

Thelodont phylogeny revisited, with inclusion of key scale-based taxa

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Abstract. Knowledge of the Thelodonti has improved greatly in recent years, but phylogenetic relationships remain poorly understood. We revised the data from an earlier phylogenetic study and added 15 scale-based species. Maximum parsimony analysis gives a well-resolved tree in which *Archipelepis* and *Boothialepis* form a basal clade, recognized here as the order Archipelepidiformes, sister group to two large clades also recognized as orders. The first is recognized as the order Furcacaudiformes, including *Nikolivia*, *Lanarkia*, *Phillipsilepis*, *Pezopallichthys*, *Drepanolepis* (in the new family Drepanolepididae), *Barlowodus*, *Apalolepis*, and Furcacaudidae. The second, here recognized as the Thelodontiformes, contains *Turinia*, *Thelodus*, *Stroinolepis*, *Loganellia*, *Longodus*, *Helenolepis*, *Phlebolepis*, *Erepsilepis*, *Trimerolepis*, *Eestilepis*, *Valiukia*, *Paralogania*, and *Shielia*.

Key words: Palaeozoic, Agnatha, Thelodonti, phylogeny.

INTRODUCTION

Our understanding of the Palaeozoic vertebrate subclass Thelodonti has improved greatly in recent years as a result of new discoveries (e.g., Wilson & Caldwell 1993, 1998; Märss 1999; Märss et al. 2002) as well as monographic revisions of articulated specimens and scale-based taxa (e.g., Märss & Ritchie 1998; Karatajūtė-Talimaa & Märss 2004; Märss et al. 2006, 2007). However, in the early years of study of thelodonts, they proved to be a difficult group for workers to deal with. Thelodont scales were first described by L. Agassiz (in Murchison 1838) but their status as a distinct group of jawless vertebrates evolved slowly over many decades (see historical review by, e.g., Turner 1991). Thelodonts preserved as articulated skeletons have been known since Powrie (1870) described '*Cephalopterus*' *pagei*, the generic name of which was subsequently found to be preoccupied. Powrie believed his species to be an acanthodian. This error was corrected by Traquair (1896), who named the genus *Turinia* to contain Powrie's species and grouped it with other well-preserved Scottish thelodonts as jawless vertebrates (Agnatha). Thelodonti were formally recognized as a higher taxon within Agnatha but distinct from other jawless vertebrates by Kiaer (1932).

In recent decades new discoveries and monographic treatments of thelodonts have included a detailed study of scale-based species from the former Soviet Union and Spitsbergen (Karatajūtė-Talimaa 1978), scale-based species of Estonia and Latvia (Märss 1986), Silurian

species based on articulated specimens from Scotland (Märss & Ritchie 1998), Silurian and Devonian species of a new group called Furcacaudiformes by Wilson & Caldwell (1993, 1998), and Silurian and Devonian species based on scales and articulated squamations from Arctic Canada (Märss et al. 2006). Thelodont studies have also been significantly advanced by publication of a reference work on thelodonts from Russia and adjacent countries (Karatajūtė-Talimaa & Märss 2004) and by the thelodont volume of the *Handbook of Paleoichthyology* (Märss et al. 2007).

However, the phylogenetic relationships within the group have remained problematic, and the question of monophyly of the Thelodonti has also been controversial (e.g., Turner 1991; Janvier 1996; Donoghue & Smith 2001; Wilson & Märss 2004).

The present contribution is our second attempt at resolving the within-group relationships of thelodonts. Our first attempt (Wilson & Märss 2004) was based almost entirely on articulated specimens (in reality, articulated squamations). In that paper 25 species of thelodonts were studied and a preliminary phylogenetic arrangement was proposed. For many of them, data were available for both scale histology and overall body form. For others, however, one of these key sets of features was absent due to imperfect preservation or lack of the needed analysis. The resulting phylogenetic tree (Wilson & Märss 2004, fig. 6; reproduced as Märss et al. 2007, fig. 34) suggested a basal split within Thelodonti between a group consisting of *Archipelepis*, *Phlebolepis*, and *Erepsilepis* and all other thelodonts.

The latter group was further divided into one that included *Turinina*, *Loganellia*, and *Phillipsilepis* and a larger separate group of remaining species. This larger group was then divided between a clade consisting of *Shiella* spp. and *Lanarkia* spp., collectively sister to the fork-tailed thelodonts or Furcacaudiformes. The basic structure of that tree is reproduced here in Fig. 1A for comparison with new findings.

However, the thelodont fossil record includes many very important species that are based solely on isolated scales. Isolated scales derived from acid dissolution

of fossiliferous rocks can often be associated with considerable assurance into suites of scales representing different parts of the body of an individual species, using the clues given by intergradations of scale structure within the samples (e.g., Märss 1999). Not only are these scale-based species important for biostratigraphy, but they also often yield the most complete data concerning scale microstructure and histology. Such details tend to be best preserved in carbonate or carbonate-cemented rocks that are processed with acetic acid to yield scale-bearing residues.

