PATTERNS OF ECOLOGICAL DIVERSIFICATION IN THELODONTS

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ABSTRACT

Ecological diversification is a key topic in evolutionary biology. Up to date, only a few studies dealing with this issue have been carried out specifically in extinct groups of early vertebrates. Here, we explore the spatial, temporal and phylogenetic patterns of ecological diversification of the whole clade of thelodonts, one of the earliest groups of vertebrates and longest-lasting of the Palaeozoic agnathans in the fossil record. Parsimony and maximum-likelihood methods were used for ancestral state reconstruction of their geographical distributions, habitats and lifestyles. Our results support that thelodonts originated during the Middle?-Late Ordovician probably in marine open waters of Laurasia, with a demersal lifestyle on hard substrates being the ancestral condition for the whole clade. After that, thelodonts underwent a complex ecological diversification and palaeobiogeographical history, comparable in many aspects to those of some major groups of living fishes. Different modes of life evolved repeatedly and a wide range of habitats were colonized by distinct groups, including deep waters and non-true marine environments. Diadromous strategies presumably appeared also on nine different occasions. The palaeobiogeographic history of thelodonts reveals significant differences in the dispersal potential of some major groups. Dispersals of thelodontiforms entailed displacements over long distances and the crossing of deep water biogeographic barriers, whereas those of furcacaudiforms were always limited to areas interconnected by shallow platforms. We propose that the evolution of pelagic larval stages in thelodontiforms might be a suitable explanation for such disparate patterns and could satisfactorily account for the greater evolutionary success of this group.

Key words: Thelodonti, early vertebrates, ecological diversification, lifestyles, habitats, dispersal events.

ECOLOGICAL diversification is the core mechanism that underlies adaptive radiations (Schluter 2000; Losos 2010) and is a major player in shaping morphological (e.g. Renaud *et al.* 2005; Von Rintelen *et al.* 2010), molecular (e.g. Duda & Palumbi 1999; Jagadeeshan & Singh 2007) and behavioural traits (e.g. McLaughlin 2001; Bird 2011). The phylogenetic patterns and the timing of appearance of different ecological characteristics have been assessed in a considerable number of vertebrates, including fishes (e.g. Winemiller *et al.* 1995; Tringali *et al.* 1999; Wellenreuther *et al.* 2007; Betancur-R 2010; Rutschmann *et al.* 2011; Betancur-R *et al.* 2012, 2015; Near *et al.* 2012; Bloom *et al.* 2013; Bloom & Lovejoy 2014), amphibians (e.g. Kozak *et al.* 2005; Gomes *et al.* 2009), reptiles (e.g. Melville *et al.* 2001; Glor *et al.* 2003; Stephens & Wiens 2003; Sanders *et al.* 2004; Ahmadzadeh *et al.* 2013), birds (e.g. Owens & Bennett 1995; Richman 1996; Cicero & Johnson 1998) and mammals (e.g. Patton *et al.* 2000; Ji *et al.* 2006; Luo 2007; Wilson *et al.* 2012; Meng *et al.* 2015; Slater 2015). However, the extension of such approaches to extinct groups involves many limitations given that ecological interpretations are difficult to support in them (mainly due to the lack of closely-related living representatives) and their phylogenetic relationships are usually poorly known. In fact, few studies deal specifically with this topic in early vertebrates (e.g. Groh 2014; Sallan *et al.* 2015, 2017; Sansom *et al.* 2015) and, as consequence, the patterns of ecological diversification during the first steps of the evolutionary history of the group remain basically unknown.

Among early vertebrates, thelodonts constitute one of first clades in the fossil record, ranging from the Upper Ordovician (Sansom *et al.* 1996; Märss & Karatajūtė-Talimaa 2002;

Turner *et al*. 2004; Märss *et al.* 2007) to the Upper Devonian (Turner 2005; Hairapetian *et al.* 2016*b*). This group includes agnathan fishes showing micromeric squamations considered as functionally analogous to those of living elasmobranchs (Turner 1982, 1991; Märss 1986; Karatajūtė-Talimaa 1998; Märss *et al.* 2007). Recently, Ferrón & Botella (2017) have established a useful comparative framework analysing the relationship between the squamation pattern and lifestyle in extant sharks and assessed the ecology of thelodonts from the study of their squamations, giving a comprehensive overview of their modes of life at species level. In addition, some other previous studies dealing with comparative anatomy (Turner 1992), isotopic data (Žigaitė *et al*. 2010; Fadel *et al.* 2015) and the sedimentology and taphonomy of several thelodont localities (Turner 1999; Märss *et al.* 2003, 2007; Märss & Männik 2013) have also provided valuable information about the environments where these fishes inhabited. Thus, the knowledge regarding the ecology, lifestyles and habitats of these animals is currently fairly broad, which, together with the recent publication of some phylogenetic trees (Wilson & Märss 2004, 2009; see also Žigaitė *et al*. 2013*a*), makes the thelodonts a suitable group for exploring different evolutionary processes in the earliest vertebrates from an ecological perspective. With this aim, here we evaluate the spatial, temporal and phylogenetic patterns of ecological diversification of the whole clade of thelodonts, providing a comprehensive interpretation of their dispersal events, habitats and lifestyles, as well as shedding light onto the ecological evolutionary history of one of the first groups of vertebrates.

METHODS

Ecological diversification of thelodonts was assessed at species level by means of ancestral character state reconstruction of their lifestyles, habitats and palaeobiogeographic distributions.

