

A review of *Neusibatrachus wilferti*, an Early Cretaceous frog from the Montsec Range, northeastern Spain

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Neusibatrachus wilferti is an anuran from the late Berriasian–early Valanginian fossiliferous lacustrine limestones that are exposed in the eastern part of the Montsec Range, province of Lleida, Spain. It was originally described by Seiffert in 1972 and its phylogenetic position has since been discussed. *Neusibatrachus* has been considered an undeterminable fossil, an abnormal individual, or a primitive palaeobatrachid. Here we redescribe the only available specimen, and clarify features, such as absence of palatines, nine presacrals, and procoelous vertebral centra, that have been the subject of previous debates. We consider the specimen to be a postmetamorphic individual and make developmental interpretations of some of its characters. In particular, we provide evidence of a living anuran (*Rana iberica*) that resembles *Neusibatrachus* in the development of intervertebral articulations. *Neusibatrachus* is considered a valid genus, which differs from other anurans, except for the pipoids, in the joint presence of an azygous frontoparietal and a parasphenoid lacking the subotic alae, although it differs from the pipoids in having nine presacral vertebrae. Morphological evidence indicates that *Neusibatrachus* is related to Xenoanura, the pipoid branch in the living Amphibia Tree of Life based on molecular data. Moreover, it might be a member of the pipoid clade proper, which presently includes the Pipidae, Rhinophrynidae, and several fossil taxa, including the Palaeobatrachidae, although the evidence is not conclusive.

Key words: Amphibia, Anura, Pipoidea, Palaeobatrachidae, *Neusibatrachus*, Cretaceous, Montsec, Spain.

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Introduction

Recent analyses based on morphological (Báez and Harrison 2005; Trueb and Báez 2006), developmental (Haas 2003), and molecular (Roelants and Bossuyt 2005; Frost et al. 2006) evidence have substantiated the monophyly of the anuran group composed of the crown taxa Pipidae Gray, 1825 and Rhinophrynidae Günther, 1859 “1858”, for which the node-based Pipoidea was applied by Ford and Cannatella (1993). This name is possibly a junior synonym of Xenoanura as proposed by Savage (1973) to include Pipidae, Rhinophrynidae, and Palaeobatrachidae Cope, 1865, the latter undergoing extinction in the Pleistocene. A number of fossil taxa, including the palaeobatrachids, appear as stem-rhinophrynids and stem-pipids, although their taxonomic placements are still unstable (Gao and Chen 2004; Báez et al. in press).

Seiffert (1972) erected the anuran genus and species *Neusibatrachus wilferti* on the basis of a single specimen preserved on two slabs as part and counterpart and acid prepared (Fig. 1). The specimen was discovered in a quarry (La Pedrera de Meià, or La Pedrera de Rúbies, or La Pedrera fossil site) at the well-known fossil locality of Santa Maria de Meià, in the lithographic limestones that crop out in the eastern part of the Serra del Montsec, province of Lleida, northeastern Spain. These lacustrine conservation deposits (Kon-

servat-Lagerstätten) have yielded numerous, exceptionally well preserved remains of plants, invertebrates and vertebrates, collected since the beginning of last century (Barale et al. 1984; Martínez-Delclòs 1991; Andreu et al. 1996). The frog bearing bed is part of the La Pedrera de Rúbies Lithographic Limestones, which consist of laminated carbonates representing open lacustrine conditions (Lacasa and Martínez 1986; Gibert et al. 2000). These deposits are part of the sedimentary filling of a complex basin that developed between the European and Iberian plates in relation to the opening of the Bay of Biscay (Souquet 1988). The age of the fossil-bearing beds was previously determined to be late Berriasian to early Valanginian, according to the evidence provided by ostracods (Peybernes and Oertli 1972; Brenner et al. 1974; Whalley and Jarzembowski 1985) and pollen (Barale et al. 1984).

Seiffert (1972) considered *Neusibatrachus* to be a representative of a stock ancestral to both palaeobatrachids, an extinct group of “archaeobatrachians”, and neobatrachian ranids. He noted the resemblance of *Neusibatrachus* to palaeobatrachids with both having an azygous frontoparietal, parasphenoid lacking subotic alae, and long metacarpals. However, he also mentioned that *Neusibatrachus* has dentate vomers and femora and tibiofibulae of similar length, traits that he considered present in ranids but not in palaeobatra-

chids. Subsequently, Estes and Reig (1973) commented that the putative ranid features of *Neusibatrachus* also occur in many other anuran groups. These authors considered *Neusibatrachus* an undoubted palaeobatrachid, although more primitive than the Tertiary representatives in the absence of a synsacrum and processus rostriformis on the coracoid, and the presence of a complete maxillary arch and free ribs on some presacral vertebrae. Špinar (1975) also advocated a close relationship between *Neusibatrachus wilfertii* and palaeobatrachids, suggesting that this species was in the direct ancestry of the group. Despite all these arguments, Sanchiz (in Sanchiz and Roček 1996, 1998) considered *Neusibatrachus* as a junior synonym of *Eodiscoglossus santonjae* Villalta, 1956, a putative discoglossid taxon described from the same deposits (Hecht 1970; Vergnaud-Grazzini and Wenz 1975), although no reasons were given other than judging it an abnormally developed specimen. More recently, a parsimony analysis of several extinct anuran taxa by Gao and Chen (2004) has shown *Neusibatrachus* nested within the pipoid clade. In their analysis, character states for *Neusibatrachus* were scored according to Seiffert's (1972) description and from comments on its features made by Vergnaud-Grazzini and Wenz (1975) and Roček (2000). However, our personal examination of the holotype of *Neusibatrachus wilfertii* housed in the Freie Universität, Berlin, revealed that some features were misinterpreted by earlier authors. In addition, this specimen presents a very peculiar set of anatomical features and is not referable to *Eodiscoglossus* or to any other known anuran taxon. Herein, we redescribe and analyze several anatomical and developmental aspects of *Neusibatrachus*, and consider its relationships to living and extinct anurans in the context of recent phylogenetic hypotheses. The pipoid affinities of *Neusibatrachus* were corroborated in a phylogenetic analysis in which the characters for this taxon were recoded according to the new observations (Báez et al. in press).

