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Taxonomie/Taxonomy

The oldest stegocephalian from the Iberian Peninsula: evidence that temnospondyls were euryhaline

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Abstract – The previous fossil record of limbed vertebrates of the Iberian peninsula started in the Triassic (245 Ma). The discovery of a new temnospondyl from the Late Carboniferous (Stephanian C, 290 Ma) extends the fossil record of stegocephalians in this region by at least 45 Ma. Early stegocephalians are usually thought to have been unable to live in salt water, but the new temnospondyl described below appears to have lived in a coastal region, presumably in salt water. © 2001 Académie des Sciences/Éditions scientifiques et médicales Elsevier SAS

Carboniferous / paleoecology / phylogeny / Stegocephali / Temnospondyli / Iberian peninsula

Résumé – **Le plus ancien stégocéphale de la péninsule Ibérique : indices de la tolérance osmotique des temnospondyles.** Jusqu'à présent, les plus anciens fossiles de stégocéphales connus de la péninsule Ibérique ne dataient que du Trias (245 Ma). La découverte d'un nouveau temnospondyle du Carbonifère Supérieur (Stéphanien C, 290 Ma) étend donc la documentation fossile des stégocéphales dans cette région d'au moins 45 Ma. Les stégocéphales anciens sont souvent considérés comme ayant été dulçaquicoles, mais le nouveau temnospondyle décrit ci-dessous semble avoir vécu dans une région côtière, probablement en eau salée. © 2001 Académie des Sciences/Éditions scientifiques et médicales Elsevier SAS

Carbonifère / paléoécologie / phylogénie / Stegocephali / Temnospondyli / péninsule Ibérique.

Version abrégée

Les temnospondyles (un clade de stégocéphales anciens, ce dernier taxon incluant les tétrapodes et les autres animaux munis d'un chiridium) ont souvent été considérés comme ayant été dulçaquicoles ou terrestres, ainsi que les amphibiens actuels. De plus, certains auteurs ont suggéré qu'un mode de vie terrestre soit primitif pour ce groupe. Quelques clades de temnospondyles euryhalins ou marins étaient connus (trimerorhachidés, trematosauridés, etc.), mais ils étaient interprétés comme des exceptions. Le nouveau temnospondyle décrit ci-dessous provient d'un site fossilifère où de nombreux chondrichthyens ont également été découverts (bassin de Puertollano, sud de l'Espagne). Des études paléoécologiques récentes montrent que ce site était côtier et marin. Ces découvertes remettent donc en question les idées reçues sur la tolérance osmotique des premiers temnospondyles, ainsi que celle des autres stégocéphales anciens. Les

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fossiles décrits ci-dessous prolongent d'au moins 45 Ma la documentation paléontologique sur les stégocéphales dans la péninsule Ibérique.

Le nouveau temnospondyle, *Iberospondylus schultzei* gen. et sp. nov. est caractérisé par la présence d'une lamelle otique qui ferme l'échancrure otique, ainsi que par la grande taille d'un processus du carré. Il conserve quelques états primitifs relativement rares parmi les temnospondyles, dont une portion du septomaxillaire exposé latéralement ainsi que l'absence du vomer de la marge de la cavité interptérygoïdienne. Il partage avec les eryopoïdés et quelques autres temnospondyles la présence d'un processus alaire sur le prémaxillaire. Ce nouveau taxon est représenté par trois spécimens, soit trois crânes plus ou moins complets ainsi qu'un squelette post-crânien incomplet. Il date du Carbonifère Supérieur (Stéphanien C). Il diffère de temnospondyles contemporains, comme *Cheliderpeton*, *Onchiodon* et *Sclerocephalus*, par l'absence du vomer de la marge de la fenêtre interptérygoïdienne, ainsi que par la possession d'une lamelle otique qui scelle l'échancrure otique et d'un processus dorsal du carré.

Une analyse phylogénétique menée avec le logiciel PAUP 3.1.1 suggère que le genre *Iberospondylus* occupe une position relativement basale parmi les temnospondyles; il forme le groupe-frère des eryopoïdés. L'inclusion du taxon *Iberospondylus* dans la matrice de données (précédemment publiée) n'altère pas beaucoup la phylogénie des temnospondyles, sauf en ce qui concerne la position du taxon *Capetus*. Ce dernier, qui était, dans une analyse antérieure, le groupe-frère de tous les temnospondyles sauf les edopoïdés, devient le groupe-frère d'un clade qui inclut les trimerorhachoïdés, *Dendrerpeton* et *Balanerpeton*.

