Morphology, Taxonomy and Interrelationships of Tristichopterid Fishes (Sarcopterygii, Tetrapodomorpha)

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Abstract

Tristichopterids (Sarcopterygii, Tetrapodomorpha) form a monophyletic group of exclusively Devonian fishes. This thesis consists of descriptions of new material of tristichopterids and closely related taxa, as well as new interpretations and descriptions of previously figured material. Redescribed specimens were originally figured as far back as 1861, and publications as old as this are almost always of limited use as anatomical and systematical references, in addition to being difficult to acquire. The possibility of using new techniques and new theoretical frameworks also provides good justification for taking a second look at such specimens. In the case of this thesis, this includes the use of computed tomography scanning methods, and the cladistic approach to describing the interrelationships of taxa.

The thesis includes a complete taxonomy of valid tristichopterid taxa, in addition to two new phylogenetic analyses incorporating the taxa that were described or redescribed. One of the analyses deals with the interrelationships of taxa along the entire tetrapod stem, and establishes the monophyly of the Tristichopteridae. The other analysis focuses on tristichopterid interrelationships.

An account is given of evolutionary trends within Tristichopteridae, and instances of parallel evolution between tristichopterids and other tetrapod groups are discussed.

The biogeographical implications of tristichopterid occurences world-wide seem to corroborate the picture provided by other vertebrate groups, and give further support to one of two main hypotheses concerning the relative positions of Gondwana and Laurussia, the two major palaeocontinents during the Late Devonian. The supported hypothesis proposes a close proximity between southern Laurussia and northwestern Gondwana, as evidenced by the wide dispersal of derived tristichopterids by the Late Devonian. A Laurussian origin of tristichopterids is proposed.

Keywords: Sarcopterygii, Tetrapodomorpha, Tristichopteridae, biogeography, phylogeny, Computed Tomography, Devonian

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urn:nbn:se:uu:diva-8625 (http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-8625)
Et ignotas animum dimittit in artes.

-Ovid, Metamorphoses VIII, 118

Trust your mechanic.

-Dead Kennedys
List of papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:


II Snitting, D. *Heddleichthys* – a new tristichopterid genus from the Dura Den Formation, Midland Valley, Scotland (Famennian, Late Devonian). Accepted, Acta Zoologica.


In Paper IV, DS coded the data matrix and gave some minor input on the text of the manuscript. In Paper V, DS wrote the manuscript, while DS and HB both performed literature searches.

**Note.** This thesis is not intended for permanent scientific record in the meaning of the International Code of Zoological Nomenclature (ICZN). Therefore, nomenclatural acts proposed here are not valid. The dissertation should not be cited as a source of nomenclatural statements.
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Most of the work included in this thesis consists of descriptions of fossil fish. More specifically, these are fossil fish that are second cousins to land vertebrates – and thus also to human beings. Our story as vertebrates, and the traits that define us, have their beginning sometime in the remote past. They can be traced back to a group of fishes, quite unlike any fish alive today, that flourished during the Devonian and then gradually went extinct, leaving land vertebrates as the sole survivors.

What is the purpose, then, of studying the anatomy of extinct organisms? The short answer would be that they offer a unique glimpse through a weird looking-glass – we get to see how the biological diversity we can observe today came to be, how the features that define groups today made their gradual appearance in the history of life, and we gain more and more insight into what the family tree of all life might look like. In short, fossils change the way we look at the diversity of extant organisms. We will never get the complete picture, but so what? The simple wonder of getting to know animals that were alive and swimming hundreds of millions of years ago, animals that are in some regards utterly different from and in other regards curiously similar to animals alive today, is part of the limitless human craving to satisfy curiosity.

The objective of this thesis has been the description of fishes belonging to a relatively crownward monophyletic group of tetrapodomorph fishes – the Tristichopteridae (more on crown groups and tetrapodomorphs below!). Historically, tristichopterids have featured extensively in the study of Palaeozoic vertebrates, especially with regard to the origin of the first land vertebrates. The most famous and extensively studied Palaeozoic fish is a tristichopterid: *Eusthenopteron*, recognized as important in the study of the emergence of tetrapods since the middle of the 19th century (Jarvik 1980). Tristichopterids are interesting in their own right: they form the largest monophyletic radiation of tetrapodomorph fishes, and in many instances parallel the morphological evolution seen in other tetrapodomorph subgroups, including tetrapods.

As more and more tristichopterid taxa are recognized and described, a picture of a diverse group with internal ecological separation appears. There are great differences in size, with total body lengths ranging from around 30 cm (*Tristichopterus*) to several meters (*Hyneria*), in addition to more subtle differences suggesting varying modes of life. Even though there seems to
have been a high diversity of tristichopterids in the Late Devonian, with an almost global distribution, no representative of the group survives past the Devonian-Carboniferous boundary.

In recent years, several new tristichopterid taxa have been described. The main point of this thesis has been to use this new information, combine it with the results of redescriptions providing a modern view of tristichopterids studied in the more remote past, and present a combined picture of the current knowledge of the evolution and distribution of the group.

The specific results of the papers included in this thesis are incorporated in the two phylogenetic analyses, the biogeographical discussion, the conclusions about tristichopterid evolutionary trends, and the taxonomic review included in this comprehensive summary.

The examined material includes fossils from Scotland (*Heddleichthys*), the Orkneys (*Tristichopterus*), East Greenland (*Spodichthys*) and Belgium (*Langlieria*). All these localities belonged to the palaeocontinent of Laurussia during the Middle and Late Devonian, when the rocks containing the fossils were deposited. Paper I deals exclusively with previously described material, while Papers II-III present new material in addition to redescriptions (Anderson 1859; Egerton 1861; Traquair 1875; Jarvik 1950, 1985).

One might wonder at the purpose of redescribing specimens already figured in the literature. The reasons can vary, as is illustrated by the papers in this thesis. Partly, the redescriptions provided here serve to give a modern view of specimens figured very long ago, with all this means in terms of scientific language, standard of illustration, and accessibility of the actual publications. When the specimens are restudied, and seen in the light of other discoveries, one often notices things that were simply not of interest to the original authors. Beginning in the first part of the 20th century, there has also been a massive shift in the general attitude towards properly illustrating details of figured material, and specifying which specimens are actually figured. In older publications, it is rare to find any reference to specimen numbers. As a consequence, unless the specimens are properly illustrated (not often the case), it is impossible to know what the original material was.

The other main rationale for these redescriptions is the simple fact that greatly enlarged volumes of data can be extracted from the specimens when modern techniques are used. This ranges from good light microscopes and cameras, to the utilization of computed tomography (CT-scanning) techniques and subsequent digital reconstructions. In fact, Papers I-III all depend to a large extent on the use of CT-scanning as a means of providing new data and new interpretations of the material. Another purpose of tackling old material is to shed light on confused matters of taxonomy. This is mainly illustrated by Paper III.
Material and methods

The *Spodichthys* material described in Paper I belongs to the Geologisk Museum, Copenhagen. It was collected during the Danish expeditions to Greenland, which took place from 1929-1956 under the leadership of Lauge Koch (Jarvik 1985). The collected material resulting from these expeditions was originally shipped to Naturhistoriska Riksmuseet in Stockholm for study, and then deposited in Copenhagen.

The *Heddleichthys* material belongs partly to the National Museums of Scotland, Edinburgh, and partly to the British Geological Survey, Nottingham. It was collected during the 19th century, with most of the specimens previously described by other authors (Anderson 1859, Jarvik 1950). One of the specimens described (NMS.G.2007.22.1) was identified during a visit to the collections in Edinburgh in 2007, and is figured for the first time in Paper II.

The *Tristichopterus* material consists of a mix of previously figured material, collected in the 19th century, and material collected during the last few decades (Egerton 1861; Traquair 1875; Jarvik 1937; Andrews and Westoll 1970b). The old material is part of the collections at the National Museums of Scotland, Edinburgh, while the new material has been recently deposited at the Natural History Museum, London. One of the new specimens (RBJ-127) is still part of a private museum collection, but will eventually be deposited at the National Museums of Scotland, Edinburgh.

The *Langlieria* material was collected during field trips in 1995 and 2003. In addition, there is material that is probably referable to *Langlieria* in the collections at the Royal Institute of Natural Sciences in Brussels, and at Liège University.

