

Habitat of early stegocephalians (Chordata, Vertebrata, Sarcopterygii): a little saltier than most paleontologists like?

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Abstract

A controversy on the degree of marine influence in the paleoenvironments represented by many Paleozoic stegocephalian-bearing fossiliferous localities has persisted for decades. Many authors have equated the absence of a typical stenohaline marine fauna with freshwater environments, but this ignores continental salt lakes and the many transitional environments (deltaic, estuarine, lagoonal, and some epicontinental seas that receive much freshwater influx, like the Baltic Sea) that separate typical marine environments from freshwater environments. This is problematic because it seems plausible that many of the late Paleozoic sediments that have been preserved were deposited on coasts in deltas and estuaries. The author had compiled a dataset of paleoenvironmental interpretations of Devonian to Early Permian stegocephalian (“tetrapod”)-bearing fossiliferous localities in 2010. How have these interpretations withstood the test of time, especially in the face of new results from different kinds of evidence? An updated dataset and a new literature review show that the case for a marine origin of stegocephalians has strengthened, especially through additional discoveries or reinterpretations of fossils that suggest marine influence in various classical vertebrate-bearing Permo-Carboniferous localities traditionally interpreted as freshwater, and a recent analysis of stable isotopes in Late Devonian localities.

Key Words

Amphibians, brackish, Carboniferous, Devonian, epicontinental seas, freshwater, marine environment, paleoenvironments, Permian, tetrapods

Introduction

Most early studies on Paleozoic stegocephalians have assumed that these taxa normally inhabited freshwater or dry land, unless their remains were clearly associated with typically marine fossils. This is exemplified by this quote from Milner (1987: 497):

“Most of the British and North American tetrapod localities represent water bodies within non-marine swamps and have generally been assumed to be in the freshwater regions of fluviodeltaic systems, not least because of the presence of amphibians as presumed freshwater indicators together with the absence of

unambiguously marine organisms.” (Emphasis mine in all quotes unless stated otherwise.)

Thus, the fact that most of the Devonian and Carboniferous stegocephalians were called “amphibians” (in the paraphyletic sense of “anamniotic limbed vertebrate”) probably played a role in this, even though parsimony does not validate the inference that these were freshwater taxa (Laurin and Soler-Gijón 2010).

This quote highlights the need for a precise nomenclature. Indeed, if the word “amphibians” had been consistently used in the sense that is now established under the PhyloCode (Cantino and de Queiroz 2020), as the lissamphibian total-group (Laurin et al. 2020), it

is possible that the paleoenvironment of many Permo-Carboniferous localities would have been interpreted more cautiously. Similarly, it may be useful to mention here the difference between Tetrapoda (or “tetrapods”), and Stegocephali (or “stegocephalians”) as used in this report. Both terms are here used as established under the PhyloCode. Namely, Stegocephali is defined as “The largest clade that includes *Eryops megacephalus* Cope 1877 (Temnospondyli) but not *Tiktaalik roseae* Daeschler et al. 2006, *Panderichthys rhombolepis* Gross 1930 (Panderichthyidae), and *Eusthenopteron foordi* Whiteaves 1881 (Osteolepiformes).” As such, it includes all known limbed vertebrates, and may conceivably contain some finned tetrapodomorphs, given that the fragmentary remains of the basalmost members of that clade, like *Elginerpeton* and *Ventastega*, cast doubt on the nature of their paired appendages (Laurin 2010). Tetrapoda is defined as the crown-group of limbed vertebrates, or the smallest clade that includes lissamphibians and amniotes, to simplify the definition provided by Laurin (2020a). As such, Tetrapoda is less inclusive than Stegocephali; it minimally excludes Devonian limbed vertebrates like *Acanthostega*, *Ichthyostega* and *Tulerpeton*, and under some phylogenies (e.g., Marjanović and Laurin 2019: fig. 14), it also excludes temnospondyls, embolomeres and seymouriamorphs. This review focuses on all stegocephalians, not only on tetrapods.

Many late Paleozoic fossiliferous localities lacking fossils of stenohaline, strictly marine organisms (such as echinoderms, cephalopods and coral reefs) have been interpreted as freshwater habitats, or the marine influence on such habitats has been minimized. However, factors other than low and fluctuating salinity may explain the absence of many stenohaline marine taxa; these include high sedimentation rates and turbidity (Feldman et al. 1993: 494), which are deleterious to filter-feeding, sessile organisms, as well as photosynthetic ones. Most contemporary estuaries and possibly tide-dominated deltas are precisely zones of maximal turbidity, because of tidal circulation and coagulation of clays resulting from mixing of fresh and salt water (Feldman et al. 1993: 494). This makes such environments difficult to recognize in the fossil record; the absence of typical marine taxa therein may well lead to erroneous interpretations of a freshwater environment.

Taxa found in these localities were often assumed to have been stenohaline, freshwater forms. Carpenter et al. (2011: 639) summarized this potential source of bias thus: “Traditionally, Pennsylvanian fishes have been classified either as marine or nonmarine (Calder 1998), the latter often taken to mean freshwater (Dick 1998).” Worse, they pointed out that “In very many cases, the mere absence of an associated stenohaline fauna and the co-occurrence of plant fossils have been cited as sure evidence for a freshwater habitat”. This comment could apply to the classical Texas Cisuralian redbeds, which include many of the most fossiliferous stegocephalian-bearing localities (Fig. 1). Yet, brackish water is not uncommon, especially along the coasts in deltas, estuaries, lagoons,

and large epicontinental seas, such as the Baltic Sea, and it seems that brackish habitats were widespread in the past too (Buatois et al. 1998, 2005; Falcon-Lang 2005). Furthermore, most sediments ultimately end up in the seas and oceans, with the continents providing only temporary storage (Hay 1998). Some rivers flow toward internal basins without connection to the seas, but these basins represent a small proportion of the emerged lands, and their main water bodies (e.g., Great Salt Lake in the USA, Dead Sea in the Middle East, etc.) typically contain saltwater (Moscatello and Belmonte 2009; Pagaling et al. 2009: 5751), which implies that the deltas and estuaries of rivers that flow into these salt lakes are brackish. Given that most sedimentation occurs in deltas and estuaries along the coasts (Peters and Husson 2017: 323) and that these environments are among the most favorable for fossilization, it seems plausible that most vertebrate fossils might come from such environments. However, the literature suggests that most Permo-Carboniferous stegocephalians that left a fossil record inhabited freshwater bodies, which may seem anomalous given where most of the long-term sedimentation occurs.

Determining the habitat of long-extinct taxa is difficult because sedimentation and regression/transgression cycles cause shorelines to move quickly in geological terms (Carpenter et al. 2011 and references therein), and carcasses can be transported before being buried and fossilized. Thus, progress on this front will ultimately require detailed inventories of taxa occurring in fairly narrow strata and with good geographic data. The literature is not as rich as we would like in such detailed studies, but the review below tries to summarize a representative sample of the data currently available, especially in the Famennian and Carboniferous and, to a lesser extent, in the Cisuralian.

Fortunately, some studies considered brackish habitats in their assessment of paleohabitats, but often still seem to have minimized the marine influence. This can be illustrated by the “Birthday Bonebed” of the Permo-Carboniferous Halgaito Formation (Utah), which was studied recently by Huttenlocker et al. (2018), who suggested (p. 87) that

Within the bonebed, microconchids, xenacanth, actinopterygians, and the lungfish Sagenodus suggest an assemblage that was to some degree dependent on permanent standing water. We interpret these stream systems, particularly those associated with the major tiered channel bodies, as primarily freshwater with little marine influence, though the microconchids and xenacanth potentially leave open the possibility of proximity to marine-influenced channel reaches (Carpenter et al., 2015; Ó Gogáin et al., 2016).

However, Huttenlocker et al. (2018: 87) concluded that the aquatic fauna preserved in the bonebed included “freshwater xenacanth, actinopterygians, and lungfish” (in addition to the aquatic to amphibious temnospondyl *Eryops* and some presumably more terrestrial



Figure 1. A *Dimetrodon grandis* chases an *Eryops megacephalus* and an *Edaphosaurus pogonias* through a *Sigillaria* forest. In the foreground, a *Meganeuropsis* flies near strobili of *Equisetum hyemale*; the ground is covered by mosses. Reconstruction of the Artinskian (Early Permian) in what is now Texas, USA. Drawing by Ruben Kooops (Haarlem, Netherlands), Rafael Albo (Corumbá, Brazil), Jacek Major (Starachowice, Poland), and Amin Khaleghparast (a biologist from Tehran, Iran); coloring by Ruben Kooops. Advisors for *Dimetrodon*: Tracy Lee Ford (San Diego, California, USA) and Russell J. Hawley (Casper, Wyoming, USA). Advice on plants was provided by Ryan Thummel and Paige K. Wilson Deibel (both at U. of Washington).

eupelycosaur amniotes). As this quote shows, a primarily freshwater interpretation is favored, despite the presence of microconchids, xenacanth, and dipnoans, three clades of marine origin. Of these, only dipnoans are still extant, and may thus have played a greater role, historically, in inferring paleoenvironments. Extant dipnoans inhabit freshwater and by the Carboniferous, some had already invaded freshwater environments, but other remained marine (Schultze and Soler-Gijón 2004: 341); thus, their presence in a Carboniferous locality does not resolve the degree of marine influence. Microconchids and xenacanth are frequently associated with early stegocephalians, which justifies a short review of their probable paleoenvironment (in dedicated sections below). The predominantly freshwater interpretation of the Halgaito Formation by Huttenlocker et al. (2018) is surprising given that they indicated (pp. 73–74) interfingering with a marine facies in the lower half of the formation. Given that the “Birthday Bonebed” is precisely in the lower half of this formation, the open sea (preserved in the marine facies) was presumably not far. Similarly, Huttenlocker et al. (2018: 86) reported results of their strontium isotopic analyses, and concluded that “These results are consistent with the hypothesis that tooth formation occurred in an environment with **some freshwater-influence**, supporting that the xenacanth associated with the

bonebed were either occasional or permanent residents of these **freshwater systems**.” Note how the indication of freshwater influence was used to infer that the xenacanth lived in freshwater. Why could the “Birthday Bonebed” not represent a marginal-marine, brackish-water environment? As we will see below, interpreting the isotopic signatures is not always straightforward.

I studied the problematic paleoenvironments inhabited by Permo-Carboniferous stegocephalians before (Laurin and Soler-Gijón 2010), but some important empirical studies were published since then, and my earlier study did not cover (or only superficially) some relevant topics, such as the probable habitat of some taxa frequently associated with Paleozoic stegocephalians; this new review attempts to fill some of these gaps, especially the probable habitat of various taxa frequently associated with stegocephalians, in the same temporal interval (Famennian to Kungurian). This paper first presents (below) evidence that marine influence has been minimized in many earlier studies, as shown for three examples; it then surveys briefly the main isotopic methods that have been used to assess paleosalinity. This is followed by sections on the paleoenvironmental significance of several taxa that are often associated with early stegocephalians. All of these data are then used to review the paleoenvironments of a few Famennian and Carboniferous localities

that have yielded stegocephalians; Cisuralian localities would be relevant too, but could not be included for lack of time and space.

Biased interpretation in favor of freshwater?

Unrecognized tidal deposits?

There are reasons to believe that the extent of marine influence in the habitat of early stegocephalians has been significantly under-estimated in the literature (see below). A similar bias against marginal-marine environments has recently been argued to be present in the paleobotanical literature, at least in the Carboniferous. DiMichele et al. (2023: 14) stated:

“Tidal environments have been identified in other areas, including in European basinal settings (e.g. Fossil Grove: Gastaldo 1986, reinterpreted as a tidal setting). Such deposits are likely much more widespread than recognized because of the difficulty of identifying tidalites in their nascent, very finely laminated stages, particularly in mudrocks (most likely to be encountered in the basal coal-roof transition strata found in mines close to channel environments, see Fig. 10a). However, the limited recognition of tidal-flat settings also may reflect that most palaeobotanists are generally unfamiliar with these kinds of strata”

This is hardly a new claim, though it remains highly relevant. Kuecher et al. (1990: 211) had already concluded, in their study of the Francis Creek Shale (in which the Mazon Creek biota is preserved) that “evidence of Westphalian tides may have been misinterpreted or overlooked in field studies elsewhere.” One of the reasons is that weathering can obscure the fine laminations; Kuecher et al. (1990: 212) indicated that cores were better for such studies, but most paleontological prospection or excavation does not entail coring. Kuecher et al. (1990: 219) observed that many Late Carboniferous coal deposits from Europe and North America were associated with fluvio-deltaic sediments interbedded with marine sediments, and that tidal rhythmites should be common in such deposits, and conjectured that many tidal rhythmites had been misinterpreted by previous authors as fluvial. The fact that the tidal rhythmites of Mazon Creek went unnoticed for about 30 years despite intensive geological field work there supports this suggestion (Kuecher et al. 1990: 219). Indeed, tidal rhythmites are now known from other Eastern Interior Coal Basin localities that were initially interpreted as non-marine (Archer et al. 1995: 408).

Schultze (2009: 127) had similarly pointed out that features typically interpreted as fluvial “can be produced by the extension of rivers into the intertidal area”, and indeed, recent research has shown previously

unrecognized similarities between sedimentary structures left by tidal channels and meanders formed by rivers (Finotello et al. 2018). More generally, Feldman et al. (1993: 485) stated that “Alternative interpretations are possible because nearly identical, varve-like, normally graded laminations can be produced in environments ranging from deep marine to shallow lagoons and freshwater lakes.” What characterizes tidal deposits is the cycles of thickness variation linked to tides and neap-spring cycles (Feldman et al. 1993: 494), but without thorough analysis, this cyclicity may go unnoticed. However, tidal currents can propagate far upstream of deltas, so that the presence of tidal rhythmites alone does not guarantee that water was brackish or of regular marine salinity (Feldman et al. 1993: 495).

Old Red Sandstone

This bias in favor of a freshwater interpretation is not restricted to formations and sites that have yielded early stegocephalians. Even older strata have arguably been affected by a similar interpretation bias. A good example is provided by the Old Red Sandstone (ORS from here on; this ranges from late Silurian to Early Carboniferous in age), which yielded many early vertebrates. Janvier (2007: 41) explained why the ORS was initially interpreted as a freshwater deposit:

“The first Silurian and Devonian fish remains described in the beginning of the nineteenth century were preserved in sandstones (e.g., the “Old Red Sandstone” of Britain and the Baltic States) and generally associated with plant remains, but rarely with marine invertebrates. In addition, these heavily armored fishes were regarded as “ganoids,” a group which classically included living bichirs, gars, and catfishes, all reputedly freshwater. Progressively, the received wisdom became that all these early fishes lived in freshwater and occasionally passed into the sea, when found in marine sediments.”

This may explain why Boucot and Janis (1983: 262) interpreted the “Vertebrate-eurypterid fauna” of the “Lyne Water Fish Beds” (Wenlock/Ludlow, Silurian) as non-marine (brackish or freshwater).

However, subsequent findings showed that some ORS was almost certainly deposited in a marginal marine environment as had been suspected already by some authors in the 1970s (e.g., Goujet and Blicek 1977). For some deposits, marine influence seems certain. Thus, Goujet and Emig (1985) described *Lingula* fossils from the top of the Wood Bay Formation (Emsian, Early Devonian) of Spitzbergen, in levels above those that yielded a diversified fauna of gnathostomes and jawless vertebrates. These deposits had previously been interpreted, based on sedimentological data and the absence of typically marine metazoans, as freshwater sediments (Friend and Moody-Stuart 1970), but

Goujet and Emig (1985) interpreted them as marine and suggested that the *Lingula* fossils represented individuals killed by a catastrophic event, such as a massive influx of freshwater following a storm or sudden short-term increase of water discharged by one of the nearby rivers. They also noted that the absence of brachiopods from the lower, vertebrate-bearing levels was not anomalous because shells of *Lingula* are fragile and are seldom preserved (Emig 1981). One of the earliest Sr isotopic studies of the ORS also concluded that at least some of its deposits seemed to be marine (Schmitz et al. 1991: 793).

Janvier (2007: 42–43) remained cautious about the paleoenvironment in which the ORS was deposited; he mentioned that some paleontologists considered that it had been deposited in marginal marine environments, whereas others viewed it as composed of freshwater deposits. Subsequently, isotopic analyses documented additional instances (in addition to the case reported by Goujet and Emig 1985) of ORS strata deposited in marginal-marine environments (Goedert et al. 2018; see section “Devonian localities”).

