well as some functional interpretations of the morphology. This part also includes new descriptions of material of *Eusthenopteron foordi* Whiteaves, 1881 and *Panderichthys rhombolepis* (Gross, 1930); and (4) a phylogenetic and taxonomic part that includes a discussion of

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concepts and methods in the study of phylogeny and taxonomy, a suggested phylogenetic model for osteolepiforms, and a resulting likewise tentative taxonomic model of osteolepiforms with some suggested amended diagnoses.

## General taxonomy

### 'Crossopterygii' and 'Rhipidistia'

The taxon Order Osteolepiformes Berg, 1937 has in a classical system been considered as belonging to the Superorder Rhipidistia Cope, 1887 within the Class Crossopterygii Cope, 1871 (Berg 1958; Romer 1966; Romer 1966; Vorob'eva & Obruchev 1967; Andrews & Westoll 1970b; Moy-Thomas & Miles 1971). Synonyms for 'Osteolepiformes' have been 'Osteolepidoidea' (Romer 1966, p. 361), 'Osteolepidiformes' (Romer 1966, p. 361) and 'Osteolepidida' (Andrews & Westoll 1970b, p. 479; Moy-Thomas & Miles 1971, p. 110; Andrews 1973, p. 174). Rhipidistia have been characterized by Moy-Thomas & Miles (1971, p. 113) by cranial dermal bone pattern, in having branched lepidotrichia, in having many more lepidotrichia than radials in the caudal fin, and in having internal nostrils (=choanae). As pointed out by Andrews (1973, p. 162) the choanae have been considered a distinctive character for Rhipidistia. Crossopterygii has by most contemporary workers been included in the taxon Sarcopterygii Romer, 1955 that includes also lungfishes. In the system suggested by Andrews (1973) Rhipidistia includes three orders; Osteolepiformes Berg, 1937, Porolepiformes Jarvik, 1942 and Rhizodontiformes Andrew & Westoll, 1970b. The former two were considered as having choanae, whereas this was unclear in Rhizodontiformes and its inclusion in Rhipidistia was tentative. Non-rhipidistian crossopterygian groups include Coelacanthiformes (=Actinistia) and Onychodontiformes (=Struniiformes, Jessen 1966, p. 334).

The validity of Crossopterygii (Stensiö 1963, p. 82; Jarvik 1968a, p. 515, 1968b, p. 226; Bjerring 1971, p. 189) and Rhipidistia (Jarvik 1942, pp. 142, 284; Andrews 1973, p. 173) has been doubted. More modern works that discuss or use these terms are Ahlberg (1991a), Cloutier & Ahlberg (1996, pp. 465, 468) and Janvier 1996 (pp. 198, 247). Ahlberg (1991a, p. 280) introduced a system where Rhipidistia has a new meaning and where it includes the superdivisions Tetrapodomorpha Ahlberg, 1991 and Dipnomorpha Ahlberg, 1991. Tetrapodomorpha are forms with choanae and includes Osteolepiformes, Rhizodontida (=Rhizodontiformes = Rhizodontoidea in the here suggested system), Panderichthyida Vorobyeva, 1981 (=Elpistostegidae = Panderichthyidae in the here suggested system) and Tetrapoda. Dipnomorpha are forms without choanae and includes (Ahlberg 1991, p. 280) porolepiforms, dipnoans and primitive genera like *Powichthys* Jessen, 1975 and *Youngolepis* Chang & Yu, 1981. Thus, Ahlberg considered that porolepiforms were without choanae. There has been a long dispute (cf. Janvier 1996, p. 204) as to whether porolepiforms show choanal passages or not. Bjerring (1991) apparently had solved this when he described the presence of a passage from the nasal sac to the mouth roof (called fenestra exotremiscalis by Bjerring) in a specimen of *Glyptolepis groenlandica* Jarvik, 1972 prepared by serial sectioning. However, Clément (2001) claimed that Bjerring's result was due to distortion of the *Glyptolepis* Agassiz, 1844 specimen and described a specimen of *Heimenia* Ørvig, 1969 that showed no choanae. The authors do not in this work take a stand in this dispute, but will mention the possibility that there – in this respect – may be variation within the porolepiform group. Thus, Rhipidistia in the new meaning proposed by Ahlberg (1991) includes also forms without choanae. It is noteworthy however that if Ahlberg's (1991a, p. 280) system is modified in the way that Panderichthyida and Rhizodontida are included in Osteolepiformes (as suggested in the model below), Tetrapodomorpha includes Osteolepiformes and Tetrapoda (see phylogenetic and taxonomic part). In this way 'Osteolepiformes' may comprise only fishes the way that it was meant by Jarvik (1942), and be used as a paraphyletic group.

The inclusion by Ahlberg (1991, p. 280) of Porolepiformes together with Dipnoi in the superdivision called Dipnomorpha, and thus separated from Osteolepiforms, is questionable. This is because of apparent synapomorphies between osteolepiforms and porolepiforms in the presence of a series of submandibulars between the gular plates and the mandibular, and the presence of more or less deep paired subethmoidal fossae. This is further discussed in the morphologic discussions.

### Osteolepiform subdivisions

Osteolepiformes was traditionally (Jarvik 1942, p. 241; Romer 1966, p. 361; 1980a, p. 202) divided into two families, Osteolepididae (Osteolepidae by Jarvik and others) and Eusthenopteridae (=Rhizodontidae = Tristichopteridae). The main character state that has been used to distinguish these families is that osteolepidids have scales with a rhombic externally exposed surface, an oblique ridge on the inner surface, and with a groove along the border between the exposed part of the scale and the part covered by the neighbouring scales (Jarvik 1980a, fig. 138A3, A4). Eusthenopterids on the other hand have round scales with an inner central boss and without the groove bordering the exposed part of the scale (Jarvik 1980b, fig. 138B3, B4). Carroll (1988, p. 611) included a larger number of families in Osteolepiformes (=Osteolepidoidea by Carroll), but still included genera like *Megalichthys* Agassiz, 1835, *Ectosteorhachis* Cope, 1880, *Glyptopomus* Agassiz, 1844 and *Gyroptychius* McCoy, 1848 in Osteolepididae (Osteolepidae by Carroll 1988).

Moy-Thomas & Miles (1971, p. 110) divided the order Osteolepiformes (=Osteolepidida by Moy-Thomas & Miles 1971) into two suborders Osteolepidoidei, which included genera like *Osteolepis* Agassiz, 1835, *Megalichthys* Agassiz, 1835 and *Gyroptychius* McCoy, 1848 and Eusthenopteroidei, which included the genera *Eusthenodon* Jarvik, 1952, *Eusthenopteron* Whiteaves, 1881 and *Platycephalichthys* Vorobyeva, 1962. The suborder Osteolepidoidei then becomes roughly the same as in earlier works was called the family Osteolepididae (=Osteolepidae). Vorobyeva (1977a) divided Osteolepididae in several subfamilies, like Osteolepidinae, Gyroptychiinae, Glyptopominae, Megistolepidinae, Thysanolepidinae and Viluichthyinae. Young *et al.* (1992, pp. 9, 20) also included the new family Canowindridae and used the family name 'Megalichthyidae'. 'Megalichthyidae' was also used by Fox *et al.* (1995, p. 107). 'Panderichthyidae' was used by Vorobyeva (1977a, p. 200), Schultze & Arsenault (1985, p. 297) and Carroll (1988, p. 611) for a family within Osteolepiformes. Panderichthyidae was considered including *Panderichthys* Gross, 1941 and *Elpistostege* Westoll, 1938. The latter genus was by Romer (1947, p. 311) included in a labyrinthodont and temnospondyl family called Elpistostegidae. Until it is known whether *Elpistostege* has fins or feet we do not know for certain whether it is a fish or tetrapod, but the current view seems to be that it is a fish (Vorobyeva & Lyarskaya 1968, p. 74; Schultze & Arsenault 1985, p. 297; Daeschler *et al.* 2006, p. 759). Vorobyeva & Schultze (1991) elevated Panderichthyidae to the order category as Panderichthyida or Elpistostegalia (Schultze 1996, p. 316). In this work is used the family name Panderichthyidae instead of Elpistostegidae, because it appears to be in common use and because *Panderichthys* is a better known genus than *Elpistostege*. Thus, 'Panderichthyidae' is more informative about what is typical for the family. The order category for this taxon is not used in this work because Panderichthyidae clearly belongs in the clade called Eopodoidea (cf. taxonomical discussion), which is a superfamily within Osteolepiformes.

Coates & Friedman (2010, p. 402) suggested the new name 'Megalichthyiformes' for 'tetrapodomorph sarcopterygians more closely related to *Megalichthys* than to *Eusthenopteron*'. This is an indefinite definition, indefinite because it does not include any diagnostic characters. It also apparently suggests that 'Megalichthyiformes' is synonymous with the earlier used 'Osteolepidoidei' (Moy-Thomas & Miles 1971). This makes 'Megalichthyiformes' redundant. The suggestion by Coates & Friedman (2010, p. 402) is also unfortunate, because it suggests a taxon in the same category as Osteolepiformes, which *Megalichthys* clearly is a part of. Besides, *Megalichthys* is among the most specialized and atypical genera within this taxon (cf. phylogenetic and taxonomic part), and to use this genus name as the basis for the name of the larger group is therefore irrational.

Thomson (1969, table 1) presented a list of the genera included in Osteolepididae. This was the osteolepiform family with the largest number of genera. Some of these genera have since been removed from the family, for instance *Canningius* (Jarvik 1950a, p. 6), *Bogdanovia* Obrucheva, 1955 (Obrucheva 1955; Vorob'eva & Obruchev 1967, p. 459; Cloutier & Forey 1991, p. 68) and *Thaumatolepis* (Obruchev 1941; Vorob'eva & Obruchev 1967, p. 456). Besides, documented descriptions of these forms apparently are lacking. They are not considered in the discussions below.

Characters other than scale configuration that have been suggested as typical for Osteolepididae in traditional meaning (Vorob'eva & Obruchev 1967, p. 449; Moy-Thomas & Miles 1971, p. 125; Vorobyeva 1977a, p. 122; Jarvik 1980a, pp. 205, 206) are the presence of an extratemporal (cf. Jarvik 1980a, p. 205), the presence of basal scutes and lobate paired fins (Moy-Thomas & Miles 1971, p. 125), and a smooth cosmine cover (Vorobyeva 1977a, p. 123). With respect to the majority of the suggested additional characters, their presence or absence is unknown in most osteolepidoids, and they are thus inefficient in a family diagnosis. This applies to most references to endocranial configurations (Vorob'eva & Obruchev 1967, pp. 448–451; Vorobyeva 1977a, p. 122; Jarvik 1980a, p. 205).

Eusthenopteridae is partly equivalent to what some authors (Romer 1966, p. 361; Jarvik 1985, p. 10) called Rhizodontidae and others (Janvier 1996, p. 221; Ahlberg & Johanson 1997; Johanson & Ahlberg 1997, 2001; Clement *et al.* 2008; Snitting 2008a–d) called Tristichopteridae. 'Rhizodontidae' was introduced by Traquair (1881) and 'Tristichopteridae' was introduced by Cope (1889, p. 855). Both are thus older than the name Eusthenopteridae which was introduced by Berg (1958). However, the time of the introduction of a name does not by necessity have priority over convenience when a more convenient name has reached frequent use (International Code of Zoological Nomenclature 1985, Chapter 6, Article 23:2). Some forms that previously were included in Rhizodontidae have been claimed to differ significantly from both osteolepiforms and porolepiforms (Andrews 1973, p. 144, fig. 2; 1985, fig. 7), and have been included in Rhizodontiformes (=Rhizodontida). It is confusing and irrational to have the name Rhizodontidae connected to the taxa that were included in Osteolepiformes and not those that were included in Rhizodontiformes. Thus, another name should be used for these forms than Rhizodontidae. Berg (1958) designed a diagnosis for this family and included only some species of *Eusthenopteron* Whiteaves, 1881 in it. Because it seems impractical to retain the name Rhizodontidae for a group not included in Rhizodontiformes 'Eusthenopteridae' is here used for the remaining genera from the Rhizodontidae. As mentioned is 'Tristichopteridae' used for this family in several relatively recent works. Firstly, Cope (1989) did not give any sort of definition of the group he called Tristichopteridae, and this family was the only group within Rhipidistia. Thus, what Cope called Tristichopteridae is far from equivalent to the taxon Berg (1958, p. 94) called Eusthenopteridae. Besides, Eusthenopteridae was in frequent use (e.g. Lebedev 1995, p. 336) before the reintroduction of Tristichopteridae and is also more convenient because *Eusthenopteron* Whiteaves, 1881, in contrast to *Tristichopterus* Egerton, 1861, is extremely well known. The name Eusthenopteridae thus associates directly to what the family represents, whereas the reintroduction of 'Tristichopteridae' was contrary to the rules (International Code of Zoological Nomenclature 1985, Chapter 6, Article 23:2) because it is inconvenient. Thus, 'Eusthenopteridae' is more informative for this taxon than 'Tristichopteridae' or 'Rhizodontidae', it is correct according to the rules, and it is therefore used in this work.

## Terminology

A terminology for the morphology of osteolepiforms has emerged particularly through the works of Jarvik (1937, 1942, 1948, and subsequent works), and it seems reasonable to use this terminology as long as it is practical. Some of the parameters that were defined and used by Jarvik (1948, fig. 12) cannot be used on specimens studied in this paper. This is because of differences in configuration and preservation between specimens studied here and by Jarvik. Some new terms and parameters have therefore been defined (Fig. 1, Appendix 1).

