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*Geological Society, London, Special Publications* 2010; v. 339; p. 151-179  
doi:10.1144/SP339.13

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# Osmotic tolerance and habitat of early stegocephalians: indirect evidence from parsimony, taphonomy, palaeobiogeography, physiology and morphology

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**Abstract:** There are probably many reasons for the widespread belief that temnospondyls and other early stegocephalians were largely restricted to freshwater, but three of the contributing factors will be discussed below. First, temnospondyls have been called amphibians (and thought to be more closely related to extant amphibians than to amniotes). Some authors may have simply concluded that, like extant amphibians, temnospondyls could not live in oceans and seas. Second, under some phylogenies, temnospondyls are more closely related to anurans (and possibly urodeles) than to gymnophionans and could be expected, for parsimony reasons, to share the intolerance of all extant amphibians to saltwater. Similarly, 'lepospondyls' are often thought to be more closely related to gymnophionans than to anurans, and could also be expected to lack saltwater tolerance. Third, extant lungfishes live exclusively in freshwater, and early sarcopterygians have long been thought to share this habitat. These interpretations probably explain the widespread belief that early amphibians and early stem-tetrapods were largely restricted to freshwater. However, these three interpretations have been refuted or questioned by recent investigations. A review of the evidence suggests that several (perhaps most) early stegocephalians tolerated saltwater, even although they also lived in freshwater.

The environment represented by several continental Palaeozoic fossiliferous localities has long been controversial. This is not surprising, because the presence of strictly or mostly marine taxa shows convincingly in several cases that a locality was marine (usually coastal, if it is located on a continental plate), but the absence of such clearly marine indicators does not necessarily imply that the locality represents a freshwater environment (Schultze 1995). Most marine organisms support only with great difficulty important variations in salinity of the water (Barnes 1987, p. 3) or large sedimentation rates, which are common in deltaic environments. The latter hampers determination of the salinity of the water that deposited many sediments.

Thus, some of the most salt-tolerant lissamphibians normally coexist along with only a few of the most euryhaline metazoans normally found in the seas (Annandale 1907). Some seas surrounded by land may have much lower salinity than most oceans and seas, and may be a hostile environment for many marine taxa. This is demonstrated by the

low biodiversity of the Baltic sea and the strong, salinity-dependent biodiversity gradient in that sea (Bonsdorff 2006; Zettler *et al.* 2007). Most sediments of the northern Baltic sea, which are devoid (or nearly so) of echinoderms, cnidarians (a few species may be abundant, such as *Aurelia aurita* and *Mnemiopsis leidyi*) and most other typically marine taxa (Bonsdorff 2006), would therefore presumably be wrongly interpreted as freshwater using the faunal association criteria which led to freshwater interpretation of many Permo-Carboniferous localities. This raises the possibility that many localities devoid of fossils of such marine taxa represent coastal, brackish water environments.

Because of this, there is considerable uncertainty about the environment (marine, brackish water or freshwater) of early stegocephalians and of their finned forerunners. Most authors have considered Palaeozoic stegocephalians a largely freshwater and terrestrial group (Hunt 1993, p. 93; Poplin 1994, p. 299; Cuny 1995, p. 57; Schoch 1995, p. 113),

whereas a few authors have argued that there is substantial evidence for widespread saltwater (and brackish water) tolerance in early stegocephalians (Schultze & Maples 1992; Schultze *et al.* 1994; Schultze 1995, 1999; Laurin & Soler-Gijón 2001, 2006). The latter point of view was eloquently summarized by Schultze (1985, p. 2):

Vertebrate remains are commonly used as terrestrial or freshwater indicators, even all the fish... This traditional interpretation is mainly based on the fact that complete vertebrates most commonly occur alone, rather than together with invertebrates. In many cases, this isolation results from preservational biases (calcium phosphate v. calcium carbonate), and not palaeoecological differences. Sometimes, the association of isolated elements of vertebrates with marine invertebrates has been explained as allochthonous, with the vertebrate remains having been washed in. No recent example of such association has been recorded.

We provide a historical review of ideas and recent evidence of the habitat of extant amphibians and lungfishes and of Palaeozoic finned sarcopterygians in a phylogenetic context. We demonstrate that in the late 19th and early 20th century, palaeontologists had objective reasons to expect early stegocephalians to be stenohaline, freshwater forms. The review also shows that these objective reasons have been refuted, and that there is no reason to expect early stegocephalians to have been confined to freshwater. We show how all data converge to suggest a marginal marine habitat for the earliest stegocephalians, and a long and widespread retention of salt- and brackish water tolerance in Palaeozoic stegocephalians.

### **Parsimony and habitat of extant and extinct sarcopterygians: a historical perspective**

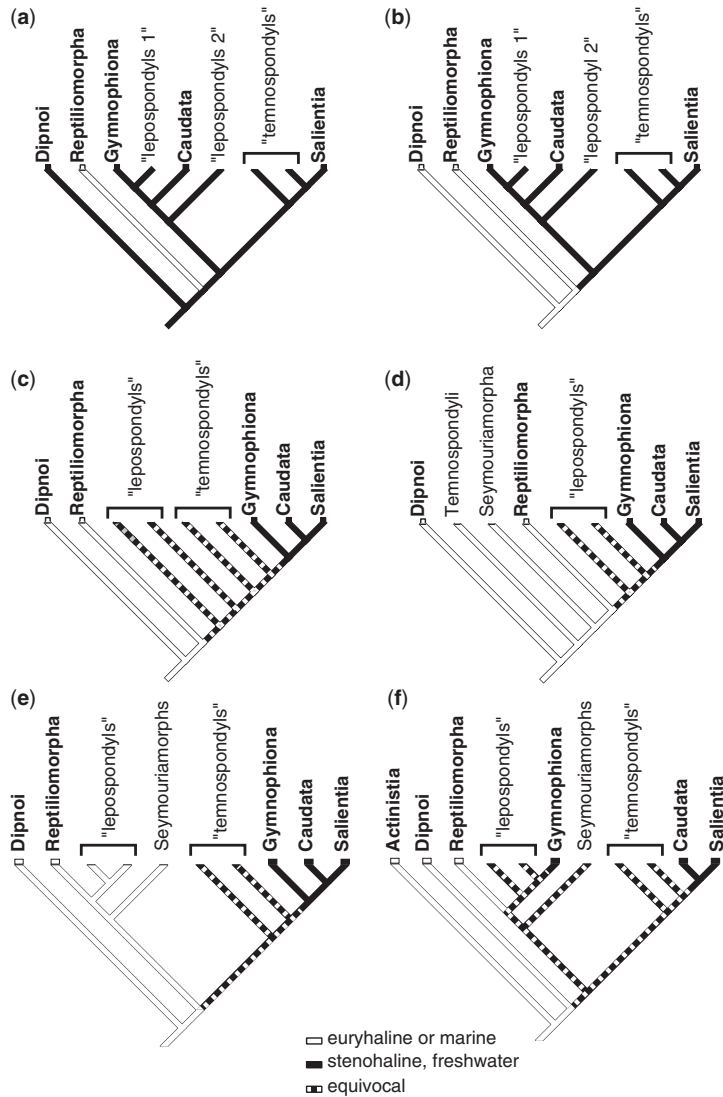
In this section, we will consider how ideas about stegocephalian phylogeny, observations of the habitat of extant sarcopterygians and more recent information about the habitat of early sarcopterygians (especially dipnomorphs) may have influenced our expectations about the habitat of early stegocephalians, using parsimony as a criterion. Parsimony may not have been explicitly invoked in early works on this problem but (at least implicitly) it has probably been used as a general scientific principle. In this section, we will disregard direct evidence about the habitat of early stegocephalians, which will be presented separately (below). This section can be seen as an attempt to use parsimony to infer habitat of early stegocephalians (globally) in the context of various phylogenies. It is analogous (except in the inclusion of data on habitat of early

dipnomorphs) to an application of Witmer's (1995) extant phylogenetic bracket.

Extant amphibians (almost all of which are freshwater or terrestrial) have been thought to be polyphyletic (Fig. 1a) for much of the 20th century (Moodie 1916, pp. 46–49). More recently, this point of view was developed by Carroll & Holmes (1980) and Carroll & Currie (1975), who argued for independent origins of urodeles and gymnophionans from 'lepospondyls' whereas anurans were thought to be derived from 'temnospondyls.' More recently, Schoch & Carroll (2003) suggested, based on developmental data, that anurans and urodeles are temnospondyls whereas gymnophionans are 'lepospondyls'. Schoch (2006) subsequently reached different conclusions, based on a much more rigorous analysis of developmental data. Furthermore, early sarcopterygians were thought to have inhabited only freshwater, as the extant lungfishes (Romer 1966).

Only reptiliomorphs were thought to include a large number of saltwater-tolerant forms, as shown by the large number of marine amniotes. For instance, Neill (1958) listed 273 species or subspecies of 'reptiles' (in his usage, contrary to ours, this excluded birds) which lived at least occasionally in salt- or brackish water. Given such premises, the parsimony criterion (although it may not have been explicitly used) suggested that most early stegocephalians were restricted to freshwater and that saltwater tolerance appeared within reptiliomorphs (Fig. 1a). This does not imply that all reptiliomorphs tolerated saltwater; these data and phylogeny make no prediction about stem-reptiliomorphs which, at the time (Romer 1966), were thought to include embolomeres, seymouriamorphs, gephyrostegids, *Solenodonsaurus* and diadectomorphs.

Later, the environments in which many early sarcopterygians were found (including lungfishes) were reinterpreted as coastal, deltaic or marine (Carroll 1988; Janvier 1996; Schultze 1999). Schultze (1997) even suggested that stegocephalians originated in an intertidal environment. Thomson (1980) also argued, on the basis of palaeogeographic arguments, that most groups of early sarcopterygians were either marine or euryhaline; in most cases, extinct stegocephalians of these two ecological categories cannot be distinguished. The term euryhaline is therefore used in this study, but it should be understood that this only means that the taxon could live in saltwater; this does not exclude the possibility that it could also live in freshwater and on land. Under such conditions, the intolerance to the marine environment could be seen as a specialization of the clade that includes at least the last common ancestor of gymnophiones, urodeles and anurans and all its descendants. Under the phylogenies advocated by Carroll & Holmes



**Fig. 1.** Habitat of early stegocephalians which could be inferred on the basis of parsimony, of the habitat of extant tetrapods, of extant and extinct sarcopterygians and according to various phylogenies. (a) Hypothesis that prevailed until the 1980s. Early lungfishes were thought to have lived in freshwater, like extant lungfishes (Romer 1966). (b) Hypothesis taking into consideration recent data on the habitat tolerance of early lungfishes (Janvier 1996). (c) Hypothesis reflecting the first phylogenies proposed in a cladistic framework (Panchen & Smithson 1988; Trueb & Cloutier 1991; Ahlberg & Milner 1994). Computer-assisted phylogenetic analyses (d) suggest a monophyletic origin of extant amphibians among ‘lepospondyls’ (Laurin & Reisz 1997; Laurin 1998a), (e) among temnospondyls (Ruta *et al.* 2003; Ruta & Coates 2007), or (f) a polyphyletic origin (Anderson 2007). Extant taxa are in bold type; paraphyletic groups are identified by quotation marks and are not capitalized. Reptiliomorpha is euryhaline, as shown by the presence of amniotes in both freshwater and in saltwater. The trees were drawn using MacClade 4 (Maddison & Maddison 2003).

(1980) and Carroll & Currie (1975), this clade included all known amphibians (or at least, all temnospondyls and most lepospondyls) (Fig. 1b).