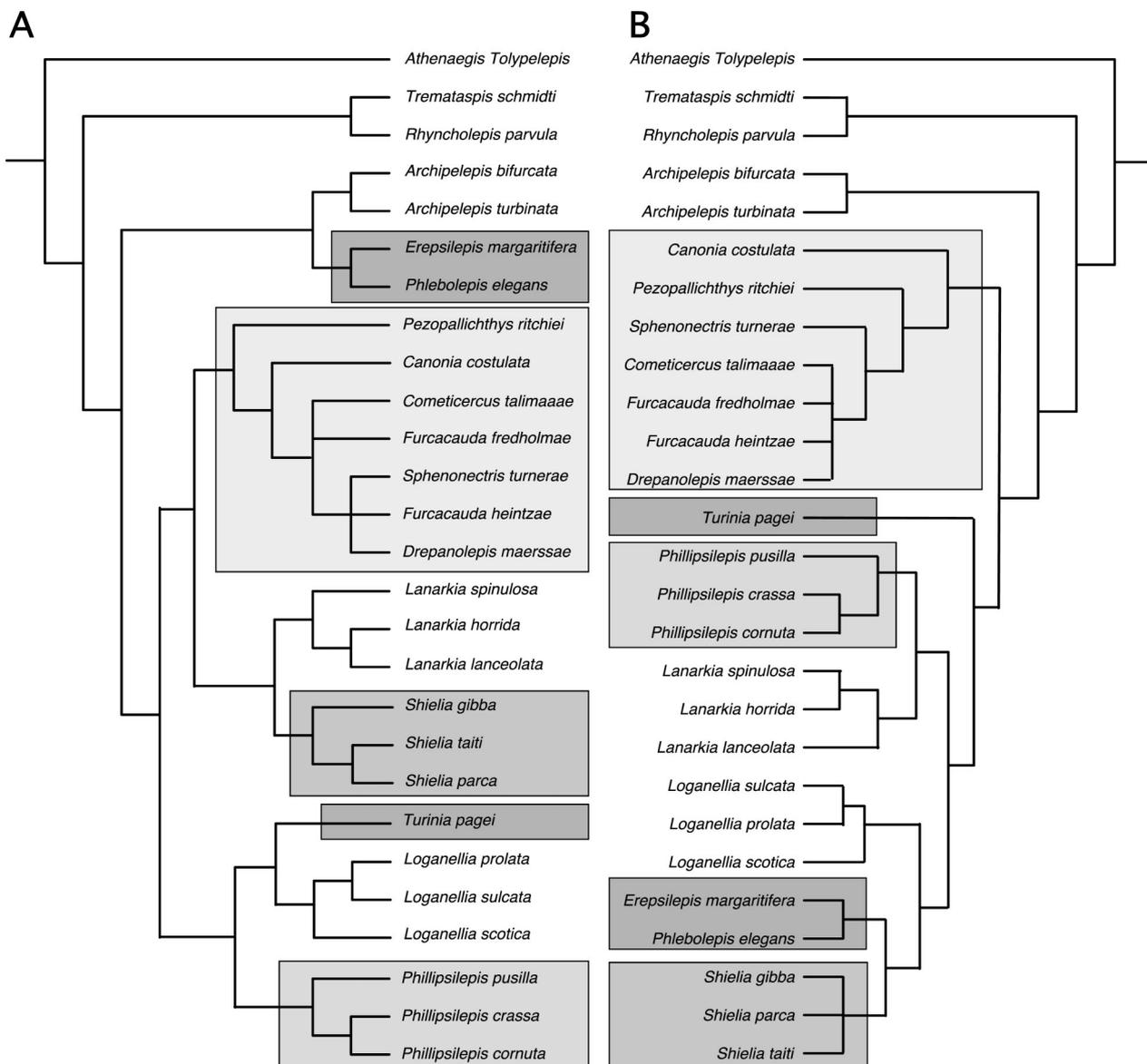


Fig. 1. Comparison of the results of the earlier analysis (A) of 24 thelodont species from Wilson & Märss (2004) with the results of analysing the same 24 species using the newly revised data matrix (B). The main differences between the two analyses (indicated by shading) are in the position of *Erepsilepis* plus *Phlebolepis*, the relationships of *Phillipsilepis* and *Lanarkia*, the position of *Shiella* spp., and the more basal position of furcacaudiforms and *Turinina* in (B).

The original study (Wilson & Märss 2004) began with data on 25 species and four outgroups scored for 53 characters, but one outgroup and one ingroup species were eliminated because of wildcard behaviour in the analyses (in multiple shortest trees, these species took radically different positions, causing a lack of resolution in the strict and majority-rule consensus trees). The final preferred phylogeny was thus based on 24 species of thelodonts and three outgroups.

In the present study we have augmented the original list of taxa from our earlier study by adding data on representative scale-based species. Some 14 scale-based species, each in a different genus, have been added for the present study, although a few of the new species are assigned to genera included in the earlier analysis. We have also revisited the list of characters and states, eliminating some and substituting others, and recoded the previous set of taxa. Our purpose is to produce a new phylogenetic analysis of 39 species of thelodonts that includes both scale-based and squamation-based species. We also compare the effect of updating the data matrix on an analysis of the original 24 species, and discuss the implications of the new phylogeny for thelodont evolution and classification.

METHODS

Our starting point was the data from our earlier study (Wilson & Märss 2004); we updated the data by editing and recoding of states and by deleting characters that were found to be highly homoplasious in the earlier study (Wilson & Märss 2004) or were rendered uninformative after editing. We modified and reduced the number of states for several characters to simplify them and to attempt to capture the major features of character evolution rather than minor variations. We also reexamined the character coding of every species critically and made a number of changes based on our current understanding of body form and of scale morphology and histology. Finally, we added a small number of new characters to replace deleted characters, including one to reflect the new information available about ultrasculpture of the scale surface (Märss 2006a). The resulting list of 52 characters and states is given here as Appendix 1 and the resulting character-taxon matrix for 42 taxa (39 ingroup species and 3 outgroups) is given as Appendix 2. Key features of thelodont scale morphologies used as the basis for character definitions in Appendix 1 are shown in Fig. 2. Similarly, key features of scale histology used for character definitions are shown in Fig. 3. Thelodont bodies and articulated squamations were illustrated in our earlier paper (Wilson & Märss 2004) and also by Märss et al. (2007). We used the

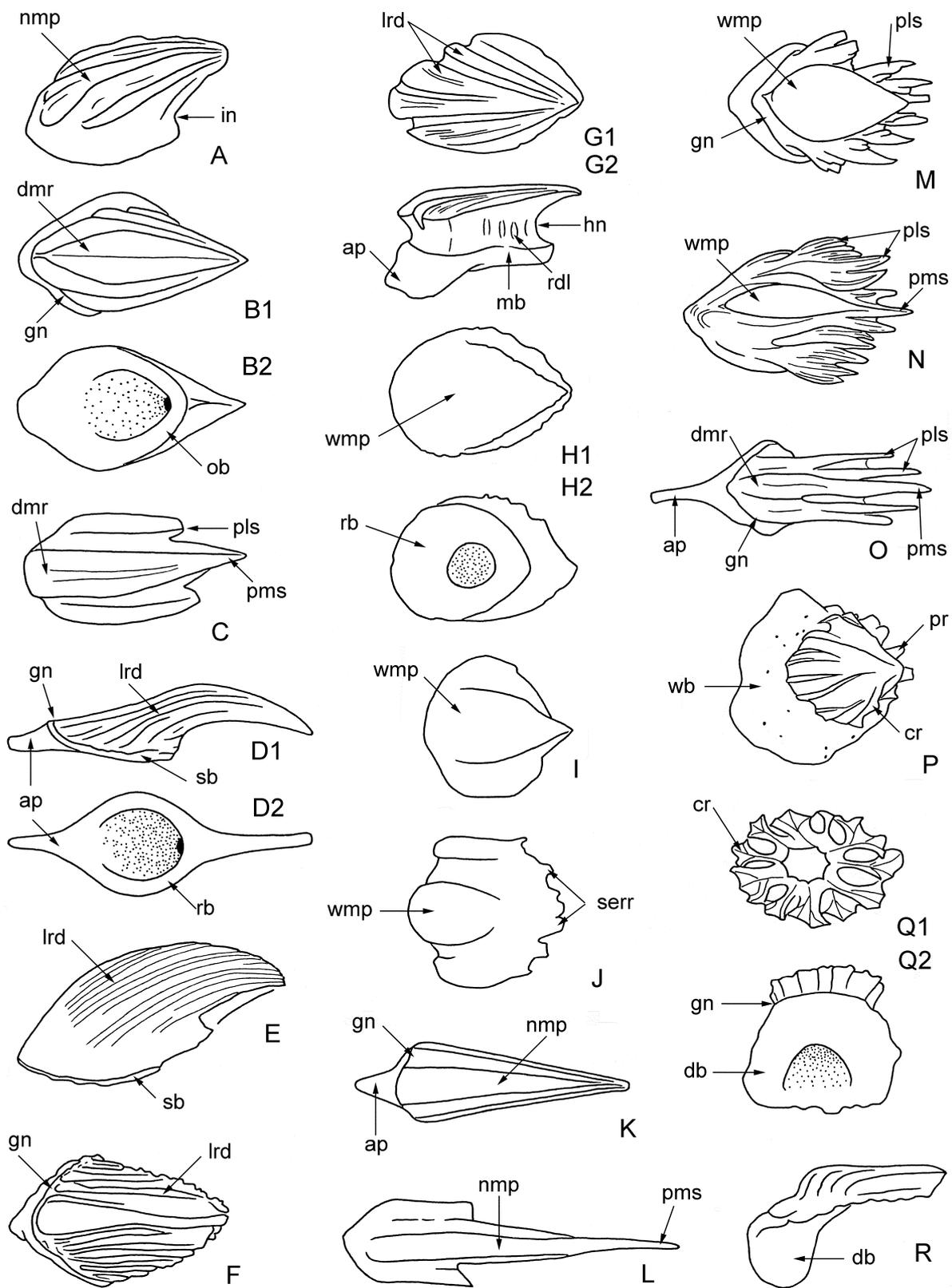
same three outgroups as in our earlier study, including '*Athenaegis Tolypelepis*' which is a composite of two of the most primitive undoubted heterostracans so far known, *Athenaegis* being the main source of body-form character states and *Tolypelepis* being the main source of histological character states. A study such as this with only three representatives of the many species in outgroup taxa is not designed to test thelodont monophyly. A more rigorous test of monophyly would involve a much larger sampling from among other jawless vertebrates, and a much larger number of characters. In the present study we have assumed thelodont monophyly, using outgroups to root the resulting tree, thereby indicating the direction of evolutionary change within the group.