Escuminac Formation

The bias against marine influence is not restricted to vertebrate paleontologists. In her monograph on freshwater ecosystems in the fossil record, Gray (1988: 24) sharply criticized previous suggestions that the Escuminac Formation was deposited in a marginal marine (probably estuarine and brackish) environment:

“Similar in its defective logic and willingness to ignore the impressive data gathered by others concerning both depositional environment and characteristics of the biota, is Schultze’s (1972; Schultze and Arsenault, 1985) conclusion that the Late Devonian, freshwater-lacustrine, vertebrate faunas of the Escuminac Formation, Miguasha, Quebec, Canada are “coastal marine, based on the fauna present” merely because some of the genera are also found in undoubted marine deposits elsewhere in the world. Unwillingness to consider that any Devonian vertebrate might have been able to flourish in both marine and freshwater environments, as is the case with many taxa today, is biologically, as well as geologically, so unrealistic as scarcely to merit serious attention. With regard to the locality at Miguasha, the nearest known marine Upper Devonian beds are no closer than the Hudson Bay region, Canada, central New York, U.S.A., and the south of England.”

Yet, shortly after, a study based on isotopes of several chemical elements concluded that the *Bothriolepis canadensis* sample that they had included yielded “a strong marine signal” (Schmitz et al. 1991: 793). Similarly, Matton et al. (2012) showed that isotopic data from specimens of several taxa (in addition to *B.*

canadensis, these include the finned tetrapodomorph *Eusthenopteron foordi*, the dipnoan *Scaumenacia curta*, the actinopterygian *Cheirolepis canadensis*, and the acanthodian *Homalacanthus concinnus*) indicate significant marine influence, and this formation is now interpreted as a brackish estuarine environment, an interpretation supported by other types of data, notably the fossil record (Cloutier 2013).

These developments illustrate the danger of relying on previous reconstructions of ancient coastlines to assess local paleoenvironments (Schultze 1995, 2009: 129); if previous paleoenvironmental interpretations were erroneous, subsequent ones risk reinforcing previous misinterpretations, which hampers scientific progress. Another spectacular case of a marine-influenced paleoenvironment recognized far from the closest reconstructed paleo-coast is the Early Carboniferous Ducabrook Formation, where Parker and Webb (2008: 525) documented estuarine conditions about 400 km from the nearest open marine sediments.

El Cobre Canyon

A possible bias against even the presence of a modest marine influence may be visible in previous works on the Permo-Carboniferous El Cobre Canyon in New Mexico, which is typically considered to be a freshwater (fluvial) environment (Fracasso 1980; Lucas and Lerner 2010). Contrary to the few cases examined above, possible marine influence in El Cobre has not been evoked in the recent literature as far as I know. Yet, in one of the earliest studies of this locality, Williston and Case (1912) reported the presence of a brachiopod (initially called *Spirifer*, but later re-named *Anthracospirifer*), a typically marine taxon. This was dismissed by Langston (1953: 412), who stated that “It is unfortunate that the material of which Case’s specimen was composed was not recorded. Had it been limestone the question might have been resolved quickly since the only limestone in El Cobre Canyon is of Jurassic age (Todilto).” Because of this, Langston (1953) considered this brachiopod fossil “as intrusive and therefore of no stratigraphic [or paleoenvironmental] significance” for the vertebrate fauna preserved in El Cobre. There are several problems with this reasoning. First, the brachiopod fossil suggests a Pennsylvanian age, not Jurassic, so Langston’s (1953) assumption about the origin of the fossil does not seem plausible. Second, brachiopods need not come from limestone; they also occur in sandstone. In fact, some brachiopods, such as orthoids, are typically associated with siliciclastic environments, even though these environments are negatively correlated with brachiopod diversity (e.g., Jakobsen et al. 2014: 196). Third, Langston summarily dismissed a finding to which Williston and Case (1912) seemed to attach great importance; it is worth quoting the short passage on this topic (Williston and Case 1912: 6–7):

*“At the south side of the cañon, the junior author found a **perfect cast** of a Spirifer, identified by Professor Schuchert as *S. rockymontanus* Marcou, a form occurring in Colorado in the Pennsylvanian. Though the specimen was found free, so that its exact horizon could not be determined, its **excellent preservation proves conclusively that it had not been carried far from its original bed**, and inasmuch as vertebrate fossils are found in the deepest strata of the cañon it seems quite certain that the specimen came from an intercalated bed among those yielding so-called Permian vertebrates. No other explanation seems possible.”*

One might tend to prefer the opinion of more recent studies that benefited from additional decades of research, but the statements by Langston (1953: 412) suggest that he did not see the brachiopod fossil; how should this be weighted against the fact that Williston and Case (1912) found and saw the fossil?

The presence of this sole brachiopod fossil does not imply that sediments of all levels of the El Cobre Canyon were deposited in a marine-influenced environment; some data suggest otherwise. For instance, Utting and Lucas (2010: 73) reported that “No evidence was found of any marine palynomorphs such as acanthomorph acritarchs or scolecodonts.” However, their sample was restricted to “a 2 m shale bed in the middle part of the El Cobre Canyon Formation”, so their findings represent a small proportion of the deposits found in the canyon and are not incompatible with marine influence in other levels of the locality.

Other evidence suggests that there might be marine influence in El Cobre Canyon. Lucas and Lerner (2010) thus reported the presence of ichnofossils attributed to cf. *Paleohelcura tridactyla*, which may have been produced by scorpions, other arachnids, or eurypterids. In their discussion of the eurypterid prosoma assigned to *Adelophthalmus* from El Cobre canyon, Lucas and Lerner (2010: 40–41) stated: “These eurypterids inhabited shallow ponds or enclosed lagoons on the deltaic plain adjacent to the ancestral Cañon del Cobre area”. Lagoons and deltas may be brackish environments, and indeed, *Adelophthalmus* from the Red Tanks Member of the Madera Formation, a few tens of km away (Kues and Kietzke 1981; Braddy et al. 2021), is clearly from a marginal-marine, brackish environment (see below, section on eurypterids). While Lucas and Lerner (2010) clearly preferred to interpret the ichnofauna that they described as a freshwater assemblage, their reference to lagoons and a deltaic plain suggests that the sea was not far. Another quote from Lucas and Lerner (2010: 41) reinforces this impression: “There is a single prior Pennsylvanian record [of cf. *Paleohelcura tridactyla*], which comes from a **tidal flat** setting in the McAlester Formation of Oklahoma (Lucas et al. 2004). There are no previous North American records of *Paleohelcura* from lacustrine settings.” One might add that the McAlester Formation of Oklahoma in which *Paleohelcura tridactyla*

was reported also yielded “a few impressions of the shells of marine gastropods” (Lucas et al. 2004: 45). Could at least some levels of El Cobre Canyon document brackish water assemblages?

Autochthonous or allochthonous stegocephalian remains?

An important consideration in paleoenvironmental studies is the autochthonous or allochthonous nature of the fossils preserved in a given locality. Only autochthonous fossils are informative in this respect. Allochthonous fossils provide information about more distant environments. In most cases, only fairly long-distance transport (several km) can be easily detected, through wear marks (erosion) on the surface of fossils, disarticulation, and the fragmentary nature of specimens (for instance, only a few isolated bones, rather than a nearly complete, articulated skeleton). Abundance of material can also be used, to an extent, in combination with quality of preservation (Bennett et al. 2021: 15), because erratics are likely to be allochthonous. However, even for localities that have been subjected to detailed taphonomic studies, such as Jarrow, it is difficult to know if the stegocephalians are preserved in their environment or if they were transported over relatively short distances (Ó Gogáin et al. 2022: 15). In other cases, it looks like some fossils are allochthonous, whereas others (including vertebrates) seem to be autochthonous (Bennett et al. 2021: 18). When there is evidence of transportation, it is generally assumed that carcasses have been carried by rivers from a more continental environment, although the possibility that it was washed in by tides or storms from a more marine environment, while less likely, cannot be ruled out either, as emphasized by Gierlowski-Kordesch and Cassle (2015: 210–211).

In a few cases, transportation can be ruled out, even for fairly short distances. Some fossils of sessile organisms are obviously preserved in situ; this may occur for brachiopods, coral-forming organisms (especially cnidarians), some echinoderms and some mollusks, among others, but not vertebrates, unless they are found in burrows (a few examples are known, notably for dipnoans). Other compelling but rarer cases are found when evidence of predation is encountered, which suggests, minimally, that predator and prey occupied the same habitat, although this does not rule out transport of the bodies over a short distance. An example is described below, of a shark (*Triodus sessilis*) that ate a temnospondyl that had eaten an acanthoderm (Kriwet et al. 2008). Such fossils provide excellent information on the local paleoenvironment, and such examples are described in a few localities below.

Another type of fossil that nearly always reflects local paleoenvironments are ichnofossils. The identity of the trackmakers is often poorly constrained, but some ichnofossils are associated with specific paleoenvironments and as such, they may be informative. They are even more

useful when the identity of the trackmaker is reasonably well-constrained. An example is provided by the ichnofossils of Puertollano (Spain), which includes an interesting assemblage of trackways left by a stegocephalian and traces left by a finned vertebrate that swam above the substrate. The trackway, called *Puertollanopus microdactylus*, was left by a small stegocephalian, tentatively identified as an amphibian (a “microsaur”) or, less probably, an amniote. The traces left by a gnathostome that swam above the substrate, presumably in shallow water, are called *Undichna britannica*, and they were probably left by the xenacanthid chondrichthyan *Orthacanthus*, which is also known by skeletal remains from the locality (Soler-Gijón 1997). Several instances of superposition of both tracks are explained by tides, with the stegocephalian footprints being left at low tide, while the swimming traces were left at high tide (Soler-Gijón and Moratalla 2001).

Isotopic signal and paleosalinity

Basic principles and limits of isotopic methods to assess paleosalinity

The isotopic ratios of various elements have been used to assess paleoenvironments, notably to shed new light on the degree of marine influence and paleosalinity in various fossiliferous localities. We saw above that Huttenlocker et al. (2018: 86) concluded, from their strontium isotopic analyses, that the Halgaito Formation had formed in a freshwater environment. Earlier, Fischer et al. (2013) had also concluded, based on isotopic analyses of oxygen and strontium, that many vertebrate-bearing European Permo-Carboniferous localities (including, among others, Buxières-les-Mines and Nýřany) represented freshwater environments lacking any detectable marine influence. Similar conclusions, following similar reasoning but based on isotopes of other elements (carbon, oxygen and sulfur), were drawn about the Bourbon-l’Archambault Basin, which contains xenacanthiform chondrichthyans, by Luccisano et al. (2023: 8).

As we will see below, some of these conclusions may rest on tenuous ground because the isotopic signature of strontium reflects freshwater input and flux between a given water body and the ocean, rather than salinity; a similar phenomenon has been documented for neodymium by Woodard et al. (2013: 57) and (to a lesser extent) for carbon by Quinton and Rygel (2023). However, a conclusion based on recent analyses of isotopes of other elements (especially on sulfur) might be more robust (Luccisano et al. 2023: 8). Strontium (Sr) has been the most intensively studied element in this respect, so to an extent, the discussion below will emphasize this, but other elements, such as carbon (C), oxygen (O) and sulfur (S), which were used in some recent studies, are also discussed below.

The $^{87}\text{Sr}/^{86}\text{Sr}$ ratio (^{87}Sr being the radiogenic isotope) has varied through time, but oceanic mixing appears to have resulted in fairly homogeneous world-wide $^{87}\text{Sr}/^{86}\text{Sr}$ oceanic values at any given time. By contrast, freshwater

bodies have much more variable ratios at any given time because these ratios depend on the $^{87}\text{Sr}/^{86}\text{Sr}$ signature of the soil and bedrock in the drainage basins. Thus, if the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of a given sediment matches the contemporary oceanic ratio, the sediments were probably deposited in oceans, although in a small minority of cases, the similarity might be coincidental. Conversely, a significant departure from the coeval $^{87}\text{Sr}/^{86}\text{Sr}$ oceanic ratio (beyond measurement error and outside two standard deviations) indicates that the Sr in the water body in which the sediments were deposited was not at equilibrium with oceanic values. This indicates that little or no exchange with the ocean took place. Several studies have interpreted such cases as representing freshwater, but this is only one of several other possibilities; the others include brackish water, which may be purely continental, far from the coasts, but also coastal (ponds, lagoons, estuaries and deltas), and even some epicontinental seas, such as the Baltic Sea.

Thus, interpreting the isotopic signature of Sr in terms of salinity is not straightforward. Purely continental salt-water lakes have a Sr isotopic signature that reflects that of the rivers that flow into it, and brackish coastal environments, such as the Baltic Sea, show strong deviations from oceanic signatures, especially where the freshwater influx is greatest; for instance, Andersson et al. (1992) reported a value as high as 0.709718 ± 41 in the most freshwater part of the Baltic (Gulf of Bothnia, close to the deltas of the Kalix and Kemi rivers), which is about 0.000568 (568 parts per million) higher than their measured value for the Atlantic Ocean (0.709150 ± 24). Fairly strong departures from the marine Sr isotopic ratio (and presumably in isotopic ratios of other elements) can occur in marginal marine basins when limited flux occurs between that basin and the ocean, especially when much of the water outflow is through evaporation; in this respect, the Baltic Sea is probably not the most spectacular example. This occurred in the Mediterranean, in the Messinian salinity crisis, and Flecker et al. (2002: 227) concluded that “excluding net evaporation from the hydrologic budget of the Mediterranean could result in an **order of magnitude error** in the palaeosalinities inferred from Sr isotope data.” Furthermore, many parts of the Mediterranean developed their own Sr isotopic signature shortly before the Messinian salinity crisis (Flecker et al. (2002: 228). This is surprising because Sr concentration in oceans is about 7.7 ppm (parts per million), which is over a hundred times more than in freshwater (Andersson et al. 1994). This great disparity in abundance should make the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio efficient to detect even a small amount of marine influence, but as shown by Flecker et al. (2002), under even moderate restriction of water flux and fairly strong evaporation, sharp departures from oceanic values can be observed.

Epeiric seas may not reflect oceanic isotopic values, as exemplified by the extant Baltic Sea (Andersson et al. 1992, 1994; Carpenter et al. 2011: 650). Large inland seas may also form, as shown by the fate of the Paratethys, which remains in a much-reduced state as the brackish Black, Caspian, and Aral seas, and in which typically

marine faunal components have fluctuated over time, depending on the opening and closing of connections with the ocean (Richards et al. 2018; Dewaele et al. 2022). Even basins located far from any coast and without any link to the sea may be brackish or even hypersaline, and in these cases, Sr isotopic values may not reflect paleosalinity. Salt lakes are not rare in deserts, and even occur in moderately dry environments (e.g., Moscatello and Belmonte 2009; Borzenko 2020). Hypersaline lakes may occur at high altitude, very far from the nearest sea; for instance, the hypersaline lake Salar Guayatayoc in Argentina is located at 3432 m above sea level (Pagaling et al. 2009: 5751). A large, perennial salt lake was present in what is now northern Germany in the Rotliegend, at least by the Guadalupian (Gast 1991), or perhaps toward the end of the Cisuralian (Verdier 1996), and smaller salt lakes may have occurred elsewhere in the Carboniferous and the Permian. The isotopic signatures of such water bodies may differ substantially from marine levels, but they are not freshwater environments.

Sulfur (S) has also been used as a paleosalinity indicator in some recent studies. As for Sr, S is highly variable in freshwater environments, with $\delta^{34}\text{S}$ values ranging from -20.0 to $+20.0$ ‰, whereas current oceans have a $\delta^{34}\text{S}$ value of about $+21.0$ ‰ (Goedert et al. 2020). $\delta^{34}\text{S}$ values are very useful paleosalinity indicators because S is much more abundant (about a hundred times) in the oceans and seas than in freshwater, so even a little oceanic water diluted in much freshwater should leave an isotopic signature. However, the same argument can be made for Sr, which does not prevent significant deviations from oceanic isotopic ratios in basins with limited (or no) exchange with the ocean, especially when much evaporation occurs (see above). The $\delta^{34}\text{S}$ values of a water body also depend on the source of S, which can come from dissolution of evaporites in a drainage basin. In that case, the $\delta^{34}\text{S}$ values would reflect those of the oceans in which the evaporites precipitated, which may be much older than the salt or brackish lake, and this creates an additional difficulty given the fluctuation of the $\delta^{34}\text{S}$ oceanic values over time, which have varied between about 10 and 40‰ just in the Phanerozoic, and with uncertainties for some ages in of up to 10‰ (Wu et al. 2014). These phenomena complicate interpretation of $\delta^{34}\text{S}$ values because atypical cases of freshwater rivers with fairly high $\delta^{34}\text{S}$ values and saline springs with fairly low $\delta^{34}\text{S}$ values have been documented even in Canada (Hitchon and Krouse 1972). Thus, purely continental, but brackish or salty lakes, can have non-marine $\delta^{34}\text{S}$ values. A well-known example is the Great Salt Lake, which is strongly hypersaline and for which $\delta^{34}\text{S}$ values of $+14.6$ and $+17.1$ ‰ have been reported (for different dates) by Mayo and Klauk (1991: table 4). Numerous saltwater lakes (some of which are hypersaline) in Eastern Transbaikalia have been studied by Borzenko (2020), who showed that their $\delta^{34}\text{S}$ display a great range of values, from -8.4 to 27.4 ‰. Such environments, which must have existed in a distant past, might be challenging to model using $\delta^{34}\text{S}$ data. Thus, as for Sr, S

isotopic data is more useful to assess the degree of marine influence than for paleosalinity.