Institutional abbreviations.—FUB, Freie Universität, Berlin, Germany; KU, Natural History Museum, The University of Kansas, Lawrence, Kansas, USA; MNHU, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; PMHU, Paläontologisches Museum, Humboldt-Universität, Berlin, Germany.

Systematic palaeontology

Class Amphibia Linnaeus, 1758

Order Anura Fischer von Waldheim, 1813

Genus *Neusibatrachus* Seiffert, 1972

Type species: *Neusibatrachus wilfertii* Seiffert, 1972.

Revised diagnosis.—Small anuran that shares only with pipoids the joint presence of an azygous frontoparietal and a parasphenoid lacking subotic alae, but differs from them in

having 9 presacral vertebrae. It differs from *Rhadinosteus* and rhinophrynids in having the atlas formed by fusion of Vertebrae I and II, and metacarpals exceeding 75% the length of the radioulna. It differs from all known pipimorphs in the presence of a complete maxillary arch and can be further distinguished from crown pipids in the presence of a T-shaped squamosal, pedicellate teeth, a parahyoid bone, and a bicondylar articulation between sacrum and urostyle. It also differs from *Thoraciliacus* and *Cordicephalus* in its narrower braincase, a frontoparietal forming a flat dorsal table, and tiny scapular cleft and it can be distinguished from palaeobatrachids in having a T-shaped squamosal lacking processes on the ventral ramus, an articulation for the lower jaw at the midlevel of the otic capsules, a monovertebral sacrum, slightly expanded sacral diapophyses, and a coracoid lacking a conspicuous rostral process and having a slightly expanded sternal end.

Neusibatrachus wilfertii Seiffert, 1972

Holotype: FUB 33A, B.

Type locality and age: Santa Maria de Meià, province of Lleida, Spain; late Berriasian–early Valanginian.

Description

The only known specimen of *Neusibatrachus wilfertii* (Fig. 1) is about 21 mm in snout-vent length. Because the specimen is irregularly split into two parts (FUB 33A, B), impressions and/or fragments of individual elements are preserved on both slabs and, thus, descriptions of most bones are composite.

Cranial skeleton

The skull is wider than it is long. The preorbital region is notably short; its anteroposterior length is slightly less than one-fifth the total length of the skull (Fig. 2).

The nasals are poorly preserved although their impressions indicate that they were delicate, relatively narrow winglike bones that incompletely roofed the nasal capsules (Fig. 2). These bones were adjacent but not in contact along the skull midline. The anterior margins of the nasals are slightly concave, whereas medially they project forward in short, blunt rostral processes. Posterolaterally, the nasals terminate near the maxillary arches.

The frontoparietal forms an ovoid dorsal skull table and lacks a median suture between the left and right halves, at least along the posterior two thirds of its length (Fig. 2). The poor preservation of its anterior part precludes assessment of the shape of its anterior margin or its relationships with the underlying bones, although it is evident that a frontoparietal fontanelle is absent. In the orbital region, the lateral margins of the dorsal table are relatively straight and do not project to form supraorbital flanges. We were not able to corroborate the presence of a pineal foramen.