As mentioned above in the introduction, CT-scanning has been extensively used in the present studies (Papers I-III). With this technique, it is possible to get at internal structures of a three-dimensionally preserved specimen without destroying the specimen with manual preparation. Parts of a specimen that are still within matrix can also be investigated, which is particularly useful when it would be difficult or very time consuming to manually surface prepare the structures in question. A CT-scan results in a series of images, representing sections of the specimen (Fig. 1).
Figure 1. Two sections from the *Heddleichthys* scan series (transverse slices).

I have used a medical software called Mimics in order to analyze the image series produced in the CT-scanner. Virtual three-dimensional models of the different anatomical structures can be constructed and exported for subsequent inclusion in publications or teaching (Fig. 2).

Figure 2. Right lower jaw and palatal elements of *Heddleichthys* in internal view. Model created in Mimics v9.11.

All scans were performed at the University of Texas in Austin.
Phylogenetic framework

Stem groups and crown groups

The relationship of an extant group of organisms to the extinct group of organisms from which it is descended can be expressed in terms of stem and crown groups. Rather than searching the fossil record for taxa that are directly ancestral to subsequent forms, the stem group concept focuses on the paraphyletic assemblage of taxa that form the lineage from which the now living group is descended. Direct ancestors are not inferred. Rather, successively more closely related (more and more crownward) sister taxa to the crown group are identified (crosses in Fig. 3). These successive taxa constitute a paraphyletic group. A crown group is defined as the least inclusive group containing all extant members of a given clade – the node of origin of the clade is the last common ancestor of all living taxa in the group. This means that a crown group will be made up of a mixture of extinct and extant organisms. A stem group, on the other hand, consists entirely of extinct organisms. A stem group and a crown group together form a total group, which is the sister taxon of another total group. Stem and crown groups can be defined at different levels (Fig. 3B). All members of the human stem group, for instance, are part of the primate crown group, and all members of the primate stem group are members of the mammalian crown group.

Popular notions of ancestors and “missing links” have little to do with the way in which the study of fossils actually proceeds. As described above, common ancestry is inferred, rather than ancestor-descendent relationships. An example of this contrast in outlook would be to look at the popularly entrenched notion that the evolution of vertebrates started off with fish, which evolved into amphibians, which evolved into reptiles, which evolved into mammals and birds. This view assumes that the interrelationships of these groups can be expressed as a chain of ancestors and descendants, and that this lineage is what palaeontologists study. Not surprisingly, this model is false. Instead, mammals and reptiles plus birds share a more recent common ancestor than do mammals and amphibians – which defines mammals and reptiles plus birds as more closely related to each other than either is to amphibians. In the figure below, this could be illustrated by the
relationship of A (substitute for mammals) and B (substitute for reptiles plus birds) to C (substitute for amphibians).

Figure 3. Stem and crown groups.
Lobe-fins and ray-fins

Bony fishes (osteichthysans) can be divided in two major radiations: ray-finned fishes (actinopterygians, Fig. 4A) and lobe-finned fishes (sarcopterygians, Fig. 4B-D).

Figure 4. A: Cod (a ray-finned fish), B: Latimeria (with tetrapod), C: Tetrapods, D: Neoceratodus (Australian lungfish).

All ray-finned fishes would in everyday conversation be considered “fish”: cod, herring, mackerel, tuna, eel, bass, pike. Some 30000 extant species of ray-finned fish have been described. The lobe-finned group, on the other hand, is almost exclusively made up of animals that in everyday conversation would be called “land vertebrates”, or “tetrapods”: shrews, elephants, turkeys, humans. The exceptions are three genera of lungfishes (the African, South American and Australian) and one genus of coelacanth (the famous Latimeria, thought to be extinct but discovered very much alive off the coast of South Africa in 1938). Of these, the lungfishes are the ones most closely related to land vertebrates. If we look at the fossil record, we get a rather different view of fish diversity. Some 360-400 million years ago,
During the Devonian, a number of now extinct piscine sarcopterygian fish groups inhabited oceans and lakes, rivers and river deltas. One of these lineages, the Tetrapodomorpha, included everything from small species, such as Spodichthys (Jarvik 1985; Paper I) to enormous predators such as Rhizodus, in some cases with body lengths of up to seven or eight meters, and equipped with fangs over 30 cm in length (Jeffery 2003). Tetrapods make their first appearance sometime in the later part of the Devonian and are descended from amongst this group of fishes. Modern lungfishes are part of another lineage, the Dipnomorpha, which also had a much higher diversity in the Devonian than the three genera observed today.

Lobe-finned fishes are defined by a number of characters, or synapomorphies. These include the presence of monobasal fins (the most proximal endoskeletal structure in the fins or limbs of a sarcopterygian is a single element, articulating with the shoulder girdle or pelvis) and a special kind of hard tissue called cosmine, that covers the external bones.

Interrelationships of tetrapodomorph fishes

The names Tetrapodomorpha and Dipnomorpha were established by Ahlberg (1991) to mean the tetrapod and lungfish total groups, respectively. Since these two lineages were defined, discussions of the interrelationships of taxa along the tetrapod stem have largely concerned the monophyly or paraphyly of the “Osteolepiformes”, a grouping that includes taxa that in the present analysis occupy positions between Kenichthys and the (Panderichthys + Tetrapoda) node (Fig. 5) (Ahlberg and Johanson 1998). Prior to Ahlberg and Johanson (1998), the monophyly or paraphyly of “Osteolepiformes” had not been demonstrated, and relationships along the tetrapod stem remained obscure (Young et al. 1992; Cloutier and Ahlberg 1996; Chang and Yu 1997). Ahlberg and Johanson (1998) recovered a paraphyletic “Osteolepiformes”, and this result has been corroborated in later studies, although the specific interrelationships of “osteolepiform” taxa are still in dispute (Johanson and Ahlberg 2001; Long et al. 2006; Friedman et al. 2007; Paper I).

For this comprehensive summary, a dataset consisting of 22 tetrapodomorph and 5 dipnomorph taxa coded for 107 morphological characters (character list, data matrix and parameter settings in Appendix 1) was analysed in PAUP* v.4b10 (Swofford 2002), resulting in 63 equally parsimonious trees (tree length=194) (Fig. 5).

The analysis recovers the same basic tetrapodomorph subgroups as other recent investigations (for instance Ahlberg and Johanson 1998; Friedman et al. 2007). These are the Rhizodontidae (represented by Gooloogongia and Barameda in this data set), Megalichthyidae (Ectosteorhachis, Cladarosymblema, Rhizodopsis and Megalichthys) and Tristichopteridae.
(Tristichopterus, Eusthenopteron, Heddleichthys, Cabonnichthys and Mandageria).

Figure 5. Strict consensus of 63 equally parsimonious trees (tree length=194 steps). Consistency index=0.629; Retention index=0.793.

This expanded data set gives the same general picture of tetrapodomorph interrelationships as the analysis presented in Paper I. Kenichthys is the most basal tetrapodomorph, in agreement with previous studies. Rhizodonts form the most basal monophyletic radiation of tetrapodomorphs thus far identified, again agreeing with previous results (Ahlberg and Johanson 1998; Friedman et al. 2007). The “osteolepid” part of the tree is not robustly resolved: Osteolepis, Gogonasus, Medoevia, Koharalepis and Gyroptychius together with Megalichthyidae represent a paraphyletic assemblage of tetrapodomorphs with a rather generalized appearance (such as cosmine-covered rhombic scales, an otoccipital that is subequal in length to the ethmosphenoid unit, a short autopalatine region of the entopterygoid, and lyre-shaped supraorbital sensory canals). Megalichthyids form a distinct radiation, characterised inter alia by a closed pineal, a reorientation of the lateral rostral and tectal around the external nostril (anterior/posterior rather than dorsal/ventral), elongate vomers with a laterally directed long axis,
absence of vestibular fontanelles and the presence of symphysial dentary fangs (Thomson 1964; Jarvik 1966; Fox et al. 1995). “Osteolepid” taxa are often relatively poorly known (with shining exceptions in Cladarosymblema, Medoevia and Gogonasus: Fox et al. 1995; Lebedev 1995; Long et al. 1997, 2006), especially when neurocrania anatomy is concerned. In addition, most of these taxa do not even have satisfyingly described lower jaws. There are massive amounts of specimens of Osteolepis and Gyroptychius in museum collections, but there is not a single detailed description in the literature of the mesial surface, or the dentition, of lower jaws belonging to either of these two taxa. Lower jaws and neurocrania are potentially very valuable, character-rich anatomical complexes.