A third element that has been used to assess paleosalinity is oxygen (O). Current oceanic seawater has a relatively uniform $\delta^{18}\text{O}$ value of 0 ± 1 ‰, although it is lower at high latitudes, ranging from about -3 to -1 ‰ (Goedert et al. 2020), and this value has changed over time (Veizer et al. 1999). Current freshwater $\delta^{18}\text{O}$ is more variable and ranges from -6 and -2 ‰ at low latitudes to about -15 ‰ at high latitudes. Hypersaline water (in lakes, lagoons and sabkhas) can have $\delta^{18}\text{O}$ values higher than 2‰. Thus, comparing the $\delta^{18}\text{O}$ inferred for an ancient water body to that inferred for the contemporary oceanic values, and considering the inferred paleolatitude of the water body, the $\delta^{18}\text{O}$ can provide valuable data about whether that water body was part of a sea, an estuary, or a purely continental environment. However, contrary to Sr and S, there is as much O in freshwater as in marine water, so the $\delta^{18}\text{O}$ should be less sensitive to detect a small proportion of seawater in a water body than methods based on Sr and S. Thus, the $\delta^{18}\text{O}$ may be less useful to assess presumed brackish environments than $\delta^{34}\text{S}$ and the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio. Also, the $\delta^{18}\text{O}$ value of apatite (found in bone, dentin and enamel) differs from that of the ambient water, but there is a linear relationship between the $\delta^{18}\text{O}$ of both substances (ambient water and apatite of animals living therein). Additional factors complicate further interpretation of apatite $\delta^{18}\text{O}$ values because it is also affected by thermo-metabolism (thus differing between ectotherms and endotherms), evaporative transcutaneous water loss, and varies among taxa (Goedert et al. 2020: fig. 1).

Paleosalinity assessed through isotopic methods: a few case studies

Isotopic analyses have been used to assess the paleoenvironment of many fossiliferous localities, but their relevance in this context can be analyzed through the example of the Joggins Formation, which has yielded a rich metazoan fauna, including many vertebrates, including some stegocephalians. On the basis of isotopic analyses, Brand (1994: 314) concluded that “The higher Sr ratio of the Joggins bivalves relative to its marine counterparts **unequivocally proves** the non-marine (continental) affinity of these fossils and their enclosing sediments.” His analyses were based on *Naiadites* bivalves, which are often interpreted as a freshwater taxon (see below, section on xiphosurans). This is not necessarily incongruent with more recent interpretations (see below), given that Brand (1994) sampled one of the most freshwater-adapted faunal elements from one of the levels with the least marine influence, but these results may not be as robust as initially suggested. For instance, in the graph of the $\delta^{13}\text{C}$ vs. $\delta^{18}\text{O}$ (Brand 1994: fig. 6), the *Naiadites* samples fall close to the marine (brachiopod) samples, but a «mineralogical adjustment» to correct for assumed diagenesis is invoked (especially for the $\delta^{13}\text{C}$) to interpret these bivalves as freshwater forms, which

suggests that diagenetic effects may hamper straightforward interpretation of these results. In any case, many factors influence carbon isotopic ratios, and their effect is neither simple nor fully understood (Quinton and Rygel 2023), and various studies have shown that carbon isotopic ratios are not suitable to discriminate between marine and freshwater environments (Luccisano et al. 2023: 10). Thus, carbon isotopes are not discussed further in this review. Similarly, Brand (1994: 314) reported a $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of >0.7093 from “two well-preserved bivalves from the uppermost unit of the Joggins Formation”, and indicated that these “are at variance with that of coeval data (<0.7085) based on marine invertebrates.” However, his graph of the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio over time (Brand 1994: fig. 7) shows a spike in the late Westphalian A at >0.7091 , which is close to the Joggins sample both temporally and in isotopic value (the difference is less than the observed range within the Baltic Sea; see above). Brand (1994) did not seriously consider the implications of this spike (which is briefly evoked in his text), probably because the spike was located, in Brand’s (1994) figure, slightly earlier than Joggins. However, considering stratigraphic uncertainties in such cases is critical, and indeed, Joggins is now considered a little older than previously thought (Carpenter et al. 2015; Rygel et al. 2015). Thus, the Sr isotopic signal found by Brand (1994) seems to give a weaker, less convincing continental signal than initially suggested, and as explained above, “continental” does not necessarily imply “freshwater”. Through comparisons with the Baltic Sea, Falcon-Lang (2005: 491) interpreted Brand’s (1994) results more categorically as “entirely consistent with brackish-water conditions.” Carpenter et al. (2015: 681) reached similar conclusions based on new analyses of two specimens.

Isotopic data are also directly relevant to assess the habitat of early stegocephalians and their associated fauna. Among the latter, xenacanthiform chondrichthyans are especially relevant and are discussed below. Some xenacanthids were found in marine sediments (Hampe and Ivanov 2007), but most were found in localities that have traditionally been interpreted as freshwater environments as suggested by Luccisano et al. (2023), who performed isotopic analyses by of the localities of Buxières-les-Mines (Bourbon-l’Archambault Basin, Allier) and the Muse (Autun Basin). These sites probably both date from the Asselian (Pellenard et al. 2017; Luccisano et al. 2022; Mercuzot et al. 2022).

Luccisano et al. (2023: 8) reported that the $\delta^{34}\text{S}$ values of the xenacanthiforms and other vertebrates from Buxières-les-Mines are “lower than 12‰ with variations from -6.0‰ to 9.6‰ for unaltered samples”, whereas those from the Muse “range from 1.2‰ to 6.9‰ ” and concluded that “Those samples are depleted in heavy isotope by at least 3‰ and on average by 10‰ compared to seawater.” The samples that displayed the highest $\delta^{34}\text{S}$ values (the closest to contemporary marine values) and might have inhabited brackish water for at least part of the time (according Luccisano et al. 2023) belong to an actinopterygian and two temnospondyl samples. Luccisano

et al. (2023) based their estimate of a marine water $\delta^{34}\text{S}$ close to 12‰ near the Carboniferous-Permian transition on Claypool et al. (1980), which is a fairly old study. Nevertheless, the more recent isotopic curves by Wu et al. (2014) yield similar values, while showing also substantial uncertainty on the estimates. The analyses of Fischer et al. (2013) also suggested a fairly continental habitat for most of the European localities that they studied, and for the chondrichthyans (hybodontiforms and xenacanthiforms) that inhabited them. To sum up, these $\delta^{34}\text{S}$ results show deviations from the inferred coeval marine values, which implies negligible water exchange with the marine environment and suggest freshwater environments, but this does not necessarily rule out purely continental brackish environments.

The $\delta^{18}\text{O}$ values obtained by Luccisano et al. (2023) from Buxières-les-Mines are less convincing. The $\delta^{18}\text{O}$ values from the Muse xenacanthiforms range from 17.3‰ to 25.1‰, whereas vertebrates from Buxières-les-Mines yielded values around 17.0‰. Permian conodonts, which are thought to be representative of contemporary seawater, have a $\delta^{18}\text{O}$ is in the range of 21‰–23‰, an interval that is encompassed by the $\delta^{18}\text{O}$ values of Buxières-les-Mines xenacanthiforms. Luccisano et al. (2023: 10) nevertheless concluded that their results “may reflect ^{18}O -enriched water due to large evaporation rates that commonly take place in arid environments.” This is plausible, but these $\delta^{18}\text{O}$ values (contrary to the $\delta^{34}\text{S}$ values) are not independent evidence that the Buxières-les-Mines xenacanthiforms had not ventured in marine-influenced environments, and large evaporation rates are compatible with continental brackish lakes. These results are not entirely congruent with those of Fischer et al. (2013) on Buxières-les-Mines, which appeared to be one of the most continental localities, with a $\delta^{18}\text{O}$ of 16.6‰. By contrast, shark teeth from Puertollano, which is probably a paralic, brackish environment (Soler-Gijón and Moratalla 2001; Laurin and Soler-Gijón 2006; Soler-Gijón and López-Martínez 2008), yielded an average $\delta^{18}\text{O}$ of 18.5‰ (with a single value at 20.2‰), and shark teeth from the marine locality of Kalinovskie Vyselki quarry of the Moscow region yielded only a slightly higher $\delta^{18}\text{O}$ of 19.6‰ (Fischer et al. 2013: table 1). The lack of discriminating power in the $\delta^{18}\text{O}$ values obtained by Luccisano et al. (2023) is unsurprising because extant taxa display considerable variability in this respect, with some significant habitat-related differences, but also some overlap between freshwater, marine and terrestrial taxa (Goedert et al. 2020: fig. 1). There is also some uncertainty about the value of oceanic $\delta^{18}\text{O}$ over time; Luccisano et al. (2023: 9) disagreed with Fischer et al. (2013) about the minimal $\delta^{18}\text{O}_p$ (the lowerscript “p” stands for “phosphate”) value (22‰ vs 18‰) that would suggest a truly marine signal. However, the fact that Fischer et al. (2013:50) reported mean values of $\delta^{18}\text{O}_p$ of 19.6‰ for shark teeth and 21.1‰ for conodonts from the “unequivocal marine facies” of the Kalinovskie Vyselki quarry near Moscow supports Fisher’s (2013) use of their lower threshold (18‰) for a marine signal.

Luccisano et al. (2023: 8) concluded that “In light of the bioapatite $\delta^{34}\text{S}$ values, the environment of Buxières-les-Mines and the Muse OSB do not seem to have been subjected to significant marine influences contrary to what was assumed in previous studies”. While this seems plausible, especially in light of the findings of Fischer et al. (2013), this only implies that Buxières-les-Mines appears to represent a continental locality, plausibly freshwater, but possibly also a brackish basin with little or no water flux with the ocean. It also suggests that the vertebrates that lived there, including the xenacanthids, appeared not to have ventured into the oceans.

A slightly different picture emerges for the xenacanthiforms from Joggins; the few Sr isotopic analyses performed by Carpenter et al. (2015), on two specimens (a xenacanthid tooth and a sarcopterygian scale) suggested that the $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of 0.710338 ± 83 (cf. *Xenacanthus*) and 0.7097772 ± 300 (cf. *Rhizodopsis*) was slightly higher than that of the Pennsylvanian oceans, which they considered to be typically ≤ 0.7083 , and this implies at least a major freshwater contribution to the environment. However, Carpenter et al. (2015: 680) noted that higher values for Pennsylvanian epicontinental seas had also been reported. Indeed, Woodard et al. (2013) reported values of up to 0.7105 for Patlanoaya (for a sample dated from about 306 Ma), but suggested that these high values reflected alteration, as suggested by the “conodont color alteration index”. Carpenter et al. (2015: 681) concluded that these results for a xenacanthid from Joggins were “equivocal, merely indicating that the environment was unlikely to have been fully marine”, which is consistent with a restricted, brackish sea similar to the Baltic Sea, when taking into consideration other sources of information, such as the fossil community found at Joggins (see section on Joggins below). Isotopic works on the habitat of the xenacanthiforms from Buxières-les-Mines and the Muse suggests a much more continental and much less salty environment, plausibly freshwater; hence, isotopic data suggest that xenacanthiforms occupied various habitats, and other lines of evidence support this conclusion (see next section).

Taxa associated with Permo-Carboniferous stegocephalians and their paleoenvironmental significance

Freshwater chondrichthyans?

Today, the vast majority of extant chondrichthyans are strictly marine; only 43 species (less than 4% of elasmobranch species currently recognized) venture into freshwater (Carpenter et al. 2011: 651 and references cited therein). Fewer still reproduce there (Feitosa et al. 2016, 2020); all of these are viviparous, as extensively documented in the only extant strictly freshwater chondrichthyans, the Potamotrygonidae, also known as

freshwater stingrays (Charvet-Almeida et al. 2005). This may not be a coincidence because only about 40% of the extant chondrichthyan species are viviparous (Dulvy and Reynolds 1997). Thus, no extant chondrichthyan lays eggs in freshwater environments. This raises doubts about the traditional interpretation of various Permo-Carboniferous localities that have yielded fossilized chondrichthyan eggs but were nevertheless interpreted as freshwater paleoenvironments. These include the Mazon Creek Lagerstätte (Schultze 2009), in which a range of marine to freshwater paleoenvironments were recognized until recently (Baird et al. 1985). However, the presence of chondrichthyan eggs, among others, suggests that there was no freshwater fauna there (Clements et al. 2019).

Xenacanthiforms are the chondrichthyans most frequently associated with Permo-Carboniferous stegocephalians (Fig. 2). They apparently lived in the same environments at least occasionally, as shown by a spectacular discovery of a *Triodus sessilis* specimen that had ingested two temnospondyls (*Cheliderpeton* [now *Glanochthon*] *latirostre* and *Archegosaurus decheni*); these temnospondyls were apparently not washed-in carcasses because the *Glanochthon* specimen had remains of *Acanthodes bronni* in its abdominal region, which suggests that all these taxa shared the same habitat (Kriwet et al. 2008). For the reassignment of *Cheliderpeton latirostre* to the more recent taxon *Glanochthon* that was erected partly for this purpose, see Schoch and Witzmann (2009). Xenacanthiforms have long been interpreted as freshwater sharks (Jain 1980; Kohring 1995: 263; Dick 1981, 1988; Kriwet et al. 2008), and would then be the first freshwater chondrichthyans (Compagno 1990). This once-widespread opinion may have resulted from their frequent occurrence in Pennsylvanian Coal Measures (Hampe 2003; Carpenter et al. 2011: 650) and with stegocephalians, which are often called (inappropriately) “amphibians”. The latter is not a good argument, but some isotopic data support this interpretation, as mentioned above (Fischer et al. 2013; Luccisano et al. 2023). However, occurrences in marine environments were subsequently documented by many studies. In fact, *Diplodoselache woodi*, which may well be one of the earliest and most basal xenacanthiform, was found in what Dick (1981: 111) interpreted as a large lagoon that was frequently isolated from the open sea by a sand bar, and *D. woodi* appears to have inhabited the lagoon (rather than representing an allochthonous element). This suggests a brackish environment. Hampe and Ivanov (2007) described xenacanthiform teeth for which they erected the nominal species *Triodus teberdaensis* in marine carbonates from the Pennsylvanian Tolstiy Bugor Formation (Moscovian) of Karachay-Cherkess Republic (Russia), and geologically older marine occurrences had been documented earlier, as in the Middle Devonian limestones of the Rhenish Schiefergebirge (Stritzke 1986). Similarly, the basal conglomerate of the Hamilton quarry has yielded teeth of *Xenacanthus*, *Orthacanthus* and a cochliodontid chondrichthyan, in a clearly marine association that includes echinoderm ossicles, brachiopods



Figure 2. The temnospondyl *Eryops megacephalus* leaps to seize a small chondrichthyan (*Xenacanthus*). While the co-existence of both taxa is well established, the environment that they occupied (freshwater, brackish water, or even a marginal marine environment) remains enigmatic. Amin Khaleghparast (a biologist from Tehran, Iran) drew the figure, which was colored by Dmitry Bogdanov (a cardiologist and paleo-artist from Chelyabinsk, Russia); Roman Yevseyev (Moscow) adjusted the legs. Anatomical advice was provided by Tracy Lee Ford (San Diego, California, USA) and Bryan Riolo (Ocala, Florida, USA).

(some of which are in growth position), fusulinids and corals (Cunningham et al. 1993). Xenacanthiforms have also been documented in coastal, probably brackish environments, such as the Kasimovian Cohn Coal Member of the Mattoon Formation in Illinois (Carpenter et al. 2011). In the Cohn Coal Member, xenacanthiforms co-occur with microconchids, often called “*Spirobis*” or “spirorbids” in the older literature, which were probably euryhaline organisms living mostly in brackish water (see below). Carpenter et al. (2011: 650) listed several other reports that showed that xenacanthiforms are “intimately associated with brackish and marine fauna”. In fact, many xenacanthiforms seem to have disappeared from the British Coal Measures in the Bolssovian substage (Hampe 2003), in which the last marine incursion in the British Pennsylvanian occurred (Waters and Davies 2006). Carpenter et al. (2011) suggested that these events are causally related; the extinctions would then imply that few xenacanthiforms could survive in freshwater. Furthermore, growth patterns in *Orthacanthus* from Spain have been interpreted as reflecting tidal cycles (Soler-Gijón 1999).