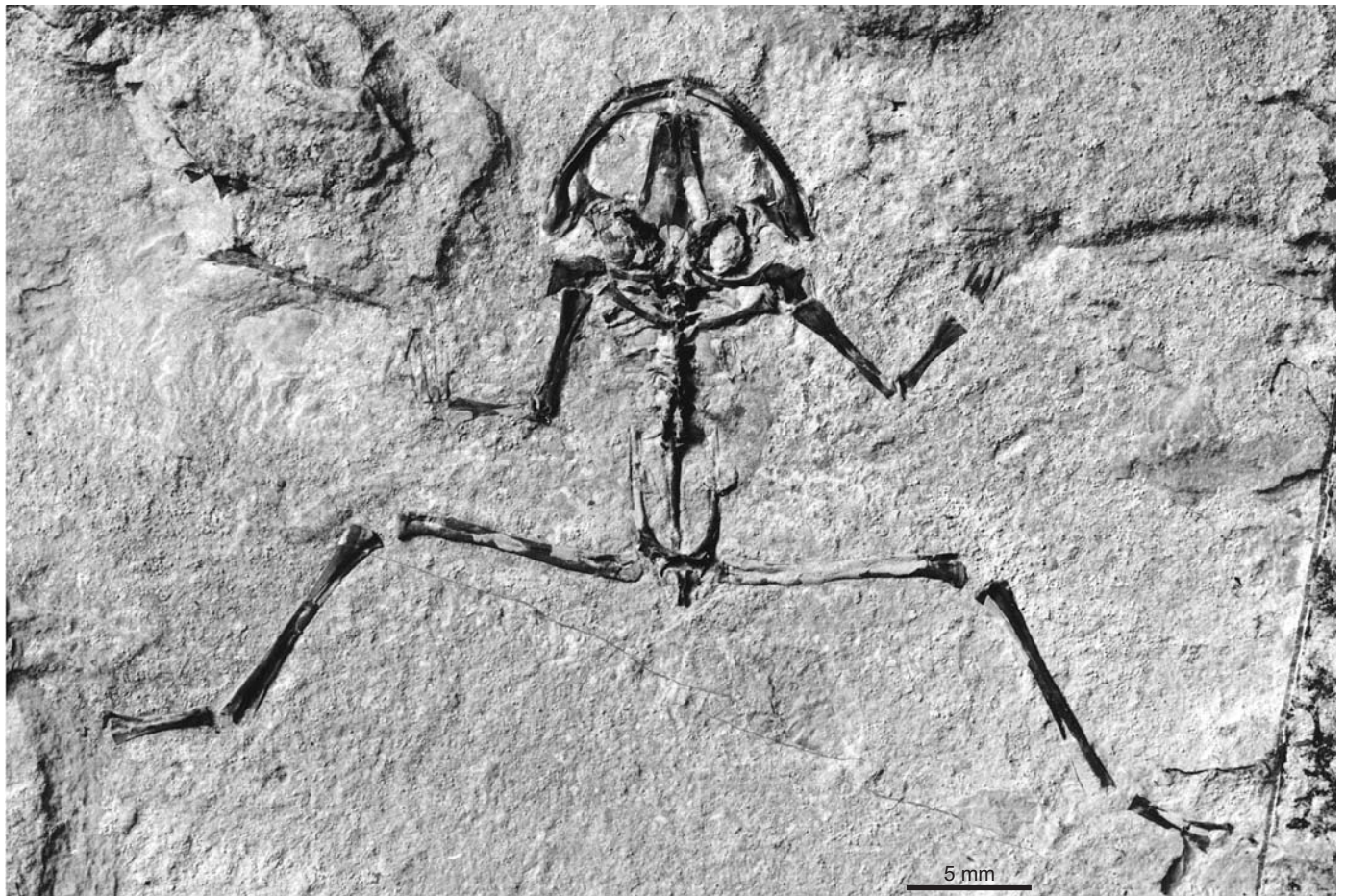


Fig. 1. *Neusibatrachus wilfertii* Seiffert, 1972, holotype (FUB 33A) from the upper Berriasian–lower Valanginian of Santa Maria de Meià, Spain, in ventral view.

The sphenethmoid, presumably single, is dorsally overlapped by the frontoparietal at least up to the level of the anterior margin of the orbits; this precludes determination as to whether it forms the boundary of the frontoparietal fenestra. There is no evidence that the sphenethmoidal ossification extended anteriorly into the medial septum that separates the olfactory capsules, or laterally into the post-nasal walls. Posteriorly, the sphenethmoid extends up to mid-orbit level; the optic nerve foramina were not enclosed by this bone (Fig. 3A). The ventral surface of the sphenethmoid is traversed by the relatively narrow cultriform process of the parasphenoid.

The prootics and the exoccipitals are only partially fused to one another to form the relatively large otic capsules, although the nature of the medial association of these latter structures is unknown. The dorsal surfaces of the prootics are poorly preserved but no crests or grooves seem to have been present. Posteriorly, the overlapping clavicles obscure the outlines of the occipital condyles. Ventrally, on both sides of the skull, a robust outgrowth projects forward from the anteromedial corner of the otic capsule (Fig. 3A). This structure is part of the palatobasal connection between the palatoquadrate and the neurocranium, possibly covered antero-

ventrally by the medial ramus of the corresponding pterygoid when *Neusibatrachus* was fully grown.

The premaxillae are anteroposteriorly long dentate bones, each being 30 per cent of the maxillary length (Fig. 3A). Although the dorsal aspect of these bones is not visible clearly, it is possible to ascertain the presence of distinct rectangular alary processes. Ventrally, the well-developed pars palatina projects posteromedially into a short palatine process. Each premaxilla bears 16 tooth positions; 11 and 13 teeth are preserved on the right and left premaxilla respectively. The maxillae are also long bones, extending posteriorly up to the level of the posterior margin of the orbit, where they articulate with the corresponding quadratojugal. The anterior portions of the maxillary pars facialis are poorly preserved on both sides; this prevents description of the joint of this bone with the adjacent premaxilla; ventrally, a transverse suture between the premaxilla and maxilla is evident (Fig. 3A). The maxillary tooth row consists of about 45 tooth positions and extends along the anterior 3/4 of the length of the bone; 28 and 31 teeth are preserved on the right and left maxilla respectively. The maxillary teeth, like those on the premaxillae, are pedicellate, bicuspid, and strongly curved lingually.

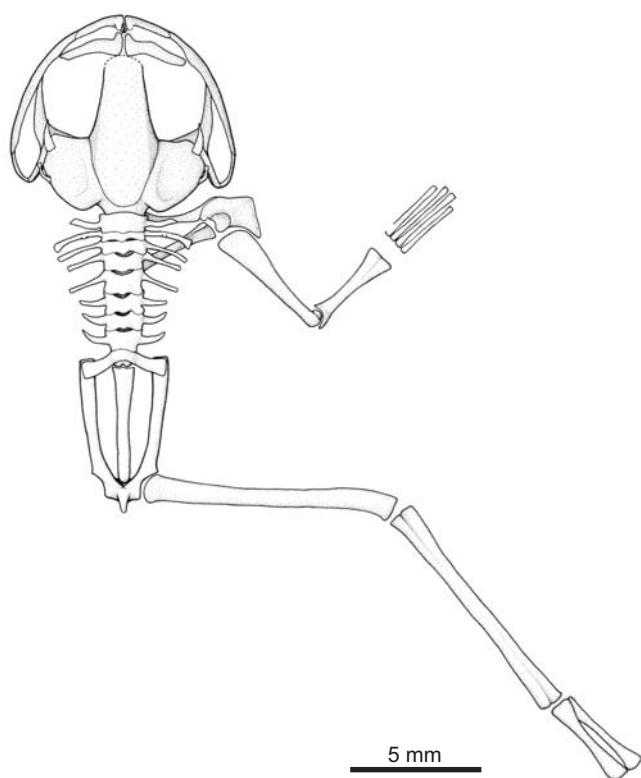


Fig. 2. *Neusibatrachus wilferti* Seiffert, 1972 from the upper Berriasian–lower Valanginian of Santa Maria de Meià, Spain. Partial restoration of the skeleton in dorsal aspect.

Paired vomers flank the anterior portion of the cultriform process of the parasphenoid at the level of the anterior margins of the orbits. These bones are well represented by their ventrally protruding dentate portions, each of which bears 5–6 tooth positions in a single row on its posterior edge, with 4 and 5 pedicellate, bicuspid teeth preserved on the right and left bone respectively. Anterior to the dentate portion on the left side, there is an irregular flat piece of bone that we interpret as part of the anterior process of the vomer. On each side of the skull, and at a level slightly anterior to the dentate portion of the vomer, there are pigmented impressions and scraps of bone that extend transversely towards the angulosplenial (Fig. 3A). These remnants have been attributed to the palatines by Seiffert (1972) and Gao and Chen (2004), but similar remnants also occur anteriorly, next to the dentaries, and it appears more likely that they correspond to the margins of the nasals. Furthermore, they coincide with the faint impressions of these bones on the counterpart slab. According to this interpretation there is no evidence for the presence of palatines.