We prepared and edited the data matrix using MacClade Version 4.08 (Maddison & Maddison 2005) and analysed the matrix under the criterion of Maximum Parsimony using PAUP 4.0b10 (Swofford 2002). Using PAUP, we obtained the set of the shortest trees, the strict and majority-rule consensus trees based on those shortest trees, and we also generated random trees for the purpose of assessing the strength of the phylogenetic signal in the data matrix. Using MacClade again, we graphically displayed the strict and majority-rule consensus trees, mapped character changes onto them, and generated tree-fit and character-specific statistics.

In PAUP, we performed heuristic searches with mostly default options, except for obtaining starting trees by random addition with 100 replicates. Branch-Swapping was by TBR (Tree Bisection-Reconnection), with the steepest descent off, multrees in effect, swapping on the best trees only, and no topological constraints. Rooting was on the single composite outgroup (*Athenaegis Tolypelepis*), although data for two other outgroups (*Rhyncholepis parvula* and *Tremataspis schmidtii*) were included in the analysis.

The character-taxon matrix contained 52 characters, all of them informative, all treated as unordered and of equal weight. The number of states per character ranged from 2 to 7, and the total number of apomorphic states was 80. Missing data per character ranged from zero to 83.3%, while inapplicable states per character ranged from zero to 85.7%.

We investigated whether the differences in the resulting phylogenies between our 2004 paper and the current study were caused mostly by changes in the characters and states or whether the difference in results was caused by addition of scale-based taxa. To examine this question, we re-analysed the same set of 24 taxa from the earlier study (Wilson & Märss 2004) but using the updated set of characters and states (Appendices 1 and 2). We then compared the resulting phylogeny with that produced by the earlier study.



We then added the 14 newly coded, scale-based taxa along with one ingroup species, *Eestilepis prominens*, that had been coded for our 2004 study but omitted because of wild-card behaviour. The complete data set was then analysed using the above-mentioned protocols. We also investigated the possibility of adding a fourth outgroup (*Poracanthodes menneri*) that we had attempted to include in 2004.

RESULTS

The analysis of the original 24 ingroup and three outgroup taxa using the original 53 characters (Wilson & Märss 2004, fig. 6) had given the preferred result illustrated here in Fig. 1A (majority-rule consensus of the 31 shortest trees of length 153 steps). When analysed with the updated data set, the same 24 species yield the arrangement in Fig. 1B (majority-rule consensus of 212 trees at 156 steps). It is evident that the updated data matrix produces a different phylogenetic arrangement for several important taxa. *Erepsilepis* and *Phlebolepis* were grouped with *Archipelepis* near the base of the tree in the 2004 study (Fig. 1A), but with the updated data they are grouped with *Loganellia* and *Shielia* (Fig. 1B). In addition, *Shielia* itself was grouped with *Lanarkia* in the 2004 study (Fig. 1A), but is united with *Loganellia*, *Erepsilepis*, and *Phlebolepis* using the updated data (Fig. 1B). *Turinia* was united with *Loganellia* in 2004 but takes a much more primitive position using the revised data.

When the 14 scale-based taxa as well as *Eestilepis prominens*, known from a partially articulated squamation, were added to the analysis, the data matrix contained 39 thelodont species and three outgroup taxa, coded for 52 characters.

As with our previous study (Wilson & Märss 2004), our attempt to include the acanthodian outgroup *Poracanthodes menneri* was not successful. The primary character-state homologies of this species, relative to the

characters designed for thelodont relationships, are difficult to determine because of the lack of comparability of its morphology and scales with the features of thelodonts. Moreover, when we included our tentative codings for *Poracanthodes* in the analysis, all structure of the phylogeny was destroyed and a large basal polytomy was generated. We therefore eliminated *Poracanthodes* as an outgroup and do not include it in our published data because we think it unwise to disseminate those preliminary but unreliable character-state codings.

In our 2004 paper we had preferred the phylogeny that omitted *Eestilepis* from consideration owing to its wild-card behaviour. Unlike our experience with *Poracanthodes menneri*, the new data matrix was much more successful in placing *Eestilepis prominens* with consistency, giving a similar relationship for this species in all shortest trees, despite its large proportion of missing data. Our preferred result, therefore, includes all 39 thelodonts for which we coded data.

The result for the inclusive analysis was 2558 shortest trees of length 204 steps. The strict consensus tree (Fig. 4A) has a high degree of resolution. The inclusive majority-rule tree (Figs 4B, 5) is only slightly more resolved than the strict consensus tree (Fig. 4A). For the shortest trees, the Consistency Index (C.I.) was 0.39, the Retention Index (R.I.) was 0.72, and the Rescaled Consistency Index (R.C.) was 0.28.

Comparing the inclusive tree for 39 thelodonts with that based on the original 24 species indicates that the inclusive majority-rule tree (Fig. 4B) is about as well resolved as the tree based only on the original 24 species (Fig. 1B). The two trees differ in that furcacaudiforms are a distinct clade in the analysis of 24 taxa (Fig. 1B) but they are united with *Lanarkia*, *Phillipsilepis*, and *Nikolivia* when the additional scale-based taxa are included (Fig. 4B).

Examination of the frequency distribution of 10 000 000 random trees generated from the inclusive data set (Appendix 2) showed a strong phylogenetic signal. The shortest tree found among the random trees

Fig. 2. Scales of thelodonts showing morphological features used for coding phylogenetic characters and states. See Appendix 1 for details. **A**, *Stroinolepis maenniki* Märss & Karatajūtė-Talimaa, 2002; **B**, *Loganellia scotica* (Traquair, 1898); **C**, *Sphenonectris turnerae* Wilson & Caldwell, 1998; **D**, *Lanarkia horrida* Traquair, 1898; **E**, *Phillipsilepis crassa* Märss et al., 2002; **F**, *Phlebolepis elegans* Pander, 1856; **G**, *Thelodus laevis* (Pander, 1856); **H**, *Nikolivia gutta* Karatajūtė-Talimaa, 1978; **I**, *Furcacauda fredholmae* Wilson & Caldwell, 1998; **J**, *Eestilepis prominens* Märss et al., 2002; **K**, *Loganellia prolata* Märss et al., 2002; **L**, *Drepanolepis maerssae* Wilson & Caldwell, 1998; **M**, *Paralogania martinsoni* (Gross, 1967); **N**, *Valiukia flabellata* Karatajūtė-Talimaa & Märss, 2002; **O**, *Shielia parca* Märss et al., 2002; **P**, *Boothialepis thorsteinssoni* Märss, 1999; **Q**, *Archipelepis bifurcata* Märss et al., 2002; **R**, *Helenolepis obruchevei* Karatajūtė-Talimaa, 1978. Scales are not drawn to the same scale.