The data regarding thelodont lifestyles were taken from Ferrón & Botella (2017), where all described species so far are classified into five ecological groups (demersal on hard substrate, demersal on soft substrate, schooling, strong swimmers and slow swimmers of the open water). Habitat interpretations were based on an extensive review of sedimentological data and associated remains of all thelodont localities (see Ferrón *et al.* 2017), assigning each of them to one (or a range of) specific environments (freshwater, brackish, marine littoral, shoal belt, open platform, subphotic distal shelf/continental slope) following Turner (1999). Finally, palaeogeographic and temporal distributions were determined for each species based on the compilation of thelodont occurrences published by Märss *et al*. (2007). These data have later been updated with more recent information provided by most of the subsequent works dealing with new descriptions of thelodont localities or species (i.e. Hairapetian *et al.* 2008, 2016*a*, *b*; Märss 2011; Burrow *et al.* 2013; Mark-Kurik *et al.* 2013; Žigaitė 2013; Žigaitė *et al.* 2013*b*).

Ancestral character state reconstruction was implemented using the software Mesquite 3.2 (Maddison & Maddison 2017). We applied parsimony analysis for reconstructing ancestral palaeobiogeographic distributions (coded as a polymorphic multistate character), and maximum likelihood method for reconstructing ancestral lifestyles (coded as a monomorphic multistate character) and habitats (each habitat coded as a different binary character). Phylogenetic relationships considered here are based on the most complete thelodont phylogeny obtained up to date (Wilson & Märss 2009), which comprises 39 species pertaining to 26 different genera (equivalent to 26 % of the total described diversity). In order to include into the phylogenetic tree as many species as possible, we added most of the remaining taxa according to different criteria. Turiniid thelodonts have been included following the phylogenetic relationships proposed by Hairapetian et al. (2016*a*). Non-represented genera were inserted as within-family polytomies together with (or as the sister group of) other representatives of the same family. Similarly, species with congeneric taxa represented in the phylogeny were inserted as within-genus polytomies. Finally, *Larolepis*, *Valyalepis*, *Sandivia*, *Angaralepis* and *Stroinolepis* were nested together within a polytomy and *Nunavutia* was considered as the sister group of the clade *Illoganellia* + *Loganellia* + *Talimaalepis*. These inclusions follow the systematic classification proposed by Märss *et al*. (2007). Even so, some taxa without representation at family level in the phylogeny or *incertae sedis* species could not be inserted in the tree but their ecological and palaeobiogeographical data have also been interpreted here despite lacking a general phylogenetic context.

RESULTS AND DISCUSSION

Ecological diversification of thelodonts

The habitat and ecology of the first vertebrates has been a matter of debate in the past (Chamberlin 1900; Romer & Grove 1935; Denison 1956; Robertson 1957; Halstead 1973, 1985; Fischer 1978; Boucot & Janis 1983; Mallatt 1984, 1985; Griffith 1987; Dineley 1988; Purnell 2001, 2002; Blieck & Turner 2003; Turner *et al.* 2004). Currently, the prevailing view among palaeontologists is that most early vertebrate groups, including thelodonts, originated in the sea as benthic detritivorous fishes (see Turner 1991, 1992; Janvier 1996; Märss *et al.* 2007; Lingham-Soliar 2014). The ancestral state reconstruction of the lifestyles and habitats of thelodonts obtained in our analysis support these ideas, suggesting that the last common ancestor of the whole clade was a demersal animal living on hard substrates of the open platform (Fig. 1 (A)). From this ancestral condition, different modes of live evolved and many habitats were later colonized by representatives of this group (Fig. 1).

Lifestyle diversification. A demersal mode of life on hard substrates is widespread among thelodonts, being the plesiomorphic condition in most cases or a derived state in few other taxa (evolved from schooling lifestyles in some nikoliviids, furcacaudids and shieliids, Fig. 1 (E, K, R); and from slow swimmers of the open water in some loganelliids, Fig. 1 (N)). According to our approach, a demersal mode of life on soft substrates appeared independently at least four times during the Silurian and the Devonian (within turiniids in Gondwana, coelolepids in Baltica and loganelliids and shieliids in Laurentia, Fig. 1 (L-N, R)) but probably more if considering some taxa with uncertain ecological assignations (i.e. archipelepidiforms, lanarkiids and phlebolepidids, Fig. 1 (B, F, Q)). Similarly, ancestral state reconstruction analysis supports that schooling lifestyle have evolved repeatedly among thelodonts. The first representatives belonging to this ecological group appeared and radiated during the Llandovery in three different occasions (i.e., once in furcacaudiforms and twice within shieliids both in Laurentia and, possibly, Baltica, Fig. 1 (C, R)). Interestingly, the monogeneans, one of the main groups of ectoparasites with vertebrate hosts, also originated in the Llandovery (Perkins 2010). The coevolution of these parasitic flatworms and vertebrates has sometimes been proposed although the reasons that promoted such an association are unknown (Perkins 2010; De Baets *et al.* 2015). We propose that, given that high densities of potential hosts increase the chances of infection by parasites with direct cycles (such as monogeneans) (Poulin 1991; Ranta 1992; Richards *et al.* 2010), the first schools of fishes could have created appropriate conditions that guaranteed their reproductive success. As consequence, the establishment of social behaviours in the earliest fishes could have triggered the evolution of parasitic flatworm groups with vertebrate hosts. After the early Silurian, schooling appears sporadically four additional times in Devonian turiniids of Gondwana (Fig. 1 (L)) and possibly in Pridolian talivaliids of Baltica (Fig. 1 (S)). Our analyses further suggest that slow swimmers of the open water also originated repeatedly in different groups of thelodonts including lanarkiids (in Avalonia, Fig. 1 (F)), coelolepids, shieliids, talivaliids (in Baltica, Fig. 1 (M, R and S)) and loganelliids (in Laurentia, followed by an important species diversification, Fig. 1 (N)). The first appearance of this lifestyle took place before or during the Rhuddanian (lower Llandovery) in the early stages of the ecological diversification of the group. Finally, adaptations to strong swimming evolved in apalolepidids (in Baltica, Fig. 1 (J)), furcacaudids (in Laurentia, Fig. 1 (K)), coelolepids (in Baltica, Fig. 1 (M)), shieliids (in Laurentia, Fig. 1 (R)) and *Skamolepis fragilis*. Ferrón & Botella (2017) already noticed that most active pelagic species, pertaining presumably to different thelodont lineages, appeared simultaneously during the Early Devonian when the competition in benthic habitats together with the availability of abundant planktonic food lead to the colonisation of the pelagic realm by many marine groups (i.e. the so called Nekton Revolution, Klug *et al.* 2010). Our results suggest that indeed pelagic thelodonts evolved independently up to five times during the Early Devonian; this supports the view that agnathan vertebrates also took part in this macroecological revolution in a most significant way acquiring the capability to swim actively in the water column on multiple occasions. Prior to that, only two species presented squamations adapted to a pelagic lifestyle (*Thelodus visvaldi* in the Sheinwoodian and