With the advent of cladistics, earlier suggestions (Bolt 1969; Schultze 1970) that extant amphibians

form a monophyletic group (that excludes all known Palaeozoic tetrapods) became much more widely accepted (Trueb & Cloutier 1991). These ideas should have cast doubts about the environmental preferences of early (stem) amphibians,

because the parsimony criterion no longer suggested that they should have been restricted to freshwater (Fig. 1c). The intolerance to saltwater, which characterizes most lissamphibians (but not all; see Schmidt 1957; Garland *et al.* 1997), could have appeared as early as the first amphibian or as late as the last common ancestor of all lissamphibians. Schultze (1985) had already reached similar conclusions, and Milner (1987, pp. 500–501) stated that

...most recent workers believe the living amphibians to form a clade (usually referred to as the Lissamphibia) definable by a series of unique characteristics, most of which are not known in any Palaeozoic amphibian-grade tetrapod (see Rage & Janvier 1982 for a recent discussion). It can thus no longer be assumed that the freshwater dependence of most living amphibians is an inheritance from the Palaeozoic amphibian-grade tetrapods; it may represent a specialization acquired later in the early stages of lissamphibian evolution.

Several recent and comprehensive computer-assisted phylogenetic analyses of tetrapods suggest that temnospondyls, formerly thought to be early amphibians, are stem-tetrapods (Laurin & Reisz 1997, 1999; Laurin 1998a; Anderson 2001; Vallin & Laurin 2004; Marjanović & Laurin 2009). Therefore, the parsimony criterion actually suggests that this group tolerated saltwater (Fig. 1d); some temnospondyls may have lived in freshwater and others probably inhabited the coastal marine environment at least during juvenile and adult stages (see also Schult 1994; Schultze *et al.* 1994). The discovery of well-preserved remains of the temnospondyl *Iberospondylus* in a coastal environment (Laurin & Soler-Gijón 2001, 2006) should not therefore be viewed as anomalous. However, this phylogeny makes no prediction about habitat preference in early amphibians ('lepospondyls').

Ruta *et al.* (2003) and Ruta & Coates (2007) proposed a monophyletic origin of extant amphibians among temnospondyls, and placed 'lepospondyls' among reptiliomorphs (Fig. 1e). According to that phylogeny, seymouriamorphs and 'lepospondyls' can be expected to retain the ancestral saltwater tolerance, but no inferences can be drawn about habitat preferences in temnospondyls.

Anderson (2007) proposed a diphyletic origin of extant amphibians, with batrachians (anurans and urodeles) nested within temnospondyls, and gymno-phonians nested among 'lepospondyls', which form a clade with seymouriamorphs and reptiliomorphs (Fig. 1f). Under this phylogeny, reptiliomorphs include only amniotes and diadectomorphs (and perhaps *Solenodonsaurus*, which was not included in the analysis). Under that phylogeny, no inferences can be drawn about the habitat preferences of most early stegocephalians (temnospondyls,

'lepospondyls', embolomeres and seymouriamorphs). This phylogeny is probably less supported than other recent alternatives because it conflicts with all published molecular phylogenies (and most morphological ones) which support the monophyly of Lissamphibia with respect to Amniota (Laurin 2002).

Other recent phylogenies do not fit the patterns presented above. For instance, McGowan (2002) suggests that many 'lepospondyls' are part of the amphibian crown (and hence should have been mostly freshwater forms) but, since his analysis does not include amniotes or reptiliomorphs, it is impossible to determine whether temnospondyls are stem-amphibians or stem-tetrapods under his proposal. His phylogeny suggests that most 'lepospondyls' did not tolerate salt or brackish water, but makes no prediction about environmental preferences of temnospondyls. This phylogeny was recently shown to be based on questionable anatomical interpretations (Marjanović & Laurin 2008b, 2009).

To summarize, in the context of phylogenies proposed early in the 20th century, parsimony suggested (Fig. 1) that Palaeozoic amphibians did not tolerate saltwater (Fig. 1a, b). More recent phylogenies usually suggest that Lissamphibia excludes all or most Palaeozoic amphibians (Fig. 1c–e), which implies no intolerance (but not necessarily tolerance either) to saltwater in amphibians (Fig. 1c–f). These trees suggest that some taxa traditionally attributed to Amphibia are stem-tetrapods (Fig. 1d) or reptiliomorphs (Fig. 1e), and this increases further the number of taxa which can be expected to have tolerated saltwater.

### Habitat of early stegocephalians and their close relatives

A review of the palaeoecological interpretations of the environment of early stegocephalians reveals much uncertainty and controversy (Tables 1 & 2). We have compiled the prevailing interpretations of the environment of these taxa. When considerable uncertainty exists, the states which were plausibly present all appear separated by slashes. However, interpretations which appear to be significantly less plausible are not considered, simply because the amount of uncertainty might be such that little signal could be extracted.

For example, *Tulerpeton* was found in a marine environment located at least 200 km from the nearest land and, given the completeness and good preservation of the specimen, it plausibly lived in the sea (Lebedev & Clack 1993). Nevertheless, Long & Gordon (2004, p. 704) suggest that the recovered bones represent a carcass which has

**Table 1.** Habitat of early stegocephalians and other early sarcopterygians. Taxa are listed in phylogenetic and stratigraphic order. Habitat 0: marine; 1: brackish water; 2: freshwater (and potentially terrestrial, in many cases). Terrestrial taxa are excluded from this analysis since the purpose is to determine if aquatic or amphibious taxa inhabited fresh, brackish or saline water, and a terrestrial habitat cannot readily be inserted into an ordered salinity gradient. The locality information is not necessarily exhaustive; at least one is given for each taxon

Taxa	Locality or formation	Habitat	Geological age	Reference for habitat
<i>Youngolepis praecursor</i>	Qujing Xian, Yunnan, China	0/1	Lochkovian	Chang (1982, p. 6)
<i>Diabolepis speratus</i>	Qujing Xian, Yunnan, China	0/1	Lochkovian	Chang (1982, p. 6)
<i>Powichthys thorsteinssoni</i>	Drake Bay Formation, Prince of Wales Island, Canada	0	Lochkovian	Jessen (1980); Clément & Janvier (2004, p. 93)
Osteolepididae	Tangil-e-Ab-Garm, Iran	0	Frasnian	Janvier & Martin (1979, p. 508); Janvier (1980, p. 228)
<i>Eusthenopteron</i>	Miguasha, Escuminac Formation, Canada	0/1	Frasnian	Chidiac (1996); Cloutier <i>et al.</i> (1996); Schultze & Cloutier (1996); Clack (2007)
<i>Gogonasmus</i>	Gogo, Australia	0	Frasnian	Clack (2007, p. 514)
<i>Panderichthys</i>	Lode, Ketleri Formation, Latvia; Rybnica, Orel region, Russia	1	Frasnian	Luksevics (1992); Vorobyeva & Kuznetsov (1992); Schultze & Cloutier (1996); Luksevics & Zupins (2004); Clack (2007, p. 512)
<i>Elpistostege</i>	Miguasha, Escuminac Formation, Canada	0/1	Frasnian	Chidiac (1996); Cloutier <i>et al.</i> (1996); Schultze & Cloutier (1996); Clack (2007, p. 512)
<i>Livoniana</i>	Ligatne, Gauja Formation, Latvia	?	Givetian	Long & Gordon (2004, p. 703)
<i>Tiktaalik</i>	Bird Fiord, Ellesmere Island, Fram Formation, Canada	2	Frasnian	Daeschler <i>et al.</i> (2006)
<i>Obruchevichthys</i>	Ketleri, Latvia	?	Frasnian	
<i>Elginerpeton</i>	Scat Craig, Scotland	1/2	Frasnian	Ahlberg (1998, p. 133); Long & Gordon (2004, p. 703); Blicek <i>et al.</i> (2007, p. 221)
<i>Metaxygnathus</i>	Jemalong, New South Wales, Australia	1/2	Frasnian	Lebedev (2004; state 1); Long & Gordon (2004, p. 703; state 2); Blicek <i>et al.</i> (2007, p. 221)
<i>Jakubsonia</i>	Gornostayevka quarry, Russia	1	Frasnian	Lebedev (2004, p. 93)
<i>Sinostega</i>	Ningxia Hui autonomous region, China	1/2	Frasnian	Zhu <i>et al.</i> (2002; state 2); Lebedev (2004; state 1)
<i>Ventastega</i>	Pavari, Ketleri Formation	0/1	Famennian	Luksevics & Zupins (2004); Lebedev (2004, p. 92); Clack (2006, p. 183); Clack (2007, p. 512)
<i>Acanthostega</i>	East Greenland	2	Famennian	Long & Gordon (2004, p. 703); Blom <i>et al.</i> (2005, p. 46)
<i>Ichthyostega</i>	East Greenland	2	Famennian	Long & Gordon (2004, p. 703); Blom <i>et al.</i> (2005, p. 46)
<i>Densignathus</i>	Red Hill, USA	1/2	Famennian	Daeschler <i>et al.</i> (1994; state 2); Lebedev (2004, p. 92; state 1); Long & Gordon (2004, p. 703; state 2)
<i>Hynerpeton</i>	Red Hill, USA	1/2	Famennian	Daeschler <i>et al.</i> (1994; state 2); Lebedev (2004, p. 92; state 1); Long & Gordon (2004, p. 703; state 2)

(Continued)

Table 1. *Continued*

Taxa	Locality or formation	Habitat	Geological age	Reference for habitat
<i>Tulerpeton</i>	Andreyevka-2, Tula, Russia	0	Famennian	Lebedev & Clack (1993)
<i>Whatcheeria deltae</i>	Delta, Iowa, USA	1/2	Viséan	Bolt <i>et al.</i> (1988); Lombard & Bolt (1995)
<i>Crassigyrynus</i>	Dora bone bed, Scotland	1/2	Viséan	Panchen (1973, p. 190; state 2); Unwin (1986; state 2); Milner (1987, p. 501; state 1)
<i>Loxomma allmanni</i>	Gilmerton ironstone, Scotland	1/2	Viséan	Beaumont (1977, p. 30; state 2); Milner (1987, p. 501; state 1)
<i>Loxomma rankini</i>	Drumgray coal, Castlehill, Scotland	1/2	Bashkirian	Beaumont (1977, p. 30; state 2); Milner (1987, p. 501; state 1)
<i>Loxomma acutirhinus</i>	Airdrie, Lanarkshire, Scotland	1/2	Moscovian	Beaumont (1977, p. 30; state 2); Milner (1987, p. 501; state 1)
<i>Megaloscephalus pachycephalus</i>	Several, Coal Measures, UK	1/2	Bashkirian, Moscovian	Beaumont (1977, p. 30; state 2); Milner (1987, p. 501; state 1)
<i>Megaloscephalus lineolatus</i>	Linton, Ohio, USA	1/2	Moscovian	Beaumont (1977, p. 30; state 2); Milner (1987, p. 501; state 1)
<i>Baphetes planiceps</i>	Albion mine, Stellarton, Nova Scotia	1/2	Moscovian	Beaumont (1977, p. 30; state 2); Milner (1987, p. 501; state 1)
<i>Baphetes kirkbyi</i>	Pirnie Colliery, Airdrie, Bradford Coal Group, Scotland	1/2	Moscovian	Beaumont (1977, p. 30; state 2); Milner (1987, p. 501; state 1)
<i>Baphetes lintonensis</i>	Linton, Ohio, USA	1/2	Moscovian	Beaumont (1977, p. 30)
<i>Baphetes bohemicus</i>	Nyrany, Czech Republic	1/2	Moscovian	Beaumont (1977, p. 30); Schultze & Maples (1992, p. 234)
<i>Spathicephalus</i>	Dora bone bed, Scotland	1/2	Viséan	Unwin (1986; state 2); Milner (1987, p. 501; state 1)
<i>Doragnathus</i>	Dora bone bed, Scotland	1/2	Viséan	Unwin (1986; state 2); Milner (1987, p. 501; state 1)
<i>Pholidogaster pisciformis</i>	Gilmerton Ironstone, Scotland	1/2	Viséan	Milner (1987, p. 501)
<i>Greererpeton burkemorani</i>	Greer, West Virginia, USA	1/2	Viséan and Serpukhovian	Schultze & Bolt (1996)
<i>Colosteus scutellatus</i>	Linton, Ohio, USA	1/2	Moscovian	Schultze & Maples (1992, p. 234); Poplin (1994, p. 316)
<i>Dendrerpeton acadianum</i>	Joggins, Nova Scotia, Canada	1/2	Bashkirian	Milner (1987, pp. 496–497; state 2); Poplin (1994, p. 315; state 1)
<i>Acroploous</i>	Keats, Riley county, Kansas, USA	0/1	Gzhelian	Schultze (1985, p. 11; 1999, p. 385; states 0/1)
<i>Trimerorhachis insignis</i>	Thrift bonebed, Wichita county, Texas, USA	0/1	Sakmarian	Parrish (1978, p. 235; states 0/1); Milner (1987, p. 501; state 1); Schultze (1999, p. 385; states 0/1)
<i>Eugyrinus</i>	Newsham, UK	1	Moscovian	Milner (1987, p. 501; state 1)
<i>Saurerpeton</i>	Mazon Creek, USA	1	Moscovian	Milner (1987, pp. 502–503; state 1)
<i>Iberospondylus</i>	Puertollano, Spain	1/2	Gzhelian	Laurin & Soler-Gijón (2001, 2006)
<i>Eryops</i>	Thrift bonebed, Wichita county, Texas, USA	1/2	Sakmarian	Parrish (1978, p. 235; states 1/2)