The dagger-like cultriform process of the parasphenoid is clearly visible beneath the sphenethmoid. The anterior end of this process terminates at the level of the anterior orbital margins, although it appears somewhat broken. The width of the cultriform process increases posteriorly up to the anterior third of the otic capsules at which point a short

process develops on each side of the bone (Fig. 3A). The posterior part of the parasphenoid is not preserved, but examination of the ventral surface of the otic capsules failed to reveal any trace of this element, strongly suggesting that it lacked subotic alae.

The squamosal is T-shaped, although the poor preservation of this bone precludes a detailed description. The distinctly pointed, well developed zygomatic process is free ending, whereas the slightly expanded otic ramus rested on the dorsolateral surface of the otic capsule. The ventral ramus, which was probably in contact with the lateral surface of the palatoquadrate cartilage, is relatively long. The plectral apparatus is represented by the well-ossified pars media plectri (Fig. 3A). This element is a strongly curved, rod-like bone, the proximal end of which is expanded into a rounded footplate that was probably applied to the fenestra ovalis. The distal end of the stylus is slightly expanded.

The pterygoids are clearly visible on each side of the skull. Each bone has an anterior ramus that is slightly curved medially and seems to have articulated with the maxilla at the midlength of the orbit. The medial and lateral rami are shorter than the anterior ramus.

The lower jaw is preserved in articulation with the skull, the jaw joint lying at the level of the midlength of the otic capsule. The angulosplenial covered the posterior two thirds of Meckel's cartilage ventrally and medially. Near the posterior end of this bone, a small, but distinct, coronoid process is visible mediodorsally. The laminar dentary extended laterally along the anterior half of the cartilage. Near the mandibular symphysis of the right dentary a terminal thickening might be interpreted as a mentomeckelian bone (Fig. 3A).

Hyobranchial skeleton

A pair of splint-like bones is clearly visible on the ventral surface of the parasphenoid between the otic capsules, and between their posterior converging ends a small, unpaired piece of bone is present. These bony elements were likely joined together to form a Y-shaped parahyoid bone. No other component of the hyobranchial apparatus has been identified with certainty. In extant frogs, the whole hyobranchial skeleton, including the parahyoid bone when present, completes its development after metamorphosis.

Postcranial skeleton

Axial skeleton.—Eight discrete vertebral elements, the sacrum, and the urostyle are clearly visible (Fig. 3B), although the total number of vertebrae is a matter of a discussion below. The neural arches of the presacral vertebrae are not completely imbricate and lack well-developed neural spines. The neural arches are wider than long, although the arches of the last three presacrals are somewhat narrower than those preceding them. The articular facets of the prezygapophyses are not exposed; thus, they can not be described. The three most anterior presacral centra are poorly preserved, but the

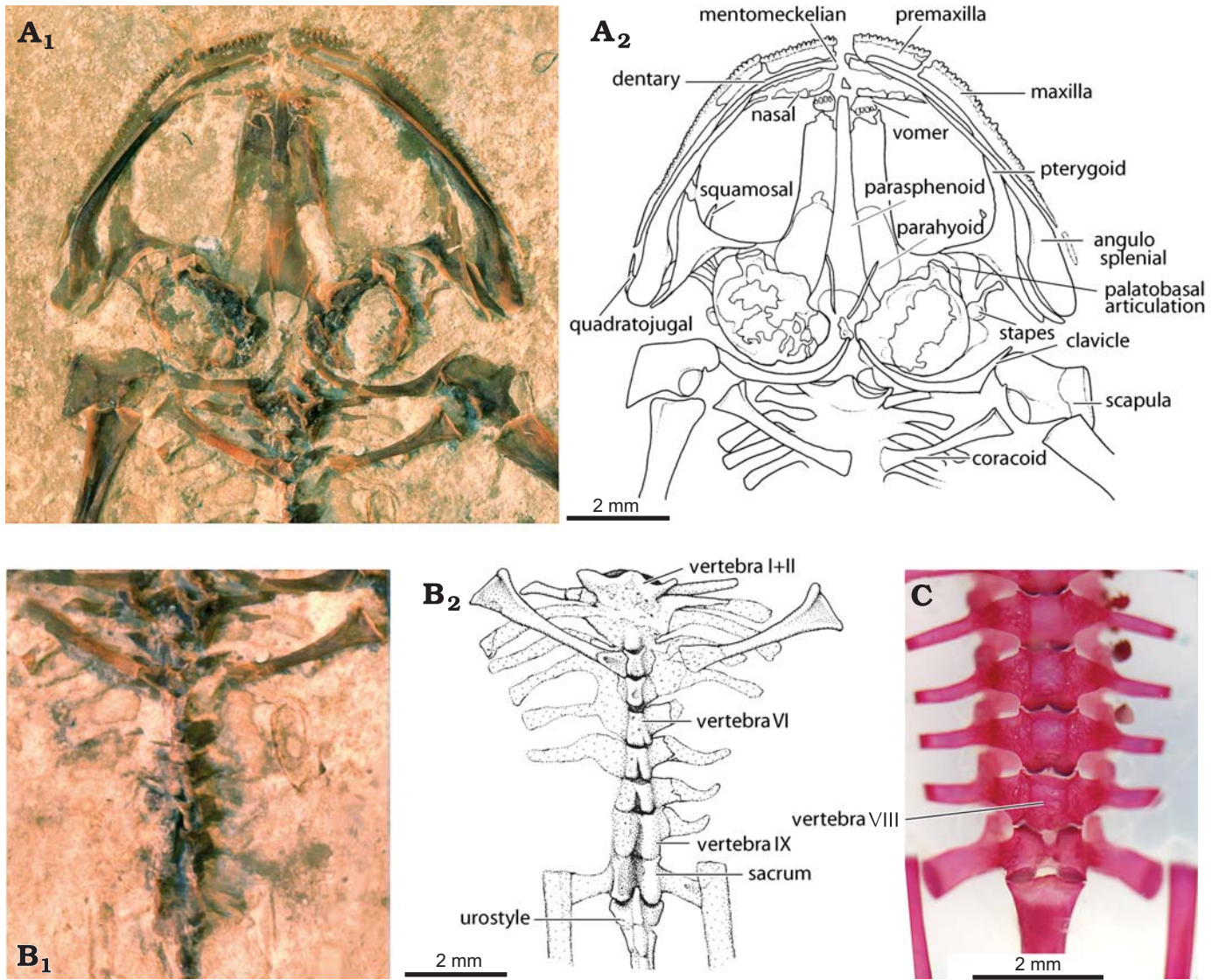


Fig. 3. **A, B.** *Neusibatrachus wilfertii* Seiffert, 1972, holotype (FUB 33A) from the upper Berriasian–lower Valanginian of Santa Maria de Meià, Spain, details in ventral view. **A.** Cranial and anterior postcranial regions, a photograph (A₁) and interpretive drawing (A₂). **B.** Vertebral column, a photograph (B₁) and interpretive drawing (B₂). **C.** *Rana iberica* Boulenger, 1879, cleared and stained wild-caught postmetamorphic froglet (MNCN 15009), posterior presacrals and sacrum in ventral view.