Praetrilogania grabion in the Pridoli) giving little support to the existence of a Silurian Nekton Revolution among Palaeozoic agnathans (Sallan *et al.* 2015, 2017).

Habitat diversification. Most thelodont species inhabited shore belt-associated areas and/or open platform environments (Fig. 1). Ancestral state reconstruction analysis reveals that colonisation of subphotic waters of the distal shelf or the continental slope took place at different times and around various continents throughout the evolutionary history of this group. Several examples can be found among nine different families (i.e. archipelepids, lanarkiids, furcacaudids, turiniids, coelolepids, loganelliids, phlebolepidids, shieliids and talivaliids, Fig. 1 (B, F, K-N, Q-S)). This contrasts with the typical habitats of most other Palaeozoic agnathans, which were usually restricted to near-shore or continental environments (with the exception of anaspids) (Janvier 1996). Our approach also suggests that most thelodonts displayed a wide tolerance to water salinities and reveals repeated invasions of non-true marine environments (Fig. 1). About 50 species have been reported from presumed brackish and/or freshwater sediments and, in fact, maximum likelihood reconstruction supports that the ancestral habitats of a considerable number of groups comprises non-true marine environments (this is the case for some lanarkiids, shieliids and talivaliids, Fig. 1 (E, F, J-L, R, S)). So far, only a few species have been found in sediments with a freshwater origin and just lanarkiids and one clade of turiniids apparently diversified from entirely non-marine ancestors (Fig. 1 (F, L)). Conversely, thelodonts with brackish affinities are better represented and it seems to be the ancestral condition for several major groups (Fig. 1 (J-L)). Many other Palaeozoic agnathans, such as galeaspids, osteostracans, heterostracans and pituriaspids, also colonised and succeed in brackish and freshwater habitats (e.g. Janvier 1996; Groh 2014; Sansom *et al.* 2015; Blieck and Elliott 2017). The invasion of non-marine environments by vertebrates has been interpreted as a gradual process with a first important occupation of brackish waters in the Wenlock and fluvial systems during the Pridoli-Lochkovian (Halstead 1985). In general, with few exceptions, the revised stratigraphic ranges and ancestral state reconstructions of the habitat of thelodonts match properly with this pattern (Fig. 1 and 2). In any case, these interpretations should be treated cautiously as the marine or freshwater origin of some thelodont localities is still under discussion (Märss *et al.* 2007; Turner *et al.* 2017) and our interpretations about the habitats of some species could be affected by sampling bias and/or lack of sedimentological evidence.

Several thelodonts (mostly Pridolian and Lochkovian species) displayed spatial distributions compatible with diadromous lifestyles, apparently occurring in both freshwater and true marine sediments. This is documented in many representatives of nikoliviids, turiniids and talivaliids (Fig. 1 (E, L, S)). Presumably, some of these species inhabited a wide range of habitats and displayed long migrations between the continental slope or the open platform and fluvial systems (e.g. *Nikolivia balabayi*, *N. oervigi*, *N. gutta*, *Lanarkia horrida*, *Turinia pagei*, *T. polita*, *Loganellia unispinata*, *Paralogania ludlowiensis* and *Talivalia elongata*). This indicates that the diadromous strategies and/or the rage of habitats occupied by some early vertebrates were comparable to those found in many living groups (Nelson *et al.* 2016; Froese & Pauly 2017). Ancestral-state reconstruction analysis supports that diadromy evolved independently up to nine times among thelodonts and was already present in the last common ancestor of all *Nikolivia* spp., some *Turinia* spp. and the whole clade of Talivaliidae (Fig. 1 (E, L, S)). Diadromous lineages rarely derived in entirely freshwater species supporting the idea that diadromy does not usually play a role as a pathway for marine/freshwater evolutionary transitions (Bloom & Lovejoy 2014 and references therein). In addition, transitions from marine to freshwater habitats seem more frequent than the contrary, as previously reported in many other groups (Betancur-R *et al.* 2015). In fact, only two freshwater lineages colonised again oceanic habitats (i.e. lanarkiids and some turiniids, Fig. 1 (F, L)).