As we saw above (isotopic section), the $\delta^{34}\text{S}$ results on xenacanthiform bioapatite obtained by Luccisano et al. (2023) from the localities of Buxières-les-Mines

(Bourbon-l’Archambault Basin, Allier) and the Muse (Autun Basin) implied that these taxa did not venture into the open ocean. This suggests that at least some xenacanthiform populations lived far from the open ocean. However, note that other studies have not excluded the possibility of at least temporary marine influence in the Bourbon-l’Archambault Basin. For instance, Steyer et al. (2012: 514) speculated that the mass mortality of the seymouriamorph *Discosauriscus* in the Franchesse locality (about 20 km North-North-East from Buxières) might have resulted from temporary and sudden flooding, potentially of salty water from the North Sea, which is plausible according to some paleogeographical reconstructions.

Collectively, xenacanthiforms appear to have inhabited both continental, plausibly freshwater (at Buxière-les-Mines and the Muse) and marine environments (represented in other localities), and most frequently environments transitional between these, but this does not imply that each xenacanthiform species inhabited all these environments. Perhaps, as in extant teleosts, there may have been freshwater, marine, and euryhaline taxa, but so far, we have a highly incomplete picture of xenacanthiform environmental preferences.

Freshwater microconchids?

Microconchids (often called “*Spirorbis*” in the older literature) are often associated with Permo-Carboniferous stegocephalians. Their paleoenvironmental significance is thus relevant to assess the habitat of early stegocephalians. Note that microconchids have often been called “*Spirorbis*” in the older literature, but the latter is an extant marine annelid, and the coiled calcitic tubes encountered in fossiliferous localities older than the Cretaceous were not formed by annelids, but rather, by microconchids (Taylor and Vinn 2006). The fossil record of microconchids extends from the Late Ordovician to the Middle Jurassic (Zatoń et al. 2012: 603). They originated in the marine environment, but subsequently became adapted to other habitats (Zatoń et al. 2012: 604). What these habitats were is to an extent controversial. Microconchids undoubtedly occurred in brackish, marine-influenced coastal environments, but their presence in truly freshwater environments is contentious. Some authors seem certain that microconchids inhabited freshwater for part of their evolutionary history, from the early Devonian to the Late Triassic (Zatoń et al. 2012: 606), but others suggested that they are not found in freshwater, but only in brackish, marine-influenced environments, such as estuaries and deltas (Gierlowski-Kordesch and Cassle 2015). A vigorous exchange took place recently between the proponents of these opposing points of view (Gierlowski-Kordesch et al. 2016; Zatoń et al. 2016).

To assess the validity of these opposing claims, I checked the most relevant data presented by Zatoń et al. (2012: table S1, appendix A). I restricted my scrutiny to the interval ranging from the Middle Devonian to the Early Permian because this is the temporal interval relevant to the origin of stegocephalians and to their great evolutionary radiation that gave rise to the first amphibians (the total clade of lissamphibians; Laurin et al. 2020) and amniotes. In that interval, four occurrences were listed as fresh to brackish water (hence, uncertain salinity), but only two (both from the Late Carboniferous, one in Ohio and the other one from England) were indicated to be freshwater (rather than brackish). These two cases should thus provide the strongest evidence supporting the presence of microconchids in freshwater and will be examined critically.

The Ohio occurrence is justified by a conference abstract (Lewis and Dunagan 2000), which indicates that this occurrence is from the Conemaugh Group. However, in a more recent assessment of this occurrence, Martino (2016: 142) interpreted the significance of microconchids differently:

“Their presence indicates a marine connection and probable brackish influence (Schultz[e], 2009; Gierlowski-Kordesch and Cassle, 2015). Two occurrences of microconchid-bearing ‘nonmarine’ limestones in the Glenshaw Formation have been re-interpreted as brackish, clear water, nearshore facies (Morris, 1967; Busch and West, 1987)”

Indeed, Busch and West (1987) had previously indicated that the microconchids, which he called “spirorbid annelids”, occurred during a major transgression, in “intertidal-supratidal ponds”. Thus, this record, rather than supporting the occurrence of microconchids in freshwater, suggests that these records occurred in a marginal-marine, brackish environment.

To support the presence of “freshwater” microconchids in the Westphalian (Late Carboniferous) of England, Zatoń et al. (2012: table S1, appendix A) cited a book on British regional geology to which I have no access. However, Lomax et al. (2016) described Westphalian microconchids from Yorkshire, which I will consider representative of the record alluded to by Zatoń et al. (2012). In that locality, microconchids co-occur with xiphosurans and shark egg capsules, both of which (especially the latter) suggest a significant marine influence (see section “Freshwater chondrichthyans”). Thus, neither of these supposedly freshwater occurrences of microconchids stands up to scrutiny.

Before closing this section, it may be useful to discuss a recent study that clearly sides with the interpretation that some microconchids occurred in freshwater, even though this concerns taxa that occur after the temporal interval considered in this paper (namely, in the latest Permian and early Triassic). Shcherbakov et al. (2021) interpreted the Early Triassic Petropavlovka Lagerstätte as a freshwater ecosystem, but its fauna includes xiphosurans, which, as I demonstrate below, (next section) suggest marine influence. They did not completely rule out the possibility that the Petropavlovka Lagerstätte represented a brackish water assemblage, but they seemed to prefer a freshwater interpretation (p. 1345) because several temnospondyls (which they call “amphibians”) “have never been recorded in assemblages with marine fossils” and because dipnoans are also present in the Lagerstätte. About the latter, they stated that “the overwhelming majority of the Permian and later dipnoans were restricted to freshwater”. This may not be entirely correct; the present study aims at demonstrating that many temnospondyls lived in brackish, coastal environments (in addition to presumably occurring in freshwater), as I previously suggested (Laurin and Soler-Gijón 2010), and Permian dipnoans frequently occurred in the same environments as early stegocephalians and xenacanthiform chondrichtynans. For instance, *Gnathorhiza* occurs in the Cisuralian Jemez Springs locality of the Cutler Group (formerly Abo Formation), along with *Xenacanthus* and a great diversity of stegocephalians (Berman 1993: 16). Furthermore, some Permian dipnoans appear to have been euryhaline (McCahon and Miller 2015). A xiphosuran head shield is encrusted with microconchids, which thus probably lived in the same environment. The Petropavlovka Lagerstätte may well represent a brackish water assemblage.

The case for a freshwater community in the latest Permian Tunguska Basin, also described by Shcherbakov et al. (2021), seems at first more convincing because it has yielded fossils of aquatic insect larvae, namely mayfly nymphs of the taxon *Khungtukunia sibirica* (Sinitshenkova

2013), and extant mayfly nymphs require a salinity inferior to 8‰ (Chadwick et al. 2002), though not necessarily freshwater. The Tunguska Basin also yielded lepisosteiforms and amiiforms, which Shcherbakov et al. (2021: 1344) interpreted as “relict freshwater” taxa, citing for this Arratia (2004). However, Arratia (2004: 306) stated, on the contrary, that early actinopterygians, including early stem- and crown-teleosts, were overwhelmingly marine, with invasions of freshwater occurring in some lineages in the Middle and Late Jurassic. The traditional interpretation of lepisosteiforms and amiiforms being adapted to freshwater is based only on extant taxa, and it has been refuted by more recent research; Guinot and Cavin (2018: 580) concluded that “Our results indicate a marine ancestry for the entire actinopterygian clade. Basal-most clades such as Cladistia, Chondrostei, Lepisosteiformes, Amiiformes, whose living representatives are known from freshwater or mixed environments all arose from a marine ancestry.” The slightly earlier study by Betancur-R et al. (2015) is congruent on this point. The “relict freshwater” neopterygian taxa mentioned by Shcherbakov et al. (2021: 1344) include *Tungusichthys acentrophoroides*, *Arctosomus sibiricus*, *Evenkia eunoptera* and *Eoperleidus bergi*. Surprisingly, three of these taxa (*Tungusichthys*, *Arctosomus*, and *Evenkia*) are included in Sepkoski’s (2002) monograph “A compendium of fossil marine animal genera”, and thus presumably occur in marine environments. The distribution of *Eoperleidus* seems to be far more limited and I could not find more information about its habitat (beyond its occurrence in the Tunguska Basin), but the three other taxa hardly constitute convincing evidence of a freshwater habitat.

Shcherbakov et al. (2021) also discussed other Permo-Triassic assemblages that contained what they interpreted as possibly freshwater microconchids. The interpretation of these assemblages is more complex than they suggest, and this will be exemplified by their discussion of the Grès à Voltzia, in which they recognize some marine influence. They report that the assemblage includes, among others, egg capsules (probably from chondrichthyans), limnomedusae, horseshoe crabs, euthycarcinoids, gilled mayfly, aquatic beetle larvae, aquatic insect egg clutches, lingulids and temnospondyls, in addition to microconchids (Shcherbakov et al. 2021: 1347). It is possible that this assemblage reflects more than one community because many (perhaps most) insect larvae normally develop in a salinity inferior to 8‰ (Chadwick et al. 2002) whereas lingulid brachiopods normally live in a much greater (at least 30‰) salinity (Hammond 1983). However, even this surprising assemblage could possibly reflect a single community because many insect larvae tolerate brackish water and occur in estuaries (Williams and Williams 1998), and a few even live in hypersaline environments (Pallares et al. 2015). That assemblage would then have to be coastal and brackish because there are no freshwater brachiopods. To sum up, the case for the Permo-Triassic microconchids described by Shcherbakov et al. (2021) as freshwater (rather than brackish water) taxa is not entirely convincing.

Thus, in this paper, I will consider that the presence of microconchids implies marine influence. Bennett et al. (2021: 17), in their analysis of the palaeoenvironment of Mississippian coastal lakes of the Ballagan Formation, likewise accepted the conclusions of Gierlowski-Kordesch and Cassle (2015) that microconchids are marine organisms and concluded that larval spirorbids are “readily transported into non-marine environments by tidal currents or storm deposits”; this may explain the occurrence of a few scattered microconchids in assemblages that show little other evidence of marine influence, but that must nevertheless have formed near the coast.

Xiphosuran habitat through time

The habitat of Permo-Carboniferous xiphosurans, which are sometimes associated with early stegocephalians, has proven particularly controversial. Extant xiphosurans (only four currently recognized species) are basically marine, even though they frequently enter brackish estuaries and less frequently, rivers where the water is almost fresh; this is documented, for *Carcinoscorpius rotundicauda* (named *Limulus rotundicauda*, in the older literature), in the Hughli river at least as far as Calcutta (Annandale 1909, 1922). This is a bit less than 100 km (as the crow flies) from the coast, but only about 40 km from the proximal part of the Hughli estuary. Størmer (1952: 630) even stated that this species can “migrate up rivers into perfectly fresh water”, but provided no reference to support this statement. However, given the obviously extreme osmotic tolerance of *C. rotundicauda*, Størmer’s (1952: 630) statement may well be correct. The three other extant xiphosuran species seem to be less euryhaline and inhabit the seas, including coasts and estuaries.

Some paleontologists argued for an early invasion of freshwater habitats by xiphosurans. For instance, Gray (1988: 60) concluded that “The Rudstangen record suggests freshwater limuloids in the Late Silurian.” Similarly, Gray (1988: 58) indicated that their occurrence in the ORS led Størmer to infer that some xiphosurans invaded brackish or fresh waters, and that by the Carboniferous, most limuloids lived in these environments. Notably, Gray (1988: 57) concluded that the xiphosuran *Kodymirus* lived in freshwater, or perhaps brackish water, because of similarities between its depositional environment and the Old Red Sandstone facies. However, the ORS no longer appears to be a freshwater deposit (Janvier 2007), partly because of marine fossils found in some strata (Goujet and Emig 1985) and because recent isotopic analyses of East Greenland ORS deposits show significant marine influence (Goedert et al. 2018). Thus, the occurrence of xiphosurans in ORS only supports presence of some xiphosurans in brackish (rather than fresh) water.

Xiphosurans occur in what was once called the Braidwood Mazon Creek fauna (Schultze 2009: 127), which was thought to include a freshwater fauna, whereas the Essex fauna from Mazon Creek was recognized to

show strong marine influence. Gray (1988: 58) considered, as was common at the time, that the Braidwood was a freshwater fauna, and concluded, on the basis of such arguments, that “There seems **no doubt** that some of the most characteristic and common limuloids in Carboniferous coal swamp assemblages of Europe and North America”, namely, the euproopaceans which occur in Mazon Creek, were “associated with **freshwater habitats**”. However, Schultze and Maples (1992: 234) concluded that the “Braidwood fauna” inhabited a “tidally influenced coastal or estuarine” environment, and more recently, Schultze (2009: 127) mentioned the presence of the brachiopod *Lingula* in the Mazon Creek biota. Clements et al. (2019: 5) went further and argued that Mazon Creek preserves faunas located at various distances from the shore but that it lacks a discrete freshwater fauna, and that “Most of the major groups found in the Mazon Creek could tolerate varying degrees of salinity”. Among these, they listed both “horseshoe crabs” (xiphosurans) and eurypterids.

Lamsdell (2016: 185) also claimed that “Colonization of the freshwater realm is shown to have occurred at least five times” in xiphosurans, and this is summarized neatly in his figure 2, which optimizes xiphosuran habitat (binary, marine vs. non-marine) onto a timetree. However, a closer look at the supporting data leads to qualify these claims. The most speciose of these putative freshwater xiphosuran clades is Belinurina. The habitat of the terminal taxa shown in the tree (Lamsdell 2016: fig. 2) is indicated, along with supporting references, in Lamsdell’s (2016) tables 1–3, and these indicate that for all taxa in Belinurina, the habitat is freshwater/brackish. Thus, there is no firm evidence that any of these taxa were truly adapted to freshwater, rather than being euryhaline, like some extant xiphosurans (Annandale 1909). The second speciose clade of “non-marine” xiphosurans, Austrolimulidae, originated in the Paleozoic but radiated in the Mesozoic. For this review, I consider only Paleozoic taxa, and extant ones, for the information that they provide about habitat. The Paleozoic austrolimulids (solely represented by ‘*Paleolimulus*’ *longispinus* in Lamsdell’s analysis), “are known from marginal marine, fluviially influenced environments”. Lamsdell (2016: 185) indicated that “Aside from these two clades [Belinurina and Austrolimulidae], xiphosurids are shown to have invaded the freshwater realm twice in the Palaeozoic (Schimper 1853; Anderson and Horrocks 1995) and once in the Mesozoic (Riek and Gill 1971).” These two additional Paleozoic “freshwater” invasions deserve additional scrutiny. Schimper (1853) reported the presence of “*Limulites Bronnii*”, subsequently renamed *Limulites bronni* by Størmer (1952), in the “grès bigarré” near Wasselonne (about 20 km W-NW of Strasbourg), which is Triassic, as reported in Lamsdell (2016: fig. 2), rather than Paleozoic. Presumably, Lamsdell (2016: 185) considered that this represented a Paleozoic freshwater invasion because the ghost lineage of *Limulites bronni* extends into the Permian. Of all the Paleozoic xiphosurans listed

by Lamsdell (2016) in his table 1, *L. bronni* is the only one listed as freshwater, rather than marine or freshwater/brackish. However, we know little about the paleoenvironmental conditions of the deposits. Schimper (1853) described no other fossil from the locality that yielded *L. bronni*, but he did report an ammonite, also from the “grès bigarré” from the quarry in Soultz-les-Bains, barely 10 km south of the *L. bronni* locality; this does not suggest a freshwater environment! The last putative Paleozoic freshwater xiphosuran mentioned by Lamsdell (2016) is *Valloisella lievinensis*. However, Anderson and Horrocks (1995) did not indicate that this was a freshwater taxon; they only indicated that “The arthropod was found associated with non-marine bivalves and the other, more commonly encountered, Coal Measures xiphosuran, *Bellinurus* [often spelled *Belinurus*] PICTET, 1846.” However, non-marine does not mean “freshwater”; brackish environments are also typically considered non-marine, and indeed, *Bellinurus* is listed in Lamsdell (2016: table 1) as freshwater/brackish. Furthermore, little is known about the fauna and stratigraphic context associated with *Valloisella lievinensis*. Anderson and Horrocks (1995) described two specimens of this taxon. For the first one, BU (University of Birmingham) 2466, Anderson and Horrocks (1995: 648) indicated:

“it was collected from a Coal Measures site near Dudley, Worcs. The Coal Measures strata in this area are Westphalian B in age (Upper Carboniferous) but unfortunately, **this is the only stratigraphic detail available**. The **nearby site** of Coseley (Westphalian B) has yielded *Bellinurus koenigianus* WOODWARD, 1872, *Bellinurus bellulus* KONIG 1851 (see SCHULTKA 1994: 347), and *Pringlia birtwelli* (WOODWARD, 1872).”