centra of the fourth and fifth discrete vertebrae are seen to be nearly cylindrical. One of them, slightly dislocated, shows an apparently procoelous condition (Fig. 3B). The presence of a notochordal canal is difficult to ascertain. The centra of the last three presacrals are incompletely ossified and their convex posterior ends are excavated by longitudinal grooves that make them appear to have posterior, paired condyles (Fig. 3B). The length and width of these grooves become progressively greater posteriorly; thus, the last presacral centrum is nearly fully divided. There is no indication of separate intervertebral bodies. The available evidence indicates that the vertebral centra are not opisthocelous; further development might have produced a procoelous condition.

All presacrals bear transverse processes, some of which might include coalesced ribs as indicated by the discontinuities visible on the first and fourth processes. The first pre-

sacral element has transverse processes that are as long as the sacral diapophyses and are slightly anterolaterally oriented. Ventrally, the anterior margin of the first presacral is acuminate and bears elongate cotyles that are not separated by an intercotylar notch. The following discrete presacral element has long transverse processes, which are oriented posterolaterally and have distinct uncinat processes on their dorsal surfaces. The distal ends of these transverse processes are slightly expanded. The transverse processes of the succeeding vertebra, almost as long as those of the second presacral, are also posterolaterally oriented. The following two vertebrae have transverse processes of similar shape and orientation, but shorter, and those of the last three presacrals are shorter still. Whereas the transverse processes of the sixth element are almost horizontal, the distal portion of the succeeding two are anteriorly directed, particularly the pro-

cesses of the last presacral. Also, the transverse processes of these two vertebrae are distinctly acuminate, unlike the distally blunt processes of all the other presacrals.

The sacrum is probably formed by one vertebra and has a bicondylar articulation with the urostyle; no neural spine is evident. There is an elongate depression on the ventral surface of the sacral centrum, flanked posteriorly by a convexity. The sacral diapophyses are deflected posteriorly and slightly expanded distally (Figs. 2, 3B). The length of the urostyle is nearly equivalent to the length of the first seven discrete presacral vertebrae. Ventrally, scars mark the fusion of the hypochord to the dorsal part of the urostyle, whereas the anterior end of the hypochord protrudes between the urostyle cotyles to fit into the ventral depression on the sacral centrum. Although the wide anterior portion of the urostyle suggests that a distinct postsacral neural arch might have been present, the presence or absence of transverse processes on the urostyle is difficult to assess because the dorsal region is poorly preserved.

Pectoral girdle.—The scapulae are relatively short bones; the glenoidal part of each scapula being almost one third of the total mediolateral length of the bone. The leading edge is straight and distinctly thinner than the rest of the scapular shaft. Medially, the slightly expanded pars acromialis and the pars glenoidalis are separated by a tiny notch (Fig. 4). The clavicles are robust and distinctly bowed anteriorly (Figs. 1, 3B). The lateral end of each clavicle is acuminate; the shape of this end and that of the pars acromialis of the scapula indicate that the clavicle rested on the anterior edge of the latter bone. The coracoids are only slightly expanded medially and laterally, the sternal ends less so than the lateral ends. A short ventral groove that sets off an anterior flattened process is visible on the lateral end of both coracoids (Fig. 4). No other parts of the pectoral girdle can be clearly discerned.

Forelimb.—The humerus is a slender bone, of slightly more than half the femoral length. The deltoid crest is moderately developed and extends along the proximal third of the diaphysis. At the distal end, the eminentia capitata remained incompletely ossified between both epicondyles. The radioulna is flattened and expanded distally. The carpus is not preserved. Faint impressions and fragments of the four metacarpals are clearly visible on both sides, whereas a few phalanges are preserved. The metacarpals are relatively long, the longest being more than 75% of the length of the radioulna (Fig. 5).

Pelvic girdle.—The articulated pelvis is visible on both slabs. The ilial shaft is oval in cross-section and appears to bear a fine crest along its dorsal margin as well as, possibly, a tuber superior. A distinct rim borders the acetabulum, its ventral part being more expanded than the dorsal one. A small ventral acetabular expansion (pars descendens) is present but the pubis is not mineralized.

Hind limb.—The femur is distinctly sigmoid. Its length is about 52% of the snout-vent length. The tibiofibula is as long as the femur and longitudinal sulci at the proximal and distal

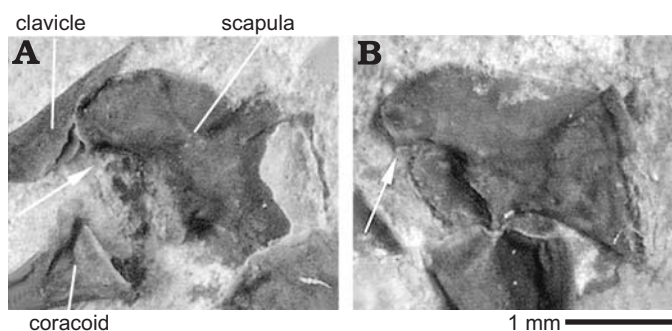


Fig. 4. *Neusibatrachus wilfertii* Seiffert, 1972 from the upper Berriasian–lower Valanginian of Santa Maria de Meià, Spain, holotype (FUB 33A). **A.** Close-up of the left scapula, ventral aspect. **B.** Right scapula of the same (reversed). White arrows indicate the position of the tiny medial notch.