Ecological diversity overview. The joint consideration of lifestyles and habitats of thelodonts allows interpreting some aspects of the ecological diversity of this group in a more comprehensive way (Fig. 3). Freshwater thelodont communities were probably characterized by a high proportion of schooling species and the absence of strong swimmers (although some non-marine gnathostomes could have already played this ecological role during the Palaeozoic, Denison 1978, 1979; Ginter *et al.* 2010). In brackish and marine environments, the best-represented ecological groups of thelodonts were demersal species on hard substrates and, to a lesser extent, schooling species. As expected, the percentage of the slow species of the open water increases towards deeper habitats and constituted an important part of the thelodont communities that resided in subphotic waters of the open platform and the slope (note that this group is also comparatively well represented in freshwaters but all these cases denote presumed diadromous species). A similar pattern is followed by demersal species of soft substrates being more common in non-marine waters and distal marine environments. This trend could be expected as muddy bottoms are usually found in the lower course of the rivers, deltas and estuaries as well as in outer shelf regions. The most distal marine environments were also characterized by a low representation of strong swimming thelodonts, which were mainly restricted to shoals and open platforms. This indicates that the potential for long-distance migrations beyond the neritic realm would be limited to thelodonts from this ecological group despite showing active swimming lifestyles (see next section for further discussion about dispersal capabilities of thelodonts).

Geographical distribution and dispersal events of thelodonts

Ancestral state reconstruction supports a Laurentian origin of thelodonts in the Middle?-Late Ordovician (Fig. 1 (A) and Fig. 4), in accordance with some previous proposals based on the location of the earliest occurrences of the group (Smith *et al.* 2002; Blieck & Turner 2003; Turner *et al.* 2004). The archipelepidiforms, which constitute the most basal group of thelodonts, and the furcacaudiforms likely originated and diversified during the early/middle Silurian also in Laurentia (Fig. 1 (B, C) and Fig. 4). Conversely, the origin of the thelodontiforms is situated in Baltica (Fig. 1 (D) and Fig. 4). Several dispersal events are predicted along the evolutionary history of the clade (Fig. 1 and Fig. 4). According to our analyses, a first dispersal wave to Baltica occurred during the Late Ordovician giving rise to the Thelodontiformes. From that moment, representatives of this group experienced a complex palaeobiogeographic history entailing several dispersal events accompanied by important diversifications. Multiple dispersals took place from Baltica to Gondwana (in the Early Devonian by turiniids and coelolepids), Laurentia (in the Late Ordovician by loganelliids, in the early Silurian by loganelliids, shieliids, coelolepids, in the middle Silurian possibly by phebolepidids, in the late Silurian by shieliids and in the Early Devonian by talivaliids) and Siberia (in the early Silurian by loganelliids and possibly in the late Silurian by helenolepidids). After that, a significant number of groups experienced a second dispersal (i.e. loganelliids dispersed from Laurentia to Baltica, Avalonia and Siberia in the early-middle Silurian; shieliids dispersed from Laurentia to Baltica and Gondwana in the middle-late

Silurian; and turiniids dispersed from Gondwana to Baltica during the early Devonian). On the other hand, Furcacaudiformes showed a simpler palaeobiogeographic history, undergoing only some dispersals from Laurentia to Avalonia (in the middle Silurian by lanarkiids and in the Early Devonian by nikoliviids) and Baltica (in the early Devonian by apalolepidids and nikoliviids). Subsequent dispersals from these continents were extremely rare and only apalolepidids dispersed to Avalonia after their arrival to Balica in the Early Devonian.

Palaeogeographic reconstructions of the early and middle Palaeozoic suggest that the dispersals of thelodontiforms entailed displacements over long distances and the crossing of deep water biogeographic barriers, whereas those of furcacaudiforms were always limited to areas interconnected by shallow platforms (Fig. 1 and Fig. 4). Such contrast in the dispersal potential of both groups may rely on differences in their swimming capabilities and/or on differences in the modes of life of their larvae (McKerrow & Cocks 1995). The first option seems unlikely in this case as most dispersal events of thelodontiforms occurred within typically demersal and/or neritic groups. Rather, the evolution of meropelagic development in the first evolutionary steps of this clade (involving neritic adults and planktonic larval stages) seems a more plausible scenario, allowing long-range larval dispersal mediated by oceanic currents (Turner & Tarling 1982; Klug *et al.* 2010). This might be proposed as a possible explanation for the greater evolutionary success of thelodontiforms, allowing them to disperse over deep ocean basins and colonize and diversify in distant regions during the early and middle Silurian (Siberia, Laurentia, Avalonia and Gondwana) (see Blieck & Janvier (1993) and Žigaitė & Blieck (2006) for further detail about the Siberian thelodontiform radiation). On the contrary, furcacaudiforms never colonized Gondwana nor Siberia and their dispersal to Baltica and Avalonia did not take place until the middle Silurian, after the formation of suitable pathways through the coastal waters of Laurassia. However, by then, thelodontiforms had already established there occupying much of the marine habitats and most Baltic and Avalonian furcacaudiforms were relegated to non-marine environments.