Thus, the locality data for this specimen are vague, stratigraphy is worse, and there is no associated fauna. The other specimen, LL 11133, has fairly precise locality data (the Bickershawe Complex colliery tip near Leigh, Wigan), but the reported associated fauna (mostly terrestrial, with the exception of the bivalve *Naiadites*) is only moderately reliable because “Unfortunately, the material is not preserved in situ, however all of the material listed above comes from a single, constrainable area of the spoil tip, and as such is likely to reflect original association.” (Anderson and Horrocks 1995: 649). Note that the bivalve *Naiadites* is usually called “non-marine”, but its distribution does not seem to fully support this assertion. At Joggins, it occurs, along with other bivalves, throughout the geological section of the coastal site of Joggins (Nova Scotia), even in the lowest levels of the section (though it is less abundant there than in higher levels), which show strong marine influence, as shown by the occurrence of punctate brachiopods and echinoderm fragments (Grey et al. 2011). Thus, the paleoenvironment of *V. lievinensis* is poorly documented, and all that can be stated about it is that it was most likely not typically marine, but it may have been either freshwater or brackish.

What should we conclude from all this? What seems to be reasonably well-established is that chelicerates most likely originated in the marine environment (Aria 2022), like most ancient metazoan taxa. Extant xiphosurans are marine and at least some taxa are euryhaline, with abilities to tolerate very low salinities, but they never venture very far from the sea. The fossil record shows that Permo-Carboniferous xiphosurans inhabited marginal-marine, probably brackish environments. They may possibly have invaded freshwater environments, but there is currently no solid evidence of this; on the contrary, when associated with early stegocephalians, it is typically in localities that show some marine influence, as in Mazon Creek and Montceau-les-Mines (which is discussed below). Given their marine origin in the early Paleozoic, parsimony suggests that until convincing proof of truly freshwater Paleozoic xiphosurans is produced, this taxon should be considered to have inhabited marine and marine-influenced environments; the burden of the proof is on authors who claim truly freshwater occurrences of xiphosurans in the Paleozoic. Goldring and Seilacher (1971: 440) reached this conclusion long ago and stressed that

“The main habitats of limulids have always been in the shallow sea; but the fossilization potential for both, carcasses and tracks, was so much lower in the true biotope than in marginal and partly nonmarine environments that the fossil representation of the limulids is now stronger in these than in their main biotopes”.

Eurypterids, marine, brackish or freshwater?

Eurypterids are rare, but a good proportion of the known Permo-Carboniferous specimens have been found in localities that yielded stegocephalians, like Joggins (Carpenter et al. 2015), the Hamilton quarry (Cunningham et al. 1993), Mazon Creek (Clements et al. 2019), and Kinney Quarry (Hunt et al. 1992; Braddy et al. 2021, 2023). A specimen was even found in the El Cobre Canyon (New Mexico), in locality 4564, low in the canyon (Hannibal et al. 2005).

The habitat of eurypterids, as for several other extinct taxa, has proven difficult to assess. Gray (1988: 62) indicated that “Much the same kind of controversy evoked in discussion of limuloid habitats has been raised with regard to eurypterids although these animals have no modern analogues.” Indeed, the fact that eurypterids are extinct adds to the difficulty in inferring their paleoenvironment. Some authors (cited in Gray 1988: 62) suggested that the first ones, in the Ordovician (Fig. 3), were marine, and many of the first discovered eurypterids were found in limestone, associated with a fairly typical marine fauna (Lebrun and Pylypenko 2023), but after that, as the group diversified taxonomically and presumably ecologically as well, the story becomes more complex. Indeed, Boucot and Janis (1983: 260) suggested that the Fish Bed Formation (Ludlow, Silurian) was “Non-marine as suggested by the

eurypterid fauna” (note that in this context, “non-marine” more likely means brackish coastal than freshwater). Kjellesvig-Waering (1958: 1108) suggested that from the Pennsylvanian on, they were restricted to freshwater. However, Kjellesvig-Waering later rejected the idea of non-marine eurypterids (Gray 1988: 62).

Nevertheless, Permo-Carboniferous eurypterids have often been interpreted as freshwater taxa (Lamsdell et al. 2019). This fact does not seem to be well-supported, as demonstrated by the citation chain that links papers that indicate that eurypterids, after the Devonian, were restricted to freshwater habitats: Lamsdell and Selden (2017: 104) cited Lamsdell and Braddy (2010) for this (in addition to an old paper from 1916 that I was unable to obtain), but the latter cited Braddy (2001) to justify the claim (and made no new contributions to this question). Braddy (2001) reanalyzed data from Plotnick (1999), which did not tackle Permo-Carboniferous eurypterids, as reflected by its title, “Habitat of Llandoveryan-Lochkovian eurypterids”. It seems dangerous to conclude, from a study based on Silurian to Early Devonian eurypterids, that all post-Devonian taxa were freshwater forms!

Furthermore, Plotnick’s (1999) interpretations seem to minimize marine influence. To demonstrate this, his ecological classification scheme needs to be explained. Plotnick (1999) classified the biofacies assemblages from least (BA0) to most marine (BA6). This was a slight modification of a scheme developed by Boucot and summarized in Boucot and Janis (1983: 252):

1 corresponds to the intertidal environment, as well as the brackish plus estuarine; 2 to the high subtidal; 3 to the remainder of the subtidal photic-phytal zone; 4 and 5 to the mid- and outer-shelf zone; and 6 to the shelf margin to upper bathyal region.

To this, Plotnick added BA0, for “probable nonmarine occurrences”. The faunal composition of some of the localities seems to match imperfectly the assigned assemblage. Out of the 94 localities, 8 are scored as BA 0, sometimes “or BA 1”, and 46 are classified as possibly BA 1, sometimes “or BA 2”, which reflects substantial uncertainty. The localities classified as BA 0 (including those that might be BA1) exhibit some signs of marine influence; some localities (like no. 2) have no associated fauna, or only plants, presumably terrestrial (like no. 62), some are associated with vertebrates (ex. localities 1, 17, 51, 54, 64), and only one (71) is associated with a more diversified biota, which includes xiphosurans. But note that while these vertebrates were once considered freshwater because they occur in the Old Red Sandstone (then considered to represent freshwater deposits), the argument no longer holds because many authors consider the ORS as a marginal marine environment (Janvier 2007), as mentioned above (section on the ORS). Thus, most of the localities classified as BA0 (non-marine) by Plotnick (1999) are ecologically difficult to assess, and rather than truly freshwater, they could well



Figure 3. *Pentecopterus*, one of the oldest (Darriwilian, mid-Ordovician) eurypteryds. Drawing by Patrick Lynch, published on Wikimedia commons (https://en.wikipedia.org/wiki/Eurypterid#/media/File:Eurypterids_Pentecopterus_Vertical.jpg) under the CC0 1.0 DEED licence.

represent marginal-marine environments, such as proximal, low-salinity deltaic areas, bays where freshwater discharge is important, and low-salinity lagoons. A more thorough ecological assessment of these localities would be worthwhile.

The localities classified as BA 1 show stronger marine influence, like brachiopods, mostly inarticulate, especially lingulids, or more rarely, articulate brachiopods like *Hindella*, *Atrypa*, *Dalejina* (like localities 7, 18, 26, 27, etc.). Some, like localities 26–30, 32–35, 38, 48,

even yielded cephalopods, which suggests a fairly typical marine environment (see below). Some have corals, in addition to cephalopods, like localities 3, 2, 68, and 79, or crinoids, like localities 37, 48. A few BA 1 localities have acritarchs (no 42), stromatolites (66), trilobite fragments (88), or possible cirripedes (92). Some BA 1 localities are hypersaline (91). Thus, most of the localities considered BA 1 by Plotnick (1999) seem to represent the marine end of the spectrum encompassed by this category, namely, intertidal environments, as well as fairly salty brackish and the distal estuarine, rather than the proximal, low-salinity estuarine environments.

Last but not least, paleobiogeographic data show that at least some eurypterids, namely, the pterygotoids “apparently could cross open oceans, and are found throughout the world in the short time span of their existence (~40 Ma)”, as Tetlie (2007: 559) concluded. However, examination of the paleobiogeographical distribution patterns of some of the geologically most recent eurypterids, namely the Adelophthalmoidea, shows that they were at least able to disperse in coastal areas, given that by the Permian, they were present in the South China Block, in addition to the core area of eurypterids in former Laurentia and Baltica (Tetlie 2007: fig. 5C). Indeed, (Tetlie 2007: 572) admitted that adelophthalmoids and pterygotoids were “the most dispersed [eurypterids] throughout the world.” Adelophthalmoids are also among the eurypterids most frequently associated with Permo-Carboniferous stegoccephalians. For instance, *Adelophthalmus brasdoensis* occurs at Joggins, *Adelophthalmus mazonensis* occurs at Mazon Creek, *Adelophthalmus sellardsi* is found in the Hamilton Quarry (in the marginal marine ostracode wackestone that also yielded rhynchonellid and productid brachiopods), and *Adelophthalmus* sp. is found in El Cobre Canyon (Cunningham et al. 1993; Hannibal et al. 2005; Tetlie 2007: table 5). More importantly, nearly 200 specimens of *Adelophthalmus luceroensis* have been found in the nearby Red Tanks Member of the Bursum Formation (Kues and Kietzke 1981; Braddy et al. 2021), which also yielded a diverse vertebrate fauna (Harris et al. 2004). These deposits are from a marine embayment, and the levels that produce *A. luceroensis* also yield microconchids, which reflect marine influence (Braddy et al. 2021:112).

Thus, the case for a freshwater interpretation of some eurypterids seems to be weak. Braddy (2001: 120) wrote “No marine fauna has ever been reported from this assemblage [Early Devonian Midland Valley of Scotland] and the presence of terrestrial plants and invertebrates indicates a freshwater lacustrine setting.” I did not try to reassess the paleoenvironment of these Early Devonian deposits because this paper focuses on the Frasnian to the Kungurian, but note that none of the three arguments given in this quote is fully satisfactory. The most convincing, the absence of marine faunas, is negative evidence, and given the controversial environmental tolerances of many Devonian taxa (such as microconchids, xiphosurans and eurypterids; see below), it is of limited value because some taxa that actually

lived in marginal-marine, brackish environments may have been misinterpreted as freshwater forms. The presence of terrestrial plants (or any terrestrial organism) is irrelevant, as pointed out by Schultze (2009: 127); such plants do grow on coasts of seas and oceans, so they only indicate that land was nearby, but give no information about paleosalinity. Last but not least, “invertebrates” are a huge paraphyletic group that is found in all environments, and if the author meant “terrestrial invertebrates” (the sentence is ambiguous on this point), just like land plants, they only indicate that the shore was nearby.

Some bias in favor of a freshwater interpretation was built into Braddy’s (2001) study. He classified benthic assemblages (B.A.) into the categories B.A. 0, “non-marine (e.g. lacustrine and fluvial settings)”, B.A. 1, for “marginal settings (e.g. lagoons, hypersaline environments, littoral settings and mud flats)”, B.A. 2, for “shallow marine settings”, and B.A. 3+, which designates “deeper marine settings”. Braddy (2001: 121) indicated (p. 121) that “In the case of disputed environmental settings the lowest B.A. [most continental] is used, for consistency.” Using this logic, with the data then available, would have led to consider the entire ORS freshwater, and indeed, a locality with no paleoenvironmental data would be considered freshwater. A similar bias seems to occur in the eurypterid literature cited by Braddy (2001). Thus, in his discussion of the Upper Silurian Bertie Waterlimes, Braddy (2001: 124) indicated that it had been

“variously interpreted as representing an upper intertidal portion of a sabkha to subtidal sequence (Hamell, 1982), a near shore lagoon showing fluctuating salinity (Heckel, 1972; Copeland and Bolton, 1985), a wide lagoonal system behind a reef (Ruedemann, 1925; Monahan, 1931), a **brackish to freshwater lagoon or estuarine deposit** (Kindle, 1934), or a **deltaic environment** (O’Connell, 1916).”

Yet, Braddy (2001: 124) indicated that evaporites occur in the Bertie Waterlimes, which “contains a diverse eurypterid fauna (Clarke and Ruedemann 1912) associated with a rare marine fauna, including **cephalopods**, bivalves, **lingulid brachiopods**, worms, gastropods, xiphosurans...”!

The eurypterids that co-occur with microconchids probably inhabited marine-influenced habitats (see above, section on microconchids). One such co-occurrence with microconchids (reported erroneously as “*Spirorbis*”) is in the Middle Devonian Gaspé Sandstone Series of New Brunswick and Québec provinces, in Canada (Gray 1988: 37). Similarly, one of the sites that yielded the most abundant and best-preserved eurypterid remains, in the Red Tanks member of the Madera Formation, contains microconchids, which were called “spirorbis worms” by Kues and Kietzke (1981: 709). This abundance and good preservation is not entirely consistent with Lamsdell et al.’s (2019: 1713) conclusion that “the eurypterid material [in coastal deposits; not specifically from the Red Tanks] was swept in from continental settings”. The Red Tanks

member also includes fusulinids and some marine and “non-marine” (possibly brackish or freshwater) strata.

More importantly, at least four specimens (at least one of which belongs to the mycteropoid *Mycterops whitei*) have been found in three Late Pennsylvanian localities in two formations (Hushpuckney Shale, Swope Formation, Iowa, and Stark Shale Member, Dennis Formation, Nebraska) that have yielded “abundant conodonts” (Schram 1984). These specimens are fairly well-preserved because Schram (1984: 208) indicated that “the holotype alone is more complete than the known specimens of *M. ordinatus* Cope, 1886; *M. mathieu* (Pruvost), 1923; or *M. (?) blairi* Waterston, 1968.” Thus, these mycteropoid remains must not have been carried far from their habitat, which suggests that they were marine.

Gray (1988: 62) cautiously concluded that she could not dismiss the possibility “that there were marine, brackish and freshwater taxa throughout eurypterid history”, but some more recent studies suggest a shift in opinion about eurypterid habitat. Thus, Tetlie and Poschmann (2008: 241) argued, after a “critical review” of this topic, that “There is much more of a marine influence in many of the sections yielding *Adelophthalmus* than has previously been acknowledged.” More precisely, they suggested that “adelophthalmoids as a whole, throughout the history of the clade, inhabited environments situated near the coastal realm, predominantly those with reduced salinities, such as lagoons, estuaries or deltas”, while recognizing that “some basal forms are known from fully marine deposits.” Tetlie and Poschmann (2008: 241) suggested that *Adelophthalmus* was found in habitats with less salinity than other adelophthalmoids, especially in freshwater. However, this apparently referred to a brief episode of eurypterid history, “during Bashkirian and Moscovian times, when they are usually encountered within **coal-bearing strata** and associated with **terrestrial organisms** and ‘freshwater bivalves’.” Terrestrial organisms cannot indicate paleosalinity, and the coal-bearing strata have recently been reinterpreted as displaying marine influence (e.g., Carpenter et al. 2015; Ó Gogáin et al. 2016). Tetlie and Poschmann (2008: 242) admitted that “These horizons were usually interpreted as reflecting freshwater conditions, but nevertheless a marine influence is commonly, but not always, encountered within the respective sequences”, and they concluded that “*Adelophthalmus* seems to be mainly confined to paralic or lowland basins, in depositional environments that had a close connection to the marginal marine realm.” This interpretation differs only slightly from my interpretation of the habitat that I infer from the associated fauna, such as microconchids, xiphosurans, and xenacanthiforms, and from more recent literature about the relevant localities. The habitats of *Adelophthalmus*, which is arguably the most “freshwater” eurypterid, were obviously close to the sea, and Tetlie and Poschmann (2008) interpret them as freshwater, whereas I suspect, based on other associated faunal elements, that they were more likely to have been brackish environments, although perhaps with a fairly low salt content.