<i>Onchiodon</i> (formerly called <i>Actinodon</i> ) <i>frossardi</i>	Montceau-les-Mines, France	1/2	Gzhelian	Schultze & Maples (1992, p. 234; state 2); Poplin (1994; state 1); Poplin <i>et al.</i> (2001, p. 299; state 1); Werneburg & Steyer (1999; synonymy)
<i>Cheliderpeton vranyi</i>	Broumov, Sudetic basin, Czech Republic	1/2	Asselian	Poplin (1994, p. 307)
<i>Zatrachys</i>	Thrift bonebed, Wichita county, Texas, USA	1/2	Sakmarian	Parrish (1978, p. 235; states 0/1)
<i>Branchiosaurus petrolei</i>	Mazon Creek, Montceau-les-Mines, Nyrany, Czech Republic	1/2	Moscovian	Schultze & Maples (1992); Poplin (1994)
<i>Micromelerpeton</i>	Montceau-les-Mines, France	1/2	Gzhelian	Schultze & Maples (1992, p. 234; state 2); Poplin (1994; state 1); Poplin <i>et al.</i> (2001, p. 299; state 1)
<i>Amphibamus</i>	Mazon Creek, Linton, Nyrany, Czech Republic	1/2	Moscovian	Schultze & Maples (1992)
<i>Caerorhachis bairdi</i>	Loanhead, Scotland	1/2	Serpukhovian	Milner (1987, p. 501)
<i>Eoherpeton</i>	Dora bone bed, Scotland	1/2	Viséan	Unwin (1986; state 2); Milner (1987, p. 501; state 1)
<i>Proterogyrinus scheelei</i>	Greer, West Virginia, USA	1/2	Viséan and Serpukhovian	Schultze & Bolt (1996)
<i>Calligenethlon watsoni</i>	Joggins, Canada	1/2	Bashkirian	Milner (1987, pp. 496–497; state 2); Poplin (1994, p. 315; state 1)
<i>Archeria</i>	Archer City bonebed, USA	1/2	Sakmarian	Parrish (1978, p. 235; states 1/2); Milner (1987, p. 501)
<i>Discosauriscus</i>	Montceau-les-Mines, France; Boskovice furrow, Czech Republic	1/2	Gzhelian	Schultze & Maples (1992, p. 234; state 2); Poplin (1994, pp. 295, 307, 308; states 1/2); Poplin <i>et al.</i> (2001, p. 299; state 1)
<i>Lethiscus</i>	Wardie Shales, Scotland	1/2	Viséan	Milner (1987, p. 501; state 1)
<i>Ophiderpeton</i>	Mazon Creek, Linton, USA; Nyrany	1/2	Moscovian	Schultze & Maples (1992)
<i>Phlegethontia</i>	Linton, Nyrany, Czech Republic	1/2	Moscovian	Schultze & Maples (1992)
<i>Ptyonius</i>	Mazon Creek, Linton, USA	1	Moscovian	Schultze & Maples (1992)
<i>Sauroplesura</i>	Linton, USA; Nyrany, Czech Republic	1/2	Moscovian	Schultze & Maples (1992)
<i>Diplocaulus</i>	Thrift bonebed, Wichita county, Texas, USA	1/2	Artinskian	Parrish (1978, p. 235; states 1/2); Milner (1987, p. 501; state 1); Schultze (1985, p. 11; 1999, p. 385; states 0/1)
<i>Euryodus</i>	Speiser shale, Wreford Megacyclotherm, Kansas, USA	1	Artinskian	Schultze (1985, p. 11)
<i>Trachystegos megalodon</i>	Joggins, Canada	1/2	Bashkirian	Milner (1987, pp. 496–497; state 2); Poplin (1994, p. 315; state 1)
<i>Leiocephalikon problematicum</i>	Joggins, Canada	1/2	Bashkirian	Milner (1987, pp. 496–497; state 2); Poplin (1994, p. 315; state 1)
<i>Hylerpeton dawsoni</i>	Joggins, Canada	1/2	Bashkirian	Milner (1987, pp. 496–497; state 2); Poplin (1994, p. 315; state 1)
<i>Ricnodon</i>	Joggins, Canada	1/2	Bashkirian	Milner (1987, pp. 496–497; state 2); Poplin (1994, p. 315; state 1)
<i>Hyloplesion</i>	Tremosna, Czech Republic	2	Moscovian	Milner (1987, p. 496–497)



**Table 1.** *Continued*

Taxa	Locality or formation	Habitat	Geological age	Reference for habitat
<i>Microbrachis pelikani</i>	Nyrany, Czech Republic	1/2	Moscovian	Beaumont (1977, p. 30); Milner (1987, p. 502); Schultze & Maples (1992, p. 234); Poplin (1994, p. 307; state 1)
<i>Brachydectes elongatus</i>	Several localities in Texas and Oklahoma, USA	1&2	Artinskian	Schultze (1985, p. 11; 1999, p. 385; states 0/1)
<i>Limnostygis relictus</i>	Florence, Nova Scotia, Canada	1/2	Moscovian	Carroll <i>et al.</i> (1972, p. 54; state 1); Milner (1987, pp. 496–497)
<i>Limnoscelis paludis</i>	El Cobre Canyon, Cutler Formation, New Mexico, USA	2	Gzhelian and/or Asselian	Vaughn (1969, p. 405); Berman <i>et al.</i> (1985, pp. 7–8; 1987, p. 1772); Eberth & Berman (1993)
<i>Limnoscelis dynatis</i>	Badger Creek Quarry, Howard, Sangre de Cristo Formation, Colorado, USA	2	Gzhelian	Vaughn (1969, p. 405)
<i>Desmatodon hesperis</i>	Badger Creek Quarry, Howard, Sangre de Cristo Formation, Colorado, USA	2	Gzhelian	Vaughn (1969, p. 405)
<i>Archaeothyris florensensis</i>	Florence, Nova Scotia, Canada	1/2	Moscovian	Carroll <i>et al.</i> (1972, p. 54; state 1); Milner (1987, pp. 496–497; state 2)
<i>Ophiacodon</i>	Thrift bonebed, Wichita county, Texas, USA	0/1	Sakmarian	Parrish (1978, p. 235)

**Table 2.** *Palaeoecological interpretations of selected fossiliferous localities which have yielded early stegocephalians or other tetrapodomorphs. The habitat attributed to each locality is scored on the basis of the data presented in the paper, rather than on the interpretation of the authors of the cited references. Habitat: as for Table 1; N/A, not applicable (terrestrial localities). Not all interpretations found in the literature have been inserted; the emphasis is on interpretations which are supported by several studies*

Locality	Habitat	Geological age	Reference for habitat
Miguasha, Escuminac Formation	0/1	Frasnian	Chidiac (1996); Cloutier <i>et al.</i> (1996); Schultze & Cloutier (1996); Clack (2007)
Scat Craig, Scotland	1/2	Frasnian	Ahlberg (1998, p. 133); Long & Gordon (2004, p. 703); Blicek <i>et al.</i> (2007, p. 221)
Gogo, Australia	0	Frasnian	Clack (2007, p. 514)
Lode, Latvia	1	Frasnian	Luksevics (1992); Vorobyeva & Kuznetsov (1992); Schultze & Cloutier (1996); Clack (2007, p. 512)
Bird Fiord, Ellesmere Island, Fram Formation, Canada	2	Frasnian	Daeschler <i>et al.</i> (2006)
Pavari, Ketleri Formation, Latvia	0/1/2	Famennian	Luksevics (1992); Luksevics & Zupins (2004); Lebedev (2004, p. 92; state 1); Long & Gordon (2004, p. 703; states 0/1/2); Clack (2006, p. 183; states 0/1); Blicek <i>et al.</i> (2007, p. 221); Clack (2007, p. 512)
Strud, Belgium	2	Famennian	Blicek <i>et al.</i> (2007, p. 221)
Jemalong, New South Wales, Australia	1/2	Frasnian	Lebedev (2004; state 1); Long & Gordon (2004, p. 703; state 2)
Gornostayevka quarry, Russia	1	early Frasnian	Lebedev (2004, p. 93); Blicek <i>et al.</i> (2007, p. 221)
Red Hill, Pennsylvania, USA	1/2	Famennian	Lebedev (2004, p. 92); Long & Gordon (2004, p. 703); Blicek <i>et al.</i> (2007, p. 221)
East Greenland	2	Famennian	Long & Gordon (2004, p. 703); Blom <i>et al.</i> (2005, p. 46); Blicek <i>et al.</i> (2007, p. 221)
Gilmerton Ironstone, Scotland	1/2	Viséan	Milner (1987, p. 501)
Dora bone bed, Scotland	1/2	Viséan	Unwin (1986; state 2); Milner (1987, p. 501; state 1)
Delta, Iowa, USA	1/2	Viséan	Bolt <i>et al.</i> (1988); Lombard & Bolt (1995); Schultze & Bolt (1996)
Glencartholm, Scotland	0/1	Viséan	Poplin (1994, p. 314)
Wardie, Scotland	1/2	Viséan	Milner (1987, p. 501; state 1); Poplin (1994, p. 314; state 2)
East Kirkton, Scotland	1/2	Viséan	Milner (1987, p. 501; state 1); Poplin (1994, p. 314; state 2)
Greer, West Virginia, USA	1/2	Viséan and Serpukhovichian	Schultze & Bolt (1996)
Loanhead, Scotland	1/2	Serpukhovichian	Milner (1987, p. 501)
Joggins, Nova Scotia, Canada	1/2	Bashkirian	Milner (1987, pp. 496–497; state 2); Poplin (1994, p. 315; state 1); Schultze (1995, p. 257; states 0/1)
Swisshelm Mountains, Arizona, USA	1	Bashkirian	Milner (1987, p. 498)
Florence, Nova Scotia, Canada	1/2	Moscovian	Carroll <i>et al.</i> (1972, p. 54; state 1); Milner (1987, pp. 496–497; state 2)
Mazon Creek, USA	0/1	Moscovian	Schultze & Maples (1992, p. 234); Poplin (1994, p. 316; states 0/1)
Linton, Ohio, USA	1/2	Moscovian	Schultze & Maples (1992, p. 234); Poplin (1994, p. 316)

(Continued)