Current limitations and future concerns

Comprehensive analytical studies compiling information from different fields are crucial for shedding light onto issues of wider scope and broader interest. Unfortunately, on some occasions the large amount of data that needs to be compiled makes these kinds of studies susceptible to inheriting (or even magnifying) errors from previous works. In the particular case of our approach, the reliability of the conclusions reached is dependent on the data quality of the ecological, environmental and phylogenetic interpretations. The ecological inferences on the lifestyle of thelodonts considered here are supported by a solid methodological framework provided by Ferrón & Botella (2017), based on the well-recognized functional analogy between the squamations of thelodonts and living sharks (Turner 1982, 1991; Märss 1986; Karatajūtė-Talimaa 1998; Märss et al. 2007). Despite the effort made by Ferrón & Botella (2017) to assess the ecology of the whole thelodont clade, lifestyle interpretations are still lacking or inconclusive for some species because of preservational particularities of their squamation. In any case, these taxa represent less than the 10% of described thelodont species and seem not to occupy key phylogenetic positions, thus not marring our understanding of the main aspects of the ecological diversification of the group (Fig. 1). On the other hand, as already mentioned above, environmental interpretations based on sedimentology and associated remains are usually difficult to assess and in most cases might be simplistic. Turner (1999) made a comprehensive and rather detailed study of the environments occupied by thelodonts known at that time, providing a helpful initial framework for exploring the major habitat changes of thelodonts from a phylogenetic and temporal perspective. Even so, our interpretations should be cautiously considered awaiting further sedimentological work and more confined facies-categorizations (Bremer & Blom 2015). Finally, the phylogenetic framework considered in our study has been constructed from the latest and most complete phylogeny of thelodonts (Wilson & Märss 2009) by inserting all the lacking taxa in polytomies following the systematic classification proposed by Märss *et al*. (2007). This kind of procedure, in which it is assumed that taxonomy reflects phylogeny, is usually applied in similar studies dealing with ancestral state reconstruction (e.g. Ackerly 2004; Staggemeier *et al*. 2010; Donoso 2014; Turcotte *et al*. 2014; Gilbert & Manica 2015) but of course is susceptible to error. Interestingly, in our study, the addition of polytomies does not seem to affect the overall conclusions significantly as very similar results are obtained if the analysis is repeated including only those species considered by Wilson & Märss (2009); i.e., a complex ecological diversification entailing the reiterated evolution of different lifestyles and the repeated colonization of different environments. Nevertheless, any new well-resolved and more complete phylogenetic tree would be helpful for future macroevolutionary analyses.

CONCLUSIONS

For the first time the ecological diversification of a whole clade of early vertebrates is explored from a spatial, temporal and phylogenetic context. Ancestral state reconstruction analysis supports that thelodonts originated in marine open waters of Laurasia as demersal fishes on hard substrates. This group underwent a complex ecological diversification and palaeobiogeographical history, comparable in many aspects to those of some major clades of living fishes. Different modes of life repeatedly evolved in non-closely related taxa and a wide range of habitats were recurrently colonized by distinct groups, including non-marine environments. On the other hand, the palaeobiogeographic history of thelodonts reveals significant differences in the dispersal potential of some major groups. It is proposed that the evolution of meropelagic development with pelagic larval stages in thelodontiforms, the most diverse clade of thelodonts, may satisfactorily account for the greater evolutionary success of this group.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository:

http://datadryad.org/review?doi=doi:10.5061/dryad.n6k72

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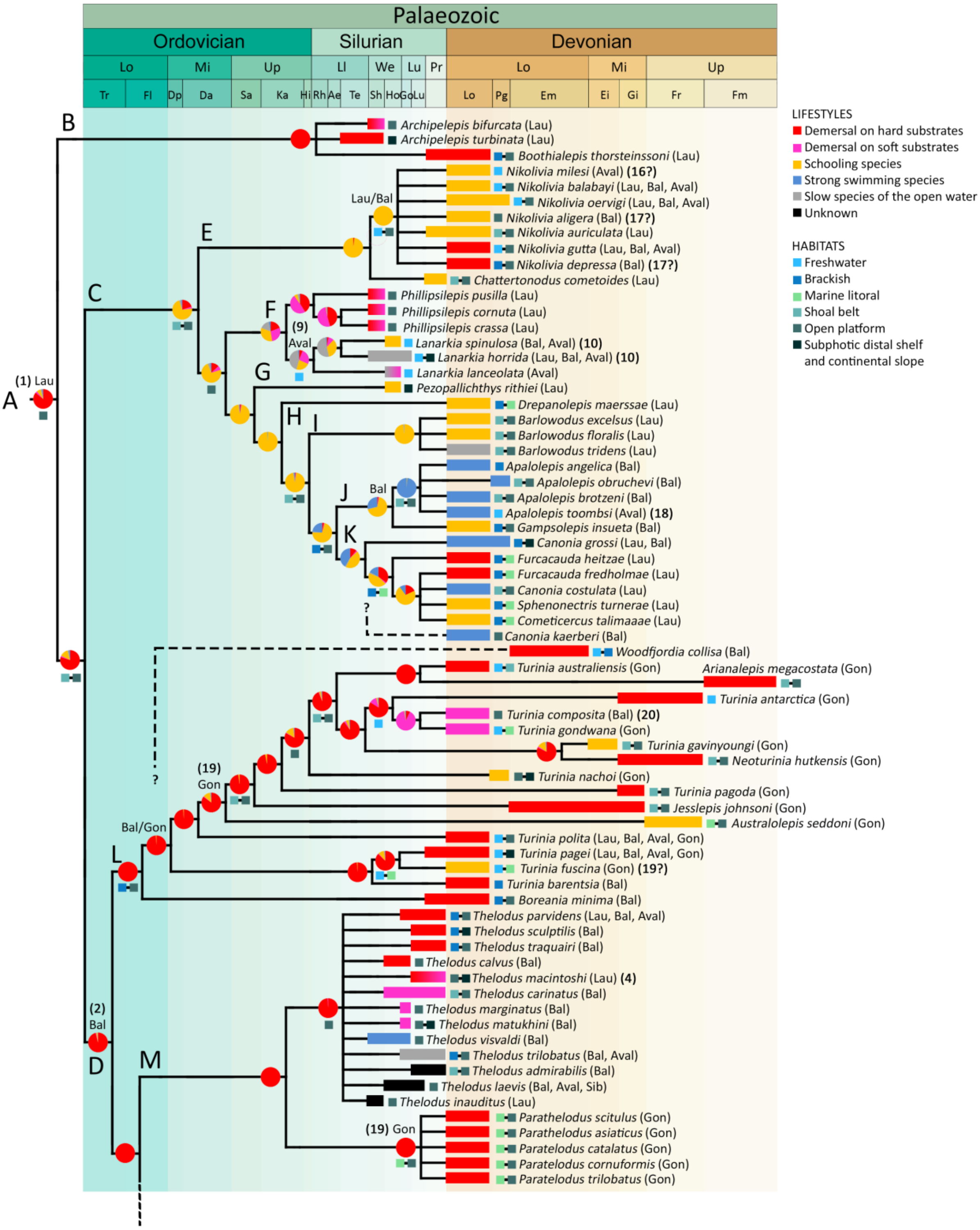