Abbreviations: ap, anterior process; cr, complicated ridge; db, deep base; dmr, double medial ridge; gn, groove-like neck; hn, high neck; in, indistinct neck; lrd, longitudinal ridges; mb, moderate base; nmp, narrow smooth median plate & side ridges; ob, oval base; pls, postero-lateral spine; pms, postero-medial spine; pr, protuberance; rb, rounded base; rdl, ridgelet on the posterolateral crown wall; sb, shallow base; serr, serration; wb, wide base; wmp, wide smooth median plate.

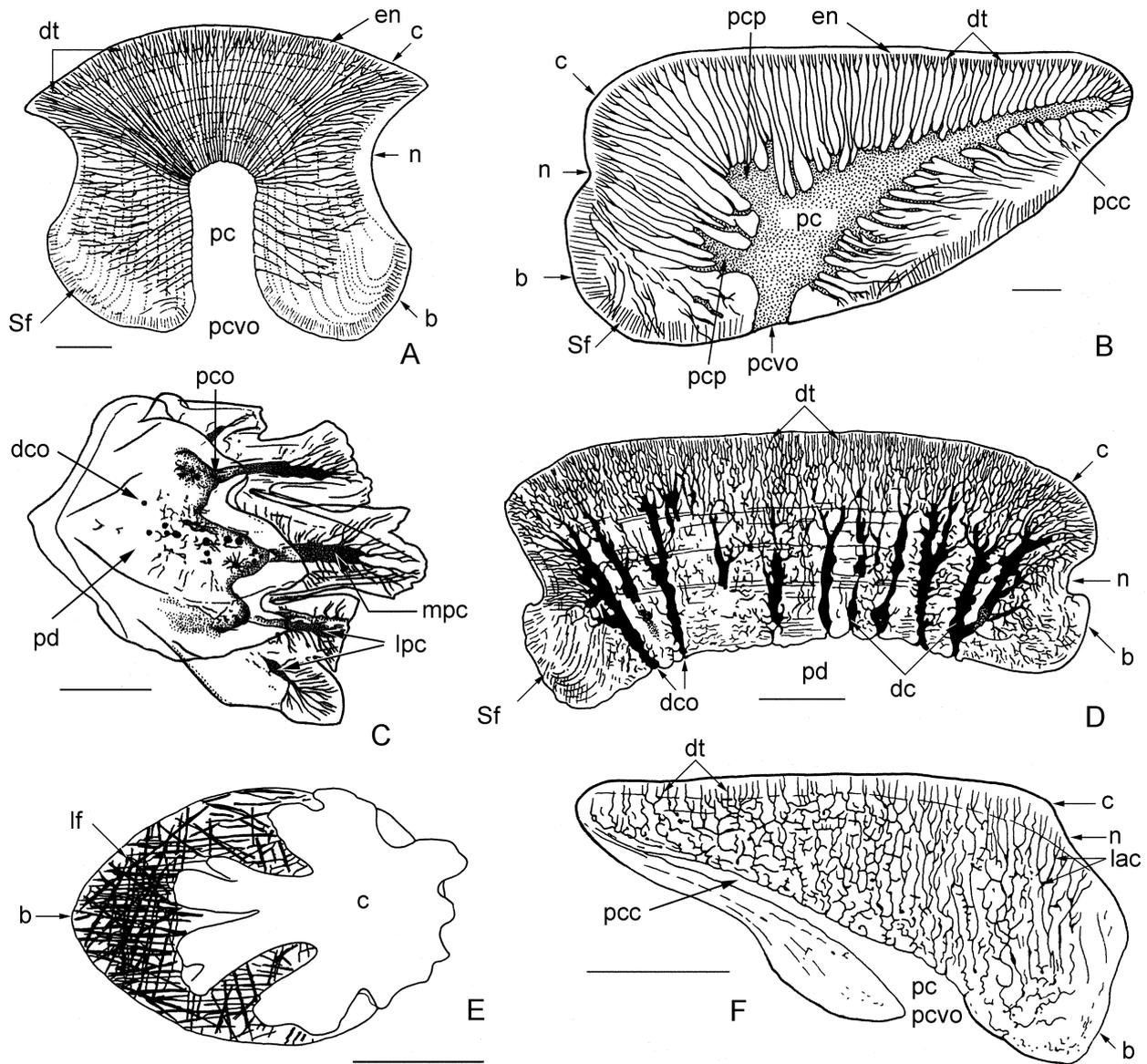


Fig. 3. Scales of thelodonts showing histological features used for phylogenetic characters and states. See Appendix 1 for details. **A**, *Thelodus parvidens* Agassiz (in Murchison 1838) from Gross 1967, fig. 11; **B**, *Turinia pagei* (Powrie, 1870) from Gross 1967, fig. 7C; **C**, *Goniporus alatus* (Gross, 1947) from Karatajütë-Talimaa 1978, fig. 12-8; **D**, *Trimerolepis timanica* (Karatajütë-Talimaa, 1970) from Karatajütë-Talimaa 1978, fig. 5-2; **E**, *Barlowodus floralis* Märss et al., 2002 from Märss et al. 2007, fig. 28B; **F**, *Canonica kaerberi* Karatajütë-Talimaa in Märss et al. 2007, fig. 30.

Abbreviations: b, base; c, crown; dc, dentine canal; dt, dentine tubule; dco, dentine canal opening; en, enameloid; lac, lacunae (widening) of dentine canals and tubules; lf, tubules for lattice fibres; lpc, lateral pulp canal; mpc, medial pulp canal; n, neck; pc, pulp cavity; pcc, pulp canal; pco, pulp canal opening; pcp, pulp cavity pocket; pcvo, pulp cavity opening; pd, pulp depression; Sf, tubules of Sharpey's fibres.

was 346 steps (compared to the shortest overall trees of 204 steps). The random trees had a mean length of 436 steps, a standard deviation of 12.4, and a skewness of -0.30; the shortest trees found by the heuristic procedure (Fig. 4) are thus more than 18 standard deviations shorter

than the average of the random trees and we conclude that the phylogenetic signal in the data is strong.

The character changes are mapped onto the majority-rule consensus tree in Fig. 5. Note that only unequivocal changes are shown; the lack of changes adjacent