**Table 2.** *Continued*

Locality	Habitat	Geological age	Reference for habitat
Nyrany, Czech Republic	1/2	Moscovian	Beaumont (1977, p. 30; state 2); Milner (1987, p. 502; state 2); Schultze & Maples (1992, p. 234); Poplin (1994, p. 307; state 1)
Tremosna, Czech Republic	2	Moscovian	Milner (1987, p. 496–497)
Kladno and Rakovnice basins	1/2	Moscovian to Gzhelian	Poplin (1994, p. 308)
Garnett, Kansas	0/1	Kasimovian	Schultze & Maples (1992, p. 234)
Hamilton, Kansas	0/1	Gzhelian	Schultze & Maples (1992, p. 234)
Robinson, Kansas	0/1	Gzhelian	Schultze & Maples (1992, p. 234)
Montceau-les-mines	1/2	Gzhelian	Schultze & Maples (1992, p. 234; state 2); Poplin (1994; state 1); Poplin <i>et al.</i> (2001, p. 299; state 1); Schultze & Soler-Gijón (2004; state 1)
Puertollano	1/2	Gzhelian	Laurin & Soler-Gijón (2001, 2006); Soler-Gijón & Moratalla (2001)
Kinney Quarry, Pine Shadow member, Wild Cow Formation, New Mexico	1/2	Gzhelian	Hunt <i>et al.</i> (1992, pp. 211, 218–219)
Badger Creek Quarry, Howard, Sangre de Cristo Formation, Colorado	2	Gzhelian	Vaughn (1969, p. 405)
Sudetic basin, Czech Republic	1/2	Gzhelian and Asselian	Poplin (1994, p. 307)
Saale basin, Germany	2	Gzhelian and Asselian	Poplin (1994, p. 310)
El Cobre Canyon, Arroyo de Agua, Cutler Formation, New Mexico	2	Gzhelian and/or Asselian	Vaughn (1969, p. 405); Berman <i>et al.</i> (1985, pp. 7–8; 1987, p. 1772); Eberth & Berman (1993)
Boskovice furrow, Czech Republic	1/2	Asselian	Poplin (1994, p. 308); Schultze & Soler-Gijón (2004; state 1)
Bromacker, Tambach basin, Germany	N/A	Artinskian	Eberth <i>et al.</i> (2000)
Dolese Brothers quarry, Fort Sill, Oklahoma, USA	N/A	Artinskian	Sullivan & Reisz (1999)

floated over a long distance. While this is not strictly impossible, this opinion is not considered further here (Table 1) for two reasons: 200 km is a very long distance to float, and this hypothesis seems to be based on pre-conceived ideas. Furthermore, Hunt *et al.* (1992, p. 219) stated that 'Tertiary freshwater frogs and salamanders are never found in lagoonal environments (A. R. Milner, pers. comm. 1991).'

Extant lissamphibians are coded as stenohaline freshwater forms because that appears to be the case in most species (see below). On the contrary, mammals, saurians and turtles are considered euryhaline because many species of these taxa are found in freshwater as well as in the seas (cetaceans, seals, sea lions, sea otters and some sirenians among

mammals; mosasaurs, marine snakes, the Galapagos iguana and several extant and extinct crocodylians among saurians; the green and leatherback turtles, among many others), as well as in freshwater.

The review (Table 1) suggests that some of our distant finned relatives, such as *Eusthenopteron*, *Panderichthys* and *Elpistostege* lived in marginal marine environments, presumably in salt or brackish water. More crownward taxa, from the Frasnian *Tik-talik* to most Permo-Carboniferous stegocephalians, appear to have more frequently inhabited brackish to freshwater bodies. Nevertheless, a few Devonian stegocephalians appear to have lived in a marine environment. Thus, the Ketleri Formation in which *Panderichthys* and *Ventastega* were found may represent a marginal marine environment

(Luksevics 1992; Clack 2006). As mentioned above, *Tulerpeton* was probably marine.

One of the first to question the freshwater, stenohaline tolerance of all Permo-Carboniferous stegocephalians was Parrish (1978). His thorough sedimentological, faunal and taphonomic study of the Thrift bonebed in Wichita county (Texas) led him to propose that

...the strong possibility exists that the fauna [which inhabited a former mudflat pond located only about 3 km from the sea and included abundant *Trimerorhynchus insignis*, as well as less numerous remains of *Xenacanthus*, *Eryops*, *Zatrachys*, *Archeria*, *Diplocaulus*, *Ophiacodon* and *Dimetrodon*] was capable of tolerating brackish, if not marine, salinities.

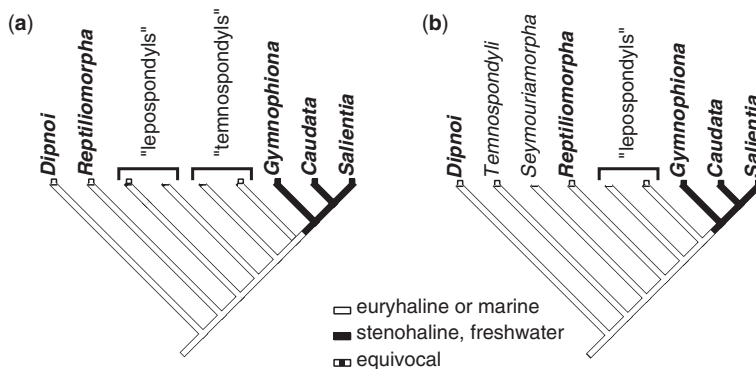
Earlier studies which suggested that Permo-Carboniferous stegocephalians were freshwater inhabitants led him to suggest that a storm had caused a massive influx of saltwater into the pond, and that 'Fresh-water species intolerant of marine salinities would have been placed in double jeopardy.' This hypothesis of the origin of at least some of the stegocephalian fossils is plausible because sudden and important variations in salinity can be lethal, even for euryhaline species such as *Fejervarya cancrivora* (Gordon *et al.* 1961, p. 662) or *Bufo viridis* (Gordon 1962). However, perhaps a massive influx of freshwater (quite likely to occur in a coastal pond during or after a storm) into a brackish to hypersaline pond might have nearly as deleterious effects on the fauna. In any case, Parrish (1978) suggested that some early stegocephalians probably tolerated brackish to saltwater. Among earlier studies, only Vaughn (1969, p. 403) came close to suggesting brackish water tolerance in some early stegocephalians

by recognizing 'crossopterygians', *Diplocaulus*, *Seymouria* and *Dimetrodon* as 'truly deltaic markers', but he did not comment on water salinity.

Several other recent studies raise doubts about the interpretation of most Permo-Carboniferous localities yielding stegocephalians as freshwater environments (Table 2). This applies particularly to North American localities such as Garnett, Hamilton and Robinson (Kansas, USA) and Las Cruces (Robledo Mountains, New Mexico, USA), and suggests that many groups of early stegocephalians inhabited marginal marine environments (at least occasionally). Thus, they may have been euryhaline (Schultze & Maples 1992; Schult 1994; Schultze *et al.* 1994; Schultze 1995, 1999).

If the results of these studies are accepted, there is actual evidence that the widespread (but not universal) intolerance of lissamphibians to the marine environment is a relatively recent feature (it probably arose in the Late Carboniferous or in the Permian) because their closest known relatives have been found in coastal environments. This conclusion can be drawn whether a traditional phylogeny (Fig. 2a) such as Panchen & Smithson (1988) or Lombard & Sumida (1992) or a more recent phylogeny such as Laurin (1998a) or Anderson (2001) is used (Fig. 2b), since both presumed sister groups of lissamphibians (lysocephalids, among lepospondyls and various dissorophoids, among temnospondyls) appear to have tolerated saltwater (Schultze 1995). This is supported not only by body fossils, which could conceivably have been transported into deltas and lagoons by rivers and streams, but also by trace fossils such as burrows and trackways (Schult 1994, 1995a, b).

In his studies of the Lower Permian Speiser Shale fauna from Kansas, Schultze (1985, 1999)



**Fig. 2.** Habitat of early stegocephalians inferred on the basis of parsimony and a review of the literature on their habitat. Whether lissamphibians are part of (a) temnospondyls (Panchen & Smithson 1988; Lombard & Sumida 1992) or of (b) 'lepospondyls' (Laurin 1998a; Vallin & Laurin 2004), a freshwater (or terrestrial) habitat is an autapomorphy of Lissamphibia. Under both phylogenies, the limited evidence of salt- or brackish water tolerance in early stegocephalians suggests that this taxon retained the saltwater tolerance inherited from their finned ancestors.

reported remains of *Acroploous* and *Trimerorhachis* (two trimerorhachid temnospondyls) and *Diplocaulus* and *Brachydictes* (two amphibians or 'lepospondyls') in coastal burrows. These would presumably have been exposed to salt- or brackish water during the tidal cycle. It could be objected that the environment represented by that locality is uncertain because Hembree *et al.* (2005) re-interpreted the locality as deposits of sporadic ephemeral ponds in a coastal plain and the burrows as a response of the tetrapods to seasonal droughts. However, despite the two different palaeoenvironmental conclusions, the deposits of the Speiser Shale represent a good example of palaeozoic transitional environments close to or connected to the sea (Park & Gierlowski-Kordesch 2007) where the organisms have to adapt to a wide range of salinities as a consequence of the combination of palaeoenvironmental (tidal cyclicity, marine incursions) and climatic factors.

Interestingly, Sequeira (1998) argued that salinity tolerance was the limiting factor explaining the patchy distribution of saurerpetontids. According to Sequeira (1998, p. 257) the saurerpetontids 'were part of a group of salinity-tolerant tetrapods, capable of living either in coastal water-bodies with some saline input, however low, or in periodically drying water-bodies which might have varying salt-content'.

The Late Carboniferous coal fields of Joggins (Nova Scotia, Canada) and Puertollano (Ciudad Real, Spain) present stegocephalians (tracks and skeletal remains) and numerous evidence (geochemical, sedimentological and palaeontological) of marine influence.

Joggins represents part of the sedimentation in a large microtidal embayment of an extensive epicontinental sea (analogous in many aspects to the Baltic Sea) which was connected to the Tethyan Ocean (Archer *et al.* 1995; Falcon-Lang 2005; Falcon-Lang *et al.* 2006; Falcon-Lang & Miller 2007). Agglutinated foraminifera (*Trochammina*, *Ammobaculites*, *Ammotium* and cf. *Textularia*) and a metazoan trace-fossil assemblage (xiphosurian trackways *Kouplichnium* and cf. *Limulocubichnus* and annelid traces *Arenicolites*, *Gordia*, *Haplotichnus*, *Plangtichnus*, *Cochlichnus* and *Treptichnus*) indicate an 'open water brackish bay' environment for at least parts of the Joggins Formation (Archer *et al.* 1995; Falcon-Lang 2005, fig. 2; Falcon-Lang *et al.* 2006, table 1 and fig. 4). The stegocephalian *Baphetes* occurred in the brackish bay together with other osteichthyans (Falcon-Lang *et al.* 2006, table 1 and fig. 5), numerous chondrichthyans (*Xenacanthus*, *Ctenacanthus*, *Ctenoptychius* and *Callopristodus*) and acanthodians (*Gyracanthus*). In addition, temnospondyls (e.g. *Dendroperon acadianum*) and lepospondyls appeared to have

populated subaerial areas of the brackish-influenced coastal plain as indicated by stegocephalian trackways in a heterolithic sandstone facies showing tidal influence (Falcon-Lang *et al.* 2006, table 2 and fig. 6).

The Puertollano basin preserves a formal coastal, marine or at least brackish environment, as shown by the presence of tidal rhythmites (a sedimentary structure which forms only in intertidal and prodeltaic environments; Mazumder & Arima 2005), acritarchs, aliphatic hydrocarbons and other geochemical evidence (Laurin & Soler-Gijón 2006, p. 295). The trackway of *Puertollanopus microdactylus*, which was produced by a small stegocephalian (pes length of about 20 mm), was left on intertidal sediments which must have been soaked with brackish water (Soler-Gijón & Moratalla 2001). The exact identity of the small trackmaker is not known because the locality in which these trackways were found did not yield skeletal remains of a size and shape matching those of the trackways. The only stegocephalian represented by skeletal remains is the much larger *Iberospondylus schultzei* (Laurin & Soler-Gijón 2001, 2006), whose skull length is about 15 cm. However, the dimensions and proportions of the tracks and size and morphology of the impressions of manus and pes suggest a microsauro or a small reptile. At least one (perhaps two) species of stegocephalians therefore ventured into salt or brackish water in Puertollano in the Stephanian C, which is equivalent to early Gzhelian, about 304–302 Ma (Davydov *et al.* 2004).