More recent research suggests that Permo-Carboniferous eurypterids may have lived closer to the seas than previously thought. Thus, Braddy et al. (2023), in their study of *Hibbertopterus* (Mycteropoidea, Stylonurina) from the Carboniferous of Kinney Quarry (New Mexico), indicated that this site included sediments from “non-marine to shallow marine settings”, but as in most other studies, “non-marine” only indicates an environment other than a typical marine setting in which coral reefs and echinoderms (among others) occur; this does not rule out brackish estuaries, deltas and lagoons. But more marine conditions were suggested by Feldman et al. (1993: 489–491) because brachiopods and crinoid debris occur there. Indeed, Braddy et al. (2023: 261) concluded that “The Kinney Quarry rocks represent a marine embayment” and that *Hibbertopterus* probably lived there (rather than the carcasses having been washed in). In light of their findings, and of a trackway of *Cyrtoctenus* reported from the Ecca Group in a paleoenvironment with possibly high salinity, Braddy et al. (2023: 261) admitted that previous ideas on Permo-Carboniferous eurypterid habitats “may need to be re-evaluated” and that they were probably euryhaline.

I conclude from the above that the presence of eurypterids in the seas and marginal-marine environments is much better established than in truly freshwater deposits; I have not seen a single solid case for the latter, although localities where *Adelophthalmus* occurs without any other faunal element suggesting marine influence (if such localities exist) could plausibly represent a freshwater environment. However, I have not studied all eurypterid-bearing localities, so my conclusions on Permo-Carboniferous eurypterid paleoenvironments remain tentative; as Tetlie and Poschmann (2008: 242) admitted, our understanding of eurypterid paleoecology “is still in its infancy”, and “only detailed examinations, i.e. bed-by-bed excavations of eurypterid-bearing sequences, may further improve our knowledge”. Nevertheless, this interpretation of the habitat of eurypterids is not new. In his summary of the three main schools of thought on this topic, Plotnick (1999: 107) indicated that according to the “facies School” (one of the three main schools), first proposed by Kjellesvig-Waering (1961), eurypterids occurred in three facies: biofacies 1, fully marine; biofacies 2, near-shore, epeiric seas and lagoons, presumed to be somewhat hypersaline; biofacies 3, presumed “near-shore, brackish, deltaic environments. Note that even biofacies 3 is considered brackish, rather than truly freshwater. Kjellesvig-Waering (1961:794) explained that it included “the more brackish part of bays, and estuaries.” This is further confirmed by Plotnick (1999: 107), who clarified that “Biofacies 3 of that school (not of his own scheme) was considered to be brackish water and landward of BA [Biofacies Assemblage] 1.” This still seems to reflect the habitat of the most continental eurypterids; I have seen no evidence of eurypterids living far from the seas, in mid- to high-altitude, freshwater lakes and rivers.

Euthycarcinoids

These enigmatic arthropods of uncertain affinities (Ortega-Hernández et al. 2010; Giribet and Edgecombe 2019) occur in some Permo-Carboniferous localities that yielded stegocephalians, like Mazon Creek and Montceau-les-Mines (Rofle 1985; Schram and Rofle 1994). The literature suggests that they inhabited a wide range of habitats from marine to freshwater, but this literature arguably displays the same problems in paleoenvironmental interpretation as that of eurypterids. Thus, Schram and Rofle (1994: 142) indicated that while many euthycarcinoids seem to have been marine, those from Montceau-les-Mines “are thought to have inhabited fresh water (Rofle 1985).” However, Rofle (1985) may have suggested that the Montceau euthycarcinoids were freshwater inhabitants only because they were associated with “amphibians”, which is not a good justification (Laurin and Soler-Gijón 2010). Simultaneously, he admitted that at Mazon Creek, they occur “only in the Essex fauna, i.e. with the most marine animals, in the distal region of the delta” (my translation throughout this paper, unless indicated otherwise). Neither paper explains why the Mazon Creek euthycarcinoids are marine, whereas the same taxa in Montceau should be considered freshwater. The euthycarcinoids of both localities are thought to be closely related; *Schramixerxes gerem* in Montceau is closely related to *Kottixerxes gloriosus* from Mazon Creek, whereas *Sottixerxes multiplex* from Montceau is related to *Pieckoxerxes pieckoae* from Mazon Creek, according to Schram and Rofle (1994: 142). Indeed, Poplin and Heyler (1994) provide a different, arguably better-justified interpretation of the same findings:

“Fossil remains of these animals were found in many regions of the world, generally in rocks derived from marine or coastal environments, such as Mazon Creek for instance. Thus their presence in the intermontane basin of Montceau-les-Mines poses a problem.”

Similarly, Racheboeuf et al. (2008: 12) interpreted the euthycarcinoids from Montceau as freshwater organisms, partly based on comparisons with euthycarcinoids from the “non-marine Braidwood facies of Mazon Creek” (p. 23). However, this quote raises two problems: first, it places these Mazon Creek euthycarcinoids in a different facies than Rofle (1985), and second, as discussed above (section on xiphosurans), Mazon Creek apparently lacks a freshwater fauna; it preserves aquatic, presumably euryhaline taxa, and terrestrial organisms (Clements et al. 2019). Furthermore, Racheboeuf et al. (2008: 14) mentioned that Schram and Rofle (1997: 211) considered euthycarcinoids to be marine.

Brachiopods

Brachiopods occasionally co-occur with stegocephalians in Permo-Carboniferous localities. Extant brachiopods are exclusively marine animals, with a fairly low tolerance

to salinity variations. Some studies have suggested that in the Paleozoic, they may have lived in slightly hypersaline or slightly brackish water (Fürsich and Hurst 1980). However, among extant brachiopods, even lingulids, which are probably the most tolerant brachiopods to salinity variations, are “only moderately euryhaline, and optimally marine”, as shown by experimental studies (Hammond 1983: 1311). They normally live in a salinity of at least 30‰ (Hammen and Lum 1977), even though lower salinities may be tolerated for short periods. The paleoenvironmental significance of lingulids has often been misinterpreted, according to Cherns (1979). In his study of two nominal species of *Lingula* from the Lower Leintwardine Beds (LLB), Ludlow, late Silurian, Cherns (1979: 42) stated that “Fossil lingulids, by analogy with modern forms, are often inferred to have lived in shallow water”, but after analyzing his data, he concluded (p. 45) that “Neither LLB species conforms to the commonly held view of *Lingula* as an intertidal, very nearshore, or even brackish water, indicator.” Thus, the presence of any brachiopod in a locality indicates a marine, fairly saline environment, contrary to what has often been suggested.

Echinoderms

Echinoderms are infrequently associated with stegocephalians, but a few such associations are mentioned below, so it is worth reviewing briefly their osmotic tolerance. This taxon is overwhelmingly marine, a constraint probably linked to the fact that echinoderms have poorly developed circulatory, excretory, and gas exchange systems (Turner 2007: 464). Very few extant echinoderms, like *Ophiura albida*, *Amphiura chiajei* and *Asterias rubens*, have adapted to brackish waters (Cognetti and Maltagliati 2000: 9). Turner and Meyer (1980: 249) reported that “brackish-water populations of at least 22 species of echinoderms” were known, but more appeared to be discovered subsequently because Turner (2007: 464) reported that about 40 species of echinoderms occur in estuaries. This is a tiny proportion of the 7584 currently recognized extant echinoderm species (as of 3 March, 2024) by the WORMS (World Register of Marine Species). Even the most euryhaline extant echinoderm (and the only one endemic to brackish water), the ophiuroid *Ophiophragmus filograneus*, which has been found occasionally in brackish water that had (momentarily) very low salinities, showed physiological stress when subjected to salinities below about 17‰ (Turner and Meyer 1980: 252), and experiments showed exposure to 8‰ salinity is deadly within 17 days (Turner 2007: 467). A record for echinoderms is a naturally-occurring population in Florida that was observed in a bay at 7.7‰ salinity in summer of 1958, but in that season, salinity fluctuated between 7.7 and 14‰ salinity, and after 1959, a subsequent study failed to recover any individuals (Turner 2007: 471), so it is possible that this bout of low salinity proved fatal for this population. Furthermore,

some estuarine populations of echinoderms are sterile and continue to exist only through immigration from more marine environments. Thus, the presence of echinoderms is strong evidence that a truly marine environment either prevailed locally, or occurred in the vicinity, and that the salinity was probably above 15‰ on average, on a yearly basis, although it may have occasionally fluctuated down to a minimum of about 8‰, below which even the most osmotolerant echinoderms are quickly killed.

Cephalopods

Extant cephalopods are among the most strictly marine mollusks. Parsimony suggests that crown-cephalopods in general were also marine, and this crown-group is ancient, given that the divergence between nautilids and coleoids harks back deep into the Paleozoic. Indeed, some molecular studies placing it around the Late Devonian (Stöger et al. 2013), which is plausible because coleoids are known from the Carboniferous at least (Klug et al. 2019) and nautiloids are much older still. What we know of the cephalopod fossil record (Leonova 2011) also suggests that they have always been exclusively marine forms. Unsurprisingly, cephalopods only infrequently co-occur with stegocephalians in Permo-Carboniferous localities, but several such examples are mentioned in this paper. Most extant cephalopod taxa tolerate only mild salinity fluctuations (Jereb and Roper 2016: 6). The most euryhaline taxa, like the squid *Lolliguncula brevis*, can survive in water that has at least 17.9‰ salinity (Bartol et al. 2002), which is about half of the normal sea water salinity (about 35‰); they die in about 48 h in water that has 16.5‰ salinity (Hendrix et al. 1981). Thus, the presence of cephalopods in a locality indicates strong marine influence, unless there is evidence of long-distance transportation.

Freshwater jellyfish?

Many articles that describe supposedly fully continental (i.e., without any marine influence) deposits reported “freshwater jellyfishes” (e.g., Poujol et al. 2023: 5). Yet, an overwhelming majority of extant cnidarians are marine, with only fewer than 35 nominal species documented in freshwater habitats (Jankowski et al. 2008), as compared to over 12 000 nominal extant cnidarian species, according to the WORMS registry (<https://www.marine-species.org/> consulted on October 3, 2023). This amounts to 0.3% of the extant cnidarian specific biodiversity in freshwater ecosystems. In Permo-Carboniferous localities, putative “freshwater jellyfishes” and other cnidarians have been reported in sites that are now known to show strong marine influence. Most interesting is the case of Mazon Creek, which has yielded a variety of cnidarians (Clements et al. 2019: table 1), including medusae and the hydroid *Devotella* (Schultze 2009: 127). The most common cnidarian at Mazon Creek is *Essexella asherae*

(Baird et al. 1985), which is a sea anemone, rather than a medusa (Plotnick et al. 2023). *Essexella asherae* appears to be autochthonous at Mazon Creek because of its abundance and its benthic lifestyle, and it was presumably a euryhaline, coastal marine taxon (Plotnick et al. 2023: 24) because Baird et al. (1986: fig. 2) showed that it is most abundant in the deepest, most marine (offshore) facies.

Devonian localities

Established ideas and recent isotopic analyses

Most Devonian localities that have yielded stegocephalians were long interpreted as freshwater by most authors. Thus, Long and Gordon (2004: 703) stated that “A reasonable generalization is that they [Devonian stegocephalians] most likely inhabited large **freshwater river and lake systems**, environments similar to those inhabited by the East Greenland forms [*Ichthyostega* and *Acanthostega*].” However, Schultze (2009: 128) argued that “The most parsimonious interpretation of the environment of the earliest (Devonian) tetrapods is coastal marine”. Subsequent isotopic study of *Ichthyostega* remains, and those of other Devonian tetrapodomorphs from East Greenland (Upper Devonian Celsius Bjerg group, *Remigolepis* series) and from the Zhongning Formation of Ningxia Hui (China), which has yielded the stegocephalian *Sinostega pani*, confirmed that these taxa “were euryhaline and inhabited transitional aquatic environments subject to high-magnitude, rapid changes in salinity, such as estuaries or deltas” (Goedert et al. 2018: 68). This result is particularly interesting because my earlier review (Laurin and Soler-Gijón 2010: fig. 4) accepted *Ichthyostega* and *Acanthostega* as the only Devonian stegocephalians for which the traditional freshwater habitat interpretation was not contradicted by indicators of marine influence; I now stand corrected! It would be interesting to perform similar analyses on other Devonian localities and formations, such as the Red Hill locality of the Catskill Formation, which yielded the stegocephalian *Hynerpeton*, and which was long interpreted as a freshwater taxon, but which might possibly have been euryhaline (Broussard et al. 2018).

Strud (Belgium)

The Famennian Strud locality (Belgium), which recently yielded a stegocephalian (Clément et al. 2004), has been interpreted as “one of the oldest continental – probably fresh-water – ecosystems” (Denayer et al. 2016). However, this hides considerable variability in the salinity of the environments represented in the strata of Strud, as the authors recognized:

“The depositional setting approximately corresponds to a ramp with both an increase in the marine influence and a deepening southwards (Thorez et al. 1977). The proximal facies (northwards) frequently

show a continental influence and are thus dominantly sandy and silty, whereas the distal facies (southwards) are more mixed with frequent carbonate intercalations (Ciney area and southwards) indicating deposition in a 'deeper' part of the basin (c. 50 m deep after Thorez & Dreesen, 1986)."

Indeed, faunal elements that indicate a fairly typical marine environment occur at various levels of the Strud succession and more generally, in the Dinant Synclinorium (Thorez et al. 1977). These will be reviewed from the base to the top. In the late Fransian/early Famennian Fasiole Formation, Denayer et al. (2016: 113, 116, 121) report spiriferid brachiopods and a sandy crinoidal limestone. The overlying Bois-des-Mouches/Citadelle de Huy Formation includes, near its top, a "coarse crinoidal limestone" (Denayer et al. 2016: 115), as well as "rhynchonellid brachiopods, locally abundant but not broken", which "suggest a more marine environment" (Denayer et al. 2016: 123). The late Famennian Poulseur Member of the Comblain-la-Tour Formation contains "some brachiopod shells, often dissolved" (Denayer et al. 2016: 115), and a "bioturbated marine sandstone" (Denayer et al. 2016: 123). Finally, near the top of the succession, the Comblain-au-Pont Formation contains a crinoidal limestone (Denayer et al. 2016: 115). Lamsdell et al. (2019: 1709) indicated that the 1.4 m thick channel-filling succession in which they found eurypterid material displayed "no evidence for marine influence". This may have been true of the 1.4 m section, but is this a large enough area to expect to find traces of marine influence in what was apparently a deltaic or estuarine environment? And eurypterids only indicate that the sea was near (see above).

The stegocephalian from Strud was found in beds B and D of the Royseux Member of the Evieux Formation (Clément et al. 2004; Denayer et al. 2016: 114), which did not yield typical marine fossils. Because of this, these beds of the Royseux Member have been interpreted as a freshwater to brackish, fluvial to estuarine environment. However, this member is between the Poulseur Member and the Comblain-au-Pont Formation, both of which contain marine fossils. Thus, the open sea was probably not very far from the habitat of the Stud stegocephalian. Indeed, Denayer et al. (2016: 123) interpreted the Royseux Member of the Evieux Formation) as "a lagoonal deposit in a back-barrier position. It consists of fining-upwards sequences associated with red beds, evaporitic dolomite (sabkha sequence) and anhydrite pseudomorphs, locally with dark shale". The presence of evaporitic dolomite and of anhydrite pseudomorphs implies saline (plausibly brackish) water, which became hypersaline at least occasionally. Were the scant remains of the stegocephalians washed in, which would be compatible with a freshwater habitat, or did this stegocephalian inhabit the estuary and other marginal-marine habitats, as apparently did the other Devonian stegocephalians? In this case, the fragmentary nature of the specimen does not preclude the possibility that it represents an allochthonous taxon.

Carboniferous localities and formations

Minto Formation (New Brunswick)

The early Moscovian (Pennsylvanian) Minto Formation of New Brunswick has yielded an interesting meta-zoan fauna that includes a few stegocephalian remains, including a jaw that plausibly belongs to a colosteid, small limb bones, and a vertebral centrum that has been plausibly attributed to an embolomere, in addition to finned tetrapodomorph material, mostly assigned to *Megalichthys* (Ó Gogáin et al. 2016). While the stegocephalian material is scant (15 specimens, out of the total of 722 vertebrate specimens), Ó Gogáin et al. (2016: 713) suggested that the vertebrate remains had undergone "minimal transportation". Nevertheless, the possibility that the fragmentary stegocephalian remains of this locality represent para-autochthonous occurrences cannot be dismissed. This site is interesting because the paleoenvironment appears to represent marginal-marine environments with a salinity gradient that ranges from open marine shallow environments to tidal estuaries. This interpretation is supported by framboidal pyrite, sponge spicules, spirorbiform microconchids, echinoid spines, bioclasts of punctate brachiopods in the most marine facies, and spirorbiform microconchids, along with the bivalve *Naiadites*, in the brackish embayment facies. The xenacanthiform remains occur in all facies (salinities), which is consistent with their inferred broad osmotic tolerance, which appears to have ranged from fully marine to freshwater (see above). Other taxa appear to have displayed osmotic preferences: dipnoans, some rhizodonts (*Archichthys*, *Strepsodus*) and *Megalichthys* occur mostly in the open marine facies, whereas *Rhizodus* and *Rhizodopsis* are most common in brackish tidal estuaries (Ó Gogáin et al. 2016: 714). The stegocephalians are most abundant in the brackish embayment. Ó Gogáin et al. (2016: 717) suggested that euryhaline habit could explain why many Permo-Carboniferous gnathostome remains "show enriched strontium isotope values indicative of continental or freshwater influences".