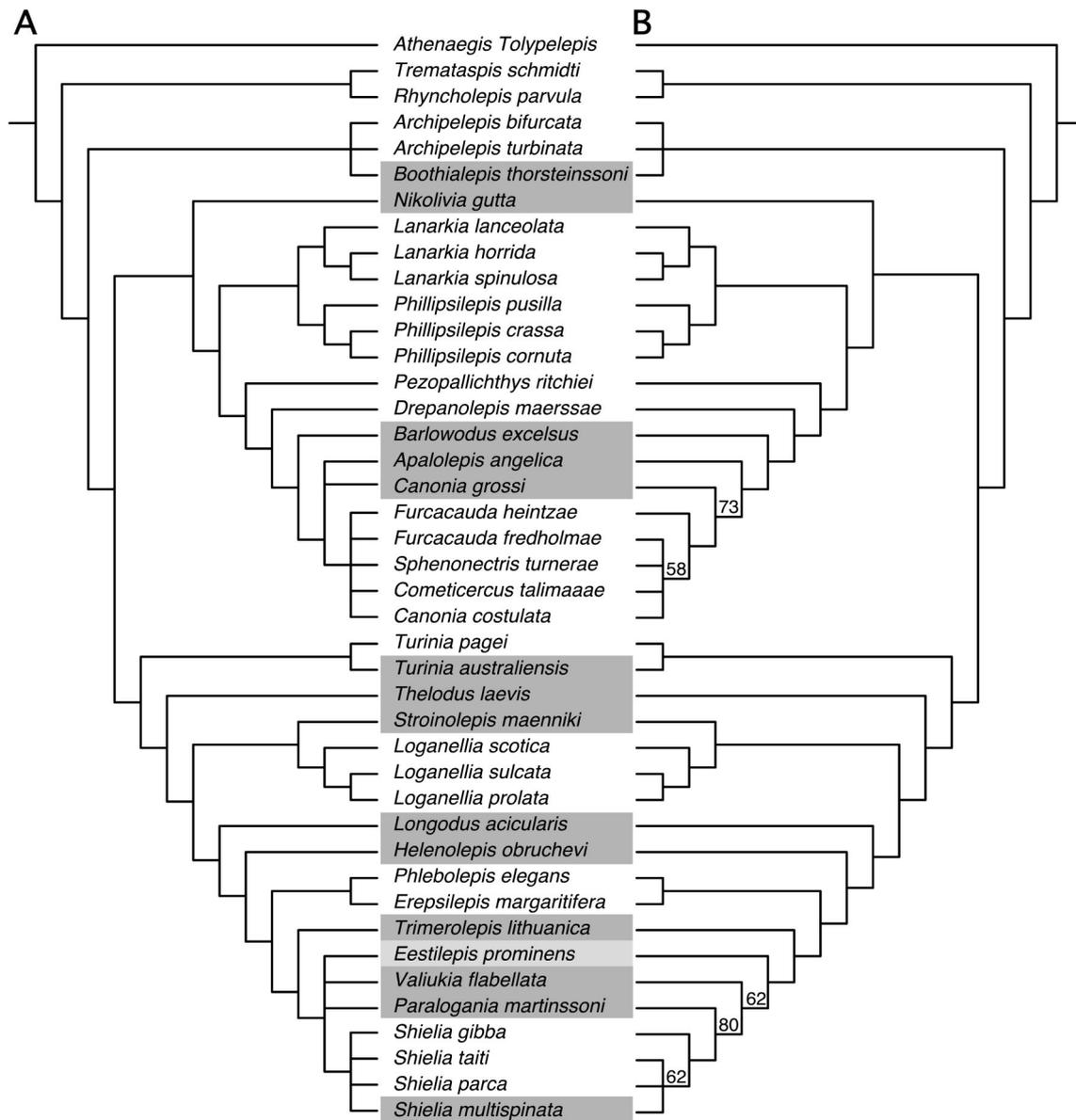
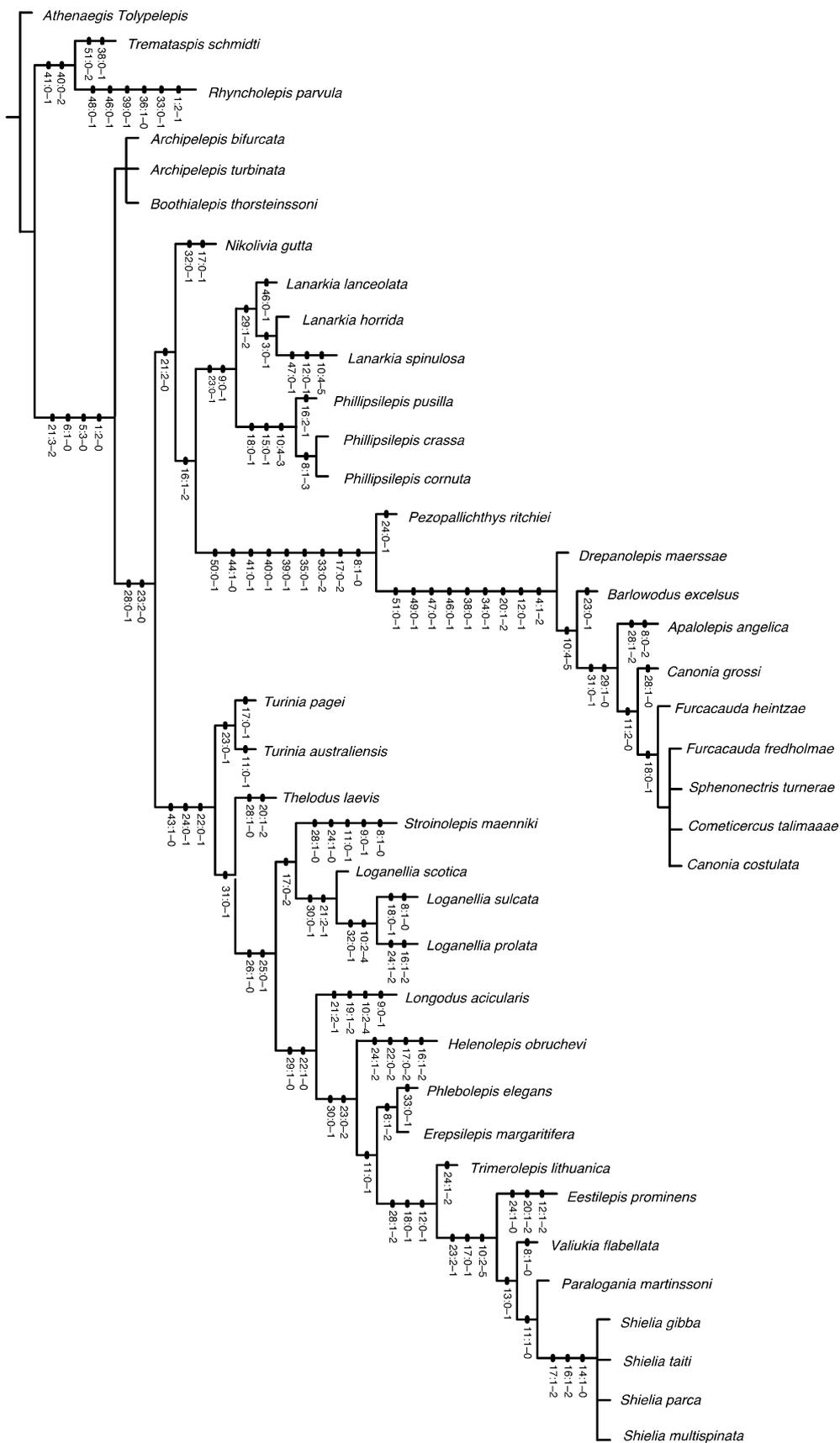


Fig. 4. Results of the present analysis (maximum parsimony, heuristic analysis, 100 random-addition starting-tree replicates) using the combined data matrix of 39 species of thelodonts and three outgroup taxa. **A**, the strict consensus obtained from all 2558 shortest trees of length 204 steps (C.I. = 0.39, R.I. = 0.72, R.C. = 0.28). **B**, the majority-rule consensus tree from the same 2558 trees of length 204 steps. All of the clades in this tree have a majority-rule percentage of 100 and appear in the strict consensus except the five clades for which percentage values are shown. Dark grey shading: the 14 scale-based species that were not included in the analysis of Wilson & Märss (2004). Light grey shading: *Eestilepis prominens*, which was eliminated from the earlier study because of wild-card behaviour but included in the present study because it did not display wild-card behaviour.

to polytomies (e.g., the clade *Archipelepis* spp. and *Boothialepis*; the polytomy among furcacauid species; the polytomy among *Shielia* species) is a product of this restriction. Different, arbitrary resolutions of these polytomies would give different suggested synapomorphies at adjacent nodes. For example, when any one of the three constituent species of the clade

Boothialepis + *Archipelepis* is placed as sister to the other two species, at least four synapomorphies are mapped unequivocally on the node: 11(1), 16(0), 17(3), and 22(2). These four synapomorphies are joined by state 4(2) if either of the two species of *Archipelepis* is placed as sister to the other two members of the clade. Characters evolving with the minimum number of



possible steps overall (C.I. = 1.0) in the majority-rule tree are characters 3, 13, 14, 15, 25, 34, 35, 42, 43, 49, and 52. Characters evolving with the most homoplasy (C.I. \leq 0.2) are characters 4, 11, 18, 24, and 46.