La présence inférée (mais douteuse) d'un tympan chez les premiers temnospondyles (en plus de la présence de doigts) a été l'un des arguments en faveur de l'hypothèse selon laquelle les premiers temnospondyles étaient terrestres. Cependant, la présence de sillons pour l'organe latéral chez *Iberospondylus* suggère que ce taxon soit aquatique. La présence de trois crânes articulés et bien conservés, dont l'un est accompagné d'un squelette post-crânien incomplet partiellement articulé, suggère que les carcasses n'aient pas été transportées loin de l'endroit où ces animaux sont morts. Il est donc vraisemblable que ce stégocéphale vivait dans l'environnement côtier marin où il a été conservé. La position relativement basale de ce taxon parmi les temnospondyles suggère que ceux-ci étaient initialement aquatiques et euryhalins. Une revue des travaux récents suggère également que les premiers stégocéphales étaient aquatiques et euryhalins. Il semble vraisemblable que l'intolérance des amphibiens actuels (lissamphibiens) à l'eau salée soit une spécialisation relativement récente de ce groupe.

1. Introduction

Temnospondyls (an early clade of stegocephalians, a taxon that includes tetrapods [1] and other limbed vertebrates [2]) are often thought to have been freshwater [3] or terrestrial animals, like extant amphibians, and some authors have inferred terrestrial habits to be primitive for this group [4]. Among temnospondyls, a single Permo-Carboniferous clade (that includes trimerorhachids and saurerpetontids), as well as two Triassic clades (one includes trematosaurs, latiscopids, and metoposaurs, and the other, luzocephalids and rhytidosteids) have been suggested for many years to have been euryhaline (i.e. to tolerate fresh and salt water). The specimens of the new genus described below (*figures 1* and *2*) come from the Puertollano basin, Southern Spain, and were found in a locality that also contains many chondrichthyan (the clade that includes sharks, rays and chimeras) remains. Recent paleoecological work on this locality demonstrates that it represents a near-shore, marine environment [5, 6, 7, 8]. Thus, the new materials described below warrant a reappraisal of the osmotic tolerance of early temnospondyls, and of early stegocephalians in general. They also extend considerably the fossil record of stegocephalians in the Iberian peninsula from the Triassic [9] to the Carboniferous.

2. Materials and methods

2.1. Specimens

Stegocephali Cope 1869
Temnospondyli Zittel 1888
Iberospondylus gen. nov.

Generic diagnosis. See specific diagnosis.

Type (and only known) species. *Iberospondylus schultzei* sp. nov.

Specific diagnosis. Temnospondyl characterized by the presence of an otic lamella of the pterygoid that occludes the temporal notch (*figure 3*), of a well-developed dorsal process on the posterior surface of the quadrate, and of a smaller dorsal process of the quadratojugal, dorsal to the medial condyle (*figures 1A, 2A,* and *3*).

It retains some primitive states found in only a few other temnospondyls: a laterally-exposed portion of the septomaxilla, the absence of a vomerine contribution to the interpterygoid vacuity, and a thick, massive stapes.

It shares with eryopoids and a few other temnospondyls the presence of an alary process of the premaxilla and of uncinate processes on the ribs.

Etymology. Ibero, in reference to the geographical distribution of this genus (only known from the Iberian pen-