Similar conclusions were expressed by Milner (1987, p. 501), who stated that

This reasoning [which implies that many localities previously interpreted as freshwater were possibly brackish] applies to all but one of the other amphibian-producing localities [Newsham was already discussed and argued to probably preserve a euryhaline fauna] from the Coal Measures of England and Scotland, which are characterized by embolomeres (Panchen 1970), loxomatids (Beaumont 1977) and the occasional keraterpetontid (Milner 1980) and lysorophid (Boyd 1980). The only exception is the Carre Heys locality which was offshore deltaic [i.e. with even more marine influence] and has produced *Eugyrinus*, a member of the Trimerorhachoidea, the other group suggested by Parrish (1978) and Schultze (1985) to be euryhaline.

Numerous Late Carboniferous–Early Permian localities with stegocephalians from western and central Europe (Massif Central in France, Saale and Saar-Nahe basins and Döhlen in Germany, Bohemian basins and Boskovice Furrow in Czech Republic) (see Table 1) have long been considered to represent intermontane freshwater basins, palaeogeographically far from the sea and located at high

altitude (Poplin 1994; Boy & Schindler 2000; Boy & Sues 2000; Sanchez *et al.* 2010).

However, Schultze & Soler-Gijón (2004) have recently suggested marine influence in these European basins because of the presence of several brackish or saline water indicators: marine calcareous algae (dasycladaceans and udoteaceans), annelids, euthycarcinoids, xiphosurans, euryhaline sharks (xenacanth, *Sphenacanthus* and *Lissodus*), the actinopterygians *Bourbonnella* and haplolepidiforms, myxinoids (Poplin *et al.* 2001) and shark egg capsules (*Fayolia*, *Palaeoxyris*, *Vetacapsula*). According to Schultze & Soler-Gijón (2004), the analysis of the distribution of fossil egg capsules in the basins is a powerful tool for the determination of palaeosalinities. This suggestion is based on the fact that no recent oviparous shark is known to deposit egg capsules in freshwater. In contrast, the few recent elasmobranchs adapted to more or less permanent life in freshwater (i.e. stenohaline freshwater) are viviparous (e.g. potamotrygonid rays). Chondrichthyan egg capsules (*Palaeoxyris* and *Vetacapsula*) have been reported in Mazon Creek and Hamilton, both localities with evidence of tides, and egg capsules have been described from Commeny (Massif Central) and from several localities of Saar-Nahe, Saale and Bohemian basins, which suggests a connection to marine areas of the Palaeotethys (Schultze & Soler-Gijón 2004).

Palaeotopographic features of the Variscan mountain chain and altitude of the western and central Permo-Carboniferous basins have important implications in the study of development and growth pattern of stegocephalians. Recently, Schoch & Fröbisch (2006) and Fröbisch & Schoch (2009) explained neoteny, very common in branchiosaurids from Saar-Nahe basin, by the high elevation (up to 2000 m or more above sea level) of the lakes where those stegocephalian lived. Sanchez *et al.* (2010) explained a double growth line pattern in bones of *Apateon* as the consequence of hibernation-estivation events similar to those which affect recent amphibians living in mountain lakes at temperate latitude (several localities in north of Portugal).

Both studies are based on a model of limnic basins located at a very high altitude (a few thousands of metres) as proposed by Becq-Giraudon *et al.* (1996) for the Stephanian basins of the Massif Central. However, recent estimations of the altitudes of the basins indicate a relative low topography (Opluštil 2005a, b; Roscher & Schneider 2006; Schneider *et al.* 2006), which suggests that the environmental factors which induced heterochrony in branchiosaurids were not low temperature; perhaps fluctuations in the salinity of the waters is a more plausible cause.

Studies of the euryhaline toad *Bufo calamita* and other recent amphibians (Gomez-Mestre & Tejedo 2002, 2005; Gomez-Mestre *et al.* 2004) which are adapted to a brackish environment show variations of thyroid hormone linked to increase in the salinity (see below for more information about salt tolerance of recent amphibians). Furthermore, double growth patterns as described in *Apateon* are also shown in several groups of recent tropical actinopterygians living in low altitudes in coastal and estuarine areas. For example, two annuli and two zones per year have been described in bones of teleosts (*Ariidae*, *Anastomidae* and *Serrasalmidae*) from French Guyana; the annual growth marks have been connected to the existence of two dry seasons and a bimodal rainfall pattern (Lecomte *et al.* 1986, 1993; Meunier *et al.* 1994).

The growth pattern of the tropical stegocephalian *Apateon* (probably a stem-tetrapod, although many authors consider it a stem-amphibian), which probably lived in a low altitude as indicated by the most recent analyses of the Permo-Carboniferous basins, probably results from factors other than the growth pattern of recent lissamphibians of Portugal living at a temperate latitude and in high altitude. For Opluštil (2005a), the recent analogue of the Late Palaeozoic continental basins of central and western Bohemia is the Tasek Bera Basin in central Peninsular Malaysia; this is a dendritic basin, located at about 3°N, 35 m above sea level, surrounded by lowland hills rising up to 240 m above sea level.

For localities of the Cutler Formation from New Mexico, other localities which yielded seymouriamorphs (Berman *et al.* 1987; Klembara & Meszáros 1992; Berman & Martens 1993) and the Sangre de Cristo Formation from Colorado, we are not aware of clear evidence of marine influence. However, many of the taxa found there (such as xenacanthiform chondrichthyans, acanthodians and dipnoans) are also known from marine and brackish environments (Table 2). Even the seymouriamorphs are also found in other, presumably brackish environments (Montceau-les-Mines, Texas redbeds). Nevertheless, the great abundance of seymouriamorphs in basins showing the least marine influence, and their lesser abundance or absence from basins which show more marine influence, suggests that they may have been less tolerant of brackish and saltwater than many other early stegocephalians.

Vaughn's (1969) palaeogeographic reconstructions placed some localities in New Mexico and Colorado in 'somewhat more upland' environments in contrast to other localities located in the 'truly deltaic' environments (or 'coastal plain', as proposed by Berman & Reisz 1980). In the Cutler Formation, the abundance of caliche (Berman *et al.* 1985, 1987), a hardened deposit of calcium

carbonate, raises the possibility that at least some of the still water bodies were brackish, even if the sea was far away. Furthermore, Eberth & Berman (1993, p. 46) seem to have interpreted the presence of the dipnoan *Sagenodus* and the osteolepidid *Lohsanias* as freshwater indicators. *Sagenodus* was probably euryhaline, however, and is thought to have occurred in marine and freshwater environments (Schultze & Chorn 1997). We have found no detailed data on the presumed habitat of *Lohsanias* but, given the general reinterpretation of osteolepidids from freshwater to marine and euryhaline forms, the freshwater interpretation of the Cutler Formation does not appear to be supported by faunistic criteria. We have provisionally accepted the conclusions of Eberth & Berman (1993) but it would be interesting to study the mollusks, arthropods and other metazoans from that formation.

### Evolutionary analysis of habitat in early stegocephalians

A time-calibrated supertree was compiled from the literature (Figs 3 & 4). Given the large time-span encompassed by the tree (Givetian to Roadian on the figure, but it really extends to the Holocene), all terminal taxa were placed within the proper geological stage. No attempt was made to achieve greater stratigraphic precision, for various reasons. First, the gained precision would not be visible on the figure, unless a non-linear timescale was used. Second, given the stratigraphic uncertainties on the age of many fossils and the still greater uncertainty about the actual (as opposed to observed) stratigraphic range of most terminal taxa (Marshall 1997; Marjanović & Laurin 2008a), the gains in precision would be more apparent than real. Among many arbitrary branch length values that could have been used, we set both terminal branches to a minimal length of 1 Ma and internal branches to a minimal length of 2 Ma. We placed the end of the stratigraphic range of all terminal taxa at the top of the geological stage to which they belong, as was done by Laurin (2004) and Marjanović & Laurin (2007). Given the large number of terminal taxa (86) and of polytomies included in the tree, this procedure results in reasonable ages for the hypothetical ancestors. Presumed terrestrial taxa were excluded because the distinction between salt and freshwater habitats does not apply to them.

Early amniotes are therefore represented by *Ophiacodon*, which may have been amphibious to aquatic (Romer 1958; Germain & Laurin 2005). *Hylonomus* is included (but not coded for habitat) to provide a temporal calibration of this part of the tree only. The tree is not exhaustive but, during its compilation, it became clear that given the

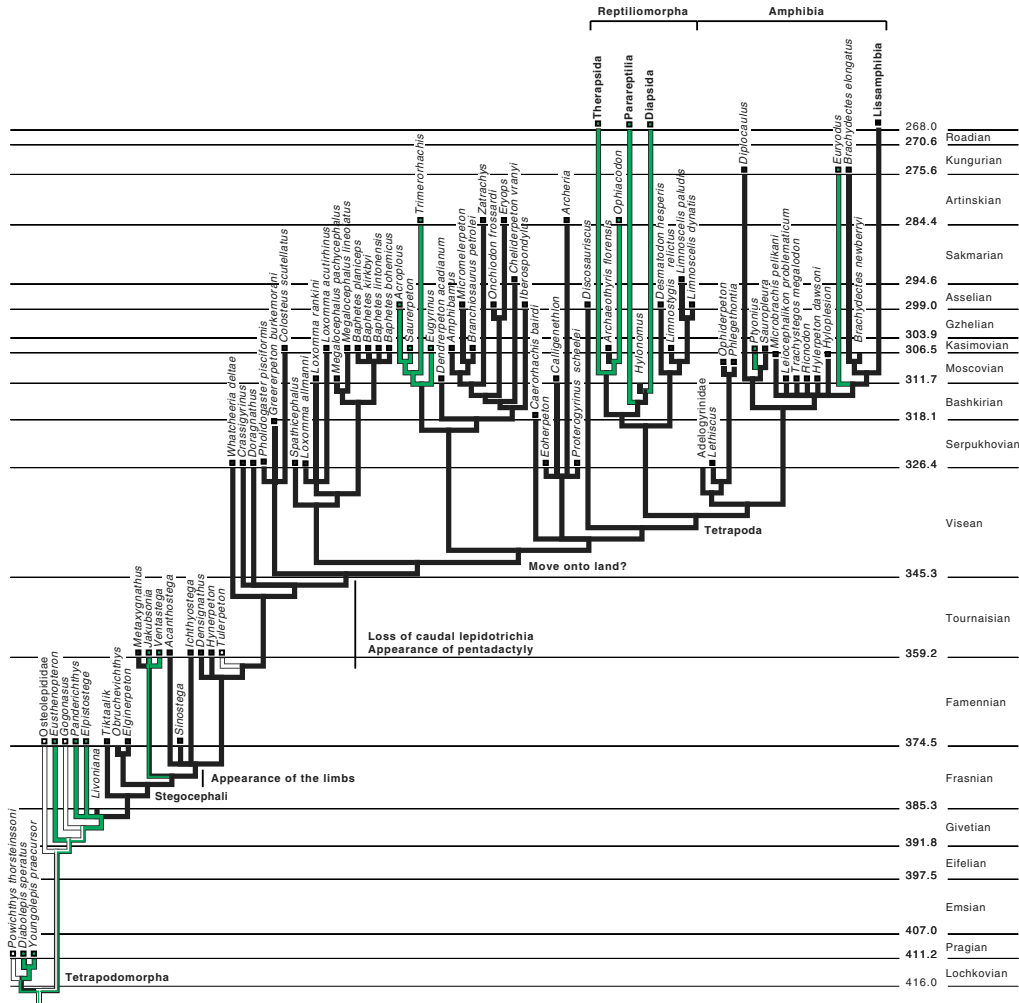
uncertainties about the palaeoenvironmental interpretation of many localities, adding more taxa would not have changed the global pattern. Furthermore, the information presented in Table 2 enables any interested palaeobiologist to expand the analysis to additional taxa.