As mentioned above, a monophyletic Tristichopteridae is recovered in this analysis, with Spodichthys as sister taxon. The latter is not included in Tristichopteridae due to the presence of an anteriorly positioned extratemporal in Spodichthys, and Tristichopteridae is diagnosed here as showing a derived condition with the extratemporal in a postspiracular position. However, Spodichthys and tristichopterids share a number of other derived character states: the anterior margin of the vestibular fontanelles extends anterior to the posterior margin of the basicranial fenestra; the parasymphysial dental plate of the lower jaw is button-like, and not posteriorly extended to reach the anterior coronoid; and the posterior margin of the floor of the fossa bridgei is transverse, thus creating a distinct posterolateral corner of the otic region, with a resulting distance between the articulation areas for the hyomandibula and the posterior margin of the floor of the fossa bridgei. In contrast for the latter character, the otic region of Panderichthys shows the “osteolepid” condition, with an oblique posterior margin of the floor of the fossa bridgei, and with the hyomandibular facets in an extreme posterior position (Ahlberg et al. 1996).

Spodichthys, Tristichopteridae and (Panderichthys + Tetrapoda) are uniquely defined by an elongated autopalatine portion of the entopterygoid, placing the anterior palatoquadrate articulation in a position far anterior to the processus ascendens; a suture between the anterio-rmost infradentary and the prearticular; a posterior coronoid which is longer than the anterior and middle coronoids; and a straight course of the supraorbital sensory canal. Derived characters of Spodichthys, Tristichopteridae and (Panderichthys + Tetrapoda) with a wider distribution within the Tetrapodomorpha include the loss of cosmine and the presence of a posterior process of the horizontal lamina of the vomer. Spodichthys and Tristichopteridae also have round scales with an internal boss, a derived character with a wider distribution among tetrapodomorphs (also seen in rhizodonts, Marsdenichthys and Rhizodopsis) (Long 1985, 1989; Schultze and Heidtke 1993).

The relative sizes of the coronoids deserves further comment. Generalized “osteolepidids” such as Medoevia and Gogonasus display a coronoid series where the anterior coronoid is the longest, and the posterior coronoid is the
shortest (Fox et al. 1995; Lebedev 1995; Long et al. 1997). Outgroup comparison with porolepiforms seems to suggest that this setup is primitive for tetrapodomorphs (Jarvik 1980). For Kenichthys, this is harder to establish because it is difficult to separate the middle and posterior coronoids (Chang and Zhu 1993; Zhu and Yu 2004). In Spodichthys, the posterior coronoid is slightly longer than the anterior (around 20%), and the middle coronoid is the shortest. Tristichopterus and Acanthostega have a posterior coronoid which is longer (between 35 and 40%) than the anterior and middle coronoids, which are almost equal in length (Ahlberg and Clack 1998). In tristichopterids other than Tristichopterus, the posterior coronoid is around twice the length of the middle and anterior coronoids (Jarvik 1980; Ahlberg and Johanson 1997; Johanson and Ahlberg 1997). Panderichthys is less extreme, but the posterior coronoid is still considerably longer than the other two, at least if the anterior coronoid is measured from the precoronoid fossa (Ahlberg and Clack 1998).

Tristichopterids, Gyroptychius, Spodichthys, Tiktaalik and Panderichthys have vomers with posterior processes, and skull tables where the posterior margins of the tabulars are at the same level as the posterior margins of the postparietals (although this is variable for Gyroptychius) (Jarvik 1948, 1985; Vorobyeva 1962; Daeschler et al. 2006). Primitively, the posterior margin of the skull roof of tetrapodomorphs is curved, with the posteriormost point medially (Jarvik 1980; Chang and Zhu 1993).

As revealed by this and previous phylogenetic analyses, tristichopterids form a distinct radiation of crownward tetrapodomorph fishes. There is variation in the appearance of tristichopterids, even though they are all constructed on a similar theme. This enables studies of evolutionary trends within the group, a meaningful endeavour when there are enough taxa available for intra-group comparison. Useful comparisons can also be made with the evolutionary trends within other tetrapodomorph radiations, and cases of parallel evolution can be documented. These issues are discussed further below.

Since tristichopterids are phylogenetically close to the origin of tetrapods, they provide useful information concerning the conditions present at the proximate fish end of the fish-tetrapod transition. Primitive tristichopterids, as well as Spodichthys, help us understand what morphological transformations took place within the most crownward fish section of the tetrapod stem. Since some of the features evolved in parallel in tristichopterids and tetrapods are unique to these two groups, understanding the fish taxa on all sides of the last common ancestor of Tristichopteridae and Tetrapoda is central to the study of both these radiations.
Historical review

Tetrapod ancestors

In 1861, T. H. Huxley wrote a review of the Devonian fishes of Great Britain. He erected the taxon “Crossopterygidae” where he included lobe-finned fossil fish, some ray-finned fossils, and the extant actinopterygian *Polypterus*. The realization that lobe-finned fishes formed a group (although this was not made explicit in Huxley’s scheme) defined chiefly by the skeleton of their fins (which are constructed on a similar pattern to the tetrapod limb) eventually led to the idea that this was where the ancestor of tetrapods could be discovered. This view was formalized by Cope (1892) who explicitly associated crossopterygians with tetrapods. Here lies part of the explanation for the subsequent iconic status of *Eusthenopteron*, classified as a crossopterygian by Cope. Not only was *Eusthenopteron* known in great anatomical detail, but it belonged to that group of fishes considered to be part of the ancestry of tetrapods – and thus also of humans. In the modern cladistic approach, this hunt for fossil ancestors has been replaced by the study of stem groups, removing the emphasis on ancestor-descendant relationships. Nevertheless, it is easy to see why the idea that we can know our ancestors is so suggestive. Since *Eusthenopteron* was sufficiently close in time and shape to the earliest known tetrapods, and was so well known and studied, it has frequently been used as a proxy for what the fish-end of the fish-tetrapod transition would have looked like. Quite apart from the philosophical implications of looking for ancestors, the view that *Eusthenopteron* is appropriate as a representative of a “fish ancestor” of tetrapods has been somewhat discredited by new findings and descriptions of fossils closely related to both *Eusthenopteron* and early tetrapods. This includes more detailed knowledge about *Tristichopterus* and *Spodichthys*, two taxa that help elucidate which features of *Eusthenopteron* were present in the last common ancestor of tristichopterids and tetrapods, and which features were derived tristichopterid characteristics.

The Stockholm School and *Eusthenopteron*

For a period of time in the middle of the 20th century, Naturhistoriska Riksmuseet in Stockholm, Sweden, was a major centre for the study of
Palaeozoic vertebrates. The so-called “Stockholm School” of vertebrate palaeontology included researchers such as Erik Stensiö, Gunnar Säve-Söderbergh, Hans Bjerring, Tor Ørvig, Egil Nielsen and Erik Jarvik. Firmly based in the practice of comparative anatomy, the group produced large numbers of often very thick and incredibly detailed volumes on various aspects of vertebrate anatomy, embryology and histology (Jarvik 1980; Janvier 1996; and references therein). Among the most impressive achievements was the successful use of the so-called Sollas grinding method, where fossils were serially ground, with each new transverse surface photographed and drawn. The drawings were then used as a basis for the construction of three-dimensional wax models of the ground specimen. In the case of the most famous grinding series, the one of the skull of the tristichopterid *Eusthenopteron* (specimen P. 222) (Fig. 6), the drawings were made at intervals of 200 μm.


This particular grinding series took almost 25 years to finish! Sollas grinding method, although incredibly laborious and time consuming, allowed for descriptions of minute details of the internal structures of the animals under study. At the end, all that was left of the fossil was a pile of dust, the information it contained instead transferred to photographic glass plates and large sheets of drawing paper (Fig. 7). The knowledge gained about the internal anatomy of the studied animals allowed for detailed comparisons with other fossil groups, as well as with recent taxa. The serial grinding technique can be compared with the use of different scanning technologies today. In a scanner, a specimen can be digitally dissected in an afternoon (although the actual interpretation and modelling of the virtual specimen can
take months), with a quality sometimes approaching that achieved by the unbelievably slow and labour-intensive serial grinding. In addition, the specimen itself is not destroyed, allowing for the technique to be used even on rare and unique fossils.