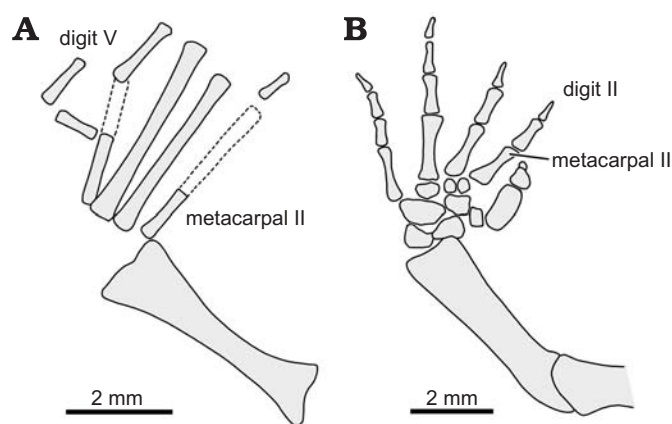


Fig. 5. Comparison of the radioulna and metacarpals of *Neusibatrachus wilfertii* Seiffert, 1972, holotype, FUB 33B (**A**) and *Eodiscoglossus santonjae* Villalta, 1956, holotype, MNCN 4723 (**B**). Both specimens are from the upper Berriasian–lower Valanginian of Santa Maria de Meià, Spain.

ends mark the former fusion between its component parts. The slender tibiale and fibulare remain separate proximally or distally. The length of these latter bones is nearly 45% of the tibiofibular length. Distal tarsal elements are not preserved but impressions and fragments of the metatarsals on one of the slabs (FUB 33B) show that they are slim and as long as the tibiale and fibulare, although the relative proportions of individual bones are not discernible.

Developmental interpretations

The only known specimen of *Neusibatrachus* is probably a recently metamorphosed individual or an early juvenile, as commented by Vergnaud-Grazzini and Wenz (1975). This is suggested by features such as the incomplete fusion of exoccipitals and prootics, and the cartilaginous, or poorly ossified, carpus. The immature state of the only known specimen forces us to extrapolate its adult features. The most difficult system to interpret from a developmental viewpoint based on the available evidence is the axial skeleton.

The single available specimen of *Neusibatrachus* arguably has nine presacrals. Atlantal transverse processes have been described occasionally in anurans, such as the Middle Jurassic basal frog *Notobatrachus degiustoi* (Báez and Nicoli 2004), and the Early Cretaceous pipoid *Shomronella jordanica* (Chipman and Tchernov 2002), or the extant basal *Ascaphus truei* (Ritland 1955). However, it seems unlikely that the long transverse processes borne by the first discrete axial element of *Neusibatrachus* are atlantal processes because those on the following element bear posterodorsally directed uncinat processes and are the longest of the entire column. Uncinate processes occur in many basal taxa and have been associated with the origin of the muscles that posteriorly insert onto the suprascapula and scapula (Ritland 1955). When a single pair of uncinat processes is present, they occur on the second pair of ribs articulated with the transverse processes of vertebra III, as in *N. degiustoi* (Estes and Reig 1973), *Vieraella herbstii* (Báez and Basso 1996), *S. jordanica* (Estes et al. 1978), *Palaeobatrachus* (*P. novotny* KU 1288, 1275; *P. luedeckei* NMHU Am 875, holotype, personal observation), *Bombina* (Madej 1965; personal observation), and *Discoglossus* (Púgener and Maglia 1997). Uncinate processes have been described on the ribs of both vertebra III and vertebra IV in *Ascaphus truei* (Ritland 1955) and in species of *Leiopelma* (Stephenson 1952; Worthy 1987), whereas they occur in the Early Jurassic basal frog *Prosalirus bitis* on ribs attached to unidentified disarticulated vertebrae (Jenkins and Shubin 1998). This evidence indicates that the second vertebra of *Neusibatrachus* probably represents vertebra III and that the preceding vertebra results from the fusion of the atlas and vertebra II. If this is so, then the sacrum is formed by vertebra X and an early fusion occurs between the atlas and vertebra II.

The cylindrical shape of the centra of vertebrae V and VI suggests that the development of these vertebrae might have been perichordal, as epichordal centra are usually distinctly shallow. The configurations of the last three presacral centra with posteriorly decreasing degrees of ossification and increasingly large longitudinal ventral grooves indicate that the axial column ossified in an anterior to posterior sequence. We can also speculate that the initial ossification of the centra occurred over the notochord to continue ventrally to eventually encircle this structure, as noted in other anuran taxa (Mookerjee 1936; Haas 2003). These grooves might correspond to the unossified ventral portion of the perichordal tube that exposes the notochordal canal and document the continuum of change between the perichordal and epichordal developmental modes commented on by Kluge and Farris (1969).

Scars on the urostyle in *Neusibatrachus* suggest that the hypochord is synostotically fused to the postsacral neural arches. This resembles the condition described for pipids and palaeobatrachids in which these structures ossify independently before fusion (Ročková and Roček 2005). As in some palaeobatrachids (Venczel 2004; Fig. 6), discoglossids (*Alytes cisternasii*, personal observation), and pelo-

dytids (Sanchiz 1978), the anterior end of the hypochord reaching the sacral centrum remains distinct as a protruding process.

Comparative morphology

In view of the debated taxonomic position of *Neusibatrachus* and our reinterpretation of some of its features, comparisons with other taxa seem pertinent.

The nasals appear less extensive than those of the holotype of *Eodiscoglossus santonjae*, although the adult *Neusibatrachus* might have had larger nasals. As in pipoids, but not *Eodiscoglossus*, there is no evidence of a suture between left and right frontoparietals and the sphenethmoid is not exposed between the acuminate anterior ends of these bones. The premaxilla, measured along the pars dentalis, is relatively wider than in juvenile *E. santonjae* (Vergnaud-Grazzini and Wenz 1975), *Palaeobatrachus*, and most living anurans, including pipids. Proportionally wide premaxillae also occur in *Prosalirus bitis* (Jenkins and Shubin 1998) and *Notobatrachus degiustoi* (Báez and Basso 1996).