To determine if character optimization yields reliable information on ancestral states, the presence of a phylogenetic signal should be assessed (Laurin 2004). The high number of polytomies constrains the choice of randomization procedure because the number of steps required by trees which include soft or hard polytomies, and of trees with randomly resolved polytomies, differs. An appropriate randomization procedure is to reshuffle terminal taxa randomly on the tree in which topology and branch lengths are kept constant, as was done by Laurin (2004). In this case, all random trees include the same number and type of polytomies.

Another solution would have been to randomly resolve the polytomies several times (ten or more) to investigate the phylogenetic signal in all of these trees and to average the probabilities; that solution would be more time consuming and potentially less accurate, however (unless a much greater number of random resolutions were examined). In both cases, the probability that the distribution of the character states is independent of the phylogeny is given by the number of random trees (produced by reshuffling) which implies the same number (or fewer) transitions as the reference tree, divided by the total number of random trees (here, 10 000). The three states (0: marine; 1: brackish; and 2: freshwater) were ordered according to a salinity gradient.

Given the controversies surrounding palaeoenvironmental interpretations of most Palaeozoic fossiliferous localities in which stegocephalians were found, two optimizations of habitat are presented. The first presents the most traditional interpretation: many localities are interpreted as freshwater environments or, when clearly marine or brackish water, stegocephalian remains are interpreted as allochthonous elements brought in by rivers (Fig. 3). Since the phylogenetic signal is highly significant ( $p = 0.0002$ ), the character can be optimized. This optimization suggests that the first sarcopterygians and tetrapodomorphs lived in a brackish or marine environment (which is not new, of course) and that the move to freshwater environments took place before the last common ancestor of *Tiktaalik* and stegocephalians. The few Palaeozoic stegocephalians which tolerated brackish water represent returns to a marginal marine environment.

The second optimization presents the alternative interpretation of a more marine (or at least brackish) environment of most fossiliferous localities. Under



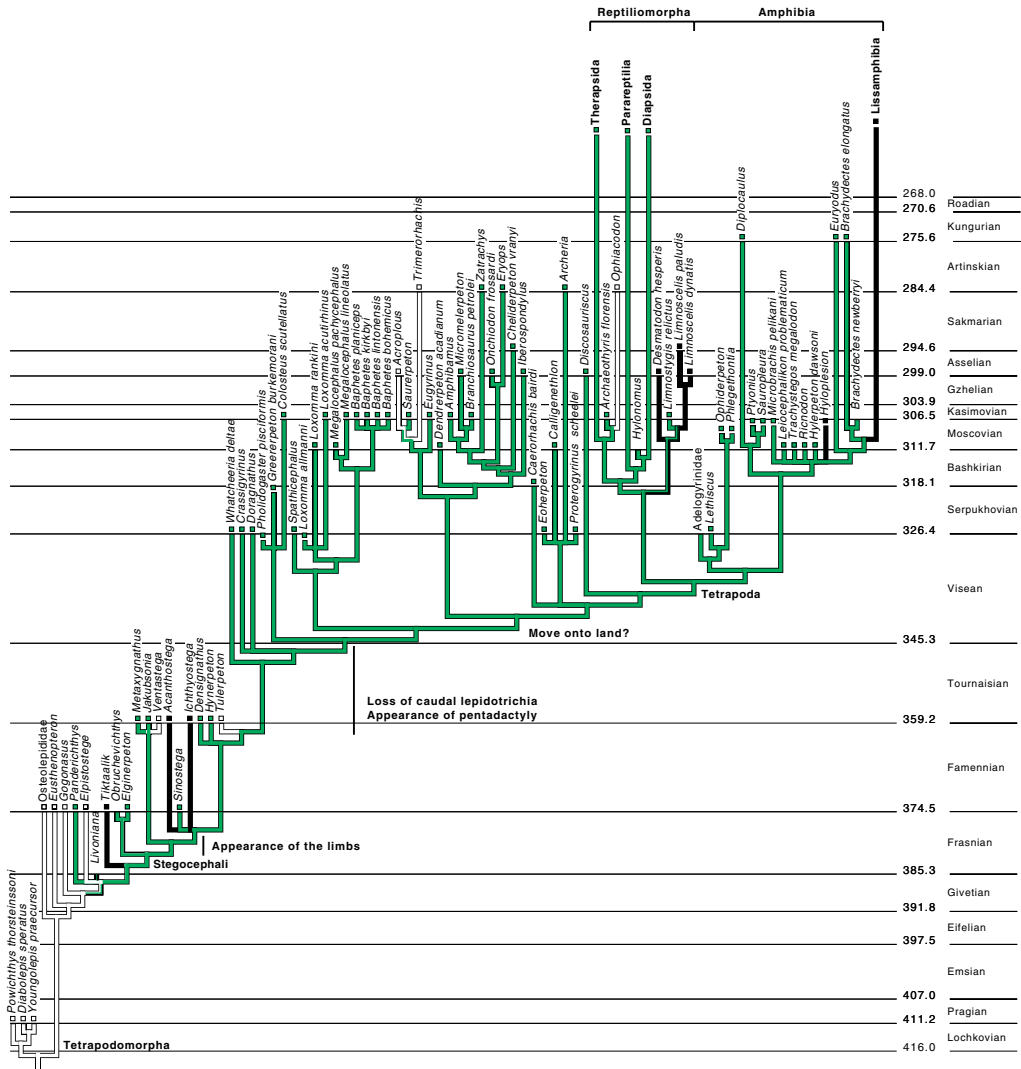
**Fig. 3.** Time-calibrated supertree of sarcopterygians emphasizing early tetrapodomorphs showing the evolution of habitat according to traditional interpretations. White: marine; grey (green in the electronic version): brackish water; black: freshwater. States were ordered. The phylogeny was compiled using the Stratigraphic Tools (Josse *et al.* 2006) for Mesquite 2.01 (Maddison & Maddison 2007) using the geological timescale of Gradstein *et al.* (2004) with trees and taxonomies from Smithson (1980), Foreman (1990), Laurin (1998a, c), Beaumont & Smithson (1998), Laurin *et al.* (2000), Zhu *et al.* (2001), Ruta *et al.* (2002, 2007), Zhu & Yu (2002), Anderson *et al.* (2003), Laurin (2004), Lebedev (2004), Long & Gordon (2004), Vallin & Laurin (2004), Clack & Finney (2005), Laurin & Soler-Gijón (2006), Clack (2007) and Ruta & Coates (2007).

that interpretation, most stegocephalian remains are interpreted as autochthonous elements which were not transported far from their habitat. This character includes a strong phylogenetic signal ( $p < 0.0001$ ). This optimization differs from the former in that the move from a marine environment to a marginal marine environment probably took place in the smallest clade which includes panderichthyids and stegocephalians. That marginal marine environment appears to have been the cradle of stegocephalian diversification, although that may well be a

taphonomic artefact (this is the environment into which most fossiliferous sediments in which stegocephalians could be preserved were deposited).

There is little evidence that some early stegocephalian species were freshwater stenohaline forms, although this could reflect the same taphonomic artefact and could result from the difficulty of demonstrating the freshwater nature of a locality. If we take this evidence at face value, the relative intolerance of most lissamphibians to moderately saline brackish (more than about 10‰) water or





**Fig. 4.** Time-calibrated supertree of sarcopterygians emphasizing early tetrapodomorphs showing the evolution of habitat according to recent works (Tables 1 & 2) which reinterpret several localities as marginal marine environments. See Figure 3 for more information. White: marine; grey: brackish water; black: freshwater.

saltwater is an autapomorphy of Lissamphibia which may have appeared in the late Carboniferous or in the Permian (Fig. 4).

Even though both optimizations are presented, this does not imply that both are equally supported or plausible. The first (Fig. 3) is presented mostly for its historical interest, and to show how much interpretations have changed in the last 20–30 years. The traditional interpretation (Fig. 3) is inconsistent with several recent discoveries of clear evidence of at least moderate marine influence of several localities (see above). The alternative (Fig. 4) appears to be much better supported

although it remains, to an extent, conjectural as is usually the case in palaeobiological and palaeoecological studies.

The conclusions drawn from the evolutionary analysis of habitat in early stegocephalians were anticipated by Milner (1987, p. 503) who stated that

... it appears to be most parsimonious to argue that the plesiomorphic tetrapod condition was to be euryhaline. Restriction to freshwater appears to have been a secondary specialization developing once or more within the Temnospondyli and at least once with the non-lysoorhian microsaurians.

Similarly, Schultze (1999, p. 388) concluded that 'The tetrapods entered the terrestrial realm through the intertidal and supratidal zones.'

### Palaeobiogeographic evidence

Saltwater tolerance for early stegocephalians would resolve the paradox of their extremely wide distribution in the Devonian (Daeschler 2000) at a time in which at least some members of this group have been argued to have been still strictly aquatic (Clack & Coates 1995). Indeed, the first undisputed record of stegocephalians dates from the Frasnian. By the Famennian, they had reached a nearly worldwide distribution; they are found in most of the Old Red Continent (eastern Greenland, European Russia, Latvia, Scotland, North America), in Australia (which was then part of Gondwana; Milner 1993; Daeschler *et al.* 1994) and northern China which was then isolated (Zhu *et al.* 2002).

Given that the Frasnian and Famennian probably lasted a total of about 26 Ma (Gradstein *et al.* 2004) and that Australia (and the rest of Gondwana) and northern China may have been isolated from Laurentia and Baltica by a fairly broad oceanic basin (Li *et al.* 1993), it is difficult to conceive how a stenohaline freshwater group could have spread so far and so fast. However, this difficulty disappears if early stegocephalians were euryhaline (Laurin & Soler-Gijón 2001; Parker & Webb 2008).

Of course, the distribution of the various continental plates in the Late Devonian is still controversial, and Scotese & McKerrow (1990) have argued for close positions of all the land masses on which early stegocephalians have been found. Milner (1993, p. 328) used the maps of Scotese & McKerrow (1990) to argue that terrestrial or freshwater-based dispersal of stegocephalians could have taken place. Scotese & McKerrow (1990, p. 1) explained that their maps differed from previous maps in that 'a narrow (rather than a wide) ocean is shown between Laurentia (North America) and Gondwana during the Devonian'.

It appears that most of Gondwana was cut off from Laurentia and Baltica by an epicontinental sea (Klapper 1995, fig. 1), even if all these plates were in contact. Therefore, the hypothesis of a strictly terrestrial or freshwater dispersal of stegocephalians and their close relatives in the Devonian does not appear to be supported by the current palaeogeographic evidence, as previously argued by Thomson (1980). The presence of skeletal remains (*Metaxygnathus*) and of trackways of a stegocephalian in Devonian rocks of Australia (Warren & Wakefield 1972; Campbell & Bell 1977) can best be explained by dispersal through a coastal marine environment. More recently, Daeschler (2000, p. 307) raised the possibility that

early stegocephalians 'retained a tolerance of marine conditions and dispersed via marine routes', based on palaeogeographic arguments.

Bray (1985) provided compelling geological and physiological arguments in support of a marine origin of stegocephalians. He pointed out that the palaeoecological interpretation of many fossiliferous localities in which Devonian stegocephalians have been found were dubious. Most of these were previously interpreted as fluvial, but they could represent tidally influenced environments. Furthermore, many Devonian inland ('freshwater') basins may have had higher ion concentrations than most of today's freshwater bodies because the vegetation cover may have been low; this would have resulted in faster weathering and leaching than in more recent times.

The difference in salinity between the marine and 'freshwater' environments may therefore have been smaller than today. Thomson (1980) had assumed that inland basins were synonymous with freshwater basins (but still argued that most early sarcopterygians were marine or euryhaline), but Bray (1985) argued that this assumption is unwarranted because these basins could have communicated with marine basins. For instance, a wrench fault system may transect a continent and bring marine influences, as was argued for the East Greenland Basin that was far from the edges of the Old Red Sandstone continent in the Upper Devonian (Ziegler 1981, 1982). These geological arguments by Bray (1985) seriously question the validity of the traditional scenario proposing freshwater origin of stegocephalians.