DISCUSSION

We consider that the present results represent a significant advance over our earlier attempt (Wilson & Märss 2004) both because of the improvements made in the data matrix and because of the more inclusive set of species in this new study.

Our analysis of the original 24 thelodont species using the updated data matrix shows that most of the changes in the relationships of these original species, compared with their relationships in the earlier study (Fig. 1A vs Figs 1B, 4), are caused by revisions to characters and states. Some other changes result from the addition of 15 mostly scale-based species to the analysis. The revised data matrix was able to place *Eestilepis prominens* with confidence; that species had acted as a wild-card and had been eliminated from the earlier analysis (Wilson & Märss 2004).

These results suggest to us that there is no fundamental barrier to the future analysis of additional, scale-based taxa despite their lack of data concerning body morphology. Similarly, the relationships of some of the articulated, squamation-based species for which ultrastructural data are currently lacking were not greatly changed by adding the scale-based taxa. This is good news for the future of thelodont phylogenetics.

Each of the three basic clades of thelodonts according to the present results has distinctive features indicated by the character-state changes mapped onto the phylogeny in Fig. 5, although the most basal clade (a trichotomy containing two species of *Archipelepis* and one of *Boothialepis*) has no unambiguous synapomorphies unless the trichotomy is arbitrarily resolved (see Results for details). This clade is distinguished from the other two clades by the following synapomorphies that the two larger clades share: scale base from wide to narrow (23:2–0), although the base configuration changes in some descendants to medium and/or wide, and pulp canals from absent to one (28:0–1), again with some subsequent changes to absent or more than one in certain descendants.

The large clade containing *Nikolivia*, *Lanarkia*, *Phillipsilepis*, and Furcacaudiformes (including *Barlowodus* and *Apalolepis*) is united by a rounded as opposed to a quadrangular scale base (21:2–0) except

Furcacauda fredholmae and the clade consisting of all of these taxa except *Nikolivia* is united by a crown that overlaps posterior scales greatly (16:1–2), again with a few exceptions.

The largest clade, which includes *Turinia*, *Thelodus*, *Loganellia*, *Phlebolepis*, *Shielia*, and relatives is united by three synapomorphies. The first is that basal members of the clade share a moderately deep scale base (22:0–1), although according to our topology subsequent evolution leads to more variation in this character. The second is that most of the clade shares (homoplasiously with *Lanarkia*) a moderate to strong anterior process on the scale base (24:0–1). The third synapomorphy uniting the clade is a long, straight intestine (43:0–1), although only in a few species can probable gut endocasts be seen. In others, one can estimate gut proportions by the length of the post-branchial, pre-caudal trunk, which is rather long and slender in most species. However, based on a similar argument about body proportions, one would also expect a long, straight intestine in *Lanarkia* spp. based on their body proportions (Märss & Ritchie 1998), and if that were confirmed, the character might be optimized differently.

The entire clade apart from *Turinia* shares sinuous or branching dentine tubules, as opposed to straight ones, in the mid-crown of scales (31:0–1), although this feature is also seen in furcacaudiforms. All members of the clade except *Turinia* and *Thelodus* share two unreversed synapomorphies: presence of a pulp depression in the scale base (25:0–1), and absence of a pulp cavity in the scale (26:1–0).

The new phylogeny makes interesting predictions about unseen features of both scale-based and squamation-based taxa. For example, the scale-based *Thelodus laevis* might be expected to have a body form something like those of *Turinia* and *Loganellia*. *Stroinolepis maenniki* is predicted to have a *Loganellia*-like body form. *Longodus* and *Helenolepis* are predicted to share additional features with *Phlebolepis* and *Shielia*. *Trimerolepis*, *Valiukia*, and *Paralogania* are predicted to share features with *Shielia*. *Valiukia* and *Paralogania* had already been united with *Shielia* in Shieliidae (Märss et al. 2006, 2007), but the inclusion of *Trimerolepis* is a novel result, the genus previously being classified in Katoporodidae (Märss et al. 2007). Similarly, *Barlowodus* and *Apalolepis* are predicted to share body-form features with Furcacaudiformes rather than with the Thelodontiformes. *Barlowodus* had been included in the Furcacaudiformes by Märss et al. (2002, 2006) but it, along with *Apalolepis*, was not classified with Furcacaudiformes by Märss et al. (2007).

Fig. 5. The preferred, majority-rule consensus tree of this study, based on 39 species of thelodonts with three outgroup taxa, showing unambiguous character changes mapped onto the tree using MacClade 4.08 (Maddison & Maddison 2005). For each change, the character is presented in the form 'X:Y–Z', where X is the character number, Y is the previous (plesiomorphic) state, and Z is the new (apomorphic) state for that clade.

Similarly, *Boothialepis* is expected to share morphological features with *Archipelepis*. When articulated specimens of these taxa are discovered, their morphologies will test the predictions of the phylogeny presented here.

Predictions concerning squamation-based taxa are focused mainly on those species for which limited data are currently available concerning histological or other ultrastructural features. *Eestilepis prominens* for example, known from a partial squamation that does not allow coding of most morphological features (Märss et al. 2002, 2006), is predicted to share histological features with *Paralogania* and *Shielia*, and morphological features with *Shielia*.

The phylogeny indicates that some aspects of the thelodont classification are in need of revision. A strict interpretation of these results indicates that the Thelodontiformes, as previously conceived (e.g., Märss et al. 2007), contained relatives of what were then classified as Loganelliiformes (e.g., *Stroinolepis*), Furcacaudiformes (e.g., *Barlowodus*, *Apalolepis*), and Shieliiformes (*Eestilepis*), as well as members of a basal clade of thelodonts (*Archipelepis* and *Boothialepis*) and basal branches from the two most diverse clades (e.g., *Nikolivia* as a basal branch of one clade and *Turinia* and *Thelodus* as successive basal branches of the other). A revised classification of thelodonts will allocate the various constituents of that paraphyletic assemblage to their various rightful groups. We here suggest a framework for that revised classification, using the ‘sequencing convention’ to indicate successive sister-group relationships, as follows:

Subclass Thelodonti Jaekel, 1911

Order Archipelepidiformes, nov.

Archipelepididae Märss (in Soehn et al. 2001)

Archipelepis Märss (in Soehn et al. 2001)

Boothialepididae Märss, 1999

Boothialepis Märss, 1999

Order Furcacaudiformes Wilson & Caldwell, 1998

Family Nikoliviidae Karatajütë-Talimaa, 1978

Nikolivia Karatajütë-Talimaa, 1978

Family Lanarkiidae Obruchev, 1949

Lanarkia Traquair, 1898

Phillipsilepis Märss et al., 2002

Family Pezopallichthyidae Wilson & Caldwell, 1998

Pezopallichthys Wilson & Caldwell, 1998

Family Drepanolepididae, nov.