The otic capsules are comparatively larger and more rounded than in *Eodiscoglossus* as the crista parotica was not extensively developed probably due to the immaturity of the specimen. The peculiar processes that project from the floor of the otic capsules may correspond to the similarly positioned structures on the prootics of *Palaeobatrachus diluvianus* (KU 124939) and *P. novotny* (KU 124909), abutting the medial pterygoid rami. In these taxa the bony contact indicates that the palatobasal articulation was immobile, but the adult condition of *Neusibatrachus* can not be ascertained on the available evidence.

The vomers are incompletely preserved, and we were unable to observe the long process depicted by Seiffert (1972) posterolateral to the dentate portion. Extensive vomers bearing 7–8 teeth are present in *Eodiscoglossus santonjae* (Vergnaud-Grazzini and Wenz 1975), although in this species the dentigerous process is more laterally elongate than in *Neusibatrachus*. In this respect, *Neusibatrachus* resembles *Palaeobatrachus* in having vomers with transversally short dentate portions, although small postchoanal processes may occur in the latter taxon (personal observation). According to Vergnaud-Grazzini and Wenz (1975: 7), *Eodiscoglossus santonjae* has a palatine "... proche de celle observée chez *Discoglossus pictus*". In this latter species, as well as in *D. sardus* (Púgener and Maglia 1997), a process extends medially from the maxilla across the planum antorbitale, but a separate palatine is not present. This maxillary element of dubious homology, termed palatine process by Púgener and Maglia (1997), is lacking in *Neusibatrachus*.

As noted above, the morphology of the region suggests that there were no parasphenoid alae underlying the ventral surface of the otic capsules. The lack of parasphenoid alae characterizes all known extinct and living pipoids and this condition differs strikingly from that in a juvenile specimen

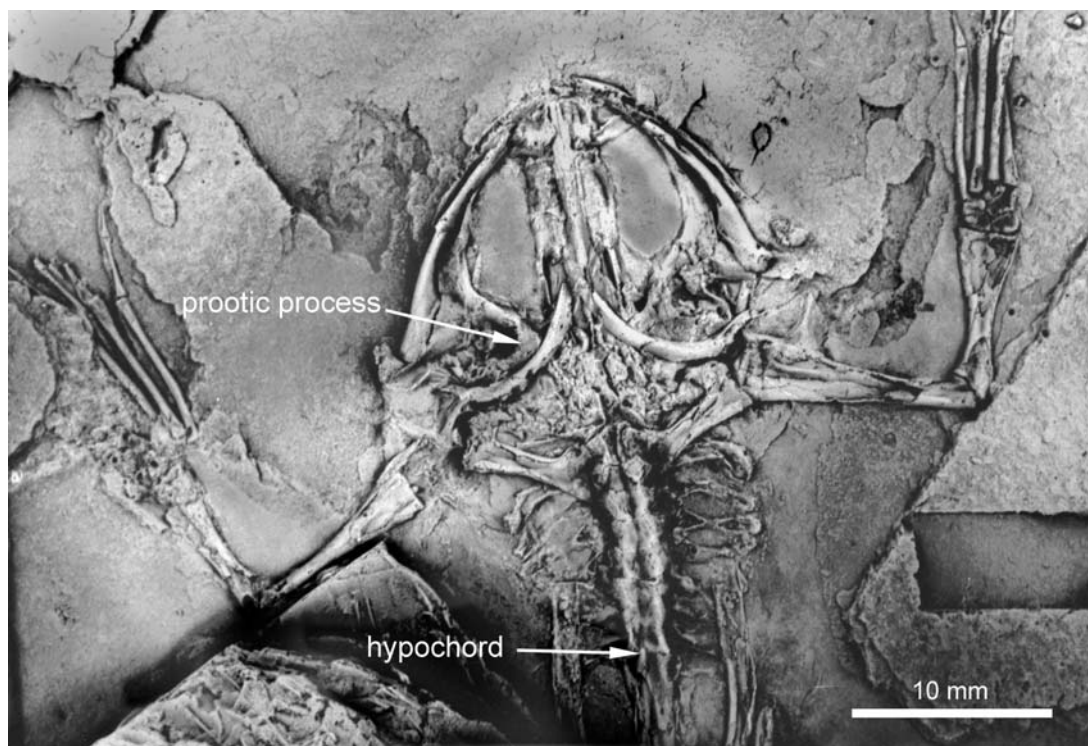


Fig. 6. *Palaeobatrachus diluvianus* (Goldfuss, 1831), KU 124939 from the upper Oligocene of Bechlejovice, Czech Republic, latex cast of the ventral aspect. Note the processes on the prootics, the ventrally grooved centra, and the protruding hypochoord.

referred to *Eodiscoglossus santonjae* (Vergnaud-Grazzini and Wenz 1975) that has well developed alae.

Nine presacrals is the standard condition in the living basal frogs *Ascaphus* and *Leiopelma*, as well as in *Notobatrachus* and in the single known specimen of *Yizhoubatrachus* from the Lower Cretaceous of China (Gao and Chen 2004). In *Neusibatrachus* the transverse processes of only the last two presacrals are distally acuminate and slightly anteriorly directed. If the distally blunt and very long processes borne by vertebrae I+II to VI include fused ribs, this taxon had five pairs of ribs, a presumably primitive condition also described in *Palaeobatrachus* (Špinar 1972; Roček 2003) and, occasionally, in *Notobatrachus* (Estes and Reig 1973). By contrast, in adult *Eodiscoglossus* vertebrae I and II are not fused and vertebrae II to IV bear short free ribs.

The deeply grooved ventral surfaces of the posterior presacral vertebral centra give these centra the appearance of having bicondylar articulations (as in the sacrum), a feature that we have not seen previously described in living forms. Nevertheless, we were able to find similar shapes in young ranid froglets (*Rana iberica*; Fig. 3C), this apparently being the normal ontogenetic pathway in these neobatrachian anurans. This developmental observation indicates that the sole specimen of *Neusibatrachus* is abnormal. Furthermore, deeply grooved centra, suggesting that the ossification involved the dorsal as well as the lateral parts of the perichordal tube, may occur in highly ossified individuals, well after the end of the metamorphosis, of Tertiary palaeobatrachids (Fig.