### Physiological and morphological evidence

Recent chondrichthyans, lungfishes, coelacanths and lissamphibians possess a full complement of enzymes for the ornithine pathway for producing urea. Furthermore, these taxa share the presence of uraemia (the retention of urea in the blood to increase its osmotic pressure and thereby prevent dehydration in a marine or terrestrial environment). Bray (1985) have argued that this evidence suggests a marine origin for these groups (and of course, two of these still live in the oceans). Actinopterygians generally have an incomplete complement of enzymes for the ornithine pathway, and Bray (1985) interprets this as a partial loss resulting from the long history of this group in freshwater (it is argued that all marine actinopterygians are derived from freshwater ancestors).

In this respect, the presence of a full complement of enzymes for this pathway in lissamphibians suggests that amphibians have left the marine environment more recently than actinopterygians (which is congruent with the optimization of

saltwater tolerance presented above, which suggests that lissamphibians have been restricted to freshwater for less than 330 Ma). Alternatively, this suggests that the ornithine pathway has been retained because of selective pressures exerted by the terrestrial environment (but this explanation applies only to relatively terrestrial lissamphibians). In any case, the presence of an ornithine cycle in lissamphibians suggests either a direct passage from the marine to the terrestrial environments, or only a short intermediate period in which stem-amphibians inhabited freshwater environments.

When reviewing evidence on whether air-breathing in osteichthyans had appeared in a freshwater or a marine environment and whether the conquest of land among sarcopterygians had started in a freshwater or a marine environment, Graham (1997) found no conclusive answers to these questions. Hypoxia is more often and more regularly a problem in stagnant freshwater than in oceans but sheltered bays, lagoons and even enclosed seas can experience hypoxia. Furthermore, hypoxia is not the only selective pressure that can favour the appearance and maintenance of air-breathing.

Farmer (1997, p. 361) indicated that 'lungs may have evolved in early fishes to support an active lifestyle by supplying oxygen to the heart and enhancing cardiac performance'. This author also pointed to the fact that air breathing is not restricted to (or even highly correlated with) hypoxic freshwater environments. Among actinopterygians several air-breathing groups inhabit coastal areas where this ability enables them to exploit parts of the habitat and resources unavailable to other actinopterygians (Graham 1997). Similar selective pressures may have driven the evolution of early stegocephalians, in which case there is no reason to expect that they would have been stenohaline freshwater forms.

In the lissamphibians that tolerate salt- or brackish water, osmotic regulation may involve the external gills. This is suggested in *Fejervarya cancrivora* (formerly known as *Rana cancrivora*) by the fact that tadpoles regulate their osmotic concentration. This varies from only 250 m-osmoles/l (milliosmoles per litre; this means 0.001 mole of solute per litre) to more than 900 m-osmoles/l when confronted with an increase in environmental osmotic pressure (Gordon & Tucker 1965, p. 439, fig. 1). On the contrary, the adults are osmoconformers (Gordon *et al.* 1961). This shows that neither gills nor impervious skin are required for amphibians to tolerate saltwater; the skin of adult *Fejervarya cancrivora* is fairly permeable (Gordon *et al.* 1961, p. 663).

Study of various ontogenetic stages shows that tadpoles of stages IV to XIX maintain an internal osmotic concentration of about 490 m-osmoles/l

in 80% seawater. In the same environment, that concentration rises from stages XX to XXV (the latter is a fully metamorphosed froglet lacking gills) to become isosmotic with the environment at stage XXV (Gordon & Tucker 1965, p. 441, fig. 2). Since the gills of teleosts are known to be involved in active salt transport, and since the loss of osmoregulation in *F. cancrivora* coincides with loss of gills in its ontogeny, Gordon & Tucker (1965) suggest that the gills of *F. cancrivora* are involved in osmoregulation.

More recent studies show that, unsurprisingly, kidneys are also important in osmoregulation. They retain urea to increase osmosis in dry or hypersaline environments, at least in *Rhinella marina* (called *Bufo marinus* by Konno *et al.* 2006). *Fejervarya cancrivora* is probably the lissamphibian with highest saltwater tolerance (Gordon 1962); Gordon *et al.* (1961, p. 665) reported that tadpoles can tolerate slightly hypersaline concentrations (up to 39‰ salinity, a salt concentration about 20% higher than seawater). Thus, it is probably among the most relevant lissamphibian species to understand saltwater tolerance (or lack thereof) in lissamphibians.

External gills are useful for osmoregulation in amphibians, but the presence of gills does not necessarily confer osmoregulatory abilities. Indeed, most tadpoles and anuran larvae have gills, but most cannot tolerate saltwater. Nevertheless, the presence of external gills in larvae of temnospondyls, seymouriamorphs and at least some amphibians (*Microbrachis* and possibly adelogyrinids and lysorophians) raises the possibility that it conferred these taxa osmoregulatory ability.

Along with the occurrence of some body fossils, trackways or burrows of these taxa in brackish or saltwater environments (Schultze 1985; Laurin & Soler-Gijón 2001, 2006), this suggests that these taxa tolerated saltwater. When they lived in the same environments and lacked gills (which apparently disappeared in ontogeny in seymouriamorphs and probably in most temnospondyls), the adults may have been osmoconformers if they had permeable skin. However, such a relatively permeable skin (a superficial layer of lipids strongly reduces its permeability in some species) may be an autapomorphy of the Lissamphibia.

The facts that the most aquatic lissamphibians have a lower skin permeability to water than most terrestrial lissamphibians (Yorio & Bentley 1978) and that even desert anurans can extract moisture from soil in their estivation burrows and secrete cocoons only when the soil becomes especially dry (Cartledge *et al.* 2006) support this suggestion; skin permeability appears to be adaptative, rather than disadvantageous, for lissamphibians in many terrestrial environments. The skin of stem-tetrapods

and some of the earliest amphibians was probably an effective barrier against water and ion flux (at least in water) for most actinopterygians (Bond 1979), aquatic lissamphibians (Yorio & Bentley 1978) and in amniotes (Pough *et al.* 2004, p. 236).

This issue should not be confused with the problem of desiccation on land; evaporative water loss in air was probably important in the first terrestrial vertebrates because the differences in efficiency and mechanism of waterproofing of the skin in lissamphibians and amniotes (Lillywhite 2006) suggests that impermeability was achieved independently in amphibians and in reptiliomorphs. Waterproofing structures in the skin of mammals and reptiles also differ, but both possess a series of layers of keratin and lipids in the stratum corneum, which was plausibly present in their last common ancestor.

The intolerance to salt- and brackish water in lissamphibians is not nearly as universal as the palaeontological literature suggests (Hunt 1993, p. 93; Poplin 1994, p. 299; Cuny 1995, p. 57; Schoch 1995, p. 113). Some reports of brackish water tolerance in lissamphibians are fairly old (e.g. Hardy 1943; Spuraway 1943) with a few from the 19th century (reviewed in Schmidt 1957), but these works may not have received the attention that they deserve from palaeontologists. Similarly, Pough *et al.* (2004, p. 234) reported that about a dozen species of urodeles and 60 species of anurans have been reported to inhabit or tolerate brackish water. At least one species (*Ambystoma subsalsum*) appears to be endemic to the brackish (8.283‰ salinity) lake Alchichica in Puebla, Mexico (Neill 1958, p. 9). Given the low number of herpetologists who study saltwater tolerance of extant lissamphibians and the common neglect of brackish and marginal marine environments by herpetological collectors (Neill 1958, p. 3), this number may still underestimate saltwater tolerance in this taxon.

## Discussion

### *The danger of model organisms*

This review illustrates the need to study a broad variety of extant taxa to understand extinct taxa. Gordon *et al.* (1961, p. 659) stated that

One result of the relatively narrow range of amphibians investigated has been the development of a firm belief that amphibians in general cannot survive for more than a few hours in external media more concentrated than about 300–350 milliosmolar... 'This belief ignores repeated observations in many parts of the world of the occurrences of a variety of [A]mphibia, virtually all anurans, in brackish and even marine environments...'

Milner (1987, p. 500) stated: 'With a few exceptions, notably the crab-eating frog *Rana cancrivora*, which inhabits mangrove swamps, all living amphibians are intolerant of brackish or salt water.' Such statements may underestimate variability in osmotic tolerance in lissamphibians. In fact, even lissamphibian species that lack adaptations for brackish water tolerance (such as *Rana pipiens* or *Rana esculenta*) can usually tolerate a salinity of up to 10‰ as adults, although eggs normally require a salinity of less than 5‰ to develop normally (Ruibal 1959).

### *The importance of nomenclature*

This paper illustrates the importance of a precise nomenclature and of recognizing only monophyletic taxa (at least, above the species level); osmotic tolerance of lissamphibians differs substantially from that of Palaeozoic amphibians and of limbed stem-tetrapods, which are often called 'amphibians' in the literature. It is possible that the recognition of a paraphyletic taxon Amphibia played a role in suggesting and maintaining the long-admitted idea that early stegocephalians were strictly freshwater and terrestrial forms, as suggested by Milner (1987, p. 500).

### *Vague similarities, phylogeny, parsimony and habitat: a proposed research program*

Previous interpretations of Palaeozoic fossiliferous localities are difficult to test for several reasons. In some cases, justification for an interpretation was not sufficiently explicit (the lack of obvious marine indicators is implicitly accepted to indicate freshwater). In others, vague similarities with extant taxa coupled with an equally vague nomenclature may have been implicitly used. This may explain many previous statements (Hunt 1993, p. 93; Poplin 1994, p. 299; Cuny 1995, p. 57; Schoch 1995, p. 113) that 'early amphibians' (stegocephalians) were essentially freshwater forms.

Several other taxa previously used as freshwater and marine indicators may need to be reassessed. For instance, Taylor & Vinn (2006) showed that Palaeozoic calcareous tube-worms previously attributed to the extant annelid *Spirorbis* (and other related forms) are actually spirorbiform microconchids, an extinct taxon plausibly related to phoronids; the latter are marine lophophorates (Temereva & Malakhov 2006). Although several authors questioned the presence of true *Spirorbis* in Palaeozoic facies in the 1970s (e.g. Burchette & Riding 1977; Taylor & Vinn 2006), the genus *Spirorbis* has been included in faunal lists of Palaeozoic localities and palaeoenvironmental implications discussed (see e.g. Falcon-Lang *et al.* 2006). Extant *Spirorbis* is a stenohaline marine form

so that the presumed presence of this genus in Permo-Carboniferous localities has been considered an indication of marine influence (e.g. Cassle *et al.* 2006). The persistence of a taxon traditionally ranked as a genus from the Carboniferous to the present should in any case have been suspect, since even *Lingula*, often considered a living fossil, does not occur in the Palaeozoic; fossils previously attributed to this taxon have been reassigned to other genera of the Lingulidae (Emig 2003). Nevertheless, this change in classification of lingulids illustrates, to an extent, the subjective nature of absolute (Linnean) ranks (Laurin 2008).

Interestingly, Palaeozoic *Spirorbis* (a microconchid) is a euryhaline form which occurs in the microtidal Joggins (Falcon-Lang *et al.* 2006), Saar-Nahe, Saale and Bohemia (Schultze & Soler-Gijón 2004). Extant (genuine) *Spirorbis*, and more generally serpulids (which include *Spirorbis*) and at least some other marine annelids, tolerate a wide range of salinity (Ushakova 2003).

It might be useful if the parsimony criterion were used in an explicit phylogenetic context (Fig. 1) to reassess the significance of palaeoenvironmental markers whenever possible. This might be feasible for at least some mollusks, brachiopods and arthropods. Also, all metazoans which do not belong to the crown-groups which appeared before the Devonian (and in some cases, well after) may plausibly have been marine, given that the oceans and seas appear to be the cradle of early metazoan diversification (Barnes 1987; Clarkson 1998). In the absence of the contrary, a marine habitat is a more reasonable null hypothesis than a freshwater habitat, although it should always be tested.