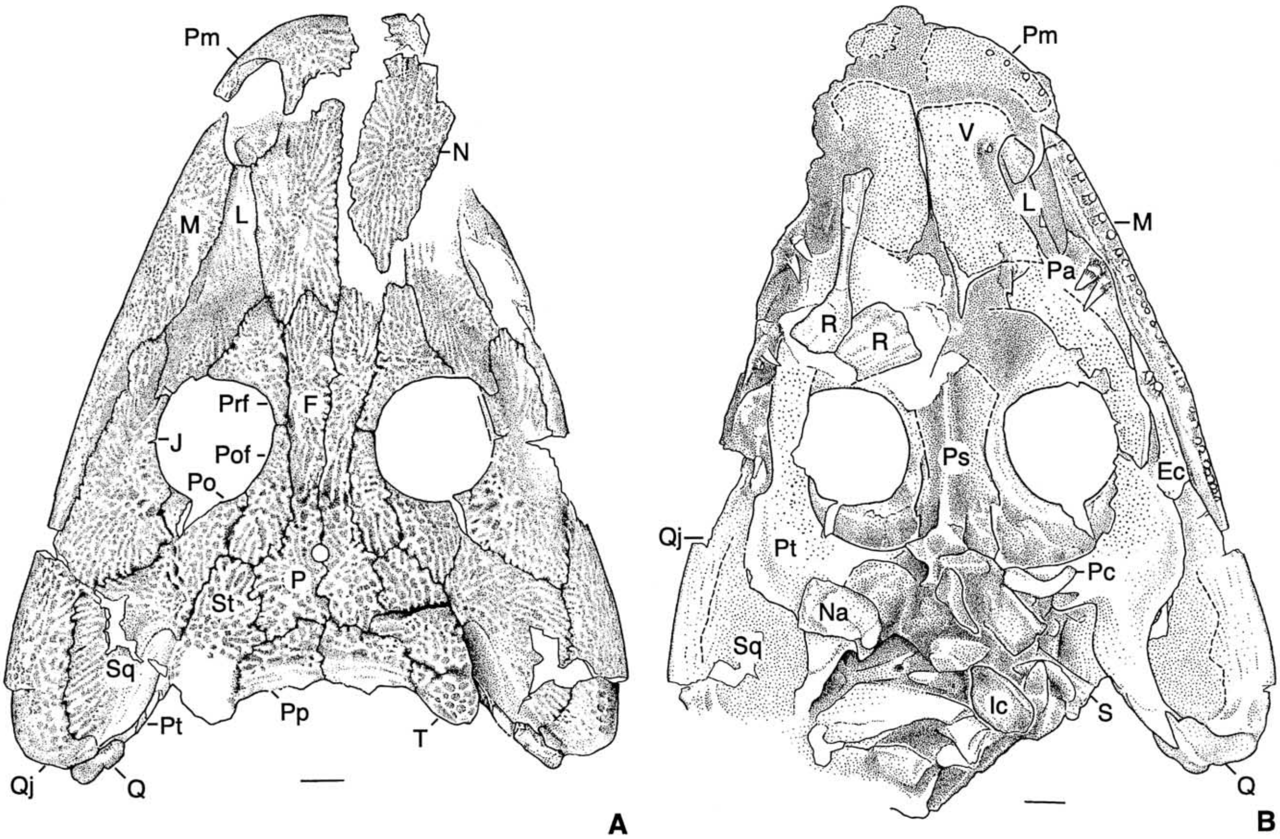

Figure 1. Drawing of the skull of holotype of *Iberospondylus schultzei*, gen. nov., sp. nov. A, dorsal view. B, palatal view. The open sutures suggest that this individual was not fully grown. The broad lateral contact between the maxilla and the quadratojugal (obscured by damage on both sides) is preserved in the other specimens. The two nearly symmetrical notches behind the orbits are breaks in the areas most strongly affected by dorso-ventral compression. The same compression gives to the otic notch a narrow appearance, but the other, less distorted specimens show that this otic notch was broad and rounded. The dorsal process of the quadrate is visible on the left quadrate. Abbreviations: Ec, ectopterygoid; F, frontal; Ic, intercentrum; J, jugal; L, lacrimal; M, maxilla; N, nasal; Na, neural arch; P, parietal; Pa, palatine; Pc, pleurocentrum; Pm, premaxilla; Po, postorbital; Pof, postfrontal; Pp, postparietal; Prf, prefrontal; Ps, parasphenoid; Pt, pterygoid; Q, quadrate; Qj, quadratojugal; R, rib; S, stapes; Sq, squamosal; St, supratemporal; T, tabular; V, vomer. Scale bar equals 1 cm.

insula, so far) plus Spondylos (Greek, vertebra). This root was chosen because it is also found in the taxon name Temnospondyli. The specific epithet is in honor of Dr. Hans-Peter Schultze, whose enthusiasm and work on Paleozoic environments and early vertebrates inspired us.