Figure 7. Two drawings of (transverse) sections from the *Eusthenopteron* grinding series. Left: at the level of the anterior part of the orbit. Right: at the level of the pineal foramen. Modified from Jarvik (1980). Original drawings at Department of Palaeozoology, Naturhistoriska Riksmuseet, Stockholm.

Because of the grinding series of *Eusthenopteron*, this genus has become the most well-known and extensively studied Palaeozoic vertebrate. Jarvik described various aspects of the anatomy of *Eusthenopteron* in a large number of publications (Jarvik 1937, 1942, 1944a, 1944b, 1950, 1954, 1963, 1966, 1980, 1996). In some regards, the level of detail to which *Eusthenopteron* could be described matched well the information that could be gathered from the study of extant fishes. In his two-volume summary of vertebrate anatomy, *Basic Structure and Evolution of Vertebrates*, Jarvik dedicated one section to the extant primitive ray-finned fish *Amia calva* and one section to *Eusthenopteron*, comparing the two in great depth (Jarvik 1980).
Tristichopterids – results and discussion

Tristichopterid taxonomy

Tristichopterids, in order of original description, with age and any additional important references specified for each taxon.


Additional species:


Additional species:


Cabonnichthys burnsi Ahlberg and Johanson, 1997. Monospecific. Frasnian or Famennian of New South Wales, Australia.

Langlieria socqueti Clément et al. Monospecific. Famennian of Belgium.

Invalidated taxa, in order of original description.

Cricodus wenjukowi Rohon, 1889. Renamed Eusthenopteron wenjukowi (Jarvik 1937).


The problem of Platycephalichthys

Three species of Platycephalichthys have been described (Vorobyeva 1959, 1962, 1977). A subfamily gathering the three species, Platycephalichthyinae, has also been erected (Vorobyeva 1977). A closer study reveals that the material assigned to Platycephalichthys almost certainly belongs to more than one genus. The diagnosis of Platycephalichthyinae includes the presence of rhombic scales (p. 192 and plate 13:7, Vorobyeva 1977), different from the round scales found in tristichopterids (Jarvik 1980; Ahlberg and Johanson 1998). Lower jaws referred to Platycephalichthys
have symphysial dentary fangs, and either one (P. bischoffi, plate 16:1b, Vorobyeva 1962) or two (P. skuenicus, plate 17:2b, Vorobyeva 1962) fangs on the posterior coronoid, the latter a synapomorphy of tristichopterids more derived than Tristichopterus (Paper III). Platycephalichthys lower jaws also differ from each other in the shape of the parasymphysial dental plate, with either a posteriorly extended plate contacting the anterior coronoid (plate 16, Vorobyeva 1962; fig. 15B, Vorobyeva 1977) or a small, drop- or kite-shaped plate not in contact with the anterior coronoid (plate 9:1, Vorobyeva 1962). The former condition is primitive for tetrapodomorphs, and the latter is a synapomorphy of Spodichthys and tristichopterids (Ahlberg and Clack 1998; Johanson and Ahlberg 2001).

It thus seems like the material referred to Platycephalichthys could be separated into at least two genera. One of these would be an (at least moderately) derived tristichopterid with symphysial dentary fangs, two fang positions on the posterior coronoid and a small kite- or drop-shaped parasymphysial plate. The other would be more similar to Panderichthys, with cosmine-free rhombic scales and a lower jaw with one posterior coronoid fang, a symphysial dentary fang and a posteriorly extended parasymphysial plate. Awaiting further clarification on the issue of the identity of material ascribed to Platycephalichthys, I have decided to omit the taxon from the phylogenetic analysis described below, and will make only brief reference to it in the discussion.

Defining Tristichopteridae

Tristichopterids are defined slightly different than previously (Jarvik 1980; Ahlberg and Johanson 1997; Johanson and Ahlberg 2001). The presence of two fang positions on the posterior coronoid and ectopterygoid turns out to be a feature of tristichopterids more derived than Tristichopterus, rather than of all tristichopterids (Johanson and Ahlberg 2001; Paper III). A fang position is here taken to mean the entire setup of fang plus associated replacement pit. Two fangs can thus be present at the same time on the same fang position, if the replacement fang is developed before the old fang is actually shed. When preservation permits, this can often be observed (such as in Gogonasus (Long et al. 1997) or Heddleichthys (Paper II)).

Primitively, tristichopterids display a characteristic, more or less asymmetrically triphycercal tail (Eusthenopteron, Tristichopterus). The caudal fin of derived tristichopterids is a truncated version of this, being diamond-shaped in a manner superficially similar to the caudal fin of Gyroptychius, but with greater external and internal symmetry (Jarvik 1948; Ahlberg and Johanson 1997; Johanson and Ahlberg 1997; Paper II).
A previously identified tristichopterid synapomorphy is the presence of a postspiracular bone in the posterior part of the skull roof. The identity of this bone as either a neomorph or a posteriorly displaced extratemporal has been somewhat unclear (Jarvik 1980). In Paper I, the postspiracular is identified as a posteriorly shifted extratemporal. This is based on the similar association of the two bones to the underlying hyomandibula (such as Gogonasus, with an anteriorly positioned extratemporal and Eusthenopteron, with a “postspiracular” extratemporal) (Fig. 42 G, Long et al. 1997; Fig. 77 A, Jarvik 1980). The presence of a postspiracular bone remains a synapomorphy of tristichopterids, although the character states are redefined.

Primitively, tetrapodomorphs have elongate, essentially antero-posteriorly directed parietal pit lines that reach the parietal-postparietal border (as exemplified by Osteolepis or Gogonasus (Jarvik 1948; Long et al. 1997)). Tristichopterids instead display short, crescent shaped pit lines that are essentially transverse, and located lateral to the pineal foramen. This character state is not unique for tristichopterids, as it is also seen in Gyroptychius (Jarvik 1948).

To summarise, tristichopterids can be diagnosed by a combination of one unique (extratemporal drop-shaped and in a postspiracular position) and several more widely distributed characters (no cosmine, round scales with an internal boss, anteriorly positioned crescent-shaped parietal pit lines, small kite-shaped parasymphysial dental plate, a transverse posterior margin of the floor of the fossa bridgei, vomers with posterior processes that suture with the lateral face of the parasphenoid, an elongate posterior coronoid). The caudal fin is also quite distinct, with a triphycercal layout that is increasingly more symmetric in derived tristichopterids. Tristichopterids more derived than Tristichopterus are uniquely characterised by having two fang positions on the posterior coronoid and ectopterygoid.

Tristichopterid interrelationships

A dataset (modified from Paper IV to exclude Platycopichalichthys and include Heddleichthys) consisting of 9 tristichopterid taxa scored for 25 morphological characters was analysed in PAUP* v4b10 (Swofford 2002) (character list, program settings and data matrix in Appendix 2). The result was a single most parsimonious tree (Fig. 8).
The tristichopterid radiation can be divided in two main parts: basal forms such as *Tristichopterus*, *Jarvikina* and *Eusthenopteron*, and derived forms such as *Mandageria* and *Eusthenodon* (Fig. 9). Total body length varies from around 30 cm (*Tristichopterus*) to several meters (*Hyneria*) (Thomson 1968).
Figure 9. Mandageria (above) and Eusthenopteron (below) representing derived and basal tristichopterids, respectively. Scale bar approximately 1 m. Modified from Ahlberg and Johanson (1998).

Among other things, derived tristichopterids are characterised by the presence of dentary fangs and an enlarged symphysial tooth on the premaxilla, a diamond-shaped caudal fin, a drop- or kite-shaped pineal series and a general increase in body size. The taxa that form the “middle part” of the Tristichopteridae (moderately derived taxa such as Platycepalichthys, Cabonnichthys, Heddleichthys and Notorhizodon) are defined by a gradual acquisition of the features defining the most derived tristichopterids, resulting in various unique combinations of the characters described in the character list and data matrix in Appendix 2. This includes varying patterns in the dermal bone cover of the cheek as well as variability in the relative position of the pineal foramen, but also other features that are harder to quantify as characters: posterior displacement and reduction in size of median fins, and changes in skull shape (the general appearance of the skull of derived tristichopterids varies from broad (Hyneria) to narrow and torpedo-shaped (Mandageria), with other taxa in between (Heddleichthys, Cabonnichthys, Eusthenodon).