A phylogenetic reduction in number of bones may be due to fusion between bones, or the disappearance of one bone in combination with an expanded growth of another bone that takes over the area of the lost bone. Which of these processes occurs is frequently difficult to say. Patterson (1977, p. 92) described the different interpretations of this process. Jarvik (1980a, p. 250) described criteria that strongly suggested that bone reductions were frequently due to fusions. The term fusion will be used here even when it is unclear which of these two processes has occurred because no matter the process, a fusion of areas has taken place.

When discussing taxonomic significance of diagnostic characters basic logical terms are used. It is in this work distinguished between sufficient characters, necessary characters, characters that are both sufficient and necessary, and indicative characters (cf. taxonomic part). This makes the significance of the characters more exact because they show the implication of the used characters. A necessary character is a character that is assumed to be present in all individuals of a taxon, but may also be present in some other taxa. A lack of a necessary character means that the specimen under study is not a member of the taxon determined by the diagnosis. A sufficient character is sufficient to determine a specimen to the taxon in question; it is not present in any other taxon. In cladistic terms it is probably equivalent to an autapomorphy. However, it is not by necessity present in all specimens of the taxon. An indicative character may not be sufficient or necessary but is seemingly more common in the taxon with the diagnosis than in other taxa.

### Cranial roof

#### *General structure*

The cranial roof consists of the fronto-ethmoidal shield (=ethmosphenoid shield), the parietal shield (=otico-occipital shield) and the extrascapular series. The fronto-ethmoidal shield includes premaxillae, rostrals, nasals, postrostrals (usually separated into anterior and posterior bones), frontals, the supraorbito-tectal series, and dermosphenotics. The premaxillae are paired bones along the upper jaw margin and usually carry the marginal teeth. The rostrals constitutes a series of bones posterior to the premaxillae and they usually carry the ethmoid sensory canal. Yu (1998, figs 1, 2) reported that also rostrals could be tooth-bearing. The nasals constitute a series of bones between the frontals and the rostrals, and they carry the supraorbital sensory canal. The postrostrals are situated between the contra-lateral

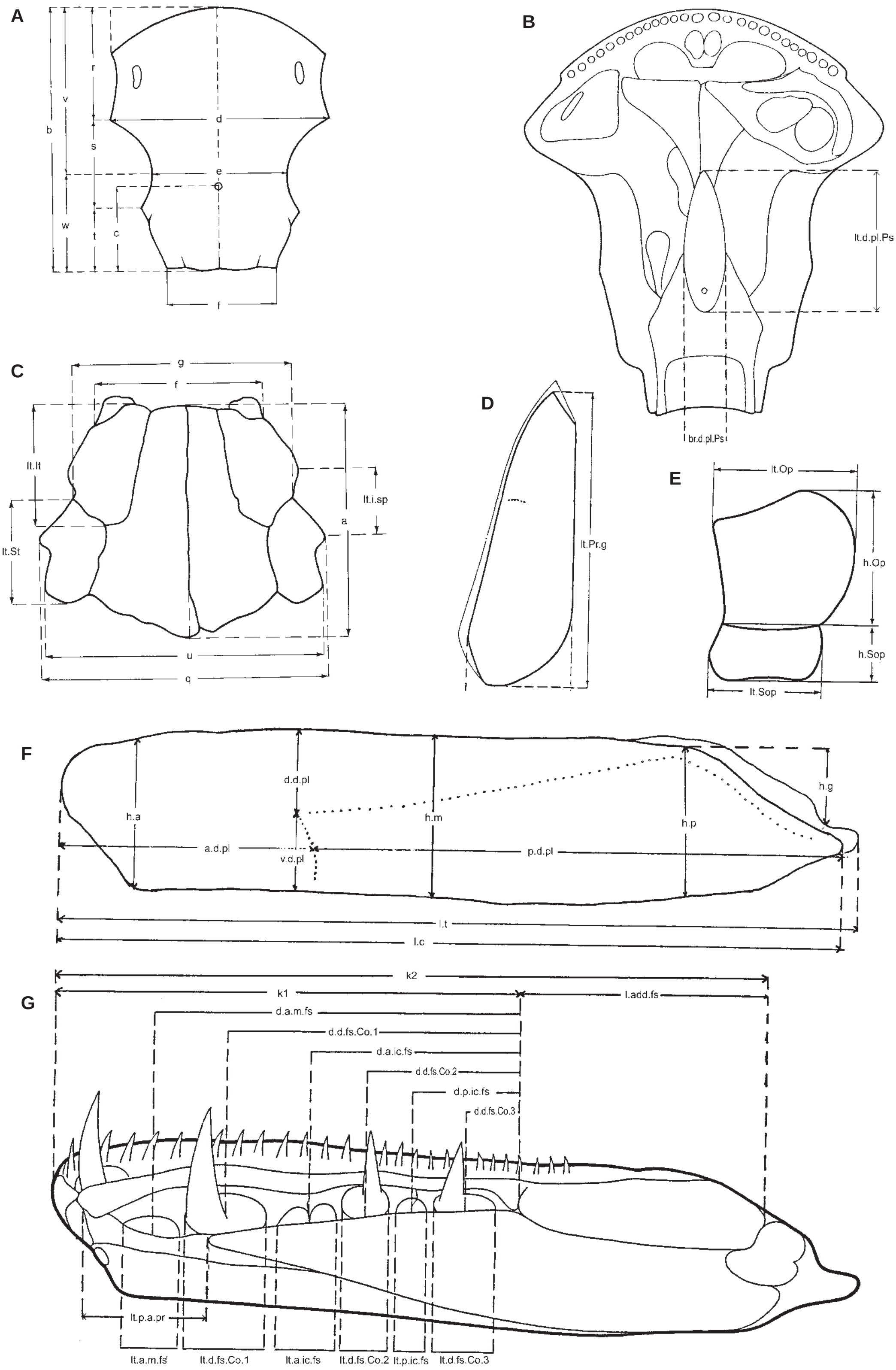

*Figure 1.* Sketches defining variables used in the tables. **A**, Fronto-ethmoidal shield in dorsal view. **B**, Fronto-ethmoidal shield in ventral view showing also the endocranium and parasphenoid. **C**, Parietal shield in dorsal view. **D**, Primary gular. **E**, Opercular and Subopercular. **F**, Lower jaw in external view. **G**, Lower jaw in internal view. Abbreviations used in illustrations and tables are explained in Appendix 1.

nasal series, posterior to the rostrals and anterior to the frontals.

The parietal shield normally includes paired parietals, intertemporals, supratemporals and extratemporals. The parietals are situated on both sides of the median line, the intertemporals are paired bones situated lateral to the anterior part of the parietals and the supratemporals are paired bones lateral to the posterior part of the parietals. The extratemporals are situated lateral to, or somewhat postero-lateral to, the supratemporals. In osteolepiforms there are usually three extrascapulars situated posterior to the supratemporals and parietals. These most posterior bones of the cranial roof carry the posterior sensory canal commissure. Skull roof parameters are defined (Fig. 1A, B; Appendix 1).

### *Premaxilla and rostrals*

Jarvik (1942, pp. 346, 347) defined premaxilla and rostral series by the respective presence on the premaxilla of a tooth row, and on the rostrals of the ethmoid cross-commissure of the sensory canal (cf. Holmgren & Stensiö 1936, p. 355). He also stated that in *Eusthenopteron* Whiteaves, 1881 and *Holoptychius* Agassiz, 1839 the premaxilla had fused with rostrals to constitute a rostro-premaxilla. In *Eusthenopteron* even a nasal was included constituting a naso-rostro-premaxilla. *Eusthenopteron* and *Holoptychius* differed in that the premaxilla of the former had fused with a median rostral leaving the more lateral rostral free, whereas in the latter it was the opposite. This pattern with separate premaxilla and rostrals may be primitive for teleostomes (=Osteichthyes = Actinopterygii + Sarcopterygii) because it has been described also in both palaeoniscoids (Nielsen 1949, fig. 73; Gardiner 1963) and in coelacanthiforms (Millot & Anthony 1958, p. 38, fig. 8). Gardiner (1963, R.pmx, figs 1–5, 18) and Nielsen (1949) also indicated the tendency of fusions of these bones in palaeoniscoids. In later works, Gardiner (1984), Ahlberg (1991a, p. 259), Vorobyeva & Schultze (1991, fig. 6) and Fox *et al.* (1995) use the name premaxilla for the bone that carries both sensory canal and tooth row, that is the bone that Jarvik (1942, p. 347, footnote) calls rostro-premaxilla. Johanson & Ahlberg (1997a, fig. 21b) reconstructed *Mandageria* Johanson & Ahlberg, 1997 with a distinct lateral rostral ventral to the fenestra exonasalis, and mesial to this lateral rostral they showed the dorsal part of a large bone they named premaxilla. It seems logical to assume that the part of the bone named premaxilla that is situated mesial to the lateral rostral, is a more mesial rostral. This has either fused with the premaxilla, or had their suture towards the premaxilla covered by cosmine. Lebedev (1995) used the terminology used by Jarvik and called the bone that constitutes the upper mouth margin naso-rostro-premaxilla. Jarvik's terminology is also provisionally followed in this work. The original premaxilla is that of tetrapods and we do not yet know whether this is homologous with the fused rostro-premaxilla we see in some osteolepiforms, or only the tooth-bearing marginal bone. However, the apparent fusion of these bones in *Panderichthys* Gross, 1941 (Vorobyeva & Schultze 1991, fig. 6), which is a member of the pretetrapod family Panderichthyidae, may indicate that the fused bone is homologous to the tetrapod premaxilla.

Jarvik (1942, p. 497, fig. 68E, D; 1980a, fig. 117) divided the naso-rostro-premaxilla into three topographic parts, a pars dentalis, a pars facialis and a pars palatina (p.d, p.f, p.pl, Fig. 106A).

Several forms show posteriorly directed processes on the palatal lamina (cf. Jarvik 1966, p. 78; 1980a, p. 171, fig. 82C), a median process and a pair of contra-lateral processes. The median process is usually tooth bearing and is therefore probably associated with the premaxilla, but as already mentioned rostrals can also be tooth-bearing (Yu 1988, figs 1, 2). Thus, it is possible that a tusk bearing median process is not only a premaxillary process, but that it consists also of a rostral, and even an endocranial part. Thus, this process is denoted antero-median palatal process (am.pl.pr, Fig. 13). It is uncertain whether the lateral processes are parts of the premaxilla, of the rostrals or of both, and they are therefore denoted 'antero-lateral palatal processes' (al.pl.pr, Figs 76, 77, 95).

### *Mesial skull roof*

Two different interpretations of the homologies between the cranial roof bones of tetrapods and the osteolepiform fishes are in use, the so-called orthodox interpretation and the interpretation suggested by Westoll (1938, 1943) and Romer (1941). These two interpretations imply different terminologies of these bones in osteolepiform fishes. The orthodox interpretation and terminology was generally used before Westoll's suggestion. The Westoll/Romer terminology and terminology (called W/R terminology) was initially used by British and American palaeoichthyologists but has spread and is today used by most workers in this field. However, an analysis of this dispute by Borgen (1983) favoured the orthodox interpretation, and the orthodox terminology is used in this work. This is, partly for reasons different from Borgen's (1983), also the terminology used by Jarvik (1937, 1996). Later works supporting the W/R terminology are Schultze & Arsenault (1985, p. 294), Panchen & Smithson

(1987, p. 410), Ahlberg (1991a, p. 246) and Daeschler *et al.* (2006). Janvier (1996, p. 262) found the W/R terminology credible, but pointed also out remaining problems with this terminology. Klembara (1992, 1993, 1994) and Jarvik (1996, p. 21) used the orthodox terminology.

At the transition from osteolepiforms to tetrapods the W/R terminology demands the following major changes in the bone pattern: (1) the whole osteolepiform extrascapular series disappears completely; (2) the sensory canal commissure crossing the extrascapular series of the osteolepiforms is transferred anteriad from the extrascapulars to the paired parietals (postparietals in the W/R terminology) and supratemporals (tabulars in the W/R terminology) of the tetrapods; (3) with the W/R interpretation and naming there has been a change in parietal position from a partly interorbital position in the osteolepiforms to a mainly postorbital position (Borgen 1983, fig. 1D) in tetrapods; (4) if the W/R terminology is correct the supraorbital sensory canal, which in tetrapods normally penetrates the frontals and avoids the parietals (Bystrow 1935, figs 6–16; Borgen 1983, fig. 4; Carroll 1988, fig. 9:14), have suddenly changed its course because in osteolepiforms, and also in other sarcopterygians (Jessen 1966, fig. 6; Jarvik 1980a, fig. 184; Andrews *et al.* 2006, fig. 4), the sensory canal according to the W/R terminology penetrates the parietals and avoids the postparietals; (5) 'Anterior' postrostrals of osteolepiforms have fused with at least some of the adjacent osteolepiform nasals constituting the nasals of tetrapods, and 'posterior' postrostrals have fused with adjacent nasals and have become frontals.

With the orthodox terminology the following changes are necessary: (1) the osteolepiform postrostrals (both 'anterior' and 'posterior') and nasals fuse constituting the tetrapod nasals. (2) In tetrapods the parietals surround the pineal opening; in most osteolepiforms the frontals surround this opening. Thus, the brain with the parapineal and pineal organs has stayed in the postorbital region, while the cranial roof bones have moved anteriad. (3) At the transition from osteolepiforms to tetrapods there has in many tetrapods been an anteriad change in the position of the frontals relative to the orbit.

The clear conclusion from comparing these lists is that the necessary number of changes at the transition between osteolepiforms and tetrapods by the W/R terminology are distinctly larger than those demanded by the orthodox terminology. Thus, the latter interpretation is more likely to be correct (more parsimonious). As will be shown below, the orthodox terminology is also more consistent with the observable changes in the proportions of the cranium.