Palaeozoic
Ordovician
Silurian
Devonian
Lo
Mi
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We
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Da
Sa
Ka
Hi
Rh
Ae
Te
Sh
Ho
Go
Lu
Lo
Pg
Em
Ei
Gi
Fr
Fm
LIFESTYLES
Demersal on hard substrates
Demersal on soft substrates
Schooling species
Strong swimming species
Slow species of the open water
Unknown
HABITATS
Freshwater
Brackish
Marine litoral
Shoal belt
Open platform
Subphotic distal shelf and continental slope
A
B
C
D
E
F
G
H
I
J
K
L
M
(1) Lau
(2) Bal
Lau/Bal
(9) Aval
Bal
(19) Gon
Bal/Gon
(19) Gon
?
?
Archipelepis bifurcata (Lau)
Archipelepis turbinata (Lau)
Boothialepis thorsteinssoni (Lau)
Nikolivia milesi (Aval) (16?)
Nikolivia balabayi (Lau, Bal, Aval)
Nikolivia oervigi (Lau, Bal, Aval)
Nikolivia aligera (Bal) (17?)
Nikolivia auriculata (Lau)
Nikolivia gutta (Lau, Bal, Aval)
Nikolivia depressa (Bal) (17?)
Chattertonodus cometoides (Lau)
Phillipsilepis pusilla (Lau)
Phillipsilepis cornuta (Lau)
Phillipsilepis crassa (Lau)
Lanarkia spinulosa (Bal, Aval) (10)
Lanarkia horrida (Lau, Bal, Aval) (10)
Lanarkia lanceolata (Aval)
Pezopallichthys rithiei (Lau)
Drepanolepis maerssae (Lau)
Barlowodus excelsus (Lau)
Barlowodus floralis (Lau)
Barlowodus tridens (Lau)
Apalolepis angelica (Bal)
Apalolepis obruchevi (Bal)
Apalolepis brotzeni (Bal)
Apalolepis toombsi (Aval) (18)
Gampsolepis insueta (Bal)
Canonia grossi (Lau, Bal)
Furcacauda heitzae (Lau)
Furcacauda fredholmae (Lau)
Canonia costulata (Lau)
Sphenonectris turnerae (Lau)
Cometicercus talimaaae (Lau)
Canonia kaerberi (Bal)
Woodfjordia collisa (Bal)
Turinia australiensis (Gon)
Arianalepis megacostata (Gon)
Turinia antarctica (Gon)
Turinia composita (Bal) (20)
Turinia gondwana (Gon)
Turinia gavinyoungi (Gon)
Neoturinia hutkensis (Gon)
Turinia nachoi (Gon)
Turinia pagoda (Gon)
Jesslepis johnsoni (Gon)
Australolepis seddoni (Gon)
Turinia polita (Lau, Bal, Aval, Gon)
Turinia pagei (Lau, Bal, Aval, Gon)
Turinia fuscina (Gon) (19?)
Turinia barentsia (Bal)
Boreania minima (Bal)
Thelodus parvidens (Lau, Bal, Aval)
Thelodus sculptilis (Bal)
Thelodus traquairi (Bal)
Thelodus calvus (Bal)
Thelodus macintoshi (Lau) (4)
Thelodus carinatus (Bal)
Thelodus marginatus (Bal)
Thelodus matukhini (Bal)
Thelodus visvaldi (Bal)
Thelodus trilobatus (Bal, Aval)
Thelodus admirabilis (Bal)
Thelodus laevis (Bal, Aval, Sib)
Thelodus inauditus (Lau)
Parathelodus scitulus (Gon)
Parathelodus asiaticus (Gon)
Paratelodus catalatus (Gon)
Paratelodus cornuformis (Gon)
Paratelodus trilobatus (Gon)