Tristichopterus, the most basal tristichopterid known, is in some regards similar to the generalized “osteolepid” morphology displayed by taxa such as Gyroptychius or Osteolepis (Jarvik 1948): the caudal fin is asymmetric (but triphycercal in Tristichopterus), overall body size is small, the snout is rather blunt, the ethmoid unit of the braincase is short relative to the otoccipital, and the lower jaws of these taxa are similar both in general shape and dentition.

Derived characters of Tristichopterus include the loss of cosmine, an elongated autopalatine division of the entopterygoid (both these character states are shared between tristichopterids, Spodichthys and Panderichthys + Tetrapoda), the presence of a triphycercal tail, a small parasymphysial plate not contacting the anterior coronoid, round scales with an internal articular boss, and a posteriorly displaced extratemporal bone in the posterolateral part of the skull roof (as discussed above, this bone was previously described
as a neomorph, “postspiracular bone” by e.g. Jarvik 1980; Ahlberg and Johanson 1997). Eusthenopteron has acquired more features characteristic of the tristichopterid radiation: there are two fang pairs on the posterior coronoid and ecompterygoid, the posterior coronoid is much longer than the penultimate coronoid, and the ethmosphenoid is longer than the otoccipital (although the last two conditions are also seen in Panderichthys + Tetrapoda) (Ahlberg and Clack 1998; Ahlberg et al. 1996). The triphycercal caudal fin of Eusthenopteron also displays a greater degree of external symmetry. As discussed above, the external symmetry of the caudal fin of derived tristichopterids is greater than in Gyroptychius. The internal symmetry, where known, is also greater with the addition of supraneural spines in the epichordal lobe. The primitive tristichopterid condition is displayed by Tristichopterus and Eusthenopteron, where the endoskeletal caudal fin support consists of haemal and epihaemal spines in the hypochordal lobe, but only neural spines in the epichordal lobe. This also seems to be the primitive tetrapodomorph condition, observed in lungfishes, actinopterygians and “osteolepid” tetrapodomorphs such as Osteolepis and Rhizodopsis (Ahlberg and Johanson 1997; Andrews and Westoll 1970b).

Derived tristichopterids represent the largest predators in the assemblages where they are found. Ecological separation between different derived tristichopterids is suggested by the co-habitance of taxa of different size at the same locality (Mandageria and Cabonnichthys at Canowindra, New South Wales; Eusthenodon and possibly another tristichopterid in East Greenland). For Langlieria and Eusthenodon, both of similar size and found at the exact same locality, the separation would seem to depend on more subtle morphological differences.

After the extinction of tristichopterids at the end of the Devonian, derived tristichopterids are replaced as the largest sarcopterygians by members of the Rhizodontidae (e.g. Rhizodus) and Megalichthyidae (e.g. Megalichthys) (Andrews 1985; Andrews and Westoll 1970b).

Parallelism
The trends described above in many instances parallel the evolution of other tetrapodomorph subgroups (Ahlberg and Johanson 1998). Curiously, derived tristichopterids independently exhibit general adaptations very similar to those seen in the panderichthyid grade and tetrapods. These include the general increase in size, the lengthened snout, a posterior coronoid which is considerably longer than the penultimate, the posterior displacement and decreased size of the median fins, the presence of dentary fangs, and (at least in some cases) a dorso-ventrally flattened skull. There is also a tristichopterid example - Mandageria - of what seems to have been a
functional neck joint, independently derived from and differently constructed than the one found in tetrapods (Johanson et al. 2003). Posteriorly displaced small median fins, symphysial dentary fangs, and greatly enlarged body size is also characteristic of derived rhizodonts (and some megalichthyids, at least as regards the dentition and increase in overall body size), although rhizodont anatomy in general is considerably less well known due to a partly poorly ossified endoskeleton (Traquair 1877, 1881; Thomson 1964; Jarvik 1966; Andrews 1985; Long 1989; Johanson and Ahlberg 1998; Jeffery 2003). For tristichopterids, “panderichthyids” and tetrapods, the changes in the skull indicate a move away from the general, broad-snouted tetrapodomorph model indicative of suction feeding. Instead, the small, posterior fins, the narrow snout and seemingly greater anterior emphasis to the bite with dentary fangs (and premaxillary pseudofangs in derived tristichopterids) appear more characteristic of an ambush-snapping type of predatory behaviour. The general body shape, if not the size, is very similar when a derived tristichopterid and a modern pike (Esox) are compared. Derived rhizodonts also appear to occupy this overall niche, although they retain the general, broad-snouted tetrapodomorph skull.

Underlying the external similarities between tristichopterids, “panderichthyids” and tetrapods are some differences in the internal architecture of the skull. An elongate snout necessarily implies different constructional demands on the structures involved in biting/feeding, even more so when the intracranial joint is considered. In the case of “panderichthyids” and tetrapods, one must also take into account that behaviours involving lifting the snout out of the supporting medium of water into the considerably less supportive medium of air are likely to make their appearance. Derived tristichopterids have a suite of specialized characters involved in creating a rigid (torsion-resistant?) internal snout structure: long posterior processes of the vomers, which interlock with the parasphenoid along its lateral margins; “accessory vomers” along the parasphenoid posterior to the posterior vomerine processes; a broad parasphenoid; and posteromedial processes of the premaxilla that bridge the apical fossa. Instead of this interlocking complex (although Panderichthys has posterior vomerine processes, shorter that those of tristichopterids), “panderichthyids” and tetrapods have a significantly lightened rostrum, with unossified nasal capsules (at least the posterior wall) in the case of Panderichthys or a completely unossified ethmoid region in the case of tetrapods; and a narrow parasphenoid (Vorobyeva 1962; Ahlberg et al. 1996). In addition, the anterior and posterior parts of the neurocranium are fused to each other in tetrapods, obliterating the intracranial joint and basicranial fenestra and therefore also the structurally weaker bipartite braincase which is primitive for sarcopterygians (Zhu et al. 1999; Zhu et al. 2001). The intracranial joint independently disappeared in the dipnomorph lineage, where stem lungfishes
such as *Youngolepis* show a fused braincase, lacking a basicranial fenestra (Chang 1982).

The actual region of elongation of the skull can be investigated when the relative positions of anatomical landmarks on the neurocranium and associated structures are analysed. In tristichopterids, the distance between the anterior and dorsal articulation areas on the lateral face of the ethmosphenoid become greater (formalized as character 68 in Appendix 1). This elongation of the autopalatine corresponds to an elongation of the ethmosphenoid in the region between the divergence of the olfactory tracts and the foramen for the trigeminal nerve. The relation between the elongation of the palatoquadrate and the elongation of the ethmosphenoid can be inferred from the position of the foramen for the trigeminal nerve (which relates to the position of the trigeminal notch in the dorsal margin of the entopterygoid), as well as the positions of the articular areas articulating with the ascending process and anterior ethmoid articulation. By contrast, in *Panderichthys* and tetrapods the elongation is exclusively preorbital. This is reflected in the dermal bone cover of the snout, where paired frontals are present anterior to the parietals.

**Biogeography**

The biogeographical implications of tristichopterid occurrences have been dealt with in a few publications over the last decade (Johanson and Ahlberg 1997; Johanson and Ahlberg 2001; Ahlberg *et al.* 2001; Johanson 2004; Clément and Boisvert 2006). A basic question is whether a place of origin for the clade can be estimated, with subsequent inferred migration and dispersal. When looking at the phylogenetic pattern of tristichopterids, it becomes immediately obvious that the most basal members (*Tristichopterus, Eusthenopteron, Jarvikina*) are exclusively Laurussian. The sister taxon of Tristichopteridae, *Spodichthys*, also occurs only in Laurussia. Derived tristichopterids, on the other hand, achieve a global distribution by the Late Devonian, with occurrences of *Mandageria* and *Cabonnichthys* in Gondwana (Australia), *Eusthenodon* in Gondwana (Australia, South Africa) and Laurussia (Greenland, Belgium, Russia, Pennsylvania), *Heddleichthys* in Laurussia (Scotland), *Platycephalichthys* in Laurussia (Baltica) and *Langlieria* in Laurussia (Belgium). This picture is somewhat complicated by the occurrence of the derived tristichopterid *Notorhizodon* from the upper parts of the ?Givetian Aztec Siltstone of Antarctica, possibly indicating a dispersal of primitive tristichopterids from Laurussia by the Middle Devonian (given that the hypothesis about a Laurussian origin of the group is correct), with a subsequent radiation of derived tristichopterids in Gondwana. The origin of derived tristichopterids would then be Gondwanan, with a subsequent dispersal back to Laurussia. A possible objection to this
hypothesis would be the total lack of occurrences of primitive tristichopterids in Gondwana. It should also be mentioned that the exact age of the Aztec Siltstone is not known with great confidence, but is referred to as Givetian or Early Frasnian, at the latest (Young et al. 1992; Johanson and Ahlberg 2001).