*Five important aspects of this dispute*

(1) The alleged disappearance of the extrascapular series at the osteolepiform-tetrapod transition that follows from the W/R interpretation. (2) The changing positions of mesial cranial roof bones, frontals, parietals and postparietals. (3) With the W/R terminology, the unexplained change of the course of the supraorbital sensory canal from penetrating the parietals and avoiding the postparietals in osteolepiforms, to penetrating the frontals and avoiding the parietals in tetrapods. (4) The fusion at the osteolepiform-tetrapod transition of the bones that in osteolepiforms are called postrostrals and nasals. (5) The transfer at the osteolepiform-tetrapod transition of the pineal opening from interfrontal to interparietal positions.

These five aspects are in the following discussed successively.

*Alleged disappearance in tetrapods of the osteolepiform extrascapular bones.* – Even if it is possible that dermal bones may disappear as separate units, the relative abrupt disappearance of the whole extrascapular series is a radical step. Because this disappearance makes no sense (cf. Pearson 1982, p. 37), and because no transitional morphotypes have been described, it is too radical to be credible.

The orthodox interpretation claims a homology between extrascapulars of osteolepiforms and the series of postparietals and tabulars in tetrapods. This is supported by (1) both series are dermal bones situated posteriorly in the cranial roof, between the occipital bones and the large paired bones posteriorly in the cranial roof; (2) the pattern of the cranial roof bones of tetrapods where the sensory canal pattern is retained is exactly similar to that in osteolepiforms, and in both patterns the extrascapular series of the osteolepiforms and the series of postparietals and tabulars of tetrapods carry the posterior commissure of the sensory canal; (3) both series show exactly the same variation in bone patterns, and (4) the bones of the two series have approximately the similar proportions. These points are in the following explained somewhat more detailed.

Between the occipital bones and the large paired posteriormost cranial roof bones, which in man and all tetrapods are called parietals, is situated a series of dermal bones. In tetrapods these bones are called postparietals (=interparietals) and tabulars. In osteolepiforms the extrascapular series is situated in the exact same position. It has been used by supporters of the W/R terminology as an explanation for the claimed disappearance of the extrascapulars that they disappeared at the transition from fishes to tetrapods because tetrapods developed a movable neck joint. However, numerous tetrapods, including man, with a movable neck joint show dermal bones in this position (Sobotta-Becher 1956, fig. 77; Starck 1979, fig. 180; Carroll 1988, figs 9:14, 10:3, 10:15, 17:8, 17:9, 17:13, 17:20, 17:22). These dermal bones in tetrapods are the interparietals (=postparietals) and the tabulars.

In tetrapods where the sensory canal system has been retained, the combined pattern of bones and sensory canals is nearly exactly the same as the pattern of osteolepiforms. This is seen in several stegocephalians (Säve-Söderbergh 1935, figs 1, 31; 1937, figs 1, 3–5, 7C; Panchen 1970, fig. 1; Borgen 1983, figs 1, 2C, 4B, C; Ivachnenko 1987, figs 1A, D, 3A, 5A; Carroll 1988, figs 9–14C, G, H, I; Klembara 1992, fig. 2B). The pair of large bones anterior to the extrascapulars in osteolepiforms and anterior to the postparietals and tabulars in tetrapods both shows the X-pattern (Andrews 1973). The pair of large bones mesially in the X-pattern is called by W/R terminology parietals in tetrapods and postparietals in osteolepiforms, whereas in the orthodox terminology they are called parietals in both groups. Posterior to the X-pattern the extrascapulars carries the posterior sensory canal commissure in fishes, and the series of postparietals and tabulars in tetrapods does the same. Sensory canals may change course but the known changes are small, one sensory canal moves from one bone to another (Borgen 1983, fig. 7). Also, the Early Permian tetrapod *Discosauriscus* (Klembara 1992, fig. 2) shows, in addition to the sensory canal on the postparietal-tabular series, also apparent pitlines on the supratemporals and frontals of the cranial roof that are reminiscent of the pitlines of the supratemporal and frontals of osteolepiforms. Some say that osteolepiforms and other stegocephalians than the Devonian are too far apart for comparisons. However, stegocephalians developed from osteolepiforms so they are not that far apart. Besides, it is irrational to assume differences in bone patterns where there are no differences. The pattern of the bones and the sensory canal of osteolepiforms clearly were sufficiently stable to persist in many tetrapods.

The postparietal-tabular series in tetrapods show exactly the same variation as the extrascapular bone series among fishes, two, three or four bones. How this variation comes about follows from the configuration of these bones in an early ontogenetic stage of the postparietal-tabular series in man (Starck 1975, fig. 542). This series (called interparietals by Starck) has a basic number of four bone precursors that may fuse in different patterns depending on what incisions, incision lateralis and/or incisura cranialis (cf. Starck 1975, fig. 542), between the precursors have been retained, and thus which of the four bones have fused. Examples showing the variation in this series in man are shown by Augier (1931, figs 141–148). There may be one, two or three bones in this series. Variation in primitive tetrapods is shown by Carroll *et al.* (2004, figs 6A, 11A). Exactly the same type of variation is shown in the extrascapulars of most osteichthyans. Osteolepiforms, and other sarcopterygians (Jarvik 1980a, fig. 184; Jessen 1966, fig. 6; Andrews *et al.* 2006, fig. 4), suggest a fusion of the two mesial contra-lateral of the four bones with the result of three extrascapulars. The presence of two extrascapulars on a specimen of *Thursius moy-thomasi* Jarvik, 1948 (see Jarvik 1948, fig. 63C) and in several early actinopterygians (Nielsen 1949, figs 21, 64; Arratia & Cloutier 1996, fig. 6B) indicates a fusion of the ipsilateral of the four bones. *Moythomasia nitida* Jessen, 1968 showed all four bones in the extrascapular series (Jessen 1968, fig. 1B). Thus, we have the same basic number of bones and variations in the extrascapular series of most primitive osteichthyan fishes as in the postparietal-tabular series of tetrapods. Like the median extrascapular among fishes are sometimes divided into two, like in *Moythomasia* Jessen, 1968 (Jessen 1968, fig. 1B), so has also the postparietal in fishes close to the fish/tetrapod transition like *Elpistostege* Westoll, 1938 (Schultze & Arsenault 1985, fig. 7) and *Tiktaalik* Daeschler, Shubin & Jenkins, 2006 (Daeschler *et al.* 2006, fig. 3).

Schultze & Arsenault (1985, fig. 7) reconstructed in *Elpistostege* a hypothetic series of three extrascapulars posterior to the postparietals. These bones will probably not be found when more complete specimens of *Elpistostege* are discovered because the postparietals and the tabulars of *Elpistostege* probably are homologous with the extrascapulars, just as in *Tiktaalik*. In these two forms the postparietals have extended anteriad due to the prolongation of the snout, just as in *Ichthyostega* Säve-Söderbergh, 1932 where the two mesial bones still are fused into a median extrascapular (Säve-Söderbergh, 1932, fig. 15; Jarvik 1996, pl. 8).

The mentioned similarities between the variation in the postparietal/tabular series of tetrapods and the extrascapular series of osteichthyan fish groups are too great to be due to coincidence. Exceptions to the basic pattern of four bones are seen in coelacanthiforms (=actinistians) that may have an even larger number of bones in the extrascapular series (Jollie 1962, figs 4:33, 4:35; Jarvik 1980a, fig. 223). This may be retention of a more primitive morphotype.

The bones that are called postparietals and tabulars in osteolepiforms according to the W/R terminology (=parietals and supratemporals in orthodox terminology), are very different in proportions from the postparietals and tabulars in tetrapods. In tetrapods the tabulars and postparietals are frequently about equally long (Borgen 1983, figs 1, 2D, 4C; Schultze & Arsenault 1985, fig. 8C; Carroll 1988, fig. 9:14) and when the tabulars sometimes are shorter than the postparietals the difference is not great. In osteolepiforms the bone that in W/R terminology are called postparietals are much longer than the more lateral tabulars. Thus, this is quite different from the postparietals and tabulars of tetrapods that are usually of about the same length. If the paired bones that in W/R terminology are called postparietals in osteolepiforms are homologous to the postparietals in tetrapods this would mean that the postparietals would have been shortened considerably at the transition from osteolepiforms to tetrapods. This is illogical considering that a main change in the cranium as a whole, at the transition from osteolepiforms to tetrapods, is a lengthening of the preorbital part of the cranium, a lengthening that is largest along the median line. The lengthening of the preorbital part, which is seen in stegocephalians (Carroll 1988, fig. 9:14) and in the osteolepiform fishes closest to the transition, *Tiktaalik* and *Elpistostege* (the subfamily Elpistosteginae, cf. taxonomic part), should logically be followed by an anteriad expansion of the dermal bones along the median line and not a posteriad withdrawal of these bones. Thus, the postparietals in tetrapods do not fit as being homologous with the long bone that in osteolepiforms according to the W/R terminology are postparietals, but fit well being homologous to the bones that are called mesial extrascapulars.

*Changes in position of the mesial cranial roof bones.* – These changes probably are crucial in this dispute. In the W/R interpretation the frontals as well as the parietals have been claimed to have moved posteriad, whereas the orthodox interpretation presumes an anteriad transfer as a following of the anteriad prolongation of the snout. Changes in proportions of the endocranium must be followed by changes in the pattern of dermal bones and the anteriad prolongation of the snout must accordingly have the effect that the cranial roof bones along the median line have moved anteriad. The positional connection between the length of the snout and the positions of the bones is proven by the variation in the cranial roofs of some stegocephalians (Borgen 1983, fig. 4; Carroll 1988, fig. 9:14). For instance, *Eryops* Cope, 1887 and *Rhinesuchus* Broom, 1908 both have a long snout that has been followed by a prolonged frontal (Carroll 1986, fig. 9:14d, f). Also the parietal bones, the median extrascapulars (=postparietals) and surrounding bones have extended anteriad as a consequence of the prolonged snout. Shorter snout means that frontal bones do not extend far anteriorly to the orbits. This is clearly shown in the bone pattern of *Metoposaurus* Lydekker, 1890 (Carroll 1986, fig. 9:14g) where the snout is not much longer than in osteolepiform fishes and the parietals and the frontals have about the same antero-posterior positions in the cranium as in osteolepiforms. Whether this similarity between *Metoposaurus* and osteolepiforms is due to a reversion of primitive proportions or that this belongs to a lineage where the primitive proportions have remained, is irrelevant. It shows the correlation between the length of the snout and the proportions of the cranial roof bones. A limited anteriad prolongation of the snout started already in the osteolepiform subfamily we have called Panderichthyinae n. subfam., but is even more distinct in the subfamily that here called Elpistosteginae n. subfam. that fishes includes *Elpistostege* and *Tiktaalik* (cf. Elpistosteginae in taxonomical part) where, as an answer to the prolonged snout, the parietal has expanded to a level anteriorly or nearly anteriorly to the orbits. *Acanthostega* Jarvik, 1952 (Ahlberg *et al.* 2008, fig. 4), where the snout is shorter than for instance in *Tiktaalik*, and the anteriad extension parietals and postparietals are likewise shorter (Clack 1994, fig. 11A; Daeschler *et al.* 2006, fig. 4d), represents an intermediate morphologic stage in this development.

The lengthening of a bone may be due to anterior growth or anterior and posterior growth of the median bones, but the result of the combined anterior and posterior growth of these bones must be an anteriad transfer of the sutures between these bones as a following up of the prolonged snout. Thus, a posteriad transfer of the parietals, as suggested by the W/R interpretation, is illogical. Bystrow (1935, fig. 13) described the ontogenetic development of the cranium of *Benthosaurus sushkini* Efremov, 1929 and showed that the growth that produced the long snout was largely at the anterior part of the frontals and the posterior part of the nasals. This is seen because the growth zones are shown by the surface sculpture of the bones (Bystrow 1935, fig. 12). In earlier stages in the ontogeny there was growth also at the anterior margin of the parietals (Bystrow 1935, fig. 15).

Correspondence in position between the frontals in *Acanthostega* on the one hand, and the naso-(posterior) postrostrals of the panderichthyid *Panderichthys* on the other, is probably considered a main argument in the support of the W/R terminology (Janvier 1996, p. 262, fig. 6:5B, C). The anterior position of the frontals in *Acanthostega* (Ahlberg 1991a, fig. 3B; Clack 1994, fig. 11A), *Ichthyostega* (Jarvik 1952, fig. 35B), *Ventastega* Ahlberg, Luksevicks & Lebedev, 1994 (Ahlberg *et al.* 2008, fig. 4), *Tiktaalik* (Daeschler *et al.* 2006, fig. 3), and *Elpistostege* (Schultze & Arsenault 1985, fig. 7), makes it easy to confuse these bones with the posterior postrostrals in classical osteolepiforms like *Eusthenopteron foordi* Whiteaves, 1881 or *Osteolepis macrolepidotus* Agassiz, 1835 and also the panderichthyid *Panderichthys rhombolepis* (Gross, 1930) (Vorobyeva & Schultze 1991, figs 4, 5). However, again it is important to note that there is virtually no prolongation of the snout in *Osteolepis macrolepidotus* and *Panderichthys rhombolepis*, whereas in *Tiktaalik* and *Elpistostege*, as well as in many tetrapods, the snout is distinctly prolonged. When this fact is taken into consideration it is seen that the assumed homology between the posterior postrostrals of osteolepiforms and the frontals of tetrapods is incorrect. If we adjust for the prolonged snout (and the following anteriad transfer of the sutures) and the enlarged eyes in, for instance, *Acanthostega* or a tetrapod like *Lyrocephalus* Wiman, 1914 (cf. Borgen 1983, fig. 5), the position of the bones that in tetrapods are called parietals will in osteolepiforms end in the position of the bones that supporters of the W/R terminology call postparietals but in the orthodox terminology are called parietals.