Joggins

Joggins has yielded many stegocephalian remains, including the oldest known amniotes (Carroll 1964; Archer et al. 2015: 662). The diversity, abundance, and quality of preservation of stegocephalian remains (e.g., Godfrey et al. 1991), many of which are articulated (Holmes et al. 1998) or at least composed of many clearly associated skeletal elements (Mann et al. 2020), suggests that little transport had occurred (Falcon-Lang et al. 2006: 561). This locality has long been interpreted as an intra-montane, freshwater basin (Carroll 1970: 17), and some isotopic analyses support this interpretation (Brand 1994). As we saw above (isotopic section), Brand (1994) suggested that the Joggins Formation sediments were

non-marine (continental), but the few Sr isotopic analyses performed by Carpenter et al. (2015) led them to conclude that these results were equivocal, and only indicated that the environment was probably not fully marine. Indeed, Carpenter et al. (2015) concluded, based on faunal data, that the marine influence at Joggins was fairly strong, at least at several stratigraphic levels.

Other recent studies support marine influence in the Joggins Formation (Davies et al. 2005), and similar conclusions had been reached much earlier by Duff and Walton (1973). The Joggins cliffs preserve a variety of habitats that reflect 14 or 15 cyclothems (probably linked to regressions and transgressions), with some levels representing marginal marine levels, and other levels that exhibit less marine influence (Grey et al. 2011; Carpenter et al. 2015). The marine levels are represented by the open water (OW) facies that contains limestone and coal; other facies include poorly drained floodplain units (PDF) and well-drained alluvial plain units (WDF). The presence of framboidal pyrite in the most marine levels also indicate normal marine salinity levels (Grey et al. 2011: 262), and agglutinating foraminifers, which are characteristic of shallow marine environments, occur both in Joggins and the nearby Sydney basin, where the Florence locality is located (Schultze 2009: 127–128).

The OW facies has been interpreted as reflecting a “brackish sea” in recent studies (e.g., Carpenter et al. 2015), but it yields fossils that show that a stenohaline, marine fauna was present nearby; these include echinoderm fragments (from blastoids, crinoids, or both), fragments of punctate brachiopods (Grey et al. 2011: 260), and actinistian scales (Schultze 2009: 127). In addition, the OW facies yields other taxa that may have been euryhaline rather than frankly marine, including microconchid tubes, chondrichthyan scales and teeth, and a lungfish tooth plate. Grey et al. (2011: 262) concluded that «The Joggins Formation records a waning marine influence over time» and that at some point (at least in the OW facies showing the strongest marine influence, especially near the base of the formation), it was close to the Paleo-Tethys Ocean. Grey et al. (2011: 262) noted “antithetic abundances of brackish ostracodes and freshwater bivalves”, but at Joggins, bivalves are present even in layers that produced fragments of punctate brachiopods (Grey et al. 2011: 260), so without a finer analysis that discriminates between the bivalve taxa present at various levels, it is unclear that these are indeed freshwater (rather than brackish water, or even marine) bivalves. Grey et al. (2011: 262) supported earlier conclusions that the Joggins Formation represents “fluvial deposition into shallow brackish waters” and suggested that this brackish environment was inhabited only by euryhaline organisms. In extant ecosystems, typical brackish faunas composed primarily of taxa with marine relatives inhabit waters where the salinity is between 5‰ and 30‰, and especially in the upper half of this salinity range (Cognetti and Maltagliati 2000). Carpenter et al. (2015: 662) suggested that a western extension of the Tethys Ocean had spread

through a hypothetical mid-Euramerican seaway and reached the area of Joggins at highstand of cyclical transgressions possibly driven by Milankovitch-scale orbital cycles. They also suggested that the brackish waters present at Joggins “probably represent the distal extension of the marine bands that characterize coal measure successions in north-west Europe”, which suggests marine influence in many other Permo-Carboniferous localities that have yielded stegocephalians. These interpretations are supported by the reinterpretation of supposedly endemic gnathostome taxa (*Ctenoptychius cristatus*, actually a synonym of the chondrichthyan *Ageleodus pectinatus*; *Gyracanthus duplicatus*, actually an undetermined gyracanthid acanthodian; *Conchodus plicatus*, actually an indeterminate *Sagenodus* dipnoan) as fairly cosmopolitan taxa that also occur in fully marine environments. Thus, Carpenter et al. (2015: 682) interpreted the Joggins aquatic gnathostome fauna “as having a distinctly euryhaline or diadromous mode of life”, and they even suggested (p. 683) that in the Pennsylvanian, a much greater proportion of gnathostomes were euryhaline than today (only 3–5% now), and that this represented an important intermediate step toward the subsequent establishment of vertebrates in freshwater habitats. Carpenter et al. (2015: 683) interpreted this as resulting from important glacio-eustatic fluctuations that resulted in the “widespread development of brackish estuaries and epeiric seaways”. Ironically, these recent works suggest that Dawson’s (1865) much earlier interpretation of Joggins as a coastal deposit was correct, after all.

Hamilton fossil-Lagerstätte

This fossil Konservat-Lagerstätte from Kansas preserves a Stephanian coastal community (Cunningham et al. 1993). The stegocephalian fauna includes temnospondyls (Trimerorhachoidea, Dissorophoidea, the second-most frequently represented vertebrate taxon, and Eryopoidea), some of which are represented by larvae, as well as amniotes (Captorhinomorpha, Diapsida, Edaphosauridae, and Ophiacodontidae). Other vertebrates include the acanthodian *Acanthodes*, which is the most common vertebrate, Xenacanthida (*Expleuracanthus?*, *Orthacanthus*, and *Xenacanthus*), Hybodontoida (*Hamiltonichthys*), Actinopterygii (*Elonichthys* and other), Dipnoi (*Gnathorhiza*, *Sagenodus*), Actinistia, and Tetrapodomorpha (Megalichthyinae). Eurypterids and numerous remains of “spirorbids” (actually microconchids) from Hamilton may represent euryhaline forms (see above), but brachiopods and echinoderms provide the best evidence of normal marine conditions in at least some levels (in the marine limestone and mudstone), which also yielded temnospondyls. Many of the vertebrates are articulated and fairly well-preserved, which suggests that they have not been transported far from where they lived, although others show signs of flotation. Furthermore, vertebrate coprolites include remains of marine metazoans

(Cunningham et al. 1993: 230), which shows that they fed in a marine environment. Much of the local fauna appears to have been preserved in its environment; Cunningham et al. (1993: 227) stated that “Some productid brachiopods, for example, are preserved in apparent growth position, nested between clasts, with their delicate spines intact. Additionally, some colonies of an encrusting cystoporate bryozoan (*Fistulipora?*) apparently are in growth position”. Other fossils from Hamilton, such as bryozoans, echinoderms, and fusulinids, are fragmented, abraded, and micritized and may be reworked from older sediments (Cunningham et al. 1993: 227). These could have been transported (not necessarily far), but they are easily distinguishable from the much better-preserved autochthonous elements. Schultze et al. (1994: 443) interpreted the temnospondyls as autochthonous and concluded that they “retained their tolerance to salinity from their marine ancestors and were able to spawn in near-shore environments.”

The Hamilton locality displays three main lithologies: a conglomerate, an ostracode wackestone, and an assemblage of laminated limestones and mudstones. Most marine and brackish fossils mentioned above occur in all three lithologies, except for the echinoderms, which may occur only as lithoclasts of wackestone, in the laminated limestones and mudstones, which also includes the vertebrate fossils. Patterns in the lamination suggest that the limestones and mudstones were deposited in a tidal environment, and Cunningham et al. (1993: 235) suggested that the high sedimentation rate and variable salinity may have enhanced fossilization. The deposits probably formed in a lagoon or estuary and some tidal creeks. Cunningham et al. (1993: 234) concluded that despite the fact that previous studies had “emphasized the freshwater nature of the laminated limestones from the Main Quarry based on some faunal elements, systematic sieving of the fossil-bearing beds has revealed the presence of marine invertebrate fossils throughout the sequence” and suggested that “The mixed composition of the fossil assemblage is interpreted as indicative of brackish or, most probably, variable paleosalinity.” Thus, the vertebrates that inhabited this locality were plausibly euryhaline, coastal forms. Hamilton is among the most marine-influenced Permo-Carboniferous localities (all of which yielded stegocephalians) compared by Schultze and Maples (1992).

Mazon Creek

Much has been written about the biota and paleoenvironment of this locality, including in various sections (above) of the present paper. Here, only a few additional points need to be added. Above, I indicated that many taxa found in Mazon Creek may have been euryhaline, but exceptions exist. Beyond the obvious case of allochthonous (mostly terrestrial) taxa, a fairly diverse cephalopod assemblage is documented (Saunders and Richardson 1979), and this even includes coleoids (Doguzhaeva et al. 2007), which have a poor fossil record. As mentioned

above, the vast majority of cephalopods are stenohaline, marine forms, and only a few taxa, like the extant squid *Lolliguncula brevis* are moderately euryhaline (Bartol et al. 2002). Shark egg capsules are also present, and this also suggests strong marine influence because extant chondrichthyans lay eggs only in the marine environment, including along the coasts, notably in estuaries, but never in freshwater (Schultze and Soler-Gijón 2004: 326; Schultze 2009: 127). Holothurians, which also occur (Baird et al. 1986), are another typically marine taxon, like most other echinoderms.

Thus, Mazon Creek undoubtedly exhibits a stronger degree of marine influence than most other classical Permo-Carboniferous stegocephalian-bearing localities. This is paradoxical because a detailed study of tidal rhythmites of various Carboniferous and Holocene localities led Archer et al. (1995: 411) to conclude that “the Francis Creek rhythmites [in the area of Mazon Creek] may have formed in a **significantly inland** setting with a **strong fluvial influence** and overprinting on the tidal cycles.” Thus, the sedimentological data point at a brackish-water estuarine environment where stenohaline marine forms could not have lived. The cephalopods documented from Mazon Creek may have ventured there at high tide when salinity was the highest and may have made only brief incursions there.

Other than the cephalopods, the obviously allochthonous elements include the remains of terrestrial embryophytes and of terrestrial arthropods, such as myriapods, arachnids (including scorpions), and insects (Clements et al. 2019: 5). The possibility that some bivalves and stegocephalians were washed-in freshwater faunal elements was considered briefly by Clements et al. (2019: 5) based on the previously assumed habitats of these taxa, but these authors admitted that the occurrence of these bivalves with “polychaetes” raised serious doubts about this interpretation, and that the habitat of the stegocephalians was equally poorly constrained. The exceptionally good preservation of these stegocephalian remains, with dermal scales (e.g., Mann et al. 2021), skin and toepads (Mann and Gee 2020) suggests that they have not been transported far, without guaranteeing that they were truly autochthonous.

Red Tanks Member of the Bursum Formation

Although not among the classical stegocephalian-bearing Permo-Carboniferous localities, the Red Tanks Member of the Bursum Formation recently yielded a fairly diversified assemblage of late Pennsylvanian stegocephalians (the temnospondyls *Eryops*, *Trimerorhachis* and an undetermined taxon, the embolomere *Archeria*, a diadectid, a caseid, *Edaphosaurus* and *Dimetrodon* cf. *D. milleri*) and other vertebrates (the chondrichthyans *Petalodus* and *Deltodus*, undetermined actinopterygians, as well as the dipnoan *Gnathorhiza bothrotreta*) from “mixed marine-nonmarine sequences” (Harris et al. 2004: 267). The presence of typically marine levels in limestone layers of this member is demonstrated by the presence of conodonts

and fusulinids, among others. In addition to this limestone, the Red Tanks Member includes “nonmarine mudstones and siltstones of a coastal plain environment”, “mudstones of a brackish to freshwater environment”, “nearshore and fluvial sandstones, limestone conglomerates of a high-energy nearshore environment, limestone horizons composed of different types of bioclastic wackestones and mudstones, and rare packstones indicating deposition in an open to restricted shallow marine shelf environment” (Harris et al. 2004: 267–268). Thus, this member seems to preserve several paleoenvironments, most of which show some marine influence, as well as some freshwater environments. The stegocephalians and other vertebrates were found in several lithologies, mostly in mudstones, siltstones, sandstones and conglomerates, but also, more rarely, in shales and in the limestone levels, as in localities 4640 and 5349 (Harris et al. 2004: fig. 2, appendix). Thus, the vertebrate community preserved in the Red Tanks Member plausibly inhabited a variety of habitats, ranging from freshwater to brackish, possibly even marine. However, given their rather fragmentary nature, some or all of these might represent allochthonous elements.

Montceau-les-Mines

Montceau-les-Mines has been considered by many authors to represent an intramontane, freshwater basin (e.g., Perrier and Charbonnier 2014). Thus, Racheboeuf et al. (2008: 12) indicated that the Montceau biota “is a mixture of both strictly aquatic, **freshwater** faunal components and terrestrial ones”. Also, they argued that “the closest Upper Carboniferous marine deposits were located at least several hundred kilometres SW of Montceau”. However, this argument rests on previous paleoenvironmental interpretations that allowed reconstructing ancient coastlines, which is weak given the numerous changes in interpretation over the years, such as those concerning the Old Red Sandstone. This paleogeographic argument was criticized long ago by Schultze (1995: 258) who pointed out that “This method stacks one interpretation on another (the palaeogeographic position on an assumed distinction of marine from freshwater, the questioned palaeoenvironment)”. Furthermore, Schultze (2009: 130) pointed out that many taxa (conchostracans, ostracodes, the bivalve *Anthraconaia*, eurypterids, *Acanthodes*, chondrichthyans, and actinopterygians) interpreted as freshwater indicators in Montceau also occur in the clearly strongly marine-influenced environment of Mazon Creek. Schultze (2009: 133) went further and stated that “The lack of undoubtedly freshwater forms in the Paleozoic is a specific problem.” This may be slightly overstated because aquatic insect larvae, though uncommon, do suggest freshwater or low salinity, if autochthonous, despite the few exceptions consisting in extant insect larvae that can develop in hypersaline water (Pallares et al. 2015).

The isotopic analyses by Fischer et al. (2013) and Luccisano et al. (2023) suggested that some localities in

the area (Buxières-les-Mines, and the Muse) represent continental environments with little or no marine influence (see section “Freshwater chondrichthyans?”), but these studies did not sample Montceau, and I am unaware of relevant isotopic analyses on that locality. Montceau is about 40 km South of the Muse, and about 110 km East of Buxières-les-Mines, so Montceau would have been a little closer to the Paleotethys than Buxières and the Muse (Schultze 2009; Mercuzot et al. 2022), and this is consistent with the presence of taxa that suggest marine influence and that have not been described from Buxières and the Muse. These include acritarchs, the annelid *Palaeocampa anthrax* (Plejdel et al. 2004), which belongs to the marine taxon Amphinomida, and abundant remains of the xiphosuran *Liomesaspis* (Anderson 1997; Racheboeuf et al. 2002). As mentioned above (section on xiphosurans), even the most euryhalic extant xiphosuran does not venture more than about 100 km from the seas. All of these were dismissed by Racheboeuf et al. (2008: 13) as indicators of marine influence, but accepted as such by Plejdel et al. (2004).