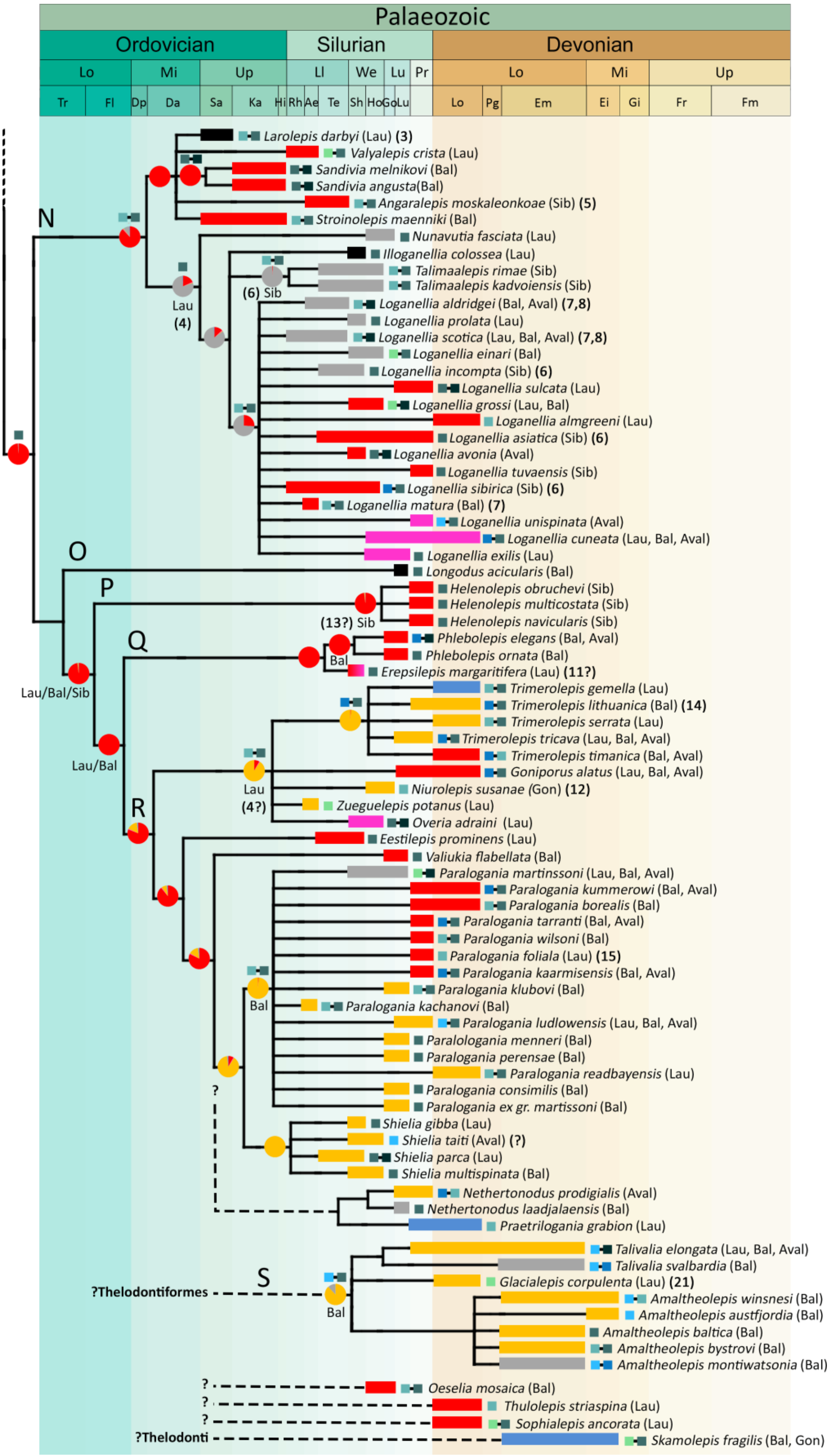

FIG. 1. Ancestral state reconstructions for lifestyles, habitats and geographical distributions of thelodonts.

Numbers in brackets indicate main dispersal events and first colonizations of palaeocontinents by major groups (see below). Series: Lo, Lower; Mi, Middel; Up, Upper; Ll, Llandovery; We, Wenlock; Lu, Ludlow; Pr, Pridoli. Stages: Tr, Tremadocian; Fl, Floian; Dp, Dapingian; Da, Darriwilian; Sa, Sandbian; Ka, Katian; Hi, Hirnantian; Rh, Rhuddanian; Ae, Aeronian; Te, Telychian; Sh, Sheinwoodian; Ho, Homerian; Go, Gorstian; Lu, Ludfordian; Lo, Lochkovian; Pg, Pragian; Em, Emsian; Ei, Eifelian; Gi, Givetian; Fr, Frasnian; Fm, Famennian. Palaeocontintents: Lau, Laurasia; Bal, Baltica; Aval, Avalonia; Sib, Siberia; Gon, Gondwana. Clades: A, Thelodonti; B, Archipelepidiformes; C, Furcacaudiformes; D, Thelodontiformes; E, Nikoliviidae; F, Lanarkiidae; G, Pezopallichthyidae; H, Drepanolepididae; I, Barlowodidae; J, Apalolepididae; K, Furcacaudidae; L, Turiniidae; M, Coelolepidae; N, Loganelliidae; O, Longodidae; P, Helenolepididae; Q, Phlebolepididae; R, Shieliidae; S, Talivaliidae. Palaeogeographic reconstructions from Scotese (2014*a*, *b*).

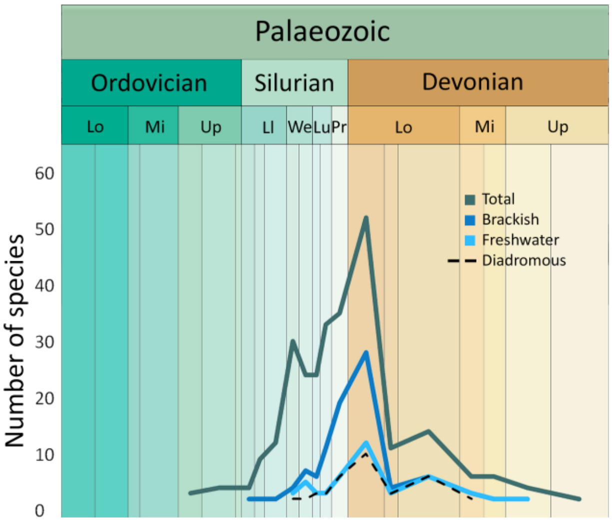

FIG. 2. Diversity dynamics of thelodonts adapted to non-marine (freshwater and brackish) habitats and presumed diadromous species. Series: Lo, Lower; Mi, Middel; Up, Upper; Ll, Llandovery; We, Wenlock; Lu, Ludlow; Pr, Pridoli. Stages are shaded on the graph.