It is relevant that the intertemporal in the Carboniferous tetrapod *Baphetes orientalis* Owen, 1854 (Milner *et al.* 2009, fig. 3) has a position that is reminiscent of a small protrusion of the postfrontal of *Tiktaalik* (Daeschler *et al.* 2006, fig. 3). Thus, the posteriorly protruding part of the postfrontal in *Tiktaalik* probably is homologous to the intertemporal. The intertemporal may have fused with the posterior supraorbital and together these bones constitute the postfrontal bone. This means that two lateral bones, the supratemporal and the intertemporal, are situated more or less lateral to the main body of the parietals. The tabular is situated posterior to the supratemporal. This interpretation of *Tiktaalik* would also fit with that the anteriad continuation of the notch lateral to the parietals of which the anterior part (called 'slightly separated scarf joint' by Daeschler *et al.* 2006, p. 760, fig. 3) corresponds to the spiracular slit of most osteolepiforms. In osteolepiforms the spiracular opening normally (*Megalichthys* may be an exception) reaches anteriorly to or close to the boundary between inter- and supratemporals (in orthodox terminology). This slit in *Tiktaalik* reaches to the boundary between the supratemporal and the part of the postfrontal that according to the pattern of *Baphetes orientalis* (Milner *et al.* 2006, fig. 3) is homologous to the intertemporal. Thus, the configuration of *Tiktaalik* corresponds well to that of osteolepiforms when using the orthodox terminology.

The narrow slit in *Tiktaalik*, presumed homologous to the spiracular slit in osteolepiforms, is posteriorly continuous with a wider gap that probably becomes the otic notch of tetrapods. Supporters of the W/R interpretation suggest that it is only the wider posterior gap that is the spiracular slit. A wide spiracular opening has been suggested above as possibly present in some specimens of *Megalichthys hibberti* Agassiz, 1835 and in *Gogonasus* Long, 1985b (Long *et al.* 2006). However, according to Starck (1979, p. 162), large spiracular openings among sharks are associated with bottom living forms. This is probably not the environment of *Tiktaalik*.

As mentioned, in both *Elpistostege* and *Tiktaalik* the postparietals bones (=median extrascapulars in orthodox terminology) have expanded anteriad to compensate for the changed proportions between the pre- and postorbital parts of the cranium, just as the median extrascapular has done in *Ichthyostega* (Carroll 1988, fig. 9:3a). Concerning *Ichthyostega*, Borgen (1983, p. 748) expressed some uncertainty in how to name the bones of the cranial roof but expressed support for Jarvik's (1967) interpretation (Borgen 1983, fig. 6A). Now, the authors consider the interpretation suggested by Säve-Söderbergh (1932, fig. 15; cf. Borgen 1983, fig. 6B) is more credible with the exception that the bone situated postero-lateral to the parietal and antero-lateral to the median extrascapular is the supratemporal and not a fusion between supratemporal and intertemporal, as suggested by Säve-Söderbergh. This is due to that *Ichthyostega* shows in Säve-Söderberghs (1932, figs 15, 16) reconstruction posterior protrusions on the bone called supraorbital 2. These protrusions are reminiscent of the protrusion from the postfrontal in *Tiktaalik* (Daeschler *et al.* 2006, fig. 3) that was, because of *Baphetes orientalis* (Milner *et al.* 2009, fig. 3), interpreted as an intertemporal that had fused with a supraorbital. This indicates that the bone Säve-Söderbergh (1932, fig. 15) considered a fusion of the inter- and supratemporal bones, instead, is only the supratemporal. In this respect the authors find that the terminology for *Ichthyostega* also presented by Carroll (1988, fig. 9:3a) is the most credible one.

*Change in the course of the supraorbital sensory canal necessitated by the W/R interpretation.* – The supraorbital sensory canal passing through the frontals and avoiding the parietals is the dominating pattern among tetrapods. Instead the canal passes through the bones lateral to the parietals (e.g. Carroll 1988, fig. 9:14c, g). If using the orthodox terminology for osteolepiforms this sensory canal passes through the same bones as they mostly do in tetrapods. However, if using the W/R-terminology for osteolepiforms the sensory canal passes through the parietals and avoids the frontals (=posterior postrostrals in W/R terminology). Thus, this is also an example where the use of the W/R terminology entails another radical change that is neither indicated by transitory stages nor functionally explicable (cf. Pearson 1982, p. 37).

The occasional extension by the sensory canal to the parietals of some tetrapods (Carroll 1988, fig. 9:14i, j) may be a parallel to the sensory canal invasion of the parietals in *Megalichthys*, or a result of a fusion of the parietal and intertemporal that probably is seen in most porolepiforms (Jarvik 1972, p. 100, figs 38, 43A, 45A). The sometimes transfer of the junction between supraorbital and suborbital sensory canals to the postorbital is illustrated by Borgen (1983, fig. 7).

In *Tiktaalik* the dermosphenotic (intertemporal in W/R terminology) has disappeared as a separate bone (Daeschler *et al.* 2006, p. 760). Normally in osteolepiforms the supra- and infraorbital sensory canals meet in the dermosphenotic but in *Tiktaalik* there has probably been a transfer of this junction to the intertemporal, possibly in the way shown by Borgen (1983, fig. 7).

*Fusion of preorbital and postrostral bones of osteolepiforms.* – Concerning the apparent fusion of the bones in the postrostral region, which in osteolepiforms are called nasals and anterior and posterior postrostrals, these bones become in the orthodox interpretation the nasals of the tetrapods. In the W/R interpretation they become both frontals and nasals. A support for the orthodox interpretation is that there is apparently a trend towards fusions between all ipsilateral postrostrals and nasals. This has the result that the small bones anterior to the paired naso-postrostrals in *Panderichthys* and *Elpistostege* also fuse with the naso-postrostrals, and all these bones become the tetrapod nasals. An indication of this trend is seen in the rhizodontiform *Barameda decipiens* (Woodward, 1906) (Long 1989, figs 1, 2, 5) where there is on the left side only one paired bone between the premaxilla (naso-rostro-premaxilla?) and frontal (orthodox interpretation) and in the claimed primitive sarcopterygian *Meemannia* Zhu, Yu, Wang, Zhao & Jia, 2006 (Zhu *et al.* 2010, fig. 3A). Also in the early palaeoniscoids *Cheirolepis* Agassiz, 1835 (Pearson 1982, fig. 1; Arratia & Cloutier 1996, figs 1A, 2, 6, 9, 10), *Moythomasia* Jessen, 1968 (Jessen 1968, fig. 1; Arratia & Cloutier 1996, fig. 1C) and in other primitive actinopterygians (Pearson 1982, fig. 3) all the bones lateral to the large median postrostral and between the rostro-premaxilla and the frontals have fused. Thus, this is a trend parallel to the fusion of all the nasals in the same position at the transition from osteolepiforms to tetrapods. The difference is that in the actinopterygians, there still remains the large median postrostral that is common also in several osteolepiforms. This is also seen in *Polypterus* Lacépède, 1803 (Jarvik 1980a, fig. 235B; Arratia & Cloutier 1996, fig. 1B). Arratia & Cloutier (1996) have, contrary to Pearson (1982, fig. 1), transferred the presumed erroneous W/R terminology of the median paired bones in osteolepiforms on to the actinopterygians.

Schultze & Arsenault (1985) and Vorobyeva & Schultze (1991) showed that in *Panderichthys* and *Elpistostege*, which are relatively close to the fish-tetrapod transition, the dermal bones between the frontals (in orthodox terminology) and the (?rostro-)premaxilla consist of two pairs of bones. The posterior pair of these bones, which are the bones that in fish terminology are called posterior postrostrals, fits as the frontal bones in the terminology followed by these authors after having fused with the adjacent nasals. The bones situated anterior to this pair of bones then become the nasals of the tetrapods after having fused with the adjacent nasals. This may be considered a support for the W/R interpretation and it is possible to imagine a transition between a panderichthyid *Panderichthys rhombolepis* and an early tetrapod like *Acanthostega gunnari* Jarvik, 1952 (Janvier 1996, fig. 6:5B; Schultze 1996, figs 7C1, D1). However, the many indications that this interpretation is wrong suggest that all the postrostral bones of osteolepiforms become parts of the tetrapod nasals.

*Transfer of the pineal opening from an interfrontal position to an interparietal position).* – The position of the pineal opening is, as stated by Parrington (1967, p. 233) and Jarvik (1967, p. 186), irrelevant for the homologizations of the bones. Jarvik (1967, p. 197) explained that the reason for the change in position of the pineal opening is that the main part of the brain including the diencephalon whose tectum includes the pineal and parapineal organs and has remained in the postorbital part of the head, whereas the frontals and to some extent even the parietals have moved anteriad as a result of the relative prolongation of the snout. The dermal bones have moved anteriad, whereas the endocranium with the brain has stayed behind (cf. Borgen 1983, fig. 2).

In most osteolepidoids the pineal fenestra and foramen is situated in an interfrontal position near the level of the orbits. In the group here called Eopodoidea (cf. phylogenetic and taxonomic part) both some eusthenopterids and panderichthyids also show an interfrontal position of the pineal opening (orthodox interpretation) but distinctly more posterior than normal in other osteolepiforms. In *Eusthenodon* (Jarvik 1952, fig. 23) the pineal fenestra reaches nearly to or to the posterior frontal margin, and in *Panderichthys rhombolepis* (Schultze & Arsenault 1985, fig. 8B; Vorobyeva & Schultze 1991, figs 4, 5) and *Elpistostege* (Schultze & Arsenault 1985, fig. 8A) the pineal foramen is positioned distinctly posterior to the orbits. Thus, we see in eopods a posteriad transfer of the pineal openings. Interesting in this connection is also the position of the pineal opening in some branchiosaurs (Boy 1972, pl. 1, fig. 1, pl. 2, figs 1–3, figs 56, 69). Here the pineal opening is situated anteriormost in the interparietal suture, in the previously mentioned anterior part of the parietals that is at a level anterior to the laterally situated supratemporal and (the presumed sometimes present) intertemporal. It is thus situated in the above-mentioned anterior expansion of the parietals that originally is due to the anteriad expansion of the tetrapod snout and that has occupied the position that in most osteolepiforms is held by the frontals (orthodox terminology). Even more revealing is the observations referred to that among recent reptiles (Trost 1956, p. 323, figs 1a, b, 2c–e) and among Permian amphibians (Boy 1972, pl. 2, fig. 1, fig. 29B), the pineal opening in several cases is situated in the suture between frontals and parietals, and in a few taxa (Trost 1956, fig. 1c) also in interfrontal position but close to the suture with the parietals. Thus, there are several recorded examples of transitional stages in the transfer of this opening from an interfrontal to an interparietal position. Schultze & Arsenault (1985, p. 295) claims that the pineal foramen (parietal foramen by Schultze and Arsenault) is interparietal in all tetrapods. This allegation is, as already mentioned, disproved by Trost (1956).

To understand homologies correctly it is necessary to follow the principle concerning comparative anatomy stated by Pearson (1982, p. 37) of viewing interpretations of homologies in a holistic (also functional) context instead of only concentrating on the position of a pair of bones relative to, for instance, the orbit or pineal foramen. The authors will add to this principle that claimed morphologic changes should preferably also be demonstrated by the observed presence of intermediate morphologic stages. The morphologic changes that are associated with the orthodox interpretation satisfy both these principles. The W/R terminology satisfies neither of these principles.

It should be pointed out that the discussed dispute concerns the bone homologies at the transition from osteolepiforms to tetrapods and that both the orthodox and W/R interpretations are based on a consensus about the homologies and terminology for tetrapods. However, Bjerring (1995) reinterpreted the homologies of the skull roof among tetrapods in a way that, if correct, has implications for the correct terminology of these bones also in fishes. This suggestion is not discussed in this paper.

The definition of the nasal bones presumably is based on man. Because of this, and because (as indicated above) the osteolepiform nasals (defined by the sensory canal) may be homologous only with the lateral part of the tetrapod nasals (considered homologous with the nasals in man), it is perhaps more correct to call the nasals of osteolepiforms 'lateral nasals', and the posterior and anterior postrostrals 'median nasals'. However, because there is still a disagreement concerning which interpretation of the skull roofing bones is correct, the normal osteolepiform terminology with anterior and posterior postrostrals, and 'nasals' defined by the sensory canal, is used in this work.

### *Circumnarial bones and supraorbito-tectals*

The circumnarial bones in *Eusthenopteron foordi* Whiteaves, 1881 include the lateral rostral and tectal bones. The tectals and the supraorbital constitute one series of bones, the supraorbito-tectal series. Thus, these bones are all discussed under the same heading.

The number of tectals has been subject of uncertainty. In *Eusthenopteron foordi* a posterior tectal was considered fused with the anterior supraorbital (Jarvik 1944a, figs 6, 7; 1980a, fig. 119). This hypothesis was based on a single specimen, SMNH P 31 (Jarvik 1944a, p. 11, fig. 4). Bjerring (1979, fig. 1) followed this interpretation, but later Jarvik (1980a, p. 159, fig. 116; E. Jarvik pers. comm. 1991) expressed uncertainty about it. The posterior tectal part of this alleged compound bone, which Jarvik called the supraorbito-tectal, constituted the preorbital corner (Jarvik 1980a, fig. 119). The pattern in this region has been studied by one of us (UB) (cf. morphologic discussions) and we will also use the term supraorbito-tectal.