Holotype. PU-ANF (Puertollano, Amphibians) 14. Complete skull and several disarticulated postcranial elements (vertebrae and ribs).

Additional material. PU-ANF 2, partial skull, fragments of lower jaw, and axial skeleton (articulated vertebrae and several disarticulated dorsal, sacral and caudal ribs); PU-ANF 15, partial skull (left half), both stapes, lower jaw, and anteriormost part of the axial skeleton.

The holotype and additional specimens are housed in the Departamento de Paleontología, Universidad Complutense de Madrid.

Type Locality. 'Emma' quarry, Puertollano basin, Ciudad Real province, southern Spain [8, 10].

Type Horizon. Bituminous bed 'Emma' above coal seam III in the 'Emma' quarry.

Specimens PU-ANF 2 and PU-ANF 15 come from the amphibian bed above coal seam III in the 'Emma' quarry.

Age. Late Carboniferous, Stephanian C [8].

2.2. Comparison with contemporaneous taxa

The general aspect of the skull is similar to that of contemporaneous temnospondyls, such as *Cheliderpeton* [11], *Onchiodon* [12] and *Sclerocephalus* [13], except that all these taxa possess a contribution of the vomer to the interpterygoid vacuity, and none seems to possess the otic lamina that occludes the otic notch or the dorsal process of the quadratojugal. The distribution of the dorsal process on the quadrate is more difficult to assess in temnospondyls; it has not been reported in Stephanian temnospondyls, to our knowledge, but the presence of a similar (but larger) process in the trematopsid *Phonerpeton pricei* [14] raises a possibility that this process is relatively widespread but that it has been seldom reported.

2.3. Phylogenetic analysis

The affinities of *Iberospondylus schultzei* were assessed by coding it into a recently published data matrix of temnospondyls [15]. The resulting data matrix (*table I*;