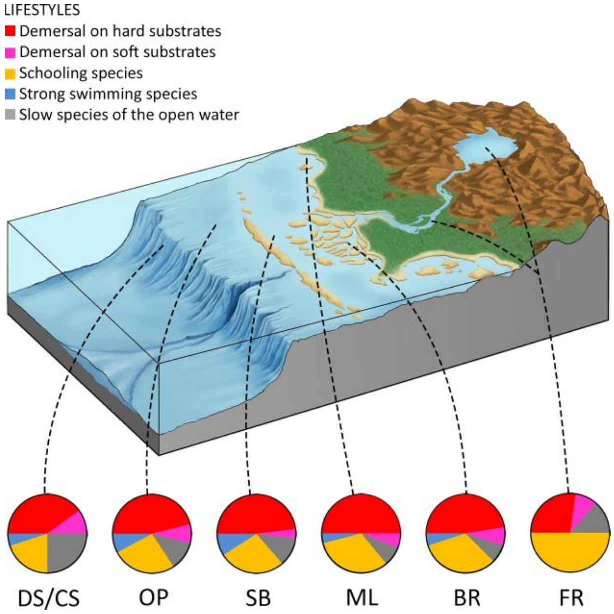

FIG. 3. Diagram showing the relative abundance of each thelodont lifestyle in the different occupied habitats. FR, Freshwater; BR, Brackish; ML, Marine litoral; SB, Shoal belt; OP, Open platform; DS/CS, Subphotic distal shelf and continental slope. Drawing of the continental margin courtesy of Hugo Saláis (HSillustration).

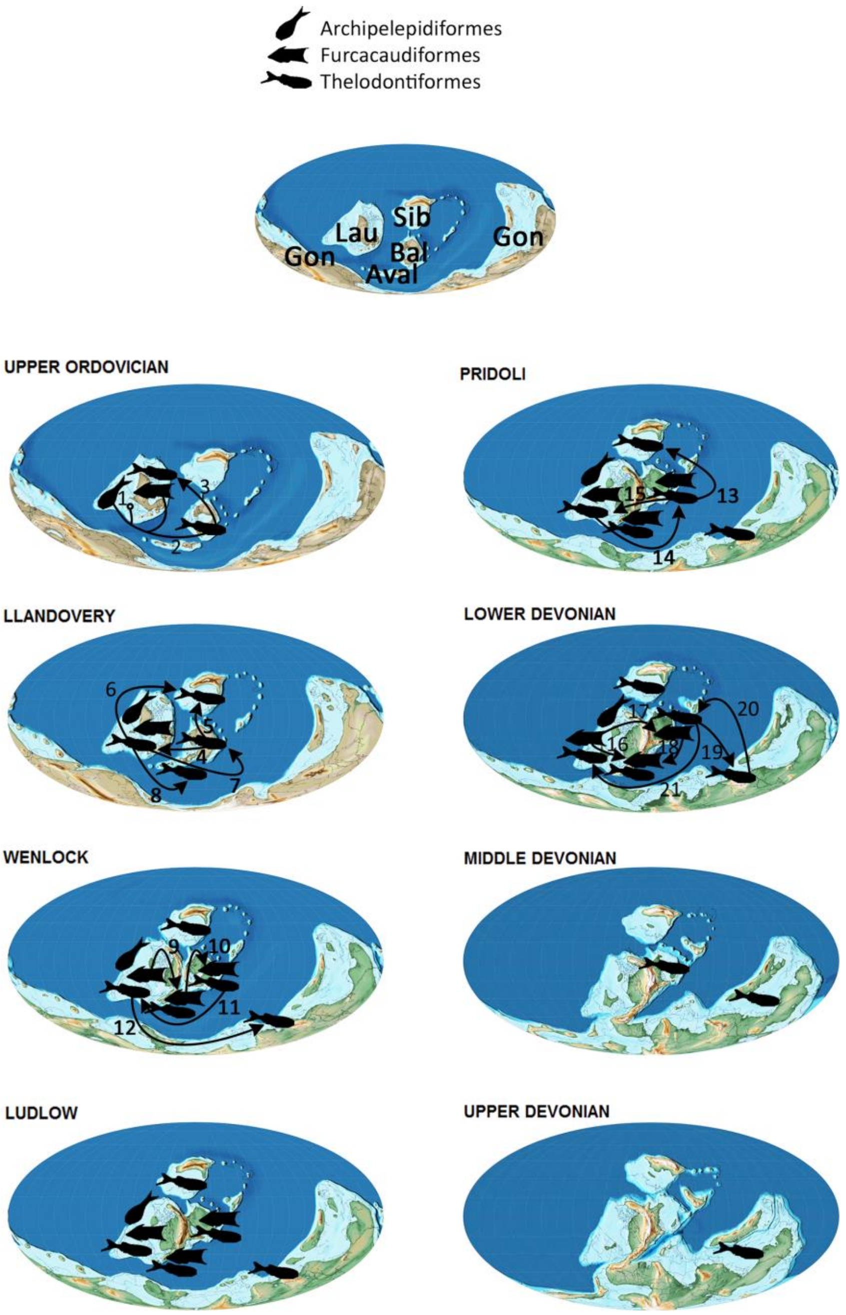

FIG. 4. Dispersal events of thelodonts through time. Numbers in brackets indicate main dispersal events and first colonizations of palaeocontinents by major groups (see also Fig. 1). Arrows on palaeomaps denote dispersal events from one palaeocontinent to another but do not intend to represent the real dispersal pathways. Palaeocontintents: Lau, Laurasia; Bal, Baltica; Aval, Avalonia; Sib, Siberia; Gon, Gondwana.