Two main hypotheses about the relationships between Laurussia and Gondwana during the Late Devonian have been formulated in recent years. The first hypothesis, mainly based on palaeomagnetic data, infers a central African position for the South Pole during the Late Devonian to Early Carboniferous. With Laurussia reconstructed entirely between 30° S and 30° N, this global reconstruction shows a stretch of open ocean between the continents (Van der Voo 1990; Li et al. 1993). This would act as a wide barrier to the migration of continental or marginal marine taxa between Laurussia and Gondwana, at least along the most proximal route between the two continents. The second hypothesis, which relies more heavily on palaeobiogeographical data, places Laurussia and Gondwana in closer proximity to each other during the Late Devonian (Li et al. 1993; Young 1993, 2005). The first model has to account for patterns of faunal distribution that seem to contradict a wide separation of Laurussia and Gondwana in Middle and Late Devonian times. For Late Devonian vertebrates, in addition to the dispersal of closely related, derived tristichopterids, this includes widely distributed taxa such as the rynchodipterid lungfish *Soederberghia* (Ahlberg et al. 2001). Given that *Eusthenodon*, together with *Mandageria* the most derived tristichopterid, is also the most cosmopolitan a continuous Late Devonian migration and dispersal between Laurussia and Gondwana is inferred. If the immediate N/NW to S/SE route between the two continents consisted of open ocean, an alternative suggested dispersal route would be via the many smaller, independent continental blocks that arched around the northern rim of what would eventually become the Tethys Sea (such as Kazakhstan, Siberia, and North and South China). This explanation seems less likely, in light of the considerable shifts in latitude such a route would suggest. The available evidence from global distributions of phyllolepid placoderms, which are found exclusively in Gondwana during the Givetian and Frasnian and eventually reach Laurussia in the Famennian, also seems to contradict a possible northern dispersal route. The regions indicated as “stepping stones” for migrations of taxa along this route (South and North China, Kazakhstan, Tarim, Siberia) have been extensively sampled with regard to Devonian fishes, but there is no clear evidence of phyllolepid occurrences in any of them (Young 2005). In conclusion, the available evidence from the dispersal patterns of Devonian vertebrates suggests that there was no open ocean barrier preventing dispersal between Gondwana and Laurussia in the Late Devonian.
Benfiskar kan delas in i två grupper: strålfeniga och kvastfeniga fiskar. I den strålfeniga gruppen ingår djur som vi i vardagligt tal betecknar som ”fiskar”, såsom gädda, torsk, sill och ål. Kvastfeningar, å andra sidan, består nästan helt av djur som vi istället kallar landrygradsdjur - exempelvis elefanter, näbmmöss, lemurer och människor. Det låter kanske överraskande att djur som går på fyra ben och lever på land klassificeras som fiskar, eftersom de egenskaperna inte riktigt ingår i vår vanliga bild av en fisk. Anledningen att de (inkluderat oss människor) klassificeras så är härkomst: alla landrygradsdjur (eller tetrapoder, fyrfota djur) härstammar från en grupp kvastfeniga fiskar, som hade fenor och levde i vattnet under Devonperioden. De enda nu levande ”fisklika” kvastfeningarna är lungfiskar (tre släkten: australiensisk, afrikansk, sydamerikansk) och Latimeria, som tillhör ett märkligt fisksläkte (coelacanthier) som länge troddes vara utdött, men som 1938 upptäcktes livs levande utanför Sydafrikas kust (Fig. 4).

I min avhandling har jag undersökt en fiskgrupp som är en del av de fyrfota djurens ursprung. Fiskarna jag tittat på kallas för tristichopterider, och kan sägas vara våra nästkusiner på ryggradsdjurens stamtavla. Tristichopteriderna dog ut i slutet av Devon (ungefär 360 miljoner år sedan), och studeras nu i form av fossil. Generellt kan man säga att man som paleontolog är intresserad av att undersöka hur fossila djur såg ut anatomiskt, och göra jämförelser med nu levnade djur. Man kan exempelvis undersöka aspekter på hur den evolutionära övergången från fiskfenor till armar och ben gick till, genom att titta både på fiskar som är nära besläktade med fyrfota djur, och tidiga representanter från den sistnämnda gruppen. Kvastfeniga fiskar har samma skelettuppsättning i fenorna som fyrfota djur har i sina ben: ett ben närmast kroppen (överarmsben i frambenen, lårben i bakbenen) följt av andra skelettelement (strålbén och armbågsben i frambenen, skenben och vadben i bakbenen). Det skelettmönster som vi ser i våra armar och ben var alltså redan på plats i fenorna hos fiskar som levde för uppemot 400 miljoner år sen! Rent praktiskt har jag använt dels traditionella metoder med mikroskop och penna och papper för att undersöka och illustrera fossil, men jag har också kunnat använda ett modernare tillvägagångssätt – att köra fossil i en CT-scanner, för att på så sätt kunna få en bild av hur de ser ut inuti. Detta kan man göra när fossilen är tredimensionellt bevarade (de allra flesta exemplar man har tillgång till är tyvärr helt tillplattade). Det man får ut efter en
CT-scanning är en serie bilder, som var och en är ett tvärsnitt av exemplaret (Figur 1 ovan). Med hjälp av datorprogram kan man sedan konstruera virtuella modeller av sina fossil, som bygger på informationen i bildserien.

När man samlat anatomiska data om olika djur kan man undersöka djurens inbördes släktskap genom en så kallad fylogenetisk analys. Då jämför man hur de olika djuren ser ut med avseende på en mängd olika detaljer, till exempel anatomiska egenskaper som de som är listade i de två appendixen i den här avhandlingen. Sedan låter man ett datorprogram undersöka vilket släktskapsförhållande som bäst förklarar (detta kan göras med avseende på olika egenskaper hos det resulterande släktträdet) den distribution av karaktärsdrag man ser hos de djur som är med i analysen. En vanlig metod är att helt enkelt undersöka vilket släktträd som med minsta möjliga antal evolutionära övergångar kan förklara hur de djur man inkluderar i studien kom att få olika tillstånd av de karaktärer man tittar på.
Thank you:

To my supervisors: Per Ahlberg, Graham Budd, Henning Blom.

To my parents, Lisbeth and Pär, and to my brother, Staffan: I’ll try to come up with a good explanation of what I’ve been doing for the past four and a half years….possibly also why it matters in the grand scheme of things, but I can’t promise anything!

To Marie: for love, support and loving support.

To Per Ahlberg: for giving me the opportunity! I remember lunch at Mickes and a trip to Naturhistoriska, after which I was told that I was welcome aboard….You are an excellent supervisor, and you are a good person! You sincerely care about the well-being of your students, and that shows.

To Henning Blom: for steering me away from invertebrates when I was an undergrad (by teaching me invertebrates), for providing a different perspective as a supervisor, for letting me beat you at badminton (well, not really), for matching my obsession about football….

To Martin and Catherine: I’ve racked my brains but I can’t think of any Canadians that I knew before you guys moved here. And now, two of my best friends are Canadian. Didn’t see that coming. For the sharing of offices, tents, rented cars, motel rooms, the bed in Paris (you know what I’m talking about Martin), nervousness, relief, anxiety, beers, tear-inducing laughs. For not bothering me with any placoderms. How do you sum up four years in a few lines of text? Like this, I suppose.

To Martin (again): for drawing the fish that went on the cover.

To Rose-Marie: without you, EO would grind to a halt. You Rule.