6). Perichordal centra occur in the Late Jurassic putative stem-rhinophrynid *Rhadinosteus parvus* (Henrici 1998), a lineage usually considered divergent from a common ancestor with pipimorphs (i.e., pipoids more closely related to pipids than to rhinophrynids). As this condition has also been described in the Early Cretaceous pipimorph *Thoraciliacus rostriceps* (Nevo 1968), this evidence is compatible with the hypothesis of perichordy being the basal pipimorph condition (Jones et al. 2003). This hypothesis would involve the loss of ossification in the ventral portion of the perichordal tube, a pedomorphic feature, to account for the epichordal centra of Cenozoic palaeobatrachids and pipids.

The inconspicuous notch separating the partes acromialis and glenoidalis contrasts strikingly with the deeper scapular medial cleft of known stem-rhinophrynids and pipimorphs, although a medial notch is absent in palaeobatrachids, as well as in *Pipa* and *Ascaphus truei*. Actually, the adult condition of *Neusibatrachus* remains unknown but it is possible that the developmental pathway of this trait might have resulted in uncleft scapulae, as it happens in *Alytes cisternasii*, where juveniles present large scapular notches that close in adults (personal observation).

Although only fragments of the metacarpals are preserved, impressions of these elements clearly show that they were rather long, thus contrasting markedly with the much shorter corresponding bones of *Eodiscoglossus santonjae* (Fig. 5). Proportionally long metacarpals, exceeding 75% of the radioulnar length, occur in all known pipimorphs, including the Early Cretaceous *Thoraciliacus* and

Table 1. Systematic placement of *Neusibatrachus wilferti* in the literature. Column M refers to the use of morphological characters.

	Author(s)	M	Systematics	Status	Evidence
[1]	Seiffert 1972	yes	incertae sedis	valid	[personal observation]
[2]	Estes and Reig 1973	yes	Palaeobatrachidae	valid	[1]
[3]	Špinar 1975	yes	Palaeobatrachidae	valid	[1] [2] [personal observation]
[4]	Vergnaud-Grazzini and Wenz 1975	yes	not determinable	valid	[1]
[5]	Sanchiz 1977	no	Palaeobatrachidae	valid	[1] [2] [3]
[6]	Estes et al. 1978	yes	Palaeobatrachidae	valid	[1] [3]
[7]	Sanchiz and Młynarski 1979	no	Palaeobatrachidae	valid	[1]
[8]	Barale et al. 1984	no	incertae sedis	valid	[1]
[9]	Fey 1988	no	Palaeobatrachidae	valid	[2] [4] [personal observation]
[10]	Wenz 1991	yes	not determinable	valid	[1]
[11]	Wenz 1995	no	Palaeobatrachidae	valid	[1]
[12]	Sanchiz and Roček 1996	no	Discoglossidae?	synonym?	[1] [2] [personal observation]
[13]	Sanchiz 1998	no	Discoglossidae	synonym	[1] [2] [3] [4] [personal observation]
[14]	Roček 2000	yes	incertae sedis	valid	[1] [2] [4] [12]
[15]	Rage and Hossini 2000	no	non Palaeobatrachidae	valid?	[1] [2] [3]
[16]	Gao and Chen 2004	yes	Pipoidea	valid	[1] [4] [13]
[17]	Báez et al. (in press)	yes	Pipoidea, Pipimorpha	valid	[1] [personal observation]

Cordicephalus (Nevo 1968). Similarly, the metatarsals are relatively longer and slimmer than those of *E. santoniae*. Elongated metapodials, considered an adaptation for efficient swimming (Trueb 1996), is one of the skeletal specializations recognized in basal members of the pipimorph lineage.

Taxonomic status

Neusibatrachus wilferti has seldom been mentioned in the palaeontological literature, with the exception of some faunal lists or accounts of palaeontological history. Table 1 includes references of articles in which an explicit taxonomic opinion concerning this taxon is provided.

Three factors have historically obscured the taxonomic placement of *Neusibatrachus wilferti*. The first is the developmental stage of the single specimen. Because the specimen is immature, the adult condition of some features remains unknown. This has prevented some authors from making a taxonomic analysis, considering the relationships of *Neusibatrachus* to be indeterminate (Vergnaud-Grazzini and Wenz 1975). A second difficulty lays in the unusual, even weird, peculiar condition of some characters, particularly the “double” posterior intervertebral articulations in the rear of the column, as described above. Prior to our observations on living ranid froglets, presented here, this condition was unknown to us, leading to our previous dismissal of the specimen as an abnormal developing froglet with unreliable taxonomic characters (Sanchiz and Roček 1996; Sanchiz 1998). However, a similar condition was described in other anurans (Kovalenko 1986). Hence, we think that an extrapolation of most characters to the

adult condition can be made reliably, and the specimen should not be considered abnormal.

A third subtle factor has obscured the taxonomic history on *Neusibatrachus*. As Špinar (1975: 59) pointed out “Even at first sight the specimen showed many features recalling Palaeobatrachidae”; this overall impression has led many authors to analyse each character with only the *Palaeobatrachus* model in mind. As a result, with the notable exception of the posterior presacral articulations, all the taxonomic characters that have been analysed were either concordant with *Palaeobatrachus* or in agreement with the expected ancestral primitive morphotype from which palaeobatrachids derive. The latter, however feasible, is not a firm indication of taxonomic placement. However, inclusion of *Neusibatrachus wilferti* in recent phylogenetic analyses of extinct and extant anuran taxa (Gao and Chen 2004; Báez et al. in press) has resulted in its placement as sister-taxon of Pipoidea or as a basal member of Pipimorpha (*sensu* Ford and Cannatella 1993), based mainly on the azygous frontoparietal and the putative lack of parasphenoid alae

The morphological analysis presented here provides a set of features, as listed in our revised diagnosis (see Systematic palaeontology), that differentiates *Neusibatrachus* from all other presently known living or extinct anuran.

This combination of characters indicates that *Neusibatrachus* Seiffert, 1972 is a valid genus closely related to Pipoidea Ford and Cannatella, 1993 (a widely used subjective synonym of Xenoanura Savage, 1973) or even a member of this clade. It contains only the type species, *N. wilferti* Seiffert, 1972, as the other species ascribed to this genus, *N. estesi* Špinar, 1975, is a synonym of *Latonia gigantea* (Sanchiz and Młynarski 1979; Roček 1994; Sanchiz 1998).

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