Jarvik (1980a, fig. 119) illustrated one single long anterior tectal in *Eusthenopteron foordi*. However, Jarvik (1966, fig. 13C) showed a groove that reaches the dorsal margin of the nasal fenestra. Jarvik (1966, fig. 14; 1980a, figs 116, 120; E. Jarvik, pers. comm. 1991) considered this a fracture and did not show a suture in this position. Also Bjerring (1979, fig. 1A) omitted this in a reconstruction, but included it in a later reconstruction (Bjerring 1989, fig. 2E). Thus, the literature may report two anterior tectals in *Eusthenopteron foordi*. This was what Jarvik (1948, fig. 17) showed in an illustration that showed the maximum number of skull roof bones in the osteolepidids examined by him. Thus, osteolepiforms have at least two anterior tectals, and a problem is how to name them. In this work all tectals anterior to the posterior tectal are called 'anterior tectals'. When there is more than one bone they are numbered from the anterior end of the series. Thus, when one form shows one anterior tectal and another form shows two or more, the homologies between these bones are unknown. Thus, the anterior tectal 1 in one form is not necessarily homologous with the anterior tectal 1 in another form. Descriptions of *Eusthenopteron foordi* specimens and following discussions that are relevant to this problem are presented in the morphologic discussions.

In works treating particularly megalichthyids the terms 'prenarial and postnarial bones' have been used (Thomson 1964a; Jarvik 1966; Schultze 1974). These names are not part of the regular series of bones that constitute the dermal cranium but are used when the homologies of the circumnarial bones in the regular system of bones are unknown. Obviously prenariale surrounds the anterior and postnariale the posterior part of this fenestra.

The maximum number of supraorbitals was by Jarvik (1948, fig. 17) given as three. In later works, his terminology has varied somewhat (Jarvik 1980a, figs 115, 116, 119). Here, the authors will use the name anterior supraorbital and number the posterior supraorbitals from the anterior end.

### *Anterior intertemporal process*

The process situated antero-lateral on the parietal shield, referred to by Bjerring (1972, p. 80) as the 'frontodermosphenotic process', has been called by Borgen (1983) 'anterior intertemporal process'. This is because it usually is advantageous to include in the term for a structure the name of the bone on which the structure is situated, and also its position on the bone.

## Endocranium

### *General structure*

The endocranium of osteolepiforms (Jarvik 1980a, fig. 86) consists of an anterior moiety that is separated from a posterior moiety by the so-called intracranial joint. The anterior moiety, which is called the ethmosphenoid, includes the ethmoid and sphenoid (also called orbitotemporal) parts of the endocranium. The border between these two parts is defined by the posterior extension of the postnasal wall. Jarvik (1942) established a detailed and well defined terminology for the different parts of the ethmosphenoid of osteolepiforms.

The posterior moiety, which is called the otico-occipital part, consists of the otic and occipital regions, respectively. The border between these two regions is defined (Jarvik 1980a, p. 39) by the opening for the vagus nerve.

*Dorsal fossa of otic region.* – The terminology concerning some endocranial fossae of the otic region was recently clarified by Bjerring (1984) who showed that the term 'fossa bridgei', as previously used on osteolepiforms (Thomson 1965, fig. 1; Bjerring 1972, figs 8, 9; Vorobyeva 1977a, figs 9, 11; Jarvik 1980a, figs 77, 88), should be changed. Bjerring suggested 'fossa supra-auditiva' which will be used here.

## Dermal bones in mouth roof

### *General structure*

The dermal mouth roof includes vomers, parasphenoid, entopterygoid, ectopterygoid, dermopalatine, paraotic plates and subotic plates. Also additional dermal plates situated in the mouth roof, and which may be more or less firmly attached to endocranium and gill arches are included here. Measured variables on the parasphenoid are defined (Fig. 1B).

*Vomers.* – Bjerring (1991) suggested that the paired tooth and tusk bearing bones situated anteriorly on the palate, which in both osteolepiforms and porolepiforms generally have been denoted vomers, are not homologous with the vomers as they originally were defined in man. Bjerring (1991, p. 227) stated that the vomer in man is the result of a fusion of two contra-lateral bones and this bone was situated beneath both the ethmoid and orbito-temporal parts of the endocranium. Because the nasal sac in man (and other mammals) has expanded posteriad and thus the posterior border of the ethmoid region has moved posteriad, the original position of the vomer in mammals may mainly have been subjacent to the interorbital region. He compared this with the vomers in urodeles and porolepiforms. In urodeles a palatal bone consisted of an anterior part situated beneath the ethmoid, and a posterior part that runs along the parasphenoid. In the porolepiform *Glyptolepis groenlandica* Jarvik, 1972 the so-called vomer is situated beneath the ethmoid region. This bone in

*Glyptolepis* was homologized with the anterior part of the bone in urodeles. The posterior part of the urodele bone was homologized with fused dental plates. The latter, which is situated in the orbitosphenoid region, is interpreted as the homologue of the vomer in man. The bone in urodeles was considered a composite bone, and that in porolepiforms a single bone called 'dacnil'. From this he concluded (Bjerring 1991, fig. 14) that the bones usually called vomers in osteolepiforms were not vomers, but also the result of fusion by a subethmoidal dacnil and a suborbitosphenoid vomer.

As shown below, the vomer in osteolepiforms is divided into two ipsilateral bones that are provisionally called anterior and posterior vomers. For two reasons this terminology is retained, in spite of Bjerring's results: (1) the gap from man to porolepiforms and osteolepiforms is a long gap for direct homologizations, particularly when one part is a structure as modified as the human cranium. This causes uncertainties. An apparently unsolved problem in Bjerring's interpretation is where the bone he called dacnil is incorporated in the human skull. One credible alternative is that the human vomer is the result of a fusion between the two dermal units in the osteolepiform palate (dacnil and vomer in Bjerring's terms), as it may be in urodeles. If so, the terms anterior and posterior vomers seem fitting; (2) because of the mentioned uncertainties, and because the term vomer is currently used for the dermal bones in this region, the authors have, also for the sake of simplicity, used the terms anterior and posterior vomer.

### Lower jaw

Measured variables are defined in Figure 1. Most length measurements on the jaw are taken parallel to an axis defined by the antero-dorsal and postero-dorsal corners. Heights are measured vertical to this axis. The two faces of the lower jaws may be called lateral and mesial sides, dorsal and ventral sides, labial and lingual sides, or external and internal sides. The latter alternative is the simplest and least ambiguous and will be used here. The two margins separating the two faces are called ventromesial and dorsal margins, respectively. The part of the dorsal margin that carries teeth is called dental margin.

In all osteolepiforms and also many other osteichthyans the lower jaws show a more or less developed antero-dorsal mandibular expansion. This usually consists to a large extent of the anterior part of the Meckelian bone, also called the mentomandibular, but also to a varying extent of other bones like the anterior part of the prearticular and the dentary.

The terminology for the infradentaries differs among different authors and needs some comments. The earlier most used terminology called the four infradentaries, from the anterior end, 'splenial', 'postsplenial', 'angular' and 'surangular'. This terminology was used by Jarvik (1937), Gross (1941), Nilsson (1943, 1944), Westoll (1943), Romer (1966, p. 50), Vorob'eva and Obruchev (1967), Thomson (1964a) and Miles (1971), with the difference that Jarvik, Gross and Nilsson used 'supra-angular' instead of 'surangular', and Nilsson used 'presplenial' instead of 'splenial'. To get a simple system free from earlier used terms Jarvik (1944) introduced 'infradentary 1', 'infradentary 2', 'infradentary 3' and 'infradentary 4'. This system has later been adopted by Gross (1956), Jessen (1966, 1973), Vorobyeva (1977a) and Young *et al.* (1992). An advantage with the number system is that it emphasizes that the bones are parts of a series of bones. One theoretical disadvantage is that there is a possibility that after a reduction of bones in a series a single bone in a jaw should have the name, for instance, infradentary 3 something which, when the jaw is studied in a non-evolutionary context, may seem awkward. Another disadvantage with the number system is that it is not consistent with the terminology used for tetrapods. In some relatively recent works (Fox *et al.* 1995; Long *et al.* 1997; Zhu & Schultze 1997) the previously used terminology was reintroduced. The authors will use the number system in this work.

A problem similar to that concerning the infradentaries exists with respect to the coronoids. These were named, from anterior to posterior, 'precoronoid', 'intercoronoid' and 'coronoid' (Gross 1941; Nilsson 1943, 1944). A number system is used by several authors like Jarvik (1944a), Vorobyeva (1962; 1977a, b), Jessen (1966, 1973), Young *et al.* (1992) and Chang & Zhu (1993). With respect to coronoids the number system may be even more problematic than with the infradentaries, since it has been claimed that there originally were more than three coronoids (Zhu & Yu 2004, fig. 8) of which one may be a bone carrying the parasymphyseal tooth plate (Jarvik 1972, p. 116). If correct we thus have a coronoid bone anterior to coronoid 1, something that constitutes an obvious terminological problem. However, since the homologies between the three osteolepiform coronoids and possible other bones in this series present in other groups is unclear, as is also the relationship to the parasymphyseal tooth plate, and also because this system now seems current, the number system is used here also for the coronoids.

The anterior mandibular fossa is normally situated posterior or postero-ventral to the antero-dorsal mandibular expansion, dorsal to the pars anterior of the prearticular and ventral to the anterior part of the coronoid ridge (a.m.fs, Figs 28, 31A, 61A, 73B). As shown in the descriptions and discussions below this fossa may sometimes also constitute a fenestra exposing the Meckelian bone. It apparently is the anteriormost of a series of cavities including also the intercoronoid fossae. Several names have been used for this fossa, 'anterior dental fenestra' (Watson 1926, p. 252), 'erste Vorcoronoidgrube' (Gross 1941, p. 8), 'anterior dentary fossa' (Thomson 1964a, p. 330, fig. 5B; Worobjewa 1975, fig. 3), 'pit for vomer tusk' (Jarvik 1972, figs 49, 50; Young *et al.* 1992, fig. 33) and 'precoronoid fossa' (Zhu & Yu 2004, fig. 4). Fox *et al.* (1995, fig. 47) used 'anterior mandibular fossa'. The latter name on this fossa is used here because it distinguishes this fossa from the other fossae associated with the coronoids. The intercoronoid fossae are, contrary to the anterior mandibular fossa, largely surrounded by coronoids, whereas this anterior fossa is bordered ventrally and antero-ventrally by the prearticular, sometimes the Meckelian bone (mentomandibular) and a parasymphyseal bone, posteriorly and dorso-laterally (sometimes even partly anteriorly) by the anterior coronoid and sometimes the dentary bone. It should not be confused with the adsymphysial fossa, which is a frequently less distinct fossa, situated anterior or antero-ventral to the anterior mandibular fossa and ventral to the antero-dorsal mandibular expansion. The term precoronoid fossa, which may seem logical, may be confused with the dental fossa on coronoid 1 which earlier was called precoronoid.

'Prearticular' seems current and will be used here, even if Nilsson's (1943, p. 15) arguments for instead using 'gonial' seem reasonable. The prearticular is usually divided into a smooth surfaced 'pars anterior' and a 'pars dentalis'. The division between these two parts of this bone is defined by the anteriormost point of the prearticular dental plate. Sometimes there is also a 'pars posterior' adjacent to and even posterior to the glenoid fossa.

Some authors (Vorobyeva 1977a, fig. 15C; Young *et al.* 1992, fig. 33A; Fox *et al.* 1995, p. 170; Long *et al.* 1997, fig. 38) have interpreted the pars anterior of the prearticular as part of the Meckelian bone. This is treated in the below morphologic discussions of the prearticular.

The above-mentioned parasymphyseal dental plate is a small tooth-covered bone situated posterior to and near the symphysis, and on the antero-dorsal mandibular expansion. Among osteolepiforms such bones were described by Vorobyeva (1962, figs 19, 30) in *Eusthenopteron saeve-soederberghi* Jarvik, 1937, *Eusthenodon wenjukowi* Rohon, 1889a, *Platycephalichthys bischoffi* Vorobyeva, 1962 and *Panderichthys rhombolepis* (Gross, 1930) under the term 'praedentale'. Thomson (1964a, fig. 4) used 'crista dentalis' and Jessen (1966, fig. 5B, C, pl. 10, fig. 1) used 'adsymphysial dental plate'. Jarvik (1972, p. 113) discussed these structures and suggested to call all such plates 'parasymphyseal dental plates', a term previously (Jarvik 1962) used by him in a study on porolepiforms. Until interrelationships between such plates in different groups is cleared up it seems reasonable to use a common term, and since 'parasymphyseal dental plate' appear to be the oldest, and in common usage (Jessen 1980, p. 186; Jarvik 1980a), this name is used in this study.

The external surface shows three grooves that sometimes are separate and sometimes continuous. One groove runs along the postero-dorsal margin. Another groove, which usually is in continuity with the former, runs obliquely antero-ventrally on the jaw. Sometimes continuous with the latter there is an approximately vertical groove on infradentary 2. As pointed out by Säve-Söderbergh (1933, pp. 14, 93) these grooves were previously interpreted as sutures. Gradually it was established that these were pitlines but the early confusion is not surprising because the suture between infradentaries and dentary frequently runs partly together with the antero-ventrally running so-called horizontal pitline. However, the suture continues to the postero-dorsal corner of the jaw, whereas the pitline turns postero-ventrally before it reaches this corner. The frequently separate pitline on infradentary 2 is, due to its normal course, called 'vertical pitline'. Distinguishing between suture and pitline may still be a problem.

## Operculo-gular bones

### *Gular bones*

The gular bones include paired principal gulars of different shapes and an anteriorly situated median gular.