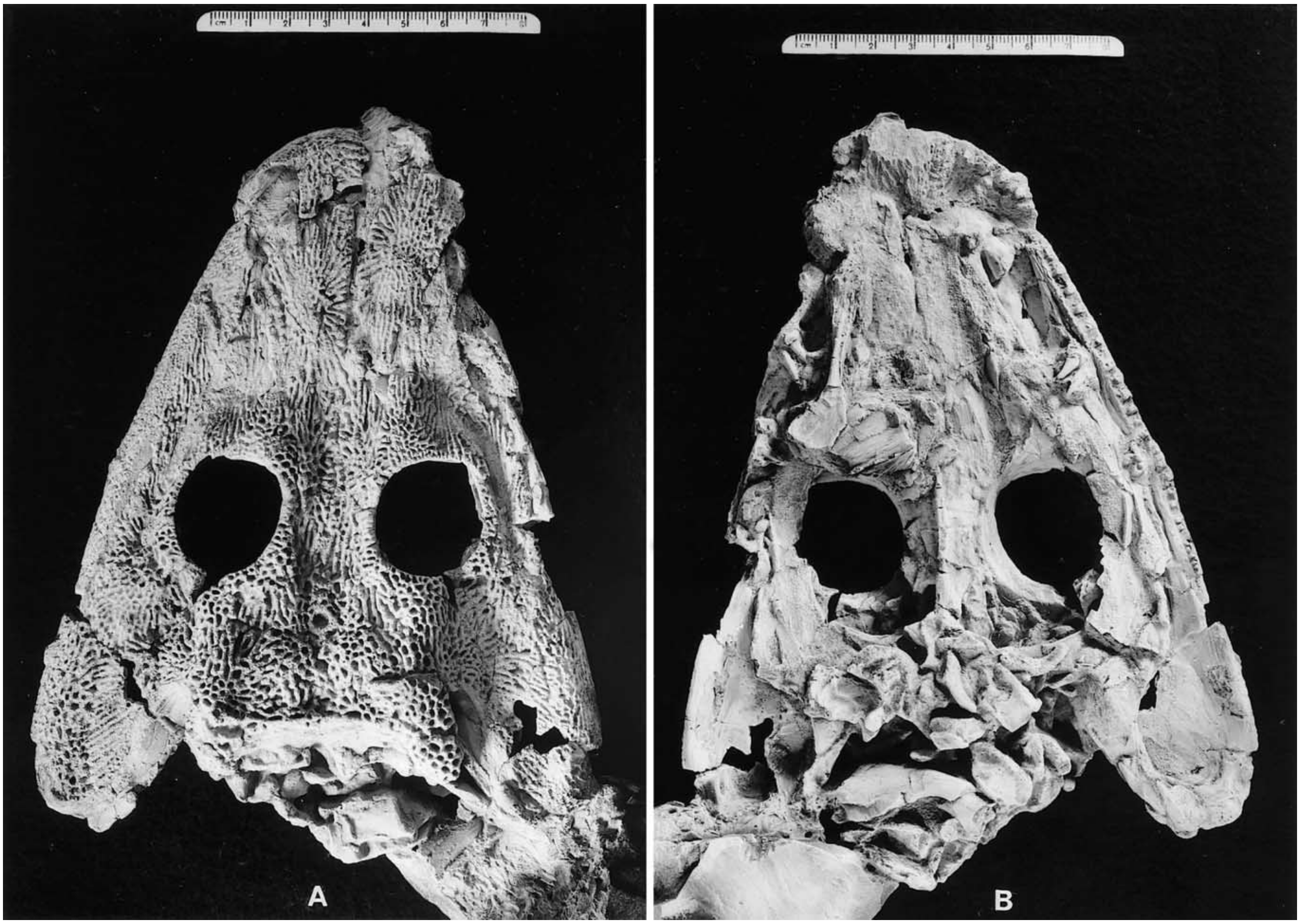

Figure 2. Picture of the skull of holotype (PU-ANF 14) of *Iberospondylus schultzei*, gen. nov., sp. nov. A, dorsal view. B, palatal view.

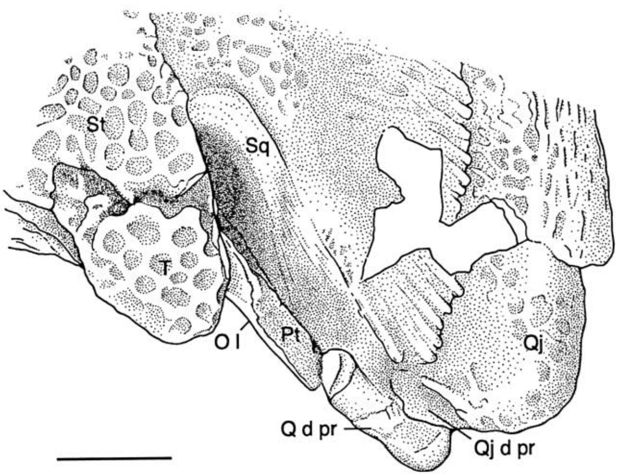

Figure 3. Specimen drawing showing a dorsal view of the otic region of PU-ANF 14, showing the otic lamella that occludes the otic notch. There is no distinct suture between the otic lamella and the pterygoid, but the limit between these two structures is obvious because the otic lamella is much thinner than the pterygoid. Abbreviations as in *figure 1*, and: O l, otic lamella; Q d pr, quadrate dorsal process; Qj d pr, quadratojugal dorsal process. Scale bar equals 1 cm.

[15]) was analysed using the branch and bound algorithm of PAUP 3.1.1 [16].

3. Results

Two shortest trees were produced. Each requires 37 steps, has a CI of 0.514 and a retention index (RI) of 0.633. In the strict consensus-tree, *Iberospondylus* occupies a fairly basal position in temnospondyl phylogeny, as the sister-group of eryopoids (*figure 4*). Except for the position of *Iberospondylus* and of *Capetus*, the strict consensus of the most parsimonious trees is compatible with the initially reported consensus tree [15]. In the previous study [15], *Capetus* was the sister-group of a clade that included all other temnospondyls except for edopoids. With the addition of *Iberospondylus* to the data matrix, *Capetus* has moved to a position nested deeper within Temnospondyli, as the sister-group of a clade that includes trimerorhachoids, *Dendrerpeton* and *Balanerpeton*.