To Johan, Anna and Patricia: welcome aboard!
To the undergraduate students who have had the (mis?)fortune of being left in my care in the lab. Life as a PhD student wouldn’t be the same without you.

For valuable help and/or discussions and/or just being overall nice people (with all three the most common combination): Hans-Peter Schultze, Matt Friedman, Brian Swartz, John Long, Zerina Johanson, Mike Coates, Gaël Clément, Sarah Finney, Philippe Janvier, Carl-Erik Cantell, Carina Östman, Gilles Cuny, Mike Taylor, Thomas Mörts, Graham Budd, Jan den Blaauwen, Roger Jones, Mike Newman, Bobbie Paton, Ted Daeschler….

Because all work and no play makes Daniel a dull boy: Mikael, Mats, Maria, Erik B and Erik H, Per, Anna, Ingemar, Ken & Kikki, Niklas, Torgny, Calle, Lina, Simon, Hallberg, Marie, Niklas, Piero, Johannes, Jocke, Martin A, Tobias (med Bajen mot Superettan), Kerem, Meta, Åsa, Sofia, Andreas, Carolina…. 

The official soundtrack to this thesis is The Great Annihilator by Swans. In the movie version, Daniel will be played by Robert Duvall.

This is the way the thesis ends.
This is the way the thesis ends.
This is the way the thesis ends.
Appendix 1

The tetrapodomorph data set was analysed using the Branch and Bound search algorithm in PAUP*. The dipnomorphs *Diabolepis*, *Glyptolepis*, *Porolepis*, *Powichthys* and *Youngolepis* were designated as outgroup.

In the character list below, **F** refers to character number in the Friedman (2007) matrix; **ALM-K** to the Ahlberg *et al.* (2000) matrix; **JA** to the Johanson and Ahlberg (2001); **AJ** to the Ahlberg and Johanson (1998) matrix; **C** to the Coates *et al.* (2002) matrix.

The data matrix follows after the character list.

[1] **Skull shape (F: 2):**
0. lateral orbits, interorbital skull roof wide and arched
1. dorsal orbits, interorbital skull roof flat or concave

[2] **Postrostral (F: 6):**
0. absent
1. mosaic
2. median postrostral

[3] **Paired bones anterior to parietals (F: 7):**
0. absent
1. present

[4] **Number of tectals (F: 9):**
0. one
1. two or more

[5] **Number of supraorbitals (F: 11):**
0. one
1. two
2. more than two

[6] **Anterior margin of parietal (F: 13):**
0. between or in front of orbits
1. slightly posterior to orbits
2. far posterior to orbits

[7] **Pineal opening (F: 14):**
0. open
1. closed

[8] **Parietal-supraorbital contact (F: 15):**
0. absent
1. present

[9] Extratemporal (F: 16):
0. absent
1. present
2. present and posteriorly displaced (postspiracular position)

[10] Intertemporal (F: 17):
0. present
1. absent

[11] Number of marginal bones alongside postparietal (F: 18):
0. single
1. two or more

[12] Dermal joint between parietal and postparietal (F: 19):
0. absent
1. present

0. median extrascapular overlapped by lateral extrascapulars
1. median extrascapular overlaps lateral extrascapulars
2. median extrascapular abuts lateral extrascapulars

[14] Dermintermedial process (F: 23):
0. absent
1. present

0. external, far from jaw margin
1. external, close to jaw margin
2. palatal

[16] Lacrimal posteriorly enclosing posterior nostril (F: 26):
0. absent
1. present

[17] Course of ethmoid commissure (F: 29):
0. middle portion through median rostral
1. sutural course
2. through bone center of premaxilla

[18] Course of supraorbital canal (F: 31):
0. straight
1. lyre-shaped

[19] Relationship of infraorbital canal to premaxilla (F: 33):
0. infraorbital canal entering premaxilla
1. infraorbital canal following dorsal margin of premaxilla

[20] Posterior end of supraorbital canal (F: 34):
0. in postparietal
1. in parietal
2. in intertemporal
[21] Contact of otic and supraorbital canals (F: 35):
0. not in contact
1. in contact

[22] Course of otic canal in relation to anterior portion of postparietal (F: 37):
0. through marginal bones alongside postparietal
1. along the margin of the postparietal
2. through postparietal

[23] Number of cheek bones bearing bearing preopercular canal posterior to jugal (F: 41):
0. one
1. two

[24] Bone bearing both preopercular canal and quadratojugal pitline (F: 42):
0. absent
1. present

[25] Subsquamosals (F: 43):
0. absent
1. present

[26] Preopercular-maxillary contact (F: 44):
0. present
1. absent

[27] Jugal-quadratojugal contact (F: 45):
0. absent
1. present

[28] Preoperculosubmandibular (F: 46):
0. absent
1. present

[29] Foramina on dermal cheek bones (F: 47):
0. absent
1. present

0. absent
1. present

[31] Parasympathial tooth whorl (F: 52):
0. absent
1. present

[32] Dentition on coronoids (F: 58):
0. broad marginal 'tooth field'
1. narrow marginal tooth row
2. single tooth row

[33] Anterior mandibular (precoronoid) fossa (F: 62):
0. absent
1. present
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<td>[34]</td>
<td>Large foramina on external surface of lower jaw (infradentary foramina) (F: 64):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[35]</td>
<td>Number of branchiostegals per side, excluding opercular, subopercular, and gular plates (F: 70):</td>
<td>0. ten or more</td>
<td>1. two or seven</td>
</tr>
<tr>
<td>[35]</td>
<td>Number of branchiostegals per side, excluding opercular, subopercular, and gular plates (F: 70):</td>
<td>2. one</td>
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<tr>
<td>[36]</td>
<td>Palatal opening surrounded by premaxilla, maxilla, dermopalatine, and vomer (choana) (F: 75):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[37]</td>
<td>Posterior process of vomer (F: 76):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[38]</td>
<td>Articulation of vomers (F: 77):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[39]</td>
<td>Parasphenoid (F: 81):</td>
<td>0. protruding forward into ethmoid region of neurocranium</td>
<td>1. behind ethmoid region of neurocranium</td>
</tr>
<tr>
<td>[40]</td>
<td>Denticulated field of parasphenoid (F: 82):</td>
<td>0. without spiracular groove</td>
<td>1. with spiracular groove</td>
</tr>
<tr>
<td>[41]</td>
<td>Endoskeletal intracranial joint (F: 86):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[42]</td>
<td>Processus descendens of sphenoid (F: 89):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[43]</td>
<td>Anterior palatal fenestra (fossa apicalis) (90):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[44]</td>
<td>Paired internasal pits (F: 91):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[45]</td>
<td>Vomer area with grooves and raised areas (F: 92):</td>
<td>0. absent</td>
<td>1. present</td>
</tr>
<tr>
<td>[46]</td>
<td>Large median (profundus canal) and several small dorsolateral openings in postnasal wall (F: 94):</td>
<td>0. absent</td>
<td></td>
</tr>
</tbody>
</table>
1. present

[47] Position of exit of pituitary vein (F: 99):
0. anterior to basipterygoid process
1. dorsal to vertical portion of basipterygoid process
2. posterior to basipterygoid process

[48] Basicranial fenestra (F: 100):
0. absent
1. present

[49] Posttemporal fossae (F: 103):
0. absent
1. present

[50] Scapulocoracoid (F: 112):
0. attached to dermal girdle, not separated by foramina
1. attached to dermal girdle by buttresses and separated from dermal girdle by foramina
2. attached to dermal girdle, foramina run through scapulocoracoid

[51] Pectoral fin radials (excluding the metapterygial ‘axis’) (F: 116):
0. unjointed
1. jointed

[52] Pectoral fin radials (F: 117):
0. 'preaxial' radials only
1. 'preaxial' radials plus 'postaxial' radials

[53] Dorsal and anal fins (F: 119):
0. present
1. absent

[54] Basal scutes on fins (F: 120):
0. absent
1. present

[55] Relative size of epichordal and hypochordal lobes of caudal fin (F: 124):
0. epichordal lobe less developed than hypochordal
1. epichordal and hypochordal lobes equally developed
2. epichordal lobe more developed than hypochordal