### *Submandibulars*

The series of bones situated between the lower jaw and the principal gulars have been called 'lateral gulars' (Moy-Thomas 1935) and 'branchiostegal rays' (Jarvik 1948; Young *et al.* 1992), but 'submandibulars' seems now to be the current term (Jarvik 1963; Moy-Thomas & Miles 1971, 1980a, b, 1985; Schultze & Arsenault 1985; Fox *et al.* 1995; Ahlberg & Johanson 1997; Long *et al.* 1997) and we will use this name. 'Branchiostegal rays' probably should be reserved for the rod-shaped bones of most actinopterygians where the principal gulars are missing. Pearson (1982, fig. 7) showed the intermandibular dermal bones of different osteichthyan groups. The submandibulars are numbered, and in early works, Jarvik (1948) considered the posteriormost bone as number 1. Later Jarvik (1980a, fig. 121C) reversed the succession. The posterior bone of this series, which is situated ventral to the subopercular, was by Jarvik (1980a, fig. 121) called 'submandibulo-branchiostegal plate'. Fox *et al.* (1995, fig. 17) called it 'subopercular 2'. Because the reduction of bone in the submandibular series takes place anteriorly the authors have followed the early terminology by Jarvik and called the posteriormost bone, the one also called submandibulo-branchiostegal plate, for 'submandibular 1'.

### *Opercular bones*

The opercular bones include a dorsal opercular and a ventrally situated subopercular. Relative heights of these bones vary.

# Upper Palaeozoic fossil locality in the Oslo Region

## Geological setting

The study area lies within the Oslo Graben, which was formed during the Late Palaeozoic tectonic activity comprising both extensional faulting and volcanism. The Oslo Graben represents the northern extension of the northwest European basin system. The formation of the Oslo rift is related to the Variscian orogeny and the main graben of the Oslo Region was formed in the Late Carboniferous (Larsen *et al.* 2008). The initial rifting event was followed by the extensive volcanism, extensive rifting and the region was uplifted by major batholiths in the latest Palaeozoic. The tectonic and volcanic activities within the Oslo Region concluded in the Early Triassic (Larsen *et al.* 2008).

## Stratigraphy

The Upper Palaeozoic sedimentary rocks in the Oslo Region overlie unconformably the Lower Palaeozoic (Cambrian–Silurian) Caledonian folded sedimentary rocks. The Late Palaeozoic succession is referred to the Asker Group (Fig. 3; Dons & Györy 1967; Larsen *et al.* 2008) and is composed of the three formations named from bottom to top, the Kolsås Formation, the Tanum Formation, and the Skaugum Formation (Fig. 3; Elder & Kanes 1966; Henningsmoen 1978; Larsen *et al.* 2008).

The Kolsås Formation (up to 20 m thick; Fig. 3) is mainly composed of red mudstone, sandstone, subordinate conglomerate, limestone and minor anhydrite characterizing a floodplain with fluvial stream channel fill and lake depositional environments that accumulated under arid conditions (Dons & Györy 1967; Henningsmoen 1978; Olausen 1981; Olaussen *et al.* 1994; Olaussen & Dahlgren 2007).

The overlying Tanum Formation is ca. 20 thick (Fig. 3). It overlies disconformably the Kolsås Formation and is composed of thick cross-bedded quartz rich sandstone, pebbly sandstone and conglomerate. Minor mudstone and fine-grained sandstone, some of them with plant remains, are present. The interpretation of the depositional environment of the Tanum Formation comprises floodplains and deltaic deposited under semi-arid conditions (Dons & Györy 1967; Olaussen *et al.* 1994).

## The Semsvik locality

The Upper Palaeozoic fossil locality at Semsvik in the township of Asker, Norway (59°51′20.28′′N, 10°24′6.13′′E), is situated about 15 km. west of Oslo (Figs 2, 3). It was discovered on a field excursion in 1931 by Olaf Holtedahl (Holtedahl 1931, p. 325). The measured stratigraphic succession is given in Table 1 and shown on Figure 3.

Of the beds exposed at Semsvik a conglomerate at the bottom is considered part of the Tanum Formation (Fig. 3), and the sandstone containing tuffs is referred to the overlying Skaugum Formation (Elder & Kanes 1966, p. 2; Dons & Györy 1967, p. 63; Henningsmoen 1978, p. 14).

The new osteolepidoid specimens were collected at the locality; fossil plants, lamellibranchs and other fish remains have also found at the locality (Fig. 2B).

### *Plant fossils*

The plant fossils from Semsvik have been described by Høeg (1936a, 1936b, 1936c). The flora consists of some poorly preserved ferns, pteridosperms of the genus *Neuropteris* and some specimens similar to *Callipteris* or *Allethopteris*, airstems and rhizosomes of species of the equisetophyt *Calamites*, presumed leaves and reproduction organs of *Calamites* named *Asterophyllites*, *Calamostachys* and *Palaeostachys*, leaves from species of *Cordaites*, seeds denoted *Samaropsis*, but considered being from a *Cordaites* species, and conifers of the taxa *Walchia* and *Ernestiodendron filiciforme* (Schlotheim) Florin. There were also remains of *Dicranophyllum*, which is considered a seed plant of unknown affinity.

In beds from the Asker Group at a locality near Tanum church (59°53′44′′N, 10°28′45′′E), silicified

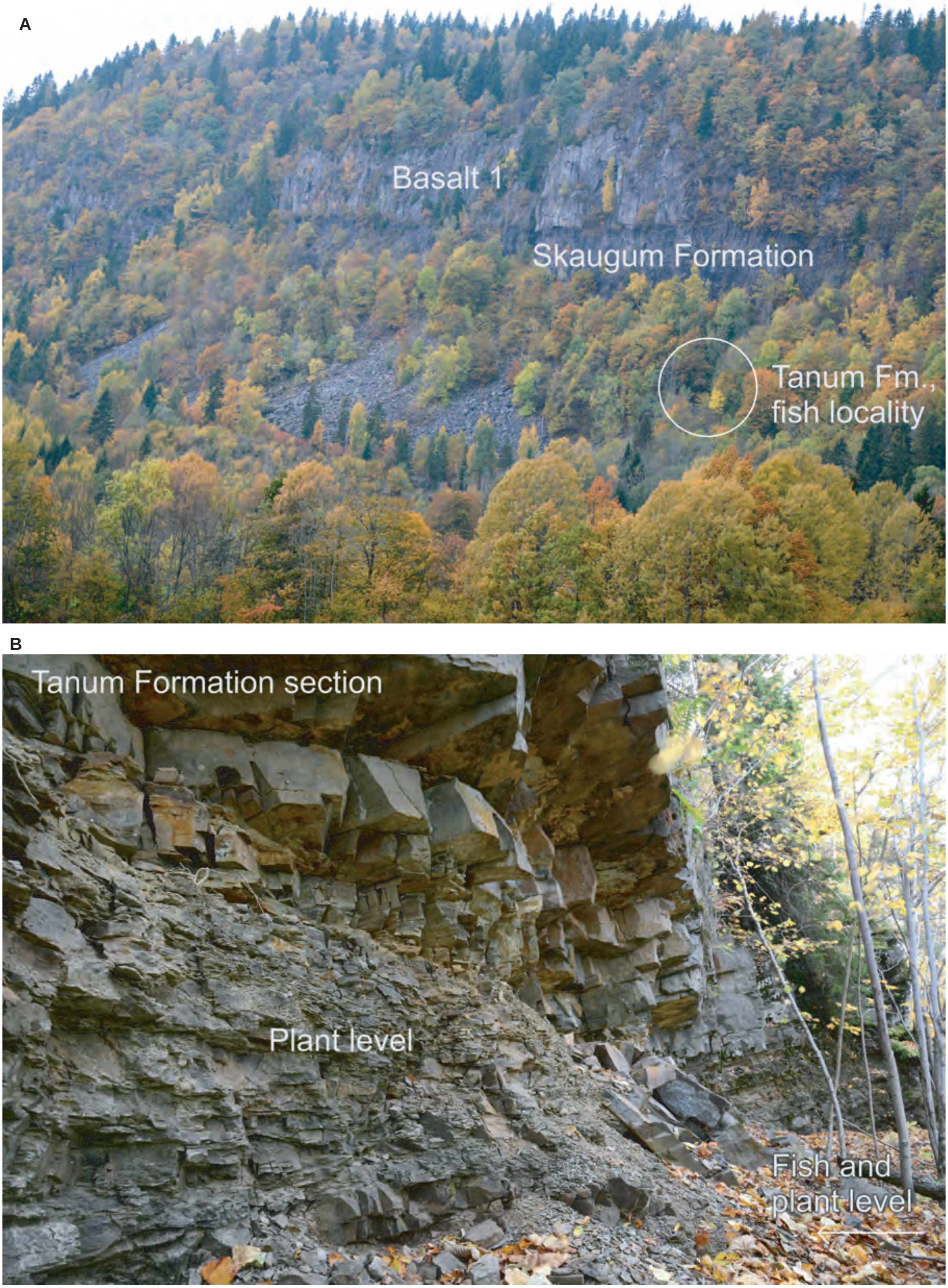

*Figure 2.* **A**, View of the Semsvik location in approximately western direction. The quarry in the Upper Palaeozic sediments is marked by the white circle. The transition between sediments and basalts is shown in the mountain side. **B**, Details of the exposure at Semsvik location.

wood has been found, which Høeg (1936c) referred to *Dadyxolon saxonicum* (Göppert) or *Dadyxolon scrollianum* (Göppert).

### *Fossil fauna*

After a preliminary examination of the fish fossils from Semsvik by Anatol Heintz, it could be stated that they were remains of osteolepidoids, probably of the genus *Megalichthys* (Holtedahl 1931, p. 329). Later, Heintz (1934) provided a fuller description of the fish fauna. The osteolepidoid remains, some scales, a head plate and one lower jaw, were identified as *Megalichthys* sp., mainly because of their general appearance and their Late Palaeozoic age (Heintz 1934, pp. 181, 185). The material also included one presumed shark tooth of a type previously called *Pleuracanthus* (concerning the use of this name see Zangerl 1981, pp. 64–65), a smaller presumed shark tooth that was indeterminable, a scale similar to those of holoptychids, a possible *Pleuracanthus* coprolite, a possible head plate and some possible neural arches of dipnoans, and some presumed palaeoniscoid remains that tentatively were determined to *Amblypterus* and *Elonichthys*. The palaeoniscoid material consisted of scales, usual and fulcra type, a 'complete specimen' consisting of the larger part of the body of a fish, a fin fragment and two lower jaw fragments.

The lamellibranchs from Semsvik were tentatively determined as possible species of *Palaeanodonta* by Dix & Trueman (1935, p. 26). Eagar (1994) restudied and revised the lamellibranchs assemblage and referred them to *Anthraconaia protracta* Eagar, 1975.

### *Age of beds*

Some doubts on the age of the sediment have prevailed. The presence of *Ernestiodendron filiciforme* (Schlotheim) Florin could indicate that the deposits at Semsvik should be referred to the Lower Permian (Høeg 1936a, p. 34). Also *Dadoxylon saxonicum* recorded from the Tanum Church locality is mainly an Early Permian (Rotliegendes) form (Høeg 1936c, p. 281).

All the described fish taxa are known both from the Carboniferous and Permian, but *Amblypterus* was considered 'more Permian than Carboniferous' (Heintz 1934, p. 192). On the assumption that they correctly had determined the lamellibranchs, Dix & Trueman (1935, p. 30) were certain that the age of the fauna was Permian. Thus, Henningsmoen (1978, p. 21) stated that the fauna and flora indicated an Early Permian age.

However, from his restudy of the lamellibranchs Eagar (1994) demonstrated that the fossil assemblage from the Tanum Formation was Late Carboniferous. Olaussen *et al.* (1994, p. 178) reviewed the results of biostratigraphic studies and conclusively referred the Tanum Formation to the Upper Carboniferous, which is followed here.

# Descriptions

The descriptions are presented from Carboniferous to Devonian forms. This is because the Carboniferous material consists of a larger number of well-preserved specimens than the Devonian material. In this way it is possible to use descriptions from the many well-preserved post-Devonian specimens as basis for the understanding of less well-preserved Devonian specimens. The material includes specimens from a new fish genus from the Upper Carboniferous beds in Norway, specimens from the Carboniferous of Great Britain referred to *Megalichthys* Agassiz, 1835 specimens from Upper Devonian beds in Germany and Balticum referred to different species of *Latvius* Jarvik, 1948, one lower jaw from Great Britain of the Middle Devonian *Osteolepis macrolepidotus* Agassiz, 1835, several also Middle Devonian specimens from Great Britain determined as *Gyroptychius milleri* Jarvik, 1948 and from Greenland referred tentatively to *Gyroptychius groenlandicus* Jarvik, 1950a.

Descriptions in this paper include only macrostructures. Discussions of possible significances of the described structures are mainly included in the next section.

## Material, methods and repository

During field work at Semsvik a detailed study of the profile was made and rock samples from the different beds were collected (Figs 2, 3; Table 1). The fossil specimens have been prepared mechanically, with vibro-tools and needles. On some specimens with only one visible side, the exposed side was covered by melted wax. After this artificial matrix had hardened the non-exposed side could be prepared. Chemical dissolution with acetic acid or sodium hydroxide had no effect on the samples.

Prior to photography several specimens were whitened with ammonium chloride to improve contrast. The photographs have not been retouched. Three specimens, two of *Askerichthys* (PMO 93549 and PMO 93553) and one of *Megalichthys hibberti* (HM G 8-52) were X-rayed to expose the course of sensory canals. The values used for the X-raying were 35–40kV and 300–750mA.