4. Discussion

The inferred (but dubious) presence of a tympanum in early temnospondyls (as well as the presence of digits) has

Table I. Coding of *Iberospondylus* in the data matrix [15].

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
State in *Iberospondylus*	1	1	?	0	0	0	?	1	0	0	0	1	0	0	1	1	?	0

been one of the major arguments used to support the idea that early temnospondyls were terrestrial [4] or at least amphibious. The more aquatic temnospondyls could then be viewed as representing a re-invasion of an aquatic environment (that has usually been assumed to be fresh water, in most cases). The presence of a lateral-line organ in *Iberospondylus* suggest that it was aquatic. The presence of three articulated, well-preserved skulls (*figures 1* and *2*), one of which is accompanied by an articulated axial skeleton, suggests that only a short post-mortem transport affected the carcasses. Therefore, *Iberospondylus* probably lived in the near-shore environment where it was preserved.

The relatively basal position of *Iberospondylus* in temnospondyl phylogeny, its apparently euryhaline physiology (or its tolerance to salt water), and recent paleoecological work [18, 19, 20, 21] suggest that temnospondyls were initially a semi-aquatic (or even aquatic), euryhaline group. The recent re-interpretation of some early stegocephalians as primitively aquatic animals [22] even raises the possibility that the (mostly) aquatic way of life of early temnospondyls such as *Iberospondylus* is primitive, although demonstrating this point would require an exhaustive review that is beyond the scope of this study. In any case, a re-examination of the habitat of most groups of stegocephalians (or rather, those in which adequate data are available) suggests that most Paleozoic stegocephalians were euryhaline [23], and that the intolerance toward salt water exhibited by most (but not all) lissamphibians is a more recent specialization of this clade. This conclusion can be reached whether the reference phylogeny is the 'traditional' one [24] (*figure 5A*), or the recent alternative based on the first computer-assisted phylogenetic analyses of most of the relevant groups [2, 25] (*figure 5B*). Indeed, in both cases, the presumed sister-group of lissamphibians (extant amphibians) appears to have been euryhaline.