Another possible indicator of marine influence is *Myxineidus gononorum*, based on a fossil that was initially described as a hagfish, even though a more recent study raised doubts about its identity and suggested that it might be a lamprey (Germain et al. 2014). Hagfishes are purely marine, but lampreys inhabit both the seas and freshwater. The fossil displays two rows of denticles forming a chevron pattern, which is characteristic of hagfishes and what appears to be an impression of a wrinkled skin, which is reminiscent of a dead hagfish, but a faint halo around the head looks like the peculiar mouth of lampreys (though it appears to be devoid of the keratinous denticles present on the mouth of extant lampreys). However, Germain et al. (2014: 133) wondered if “this pattern [reminiscent of a lamprey’s mouth] somewhat reflects the original body shape of the animal, or is merely and incidental artefact due to the distribution of microbially induced films during the decay of the animal”, and they also admitted that “Quite a similar halo is sometimes observed in other fossiliferous nodules from Montceau-les-Mines, not necessarily associated with soft tissue preservations.” In the end, their suggestion that the fossil represented a lamprey seemed to depend as much on the presumed freshwater habitat of Montceau as on its morphology, because they stated that their new interpretation “would perhaps resolve the controversial problem of the presence of a hagfish in the reputedly fresh-water, intramontane basin of Montceau-les-Mines”. Indeed, Germain et al. (2014: 134) stated that the Montceau basin “provides no clear evidence for any marine influence, be it temporarily.” Given the evidence mentioned above that suggests marine influence in that basin, especially the annelid *Palaeocampa* and the xiphosuran *Liomesaspis*, it seems better to base a taxonomic assignment of *Myxineidus* on its morphology, which unfortunately leaves serious doubts about its affinities.

Stegocephalians are represented by temnospondyls (*Branchiosaurus petrolei*, *Micromelerpeton boyi*, and fragments of *Actinodon*), neotridians (*Sauravus costei*, *S. spinosus*, and *Montcellia longicaudata*), the aistopod *Phlegethonia longissima*, and fragments of a synapsid (*Stereorachis? blanziacensis*); none of these are very well-preserved, even though several specimens preserve traces of soft tissues (Perrier and Charbonnier 2014). It is thus unclear if this fauna was autochthonous; significant transport cannot be excluded.

German basins

In my previous review (Laurin and Soler-Gijón 2010), I presented various arguments supporting marine influence in the Saar-Nahe basin. These obviate the need for a detailed treatment of this basin, but a few additional points can be made. The presence of glauconite in that basin also supports marine influence (Schultze 2009: 131) because it normally forms in the marine environment (Baldermann et al. 2013). In addition, microconchids are present in various horizons in the basin (Schultze 2009: 131 and references cited therein), and as indicated above (section “Freshwater microconchids?”), these indicate marine influence.

In the central German basins, which extend from the Thüringer Wald Permo-Carboniferous basins to the Döhlen Basin farther east, Schultze (2009: 132) reported the presence of chondrichthyan egg capsules. As indicated above (section on Mazon Creek), these suggest fairly strong marine influence. In addition, xiphosurans (the limulid *Euproops*) occur there, in several levels, and they can be locally abundant given that Schultka (2000) described 45 individuals from at least four levels of a single locality. As explained in the section “Xiphosuran habitat through time”, this suggests at the very least proximity to the sea. In north-east Germany, the Rotliegend has yielded “hydromedusas” (Legler et al. 2004), which also suggests marine influence (Schultze 2009: 132).

It is impossible to assess the allochthonous or autochthonous nature of all stegocephalian remains found in all localities of the German basins, but the *Glanochthon latirostre* and *Archehosaurus decheni* found in a shark (*Triodus sessilis*) in the Lower Permian Lake Humberg, in the Saar-Nahe Basin, probably all lived in the same environment and there is no reason to infer significant transport (Kriwet et al. 2008).

Bohemia

The Bohemian basins in the Czech Republic were already discussed by Laurin and Soler-Gijón (2010), so only a few comments are needed here. These basins are best known for the famous Late Carboniferous (Westphalian D, Kasimovian) Nýřany locality (Schoch 2022: 14) in the Plzeň-Manětín Basin (Klembara et al. 2014). Nýřany yielded a great diversity of stegocephalians:

temnospondyls, such as *Cochleosaurus bohemicus* (Sequeira 2003), *Cheliderpeton vranji* (Werneburg and Steyer 2002), *Anthracobamus fritschi*, *Branchiosaurus salamandroides*, ‘*Platyrhinops*’ *fritschi*, *Mordex calliprepes*, *Mattauschia laticeps* (Schoch 2022), the baphetid *Loxomma bohemicum* (Fritsch 1883), the enigmatic *Gephyrostegus bohemicus* (Godfrey and Reisz 1991), which has long been considered an anthracosaur, although some analyses suggest a more crownward position (Marjanović and Laurin 2019), amphibians that are still often referred to as “microsaurs” (a paraphyletic group), such as *Microbrachis pelikani* (Vallin and Laurin 2004), *Crinodon limnophyes*, *Ricnodon copei*, *Sparodus validus*, *Hyloplezion longicostatum* (Carroll and Gaskill 1978), as well as other amphibians, such as the neotridians *Sauroplesura scalaris* and *Urocordylus angustatus* (Fritsch 1883), and some amniotes, among others. Nýřany and other nearby Carboniferous strata have typically been interpreted as freshwater environments (Sequeira 2003: 21; Opluštil et al. 2005), but Laurin and Soler-Gijón (2010) presented an alternative interpretation. In addition to the presence of chondrichthyan egg capsules and microconchids already evoked by Laurin and Soler-Gijón (2010), the presence of limulid xiphosurans and of the eurypterid *Adelophthalmus* (Schultze 2009: 132) suggest marine influence in at least some parts of the basin and some horizons. Medusae have been described there; they have been interpreted as freshwater taxa (Kozur 1984), but see above (section “Freshwater jellyfish?”) for reasons to question this interpretation. The taxonomic diversity suggests that most stegocephalians found in that locality were probably amphibious or aquatic. The Nýřany assemblage has been interpreted as representing a brief, local accumulation, which seems plausible given the good preservation of most specimens (Sequeira 2003: 21). Ichnofossils also show that temnospondyls occurred locally (Turek 1989). All of this supports the hypothesis that most of these specimens were not carried far.

Conclusion

This literature survey illustrates a recurring theme that pervades the history of paleontological research on the Paleozoic paleoenvironments. The absence of typically marine indicators, such as coral reefs, echinoderms, and a diversified brachiopod fauna has been interpreted as indicating a “non-marine environment”, which was often implicitly or explicitly assumed to be freshwater. However, “non-marine environments” thus defined (very broadly) include estuaries, deltas, coastal mangroves, lagoons and salt marshes, which occur between truly marine and freshwater environments on, or near the coast, as well as brackish or salt lakes, which occur even far from coasts. This seems to have been too often forgotten. Thus, the paleoenvironment of many Permo-Carboniferous localities that have yielded stegocephalians need to be reassessed, even in the comparatively well-studied Permian redbeds of Texas (Fig. 1).

Freshwater ecosystems may well be very ancient; Gray (1988: 1) even boldly suggested that “The freshwater ecosystem may be as old as most life.” That may well be, but various factors may have conspired to yield a very fragmentary picture of the history of freshwater ecosystems. The ichnofossil record, which is more abundant than body fossils for many taxa, suggests a marine origin of early life; Buatois et al. (2005: 322) stated that “Virtually all Precambrian ichnofaunas represent the activity of open-marine biotas that presumably inhabited nearshore to deep-marine areas under normal salinity conditions”. Oceans and seas cover more of the Earth’s surface than continents, and more importantly, most sediments are deposited by the largest, most powerful rivers, in deltas that are predominantly located at the edge of seas (including epicontinental seas) and oceans. In fact, Peters and Husson (2017: 323) concluded that “Most of the surviving volume of sedimentary rock (~75%) was deposited in and adjacent to shallow seas on continental crust”. By contrast, non-marine sediments decrease in quantity with increasing age. This implies that in the Permo-Carboniferous, we expect far more fossiliferous localities (though not necessarily those that yielded stegocephalians) to represent marine and coastal (plausibly brackish) environments than freshwater ones. These factors, plus the higher erosion rates of high-altitude deposits compared to low-altitude sediments that we can expect from basic physical principles, may result in a low fossilization potential of freshwater organisms, especially ancient ones, except for those living close to the seas, where their remains may be carried after death.

On the contrary, marginal-marine environments, where much sedimentation occurs, should be fairly well-represented in the fossil record, but they may be difficult to interpret because coastlines can vary quickly, especially in deltas, and even on a daily basis, tides result in short-term salinity variations in some coastal habitats. Thus, the exact environmental preferences and tolerances of long-extinct organisms that inhabited these coastal environments are difficult to assess. These organisms appear to have included many Paleozoic stegocephalians. Of course, this does not mean that all Paleozoic stegocephalians lived in brackish or normal-marine salt water. Like extant teleosts that occupy a great range of aquatic environments, many stegocephalians may have been adapted to freshwater habitats, and in some cases, independent evidence exists for this (e.g., Witzmann and Brainerd 2017).

Above, I raised the question of a bias in favor of freshwater interpretation of localities devoid of typically marine fossils, and discussed some cases for which marginal-marine, brackish environments seem more plausible. While I focused on the body fossil record which I know best, I note that Buatois et al.’s (2005) review of the ichnological record suggests a similar pattern. Localities or formations that were initially interpreted as freshwater and now seem to more plausibly represent brackish environments include the Sequatchie Formation (Upper Ordovician) from Georgia and Tennessee (p. 325), the Kanawa

Formation (Middle Pennsylvanian) from West Virginia (p. 327), the Permian Rio Bonito Formation from southern Brazil (p. 328), “many Cretaceous units” (p. 331), and the Ekalaka Member of the Paleocene Fort Union Formation in Montana (p. 334), just to mention the cases reported by Buatois et al. (2005). Furthermore, “in virtually every case, ichnological interpretations were supported fully by the companion microfossil studies” (Buatois et al. 2005: 331), as well as by neoichnological studies (p. 337).

This review mostly supports the preliminary conclusions that I presented more than a decade ago (Laurin and Soler-Gijón 2010). For most of the localities that I had discussed earlier, like Joggins, my suspicions of some marine influence have been strengthened by this new literature review. One notable exception is the habitat of some Famennian (Late Devonian) stegocephalians from Greenland. At that time, nothing suggested marine influence, so I had accepted the freshwater habitat that had been inferred in the literature, even though it appeared anomalous in an optimization of habitat use in early stegocephalians (Laurin and Soler-Gijón 2010: fig. 4), in which *Ichthyostega* and *Acanthostega* displayed an acquisition of a freshwater lifestyle from an ancestor that was inferred to have lived in brackish water. The isotopic analyses performed by Goedert et al. (2018) show that there is no need to invoke such transitions to a freshwater habitat in these Devonian taxa, which appear to have inhabited brackish, coastal marine environments. A new optimization of lifestyle on a stegocephalian phylogeny (Fig. 4) shows the updated scores for *Ichthyostega* and *Acanthostega*. Laurin and Soler-Gijón (2010: table 2) had also considered Strud to be a freshwater locality, and while the recent literature still interprets it this way (Denayer et al. 2016), most levels in the Dinant Synclinorium are clearly marine (Thorez and Dreesen 1986), and even in the more continental strata (on the northern edge of the basin) that have yielded stegocephalian remains, the sea could not have been far. More research on the habitat of Devonian stegocephalians would be useful.

The picture that emerges from all this is that early stegocephalian diversification seems to have occurred to a large extent close to coasts, including those of epicontinental seas, and to a lesser extent farther inland, and on land and possibly in freshwater. Is this pattern genuine, or does it reflect a taphonomic artefact that reflects the extent of sedimentation in deltas of the largest rivers on the coasts, along with erosion of sediments deposited farther from the coasts? If the latter is correct, a large evolutionary radiation of stegocephalians may have occurred in freshwater habitats but be poorly known because of taphonomic bias. Some localities, like Buxière-les-Mines, the Muse and Nýřany, may represent these freshwater localities, as suggested by the traditional interpretations. What was the salinity of the coastal environments in which stegocephalians diversified? As we saw above, the mere fact that tides occurred, as shown by tidal rhythmites, does not necessarily indicate brackish water because tidal effects can propagate inland along rivers (Feldman et al. 1993: 495), but most localities

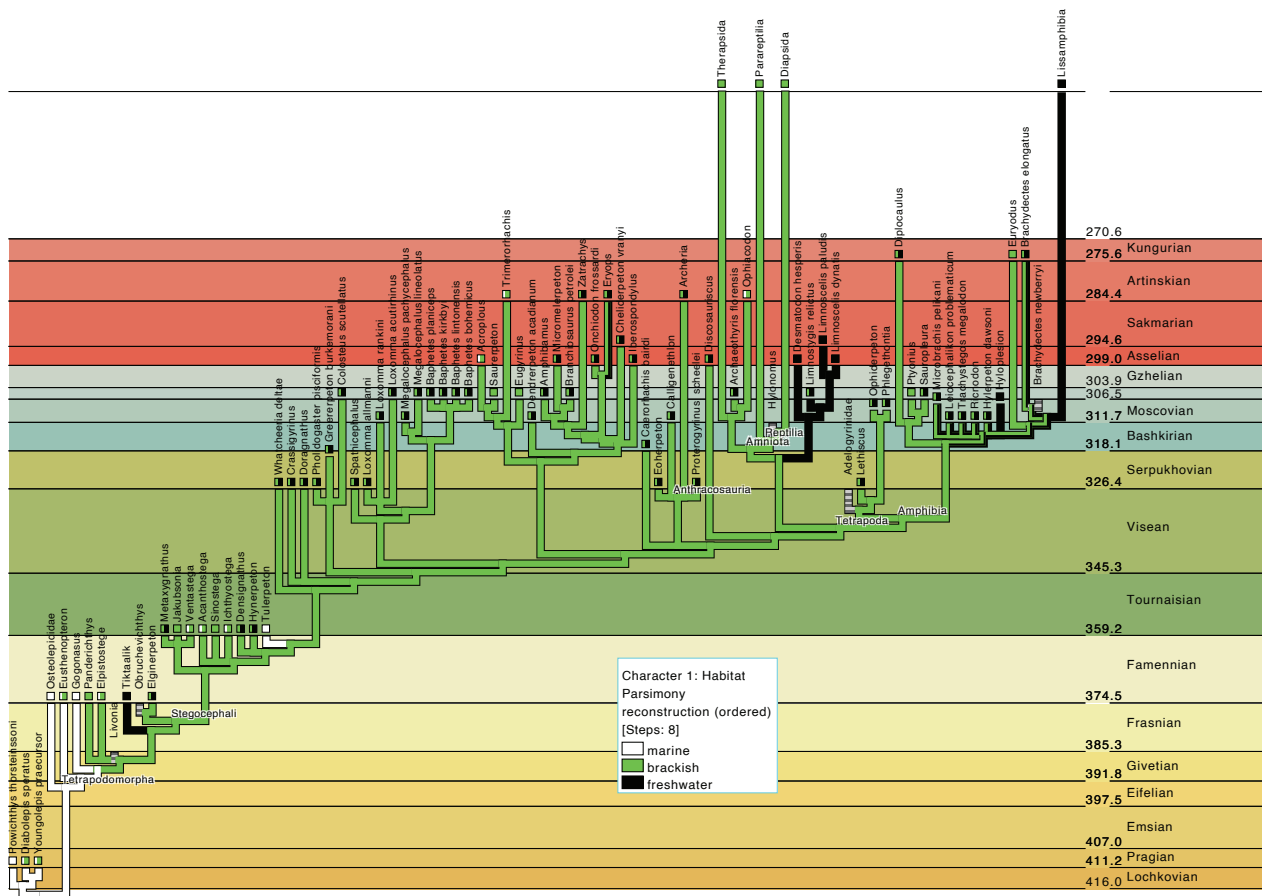


Figure 4. Optimization of habitat in stegocephalians (with a few other sarcopterygians provided to better optimize near the base of Stegocephali) on a phylogeny. This figure is slightly updated from Laurin and Soler-Gijón (2010: fig. 4), which represented the interpretations of the authors at the time. For the data shown, only the habitat of *Ichthyostega* and *Acanthostega* has been updated to reflect the findings of Goedert et al. (2018), along with the geological age of *Simostega*. To facilitate comparisons, the phylogeny was kept the same as in Laurin and Soler-Gijón (2010: fig. 4); in any case, minor changes in the phylogeny of various taxa would not change the overall pattern, and the relationships between the main clades have been confirmed by two recent studies based on extensive datasets (Marjanović and Laurin 2019; Laurin et al. 2022). The geological timescale, shown only from the Devonian through the Cisuralian, has been colored using the RGB Color Code provided by the Commission for the Geological Map of the World.

where tidal rhythmites have been recognized yielded fossils of taxa of marine origin, which suggests brackish water.

This survey may have raised more problems than it has solved, and unfortunately, time constraints prevented me from reassessing the paleoenvironment of the many Carboniferous stegocephalian-bearing localities and formations, such as the Garnett quarry, and of the more numerous Cisuralian localities. Hopefully, this review has shown that it is time to have a fresh look at the development of continental ecosystems from the Late Devonian through the Cisuralian.

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