The fossil material collected from Semsvik in Asker belongs to the Natural History Museum in Oslo. The numbers of these specimens have the prefix PMO. Material of *Megalichthys* is borrowed from the Natural History Museum in London and Hancock Museum in Newcastle. Their specimens have respective prefixes BMNH PV and HM. The material of *Latvius*, and also other specimens from the Baltic Upper Devonian, belongs partly to Swedish Museum of Natural History, specimens with prefix SMNH, and partly to the Museum für

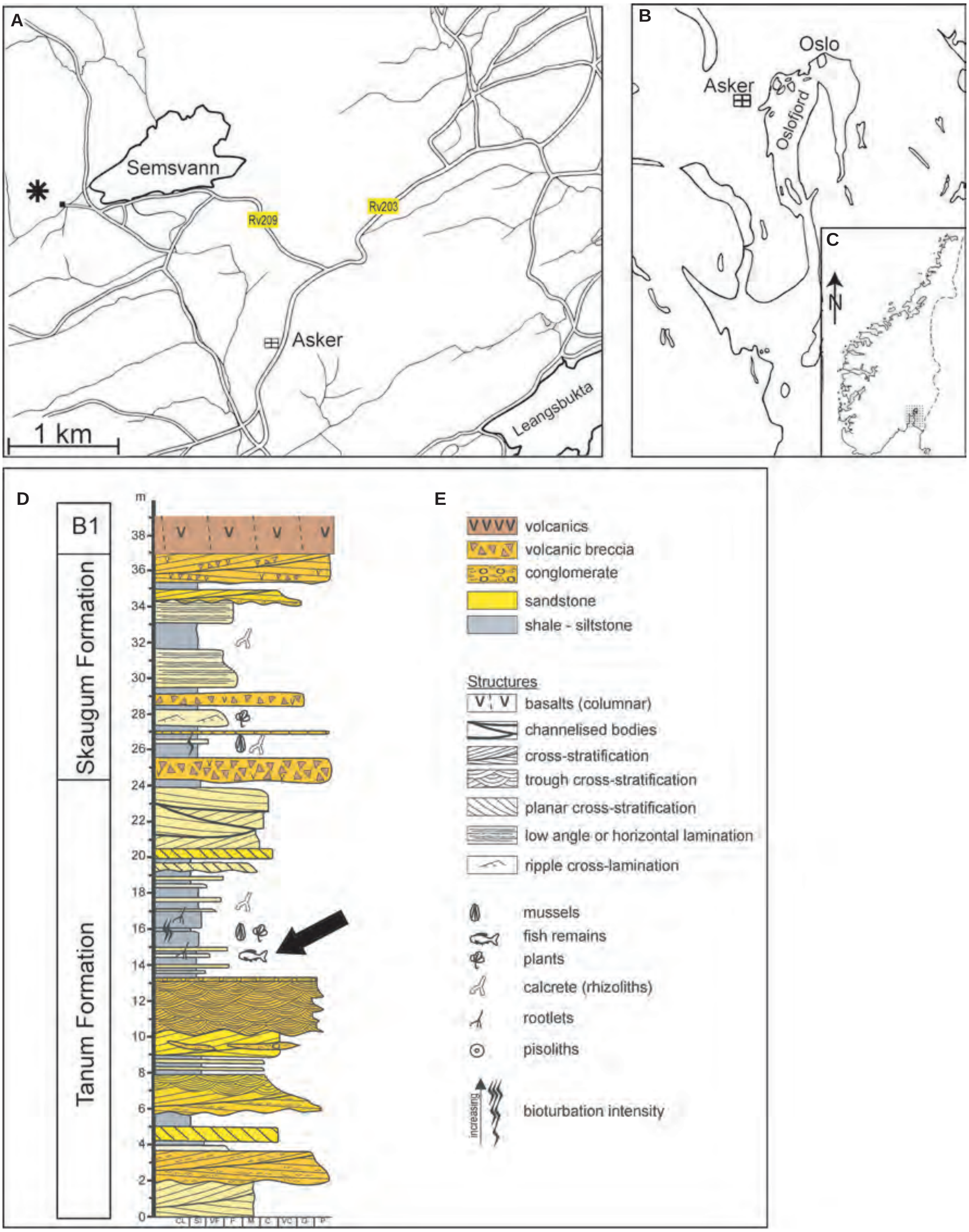

*Figure 3.* Maps showing the position of the fossil locality at Semsvannet W of the NW part of the Oslofjord. **A**, Map showing location of fossil locality relative to the lake Semsvannet and Asker church. The asterisk shows the fossil locality and the square the Semsvik farm. Asker church is also marked. **B**, The inner region of the Oslo fjord also showing the position of the Asker church. **C**, Southern Norway with area shown in map B indicated by shading. **D**, A general section of the sediments at Semsvik and of the whole Asker Group below the basalt (B1) (Snorre Olausson pers. com., 2010). **E**, Legend.

Naturkunde Berlin, which have the prefix MB. The material from Greenland has the prefix MGUH. The specimens are kept at the Natural History Museum of Denmark, University of Copenhagen, Denmark. For comparisons with materials from Palaeontological Museum of Uppsala (PMU) have been included; the Manchester Museum (MM); The Sedgwick Museum (SM); the Royal Scottish Museum (RSM); Australian National university (ANU); Australian Museum, Sydney (AMF); Commonwealth Palaeontological Collection (CPC), which is housed in the Bureau of Mineral Resources, Geology and Geophysics, Canberra, Australia; Queensland Museum QMF, Peabody Museum, Yale University (YPM); Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing (V).

## Genus *Askerichthys* n. gen.

*Type species.* – *Askerichthys heintzi* n. sp.

*Species included.* – The type species is the only known species of the genus.

*Diagnostic characters.* – (1) Lachrymo-maxillary notch angular; necessary character. (2) Nasal fenestra situated close to the dorsal margin of the lachrymo-maxillary notch, and mostly situated posterior to the corner of the notch. (3) Large triangular retroarticular process on the lower jaw. (4) Two pairs of coronoid tusks and thus only two coronoids. Characters 2–4 are all necessary and probably sufficient characters.

*Derivation of name.* – The genus is named for the township of Asker from which the fish is known.

## *Askerichthys heintzi* n. sp.

Figures 4–39, 110B, 117, 119D, 121D, 125F, 126A, 127B, 158A, 133B, 134D, 137B, 143A, 147A, 148A, 149H, 158A, 159A, 160A, 162A and 164B

1934 *Megalichthys* sp. Heintz, pp. 181, 185, pl. 1, figs 8–12; fig. 2B.

1995 'Borgen's new Norwegian genus'; Fox, Campbell, Barwick & Long, pp. 109–111, 129.

*Holotype.* – PMO 93555 (Figs 4, 5, 6, 21, 22, 23A, B, 24A, B, 26, 32, 36, 37, 38), Tanum Formation, Semsvik, Asker, Norway.

*Material.* – The holotype of *Askerichthys heintzi* is PMO 93555. It was collected by J. F. Bockelie at the type locality at Semsvik in 1965, and consists of a main specimen PMO 93555a (Figs 4, 5) and its counterpart PMO 93555b (Fig. 6). A posterior part of a left lower jaw that is prepared free from PMO 93555a constitutes PMO 93555c (Figs 23B, 24B, 26), a probable left maxilla, stuck on a latex mould of the counterpart, constitute PMO 93555d (Fig. 7) and the right preopercular that is prepared free from PMO 93555b is numbered PMO 93555e (Fig. 7B). The main specimen of the holotype shows remains of a body seen in ventral view. It shows some operculo-gular bones, a complete lower jaw (Figs 5, 23, 24), the left maxilla, an incomplete pectoral girdle (Clt, Figs 4, 37), scales from the ventral side, the caudal fin and remains of some median and paired fins (Figs 4, 6, 37).

There are four more or less complete specimens of the anterior cranial division (Figs 8, 9). PMO 73855 (Figs 8A, 9A) is an imprint of a fronto-ethmoidal shield whose reference to *Askerichthys* is uncertain. PMO 93549, PMO 93553 and PMO 93554 are more typical osteolepiform anterior cranial divisions (Figs 8B–D, 9B–D, 10–13). There is one incomplete posterior cranial division PMO 73876 (Figs 15–19) that, like the holotype, was collected by J. F. Bockelie. In addition to the bones on the holotype there is one separate opercular PMO 73879 (Fig. 35), and three separate lower jaws, PMO 51005 that is incomplete (Heintz 1934, pl. 10), PMO 93546, and PMO 93548 (Figs 23A–C, 24A–C, 25, 27–31). The latter specimen is complete. These are paratypes.

*Stratigraphic and geographic distribution.* – The species is known from the Upper Carboniferous beds at Semsvik in Asker west of Oslo (Fig. 3). The beds are referred to the Tanum Formation in the Asker Group (Table 1, Fig. 3).

*Derivation of name.* – The species is named after the late Professor Anatol Heintz, who was the first to describe remains of this fish. Together with his daughter Natascha Heintz he kept vertebrate palaeontology alive as a science in Norway for about six decades.

*Diagnostic characters.* – (1) Lachrymo-maxillary notch angular; necessary character. (2) Nasal fenestra situated close to the dorsal margin of the lachrymo-maxillary notch, and mostly situated posterior to the corner of the notch. (3) Large triangular retroarticular process on the lower jaw. (4) Two pairs of coronoid tusks and thus only two coronoids.

Characters 2–4 are all necessary and probably sufficient characters.

Description

*Fronto-ethmoidal shield*

*Shape.* – The general shape of the fronto-ethmoidal shields is shown in the illustrations (Figs 8–10). PMO 93553 (Figs 8C, 9C) is shorter and broader than PMO 93549 (Figs 8D, 9D). In PMO 93549 the dorsal mouth margin is visible from above. In PMO 93553 and PMO 93554 the margin is not visible in dorsal view, but this is probably due to the margin being secondarily bent underneath the anterior part of the shield because a fracture apparently resulting from such a break is visible. The shape of the subnarial corners (sn.c, Figs 8D, 10B, C–E, 12B, 13) appears approximately right-angled on PMO 93553 and slightly acute on PMO 93549 and PMO 93554. Anteriorly on the dorsal side of the shields the dermal bones are covered by a more or less continuous cosmine sheet, which also covers several sutures. More posteriorly the sutures are visible.

In PMO 73855 (Figs 8A, 9A) the interpretations of different bones are less obvious than on the other specimens. It is an imprint and thus cannot be prepared further. A notch on the left side of PMO 73855 looks somewhat like an orbital fenestra (?fe.orb, Fig. 8A), and if so a pair of bones mesial to this notch may be supraorbitals. An argument against this interpretation is that the posteriormost bone has a groove that looks like a pitline (?pl.Fr, Figs 8A, 9A) suggesting that this bone is the frontal (?Fr, Figs 8A, 9A). With this latter interpretation the above-mentioned notch (?fe.orb, Fig. 8A) must be a notch between the frontal and the posteriormost nasal (?Na. 7, Fig. 9A). Such a notch is present also on PMO 93549 and PMO 93554, but is on these specimens much shallower (Figs 8C, D, 9C, D). This latter interpretation fits well with the shape of the central bone that is reminiscent of the median posterior postrostral of PMO 93549 and PMO 93553 (M.p.pr, Figs 9C, D, cf. Fig. 8), and may thus represent this bone (?M.p.pr, Fig. 9A, B). The right antero-lateral part shows a possible fenestra exonasalis (?fe.ex, Figs 8A, 9A). Tentatively, this specimen is assigned to ?*Askerichthys heintzi*.

*Premaxilla.* – Neither the postero-dorsal suture of the premaxilla nor the postero-dorsal suture of the rostro-premaxilla is distinguishable on the external surface of PMO 93549, PMO 93553 or PMO 93554 (Fig. 8B–D). Except for the left lateralmost part on PMO 93553, the mouth margin of both PMO 93549 and PMO 93553 is complete between the subnarial corners. These two specimens have both been prepared in ventral view.

The anterior margin of the lachrymo-maxillary notch can best be studied on PMO 93549 (Fig. 10A, B, D), but is observable also on PMO 93553 (Figs 8C, 9C, 10E) and PMO 93554 (Figs 8B, 9B). On the latter two specimens the margin shows no specific structures except for a foramen (fr, Fig. 10E) that

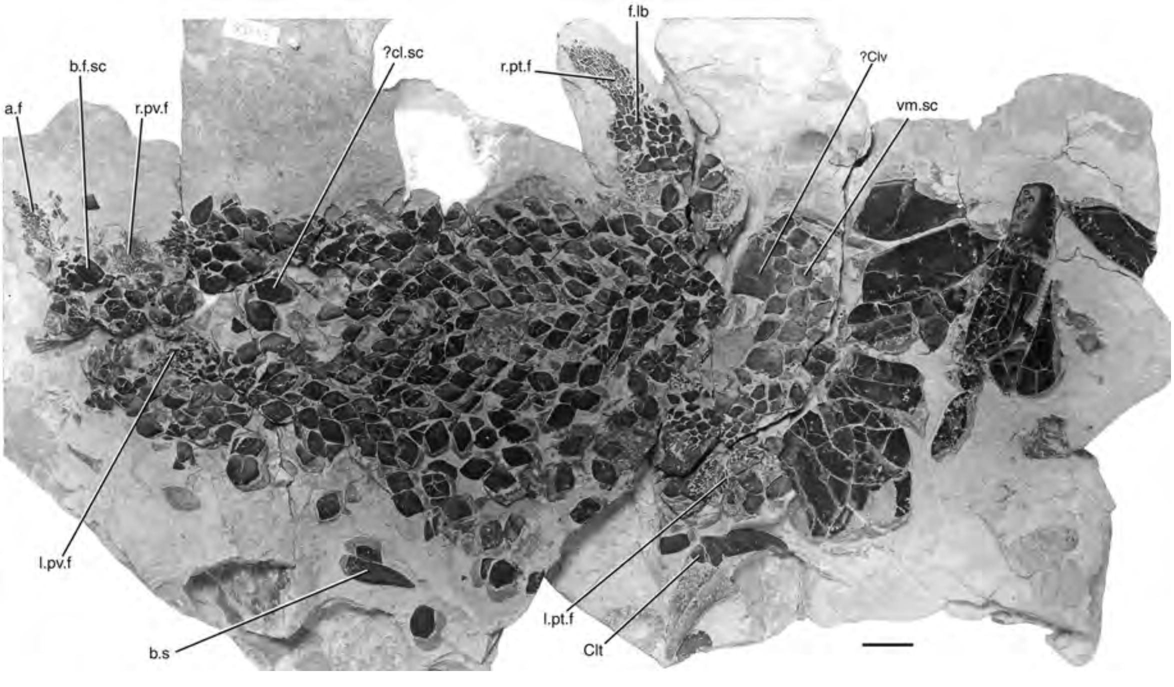

*Figure 4. Askerichthys heintziorum* n. gen. et n. sp. Tanum Formation, Semsvik, Asker, Norway, Late Carboniferous. PMO 93555a. Main specimen of the holotype. Scale bar = 1 cm. Abbreviations explained in Appendix 1.