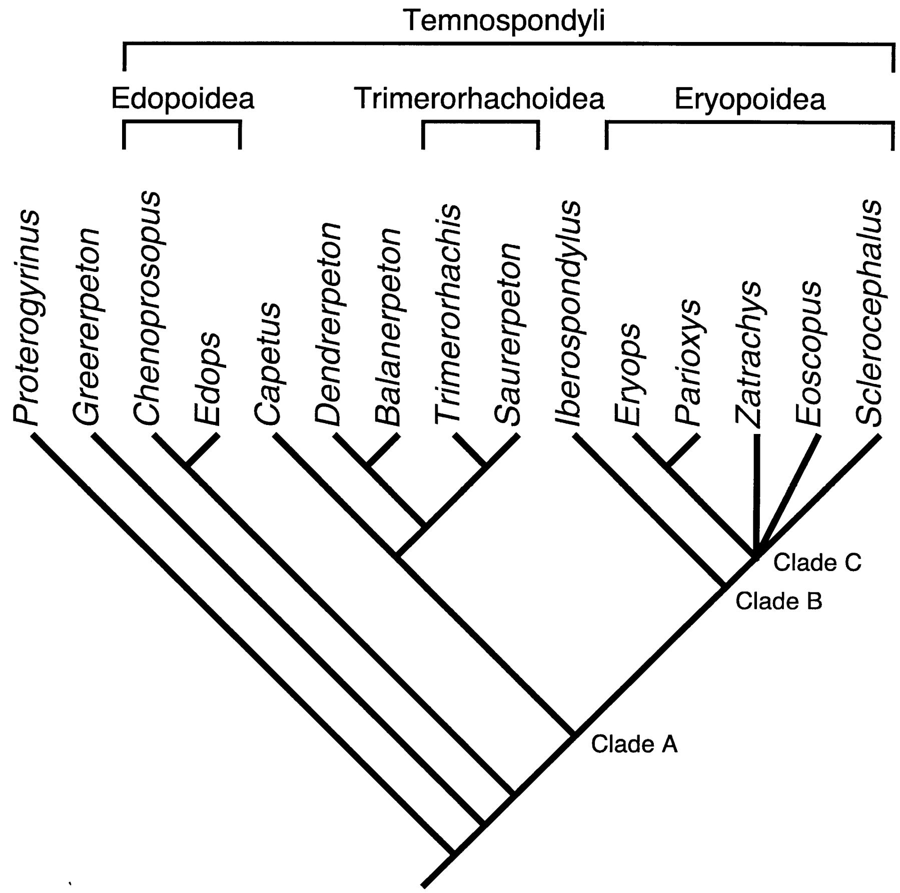

Figure 4. Position of *Iberospondylus* in temnospondyl phylogeny. Strict consensus of the two most parsimonious trees. Synapomorphies: Clade A, presence of an alary process of the premaxilla; Clade B, occipital condyle formed mostly by exoccipital; intertemporal absent; Clade C, vomer contributes to anterior edge of interpterygoid vacuity. *Proterogyrinus* and *Greererpeton* were the outgroups.

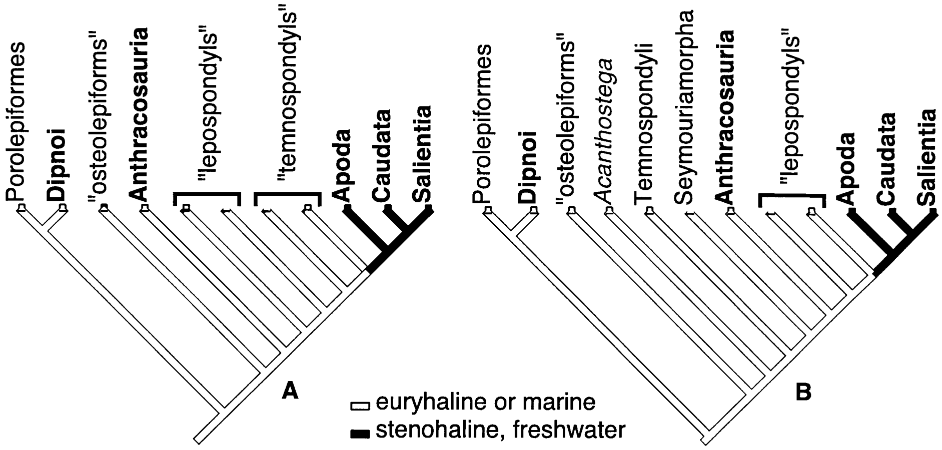

Figure 5. Evolution of environmental tolerances of choanates. A, hypothesis based on a 'traditional' phylogeny [24]. B, hypothesis based on recent, computer-assisted phylogenetic analyses of most of the relevant groups [2, 25] of stegocephalians (relationships between early sarcopterygians based on [28], and between lissamphibians taxa, on [29]). These trees were drawn using MacClade 3.08 [30] and Adobe Illustrator 5. The presence of a data box indicates that data on the physiology of the taxon exist; the absence of a data box indicates that no data exist (in some groups of lepospondyls and of temnospondyls), and that the environmental tolerance must be reconstructed using parsimony. Anthracosauria includes amniotes and all the extinct groups that are more closely related to amniotes than to lissamphibians [1, 2]. Anthracosauria is euryhaline, as shown by the presence of amniotes in both fresh water and in salt water.

These are dissorophids (the group that includes *Doleserpeton*) or some branchiosaurs, according to the 'traditional phylogeny' [24], and lysorophians, according to the newly proposed phylogeny [2]. Recent paleoecological work has suggested that all these groups were euryhaline [23].

Euryhaline habits for early stegocephalians would resolve the paradox of their extremely wide distribution in the Devonian. The first undisputed record of stegocephalians dates from the Frasnian, and by the Famennian, they had reached a nearly worldwide distribution; they were found in eastern Greenland, European Russia, Latvia, Scotland, North America, and Australia [26, 27]. The distribution of the various continental plates in the Late Devonian is still controversial, but broad epicontinental seas apparently isolated most of Gondwana from Laurentia and Baltica in the Upper Devonian [17]. Therefore, the distribution of early stegocephalians can only be explained if this group was euryhaline (at least in the Devonian; by the Carboniferous, dispersal through terrestrial or freshwater environments may have become possible).

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