[56] Well-ossified ribs (F: 126):
0. absent
1. present

[57] Scales (F: 127):
0. rhombic
1. rounded

[58] Pore-canal network (F: 131):
0. absent
1. present

[59] Enamel lining pore canals (F: 133):
<table>
<thead>
<tr>
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</tr>
</thead>
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<tr>
<td>Rostral tubuli (F: 136)</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Plicidentine (F: 140)</td>
<td>absent</td>
<td>present, labyrinthodont, dendrodont</td>
</tr>
<tr>
<td>Pineal eminence (in those taxa with no pineal foramen) (F: 146)</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Premaxillae with inturned symphysial processes (F: 149)</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Opercular (F: 153)</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Large ventromesially directed flange of anteriormost dentary (F: 156)</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Teeth of outer dental arcade (F: 157)</td>
<td>several rows of disorganized teeth</td>
<td>two rows, with large teeth lingually and small teeth labially, single row of teeth</td>
</tr>
<tr>
<td>'Urohyal' morphology (F: 165)</td>
<td>dorsoventrally compressed and rod-like, may bifurcate posteriorly</td>
<td>vertical plate</td>
</tr>
<tr>
<td>Entopterygoid proportions (AJ: 18)</td>
<td>anterior end level with processus ascendens</td>
<td>anterior end considerably anterior to processus ascendens</td>
</tr>
<tr>
<td>Ethmoid articulation for palatoquadrate (F: 172)</td>
<td>placed on postnasal wall</td>
<td>majority of facet located anterior to postnasal wall, extends posteriorly to the level of N.II</td>
</tr>
<tr>
<td>Autopalatine fossa bearing unfinished articular surfaces (F: 173)</td>
<td>absent</td>
<td>present</td>
</tr>
<tr>
<td>Vestibular fontanelles (F: 180)</td>
<td>absent</td>
<td>present</td>
</tr>
</tbody>
</table>
[72] Accessory fenestration in otic capsule (F: 181):
0. absent
1. present

[73] Parachordal plates (F: 182):
0. separated from the otic capsule
1. sutured or co-mineralised with the otic capsule

[74] Otoccipital fissure (F: 184):
0. absent
1. present

[75] Ethmosphenoid region significantly longer than otoccipital region:
0. no
1. yes

[76] Premaxillary fang (JA: 3):
0. absent
1. present

[77] Jugal extends anterior to middle of orbit (ALM-K: 24):
0. no
1. yes

[78] Extratemporal/supratemporal contact (JA: 6):
0. absent
1. present

[79] Dentary fang:
0. absent
1. present

[80] Anterior infradentary (splenial) sutured to prearticular (AJ 2):
0. no
1. yes

[81] Posterior coronoid (AJ: 8):
0. subequal
1. much longer than penultimate coronoid

[82] Extrascapular series:
0. present
1. absent

[83] Anocleithrum (AJ 85):
0. subdermal
1. exposed

[84] Position of scapulocoracoid on cleithrum (JA: 12):
0. ventrally positioned
1. dorsally positioned

[85] Basal segments of pectoral lepidotrichia (AJ: 92):
0. elongated
1. short
[86] Pectoral fin web:
0. asymmetrical
1. symmetrical

[87] Pectoral radials (excluding metapterygial ‘axis’):
0. do not bifurcate
1. bifurcate

[88] Body of humerus (AJ: 89):
0. cylindrical
1. flattened with rectangular cross-section

[89] Radius of equal length or shorter than humerus (C: 17):
0. no
1. yes

[90] Posterior process on distal mesomere(s):
0. absent
1. present

[91] Distal fin or limb domain expanded across A-P axis (C: 1):
0. no
1. yes

[92] Ossified ring centra:
0. absent
1. present

[93] Parasymphysial tooth plate:
0. long, with posterior extension reaching anterior coronoid
1. short, kite- or button-shaped
2. carrying tooth whorl

[94] Hyomandibular facets on lateral face of otoccipital:
0. dorsal directly above ventral
1. ventral anterior to dorsal
2. dorsal anterior to ventral

[95] Pit lines on parietal:
0. anteroposterior, reaching or almost reaching parietal-postparietal border
1. crescent-shaped, essentially transverse, anterior or mostly anterior to pineal foramen/pineal eminence

[96] Vestibular fontanelles extend anterior to posterior margin of basicranial fenestra:
0. no
1. yes

[97] Relationship of vomer to parasphenoid (AJ 23):
0. no contact, or simple abutment
1. dorsal/ventral overlap anteriorly
2. intimate suture with lateral edge of parasphenoid

[98] Prearticular (AJ 5):
0. rear part flat
1. rear part with conspicuous horizontal ledge

[99] Retroarticular process (AJ 6)
0. absent
1. present

[100] Posterior margin of tabulars (AJ 42):
0. anterior to posterior margin of postparietals
1. level with posterior margin of postparietals

[101] Contact margin for clavicle on cleithrum (AJ 84):
0. straight or faintly convex
1. strongly concave

[102] Direction of posterior margin of floor of fossa bridgei:
0. oblique
1. transverse

[103] Cosmine:
0. present
1. absent

[104] Postorbital (AJ 54):
0. contributes to orbital margin
1. does not contribute to orbital margin

[105] Anterior margin of median extrascapular (AJ 65):
0. long
1. very short

[106] Orientation of tectal and lateral rostral relative to external nostril:
0. dorsal/ventral
1. anterior/posterior

[107] Number of fangs on posterior coronoid (AJ 13):
0. One
1. Two
2. Zero
<table>
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<th>Data</th>
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<tbody>
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Appendix 2

The tristichopterid data set was analysed in PAUP*, using the Branch and Bound search algorithm. The outgroup consisted of *Spodichthys*, *Gogonasus*, *Medoevia* and *Gyroptychius*.

Character list used in the analysis of tristichopterid interrelationships, followed by data matrix:

[1] Epichordal radials in caudal fin:
0. absent
1. present

[2] Shape of caudal fin:
0. epichordal lobe less developed than hypochordal
1. epichordal and hypochordal lobes equally developed

[3] Relationship of jugal to orbit:
0. contributes to orbital margin
1. excluded from orbital margin

[4] Relationship of postorbital to orbit:
0. contributes to orbital margin
1. excluded from orbital margin

[5] Contact between posterior supraorbital and intertemporal:
0. present
1. absent

[6] Contact between posterior supraorbital and lachrymal:
0. present
1. absent

[7] Shape of posterior supraorbital:
0. posterior process shorter than diameter of orbit
1. posterior process much longer than diameter of orbit

[8] Shape of pineal series:
0. round or oval
1. kite-shaped with posterior corner

[9] Location of pineal foramen:
0. level with posterior margin of orbits
1. well posterior to orbits

[10] Enlarged anterior tooth on premaxilla:
0. absent
1. present

[11] Number of fang positions on ectopterygoid:
0. one
1. two

[12] Number of fang positions on posterior coronoid:
0. one
1. two

[13] Length of posterior coronoid:
0. subequal to penultimate coronoid
1. much longer than penultimate coronoid

[14] Marginal dentition on dentary reaches lower jaw symphysis:
0. yes
1. no

[15] Vertical lamina present lateral to coronoid fang on anterior coronoid:
0. yes
1. no

[16] Accessory vomers
0. absent
1. present

[17] Cutting edges on fangs:
0. absent
1. present

[18] Location of posterior point of median postrostral:
0. anterior to orbits
1. posterior to orbits

[19] Marginal tooth row present anterior to dermopalatine fang:
0. yes
1. no

[20] Marginal teeth present on all coronoids:
0. yes
1. no

[21] Symphysial dentary fang:
0. absent
1. present

[22] Posterior process of vomer:
0. straight of slightly concave
1. distinct posterolateral corner present

[23] Apical fossa subdivided by posteromedial process of premaxilla:
0. no
1. yes
[24] **Extratemporal**
0. present lateral to tabular
1. present in postspiracular position

[25] **Denticulated field of parasphenoid:**
0. stands proud of body of parasphenoid, supported anteriorly by midline keel
1. slightly recessed into body of parasphenoid

<table>
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<td><em>Tristichopterus</em></td>
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<td><em>Notorhizodon</em></td>
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<td><em>Gogonasus</em></td>
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<td><em>Medoevia</em></td>
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<td><em>Spodichthys</em></td>
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<td><em>Gyroptychius</em></td>
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</table>
References


Permo-Carboniferous Faunas, pp 133-142. POLLICHIA-Buch Nr 29, Bad Dürkheim.


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