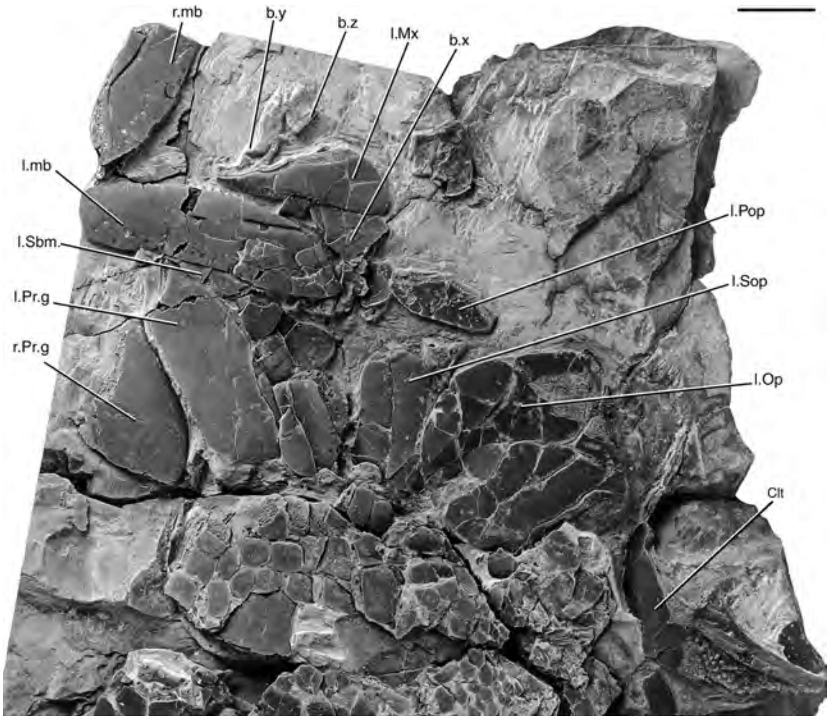

*Figure 5.* *Askerichthys heintziorum* n. gen. et n. sp. Tanum Formation, Semsvik, Asker, Norway, Late Carboniferous. Head section of holotype PMO 93555a. The half right mandible in the upper left corner of the specimen was later prepared free and is PMO 93555c. Scale bar = 1 cm. Abbreviations explained in Appendix 1.

*Figure 6.* *Askerichthys heintziorum* n. gen. et n. sp. Tanum Formation, Semsvik, Asker, Norway, Late Carboniferous. PMO 93555b. Holotype. Counterpart of PMO 93555a showing remains of the caudal fin and submandibulars. On this specimen, the main part of the fish is shown as an imprint. Scale bar = 1 cm. Abbreviations explained in Appendix 1.

covers a large part of the margin. It cannot be determined whether this is the opening for the infraorbital sensory canal, or the so-called premaxillary canal. The lack of other structures is partly because of incomplete preparation due to the fragility of the specimen. On PMO 93549 this region is slightly damaged, but shows more structures than the other specimens. A lateral distinct foramen is interpreted as the opening for the premaxillary canal (fr.c.Pm, Fig. 10D). Mesial to this foramen there are some pits that probably are secondary, and mesialmost on the margin there are two foramina that have tentatively been interpreted as, respectively, the opening for the infraorbital sensory canal (fr.io.sc, Fig. 10D) and a branch of this canal. A groove running along the ventral margin of the narrow bar ventral to the nasal fenestra, possibly led the infraorbital sensory canal (gr.io.sc, Fig. 10D).

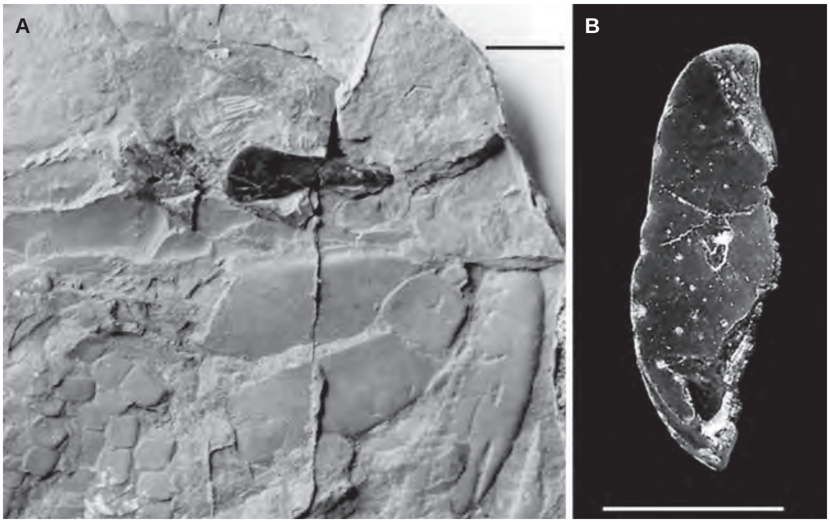

*Figure 7. Askerichthys heintziorum* n. gen. et n. sp. Tanum Formation, Semsvik, Asker, Norway, Late Carboniferous. **A**, Detail of holotype. PMO 93555d. Part of the latex mould of PMO 93555b on which is stuck a dermal bone, probably the right maxilla. **B**, The right preopercular is prepared loose from PMO 93555b and is numbered PMO 93555e. Scale bar = 1 cm. Abbreviations explained in Appendix 1.

In ventral view the subnarial corner on PMO 93553 (sn.c, Fig. 13) is positioned approximately at the level of the mid-point of the lateral margin of the fenestra endochoanalis, whereas on PMO 93549 it is positioned nearer to the anterior end of this margin (sn.c, Fig. 12B).

On both PMO 93549 and PMO 93553 the ventral side of the mouth margin shows pits for premaxillary marginal teeth that are situated on a premaxillary shelf (sh.Pm, Fig. 13). Mesially this shelf is expanded constituting the ventral part of an antero-median palatal process (am.pl.pr, Fig. 13). This process functions as the base for premaxillary tusks (tu.Pm, Figs 12B, 13). On PMO 93549 part of the process seems to be in contact posteriorly with anterior remnants of the parasphenoid (Fig. 12B). On PMO 93553 such a contact is not observable (Figs 12A, 13). There are no marginal teeth anterior to the antero-median palatal tusks on any of the two specimens.

PMO 93553 had on the right side apparently 15 premaxillary teeth (t.Pm, Fig. 13) not counting the tusk (tu.Pm, Figs 12, 13). On the incomplete left side of PMO 93553 there are observable remains of 9 teeth, but the ninth tooth is situated in the same position as the ninth tooth on the right side, suggesting a similar number on both sides. On PMO 93549 the number of teeth is less clear. An estimated number of teeth and empty pits on the right side suggests, not counting the tusk, 13–14 teeth. On the left side an estimate gives 11–13 premaxillary teeth.

On PMO 93553 the palatal lamina on the left side shows a shallow groove posterior to the premaxillary shelf. On PMO 93549 there is such a groove on both sides. These grooves are rather indistinct, and may be secondary features, but for reasons outlined in the morphologic discussions they are tentatively interpreted as sutures between premaxilla and the rostral series (s.Pm/Ro, Figs 12B, 13).

Laterally, on both sides, there are posterior expansions from the palatal lamina constituting the lateral walls of the anterior palatal fenestra. These antero-lateral palatal processes (al.pl.pr, Fig. 13) are directed postero-mesially. They are seen on both sides of both specimens, but are most distinct on the right side of PMO 93553. This process meets antero-laterally directed parts that have been interpreted as being endocranial. Since the ventralmost part of the process on the right side of PMO 93553 is situated also at a level ventral to the endocranial part, and since the process on the left side of PMO 93553 meets structures that possibly are remains of the anterior vomer (?Vo, Fig. 13), also the right antero-lateral palatal process possibly also met the anterior vomer. A possible anterior suture of the anterior vomer runs across the bone mesial to the left nasal cavity.

*Rostrals.* – If the above-mentioned groove observable on the palatal lamina is the suture between premaxilla and the rostral series, the part of the anterior wall of the apical fossa dorsal to this groove is part of the rostral bones (?Ro, Fig. 13). The suture

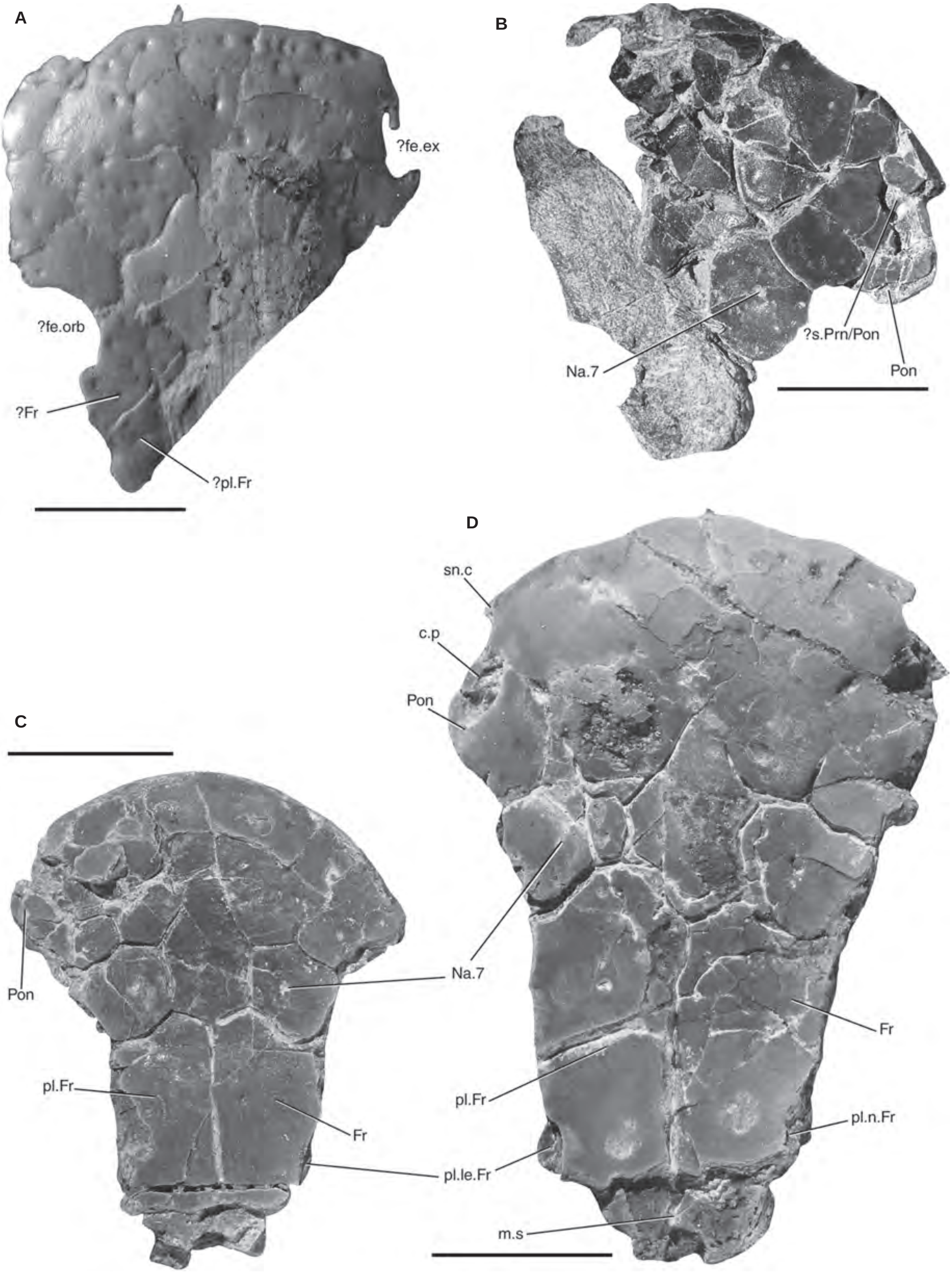

*Figure 8.* Fronto-ethmoidal shields in dorsal view. Tanum Formation, Semsvik, Asker, Norway, Late Carboniferous. **A**, *Askerichthys*? PMO 73855. **B**–**D**, *Askerichthys heintziorum* n. gen. et n. sp. **B**, PMO 93554; **C**, PMO 93553; **D**, PMO 93549. Scale bars = 1 cm. Abbreviations explained in Appendix 1.