Detailed phylogenies are now available for many relevant clades, and some of these include extinct taxa (Wheeler *et al.* 1993; Waggoner 1996) or include enough morphological characters to enable inference of the position of extinct taxa (Jenner & Schram 1999; Giribet *et al.* 2001; Collins 2002; Jacobs *et al.* 2005; Collins *et al.* 2006); use of parsimony and of an explicit phylogeny might therefore yield additional data. For instance, the tenuous interpretations by vertebrate palaeontologists of several Palaeozoic localities as freshwater environments may have influenced other palaeontologists. The suggestion that in the Devonian, 'spirorbiform microconchids began to inhabit brackish and freshwater environments in addition to marine settings' (Taylor & Vinn 2006, p. 227) may rest partly on the interpretation of palaeoenvironmental preferences of stegocephalians.

It would be useful to try to resolve the phylogenetic position of microconchids and use the parsimony criterion to assess their environmental preferences. Given the number of problems (noted above) which have marked the freshwater/marine

controversy, such an approach might yield useful new insights.

Note that much of the discussion above has treated saltwater tolerance as a discrete character because, when little detailed information is available, this is the only applicable technique. When more quantitative data are available (as for salinity tolerance in some species of lissamphibians and *Nereis*) however, squared-change parsimony and independent contrasts could conceivably be used to estimate environmental tolerance with confidence intervals. Such techniques were recently used to study body size evolution (Laurin 2004). Another possible approach to determine habitat preference and breadth of ancient organisms might be inference models built upon observable characters which can be shown to be correlated to the relevant environmental variable. However, such models should be applied only within the clades in which such correlations have been tested, as suggested by an extension of the extant phylogenetic bracket principle to continuous characters (Laurin *et al.* 2004, p. 607).

#### *Habitat and the fossil record*

The frequent, relative intolerance of lissamphibians to saltwater could explain (at least partly) why their fossil record is so much poorer than that of most other groups of stegocephalians. Stem-amphibians closer to lissamphibians than to lysorophians (or dissorophoids) may have lived away from the coast, possibly in upland environments, from which the fossil record is generally poor. Sediments deposited inland, above the sea level, are much more likely to be eroded quickly than sediments deposited in coastal areas, just below the sea level. Even rocky shores have an extremely poor fossil record because, despite their low altitude, they are areas of erosion (Schultze 1999, p. 373). This could explain the large stratigraphic gap between presumed sister-groups of lissamphibians (which appear in the middle Upper Carboniferous, such as lysorophians and dissorophoids) and the oldest known lissamphibians, such as *Triadobatrachus* (Rage & Rocek 1989) and *Czatkobatrachus* (Evans & Borsuk-Bialynicka 1998), from the Early Triassic. That poor record hampers direct comparisons between molecular and palaeontological estimates of the age of Lissamphibia (Zhang *et al.* 2005), although indirect comparisons show no incompatibility and suggest that the record is sufficiently good to assess the age of origin of several lissamphibian taxa (Marjanović & Laurin 2007).

#### *Habitat of early stegocephalians*

This review attempts to shed new light on the long-debated problem of the original environment

(marine v. freshwater) of our aquatic ancestors. The problem is far from solved because there is considerable uncertainty about the environment represented by many fossiliferous localities; some authors (Schultze 1985; Schultze & Maples 1992; Cunningham *et al.* 1993; Schultze *et al.* 1994; Lebedev 2004) interpret as brackish or marine several localities which are interpreted by others (Zhu *et al.* 2002; Long & Gordon 2004; Hembree *et al.* 2005) as freshwater.

For instance, Campbell & Bell (1977, p. 372) interpreted as overbank deposits (hence, presumably freshwater) the locality in which *Metaxygnathus* was found. Yet, some horizons, including the most fossiliferous ones, contain 'calcareous algal structures of the kind previously reported by Wolf & Conolly (1965)' (Campbell & Bell 1977, p. 371). These 'calcareous algal structures' cannot be identified with certainty; hence, their palaeoenvironmental implications are uncertain (Wolf & Conolly 1965, p. 99). Some stromatolites (oncoids) formed by communities of cyanobacteria, which are often considered 'algae', occur in freshwater environments (Hägele *et al.* 2006). However, calcareous macrophytic 'algae' such as rhizophytes are usually found in marine settings (Prothero 2004, p. 440; Biber & Irandi 2006), normally require high constant salinity to thrive and are major contributors of carbonates (Wefer 1980). *Metaxygnathus* may therefore have tolerated saltwater.

We have revealed many uncertainties and inconsistencies in the palaeoenvironmental interpretation of several Permo-Carboniferous fossiliferous localities. Even only a few fossils of typically marine organisms shed serious doubt about the freshwater nature of a locality, since the bodies of such organisms cannot move far upstream to freshwater continental environments. Tides could conceivably move them slightly upstream of their normal habitat, but only into an estuary where the water would in any case be mainly salty or brackish (freshwater only appears in the uppermost (proximal) zone of the estuary, close to the fluvio-estuarine transition). On the other hand, stegocephalians deposited in such environments may in many cases have been carried at least a short distance by rivers.

Nevertheless, the reinterpretation of several localities formerly interpreted as freshwater environments as marine to brackish environments might make more sense to the extent that most sediments deposited relatively high above the sea level in intramontane basins should be far more subject to erosion than sediments deposited slightly below the sea level. Thus, the traditional interpretation of many Permo-Carboniferous localities which have yielded stegocephalians as freshwater, inland and (sometimes) intramontane environments is perhaps

not the most plausible, in this respect. This question might be profitably explored using sophisticated geological models.

The evidence of marine influence in many classical Permo-Carboniferous localities is not all recent. Some evidence has been available for a long time, but was dismissed. For instance, fossils attributed apparently wrongly (Burchette & Riding 1977; Taylor & Vinn 2006) to the marine annelid *Spirorbis* have been known to occur in Joggins since the mid-19th century (Dawson 1845, 1853). Perhaps the expectation that 'amphibians' lived in freshwater led to these interpretations. Schultze (1995, p. 260) similarly explained earlier interpretations of Robinson (Gzhelian, Kansas, USA) as a freshwater locality despite the presence of marine indicators. This would explain why mostly vertebrate palaeontologists interpreted the localities of Robinson and Hamilton as freshwater deposits (Schultze 1995, p. 269).

It is not always clear if the stegocephalians lived in the environment into which their remains were deposited. Long-distance transport can usually be ruled out when specimens are well-preserved, complete and articulated, but short transport is extremely difficult to detect. Given the fact that many early stegocephalians were found in coastal areas, it is possible that some were transported a short distance from freshwater bodies near the coast.

#### *The move onto land: from where?*

It may be appropriate to discuss some recent evolutionary scenarios about the origin of limbed vertebrates and of a terrestrial lifestyle in vertebrates. Graham & Lee (2004, p. 720) recently argued that

...selection pressures imposed by life in the intertidal zone are insufficient to have resulted in the requisite aerial respiratory capacity or the degree of separation from water required for the vertebrate land transition. The extant marine amphibious fishes, which occur mainly on rocky shores or mudflats, have reached the limit of their niche expansion onto land and remain tied to water by respiratory structures that are less efficient in air and more vulnerable to desiccation than lungs.

This argument is weak because the failure of amphibious teleosts to colonize more inland habitats may simply result from the presence of tetrapods in these habitats, as indirectly suggested by the extent and diversity of adaptations to life on land in this taxon (Gordon *et al.* 1969; Graham 1997).

Here, an analogy with arthropods may be the best line of argument. Several groups of crustaceans have become terrestrial, but only isopods have succeeded in invading terrestrial habitats located far from the coasts. Most terrestrial crabs live on the coast; several of the most notable exceptions are

found on islands located sufficiently far from the nearest continent to have few insects and arachnids (such as Guadeloupe; personal observation), although some occur on the continent such as *Potamon* in the Alborz range (Iran; P. Janvier, pers. comm., 2009). Yet, several primitively marine crustaceans have perfectly functional walking appendages that can be used to walk on land with little or no modification. In this respect, it should be less difficult for arthropods to adapt to terrestrial locomotion than for teleosts, whose paired fins are poorly suited for this task. Despite all this, very few crustaceans have invaded inland habitats, presumably because numerous insects and arachnids already occupy these habitats.

This suggests that the failure of mudskippers (Periophthalmidae and close relatives) and other amphibious teleosts to become more fully terrestrial may reflect competitive exclusion, rather than intrinsic limitations of their bauplan or incompatible evolutionary pressures exerted by the intertidal environment. Another possibility is that these teleosts never acquired metabolic adaptations as good as those found in tetrapods to deal with nitrogen excretion outside the water. This possibility is raised by recent works which shows that most amphibious teleosts are ammonotelic (they produce ammonia, which is toxic and difficult to excrete in air) rather than ureotelic (Ip *et al.* 2004, p. 774). One of the few exceptions is *Periophthalmus sobrinus*, which excretes about as much urea as ammonia and can shift towards ureotelism when out of the water (Gordon *et al.* 1969). The infrequent occurrence of ureotelism in amphibious actinopterygians appears to be linked partly to its metabolic cost, which may be prohibitive in most teleosts species which developed alternative strategies for dealing with nitrogenous waste when out of the water (Ip *et al.* 2004).

Finally, Graham & Lee's (2004) analysis seems to rest on the hypothesis of 'tetrapod land life selection being driven by alternating (likely seasonal) periods of rain and drought.' That scenario was popular through much of the 20th century but has been discarded because, among other reasons, the redbeds on which that hypothesis rests are now known not to require seasonal aridity to form (Czyscinski *et al.* 1978; Laurin *et al.* 2007). This therefore deprives Graham & Lee's (2004) hypothesis from geological support.

Other arguments against a marine origin of terrestrial vertebrates proposed by Graham & Lee (2004) are similarly of limited value. Their argument (p. 727) that the waves exert an evolutionary pressure to increase body density is interesting, but it would not apply to most mangrove and lagoonal habitats. It might also apply less to large taxa (about 1 m body length) than to the much smaller

mudskippers, most of which are less than 15 cm in length (Graham & Lee 2004, p. 727). Thus, the reliance of extant tetrapods on lung ventilation is not a strong argument against their origin from coastal areas because the lung is probably an osteichthyan synapomorphy (Sullivan *et al.* 1998). It is not established that Devonian stegocephalians had larger or more complex lungs than their finned sarcopterygian relatives. Lung complexification in tetrapods may have occurred shortly before the origin of the crown-group, whose composition is controversial (Laurin 1998a, b; Ruta *et al.* 2003; Vallin & Laurin 2004; Ruta & Coates 2007) but which probably appeared only in the Early Carboniferous. Under some topologies, a terrestrial lifestyle may have been acquired in stem-tetrapods well before the origin of the crown because Seymouriamorphs and several temnospondyls, which may be stem-tetrapods, appear to have had terrestrial adults (Sumida *et al.* 1998; Sullivan & Reisz 1999; Laurin 2000; Laurin *et al.* 2004).

This brief discussion suggests a marginal-marine origin of terrestrial vertebrates, and reveals weaknesses in arguments that were presented to refute this hypothesis. However, the large amount of uncertainty in the data plainly shows that much additional work is required to reach a well-corroborated resolution. This will probably not be easy because similar controversies affect the habitat of other Palaeozoic taxa such as ostracodes; the oldest (Devonian) occurrence of that taxon in presumed freshwater is partly supported by association with 'freshwater fishes' (Friedman & Lundin 2001, p. 73)!

We thank P. Janvier and G. Clément for numerous suggestions which substantially improved the text. This research was funded by the CNRS and the French Ministry of Research (grants to UMRs 7179 and 7207). Funds for work in the Puertollano basin were provided by DGES projects PB95-0398 and PB98-0813 (MEC, Spain) and BET2002-1430 (Spanish Science and Technology Ministry).

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