Drepanolepis Wilson & Caldwell, 1998

Family Barlowodidae Märss et al., 2002

Barlowodus Märss et al., 2002

Family Apalolepididae Turner, 1976

Apalolepis Karatajütë-Talimaa, 1968

Family Furcacaudidae Wilson & Caldwell, 1998

Canonias Vieth, 1980

Furcacauda Wilson & Caldwell, 1998

Cometicercus Wilson & Caldwell, 1998

Sphenonectris Wilson & Caldwell, 1998

Order Thelodontiformes Kiaer, 1932

Family Turiniidae Obruchev, 1964

Turinia Traquair, 1896

Family Coelolepididae Pander, 1856

Thelodus Agassiz (in Murchison 1838)

Family Loganelliidae Märss et al., 2002

Stroinolepis Märss & Karatajütë-Talimaa, 2002

Loganellia Fredholm, 1990

Family Longodidae Märss, 2006b

Longodus Märss, 2006b

Family Helenolepididae, nov.

Helenolepis Karatajütë-Talimaa, 1978

Family Phlebolepididae Berg, 1940

Phlebolepis Pander, 1856

Erepsilepis Märss et al., 2002

Family Shieliidae Märss et al., 2002

Trimerolepis Obruchev & Karatajütë-Talimaa, 1967

Eestilepis Märss et al., 2002

Valiukia Karatajütë-Talimaa & Märss, 2002

Paralogania Karatajütë-Talimaa, 1997

Shielia Märss (in Märss & Ritchie 1998)

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Appendix 1. List of characters and states for phylogenetic analysis of 39 species of thelodonts and three outgroup taxa. Illustrations of important character states are found in the cited references and/or in Figs 2 and 3. Important summaries of the features of thelodonts can be found in Karatajütë-Talimaa (1978), Märss (1986), Turner (1991), Wilson & Caldwell (1993, 1998), Märss & Ritchie (1998), and Märss et al. (2002, 2006, 2007).

Exoskeleton

1. Head plates: absent = 0; many small = 1; few large = 2
2. Dermal skeleton of trunk: monodontodia = 0; polyodontodia = 1; other = 2

General scale arrangement

3. Longitudinal rows of larger scales among smaller ones: absent = 0; present = 1
4. Scale distribution on trunk: irregular or in longitudinal rows = 1; in diagonal rows = 2

Scale regions

5. Specialized scales immediately anterior to or surrounding orbits: low-crowned as head scales = 0; high-crowned, with one point = 1; multipointed = 2; enlarged scales/small platelet(s) = 3

6. Distinct mid-dorsal and mid-ventral body scales: absent = 0; present = 1
 7. Distinct scales of leading edges of fins: absent = 0; present = 1

Trunk scales*Size of scales*

8. Size of scales (length): very small (0.1–0.5 mm) = 0; small (0.5–1.0 mm) = 1; medium (1–2 mm) = 2; large (2–4 mm) = 3
 9. Scales of very different sizes: absent = 0; present = 1

Crown shape

10. Configuration: irregular = 0; water drop-like = 1; diamond = 2; elongate oval = 3; cuneiform = 4; flammate = 5; slender and high = 6 (Fig. 2P, Q; Fig. 2H; Fig. 2B, F, G; Fig. 2E; Fig. 2D, K, L; Fig. 2M, N, O; state 6 not illustrated)
 11. Crown surface: flattened = 0; moderately raised (<45 deg.) = 1; strongly raised (>45 deg.) = 2 (Fig. 2G, R; Fig. 2A; Fig. 2D, E)
 12. Crown posterior structures: one point = 0; three or more points = 1; fine serration = 2 (Fig. 2A, B, D, G, K; Fig. 2C, M–O; Fig. 2J)
 13. Postero-lateral spines on crown: absent = 0; present = 1 (Fig. 2A–L, P–R; Fig. 2M–O)
 14. Postero-lateral spines attached: horizontally = 0; vertically = 1 (Märss et al. 2007, figs 60–62; Märss 2003, pl. 2, fig. 11)
 15. High crests on body scales: none = 0; one central = 1 (Fig. 2G; Fig. 2E)
 16. Crown overlaps base posteriorly: no = 0; slightly or moderately (<1/2 of crown length) = 1; greatly (>1/2 of crown length) = 2 (Fig. 2P, Q; Fig. 2A, B, G, H; Fig. 2D, K, L, O, R)

Crown sculpture

17. Crown upper side ornamented with: simple longitudinal ridges = 0; relatively wide smooth medial plate = 1; narrow median plate or double median ridge plus side longitudinal ridge(s) = 2; radiating bifurcating ridges = 3 (Fig. 2D–G; Fig. 2H, I, M, N; Fig. 2A–C, K, L, O; Fig. 2Q)
 18. Crown posterior lower side: smooth = 0; sculptured = 1 (Fig. 2A, B2, D2, H2; Fig. 2E, Q2)

Crown ultrasculpture

19. None = 0; fine longitudinal striation = 1; wavy tranverse lamellae and irregular polygons = 2; (Märss 2006a, fig. 11A; Märss 2006a, figs 1C, O, 2D, F, 11D; Märss 2006a, figs 2I–Q, 11G)

Neck

20. Absent or as narrow groove = 1; high and distinct = 2 (Fig. 2A, D1, Q2; Fig. 2G2)

Base

21. Configuration: rounded = 0; oval = 1; quadrangular = 2; elongate rhombic = 3 (Fig. 2B2, D2, H2; Fig. 2B2; Fig. 2M–P, Q2; not illustrated)

22. Depth: shallow = 0; moderate = 1; very deep = 2 (Fig. 2D1, E; Fig. 2G2; Fig. 2Q2, R)
 23. Width: narrow = 0, moderate = 1; wide = 2 (Fig. 2B2, H2; Fig. 2D, F, M–O; Fig. 2P, Q)
 24. Anterior process: absent = 0; moderate = 1; long to very long = 2 (Fig. 2A, C, E, H, I, J, Q; Fig. 2B, G2, M, N; Fig. 2D, K, O, R)

Microstructure of adult scales

25. Pulp depression: absent = 0; present = 1 (Fig. 3A, B, F; Fig. 3C, D)
 26. Pulp cavity: absent = 0; present = 1 (Fig. 3C, D; Fig. 3A, B, F)
 27. Pulp cavity ‘pockets’: absent = 0; present = 1 (Fig. 3A, F; Fig. 3B)
 28. Pulp canals: absent = 0; single = 1; multiple = 2 (Fig. 3A; Fig. 3B, F; Fig. 3C)
 29. Length of (main) pulp canal: short = 0; medium = 1 (<1/2 length of crown); long = 2 (>1/2 length of crown) (Märss 1986, pl. 3, fig. 2; Märss et al. 2006, fig. 8D; Märss et al. 2007, fig. 23)
 30. Dentine canals in mid crown: absent = 0; present = 1 (Fig. 3A, B, F; Fig. 3C, D)
 31. Dentine tubules in mid crown: straight = 0; sinuous/branching = 1 (Fig. 3A, B; Fig. 3D, F)
 32. Sharpey fibre tubules: fine = 0; medium = 1; long & strong = 2 (Karatajūtė-Talimaa & Märss 2002, fig. 6A, B; Märss et al. 2006, text-fig. 11D; Märss et al. 2006, text-fig. 63A)

Body shape

33. Body shape: depressed = 0; fusiform = 1; compressed = 2
 34. Distinct anal notch: absent = 0; present = 1
 35. Caudal peduncle and tail: long and slender = 0; short and very deep = 1

Cephalopectoral area

36. Cephalopectoral area: short = 0; moderately long to very long = 1
 37. Orbit location: lateral or behind anterolateral corners of head = 0; at anterolateral corners of head = 1
 38. Orbits: small = 0; large = 1
 39. Mouth shape: subterminal, transverse, broad = 0; terminal, nearly circular = 1
 40. Head: broad, rectangular = 0; conical, tapered = 1; bluntly rounded = 2

Gut

41. Branchial row (where known): more or less horizontal = 0; strongly oblique = 1
 42. ‘Stomach’ chamber: funnel-shaped = 0; barrel-shaped = 1
 43. Intestine: long and slender = 0; short and wide = 1

Fins*Paired fins*

44. Pectoral/suprabranchial fins: absent = 0; present = 1 (see Wilson et al. 2007)

- 45. Pectoral fins: ‘rays’ of subparallel scale rows = 0; fleshy base of scale covered skin = 1 (see Wilson et al. 2007)
- 46. Pelvic/ventral fins: absent = 0; present = 1 (see Wilson et al. 2007)
- Dorsal and anal fins*
- 47. Dorsal fin(s): absent = 0; one or two = 1
- 48. Anal fin: absent = 0; present = 1
- Caudal fin*
- 49. Caudal fin length as proportion of total body: less than 30% = 0; more than 40% = 1

- 50. Caudal fin main lobes: dorsal and ventral lobes differ greatly in size or shape = 0; d and v lobes similar in size and shape = 1
- 51. Caudal fin web supported by many, slender, ray-like scale rows = 0; supported by few, large lobes = 1; without obvious lobes or rays = 2

Lateral line system

- 52. Arrangement of lateral line system on body: longitudinal lines = 0; short segments forming right-angled network = 1

Appendix 2. Character-taxon matrix for 39 species of thelodonts and three outgroups scored for 52 characters. Missing data = ‘?’; inapplicable state = ‘-’.

	1	5	1	1	2	2	3	3	4	4	5
			0	5	0	5	0	5	0	5	0
<i>Stroinolepis maenniki</i>	00	???	012	100	-0120	?12100	1000	-01	????	????	????
<i>Loganellia scotica</i>	0002	101102	000	-01200	11101100	111100	00010000	?0100	11000?	0100	11000?
<i>Loganellia sulcata</i>	0001	101004	000	-01210	11101100	111110	?00?000	???	1???	???	000?
<i>Loganellia prolata</i>	0001	?01104	000	-02200	11102100	111110	?00?000	???	1???	???	000?
<i>Shielia taiti</i>	0001	201005	01100	221?	?2011100	22110100	10000?	0?	?01100	002?	
<i>Shielia parca</i>	0001	201005	01100	22111	2012100	2???	?1?01?	?00???	?1???	?0???	
<i>Shielia gibba</i>	0001	?01105	01100	221?	?2112100	22???	?01?	?00???	?1???	?0???	
<i>Shielia multispinata</i>	00???	01005	01100	22111	2012100	22110???	????	????	????	????	????
<i>Paralogania martinssoni</i>	00???	01105	01110	11112	111100	22110???	????	????	????	????	????
<i>Valiukia flabellata</i>	00???	0?005	11101	111?	?2011100	2211???	????	????	????	????	????
<i>Phlebolepis elegans</i>	0002	300202	100	-0100	112021100	1010100	10000?	00100	110101		
<i>Erepsilepis margaritifera</i>	000???	?202100	-0100	?12021100	?????	0???	?0???	?1???	?0???		
<i>Helenolepis obruchevi</i>	00???	0?102	000	-0220	?12222100	10110???	????	????	????	????	????
<i>Trimerolepis lithuanica</i>	00???	0?102	110	-0101	?12022100	21110???	????	????	????	????	????
<i>Thelodus laevis</i>	000???	01102	000	-0100	1221010100	-010???	????	????	????	????	????
<i>Eestilepis prominens</i>	0002	?01105	120	-011???	?2?110???	?????	0???	?1???	????	????	????
<i>Lanarkia horrida</i>	00111	11114	200	-0200	?100120101200	?000010000	?1100000?				
<i>Lanarkia spinulosa</i>	0011???	11152	10	-0200	?100120???	???	0?0?	10000?	?1???	0???	
<i>Lanarkia lanceolata</i>	0001?	01114	200	-0200	?10011???	?12???	0000?	0000?	?1?	100000?	
<i>Phillipsilepis crassa</i>	0001?	01313	200	-1201?	?10010010110000	?0???	000???	????	????	000?	
<i>Phillipsilepis cornuta</i>	0001?	0?313	200	-1201?	?100100101100	????	????	????	????	????	????
<i>Phillipsilepis pusilla</i>	0001?	0?113	200	-1101?	?1001001???	???	0?0?	????	????	0???	
<i>Archipelepis bifurcata</i>	0002?	0?200	100	-0031?	?122200100	-0010?	0???	0???	????	0???	
<i>Archipelepis turbinata</i>	000200?	100100	-003?	?1222001	?????	0?0?	000???	1-???	000?		
<i>Boothialepis thorsteinssoni</i>	000???	0?200	100	-00301	?122210110	-000???	????	????	????	????	????
<i>Turinia pagei</i>	000100	1202000	-0110?	?121101111000	0001100000011	???	0?2?				
<i>Turinia australiensis</i>	00???	???	202100	-0100	?11211101?	?11000	????	????	????	????	????
<i>Barlowodus excelsus</i>	00???	???	005210	-0120	?12001001011002	????	????	????	????	????	????
<i>Nikolivia gutta</i>	00???	0?101	000	-0110?	?1000001011001	????	????	????	????	????	????
<i>Apalolepis angelica</i>	00???	???	205210	-0100	?2000001?	?2001	????	????	????	????	????
<i>Pezopallichthys ritchiei</i>	000100000	4100	-0220	?1000101	?????	?201000	111110	-0000	10?		
<i>Furcacauda heintzae</i>	000221	1005010	-0221?	?2000001	?????	?21100	1111110	-1101	1110		
<i>Furcacauda fredholmae</i>	000211	1002010	-0211?	?2200001	?????	?21100	1111110	-1101	1110		
<i>Sphenonectris turnerae</i>	000221	1002010	-0221?	?2000001	?????	?21100	1110110	-0001	1110		
<i>Drepanolepis maerssae</i>	000200000	4110	-022??	?2000001	?????	?21100	1111110	-1101	1110		
<i>Cometicercus talimaaae</i>	0002?	11002010	-022??	?2000001	?????	?211?	0???	???	10	-1101	1110
<i>Canonia costulata</i>	00???	???	002000	-0201	?22000001?	?10012	????	????	????	????	????
<i>Canonia grossi</i>	00???	???	005010	-0200	?2200000110	-01	????	????	????	????	????
<i>Longodus acicularis</i>	00???	???	114000	-0100	?21100110010010	????	????	????	????	????	????
<i>Athenaegis Tolypelepis</i>	2101311	2600	-0-010	-?130200	112000	-000100000	?10	-0000	111		
<i>Tremataspis schmidtii</i>	2201	-1-2060	-0-01	--?	?130200000	-00-0001	-1021	???	11000002?		
<i>Rhyncholepis parvula</i>	120131	-2060	-0-01	--	0130200	-----	01000001	21???	0-101000?		

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Telodontide fülogeneesiuringud soomustepõhiste taksonite kaasamisega

Mark V. H. Wilson ja Tiiu Märss

On käsitletud seni vähe uuritud varajaste selgroogsete, telodontide fülogeneesi. On ümber hinnatud varasema uuringu andmed, mille aluseks olid telodontide terved välisskeletid, ja lisatud 15 liigi soomuste iseloomulikud tunnused. On revideeritud alamklassi Thelodonti süstemaatikat, eraldades selles kolm seltsi: Archipelepidiformes kahe, Furcacauid-formes nelja ja Thelodontiformes seitsme sugukonnaga.